The Crato Fossil Beds of Brazil

Window into an Ancient World

EDITED BY

David M. Martill, Günter Bechly and Robert F. Loveridge

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THE CRATO FOSSIL BEDS OF BRAZIL

Window into an Ancient World

This beautifully illustrated volume describes the entire flora and fauna of the famous Lower Cretaceous Crato Formation of Brazil – one of the world's most important fossil deposits, exhibiting exceptional preservation. For the first time, the entire fossil assemblage is brought together in a single volume.

Chapters on the fauna cover a range of invertebrates including arachnids, crustaceans and an immense number of insect groups, while vertebrates are treated in chapters on fishes, anurans, lizards, turtles, crocodiles, pterosaurs and birds. A diverse flora is described in chapters on macrophytes ranging from ferns to some of the earliest angiosperms, including eudicots. Palynomorphs are also considered. Virtually all species are illustrated, many for the first time and some in full colour, while numerous interpretative drawings add to the scientific value of this work. Many new species and higher taxa are described. The fossil descriptions are supported by detailed explanations of the geological history of the deposit and its tectonic setting. Each chapter also contains a comprehensive bibliography.

Drawing on expertise from around the world and specimens from the most important museum collections, this book forms an essential reference for all researchers and enthusiasts with an interest in Mesozoic fossils, and will provide a springboard for further research.

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Preface

In the late 1830s Scottish botanist, surgeon and explorer George Gardner (1810–1849) made his way on horseback from the picturesque spring-line village of Brejo Grande towards the now palaeontologically famous town of Santana do Cariri on the flanks of the Chapada do Araripe. In his published diaries (Gardner, 1846) it is noted that parts of the track were naturally paved in a slabby limestone. Some of these exposures still exist, although this picturesque country track has recently been resurfaced. What Gardner didn't record was that these limestones contain a wealth of fossils, some of which are spectacularly preserved and the *raison d'être* for this book. Although primarily a botanist, Gardner had a keen interest in fossils and, just a few weeks earlier, he had been exploring outcrops where carbonate nodules contained three-dimensionally preserved fishes: the so-called Santana Formation fish nodules, often seen for sale in fossil shops around the world.

Gardner shipped many of the fish-bearing nodules back to Scotland where they formed the basis of studies by the famous ichthyologist Louis Agassiz (1807–1873; Agassiz, 1841, 1833–1844a, 1844b), but the fossils in the slabby limestones seemed to pass him by. Perhaps it was because few quarries excavated the stone at this time, houses then being constructed mainly of mud and sticks or, for the wealthier, bricks made in the traditional style using locally dug alluvial clays.

Even 20 years ago fossils from the Crato Formation were still hardly known. Description of the fossil fish *Dastilbe*, the commonest macrofossil in the Crato Formation, didn't occur until 1947, over 100 years after Gardner's first mention of the rocks (Silva Santos, 1947). Shortly after the description of the fish the first fossil insects from the limestones were described (Costa Lima, 1950), but serious palaeontological research did not commence until the 1980s when Brito (1984, 1987), Campos (1986), Kellner and Campos (1986) and Martins-Neto and Kellner (1988) described elements of the fauna and Duarte (1985) described the first floral remains.

These announcements coincided with the commencement of a major increase in the commercial extraction of the Crato limestones or so-called *pedra de larje*. Today, specimens of *Dastilbe* can be purchased in fossil shops around the world or on the Internet, and the number of scientific papers describing Crato fossils is in the hundreds. From an initial faunal list of a single fish and an unnamed mayfly larva in the middle of the twentieth century, the faunal and floral list today includes over 100 insect species, nine species of fish and nearly a dozen arachnids. Turtles, lizards and even a bird are known, but among the vertebrates the formation is gaining prominence for the diversity and spectacular preservation of its pterosaurs.

The Crato Formation has the most diverse fossil assemblage for any non-marine Cretaceous locality in Gondwana, and perhaps Laurasia too. Museum collections around the world are full of new species of Crato insects, plants and even pterosaurs just waiting to be described. This book brings together the various components of the palaeobiota and attempts to describe the ancient environments represented by the formation. It is one of the clearest windows yet into the Mesozoic, and although its edges may still be misty, a picture of a Cretaceous low-latitude environment is becoming much, much clearer.

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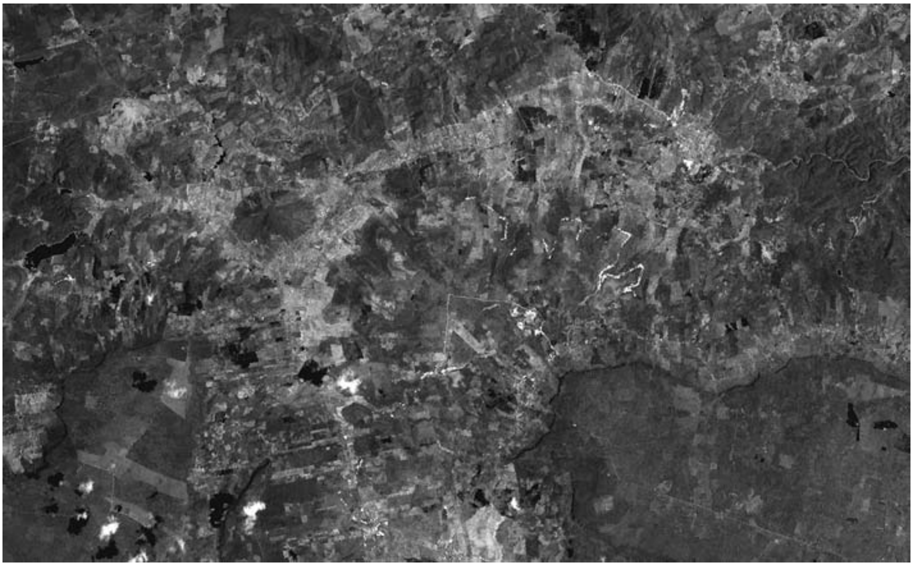
Part I

The Crato Formation Konservat Lagerstätte



1

Introduction to the Crato Formation

David M. Martill and Günter Bechly

The Crato Formation takes its name from the university town of Crato, Ceará, situated in a forested cirque in the north central part of the Chapada do Araripe, a large tableland in north-eastern Brazil (Plate 1a). Its outcrop pattern forms a narrow strip along the flanks of the plateau, and is also present as a few isolated outliers to the south of the plateau. As one of the few limestone units in the region, the Crato Formation supports a unique flora of lime-loving species, and even appears to have an endemic bird, the Araripe manakin, *Antilophia bokermanni*, living on the outcrop near Arajara. This bird was only discovered in 1996 (Coelho and Silva, 1998) and apparently has the smallest geographic range of any bird species, only 1 km^2.

The Crato Formation is mined commercially for cement manufacture and paving stones, and is thus of considerable economic importance to the region, providing both raw materials and employment in its extraction (Plate 1b). It is in the quarries where the slabby limestones are extracted for paving stones that an astonishingly high number of rare and beautiful fossils occur. The preservation of the fossils is often exquisite, and many form the centre pieces of museum exhibitions. Although the formation is some 50–60 m thick, and comprises a varied series of rock types, it is only the basal unit, a 0–13-m-thick series of laminated limestones known as the Nova Olinda Member, that yields the spectacular fossils, and earns the formation its status as a Fossil Konservat Lagerstätte. Elsewhere in the succession fossils are extremely rare, or absent altogether.

But it is not just the beauty and quality of preservation of the fossils that makes the Crato Formation a world-class Fossil Lagerstätte. It was deposited when Gondwana was still reasonably intact and in a sedimentary basin located close to the heart of that supercontinent. It also is of an age when angiosperms were beginning to diversify, and the co-evolution of insects as their pollinators was just beginning. It thus forms one of the best windows into a Cretaceous Gondwanan ecosystem and, perhaps uniquely, allows the co-evolution of the flowering plants and their pollinators to be investigated. Indeed, it may prove to be one of the most diverse assemblages of a Cretaceous terrestrial biota known anywhere, for although it has only been studied palaeontologically since the early 1980s (Brito, 1984), in just a little over 20 years over 200 new species have been discovered and described from this exceptional deposit.

The relationship of the Crato Formation with other sedimentary units in the basin has been covered extensively (da Silva, 1986; Ponte and Appi, 1990; Assine, 1992; Ponte and Ponte Filho, 1996) but there are still problems for intraformational correlation, especially between the sub-basins. There have also been a number of attempts to date the formation using palynomorphs (Lima, 1978, Pons *et al.*, 1990), but despite the palaeontological attention that this deposit has attracted (e.g. Grimaldi, 1990; Maisey, 1991; Martill, 1993), there have been few detailed studies on its general geology, and sedimentology.

A number of aspects of the Crato Formation remain problematic. Indeed, the name itself is controversial. Although first designated a formation by Beurlen (1963), he later relegated the unit to a member (Beurlen 1971), and although Martill and Wilby (1993) made a case for reinstating its formation status, some workers have been reluctant to recognize this. The depositional environment of the Nova Olinda Member is also problematic, and has been claimed to have occurred in fresh (Maisey, 1990, 1996), hypersaline (Martill and Wilby, 1993) or brackish water (Bechly, 1998; Neumann *et al.*, 2003). Similarly, the water depth has been considered to have been shallow (Maisey, 1990) or relatively deep (Martill and Loveridge, 2006), although few workers have attempted to put figures on the depth. Furthermore, the size of the water body is in some doubt. Those who argue for a freshwater lake environment have indicated that the water body was restricted to the Araripe Basin and contained within its fault bounded margins (Ponte and Appi, 1990), while Beurlen (1971) indicated that it may have had connections with adjacent basins to both the west and north, and possibly the south. In terms of semantics, some call it a lake or palaeolake, while others refer to it as a lagoon (e.g. Martill, 1993). Even the age of the deposit is in some doubt, and is nearly always cited as possibly late Aptian or early Albian (Berthou *et al.*, 1990). The unit was mapped as part of Projeto Santana during the 1970s, but ‘ground truthing’ reveals many inaccuracies. Thus it would seem that there remains ample scope for much interesting research on this important formation.

The Crato Formation has been proposed as a potential World Heritage Site by Viana and Neumann (1999), and there is no doubting its extreme scientific importance. However, most of the fossils that exist in scientific collections are a consequence of commercial activities, including the trading of fossils. Essentially, the fossils are found by quarry workers who manually extract the Nova Olinda Member limestone, and have a good eye for finding even the smallest of fossils. The fossils that they find are sold at very low prices to a group of 'middle-men' based mainly in Santana do Cariri and Nova Olinda. These gentlemen, who are acutely aware of the worth of the fossils, then sell them on to dealers based in São Paulo and abroad. Without this trade, there would be very few fossils for scientists to study. Although it is possible to undertake scientific excavations, the chances of finding exceptional material are slim, and certainly would be limited by expense of such excavations: thus, scientific palaeontology needs this trade (Martill, 2001). In a few quarries the owners have issued strict instructions for the workers not to collect and sell the fossils. In these quarries potentially valuable fossils are simply thrown on the spoil dumps and carted off to be ground into cement.

It is the aim of this book to summarize the work undertaken so far and to synthesize the present understanding of the geology, sedimentology and palaeoenvironmental setting of this important deposit. It is also an aim to introduce as much of the palaeobiota as is practicably possible within the confines of these pages. Some authors, in reviewing the fossils in their collections, have discovered new species, or have re-evaluated the status of previously described taxa. Thus, this book is hopefully more than just an introduction to the fossil assemblage; it also contains the results of some new and innovative studies published for the very first time.

Many of the chapters in this book refer to specimens in collections indicated by their museum number, with the following abbreviations being used:

AMA-I, Universidad Federal de Ceará, Fortaleza, Brazil; AMNH, American Museum of Natural History, New York, USA; BSPGM, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; CAMSM, Sedgwick Museum, Cambridge, UK; CJW, Collection Wunderlich, Straubenhardt, Germany; CV, collection Vulcano, Brazil; DNPM, Departamento Nacional Produçao Mineral, Rio de Janeiro, Brazil; GP/It Universidad Guaralhos, São Paulo, Brazil; IMCF, Iwaki Coal and Fossil Museum, Iwaki, Japan; IVPP, Institute for Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; JME, Jura-Museum, Eichstätt, Germany; KMINH, Kitakyushu Museum of Natural History & Human History, Kitakyushu, Japan; LEIUG, Geology Department of the University of Leicester, Leicester, UK; MCSNM, Museo Civico di Storia Naturale, Milano, Italy; MCT, Paleontological Collection of the Setor de Paleontologia do Departamento Nacional de Produção Mineral (DNPM), Rio de Janeiro, Brazil; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MNB, Museum für Naturkunde, Berlin, Germany; MNHM, Museum National d'Histoire Naturelle, Paris, France; MSF, ms-fossil, Sulzbachtal, Germany; MURJ, collection Masayuki Murata, Kyoto, Japan; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NHM, Natural History Museum, London, UK; NSMT, National Science Museum/Tokyo University, Tokyo, Japan; RGMN, Martins-Neto Collection, Sociedad Brasileira de Paleoartropodologia de Ribeirão Preto and at MZUSP (see above); PMSC, Palaeontological Museum, Santana do Cariri, Brazil; SMF, Naturmuseum Senckenberg, Frankfurt am Main, Germany; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TMM, Texas Memorial Museum, Austin, Texas, USA; UM, Ulster Museum, Belfast, UK; UOP, Department of Earth and Environmental Sciences, University of Portsmouth, Portsmouth, UK.

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2

The geology of the Crato Formation

David M. Martill

Introduction

The Crato Formation crops out around the northern, eastern and south-eastern flanks of the Chapada do Araripe plateau that sits at the boundaries of southern Ceará, western Pernambuco and south-eastern Piauí in north-eastern Brazilian caatinga (Martill, 1993; Neumann and Cabrera, 1999).

The formation comprises a heterolithic sequence of clastic and carbonate strata currently restricted to within the Araripe Basin and a few smaller, interconnected basins such as the Serra do Vermelha and Cedro Basins (Assine, 1990, 1992; Carvalho, 2001). It is remarkable for its exceptionally well-preserved fossil assemblages and its limestones are economically important for cement manufacture and building materials (see Chapter 5). Parts of the formation, especially some of the limestone units, are also remarkable for their lateral continuity considering how thin some of the units are and how lithologically variable the sequence is vertically. There have been few detailed studies of the geology, stratigraphy or sedimentology of the Crato Formation as a stratigraphic unit, but the palaeontology of the lowermost of its limestone members has received considerable attention. The unit was first mapped in detail during the Projeto Santana as a separate entity (Moraes *et al.*, 1976), although its definition was unclear. Beurlen (1962, 1963) provided a series of cross-sections across the Chapada do Araripe demonstrating its unconformable relationship with the basement and overlap by younger strata. Since that time there have been few studies of the unit as a whole, although several workers have examined the tectono-stratigraphic evolution of the Araripe Basin, especially its relationship to the opening of the South Atlantic Ocean (Brito-Neves, 1990; Ponte, 1994; Ponte and Ponte Filho, 1996a, 1996b; Medeiros *et al.*, 1997; Ponte *et al.*, 1997; Valença *et al.*, 2003) (Figure 2.1).

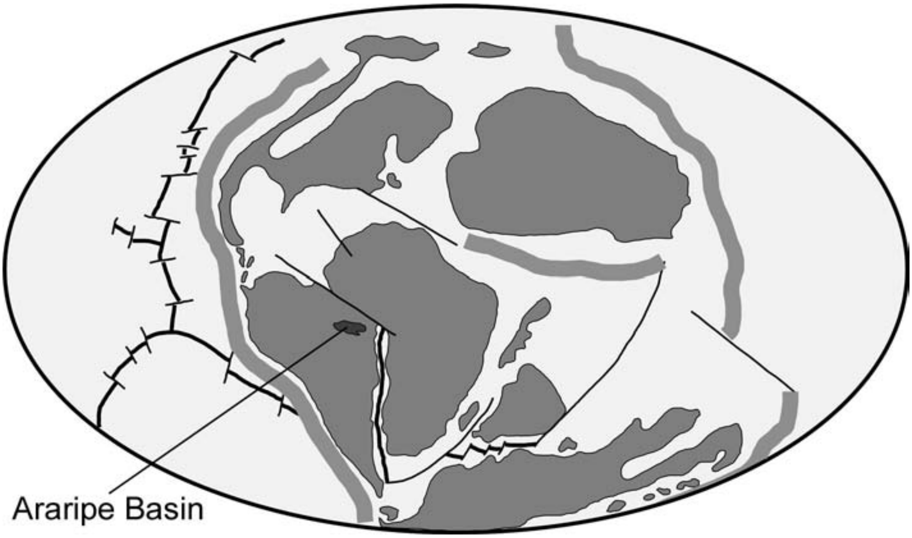

Fig. 2.1. Palaeogeographic reconstruction of the Early Cretaceous world with the location of the Araripe Basin indicated.

Tectono-stratigraphic evolution of the Araripe Basin

The Araripe Basin comprises a largely Mesozoic intracratonic sedimentary system deposited within a complex of horsts and grabens (Figure 2.2) developed in the crystalline basement of the Neoproterozoic Borborema Massif of north-eastern Brazil (Figure 2.3). It lies between two major east–west-trending megafractures, the Patos Lineament in the north and the Pernambuco Lineament to the south (Corsini *et al.*, 1991) (Figure 2.3). The basement rocks between these two structures are composed largely of sequences of schists and phyllites, schists and gneises, and gneises with migmatites, all intruded by calc-alkaline granites and granitoids with trondheimite affinities (Sial, 1986) which form the Cachoeirinha–Salgueiro fold belt (Corsini *et al.*, 1991). The rocks of the Borborema Province comprise a series of supracrustals and older basement effected by late Neoproterozoic metamorphism associated with the Brasiliano-Pan-African Orogeny between 700 and 550 Mya (Vauchez and da Silva, 1992). The Pernambuco Lineament is a late Precambrian shear zone, but underwent reactivation on a number of occasions during the Mesozoic and perhaps later (Arai *et al.*, 1989).

During the opening of the South Atlantic Ocean reactivation of structures within the Borborema Province resulted in the formation of the Araripe Basin, along with several other sedimentary basins in the north-east region of Brazil (Assine, 1994; Ponte, 1996). Estimating the exact timing of these reactivation events is somewhat hampered by a lack of diagnostic fossils in the sedimentary fills, the earliest of which

Fig. 2.2. Brazilian major sedimentary basins. Based in part on Arai (2000).

are coarse siliciclastics largely of fluvial origin probably from the Late Jurassic (Arai *et al*., 1989). Seismic profiles and some borehole data show that the Araripe Basin comprises two sub-basins, which acted as separate depocentres at least for the early part of the basin's history: these are the Feitoria sub-basin in the west and the Cariri sub-basin in the east. Although these were independent depocentres in the Jurassic, they were probably less influential on sedimentation during the mid-to-Late Cretaceous (Ponte and Ponte Filho, 1996b).

Some workers have suggested that the most basal strata within the Cariri sub-basin are of Siluro-Devonian age, but this conclusion has been reached largely on the grounds of lithological similarity with Siluro-Devonian sequences in the nearby (~200 km) Parnaiba Basin. The presence of well-preserved, reworked Devonian palynomorphs (Brito and Quadros, 1995) at the Crato Formation/Bataterias Formation transition beds in the same sub-basin may support this hypothesis (see

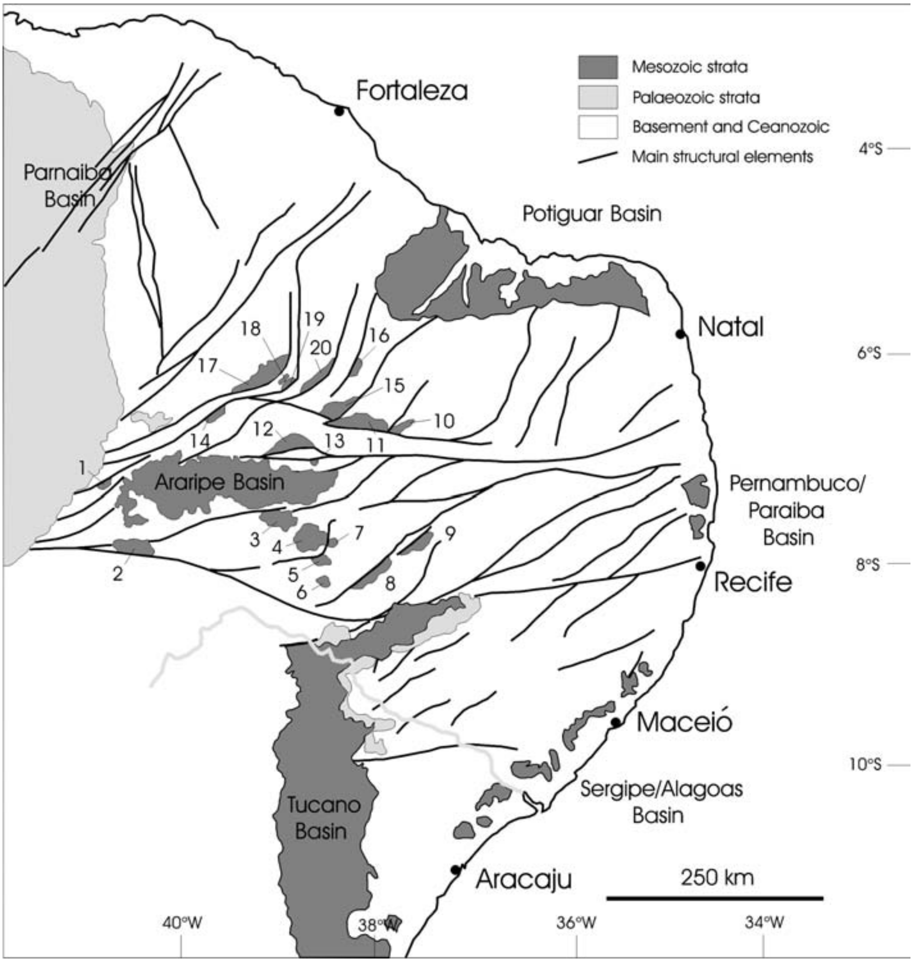

Fig. 2.3. Major and minor Mesozoic sedimentary basins in the north-east of Brazil and main structural elements of the Borborema and adjacent basement terranes. 1, Padre Marcos; 2, Serra do Vermelha; 3, Cedro; 4, São José de Belmonte; 5, Mirandiba; 6, Pajeú; 7, Bom Nome; 8, Betãnia; 9, Afogados da Ingazeira; 10, Pombal; 11, Souza; 12, Lavras de Mangabeira; 13, Barro; 14, Bastões; 15, Triunfo; 16, Rio Nazaré; 17, Iguatu; 18, Malhada de Vermelha; 19, Lima Campos; 20, Icó. Based in part on Assine (1994).

also Chapter 20). However, the supposed Siluro-Devonian strata are largely fanglomerates of fluvial origin, while the derived palynomorphs are marine forms, suggesting derivation from more distant outcrops. Certainly some of these basal units currently lie at high angles to younger stratigraphic units within the basin, and are overstepped by them in some places, proving that they were deposited prior to at least some tectonic activity within the basin. Around Nova Olinda a series of sandstones dip at high angles underneath the Cretaceous sediment fill

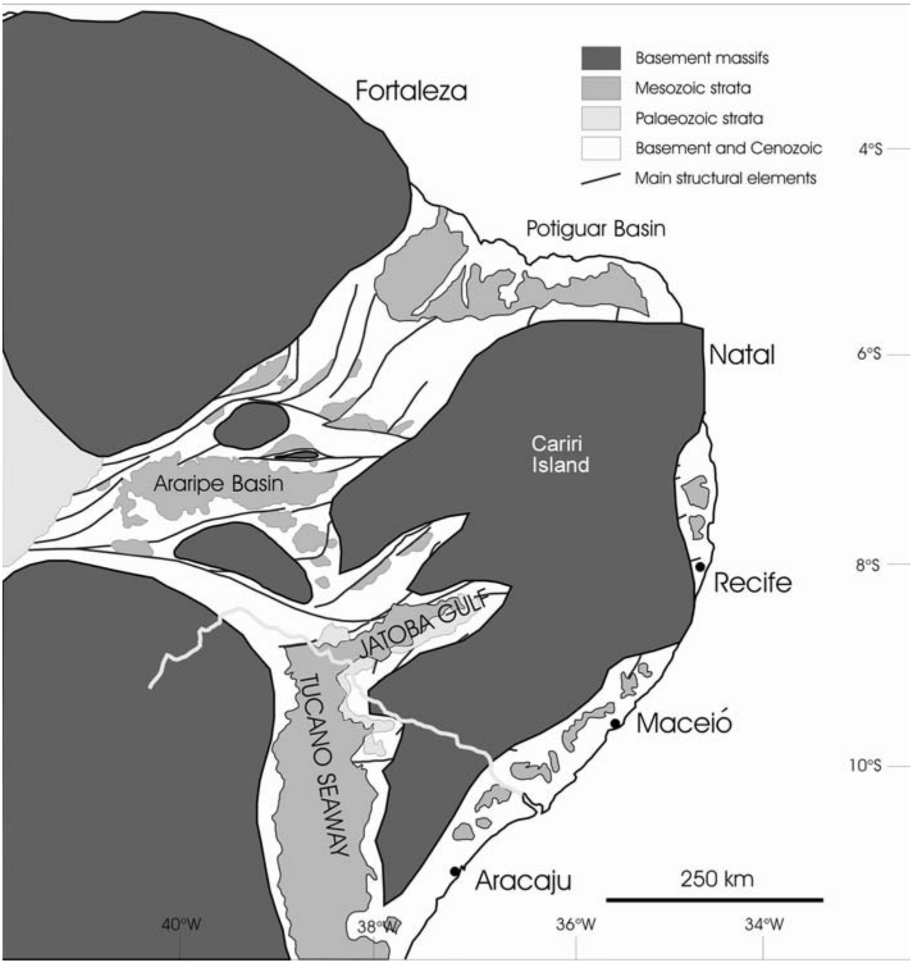

Fig. 2.4. Possible extent of a north-east Brazilian interior seaway during the mid Cretaceous. Intermittent links between the South Atlantic Ocean and the North Atlantic may have existed via a north-east Brazilian seaway. The Araripe Basin records marine 'pulses' in the Aptian and Albian. The basement massifs were the source of the terrestrial flora and fauna of the Crato Formation.

and may form part of a duplex sandwiched between east–west-trending shear zones.

The Araripe Basin is a fault-bounded interior basin (Figure 2.4), the formation of which is directly related to extensional deformation accompanying the opening of the southern and equatorial branches of the South Atlantic Rift System (Ponte and Ponte Filho, 1996a, 1996b; de Matos, 1992). The reactivation of pre-Mesozoic lineaments and fracture zones during the early rifting had a strong influence on the geometry and orientation of the later rift basins. In general, four successive tectono-sedimentary sequences can be distinguished which reflect the different stages of extensional deformation of the initially intracratonic rift basins in north-east Brazil (Chang *et al.*, 1988; de Matos, 1992). These phases are partly reflected in the infill history of the Araripe Basin. An initial pre-rift sequence covers the Late Jurassic–early Berriasian interval and resulted in the widespread deposition of siliciclastics in the extensive and shallow intracontinental ‘African-Brazilian Depression’ of Ponte (1996). According to de Matos (1992) the Jurassic succession of the Araripe Basin (Brejo Santo and Missão Velha Formations) represents the northernmost occurrence of sediments associated with this early phase. The main syn-rift stage (Berriasian to early Barremian) resulted in the development of elongated intracratonic rift valleys which are characterized by sets of north-east-trending, asymmetric, tilted half-graben structures separated by basement highs, transfer faults and/or accommodation zones (de Matos, 1992). Deposition in the rift valleys was characterized by fluvial, deltaic and deep-water lacustrine sedimentation with total syn-rift sedimentary thicknesses reaching >10 000 m in the depocentres of the Recôncavo and South Tucano Basins. In western Pernambuco and southern Ceará, north-west south-east-directed extension resulted in the reactivation of pre-existing sigmoidal shear zones related to the Pernambuco and Patos megashears, generating a suit of north-east south-west trending half-grabens including the Araripe, Rio do Peixe and Iguatu Basins (de Matos, 1987) (Figure 2.3). In the Araripe Basin, gravity, magnetic and seismic data revealed the occurrence of two sub-basins, the Feira Nova in the east and the Crato sub-basin in the west, which are both bound by north-east-trending normal faults (de Castro and Castelo Branco, 1999). The sedimentary infill of the syn-rift stage consists of fluvial deltaic deposits, the Abaiara Formation, probably ranging in age from Berriasian to Barremian (Arai *et al.*, 1989). With the cessation of extension during the Aptian, the north-east Brazilian rift basins entered the transitional post-rift phase. Above a major unconformity representing a significant hiatus (Coimbra *et al.*, 2002), the post-rift stage in the Araripe Basin is represented by the deposits of the Araripe Group. During this stage, low subsidence resulted in the deposition of deltaic to lacustrine sediments (Rio da Batateiras Formation and Crato Formation) followed by evaporites (Ipubi Formation) and marginal marine shales (Romualdo Member of the Santana Formation). Above a major unconformity the Araripe Group is overlain by a massive pile of fluvial siliciclastics of most probably post-Albian age (Exu Formation).

Outcrop

Outcrops in the western Feitoria sub-basin in the region of Ipubi can be attributed to the Crato Formation, as well as outliers in small sub-basins to the south of

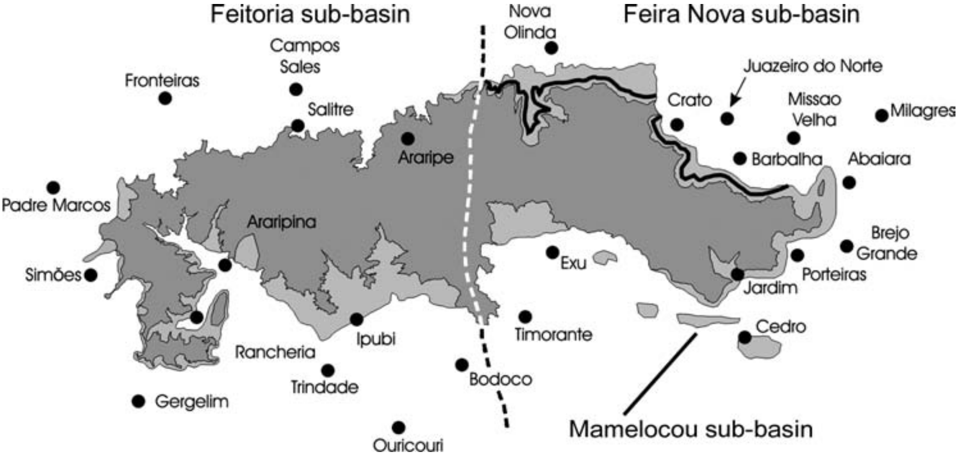

Fig. 2.5. Simplified geological map of the Chapada do Araripe and major towns and villages. Dark grey: Exu Formation forming top of plateau; light grey: Combined outcrop of the Santana, Ipubi, Crato and Rio da Batateiras Formations; Black: extent of the fossil-bearing Nova Olinda Member.

the Chapada do Araripe between Cedro and Exu (Figure 2.5). The outcrop pattern largely follows the contours of the chapada at an altititude of between 420 and 560 m in the north and a little higher in the east. Exposures of the laminated limestone are often conspicuous, where they can form minor escarpments, as in the region to the south of Nova Olinda, but intervening softer strata are usually only exposed in stream sections and some of the larger quarries near Barbalha and between Santana do Cariri and Nova Olinda (Figure 2.6). In places the outcrop is obscured by landslips of the overlying Exu Formation, and at a few locations high basement relief on a topographic unconformity may allow younger strata to overlap, and thus obscure the Crato Formation. This is particularly obvious at Tatajuba, Ceará and between Exu and Jardim in Pernambuco. In the western Feitoria sub-basin much of the Crato Formation is known only from boreholes and in the bottom of gypsum quarries (da Silva, 1986a, 1988). Between Tatajuba and Brezhino the Crato Formation may be truncated by a fault.

Isolated outliers of the Crato Formation are few, but significant outcrops of laminated limestones comparable with those of the Crato Formation occur on the north-western flank of the Serra do Vermelha in Piauí. These limestones occur at a stratigraphic position permitting correlation with the main exposures of the Crato Formation, although they occur some 50 km or more from the main outcrop. Here they are extensively silicified, show contorted laminae, and occur within a sequence of immature white sandstones. They are overlain by a thick sequence of evaporites and fish-bearing nodule beds of the Ipubi and Santana formations respectively.

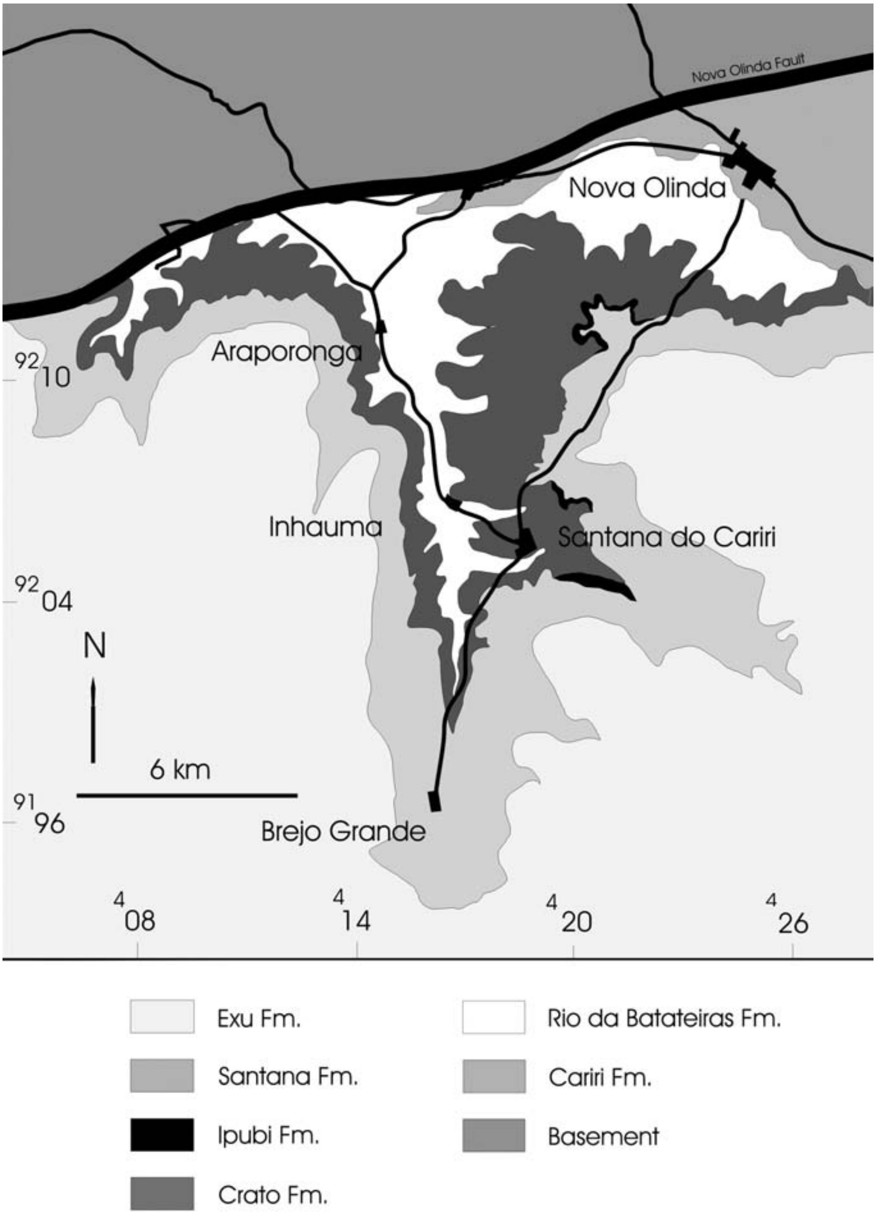

Fig. 2.6. Simplified geological map of the Nova Olinda region. Fm, formation.

The presence of such distant outliers from the main outcrops of the Crato Formation has some bearing on estimates of the size of the Crato Formation water body. Including the Sera do Vermelha outlier, the maximum east–west outcrop distance of the Crato Formation exceeds 180 km while the north–south distance is approximately 100 km, suggesting a water body with a minimum extent of some

18 000 km^2. Presently, some 160 km of near-continuous outcrop of the Crato Formation can be traced around the northern and eastern flanks of the Chapada do Araripe, with additional, though not well-known, outcrops on the southern flank of the chapada.

Relationship to other strata

In many places, especially in the eastern parts the Chapada do Araripe, the Crato Formation forms part of a largely continuous sedimentary sequence and lies generally horizontally. However, the formation rests on different strata depending on location. In the vicinity of Crato it rests on a series of clay-rich sands and silts of the Batateiras Formation, whereas in Nova Olinda it rests on a series of red and brown clays used in the region for brick manufacture. At Sobradinho the Crato Formation rests on a thick sequence of white sandstones, but in many places it rests unconformably on the basement, or occasionally on coarse sandstones and conglomerates of the ?Palaeozoic Mauriti (? = Cariri) Formation. Contacts of the Crato Formation with the underlying metamorphic basement are especially well seen at Tatajuba Alta and valleys feeding the Tatajuba reservoir, whereas its contact with the Mauriti Formation is seen to the south east of Nova Olinda. Near Santa Fé it can be inferred by mapping to contact with late Proterozoic granites intruded into the metamorphic basement. Some of these contacts may be faults, topographic unconformities, or a combination of both.

Where the Crato Formation rests unconformably on the basement the contact is often obscured, but at Tatajuba laminated limestones rest directly on a weathered surface of banded gneiss. Perhaps somewhat surprisingly, no basal conglomerate is developed, and the limestones do not show any facies variation at the contact, but there is little evidence to suggest the contact is a fault.

Palaeogeography of the Crato Formation

The Crato Formation outcrop is presently situated between approximately 7° and 8° south of the equator and between 39° and 41° west of the Greenwich Meridian. During mid Cretaceous times Gondwana was undergoing extensive rifting and lay a little further south than its present position, such that the Crato Formation was deposited in a basin situated at approximately 10–15° south of the palaeoequator (Figure 2.1), and thus well within the tropics (Skelton, 2003).

Although the precise age of separation of South America from Africa is controversial, it is considered that the northern part of South America remained attached to Africa during the Aptian and that the ocean floor was not emplaced until at least Albian times (Berthou, 1990). Thus, the Crato Formation was deposited in an equatorial mid-continental setting.

Active rifting of the northern part of the South Atlantic Ocean was occurring and reactivation of numerous structural elements of the Brazilian basement lead to the development of numerous fault-bounded sedimentary basins (Ponte and Ponte Filho, 1996a, 1996b). However, while much pre-rift fluvial sedimentation occurred within the confines of these basins, an estimated 300-m rise in sea level during the Cretaceous provided extra basinal sedimentation. The Crato Formation may have been one of these units. Arai (1995, 2000) has proposed that high sea levels during the mid Cretaceous resulted in much more widespread deposition than is indicated by the present outcrop pattern. Indeed, Arai (2000) suggests the presence of an extensive seaway (Figure 2.4), or series of seaways, over considerable areas of South America, that may have linked the central Atlantic with the South Atlantic and, perhaps also the Pacific Ocean, via an epeiric sea. Always a difficult proposition to demonstrate, as clearly it relies on much negative data, Arai draws his evidence from five main sources: geomorphological, stratigraphical, sedimentological, geochemical and palaeontological. An examination of Arai's criteria, and some further considerations are presented here.

The Araripe Basin is currently located some 400–500 km from the Brazilian continental margin and a little less distant from two sedimentary basins that were open to the newly opening Atlantic Ocean, namely the Potiguar Basin to the north and the Tucano–Jatoba basin complex to the south. Marine waters certainly entered the Araripe Basin during deposition of the Santana Formation, as evidenced by the presence of echinoids in the higher parts of the sequence (Beurlen, 1963, 1971), but it is highly likely that the influence of freshwater fluvial input, and perhaps restricted circulation, prevented normal marine salinities dominating some of the slightly older deposits of the Araripe Group. Thus, many of the strata represent hypersaline (Ipubi Formation) or brackish (basal Crato Formation) environments, depending on location and relative age. The only time that marine conditions with near-normal marine salinities were evident was during deposition of the thin gastropod- and echinoid-bearing limestones occurring towards the top of the Romualdo Member of the Santana Formation (Martill and Wilby, 1993) and representing a high sea stand. The precise dating of this event is uncertain, but the highest Cretaceous sea stands were between the Cenomanina and Turonian (Haq *et al.*, 1987; Hancock, 2003).

Geomorphological evidence

The only geomorphological evidence that Arai presents for an extensive continental seaway is that of the 'chapada' tableland topography. The Brazilian tablelands

(Chapada do Araripe, Chapada Meio-Norte, Sanfransiscan, Paracis) are considered to represent an abrupt halt in sedimentation rather than a peneplained or exhumed surface (Arai, 2000). In such a case, the top of the Exu Formation thus represents a retreat of a shallow sea followed by infilling by prograding fluvial material. Thus, the top of the Chapada do Araripe and, therefore, the top of the Exu Formation, may represent the highest of the Cretaceous sea stands, which could make it Turonian age. Following the Turonian, Cretaceous sea levels began to fall, albeit gradually (Haq *et al.*, 1987). However, gentle folding of the Exu sandstone, as seen near Simoes, and its later erosion to form the flat top to the chapada in that region, suggest that peneplanation did play a part in shaping the morphology of the tabeland.

It should also be noted that there exists a peneplained surface on the Precambrian basement to the north of the Araripe Basin with an average altitude of 600 m and, although now deeply incised, viewed from a distance the topography appears flat. This peneplained surface lies some 400 m below the top of the Chapada do Araripe in the region to the west of Crato, but to the west around Araripe the difference in height is less marked; the difference perhaps being related to post mid Cretaceous tectonics. Between Brejino and Araripe the peneplained surface of the Precambrian basement is seen to be overlain by the Exu Formation. This peneplained surface may represent a surface that was close to sea level during the Early Cretaceous and was inundated by rising sea levels from the Aptian onwards.

In the vicinity of Nova Olinda the Crato Formation outcrop presently lies below this peneplained surface, but its outcrop is restricted to the south of the Paraiba Lineament. Near Tatajuba, however, the Crato Formation rests directly on down-faulted basement, suggesting that in this region it was the first deposit to transgress on this surface. If this is to be accepted, then the Crato limestones would also have been present north of the Paraiba Lineament, but subsequently removed by erosion. Evidence for its former continued presence north of the lineament is somewhat circumstantial. Essentially there is no facies change of the Crato Formation laminites close to the fault (the outcrop can be traced to within less than 50 m of the fault line at Triumfo and Tatajuba). Close to the fault at Tatajuba, the Nova Olinda Member reaches its thickest sequence of 14 m, suggesting active fault movement controlling the depth of the depocentre with downthrow to the south. The corollary of this is that the Crato Formation in the Araripe Basin is merely an erosional relict of a formerly more widespread unit.

An additional line of evidence is that of the present-day altitude of the Araripe Group strata with respect to the surrounding basement. In the east of the Chapada do Araripe these strata crop out on the flanks of the plateau between 600 and 1000 m above sea level. Projection of this outcrop to the basin margins indicates that these strata would pass above the present peneplained surface of the basement rocks to the north except in a few isolated places. To the north east there is no ground presently higher than 2500 m between the Chapada do Araripe and the present-day coast at Macáu, Rio Grande do Norte, with most ground lying below 300 m. Similarly, to the west of the Chapada the outcrop of the Araripe Group can be projected as far as the Maranhao Basin where the Codó Formation is of similar age and lithofacies to the Araripe Group (Paz and Rossetti, 2005). It is therefore possible that immense tracts of Cretaceous strata have been removed by post-Cretaceous erosion.

Stratigraphical evidence

Arai (2000) cites the lateral continuity of many of the stratigraphic units present in the Brazilian chapadas. In the Araripe Basin the stratigraphic continuity of some of its formations is quite striking, especially when considering the remarkable variation vertically. The Romualdo Member concretion-bearing horizon of the Santana Formation, for example, can be traced for over 180 km, and certain characteristics, such as tabular concretions at the base, and ovoid concretions towards the top, are features of the member over the entire outcrop. This is remarkable in that, if the Romualdo Member had been confined to the Araripe Basin, then where are the impinging deltas from rivers draining into it, or the shoreline facies? In the Crato Formation the Jamacaru Member laminated limestone is never more than 3–4 m thick, but a silicified, halite pseudomorph-bearing horizon at its top can be traced for more than 200 km from Porteiras to the Serra do Vermelha. This lateral continuity of some, but not all of the stratigraphic units, is put into perspective when it is considered that it is almost impossible to correlate the intervening strata over more than a few kilometres and sometimes less.

Although there have been few direct correlations made between the various basins, some names have been used between basins because of a remarkable similarity of rock types. The Codó Formation of the Paraiba Basin, for example, has an overall stratigraphic sequence that is similar, though not identical to, the Araripe sequence (Paz and Rosetti, 2005). There are also some lithological similarities between the Tucano/Jatoba Basin complex and the Araripe Basin. What has perhaps not been noticed is that some of these lithological similarities extend beyond the boundaries of Brazil, with facies remarkably similar to the Romualdo Member nodule beds occurring in the Magdalena Valley of Columbia (Weeks, 1956) and the Apon Formation of Venezuela (Moody and Maisey, 1994). It is certainly the case that strata deposited in epeiric seas can, at times of high sea stand, be remarkably continuous for hundreds of kilometres, as exemplified by the Posidonia Shale/Lias Epsilon of Germany, which can be traced through France, The Netherlands and into northern England and south to the English Midlands: facies continuity in an epeiric sea for nearly 1000 km.

Sedimentological evidence

Sedimentological evidence for an extensive interior marine seaway is ambiguous. Marine strata have been recognized in the Araripe Basin, but only the top part of the Santana Formation provides the convincing palaeontological evidence (see below). Evidence for marine deposition on the basis of sedimentary structures is lacking. Herring-bone cross-stratification is not present, but, on the other hand, tidal influence is not necessarily great in shallow epicontinental seas or restricted water bodies, as exemplified by the Black Sea and Mediterranean Sea today.

Other primary sedimentary structures, such as hummocky cross-stratification, can occur in shallow lakes as well as parallic or marginal marine settings and are thus of limited value in this context. Arai's (2000) main line of evidence is that palaeocurrent data for some fluvial deposits indicate drainage toward the west, implying that the sea may have lain in that direction rather than the north (central Atlantic) or east (South Atlantic).

There is a tenuous line of evidence suggesting that the Araripe Group was formerly much more widespread. At Mina Pedra Branca a 1–2-m-thick conglomerate within the basal Santana Formation (the Araporanga Member of Martill and Wilby, 1993) contains a mixture of sub-rounded grey quartz, rotten gneiss and rare clasts of laminated limestone resembling that of the Crato Formation. However, nowhere in the immediate vicinity within the basin is there evidence for erosion of the Crato Formation. Hence, this material must be derived from outside the present boundary of the basin, as suggested by the presence of derived basement pebbles. This suggests that removal of extra-basinal Crato Formation strata was already taking place during Santana Formation times. This is wholly consistent with the basin-wide disconformity detected by da Silva (1986b) at the top of the Ipubi Formation.

Geochemical evidence

Arai (2000) cites $^{86}Sr/^{87}Sr$ ratios for the Codó Formation evaporites as evidence for precipitation from marine waters. Similarly Berthou and Pierre (1990) reported on sulphur isotopic composition of evaporites from the Ipubi Formation as evidence for a marine source. Indeed, it seems almost inconceivable that such thick deposits (in excess of 20 m) of gypsum and anhydrite would not have a marine, albeit highly restricted, origin.

In addition to the strontium isotope ratios, the presence of marine organic biomarkers beneath evaporites in the Codó Basin, including dinosterane and C_{30} sterane, has been used by Arai (2000) to support the notion of an extensive epeiric sea.

Palaeontological evidence

Perhaps the strongest case for support for marine waters in any of the chapadas comes from palaeontology. The salinity tolerance of the fish assemblages from the Crato and Santana Formations has often been debated (e.g. Maisey, 1991; Martill, 1993), and although a case has sometimes been made for a freshwater origin for the Crato Formation (Maisey, 1990, 1996), most fish taxa appear to be known from fully marine strata elsewhere (Maisey, 2000).

Marine dinoflagellates, mainly species of *Subtilisphaera* and *Spiniferites*, are reported from several horizons in the Araripe Basin, including early in the succession in the Batateiras Formation, below the Crato Formation (Arai and Coimbra, 1990). However, typical open marine nekton is absent from all of the Brazilian interior basins, with no reports of cephalopods from any basin except those fronting the present-day coast.

Foraminifera have been discovered in the Santana Formation (Berthou *et al.*, 1990) and marine turtles have been reported by Hirayama (1998), but there have been no reported occurrences of plesiosaurs or mosasaurs from these deposits. Thus, although marine waters may have been entering the Araripe Basin, there appear to have been filters in place that severely restricted the biota.

Remarks

Despite several projects to map the strata of the Chapada do Araripe and the Crato, Ipubi and Santana Formations in particular, there remains considerable scope for elucidating the tectono-sedimentary history of the basin. Of particular interest is the relationship of the Araripe Group strata to the basin's boundary faults, and the timing of movements of these faults. More detailed sedimentological studies, perhaps concentrating on the strata between the richly fossiliferous horizons of the Crato and Santana Formations, would help to elucidate the basin's sedimentary dynamics.

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3

Stratigraphy of the Crato Formation

David M. Martill and Ulrich Heimhofer

Introduction

The Crato Formation comprises a series of laminated limestones inter-bedded with sandstones, marls and clays, sandwiched between a highly variable sequence of strata in the mainly Mesozoic Araripe Basin. Its distribution has not been completely mapped as an integral stratigraphic unit, although some beds of limestone were mapped by the Projeto Santana team in the 1970s (Moraes *et al.*, 1976). The formation has never been formally defined, although Martill and Wilby (1993) proposed a type section in the river at Cascata near Crato, but exposures of the upper part of the Crato Formation sequence are only poorly exposed here compared with elsewhere. There have been a few attempts to define the unit (e.g. Martill and Wilby, 1993; Berthou *et al.*, 1994), but it is not always clear what authors are referring to when discussing the Crato sedimentary unit, partly due to terminology and partly due to concept. Here we consider the Crato Formation to comprise a heterolithic suite of strata lying above the Rio da Batateiras Formation of Ponte and Appi (1990) and beneath a unit of evaporites termed the Ipubi Formation by Martill and Wilby (1993) (Figure 3.1). Its base is defined as the first appearance of laminated limestones and its top by the first appearance of the evaporites of the overlying Ipubi Formation (see Figures 3.4 and 3.8, respectively, below). Although this definition works well in most areas of the Crato Formation's outcrop, Berthou *et al.* (1994) noted problems in defining the upper limit where the gypsum deposits of the Ipubi Formation appear to be missing. In our experience it is rare to find a section in which the Ipubi evaporites are absent due to non-deposition, although they may be missing locally due to dissolution at the surface with a concomitant collapse of surrounding strata, or simply lack of exposure. It is possible that in some places the evaporites may have been removed by lateral migration due to halokinesis or pressure solution.

GROUP	FORMATION	MEMBER	LITHOLOGY
ARARIPE	IPUBI		Mainly gypsum
	CRATO	CASA DE PEDRA	Heterolithic - including black shales and muddy ssts
		JAMACARU	Laminated lst
		CALDAS (Barbalha Mbr of Martill & Wilby 1993)	Heterolithic - including silty mudstones, silts and fine to medium ssts. Some thin laminated lsts
		NOVA OLINDA	Laminated lst
		Transition beds	
	BATATEIRAS		

Fig. 3.1. Stratigraphic scheme employed for the Crato Formation. Modified from Martill and Wilby (1993). lst, limestone; Mbr, member; sst, sandstone.

Stratigraphic nomenclature

The limestones of the Crato Formation are presumably what prompted Small (1913) to call strata between the lower and upper sandstones of the Araripe Basin the 'Calcareo do Sant'Anna'. This extensive suite of strata eventually became known as the Santana Formation, a name that has become famous among palaeontologists and is synonymous with exquisitely preserved fossil fishes (Maisey, 1991; Martill, 1993).

The Crato Formation has, in the past, been referred to as an unnamed part of the Santana Formation (Beurlen, 1962), the Crato Member of the Santana Formation (Beurlen, 1971), the Crato Member of the Araripina Formation (da Silva, 1986a) and the Crato Lithological unit (Berthou *et al.*, 1994). It was first called the Crato Formation by Beurlen (1963), but in later works he referred to it as the Crato Member (Beurlen 1971). A similar lack of consistency with regard to the unit's nomenclature and stratigraphic status may also be seen in its stratigraphic scope and considerations of its age. To complicate matters further, the Crato Formation has variously been placed within an Araripe Group (Ponte and Ponte Filho, 1996) or a Santana Group (Neumann and Cabrera, 1999), both with subtly different definitions. It would appear that the unit was originally defined to include all of the laminated limestones that occur around the Chapada do Araripe that lie above a lower, mainly red bed sequence and beneath a thick series of evaporites, now called the Ipubi Formation (Martill and Wilby, 1993). Here we regard the Crato lithological unit as a distinct formation, as originally proposed by Beurlen (1963). We also propose here a type section for the unit and attempt to define the unit on the basis of this section. In an attempt to avoid confusion a conservative approach is adopted for the use of new names. The rationale for regarding the Crato Formation as a distinct formation can be summarized as follows.

1. The unit can be easily mapped on account of its distinctive laminated limestones.
2. There is a basin-wide disconformity within the so-called Santana Formation of earlier authors that separates the Crato and Ipubi Formations from the Romualdo Member, the horizon famous for its three-dimensional fishes in calcareous concretions (da Silva, 1986b). This disconformity may correspond to a global sequence boundary event, but its precise date and origin remain ambiguous.
3. The palaeobiota and preservation of fossils in the Crato Formation are distinct from that of the Romualdo Member. In this regard, many workers simply refer to fossils from the Crato limestones as being from the 'Santana Formation', resulting in considerable confusion as to the composition of the respective assemblages and their relative ages.

A number of workers have been reluctant to adopt the term Crato Formation, but among European and North American workers the scheme of Martill and Wilby is increasingly accepted (Dilcher *et al.*, 2005; Selden *et al.*, 2006). Neumann and Cabrera (1999) also consider the Crato unit as a distinct formation.

Historical background

Strata that are now included in the Crato Formation were first mentioned by George Gardner in his 1846 *Travels in the Interior of Brazil.* After having left Crato on horseback Gardner describes a 'horizontal bed of limestone in thin layers' that forms a natural pavement on the road from Brejo Grande to Santa Anna (now called

Santana do Cariri; Gardner, 1846, p. 227). This road is still the main route between Santana do Cariri and Brejo Grande and the limestone can still be seen cropping out in the track. There appears to be little or no mention of the unit in readily available geological literature until aspects of its palaeontology were brought to light by da Silva Santos (1947), who described the occurrence of the small gonorhynchiform fish *Dastilbe crandalli*. At this time the unit had still not received any formal name and was widely regarded as a bed of limestone within the 'Calcareo do Santa Anna' (= Santana Formation) of Small (1913). The unit first received a formal name when Beurlen (1963) called it the Crato Formation.

The first fossil insects from the Crato Formation were briefly noted by Costa Lima (1950), who figured several larval ephemeroptera from the limestone near Santa Fé in the municipality of Crato. However, fossil insects from the now famously fossiliferous outcrops around Nova Olinda were not reported until as late as the 1980s (Brito, 1987; Brito *et al.*, 1984).

Since the beginning of the 1980s extraction of limestone for building and paving stone from the outcrops of the Crato Formation between Nova Olinda, Santana do Cariri and Tatajuba has exposed the lowermost limestones extensively (see Chapter 5) and has brought to light huge numbers of fossils, especially of fishes, insects and plants. During this period a considerable body of work has been generated on the palaeontology, but very little on the sedimentology, stratigraphy or geochemistry. An exception is the study by Neumann *et al.* (2003) on the preservation of organic matter in the Crato Formation.

The Crato Formation is well exposed around the Chapada do Araripe, although in stream sections natural outcrops are usually restricted to the thicker beds of laminated limestone, as in the region between Nova Olinda, Santana do Cariri and Tatajuba where a dissected plateau is capped by the formation. The outcrop is almost continuous on the flanks of the Chapada do Araripe between Tatajuba in the north west and Jardim in the south east of the chapada, with only a minor break where it is overlapped by younger strata onto a high of crystalline basement to the west of Crato, near Santa Fé. In the region between Jardim and Exu in Pernambuco, outcrops of the laminated limestones occur in small isolated sub-basins, as at Mamelocou and Ori. Beurlen (1963) noted the presence of laminated limestones near Bodoco. A highly silicified laminated limestone facies occurs just beneath the Ipubi Formation evaporites on the northern flank of the Serra do Vermelha in Piaui, which may represent lateral equivalents of the higher parts of the Crato Formation; similar blocks occur in field brash beneath typical Romualdo fish nodules near Simões. Elsewhere in the west of the Araripe Basin strata beneath the Ipubi Formation evaporites include several metres of laminated bituminous shales, which may in part be lateral equivalents of laminated limestones in the east of the basin.

Definition of the Crato Formation and proposal for a type area

Martill and Wilby (1993) proposed a section along the Rio Batateiras, to the west of Crato, as a type locality for the Crato Formation. This suggestion was adopted by Berthou *et al.* (1994) for their 'Crato Lithological Term', who published a lithological log for the river section. Martill and Wilby (1993) also proposed a number of localities as type sections for various members which they recognized within the Crato Formation. The utility of these sections and the status of the various members erected by Martill and Wilby are considered below. Since the early 1990s additional fieldwork has shown that several other sections offer excellent opportunities to examine the Crato Formation, or parts of it. It is apparent that a single type section is insufficient to define the Crato Formation as a whole. Accordingly, a series of localities are proposed as type sections in the region between Nova Olinda, Santana do Cariri and Tatajuba. This area permits observation of the base of the formation, all of the various laminated limestone members, and the contact with the overlying Ipubi Formation evaporites (Figures 3.2 and 3.3). In this area it is also possible to observe the unconformable contact with the metamorphic basement and map its relationship to basin margin faults.

The Crato Formation (Beurlen, 1963)

Several natural sections and a number of quarries around the Chapada do Araripe expose informative sections through the Crato Formation. Logging of these sections reveals considerable differences in thickness and lithological content between exposures in the east of the Chapada do Araripe and those in the vicinity of Crato and Nova Olinda (Figure 3.3). Most notably, sandstones are dominant in the east and some of the more prominent laminated limestones appear to be absent, which may reflect an interdigitation between two distinct formations. In the north of the Chapada do Araripe complete or near-complete sections through the Crato Formation can be seen in the stream section of the Riacho Jacu between Nova Olinda and Pedra Branca Hill, in a small tributary of the Riacho Jacu to the east of the road between Nova Olinda and Santana do Cariri, at Sitio Estiva near Araporanga and in a stream adjacent to the old gypsum mine 2 km north of Santana do Cariri (Figure 3.4). The Riacho Jacu and tributaries section is somewhat patchy, but does show the basal contact with the underlying Rio da Batateiras Formation (Figure 3.4) and the transition at the top of the sequence into the overlying evaporites. This latter boundary is particularly well seen in the section near the old gypsum mine (see Figure 3.8b, below). The section at Estiva is one of the most complete and displays at least four laminated limestone horizons. Another reasonably complete sequence is that of the IBACIP Mina Caldas quarry near Barbalha. Here extensive

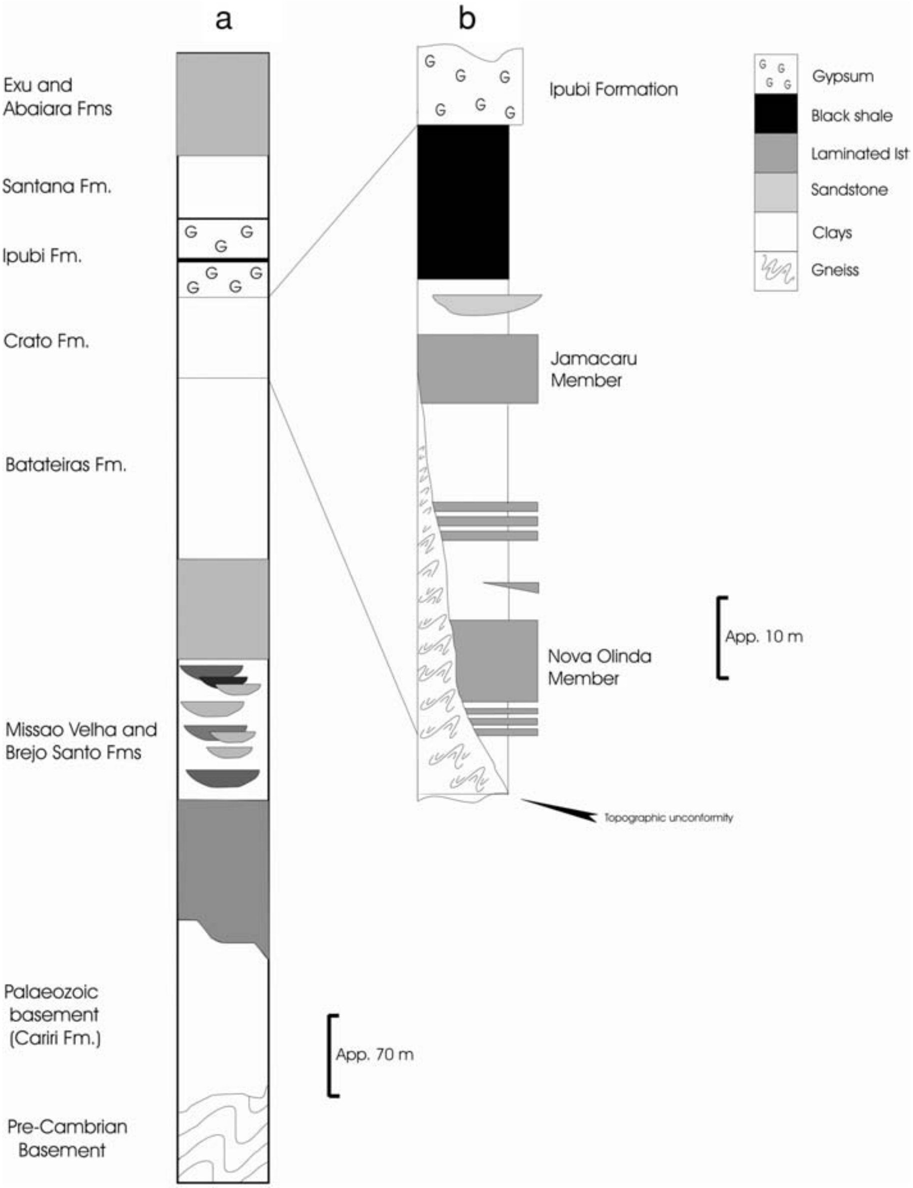

Fig. 3.2. Simplified lithological section for the Crato Formation. (a) Generalized lithological log for the north central part of the Araripe Basin; (b) simplified lithological log of the Crato Formation for the Nova Olinda region, based on sections seen at Estiva and between Nova Olinda and Pedra Branca hill. The black shale unit may not be as thick as estimated. App., Approximately; Fm., Formation; lst, limestone; sst, sandstone.

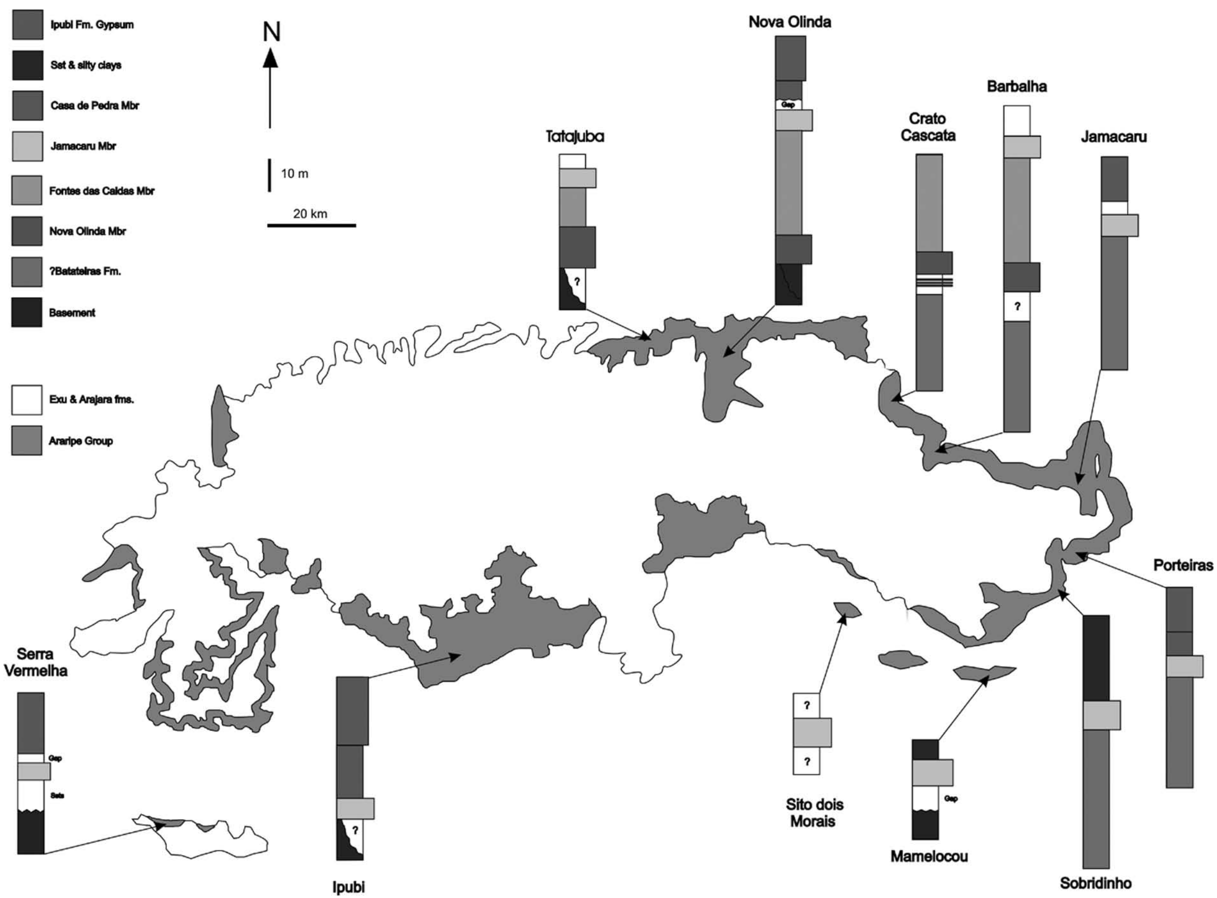

Fig. 3.3. Stratigraphic variation of the various members of the Crato Formation around the Araripe Basin. Mbr, Member.

Fig. 3.4. The base of the Crato Formation: (a) transition beds between the Rio da Batateiras Formation and the Crato Formation at Cascata, near Crato, Ceará, comprising a series of alternating clays and laminated organic-rich limestones rich in ostracods; (b) stream section approximately 3 km south of Nova Olinda, Ceará, showing Crato Formation limestones unconformably overlying probably Devonian sandstones of the Cariri Formation. The hammer is resting on the boundary.

quarrying has exposed much of the sequence (see Figure 3.6, below), and the basal most beds can sometimes be seen in drainage ditches in the floor of the pit. The adjacent stream exposes higher beds not seen in the quarry faces, but unfortunately does not show a contact with the overlying Ipubi Formation evaporites.

At least two schemes have been proposed to subdivide the Crato Formation. Martill and Wilby (1993) recognized a basal laminated limestone, the main fossil-bearing unit, as a distinct member which they called the Nova Olinda Member: a term adopted here (Figure 3.5). They also recognized two higher laminated limestones which they called the Barbalha and Jamacaru members respectively. The uppermost Jamacaru Member is readily recognizable in the field (see Figure 3.7a, below), as in most places it is capped by a silicified, halite pseudomorph-bearing limestone (see Chapter 4). However, the Barabalha Member of Martill and Wilby (1993) is here renamed and redefined (see below). Berthou *et al.* (1994) divided their Crato lithological unit into two 'terms'; a lower 'Crato Cascata Term', which includes a series of alternating clays, laminated limestones and silty clays with plant remains and the Nova Olinda Member of Martill and Wilby (1993), and an upper 'Crato Bebida Term', which includes a variable sequence of silts, laminated limestones and the Barbalha and Jamacaru Members of Martill and Wilby (1993). These workers also recognized a 'Crato Sao João Term' but they could not decide whether it belonged in the Crato or Ipubi formations. These workers specifically did not want their 'terms' to be recognized as members or formations. Here we recognize four members within the Crato Formation. We retain the Nova Olinda Member of Martill and Wilby (1993). The name Barbalha Member is replaced with the new name Caldas Member for reasons of priority (see below). The Jamacaru Member of Martill and Wilby (1993) is also retained. Laminated black shales beneath the Ipubi Formation evaporites in the western Araripe Basin are here included in the Crato Formation and are considered to represent a distinct member for which the name Casa do Pedra Member is proposed (Figure 3.1).

The Nova Olinda Member (Martill and Wilby, 1993)

Name. From the town of Nova Olinda where most of the stone cutting of this member takes place (Figure 3.5). This is the unit that contains an abundance of exceptionally well-preserved fossils and constitutes the Crato Formation Konservat Lagerstätte.

Type locality. Exposures in the banks of the Riacho Jacu and the numerous quarries in this member approximately 3 km south of Nova Olinda. The base of this unit and the transition from the underlying Rio da Batateiras Formation is extremely well exposed at Cascata, near Crato (Figure 3.4a). To the south west of Nova Olinda some exposures show this member resting unconformably on presumed Devonian sandstones of the Cariri Formation (Figure 3.4b)

Fig. 3.5. The Nova Olinda Member: a complete section through the Nova Olinda Member exposed in a quarry and stream section south of Nova Olinda, Ceará. The palaeontologist's left hand is pointing to the base.

Definition. The base is the first substantial laminated limestone of the Crato Formation. The top is a 0.20–0.30-m-thick, conspicuous, buff weathering, non-laminated limestone before the unit passes sharply into the heterolithic siliciclastics of the Caldas Member (see below). At Mina Caldas the upper part of the Nova Olinda Member comprises more than 1.5 m of non-laminated limestone.

Lithology. Parallel, millimetrically laminated limestone. Blue/grey when fresh, weathering to hues of buffs, pink and white.

Distribution. Present at outcrop between Tatajuba in the north west of the Chapada do Araripe extending eastwards to Barbalha, but disappears eastwards between Sitio Santa Rita and Jamacaru. Not definitely known in south west of the chapada and its relationship to similar facies in the south, for example the Mamelocou sub-basin, is not clear.

Thickness. This member reaches a maximum of 13–14 m in thickness at Tatajuba, but is between 6 and 8 m thick at Nova Olinda, and about 8 m thick at Barbalha.

Palaeontology. Diverse in the Nova Olinda region (the Crato Formation Fossil Lagerstätte), but restricted elsewhere. At Mina Caldas rare specimens of *Dastilbe* occur. Ostracods and a species of the conchostracan *Cyzicus* are extremely abundant in the transition beds with the Rio da Batateiras Formation at Cascata.

Caldas Member (replacement name) = Barbalha Member (Martill and Wilby, 1993)

Name. This name is offered as a replacement name for Barbalha Member of Martill and Wilby (1993) with a redefinition of that unit. The name is after the Fontes dos Caldas, a spring that emanates at the base of the chapada escarpment above Barbalha. Originally termed the Barbalha Member by Martill and Wilby (1993), Assine (1992) proposed the name Barbalha Formation while the chapter by Martill and Wilby (1993) was in press for a suite of strata below the Crato Formation. These strata were formerly the upper part of the Missao Velha Formation of earlier authors (e.g. Lima, 1978) and are more frequently called the Rio da Batateiras Formation by most recent authors (e.g. Berthou, 1990; Ponte and Appi, 1990). Due to a lack of published detailed lithological logs, it is not clear if the Barbalha Formation of Assine (1992) and the Rio da Batateiras Formation of Ponte and Appi (1990) are exactly synonymous. To avoid any possible confusion, should the term Barbalha Formation gain widespread acceptance, the term Barbalha Member as a lithostratigraphic unit within the Crato Formation is here abandoned and the name Fontes dos Caldas Member offered as a replacement.

Type locality. The Mina Caldas quarry between Barbalha and Arajara (Figure 3.6).

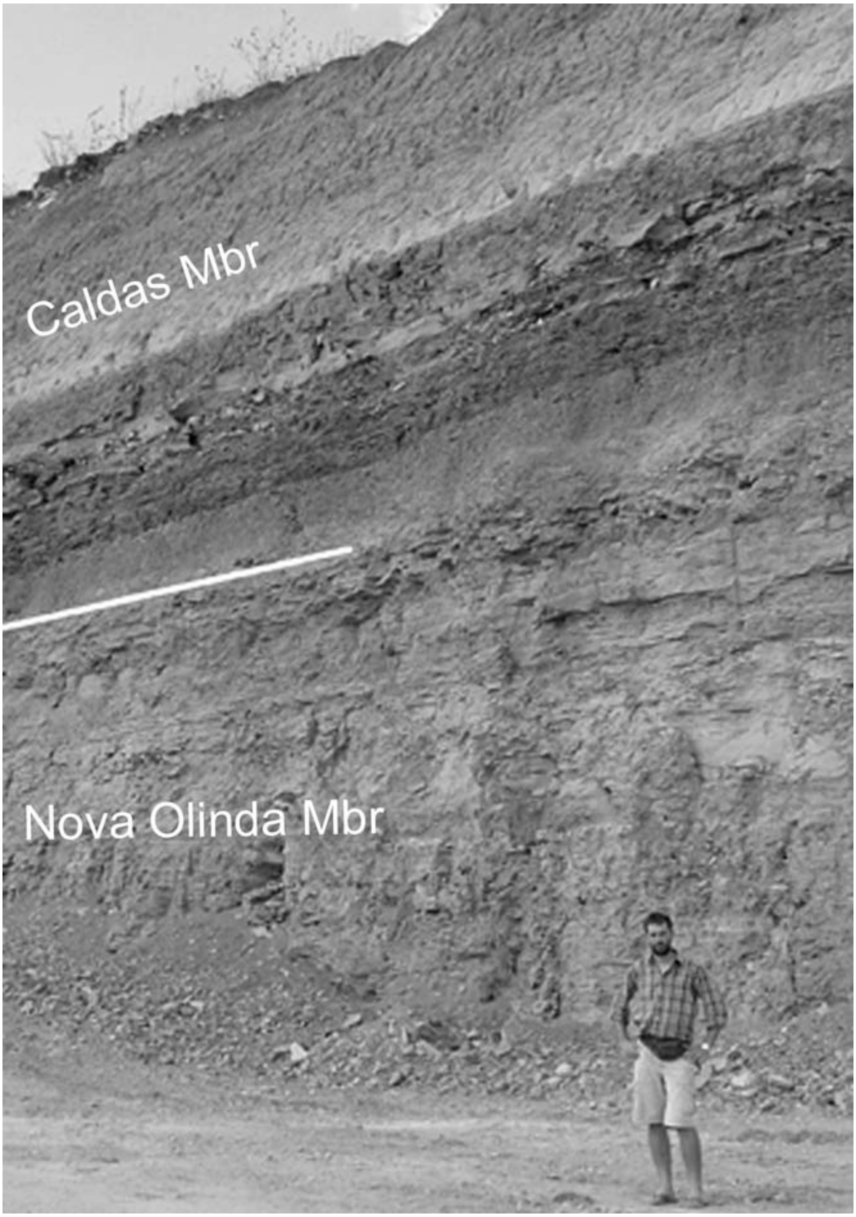

Fig. 3.6. The Nova Olinda Member (Mbr) and overlying Caldas Member exposed in the IBACIP cement company's Caldas mine (Mina Caldas) near Arajara, Ceará.

Definition. The base rests on a 1-m-thick bed of non-laminated limestone of the Nova Olinda Member. The basal boundary is sharp everywhere. The top is defined as the base of the overlying Jamacaru Member.

Lithology. A heterolithic siliciclastic and carbonate sequence comprising well-bedded thin black shales, silty shales, variegated clays and sandstones with thin laminated and micritic limestones.

Distribution. This unit is present from Tatajuba in the west to Barbalha in the north of the chapada, but appears to be replaced by thick sandstone units eastwards (see Martill and Wilby, 1993).

Thickness. Reaches at least 10 m in Mina Caldas, and may be more elsewhere. In the Riacho Jacu it may reach 30 m in thickness.

Palaeontology. Rare, poorly preserved bivalves. Some horizons are exceptionally rich in ostracods and conchostracans.

Jamacaru Member (Martill and Wilby, 1993)

Name. After the village of Jamacaru, Ceará, on the north-eastern flank of the Chapada do Araripe overlooking the isolated mesa of Serra da Mãozina.

Type locality. Stream below Jamacaru. Other good exposures of this member are at Sobradinho (Figure 3.7a) and Estiva.

Definition. The first substantial laminated limestone above the Nova Olinda Member and possibly the only laminite present in the eastern chapada. The top is marked by a distinctive silicified limestone, often with salt pseudomorphs replaced by black and grey silica with vuggy cavities lined with small quartz crystals. Between Tatajuba and Barbalha it rests on the Fontes das Caldas Member, but eastwards from Jamacaru to Porteiras and Sobradinho it is found resting on a thick sequence of fine sandstones and siltstones that might correlate with the Rio da Batateiras Formation.

Lithology. Lithologically similar to the Nova Olinda Member and almost indistinguishable in small outcrops. It can be recognized by its silicified stromatolitic top rich in halite pseudomorphs. Fossils appear to be rare, but this may be an artefact of the small exposure area compared with the Nova Olinda Member. A slumped horizon occurs near the top of this unit at several localities that may represent a near basin wide event.

Distribution. This unit is seen in many of the streams that drain the eastern chapada. It can be traced from as far west as Tatajuba eastwards in an almost continuous outcrop as far as Sobradinho near Jardim. Laminated limestones of similar facies occur at Mamelocou and near Ori south of the chapada in Pernambuco and may correlate with this unit. At Mina Casa de Pedra laminated limestones described by da Silva (1986a) beneath the Ipubi Formation evaporites and some black shales

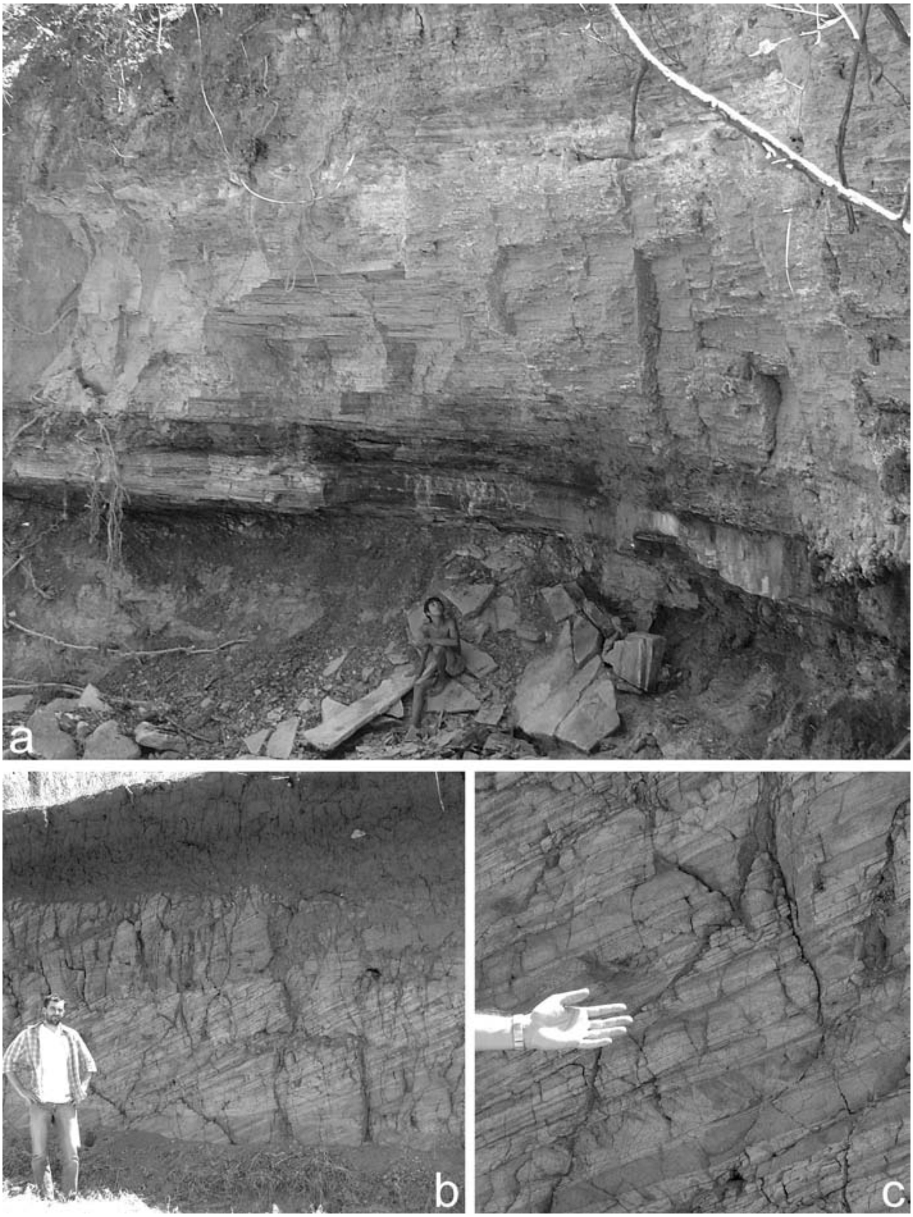

Fig. 3.7. Higher beds of the Crato Formation: (a) laminated limestones of the Jamacaru Member exposed in a stream section at Sobradinho, Ceará; (b, c) coarse cross-bedded sandstones resting above one of the laminated limestones in the Mamelocou sub-basin exposed in a road cutting between Jardim and Cedro, Pernambuco.

might correlate with the Jamacaru Member. Silicified laminated limestones in the north-western flank of the Serra do Vermelha, an outlier of the Chapada do Araripe, are tentatively correlated with this unit.

Thickness. Generally around 4 m thick, usually with a basal limestone unit of less than 1 m separated from the main limestone by a bed of silty shale of about 0.5 m (Figure 3.7a).

Palaeontology. Very rare *Dastilbe* sp. Conchostracans have been reported at Porteiras (Martill and Wilby, 1993), and fossil wood was noted at the type locality.

Casa de Pedra Black Shale Member (new name)

Name. From the *sitio* of Casa de Pedra in western Pernambuco where several nearby gypsum mines expose the member in drainage ditches in the base of the workings (Figure 3.8a).

Type locality. Mina Casa de Pedra, between Trindade and Ipubi in western Pernambuco, and adjacent mines.

Lithology. Laminated pyritous black shale, with some thin sandy layers. At least one fine sand layer was seen exhibiting mudcracks close to the contact with the evaporites.

Distribution. This facies has been seen in drainage ditches beneath the Ipubi evaporites at Mina Lagoa de Dentro, Ipubi, near Gergelim, Casa de Pedra and Mina Pedra Branca. Thus it appears to be present in both the Feitora and Cariri sub-basins. Variations in its thickness are not known.

Thickness. Three boreholes penetrating the full thickness of this unit were described by da Silva (1986a, 1986b, 1988), who reported some 10 m or more of algal-rich black shale in the type Ipubi district.

Palaeontology. Rich in ostracods and occasional small fish, such as *Dastilbe* sp.

Lithology

Although the Crato Formation is famous for its fossiliferous laminated limestones of the Nova Olinda Member, the formation comprises a heterogenous suit of lithologies, including both carbonates and siliciclastics. In fact, there is a greater diversity and overall a greater thickness of siliciclastics than of carbonates. Parts of the sequence are represented by laminated, fissile black shales, often rich in ostracods and small fishes, as in Mina Pedra Branca and the vicinity of Araripina. Many parts of the sequence contain siltstones and sandstones (Figures 3.7b and c) interbedded with green, yellow and brown clays with bivalves. Some of the clays are peppered with friable, white caliche concretions that may represent palaeosols, while silty

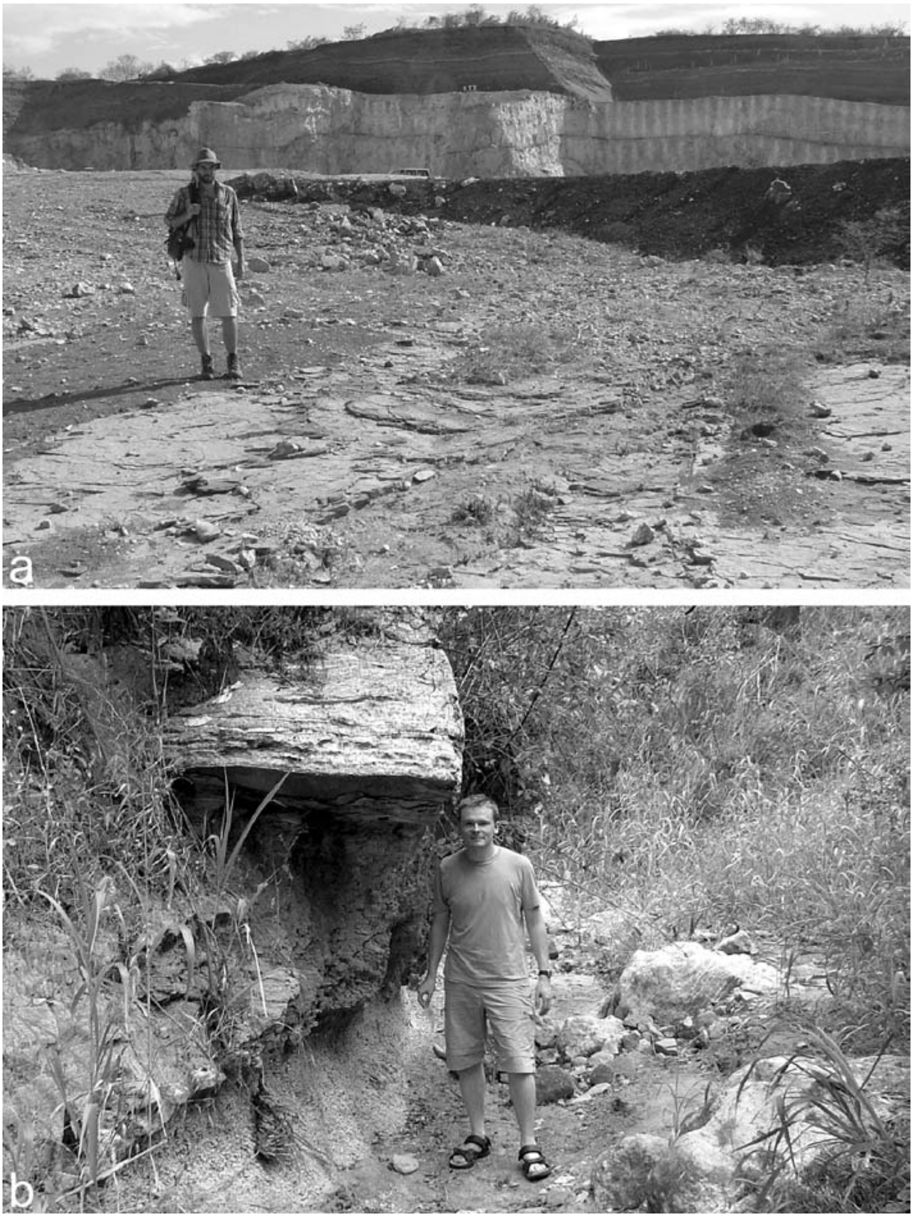

Fig. 3.8. The top of the Crato Formation: (a) gypsum mine at Ipubi with fissile black shales of the Casa de Pedra Member of the Crato Formation overlain by massive bedded gypsum of the Ipubi Formation, in turn overlain by the Santana Formation; (b) junction between the Crato and Ipubi Formations exposed in a stream section 2 km north of Santana do Cariri, Ceará. The massive bluff is laminated gypsum (Ipubi Formation) resting with sharp contact on black shales of the Casa de Pedra Member of the Crato Formation.

clays at Cascata, near Crato, are rich in plant remains and may represent parts of a distal subaqueous fan.

Age

Although the age of the Crato Formation remains to be determined precisely, several workers have considered it to be of Aptian age, while Berthou (1994) considers that the Aptian/Albian boundary lies within the formation, but its position remains to be located precisely. Early attempts to date strata in the Araripe Basin by Braun (1966) compared the ostracod assemblages with those of west Africa that had been dated as Aptian by Krommelbein (1966). A study by Lima (1979a, 1979b, 1980) on the palynology of the Araripe sequence also arrived at an Aptian age. However, a problem with these early studies is that it has never been clear which part of the stratigraphic sequence the fossil assemblages came from, rendering them rather imprecise. Considering the thickness of the Araripe sequence, the poor definition of the stratigraphic units at the time of these studies and the recognition of a number of disconformities within the basin, it seems unlikely that the entire sequence lies within the Aptian. Medus *et al.* (2001), in a brief review of the palynology, re-evaluated the dating by previous workers. They considered a late Aptian to early Albian age for the Crato Formation (although they called it Crato Member). Again, this study failed to say which parts of the sequence were attributed to which ages. Presumably the lowest part of the sequence which includes the Nova Olinda Member, must be late Aptian. In considering the palynology Batten (see Chapter 20) considers that the formation as a whole cannot be older than Barremian or younger than Cenomanian, and makes a reasoned argument for a late Aptian age.

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4

The sedimentology and depositional environment of the Crato Formation

Ulrich Heimhofer and David M. Martill

Although the exceptionally preserved fossils from the Crato Formation have attracted a multitude of palaeontological studies dealing predominantly with the systematics and taxonomy of the assemblage, reports on the sedimentology and depositional environment of this important Fossil Lagerstätte are rather scarce. There are even fewer studies on the geochemistry and sedimentary diagenesis of the formation. A few exceptions include analyses of the organic matter composition (Baudin and Berthou, 1996; Neumann, 1999; Neumann *et al.*, 2003) and a study of evaporite mineral pseudomorphism in the Nova Olinda Member (Martill *et al.*, 2007). Some workers have examined spot samples from the Crato Formation in studies on the Araripe Group as a whole (e.g. Berthou *et al.*, 1990) and a few assessments of the palaeoenvironment have been undertaken (Cavalcanti and Viana, 1990; Martill and Wilby, 1993). For a better understanding of the unusual taphonomy and exceptional preservation of the Crato fossils, a more detailed knowledge of the physico-chemical conditions of the aquatic palaeoenvironment is necessary. Because the Crato Formation is a heterolithic sequence with both clastic and carbonate deposition, it is clear that many different and often contrasting environments are represented by the sedimentary sequence. Many previous analyses fail to address the situation, preferring to summarize the unit as a whole, and providing generally unsatisfactory interpretations. Here we concentrate on the sedimentology and geochemistry of the Nova Olinda Member of the Crato Formation, with a view to elucidating the sedimentary and diagenetic environment that resulted in the exquisite preservation of the fossil assemblage. We draw on data from other parts of the Crato Formation sequence to enable us to place the Nova Olinda Member sedimentary environment in its wider context.

Problems that remain to be elucidated regarding the water body under which the Nova Olinda Member was deposited include the absolute salinity, or the range within which salinity may have varied, and the water depth. Furthermore, the rate of sedimentation, the substrate consistency and the eodiagenetic environment remain to be fully understood.

Origin of the carbonate

The most striking aspect of the Nova Olinda Member carbonate is the fine-scale parallel lamination (Figures 4.1–4.3). This distinct pale/dark banding is formed by 3.0–6.0-mm-thick couplets of laminae consisting of a carbonate-rich and a carbonate-poor layer, which split when weathered in typical *plattenkalk* style. The individual couplets add up to form the thick limestone unit of the Nova Olinda Member, which represents the primary target of the quarry men in the area. From a petrographic point of view, the Crato *plattenkalk* is a micritic limestone consisting of very fine-grained carbonate particles (Figure 4.1e) with only very few larger bioclastic grains such as ostracod shells and fish bones. In general, micritic limestones originate from the lithification of carbonate ooze and can be formed in depositional environments ranging from deep ocean basins to continental lakes. In modern pelagic marine settings, the source of the fine-grained carbonate particles is usually the disintegrated remains of micrometre-sized calcareous microfossils, including for example coccolithophorids and planktonic foraminifera. In shallow marine environments, calcareous algae, fecal pellets and reworked skeletal grains account for most of the calcareous ooze which gets deposited in the protected areas of carbonate platforms and around their slopes. Carbonate minerals are also a common constituent of lacustrine sediments. But, in contrast to the marine environment, the contribution to carbonate production by calcifying organisms (including mainly gastropods, bivalves, charophytes and ostracods) is comparatively small, and mostly restricted to the littoral realm. In modern lakes, the bulk of the primary lacustrine carbonates are inorganic chemical precipitates which form in the upper water column (the epilimnion). The precipitation of these authigenic carbonates occurs often in association with seasonal phytoplankton blooms, which produce chemical disequilibrium by abstracting large volumes of CO_2 from surface waters (Kelts and Hsü, 1978). The biological withdrawal of CO_2 out of the lake water causes a rise in pH, resulting in increased supersaturation with respect to calcium carbonate. The combination of seasonality-controlled phytoplankton activity and temperature increase during summer initiates the authigenic precipitation of calcite crystals in the upper water column, which sink and accumulate at the bottom. Thus, if the biological productivity of a lake or lagoon is controlled by seasonal climatic variations, the annual cycle can be preserved in the sediments as non-glacial varves. This varve type is made up of characteristic couplets which consist of a pale calcite layer formed during the warmest season and a dark,

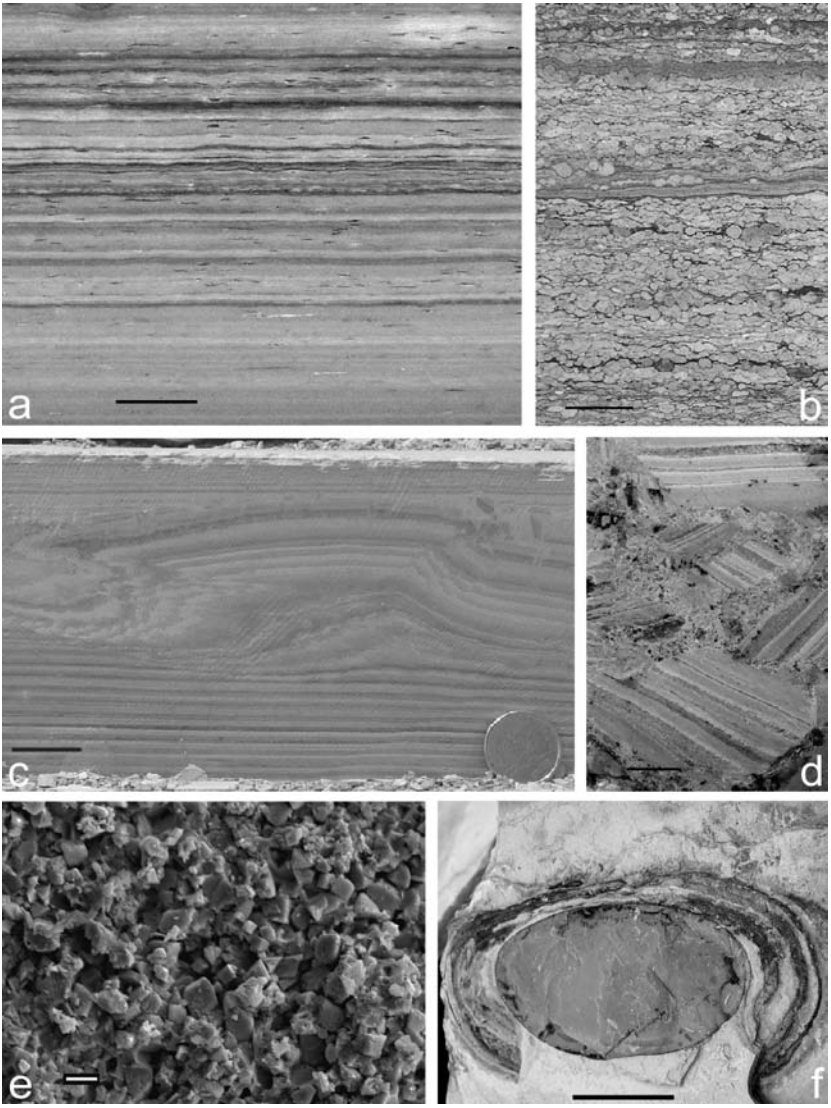

Fig. 4.1. Sedimentary laminae of the Nova Olinda Member. (a) Petrographic thin section showing planar laminae comprising an alternating sequence of carbonate and thin organic layers. Small dash-like marks are sections through crushed ostracod carapaces. This sample was obtained from the transition beds at the base of the Crato Formation. (b) Pelleted laminite comprising carbonate layers in the form of 0.5-mm-diameter pellets and organic-rich laminae. The pellets were cemented during early diagenesis and resisted compaction, retaining their circular cross-section. This sample from the base of the Nova Olinda Member between Barbalha and Arajara. (c) Small-scale soft sediment deformation in Nova Olinda Member laminite. (d) Brecciated laminite, probably as a result of the dissolution of interbedded evaporite minerals. This sample from a carbonate horizon approximately 1 m above the Nova Olinda Member at Tatajuba. (e) Carbonate-rich laminae with abundant euhedral crystallites of calcite; scale bar, 10 µm. (f) An early diagenetic chert concretion; scale bar, 25 mm.

Fig. 4.2. Synsedimentary deformation. (a) At Tatajuba Baixa, a prominent horizon towards the top of the Nova Olinda Member comprises a series of highly contorted laminae. The outcrop here is situated on the Nova Olinda branch of the Aurora Fault Zone. (b) Close up showing overturned, folded laminite.

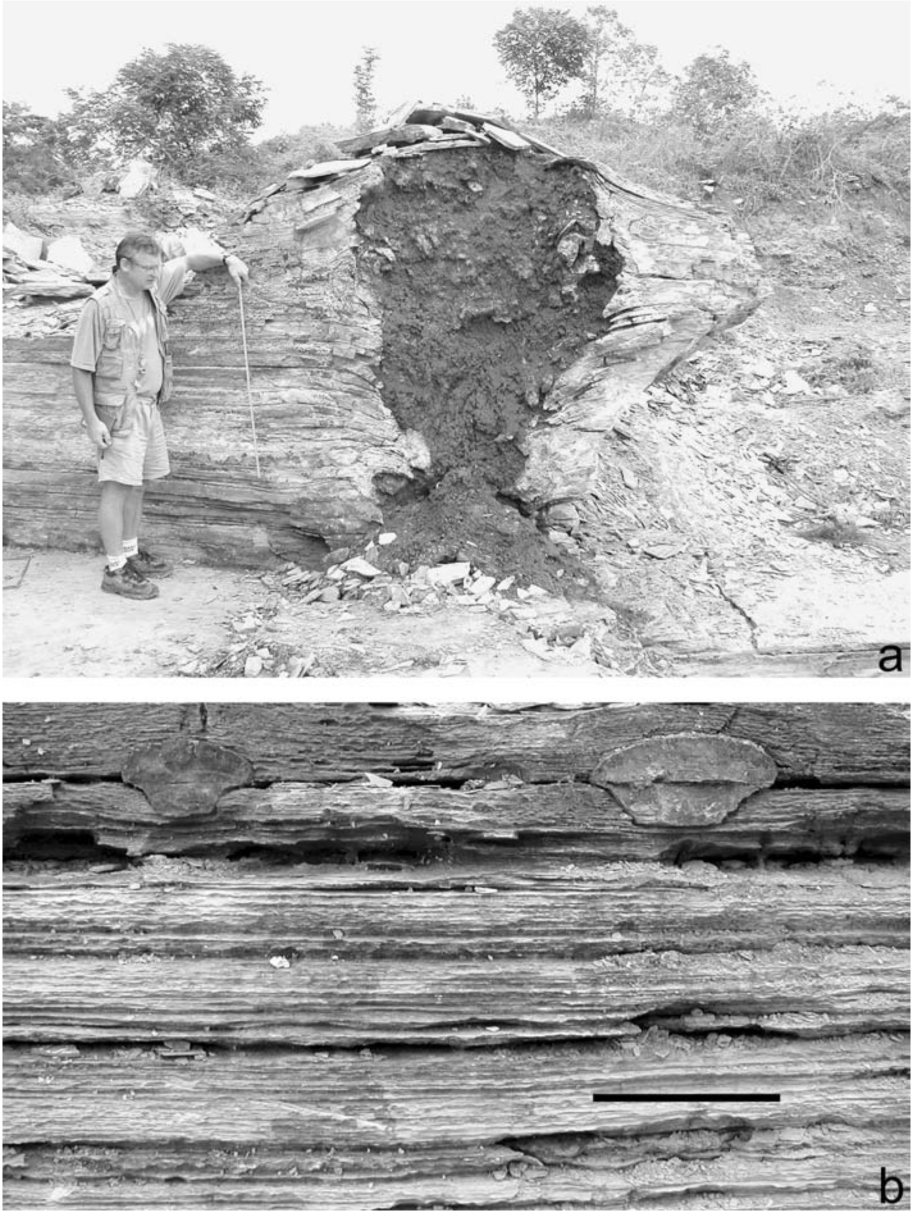

Fig. 4.3. Diagenesis in the Nova Olinda Member. (a) Dolomite pipe outcrop between Nova Olinda and Santana do Cariri. Later dissolution of the dolomitic part of this structure resulted in fissure development, which later became filled with a Holocene soil and limestone breccia. This outcrop has now been destroyed by quarrying. (b) Early diagenetic carbonate concretion growth within the laminite. Such concretions sometimes develop around body fossils. These concretions may sometimes be linear with sub-parallel orientations. Scale bar, 30 cm.

carbonate-poor layer arising from the settling out of detrital and organic material (Kelts and Hsü, 1978; Zolitschka, 2003). The process of seasonality-controlled, bio-induced calcite precipitation has been reported from many modern mid- to low-latitude settings, including a variety of European lakes as well as some of the large African rift lakes. In more arid regions, seasonal changes in the salinity of the lake water caused by evaporation might trigger the physico-chemical precipitation of calcium carbonate and other minerals (e.g. gypsum and halite). The individual laminae are often interbedded with bacterial mats or terrigenous detrital material, resulting in the characteristic pale/dark couplets (Zolitschka, 2003). Modern examples of seasonal calcite formation in evaporative basins are the Dead Sea (Israel) and Lake Van (Turkey). Seasonality-controlled authigenic calcite precipitation has also been suggested to explain the laminated sedimentary patterns observed in many fossil freshwater carbonates, including for example the Orcadian Basin (Devonian; UK; Stephenson *et al.*, 2006), Slawkow Graben (Permian; Poland; Szulc and Cwizewicz, 1989) and Krkonoše Piedmont Basin (Permian; Czech Republic; Martínek *et al.*, 2006). To decipher the nature of the carbonate particles in the fine-grained Crato limestone, it is necessary to use scanning electron microscopy (SEM). Our observations show that the bulk of the carbonate consists of individual calcite crystals ranging between 5 and 10 μm in diameter (Figure 4.1e). The grain-size distribution appears to be relatively narrow. In the clay-rich facies, individual calcite crystals are well-developed rhombs with relatively even crystal faces. Cavities between individual grains are open, pointing towards a high primary porosity and the absence of strong cementation or recrystallization during burial. Evidence for a biological origin for the carbonate particles is restricted to the scarce occurrence of ostracod carapaces in a few of the basal horizons.

In the case of the famous Solnhofen micritic limestone, Keupp (1977) argues for an important contribution of carbonate-secreting cyanobacteria for the carbonate. Keupp's argument is based on the common occurrence of spherical cavities that he interprets to reflect the activity of coccoid cyanobacteria on the sediment surface. Similarly, *in situ* precipitation of the carbonate by benthic microbial mat communities has been suggested by Martill and Wilby (1993) as a possible mechanism for the Nova Olinda Member limestone. However, SEM analyses of the limestone does not show the spherical structures or shells which might have pointed towards a strong contribution by calcifying coccoid bacteria. In contrast, the shape and size of the calcite crystals in combination with the virtual absence of biogenic or detrital carbonate grains suggests that the bulk of the carbonate formed by authigenic calcite precipitation, most probably due to oversaturation with respect to calcium carbonate by phytoplankton activity or by changes in evaporation in the surface waters of the Crato lagoon.

Style and nature of the lamination

The distinct pale/dark lamination is laterally consistent and individual laminae can be traced along the full length of the outcrop without change in their character. The vertical stacking pattern is similarly consistent and shows rhythmical bedding of pale/dark couplets with only minor changes in thickness across the entire accessible quarry face (Chapter 3, Figure 3.5).

According to Neumann *et al.* (2003), two types of laminated limestone facies can be generally distinguished based on their lithological composition and style of lamination. (1) The clay-carbonate rhythmite facies is characterized by relatively high detrital clay contents and by rather thin laminae couplets ranging in thickness between 0.5 and 0.8 mm. The pale/dark banding is very distinct and the dark part of the couplet is rich in continent-derived detrital grains and organic debris including pyritized phytoclasts. The pale laminae are dominated by calcite crystals between 5 and 10 μm in size whereas cement phases are virtually absent. (2) The laminated limestone facies corresponds to the typical 'blue' laminated carbonates which are preferentially mined in the quarries between Nova Olinda, Santana do Cariri and Tatajuba. Here, the distinct pale/dark couplets are much thicker and measure between 3.0 and 6.0 mm (Figure 4.1a). The dark-grey part of the couplets often exhibits an internal sub-lamination and is characterized by the occurrence of finely disseminated pyrite grains which generate the dark-grey colouring. Identifiable organic remains are restricted to a few phytoclast particles and rare fish remains. In contrast, the pale part of the couplets is made up of calcite rhombs (5–15 μm) that are partly cemented by coarse, poikilotopic calcite spar. Compared to the clay-carbonate rhythmite facies, the laminated limestone facies contains less terrestrially derived detrital material indicating a more distal position, with deposition during a water level high-stand (Neumann *et al.*, 2003). An alternative explanation might be that this represents a climatic shift to an arid or semi-arid period.

The occurrence of a distinct laminated pattern corresponds well with the concept of authigenic carbonate precipitation as the main source of the carbonate in the Crato limestone. As previously stated, precipitation of authigenic carbonate in modern lakes often reflects changing physico-chemical conditions of the lake waters throughout the seasonal cycle, for example due to phytoplankton blooms or changes in evaporative concentration. Under certain conditions, this can result in the preservation of the annual cycle in the form of non-glacial varves. The rhythmically stratified pattern observed in the clay-carbonate rhythmites strongly resembles modern non-glacial lacustrine varves in terms of thickness and composition. Seasonal changes in lake-water chemistry are suggested as the most likely trigger mechanism to form the observed lamination pattern. However, apart from annual changes there is a wide range of forcing factors working on non-annual time scales which can cause the deposition of rhythmically laminated sequences (Glenn and Kelts, 1991).

Other sedimentary features of the Nova Olinda Member

Although the dominant rock type of the Nova Olinda Member is laminite, occasionally other facies are developed. At the base of the sequence thin horizons of oncolitic limestone occur (Figure 4.4f), which appear to be patchily distributed, perhaps concentrated in nearly imperceptible hollows. Rare carbonate horizons containing coarse-grained siliciclastics occur towards the top of the Nova Olinda Member at Tatajuba (Martill and Wilby, 1993), but these horizons are usually only a few centimetres thick at most and clastic material is quite sparse, poorly sorted, and suggestive of sudden input, perhaps due to flash flooding (Figure 4.4e). Elsewhere in the Crato Formation succession siliciclastics, including some coarse sands, occur frequently, and may be several metres thick.

At some horizons in the Nova Olinda Member concretions of early diagenetic calcite occur. These usually have diameters of between 20 and 60 cm, and are usually flattened spheroids. The laminations can be seen to pass through them, but are somewhat thicker as a consequence of the earlier, precompaction diagenesis of the concretions. The cross-sectional shape may be an inverted bell shape (Figure 4.4b). In some places similar concretions are elongate and several may lie parallel to one another, and reach lengths of 2.3 m, but with widths of only 20 cm. Occasionally small concretions of black chert may occur (Figure 4.1f).

Wet sediment deformation

In many places the fine-scale lamination of the Nova Olinda Member is convoluted, pinched, overfolded and occasionally micro-faulted. Such structures may be restricted to a few laminae (Figure 4.1c) or to a horizon up to 1 m thick (Figures 4.2a and b). In all cases both the underlying and overlying strata are undeformed, demonstrating the penecontemporaneous nature of the deformation. Such deformation may have been triggered by tectonic activity on nearby, or underlying, faults in the basement rocks associated with strike slip movement on the Aurora Fault Zone.

Debris slides

At Tatajuba Baixa a series of small quarries exposes approximately 6 m of laminated limestone lying to the north of the Nova Olinda Fault, an offshoot of the Lineamento da Paraiba (Ponte, 1996). This limestone has an upper horizon with extensive

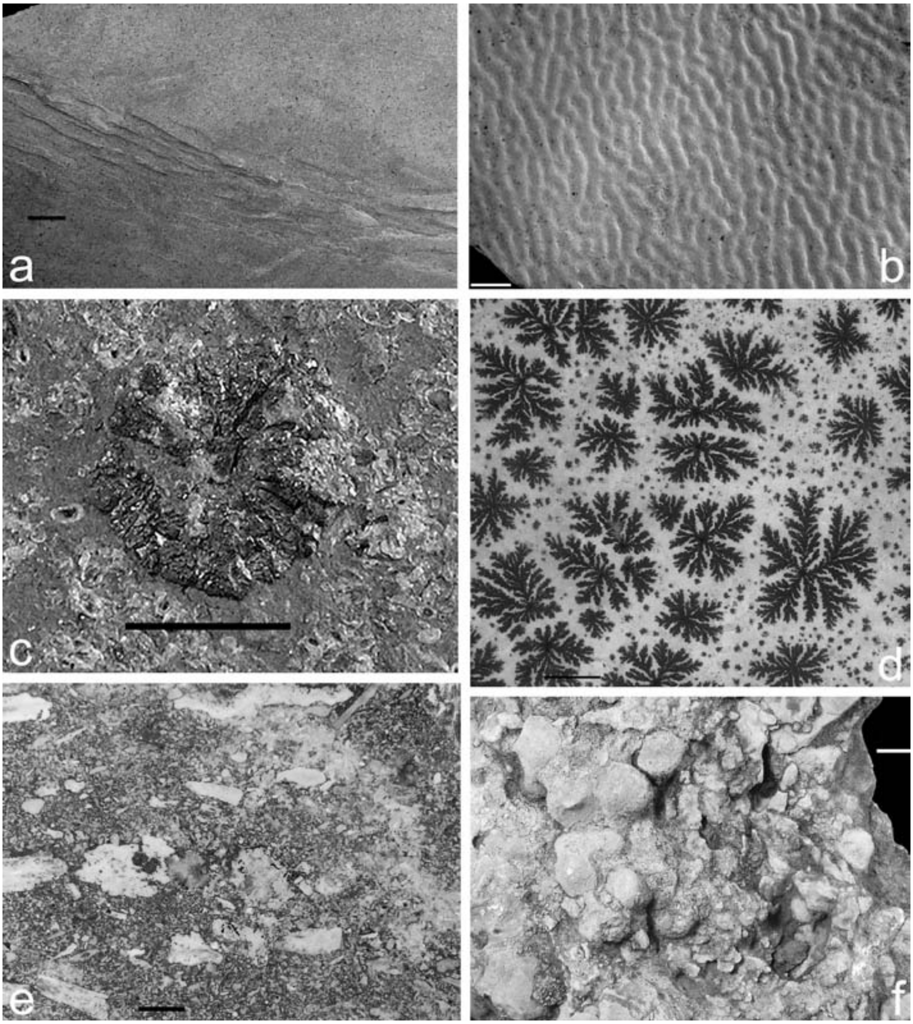

Fig. 4.4. Sedimentary features of the Crato Formation: (a), folded and 'rucked-up' lamina of the Nova Olinda Member, scale bar, 10 cm. (b) Ripple-like lithified microbial mat in Nova Olinda Member. (c) Concretion of radially arranged galena crystals in ostracod mass mortality horizon, from Rio da Batateiras/Nova Olinda Member transition zone at Cascata, near Crato. (d) Manganese dendrites on bedding plane of Nova Olinda Member laminite. (e) Carbonate conglomerate from base of Caldas Member. (f) Unusual oncolitic facies from base of an unidentified laminite in the Mameloucou sub-basin, between Mameloucou and Cedro, Pernambuco. Scale bars b–f, 10 mm.

slumping of the laminite (Figure 4.4). The slumped horizon is between 0.5 and 1 m thick (seen) and appears to cut down into the undeformed laminite below with a sharp basal contact. At its margins in one part of the quarry the laminite appears to be brecciated, suggesting that the slumped horizon cut through semi-lithified laminite as it moved downslope.

At this same locality, a thin (≈0.75 m) debris flow deposit occurs above the slumped horizon and includes a mixture of poorly sorted clasts of basement-derived quartz and intraclasts of sub-rounded laminite (Figure 4.5e). Although this mixture of material may have been derived from the nearby basin margins in a flash flood, it is not improbable that it is derived from a tsunami backwash.

Pseudomorphs after halite

Many bedding planes of the Nova Olinda Member exhibit circular to quadrangular structures with a four-pointed cross in the centre. These vary in size from a few millimetres to several centimetres (Figures 4.5d–f) and have been interpreted as compacted pseudomorphs after hopper-faced halite (Martill *et al.*, 2007). The central circular structure appears to be a consequence of compaction and micro-faulting of laminae draped over the pseudomorph. In some examples it appears that burial of the halite occurred and that its surface became a site for halophilic sulphate-reducing bacteria that generated a thin veneer of pyrite or marcasite on their surfaces. Subsequent dissolution of the halite resulted in collapse, or partial collapse, of the pyrite/marcasite skin.

Pseudomorphs after halite also occur in limestones within the Crato Formation south of the Chapada do Araripe near Sitio dos Moreiras, where they exhibit complex dissolution and replacement phases involving calcite, quartz and marcasite (Figures 4.2a and b). Silica pseudomorphs after halite also occur at the top of the Jamacaru Member (Figure 4.2c).

Algal mats and biofilms

At Nova Olinda one of the stone yards contained a number of slabs of typical Nova Olinda Member laminite in which bedding planes exhibited fine-amplitude ripple-like textures (Figure 4.5b), and creased and torn-off laminae, which we interpret as a damaged biofilm (Figure 4.5a). If this interpretation is correct, it is intriguing how the film became damaged. Unfortunately, this material was not seen *in situ*.

Occasionally irregular, contorted masses of filamentous material preserved as thin buff-coloured films occur and are interpreted as patches of filamentous algae. This material may occur as small patches of just a few centimetres in diameter, or

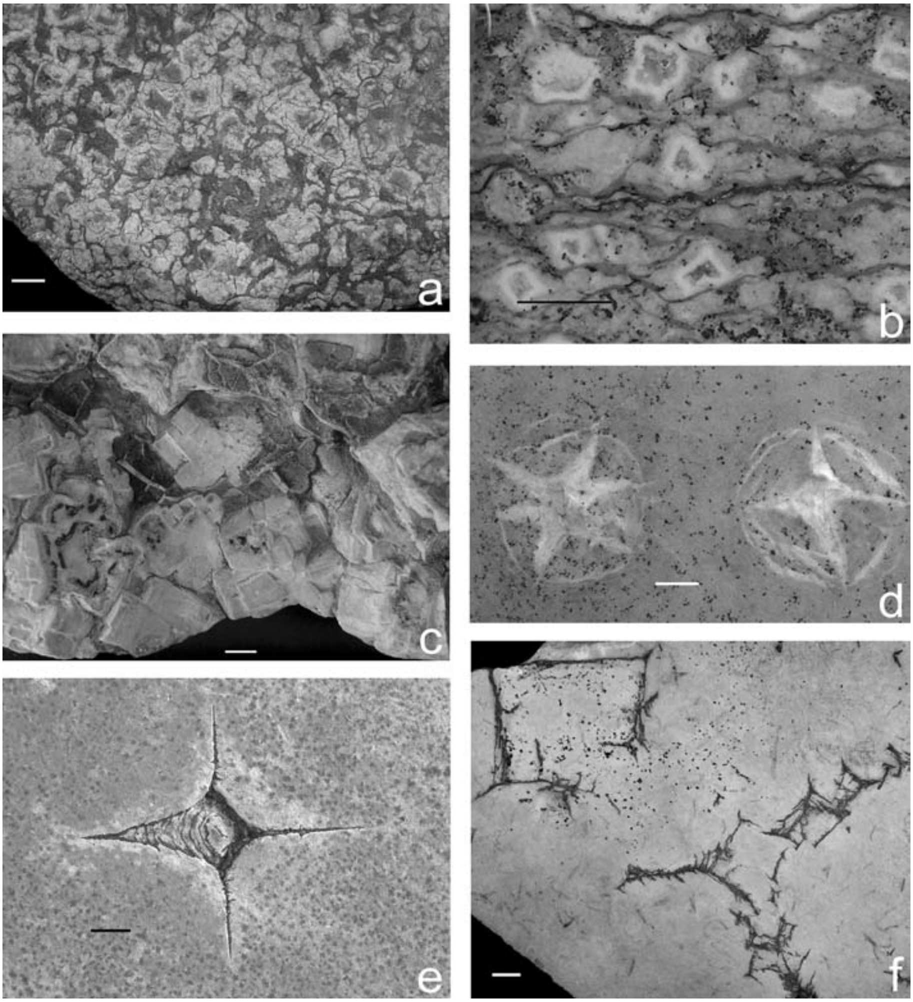

Fig. 4.5. Pseudomorphs after halite: evidence for hypersalinity in the Crato Lagoon. (a) Laminated limestone composed of aggregated quartz, calcite and marcasite complex pseudomorphs after halite. Specimen from southern side of Chapada do Araripe. (b) Thin section through same specimen, showing internal zoning of pseudomorphs and retention of cubic outline. The centre is quartz, with a white calcite overgrowth and a thin marcasite rim. (c) Pseudomorphs of silica after inter-grown halite. (d) Halite ghosts revealed as tears in laminae of Nova Olinda Member limestone. (e) Ghost halite crystal picked out as series of weathered marcasite overgrowths now themselves pseudomorphed by goethite. (f) Syntaxial aggregates of halite ghosts overgrown by marcasite. All Scale bars, 5 mm.

as larger patches of up to 30 cm across. It is common to find euhedral sphalerite associated with this material and on occasions to find several small insects seemingly trapped within it (see Chapter 21, Figure 21.2c and d). This material attests to the presence of algae within the basin, but it clearly was not benthic, and is unlike the benthic mat.

Fluid-escape structures

Rare dolomitic pipes occur in the region between Nova Olinda and Santana do Cariri, where zones of dolomitized laminites appear to surround brecciated material associated with intense ferruginous staining, numerous cross-cutting calcite veins and irregular silicification (Figure 4.4a). These pipes can reach up to 1 m in diameter and may be two or more metres in height. The lamination is compacted around them, suggesting an early origin, perhaps associated with fluid escape on the lagoon floor (Martill *et al.*, 2007).

Diagenetic alteration and weathering

The Crato limestone has not been subject to deep burial and severe thermal alteration, which is clearly indicated by the preservation and colouring of the palynomorphs (Chapter 20, Plate 32), and the exceptional preservation state of its macroscopic fossil content. The lack of evidence for strong physical and chemical compaction in the Crato limestone (for example in the form of pressure-solution seams or fracturing) additionally highlights the relatively shallow burial depth of the sediment stack. However, despite the absence of strong burial diagenetic overprinting, petrographic analyses of the carbonates show some evidence for diagenetic alteration, mainly in the form of cement growth. During an early phase of burial, compression of the carbonate ooze resulted in compaction and dewatering of the sediment pile, a process which was accompanied by a decrease in primary porosity and permeability. Circulation of calcium carbonate-rich pore fluids between the carbonate particles resulted in precipitation of sparry cements in cavities between the individual grains, causing the lithification of the former soft sediment. In the laminated limestone facies, individual cement crystals are relatively large, measuring between 1 and 3 mm in diameter and incorporating several grains. This type of cement, known as poikilotopic calcite spar, typically forms due to slow crystal growth and low nucleation rates in the burial environment (Tucker and Wright, 1990). The two types of laminated facies display distinct differences with regard to cement growth and recrystallization. Whereas the laminated limestone facies shows a significant porosity decrease due to widespread sparry cementation, the clay-carbonate rhythmites are virtually unaffected by cement formation. This might be the result of the higher clay content in the latter, which causes a significant reduction in permeability, in turn limiting circulation of calcium carbonate-rich fluids. In addition, clay minerals draped around individual crystal grains may have hampered the nucleation and subsequent growth of carbonate cements.

Other diagenetic minerals occur less frequently. At Cascata in the rhythmic alternations of clay and laminite it is possible to find small (10–15-mm diameter) discoidal aggregates of galena (Figure 4.5c), whereas near Triunfo the basal part of the Nova Olinda Member contains small aggregates of sphalerite. The presence of sulphide minerals attests to the strongly reducing conditions present in the basin. Tabular crystals of baryte up to 20 mm in length occur in loose clusters rarely within the Nova Olinda Member, but their genesis has not been investigated.

Probably the most visible effect of secondary alteration of the Nova Olinda Member is the distinct change in colour which can be seen within the thick stack of the Crato limestone in most of the quarries. Whereas the deeper parts of the succession exhibit a characteristic grey-blue tinge, the upper few metres are usually yellowish-brown to ochre in appearance, often with manganese dendrites (Figure 4.5d). This distinct colour change is a secondary effect and most probably reflects the influence of meteoric waters which percolated through the ground and affected the upper part of the limestone. Oxygen dissolved in the meteoric waters caused oxidation of the organic matter and associated pyrite (FeS_2), which resulted in the *in situ* formation of iron oxides and hydroxides (e.g. hematite and goethite). These secondary mineral phases are responsible for the yellowish-brown colouring which characterizes the altered, upper part of the limestone succession today.

Sedimentary pattern and palaeoenvironment

In general, the preservation of lamination in aquatic deposits depends on two factors, which are (1) the absence of bottom currents and (2) negligible benthic activity on and in the substrate. The carbonates of the Crato Formation provide no evidence for any turbulence or current activity at the lagoon bottom during or after deposition. Sedimentary features such as ripple marks, graded or cross-bedding, erosive channels or lag deposits are noticeably absent. Only one locality is known in the entire basin (at Tatajuba Baixa) where the occurrence of well-rounded laminated limestone clasts indicates reworking and subsequent deposition in the basin, most probably in form of a debris flow deposit (Figure 4.5e). Storm-winnowed horizons are absent and the Nova Olinda laminite is vertically continuous for up to 13 m (perhaps a little more at Tatajuba Baixa). This strongly hints at a basin floor beneath the normal storm wave base for inland water bodies in tropical regions. Indeed, if the laminations are seasonal, then the normal storm wavebase criteria should be extended to include larger tempests, as the sequence may represent continuous sedimentation for several thousand years without interruption.

Mud-cracked horizons are absent from the Nova Olinda Member, although they do occur in other parts of the Crato Formation, notably beneath the Ipubi Formation evaporites at Ipubi. Similarly, dinosaur footprints have failed to be reported, but are known elsewhere in the basin (Carvalho, 2000). Neither can the Nova Olinda laminites be traced laterally into a shallow water carbonate or shore-line facies, even close to the basin's suspected northern margin. The persistent occurrence of a virtually undisturbed lamination pattern throughout several metres of limestone clearly proves that the Crato carbonates were deposited in a very quiet and protected depositional environment, certainly below the wave base of the lagoon and probably in a water depth in excess of 50 m or more.

Evidence for anoxic conditions

The virtual absence of sediment mixing by bioturbation indicates that conditions in the deeper water body of the lake (hypolimnion) were unfavourable for bottom-dwelling organisms. Such hostile environments are often caused by oxygen depletion or anoxia, when nothing apart from a specialized microbial community is able to survive. Oxygen deficiency of the hypolimnion is a common feature of many modern lakes and lagoons and is often caused by insufficient water mixing in combination with high primary productivity in surface waters (eutrophic conditions). Decay of the organic detritus during sinking causes enhanced oxygen demand, eventually causing anoxia at the lake bottom, and sometimes extending up into the lower part of the water column.

Analysis of organic biomolecules (biomarkers) preserved in the sediments of the Crato lagoon provide important information on the structure of the water column and the prevailing redox conditions during deposition of the carbonates. Biomarkers of special interest are pigments produced by a group of bacteria which can only thrive under certain conditions in the waters. These compounds, known as isorenieratene derivatives, are produced by the brown strain of the green sulphur bacteria (*Chlorobiaceae*). These bacteria require hydrogen sulphide to perform anoxygenic photosynthesis and therefore are restricted to oxygen-free, hydrogen sulphide-saturated waters. As these bacteria are phototrophic they also require a certain amount of light to thrive in the water column. In modern environments (e.g. Norwegian fjords or the Black Sea) the highest concentrations of these bacteria occur at the chemocline, where sulphidic bottom waters and oxygenated surface waters meet. The occurrence of isorenieratene derivatives in ancient sediments of the Black Sea has been used to demonstrate that this basin experienced several phases of photic-zone euxinia (that is, anoxic conditions reaching up into the photic zone) during the last couple of thousands years (Sinninghe Damsté *et al.*, 1993). In addition, these compounds are ubiquitous in Cretaceous black shales deposited during global oceanic anoxic events (OAEs) and prove the occurrence of photic-zone euxinia of entire ocean basins during these events (e.g. Pancost *et al.*, 2004). The occurrence of isorenieratene derivatives in the laminated carbonates of the Crato Formation confirms the sedimentological evidence and indicates anoxic conditions prevailing in the hypolimnion. In addition, these findings show that the waters of the Crato lagoon were, at least seasonally, stratified and saturated with respect to hydrogen sulphide below a shallow chemocline.

Evidence for hypersalinity

Apart from oxygen deficiency, excessive concentration of salt in the bottom waters of a stagnant water body can explain the lack of sediment mixing by benthic organisms. Intensive evaporation, generally under arid conditions, can result in the formation of a brine, which collects at the bottom of the basin due to its higher density compared to fresh- or normal marine water. If mixing of the water body is limited, because of the geometry of the basin or the lack of intense storm activity, the accumulation of hypersaline waters at the bottom of a lake can prevent the colonization of the substrate by bottom-dwelling organisms and therefore preserve the primary sedimentary pattern. The tolerance of most freshwater and marine macrobenthic organisms towards increased salinities is rather limited. This results from the osmotically driven withdrawal of water from their body tissue in hypersaline solutions.

The Crato limestone provides evidence for at least episodic occurrence of hypersaline bottom waters in the form of salt pseudomorphs. These types of structure form due to dissolution of a primary salt precipitate, usually during an early phase of diagenesis, and replacement by calcite which preserves the shape of the former salt crystal. Salt pseudomorphs with circular compaction faults have been described by Martill and Wilby (1993) from the Crato limestone. More recently, Martill *et al.* (2007) reported on five different types of pseudomoph after halite (NaCl), providing strong support to the idea of at least episodically hypersaline bottom waters persisting during deposition of the laminated carbonates (Figure 4.2). Some breccias of laminite found within the Fonts do Caldas Member at Tatajuba may represent collapse breccias generated by the dissolution of interbedded halite (Figure 4.1d).

An evaporative scenario causing salinity-driven stratification in the lake fits well with the overall palaeoclimatic pattern of the area. During the late Aptian to early Albian, the Araripe Basin was situated at a palaeolatitude of about 10°S. The corresponding region was part of a vast climatic belt characterized by semi-arid to arid conditions (termed the tropical-equatorial hot arid belt in Chumakov *et al.* 1995). This palaeoclimatic reconstruction is primarily based on sedimentological and palaeobotanical evidence including the widespread occurrence of evaporites along the evolving South Atlantic rift system, the absence of coal deposits and the dominance of drought-resistant savanna-type vegetation (Doyle *et al.* 1982). This interpretation is in good agreement with the high abundances of *Classopollis* pollen in the sediments of the Crato lagoon. *Classopollis* pollen is produced by plants of the family Cheirolepidiaceae, an extinct group of conifers whose leaf structure indicates adaptation to at least seasonally arid conditions (see Chapter 20). Additional evidence for low precipitation rates is provided by the low concentration of leaf-wax lipids in the Crato carbonates. Leaf-wax lipids are produced by terrestrial plants and their abundance in sediments can be used as an indicator for the overall input of terrestrially derived organic matter to the basin. Exceptionally low abundances of leaf wax lipids in the laminated carbonates point towards low riverine fresh water input and a rather meagre vegetation in the vicinity of the basin.

Implications for fossil preservation

In freshwater or normal marine water, any type of animal carcass deposited on the sediment surface is scavenged by a variety of organisms (detritivores) and its disseminated remains get rapidly populated by a mixed microbial community of aerobic heterotrophic bacteria. This will result in effective decomposition and remineralization of almost all body parts (and in the release of dissolved organic compounds and nutrients back into the water column), leaving behind only certain resistant hard parts (e.g. teeth) which might then enter the geological record. However, the peculiar physico-chemical conditions of the Crato waters inhibited the efficient decomposition and disarticulation of the deposited animal corpses, allowing for undisturbed embedding and burial in the sediments, which finally resulted in the exceptional preservation of the fossils.

Based on the existing evidence, the Crato basin can be typified as a meromictic water body characterized by a well-mixed and productive epilimnion which was separated by a pronounced chemocline from a permanently stagnant hypolimnion. Insufficient water mixing in combination with a strong oxygen demand within the water column (due to the decay of settling organic matter) is suggested to have caused anoxic conditions in the lower water column. The process of oxygen depletion might have been amplified by a concomitant increase in the water salinity caused by strong evaporation (in a relatively arid environment) as oxygen solubility in water is known to decrease with increasing salinity. The existence of a hypersaline brine completely depleted in oxygen drastically constricted the activity of macrobenthic detritivores at the bottom of the Crato lake/lagoon. This resulted in a significant reduction in the reworking of organic detritus and sediment mixing by bioturbation. Once an anoxic and hypersaline bottom water body was established, the organic matter produced in the surface waters was no longer broken down by aerobic heterotrophic bacteria and accumulated in the sediment. Similarly, carcasses of fish and reptiles as well as insects that had been blown in were not severely attacked and remained virtually ‘untouched’. Bacterial decomposition and remineralization of organic matter continues under anoxic conditions due to the activity of various anaerobic bacteria, but is less efficient and the overall turnover rate is significantly lower. The saline waters present in the hypolimnion most probably provided the sulphate necessary for bacterial sulphate reduction, which represents an important pathway for organic matter decomposition under anaerobic conditions. Many sulphate-reducing bacteria cannot tolerate hypersaline conditions, but a number of halophilic sulphate-reducing anaerobes have been documented. Bacterial sulphate reduction generates hydrogen sulphide as a main by-product, which is known to be extremely toxic to most organisms and therefore further reduces the activity of other bacterial consortia. On the other hand, free hydrogen sulphide is an essential requirement for Chlorobiaceae to perform photosynthesis under oxygen-free conditions, allowing these bacteria to thrive along the chemocline in the photic zone of the basin.

In summary, the exceptional preservation of fossils in the Crato limestone represents the result of a combination of different processes that controlled the peculiar physico-chemical conditions of the depositional environment. The presence of an oxygen-free, hydrogen sulphide saturated lower water column is the most important factor in providing an extremely hostile environment devoid of any macrobenthic life. Anaerobic bacterial decomposition rates were most probably too low to cause significant disintegration of the carcasses. These factors were amplified by hypersaline bottom waters, which limited oxygen concentration in the hypolimnion and further reduced bacterial activity, finally promoting undisturbed burial and exceptional preservation of the fossils.

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5

Commercial exploitation of the Crato Formation

José Artur Ferreira Gomes de Andrade

Despite the varied nature of the Crato Formation succession, comprising a mix of carbonates and silicilastics, only the Nova Olinda Member, the source of the exceptionally preserved fossils, and some of the overlying argillaceous strata, are exploited commercially. The finely laminated limestones of the Nova Olinda Member have been excavated as a building stone, because of the easy way in which they split, and have been used for table tops and paving slabs, probably since historic times.

At present, the Crato Formation is quarried extensively in only two main areas, although in former times small quarries were operated in many places around the Chapada do Araripe, where it was extracted as a source of agricultural lime as well as for building materials. One of the higher laminated limestones of the Crato Formation, the Jamacaru Member, was formerly excavated on the northern flanks of the Serra do Moazina, near Abaiara.

Cement production

To the south and west of Barbalha several large-scale excavations of the Nova Olinda Member limestone and the overlying clays and muddy sands are used in cement manufacture. Quarries formerly operated at Sitio Santa Rita on both sides of the road leading from Barbalha to Jardim, but these sections are now becoming overgrown. A quarry at Sitio Correntinho and the adjacent stream section exhibit a near-complete section of the Crato Formation and are currently the main source of material for cement production at the IBACIP cement works in Barbalha (Figure 5.1a). A new quarry to supply this works was opened in 2005 just to the

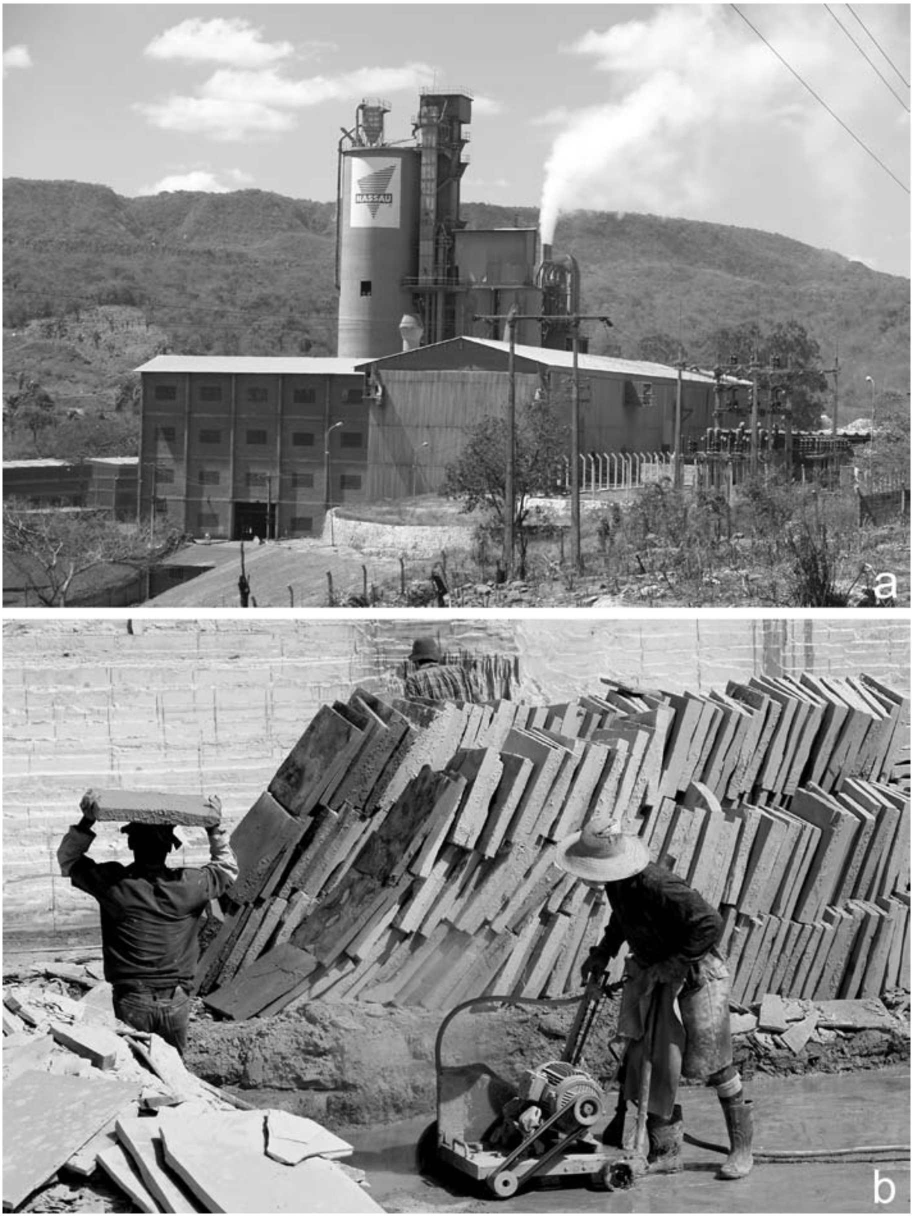

Fig. 5.1. Economic uses of the Crato Formation. (a) Cement production at Barbalha using both the limestones and clays of the Crato Formation supplies the rapidly growing conurbation of Crato/Juazeiro do Norte. (b) *In situ* cutting of the Nova Olinda Member laminites produces paving slabs with very little wastage of this valuable stone.

north east of Arajara. The IBACIP cement factory, the only one in southern Ceará, supplies material to as far as 600 km away.

Paving and ornamental stone

In the region forming the triangle of Nova Olinda–Santana do Cariri–Tatajuba there are numerous quarries excavating the Nova Olinda Member for paving stone and, to a lesser degree, for building stone (Figures 5.1b and 5.2). It is unusual to find houses constructed of the limestone, partly as traditional low-cost housing is built from adobe, while slightly more expensive properties are usually built from extruded terracotta blocks or locally fired bricks. Nevertheless, a few houses, especially in villages and farmsteads located on the outcrop, have some housing built from the Crato limestone (Figure 5.3a).

Until the 1980s there were only a few small quarries working the Nova Olinda Member, and the market for the paving stone, sometimes called *pedra de laje*, was mainly local. Demand for stone varied and many quarries closed, including those to the south of Crato, but during the 1990s the stone became popular and new markets were established as far as Recife and even Rio de Janeiro and São Paulo. The development of these markets and the rising popularity of the stone resulted in the rapid expansion of the quarries in the main stone-producing area. Although not licenced by the DNPM, there are now more than 400 active quarries in the region, providing work for a little over 1000 families. Initially the stone was always worked using traditional, labour-intensive techniques, and often worked slumped blocks along the outcrop, rather than the stone *in situ*. However, the rising wealth of the stoneyard owners and the increase in demand for the stone saw the introduction of mechanization, at first for overburden removal, and more recently for cutting the stone *in situ* (Figure 5.1b). Prior to the introduction of machinery for excavation, much of the supplied stone was a yellow, buff or cream colour, and not especially hard-wearing, but as increasingly thicker amounts of overburden were removed to expose the stone, less-weathered, darker grey and harder-wearing stone was produced.

At Tatajuba the quarries of Anton Felipe produce large slabs of unweathered stone that takes a high polish and is used for very high-quality ornamental tables (Figure 5.3b).

Geotourism and artisan products

Part of the Chapada do Araripe was designated a National Forest in 1942, and was one of the first in Brazil to be so designated. More recently the entire Chapada

Fig. 5.2. Stone cutting in Nova Olinda: the stone quarries around Nova Olinda are the source of the beautiful Crato Formation fossils. (a) Many fossils are discovered in the cutting yards where rough slabs are turned into paving stones. (b) Splitting of the laminite in the quarry means that quarry workers discover fossils on a regular basis.

Fig. 5.3. Economic uses of the Nova Olinda Member limestone. (a) Historically used as building stone, Araraporanga, Ceará. (b) Ornamental use of unweathered stone for tables and 'neo-classical' columns, manufactured by Sr Anton Filipe, Nova Olinda.

Fig. 5.4. Educational use: the UNESCO-supported Araripe Geopark includes a Geotope on the Nova Olinda Member of the Crato Formation, providing an important resource for the Regional University of the Val do Cariri and an educational tourist attraction.

do Araripe region has come under new legislation to protect the environment (Anon, 1999), and work has now commenced to establish the Araripe Geopark (Figure 5.4). This is the first geopark to be established in Brazil, and indeed is probably the first in South America. Its establishment will guarantee the protection of a number of internationally significant localities, as well as provide a series of easily accessible localities of educational value that highlight the palaeontology and geological evolution of the region. Presently, sites have been established that show sections through the Nova Olinda Member limestones, the Ipubi Formation evaporites and the Romualdo Member nodule beds of the Santana Formation. In addition, a viewpoint providing spectacular vistas over the valley of the Riacho Caririaru at Cancau overlooking the town of Santana do Cariri makes an excellent place to end a fieldtrip, having a rather nice restaurant. Although early days, this project will surely attract visitors, not just from Brazil, but also from abroad, such is the palaeontological importance of the Araripe Basin.

Although in its infancy, a spin-off from the stone quarrying around Nova Olinda is the development of an artisan industry producing stone carvings and artwork made from the Nova Olinda limestone. Such products, including carvings, acid-etched pictures and stone plates and other items, are very attractive and inexpensive.

Reference

Anon. 1999. Politica ambiental e gestao dos recursos naturais para a bio-regiao do Araripe. *Proposta da FUNDETEC para o Conselho Gestor da APA Chapada do Araripe, Crato, CE, Brasil, Juhno 1999.*

6

Preparation techniques for Crato Formation fossils

Michael Schwickert

Fossils are abundant throughout the Nova Olinda Member of the Crato Formation and occur at most levels within the laminated parts of the sequence. They occur in a variety of styles of preservation depending on the degree of weathering of the deposit and, to a lesser degree, on localized diagenetic anomalies. Accordingly, a number of different techniques are employed for their preparation depending on the nature of the matrix and on the style of preservation of the fossil itself. In general, all fossils from the Nova Olinda Member are fragile, being composed of either a soft, sometimes powdery goethite in the buff-coloured weathered stone, or a powdery carbonaceous material in the fresh blue-grey limestones. Many fossils are discovered when the limestone is split along well-defined bedding planes, resulting in the splitting of the fossil into two halves, often referred to as part and counterpart. Such discoveries, while damaging the fossil, may reveal details of the internal anatomy and, in the case of larger examples of the fish *Dastilbe*, may reveal stomach contents. Such fossils often require little or no preparation.

Many Crato fossils, however, occur beneath several laminae and are discovered, often by the quarry workers, as almost imperceptible swellings on bedding-plane surfaces (Figure 6.1c). These slight swellings may be accompanied by whitening of the surface, and occasionally a halo of orange-brown goethite (Figure 6.1c). Such fossils may lie at depths of more than 10 mm (Figure 6.1d) and always require mechanical preparation to expose them. When undertaken by professional preparators these fossils are often found to be exquisitely preserved (Figures 6.1d). Here I outline a number of preparation techniques that yield good results on the Crato Formation fossils.

When collecting Crato fossils in the field it is important not to touch them, but to wrap them in such away as to avoid abrasion. A continual problem for palaeontologists is inappropriate preparation by quarry workers.

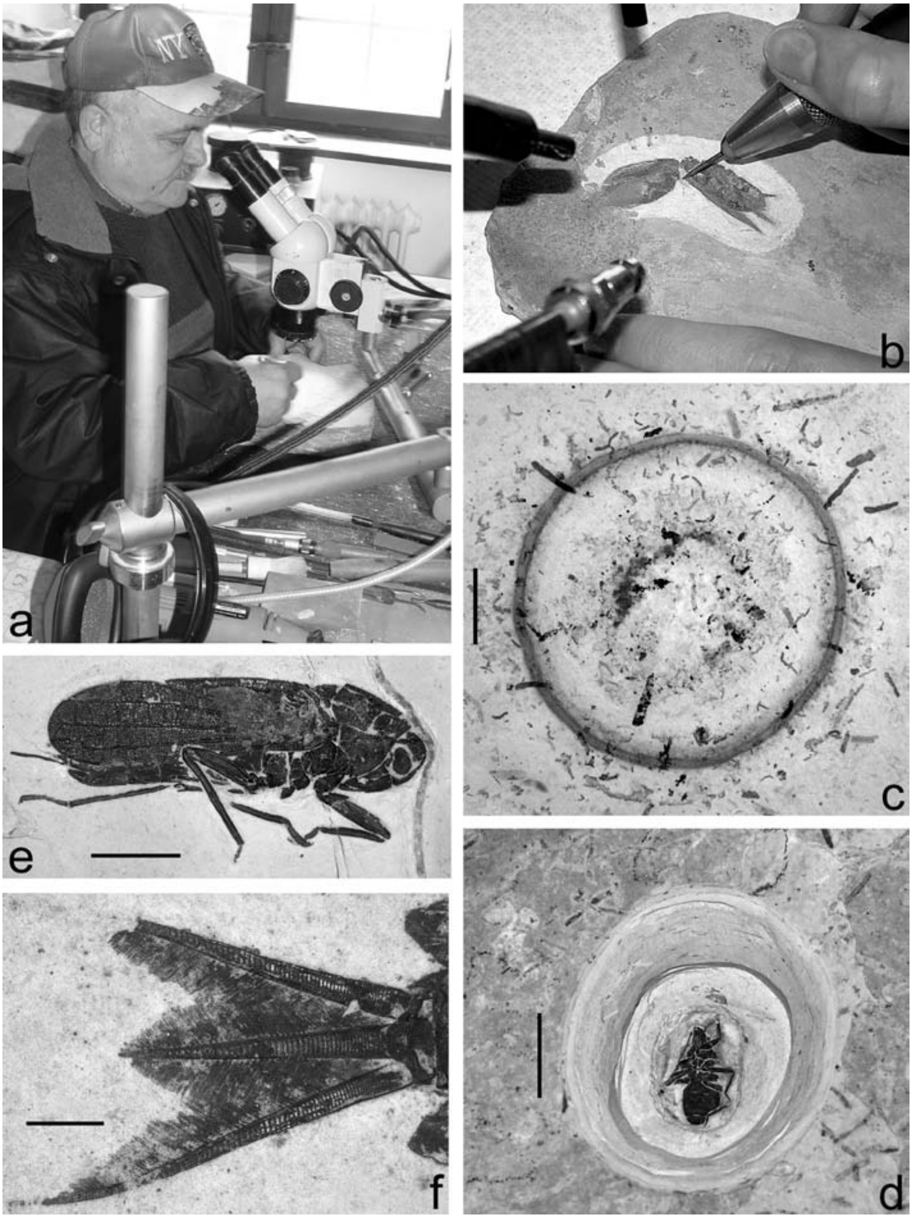

Fig. 6.1. Preparation of fossils from the Nova Olinda Member laminite. (a) Preparation is best undertaken with a binocular microscope. (b) The use of needles working with directed light yields the best results. (c) The presence of fossils is often indicated by a slight swelling of the laminae or the presence of a halo of goethite. Here both indicate a fossil just a few millimetres below the surface. (d) Fossils found below lamina are often in perfect condition but must be exposed by careful preparation. (e, f) Examples of fine preparation using acid. Scale bars, 10 mm (c, d); 5 mm (e); 1 mm (f).

Field techniques

Although Crato Formation fossils are abundant, there is currently little to be gained by opening excavations solely to obtain fossils as there are numerous small quarries operating between Nova Olinda, Santana do Cariri and Tatajuba. In these quarries fresh rock is being exposed every day and fossils can be obtained from the quarry workers, or by searching the spoil dumps. Searches are usually more productive after light rain due to the large quantities of dust that accumulates during dry periods. While a search for fossils will always reveal small fishes and the more obvious insects on bedding planes at most times of the day, discoveries are more frequent when the sun is low in the sky; the low-angle light emphasizing the low swellings and faint discolouration that indicates a fossil at depth in the slabs.

Laboratory techniques: mechanical preparation

Because many of the Crato Formation fossils are small, it is necessary to undertake most preparation under a binocular microscope with variable magnification (Figure 6.1a). Even though Crato fossils generally contrast well with their surrounding matrix, good lighting is essential. Commercial cold-light lamps with a swan neck are best because of their flexibility and ease of positioning the light.

Fossils can be prepared using hand tools, with a pin-vice (Figure 6.1b) and medical-grade scalpels being particularly useful, or a pneumatic air stylus (e.g. W224). The latter has a top for changeable tips in sizes W218 (chisel needle, 48 mm), W213 (point needle, 48 mm), W219 (knife needle, 48 mm) and W226D (replacement needle holder), which can be obtained from the Krantz company in Bonn (*http:// www.krantz-online.de*).

When using any of these tools, it is essential to practise on a piece of unimportant stone first to gain some experience of the Crato stone. While some of the weathered parts of the formation can be soft and easily worked with hand-held tools, the bluish-grey limestone can be extremely hard and is better worked with a pneumatic stylus.

Scraping away the soft limestone with hand-held needles and scrapers generates dust that quickly accumulates to conceal the worked area. Accordingly, Selden (2003) developed a technique in which hypodermic needles of various sizes are connected to a small fish-tank air pump via a flexible plastic tube. A continuous gentle airflow from the hypodermic needle maintains a constantly clear working area.

With the use of any pneumatic tools, care must be taken to avoid extreme air pressures, as it is possible to blow away delicate fossils: when in doubt, use hand-held tools.

For extremely friable fossils, it may be necessary to consolidate parts of the fossil prior to preparation using cyanoacrylate adhesives or paraloid. Sometimes very thinly diluted paraloid (dilute with acetone) can be dropped close to the fossil and allowed to diffuse through the porous matrix into fossil.

Laboratory techniques: synthetic resin transfer

Because the Nova Olinda Member is a nearly pure limestone, it is easily broken down using mineral and organic acids. The weathered parts of the succession dissolve readily in hydrochloric acid and many of the highly oxidized, but less porous, insect fossils can be partially prepared using hydrochloric acid at 5% without causing any damage (acetic and formic acids may also be used). Acid preparation can be performed either as a wash over the surface of a partially exposed insect, or with the fossil immersed for a prolonged period.

This technique has some limitations, in that some fossils, notably small fishes, may have a thin zone around them which appears to be partially resistant to acid dissolution. Also, bones of small *Dastilbe* are likely to dissolve in hydrochloric acid, and it is best to employ acetic or formic acid for the vertebrates. I have successfully employed the acid-transfer technique to small specimens of *Dastilbe*, leaving the exposed fossil embedded in a resin block. A variation of this technique has now been successfully developed for the insects. Where insects have been damaged by poor handling in the field, it is sometimes clear that the surface embedded within the rock remains in good condition. Under ordinary circumstances preparation of the fossil from the other side of the slab would, without some means of stabilizing the specimen, result in its destruction.

This method is similar to the transfer method, used for Eocene fossils from the famous Messel Pit in Germany (von Koeningswald and Storch, 1998). Damaged insects should be embedded in a clear resin by constructing a small plasticine ‘dam’ around the fossil and filling the ‘bowl’ with a hard, clear-drying resin such as two-component polyester resin. It requires 24 h to completely harden, although the hardening process can be accelerated by immersing the specimen in water at 70–80°C. To avoid bubbles forming it is important to pour the resin very carefully and slowly into the bowl. It is also possible to use a small shaking plate or autoclave to help avoid the formation of bubbles. A homemade shaking plate can be made from an electric sander.

The resin can be polished once it has hardened to provide a smooth, flat, clear surface. Provided that the surface has hardened and clarified satisfactorily, the specimen can now be prepared from the reverse side, either mechanically or by using acids (Plate 2f).

Focused acid preparation

Because of the delicate nature of some of the fossils, wholesale acid digestion may be inappropriate. Nevertheless, there may be parts of a specimen that require exposure, or the removal of small amounts of matrix to expose such structures as compound eyes or genitalia. As an alternative to using mechanical methods, acid applied to specific areas can achieve excellent results (Figures 6.1e and f). However, because of the highly fluid nature of acids, it is more convenient to combine them with a thixotropic gel such as Aerosil (from R & G Faserve, Bundwerkstoffe GmbH, Waldenbuch, Germany). The paste can be easily applied with a spatula to specific parts of the fossil.

Airabrasives

The use of airabrasives for the preparation of fossils is a well-known technique, and has been widely employed for developing Crato Formation vertebrate remains, where the bone is relatively strong. Recently, the use of very soft powders such as talcum powder has been employed with some considerable success. Formerly it was thought that the delicate goethitic preservation rendered the insect fossils too soft for such aggressive preparation, and great care is essential if airabrasives are to be used.

Computed tomography (CT) scanning

The development of small-scale CT scanners has opened up tremendous opportunities for palaeontology, and fossils from the Crato Formation are among the first to be analysed using this technique. In essence, high-resolution CT scanning removes the necessity to prepare the fossils, and thus is especially useful where it is deemed ‘impossible’ to remove the matrix without harming the fossil. Grimaldi and Engel (2005) were able to reveal not only the surface morphology of fossil Belostomatidae, but were also able to show details of the internal structure, which otherwise could only be revealed by damaging the fossil. An additional advantage of this technique is that digital images can be manipulated to examine the specimen as a three-dimensional entity that can be rotated to view from any angle, or slices can be generated to view the cross-sectional morphology (see Chapter 11, Figure 11.34).

Fabricated Crato fossils

Some fossil preparators, especially some operating in Nova Olinda, are skilled at producing forgeries. It has become common practice for unscrupulous dealers to fabricate fossils from less well-preserved examples. Some of these are difficult

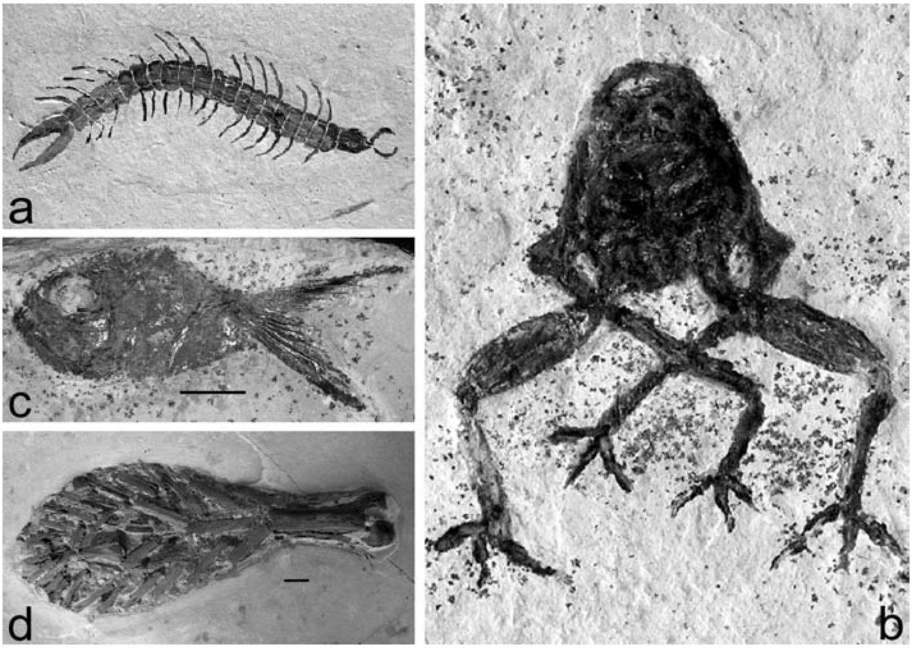

Fig. 6.2. Examples of fabricated fossils from the preparators of Nova Olinda. (a) This ‘centipede’ is a modified plant stem. (b) This small space monster was originally a seed of *Priscowelwitschia*. (c) The very long fish *Cladocylus* modified to create a new family of very short fishes, the ‘Fakeichthyidae’. The pectoral fin has been sculpted to resemble a caudal fin, and the outline is a fabrication. (d) This ‘pineapple’ is an assemblage of lots of pieces of plant stem. All specimens photographed in the Museum of Palaeontology, Santana do Cariri. Scale bars, 10 mm.

to detect to the untrained eye, as the basic fossil material that remains serves to make the fossil appear genuine. Some creations represent new and ‘improved’ body outlines from original fossils, but others include the addition of limbs, wings and other imaginative structures (Figure 6.2). A common method of forging is to elaborate a small genuine fossil by scribing additional or larger, more fearsome appendages into the limestone and rubbing brown crayon into the groove. This method can generate impressive and genuine-looking fossils, but the addition of a little acetone or alcohol will result in the ink bleeding into the rock and thus revealing the forgery.

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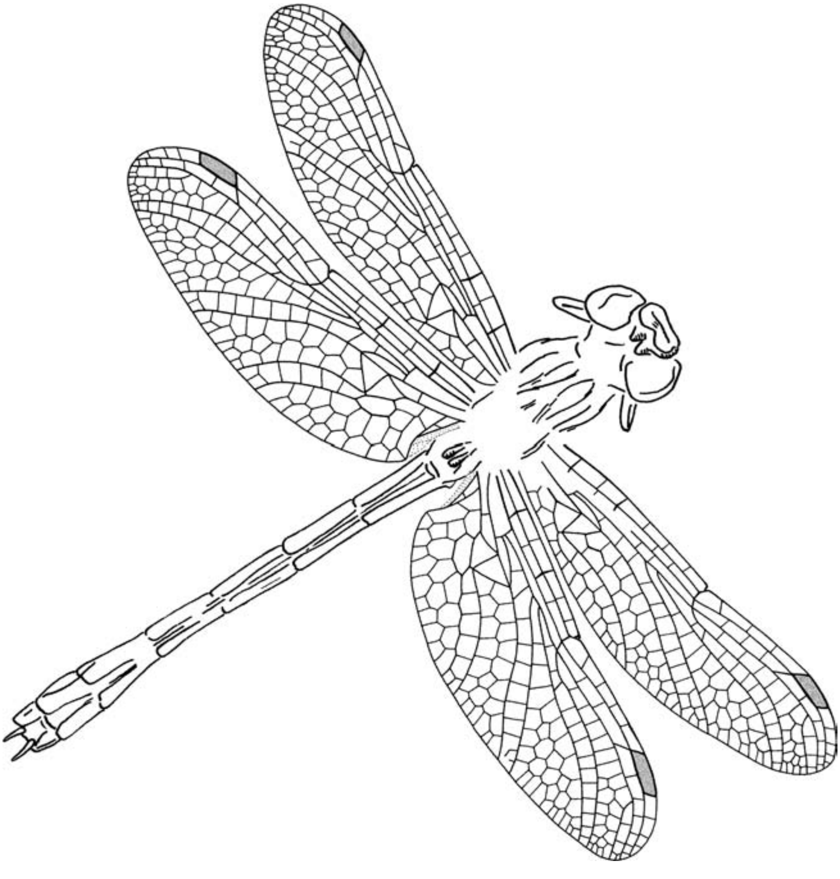
Part II

The invertebrate fauna



7

Taphonomy and preservation of Crato Formation arthropods

Federica Menon and David M. Martill

The fossil assemblage of the Nova Olinda Member of the Crato Formation is highly distinctive in comparison with coeval assemblages elsewhere. It is dominated by arthropods and, in particular, by insects in both numerical abundance and taxonomic diversity. Despite being an aquatic deposit, typical aquatic arthropods such as decapods and ostracods are either rare or absent from large parts of the succession. Furthermore, the taxonomic diversity of its insects differs from that of other aquatic insect-bearing deposits. Notable by their abundance and diversity are terrestrial adult orthopterans, hemipterans (including all bugs, cicadas and hoppers), ephemeropterans and odonatans, whereas beetles, often highly abundant in Cretaceous insect assemblages elsewhere, such as Baissa, Siberia (Vrsansky *et al.*, 2002), are relatively scarce in the Nova Olinda Member.

In addition to its taxonomic distinctiveness, the Nova Olinda Member assemblage is also noteworthy for the ecological character of its fossils, apparent in both the vertebrates and arthropods. Ostracods, abundant in basal parts of the sequence at several localities (such as at Cascata, near Crato), occur in association with conchostracans, but are not present in the bulk of the Nova Olinda Member, despite the lithological similarity, while decapod crustaceans are known from a single taxon *Beurlenia araripensis* (Martins-Neto and Mezzalira, 1991), which is extremely rare, though often beautifully preserved (see Chapter 10). By contrast, terrestrial, fossorial or cryptic taxa occur quite frequently, and include scorpions at various stages of development, camel spiders, diplurans and centipedes (see Chapters 8–11). Spiders, although of low taxonomic diversity, are also relatively abundant. Some aquatic adult insects have been reported, including hydrometrids, water scorpions, dytiscid beetles and Nepomorpha (see Chapter 11), but many of these groups appear to be rarer than some wholly terrestrial taxa.

The distinctiveness of the assemblage and the perceived distance of the nearest palaeoshoreline, of at least 3 km from the main fossil-bearing localities, suggest that it is largely allochthonous (Figure 7.1). However, the assemblage is remarkably well preserved, and most arthropod specimens are examples of complete or near-complete specimens, suggesting, in most cases, short transport distances with little scavenger activity or prolonged decay.

Preservation

Preservation of Nova Olinda Member arthropods can be highly variable. This is in part due to the nature of the rock at outcrop, and in part due to the original morphology of the animal. Essentially, two types of preservation occur; replacement in a dark-brown to orange-brown goethite, a hydrated iron oxide (e.g. specimens on Plates 7, 8 and 23) or as black, carbonaceous replicas with finely disseminated pyrite (e.g. specimens on Plates 9e and g, and 25c). The former preservation style occurs when deeply weathered limestone is quarried at shallow depths, the latter where unweathered, blue-grey limestone is excavated from under several metres of overburden. In both preservational types the fossils are delicate, and can easily be damaged by even gentle abrasion. Most common are those preserved as goethitic replacements, but this may simply be a reflection of the dominance of shallow surface workings for the limestone. In more recent years the introduction of machinery for overburden removal has resulted in a greater occurrence of black, carbonaceous specimens. In both preservational types, detail is exquisite, with even delicate hairs, eyes and other equally fine structures retained. This strongly suggests that the presumed transformation from black, carbonaceous fossil, to weathered, goethitic fossil results in only limited loss of morphological detail, even though the molecular composition may be changed significantly.

Specimens may be preserved three-dimensionally (Figure 7.2a and b), or at least partly so, with only minor compaction (Figure 7.2c). In complete articulated specimens, it is not uncommon to find limbs and other appendages at high angles to bedding. Thorax and abdomen may by three-dimensional in small fossils, although in larger insects there is usually some compaction. Void spaces in three-dimensional fossils are usually filled with a clear calcite, but in some specimens phosphatized muscle tissue may be present. It is doubtful if any cuticle is preserved, although some of the goethitic specimens may possess a cuticle-like glossy sheen, but this is attributed to the very fine grain size of the preserving medium. At least one example of an odonatan is known with original metallic lustre preserved (Plate 2c).

Colour patterns may be preserved, especially on the wings of neuropterans and odonatans (Plates 2 and 9), some cicadomorpha and small blattellids, and may even be discernible in weathered goethitic specimens (Martill and Frey, 1995; Heads

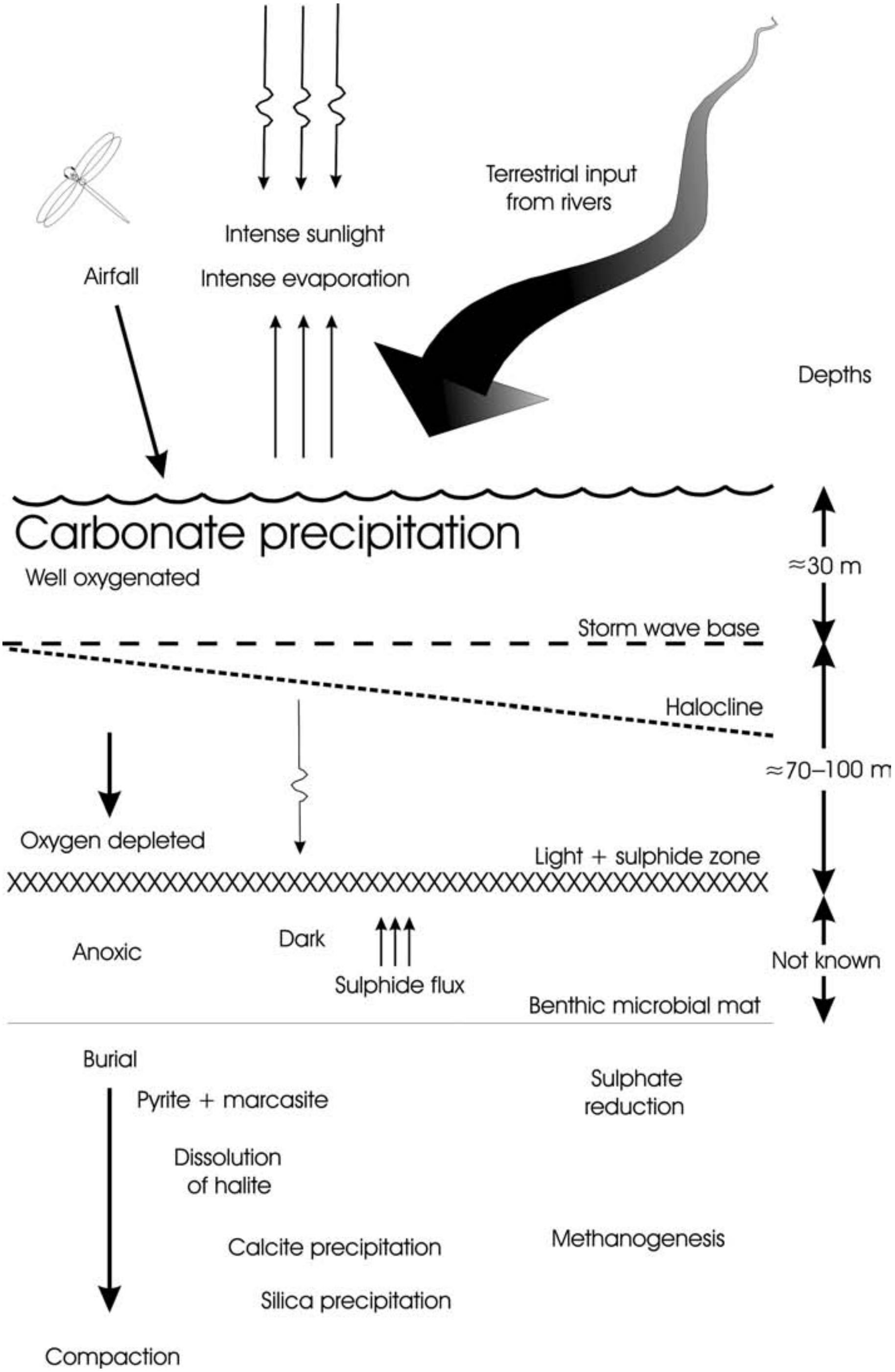


Fig. 7.1. Physical, chemical and biochemical parameters operating in the Crato lagoon during deposition of the Nova Olinda Member: although the physical properties of the terrestrial environment may act to destroy bio-products, the combined salinity, pH, oxygen levels and microbial communities acting together provide an ideal environment for fossilization.

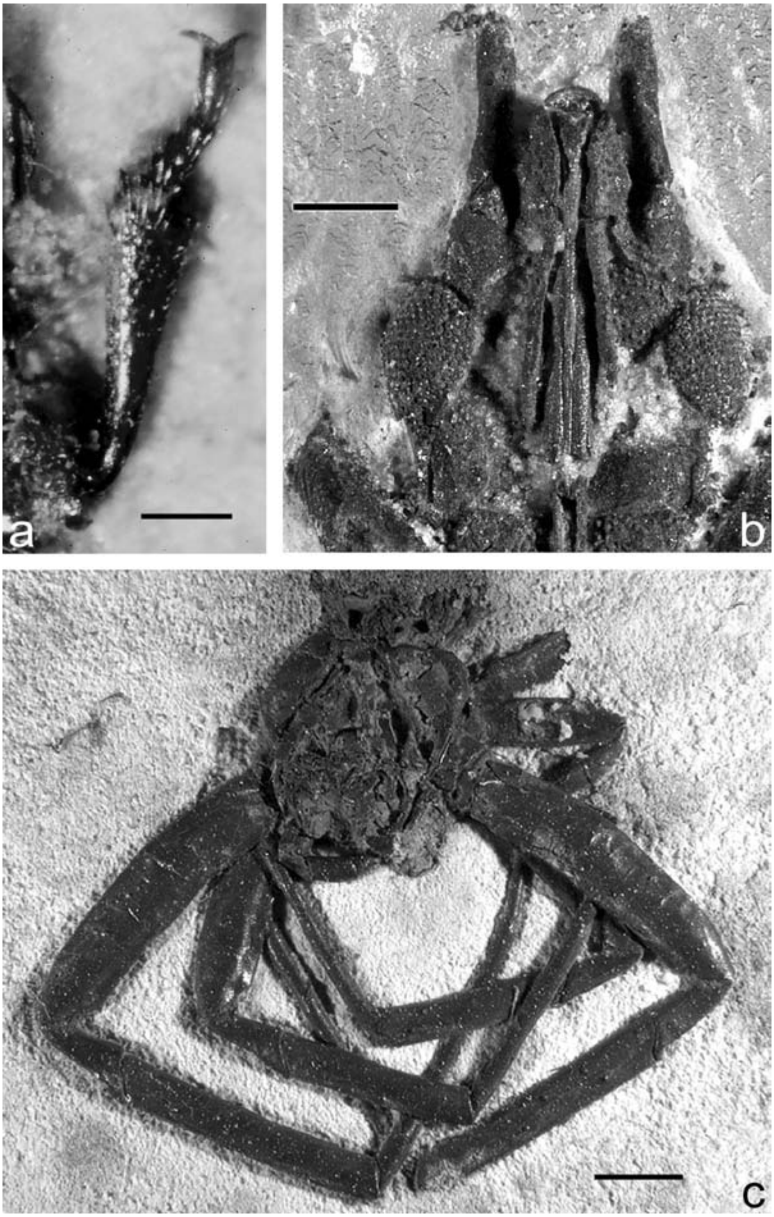


Fig. 7.2. Three-dimensional preservation (preparation with acetic acid): (a) leg of a beetle with delicate hairs preserved intact; (b) head of plant hopper with intact eyes and lenses preserved; (c) partial three-dimensional preservation of a small spider. Scale bars, 0.5 mm.

et al., 2005). Unlike the preservation seen in some black shales, however (e.g. the Eocene Messel oil shale), original colour pigment, has not been reported. Rarely, invertebrates may be silicified in concretions, as in the case of the centipede *Velocipede bettimari* (Martill and Barker, 1998; Plate 3a).

Many arthropods are preserved in their usual resting attitude; thus, typically complete dragonflies are preserved with wings outstretched, while damselflies have their wings closed above the thorax (Plates 9b and d). In contrast, cockroaches may be preserved with wings open or, quite commonly, with only a single elytron open, or with both wings closed. It is rare to find arthropods that are complete, but in a disarticulated condition, suggesting that rapid burial, or perhaps bacterial sealing, *sensu* Gall (1990), occurred to prevent disarticulation on the lagoon floor. Scanning electron microscopy reveals that some preservation can be attributed to bacterial autolithification (*sensu* Wüttke, 1983), whereby bacteria infesting the arthropod carcass are preserved *en masse* (Martill and Frey, 1995; see Chapter 18, Figure 18.1f).

Taphonomy

The taphonomy of the Nova Olinda Member arthropod assemblage can potentially provide important clues to the nature of the palaeoenvironment of the Araripe Basin as well as the palaeoecology of the biota. For the purposes of this chapter taphonomy includes all processes acting upon arthropods from the moment of death to their discovery as a fossil. Thus the arrival of the animal in the lagoon, its decomposition, burial, mineralization and subsequent weathering at the surface is considered a part of the story. In addition, the attitude and state of the fossils and their abundance is examined.

The character of a fossil assemblage can be assessed informally on the basis of field experience (and a selective memory!), from an overall impression of museum collections or, preferably, on the basis of carefully collected scientific field observations and collection data. Neither method is perfect, due to the vagaries of the fossil record, but here we present some observations based on field experience, and the results of a statistical analysis of both in-field and museum collections. Of importance is a discrepancy between our statistical analysis and an analysis by Bechly 1998c. One of us (DMM) was of the opinion (based on 18 years of field observations) that larval ephemeroptera were most abundant, followed by orthopterans and blattoids in approximately equal numbers. The statistical data do not reflect this perception, and until a more scientific survey is undertaken, the results presented here must be considered preliminary.

The data presented here are derived from several sources, including field data pertaining to arthropod abundance, stratigraphic position and locality collected over several years. Several thousand specimens were examined in museum collections

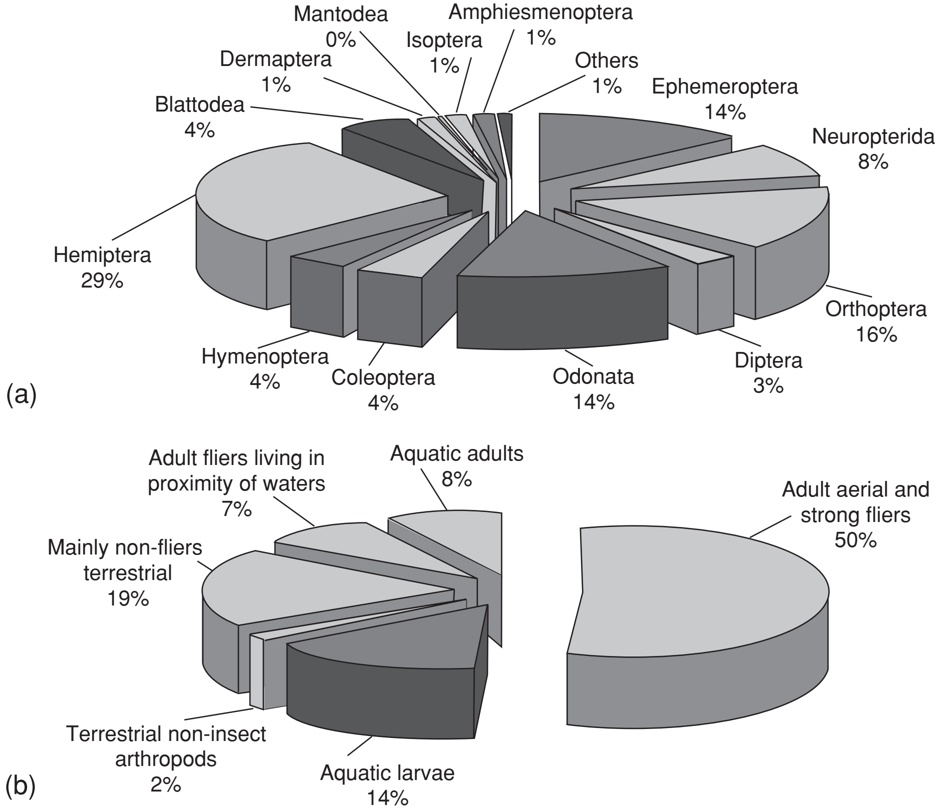


Fig. 7.3. Nova Olinda Member insect diversity. (a) Diversity by group. Percentages represent the number of individuals within each group. (b) Insect life strategies. Strong fliers dominate the assemblage in terms of overall abundance.

obtained by commercial collecting of the Crato Formation that probably began in the 1980s. Such collections can be heavily biased due to the preferences of curators for certain taxonomic groups, rare or well-preserved, exhibition-quality examples. The sample size, however, is considered sufficiently large to provide a realistic idea of the taxonomic diversity (Figure 7.3), but perhaps not for relative abundances.

Bechly (1998c) studied 3.651 arthropods from the Crato Formation, obtaining very different results regarding relative abundances: Ephemeroptera 7%; Odonata 2%; Blattaria 26%; Orthoptera 27%; Hemiptera 23%; Neuropterida 4%; Coleoptera 3%; Hymenoptera 2%; Diptera 2%; all others > 1%. Blattaria, Orthoptera and Hemiptera are also the most abundant among thousands of specimens held by a German trader (G. Bechly, personal communication).

To enter the fossil record insects have to be transported from their source habitat to the water surface, break the surface tension and descend through the water column to be deposited on the bottom of the lake/lagoon before they are blown to the shoreline. Transport occurs by wind and water, local floods and sudden rain falls, with associated flash flooding. The proximity of the original habitat to the water body is, understandably, crucial and affects the assemblage composition.

During transport, arthropods face breakage, sorting, predation and decomposition. The degree of breakage depends very much on the mode of transport: strong water currents tend to be more damaging than wind, whereas sorting is influenced by size and density. Large, bulky insects, such as some beetles, may not travel for long distances, while light insects with large wing spans, such as dragonflies and lacewings, could potentially be transported for hundreds of kilometres (Archibald and Makarkin, 2005). Predation and scavenging, and decomposition, can operate both during transport and post-settling stages. Capacity for active flight, migratory behaviour and ecology may also be contributory factors. Nova Olinda Member arthropods appear to have by-passed some of these process. Indeed, most specimens are entire and retain delicate structures (Figure 7.2a). Such quality of preservation demands minimum transport distance under aggressive regimes, rapid descent to the lagoon floor and limited or no decay during the transport phase. Scavenging during transport must be minimized or excluded and burial or sealing must be rapid. The by-passing of these processes must have been the norm in this setting.

That much of the assemblage is allochthonous poses some problems. Those insects with powerful flying abilities may represent airborne fallout, and their presence in the assemblage is relatively easily explained. Wholly terrestrial, flightless arthropods such as spiders and scorpions can be considered as flotsam brought into the lagoon by local rivers and drifted away from the shore by wind-generated currents. More problematic, however, are forms such as the aquatic larva of the Ephemeroptera and Odonata and aquatic imagoes such as dysticid beetles. Although these presumably could have been living in the lagoon, the high salinity present during deposition of the Nova Olinda Member (see Chapter 4) would have excluded all freshwater arthropods. It is possible that the water column was stratified in close proximity to deltas with a surface layer of well-oxygenated freshwater, which may have been inhabited by some surface-dwelling arthropods. Benthic arthropods, such as ostracods and conchostracans, are absent from the laminated limestones, probably due to a combination of elevated salinity and bottom-water anoxia. However, they occur in abundance in clays and thin-laminated limestones just below the base of the Nova Olinda Member (e.g. at Cascata near Crato; see Chapter 10). Thus even the rarer aquatic arthropods probably represent part of a wholly allochthonous assemblage.

Representation of the fossil assemblage

Based on observation of specimens examined both in the field and in museum collections, the assemblage comprises mainly complete adults, most of which represent Orthoptera and Hemiptera. Blattodea, Odonata and Ephemeroptera (larvae and adults) are also abundant. Although there is little concrete evidence for mass mortality among the arthropods, small accumulations of more than three insects in close proximity on the same bedding plane are known, but such aggregations are rare (e.g. see Bechly, 2001, p. 21, Figure 12). Particularly noticeable is the abundance of bugs, grasshoppers and crickets and an apparent under-representation of beetles (Figure 7.3). Hemiptera are numerous and taxonomically diverse (see Chapter 11), presumably a reflection of a greater presence in the regional insect community, but the limited presence of beetles is noteworthy. At first sight, it appears that crawling insects occur far less frequently than what might be called frequent flyers. Martinez-Delclos *et al.* (2004) consider that insect assemblages in limestones are often subject to selective preservation. In the Nova Olinda Member, such selection is clearly not size-controlled, as both very large (wing spans >150 mm) and very small (wing spans 4–5 mm) insects occur together. Similarly, the robustness of the arthropods does not appear to be limiting, as thick-cuticled beetles occur with delicate dipterans. Thus it appears that arthropod ecology and habitat played an important role, hence the abundance of mayflies and dragonflies.

The number of disarticulated wings, limbs and bodies relative to the number of complete (or nearly complete) specimens is insignificant, accounting for less than 6% of the specimens (Figure 7.4). The degree to which arthropod diversity is linked to taphonomy is difficult to establish and the analysis here considers each major group separately.

Orthoptera

Grasshoppers, crickets and locusts constitute 16% of the total specimens examined, and were 25% of the specimens collected in one of the mines south of Nova Olinda. Some workers find an even higher abundance of around 27% (Bechly, 1998c). Orthoptera are composed of 11 families, each including only a few species (see Chapter 11), mostly occurring as adults, with early instars uncommon. The majority are preserved in lateral aspect with the wings folded over the abdomen in the 'rest position' (Martins-Neto, 1992), but many crickets are preserved dorso-ventrally. Their relatively high abundance in collections and in field-collected samples may reflect a real numerical abundance in the original population, but it may be that saltatorial insects could more easily land on water by accident.

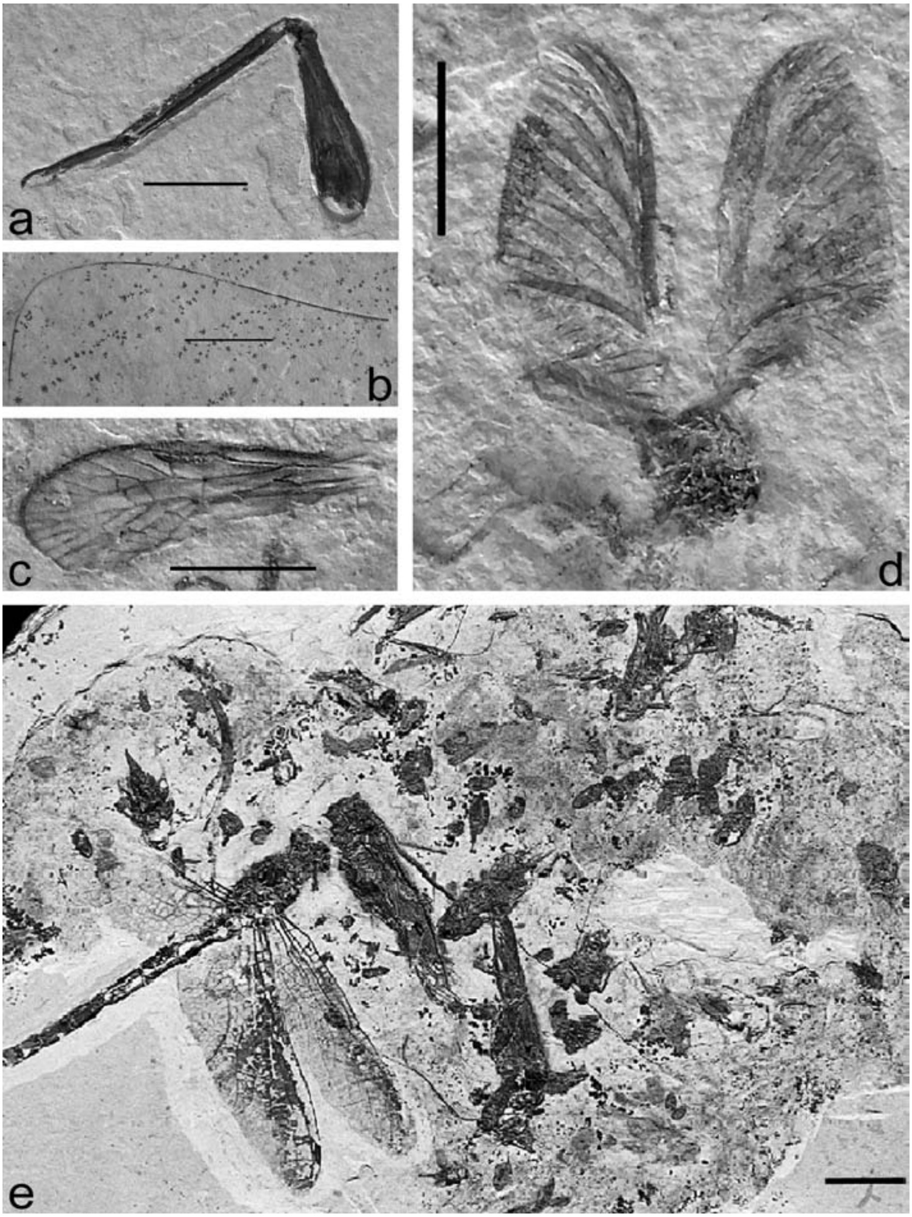


Fig. 7.4. Insect taphonomy: some insect fossils in the Nova Olinda Member are fragmentary and include (a) isolated limbs, (b) antennae, (c) wings and (d) portions of insects. Such remains are probably a consequence of predation. (e) Aggregates of several tens, perhaps even hundreds of insects occur occasionally, representing some as yet unidentified concentration process. Perhaps they accumulated against overhanging vegetation in slowly flowing rivers as 'insect flotsam' which was subsequently flushed into the lagoon as an insect/plant debris mat. Scale bars, 10 mm.

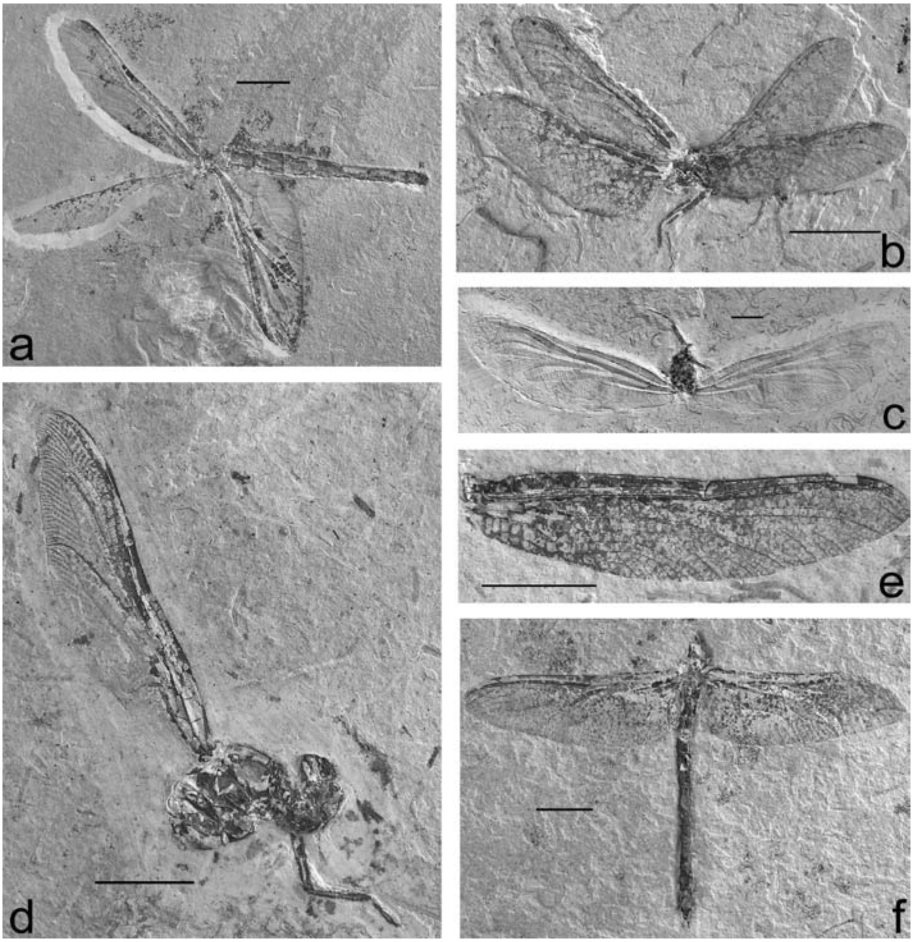


Fig. 7.5. Dragonfly taphonomy: odonatans are often spectacularly preserved but, due to predation, they may occur in varying degrees of completeness. (a) Head, part of the thorax and one wing missing; (b) abdomen missing; (c) abdomen and hind wings missing; (d) abdomen and three wings missing; (e) isolated forewing; (f) head and forewings missing. Scale bars, 10 mm (a, c, d, f); 20 mm (b, e).

Odonata

Adults and larvae occur mostly as complete specimens, preserved in the dorsal or ventral aspect in dragonflies and in a lateral aspect in damselflies. Isolated wings and other fragments are also common and may represent the rejects of predators (Figure 7.5). Many adult specimens are missing the abdomen, possibly as a consequence of predation. The abdomen is the body part that tends to detach first during decay and although isolated abdomens are known, they are rare; most are presumably eaten. By contrast, all larvae examined were complete. The large wingspan, the facility of being transported and the proximity of the original habitat to the water body may account for the high abundance of odonatans, even though they are active and effective fliers. Odonata may appear over-represented, up to 14% in museum collections, when compared with the modern insect assemblage. They are large and beautiful insects of wide appeal and it is unsurprising that so many specimens were obtained by museums. However, the high diversity of the Odonata in the Crato Formation (see Chapter 11) might suggest very high abundances.

Ephemeroptera

Mayflies are abundant both as adults and larvae and numerically constitute 14% (including imagines and larvae) of the total specimens examined during a field study. The highest representation was 24%, which was calculated from observations at one locality and is largely due to the high number of Hexagenitidae (Chapter 11), but recorded only 7% Bechly (1998c, p. 60). Undoubtedly ephemeropterans were extremely abundant, but not diverse in the number of families. All larval stages occur, usually preserved in dorsal or ventral aspects, mostly complete, while the attitude of adults differs greatly (to include dorsal, ventral and lateral aspects); isolated wings are also quite common. The vicinity of the original habitat to the water body must have played a role in the abundance of the Ephemeroptera. However, some families could possibly be under-represented: an example is the Euthyplociidae, the larvae of which inhabit fresh, running waters. Only two larval specimens are known, while the adult form is well known (McAfferty, 1990) and occurs frequently, although it may not be as abundant as imagoes of other ephemeropteran families. Larvae would have to be transported for longer distances in strong currents and would have been subject to predation and disarticulation, thus their scarcity can be easily explained. The rarity of the larvae is a direct reflection of their distinctive ecology, while the slightly elevated abundance of imagoes reflects their greater mobility.

Neuropteroidea

Lacewings and antlions represent 5% of the sample population, 8% when considered together with snakeflies (Raphidioptera), dobsonflies and alderflies (Megaloptera); an abnormally high percentage, even considering collecting bias and the attractiveness of these insects. Stork (1988) recorded Neuroptera to be less than 1% of recent tropical forest canopy insect fauna. In the Nova Olinda Member both isolated wings and complete specimens are equally present. Families of medium or large neuropterans seem to be in a majority (Myrmeleontidae, Palaeoleontindae and Araripeneuridae) while Coniopterygidae, the smallest neuropterans, are absent, but are known to occur in Barremian Lebanese amber (V. N. Makarkin, personal communication). Although there is little evidence for a bias in favor of larger insects, it is possible that large fossils are also more easily noticed by quarry workers.

Raphidioptera are less diverse, represented by only a few species (see Chapter 11) belonging to three families. Raphidioptera are found today in fresher, temperate regions in the Northern Hemisphere; back in the Early Cretaceous of Brazil they probably lived in restricted areas, perhaps in highlands or in denser, fresher forests on hill tops; their original habitat could have been far from the water body, a fact that could explain their scarcity in the Nova Olinda Member.

Diptera

Diptera account for 2–3% of the total insect assemblage of the Nova Olinda Member with Tipulomorpha by far the most abundant, in terms of both number of specimens and species. Their representation may appear to be limited, considering that they are one of the most important groups of insects today. Diptera are, in general, very active fliers and are, possibly, able to compete effectively against winds. Furthermore, they can be fragile and unable to break the water tension when on the surface. However, there are many such small insects in the Nova Olinda Member, which suggests that the paucity of dipterans is the result of another, perhaps ecological, taphonomic filter.

Hymenoptera

Hymenoptera are one of the five most abundant orders of insects today, together with Coleoptera, Lepidoptera, Diptera and Hemiptera, but the group represents only 3–4% of the Crato insects. Typically they are strong fliers and do not necessarily live near water. Families represented include Scoliidae, Siricidae, Anaxeylidae, Scelionidae, Ephialtidae, Protoctupridae, Tiphiidae, Rhopalosomatidae and, most commonly, Sphecidae (Darling and Sharkey, 1990), which alone constitutes almost half of the hymenopteran assemblage (see Chapter 11). The high number of sphecids and the absence of apids is not surprising. Bees are not expected to be found in the Lower Cretaceous as currently the oldest bees date from the Upper Cretaceous, while the first fossil *Apis* comes from the lower Miocene (Grimaldi and Engel, 2005). Sphecids, on the other hand, dominated warmer climates as early as the Lower Cretaceous (Rasnitsyn, 2002).

Blattaria

In a study by Bechly (1998c) based on 3651 specimens, 26% were ‘roaches’. However, in a study by Menon (2005) in 2004 based on 2215 specimens, of which 819 were field observations at six localities near Nova Olinda, only 4% of specimens were ‘roaches’. Roaches inhabit damp habitats, but are somewhat cryptic; nevertheless, their preservation potential is probably quite high due to their sclerotized forewing. Thus the discrepancy in abundances in these two analyses may be a combination of selective collecting of specimens and differences between localities and different stratigraphic levels within the Nova Olinda Member.

‘Roaches’ are one of the orders of crawling insects that could be under-represented. They are composed of only five families: Blattellidae (dominant), Blattulidae, Umenocoleidae, Mesoblattiindae (A. Ross, personal communication) and possibly Raphidiomimidae (see Chapter 11), but it is difficult to evaluate whether this composition reflects the original assemblage. Blattodea are preserved in all aspects, mostly complete, usually with both fore- and hind wings. Exceptional examples of adults with fore- and hind wings open at both sides of the body are also found. Study of the Crato Blattodea is ongoing and the exact species composition is not yet clear (Chapter 11).

Coleoptera

Beetles appear to be under-represented in the Nova Olinda Member, which is surprising. Today beetles represent approximately 40% of the estimated total of insect species (Grimaldi and Engel, 2005) and are especially numerous, both in number of individuals and number of species, in the tropics. However, in the Crato Formation they constitute only 4–5% of the insect assemblage in numerical abundance (Figure 7.3). Insects with highly sclerotized cuticles are thought to be more resistant to the negative taphonomic factors such as transport. Thus, the high probability of remaining intact during sinking and the incapacity to float for prolonged periods should have ensured beetles a more significant presence in the Nova Olinda Member, unless they were prevented from reaching the waters in the first place.

Hemiptera

This group has the highest diversity at the familial level and is the best represented in number of specimens (23% of the total), comprising 30 families and at least as many species. However, the Crato hemipterans have not been as well studied as other taxa, especially with regards to the Heteroptera or true bugs, and therefore it is difficult to estimate their diversity (see Chapter 11). Most of the material in collections can be assigned to modern taxa, the most abundant of which are Belostomatidae, Naucoridae and Miridae, including all water bugs and hemipterans whose habitats are strictly linked to aquatic environments. Cicadomorpha (Palaeontinidae, Tettigarctidae, Cercopionidae, Cicadellidae and Jascopidae) are also abundant. In this group, recent forms are dominant, but extinct families are also present, for example Palaeontinidae (Martins-Neto, 1998; Menon and Heads 2005; Menon *et al.*, 2005), Jascopidae and Cercopionidae (Hamilton, 1990). Abundant also are Tettigarctidae (Menon, 2005), with two described and several undescribed species (R. G. Martins-Neto, personal communication) in the Brazilian RGMN collection. Like other insect groups in the Crato Formation, specimens are usually complete, but isolated wings and partial specimens also occur.

Other less well-represented arthropod groups

Dermaptera, Isoptera, Amphiesmenoptera, Phasmatodea, Chilopoda, Arachnida and Crustacea are included here. These groups are rare probably due to a combination of low abundance in the original community and their autecology. The scarcity of Lepidoptera is not a surprise; the group evolved and diversified mostly during the Tertiary and only small forms are recorded (Martins-Neto 1999; Chapter 11). Trichoptera are also scarce, with only three families (F. Menon, personal observations). Dermaptera are represented by two families and Isoptera by only one. The presence of Collembola, Plecoptera and Psocoptera is not certain.

A number of non-insect terrestrial arthropods have been described from the Nova Olinda Member, including four species of Chilopoda (Martill and Barker, 1998; Wilson, 2001, 2003; Menon *et al.*, 2003), representing two families. Centipedes are in general extremely rare in the fossil record, and all Early Cretaceous species come from the Crato Formation. Arachnids (scorpions, spiders, whipscorpions and pseudoscorpions) are also known (see Chapter 9); and are often extremely well preserved. Hundreds of specimens of spiders have been recovered in the last few years, as have many scorpions. However, most of the spiders are of a single species, and are undoubtedly far less numerous than the insects in terms of number of individuals.

The role of the microbial community

Microbes are ubiquitous in most environments where they are responsible for processing vast amounts of organic material and, in so doing, generate a wide variety of by-products, some of which aid fossilization. A few of these microbial processes contribute to exceptional fossil preservation, and this appears to have been the case in the Crato Formation.

A lack of reworked horizons within as much as 13 m of laminite in the Nova Olinda Member suggests considerable water depth, while the presence of salt pseudomorphs indicates elevated salinity (Figure 7.1; see also Chapter 4). These conditions strongly influence the nature of the microbial communities present both in the water column and in the bottom sediment. They can also assist to some degree in exceptional preservation. High salinities may inhibit macro-scavengers and bioturbation, and consequently can allow carcasses to remain intact for a considerable time. However, high salinities do not necessarily inhibit all microbial breakdown. Similarly, anoxic bottom waters inhibit macro-scavengers and bioturbation, but certainly do not inhibit microbial activity, although the microbial faunas differ considerably, and decay may be slowed or restricted to certain microbial pathways (Allison, 1990). The presence of microbial mats in the Nova Olinda Member (see Chapter 4) suggests that bacterial sealing was a factor in retaining the integrity of arthropod carcasses. The role of microbial mats in insect preservation has been discussed by Gall (1990) and Martinez-Delclos *et al.* (2004), who note that microbial mats develop around the insect body from the initial fall on to the water surface. The mat continues to develop until the carcass sinks, perhaps even aiding sinking, and is partly responsible for limiting attacks from scavengers and preventing disarticulation. The exceptional preservation witnessed in Crato might be partially due to this process. On the bottom it is possible that benthic microbial communities have the same effect.

The millimetrically laminated nature of the Nova Olinda Member and the absence of bioturbation combined with the abundance of finely disseminated pyrite implies anoxic bottom waters, and therefore benthic microbial communities would have been dominated by dysaerobic and anaerobic bacteria. Disseminated pyrite indicates the presence of sulphate-reducing bacteria such as *Desulfovibrium* spp., but these probably lived within the sediment, and while they are most likely responsible for the early pyritization of the Crato fossils, they are part of the diagenetic, post-burial phase of preservation.

The presence of the biomarker molecule isorenieratane in the Nova Olinda Member laminites (see Chapter 4) provides compelling evidence for photoautotrophic green sulphur bacteria (Chlorobiaceae) such as *Chlorobium* spp. Such bacteria are known to be part of bacterial mat communities, but are not necessarily major mat formers. However, as photoautotrophs, they require light, albeit only low levels, and as such live in the top 1 mm of the sediment or at a chemocline in the water column (in the Black Sea today this is at a depth of between 68 and 98 m) at the interface between light and sulphide-rich waters. These bacteria may be responsible for additional mat formation on biogenic flotsam descending through the water column. Other bacterial species may also have been present, but all must have been tolerant of sulphide-rich water, anoxia and perhaps hypersalinity (it is possible that dense benthic brine pools existed). At least some bacteria are known to have proliferated on Crato Formation fossils, as shown by autolithified bacteria on fossil feathers (Martill and Frey, 1995).

Conclusions

The Nova Olinda arthropod assemblage represents a taphocoenosis that may reflect an unusual terrestrial assemblage adapted to riparian settings in an arid or semi-arid hinterland. Individuals arrived in the lagoon mainly as airfalls (hence the abundance of aerial and strong flyers) and by floating in river systems draining into the basin. Fossorial, cryptic taxa and purely terrestrial arthropods were introduced into the system as rivers eroded their banks and during flash-flood events. Some possible cooler-climate-adapted insects may have been derived from highland areas to the east.

The fossils are exceptionally well preserved as a consequence of several factors: scavenging was inhibited by both bottom-water anoxia and elevated salinities, and rapid microbial mat development may also have played a role. Microbial mat development may also have been responsible for retaining the integrity of carcasses while on the lagoon floor for prolonged periods. Early diagenesis in the form of pyrite or marcasite formation during sulphate reduction both on the lagoon floor and during the early stages of burial resulted in early replacement of cuticle synchronous with its bacterial decay, producing a mixture of organic breakdown products and a mineral phase. Early diagenetic phosphatization occasionally replaced muscle and other labile tissues. Only moderate compaction affected the insect carcasses but, oddly, was sufficient to crush pterosaur bones. The degree of compaction is thus probably linked to size and shape as well as overall strength. Later, *in situ*, deep weathering oxidized the pyrite and removed the organic component to leave highly porous and delicate goethite pseudomorphs with retained microscopic detail. This assemblage is thus unique in terms of its taxonomic composition and style of preservation.

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8

Chilopoda: centipedes

David M. Martill

The taxon Myriapoda, grouping together the centipedes and millipedes, proved to represent a paraphyletic assemblage. However, the centipedes, or Chilopoda, are a monophyletic assemblage of ancient, multi-segmented, predatory arthropods with highly elongate bodies, a single pair of legs per body segment and a pair of poisonous fangs. All are terrestrial, living under stones, in bark or in burrows and are globally distributed, but with higher diversity in the tropics. Their exoskeleton is rather soft, unmineralized and, consequently they are extremely rare in the fossil record. The oldest examples are Scutigeromorpha from the Devonian (Shear *et al.*, 1998), but centipedes generally occur more frequently in Paleogene and Neogene ambers (Keilbach, 1982; Poinar, 1992). Several specimens representing at least four species in three genera have been recovered from the Crato Formation limestones, and together with a single example from the Late Jurassic of Germany (Schweigert and Dietl, 1997), constitute the only record of Mesozoic centipedes. All of these are remarkably similar to forms living in the tropics today, and at least one form is tentatively referred to the extant genus *Rhysida* Wood, 1862 (F. Menon, personal communication).

The classification of centipedes is relatively straightforward, with two distinct groups recognized, the Scutigeromorpha and the Pleurostigmophora (Figure 8.1). The Scutigeromorpha, otherwise known as the house centipedes, are characterized by highly elongate antennae, 15 pairs of long legs, especially those on the hind-most segments, and a rapid turn of speed. A scutigeromorph from the Crato Formation is the only known example of these familiar animals from the Mesozoic. The Pleurostigmophora include four distinct groups (Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha, Geophilomorpha) that in general have more than 15 pairs of legs, reaching 181 pairs in some species of geophilomorphs. Some

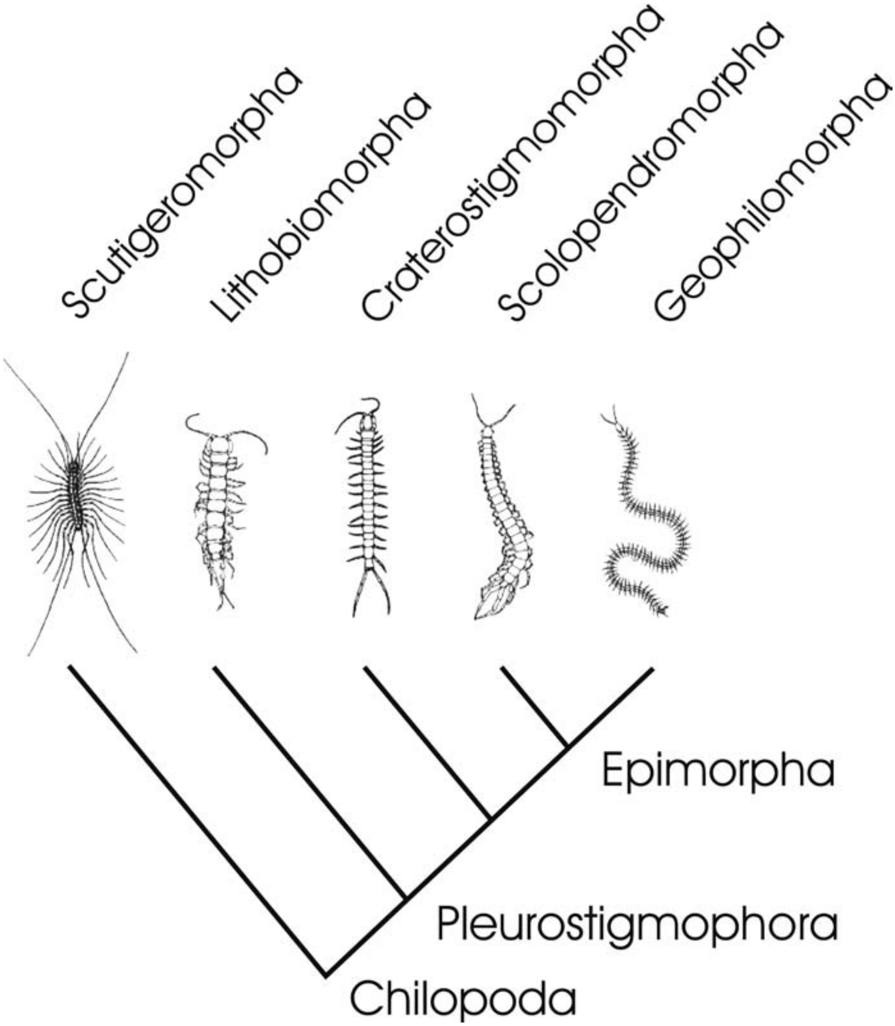

Fig. 8.1. Interrelationships of the main groups of Chilopoda. Modified from Edgecombe and Giribet (2002).

scolopendromorphs can reach lengths of 26 cm, although these centipedes are usually in the range of 4–8 cm.

Crato Formation Chilopoda

Only one species of Scutigeromorpha and three species of Scolopendromorpha occur in the Crato Formation, but the presence of scolopendromorphs in the Carboniferous of the USA (Mundel, 1979) and of a geophilomorph centipede in the Upper Jurassic of Germany (Schweigert and Dietl, 1997), suggests that the other two pleurostigmophoran centipede groups (*viz* Geophilomorpha and Lithobiomorpha), which have a worldwide distribution today, can be expected to occur in the Mesozoic of South America as well. The Palaeozoic fossil group Devonobiomorpha and the recent Tasmanian relict group Craterostigmomorpha are very probably not to be expected in the Crato taphocoenosis.

Chilopoda Latreille, 1817

Scolopendromorpha Attems, 1930

Scolopendridae Newport, 1844

Sterropristinae Verhoeff, 1937

cf. *Rhysida* Wood, 1862

Material: SMNS 66005, only known specimen.

A specimen of cf. *Rhysida* is preserved in right lateral view and is a medium-sized centipede with a body length of around 54 mm and a head length of 2.5 mm. The antennae are short, composed of just 14 hairless antennomeres. The forcipules (poison claws) borne on the first segment and fused with the head are also around 2.5 mm in length and hairless. There are 21 leg-bearing segments, hence its placement in Scolopendridae, and the legs all appear smooth, seemingly lacking evidence of setae or spines. Spiracles are rounded, open, concave with no flaps and preserved on segments VII and XIV. An affiliation with Sterropristinae is confirmed by the presence of spiracles in segment VII.

Subfamily *incertae sedis*

Genus *Cratoraricus* Wilson, 2003

Cratoraricus oberlii Wilson, 2003

Material: holotype SMNS 64431.

This taxon (Plate 3b; Figure 8.2c) is characterized by having bisegmented tarsi, paramedial syternal grooves and, in the ultimate legs, a prefumur and femur in which the length/width ratio is 5:1. The holotype specimen is 54 mm long, with 21 pairs of legs. The specimen has been damaged such that along its length parts of the internal surface of the sternites can be seen.

Subfamily *incertae sedis*

Genus *Velocipede* Martill and Barker, 1998

Velocipede bettimari Martill and Barker, 1998

Material: holotype SMNK 2345 PAL.

Velocipede bettimari was the first centipede described from the Crato Formation and is known from a single, rather poorly preserved specimen of 85 mm in length seen

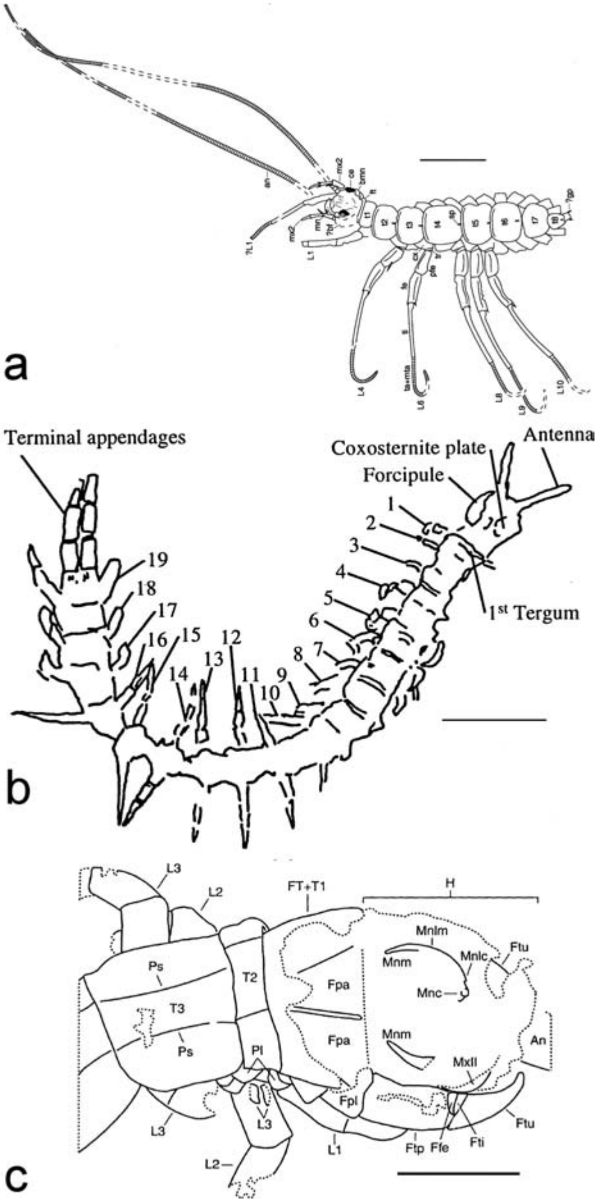

Fig. 8.2. Interpretative diagrams of centipedes from the Nova Olinda Member: (a) scutigeromorph *Fulmenocursor tenax* Wilson, 2001; (b) scolopendroid *Velocipede bettimari* Martill and Barker, 1998; (c) details of the head of scolopendroid *Cratoraricus oberlii* Wilson, 2003. (a) Reproduced by kind permission of the Palaeontological Association; (b) after Martill and Barker (1998); (c) after Wilson (2003).

in dorsal aspect (Plate 3a; Figure 8.2b). F. Menon (personal communication) noted that several of the more important features, such as spiracles, allowing its precise systematic position to be established, are not visible. Thus it can only tentatively be assigned to the Sterropristinae, but is certainly a member of the Scolopendridae. It is distinguished from *Cratoraricus oberlii* by the greater size, the prefemur and femur of the terminal appendages being much stouter, with a length/width ratio of 2:1.

Scutigeromorpha Leach, 1814

Scutigeridae Newport, 1844

Genus *Fulmenocursor* Wilson, 2001

Fulmenocursor tenax Wilson, 2001

Material: holotype SMNS 64275.
Although scutigeromorph centipedes are known from fragmentary material from as far back as the middle Devonian (Shear *et al.*, 1998) the holotype of *Fulmenocursor* is the only known record of the group from the Mesozoic. Found in the Nova Olinda Member, and described by Wilson (2001), *Fulmenocursor tenax* is a typical scutigeromorph, sharing with extant forms the 15 leg-bearing segments, a fusiform body and highly elongate legs (Plate 3d; Figure 8.2a). The body and head together are 17 mm long by 4.8 mm wide, and the antennae are approximately 32 mm long. Only six legs on the left side are exposed in the holotype, although bases of the other legs of the left side can be discerned, and a possible anteriormost leg from the right side is present. The longest leg is approximately 13 mm in length.

Today scutigeromorph centipedes are widespread in the tropics and it is noteworthy that while searching for fossils in the Crato Formation stone quarries, recent species of scutigeromorphs are commonly encountered under slabs of limestone.

Discussion

Although centipedes are very rare in the Crato Formation, they nevertheless appear to be diverse, with at least four species present. A still-undescribed specimen is featured in Plate 3c, and deposited in coll. MURJ. The three described scolopendrids, although looking somewhat similar, can be distinguished from each other even though it is not always possible to assign them to a particular subfamily. Wilson (2003) noted that Mesozoic centipedes are indistinguishable from their modern counterparts. The presence of cf. *Rhysida* Wood, 1862, an extant taxon, in the Crato Formation is a remarkable example of evolutionary stasis, giving the genus a minimum temporal range of approximately 110 mya.

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9

Arachnida: spiders, scorpions and allies

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The Crato Formation of Brazil is one of the most important localities for fossil arachnids to be found in recent years. Before its discovery there were few reliable records of spiders and their relatives throughout the entire Mesozoic era (265–248 mya) to the point that we actually knew more about the older Palaeozoic arachnid fauna; see e.g. Selden (1993) for a summary and review. Mesozoic spiders have since been found in France, Spain, southern Africa, Mexico, the USA and China (see below) – all as compression fossils in shales – as well as in various Cretaceous ambers. The Crato arachnids are generally better preserved than other records from Mesozoic shales and are in some cases easier to study than inclusions in amber. In addition to spiders, the Mesozoic record of the other arachnid orders remains patchy by comparison, but scorpions, harvestmen and mites have been described from a few localities other than the Crato Formation and our knowledge of Mesozoic arachnids is slowly improving.

The Nova Olinda Member of the Crato Formation gains its significance as an arachnid Konservat Lagerstätte through yielding the most complete fauna – with the widest range of arachnid groups (see below) – of any single Mesozoic locality known to date. The camel spider, whipspider and whipscorpion described from the Crato Formation represent the first, and so far only, record of these groups from the entire Mesozoic. Furthermore, the Crato Formation preserves these arachnids beautifully (Plates 4 and 5), often in considerable anatomical detail that allows them to be compared directly with the modern families, to which these Brazilian arachnid fossils can often be quite confidently referred. This implies a remarkable degree of evolutionary stasis, whereby these arachnids have changed little since at least the Early Cretaceous. Finally, most fossil sites yielding arachnids are found in the Northern Hemisphere. The Nova Olinda Member is one of only a handful of arachnid-bearing strata from the Southern Hemisphere and dates from about the time of the break up of Gondwanaland, during which South America is thought to have separated from Africa. It is thus of considerable interest with respect to arachnid biogeography and individual case studies are outlined below.

Preservation

As with the insects, the Crato Formation arachnids are usually preserved as reddish-brown goethitic pseudomorphs (see Chapter 7). Although compressed, the fossils exhibit a certain degree of three-dimensionality and can sometimes be partially excavated from the surrounding matrix. They are usually recovered either in dorsal or ventral view, but occasionally they are discovered lying on their side (e.g. Dunlop and Martill, 2004). In some cases (e.g. Dunlop and Martill, 2002, figure 1b) one surface of the body may have broken away to reveal the other surface beneath it. Sometimes the fossils are only preserved rather crudely in outline (Dunlop, 1998), but often there is excellent preservation of taxonomically significant details such as hairs, spines and claws (e.g. Selden and Shear, 1996; Selden *et al.* 2006; Menon, 2007).

Arachnids are much rarer in the Crato Formation than insects. This is unsurprising for two reasons. First, even in modern ecosystems arachnids are generally less common, in terms of both diversity and sheer number of individuals, than the insects which form the bulk of their prey. Second, apart from tiny or juvenile spiders, which can 'balloon' on strands of silk, arachnids do not fly. This begs the obvious question of how they came to end up deposited in the middle of a lagoon, apparently some distance from the original shoreline. Dunlop and Martill (2004) offered a possible mechanism. Noting the fact that many plants are preserved in their entirety, including roots, they suggested that rivers feeding the lagoon system were eroded during floods and that terrestrial arachnids may have been transported accidentally with the plant and soil debris, before finally becoming deposited in deeper water. Further support for this hypothesis comes from three of these groups: whipscorpions, whipspiders and (perhaps) scorpions. In modern arid ecosystems members of all these groups have been observed emerging from soil or their burrows and becoming active on the surface specifically in the immediate aftermath of (heavy) rainfall. If this also applies to the Crato examples, we might have a scenario in which some of these animals emerged after rains, only to be caught up in flash floods resulting from this rainfall. In general, the Crato Formation arachnid fauna shows some similarities to that of modern desert or semi-desert regions in the southern USA and Mexico.

Araneae: spiders

Spiders are the most familiar of arachnids and, along with insects and mites, are among the most diverse animals on land today. They are the most abundant terrestrial predators, and populations of their main prey, the insects, are kept in check by the activities of spiders. They occur in almost all terrestrial, and a few aquatic, habitats and their biology has been summarized by Foelix (1996). They differ from other arachnids in three obvious ways: by their ingenious exploitation of silk produced from opisthosomal glands, by the modified palpal organ used as a sperm-transfer device by males and the use of venom from prosomal glands, opening on the chelicerae, to subdue prey. As a group they are both morphologically and ecologically diverse and can be broadly divided ecologically into web-building and free-living forms. Over 39,000 extant species in 110 families are currently known and there is some broad consensus on their evolutionary relationships (see Coddington and Levi, 1991).

Spider fossil record

The earliest fossil spider dates from around 380 mya, from the middle Devonian of Gilboa, New York (Selden *et al.*, 1991). Only members of the most primitive suborder, the Mesothelae, are known from the Palaeozoic, but by the Triassic both mygalomorphs ('tarantulas', bird-eating spiders and trap-door spiders) and araneomorphs ('true' spiders) had evolved. *Rosamygale* from the Triassic of France (Selden and Gall, 1992) was placed in the modern family Hexathelidae, and whereas the araneomorphs *Triassaraneus* from South Africa and *Argyrarachne* from Virginia could not be identified with greater precision, their resemblance to orb-web weaving Araneoidea is striking (Selden *et al.*, 1999). There are few Jurassic spider records. Eskov (1984) described the new family Juraraneidae, based on *Juraraneus rasnitsyni*, a single adult male from the Jurassic of Transbaikalia, Siberia. The interpretation of *Juraraneus* as an araneoid was based on the complexity of the male palp. Wunderlich (1986) suggested that *Juraraneus* could be accommodated in the modern family of garden spiders, Araneidae. Eskov (1987) described an archaeid spider, *Jurarchaea zherikhini*, from the Jurassic of Kazakhstan. The find of an archaeid in Jurassic strata was interesting because this family of small, araneophage (i.e. specialist spider-eating) spiders was already well known from Baltic amber and the Recent Gondwana fauna.

More recently, fossil spiders have turned up in rocks of Jurassic age in China, but there is some dispute over the exact age of these strata. There are two horizons: the younger, Yixian Formation, famous for its so-called Jehol Biota including feathered dinosaurs and insects, is more likely to be Early Cretaceous in age (Zhou *et al.*, 2003), but the older Jiulongshan Formation is probably Jurassic. Spiders in the Jiulongshan Formation include mygalomorphs, araneoids, uloborids and palpimanoids, including archaeids. Therefore, a Jurassic araneofauna existed of orb-web weavers (Orbiculariae) including both cribellate uloborids and ecribellate araneoids. Since the orb web is considered to have originated among cribellate orbicularians (Coddington, 1986), the presence of ecribellate araneoids is evidence of the split of ecribellate from cribellate orbicularians in at least Late Jurassic times, and therefore possibly earlier.

Cretaceous non-amber spiders include those (as yet undescribed) from the Chinese Yixian Formation; single, poorly preserved specimens from Botswana (Rayner and Dippenaar-Schoeman, 1995), Mexico (Feldmann *et al.*, 1998), and Australia (Jell and Duncan, 1986), an interesting fauna from two localities in Spain (Selden, 1989, 1990; Selden and Penney, 2003), which also includes both cribellate and ecribellate orb-weavers, and some mygalomorphs from Asia (Eskov and Zonshtein, 1990). The Crato Formation is therefore one of the most abundant sources of non-amber Mesozoic spiders. Like the Chinese material, the Crato finds (see below) are still relatively new, and much of the araneofauna from this locality has yet to be described. Undescribed material of fossil spiders from the Crato Formation is deposited at SMNS, MNB, NSMT, MURJ and other institutions (see Chapter 1 for definitions of these abbreviations).

Suborder Opisthothelae Pocock, 1892

Infraorder Araneomorphae Smith, 1902

Suborder Araneoidea Latreille, 1806

Family uncertain

Genus *Cretaraneus* Selden, 1990

Cretaraneus martinsnetoi Mesquita, 1996

1988 Araneida, Campos, Costa and Martins-Neto, p. 494.
1996 *Cretaraneus martinsnetoi* Mesquita, pp. 25–26, text figure 2, plates 1–3.

Material: holotype UnG/1T-50 D in Laboratoria de Geosciences, Universidade Guarhulos, São Paulo, Brazil.

The first Crato spider to be described was *Cretaraneus martinsnetoi* (Figure 9.1b). Mesquita (1996) compared the specimen with the type of the genus *Cretaraneus* from the Lower Cretaceous of Montsech, Spain (Selden, 1990), which was one of the few Cretaceous spiders described at that time. A study of the Crato holotype by PAS during a visit to Brazil suggested some misinterpretations in the

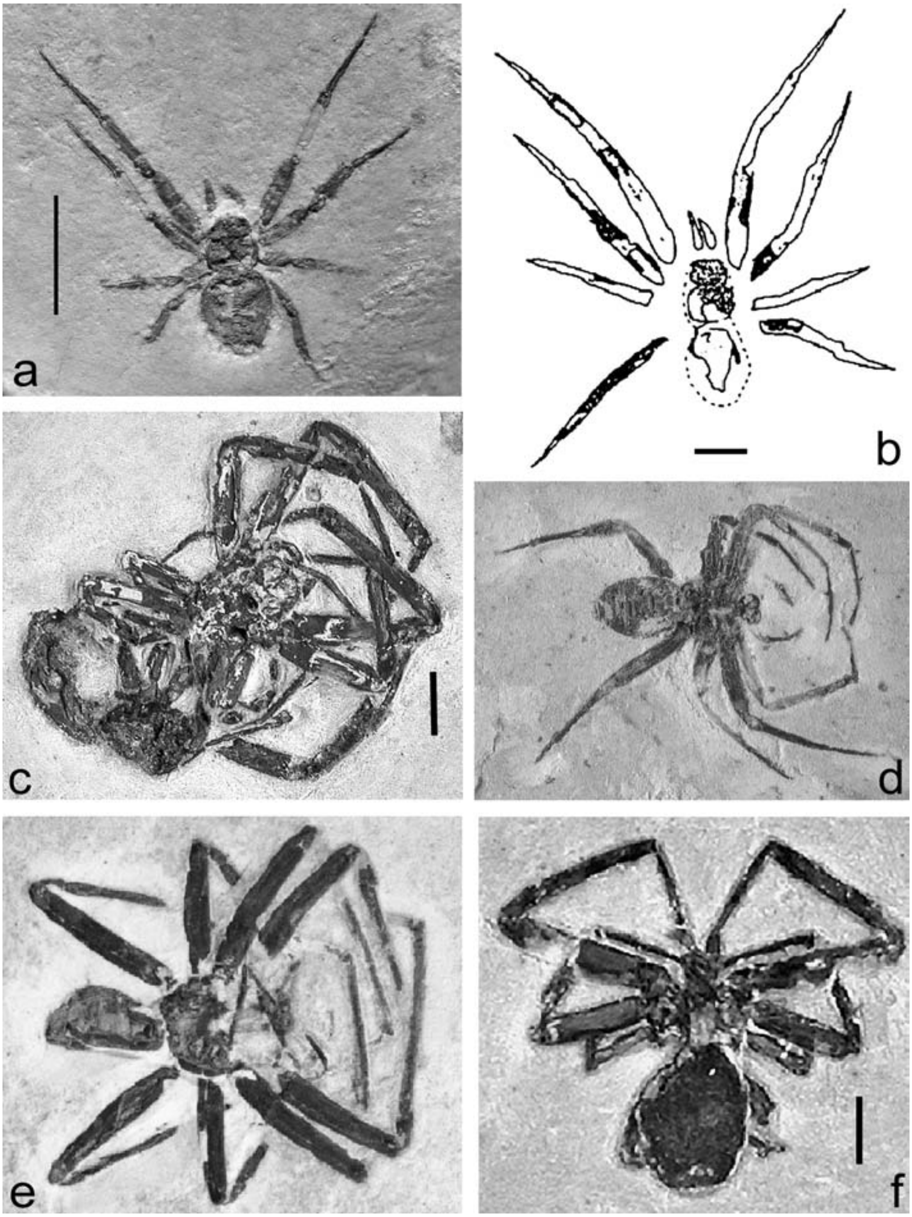

Fig. 9.1. Crato Formation small spiders. (a) A fine example with appendages out-splayed. (b) Interpretive drawing of holotype of *Cretaraneus martinsnetoi* Mesquita, 1996. (c) A rare example of two spiders in association. The nature of this association is unknown, perhaps representing two competing individuals or a single individual undergoing ecdysis, but it may simply be a chance association. (d–f) examples of cf. *Cretaraneus* with appendages turned inwards, a typical pose for Crato Formation spiders. Scale bars, 5 mm (d), 1 mm (d–f). (b) Redrawn after Mesquita (1996).

original description, so that it is unlikely to be congeneric with *Cretaraneus*. The species, however, is the commonest in the Crato fauna, so a redescription with the abundant additional material should be straightforward. There are now hundreds of specimens of Araneae known from the Crato Lagerstätte; this is in great contrast to the handful known from the entire Mesozoic Era when the type of *Cretaraneus* was described from Spain less than 20 years ago. The commonest spiders from the Crato Formation appear to be araneoids (Figure 9.1), although no definite ecribellate orb-web weavers have yet been determined.

Infraorder Mygalomorphae Pocock, 1892

Family Dipluridae Simon, 1879

Subfamily Diplurinae Simon, 1889

Cretadiplura Selden, in Selden *et al.,* 2006

Cretadiplura ceara Selden, in Selden *et al.,* 2006

2002 Dipluridae Selden *et al.*, pp. 89–91.

2006 *Cretadiplura ceara* Selden, *in* Selden *et al.*, pp. 819–820; text figures 1, 2; plate 1.

Material: holotype MB.A.979; allotype A11 in Laboratoria de Geosciences, Universidade Guarhulos, São Paulo, Brazil (Figure 9.2).

Dinodiplura Selden, in Selden *et al.,* 2006

Dinodiplura ambulacra Selden, in Selden *et al.,* 2006

2006 *Dinodiplura ambulacra* Selden, *in* Selden *et al.* 2006, pp. 820–824, text figures 4-4; plate 2.

Material: holotype SMNK-Pal.3995; counterpart MPSC A883; allotype F1417/SAB/AR/DIP/CJW Wunderlich collection, Hirschberg, Germany (Figure 9.2).

The first major group of spiders to be described in detail from the Crato Formation was the Mygalomorphae. Some quite large and spectacular specimens (Plate 5; Figure 9.2) have been referred to the modern family Dipluridae on account of their elongated posterior lateral spinnerets. The presence of diplurid spiders in the Crato Formation was first reported by Selden *et al.* (2002). Two new genera and species were described by Selden in Selden *et al.* (2006), from adult males and females as well as juveniles. The largest is *Dinodiplura ambulacra*, named in honour of Dino Frey, who acquired the specimen for scientific study. The holotype adult female (part) is in the Staatliches Museum für Naturkunde, Karlsruhe, Germany (Figures 9.2c and 9.3a), but its counterpart is on display in the Museum of Palaeontology in Santana do Cariri, Ceará, Brazil (Figure 9.3b). The allotype adult male (Figure 9.2d)

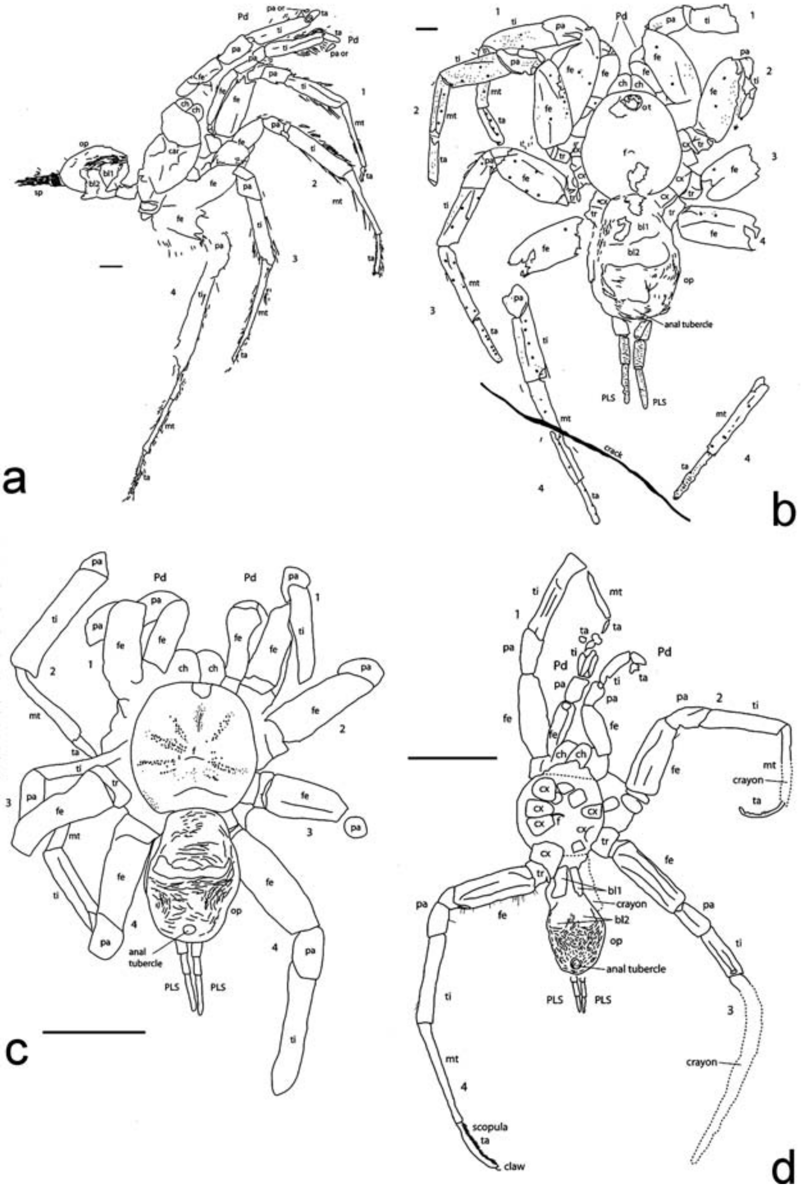

Fig. 9.2. Diplurid spiders: (a) *Cretadiplura ceara* Selden, in Selden *et al.* 2006, allotype adult, no. A11; (b) *C. ceara* holotype adult, no. MB.A.079; (c) *Dinodiplura ambulacra* Selden, in Selden *et al.* 2006, holotype, adult, SMNK-Pal.3995; (d) *D. ambulacra*, adult, allotype, F1417/SAN/AR/DIP in CJW collection.

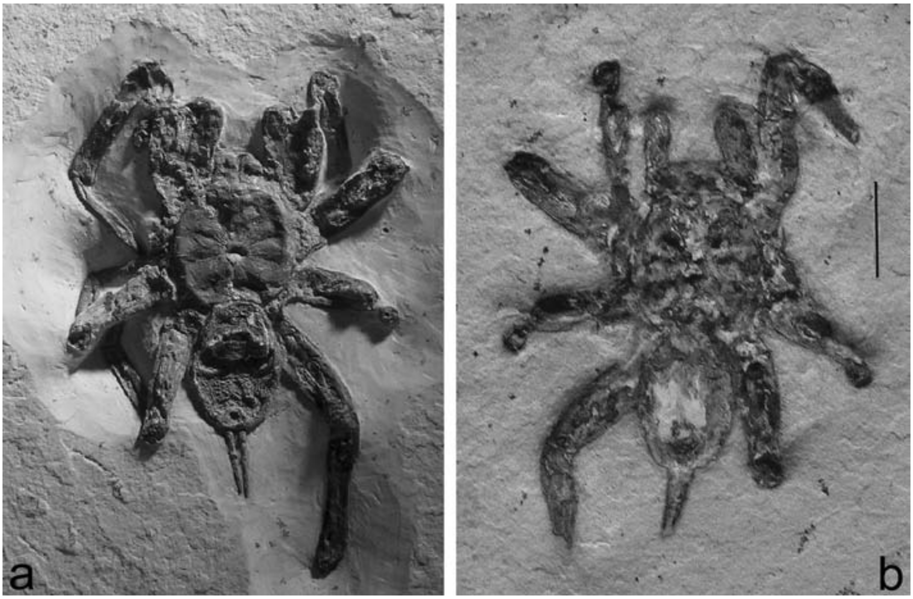

Fig. 9.3. *Dinodiplura*: (a) the holotype of *Dinodiplura ambulacra* Selden, 2006, obtained from a commercial source; (b) the counterpart located during a visit to the Museum of Paleontology in Santana do Cariri, Ceará, Brazil; scale bar, 10 mm.

is in the collection of Jörg Wunderlich, Hirschberg, Germany. The other diplurid is *Cretadiplura ceara*, which is also known from a holotype adult female (Figure 9.2b) held in the Museum für Naturkunde der Humboldt-Universität, Berlin, Germany. The allotype adult male (Figure 9.2a) is in the collections of the Laboratório de Geociências, Universidade Guarulhos, São Paulo, Brazil.

Discussion: the discovery of members of the Dipluridae in the Early Cretaceous pushes the age of the this group back some 90 mya because the previously described earliest diplurid, *Clostes priscus*, plus two indeterminate genera, are from Eocene (*c*.35 mya) Baltic amber (e.g. Wunderlich, 2004). Three genera (including two extant) of diplurids are known from (?)Miocene Dominican amber (Schawaller, 1982; Wunderlich, 1988, 2004). The presence of Dipluridae in the Early Cretaceous had been predicted by the presence of its likely sister group (Nemesiidae; see Goloboff, 1993) in strata of this age (Selden, 2002). Dipluridae is widespread in tropical to temperate regions, but the subfamily Diplurinae, to which the Crato fossils belong, is restricted to Central and South America. Whereas a few genera are burrowers, diplurids are characteristically weavers of funnel-webs; their long, manoeuvrable posterior lateral spinnerets are adapted to this purpose (Coyle, 1986). Indeed, one of the most common spiders to be found in the quarries in Crato limestone around Nova Olinda, weaving its funnel-webs beneath loose slabs of limestone, is the ischnotheline diplurid *Ischnothele annulata*. Funnel-webs are constructed to catch jumping prey, such as orthopteran insects. The long posterior lateral spinnerets of the fossil genera suggests they, too, would have woven funnel-webs and, because Orthoptera are abundant in the Crato limestone, there was plenty of food available for the spiders in the Early Cretaceous. The suggested palaeoenvironment of the Early Cretaceous of north-east Brazil is arid or semi-arid (Martill, 1993), and both diplurids and their orthopteran prey are plentiful in semi-arid environments today (Main, 1982; Hunter *et al.*, 2001).

Scorpiones: scorpions

Scorpions are an instantly recognizable group, characterized primarily by their large pedipalpal claws, their highly mobile tail ending in a venomous sting and a pair of comb-like sensory organs on the underside of the body called pectines. A good recent summary of their biology is by Brownell and Polis (2001). Scorpions are primarily nocturnal predators, mostly eating other arthropods. Their vision is poor and prey is detected to a large extent using very fine, sensory hairs on the limbs, called trichobothria, which can detect air currents. Prey is caught initially with the claws. If it still needs to be subdued it is subsequently injected with venom via the sting. Fet *et al.* (2000) recognized 1259 Recent scorpion species in 16 families. Nevertheless, scorpion higher systematics and their familial and suprafamilial classification remains controversial (see e.g. Fet and Soleglad, 2005; Prendini and Wheeler, 2005, and references therein). Living scorpions are widely distributed throughout warmer regions of the world and can be found from rainforest through to desert environments. Unlike other arthropods, their diversity tends to be greater in arid habitats as opposed to tropical forests (Polis, 1990).

Scorpion fossil record

The scorpion fossil record goes back to the mid Silurian, about 430 mya, when the earliest forms may have been aquatic, but they were certainly living on land by the Early Carboniferous (*c.*340 mya). An older summary of the approximately 100 (mostly Palaeozoic) fossil species can be found in Kjellesvig-Waering (1986), with a more up-to-date account of their relationships by Jeram in Brownell and Polis (2001). Evidence of scorpions in the Cretaceous is scarce, with the majority being found in amber deposits (e.g. Lourenço, 2003; Santiago-Blay *et al.*, 2004). In the Crato Formation scorpions are represented by two species: *Araripescorpius ligabuei* Campos, 1986 and *Protoischnurus axelrodorum* Carvalho and Lourenço, 2001 (Plate 4; Figure 9.4). The affinities of both have recently been revised (Menon, 2007) and they can be placed within the superfamilies Chactoidea and Scorpionoidea. Undescribed material of fossil scorpions from the Crato Formation is deposited at SMNS, MNB, NSMT, MURJ and other institutions.

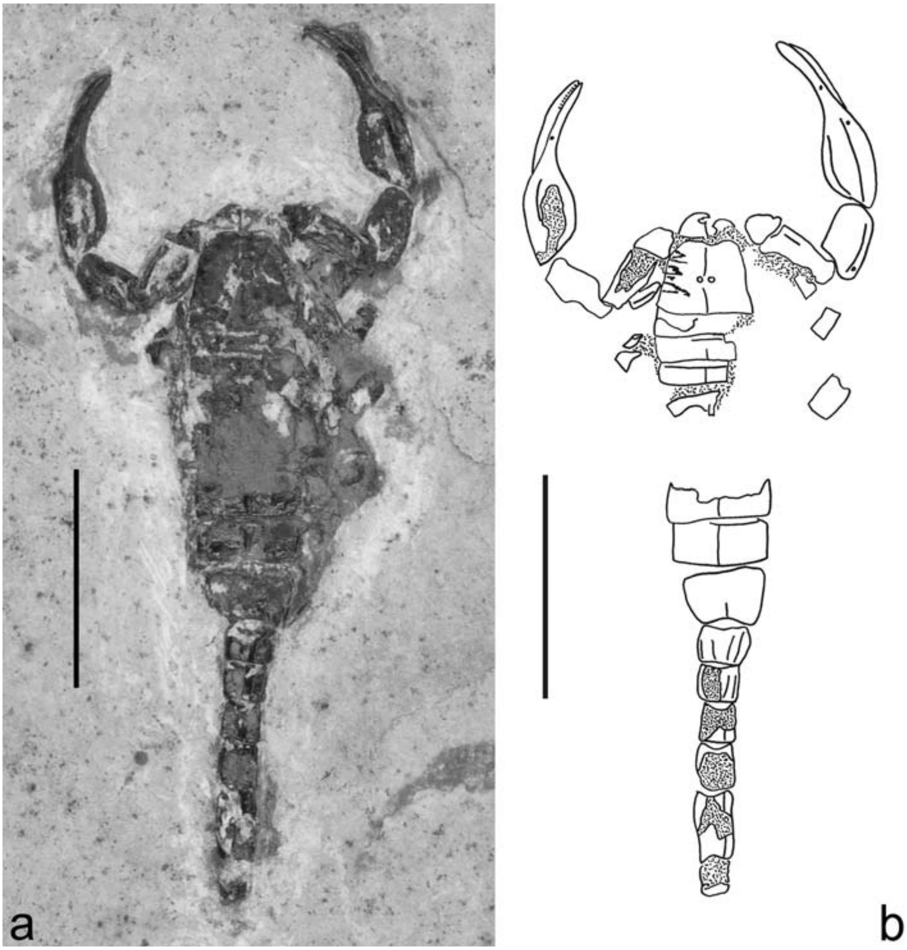

Fig. 9.4. Crato scorpion *Araripescorpius ligabuei* Campos, 1986: (a) specimen VII21 from Senckenberg Museum Frankfurt; (b) interpretive drawing of the same specimen. Scale bars, 5 mm.

Superfamily Chactoidea Pocock, 1893

Family Chactidae Pocock, 1893

Genus *Araripescorpius* Campos, 1986

Araripescorpius ligabuei Campos, 1986

1986 *Araripescorpius ligabuei* Campos, p. 136, figures 1, 1a.
1991 *Araripescorpius ligabuei* Campos; Maisey, p. 406, unnumbered figure.
2001 *Araripescorpius ligabuei* Campos; Carvalho and Lourenço, p. 714.
2002 *Araripescorpius ligabuei* Campos; Dunlop and Martill, p. 325.

Material: holotype DGM6.216-1 held in the Departamento Nacional da Produção Mineral, Rio de Janeiro.

The original diagnosis of this species (Campos, 1986) was based on a poorly preserved specimen and the description gave no details of the arrangement of carina (ridges) on the tail, trichobothrial patterns or morphometric data. The holotype was assigned to Scorpionoidea based only on its general appearance, but a re-examination by Carvalho and Lourenço (2001) supported this placement (as ?Protoischnuridae; see below). Menon (2007) examined additional, well-preserved material (Plate 4; Figure 9.4a), which showed that the species should in fact be assigned to a different superfamily, Chactoidea, and is thus the oldest chactoid known to date. This assignment is confirmed by neobothriotaxy (a characteristic pattern of trichobothrial distribution) displayed on the ventral side of the right patella of the claw, which can also be seen in Recent chactids. In fact, all modern South American chactids show neobothriotaxy on this claw surface (Soleglad and Fet, 2003). Chactidae is a large, widespread family, currently recorded from Europe and the Americas. Their fossil record dates back to the Early Cretaceous of the Crato Formation and to French Cretaceous amber (Lourenço, 2003), although the family probably originated much earlier. Chactids are typically small scorpions (body length $\approx$ 11–27 mm), with short and bulky pedipalpal claws. They can be recognized by having a type 2 pentagonal sternum, an oval telson without a subaculear tooth, a pair of ventral lateral carinae on the fifth metasomal (tail) segment and a so-called C pattern of the trichobothria (*sensu* Vachon 1974); see also Menon (2007) for details.

Superfamily Scorpionoidea Latreille, 1802

Family Hemiscorpiidae Pocock, 1893

Subfamily Hormurinae Laurie, 1896

Genus *Protoischnurus* Carvalho and Lourenço, 2001

Protoischnurus axelrodorum Carvalho and Lourenço, 2001

1993 Scorpion, Martill, plate, figure 2.
2001 *Protoischnurus axelrodorum* Carvalho and Lourenço, p. 714, figures 1–3.
2003 Undescribed scorpion, Selden, p. 338, figure 2.
2005 *Protoischnurus* [*axelrodorum*] Carvalho and Lourenço; Soleglad *et al.*, p. 34.

Material: holotype MN-7601-I National Museum, Rio de Janeiro. Also A355, 884, 704, 886 Santana Museum, Santana do Cariri; LL 12484 Manchester Museum; MBA974, A971, A972 Berlin; SMNS 65534, 65535; SF122-4 School of Earth, Atmospheric and Environmental Sciences, University of Manchester.

Formally described by Carvalho and Lourenço (2001), the type material of *Protoischnurus axelrodorum* is held in the Museu Nacional, Rio de Janeiro, Brazil and the American Museum of Natural History in New York, USA. Its referral to Scorpionoidea is based on the inverse Y-shape of the posterior end of the central suture on the carapace, the arrangement of carinae on the fourth and fifth segments of the metasoma (tail), the position of the *Est* trichobothrium and a sternum which is longer than it is wide (see Menon, 2007). Within this clade, Hemiscorpiidae (= Ischnuridae; Liochelidae) is a small family, which includes some Recent species known from Africa, South America and Asia. Fossil Hemiscorpiidae from the neotropics were previously unknown and *Protoischnurus* is thus the first record of a Cretaceous hemiscorpiid. It should be noted that Carvalho and Lourenço (2001) erected a new family, Protoischnuridae, to accommodate *Protoischnurus*. However, they failed to define the differences between Protoischnuridae and Hemiscorpiidae (as Ischnuridae); but did suggest, as the name implies, a close relationship between the two. Menon (2007) concluded that Protischnuridae is a junior synonym of Hemiscorpiidae, an interpretation also upheld by Soleglad *et al.* (2005) and Fet and Soleglad (2005). *Protoischnurus* can be recognized by slit-like spiracles, a pentagonal sternum, large pectines, a telson without a subaculear tooth and a C-type trichobothrial disposition (*sensu* Vachon, 1974). It also shows a single, linear row of differently sized granules on the movable finger of the claw; see Menon (2007) for further details.

Discussion: Soleglad *et al.* (2005) and Menon (2007) discussed the phylogenetic implications of the Crato Formation scorpions, as inferred from an analysis of modern scorpion distribution. The neobothriotaxy in *Araripescorpius* is only the second example of this morphology recorded from the Cretaceous, and the only case encountered for the Southern Hemisphere. The only other record, *Palaeoeuscorpius gallicus* (Palaeoeuscorpiidae), occurs in Early Cretaceous French amber (Lourenço, 2003). Chactoidea was probably already established by the Mesozoic, and contains one modern family, Chactidae. In the other major clade preserved in the Crato Formation, the scorpionids, the Hormurinae is distributed today in several Gondwanan fragments (Soleglad *et al.*, 2005), which suggests that it was present across Gondwanaland well before the continent's fragmentation. Analysing several morphological characters of many Recent genera of Scorpionoidea, Soleglad *et al.* (2005, figure 72) offered a phylogenetic analysis of Hemiscorpiidae and its sister group Scorpionidae and concluded that the putative (Hemiscorpiidae+Scorpionidae) clade was present during Pangaean times (i.e. Late Permian–Triassic).

Ecologically, scorpions can be broadly divided into lithophilic (rock-living), psammophilic (sand-living) and fossorial (burrowing) morphotypes (e.g. Polis, 1990). The large claws of at least the Crato Formation chactid, *Protoischnurus*, tend to suggest a fossorial scorpion, in which the claws help with burrow construction. Fossorial scorpions tend to hunt close to their burrow, although the majority of their life – perhaps up to 97% in some species (Polis, 1990) – is spent within the safety of the burrow; which in desert species also offers protection from the heat of the day. The Crato Formation scorpions may, therefore, be animals caught out of their burrows, or even driven out by flooding events. In this context, some extant species emerge after rains to feed, but this is not a universal phenomenon in all scorpions.

Acari: mites

Mites are the most diverse arachnids, with over 48,000 living species known so far and probably a great many unknown species still awaiting discovery. Mites are, with a few exceptions (see below), tiny creatures and all share a characteristic form of the mouthparts called the gnathosoma. Here the chelicerae and pedipalps articulate together as a moveable unit, offset from the rest of the body, or idiosoma. The mite body is usually rather compact, can be quite hairy, and its division into a prosoma and opisthosoma is often obscure. Early larval instars have only six legs, not eight, but given the diversity within the mites it is difficult to make further morphological generalizations and not all workers are convinced that the group is monophyletic. Most acarologists recognize two major clades: Acariformes (oribatid or soil mites, cheese mites, water mites, follicle mites, etc.) and Parasitiformes (mostly predatory gamasid mites and ticks). As a group, mites are found almost everywhere and occupy a huge range of habitats and lifestyles encompassing free-living predators, detritivores, saprophages, phytophages and ectoparasites. Good general texts on mite biology and systematics include Evans (1992) and Walter and Proctor (1999).

Acari fossil record

A valuable summary of fossil mites can be found in Bernini (1991) and amber inclusions were listed by Spahr (1993). In total, there are probably about 170 fossil species. Recent work suggests that acariform mites *may* go back as far as the Ordovician and they are certainly present in terrestrial habitats in the early to mid-Devonian about 400–380 mya. Fossil parasitiform mites are so far only known from the Mesozoic–Tertiary. This is probably an artefact and a similarly long fossil record would be expected. Mesozoic mites (mostly oribatids) include records from Cretaceous ambers (e.g. Krivolutsky, 1979, and references therein), as well as argasid (bird) ticks (Klompen and Grimaldi, 2001) and numerous undescribed specimens from Lebanese and Burmese amber. There are three putative records of mites, or mite activity, in the Crato Formation, each of which is dealt with separately below.

Feather mites?

Martill and Davis (1998) reported tiny, spherical structures preserved on Crato feathers (e.g. specimen PV20059 at NSMT). These egg-like objects have a diameter of approximately 70 µm and a circular aperture of about 35–40 µm (see Chapter 18; Figures 18.1b–e). They were interpreted by these authors as evidence of ectoparasitism. Bird lice were excluded as potential producers due to the small size of the spheres. Instead, these authors suggested that the feathers hosted mites, several groups of which are known from modern bird families and which lay their eggs attached directly to the feathers. However, Martill and Davis (1998) were unable to assign the eggs to any particular mite taxon. In her review of feather mite biology, Proctor (2003) disputed this hypothesis, pointing out that eggs of Recent feather mites (Acari: Astigmata) are typically larger (150–400 µm), sausage-shaped and have a longitudinal seam rather than an aperture. She suggested ostracods as an alternative source, a group known to lay spherical eggs on aquatic detritus, such as a feather washed into a lake. The identity of these spheres on the feathers thus remains open.

Leaf-inhabiting mites?

Scanning electron microscopy (SEM) of a piece of a fossil fern from the Crato Formation held in the Portsmouth University collections and belonging to the family Schizaceae (ray ferns) has revealed a possible arthropod embedded within the fern tissue. As yet undescribed, it consists of a tiny, flattened body, only about 15 µm long, possibly divided into two sections, or tagma, and with what looks like at least one short appendage visible towards the front end of the body (Figure 9.5). Further details are lacking, making its unequivocal identification difficult, but one tentative interpretation would be that this is some sort of leaf-inhabiting mite. Among modern taxa at least two phytophageous groups, Eriophyidae (gall, rust or blister mites) and Tenuipalpidae (false spider or flat mites) are known to live within plant tissues. In crude morphology, the specimen seen under SEM is more reminiscent of the latter group (see e.g. Welbourn *et al.*, 2003), but there is a problem in that the smallest modern mites are known to be about 80–250 µm long (including their smallest hatching stages), making the Crato Formation example almost an order of magnitude too small. Further work is required to assess whether this really is an animal remain, or merely some sort of fortuitous artefact.

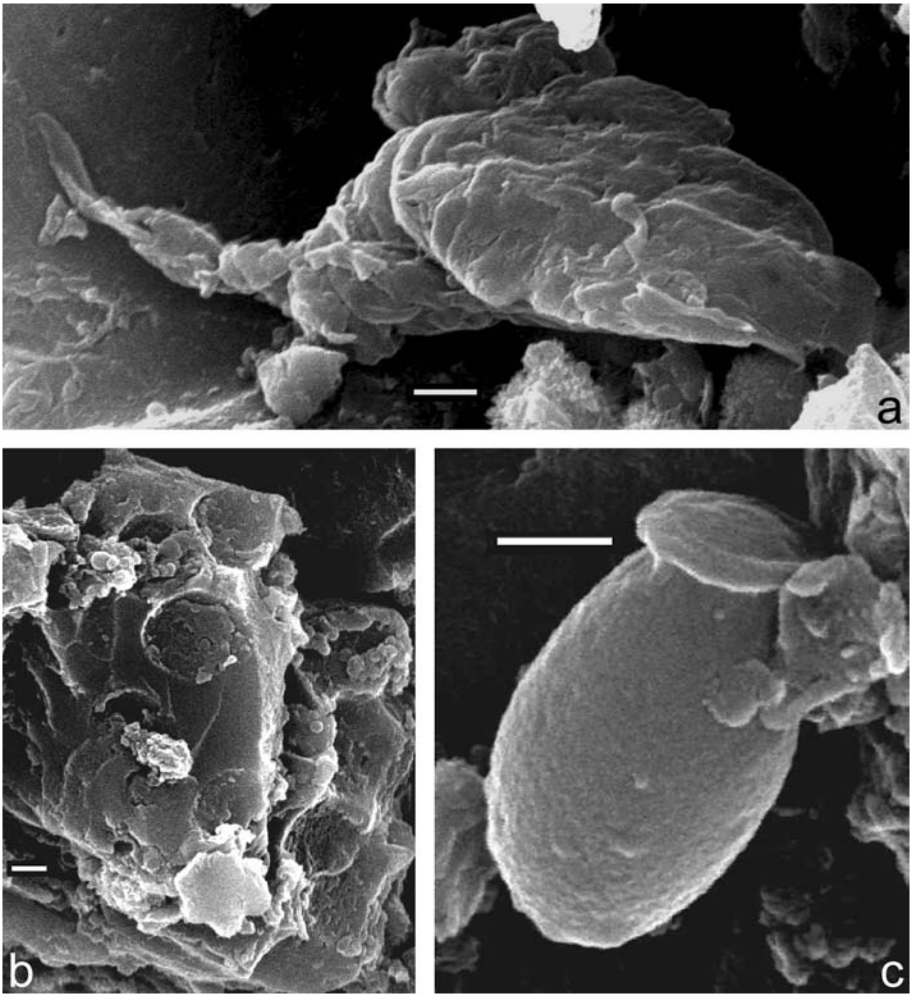

Fig. 9.5. Scanning electron micrographs of a possible phytophagous leaf mite: (a) the mite; (b) possible boring made by the mite; (c) an associated flask-shaped, egg-like structure with flanged opening. These were discovered by Robert Loveridge and all occur within a crevice on a frond of the schizeaecean fern cf. *Ruffordia* sp. Scale bars, 1 μm.

Erythraeoid mites

Erythraeoids (Acari: Parasitengona: Erythraeoidea) are a large group of terrestrial, free-living mites whose biology was summarized by Southcott (1961). Cosmopolitan in distribution, there are at least 200 living species (Welbourn, 1991). Typically with a reddish colour in life which gives the group its name, these mites tend to occur in litter or on open ground and occasionally in trees or under bark. Like other parasitengonids, they have a complex life history with an ectoparasitic instar, and their larvae usually parasitize other arthropods.

Fossil erythraeoid mites are known from Cretaceous and Tertiary (particularly Baltic) amber (see e.g. Spahr, 1993). A Late Cretaceous species was formally described from Canadian amber by Vercammen-Grandjean (1973). However, not all of these amber fossils have been described in detail, and the generic placements of those that have were mostly based on superficial characters and merit revision. All these other fossils are considerably smaller than the Crato example, which is to the best of our knowledge the oldest erythraeoid and the largest fossil mite ever recorded.

Cohort Parasitengona Oudemans, 1909

Superfamily Erythraeoidea Grandjean, 1947

Family ?Erythraeidae Robineau-Desvoidy, 1828

Genus

Pararainbowia Dunlop, 2007

Pararainbowia martilli Dunlop, 2007

The single Crato example (MNB.A. 982) appears to show the ventral surface (Figure 9.6). The counterpart is in coll. MURJ in Japan. The body is preserved in outline only, but the legs and mouthparts are rather better and show an obvious gnathosoma, indicating that it is a mite. It therefore represents the least equivocal of all the Crato mites and indeed it is quite unusual to find a mite preserved in a limestone, rather than in a macerate or in amber. The sheer size of the Crato mite, with a body length of approximately 5 mm, is remarkable and only a few extant taxa reach these proportions, such as certain ticks (Ixodida) and velvet mites (Trombidiformes). However, the legs in this Crato fossil are far too long and slender for either a tick or a velvet mite and a velvet mite would also be expected to be much more stocky and hairy. Instead, the general body shape strongly implies an erythraeoid. Most living examples of this group are about 1–3 mm long, but some extant Australian species are noticeably larger (Southcott, 1961) and are of a similar size to the Crato fossil. For a full description of *P. martilli* see Dunlop (2007).

Solifugae: camel spiders or sun spiders

Camel spiders are also known as sun spiders or wind scorpions. A summary of camel spider biology can be found in Punzo (1998). Most of their common names refer either to their remarkable running abilities – thanks partly to an extensive system of tracheae – or their occurrence (like camels) in predominantly arid habitats. Camel

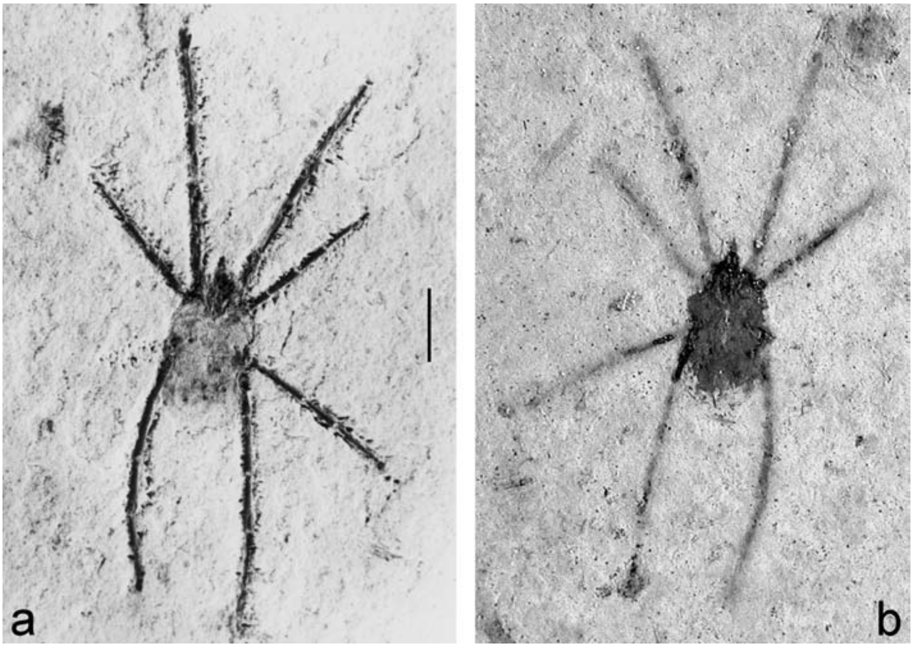

Fig. 9.6. Acari, ?Erythraeidae. Part (MURJ), (a); and counterpart (MNB.A. 982), (b) of *Pararainbowia martilli* Dunlop (2007). Scale bar, 2.5 mm.

spiders are predators with formidable chelicerae which can make up a sizable proportion of the body length. Adult males have a projection called the flagellum on the upper surface of each chelicera, which can be quite elaborate in some groups and is of considerable taxonomic value. Camel spiders mostly eat other arthropods, but large, extant species are quite capable of tackling small vertebrates. On first appearances they appear to have 10 legs, since their pedipalps are large and leg-like, often bearing strong, inward-facing spines which help with prey capture. Camel spiders are usually extremely hairy and rely heavily on their long, tactile hairs to sense the world around them. They also have, uniquely among arachnids, a series of club-shaped, probably chemosensory organs on the underside of the bases of the back legs called malleoli or racquet organs. Around 1075 species of extant camel spiders have been described and these can be placed in 12 families (Harvey, 2003). As a group they can be found in most tropical to sub-tropical arid regions of the world, with the curious exception of Australia.

Camel spider fossil record

Camel spiders have an extremely poor fossil record. There is an enigmatic Early Carboniferous fossil, about 330 myr old, which shows possible camel spider features. This is followed by a poorly preserved, but recognizable, *c*.305 myr-old late Carboniferous example – redescribed by Shear in Selden and Shear (1996). Next come the Crato examples, six of which have been formally described and figured as *Cratosolpuga wunderlichi* in the extant family Ceromidae (Selden in Selden and Shear, 1996). Finally, there are two younger Tertiary examples from Dominican and Baltic amber, both of which can confidently be assigned to extant families known today from the Neotropics and southern Europe respectively.

Family Ceromidae Roewer, 1934

Genus *Cratosolpuga* Selden, in Selden and Shear, 1996

Cratosolpuga wunderlichi Selden, in Selden and Shear, 1996

1996	*Cratosolpuga wunderlichi* Selden, in Selden and Shear, pp. 601–603, plate 1, figures 3 and 4, plate 2, text figures 1, 3–6.
1996	*Cratosolpuga* [*wunderlichi*] Selden; Dunlop, pp. 84, 86, figure 5.
1998	*Cratosolpuga wunderlichi* Selden; Punzo, pp. 213–214, figures 7.7.–7.10.
2002	*Cratosolpuga wunderlichi* Selden; Harvey, p. 366.
2003	*Cratosolpuga wunderlichi* Selden; Harvey, p. 212.
2004	*Cratosolpuga wunderlichi* Selden; Dunlop and Martill, pp. 145–151, figures 1–8.

Material: holotype no. Sol-1 in coll. J. Wunderlich (Hirschberg, Germany); specimen SMNK 1268 PAL (not a paratype); specimens MB.A.1087 and MB.A.1088 at MNB; specimens SMNS 65417 and SMNS 65418; three well-preserved specimens without number at coll. MURJ.

The Crato Formation camel spider was assigned by Selden (in Selden and Shear 1996) to the extant family Ceromidae based principally on the presence of a styliform, backwards-pointing flagellum originating from a bulbous base, a characteristic shape for this group (Figures 9.7 and 9.8). Selden (1996) described a relatively complete adult male – the holotype, held in the private collection of J. Wunderlich, Hirschberg – and a smaller juvenile deposited in SMNK Karlsruhe. Dunlop (1996) figured the holotype in a review of fossil arachnids and Punzo (1998) showed it in his book on camel spider biology. Dunlop and Martill (2004) described four additional Crato Formation camel spiders from the Berlin and Stuttgart collections. These revealed some new features, such as the dorsal surface of the abdomen, and one specimen represents an unusual lateral preservation showing the folded membrane between the tergites and sternites very nicely. All four examples were referred to *C. wunderlichi*. In their discussion, Dunlop and Martill recognized some minor differences between the six Crato Formation camel spiders, which range in body length from about 6 to 23 mm. However, they cautioned that among living species

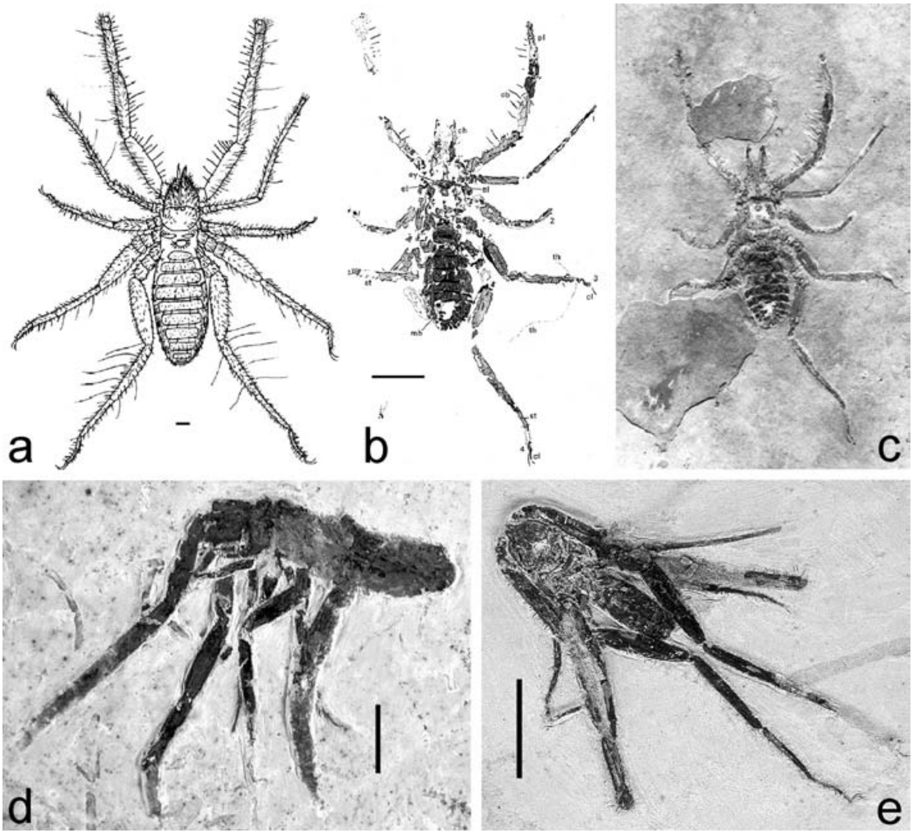

Fig. 9.7. Camel spiders: (a) reconstruction of *Cratosolpuga wunderlichi* Selden in Selden and Shear, 1996; (b) interpretive diagram of specimen in (c); (c) specimen MB.A. 1087; (d) cf. *Cratosolpuga* in lateral aspect; (e) an unusual specimen with folded appendages. Scale bars, 1 mm (a), 5 mm (b, c), 5 mm (d), 10 mm (e). (a) Courtesy of the Palaeontological Association; (b) courtesy of GIA/SEA.

some characters are so variable – for example, the size of the abdomen – that they are effectively taxonomically irrelevant. Size and proportion-related characters in these Brazilian camel spiders are poor grounds for creating new fossil taxa.

Discussion: The presence of camel spiders in the Crato Formation supports the general interpretation of an arid local environment, since this sort of habitat is typical for the majority of living Solifugae. The assignment of the fossils to Ceromidae is of particular biogeographic interest since this family is currently restricted to southern Africa and does not occur in the Americas today. As discussed by Selden and Shear (1996), the Crato fossils suggest that Ceromidae was present in Pangaea before the rifting event in the Cretaceous, which eventually led to the formation of the Atlantic Ocean. It appears that the ceromid lineage survived in what became Africa, but died out on the South American side.

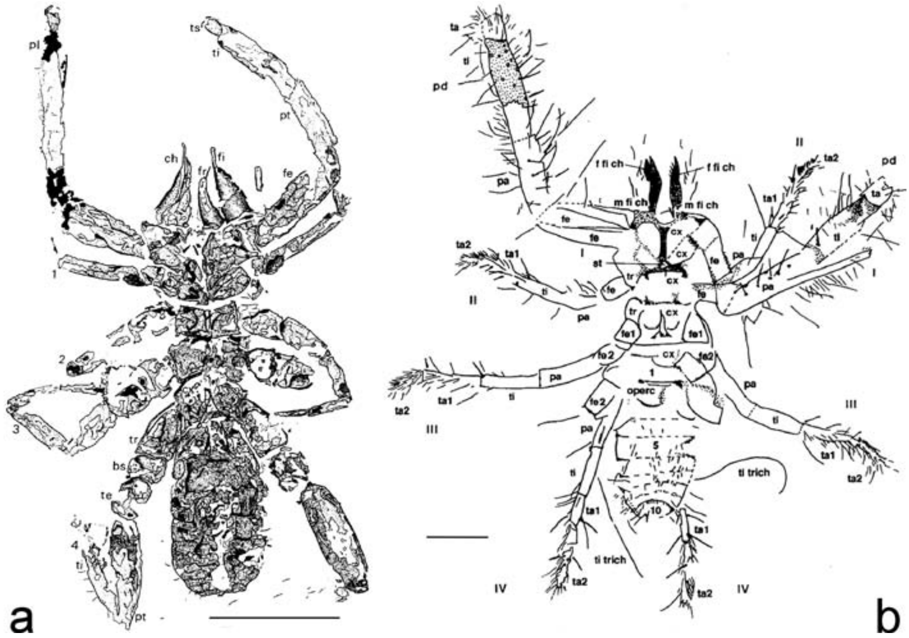

Fig. 9.8. Camera lucida drawings of two specimens of *Cratosolpuga wunderlichi*: (a) specimen MB.A. 1088; (b) juvenile example, SMNK 1268 Pal. Scale bars, 5 mm (a), 1 mm (b). (a) Courtesy of GIA/SEA; (b) courtesy of the Palaeontological Association.

Uropygi/Thelyphonida: whipscorpions

Whipscorpions superficially resemble scorpions, but in fact they are more closely related to spiders with which they share features of the mouthparts and the number of book-lungs. A summary of their biology can be found in Haupt (2000). Unlike scorpions, which have truly chelate palps, the pedipalps of whipscorpions are only sub-chelate. These robust pedipalps are likewise used for grasping prey, which is attacked opportunistically and consists mostly of other small arthropods (see e.g. Punzo, 2000). Whipscorpions do not have a sting, but they can raise their opisthosoma in a behaviour called aggressive posturing. This mimicry makes them look more like real scorpions and presumably fools predators into thinking they face a more dangerous animal. Failing this, they can also squirt an irritant secretion from glands near the base of the tail and this vinegar-like defensive spray gives them another vernacular name: vinegaroons. The ‘whip’ in whipscorpions refers to the long, segmented tail called the flagellum at the back of the animal. Whipscorpions are generally nocturnal and many species have been observed to burrow. They are, with one important exception (see below), generally found in rainforest habitats and occur throughout the tropics in west Africa, South-East Asia, the islands of the Pacific and the Americas. Whipscorpions are an extremely homogeneous group and most authors (e.g. Harvey, 2003) refer all 103 Recent species to a single family.

Whipscorpion fossil record

Before the discovery of the Crato Formation material (Dunlop, 1998) – described as *Mesoproctus rowlandi* – whipscorpions were mostly known as fossils only from the Late Carboniferous Coal Measures of Europe and North America. Most of these approximately 300 myr-old examples are essentially modern in appearance and can probably even be placed in the extant family Thelyphonidae. A Miocene fossil from California assigned to the whipscorpions is a misidentification (Dunlop and Tetlie, 2007).

Family ?Thelyphonidae Lucas, 1835

Subfamily ?Mastigoproctinae Speijer, 1933

Genus *Mesoproctus* Dunlop, 1998

Mesoproctus rowlandi Dunlop, 1998

1998 *Mesoproctus rowlandi* Dunlop, p. 294, figures 1 and 2.
2002 *Mesoproctus rowlandi* Dunlop; Dunlop and Martill, pp. 331–332, figures 1b, 2b, 3a, 4a.

Material: holotype UM no. K28006 deposited in the Ulster Museum, Belfast, UK; specimen SMNS 64331; specimens MB.A.975 and MB.A.1041 at MNB; four specimens (two very well-preserved) without number at coll. MURJ.

The holotype of the single Crato Formation species is preserved only in outline and while clearly recognizable as a whipscorpion on account of the robust pedipalps, this 24-mm-long fossil could not be diagnosed on anything other than its Mesozoic age. Subsequently two better-preserved specimens (Figure 9.9) from the Berlin and Stuttgart collections were described (Dunlop and Martill, 2002). They were also assigned to *M. rowlandi* and confirm the essentially modern appearance of the Crato fossils. The Berlin example (MB.A.975) is a ventral view in which the sternites have partly broken away to reveal the tergites. Details such as the flagellum, claws at the ends of the legs and even tiny sclerites embedded within certain joint membranes (also seen in living taxa) are preserved. This fossil is smaller than the holotype and, compared to living species, the shape of the anterior sternum between the leg coxae implies an immature animal. The Stuttgart example (SMNS 64331) is also quite small and poorly preserved, but retains a longer flagellum. Here the individual flagellum articles are more quadrate than in the Berlin example, but Dunlop and Martill (2002) did not feel that this minor difference warranted a separate species.

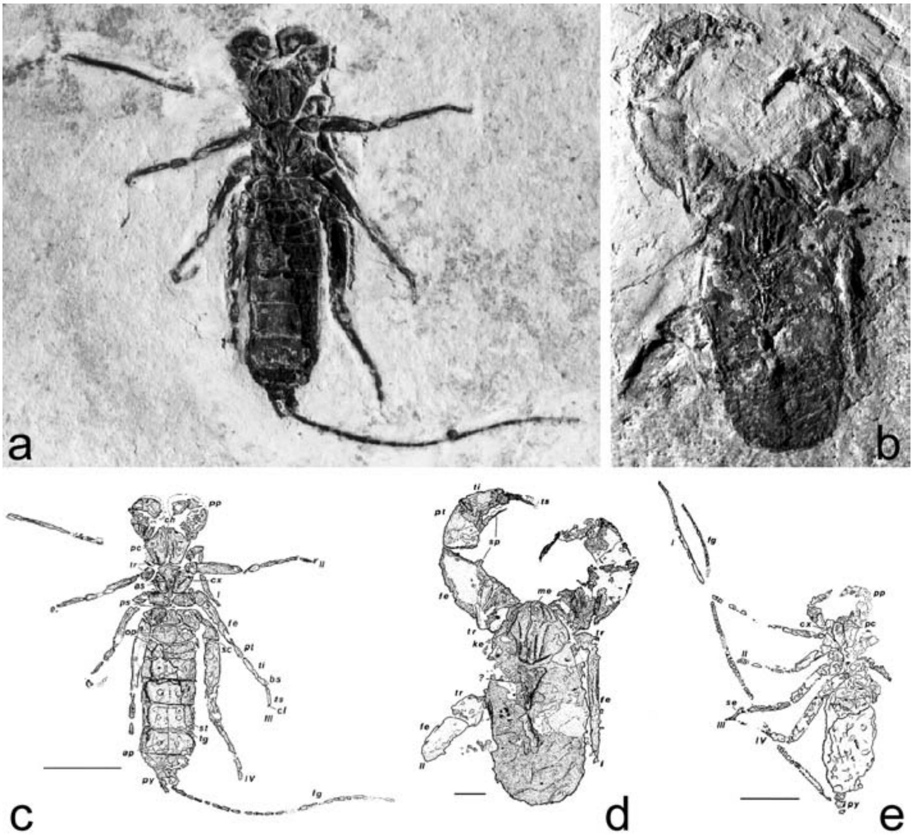

Fig. 9.9. Whipscorpion *Mesoproctus rowlandi* Dunlop, 1998: (a) near-complete specimen, MB.A 975; (b) *Mesoproctus* sp. anterior portion of large example; (c) interpretative diagram of (a); (d) camera lucida diagram of (b); (e) diagram of an additional specimen SMNS 64331. Scale bars, 5 mm.

A further whipscorpion in Berlin (MB.A.1041) consists of the prosoma only, including the pedipalps, but excluding most of the legs (Figure 9.9b). Given its incompleteness Dunlop and Martill (2002) only felt confident referring this specimen to *Mesoproctus* sp., but speculated that this might be the adult of *Me. rowlandi*. The significance of this specimen is its size. With a carapace over 32 mm long it exceeds slightly both published and unpublished size records for the living whipscorpion genus *Mastigoproctus*. The Crato fossil is thus potentially the largest whipscorpion ever recorded. There are further, undescribed, specimens of very large and more complete whipscorpions from the Crato Formation (P. van Roy, personal communication). Provisionally, these seem to be conspecific with the smaller (juvenile) specimens, and if this can be confirmed all the Crato whipscorpions can probably be referred to *Me. rowlandi*. Harvey (2003) recognized four extant subfamilies of whipscorpion, but felt unable to place the Crato fossils in this scheme. Intuitively *Me. rowlandi* probably belongs in the Mastigoproctinae, which includes a number of very large extant species – in fact only the fossil *Mesoproctus* and living *Mastigoproctus* reach this size – and is the only subfamily currently recorded from the Americas.

Discussion: one of the best-known and most thoroughly investigated Recent taxa, *Mastigoproctus giganteus*, is a large species which lives in arid environments across the southern USA and Mexico, such as the Sonoran and Chicuahuan Deserts. These places might be reasonable models for the original Crato Formation local environment. *Ma. giganteus* may thus offer clues about the ecology of *Me. rowlandi*. Physiological and behavioural studies (Ahearn, 1970; Crawford and Cloudsley-Thompson, 1971; Punzo, 2000, and references therein) of *Ma. giganteus* indicate that this extant species is not particularly well adapted to resist water loss across the cuticle and that it avoids desiccation instead by burrowing during the day and emerging at night or after heavy rains to feed. As with the scorpions, we might again speculate that the Crato Formation whipscorpions represent animals which emerged to feed after rains, only to be washed into the lagoon during flash floods.

Amblypygi: whipspiders

Whipspiders resemble whipscorpions and are related both to these arachnids and to spiders. Weygoldt (2000) gave an excellent summary of their biology. Whipspiders differ from whipscorpions in having a more rounded prosoma, in not having a flagellum at the back of the opisthosoma and in having legs which are even more slender and elongate. This gives them a delicate and rather fragile appearance. The first pair of legs are particularly whip-like and are used in a similar fashion to insect antennae to probe ahead of the animal and search for prey. As in whipscorpions, their pedipalps are subchelate, but tend to be less robust and more spiny. Whipspider pedipalps form a ‘catching-basket’ of spines to ensnare prey with a rapid grabbing motion. Like spiders, whipspiders have a very narrow waist or pedicel between the prosoma and opisthosoma, but unlike spiders they lack venom and do not produce silk. They are typically nocturnal. Around 136 living species (Harvey, 2003) in five families (*sensu* Weygoldt, 1996) are currently recognized and they can be found throughout the world in tropical to sub-tropical regions.

Whipspider fossil record

The whipspider fossil record is very sparse. Some Early Devonian cuticle fragments show similarities to modern whipspiders, but – like whipscorpions – they are first known as complete fossils from the Late Carboniferous Coal Measures of Europe

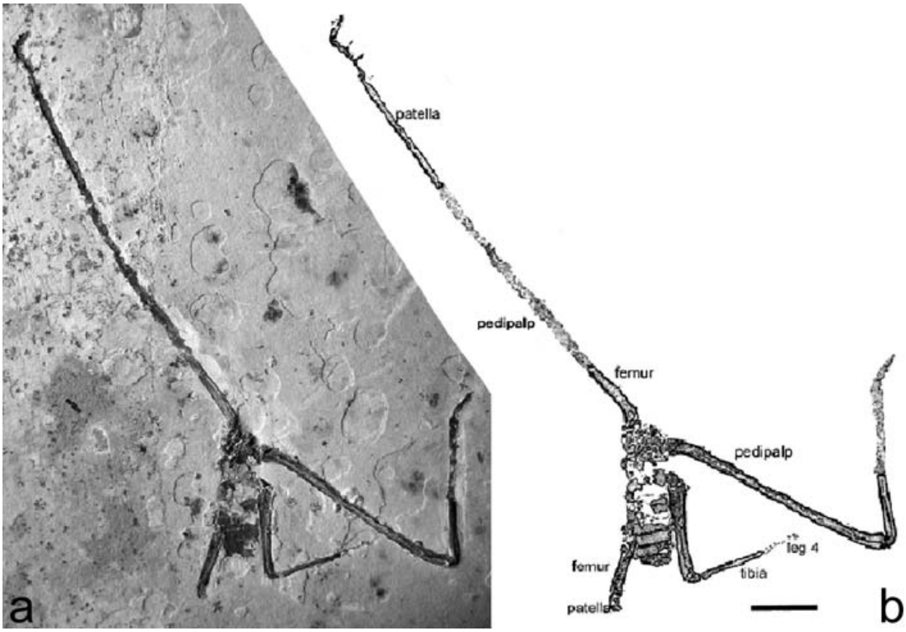

Fig. 9.10. Whipspider *Britopygus weygoldti* Dunlop and Martill, 2002: (a) specimen SMNS 66123 exposed in ventral view; (b) camera lucida drawing of specimen. Scale bar, 2 mm.

and North America. The only other fossil records are the Crato examples (Dunlop and Martill, 2002), all referred to *Britopygus weygoldti* (Figure 9.10), and material assignable to living Neotropical groups from Tertiary ambers of the Dominican Republic and Mexico.

Infraorder Neoamblypygi Weygoldt, 1996

Family ?Phrynidae Blanchard, 1852

Genus *Britopygus* Dunlop and Martill, 2002

Britopygus weygoldti Dunlop and Martill, 2002

2002 *Britopygus weygoldti* Dunlop and Martill, pp. 330–331, figures 1a, 2a.
2003 *Britopygus weygoldti* Dunlop and Martill; Giupponi and Baptista, p. 104.
2005 *Britopygus weygoldti* Dunlop and Martill; Dunlop and Barov, p. 61, figures 1–11.

Material: holotype SMNS 64332; specimen SMNS 66123.

Only two whipspiders have been formally described from the Crato Formation, both as *B. weygoldti* and both in the Stuttgart Museum collections, Germany. The smaller holotype is only known from the ventral surface, but is easily recognizable as belonging to Amblypygi from the shape and orientation of the limbs. The slender first pair of legs and the opisthosoma are missing, possibly having broken off while the carcass was being transported. The remaining legs are flattened onto their sides and this may well be pretty close to their original position in life as this leg orientation allows modern species to hug the ground and crawl easily into narrow spaces. The fossil is quite small compared to living whipspiders, about 5 mm wide across the prosoma, and may well be a juvenile. Dunlop and Martill (2002) discussed its family placement and concluded from the form of the pedipalp that it probably belongs in either the Phrynidae or Charinidae.

The second specimen SMNS 66123 was described by Dunlop and Barov (2005) and is again essentially a ventral view including good details of the mouthparts. Although considerably larger (perhaps 15 cm across the outstretched limbs) with proportionately longer pedipalps, these authors noted that the pedipalps grow allometrically in modern whipspiders and that males can have longer palps than females. Since modern whipspiders tend to occur allopatrically – only one species at any given locality – they could not rule out the possibility that the two specimens represent extremes (a first instar juvenile and a mature male?) of a single species. The second fossil was therefore also assigned to *B. weygoldti* and morphological details, in particular of the pedipalp trochanter, suggested that the fossil species does indeed belong in Phrynidae: a family distributed today across Central and South America which would make biogeographic sense for a Brazilian fossil. A further, well-preserved, Crato whipspider is known from a private collection in Brazil and was mentioned by Giupponi and Baptista (2003).

Discussion: with respect to the Crato palaeoenvironment, whipspiders are (like whipscorpions) not typical desert creatures and tend to occur in secluded, humid places. Nevertheless there is also a parallel to *Mastiogoproctus giganteus*, whereby some extant species of the Neotropical whipspider *Paraphrynus* (family Phrynidae) have been recorded from arid environments in the southern USA and Mexico. The most comprehensive study of the genus (Mullinex, 1975) lacks detailed ecological data, but there are general accounts from natural history websites of species like *Paraphrynus mexicanus* living in dry areas and emerging to feed on moist summer nights. In summary, it is not implausible to find a whipspider in an arid habitat. In any case some Crato Formation plants suggest local moist settings (oases?) too, such that there may have been less-xeric habitats around the original lagoon hosting parts of the arachnid fauna.

Other arachnids

Representatives of other arachnid orders have not been found thus far in the Crato Formation, with the possible exception of an erratic fossil arachnid specimen in coll. ms-fossil that is featured in Figure 11.90a. The Palaeozoic yields three extinct groups (Trigonotarbida, Phalangiotarbida and Haptopoda), none of which have been recorded beyond the Permian. With respect to extant orders, the absence of pseudoscorpions (Pseudoscorpiones), schizomids (Schizomida) and palpigrades (Palpigradi) from the Crato Formation is unsurprising since all three are tiny, mostly soil-living, animals with weak sclerotization and a poor chance of preservation. Ricinuleids (Ricinulei) are larger, but are very rare and today only known from a few localities in tropical forest litter and caves. The one slightly puzzling absence from the Crato Formation are the harvestmen (Opiliones), which are fairly diverse and abundant in modern ecosystems. The New World in particular yields many Recent species of Laniatores, which can be quite large and heavily sclerotized, often with remarkable spines and tubercles; all of which should improve their chances of preservation. However, living Laniatores are strongly correlated to forest habitats (A. Kury, personal communication) and their absence from Crato *might* be a result of the unsuitable habitat in the supposedly arid hinterland. Nevertheless, a diverse flora is also preserved in the Crato Formation so perhaps the ‘missing’ harvestmen are only an artefact, and require another explanation.

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10

Crustacea of the Crato Formation

Günter Schweigert, David M. Martill and Mark Williams

Although crustaceans are often abundant and diverse in fossil Konservat Lagerstätten, their remains are remarkably rare in the Nova Olinda Member and, indeed, they are only abundant at a few localized horizons in the Crato Formation as a whole. Reasons for this rarity compared with other fossil Lagerstätten are unclear, but are probably related to salinity levels and substrate chemistry. By far the most abundant crustaceans are ostracods, which occur in rock-forming quantities in shales and fissile laminated muddy limestones at the transition between the Rio da Batateiras Formation and the Crato Formation at Cascata, near Crato. In these same deposits conchostracans occur with the ostracods at Cascata, although they are not as abundant, and in dark-coloured silty shales beneath a series of laminated limestones at Estiva, near Araporanga. Here they occur without ostracods, but in a sequence that is similar to, though slightly younger than, that at Cascata. Decapod crustaceans have only been reported from the laminites of the Nova Olinda Member in the Crato Formation.

Decapoda: *Beurlenia*, the 'sole' shrimp from the Crato Formation

The Crato Formation yields only a single species of decapod crustacean: *Beurlenia araripensis*. Originally described as a palaemonid shrimp by Martins-Neto and Mezzalira (1991), Maisey and Carvalho (1995) cast doubt on its palaemonid affinities, referring it to ?Palaemonidae. Palaemonids are a family within Caridea that are scarcely recorded from the fossil record. We here concur with Maisey and Carvalho (1995) and transfer *B. araripensis* to Familia *incertae sedis* within Caridea. Garassino and Jakobsen (2005) provide a comprehensive summary of most recently known caridean genera.

Systematic palaeontology

Crustacea

Decapoda Latreille, 1802

Caridea Burkenroad, 1963

Familia incertae sedis

Beurlenia Martins-Neto and Mezzalira, 1991

Beurlenia araripensis Martins-Neto and Mezzalira, 1991

Material: holotype no. CD-I-161 in coll. Desiree, Rio de Janeiro, Brazil; three specimens AMNH 44984, AMNH 44900 and AMNH 44991; two specimens SMNS 66124/1 SMNS 66124/2, and SMNS 66124/3; two well-preserved specimens without number in coll. MURJ.

The genus *Beurlenia* is named after Karl Beurlen (1901–1985), a German palaeontologist and specialist in decapod crustaceans, who lived and worked for many years in Brazil. *B. araripensis* appears to be rather rare in the Crato Formation, and so far it has only been recorded from the Nova Olinda Member in the region between Nova Olinda and Santana do Cariri. When it was described for the first time there was only a single specimen known, which did not permit study of all its morphological features with accuracy. *B. araripensis* reaches a length of a little less than 50 mm (Figure 10.1), and shows a short, dorsally finely serrate rostrum, which ventrally bears three teeth. The uropodal exopodites of the tail fan exhibit a diaeresis which was unrecognized in both the original description and the review by Maisey and Carvalho (1995). The first two pairs of pereiopods bear somewhat enlarged, pincer-like chelae. The posterior three pairs of pereiopods are achelate and almost equal in size. In the original description only the second pair of pereiopods was reconstructed as being chelate. The outline of these chelae points to a detritus-feeding lifestyle. Antennae and antennules are moderately long, compared with other taxa, and the stalked eyes are well-developed. The antennae reach about one and a half times the length of the body. Thus, these shrimps either lived in a shallow, littoral environment, or they inhabited algal mats close to the water surface.

Unfortunately, it is not possible to comment further on the environmental significance of this shrimp's occurrence in the Crato Formation because *Beurlenia* is an extinct, monospecific genus. In addition, Recent palaemonids are known from a wide range of distinctive habitats, ranging from the deep sea to freshwater lakes and rivers, while some species are adapted to brackish and even hypersaline conditions (e.g. Bayly, 1972). However, the undoubted lack of articulate setae on the telson as well as the presence of biflagellate instead of triflagellate antennules, and the

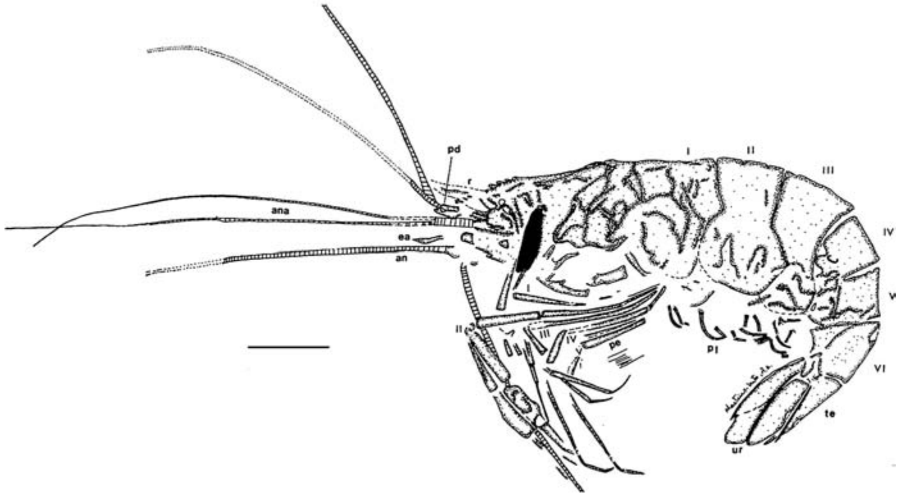

Fig. 10.1. Crato Formation decapod shrimp: *Beurlenia araripensis* Martins-Neto and Mezzalira, 1991; scale bar, 5 mm. Modified from Martins-Neto and Mezzalira, 1991.

absence of lateral spines at the tip of the telson, seriously question the previous attribution of *Beurlenia* to palaemonids (see also Maisey and Carvalho, 1995). The presence of a uropodal diaeresis hints at a basal position within Caridea, although this feature does occur in some other fossil and Recent palaemonids (e.g. *Palaemon antonellae* Garassino and Bravi, 2003, from the Lower Cretaceous of Italy). There seems to be a closer resemblance to carideans known from marine deposits of the Upper Jurassic, like *Hefriga* Münster, 1839 (see Förster, 1967).

The monospecific occurrence of a natant shrimp is mirrored in a number of other non-marine deposits from the Lower Cretaceous such as Las Hoyas and Montsec de Rúbies, Spain (Rabadà, 1990, 1993; Garassino, 1997). Similarly, the Eocene Green River Formation of the USA also yields a low-diversity decapod fauna (Feldmann *et al.*, 1981), as does the Miocene of Bohemia (Hoŭsa, 1956). In contrast, fully marine deposits, like the famous lithographic limestones in the Upper Jurassic of southern Germany (Schweigert and Garassino, 2003, 2004) or the platy limestones from the Upper Cretaceous of Lebanon (Glaessner, 1945; Garassino, 1994, 2001), exhibit highly diverse decapod faunas containing various groups of shrimps and lobsters. Also the Santana Formation overlying the Crato Formation yields somewhat more but only poorly preserved decapods (Martins-Neto and Mezzalira, 1991; Maisey and Carvalho, 1995; Martins-Neto, 2001).

Decapods can be fossilized in two different types of preservation: either as moults or as true-body fossils. Some of the studied specimens from the Crato Formation are filled with a fine, greyish material interpreted as phosphatized soft tissues. Hence these specimens do not represent moults. In those specimens thought to represent moults, post-mortem decay or transport preburial has led to the loss of some appendages.

Ostracoda, the seed shrimps, and Conchostraca, the clam shrimps

Ostracods, or seed shrimps, are minute (typically sub-millimetre) bivalved maxillopod crustaceans in which the valves of the carapace are composed of calcite and are shed at regular growth stages, usually six to eight, before adulthood. Conchostracans, or clam shrimps, are bivalved branchiopod crustaceans that retain all of the growth phases of the carapace. They add regular growth increments, producing a carapace that superficially resembles that of bivalve molluscs. The carapace of conchostracans is usually composed of an organic material that although not mineralized, is readily fossilized. Both groups of fossils are used widely for biostratigraphy and palaeoenvironmental analysis.

Ostracods occur in superabundance at several horizons in the Crato Formation, and are sometimes accompanied by smaller numbers of conchostracans. Diversity is low, with ostracods mainly represented by a few species of smooth-shelled cypridids. A number of studies of the ostracods of the Araripe Basin have been undertaken in an attempt to investigate their taxonomy, biostratigraphic utility and palaeoenvironmental signature (Silva, 1978a–c, 1979; Depeche *et al.*, 1990; Silva-Telles and Viana, 1990), while Bate (1971, 1972), Martill (1993) and Smith (2000) have reported on forms with soft tissues preserved in the Romualdo Member of the Santana Formation where they are associated with fossil fish.

The conchostracans from the Crato Formation (Figures 10.2a–c and h) have only been studied briefly. Martill (1993) figured examples from the Crato Formation of Barbalha and Cascata near Crato, whereas Carvalho and Viana (1993) described three taxa of *Cyzicus* in open nomenclature from Nova Olinda. Viana and Neumann (1999) also mentioned conchostracans in the Crato Formation at Nova Olinda. Elsewhere in the Araripe Basin succession conchostracans are found at a few horizons within the Missao Velha Formation and Ipubi Formation and in clays both above and below the Romualdo Member fish nodules, but not in the nodules themselves.

In some parts of the Araripe succession ostracods occur in such abundance as to constitute ostracod limestones, sometimes up to 30 cm thick. Examples occur near Barbalha in the Crato Formation and at most localities where the base of the Romualdo Member nodule horizon is exposed. In the Crato Formation ostracods are common in beds between the laminated limestones, but in general they do not occur in the Nova Olinda Member. At Cascata, thin laminated, organic-rich limestones marking the transition from the Rio da Batateiras Formation to the Crato Formation

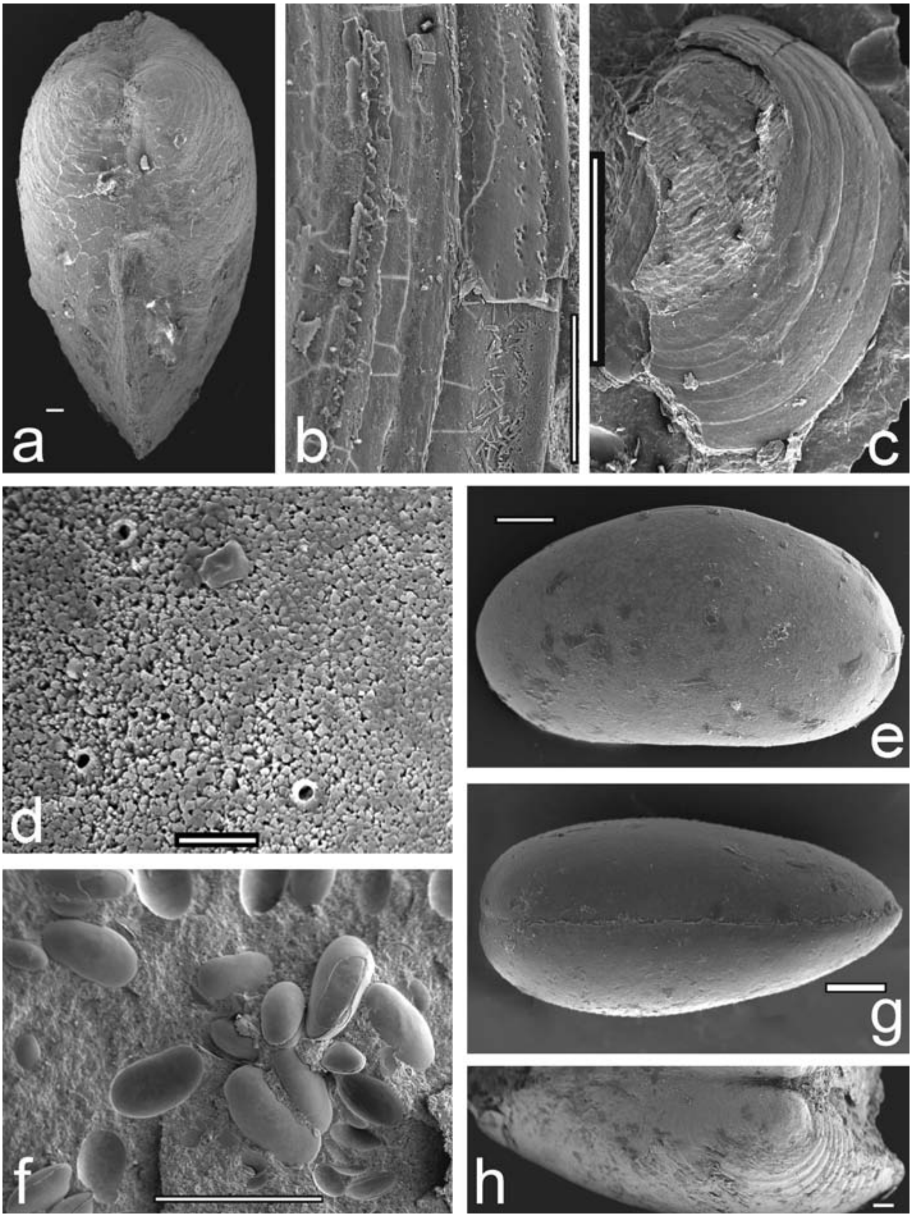

Fig. 10.2. Scanning electron micrographs of ostracods and conchostracans from the Rio da Bataterias/Crato Formation transition beds. (a, b, c, h) Conchostracan *Cyzicus* sp.; (d, e, f, g) cypridid ostracod; (a) *Cyzicus* sp. in umbonal view; (b) ornamentation on growth ring; (c) growth rings; (d) surface detail of cypridid ostracod showing pores for sensory setae; (e) cypridid ostracod in lateral and (g) ventral views; (f) probable mass-mortality assemblage comprising carapaces of several instars. Scale bars, 1 mm (a, c, f) 100 μm (b, e, g, h), 10 μm (d).

are rich in ostracods, which occur in thin laminae as ostracod-dense patches where they are often crushed, but usually articulated carapaces (Figure 10.2f; see also Chapter 3, Figure 3.4a).

The collective assemblage of named ostracod species given by Depeche *et al.* (1990, p. 297), Silva-Telles and Viana (1990, p. 311) and Carmo *et al.* (2004) for the Crato Formation comprises *Theriosynoecum silvai* (Silva, 1978), *Theriosynoecum munizi* (Silva, 1978a 1978b), *Theriosynoecum quadrinodosa* (Silva, 1978b), *Harbinia micropapillosa* (Bate, 1972), *Harbinia angulata angulata* (Krömmelbein and Weber, 1971), *Darwinula martinsi* Silva, 1978 and *Cyrpridea araripensis* Silva, 1978. A number of taxa remain in open nomenclature, including species of *Harbinia, Brasacypris, Candona* and *Zonocypris*(?), for which see Carmo *et al.* (2004).

Although Abreu (1922) notes the occurrence of 'estherias' in black shales near Crato, these supposed conchostracans were not figured, and it is possible that it was a reference to abundant ostracods.

Geological significance of the ostracods and conchostracans

Since their origins in the Early Ordovician ostracods have evolved to colonize most aquatic environments, from the ocean abyssal planes to damp leaf litter on forest floors. The Crato Formation is interpreted as a dominantly lacustrine deposit and the low-diversity ostracod assemblages have generally been regarded as non-marine (e.g. Carmo *et al.*, 2005), to include species that are both limnetic (e.g. *Candona* sp.; see Gobbo-Rodrigues *et al.*, 2005) and those that could tolerate a wider range of salinities including brackish water (e.g. *Darwinula martinsi*; see Syrio and Rios-Netto, 2002). There is, however, still no detailed assessment of the distribution of the ostracods in space and time throughout the Crato Formation, and the group is likely to provide a much clearer indication of palaeosalinity and environment if such a study is undertaken (e.g. see Keen, 1977).

Conchostracans typically inhabit ephemeral water bodies and are tolerant of fresh and brackish water. They have been reported from non-marine sediments elsewhere in the Cretaceous of Brazil (Cunha and Carvalho, 2002), but their occurrence in the Crato Formation is at best sporadic. For example, Viana (1992, figure 1) records only a single conchostracan at the level of her 'bed 3'. A detailed systematic analysis of the Crato Formation conchostracans is needed, not least because a number of authors (e.g. Carvalho and Viana, 1993; Aria and Carvalho, 1999) have noted similarities between the Lower Cretaceous conchostracan faunas of north-east Brazil and those of Australia and West Africa. Similarities with West African faunas are not surprising given the palaeogeographical proximity of these two regions at that time (e.g. Martill, 1993, figure 2.1).

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11

Insects of the Crato Formation

11.1 Introduction

Günter Bechly

Insects are by far the most diverse group of multicellular organisms on our planet. Of about 1,625,000 described species of prokaryotes, protoctists, fungi, plants and animals, more than 1 million is represented by arthropods, of which insects constitute the largest group with about 854,000 described species. The estimations of the number of still undescribed species, especially in the vanishing tropical rainforests, are ranging from 2 million to 80 million species! The most species-rich groups within insects are the holometabolous orders Coleoptera (beetles), Hymenoptera (ants, wasps and bees), Diptera (mosquitoes and flies) and Lepidoptera (moths and butterflies). Among the hemimetabolous orders, which lack a pupal stage in their ontogenetic development, the Hemiptera (aphids, scale insects, cicadas and bugs) are the largest group, while all other insect orders have much fewer species.

Even though relatively small animals, the extremely large number of individuals makes insects a very significant part of the total terrestrial biomass in many biotopes. For example, in tropical rainforests, the ants and termites have a higher total biomass than all the vertebrates combined.

Insects are not only diverse in terms of species number and number of individuals, but also in their astonishing anatomical and ecological variability. Insects populate nearly every available habitat on the planet, except for the open seas and the frozen polar regions. They live under water, on the water surface, in soil, in wood, in deserts and in forests, in arid and humid regions, in mountains and in caves, and they were the first organisms to conquer the skies.

Insects have developed appendages for all kinds of locomotion, from wings for flight, to burrowing legs for digging, strong hind legs for jumping, predatorial legs for catching prey, cursorial legs for running on the ground and climbing in vegetation, and specialized legs for walking on the water surface or for diving and swimming. Even subaqueous jet propulsion is found in some dragonfly larvae.

They have developed an equal diversity of mouthparts that allows nearly any kind of feeding, from chewing mouthparts for herbivory and carnivory or omnivory, licking mouth parts for feeding on nectar and pollen, to piercing mouth parts for sucking plant juices or the blood of other animals.

Insects are also masters of camouflage and no other group of organisms has developed so many and striking cases of mimesis and mimicry. Even communication with sounds and voices is not the exclusive domain of vertebrates, with stridulation independently developed in unrelated insect groups from cicadas (Hemiptera) and orthopterans (Ensifera and Caelifera) to longhorn beetles (Cerambycidae). There is even an aquatic larva, the Japanese relict dragonfly *Epiophlebia superstes*, that can utter a sound.

Finally, some insect groups, especially among the termites, ants and bees, alongside humans, have developed eusocial states with distinct castes and tremendous 'cultural achievements'. These include war campaigns, mass defensive attacks, enslavement of other species, the cultivation of fungi, animal husbandry, and construction of buildings that are a million times bigger than themselves and made comfortable with sophisticated climatization systems. All of this was achieved in animals with tiny brains and their skeletons on the outside. Insects are truly remarkable animals.

Insect evolution

The enormous diversity and evolutionary success of the insects can perhaps be attributed to three major evolutionary innovations: moving from water to dry land, development of wings and flight and an adaptive radiation in co-evolution with flowering plants.

Contrary to earlier theories that insects are most closely related to terrestrial myriapods, new molecular and ontogenetic evidence suggests that insects are *just* terrestrial crustaceans of remipedian and malacostracan affinity (Richter, 2002; Fanenbruck *et al.*, 2004). Insects are thus derived from marine crustacean-like arthropods that already had an exoskeleton, walking limbs, compound eyes and sensory antennae. These features were excellent pre-adaptations for the first evolutionary leap, the conquest of the land in the late Silurian and Lower Devonian (about 430 mya). The oldest known insects were small primarily wingless forms and stem from this era, like the famous fossil springtail *Rhyniella praecursor* from the Devonian Rhynie cherts of Scotland.

While adapting to a terrestrial lifestyle, the number of legs was reduced to just three pairs, the number of antennae reduced to a single pair, and the mode of reproduction changed from external insemination with liquid sperm under water, to an external insemination with terrestrial deposition of spermatophores. The first terrestrial insect ancestors were probably very small animals capable of breathing through their skin in moist habitats. This method of gaseous exchange paved the way for the later evolutionary development of sophisticated cuticular invaginations (tracheae) as respiratory organs.

The second major evolutionary innovation occurred during the Lower Carboniferous (or perhaps in the Late Devonian), when insects developed wings and conquered the air. This achievement led to the first radiation and increase in diversity and population density of insects, although the biggest evolutionary leap was yet to come. Among the numerous advantages of flight is the ability to escape easily from predators, a greater chance to locate food, suitable habitats or sexual mates and an improved panmixia of the gene pool. Correlated with the evolution of insect flight, some spiders developed the ability to construct complex webs to exploit this new resource of airborne protein. The oldest fossil records of pterygote insects stem from the lower Namurian (about 324 mya) of Germany (*Delitzschala bitterfeldensis* Brauckmann and Schneider, 1996) and the Czech Republic (unnamed Archaeoptera; Prokop *et al.*, 2005). Wings developed either from mobile lateral thoracic gills of aquatic insect larvae, similar to the abdominal gills of modern mayfly larvae, or from originally immobile lateral expansions of the thoracic tergae, known as paranota. Both of these conflicting hypotheses are supported by substantial neontological and palaeontological evidence, so that a final decision is not possible with the current state of knowledge. During the Carboniferous and Permian some winged insects reached tremendous sizes with wing spans of up to 60–75 cm. This era of flying giants ended in the Triassic, perhaps correlating with the appearance of pterosaurs as the first active flying vertebrates to feed on airborne insects. Due to the successive evolution of different flying vertebrates (pterosaurs, birds and bats) it appears that no giant flying insects ever evolved again. Of course, the great Permian mass extinction might also have contributed to the decline of the giant pterygotes.

The third and final great leap in evolution is the remarkable co-evolution of flowering between the flowering plants and some insect groups as their pollinators. This co-evolution started at least as early as the Early Cretaceous, thus exactly at the time that the Crato Formation limestones were deposited. Early modes of this symbiosis were probably rather crude, perhaps similar to the way modern tropical water lilies, *Nymphaea* spp., are pollinated by certain beetles that became enclosed within the flowers at night and literally ransack their floral "prison" in a futile attempt to escape. Later, more sophisticated mechanisms evolved involving highly complex flower organs and specialized mouth parts of their pollinators. In many cases these plants became dependent on a single insect species for pollination, which themselves solely depend on one plant species as a source of food. The most highly evolved mechanisms are found in orchids, which ‘betray’ their pollinators with flowers that mimic female insects in shape, colour, setation and even the scent of their sexual pheromones. The co-evolution of plants and insects led to the biggest radiation in the evolution of life, which is not only documented by the enormous number of species of flowering plants compared to that of gymnosperms, but also by the fact that precisely those insect orders that are associated with angiosperms belong to the groups with the highest number of species (see above).

This co-evolution seems to have reached a maximum in the beginning of the Caenozoic era, as nearly all fossil insects from Eocene amber more or less equal their Recent relatives, and can often be classified in modern genera. The only significant changes in insect evolution during the Tertiary have been major shifts of biogeographical ranges due to dramatic changes of the climate and vegetation. For example, there are numerous insects found in Baltic amber that are today restricted to tropical forests in Latin America, Africa or Oceania.

The destruction of these tropical forests at an alarming rate of nearly 10,000 m^2/s is the cause a dramatic human-made mass extinction event the likes of which this planet has not seen before. This could even represent the final major event in the evolution of insect diversity, since it is calculated that around 140 species are disappear every single day from our planet.

Insect phylogeny and palaeoentomology

A revolution in insect systematics and phylogenetic research was instigated by German entomologist Willi Hennig (1969), the founder of modern phylogenetic systematics. Numerous subsequent cladistic analyses have greatly expanded our knowledge of the evolutionary relationships of the various insect higher taxa. Especially important has been the rise of molecular research which has led to new insights (some highly surprising) into our understanding of insect interrelationships, for example concerning the sister group of Hexapoda or the relationships of the recently discovered new living insect order Mantophasmatodea. Excellent summaries of the current knowledge of insect phylogeny have been provided by Kristensen (1995) and Grimaldi (2001), and particularly important is the seminal work by Grimaldi and Engel (2005). The first comprehensive treatment of fossil insects was provided by Handlirsch (1906–1908), followed by Rohdendorf (1969; translated into English in 1991), Hennig (1969), Carpenter (1992) and Rasnitsyn and Quicke (2002), and again important analyses of fossil insects are included in Grimaldi and Engel (2005).

Scientific importance of the Crato insects

The limestone quarries of the Crato Formation represent a particularly interesting fossil locality, because not only were they deposited at a time when plant/insect co-evolution was in its early stages, but also these limestones yield both plant and insect fossils in the same strata. This importance is further increased by the fortunate circumstance that many tens of thousands of fossils have been discovered already, representing most orders of insects, and generally with excellent preservation of delicate details, sometimes even of soft tissues or colour pattern (see Chapter 7).

Important collections of Crato Formation insects can be studied in the following institutions:

- Brazil: Sociedad Brasileira de Paleoartropodologia (RGMN) in Ribeirão Preto/São Paulo, Museu de Zoologia in São Paulo; Museu do Paleontologia Santana do Cariri; Centro de Pesquisas Paleontologicas da Chapada do Araripe in Crato.
- USA: American Museum of Natural History (AMNH) in New York.
- Japan: Kitakyushu Museum of Natural History & Human History (KMINH) in Kitakyushu, Tokyo University/National Science Museum (NSMT) in Tokyo, and collection Masayuki Murata (MURJ) in Kyoto (deposited partly at KMNH).
- France: Museum National d'Histoire Naturelle (MNHN) in Paris.
- United Kingdom: Geology Department of the University of Leicester (LEIUG), and Natural History Museum (NHM) in London.
- Germany: Museum für Naturkunde in Berlin (MNB), Bayerische Staatssammlung für Paläontologie und Historische Geologie *BSPGM* in Munich, Naturmuseum Senckenberg (SMF) in Frankfurt, Staatliches Museum für Naturkunde Karlsruhe (SMNK), Staatliches Museum für Naturkunde Stuttgart (SMNS), Jura-Museum Eichstätt (JME), and ms-fossil (MSF) in Sulzbachtal.
- Italy: Museo Civico di Storia Naturale (MCSNM) in Milan.

Until recently there were hardly any fossil insects known from this crucial period of Earth's history, such that Willi Hennig (1969) even commented "Einer der beklagenswertesten Mängel in unseren Kenntnissen der Stammesgeschichte der Insekten ist das fast völlige Fehlen von Fossilfunden aus der Kreide" ["One of the most unfortunate gaps in our knowledge of insect phylogeny is the nearly complete lack of fossils from the Cretaceous"]. Since then numerous localities yielding Cretaceous insects have been discovered, for example in Southern England (Weald), Spain (Sierra de Montsech and Las Hoyas), Commonwealth of Independent States (Magadan, South Kasakhstan and Transbaikals), Western Mongolia, China (Gansu, Hebei, Shandong, Liaoning and Inner Mongolia), Botswana (Orapa), South-west Egypt (Abu Ras), the USA (Fox Hill, Colorado), Australia (Koonwarra, Victoria) and various Cretaceous amber sites from Lebanon, Siberia (Taymyr), Myanmar (Burma), Spain (Alava), France (Besonnais), Canada (Cedar Lake and Medicine

Hat) and the USA (Alaska and New Jersey). These localities provide an exciting opportunity for interesting comparisons of the Cretaceous insect faunas in both the New and Old Worlds, and the southern (Gondwana) and northern (Laurasia) hemispheres. However, none of these localities can match the Crato Formation in the sheer number of fossils, their diversity and their quality of preservation. Consequently, the Crato Formation is considered by palaeoentomologists as one of the most important Mesozoic localities of all for fossil insects.

The first record of insects from the Crato Formation was a mayfly nymph discussed by Costa-Lima (1950) and described by Demoulin (1955). Since then, numerous contributions by various specialists followed and have been summarized by Brito (1984), Schlüter (1990), Grimaldi (1990, 1991), Martill (1993), Bechly (1998a–c), Bechly *et al.* (2001a), Martins-Neto (1991a–d, 1992d, 1996b, 2005a, 2005b), and Grimaldi and Engel (2005).

The missing groups of insects

The number of arthropod taxa from the Crato Formation is impressive: Scorpiones, Uropygi, Amplypygi, Araneae (Orthognatha and Labidognatha), Solifugae, Acari, Ostracoda, Conchostraca, Decapoda and Chilopoda have all been reported from among the non-hexapods. Even a brief glance at this list demonstrates an unusual mix of aquatic and terrestrial forms. In the Hexapoda, the insects, the list is even longer: Diplura, Zygentoma, Ephemeroptera, Odonata, Dermaptera, Mantodea, Blattaria (including Umenocoleoidea), Isoptera, Chresmododea, Phasmatodea, Orthoptera (Ensifera and Caelifera), 'Auchenorrhyncha' (Cicadomorpha and Fulgoromorpha), Coleorrhyncha, Heteroptera, Megaloptera, Raphidioptera, Neuroptera (Planipennia), Coleoptera, Hymenoptera, Mecoptera, Diptera, Trichoptera and Lepidoptera. The most frequent groups are Orthoptera, Blattaria, Hemiptera and Ephemeroptera (larvae of the type *Protoligoneuria*), which together represent more than 80% of the fossil arthropod material based on a study of 3,651 fossil arthropods from the Crato Formation that had not been selected in preference of certain taxa (Bechly, 1998c).

But while the taxa present in the formation suggest an unusual taphocoenosis, the absence of certain groups is also perplexing. Completely missing (so far) are most of the tiny, ground-dwelling or ectoparasitic (often wingless) insect orders (Collembola, Protura, Archaeognatha, Zoraptera, Embioptera, Psocoptera, 'Mallophaga', Thysanoptera, Sternorrhyncha, Anoplura, Siphonaptera and Strepsiptera), but their absence can be relatively easily explained by their cryptic lifestyle and their small size, which makes their fossilization unlikely (however, Martill and Davis (1998) reported putative eggs of lice or mites in a fossil feather from this locality). The same is also true for the absence of the smaller arachnid groups Ricinulei, Palpigradi and Acari (only a single specimen is known), and the myriapod groups Pauropoda, Symphyla and Diplopoda. The rarity of centipedes (four specimens), and of Diplura (two specimens) and Zygentoma (three specimens) is propably due to the same reasons. The complete absence of terrestrial Isopoda and of Opiliones is harder to explain. The absence of Mantophasmatodea may be due to the biogeographical absence of this order from South America, but on the other hand this appears unlikely considering the Recent occurrence in southern Africa and Baltic amber. Maybe they have just been overlooked or misidentified. The absence of Grylloblattodea is easily explained by their ecology, which confines them to mountainous cool and humid areas of the Northern Hemisphere. The extreme rarity of Mecoptera, of which only two specimens have been discovered, can similarly be attributed to their preference for moist habitats. The absence of Macrolepidoptera and especially of diurnal butterflies (Papilionoidea) is presumably due to the late occurrence of these groups in the evolution of insects (the oldest known fossils are from the Paleocene Fur Formation of Denmark). However, the complete absence of any Plecoptera (adults and larvae) is odd and cannot easily be explained, especially considering the striking abundance of both adults and larvae of nearly all other groups of aquatic insects, including clearly rheophilic ephemeropteran and odonatan families that usually co-exist with several species of plecopterans in Recent Neotropical habitats.

A further ‘missing taxon’ is Gerridae. These water striders are present in Recent South America so their absence may be due to a major biogeographical shift in their distribution since the Cretaceous. Considering the relatively frequent occurrence of adult Trichoptera, the complete absence of larval specimens and the extreme rarity of aquatic larvae of Diptera and Coleoptera is also unusual, because the aquatic larvae of Heteroptera, Odonata and Ephemeroptera are found in abundance. Until recently the absence of the odonate suborder ‘Anisozygoptera’, that represents a paraphyletic grade in the stem group of Anisoptera and is abundant in nearly all other Mesozoic sites with fossil dragonflies, was perplexing. However, recently two specimens of Stenophlebiidae have been discovered from the Crato Formation and are described below. Such ‘late’ discoveries clearly demonstrate a continued need for collecting. Finally, a surprising phenomenon is the presence of several species of Raphidioptera in the Crato Formation. It is surprising because Recent snake-flies are confined to the Northern Hemisphere. Thus a plausible explanation is required to explain their extinction in South America and determine when it happened.

Some taxonomic problems

During work on this chapter, the contributors discovered that several scientific publications on Crato Formation insects do not comply with the common international standards of scientific work, and often fail to satisfy the criteria of the International Rules of Zoological Nomenclature (ICZN). Numerous taxa have been established with inadequate diagnoses, creating *nomina dubia*, and many are in diploma and PhD theses, and technically are invalid, but nevertheless cited by subsequent workers. Many species names have been established in conference proceedings abstracts with the creation of *nomina nuda* and on several occasions different spellings are used from the original description by the same author. There are many incorrect citations of authorship and year of publication, as well several taxa erected on holotypes in private collections. The result is a plethora of dubiously established species and considerable taxonomic confusion.

11.2 Apterygota: primarily wingless insects

Arnold H. Staniczek and Günter Bechly

There are several small-taxa at the base of the Hexapoda lacking wings that formerly were referred to as 'Apterygota', until Hennig (1953) recognized its paraphyly with respect to the winged insects, the Pterygota. Usually five Recent higher taxa are recognized among apterygotes: Collembola (springtails), Protura, Diplura, Archaeognatha (bristletails) and Zygentoma (silverfish and firebrats), the former three often united as the Entognatha, as their mouthparts are enclosed within a gnathal pouch. Recently it has been proposed that Diplura are more closely related to the insects than to Protura and Collembola (Bitsch and Bitsch, 2000). It is generally accepted that Archaeognatha and Zygentoma have closer phylogenetic affinities to the Pterygota than to the entognathous taxa. All of these taxa, however, share a number of plesiomorphic characters such as the retention of abdominal leglets and moulting even in the adult stage.

In the Crato Formation, so far only one species each of Diplura (two specimens) and Zygentoma (two specimens) have been discovered (Figure 11.1; Plates 7a and b). The other orders are certainly to be expected in the Mesozoic of South America as well, but probably have a very low preservation potential due to a combination of their delicate anatomy, tiny size and cryptic lifestyle as soil-dwelling organisms.

Order Diplura: diplurans

Diplura is a globally distributed taxon comprising about 850 Recent species. They are generally classified into two different lineages, the Campodeomorpha (Rhabdura) and Japygomorpha (Dicellurata), which have a rather different appearance. Campodeomorph diplurans have long slender legs that enable fast movement and high agility, whereas japygomorphs are better adapted for a life within soil

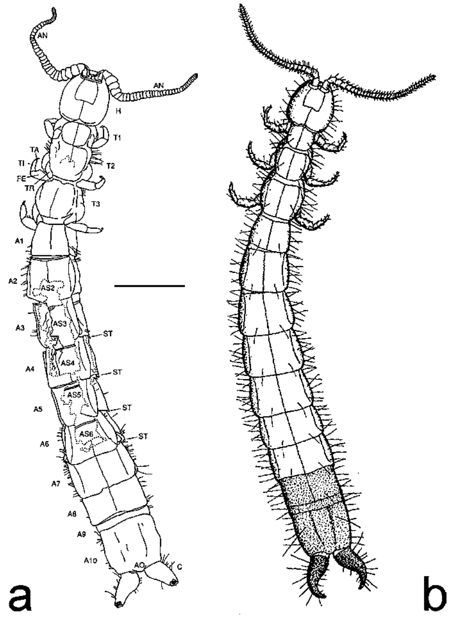

Fig. 11.1. Crato Formation dipluran: *Ferrojapyx vivax* Wilson and Martill, 2001; (a) interpretative diagram of holotype SMNS 64276; (b) restoration of the animal in life. After Wilson and Martill (2001); reproduced with kind permission of the Palaeontological Association.

interstices. While the campodeomorphs have filiform cerci consisting of many segments, the cerci of japygomorphs are transformed into unsegmented forceps. Both groups, however, are cryptozoic and confined to soil. Campodeiform diplurans are mostly omnivorous or herbivorous animals, which feed on a variety of plant matter, often rotten leaves. The japygomorphs are predominantly predators and feed on other soil-dwelling arthropods such as other entognathous insects, myriapods and mites. They generally catch their prey by grasping it with the abdominal forceps. All diplurans are small and soft-bodied hexapods of whitish colour that generally only reach a body size of a few millimetres, but some japygomorphs may achieve a larger body size, of up to 6 cm. The Campodeomorpha have long filiform antennae with up to 70 segments. As in all primarily apterous hexapods, all antennal segments are equipped with intrinsic muscles. The antennae of japygomorphs are comparably short and stout, and in some they even resemble a telescope with retractable segments.

The head of diplurans is dorsoventrally flattened and bears prognathous mouthparts that lie within a single gnathal pouch. The internal head skeleton, the tentorium, is lacking. The maxillae are specifically interlocked with the lateral lobes of the hypopharynx and the mandible of campodeomorph diplurans bears a mobile lobe, the prostheca. All Recent diplurans lack compound eyes, but the entire body is equipped with a variety of sensory hairs. Their abdomen is composed of 10 segments, the anterior seven bearing paired leglets and often also ventral eversible vesicles that are actively used to absorb water.

Systematics and phylogeny

The phylogenetic affinities of the Diplura remain controversial, and although their monophyly has been challenged recently, the unique interlocking of the maxillae with the hypopharyngeal superlinguae, uniquely arranged leg muscles and leg pivots, the modified position of the gonopore, and the reduced eyes, mandibular molar and tentorium clearly demonstrate their monophyly (Kristensen, 1998). However, the sister group of Diplura remains debatable. Most recent authors unite Diplura and Ellipura (Collembola+Protura) in the Entognatha because the mouthparts of entognatheous hexapods lie with a gnathal pouch formed by the lateral head capsule (Hennig, 1953). On the other hand, some authors interpret filamentous cerci, an epimorphous development (the larva hatches with the final number of abdominal segments) and the 9+9+2 axonem sperm pattern as derived characters of Diplura+Insecta, the so-called Cercophora. These authors consequently assume a parallel development of entognatheous mouthparts in Diplura and Ellipura (e.g. Koch, 1997).

The extant Diplura are divided into the Rhabdura (Campodeomorpha) with two superfamilies, and the Dicellurata (Japygomorpha) with only one superfamily. The Campodeoidea comprise about 300 species and include the Procampodeidae and the Campodeidae. The Projapygoidea include only some 20 species in three families; among these the Projapygidae and Anajapygidae. The Dicellurata are represented by the superfamily Japygoidea that includes five families, among these the Japygidae, Parajapygidae and Dinjapygidae.

Evolution

Judging from their phylogenetic position as basal hexapods Diplura must have already originated by the Early Devonian, but unfortunately there are no fossils from this period that could shed light on their early evolution. The enigmatic *Testajapyx thomasi* from the Upper Carboniferous of Mazon Creek of Illinois (Kukalová-Peck, 1987) bears well-developed compound eyes, long maxillary and labial palps, and multi-articulated abdominal leglets. Its abdomen bears the typical forceps of the Rhabdura. If its description and assignment is correct, the reduction of eyes, palps and abdominal leglets in Diplura has to have been achieved independently within Rhabdura and Dicellurata.

Fossil record

The fossil record of Diplura is extremely poor. Except for the controversial *Testajapyx thomasi* there is only one Mesozoic record of Japygoidea from the Lower Cretaceous of Brazil (Wilson and Martill, 2001). A few other diplurans are recorded from Eocene Baltic amber (Weitschat and Wichard, 1998), the Pliocene of Arizona (Pierce, 1950, 1951), and from Miocene Dominican amber (Grimaldi and Engel, 2005). Unfortunately, the scarcity of fossil diplurans does not allow any substantial conclusions regarding their palaeobiology.

Crato Formation fossils

Ferrojapyx vivax (Plate 7b; Figure 11.1) is the sole japygoid described from the Crato Formation (Wilson and Martill, 2001). Due to its mode of preservation, insufficient features of *F. vivax* can be seen, preventing its attribution to any of the Recent families of Japygoidea.

Japygoidea

Family *incertae sedis*

Ferrojapyx vivax Wilson & Martill, 2001

Material: holotype SMNS 64276 (Plate 7b; Figure 11.1); specimen MB.1999.9 MB. J.2017 at MNB.

Diagnosis: body length 17 mm; antennae with 40 segments; abdominal tergites 1–8 with median suture, abdominal tergite 9 significantly shorter, and abdominal tergite 10 significantly longer with pair of paramedian grooves; abdominal styli conical; forcipate cerci with similar arms, each with a curved inner margin and lacking obvious denticles.

Order Zygentoma: silverfishes and firebrats

The Zygentoma comprise only about 470 Recent species, all of which are small, ranging between 1.5 and 2 mm in body length. Their general appearance is rather uniform, with a dorsovenrally flattened wingless body, long antennae and three long terminal appendages. Some species, such as the well-known silverfish *Lepisma saccharina* and the firebrat *Thermobia domestica*, are cosmopolitan. Others, such as the relic *Tricholepidion gertschi* from California, have a very restricted distribution. It is generally accepted that the Zygentoma form the sister group of pterygote insects. They are herbivorous, feeding mainly on algae and fungi. Their body is mostly covered with scales and the head bears orthognathous mouthparts with dicondylous mandibles. Compound eyes and ocelli are largely reduced or entirely lacking and the abdomen bears styli and coxal vesicles on different abdominal segments.

Systematics and phylogeny

The Zygentoma are often considered to be monophyletic, although *T. gertschi* retains many plesiomorphic features not otherwise found in the remaining taxa. Putative shared derived characters such as a special mode of cleavage (but not confirmed in *Tricholepidion*), a special mode of sperm deposit, and a unique specialized articulation between the cercal base and tergum X however support its monophyly (Koch, 2003). Other characters, including the loose dicondylous mandible, the loss of hypopharyngeal superlinguae, and the fused tentorium are either groundplan characters of insects, reductions or are absent in the basal taxon *Tricholepidion* (Staniczek, 2000).

Zygentoma are classified into five families; Lepidothrichidae, Nicoletiidae, Protrinemuridae, Maindroniidae and Lepismatidae. The Zygentoma generally retain an arrangement of mandibular musculature similar to that seen in primitive Pterygota. Additionally, *T. gertschi* retains a zygomatic mandibular muscle. Anterior and posterior tentorial arms are generally separated from each other, but in the Maindroniidae there is a fused tentorium, as in Pterygota. If the Zygentoma prove to be monophyletic, the Lepidothrichidae would be the sister group of the remaining Zygentoma. In this case, the changes in mandibular musculature and tentorium would have occurred twice within the Zygentoma and in the Pterygota, respectively.

Evolution

The Recent relic silverfish *T. gertschi* (Wygodzinsky, 1961) shows that many of the characters generally attributed to the Zygentoma evolved within the order, but their scarce fossil record unfortunately provides few clues to the early events in their evolution. As in Diplura, the meagre fossil record allows few conclusions regarding the palaeobiology of Zygentoma.

Fossil record

Except for a single Mesozoic record (Sturm, 1998), the Zygentoma are known mostly from Tertiary amber (Mendes, 1997a, 1998a; Sturm and Mendes, 1998; Weitschat and Wichard, 1998; Sturm and Machida, 2001). Even fossil Lepidothrichidae are known only from Baltic amber (Silvestri, 1912), but clearly the splitting of the different higher taxa within Zygentoma had already occurred by the Caenozoic. There are some other early records of insects that have been tentatively assigned to Zygentoma, but their state of preservation does not allow a definite assignment (Shear *et al.*, 1984; Kukalová-Peck, 1987; Kluge, 1996).

Crato fossils

The first records of Zygentoma from the Crato Formation are those of Bechly (1998a). Two specimens of Lepismatidae were described by Sturm (1998). Since then, a further undescribed specimen (Plate 7a) was found in the Stuttgart (SMNS) collection. Due to their relatively poor state of preservation, neither a determination of the sex, nor a formal taxonomic description as a new species, has been possible. Consequently, these specimens have only been determined as "Lepismatidae gen. spec. 'Araripe'" by Sturm (1998).

Lepismatidae

Lepismatidae gen. spec. 'Araripe' Sturm, 1998

Material: no. B 99 at SMF; no 1998 III/4 at BSPGM; and no. SMNS 66535 (Plate a). A fourth specimen without number from AMNH was figured by Grimaldi and Engel (2005: 152, figure 5.6).

Diagnosis: body 10.5–14 mm long and 3–4 mm wide; head orthognathous; filiform antennae 10.5–13.5 mm long; filiform cerci (12–18 mm long, the only 8.8-mm-long cerci in specimen B 99 are obviously broken off) and terminal filum (13–21 mm long), all provided with setae; wingless; body robust; legs stout with flattened, broad and oval-shaped coxae.

11.3 Persisting-type stem group Ephemeroptera

Rainer Willmann

Organisms do not evolve at equal rates. While many Recent taxa are of entirely modern appearance, others are plesiomorphic in many respects, and in some insects plesiomorphic structures determine their body plan. This is not necessarily related to the age of the respective taxa, but of course some taxa, be it species or large species groups, have become separated from their sister group only recently, while others are very old and have changed little, even over several tens of millions of years. In both cases the latter types of organism have been called living fossils, a term introduced by Charles Darwin. However, such types have lived at any time in the history of life. As the term living fossil cannot well be applied to relatively plesiomorphic fossil species or species groups, the term persisting type, first introduced by Huxley, may be applied. Such types belonging to ephemeropteroid insects in its widest sense were in existence in the Lower Cretaceous of Brazil (Figures 11.2 and 11.3; Plates 7c–h).

Numerous mayflies of the crown group Ephemeroptera (about 3,100 described Recent species) have been described from Triassic, Jurassic, Cretaceous and Cenozoic strata including the Crato Formation (see review by McCafferty, 1990). No

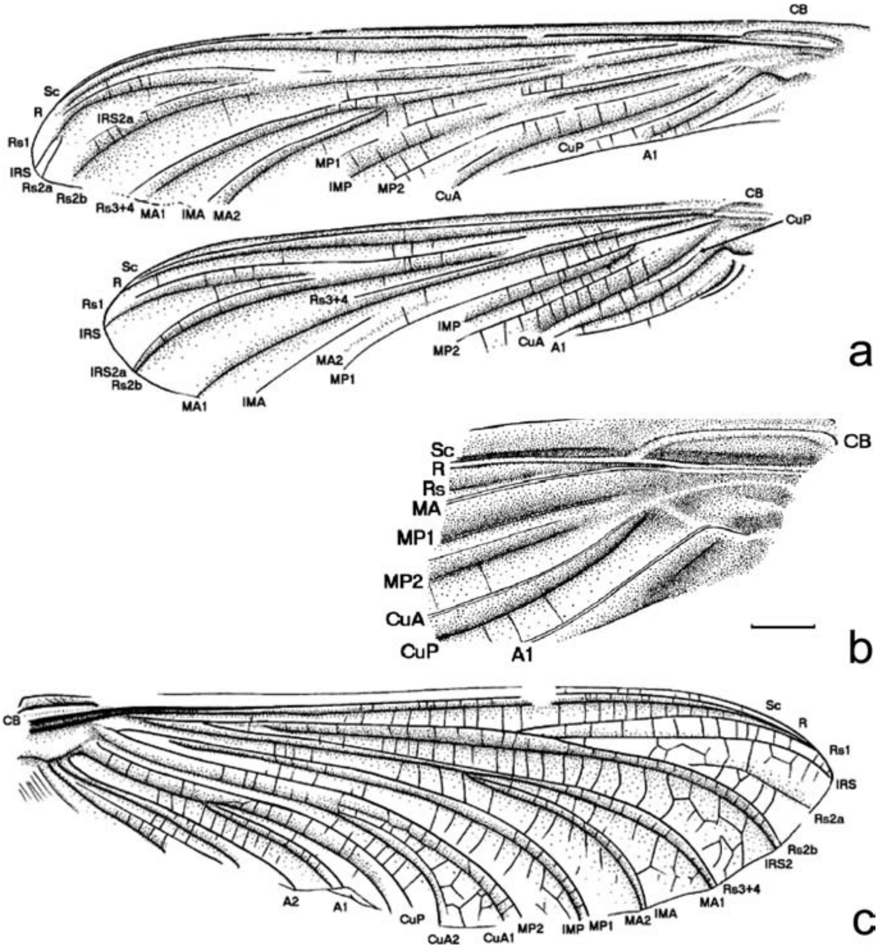

Fig. 11.2. Stem group Ephemeroptera; *Cretereisma* spp. wing venation of holotypes: (a) *Cretereisma antiqua* sp. nov., SMNS 66546, left fore- and hind wings (right wings of the living animal); (b) same specimen as (a), showing basis of left forewing (right wing of the living animal) with additional structures as observed in the right wing; (c) *Cretereisma schwickertorum*, SMNS 66598. Right forewing (left forewing of the living animal). Note the costal brace which does not reach the anterior wing margin. Both original specimens are seen in ventral view and convex veins are preserved as concave and vice versa. Drawings by R. Willmann.

such form is known from the Palaeozoic. On the other hand, numerous stem group representatives of Ephemeroptera are known from the Carboniferous and Permian, and it has been assumed that most of them, and all of those with more than seven pairs of nymphal abdominal gills, were extinct by the end of the Permian.

During a meeting of the fossil-insects network of the European Scientific Foundation in Portsmouth in 1998, David Martill exhibited specimens of a nymph from

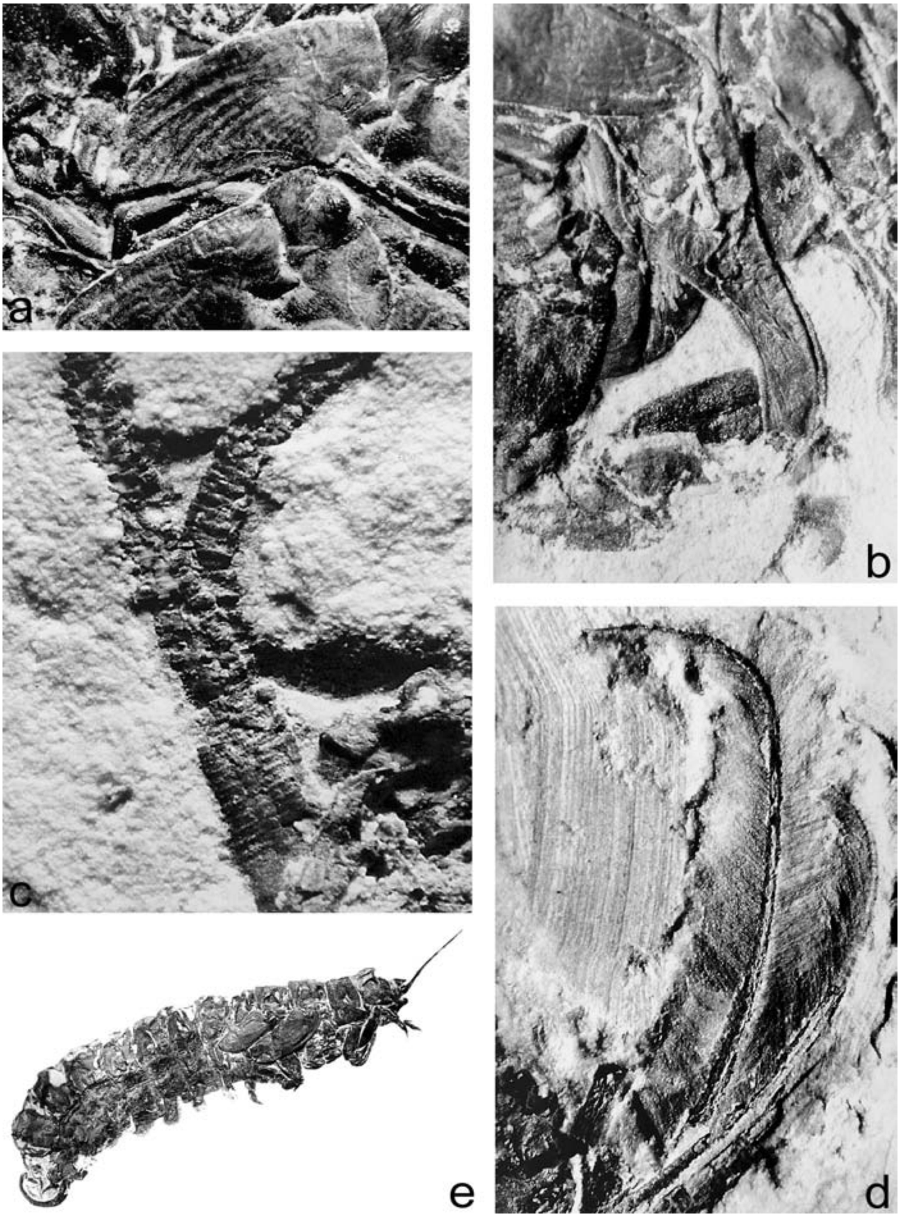

Fig. 11.3. Stem group Ephemeroptera; *Cretereisma* sp. nov., anatomical details of nymphs. (a) Forewing pad and proximal part of hind wing pad, SMNS 66673. (b) First abdominal left gill plate overlying femur-tibia-joint of hind leg. Its basal area is overlain by the tip of the hind wing pad. The dark area near the left margin is the posterior part of the coxa, SMNS 66673. (c) Bases of terminal appendages, SMNS 66601. (d) Left circus (on the right) and paracercus, showing setation, SMNS 66604. (e) *Cretereisma* sp., nymph, no. 512 MURJ. Photographs (a)–(d) by R. Willmann, photograph (e) by G. Bechly.

the Crato Beds that appeared to belong in mayflies but clearly not into any taxon previously known from the late Mesozoic. Comparison with stem group representatives of mayflies showed that the new finds belong here. Later, Günter Bechly obtained specimens of large adult mayflies that showed characters that were as plesiomorphic as those of the nymphs. I completely agree with Bechly *et al.* (2001a), who discussed and figured beautiful larval and adult specimens as ancestral mayflies similar to Protereismatidae, that both nymphs and adults belong to the same archaic taxon. These specimens are described below.

Systematics

Including ephemeroid-like insects, the mayflies have been classified into the crown group and the stem group representatives. An early example is Handlirsch (1908: 1292 and plate LX), who distinguished between a subclass Ephemeroidea including the Plectoptera (= Agnatha), and the Protephemeroidea. Crampton (1938: 170) wrote that the Ephemerida were probably derived from the Protephemerida, and that the Ephemerida and Protephemerida might be grouped into a superorder called the Panephemeroptera or Ephemeropteria. The names Protephemeroptera and Protephemerida refer to the Carboniferous *Triplosoba pulchella* (Brongniart, 1893), which is, however, possibly not a stem group representative of the mayflies (Willmann, 1999). Therefore, one might abandon the names Panephemeroptera or Ephemeria. Lauterbach (1973), however, proposed to call a crown group and the entirety of its stem group representatives with the prefix Pan-, and accordingly, under a phylogenetic view, the name Panephemerida would still be both useful and acceptable. Numerous stem group representatives of the mayflies have been described since the discovery of *Triplosoba*.

Categorical ranks have varied from subclass (Ephemeroidea *sensu* Handlirsch, 1908) through superorder (Ephemeroidea *sensu* Weber, 1933), cohorts (Ephemeriformes; Rohdendorf, 1977) to order (Ephemeroptera), suborder and infraorder. The latter two ranks have been applied to the crown group mayflies, or Euplectoptera, which were, however, consistently called Ephemeroptera, Ephemerida or Plectoptera when only Recent species were considered. Carpenter (1992) called the mayflies *sensu latissimo* (including *Triplosoba*) Ephemeroptera and assigned them ordinal rank. Categorical ranks will not be used here because of the inapplicability in a phylogenetic context.

Several taxon names for stem group representatives do not refer to monophyla and should be abandoned (for Permoplectoptera, see remark of Illies, 1968: 6). Willmann (2006) reviewed the phylogenetic relationships among the early mayflies *sensu lato* and systematized the stem group representatives, including *Cretereisma*, as follows, attempting to preserve established names (synonyms are given only as examples).

1. Panephemeroptera Crampton (= Ephemerata Boudreaux; = Ephemeridea Rasnitsyn, 2002 (in Rasnitsyn and Quicke, 2002), = Ephemeroptera *sensu* Tshernova, 1962, Carpenter, 1992 and others, = Ephemerida *sensu* Kukalová-Peck, 1985)

? 1.1 *Triplosoba* ('Protephemeroptera')
1.2.1 *Bojophlebia*
1.2.2 Ephemerontoida (= Ephemerida *sensu* Boudreaux, 1979: 271)
1.2.2.1 *Syntonoptera*
1.2.2.2 Ephemeronta
1.2.2.2.1 *Lithoneura*
1.2.2.2.2 Reticulata (= Plectoptera *sensu* Tshernova, 1962, 1970, = Ephemerida *sensu* Kluge and Sinitshenkova, 2002 (in Rasnitsyn and Quicke, 2002) and others, = Ephemeroptera *sensu* Grimaldi and Engel, 2005)
1.2.2.2.2.1 *Protereisma* (+*Misthodotes*?)
1.2.2.2.2.2 Heptabranchia
1.2.2.2.2.2.1 *Cretereisma*
1.2.2.2.2.2.2 n.n.
1.2.2.2.2.2.2.1 *Litophlebia*
1.2.2.2.2.2.2.2 Triangulifera (= Euplectoptera *sensu* Tshernova, 1962, 1970,? = Euplectoptera *sensu* Tillyard, 1932) (= *Paedephemera multinervosa*+remaining ephemeroids, which include, among others, the Ephemerida) (Ephemereida = Ephemeroptera *vel* Plectoptera auct., = Euplectoptera *sensu* Grimaldi and Engel, 2005,? = Euplectoptera *sensu* Tillyard, 1932; = crown group of the entire ephemeropteran lineage).

In the following, the vernacular term ephemeroid is used for any taxon which is considered to be more closely related to modern mayflies (Ephemerida) than to any other Recent taxon.

Cretereisma gen. nov.

Type species: *C. antiqua* sp. nov., by present designation.

Etymology: named after the Cretaceous age and the similar fossil genus *Protereisma*.

Diagnosis: adult fore- and hind wings of almost equal size, narrow, distal portions only slightly broader than their basal parts. Costal brace long and only slightly arched. Anal veins long, meeting the hind margin of the wings at low angle (plesiomorphies shared with *Protereisma* and, in part, earlier branches of ephemeroids). Several longitudinal veins run pairwise and almost parallel to each other towards the wing margin, each pair consisting of a concave and a convex vein (IRS_{2a} and R_{2b}; RS_{3+4} and MA_1; IMA and MA_2; MP_1 and IMP; MP_2 and CuA_1; ICuA and CuA_2 respectively). Nomenclature of veins as developed by Tillyard (1932) for *Protereisma*. The main CuA vein appears to be CuA_2, while this is CuA_1 in *Protereisma*.

Nymph caterpillar-like or gammarid-like in appearance, with undivided tarsus bearing one claw. Pro-, meso- and metathorax subequal in size, hind wing pads only slightly shorter than forewing pads. Abdomen with seven pairs of elongated plate-like gill appendages.

Comment: these generic characters – that is, characters found in both species of *Cretereisma* – are not repeated in the following descriptions of the two species.

Cretereisma antiqua sp. nov. (Figures 11.2a and b; Plate 7c)

Material: holotype SMNS 66546 (old no. 28) (figured by Bechly *et al.*, 2001a: 48, Abb. 37).

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Etymology: *antiquus*, Latin, old. The name refers to the very archaic structure of the species, which resembles the Permian *Protereisma* in many aspects.

Description (Figures 11.2a and b): specimen with all four wings spread out, visible from its ventral side. Body length 18 mm. Forewing length 24 mm. Hind wing measuring about four-fifths of forewing length. Sc running towards wing apex, curving posteriorly towards R. CuA and CuP simple. A_1 short (not extending beyond the first quarter of the wing), probably simple; remaining anals difficult to trace (the veinal description applies for both the fore- and the hind wings). Abdominal segments as broad as those of the thorax, head as broad as thorax, with large bulging eyes. Antennae and abdominal appendages not preserved.

Cretereisma schwickertorum sp. nov. (Figure 11.2c; Plate 7d)

Material: holotype SMNS 66598 (old no. H51).

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Etymology: the species is named in honour of Mr and Mrs Schwickert, Sulzbachtal, Germany, for generously supporting scientific research on Crato Formation fossils for nearly 15 years.

Description (Figure 11.2c): left wings missing except the very bases, right hind wing very fragmentary. Body length 32 mm. Forewing length 31 mm. Wing venation as in *C. antiqua* but A_1 almost extending to the middle of the wing and with a well-developed triad. With more anal veins behind A_1 than in the previous species.

Head, thorax and abdomen of almost the same width. Antennae, legs and abdominal appendages not preserved.

Comment: the circumstance that almost no crossveins have been noticed in the costal areas of both *C. antiqua* and *C. schwickertorum* is certainly due to preservation.

Comparison with *C. antiqua*: the differences in venation between the two species are a result of size differences, *C. schwickertorum* being considerably larger. In the latter, more anal branches are present to strengthen the posterior basal wing area. I do not believe that the differences, especially the absence/presence of a well-pronounced triad on A_1, is due to intraspecific variation or sexual dimorphism.

Two further well-preserved adult specimens of *Cretereisma* spp. are deposited without number in the collection of SMF.

Nymphs (Figures 11.3a–d; Plates 7e–h)

According to the size and morphology of the flying stages, the nymphs of the two species described above must have been of considerable size, have had four wing pads of almost equal size and, as a necessity of the latter property, a well-developed meso- and metathorax. Many specimens fulfilling these requirements have been found in the Crato Formation and are considered to be members of *Cretereisma*. These nymphs are not so rare in the Crato Formation, and are well-known to the local quarry workers under the vernacular term *Ananas* or pineapple.

Material: there are 10 nymphs with the nos SMNS 66547 (old no. 33; figured by Bechly *et al.*, 2001a: 47, Abb. 36), SMNS 66548 (old no. L74), SMNS 66549, SMNS 66599 (old no. 30), SMNS 66600 (old no. 31), SMNS 66601 (old no. 32), SMNS 66602 (old no. H54), SMNS 66603 (old no. L73), SMNS 66604 (old no. H52), and SMNS 66605 (old no. 29); three further specimens have been recently donated to SMNS (SMNS 66673, SMNS 66674, SMNS 66675). A very nice nymph is specimen MB.I.2028 at MNB, and additional specimens are held by SMF. One of the best-preserved nymphs is specimen no. 512 in coll. MURJ (Figure 11.3e). Another nymph from AMNH was figured by Grimaldi and Engel (2005: 166, figure 6.13).

Specimen SMNS 66673 (Figures 11.3a and b; Plate 7e) was chosen as the basis of nymphal description mainly because of its good general state and the complete preservation of its left wing pads): the animal is visible from its left side. Body length 33 mm. Thoracomeres and abdominal segments are very high (body not flattened), which give the animal a somewhat caterpillar-like appearance. Sclerites with numerous fine pores are present which may have been the insertion points of bristles (see description of additional material).

Description (Figures 11.3a and b): head short, about as long as prothorax, and probably with burrowing devices. Mouthparts only fragmentarily preserved.

Antenna long, with big basal segments (only a very faint impression of one antenna directed forwards is left). Pro-, meso- and metathorax of almost equal length, mesothorax slightly longer than the other two thoracomeres. Thoracic terga with pronounced hind margins. Meso- and metathorax with wing pads of subequal shape, the hind wing pad being slightly shorter than that of the forewing. The forewing base is attached to the thorax as follows: laterally, the tergite has two knob-like elevations opposite to the anterior basal wing area; these elevations being set apart from the wing pad by a deep longitudinal incision. The posterior lateral area of the tergite is slightly elevated and separated by a longitudinal groove from a still more lateral elevation near the middle of the wing base. The hind margin of the wing pad runs continuously into the hind margin of the mesothoracic tergite. The situation in the metathorax is the same, but the structures are less pronounced due to the slightly smaller size of the hind wing pad. As already proposed by Bechly *et al.* (2001a: 48), it appears that the wing pads were moveable along the deep incision mentioned above. Such moveable wing pads represent a very archaic character state, which is otherwise only known from Palaeozoic pterygote larvae. Legs stout; coxae very large and broad. Fore coxa slightly shorter than the fore femur, middle and hind coxae almost as long as the respective femora. The fore legs are the longest.

The first eight abdominal segments are of subequal length, the remaining ones being considerably shorter. Segments 1–7 each with a pair of strongly scleritized elongated lateral gill appendices which are directed downwards in the fossil. Their distal parts appear to have been strongly scleritized into plate-like structures and are slightly curved forwards. Gill plates with a pronounced margin around their distal portions. The gill appendices insert laterally at the abdomen with a broad base. As the bases are irregularly crumbled it appears that this portion was not developed as a plate in the living animal. Abdominal tergites 8–10 extend more ventrally than the preceding ones. Cerci are lacking in this specimen due to preservation.

Additional material as listed above shows well-preserved long antennae and fairly long cerci and paracercus. Antennae about as long as head and thorax combined (e.g. SMNS 66599, SMNS 66600, SMNS 66547). Paracercus with row of long setae on each side, cerci with one row of setae only. Cercal joints and joints of paracercus short. Femora with strong bristles or hairs (SMNS 66599 and SMNS 66604), coxa similarly equipped (SMNS 66547; other leg segments do not show such structures possibly due to preservation of the specimens available for study). Tarsi one-segmented, claws pointed. Specimen SMNS 66674, which is partly preserved as a negative imprint, shows impressions of longitudinally directed long body hairs on the abdomen. The small pores on the sclerites of other specimens may correspond to these hairs and might have been insertion places. Gill appendages fringed with hairs.

Body lengths in the additional material range from 10.5 mm (SMNS 66605) to 26 mm (SMNS 66547 and SMNS 66604) and even 30 mm in one specimen (SMNS 66549), without antennae and abdominal appendages.

It was not possible to distinguish, in the nymphs, between the two species described above from adult specimens.

With exception of specimen no. MSF Z78, all nymphs of *Cretereisma* are embedded in a lateral position. Furthermore, these nymphs clearly have a laterally compressed body, which seems to be a unique autapomorphy, because such a habitus is unknown from other fossil and Recent mayfly nymphs. Bechly *et al.* (2001a: 49) therefore suggested that these peculiar larvae had a very different lifestyle than all other known mayflies.

Comparisons

The general wing structure of *Cretereisma* resembles closely that of *Protereisma*. A main difference is the pairwise alignment of some of the longitudinal veins which is an autapomorphy of *Cretereisma*. Another difference lies in the structure of the first anal vein, which is simple in the forewing of *Protereisma* and *Misthodotes* while it has a triad in the hind wing (Carpenter, 1933). In *Cretereisma*, however, A_1 is apparently either simple in both wings (*C. antiqua*) or has a triad at least in the forewing (*C. schwickertorum*; structure of hind wing anals unknown). The general tendency towards a reduction of anal branches is probably correlated to the reduction of wing width. Nymphs are different from those of *Protereisma* (and *Phthartus*) in their unique body shape and their plate-like gill appendages, and both *Protereisma* and *Phthartus* have nine abdominal gill pairs while *Cretereisma* is more derived in having seven. Epeoromimidae have seven pairs of plate-like gill appendages as well; however, this is the only remarkable similarity worth mentioning. In other structures, epeoromimid nymphs differ fundamentally from *Cretereisma*, for example in body shape, a small prothorax and posteriorly directed wing pads, of which the hind pair is only small.

Phylogenetic position

Cretereisma shares with the Permian *Protereisma* and *Misthodotes* a reduced anal area in the hind wing and the possession of a costal brace which is only slightly curved and does not reach the costal margin. These characters were not present (or have not been observed) in earlier ephemeroids. *Cretereisma* is more derived than *Protereisma* in having only seven gill appendages in the nymph. On the other hand, the Upper Triassic *Litophlebia*, which resembles *Protereisma* in many aspects, possibly shares at least one synapomorphy (shortened anal veins) with the

Triangulifera but not with *Cretereisma*. Thus it appears that *Cretereisma* is the sister taxon of *Litophlebia*+Triangulifera. *Protereisma* and *Misthodotes* were abundant in the Lower Permian while *Litophlebia* lived about 60 myr later. Hence *Cretereisma*, with a phylogenetic position between *Litophlebia* and the two Permian taxa, is the only known representative of an ephemeroid lineage which had retained many plesiomorphic features for about 110–160 myr.

11.4 Ephemeroptera: mayflies

Arnold H. Staniczek

Mayflies represent one of the basal branches of winged insects and have a world wide distribution. Stem group representatives of mayflies date back to the Carboniferous. More than 3,000 Recent species have been described.

The larvae of mayflies are obligatorily bound to freshwater habitats. The imagines of mayflies are short-lived insects with a life span that varies from a few hours to a few days. Mayflies are the only pterygote insects to retain more than one fully winged stage. The subimago is the alate penultimate stage and undergoes another moulting to become the imago. The subimaginal moulting is generally regarded as a vestigial adult moulting as it is present in the apterygote insect groups. The adult stages of mayflies are easily recognized by the presence of usually very long cerci, often accompanied by a median long terminal filament (paracercus). At rest the wings are folded vertically over the abdomen. The hind wings are considerably smaller than the forewings and can also be entirely lost in some taxa. The imaginal wings are generally translucent and glabrous, but the subimaginal wings usually have a greyish or milky tinge and are equipped with setae. The venation is characterized by the presence of multiple crossveins, a pronounced costal brace especially in the forewing, and the presence of vein MP. The wings generally retain a pronounced pleating and corrugation of the longitudinal veins. The adult stages of mayflies do not feed, and their mouth parts are atrophied. The antennae are very short and bristle-like, convergent on Odonata. Other features are connected with the aerial mating flight that the males perform above the water: the male eyes are generally larger than the female ones, in some taxa (Baetidae, Leptophlebiidae) they are extended to so-called turbinate eyes, which are also morphologically divergent. The male forelegs are elongated to grasp the females around the base of the forewing during copulation. The male claspers, modified abdominal leglets of abdominal segment VIII, additionally clutch the female abdomen during copulation. Males have paired penes, and females have paired gonopores, respectively. The female ovipositor is completely reduced, and only some taxa have developed a secondary egg guide. After mating the female mayfly simply drops its eggs into the water. The eggs are equipped with highly variable adhesive structures to prevent drifting.

The larvae of mayflies undergo numerous moults until they reach the final instar. Extant species usually bear seven pairs of tracheal gills, which insert laterally on the first seven abdominal segments. The gills are of variable shape but often specific for higher taxa. They can be either simple or may be composed of an upper and a lower branch. The gills can be shaped like a leaf (Baetidae), fringed (Ephemeroidea), finger-like in some Leptophlebiidae, miniaturized in the Oligoneuriidae, or may be located beneath a specialized gill that functions as a gill cover (Caenidae). In the Heptageniidae the upper gill portion is leaf-like, and the lower portion is represented by a gill tuft. The larvae are also characterized by the presence of the tail filaments. The chewing mouth parts of mayfly larvae are well developed. The secondary mandibular joint is not fixed as a ball-and-socket joint, and the mandible is able to perform gliding movements similar to the conditions in silverfish. The hypopharynx retains side lobes (superlinguae), and maxillary and labial palps are both three-segmented. Mayfly larvae mostly feed on detritus accumulated with their maxillae and mandibles. The filter-feeding Setisura even use specialized setae to filter their food out of the water currents with their forelegs. A few taxa (Behningiidae, Ameletopsidae) have carnivorous larvae. Mayflies are important elements of the freshwater food chain and the nutrient base for many carnivorous fish. The emergence of mayflies is often highly synchronized, and at times millions of specimens can be observed in dense swarms.

Systematics and phylogeny

The monophyly of mayflies is well established and supported by numerous apomorphic characters such as the Palmen body, the atrophy of mouth parts, and an air-filled gut with aerostatic function. Apart from the Ephemeroptera, there are only two other Recent basal lineages of pterygote insects, the Odonata and Neoptera. There is, however, no general agreement on the sister group of Ephemeroptera. A potential sister-group relationship between Odonata and Ephemeroptera+Neoptera is only substantiated by few putative synapomorphic characters, namely by the presence of a direct sperm transfer in Ephemeroptera+Neoptera. A monophyletic taxon Paleoptera (Martynov, 1925; Ephemeroptera+Odonata) has mainly been advocated by Kukalová-Peck (1985, 1987, 1991). Potential synapomorphies of the Paleoptera include an anal wing brace that is similarly developed in stem group representatives of both groups, a media with common stem, and the presence of intercalary veins. Other workers have proposed a sister-group relationship between Ephemeroptera and all other pterygote insects, the Metapterygota (Börner, 1909). The rigid secondary mandibular joint together with a different arrangement of mandibular musculature, the loss of the terminal filament and superlinguae, and the loss of the imaginal moults are regarded as apomorphic characters of the

Metaptygota (see Kristensen, 1995 and Staniczek, 2000 for a detailed discussion). Molecular data are inconclusive (Ogden and Whiting, 2003), and a final decision cannot be made at present.

The phylogenetic systematics of Ephemeroptera is far from being fully resolved and remains controversial with regard to the composition and branching sequence of many higher taxa. There are about 37 monophyletic taxa recognized that are categorized as families. McCafferty and Edmunds (1979) divided the Ephemeroptera into the paraphyletic Schistonota and the Pannota, which are defined by medially fused larval wing pads. Later Kluge (in an oral conference contribution in 1992; and 1998) and then McCafferty (1997) excluded the Batiscidae+Prosopistomatidae from the Pannota and assumed the Prosopistomatoidea (Carapacea *sensu* McCafferty, 1997; Posteritorna *sensu* Kluge, 1998) to be the sister group of all other mayflies. Other similarities in both systematics are a proposed taxon of several rather plesiomorphic families, the Tridentiseta (Kluge, 2004) or Pisciforma (McCafferty, 1998), that consist of the Siphlonuroidea (Kluge *et al.*, 1995) and Baetoidea (Staniczek, 1997). There is also congruence in uniting all filter-feeding taxa with the Heptageniidae to a taxon Setisura (McCafferty, 1997) or Branchitergaliae (Kluge, 2004). The remaining groups, united into a taxon Furcatergaliae by Kluge (2004), are also considered to be monophyletic. Within these higher taxa, however, the arrangement of the different families differs considerably. Moreover, recent molecular systematics by Ogden and Whiting (2005) failed to support most of these groupings.

Evolution

One of the most important steps in insect evolution was the acquisition of wings. The development of insect wings from thoracic side lobes, the paranota, has been the prevailing hypothesis for a long time (Snodgrass, 1935), until Kukalová-Peck (1978, 1983) publicized the development of insect wings from modified thoracic gills. Both hypotheses claim to gain support from fossil evidence. The Recent ephemeropteran lineage is only one of several branches of early winged insects. The †Paleodictyopterida comprise several distinctive groups, all of which became extinct by the end of the Permian. At present there are some doubts whether the †Paleodictyopterida are monophyletic, as often assumed, because of the characteristic elongated, sucking mouth parts they share. In several groups of these Palaeozoic insects, huge prothoracic side lobes were developed as winglets. These prothoracic paranotal lobes had a similar venation to the meso- and metathoracic wings. The presence of prothoracic winglets in many of these Palaeozoic insects is generally taken as support for the above-mentioned paranotal hypothesis. However, paranota are rigid outgrowths that do not have any articulation with the prothorax. The gill hypothesis assumes that insect wings are serially homologous with the gills of mayfly larvae (Kukalová-Peck, 1991). In particular, gills and wing pads of Permian larvae of †Protereismatidae look similar to each other, and the wing pads, unlike in modern mayfly larvae, seem to articulate with the thorax. Consequently, an aquatic origin of pterygote insects has been postulated by the advocates of the gill hypothesis. On the other hand, all primarily apterous insect groups are terrestrial, and the basal taxa of ptergote insects with aquatic larvae (Ephemeroptera, Odonata, Plecoptera) have developed very different modes of respiration. This makes it unlikely that the pterygotes evolved in an aquatic environment (Pritchard *et al.*, 1993), although there are no terrestrial larvae of stem group representatives of mayflies known. Recently the gill hypothesis has been modified and the use of wings as a skimming device has been proposed as the trigger of wing development (Marden and Thomas, 2005). Given the fact that skimming in Recent mayflies and stoneflies only occurs in a few derived taxa, this scenario is not very likely.

However, notable differences from early stem group representatives of mayflies to modern Ephemeroptera can be observed. While a costal brace is present in most fossil and modern taxa, its basal course is slightly different in early groups such as the †Protereismatidae, where the costal brace is still well separated from the costal vein. Fore- and hind wings in the first fossil taxa are of the same size. Heteronomous wings first appear in the Jurassic, and all modern mayflies have significantly reduced hind wings. Other differences concern the development of a wing tornus in modern mayflies, while the hind margin of the wing in Palaeozoic stem group representatives has no sharp angle (Kluge, 2004). Generally the size of mayflies diminished during their evolution. Adults of Palaeozoic stem group representatives like the †Protereismatidae are also assumed to have functional mouth parts (Grimaldi and Engel, 2005). The articulated wing pads of the associated larvae grew out in a laterocaudad direction. In modern mayflies the wing pads are fused with the mesonotum and grow parallel to the longitudinal body axis. The amount of gill numbers has become reduced from nine pairs to seven.

Fossil record

Winged insects were already abundant in the Late Cretaceous, but the discovery of the Early Devonian *Rhyniognatha hirsti*, a species that may belong within the lineage of Metapterygota, suggests that the age of the Metapterygota and of its putative sister group, the Ephemeroptera, dates back to that time (Engel and Grimaldi, 2004). The first fossils that have been assigned to the ephemeropteran lineage date back to the Late Carboniferous. While the assignment of two enigmatic fossils, *Triblosoba pulchella* from the Late Carboniferous of Commentry and *Lithoneura lameerei* from the Late Carboniferous of Mazon Creek, to the stem group of mayflies is controversial (Willmann, 1999), most researchers agree on the assignment of *Bojophlebia prokopi*, from the Upper Carboniferous of Bohemia, to the stem group of mayflies (Kukalová-Peck, 1985). With a wing span of 45 cm it is also the largest mayfly precursor ever found.

There are many fossil stem group representatives from the Permian fauna preserved, among them the well-known †Protereismatidae from the Early Permian of Kansas, Oklahoma, Moravia and the Urals (Tillyard, 1932; Carpenter, 1979; Hubbard and Kukalová-Peck, 1980). Another well-known taxon is the †Misthodotidae that together with the †Protereismatidae disappeared by the end of the Permian (Tshernova, 1965). The stem group representatives were often placed in a separate suborder, '†Permoplectoptera', which is, however, regarded as paraphyletic with respect to the crown group. Most of these early taxa went extinct by the end of the Permian, but others could be recorded from the Triassic (Sinitshenkova *et al.*, 2005). The youngest stem group representatives of Ephemeroptera have been found within the Crato Formation and are described in detail in the preceding Section 11.3, by Willmann. A further, undescribed, stem group mayfly from this locality is featured in Figures 11.90i and j. For recent reviews on all stem group representatives of mayflies, see Kluge (2004) and Willmann (this volume, Section 11.3).

The first species that are positioned within the crown group of Ephemeroptera appear in the Lower Jurassic (Tshernova, 1967): *Stackelbergisca sibirica* turned out to be closely related to the Recent *Siphluriscus chinensis* (Siphluriscidae; Zhou and Peters, 2003). Species that are attributed to the Leptophlebiidae can be traced back to the Jurassic (Hubbard and Savage, 1981). Numerous other Jurassic genera have been placed in the extinct taxa †Epeoromimidae, †Aenigmephemeridae, †Mesephemeridae and †Hexagenitidae (McCafferty, 1990). The affinities to Recent mayfly groups remain mostly uncertain (Kluge, 2004).

The Cretaceous mayfly fauna apart from the Crato Formation has been documented by fossil records from Transbaykalia (Tshernova and Sinitshenkova, 1974; Sinitshenkova, 1986), China (Lin and Huang, 2001), England (Sinitshenkova and Coram, 2002), Australia (Jell and Duncan, 1986) and Algeria (Sinitshenkova, 1975).

The oldest mayflies in amber have been recorded from the mid-Cretaceous of Myanmar (Sinitshenkova, 2000), Lebanon (McCafferty, 1997) and New Jersey (Peters and Peters, 2000; Sinitshenkova, 2000). Several mayfly fossils from Baltic and Dominican amber have been recorded from the Eocene and Miocene that mostly reflect the modern fauna (Staniczek and Bechly, 2002; Staniczek, 2003; Godunko, 2004; Godunko and Neumann, 2006). New families of mayflies are defined only rarely, which, however, can all be attributed to Recent monophyletic groups (Kluge *et al.*, 2006). Kluge (1986) even reports a putative Recent species from Baltic amber.

Palaeobiology and palaeoecology

Mayflies are obligatorily bound to fresh water. Extant species of mayfly are generally halophobic and only a few species are reported to tolerate elevated salt concentrations as they are present in brackish water (Chadwick *et al.*, 2002). *Protoligoneuria limai* (Figures 11.4a and 11.9c; Plates 7i and 8a–c) is reported to be the most common fossil insect species of the Crato Formation (Martins-Neto, 1996a; D. Martill, personal communication), although mayflies only make up about 7% of the described Crato species (Bechly, 1998c). The mass occurrence of thousands of fossil larval mayflies in the Crato limestones clearly points to the presence of streams in the immediate vicinity of the deposit. McCafferty (1990) and Tshernova (1970) hypothesized quiet waters as a habitat for *P. limai* because of its larval swimming adaptations such as the minnow-like body shape, siphlonuroid caudal appendages and its enlarged seventh gill. The larvae of the burrowing Ephemeroidea (Figures 11.4c and g, 11.5a and b and 11.6h and i; Plate 8f) found in Crato also point to the presence of streams or at least stream sections with a rather low flow rate. However, a rheophilic habitat cannot entirely be ruled out. Similar to the Odonata fauna with a high percentage of Gomphidae found here, the oligoneuriid species found were probably more adapted to a lotic environment and generally depended on a high amount of oxygen. Most probably the Crato environment provided a diverse habitat suitable for both lotic and lentic species. The few adult records compared to the enormous amount of larval specimens found may be explained by two factors: mayfly larvae are sensitive to downstream drift, and this is counterbalanced by an upstream compensation flight of the female adults. Both effects may lead to a spatial separation of larvae and adults with the effect of an accumulation of larvae which have been swept into the area of deposition.

Crato fossils

The first fossil mayfly from this locality was reported by Costa-Lima (1950) and described by Demoulin (1955). According to Martins-Neto (2005b) there have been 15 species of fossil Crato mayflies described, not including the two species of stem group mayflies described by Willmann in Section 11.3 (a further undescribed specimen is featured on Figures 11.90i and j). Important contributions to Crato mayflies were made by McCafferty (1990) and Martins-Neto (1996a). Shorter contributions were provided by Brito (1987), Martins-Neto and Caldas (1990), Polegato and Zamboni (2001), Zamboni (2001) and Bechly *et al.* (2001a: figures 28, 30, 36 and 37).

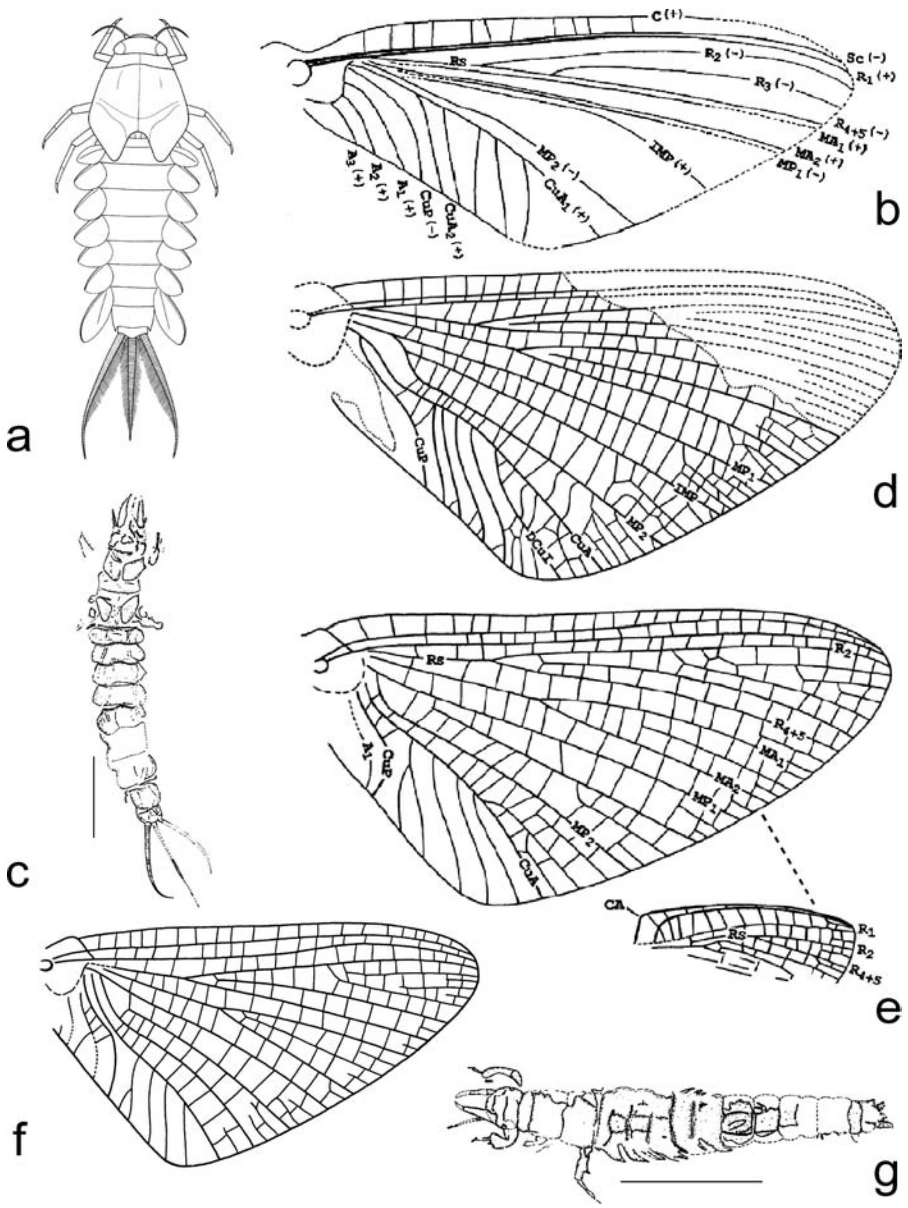

Fig. 11.4. Crato Formation Ephemeroptera: (a) Hexagenitidae, *Protoligoneuria limai*, composite reconstruction of larva (after McCafferty, 1990: figure 1); (b) Oligoneuriidae, *Colocrus indivicum*, reconstruction of forewing, adult paratype AMNH 43499 (after McCafferty, 1990: figure 19); (c) Ephemeroidea (Potamanthidae?), *Olindinella gracilis*, larval holotype AMA-I-028 (after Martins-Neto and Caldas 1990: figure 2); (d) Euthyplociidae, *Pristiplocia rupestris*, forewing, adult holotype AMNH 44308 (after McCafferty, 1990: figure 23); (e) Ephemeridae, *Australiephemera revelata*, forewing and hind wing fragment, composite from adult holotype AMNH 44300 and adult paratype AMNH 44310 (after McCafferty, 1990: figures 20 and 21); (f) Ephemeridae, *Microephemera neotropica*, forewing, adult holotype AMNH 43303 (after McCafferty, 1990: figure 22); (g) Ephemeroidea, (Ephemeridae?), *Cratonympha microcelata*, larval holotype GP/1T-1677 (after Martins-Neto and Caldas 1990: figure 1A).

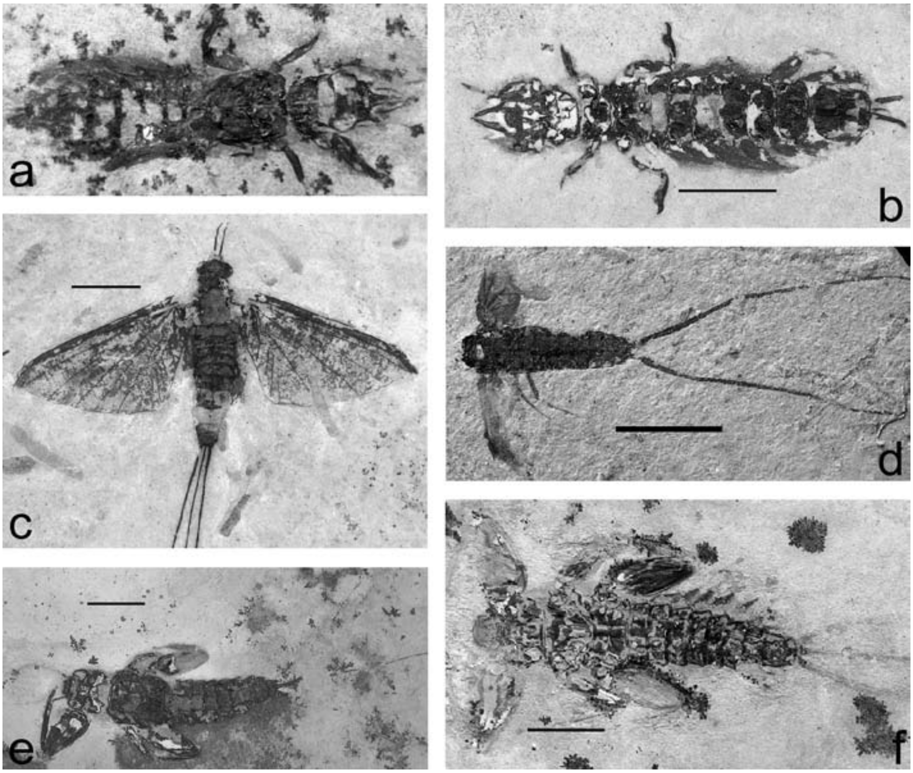

Fig. 11.5. Crato Formation Ephemeroptera: (a) Ephemeroidea indet., larva, SMNS 66630; (b) Ephemeroidea indet., larva, coll. MSF; (c) Ephemeroidea indet., adult, coll. MSF; (d) Leptophlebiidae (?) sp. 1 (*sensu* McCafferty 1990), subimago?, SMNS 66639; (e) Familia *incertae sedis*, gen. et sp. nov., larva Z2 coll. MSF; (f) Familia *incertae sedis*, gen. et sp. nov., larva, SMNS 66622. Scale bars, 5 mm.

†**Hexagenitidae** Lameere, 1917

Apart from the Crato fossils, there are five more genera that have been placed in the extinct †Hexagenitidae: *Hexagenites* Scudder 1880, *Ephemeropsis* Eichwald 1864, *Hexameropsis* Tshernova and Sinitshenkova 1974, *Mongologenites* Sinitshenkova 1986 and *Caenoephemera* Lin and Huang 2001. The first mayfly ever from Crato was mentioned by Costa-Lima (1950), who assigned three larval specimens to the Baetidae (equivalent to today's 'Siphlonuroidea'); however, no formal description was given. Based on these specimens, Demoulin (1955) formally named the species as *Protoligoneuria limai*, and placed it in the Oligoneuriidae. Brito (1987) described a new genus and species *Palaeobaetodes limai* but McCafferty (1990) synonymized Brito's species with *Protoligoneuria limai*. He placed the species in the †Hexagenitidae, based on the characteristic, significantly enlarged and outspread seventh gill that is also present in other hexagenitid larvae. This enlarged seventh gill is regarded as an autapomorphic larval character of the †Hexagenitidae

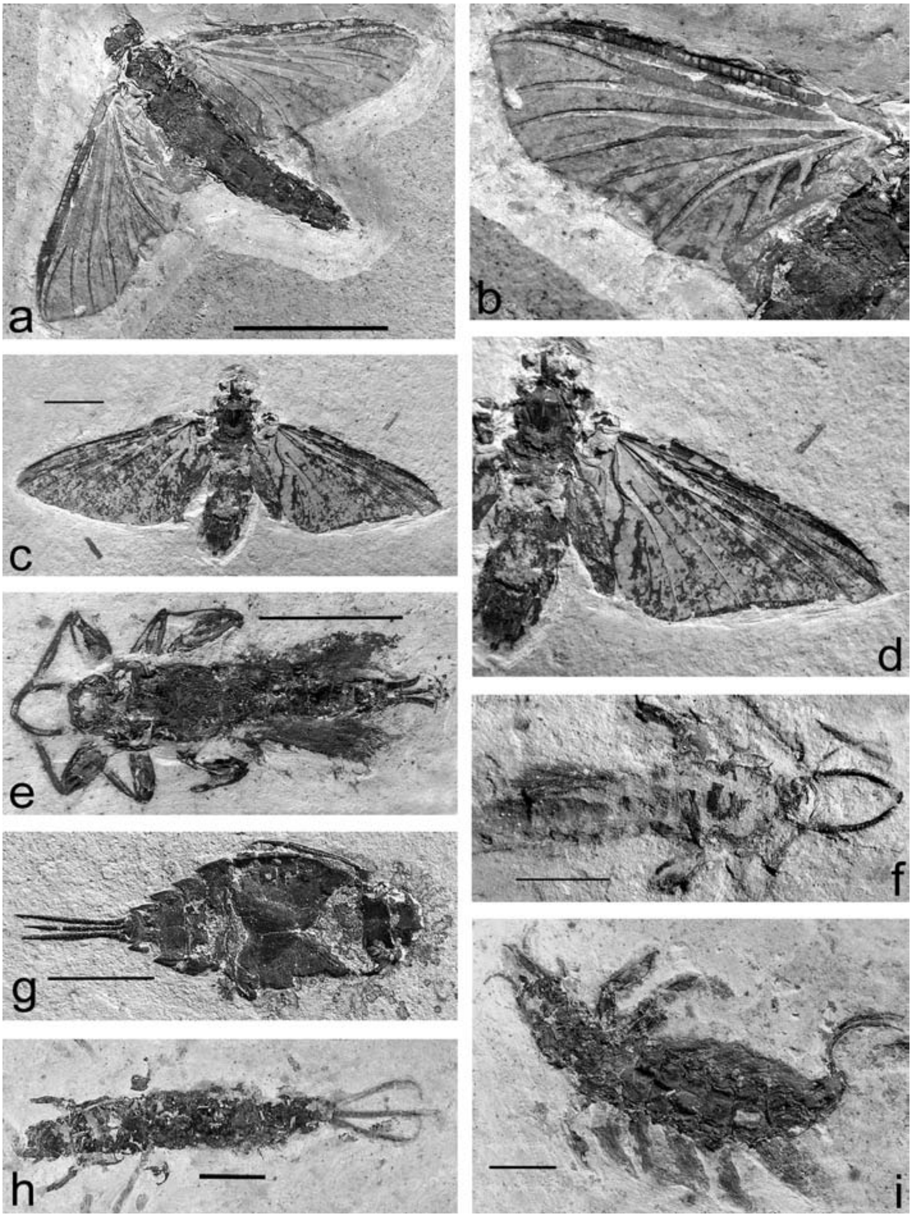

Fig. 11.6. Crato Formation Ephemeroptera: (a) Oligoneuriidae, *Colocrus magnum* sp. nov., putative adult, SMNS 66623; scale bar, 10 mm; (b) Oligoneuridae, *Colocrus magnum* sp. nov., left wings of adult, SMNS 66623; (c) Euthyplociidae, *Pristiplocia rupestris*, adult, SMNS 66541; scale bar, 5 mm; (d) Euthyplociidae, *Pristiplocia rupestris*, right wings of adult, SMNS 66541; (e) Euthyplociidae, *Pristiplocia* sp., larva, SMNS 66539; scale bar, 5 mm; (f) Euthyplociidae, *Pristiplocia* sp., larva, SMNS 66621; scale bar, 3 mm; (g) Baetiscidae, *Protobaetisca bechlyi* gen. et sp. nov., larval holotype SMNS 66620, scale bar, 3 mm; (h) Ephemeroidea indet., larva, MURJ without number; scale bar, 3 mm; (i) Ephemeroidea indet., larva, SMNS 66634; scale bar, 3 mm.

(Kluge, 2004), but according to McCafferty (1990) it may only be a synapomorphic character between some taxa within the †Hexagenitidae. Martins-Neto (1996a) reinstated *Palaeobaetodes* and described a second species, *Palaeobaetodes britoi*, from larvae, and also described a third genus *Cratogenites*, including *C. corradiniae*, from larvae.

The known imagines of the †Hexagenitidae all have a characteristic wing pattern with a branched CuA in the forewing and several successive triads present between CuA_1 and CuA_2. The first adult specimen of †Hexagenitidae from Crato was described as yet another new genus and species, namely *Cratogenitoides delclosi*, by Martins-Neto (1996a).

Protoligoneuria limai Demoulin, 1955

Baetidae (Siphlonurinae), Costa-Lima, 1950: 419

Protoligoneuria limai Demoulin, 1955: 271. (Figures 11.4a and 11.9c; Plates 7i and 8a–c)

Paleobaetodes costalima Brito, 1987. Restored status as Syn. (Figure 11.7a)

Siphgondwanus occidentalis McCafferty, 1990 Syn. nov. (Figure 11.7h)

Palaeobaetodes britoi Martins-Neto, 1996a Syn. nov. (Figures 11.7c–d)

Cratogenites corradiniae Martins-Neto, 1996a Syn. nov. (Figures 11.7e–f)

Cratogenitoides delclosi Martins-Neto, 1996a Syn. nov. (Figure 11.8b)

Material: larval holotype specimen CD 6616, Vulcano collection (according to Martins-Neto (2005a) it is the only specimen that is left from the original three syntypes, and thus it is here designated as lectotype); more than 2,000 specimens deposited in the collection Martins-Neto, São Paulo; 77+4 larval specimens deposited at AMNH, and specimen AMNH 43404 (holotype of *Siphgondwanus occidentalis*); 236 larval specimens deposited at SMF, including the two specimens with preliminary nos Q4 and Q9 (Plates 7i and 8a); three very well-preserved specimens SMNS 66536, SMNS 66537 (Figure 11.9c) and SMNS 66672; and numerous specimens in other collections. Two putative alate specimens are no. RGMN-T002 (holotype of *Cratogenitodes delclosi*) in the Martins-Neto collection at the University of São Paulo, and specimen SMNS 66635 (Figures 11.9a and b).

Diagnosis: putative alate stages (Figures 11.9a and b) with compact anteritornous wing, relation of wing length to width of about 2:1. Length of forewing about 18–20 mm. C, Sc and R_1 not branched; Sc not shortened. Costal field and entire wing with numerous crossveins. RS basally branched at about one-quarter of wing length. MA branched in apical half of wing at about three-quarters of wing length. MP basally branched, with very short common stem, CuA basally branched at about one-third of distance between wing base and tornus. CuA field with four successive 'hexagenitid' triads. CuP not branched. A_1 with common short stem and basally branched. Hind wing significantly reduced, without costal process, with RS, MA and MP apically branched. No conspicuous gemination of longitudinal veins.

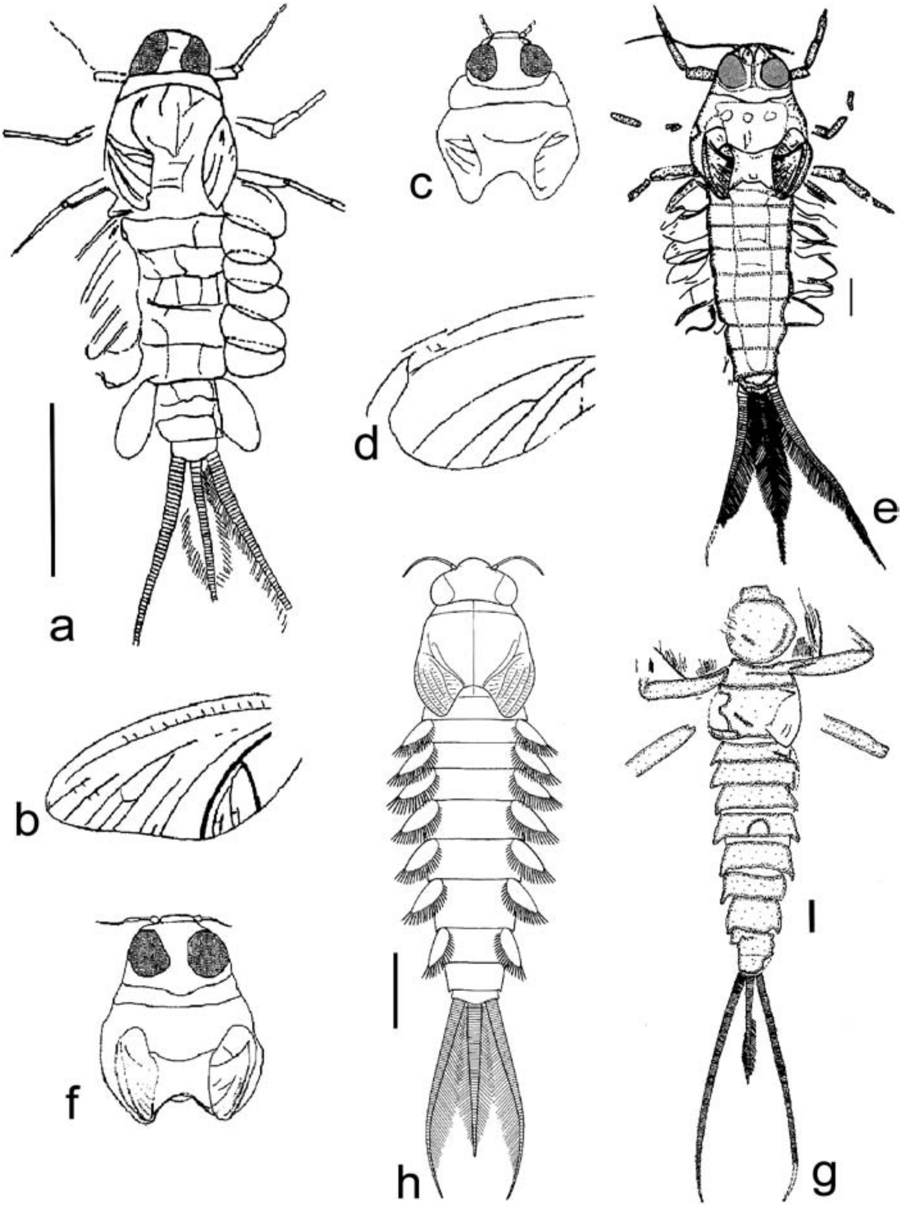

Fig. 11.7. Crato Formation Ephemeroptera (invalid taxa): (a, b) *Palaeobaetodes costalimai* Brito, 1987 (= *Protoligoneuria limai*); (a) mature nymph; scale bar, 5 mm, (b) alar; (c, d) *Palaeobaetodes britoi* Martins-Neto, 1996a (= *Protoligoneuria limai*); (c) head and thorax, RGMN-T006; (d) alar; (e, f) *Cratogenites corradiniae* Martins-Neto, 1996a (= *Protoligoneuria limai*), holotype, RGMN-T001; (e) mature larva; scale bar, 1 mm; (f) head and thorax; (g) *Cratoligoneuriella leonardii* Martins-Neto, 1996a (= *Colocrus indivicum*), holotype nymph, RGMN-T005; (h) *Siphgondwanus occidentalis* McCafferty, 1990 (= *Protoligoneuria limai*), larva in dorsal view, legs ommitted; scale bar, 1 mm. (a–h) After Martins-Neto (1996a); (i) after McCafferty (1990).

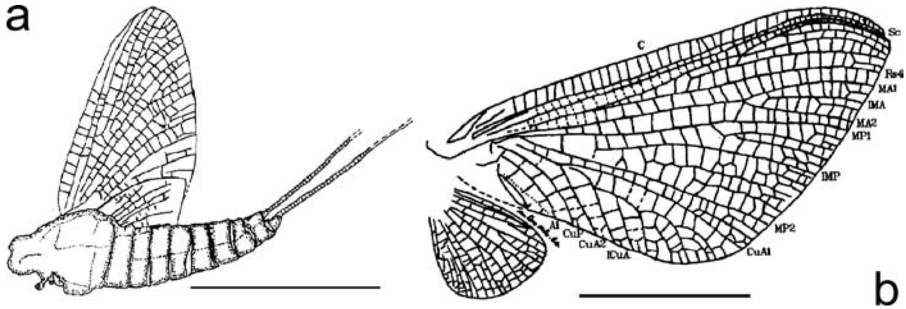

Fig. 11.8. Crato Formation Ephemeroptera: (a) Ephemeroptera *incertae sedis*, *Costalimella nordestina* Martins-Neto, 1996a, holotype, RGMN-T004; (b) *Cratogenites delclosi* Martins-Neto, 1996a (synonym of *Protoligoneuria limai*), holotype, RGMN T002. Scale bars, 5 mm. After Martins-Neto (1996a).

Larvae (Figures 11.4a and 11.9c; Plates 7i and 8a–c): body length up to 16 mm, excluding cerci. Siphlonuroid minnow-like appearance (Figures 11.4a and 11.9c), cerci at their inner sides and terminal filum with fringes of swimming hairs, cerci slightly longer than terminal filament, abdomen with seven pairs of tracheal gills, gill VII distinctively longer than other gills, all gills consisting of a leaf-like upper part and a lower gill tuft (Plates 7i and 8a) that previously had been overlooked. Anterior margin of gills I–VII strengthened, gill VII (Plate 8b) also with a second longitudinal rib in the posterior half of the gill, well apart from its posterior strengthened margin (often a small but distinctly protruding apical lobe is visible at the posterior end of this gill plate). Wing pads medially partially fused as in Recent species of Setisura (Plate 8c).

Comments: Brito (1987) described with *Palaeobaetodes costalima* (Figures 11.7a and b) a new genus and species of †Hexagenitidae from Crato. McCafferty (1990) synonymized *Palaeobaetodes* with *Protoligoneuria*, but Martins-Neto (1996a) reinstated the latter genus and described a second species, *Palaeobaetodes britoi* (Figures 11.7c and d). However, these authors mention only few differences to *Protoligoneuria*: according to Martins-Neto (1996a), *Paleobaetodes* differs from *Protoligoneuria* mainly in larger eyes, which occupy 50% of the head in *Palaeobaetodes* instead of 30% in *Protoligoneuria*. Obviously the author did not consider the sexual dimorphism of the eyes in many mayfly species. It is very common that male larvae have larger eyes than the females, and this has to be assumed in this case as well. A different ratio of gill lengths VII/VI was claimed to be the significant difference between the two described species of *Paleobaetodes* (Martins-Neto, 1996a), but I could not confirm a significant grouping in the material available (several hundred larvae). Consequently, both species of *Paleobaetodes* are here regarded as junior synonyms of *Protoligoneuria limai*.

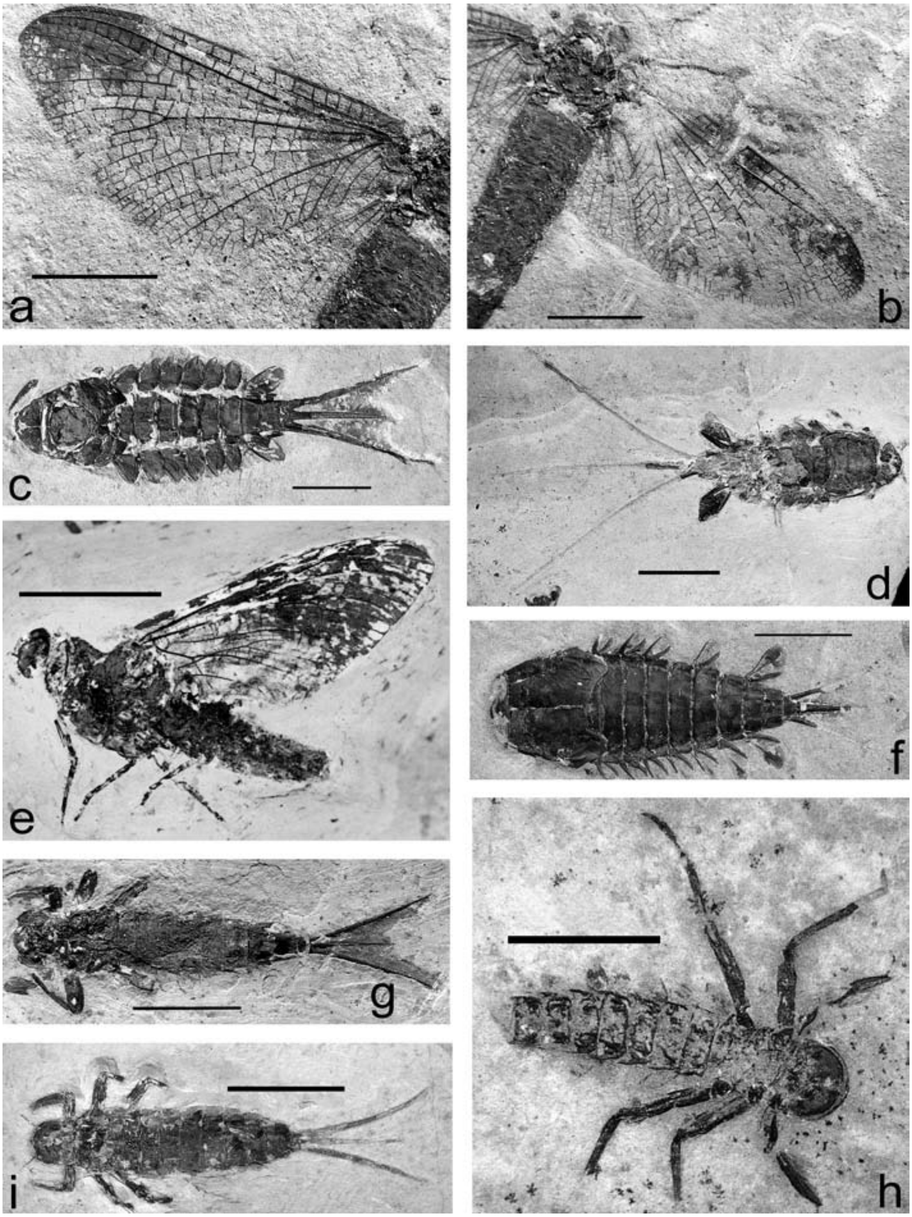

Fig. 11.9. Crato Formation Ephemeroptera: (a, b) Hexagenitidae, *Protoligoneuria limai* Demoulin, 1955, wings of adult, SMNS 66635; (a), left wings; (b) right wings; (c) *Protoligoneuria limai*, larva, SMNS 66537; (d) *Cratohexagenites longicercus* gen. et sp. nov., larva, holotype no. 447 MURJ; (e) *Cratohexagenites longicercus* gen. et sp. nov., putative adult, no. O46 coll. MSF; (f) *Cratohexagenites minor* gen. et sp. nov., larva, holotype MB.I.2026; (g) Oligoneuriidae, *Colocrus indivicum*, larva, SMNS 66538; (h) Oligoneuriidae, *Colocrus indivicum*, larva, MB.I.2025; (i) Oligoneuriidae, *Colocrus magnum* sp. nov., larva, holotype, SMNS 66624.

Martins-Neto (1996a) also described *Cratogenites corradiniae* (Figures 11.7e and f). Apart from larger eyes the only differences to *P. limai* mentioned are longer antennae (about twice the head width) in *C. corradiniae*. However, while the line drawing of the holotype (Martins-Neto, 1996a: figure 2A) shows an elongated left antenna, the corresponding photograph (Martins-Neto, 1996a: Plate 1, figure 1) does not support this view. Hence I also synonymize *Cratogenites corradiniae* with *Protoligoneuria*, until there is sound proof that it can indeed be distinguished as a separate species from *P. limai*.

Martins-Neto also noted differences in the larval head shape of the specimens he investigated and tried to link these differences with different species. However, it seems more likely to me that the observed differences are due to different positions of the head. I also noted slight differences in the body shape, but this could be caused by a different state of nutrition or by a different phase of the moulting period.

The body length of *Cratogenitoides delclosi* (Figure 11.8b), the only hexagenitid species described in the alate state, closely matches the length of the largest larvae of *P. limai* found. So *C. delclosi* is regarded as a junior synonym of *P. limai* herein. A very well-preserved adult specimen is SMNS 66635 (Figures 11.9a and b).

None of the previous authors observed ventral gill tufts in the larvae they investigated. This may be due to the fact that the gill tufts are inconspicuous and only visible in very well-preserved specimens. However, once I had encountered well-preserved specimens with clearly visible gill tufts, they could be observed quite frequently in many specimens (Plates 7i and 8a). In some specimens the fibrillous endings of the tufts just slightly protrude the rear margin of the upper gill portion and give the leaf-like gills the appearance of having a fringed rear margin. McCafferty (1990) described a single siphlonurid larva as *Siphgondwanus occidentalis* (Figure 11.7h) having exactly the same gill shape as mentioned above. Furthermore, the seventh pair of gills is not well preserved in this specimen. It is very probable that this in fact is nothing but a badly preserved specimen of *P. limai*. Hence *Siphgondwanus occidentalis* is also synonymized with *Protoligoneuria limai*.

Demoulin (1955) assigned *P. limai* to the Oligoneuriidae, but McCafferty (1990) demonstrated that there are larval and imaginal apomorphies present that clearly point to a position of *P. limai* within the †Hexagenitidae.

The phylogenetic relationships of the †Hexagenitidae have been enigmatic for a long time. Tshernova and Sinitshenkova (1974) maintain affinities between the †Hexagenitidae and Siphlonuridae, but the characters they have in common are genererally thought to be plesiomorphic. Demoulin (1971) emphasized similarities between the basal Recent oligoneuriid genus *Chromarcys* and the †Hexagenitidae, assuming a closer phylogenetic relationship between these taxa. However, *Chromarcys* is generally regarded as the sister group to all other Recent Oligoneuriidae (McCafferty, 1991), and the †Hexagenitidae are clearly lacking the autapomorphies of the Oligoneuriidae, so the †Hexagenitidae cannot be an ingroup taxon of the Oligoneuriidae. If the gill tufts now found in *P. limai* should be confirmed as groundplan characters of the †Hexagenitidae, a position of the †Hexagenitidae within the Setisura (McCafferty, 1991) = Branchitergaliae (Kluge, 2004), or a sister-group relationship between the two taxa, would be likely. However, a detailed structural analysis of the gill tufts is yet to be undertaken. A second character also supports this hypothesis: in some very well-preserved specimens a partial medial fusion of the wing pads is visible (Plate 8c). The same character state is also present in the filter-feeding taxa of the Branchitergaliae.

Cratohexagenites gen. nov.

Type species: *C. longicercus* sp. nov., by present designation.

Derivation of name: named after the type locality and the genus *Hexagenites*.

Diagnosis: Body of broader drop-like shape; seventh gill distinctly larger in proportion to the other gills than in *Protoligoneuria*, and of trapezoidal shape with angular instead of rounded hind margin.

Cratohexagenites longicercus sp. nov.

Material: larval holotype (Figure 11.9d) no. 447 (old no. G76) in coll. MURJ; larval paratype MB.I.2026 at MNB; putative adult specimen no. MSF O46 (Figure 11.9e), deduced from the corresponding large size of this imaginal hexagenitid.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after its elongated caudal filaments.

Diagnosis and description (Figure 11.9d): hexagenitid larva with enlarged seventh gill of trapezoid shape, differs from *P. limai* by body length of about 27 mm, length of cerci 28 mm, length of terminal filament 24 mm. General body shape is drop-like. Length of gills I–VI is about 5 mm, length of gill VII is 11 mm. Otherwise quite similar to *P. limai*.

Comment: adult specimen no. MSF O46 has the characteristic CuA branch and apical MA branch of †Hexagenitidae (CuA field not preserved). Its body length of 23.5 mm corresponds to the large size of the holotypical larva. Like *Protoligoneuria* and Recent Setisura this new taxon also has the larval wing pads medially partially fused (Figure 11.9d).

Cratohexagenites minor sp. nov.

Material: larval holotype (Figure 11.9f) no. MB.I.2026 at MNB.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after its smaller size compared to the type species.

Diagnosis and description (Figure 11.9f): hexagenitid larva with enlarged seventh gill of trapezoid shape, differs from type species by body length of 15.5 mm, length of terminal filaments about 6 mm (comparatively shorter than in type species). General body shape is drop-like (maximum width of body, 6.1 mm). Length of gill VII is about 2.4 mm. Otherwise it is very similar to the type species, including the larval wing pads that are medially partially fused (Figure 11.9f). Adults are still unknown.

Oligoneuriidae

Colocrus McCafferty, 1990 (see Figure 11.4b)

Cratoligoneuriella Martins-Neto, 1996a Syn. nov.

Diagnosis: larva: abdomen with pronounced posterolateral projections. Paracercus significantly shorter than cerci. Siphlonuroid setation of terminal filaments: cerci at their inner sides and terminal filum with swimming hairs. Abdomen with leaf-like tracheal gills preserved on segments I–VI (I–III in holotype AMNH 43483, III–V in SMNS larva 66538, I–VI in SMNS larva 66619). Gill I with dorsal insertion (McCafferty, 1990). Ventral gill tufts are not present or not preserved. Abdominal segments with posterolateral projections are present on segments IV–IX. Fore femora and fore tibiae on inner sides are equipped with a row of filtering setae (Plate 8d). Head capsule is broadened; the labium with enlarged and basally fused glossae forms a labial plate (Figure 11.9h; Plate 8e).

Alate stages: forewing with crossveins in costal field only. Gemination of Sc and R_1, R_{4+5} and MA_1, MA_2 and MP_1, MP_2 and CuA. Series of veins running from CuA to posterior wing margin. Intercalaries absent except IMP.

Comments: Martins-Neto (1996a) established a new genus, *Cratoligoneuriella*, based on putative differences of the femoral base of the larval filter hairs. He claimed the presence of a ‘sclerotic process in the middle length of the fore femur’ of *Cratoligoneuriella* without further explanation or figure. Judging from the picture he gives, there is no difference between the detailed structure and origin of the filtering hairs in *Cratoligoneuriella* and *Colocrus*. However, the row of filtering hairs is sometimes detached and dislocated in some specimens (Figure 11.9g; Plate 8d). It is likely that Martins-Neto’s observation can be traced back to this artefact. I regard *Cratoligoneuriella leonardii* as a synonym of *Colocrus*.

Martins-Neto (2002b), in his unpublished doctoral thesis, described another species, *Cratoligoneuriella ninae*, and listed this species in a recent publication (Martins-Neto, 2005a). As the description in this doctoral thesis was never properly published, *Cratoligoneuriella ninae* has to be considered as a *nomen nudum*. This thesis was not available to me, so that I cannot comment on the description given there.

Colocrus indivicum McCafferty, 1990

Cratoligoneuriella leonardii (Martins-Neto, 1996a) Syn. nov.
Cratoligoneuriella ninae (Martins-Neto, 2005b) *nomen nudum*

Material: larval holotype AMNH 43484; adult paratype AMNH 43499 (Figure 11.4b); larvae SMNS 66538 (Figure 11.9g; Plate 8d) and SMNS 66619 (Plate 8e); larva RGMN-T005 coll. Martins-Neto; larvae MB.I.2025 (Figure 11.9h) and MB.I.2027 at MNB.

Diagnosis: larva (Figures 11.9g and h; Plate 8d and e): body length up to 15 mm excluding terminal filaments. Length of cerci up to 7 mm. Fore femora short and broad, middle and hind legs longer and slender. Filtering hairs on forelegs.

Alate stage (Figure 11.4b): forewing length 11 mm. Body length 13.2 mm. Wing venation see generic diagnosis, above.

Comment: McCafferty (1990) assigned an adult specimen (Figure 11.4b) of an oligoneuriid with a body length of 13.2 mm to *Colocrus indivicum*. Judging from the size of the holotype larva, it is most likely that it is indeed the alate stage of *C. indivicum*. Figure 11.9h and Plate 8e show in excellent preservation the labial plate that is characteristic for the larvae of all Oligoneuriidae. The filter apparatus is very well visible in specimen SMNS 66538 (Figure 11.9g; Plate 8d).

Colocrus? magnum sp. nov.

Material: larval holotype SMNS 66624 (Figure 11.9i). Putative adults are not rare in the collections; for example, specimen SMNS 66623 (Figures 11.6a and b), which is a fossil oligoneuriid of corresponding size, but the wing venation (Figures 11.6a and b) differs significantly from the adults attributed to *Colocrus indivicum*, so that the generic attribution is only very preliminary.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after its large body size compared to the other species of the genus.

Diagnosis and description (Figure 11.9i): body length 22.5 mm without terminal filaments. Length of cerci 12 mm; length of terminal filament 9 mm. Femora short and broad.

Ephemeroidea (*sensu* McCafferty, 1991)

There are currently eight different species in eight different genera of Ephemeroidea described from Crato by McCafferty (1990) and Martins-Neto and Caldas (1990). While McCafferty (1990) described only alate stages, the contribution of Martins-Neto and Caldas (1990) only deals with larval specimens. A definite attribution of all larval and imaginal specimens to each other cannot be made at present.

Moreover, the larval specimens are not adequately described, and judging from the figures presented there, the contribution of Martins-Neto and Caldas rather deals with three specimens of a single species than three different genera and species from three different families. However, as I do not have the type material at hand, I here still refrain from synonymizing the three larval specimens described by Martins-Neto and Caldas (1990). The material and diagnoses given by the authors are merely listed.

Four undetermined larval specimens (two specimens SMNS 66630 and SMNS 66634, as well as two specimens without number in collections MURJ and MSF, respectively) and an undetermined adult specimen (MSF without number) of Ephemeroidea are featured in Figures 11.5a–c and 11.6h and i and Plate 8f.

Potamanthidae?

Olindinella gracilis Martins-Neto and Caldas, 1990

Material: larval holotype AMA-I-028 (Figure 11.4c), coll. Federal University of Ceará.

Diagnosis: burrowing larva with rostrum, long mandibular tusk, pubescent, robust tibia, paracercus longer than cercus.

Comment: validity and status doubtful, as discussed above.

Euthyplociidae

Pristiplocia rupestris McCafferty, 1990

Material: adult holotype AMNH 44308 (Figure 11.4d); adult SMNS 66541 (Figures 11.6c and d); various adult specimens in coll. MSF; larvae SMNS 66539 (Figure 11.6e) and SMNS 66621 (Figure 11.6f; Plates 8g and h) (probably two different species).

Diagnosis: alate stage (Figures 11.4d and 11.6c and d): body length 13–14 mm. Forelegs developed, about 4 mm long. Length of forewing 13 mm. Extensive crossvenation throughout wing. RS fork at one-quarter distance from base, MA fork in basal third of wing, MP_2 and CuA strongly decurved posteriorly at base. Cubital field with sigmoid veinlets from CuA to hind margin. A_1 not forked.

Larva (specimen SMNS 66621; Figure 11.6f; Plates 8g and h): body length up to 12 mm excluding terminal filaments (Figure 11.6f). Length of cerci and paracercus up to 2 mm. Abdominal segments II(?)–VII with fringed, doubled, lateral tracheal gills (Plate 8g). Femora flat and broad. Tibial spur not visible. Long, convex mandibular tusks up to 3 mm length, with numerous hairs (Plate 8h).

Comment: the very characteristic larval mandibular tusks equipped with long hairs unambiguously determine the larva as belonging to the Euthylociidae. As there have been only adult specimens of *P. rupestris* found so far, and because there are probably at least two species (Figures 11.6e and f) of euthyplociid larvae (compare the different length and shape of mandibles) from this locality, a definite attribution of one of these two types to the present species is not possible.

Ephemeridae

Australiephemera revelata McCafferty, 1990

Material: adult holotype AMNH 44300 (Figure 11.4e); adult paratype AMNH 44310 (Figure 11.4e).

Diagnosis: ephemeroid forewing, MA forked at midlength, distinct distal arch of CuP, A_1 nearly straight, no cubital intercalaries, hind wing with costal angulation, RS shorter than R_2 and R_{4+5}.

Microephemera neotropica McCafferty, 1990

Material: adult holotype AMNH 43303 (Figure 11.4f).

Diagnosis: ephemeroid forewing, MA forked in basal half of wing, moderate distal arch of CuP, A_1 not forked.

Cratonympha microcelata Martins-Neto & Caldas, 1990

Material: larval holotype USP GP/1T-1677 (Figure 11.4g).

Diagnosis: burrowing nymphs with rounded head, mandible long and smooth, foreleg with expanded tibia, apically with at least two spines.

Comment: validity and status doubtful, as discussed above.

Polymitarcyidae?

Caririnympha mandibulata Martins-Neto & Caldas, 1990

Material: larval holotype GP/1T-1678 coll. University of São Paulo.

Diagnosis: burrowing nymphs with trapezoid head, without rostrum, mandibular tusk short, foreleg with femur and tibia of same length.

Comment: validity and status doubtful, as discussed above.

Baetiscidae

Protobaetisca gen. nov.

Type species: *Protobaetisca bechlyi* sp. nov., by present designation.

Derivation of name: compound noun made up of the Greek prefix *protos* (first) and the Recent genus *Baetisca*.

Diagnosis: as for type species, since it is monotypic.

Protobaetisca bechlyi sp. nov.

Material: larval holotype SMNS 66620 (Figure 11.6g).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after my colleague Günter Bechly, curator of fossil insects and amber at the SMNS, who pointed me to fossil mayflies.

Diagnosis and description (Figure 11.6g): larva with stout, rotund body of ovoid shape. Length 8 mm without terminal filaments. Length of cerci 3 mm. Abdominal segments VI–IX with prominent posterolateral projections, without median spines. Lateral margins of abdominal segments I–V bent up. Abdominal segment VI slightly enlarged, longest abdominal segment, with prominent longitudinal crest most probably representing the caudal closure of a gill chamber. Mesonotum posteriorly extending up to abdominal segment VI, forming a gill chamber (‘carapace’). Anterior part of gill chamber torn and flaked off. It cannot be decided with certainty if the pronotal part of the gill chamber is preserved in its entity or partly broken off together with the anterior part of the mesonotum). Carapace without dorsal spines, lateral parts of carapace not preserved. Length of preserved part of foreleg 4 mm, length of femur 2 mm, length of tibia 0.8 mm. Head with two frontal carinae. Antennae not preserved.

Comment: apparently, this is the fourth record of a fossil stem group representative of the Prosopistomatoidea. Staniczek and Bechly (2002) described *Balticobaetisca velteni* from Eocene Baltic amber extending the distribution of the

Baetiscidae to the Palaearctic. Jell and Duncan (1986) described a specimen from the Lower Cretaceous as Siphlonuridae? gen. nov. It has the general shape of a baetiscid mayfly with a mesonotum that extends posteriorly to abdominal segment VI. The pronotum is separated from the mesonotum. The authors mentioned its similarities to Baetiscidae but refrained from assigning the fossil to this family because its Recent distribution is Nearctic. Nevertheless this fossil either belongs to the stem group of Baetiscidae or Prosopistomatoidea. Sinitshenkova (2000) described *Cretomitarcys luzzi* from the Upper Cretaceous of New Jersey. She assigned the adult male specimen to the †Cretomitarcyinae, a new subfamily of the Polymitarcyidae. McCafferty (2004) realized its affinities and transferred the fossil to the Prosopistomatoidea (= Carapacea *sensu* McCafferty = Posteritorna *sensu* Kluge). He placed it in a new family, the †Cretomitarcyidae. Judging from the figures given in Sinitshenkova (2000), *C. luzzi* indeed clearly belongs to the Prosopistomatoidea: the wing tornus is situated posterior to A_1. The rounded hind wing with multiple intercalaries points to a phylogenetic position in the stemline of Baetiscidae. *C. luzzi* is plesiomorphic in retaining gonopods with several segments and an entirely separated basitarsus of the foreleg. However, I see no reason in placing this species in a separate family.

Protobaetisca bechlyi sp. nov. is the first record of a fossil Baetiscidae from the Crato Formation. The frontal head projections confirm its placement at least in the stem group of Baetiscidae. If the pronotum was separated a placement in the stem group of Prosopistomatoidea cannot be excluded.

The alleged fossil Baetiscidae *Cariephemera marquesi* (Zamboni, 2001) definitely does not belong to the Baetiscidae (see below).

Other records of unnamed Ephemeroptera

- Siphlonuridae (?) sp. 1 McCafferty (1990: 30, figure 11; AMNH 44306, adult)
- Siphlonuridae (?) sp. 2 McCafferty (1990: 30, figure 12; AMNH 44313, adult)
- Siphlonuridae (?) sp. 3 McCafferty (1990: 31, figure 13; AMNH 43477, adult)
- Oligoneuriidae gen. et sp. indet. Martins-Neto (1996a: 188, figure 6c; adult)
- Ephemeroidea *incertae sedis* (Figures 11.5a and b and 11.6h and i; Plate 8f); larval specimens SMNS 66630, SMNS 66634, without number in collections MURJ and MSF)
- Ephemeroidea *incertae sedis* (Figure 11.5c; adult specimen, MSF without number)
- Ephemeroidea sp. 1 McCafferty (1990: 42, figure 30; AMNH 44311, adult)
- Ephemeroidea sp. 2 McCafferty (1990: 42–43, figure 31; AMNH 43480, adult)
- Leptophlebiidae (?) sp. 1 McCafferty (1990: 43, figure 32; AMNH 43474, adult)
- *Comment*: this taxon is relatively frequently found. Other specimens (e.g. SMNS 66639, Figure 11.5d) demonstrate that specimen AMNH 43474 is not a larva, but an adult without preserved wings. The other fossils generally have entangled or wizened wings (probably subimagines) and also only two terminal filaments (cerci).

- Leptophlebiidae (?) sp. 2 McCafferty (1990: 43–44; figure 33; AMNH 43476, adult)
- Leptophlebiidae (?) sp. 3 McCafferty (1990: 44, figure 34; AMNH 44312, adult)
- Family *incertae sedis* sp. 1 McCafferty (1990: 44; AMNH 43453, larva)
- Family *incertae sedis* sp. 2 McCafferty (1990: 44–45; AMNH 43423, larva)
- Family *incertae sedis* Grimaldi and Engel (2005: 166, figure 6.12; AMNH without number; small alate stage with two extremely long cerci but without paracercus)
- Family *incertae sedis* Bechly *et al.* (2001a: figure 30)
- Familia *incertae sedis* (Figures 11.5e and f); larval specimens SMNS 66622, SMNS 66625 and MSF Z2)
- *Comment*: these strange mayfly larvae (body length about 23 mm) have an absolutely unique habitus with broadened and flattened fore and hind femora, but slender mid femora.

Ephemeroptera *incertae sedis*

Costalimella nordestina Martins-Neto, 1996a (Figure 11.8a)
Costalimella zuechii Zamboni, 2001

Comment: these two species have each been described from a single adult specimen. Possibly both specimens resemble small species of †Hexagenitidae. In the forewing, the MA branch is located in the apical fourth of the wing, and in *C. zuechii* the branching of CuA is reported.

Insecta *incertae sedis*

Caririephemera marquesi Zamboni, 2001

Comment: Zamboni, 2001 described an insect larva with eight visible abdominal segments and without abdominal gills as a mayfly larva. Terminal filaments are either not present or not preserved. The author tentatively places the fossil within the Baetiscidae, because 'the lack of gills . . . occurs only in Baetiscidae'. In fact, the gills of the Baetiscidae lie under a gill chamber formed by the enlarged mesonotum. This fossil has no such gill chamber and nor does it exhibit any character that could identify it as a mayfly nymph, even though it might well represent a poorly preserved specimen of *Protoligoneuria limai*.

11.5 Odonata: damselflies and dragonflies

Günter Bechly

The order Odonata includes three Recent suborders (Zygoptera, 'Anisozygoptera' – Epiophlebiidae, and Anisoptera) with a total of 635 Recent genera and 5,538 described species. Odonates are relatively large insects and well known for their beautiful colours, their swift flight and the curious mating in the wheel-position.

Odonates have bristle-like antennae, biting mouthparts and large compound eyes. The thoracic segments have a distinct skew, so that their spiny legs are tilted anteriorly to form a 'catching basket'. The very powerful flight mechanism is driven by a unique combination of upstroke operated by indirect dorso-ventral muscles and a downstroke using direct flight musculature. The wings have a complete and dense venation with a characteristic that includes arculus, nodus, apical pterostigma, intercalary veins IR_1 and IR_2, and a distinct discoidal cell or discoidal triangle. The wing margins and wing veins are covered with spines, and the wing membrane is strongly pleated. The abdomen is long and slender. The primary genitalia are reduced in males, and in the females an ovipositor can be normally developed, hypertrophied or completely reduced. A unique feature within insects is the male secondary copulatory apparatus that is developed on the sternites of the second and third abdominal segments. In the three Recent suborders of Odonata different parts of this apparatus have been independently developed as copulation organs (Bechly *et al.*, 2001b), with structures for the removal of foreign sperm on the intromittent organ (ligula in Zygoptera, hamuli posteriores in Epiophlebiidae and vesicula spermalis in Anisoptera). The apex of the abdomen is provided with a grasping apparatus that is used in the formation of the mating wheel. This grasping apparatus comprises two pairs of claspers (cerci and paraprocts) in Zygoptera, but only a single pair of claspers (cerci), plus an unpaired appendage (epiproctal process) in Epiophlebiidae and Anisoptera.

Development is hemimetabolous, with a distinct aquatic larval stage. Larvae are characterized by a prehensile mask, twisted wing sheaths (convergent with Orthoptera), rectal gills (in Zygoptera also three caudal gill filaments). The larvae of Anisoptera are capable of locomotion by jet propulsion, except for the amphibious larvae of Petaluridae. Adult Odonata are important predators on other insects and have a worldwide distribution. They are only absent from very cold or very arid regions, and the larvae can be found in running water, stagnant water, swamps and phytotelmata, and a few even in brackish water.

Systematics and phylogeny

The systematics of Odonata is still largely based on the typological classification by Fraser (1957), but in the last two decades there have been attempts towards a phylogenetic classification (Carle, 1982; Lohmann, 1996; Trueman, 1996; Bechly, 1999a, 2002, 2003; Rehn, 2003; Hovmöller, 2006). Differences between the results of these attempts are based on different selection of characters or, perhaps even more so, on different methodological approaches (e.g. traditional Hennigian phylogenetic systematics and computer-based numerical cladistics).

There is a broad consensus that Epiophlebiidae and Anisoptera are both monophyletic sister groups, while 'Anisozygoptera' is a paraphyletic assemblage of Recent Epiophlebiidae (a single genus with only two relict species) and fossil stem group representatives of Anisoptera. In modern works there is also a wide consensus that ‘protodonates’ (e.g. †Meganisoptera), †Protanisoptera, †Triadophlebiomorpha and †Protozygoptera+†Archizygoptera are successive basal branches on the stemline of Odonata, and that the Mesozoic family †Tarsophlebiidae represents the sister group of crown group Odonata.

The monophyly of Anisoptera is supported by numerous morphological autapomorphies (sperm vesicle developed as a copulation organ, wing venation with hypertriangle, triangle, subtriangle and anal loop, and larval locomotion with jet propulsion) and this is also the case for Epiophlebiidae (hamuli posteriores developed as a copulation organ, interocellar lobe, ovoid pedicel, hairy eye tubercle and larval stridulation organs). It is also undisputed that Epiophlebiidae is the sister group of Anisoptera, because there are several good synapomorphies (discoidal cell distally distinctly widened in hind wing, male hind wing with anal angle, males with a secondary epiproctal projection, synthorax with the dorsal portion of the interpleural suture suppressed, and larvae with anal pyramid).

Most recent authors consider Zygoptera monophyletic, while Trueman (1996), in a cladistic analysis of wing venational characters, suggested that Zygoptera is a highly paraphyletic group, as previously indicated by Fraser (1957). However, the monophyly of Zygoptera is supported by several strong putative autapomorphies, including the transverse head, the more oblique pterothorax, abdominal sternites with triangular cross-section and longitudinal keel, formation of an ovipositor pouch by the enlarged outer valves (valvula 3 = gonoplacs) of the ninth abdominal sternite, and the highly specialized ligula developed as a copulatory organ. The presence of caudal gills, even though uniquely present in Zygoptera among Recent odonates, has been demonstrated to be a symplesiomorphy by the discovery of a fossil dragonfly larva. This larva has wing sheaths that clearly show the characteristic veinal features of the isophlebiid stem group representatives of Anisoptera, but still possesses three caudal gills.

A detailed phylogenetic system of fossil and Recent odonates with all synapomorphies, based on my results, is available at http://www.bernstein.naturkundemuseum-bw.de/odonata/phylosys.htm Bechly, 2002).

A comprehensive cladistic study of 122 morphological characters by Rehn (2003) basically confirmed this phylogeny: this includes the sister group relationship of †Tarsophlebiidae and crown group Odonata, the monophyly of Zygoptera, a lestinoid+coenagrionoid clade that is sister-group to Calopterygoidea, the position of the relict damselfly *Hemiphlebia* at the very base of lestinoid zygopteres, the position of Petaluridae at the base of Anisoptera, and the sister-group relationship of African Coryphagrionidae to the Neotropical Pseudostigmatidae. The only clear differences concern the positions of amphipterygid and megapodagrionid damselflies, which Rehn (2003) regards as a paraphyletic basal grade towards the lestinoid+coenagrionoid clade. However, the widely separated Zygoptera genera *Diphlebia* and *Philoganga* in this phylogeny indicate an artefact of the cladistic method without proper character weighting, because these two genera are united by very strong larval synapomorphies and some synapomorphies of the imagines.

Recent molecular studies concerning the higher phylogeny of odonates (Misof and Rickert, 1999a, 1999b) did not resolve the Zygoptera problem and in part conflicted with some monophyla; for example, Cavilabiata (Cordulegastridae, Neopetaliidae, Chlorogomphidae and libelluoids) that are very well established by morphological evidence beyond reasonable doubt. Methodological artefacts like long-branch attraction and 'noise' seem to be prevalent. Based on a study of rDNA, Hasegawa and Kasuya (2006) suggested that Zygoptera is paraphyletic (and incorrectly cited Bechly (1996) in support of this hypothesis) and confirmed that Epiophlebiidae is the sister group of Anisoptera.

The phylogenetic position of the Odonata in the tree of insects remains ambiguous. Fossil evidence and some morphological and molecular characters support the monophyly of Palaeoptera (†Palaeodictyopteroida+Ephemeroptera+Odonata), while rather strong characters of the Recent head morphology (Staniczek, 2000) and some molecular data support the monophyly of Metapterygota (Odonata+ Neoptera). Consequently, this issue still has to be considered unresolved.

Fossil record

The fossil record of Odonata is relatively well documented, with about 700 fossil species extending from Tertiary representatives of Recent families back to primitive protodonates of the lower-most Upper Carboniferous (320 mya). The biggest insect in Earth history was the protodonate *Meganeuropsis* from the Permian of North America, with a 75 cm wing span, while some protodonates from the Namurian belong to the oldest-known fossils of winged insects. Other Mesozoic localities with very diverse odonate faunas include the Madygan/Ferghana Basin (Late Triassic, Kyrgyzstan), the Solnhofen lithographic limestone (Upper Jurassic, Germany), the Weald Clay (Lower Cretaceous, southern England) and Liaoning (Lower Cretaceous, China).

Palaeobiology and palaeoecology

The large number of odonate species from the Crato Formation is typical for subtropical and tropical habitats with rather diverse aquatic biotopes. Some taxa, like libelluloid dragonflies, could indicate the presence of lacustrine biotopes, especially as no larvae of these dragonflies have been discovered yet. This is also supported by the occurrence of water striders (Hydrometridae) that are usually confined to standing water bodies or at least calmer water. Bechly (1998c) studied 351 fossil odonates from the Crato Formation (241 adults and 110 larvae): 54% of the adults and 56% of the larvae belonged to the gomphid clade (Plate 9a), and thus to a taxon of Anisoptera that is mostly adapted to lotic habitats. The presence of fast-flowing streams and rivers is therefore very likely, and also supported by the abundance of fossil mayfly larvae.

The somewhat larger percentage of female specimens among the Crato dragonflies (e.g. of the 46 adult holotypes and projected types, one is a larva, nine are of indeterminate sex, 21 are female and only 15 are male) could indicate that many specimens drowned during oviposition attempts.

Crato fossils

Even though they constitute only about 2% of the fossil insects found (Bechly, 1998c), dragonflies are not rare in the Crato Formation, so that more than 1,000 specimens of about 46 different species have been discovered so far. No other fossil locality yields more fossil odonates, either in the number of individuals or in the number of species, than the limestones of the Crato Formation. Furthermore, Crato Formation examples are outstanding because of their completeness and very beautiful preservation. A detailed statistical analysis of the Crato Formation odonate fauna was provided by Bechly (1998c: Table 1 and Appendix).

The first fossil dragonfly from this locality was mentioned by Westfall (1980) and described by Wighton (1987). Subsequently, important contributions with numerous descriptions of new species have been provided by Wighton (1988), Carle and Wighton (1990), Grimaldi (1991), Nel and Escuillié (1994), Nel and Paicheler (1994a, 1994b), Martill and Nel (1996), Bechly (1997a, 1997b, 1997c, 1998a, 1998b, 1998c), Nel *et al.* (1998), Jarzembowski *et al.* (1998), Bechly (1999a, 2000), Bechly *et al.* (2001b, 2001c), Bechly and Ueda (2002), Fleck *et al.* (2002), Martins-Neto (2005a, 2005b) and Grimaldi and Engel (2005).

Occasionally, falsified fossil dragonflies are offered for sale by local traders in Brazil. Such specimens often include the wings of a Recent dragonfly glued to a slab of Crato limestone, combined with a carved body. Such a specimen is deposited in the Paläontologische Staatssammlung (BSPGM) in Munich and was figured by Bechly *et al.* (2001b: Abb. 23), while a similar example was figured by Martill (1994).

Zygoptera: damselflies

Diagnosis: small-to-medium-sized damselflies (wing span less than 6 cm), with delicate bodies and a transverse head with large compound eyes; forewings and hind wings of very similar shape and venation, and without sexual dimorphism; wing venation of both pairs of wings with basally open or closed discoidal cells and a subdiscoidal cell. About 278 genera with more than 2,664 species. Up to now, no larvae of Zygoptera have been discovered among the hundreds of fossil dragonfly larvae from the Crato Formation, which suggests that they all lived in lacustrine habitats outside the Crato lagoon.

Family *incertae sedis* (probably Hemiphlebiidae)

Cretarchistigma Jarzembowski *et al.,* 1998

Cretarchistigma (?) essweini Bechly, 1998c

Material: female holotype SMNS 63071 (Figure 11.10a); female paratypes no. 51 and no. 1007 at NSMT; female paratype no. 101 at KMNH; specimen SMNS 66393 (Plate 2c); specimens no. MB.1999.3 MB.I.2055 (old no. D52) and no. MB.1999.3 MB.I.2056 (old no. C24) at MNB (ex MSF); several specimens in other collections (Plate 9b).

Diagnosis: wing length 9.8–10.5 mm; hind wing discoidal cell closed, elongate and narrow; pterostigmal brace distinct but not very oblique; IR_1 originates one cell basal of pterostigma or beneath stigmal brace; cell beneath pterostigma not widened; pterostigma with ‘micraster-type’ microsculptures; arculus aligned with Ax2; six non-aligned postnodal crossveins; thorax more gracile than in *Parahemiphlebia*; anal appendages very long and slender in males, but strongly reduced in females.

Comment: the new specimen SMNS 66393 (Plate 2c) demonstrates very rare preservation of the original metallic-green body colour (previously noted by Bechly, 1998c for *Parahemiphlebia cretacica*, Plate 9c), very similar to the colour of Recent Hemiphlebiidae. This is further evidence for referral of this species to Hemiphlebiidae. It is the first Mesozoic fossil record for preservation of interference colours.

Hemiphlebiidae Tillyard, 1926

Parahemiphlebia Jarzembowski *et al.,* 1998

Diagnosis: wings hardly petiolated; discoidal cell basally open in forewings; arculus somewhat distal of Ax2 in forewings; maximum of four to seven postnodal crossveins that are non-aligned; no intercalary veins (except IR_1 and IR_2) and no lestine oblique vein; RP_1 strongly kinked at stigmal brace; MP strongly bent at discoidal cell; anal area crossed by two transverse veinlets between AA and AP; head with distinct suture between vertex and occiput; metallic green body coloration (rarely preserved); males with long paraprocts (Bechly, 1998c, *contra* Jarzembowski *et al.*, 1998).

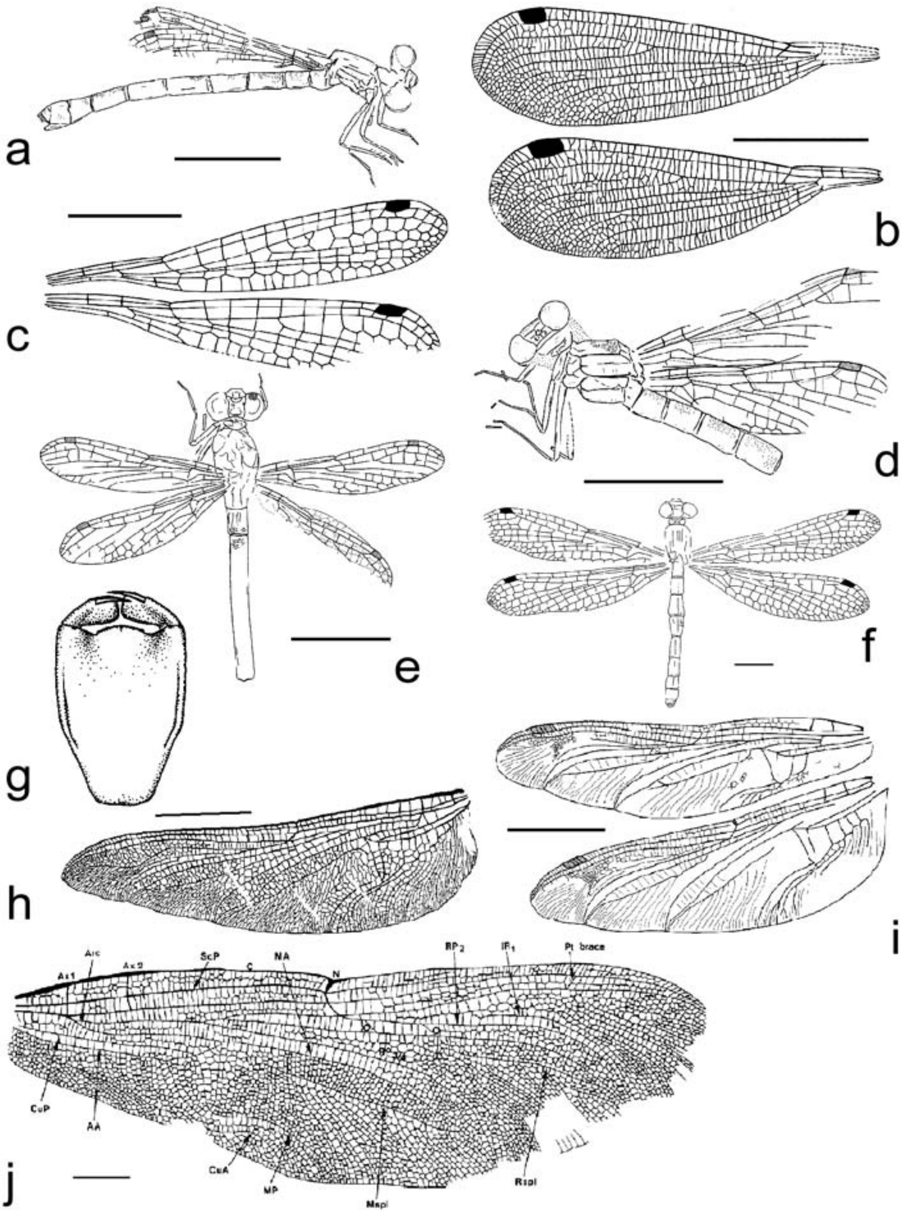

Fig. 11.10. Crato Formation Odonata: (a) Hemiphlebiidae?, *Cretarchistigma essweini*, female, holotype SMNS 63071; scale bar, 5 mm (after Bechly, 1998: figure 17): (b) Thaumatoneuridae, *Euarchistigma atrophium*, holotype AMNH 44204; scale bar, 3 mm (combined after Carle and Wighton, 1990: figures 2 and 3): (c) Protoneuridae, *Eoprotoneura hyperstigma*, male, holotype AMNH 44203; scale bar, 5 mm (after Carle and Wighton, 1990: figure 8); (d) Hemiphlebiidae, *Parahemiphlebia mickoleiti*, paratype SMNS 63072; scale bar, 5 mm (after Bechly, 1998: figure 16); (e) Hemiphlebiidae, *Parahemiphlebia mickoleiti*, holotype

Comment: about 11% of the Crato fossil odonates belong to the primitive damselfly family Hemiphlebiidae, which has only a single Recent relict species, *Hemiphlebia mirabilis*, in Australia.

Parahemiphlebia cretacica Jarzembowski *et al.*, 1998

Material: male holotype MNHN-LP-R.10451 (Figure 11.10f); female allotype MNHN-LP-R.10452; and male paratype MNHN-LP-R.10453 (Figure 11.10f); many specimens on other collections (Plate 9c).

Diagnosis: wing length 12.5–15.5 mm; five to seven postnodal crossveins; pterostigmal brace extremely oblique; IR_1 originates basal of pterostigma.

Parahemiphlebia mickoleiti Bechly, 1998c

Material: holotype without number (also figured in Grimaldi and Engel, 2005: figure 6.44) at AMNH, New York (Figure 11.10e); paratype SMNS 63072 (Figure 11.10d). Additional specimen SMNS 66385.

Diagnosis: wing length 8.9–9.9 mm; only four postnodal crossveins; pterostigmal brace highly oblique, but not as extreme as in *P. cretacica*; IR_1 originates beneath the distal side of pterostigma.

Parahemiphlebia spec. nov. (?) Bechly, 1998c

Material: specimen no. NSMT 563, and a further specimen mentioned by Bechly (1998c: 62).

Diagnosis: habitus, venation, and size similar to *P. cretacica* (wing length 13–14 mm), but pterostigmal brace not very oblique.

Comment: it is not yet possible to decide whether these two specimens really represent a new species or just slightly aberrant specimens of *P. cretacica*.

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AMNH without number; scale bar, 5 mm (after Bechly, 1998: figure 14); (f) Hemiphlebiidae, *Parahemiphlebia cretacica*, reconstruction from holotype wings and paratype body (combined after Jarzembowski *et al.*, 1998: figures 3A–D, figure 4A); (g) Nothomacromiidae, *Nothomacromia sensibilis*, mask (after Carle and Wighton, 1990: figure 22); (h) Aeschnidiidae, *Wightonia araripina*, holotype AMNH 43268; scale bar, 10 mm (redrawn after Carle and Wighton, 1990: figure 21); (i) Aeschnidiidae, *Wightonia araripina*, B10 coll. MSF; scale bar, 10 mm (after Bechly, 1998: figure 24); (j) Aeschnidiidae, *Santanoptera gabbotti*, holotype LEIUG 115858; scale bar, 10 mm (after Martill and Nel, 1996: figure 2).

Protoneuridae Jacobson and Bianchi, 1905

Isostictinae Fraser, 1955

†Eoprotoneurini Carle and Wighton, 1990

Eoprotoneura Carle and Wighton, 1990

Eoprotoneura hyperstigma Carle and Wighton, 1990

Material: male holotype AMNH 44203 (also figured in Grimaldi and Engel, 2005: figure 6.39) (Figure 11.10c); female paratypes AMNH 44201 and AMNH 44202. A very nice female specimen with ovipositor is SMNS 66386; numerous specimens in other collections (Plate 9d).

Diagnosis: wing length 16.0–18.5 mm; only two antenodal crossveins and arculus somewhat distal of Ax2; discoidal cell rectangular, undivided, and closed in both pairs of wings; postnodal crossveins aligned; pterostigma braced; veins AA and CuA totally fused with hind margin; vein MP strongly shortened, ending at the level of the nodus.

Comment: about 6–7% of the fossil odonates belong to this taxon.

Thaumatoneuridae Tillyard and Fraser, 1938

Thaumatoneurinae Tillyard and Fraser, 1938

†Euarchistigmatini Carle and Wighton, 1990

Euarchistigma Carle and Wighton, 1990

Diagnosis: wings petiolated and apically broadened with a very dense venation; discoidal cell rectangular and undivided; subdiscoidal cell undivided; only two antenodal crossveins and Ax2 aligned with arculus; postnodal crossveins not well-aligned; nodus in very basal position at 25% of wing length; subnodus slightly distal of origin of IR_2, but far basal of origin of RP_2; pterostigma very broad and unbraced; all longitudinal veins strongly bent towards hind margin, especially at apex; RA, RP_1 and IR_1 apically converging; only a single row of cells between CuA and hind margin. The original diagnosis by Carle and Wighton (1990) was revised by Bechly (1998c).

Comment: approximately 1.5% of the Crato odonates belong to this taxon.

Euarchistigma atrophium Carle and Wighton, 1990

Material: holotype AMNH 44204 (Figure 11.10b); four further specimens were described by Bechly (1998c: 41–43) from SMNK, NSMT (no. 46), and MSF; specimen no. SMF Q55. SMNS 66387 (old no. H6) is a particularly nice example (wing length 32 mm) with anal appendages preserved.

Diagnosis: forewing length 30–35 mm; discoidal cell similar in both pairs of wings.

Comment: a new specimen no. SMF Q55 (Plate 9e) shows for the first time the original colour pattern of this calopterygoid-like damselfly, which has the basal two-thirds of all wings tinted in dark colour, while the apical thirds are hyaline.

Euarchistigma marialuiseae sp. nov.

Material: holotype with preliminary number Q56 (Plate 9f) and paratype no. Q87, deposited at SMF; paratype no. MB.1999.3 MB.I.2050 (old no. D29) (figured by Bechly, 1998c: figure 19) deposited at MNB (ex MSF); a further specimen with a wing length of only 26.5 mm is no. MSF O35.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after my dear wife Maria Luise.

Diagnosis and description (Plate 9f): distinctly smaller than type species; forewing length only 26.5–28.5 mm; discoidal cell longer and narrower in hind wings. Otherwise, very similar to the *E. atrophium*, but potential colour pattern not preserved as in most specimens of *E. atrophium*.

‘Anisozygoptera’: ancient dragonflies

†Stenophlebioptera Bechly, 1996

†Stenophlebiidae Needham, 1903

Diagnosis: large dragonflies with a very dense wing venation with numerous small cells and many intercalary veins; both pairs of wings of similar shape and venation, long and slender, and more or less petiolated (at least in hind wings); both pairs of wings with hypertriangle and triangle; distinct subdiscoidal cell instead of a subtriangle; nodal and subnodal veinlets very oblique and elongated; IR_2 close to $RP_3{+}_4$, but far basal of RP_2; pterostigmata very long and shifted in a more basal position; hind wings of males often with an anal angle; larvae still unknown, but certainly of anisopterid type with anal pyramid instead of caudal gills (as in Epiophlebiidae).

Comment: new diagnoses and phylogenetic analyses of all Stenophlebiidae, as well as several descriptions of new species, are provided by Nel *et al.* (1993) and Fleck *et al.* (2003). A further new species *S. nusplingensis* was described by Bechly *et al.* (2003), while *S. casta* was re-described by Bechly (2005) and transferred from Stenophlebiidae to a new isophlebioid family Parastenophlebiidae.

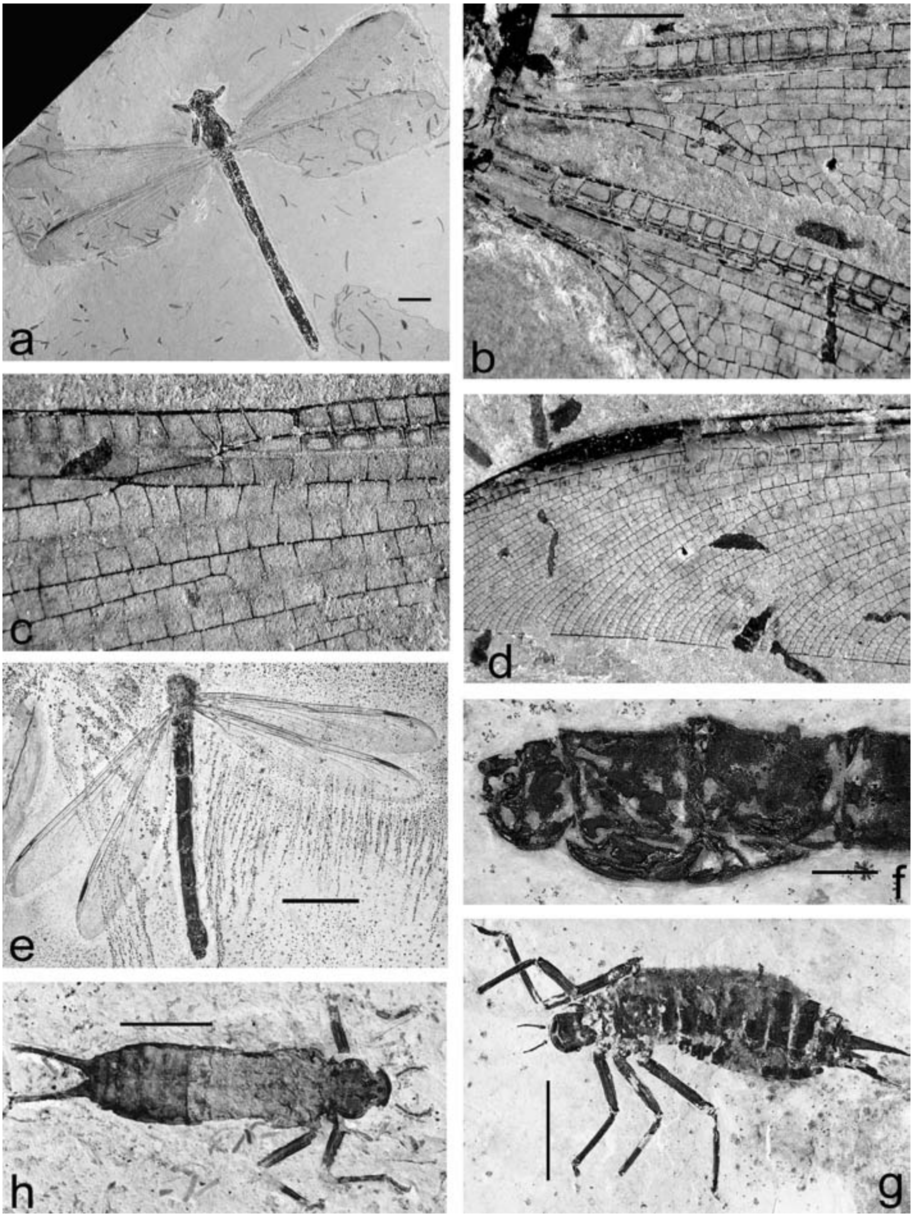

Fig. 11.11. Crato Formation Odonata: (a) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., male, holotype SMNS Z109; scale bar, 10 mm; (b) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., male, right wing bases, holotype SMNS Z109; scale bar, 5 mm; (c) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., male, left hind wing nodus, holotype SMNS Z109; (d) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., male, left hind wing pterostigma, holotype SMNS Z109; (e) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., female, paratype and allotype

Cratostenophlebia gen. nov.

Type species: *C. schwickerti* sp. nov., by present designation.

Derivation of name: named after the type locality and the fossil genus *Stenophlebia*.

Diagnosis: as for type species.

Cratostenophlebia schwickerti sp. nov.

Material: male holotype SMNS no. Z109 (Figures 11.11a–d; Plates 9g and h) and female paratype and allotype SMNS no. Z110 (Figures 11.11e and f; Plate 9i), both donated as permanent loans with later inheritance to SMNS by coll. MSF.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: in honour of the collector Mr Michael Schwickert (Sulzbachtal, Germany).

Diagnosis and description (Figures 11.11a–f; Plates 9g–i): very large dragonfly with more than 140 mm wing span and a total body length of 94 mm; Anisoptera-like robust body and globular head with very large compound eyes that are only separated by a single-millimetre distance (Plate 9g); cerci short and stout (about 2.3 mm long and 1.0 mm broad) (Plate 9h); wings elongate and falcate, and both pairs of wings of very similar size, shape and venation (Figures 11.11a and e); discoidal cell indistinctly divided into hypertriangle and triangle by a crossvein that is not ending at the distal angle of triangle (Figure 11.11b); hypertriangle and triangle each divided by a crossvein (autapomorphy, unlike other Stenophlebiidae); triangles and subdiscoidal cells not transverse, because veins MP+Cu and AA are nearly straight (symplesiomorphy with *Prostenophlebia* and *Hispanostenophlebia*); nodal vein as in *Stenophlebia latreillei* with one or two postnodal crossveins above it, but none below it (Fig. 11.11c); subnodus elongate (about as long as nodal veinlet) but with only one crossvein above it and none below it (Figure 11.11c); in the putative male holotype RP_2 originates at subnodus in all four wings (symplesiomorphy with *Prostenophlebia* and *Cretastenophlebia*, unlike *Hispanostenophlebia* and *Stenophlebia*, which possess the characteristic stenophlebiid oblique veinlet beneath the subnodus between RP_1 and RP_2), while in the female paratype the ‘stenophlebiid oblique veinlet’ is completely absent only

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SMNS Z110; scale bar, 20 mm; (f) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., female, ovipositor,, paratype and allotype SMNS Z110; scale bar, 2 mm; (g) Nothomacromiidae, *Nothomacromia sensibilis*, SMNS 66399; scale bar, 10 mm; (h) Nothomacromiidae, *Nothomacromia sensibilis*, SMF no. 1002; scale bar, 15 mm.

in the right forewing, very tiny and indistinct in the right hind wing, but very distinct with two 'origins' of RP_2 in the left fore- and hind wing (consequently this feature seems to be much more variable than previously believed); origins of RP and MA widely separated in arculus; three rows of cells in basal area of postdiscoidal space in both pairs of wings (autapomorphy, unlike other Stenophlebiidae); Mspl well-defined; primary antenodals Ax1 and Ax2 as in *Cretastenophlebia*, with Ax0 in relatively distal position; no accessory antenodal crossveins between Ax0 and Ax1 and Ax2 (symplesiomorphy with *Cretastenophlebia*); pterostigmata very elongate and unbraced (Figure 11.11d); no distinct lestine oblique vein 'O'; both wings are strongly petiolated with a very long petiole and thus much reduced submedian area even in the forewing (autapomorphic difference to *Stenophlebia*, maybe similar to *Hispanostenophlebia* of which the forewing is unknown); the female has a normally developed endophytic ovipositor as in Aeshnidae (Figure 11.11f).

Anisoptera: dragonflies

Diagnosis: medium-sized to very large dragonflies (wing span at least 3–4 cm), with robust bodies and a globular head with very large compound eyes; hind wings distinctly broader than forewings; wing venation of both pairs of wings with discoidal triangles, hypertriangles and subtriangles (instead of a subdiscoidal cell), and often with an anal loop; sexual dimorphism of hind wings, with rounded anal margin in females, but with angulated anal margin (anal angle and anal triangle) in males of most taxa. About 356 Recent genera with more than 2,872 species.

†Nothomacromiidae Carle, 1995 (stat. rest.)

(subst. name for Pseudomacromiidae Carle and Wighton, 1990)

Nothomacromia Carle, 1995

(subst. name for *Pseudomacromia* Carle and Wighton, 1990)

(= genus *Conan* Martins-Neto, 1998c, new synonymy)

Nothomacromia sensibilis (Carle and Wighton, 1990)

(*Conan barbarica* Martins-Neto, 1998c, new synonymy)

Material: holotype AMNH 44205 (also figured in Grimaldi and Engel, 2005: figure 6.45) (Figure 11.10g); four specimens with nos SMNS 66397 (Figure 11.12a), SMNS 66398, SMNS 66399 (Figure 11.11g) and SMNS 66404; five specimens with no. MB.1999.3 MB.I.2036, no. MB.1999.3 MB.I.2037 (old no. B47), no. MB.1999.3 MB.I.2038 (old no. C47), no. MB.1999.3 MB.I.2039 (old no. C48a) and no. MB.1999.3 MB.I.2040 (old no. 1005) deposited at MNB; specimen no. SMF 1002 (Figure 11.11h); and specimens nos B42 (Plate 13c) and B53 in coll. MSF (figured by Bechly, 1998c: figures 28 and 29).

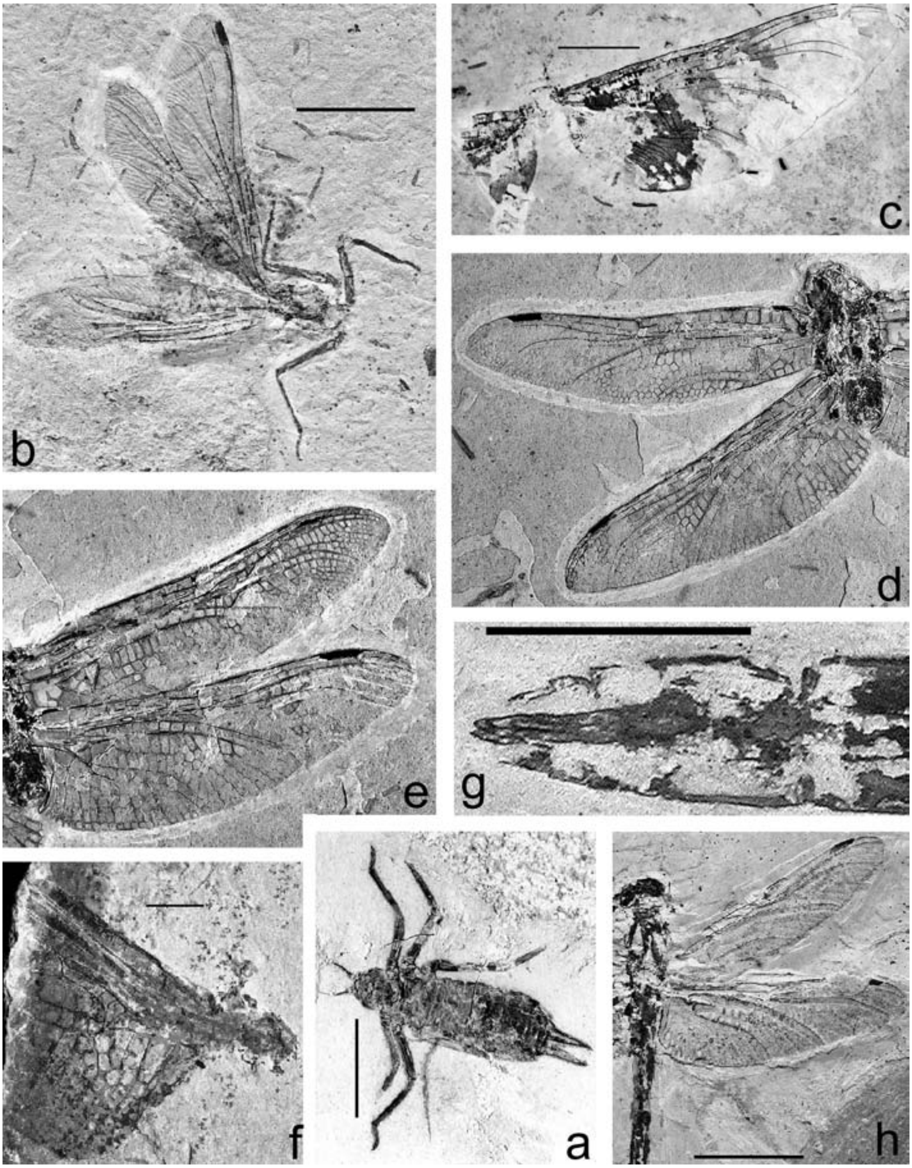

Fig. 11.12. Crato Formation Odonata: (a) Nothomacromiidae, *Nothomacromia sensibilis*, SMNS 66397; scale bar, 10 mm; (b) Aeschnidiidae, *Wightonia* cf. *araripina*, SMNS 66611; scale bar, 15 mm; (c) Aeschnidiidae, *Santanoptera gabbotti*, R4 coll. MSF; (d) Cretapetaluridae, *Eotanypteryx paradoxa* gen. et sp. nov., male, left wings, holotype SMF Q90; (e) Cretapetaluridae, *Eotanypteryx paradoxa* gen. et sp. nov., male, right wings, holotype SMF Q90; (f) Liupanshaniidae, *Paramesuropetala gigantea*, female, left hind wing base, SMNS 66613; (g) Araripegomphidae, *Araripegomphus andreneli*, female, ovipositor, SMNS 66392; (h) Anisoptera, gen. et sp. nov., male, SMNS 66592. Scale bars: f,g, 5 mm; a, 10 mm; b,c,h, 15 mm.

Diagnosis (Figures 11.10g, 11.12a and 11.11g and h; Plate 13c): body length 14.3–63.5 mm without antennae and anal appendages; antennae lyra-shaped; paraprocts hypertrophied and forcep-like (as in Aeschnidiidae); epiproct small and needle-like; mask of the flat gomphoid type with broad palps (Figure 11.10g); legs very long (as in Aeschnidiidae); the corresponding adults are still unknown.

Comment: about 7% of the Crato odonates belong to this family, and 22% of all the dragonfly larvae. Fleck *et al.* (2002: 178–179) demonstrated that the aeschnidiid affinities proposed by Bechly (1998c) cannot be upheld, and discussed possible affinities of the nothomacromiid larvae with anisozygopterous dragonflies, but dismissed this hypothesis (as did Bechly, 1998c) because of the complete lack of adult fossil anisozygopteres in the Crato Formation at the time of writing. However, the present discovery of two specimens of Stenophlebiidae from this locality, described above, suggests that the possibility of a correspondence with the *Nothomacromia*-type of larvae has to be reconsidered, also because the very large size of these adult Stenophlebiidae from Crato corresponds well with the giant size of the ultimate instar larvae.

Some apparent differences in the structure of the paraprocts (compare Figures 11.12a and 11.11g and h, and Plate 13c), for example the length and shape as well as the presence or absence of a serrated margin, previously seemed to suggest that there is more than one species of *Nothomacromia* larvae. However, specimen no. MB.1999.3 MB.I.2040 from MNB clearly shows that the apparent difference between broader forcep-like paraprocts (as in the holotype of *Nothomacromia sensibilis* and most other specimens) and very slim needle-like paraprocts (as in the holotype of *Conan barbarica*, or specimens no. SMF 1002 and no. B53) are an artefact of preservation, because the paraprocts are enforced by a tube-like structure, which sometimes is the only part preserved, while mostly the complete paraprocts are preserved. The absence or presence of a serrated margin is similarly due to differential preservation.

Conan barbarica was erroneously described as a larva of the beetle family Coptoclavidae by Martins-Neto (1998c), but was correctly recognized by Zamboni (2001) as a dragonfly nymph similar to *Nothomacromia*. There are no characters that justify generic separation of *C. barbarica* (*contra* Zamboni, 2001). Most differences (size, proportions and shape of body) are due to ontogeny, and the apparently different shape of the paraprocts is explained above. Furthermore, the different size is an insufficient criterion for generic distinction: for example specimen SMNS 66398 has all characters of *N. sensibilis* (including the shape of the paraprocts), but a larger size (body length about 4 cm) combined still with small wing sheaths (length only 6–7 mm), so that it would have even exceeded the size of *C. barbarica* in the final instar with fully developed wing sheaths. Finally, the different shape of the abdomen is a spurious character, as this is very flexible in Recent dragonfly larvae.

Consequently, *C. barbarica* is here regarded as a junior synonym of *Nothomacromia sensibilis*.

†Aeschnidiidae Needham, 1903

Diagnosis: large dragonflies; both pairs of wings of equal length, with a very dense venation, often partly or totally dark coloured; arculus close to Ax1; both pairs of wings with transverse and narrow triangles that are far removed from arculus, long and narrow hypertriangles, and hypertrophied subtriangles; a vein pseudo-ScP is developed in the postnodal area; two lestine oblique veins; Mspl and Rspl; anal area distinctly fan-like; hind wing strongly broadened, without anal angle and anal triangle in males; all wing spaces (e.g. median space, submedian space, triangle, and hypertriangle, etc.) traversed by numerous crossveins; compound eyes separated; abdomen thick and shorter than wings; females with very hypertrophied, long and thin ovipositor; larvae (still unknown from Crato) with concave spoon-shaped mask (unlike Nothomacromiidae), very long legs (like Nothomacromiidae), large forcep-like paraprocts (like Nothomacromiidae) and long ovipositor in female larvae (unlike Nothomacromiidae).

Wightonia Carle in Carle & Wighton, 1990

Wightonia araripina Carle in Carle & Wighton, 1990

Material: holotype AMNH 43268 (Figure 11.10h); female specimen no. KMNH; specimens SMNS 66610 and SMNS 66611 (Figure 11.12b); specimen MSF B10 (Figure 11.10i; also figured in Bechly, 1998c: figures 23–26); female specimen D28 at MNB (figured Bechly, 1998c: figure 22).

Diagnosis: forewing length 38–47.0 mm and hind wing length 38.0–46.0 mm; pterostigma well defined (Bechly, 1998c, *contra* Carle and Wighton, 1990), but traversed by about four crossveins and not always bulged, thus not visible in fossils without preserved colour of the stigma (e.g. in the holotype or in the isolated forewing SMNS 66610); stigmal brace present in some fossils, but very indistinct; triangle very narrow and divided into a single vertical row of about six cells; only one row of cells between ScP and C; one or two rows of cells between RA and RP_1; undulating complex intercalary vein (not IR_1) between RP_1 and RP_2.

Comment: the phylogenetic position was discussed by Nel and Martínez-Delclòs (1993: 64–65) and the original diagnosis was corrected and amended by Bechly (1998c: 43–47, figures 22–27), who described and figured additional specimens.

Some smaller specimens (e.g. SMNS 66610, SMNS 66611 = G28 and no. MSF B10 described by Bechly, 1998c) have a wing length of only about 38–40 mm. Specimen SMNS 66611 even has a preserved forewing length of only 35 mm, and an estimated total length of maximum 38 mm (Figure 11.12b). These fossils could belong to a new species, because a wing-length range of 38–47 mm seems to be too high to be attributed to infraspecific variability.

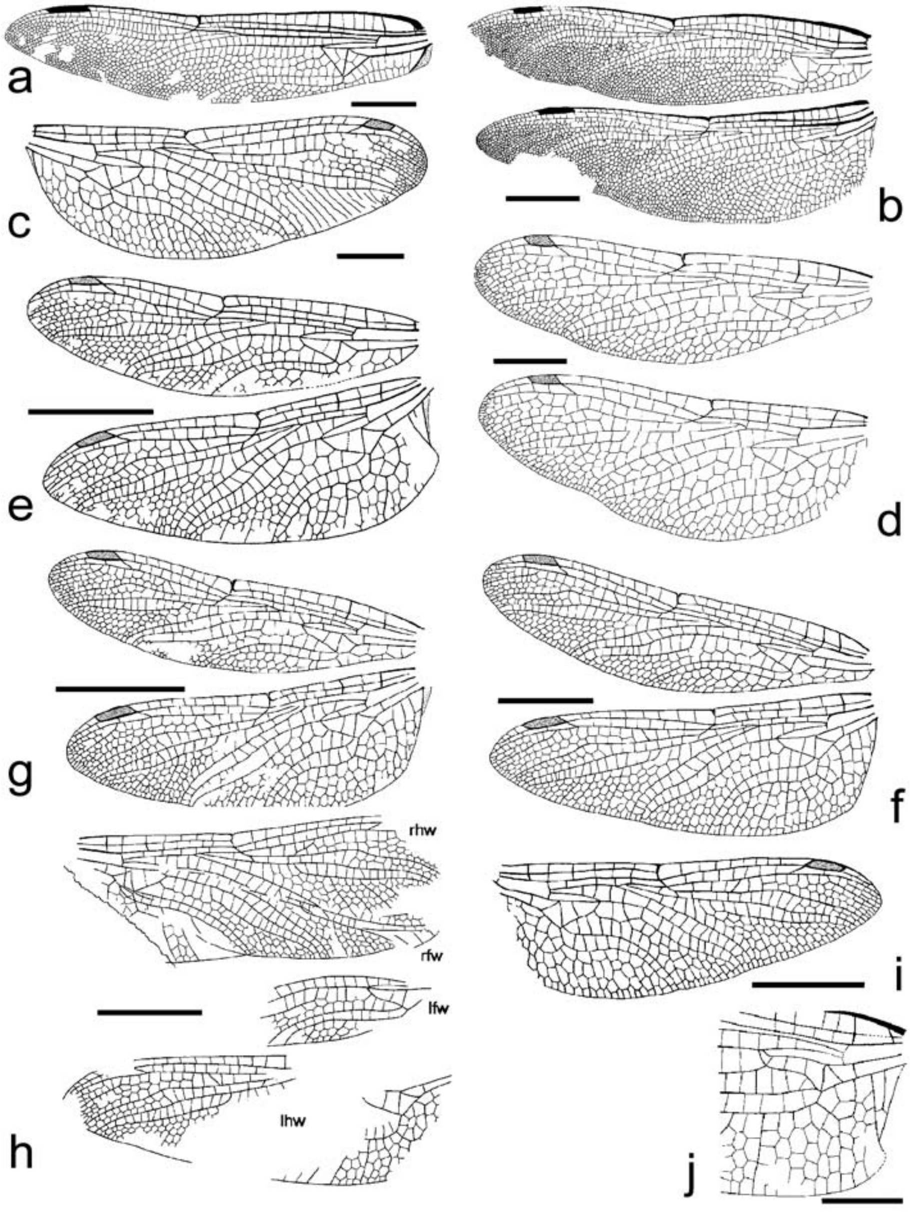

Fig. 11.13. Crato Formation Odonata: (a) Liupanshaniidae, *Paramesuropetala gigantea*, holotype MNHN-LP-R.55194; scale bar, 10 mm (after Bechly *et al.*, 2001: figure 28); (b) Cretapetaluridae, *Cretapetalura brasiliensis*, female, holotype MCSNM I 9562; scale bar, 10 mm (redrawn after Nel *et al.*, 1998: figures 43 and 44); (c) Gomphaeschnidae, *Progomphaeschnaoides staniczeki*, female, holotype JME AP 1997–4a,b; scale bar, 5 mm (after Bechly *et al.*, 2001: figure 114); (d) Gomphaeschnidae, *Progomphaeschnaoides ursulae*, female, holotype SMNK 2357 PAL, scale bar, 5 mm (combined after Bechly *et al.*, 2001: figures 111 and

Santanoptera Martill & Nel, 1996

Santanoptera gabotti Martill & Nel, 1996

Material: holotype LEIUG 115858 (Figure 11.10j); SMNS 66609; nos R3 and R4 (Figure 11.12c) in coll. MSF.

Diagnosis: forewing length 62.3–64.1 mm; hind wing length 62–63 mm; arculus obliterated; pterostigma completely reduced, but a distinct stigmal brace is still present; triangle divided into two or three vertical rows of cells; two or three rows of cells between ScP and C; two or four rows of cells between RA and RP_1.

Comment: there is a fragmentary new specimen SMNS 66609 with two connected hind wings, which are 62 mm long and a maximum of 25 mm wide. Two further specimens, no. R3 (forewing length 64.1 mm) and R4 (hind wing length 63 mm), were in coll. MSF, and show more details of the hind wing venation (no pterostigma, narrow and oblique triangle with numerous cells, very broad and densely veined anal area; Figure 11.12c).

†Cretapetaluridae Nel *et al.*, 1998

Cretapetalura Nel *et al.*, 1998

Cretapetalura brasiliensis Nel *et al.*, 1998

Material: female holotype no. I 9562 at MCSNM (Figure 11.13b).

Diagnosis: length of fore- and hind wings 67.0 mm; two lestine oblique veins, the first one only one cell distal of subnodus; distal side of hind wing triangle strongly angulated, with a strong post-trigonal intercalary vein originating at the angle; triangle transverse and undivided in forewings, but elongate and two-celled in hind wings; forewing subtriangle large and three-celled, hind wing subtriangle widened and divided by a crossvein; very long and distinct vein IR_1 between RP_1 and RP_2; pterostigma very long and in basal position, with the stigmal brace displaced between stigma and nodus; hind wing anal loop longitudinally elongated.

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112); (e) Gomphaeschnidae, *Gomphaeschnaoides obliquus*, male, SMNS 63069; scale bar, 10 mm (after Bechly *et al.*, 2001: figure 118); (f) Gomphaeschnidae, *Gomphaeschnaoides magnus*, female, holotype JME AP 1997–2; scale bar, 10 mm (after Bechly *et al.*, 2001: figure 120); (g) Gomphaeschnidae, *Gomphaeschnaoides betoreti*, female, holotype BSPGM no. 11; scale bar, 10 mm (after Bechly *et al.*, 2001: figure 123); (h) Gomphaeschnidae, *Gomphaeschnaoides petersi*, male, holotype JME AP 1997–3; scale bar, 10 mm (combined after Bechly *et al.*, 2001: figures 121 and 122); (i) Gomphaeschnidae, *Gomphaeschnaoides obliquus*, female holotype AMNH 43257; scale bar, 10 mm (redrawn after Wighton, 1987: figure 2); (j) Liupanshaniidae, *Araripeliupanshania annesusaea*, male, hind wing base, holotype MB.1999.3 MB.I.2047; scale bar, 5 mm (after Bechly *et al.*, 2001: figure 26).

Eotanypteryx gen. nov.

Type species: *E. paradoxa* sp. nov., by present designation.

Derivation of name: after the similarity to the Recent genus *Tanypteryx*.

Diagnosis: same as type species, since it is monotypic.

Eotanypteryx paradoxa sp. nov.

Material: male holotype (Figures 11.12d and e) no. SMF Q90.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after the strange combination of plesiomorphic and apomorphic character states.

Diagnosis and description (Figures 11.12d and e): a thorax with all four wings; wing span 99 mm; forewing 45.1 mm long; hind wing 43.9 mm long and a maximum of 14.6 mm wide; stigmal brace shifted midway between nodus and pterostigma; only a single lestine oblique vein two cells distal of subnodus; hypertriangles free; forewing triangle free and very transverse and narrow; hind wing triangle free and acute; forewing subtriangle large and two-celled; hind wing subtriangle free and not enlarged; no Mspl or Rspl; IR_1 not hypertrophied; post-trigonal area with two rows of cells and a convex intercalary vein in both pairs of wings; anal loop posteriorly closed and two-celled; hind wing with anal angle and three-celled anal triangle (male).

Comment: this new genus and species is clearly a Petalurida and it looks quite similar to the Recent North American genus *Tanypteryx*, because it shares the autapomorphies of the subfamily Tachopteryginae (distal lestine oblique vein reduced) and the tribe Tanypterygini (wings shorter than 50 mm; IR_1 shorter and zigzagged; wing space between RP_1 and RP_2 not expanded, with less than eight to nine rows of cells; bridge-space less narrowed; hind wing triangle free; area between RP_3+_4 and MA not strongly widened near wing margin, and MA not undulate; distal side of hind wing triangle slightly angled, correlated with a convex intercalary vein in the post-trigonal area; basal part of post-trigonal area only with two rows of cells). However, the distal position of the forewing nodus at about 50% of the wing length, the long hind wing CuAa that nearly reaches the level of the nodus and the short pterostigmata (only two or three cells long) that do not reach the basally shifted stigmal brace are symplesiomorphies with Cretapetaluridae, that exclude a position within crown group Petaluridae.

†Liupanshaniidae Bechly *et al.*, 2001b

Diagnosis: hind wing triangle at least three-celled, longitudinally elongate, and narrow (anterior side distally curved and ending on the anterior side; distal side sigmoidally curved and with a strong angle); forewing triangle equilateral and three-celled; both pairs of wings with a strong intercalary vein in post-trigonal area; only a single lestine oblique vein; area between RP_1 and RP_2 very narrow; RP_2 and IR_2 distally undulate.

Comment: a phylogenetic analysis of this enigmatic fossil family was provided by Lin *et al.* (2002).

Paramesuropetala Bechly *et al.,* 2001b

Paramesuropetala gigantea Bechly *et al.,* 2001b

Material: holotype MNHN-LP.R.55194 (Figure 11.13a); specimen SMNS 66613 (Figure 11.12f).

Diagnosis: forewing length 67.0 mm; post-trigonal area with three rows of cells in forewing.

Comment: specimen SMNS 66613 is a basal fragment of a female hind wing (Figure 11.12f). The anal loop is indistinctly closed and the anal margin is rounded without anal angle and anal triangle (female), but otherwise the venation is identical to *Araripeliupanshania*, including the structure of the peculiar triangle. However, this fossil is much bigger than *Araripeliupanshania annesuseae*, with a maximum width of 19 mm (instead of only 12 mm in the holotype of *A. annesuseae*, which has a hind wing length of 38.5 mm) and a triangle that is about 7 mm long (instead of 4 mm in the holotype of *A. annesuseae*). Consequently, the estimated total hind wing length of this specimen is 61 mm, which corresponds quite well with the forewing length of the holotype of *Paramesurometala gigantea*. Therefore, this specimen strongly confirms the attribution of *Paramesurometala* to Liupanshaniidae.

Araripeliupanshania Bechly *et al.,* 2001b

Araripeliupanshania annesuseae Bechly *et al.,* 2001b

Material: male holotype MB.1999.3 MB.I.2047 (old no. D58) at the Museum für Naturkunde in Berlin (Figure 11.13j; Plate 10a); paratype and female allotype SMNS 64345 (old no. 72); male paratype SMNS 64343; a very well-preserved isolated forewing SMNS 66616 (old no. R9); an isolated hind wing without number in coll. MURJ; and two beautiful specimens with nos M56 and L75 in coll. MSF.

Diagnosis: forewing length 35.3–40.2 mm and hind wing length 34.7–38.5 mm; post-trigonal area with two rows of cells in forewing.

Comment: this species was previously mentioned (as *nomen nudum*) and figured by Bechly (1998c: figure 30).

Gomphaeschnidae Tillyard and Fraser, 1940

†Gomphaeschnaoidinae Bechly *et al.*, 2001b

Diagnosis: triangles elongate and two-celled; hypertriangles usually free (except in *Gomphaeschnaoides betoreti*); subtriangles free; only one secondary antenodal between Ax1 and Ax2 in forewings (except in *Progomphaeschnaoides*); short ‘cordulegastrid gap’ of antesubnodal crossveins; no accessory cubito-anal crossveins in the submedian space; pterostigmal brace very oblique and sigmoidal; a single lestine oblique vein one cell distal of subnodus; RP_2 strongly undulating, but IR_2 more or less straight; Mspl and Rspl present; anal loop closed and at least four cells large.

Comment: about 10% of the Crato fossil odonate larvae and adults belong to this family.

Gomphaeschnaoides Carle and Wighton, 1990

Type species: *Gomphaeschnaoides obliquus* (Wighton, 1987).

Diagnosis: wings usually longer than 30 mm (except in *Gomphaeschnaoides betoreti*); pseudo-IR_1 originates beneath middle of pterostigma; oblique crossvein slanted towards stigma between RP_1 and RP_2 about three or four cells distal of subnodus; one or two rows of cells between RP_2 and IR_2; posterior branches of CuAa well-defined; anal loop about circular; distinct posterior branches of AA basal of anal loop in females.

Gomphaeschnaoides obliquus (Wighton, 1987)

Material: female holotype AMNH 43257 (Figure 11.13i); numerous further specimens have been described by Bechly *et al.* (2001c), for example male specimen SMNS 63069 (Figure 11.13e).

Diagnosis: forewing length 31.0–35.0 mm and hind wing length 32.0–37.0 mm; six postnodals in forewing and seven or eight in hind wing; anal loop with four or five cells.

Gomphaeschnaoides petersi Bechly *et al.*, 2001b

Material: male holotype JME AP 1997/3 (Figure 11.13h); possible further specimen no. MSF G9/G24.

Diagnosis: wing length about 37.5 mm; nine or ten postnodal crossveins; anal loop with eight cells.

Gomphaeschnaoides betoreti Bechly *et al.*, 2001b

Material: female holotype no. 11 (old no. D9) at BSPGM (Figure 11.13g).

Diagnosis: forewing length 29.1 mm and hind wing length 28.2 mm; hypertriangles divided by a crossvein; eight postnodals in forewing and nine in hind wing; anal loop with seven cells.

Gomphaeschnaoides magnus Bechly *et al.*, 2001b

Material: female holotype JME AP 1997/2 (Figure 11.13f); paratypes SMNS 64344 and no. MSF M62; further specimen LEIUG 113603, figured in Martill (1993: plate 8, figure 2).

Diagnosis: wing span about 85 mm; forewing length 42.1–45.0 mm and hind wing length 41.0–43.0 mm.

Progomphaeschnaoides Bechly *et al.*, 2001b

Type species: *Progomphaeschnaoides ursulae* Bechly *et al.*, 2001b.

Diagnosis: wing length less than 30 mm; pseudo-IR_1 does not originate beneath middle of pterostigma; two antenodals between Ax1 and Ax2; two or three rows of cells between RP_2 and IR_2; basal posterior branches of CuAa weakly defined; anal loop longer than wide; no posterior branch of AA basal of anal loop in females; no oblique crossvein slanted towards stigma between RP_1 and RP_2.

Progomphaeschnaoides ursulae Bechly *et al.*, 2001b

Material: female holotype SMNK 2357 PAL (Figure 11.13d).

Diagnosis: forewing length 27.5 mm and hind wing length 25.0–26.9 mm; pseudo-IR_1 originates beneath distal of pterostigma; five postnodals in forewing and seven in hind wing; Ax1 distinctly slanted towards wing base in hind wing; two rows of cells between RP_3+_4 and MA; one to three rows of cells between pseudo-IR_1 and RP_1 or RP_2 respectively.

Progomphaeschnaoides staniczeki Bechly *et al.,* 2001b

Material: female holotype JME AP 1197/4a,b an isolated hind wing (Figure 11.13c).

Diagnosis: hind wing length 29.3 mm; pseudo-IR_1 originates beneath basal side of pterostigma; 12 postnodals in hind wing; Ax1 not slanted towards wing base in hind wing; only a single row of cells between RP_3+_4 and MA; two to five rows of cells between pseudo-IR_1 and RP_1 or RP_2 respectively.

Paramorbaeschna Bechly *et al.,* 2001b

Paramorbaeschna araripensis Bechly *et al.,* 2001b

Material: female holotype SMNS 63068a,b (Figure 11.14e); paratypes MNHN-LP-R.55180, no. NSMT 29, SMNS 64218 and no. MURJ 518.

Diagnosis: forewing length 40.0–41.7 mm and hind wing length 37.7–40.6 mm; RP_2 distinctly undulate; three rows of cells between RP_2 and IR_2; two rows of

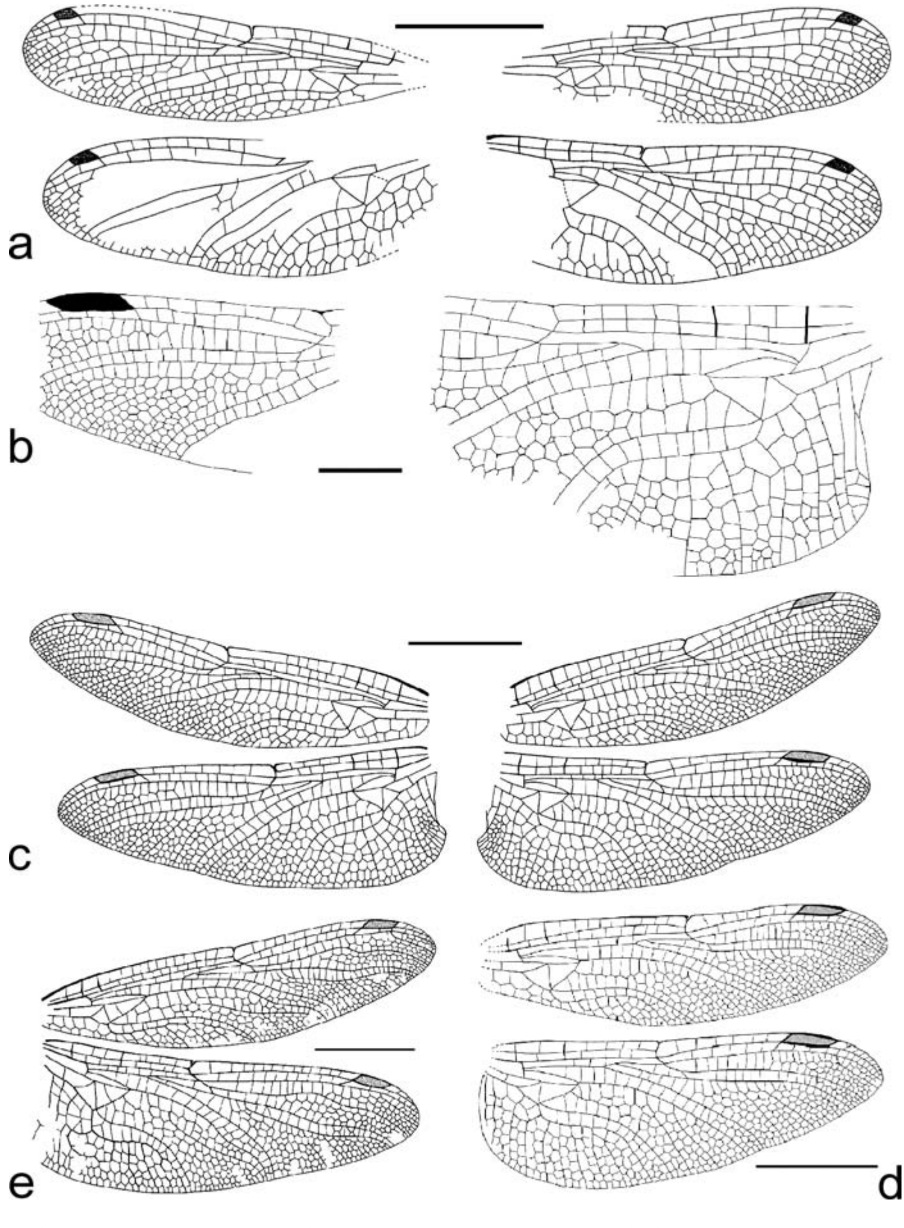

Fig. 11.14. Crato Formation Odonata: (a) Gomphaeschnidae, *Anomalaeschna berndschusteri*, female, holotype no. 515 MURJ (combined after Bechly *et al.*, 2001: figures 134–136); (b) Araripegomphidae, *Araripegomphus cretacicus*, female, holotype, forewing (left) and hind wing (right) (combined after Nel and Paichler, 1994: figures 5 and 6); (c) Araripegomphidae, *Araripegomphus andreneli*, male, holotype SMNS 63651 (after Bechly, 1998: figure 1); (d) Araripegomphidae, *Araripegomphus hanseggeri*, female, holotype SMNS 64415 (after Bechly, 2000: figure 1); (e) Gomphaeschnidae, *Paramorbaeschna araripensis*, female, holotype SMNS 53068 (after Bechly *et al.*, 2001: figure 109). Scale bars, 10 mm; except b, 4 mm.

cells between MA and Mspl; CuAa with five poorly defined posterior branches; accessory second anal loop (eight or nine cells) in hind wing.

Comment: a specimen that is nearly completely preserved in a large aggregation of insect remains and plant debris is featured in Figure 7.4e.

Anomalaeschna Bechly *et al.,* 2001b

Anomalaeschna berndschusteri Bechly *et al.,* 2001b

Material: female holotype no. 515 (old no. G22) at MURJ (Figure 11.14a).

Diagnosis: forewing length 28.4 mm and hind wing length 27.4 mm; triangles free (unique within subfamily); RP_2 originates distal of subnodus (unique autapomorphy within Anisoptera); RP_1 and RP_2 divergent; pterostigma only one cell long.

Araripegomphidae Bechly, 1996

Araripegomphus Nel and Paicheler, 1994d

Diagnosis: secondary antenodals between Ax1 and Ax2 more or less aligned (but not precisely so); arculus close to Ax1; hypertriangles, triangles and subtriangles free; anal loop reduced and posteriorly open; 'cordulegastrid gap'; bases of RP and MA approximated at arculus; three or four antefurcal crossveins (not oblique) in hind wings; no Mspl or Rspl; pterostigma three cells long and braced; compound eyes distinctly approximated but not connected (specimens with apparently widely separated eyes are preserved in ventral aspect).

Comment: about 5% of the adult fossil dragonflies from this locality belong to this taxon. The well-preserved female *Araripegomphus andreneli* specimen SMNS 66392 (old no. I38) shows a distinct ovipositor of about 3 mm length (Figure 11.12g; Plate 10b) with four valves, which strongly confirms the most basal position of Araripegomphidae within the gomphoid clade, as previously suggested by Bechly (2002), because all crown group gomphids have an obliterated ovipositor.

Araripegomphus cretacicus Nel and Paicheler, 1994d

Material: female holotype without number (Figure 11.14b) in coll. Baraffe in Paris, France.

Diagnosis: forewing length 38.5 mm and hind wing length 37.8 mm; posttrigonal area with three rows of cells in forewings.

Araripegomphus andreneli Bechly, 1998c

Material: male holotype SMNS 63651 (Figure 11.14c); paratypes no. 31, 47 (female allotype) and no. NSMT 1006; specimen MB.1999.3 MB.I.2057 (old no. D10) at MNB; male specimen SMNS 66394 and female specimen SMNS 66392, and numerous specimens in various collections.

Diagnosis: forewing length 32.0–36.7 mm (usually about 35 mm) and hind wing length 30.5–36.0 mm (usually about 34 mm); post-trigonal area with only two rows of cells in forewings.

Comment: the beautiful fossil dragonfly from the local museum in Santana do Cariri, figured by Martill (1993: front cover and text-figure 4.1), most probably belongs to this species. Specimen SMNS 66392 shows the female ovipositor (Figure 11.12g; Plate 10b), and a few male specimens (e.g. no. MSF G10) show extremely long cerci (4 mm) and an acute epiproct (Plate 10c). Specimen MSF G10 also shows the structure of the compound eyes in the same way as in the type species, *contra* Bechly (1998c), who was misled by ventrally preserved specimens.

Araripegomphus hanseggeri Bechly, 2000

Material: female holotype SMNS 64415 (Figure 11.14d); male paratype and allotype SMNS 64416a,b (Figure 11.15e).

Diagnosis: forewing length 32.9–33.6 mm and hind wing length 31.4–32.7 mm; only a single secondary antenodal between Ax1 and Ax2 in forewings; hind wing CuAa with five or six posterior branches; gap of crossveins distal of lestine oblique vein; area between RP_2 and IR_2 distally widened with two to four rows of cells in-between; hypertriangle quadrangular; anal loop posteriorly closed and divided into two or three cells; only two rows of cells in post-trigonal area in both pairs of wings.

Araripegomphus sp. nov. (?) Bechly, 1998c

Material: male specimen SMNS 63070.

Diagnosis: hind wing length only 30.5 mm; compound eyes apparently distinctly separated (distance 1.3 mm, head width 6.5 mm); otherwise very similar to *A. cretacicus* and *A. andreneli*.

Comment: a more detailed description, photograph and drawing, as well as phylogenetic discussion, was already provided by Bechly (1998c: 14–15, figures 4–5). It cannot be totally excluded that the apparently wide separation of the compound eyes is an artefact due to preservation of the head in ventral aspect. Therefore, this poorly preserved specimen could well represent a small male specimen of *A. andreneli*. The mention of the new species name '*A. imperfectus* n. sp.' in the acknowledgements section of Bechly (1998c: 64) was a *lapsus calami* and has to be considered as a *nomen nudum*.

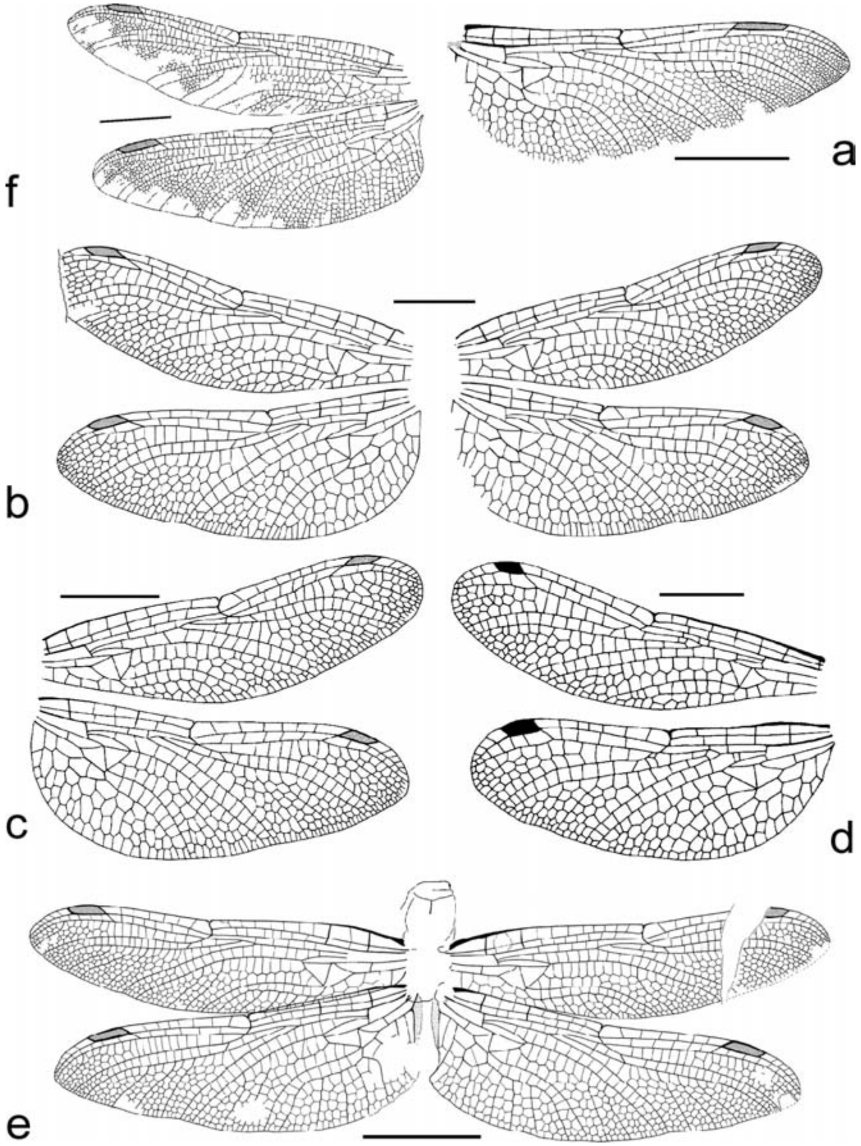

Fig. 11.15. Crato Formation Odonata: (a) Proterogomphidae, *Cordulagomphus winkelhoferi* sp. nov., female, paratype no. 513 MURJ (after Bechly, 1998: figure 31); (b) Proterogomphidae, *Cordulagomphus tuberculatus*, female, BSPGM C6 (after Bechly, 1998: figure 36); (c) Proterogomphidae, *Cordulagomphus fenestratus*, female, SMNS C13 (after Bechly, 1998: figure 35); (d) Proterogomphidae, *Procordulagomphus xavieri*, female, holotype MNHN-LP-R.10406 (redrawn after Nel and Escuillé, 1994: figure 2); (e) Araripegomphidae, *Araripegomphus hanseggeri*, male, allotype SMNS 64416a (after Bechly, 1998: figure 6); (f) Lindeniidae, *Cratolindenia knuepfae*, female, holotype SMNS 64414 (after Bechly, 2000: figure 9). Scale bars: d, 4 mm; b,c, 5 mm; a,e,f, 10 mm.

†Proterogomphidae Bechly *et al.*, 1998

†Cordulagomphinae Carle and Wighton, 1990

Diagnosis: 'cordulegastrid gap'; hypertriangles, triangles and subtriangles free; pterostigma two cells long and braced; pseudo-IR_1 originates beneath distal side of pterostigma; anal loop longer than wide and with only one or two cells; most basal postnodal crossveins very oblique; only two antefurcal crossveins in both pairs of wings; CuAa shortened and with reduced branching in hind wings (except in two new species).

Comment: about 44% of the fossil odonate larvae (41%) and adults (47%) belong to this taxon.

Cordulagomphus Carle and Wighton, 1990

Diagnosis: the second, distal antefurcal crossvein is very oblique in the hind wing (unique autapomorphy); anal loop usually divided in two cells; distal side of triangle angled; hind wing anal and cubito-anal area with at least three or four rows of cells and CuAa with visible posterior branches; hind wing with at least five antenodal crossveins.

Comment: Bechly (1998c) described new species and demonstrated great insufficiencies in the diagnoses of *Cordulagomphus tuberculatus* and *Cordulagomphus fenestratus*, based on a study of 98 specimens. Bechly (1998c: 57–58, figure 38) also identified the putative larvae of Cordulagomphinae and recognized that "*Cordulagomphus santanensis* Carle and Wighton, 1990' (specimen AMNH 43258) is not a dragonfly larva but a fossil earwig (see Section 11.6).

Cordulagomphus tuberculatus Carle and Wighton, 1990

Material: female holotype AMNH 43256; female specimen no. BSPGM C6 (described and figured by Bechly, 1998c: figures 36 and 37) (Figure 11.15b).

Diagnosis: forewing length 22.0–29.0 mm and hind wing length 21.0–28.0 mm; secondary antenodals usually non-aligned; distally two rows of cells between RP_{3+4} and MA; usually four or five postnodals in forewings and five or six in hind wings.

Comment: there could be a second, somewhat bigger, species 'hidden' among the very variable material (Plate 10d), because there are several specimens (e.g. SMNS 64362 = H10, SMNS 64361 = H11 and SMNS 66593 = M69) of very large size (forewing length 27–29 mm), but with more or less the same wing venation as the holotype. These specimens distinctly differ in size and venation from the two new large species of the same genus described below.

Cordulagomphus fenestratus Carle & Wighton, 1990

Material: male holotype AMNH 43262; female paratype and allotype AMNH 44200; female specimen SMNS C13 (described and figured by Bechly, 1998c: figure 35) (Figure 11.15c).

Diagnosis: forewing length 18.0–19.8 mm and hind wing length 17.5–19.6 mm; all antenodals aligned; distally only a single row of cells between RP_{3+4} and MA; usually five or six postnodals in forewings and six or seven in hind wings.

Cordulagomphus winkelhoferi sp. nov.

Material: male holotype SMNS 66607 (old no. M58; a very well-preserved hind wing; Plate 10e); female paratype and allotype no. 513 (old no. C20) at MURJ (Figure 11.15a).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named in honour of my father-in-law, Mr Dipl.-Ing. Othmar Winkelhofer, Schwarzenau, Austria.

Diagnosis and description (Figure 11.15a; Plate 10e): hind wing length about 35 mm; CuAa with five or six well-defined posterior branches; six rows of cells in cubito-anal area; pterostigma and pseudo-IR_1 distinctly longer than in the other species of *Cordulagomphus*. Otherwise, the wing is very similar to *C. tuberculatus*, but with a more dense venation because of the much bigger size. A more detailed description, photo and drawing of this new species was already provided by Bechly (1998c: 51, figures 31 and 32), who also discussed the phylogenetic position as being most basal Cordulagomphinae. However, due to preservational circumstances Ax2 was incorrectly drawn by Bechly (1998c: figure 31); it is on the level of the distal angle of the triangle. In the hind wing there are two non-aligned secondary antenodals between Ax1 and Ax2 in the first row and three in the second row. Furthermore, there is a well-defined 'cordulegastrid gap' in the holotype.

Cordulagomphus hanneloreae sp. nov.

Material: female holotype SMNS 66591 (old no. O21; Plate 10f).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after my dear aunt Hannelore Krause (née Schmidt; Kassel, Germany, 1943–2005).

Diagnosis and description (Plate 10f): the holotype is a nearly complete female dragonfly, of which only the abdomen is missing; the wing venation is very similar to *Cordulagomphus winkelhoferi* sp. nov., but pseudo-IR_1 is originating far distal of the pterostigma and the specimen is distinctly bigger (wing span 86 mm, hind wing 39 mm long and a maximum of 13.5 mm wide). This size difference to *C. winkelhoferi* (hind wing 35 mm long and a maximum of 11.5 mm wide) might appear minor at first sight, but is very obvious and striking in direct comparison. There is also a long 'cordulegastrid gap', and Ax2 is on the level of the distal angle of the triangle in both pairs of wings. In the forewing there is only one secondary antenodal between Ax1 and Ax2 in the first row but four antenodals in the second row, while in the hind wing there are two antenodals between Ax1 and Ax2 in the first row and five in the second row. Consequently, there is little doubt that this is a further new species of *Cordulagomphus*.

Cordulagomphus Carle and Wighton, 1990

Subgenus *Procordulagomphus* Nel and Escuillié, 1994

Diagnosis: anal loop unicellular; hind wing anal and cubito-anal area strongly reduced with only about three rows of cells and CuAa without distinct posterior branches; hind wing only with four antenodal crossveins (six in the new species).

C. (Procordulagomphus) xavieri Nel and Escuillié, 1994

Material: female holotype MNHN-LP-R.10406 (Figure 11.15d); male allotype MNHN-LP-R.10407; a further female specimen, with excellent three-dimensional preservation of the body, is SMNS 66391; specimens SMF Q79 and SMF Q82; MSF no. 37 and other specimens without numbers.

Diagnosis: forewing length 16.6–18.4 mm and hind wing length 15.6–17.5 mm; triangle slightly quadrangular; distal side of triangle MAb relatively straight, especially in hind wings; distal antefurcal crossvein usually not oblique or slanted but transverse; male anal triangle undivided; RP_1 bent posteriorly at stigmal brace; RP_3+_4 and MA closely parallel in forewings, with only a single row of cells in between (two rows at wing margin); anal area in forewings with only a single row of cells and without an enlarged elongate cell; anal loop usually unicellular, rarely two-celled in one wing. The secondary antenodal crossvein between Ax1 and Ax2 may be non-aligned in a few specimens.

Comment: the biggest specimen that otherwise completely agrees with all characters of the holotype, and strongly differs from *C. primaerensis*, is no. MSF 37, with a forewing length of 18.4 mm and a hind wing length of 17.5 mm.

C. (Procordulagomphus) senckenbergi Bechly, 1998

Material: male holotype SMF C7 (Figure 11.16c).

Diagnosis: forewing length 17.4 mm and hind wing length 16.8 mm; distal antefurcal antefurcal crossvein distinctly oblique; male anal triangle divided; forewings with only three postnodal crossveins; $RP_3{+}_4$ and MA closely parallel in forewings, with only a single row of cells in between (two rows at wing margin).

C. (Procordulagomphus) primaerensis Petrulevičius and Martins-Neto, 2007

Material: female holotype RGMN-T165 (Figure 11.16a).

Diagnosis: forewing length 20.6 mm and hind wing length 19.8 mm; distal antefurcal antefurcal crossvein distinctly oblique; forewings with five postnodal crossveins; $RP_3{+}_4$ and MA distally divergent in forewings, with two rows of cells in-between (three or four rows at wing margin); anal area of forewings with two rows of cells but without enlarged cell (or enlarged cell divided?).

Comment: the accessory cubito-anal crossvein in one forewing of the holotype is most probably not a diagnostic character, but an individual aberration.

C. (Procordulagomphus) michaeli sp. nov.

Material: male holotype no. 514 (old no. C14) at MURJ (Figure 11.16b; Plate 10g); further specimen nos E4 and E10 in coll. MSF.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after Mr Michael Schwickert (Sulzbachtal, Germany).

Diagnosis and description (Figure 11.16b; Plate 10g): forewing length 17.0–21.5 mm and hind wing length 16.9–20.0 mm; forewings with seven and hind wings with six antenodal crossveins; forewings with four postnodal crossveins; distal antefurcal crossvein not very oblique; $RP_3{+}_4$ and MA distally divergent in forewings, with two rows of cells in between (four rows at wing margin); anal triangle very narrow and two-celled.

Comment: a more detailed description, photograph and drawing, as well as phylogenetic discussion, was provided by Bechly (1998c: 52–53, figures 33 and 34).

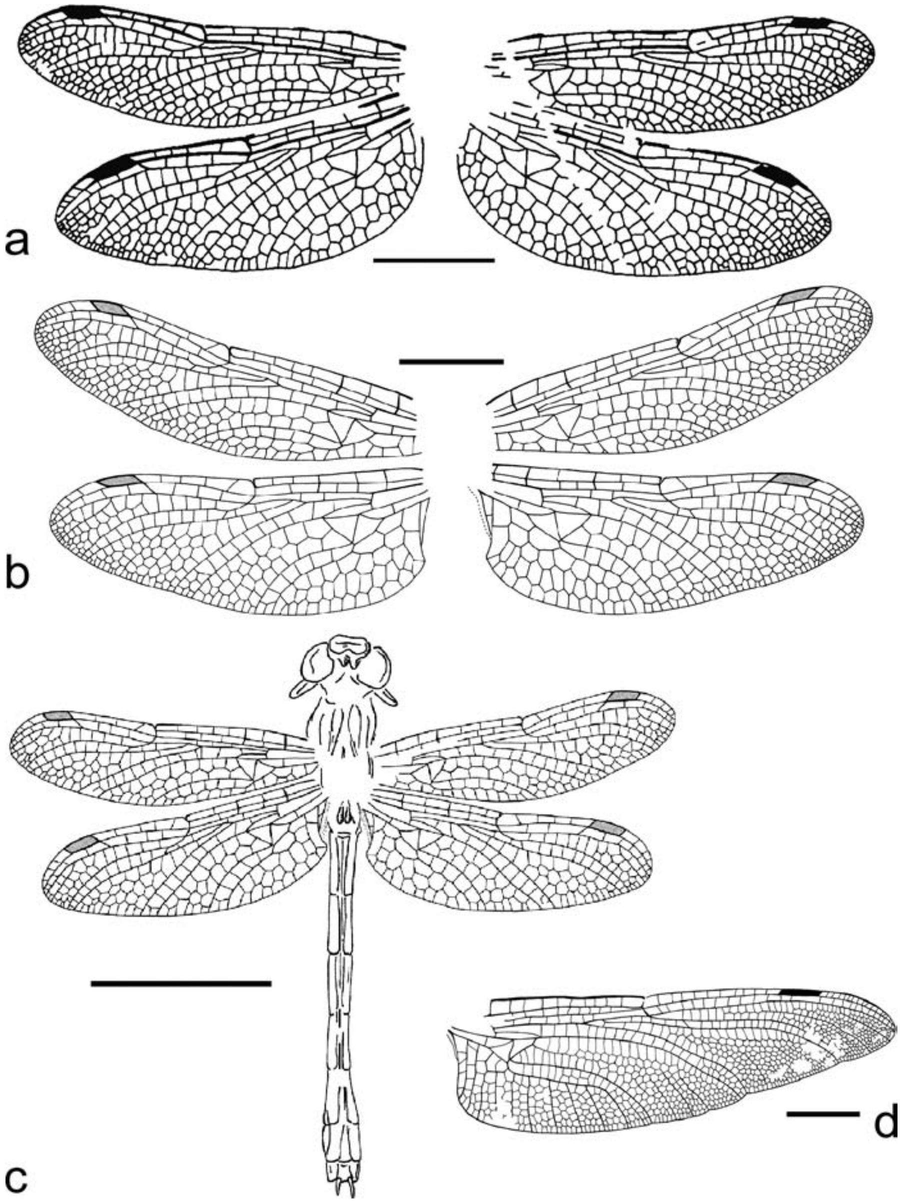

Fig. 11.16. Crato Formation Odonata: (a) Proterogomphidae, *Cordulagomphus (Procordulagomphus) primaerensis*, female, holotype RGMN-T165 (after Petrulevicius and Martins-Neto, 2007: figure 3); (b) Proterogomphidae *Cordulagomphus (Procordulagomphus) michaeli* sp. nov., male, holotype no. 514 MURJ (after Bechly, 1998: figure 33); (c) Proterogomphidae, *Cordulagomphus (Procordulagomphus) senckenbergi*, male, holotype SMF C7 (after Bechly, 1998: figure 6); (d) Petalurida? gen. et sp. nov., female, right hind wing, SMNS 66567. Scale bars: (a), 4 mm; b, 5 mm; c,d, 10 mm.

Lindeniidae Jacobson and Bianchi, 1905

Lindeniinae Jacobson and Bianchi, 1905

Cratolindenia Bechly, 2000

Cratolindenia knuepfae Bechly, 2000

Material: female holotype SMNS 64414 (Figure 11.15f).

Diagnosis: forewing length 49.6 mm and hind wing length 47.6 mm; short 'libelluloid gap' of postsubnodal crossveins and long 'cordulastrid gap' of antesubnodal crossveins; hypertriangle two-celled in forewing and undivided in hind wing; subtriangle large and three-celled in forewing and unicellular in hind wing; triangle transverse and three-celled in forewing and longitudinal elongate and two-celled in hind wing; costal side of triangle ends on its distal side below the distal angle in both wings (hypertriangle secondarily quadrangular); distal side of triangles strongly kinked in both wings with an post-trigonal intercalary vein originating at the kink; pterostigmata strongly braced and six cells long; IR_2 unforked; no Mspl or Rspl; only one lestine oblique vein three cells distal of subnodus; no accessory cubito-anal crossveins; anal loop elongate and two-celled; arculus close to Ax1 and about three secondary antenodals between Ax1 and Ax2.

†Araripephlebiidae Bechly, 1998c

Araripephlebia Bechly, 1998c

Araripephlebia mirabilis Bechly, 1998c

Material: female holotype no. 49 (Figure 11.17a) at NSMT; paratype no. 14 at KMNH; specimen MB.1999.3 MB.I.2058 (old no. D45) at MNB; SMNS 66618 (old no.K30), an isolated hind wing (Plate 10h); and complete specimen MSF G16 (Plate 10i).

Diagnosis: compound eyes approximated but not fused; forewing length 33.6–34.2 mm and hind wing length 32.5–36.0 mm; unique venation in the cubito-anal area with a very long anal loop with concave midrib (not homologous to libelluloid "italian loop"); a concave secondary vein beneath the anal loop, delimiting an elongate accessory anal loop with a single row of cells (Plates 10h and i); hind wing CuA short without CuAb and only a single dichotomic branching of CuAa (Plates 10h and i) or none at all (holotype); hypertriangles and subtriangles free; forewing triangle equilateral and free; hind wing triangle more transverse and divided by a horizontal crossvein; only a single antenodal between Ax1 and Ax2; 'cordulegastrid gap' of antesubnodal crossveins; a single lestine oblique vein two or three cells distal of subnodus; pterostigma two cells long and braced.

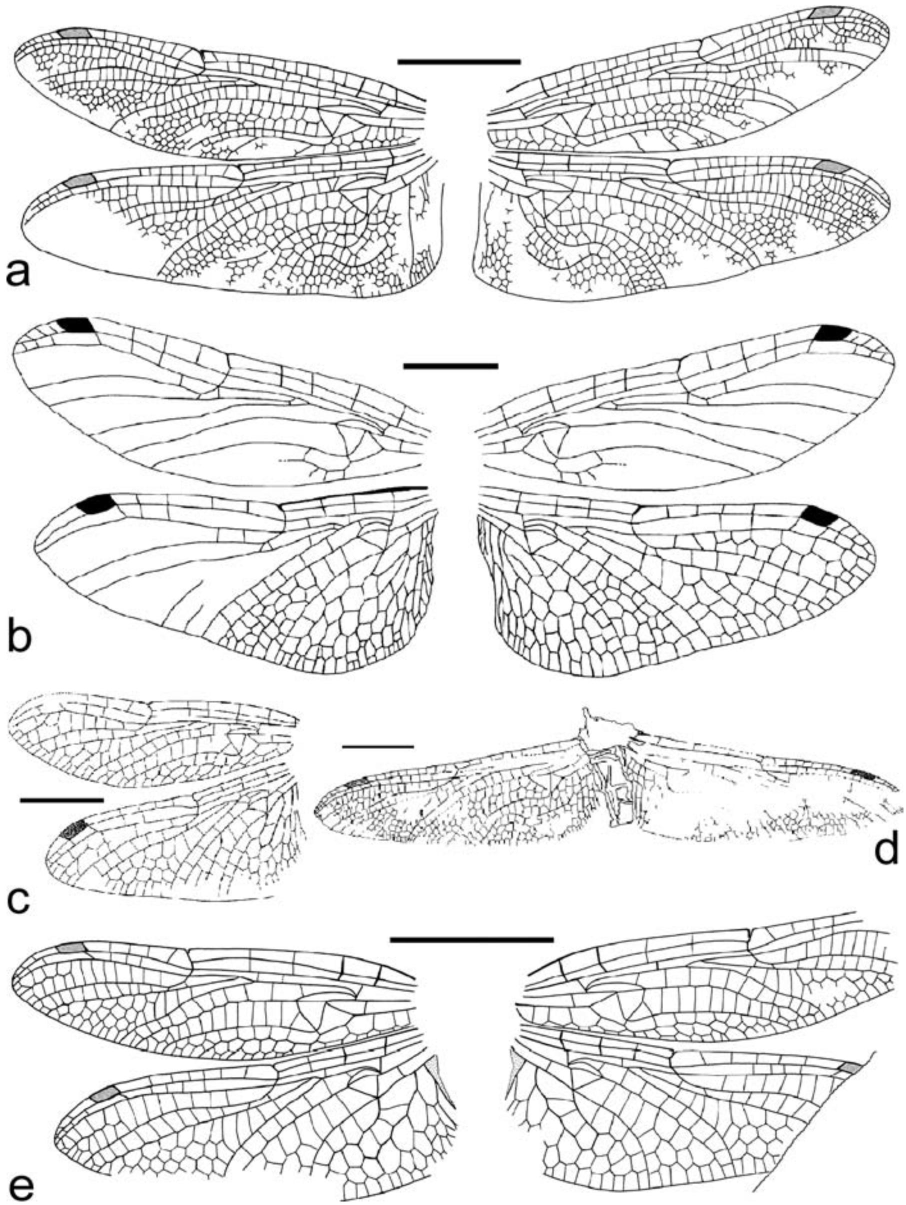

Fig. 11.17. Crato Formation Odonata: (a) Araripephlebiidae, *Araripephlebia mirabilis*, female, holotype NSM Tokyo 49 (after Bechly, 1998: figure 8); (b) Araripelibellulidae, *Araripelibellula martinsnetoi*, holotype MNHN-LP-R54376 (combined after Nel and Paichler, 1994: figures 1–3); (c) Araripelibellulidae, *Araripelibellula martinsnetoi*, female, B39 coll. MSF (after Bechly, 1998: figure 13); (d) Araripechlorogomphidae, *Araripechlorogomphus muratai*, female, holotype KMNH IP 000004 (after Bechly and Ueda, 2002: figure 1); (e) Araripelibellulidae, *Cratocordulia borschukewitzi*, female, holotype MNHN C5 (after Bechly, 1998: figure 11). Scale bars: b, 4 mm; c,d, 5 mm; a,e, 10 mm.

Comment: specimen no. G16 (complete dragonfly, forewing 33.6 mm long, hind wing 32.5 mm long) in coll. MSF, and specimen SMNS K30 (an isolated hind wing with 36 mm length) belong to the same species and show further details of the strange cubito-anal area (Plates 10h and i). All three known specimens with preserved hind wings lack an anal angle and anal triangle, thus they are either all females, or this taxon has reduced these structures in the male hind wing. Bechly (1998c) listed as a further diagnostic character the 'distal half of MA distinctly zigzagged in hind wings', but this is probably rather an individual aberration of the holotype, because this state is absent in the other specimens.

†Araripechlorogomphidae Bechly and Ueda, 2002

Araripechlorogomphus Bechly and Ueda, 2002

Araripechlorogomphus muratai Bechly and Ueda, 2002

Material: female holotype KMNH IP 000004 (Figure 11.17d), (ex coll. MURJ). This holotype was previously discussed and figured by Bechly (1998c: figure 39) and Bechly *et al.* (2001b: Abb. 40).

Diagnosis: hind wing length 39.4 mm; short 'libelluloid gap' of postsubnodal crossveins; triangle and subtriangle transverse and undivided; basal space free; CuAa with only two posterior branches; anal loop large, transverse, hexagonal, and seven-celled; very long 'gaff'; only a single lestine oblique vein two or three cells distal of subnodus; no Mspl or Rspl; pterostigma unbraced and covering two or three cells.

†Araripelibellulidae Bechly, 1996

†Araripelibellulinae Bechly, 1996

Diagnosis: all antenodal crossveins aligned; no antenodals between Ax1 and Ax2 and only two or three antenodals distal of Ax2; 'cordulegastrid gap' (only one or two antesubnodal crossveins); forewing with only three or four postnodals; pterostigma braced and short (one cell long); hypertriangle strongly curved in hind wings; hypertriangles, triangles and subtriangles free; post-trigonal area very narrow in the forewings with only a single row of cells; anal loop transversely elongate, narrow, with a single row of two to four cells; area between RP_2 and IR_2 very narrow near the single lestine oblique vein; PsA and subtriangle suppressed in the hind wing.

Comment: only about 2% of the Crato odonates belong to this taxon.

Araripelibellula Nel and Paicheler, 1994

Araripelibellula martinsnetoi Nel and Paicheler, 1994

Material: holotype MNHN-LP-R.54376 (Figure 11.17b); specimen no. MSF B39 (discussed and figured by Bechly, 1998c: 31–32, figure 13) (Figure 11.17c); and several further specimens in other collections.

Diagnosis: forewing length 17.4–18.0 mm and hind wing length 16.5–17.1 mm; anal loop two-celled.

Cratocordulia Bechly, 1998c

Cratocordulia borschukewitzi Bechly, 1998c

Material: female holotype with preliminary no. C5 (Figure 11.17e) at the MNHN in Paris (coll. A. Nel, Laborat. Paleont.). A further putative specimen (two connected forewings) is SMF Q66.

Diagnosis: forewing length 23.5–25.1 mm and hind wing length 24.2 mm; anal loop with row of four cells.

Undescribed new taxa

Several further species of Anisoptera remain to be described, but due to time constraints it has not been possible to include all these new descriptions, which therefore will be published elsewhere. Among these new taxa are the following new genera and species.

Specimen SMNS 66567 (Figure 11.16d; Plate 10j): an isolated but complete and very well-preserved female hind wing (length 57.3 mm, maximum width 17 mm): pterostigma long, unbraced and in basal position and a well-defined and long vein IR_1 (all characters as in Petaluridae), but only a single lestine oblique vein (as in Recent Petaluridae-Tachopteryginae) 3.5 cells distal of subnodus; pseudo-IR_1 originating far distal of pterostigma; no Mspl or Rspl; RP and MA separated in arculus (unstalked); four antefurcal crossveins (none oblique); hypertriangle free; triangle transverse, free and with a strongly kinked distal side; distinct intercalary vein originating at this kink, dividing the post-trigonal area into two rows of cells; subtriangle free; CuAa with six posterior branches; anal loop round, posteriorly closed, and two-celled; anal margin rounded without anal angle or anal triangle (female); no accessory veins. This undescribed new genus and species most probably represents a further fossil petalurid that has some similarities to the Recent North American genera *Tachopteryx* and *Tanypteryx*, but differs from all crown group Petaluridae by its very long and multi-branched CuAa in the hind wing and the structure of the pterostigma.

Specimen SMNS 66608 (old no. H19) (Plate 10k): head, thorax, two forelegs and both forewings (complete but poorly preserved): compound eyes approximated but not fused; forelegs very short; wing length 38 mm; pterostigma elongate (4.5–5 cells long) and braced; pseudo-IR$_1$ originates distal of pterostigma; RP$_2$ closely parallel to RP$_1$ with only one row of cells in between them, even below basal part of pterostigma (strongly different from *Araripegomphus*, which otherwise looks quite similar); RP$_2$ and IR$_2$ as well as RP$_3$+$_4$ and MA slightly undulate; lestine oblique vein one cell distal of subnodus; triangle somewhat transverse, distal side straight; hypertriangles elongate, narrow and apparently undivided; subtriangle transverse, narrow and apparently undivided; no Mspl or Rspl, and no post-trigonal intercalary vein at triangle; only two rows of cells in post-trigonal area. Most probably it is a new species of †Mesuropetalidae or rather †Liupanshaniidae.

Specimen SMNS 66614 (old no. M67) (Plate 10.l): left pair of wings with thorax fragment (rather poorly preserved): forewing 30.4 mm long and 8 mm wide, hind wing 29 mm long and a maximum of 10.5 mm wide; pterostigma only two cells long and distinctly braced; anal loop closed and elongate; hind wing with anal angle and a very broad and three-celled anal triangle (male). Overall the visible venation is quite similar to *Cordulagomphus tuberculatus*, but the wings are of very different shape and there are three post-trigonal rows of cells in the hind wing (beginning two cells distal of triangle). Probably it is a new species of †Cordulagomphinae.

Specimen SMNS 66592 (old no. H29) (Figure 11.12h): a complete and well-preserved male dragonfly; body length about 5 cm; compound eyes separated; forewing length 34.0 mm, hind wing length 32.5 mm; pterostigma elongate and braced; space between RP$_1$ and RP$_2$ basally very narrow; no Mspl or Rspl; a single lestine oblique vein one cell distal of subnodus; apparently only two antefurcal crossveins in hind wing (none oblique); the anterior side of the triangles ends on the distal side MAb beneath the distal angle (hypertriangles quadrangular) in all four wings; forewing triangle transverse and two-celled (as in *Mesuropetala*); hind wing triangle elongated, two-celled, and with sigmoidal distal side; distinct posttrigonal intercalary vein originating at distal side of triangle in both pairs of wings; subtriangle large and three-celled in forewing, but smaller and unicellular in hind wing; CuAa with four posterior branches in hind wing; anal loop closed and three-celled; anal triangle three-celled but extremely narrow and anal angle much reduced (a unique feature). A second specimen (SMNS 66612, old no. R5, forewings 38 mm long, hind wings 37 mm long) is preserved in lateral aspect with superimposed wings (Figure 11.18a). A third specimen (SMNS 66615a, b, old no. M71a,b, plate and counterplate of a female dragonfly thorax with all four wings, forewings 38.3 mm long, hind wing 37.0 mm long) also agrees with the above description, but there are three or four antefurcals in the hind wings (none oblique), a short ‘libellulid gap’ and a long ‘cordulegastrid gap’ are visible, and vein

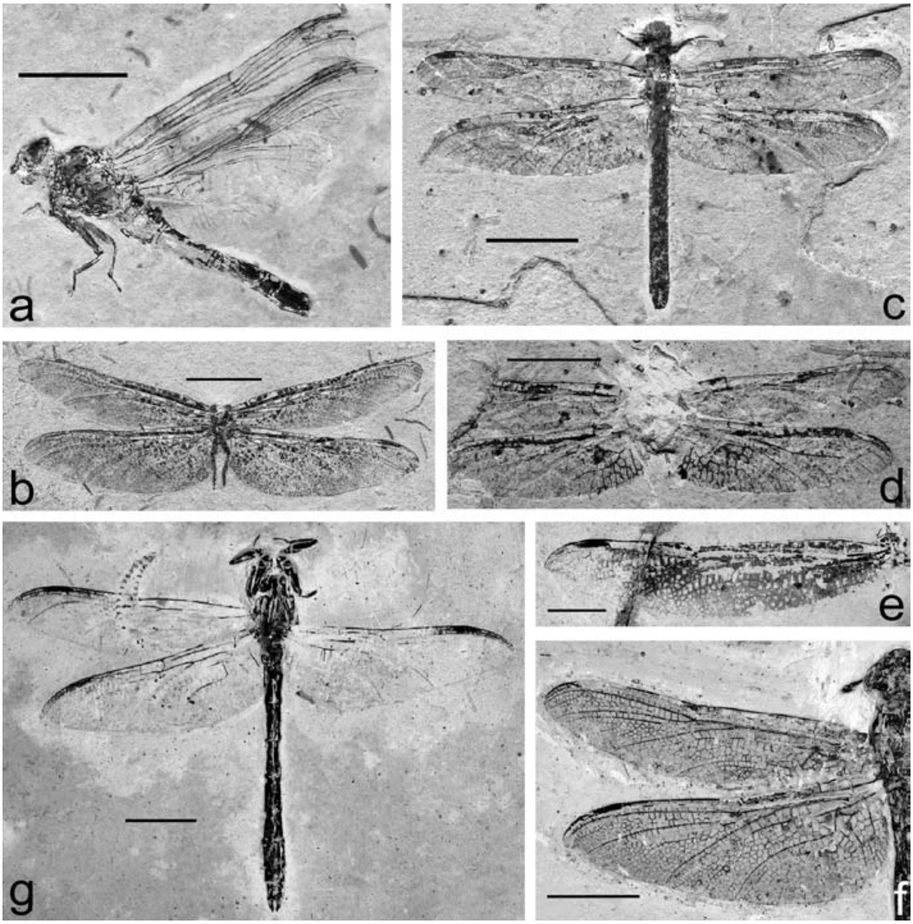

Fig. 11.18. Crato Formation Odonata: (a) Anisoptera, gen. et sp. nov., SMNS 66612; (b) Anisoptera, gen. et sp. nov., female, SMNS 66615b; (c) Anisoptera, gen. et sp. nov., male, SMNS 66606a; (d) Anisoptera, gen. et sp. nov., male, SMNS 66606b; (e) Anisoptera, gen. et sp. nov., SMNS 66617; (f) Anisoptera, gen. et sp. nov., female, Z43 coll. MSF; (g) Anisoptera, gen. et sp. nov., male, Z52 coll. MSF. Scale bars: a,b, 15 mm; c–g, 10 mm.

pseudo-IR_1 originates beneath distal side of stigma (Figure 11.18b). Most probably all these specimens belong to the same new genus and species of gomphid relationship, because they share the same combination of characters and show only a minor difference in size. The small numbers of antefurcals and the shape of the triangle in the hind wings suggests an attribution to the superfamily Hagenioidea.

Specimens SMNS 66606b (old no. L17) and SMNS 66606a (old no. L43) (Figures 11.18c–d): plate and counterplate of a complete male dragonfly; forewing length 24.0 mm, hind wing length 23.0 mm; pterostigma braced, relatively short

(2.5 cells long) and broad; pseudo-IR_1 originates beneath middle of pterostigma; only a single row of cells between pseudo-IR_1 and RP_1; only a single row of cells between RP_1 and RP_2 up to level of stigmal brace; Ax1 and Ax2 close together without secondary antenodals between them; the arculus is straight; very long ‘libellulid gap’ of antesubnodal crossveins and long ‘cordulegastrid gap’ of postsubnodal crossveins in both pairs of wings; three antefurcal crossveins in hind wing (not oblique); a single lestine oblique vein 1.5–2 cells distal of subnodus; no Mspl or Rspl; hypertriangles and subtriangles free; forewing triangle transverse, hind wing triangle elongate; triangles free and with slightly angled distal side in both pairs of wings; two rows of cells in posttrigonal area in both pairs of wings; CuAa long and with six posterior branches; cubito-anal area with three rows of cells, anal area with four rows; anal loop elongate and undivided (as in *Procordulagomphus*); hind wing with anal angle and three-celled anal triangle (male). Specimen MSF O40 is a very well-preserved isolated hind wing (length 28 mm) of the same taxon. The combination of characters is rather strange and very unusual. It is certainly a new gomphid genus and species, most probably closely related to †Araripegomphidae or †Cordulagomphinae.

Specimen SMNS 66617 (old no. R6) (Figure 11.18e): a well-preserved isolated forewing with the enormous length of 58.7 mm; a single secondary antenodal between Ax1 and Ax2; pterostigma about two cells long and braced; pseudo-IR_1 originates beneath distal end of stigma, with a very broad area between pseudo-IR_1 and RP_1; RP_2 and IR_2 distally divergent with two or three rows of cells in between; Rspl present and parallel to IR_2, with a single row of cells in between; a single lestine oblique vein 3.5 cells distal of subnodus; RP_{3+4} and MA strongly undulate, but closely parallel, with a single row of cells in between; post-trigonal area narrow, basally with only two rows of cells, and a convex intercalary vein; hypertriangle free; triangle elongate (aeshnoid-like) and free; subtriangle small and free; nodus in extremely distal position at about 56% of the forewing length (32.7 mm); no ‘libellulid gap’ of postsubnodal crossveins; no accessory veins. Again, no familial attribution of this new taxon is possible yet.

Specimen MSF Z43 (Figure 11.18f): a complete and very well-preserved female dragonfly; body length 56.1 mm; compound eyes widely separated; wing span 79.7 mm; forewings 37.5 mm long; hind wings 36.8 mm long and a maximum of 13.2 mm wide; pterostigma 4.5–5 cells long and braced; pseudo-IR_1 originates between distal part of pterostigma (two or three rows of cells between RP_1 and pseudo-IR_1); RP_1 and RP_2 strongly divergent with three or four rows of cells in between at stigmal brace; one lestine oblique vein one or two cells distal of subnodus; two rows of cells between RP_{3+4} and MA from the level of oblique vein up to hind margin; no Mspl or Rspl; triangles equilateral and two-celled in both pairs of wings; subtriangles elongate in forewings and two-celled in both pairs of wings;

anal loop absent (not posteriorly closed); three rows of cells in basal part of post-trigonal area in forewings, and four rows in hind wings; hind wing CuA with six distinct posterior branches (including CuAb); about two antenodals between Ax1 and Ax2; arculus close to Ax1 in hind wing (Ax2 aligned with distal angle of hind wing triangle), and apparently even basal of Ax1 in forewings (Ax2 aligned with basal angle of forewing triangle); a short but distinct 'libelluloid gap' of postsubnodal crossveins is visible. It is a new genus and species of uncertain familial affinity.

Specimen MSF Z52 (Figure 11.18g): a nearly complete male dragonfly, of which only the head and one forewing is missing; unfortunately the wing venation is poorly preserved; forewing 34.0 mm long; hind wing 32.5 mm long and a maximum of 11.0 mm wide; hind wing triangle and subtriangle transverse and free; RP_1 and RP_2 very close together up to level of the pterostigma; pterostigma long with a very acute basal edge and a very slightly basally displaced stigmal brace, which is very oblique as well; apparently no Mspl or Rspl, and no hypertrophied vein IR_1; two rows of cells in post-trigonal area of both wings; hind wing with anal triangle (male); cerci 1.9 mm long. Familial attribution of this new taxon is not possible.

11.6 Dermaptera: earwigs

Fabian Haas

Dermaptera constitute a uniform and highly derived monophyletic taxon among the insects, with a moderate diversity of about 2,200 species, including fossils. Almost all species belong to the Forficulina: the earwigs of common parlance. Earwigs are rather long and slender insects, often 10–20 mm in length, with a disc-like pronotum, short to moderately long walking legs, and have, without exception, forceps-like cerci. Earwigs are omnivorous. The common or European earwig (*Forficula auricularia* Linnaeus, 1758) provides a typical example for description. The extremes, however, are quite different: the smallest earwig is *Eugerax peocilium* Hebard, 1917, at 3 mm long, while the largest, now probably extinct, was *Labidura herculeana* (Fabricius, 1798), from St. Helena in the Atlantic Ocean, at 80 mm in length. *Titanolabis colossea* (Dohrn, 1864) from Australia is the largest Recent species at 55–60 mm long. The nutrition, as far is known at all, varies between carnivory (*Labidura riparia* (Pallas, 1773)), omnivory, herbivory and spongivory in many Spongiphoridae, although no species seems to be highly specialized on a food source (for an exception see below). Earwigs usually prefer narrow spaces and hide under stones, under bark, in decaying wood, in leaf axles, in leaf litter or in flowers, in a wide range of habitats.

One of their most interesting features is the complex folding mechanics of the hind wings. They are unfolded by the cerci and, due to intrinsic elasticity, folded to only a tenth of the surface area of the unfolded wing (Haas *et al.*, 2000). The mechanism of folding evolved early and the oldest known earwig fossil with expanded hind wings suggests that the venation and folding pattern has not changed significantly at least since the Cretaceous.

There is considerable variation and independent reductions in the female external genitalia, which correlates with various egg-laying behaviours (Haas and Klass, 2003). As far is known, all species show maternal care for eggs and first instars (Matzke and Klass, 2005). There are two notable exceptions to this ethology and morphology. The first is the Hemimerina (11 species in two genera) living epizooically on hamster rats in sub-Saharan Africa. The relationship with their hosts is so close that they hardly every leave them and die fairly soon after being separated from the hamster rats. The second is the Arixeniina (five species in two genera) living on bats and in their resting caves on Sarawak and the Philippines. The derived structure and ecology of these two epizoons led to several important modifications in structure and physiology: incomplete eye reduction and highly derived tarsal attachment pads in Hemimerina, and vivipary in all species (also in the spongiphoridan *Marava arachidis* (Yersin, 1860)). There is no fossil record of these two groups.

Most Dermaptera are easily recognized by the short tegmina and modified cerci, with incorrect identifications at high taxonomic levels being rare. On the other hand, Diplura-Japigydae, larval Anisoptera and Staphylinidae are sometimes misidentified as dermapterans, sharing a generally elongate and slender habitus, short (or no) tegmina and elytra, and forceps-like abdominal protrusions (cerci in case of the Japygidae). This similarity might pose special problems in the fossil record with its reduced number of accessible characters. However, only one fossil from the Crato Formation was erroneously assigned to Dermaptera (see below).

Ecology

Earwigs as a whole have no habitat preference and there is no indication that fossil species were any different. There are species over most vegetation types, including some with preferences for grasses, bushes and trees, or hiding under bark and stones. Their feeding is equally diverse, ranging from strict carnivory (*Labidura riparia* (Pallas, 1773)), over a mixed diet (*Forficula auricularia* Linnaeus, 1758), to fungivory and herbivory. These preferences are reflected in small variations in the mouth parts (Waller *et al.*, 1996) and are not visible in the fossils.

Some species have a closer relation to water, such as *L. riparia*, which is most often found on sandy river banks or sea shores. Other species (*Forcipula* spp.) are reported to move swiftly over water and on the beds of small rivers (Haas and Gorb, 2004). However, these traits and preferences are not discernible as morphological adaptations.

Reproductive seasonality occurs in the life cycle of earwigs and usually they produce only one generation per year, rarely two. It is determined either by the yearly temperature cycle in the moderate climate or, in tropical areas, by the change of wet and dry seasons. The wet season with its abundant plant growth and insect diversity is preferred for breeding (Boukary *et al.*, 1996). Breeding, as well as foraging, requires animals to move about to find prey, mates and nesting places, such as leaf sheaths, tunnels and caves under stones. In addition to this increased activity, more rain increases the chance to be washed into creeks and lakes. Surprisingly, no nymph has been identified with certainty in the Crato Formation. If there are adults there should be nymphs as well because, due to maternal care, there is an obligatory overlap of generations and occupancy of the same habitat. However, the nymphs seemed to have a significantly lower risk of fossilization than the adults. This is possibly because they were non-flying or the larger part of their ontogeny took place when water was scarce, simultaneously reducing their preservation potential. Thus the occurrence of only adults in the Crato Formation might be a consequence of seasonality.

Recent Dermaptera prefer a warm and humid climate, such as the Mediterranean and the tropics, and hence there is only a poor earwig fauna in colder and dryer regions: presently, Europe (as defined by the Fauna Europaea database) and Australia hold only about 90 species each, whereas the tropical Brazil has approximately 150 species, eastern Africa about 167 species and India about 300 species.

Systematics and phylogeny

There is no doubt that Dermaptera are monophyletic (i.e. Forficulina), due to their general uniformity and the many derived characters found throughout the taxon. This includes the lack of ocelli, transformation of the forewings to short and veinless tegmina, highly derived hind wings (including venation, folding pattern and mechanics), three tarsomeres, modified cerci, holocentric chromosomes (also in Hemimerina and Arixeniina) and maternal care for eggs and first nymphal instars.

The situation is somewhat complicated by the derived structure and biology of Hemimerina and Arixeniina. They were often considered as suborders of the Dermaptera, but a recent study (Haas and Klass, 2003) indicates that both taxa are nested well within the Forficulina.

Within Forficulina, nine taxa with family rank are recognized: Karschiellidae, Diplatyidae, Pygidicranidae, Apachyidae, Anisolabididae, Labiduridae, Spongiphoridae, Chelisochidae and Forficulidae. However, only for Karschiellidae, Apachyidae, Chelisochidae and Forficulidae are unequivocal autapomorphies known. In the other ‘families’, no or only ambigous apomorphies were identified in an extensive phylogenetic analyses (Haas and Kukalová-Peck, 2001). In addition, the Eudermaptera, (Spongiphoridae+Chelisochidae)+Forficulidae, can be diagnosed by a great many autapomorphies. The most easily recognized and widely used character in their taxonomy is the reduction of the genitalia to a single penis lobe.

Evolution

The phylogeny and character evolution of the Dermaptera was analysed by Haas and Kukalová-Peck (2001). The general morphology of the Jurassic stem group Dermaptera from Kazakhstan is almost identical to that of Recent representatives, and consequently most fossil Dermaptera are easily recognized as such. The body is long and slender, the head prognathous, with a disc-like pronotum, followed by a compact mesothorax with abbreviated tegmina and the metathorax with the densely folded hind wings. These are folded to the wing packages so characteristically of the Dermaptera and this implies that the same unfolding and folding mechanism (Haas *et al.*, 2000) evolved before the Jurassic. The first positive confirmation that these hind wings had a similar venation pattern as Recent earwigs is seen in the *Cratoborellia gorbi* specimen shown here (Figure 11.19e). It is the oldest known fossil with expanded hind wings, including the dermapterans with unfolded wings occasionally found in amber. The lateral overlap of abdominal tergites and sternites form the typical zig-zag pattern in lateral view.

For the present context and in the context of inter-ordinal relationships, four characters are important and the phylogenetic analyses suggest that these transformations are synapomorphies for the ‘modern’ Dermaptera.

1. Ocelli: three ocelli are present in some Jurassic earwigs but they are reduced (derived character state) in other fossil specimens and Recent Dermaptera.
2. Adult cerci: in some of the Jurassic taxa, the adult cerci are annulated, representing the plesiomporphic condition. In all Recent Dermaptera, the adult cerci lack annulae (sometimes called un-segmented). Annulated cerci, however, are present in the nymphs of two basal taxa, the Karschiellidae and Diplatyidae. All other, more derived, taxa show the adult character state in the nymphal cerci.
3. Tarsi: in Jurassic fossils, there are taxa with five tarsomeres, representing a plesiomorphic character state, while all Recent Dermaptera have three tarsomeres with a variety of attachment structures. However, there were no such pads in the last common ancestor of all Recent earwigs (see Haas and Gorb, 2004, for review and phylogenetic interpretation).
4. Ovipositor: in some Jurassic fossils an ovipositor is visible, which is not discernible without dissection in most ‘modern’ Dermaptera. However, basal Dermaptera, such as *Tagalina* spp. (Haas and Klass, 2003), do have thin and flexible ovipositors projecting beyond the ultimate sternite.

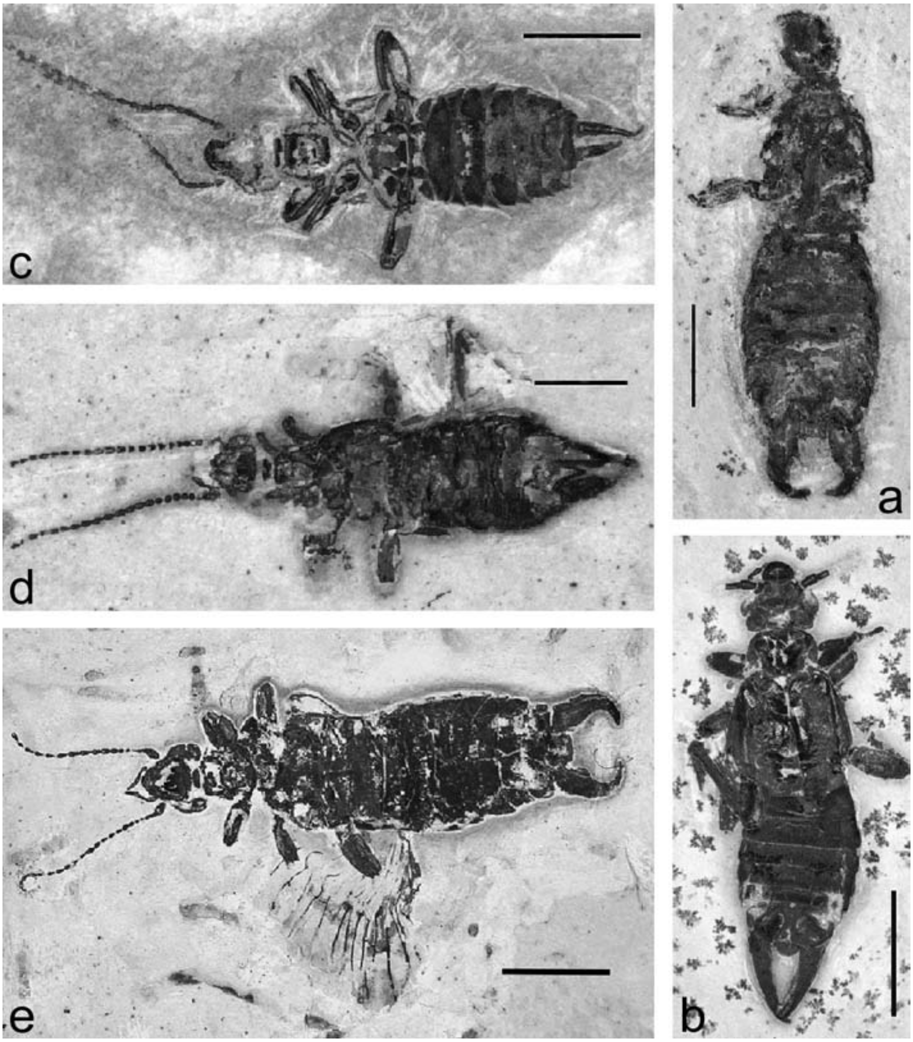

Fig. 11.19. Crato Formation Dermaptera: (a) Anisolabididae, *Cratoborellia gorbi* gen. et sp. nov., holotype SMNS 66556; (b) Labiduridae, *Caririlabia berghoffi* sp. nov., holotype SMNS 66555; (c) Spongiphoridae, *Kotejalabis haeuseri* sp. nov., holotype SMNS 66557; (d) Spongiphoridae, *Kotejalabis goethitica*, SMNS 66515; (e) Anisolabididae, *Cratoborellia gorbi*, specimen with exposed hind wing, MSF Z10. Scale bars: a,b,e, 5 mm; c,d, 2 mm.

Thus, ovipositor reduction, unsegmented cerci and attachment pads are clearly not synapomorphies for Blattaria, Embioptera or Zoraptera (to name but a few), as has previously been discussed. The fossil record and the ground-pattern reconstruction show that these reductions and modifications are parallel developments in other taxa, having evolved several times since the Jurassic.

Fossil history

The fossil history of the Dermaptera was summarized by Carpenter (1992), Shcherbakov (2002) and Wappler *et al.* (2005), and these sources should be addressed for the primary references. The earliest stem-lineage representatives are Protelytroptera from the Permian, which superficially resemble Recent cockroaches but clearly share some derived characters with the Dermaptera. Protelytroptera+ Dermaptera are sometimes considered to form a monophyletic taxon, Forficulida (Shcherbakov, 2002).

From the Jurassic onwards (Triassic records are currently undescribed and will not be considered further), a number of specimens are known from the Old World (Europe, Russia, Kazakhstan, China). These taxa are often considered to be Archidermaptera (a paraphyletic assemblage); however, some of them already show derived character states in the reduction of ocelli, reduction to three tarsomeres and adult cerci without annulations. Hence, the basal and monophyletic (singular) split separating the modern from the plesiomorphic Dermaptera occurred before or early in the Jurassic. Nonetheless, the Jurassic fossils give important clues on the evolution of characters, with consequences for reconstructing the inter-ordinal relationships among Insecta.

In the Cretaceous, predominately 'modern' Dermaptera are found, with the notable exception of the genus *Longicerciata* (the stratum was erroneously cited as Late Jurassic by Zhang, 1994; see Wappler *et al.*, 2005). The Tertiary and Quaternary fossil record is more abundant, and the dermapteran species are often assigned to Recent genera, therefore it is not considered further (Wappler *et al.*, 2005).

Fossil Dermaptera with outspread hind wings were previously only known from amber inclusions, except for the Permian stem group earwig *Protelytron*. In Figure 11.19e the first specimen from the Crato Formation and oldest crown group dermateran is shown that is preserved with a visible hind wing. It is a specimen of the new species *Cratoborellia gorbi*.

Fossils give an indication of how ancient single taxa are. This requires, however, that the taxa in question are monophyletic and that there is a reliable phylogeny available to infer the age on the basis of sister-group relationships. The latter requirement is fulfilled (Haas and Kukalová-Peck, 2001; molecular studies (Colgan *et al.*, 2003; Jarvis *et al.*, 2005) largely confirm their findings); the former is not. The issue is twofold. First, not all of the so-called 'families' of the Dermaptera are clearly defined by autapomorphies, and second, not all the characters are preserved in the fossil specimens: for example, modifications of tarsomeres and, except for rare cases, hind wing characters. Based on the newly described fossil species and the first record of an Anisolabididae, as well as literature data (Carpenter, 1992; Wappler *et al.*, 2005), following suggestions about the age and occurrence of splitting events can reasonably be given:

- Protelytroptera: Permian
- Archidermaptera (paraphyletic): Lower Jurassic to Lower Cretaceous
- Hemimerina: no fossil record
- Arixeniina: no fossil record
- Forficulina: Jurassic to Recent
  - Karschiellidae: no fossil record
  - Diplatyidae: no fossil record
  - Pygidicranidae: Jurassic to Recent
  - Anisolabididae: Cretaceous to Recent
  - Apachyidae: no fossil record
  - Labiduridae: Cretaceous to Recent
    - Eudermaptera: Cretaceous to Recent
      - Spongiphoridae: Cretaceous to Recent
      - Chelisochidae: Eocene to Recent
      - Forficulidae: Eocene, Miocene

So, although the Permian is the starting point of the lineage leading to Recent Dermaptera, the major modification and diversification of taxa occurred no earlier than in the Jurassic. Since fossil specimens of Anisolabididae and Labiduridae were found in Cretaceous beds, the splitting into the Recent 'family' rank taxa took place somewhat before that period (i.e. Upper Jurassic). The Cretaceous Spongiphoridae suggest that even the Eudermaptera split from other taxa took place as early as the Cretaceous. The Recent fauna and biodiversity found in the Dermaptera date back to this period, well before the rise and fall of some other vertebrate taxa, which agrees with many other hexapod taxa.

Crato fossils

Several Dermaptera species have been recovered from the Crato Formation (Figures 11.19 and 11.20), and while not especially common, their remains occur regularly. The first studies of Crato earwigs were by Popham (1990) and Martins-Neto (1990a), although at least one taxon described by Martins-Neto proved not to be Dermaptera (see below). Since those early studies, much new material has become available (e.g. Engel and Chatzimanolis, 2005) and several new taxa are described below.

Anisolabididae

Diagnosis: the following features are apomorphic: neck forficuloid-type; fustis with embayment; costal area long and broad; end of CuA_3+_4 between seventh and eighth branch of AP_1+_2; CuP indistinct; concave longitudinal fold runs laterally

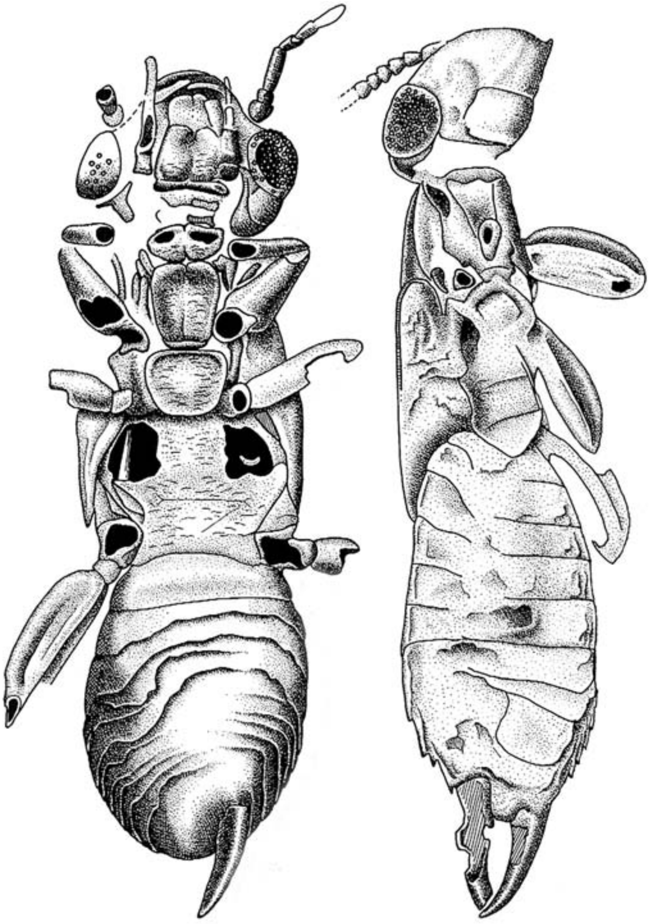

Fig. 11.20. Crato Formation Dermaptera: *Cretolabia cearae* Popham, 1990: left: holotype, AMNH 43798, original specimen 7 mm total length; right: paratype, AMNH 43799. After Popham, 1990: figures 1 and 2.

between CuA and AP. AA_3 close to $BAA_{1}+_{2}$. $JP_{3}+_{4}$; veinal portion posterior to RC absent; femur without keels on dorsal surface, i.e. rounded; each penis with one opening of the ejaculatory duct and both penes pointing in different directions; basal vesicle absent (vesicular structure in the ejaculatory duct); telson fused; nymphal cerci without annulation, as in the adult. The following are plesiomorphic: tegminal cranial margin curved; fustis not separated by groove from its base; jugal cell and anojugal cell of similar size; male genitalia with two penes.

Comments: a large (450 Recent species) and confusing taxon with unclear monophyly that has been referred to as 'c'est un bordel' or 'It's a pig sty'. Many species have considerable body length and the group includes 55–60-mm-long *Titanolabis* *colossea* (see above). Tegmina and/or wing reduction is common but some fully winged and flying species occur. In many species the habitus is homogenous, robust, with short legs, and of a shiny brown to black colour. Identification of species requires dissection of the male genitalia while females and nymphs are often not identifiable to species.

Cratoborellia gen. nov.

Type species: *Cratoborellia gorbi* sp. nov.

Etymology: the generic name is derived from the Crato Formation in which the specimen was found and *–borellia* to express the similarity of the cerci shape with that found in species of the genus *Euborellia*.

Description: large earwigs, about 20 mm long (including forceps). Wings present. Cerci short, with a broad, fairly straight, anterior half and a thinner strongly curved posterior half. No ornamentation with denticles and teeth. Cercal base wide and with broad and transverse pygidium.

Cratoborellia gorbi sp. nov.

Material: holotype SMNS 66556 (Figure 11.19a). A further specimen with preliminary no. MNS Z10 is featured in Figure 11.19e).

Etymology: dedicated to Dr Stanislav Gorb (MPI, Stuttgart), with whom I had the pleasure to explore various aspects of the functional morphology of wing folding and attachment pads in Dermaptera.

Description: as for the genus, by monotypy.

Comments: the specimen is not well preserved but it is complete. The hind wing package indicates an adult and the strongly curved cerci, similar to those of the Recent *Euborellia janeirensis* (Dohrn, 1864) are clearly different from those of other species from the Crato beds. In Recent Dermaptera, earwigs with similar cerci shape are not found in the Labiduridae; this, and the occurrence of *Euborellia* species in Brazil, justifies the placement into the Anisolabididae, which have representatives with similar cerci shape, and in a new genus. The cerci shape suggests a male specimen. This is the first genus and species of the Anisolabididae described from the Cretaceous.

A second specimen of this species (Figure 11.19e) is the oldest confirmation that venation and thus folding pattern were similar to those of Recent species, at least since the Cretaceous. This specimen is the oldest earwig fossil known to us with unfolded wings; however, there is a small number of dermapterans of later periods which were obviously fossilized after being trapped by tree resins (amber) while on the wing.

Labiduridae

Diagnosis: the following are apomorphic: neck forficuloid-type; costal area long and broad; jugal cell smaller than anojugal cells; end of CuA_3+_4 between sixth and seventh branch of AP_1+_2; CuP indistinct; concave longitudinal fold runs laterally between CuA and AP; AA_3 close to BAA_1+_2; femur without keels on dorsal surface, i.e. rounded; fustis with embayment; telson fused; nymphal cerci without annulation, as in the adult; both paired penes with one opening of the ejaculatory duct, and both penes pointing in different directions. The following are plesiomorphic: tegminal cranial margin curved; fustis not separated by groove from its base; JP3+4, veinal portion posterior to rc present; male genitalia with two penes; basal vesicle present.

Comment: a taxon which is not clearly monophyletic. Haas and Kukalová-Peck (2001) suggest a sister-group relationship to Eudermaptera, based mainly on wing characters; however, the monophyly is still equivocal.

Caririlabia Martins-Neto, 1990a

A new species of labidurid agrees with the diagnosis of the genus *Caririlabia* provided by Engel and Chatzimanolis (2005).

Caririlabia berghoffi sp. nov.

Material: the holotype is SMNS 66555 (Figure 11.19b).

Etymology: the epithet is dedicated to fellow entomologist Dr Stefanie Berghoff, even though she never worked on Dermaptera.

Description: dorsal view. Length of body (including cerci) 19 mm. Head large and stout (3.1 mm wide, 2.6 mm wide); compound eyes large; antenna with no more than four articles preserved, second article very short; impressions of four more articles on right antenna visible; antennal bases widely separated, wider than the second antennal article long (0.7 mm); coronal sutures visible; head slightly concave on posterior margin. Pronotum as wide as head and transverse, distinctly rounded, i.e. almost ellipsoid. Tegmina partly open, possibly with lateral keel, extending to the first abdominal tergite. Left wing partly unfolded without yielding further detail; right hind wing folded with squama visible. Abdomen with seven visible tergites, suggesting female, widest at about the middle of the abdomen. Cerci 3 mm long with widely separated bases, gently curved, apices crossing, and lacking ornamentation with denticles or teeth. Pygidium short, semi-circular.

Comments: this specimen resembles members of the Labiduridae in its size and robustness, including the coronal sutures on the head. The new species differs from *Caririlabia brandaoi* (Martins-Neto, 1990a) in being 3 mm smaller; the head is larger and less rounded; the pronotum is distinctly ellipsoid. It differs from the specimens figured in Carle and Wighton (1990) by having a visible pygidium.

Today, only two species of Labiduridae occur in Brazil. Although the low diversity might suggest a poor chance of fossilization, *Labidura riparia* (Pallas, 1773) has a preference for sandy habitats along river banks, thus increasing significantly the chances of preservation.

Caririlabia brandaoi Martins-Neto, 1990a

Synonyms: *Cordulagomphus santanensis* Carle and Wighton, 1990 clearly is an adult earwig and not an odonatan nymph (first recognized by Bechly, 1998c). Martins-Neto (2001a) erected a new genus *Lapsoderma* for this species and incorrectly attributed it to Labiidae(?), which is still cited this way by Martins-Neto (2005a, 2005b). However, Engel and Chatzimanolis (2005) demonstrated that *Lapsoderma* is a *nomen nudum* and finally synonymized *C. sanatanensis* with *C. brandaoi*.

Comment: Martins-Neto (1990a) might have actually described a nymph because there are neither tegmina nor wings clearly illustrated (Martins-Neto, 1990: 780, figure 2) and there seems to be a concave suture on the thorax, which is typical for dermapteran nymphs (the holotype was not examined). He suggested a relationship of this genus to the Pygidicranidae, which is rejected here, because no carina is present on the femur. This agrees with the suggestion of Engel and Chatzimanolis (2005), who prefer an Anisolabidoidea or Labiduroidea relationship.

Martins-Neto (2005a) mentions the discovery of a new species of *Lapsoderma*, and Martins-Neto (2005b) lists two species, *Lapsoderma araripensis* and *Lapsoderma nordestina*, with the citation Martins-Neto (2002) as source for their description. However, I could not locate such a publication and thus cannot comment on the validity and attribution of these two species, which might still represent *nomina nuda*.

Eudermaptera

Diagnosis: the following are all apomorphic: neck forficuloid-type; tegminal cranial margin straight; fustis with notch; fustis separated by groove from its base; costal area long and broad; jugal cell smaller than anojugal cells; CuP indistinct; concave longitudinal fold runs laterally between CuA and AP; AA_3 close to BAA_{1+2}; JP_{3+4}, veinal portion posterior to RC absent; femur without keels on dorsal surface, i.e. rounded; male genitalia with one penis, with one opening of the ejaculatory duct; telson fused; nymphal cerci without annulation, as in the adult.

Comments: the Eudermaptera are the one earwig taxon defined by the highest number of autapomorphies derived from all organ systems, so that there is little doubt about their monophyly. The most easily recognized and widely used character to identify them is the reduction of the male genitalia to one penis lobe. The phylogenetic relationship of the three taxa within Eudermaptera is not finally resolved: a relationship of (Spongiphoridae+Chelisochidae)+Forficulidae is probable.

Spongiphoridae

Diagnosis: Eudermaptera with unmodified second tarsomere (plesiomorphy) and basal vesicle absent (vesicular structure in the ejaculatory duct, apomorphy).

Comment: quite often, small and slender species and *Eugerax peocilium* Hebard, 1917, is, with a mere 3 mm body length, the smallest dermapteran known. The pygidium (in males more often than in females) regularly reaches considerable size, up to half of the cerci length, and has a pronounced sculpturing. Tegmina and/or hind wing reduction is rare.

Cretolabia Popham, 1990

Cretolabia cearae Popham, 1990 (Figures 11.20)

Synonyms: *Araripelabia costae* (Martins-Neto, 1990a) by Engel and Chatzimanolis (2005).

Comment: Popham (1990) suggested that *Cretolabia* is related to the Spongiphoridae (= his Labiidae) because of some similarities, while Engel and Chatzimanolis (2005) do not suggest close affinities, instead placing *C. cearae* in Epidermaptera (see Grimaldi and Engel, 2005), which include Eudermaptera, Labiduridae and Anisolabididae. Here, I agree with Popham (1990) and suggest a close spongiphoridan relationship.

Kotejalabis Engel and Chatzimanolis, 2005

The new species described below agrees with the generic description provided by Engel and Chatzimanolis (2005).

Kotejalabis haeuseri sp. nov.

Material: holotype SMNS 66557 (Figure 11.19c).

Etymology: the specific name is dedicated to Dr Christoph L. Häuser (SMNS), with whom I had the pleasure to work on the Global Taxonomy Initiative (GTI).

Description: ventral view. Length of body (including cerci) 7.5 mm. Head 1.75 mm long and somewhat wider than the prothorax; compound eyes large. Antenna with no more than 11 preserved articles, a few more impressions visible; basal article large, the distal ones becoming increasingly conical. Prosternum rectangular; mesosternum large, with two small lobe-like extensions at the latero-posterior corners; femora rounded; tarsomeres without expansions. Seven abdominal segments visible, suggesting a female; base of cerci contiguous but not abutting; cerci 1.25 mm long, almost straight without ornamentation, but with denticles; no pygidium visible.

Comment: this specimen is preserved in ventral view and so the head appears to be wider than the prothorax. Since the disc-like pronotum is usually wider than the remaining prothorax, the head is probably as wide as the pronotum in the standard dorsal view. The number of visible abdominal segments and the simple shape of the cerci suggest a female specimen. It is significantly smaller than *Kotejalabis goethitica* and lacks a pygidium, which are the reasons for establishing a new species.

Kotejalabis goethitica Engel and Chatzimanolis, 2005

A new specimen identified as this species (SMNS 66515) is featured in Figure 11.19d. This fossil is somewhat smaller (9 mm including cerci) than the holotype of *K. goethitica* figured by Engel and Chatzimanolis (2005) but otherwise is in accordance with the description. The cerci shape and pygidium structure are very similar and both are used as diacritical characters among Recent species. It is noteworthy that the right hind wing is partly open without yielding any further details. Adult specimen of unknown sex.

Comments: Engel and Chatzimanolis (2005) considered *K. goethitica* to be a representative of the Epidermaptera, which includes a number of ‘family’-rank taxa, including the Spongiphoridae (Grimaldi and Engel, 2005). Assuming closer affinities to the latter taxon seems to be justified based on the size, general morphology and the large pygidium which frequently (but not exclusively) occurs in this taxon.

Fossil erroneously identified as Dermaptera

Caririderma pilosa Martins-Neto, 1990a

Comment: this species is a staphylinid beetle. The general habitus of Dermaptera and Staphylinidae is fairly similar; however, the expanded hind wings of *C. pilosa* shows a clearly coleopterous–staphylinid wing venation. It was shown elsewhere (Haas and Kukalová-Peck, 2001; Haas and Gorb, 2004) that in Dermaptera the hind wing venation is conserved with little variation, and so the hind wing venation of *C. pilosa* cannot be that of a modified dermapteran.

11.7 Mantodea: praying mantises

David A. Grimaldi

The Mantodea, or mantises, are among the most recognizable of insects. They are generally quite large (adults have body lengths generally of 2–10 cm, although some are up to 15 cm long or longer), and they have distinctive, spiny raptorial forelegs at the anterior end of the prothorax that are used for grasping prey. The forelegs are folded under the prothorax at rest, giving rise to the common name ‘praying’ mantis. Eyes are large and bulging, with keen vision for detecting movements, but otherwise the head has a basic neopteran structure including three large ocelli, filiform antennae and mandibulate mouthparts. Most mantises have a long prothorax, which extends the reach of the forelegs, and which also allows the head a remarkable degree of pivoting. The basal genera of mantises (i.e. *Chaeteessa*, *Mantoida*, *Metallyticus*, *Amorphoscelis* and *Eremiaphila*) actually have a short prothorax, and consequently the head is more sessile. Many mantises also sway from side to side, which, with the large eyes and pivoting head, allows them excellent depth perception and thus improves their strike, which is important for ambush-type predators. Mantises strike at prey by simultaneously extending the long fore coxae, thick femora and the tibiae and tarsi, and when the spiny tibia and femur suddenly fold against each other this grasps the prey, which is immediately brought to the mouth and devoured, usually wings and all. The strike of mantises is remarkably quick, being faster than the reflexes of cats. Mantises in the basal genera, though, are cursorial predators that scurry along tree trunks and logs, chasing down prey.

The most popularized aspect of mantis biology is their mating behavior; specifically, cannibalism of males by their female partners. While this does occur, it is not the norm (and certainly unnecessary for copulation), but it may be a consequence of the voracious habits of mantises in general and the fact that males are smaller than females, sometimes up to one-half their size. Considerably less well known is the impressive array of mimics among the mantises. Many mantises are green, which camouflages them among living foliage. Others are brown, or mottled grey-brown like lichens, particularly ones that live on tree trunks, or among dead branches and forest leaf litter. Among these, some have leaf-like extensions on their prothorax and legs (e.g. *Deroplatys*, *Gongylus*, *Idolomantis*, *Phyllocrania* and *Zoolea*), making them appear astonishingly plant-like. This camouflages them from birds and other predators, but also allows prey to closely approach them. *Hymenopus coronatus* from South-East Asia, for example, is often found on flowers. It is usually pure white with fringes of pink or purple, which makes it virtually unrecognizable to pollinators.

Mantises probably first evolved in the Late Jurassic, but radiated in the Tertiary, giving rise to the spectacular array of some 2,300 living species. Recent understanding of their phylogeny and fossil record has more clearly revealed their evolutionary history.

Systematics and phylogeny

Despite common awareness of mantises, it is little known that mantises are dictyopterans, closely related to the roaches (Blattaria) and termites (Isoptera). This relationship is based on several obscure characters (such as perforations in the internal strut system of the head, the tentorium), but most obviously on the basis of the female reproductive system. Female Dictyoptera have the ovipositor significantly reduced or entirely lost, and mantises and roaches lay their eggs in a hardened sac, the ootheca. Almost all combinations of relationships among these three 'orders' have been proposed, but the one that is best supported has Mantodea as the sister group to Blattaria+Isoptera (indeed, Blattaria is paraphyletic to Isoptera). Mantises have retained primitive features that the other dictyopterans have lost: the gonoplacs and gonaphyses (appendages in the ovipositor) are least reduced; three large ocelli are present; and the wing venation is the most generalized. This set of relationships in no way implies that mantises are Palaeozoic in age, since roach-like insects ('roachoids') existed since the Carboniferous. In fact, Palaeozoic and many Mesozoic roachoids are stem group Dictyoptera that had well-developed ovipositors (see section 11.8 in this volume).

The traditional classification of mantises is by Beier (1968), who recognized eight families. Ehrmann (2002), in his comprehensive catalogue of the world species of mantises, essentially used Ehrmann's classification, but he employed 15 families because seven subfamilies were elevated in rank. All classifications recognize three families as the most basal: Mantoididae (one Neotropical genus, with nine species), Chaeteessidae (one Neotropical genus, with four species) and Metallyticidae (one South-East Asian genus, with four species; Klass, 1997a; Grimaldi, 2003; Wieland, 2006). Further, families commonly recognized of 'intermediate' phylogenetic position are Amorphoscelididae, Eremiaphilidae, Hymenopodidae and Liturgusidae. The main classificatory differences are whether some subfamilies that are Mantidae *sensu lato* are recognized as subfamilies. Indeed, the one study thus far on mantis DNA sequences (Svenson and Whiting, 2004) found widespread polyphyly of the families Mantidae and Threspidae, as well as paraphyly. Thus, classification of the 'higher' mantises (superfamily Mantoidea) requires complete revision. Interestingly, species in the basal families are uniformly small, cryptic brown, short-bodied, cursorial predators, with the notable exception of *Metallyticus*. That genus has a striking bright metallic iridescence.

Fossil record and significance of the Crato fossils

Fossil mantises are scarce, with only approximately 25 described species. The earliest definitive fossils of the order are from the Valangian-Hauterivian (*c.*135 mya) of Baissa, Siberia (Gratshev and Zherikhin, 1993). Fossil mantises are equally represented as compressions and in amber (the latter primarily as nymphs). Evolutionarily, the most interesting fossils are from the Mesozoic, since this seems to be the nascent stage in mantis diversification.

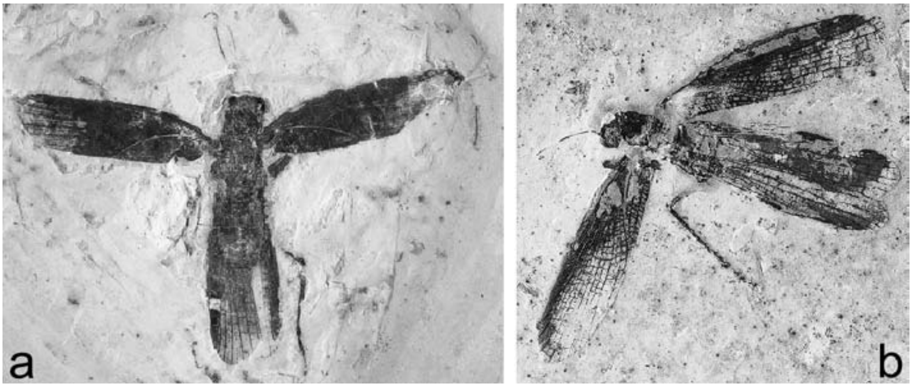

Fig. 11.21. Crato Formation Mantodea *Santanmantis axelrodi* Grimaldi, 2003: (a) specimen SMNS 66677 (old no. 112); (b) paratype SMNS 66680 (old no. 113).

Gratshev and Zherikhin (1993) published the first major paper on Mesozoic mantises, which included 11 taxa (10 of them compressions from the Early to Late Cretaceous of Eurasia, some 135–90 mya). Grimaldi (2003) expanded on that work, based on restudy of the prior material and descriptions of five new Cretaceous taxa (most of them in amber). In that paper a phylogeny of basal mantises was proposed, which indicated that the Cretaceous taxa represent an extensive paraphyletic grade to all living mantises (the monophyletic infraorder Eumantodea). Some Cretaceous mantises, for example, are missing the key feature of a patch of microscopic scales inside each fore femur, which is used in modern mantises to wipe the eyes and head after a meal. The phylogenetic pattern thus indicates that mantises evolved in the Late Jurassic, had their basal diversification in the Cretaceous, and explosively diversified (as the Mantoidea) in the Tertiary.

The first record of fossil mantids from the Crato Formation was provided by Bechly *et al.* (2001: 56, figure 46). Meanwhile, the Crato Formation has yielded two species of mantis. One is based on a unique specimen in the Stuttgart Museum (SMNS 66528 with the old no. SMNS 114; Grimaldi, 2003: 33). This species had apparently pedunculate eyes and a very short and stout fore femur and tibia, not unlike *Cretomantis larvalis* Gratshev and Zherikhin, known as a compressed nymph from the Early Cretaceous of Siberia. Unfortunately, the wing venation of SMNS 66528 is obscured, which is why it was not named.

The second species is the primitive mantis *Santanmantis axelrodi* Grimaldi, 2003 (Figures 11.21a and b and 11.22) and is based on a spectacular series: holotype specimen AMNH 1957, and paratypes AMNH 1956, SMNS 66677 (old no. 112), SMNS 66680 (old no. 113), SMNS 66678 (old no. 115), SMNS 66679 (old no. L72, 172 or 174 as stated by Grimaldi, 2003) and a new specimen SMNS 66519. This was a relatively small mantis, approximately 9.5–10.5 mm in body length. As

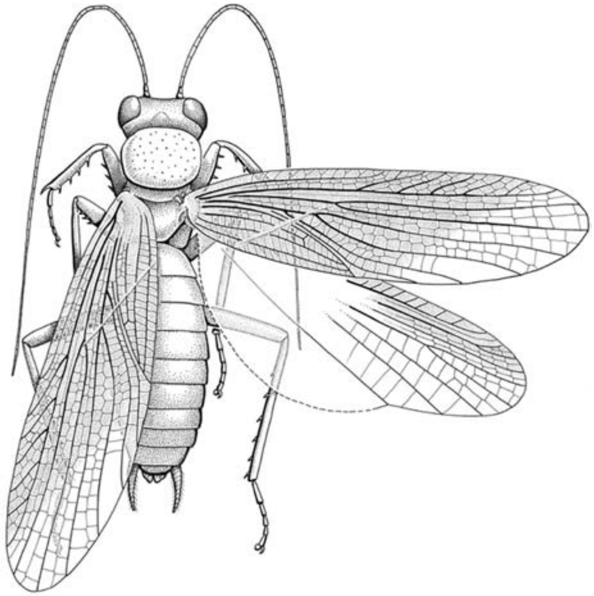

Fig. 11.22. Crato Formation Mantodea: life restoration of *Santanmantis axelrodi* Grimaldi, 2003. From Engel and Grimaldi (2005).

expected, its proportions were very similar to that of living basal mantises, with notably a short abdomen and body, including a nearly square pronotum; and the fore- and hind wings extended well beyond the apex of the abdomen. The forelegs were folded under the thorax and apparently raptorial, and the mid- and hind legs were long, gracile and obviously the ones employed for walking. Its forewings were partially sclerotized (the distal third less so, and often lost in the fossils), and this pair of wings primitively bore a very well-developed claval suture, as well as a prominent pseudovein. The pseudovein, oddly enough, is larger than in any other living or extinct mantis.

The density of Crato concretions compared to the limestone matrix has allowed high-resolution (<5 µm) X-ray computed-tomography scanning of fossils from the deposit (e.g. Grimaldi and Engel, 2005: figure 2.9), including *Santanmantis* (Grimaldi, 2003: 30–31). These images have thus allowed detailed reconstructions of some Crato insects (e.g. Figure 11.22), since the images are three-dimensional and provide views of surfaces hidden deep in matrix. Although the high-resolution computed tomography (HRCT) scanning has been unable to resolve the details of foreleg spination (which newer-generation instruments may eventually resolve), an extensive series of *Santanmantis* specimens and their study with HRCT scanning provides a remarkably complete picture of one of the oldest and most primitive mantises.

11.8 'Blattaria': cockroaches and roachoids

Günter Bechly

Cockroaches and their relatives are often found in abundance and are familiar insects, especially in the tropics. Fossil cockroaches and roachoids are also often abundant, and are especially common in the Crato Formation. About 4,000 Recent species of cockroaches plus about 1,000 fossil roachoid species have been described (Vršanský, 2005). Living cockroaches are usually small to large insects with long filiform antennae. They possess hypognathous chewing mouthparts with well-developed mandibles. The compound eyes are large with two lateral ocelli present. Usually they have two pairs of wings, but some are secondarily wingless. The forewings are heavily sclerotized as tegmina and are much more slender than the broad hind wings, which have a large anal fan. In the forewings vein CuP is strongly curved and delimits a rounded anal field. The abdominal cerci are relatively long with numerous segments and the female ovipositor is reduced in modern cockroaches, but is still present in fossil roachoids that seem to belong to stem group Dictyoptera rather than the crown group Blattaria. The discovery of an undescribed living cockroach with ovipositor is mentioned by Vršanský (2003a: 30). All living cockroaches lay large pods of eggs called oothecae. Development is paurometabolous with a gradual development from larva to imago. Cockroaches are omnivores with cosmopolitan distribution in arid as well as humid environments, and a few species are considered pests.

Systematics and phylogeny

Within modern pterygote insects (Pterygota: Neoptera) the cockroaches belong to the clade Dictyoptera, which also includes Isoptera (termites) and Mantodea (praying mantids).

Almost certainly the Recent roaches do not constitute a monophyletic clade, but have to be considered as paraphyletic with regard to termites, because polyphagid roaches in general, and the genus *Cryptocercus* in particular, are more closely related to termites than to other roach taxa (see Section 11.9). Furthermore, many of the 'fossil roachoids', especially from the Palaeozoic, possess a long ovipositor and therefore cannot be Blattaria but have to be attributed to the stem group of all Dictyoptera. These forms look like roaches because a roach-like habitus is the typical 'groundplan' of Dictyoptera. Such stem group roachoids with long ovipositors also occur in the Lower Cretaceous of Mongolia (Vršanský, 2003b), but have yet to be discovered in the Crato Formation. The Jurassic and Cretaceous Umenocoleidae also retain an ovipositor, albeit a short one, and therefore also probably belong to the stem group Dictyoptera rather than to Blattaria (+Isoptera) (see below).

The true cockroaches are usually classified in nine Recent families with the following relationships (Klass, 2001; Bohn, 2003a; Grimaldi and Engel, 2005): (Blattidae+(Tryonicidae+((Polyphagidae+Lamproblattidae)+(Cryptocercidae+termites)) + (Nocticolidae? + Anaplectidae + ("Blattellidae" + Blaberidae)))). Of these Recent families only the family Blattellidae, which has to be regarded as highly paraphyletic with the subfamilies Anaplectinae and 'Plectopterinae' being most basal, is known from the Crato Formation.

Fossil record

Unlike many other groups of fossil insects there is no up-to-date revision of fossil roaches. Most works recording the presence of fossil roaches note the urgent need of such a revision and refrain from describing new species (e.g. Maisey, 1991; Grimaldi and Engel, 2005) because of the taxonomic mess in 'palaeocockroachology'. Consequently, despite the abundance of material and quality of preservation of Crato Formation roaches, they have hardly been studied. The current state of knowledge of the fossil record of Blattaria in general, and of Cretaceous roaches in particular, has been summarized by Carpenter (1992), Vršanský (1999a, 2004), Vršanský *et al.* (2002a) and Grimaldi and Engel (2005).

Palaeobiology and palaeoecology

Cockroaches are sometimes highly habitat-specific and their presence and general abundance can provide useful clues for the reconstruction of palaeoenvironments and palaeoclimate (Vršanský *et al.*, 2002b). The large percentage of roaches in the Crato taphocoenosis is typical for a warm climate, probably more arid than humid or with strong seasonality. A similar composition of Recent terrestrial arthropods dominated by roaches, orthopterans and spiders is, for example, found in the seasonal forests of Hong Kong (Kwok and Corlett, 2002). According to Vršanský (personal communication) most cockroach species from Crato are characteristic of shrub vegetation.

Crato fossils

Fossil cockroaches were first described from the Crato Formation by Pinto and Purper (1986) and Pinto (1989). Even though many hundreds of specimens have been discovered already, such that cockroaches are one of the most abundant fossils in the Nova Olinda Member, only a few species have been formally described. Photographs and brief discussions of Crato cockroaches have appeared in Grimaldi and Maisey (1990: 10, figure 3), Maisey (1991: 381 and 386), Martill (1993: plate 6, figure 5), Mendes (1991a, 1991b, 1993, 1995, 1997b, 1998b, 2000), Bechly (1998: 151, Abb. 5), Bechly *et al.* (2001a: 26, Abb. 17), Vršanský (1999a, 2002, 2004), Martins-Neto (2005b) and Grimaldi and Engel (2005: 235, figure 7.72).

About 26% (960 from a sample of 3,651 fossil insects) of the many thousands of Crato insects discovered are cockroaches and roachoids. According to Vršanský (2004), among the hundreds specimens only seven different species are present, dominated by Blattellidae (60%), with subdominant †Blattulidae (25%), as well as †Umenocoleidae (15%) and a single species of †Mesoblattinidae. Even though there may be a few more species, this is a relatively small diversity of species compared to the thousands of specimens collected.

Some of the Crato cockroaches have an exceptional quality of preservation, with preserved colour pattern of the wings (Bechly *et al.*, 2001a: Abb. 17; Martill and Frey, 1995: incorrectly identified as a bug) and sometimes even preserved soft parts including nerves, eye lenses (Vršanský, 2003a), guts and oothecae (Grimaldi and Engel, 2005).

†Mesoblattinidae

Although Mendes (1995) mentions three undescribed species of *Mesoblattina*, according to Vršanský (2004) only a single species of this extinct family is present among the Crato roaches and represents a new undescribed genus and species. †Mesoblattinidae belong to the stem group of all Dictyoptera (Vršanský *et al.*, 2002a; Grimaldi and Engel, 2005) because their females have retained a relatively distinct external ovipositor. Unfortunately, I did not find any material with mesoblattinid affinities among the numerous fossil roaches from this locality that I have studied.

†Raphidiomimidae

An undescribed member of this erratic and predatory Mesozoic roach family, which seems to be the sister group of Mesoblattinidae (Grimaldi and Engel, 2005: 229), is recorded from the Crato Formation by Mendes (1991b). A possible fossil of this family is also featured on Figure 11.90c.

†Umenocoleoidea

Diagnosis: small roachoid habitus but with beetle-like appearance; large compound eyes; antennae filiform but shorter than body; forewing sclerotized; hind wings membranous and with prominent pterostigma; hind wing venation similar to Blattulidae; roach-like cerci.

Comment: here re-defined to include the three fossil families †Vitismidae, †Cratovitismidae fam. nov. and †Umenocoleidae, but excluding the Recent taxa Anaplectidae and Oulopterygidae that are here considered as unrelated to †Umenocoleidae (*contra* Vršanský, 2003a).

†Cratovitismidae fam. nov.

Type genus: *Cratovitisma* gen. nov., by present designation.

Diagnosis: like †Vitismidae, intermediate between Blattulidae and †Umenocoleidae; with strongly sclerotized forewings, pterostigmata in the hind wings, transverse head (different to Vitismidae) with relatively short antennae and a short ovipositor, but with curved CuP in the broader forewings, a more dense venation in the hind wings, and a disc-like pronotum (different to most Umenocoleidae).

Comment: Peter Vršanský (personal communication) thinks that this new taxon could rather represent a transition between †Liberiblattinidae and †Umenocoleidae. He doubts that it is related to †Vitisminae, which belong to †Holocompsidae and have a reduced ovipositor and a very different forewing venation. A very similar animal, belonging to a closely related new genus, was recently discovered in deposits 50 myr older from Asia, and is the oldest representative of the Umenocoleoidea.

Cratovitisma gen. nov.

Type species: *Cratovitisma oldreadi* sp. nov., by present designation.

Derivation of name: named after the Crato Formation and the similar fossil roach genus *Vitisma*.

Diagnosis: as for type species, since monotypic.

Cratovitisma oldreadi sp. nov.

Material: holotype SMNS 66000-127 (Figure 11.23a); paratype without number at SMF; and a third specimen with no. N63 in coll. MSF.

Type locality: vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after Mr Chuck Oldread from Summerville, South Carolina, USA, for his invaluable help preparing Crato fossils.

Diagnosis and description: cockroach with adult body length of 6.9 mm and forewing length of 5.3 mm. As in *Vitisma*, the forewings are broader than in *Ponopterix* (maximum 2 mm wide), strongly sclerotized, but with vestiges of the wing veins still clearly visible. Vein CuP is strongly curved and delimits a typical roachoid anal field in the forewings. The hind wing venation is very similar to *Vitisma*, and thus more dense than in *Ponopterix*, but of similar pattern and with

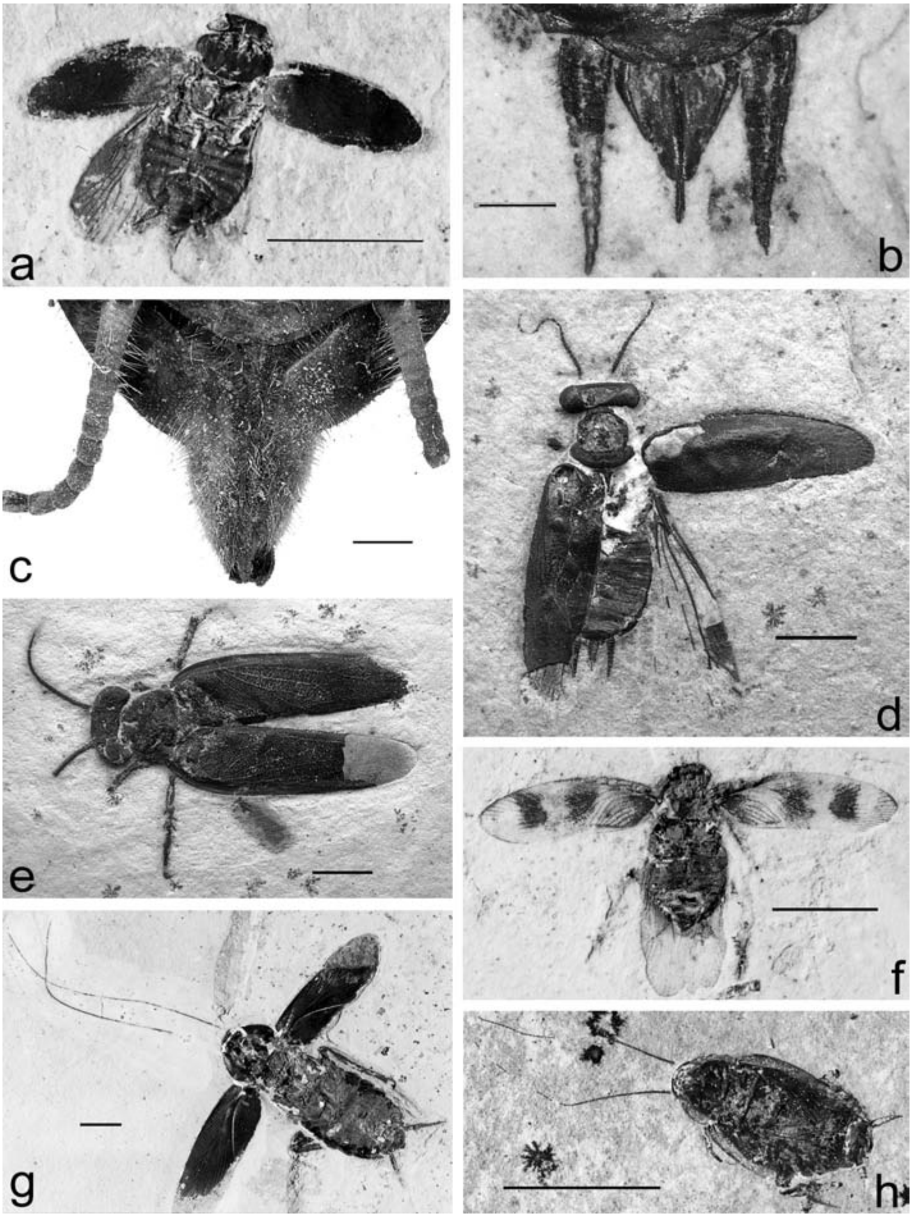

Fig. 11.23. Crato Formation cockroaches: (a) Umenocoleoidea, Cratovitismidae fam. nov., *Cratovitisma oldreadi* gen. et sp. nov, holotype SMNS 66000-127; scale bar, 5 mm; (b) Umenocoleoidea, Umencoleidae, *Ponopterix maxima* sp. nov., SMNS 66328, ovipositor; scale bar, 5 mm; (c) Mantodea, Mantidae, *Sphodromantis viridis*, ovipositor, Recent; scale bar, 1 mm; (d) Umenocoleoidea, Umencoleidae, *Ponopterix axelrodi*, SMNS 66338; scale bar, 2 mm; (e) Umenocoleoidea, Umencoleidae, *Ponopterix maxima* sp. nov., holotype SMNS 66332; scale bar, 2 mm; (f) Blattulidae, *Elisama americana*, SMNS 66558, with original colour pattern preservation; scale bar, 5 mm; (g) Blattellidae, undescribed new genus and species, SMNS 66318; scale bar, 5 mm; (h) Blattaria, Familia *incerae sedis*, undescribed new genus and species, SMNS 66308; scale bar, 5 mm.

pterostigma. The head is transverse as in Umenocoleidae (different from *Vitisma*) and the antennae are also similar to Umenocoleidae, and thus shorter than the body. The pronotum is flat and disc-like as in *Vitisma* and true cockroaches, but very different from *Ponopterix* and *Umenocoleus*. A protruding ovipositor seems to be present, but is somewhat less conspicuous than in *Ponopterix* (similar to Blattulidae).

Comment: the transverse head seems to place this new genus and species closer to †Umenocoleidae than *Vitisma*, so that a new family would be justified.

†Umenocoleidae

Diagnosis: head transverse; pronotum saddle-like and much narrower than head (except in the most basal *Jantaropterix lebani*); sclerotized forewing only with vestiges of the reduced wing venation still visible (CuP curved in basal genera, but not curved in the more derived ones); derived cup-like ultrastructures on forewings (Vršanský, 2003a); legs spiny and tarsi very long (nearly as long as tibia) and apparently five-segmented (first segment the longest, second segment the second longest) as in cockroaches; cerci with about 13 segments; females with a short but distinctly prominent ovipositor (Figure 11.23b).

Comments: according to Vršanský (2004) about 15% of the fossil roaches from the Crato Formation belong to †Umenocoleidae. Currently †Umenocoleidae contains six genera with 11 species from the Lower Cretaceous of Gansu, China (*Blattapterix* Vršanský, 2003b; *Umenocoleus* Chen and Tian, 1973; *Petropterix* Vršanský, 2003b), Baissa, Transbaikalia, Siberia (*Petropterix* Vršanský, 2003b), Bon Tsagaan Mongolia (*Elytropterix* Vršanský, 2003b; *Petropterix* Vršanský, 2003b), Lebanon amber (*Jantaropterix* Vršanský, 2003b) and the Crato Formation of Brazil (*Ponopterix* Vršanský and Grimaldi in Vršanský, 1999a). *Jantaropterix* is also known from Upper Cretaceous New Jersey amber.

Originally described as a family of fossil Coleoptera by Chen and Tian (1973), it was incorrectly transferred by Carpenter (1992: 149–150) to †Protelytroptera (= Protocoleoptera), but considered as Blattaria by Vršanský *et al.* (2002a) and Andrew Ross (personal communication). More recently it was considered a stem group dictyopteran by Grimaldi and Engel (2005). This latter view seems reasonable, because the distinct external ovipositor (Figure 11.23b) excludes it from a position within crown group Dictyoptera. On the other hand, a polyphagoid relationship, as proposed by Vršanský (1999b, 2003a), would not necessarily imply an unlikely convergent evolution of the dictyopteran genital chamber and oviposition with oothecae (Vršanský, 2003a: 30; *contra* Vršanský, 1999a), because Recent Mantodea also have a small external ovipositor that is not much less developed than that seen in †Umenocoleidae (see Figure 11.23c). Consequently, the only implied assumption would be the multiple parallel invagination of the ovipositor into the genital chamber within the various lineages of Recent cockroaches.

An alleged relationship of †Umenocoleidae with Mantodea, proposed by Gorochov (2001: 357), was convincingly ruled out by Grimaldi (2003).

Similarities of †Umenocoleidae with the fossil roach genus *Vitisma*, described by Vršanský (1999b) as the most basal Polyphagidae (Vitisminae), include a strongly sclerotized forewing, a distinct pterostigma in the hind wing, and a near-identical hind wing venation. However, the forewing venation, which lacks the typical roachoid CuP curvature, is very different between some †Umenocoleidae (*Ponopterix* and *Blattapterix*) and the remaining †Umenocoleoidea (e.g. *Vitisma*, *Elytropterix* and *Petropterix*) and is strikingly different between these umenocoleidids and any other Blattaria (including roachoid stem group Dictyoptera from the Carboniferous). The presence of a saddle-shaped pronotum instead of a shield-like pronotal disc is a further difference between roaches and roachoids. Both characters have to be considered as autapomorphic reversals.

Jantaropterix lebani described by Vršanský and Grimaldi (in Vršanský, 2003a) had previously been figured by Grimaldi (1996: 37) and is noteworthy because of two striking symplesiomorphies with *Vitisma*: a strongly curved CuP in the forewings and a shield-like pronotum; furthermore it has a fore- and hind wing venation that is nearly identical to *Vitisma*. This heterobathmic (*sensu* Hennig) distribution of character states suggests that †Umenocoleidae evolved from more roach-like ancestors like *Vitisma* (which should be transferred from Polyphagidae to †Umenocoleoidea as its most basal member) with *Cratovitisma* gen. nov. and *Jantaropterix lebani* as intermediate links between Vitismidae and 'higher' †Umenocoleidae. The similarities in hind wing venation of †Umenocoleidae, †Vitismidae stat. nov., Blattulidae and modern Polyphagidae could well be symplesiomorphic and are not reliable evidence for a polyphagoid relationship.

According to Grimaldi and Engel (2005: 235), Vršanský has described a putative living species of †Umenocoleidae. If the phylogenetic analysis of this Recent species supports a position outside crown group Dictyoptera, a new Recent insect order should be erected for this species!

For such a new order the name †Protocoleoptera should not be used (*contra* Bechly *et al.*, 2001b: 49) because it was recently re-defined as a coleopteroid clade including †Tshekardocoleidae (Grimaldi and Engel, 2005: 361–362). *Contra* Carpenter (1992), †Protocoleoptera is also not a synonym of the dermapteroid stem group †Protelytroptera, because †*Protocoleus* Tillyard, 1924 is not sharing the typical patches in the hind wing venation that are very well defined in †Protelytridae and Recent Dermaptera.

With regard to alleged living Umenocoleoidea it should be noted that the statement by Vršanský (2003a: 6, 30), that living genera of beetle-mimicking cockroaches like *Anaplecta* (Anaplectidae) and Melyroidea, *Prosoplecta* and *Oulopteryx* are probably Umenocoleoidea, has to be considered erroneous, as these insects are typical cockroaches with reduced ovipositor, broad shield-like pronotum, broad head and very different wing venation with blattoid curved CuP in the forewings and without the umenocoleoid pterostigmata in the hind wings. Furthermore, the latter three genera are placed in subordinate position within Blattellidae-Pseudophyllodromiinae by the leading specialist on Recent cockroaches (Roth, 1994), who also considers the former family Oulopterygidae as a synonym of Blatellidae-Pseudophyllodromiinae. Until the existence of an unambiguous surviving Umenocoleoidea is demonstrated this group has to be considered extinct.

Ponopterix axelrodi Vršanský and Grimaldi in Vršanský, 1999a

Material: holotype AMNH 43800 and six additional specimens (SMNS 66326, 66329, 66334, 66335, 66336 and 66338) at SMNS (the very well-preserved specimen SMNS 66338 is featured in Figure 11.23d). Two further specimens (SMNS 66325 and SMNS 66331) are just in between the size range of *P. axelrodi* and the new species described below.

Diagnosis: body length 4.9–7.5 mm; forewing length 4.3–6.5 mm; head capsule distinctly narrowed between the large and globular compound eyes; pronotum very small and bell-shaped; vestigial wing venation on elytra usually less distinct than in the following new species.

Ponopterix maxima spec. nov.

Material: specimen no. SMNS 66332 (holotype) (Figure 11.23e) and eight further specimens (SMNS 66323, 66324, 66327, 66328 (Figure 11.23b), 66330, 66333, 66337 and 66562) at SMNS.

Type locality: vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named because of its larger body size than *Ponopterix axelrodi*.

Diagnosis: body length 7.5–12.5 mm; forewing length 6.5–10.5 mm; head broader than in previous species, especially between the compound eyes; pronotum comparatively larger and broader and saddle-shaped; otherwise very similar to *P. axelrodi*, therefore very probably belonging to the same genus.

Comment: this new species was figured by Bechly *et al.* (2001: 49, Abb. 38) as Protocoleoptera.

Cercopisblatta Martins-Neto, 2005a

Comment: this genus was mentioned without specific designation by Martins-Neto (2005b) and is here regarded as a *nomen nudum* until a proper designation, diagnosis and figure are published.

†Blattulidae

Comment: †Blattulidae are represented in the Crato Formation by two genera and species; *Elisama americana* and an undescribed genus and species. This family could either belong to the stem group of Dictyoptera (Grimaldi and Engel, 2005) or might be related to Polyphagidae (Vršanský, 1999b). Vršanský (2003b) described structural similarities of the external ovipositor in †Blattulidae and †Umenocoleidae.

Elisama americana Vršanský, 2002

Material: holotype AMNH XX (stated this way by Vršanský, 2002, probably due to a lapse) at the American Museum of Natural History in New York, USA; and three additional specimens, SMNS 66558 with colour preservation (Figure 11.23f), SMNS 66000-125, and SMNS 66316.

Diagnosis: body length 6.5–8.5 mm; antennae about as long as body; head with very large and globular compound eyes; width of pronotum is 146% of head width; pronotum is broadest in the middle, thus with about equal anterior and posterior halves; forewing length 7.5–10.2 mm; forewing venation with an extremely curved CuP and anal veins that reach the hind margin; Sc very short; M with three or four branches; R/RS with nine to 10 branches; forewings sometimes preserved with a distinctly banded color pattern (Bechly *et al.*, 2001a: Abb. 17), for example in specimen SMNS 66558 (Figure 11.23f).

Comment: because of the long and free fore coxae and the structure of styli and cerci Vršanský (2002) considers this species and some other polyphagoid cockroaches to be more closely related to Mantodea. I strongly disagree with this view, because it is contradicted by molecular data and by several unique plesiomorphies of Mantodea (three ocelli, long vein Sc) that are synapomorphically absent in all Recent cockroaches and termites.

Blattellidae

Two species of Blattelidae occur in the Crato Formation, each in its own genus. One of these species was described by Pinto and Purper (1986), but incorrectly placed in the mesoblattinid genus *Mesoblattina* (see below), and the other is currently still undescribed. A preliminary analysis suggests that blatellids represent the most

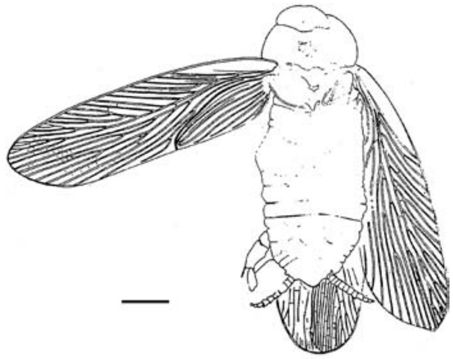

Fig. 11.24. Crato Formation cockroach: Blattellidae, *Mesoblattina limai* Pinto and Purper, 1986, holotype, MP-1–6400; scale bar, 2 mm. Based on Pinto and Purper (1986).

abundant cockroaches in the Crato Formation, comprising 60% of all fossil roaches (Vršanský, 2004). An appraisal of Crato Blattellidae and a formal description of the undescribed taxon seem to be in progress (F. Menon, personal communication).

'Mesoblattina' limai Pinto and Purper, 1986

Material: holotype no. MP-I-6400 (Figure 11.24) at the coll. Prof. Lima at the University of São Paulo and four specimens (SMNS 66314, 66315, 66319 and maybe 66311) at SMNS.

Diagnosis: body length 11–14 mm; antenna about as long as body; pronotum subcircular, very broad (about 200–233% of head width) with very broad lateral lobes; forewing venation typically blattellid with Sc bifurcated, R with eight to 11 branches (some of them bifurcated), MA and CuA free and branched, several anal veins simple and ending on CuP, intercalary veins and crossveins present (not as few as mentioned in the original description).

Comment: this species was incorrectly placed in *Mesoblattina*, belonging instead to a distinct, but undescribed new blattellid genus according to Vršanský (2004).

Unnamed new genus and species A

Material: three specimens with nos SMNS 66313, SMNS 66317 and SMNS 66318 (Figure 11.23g), as well as a putative further specimen with preliminary no. SMNS 0116 (K9).

Diagnosis: body length 18.3–27.0 mm; antennae distinctly longer than body (31 mm in a specimen with 25 mm body length); pronotum very large, with 215–233% of head width and with very broad lateral lobes; pronotum broadest in the middle of the posterior half; forewing venation typically blattellid.

Comment: very similar to '*M.*' *limai*, except for the distinctly larger size, and thus probably belonging to the same new genus. It has not been possible to determine whether this new taxon is conspecific with the undescribed new genus and species mentioned by Vršanský (2004) or instead represents a third blattellid taxon from Crato.

Blattidae

The presence of the Blattidae in the Crato Formation was first noted by Mendes (1993), who recognized that *Mesoblattinopsis schneideri* Pinto, 1989 was a blattid.

Mesoblattinopsis schneideri Pinto, 1989

Comment: two further new species of *Mesoblattinopsis* are reported by Mendes (1997b).

Family *incertae sedis*

Unnamed new genus and species B

Material: three specimens with nos SMNS 66321, SMNS 66308 (Figure 11.23h) and SMNS 66309.

Diagnosis: body length about 8.7–9.5 mm; shape of body longish oval; antennae about as long as body; pronotum much broader than head (width 3.0–3.7 mm, thus 180–195% of head width), posteriorly broader than anteriorly, but with narrower lateral lobes than the new blattellid species mentioned above; forewing venation unknown, but with a broad costal margin; cerci with about 10 segments.

11.9 Isoptera: termites

Günter Bechly

There are about 2,800 Recent and about 130 fossil termite species, usually classified in seven families (see below). Termites are relatively small insects with a body length that is usually much less than 3 cm. They are soft-bodied and often called white ants because they are small colonial insects of more or less whitish color. They are, however, completely unrelated to ants, but closely related to cockroaches and mantids. Their antennae are filiform or moniliform, usually relatively short, with 10–32 segments. They possess prognathous chewing mouthparts with well-developed mandibles, and their compound eyes and ocelli are often reduced, except in alate stages. Wings are only present in the reproductive stages and are shed after the mating flight. Both pairs of wings are membranous and much longer than the abdomen. Fore- and hind wings are similar in size (hence their scientific name Isoptera) and are similar in shape and venation, except in the most basal family Mastotermitidae that have retained a broader hind wing. The abdominal cerci are relatively short with one to eight segments (usually two to four segments) and the female ovipositor is reduced, as are all other genital appendages. Termites lay single eggs, except Mastotermitidae, which lay pods of up to 24 eggs. The development is paurometabolous with a gradual development from larva to imago. Termites mainly feed on cellulose but also feed on fungi and organic detritus. Consequently, they are often considered a pest. They are polymorphic eusocial insects with different castes, either nesting in small colonies in their feeding wood ("one-piece nesting") or in large colonies in the soil from which they forage in search for wood. Termites have a worldwide distribution in all subtropical and tropical regions where woody plants are available. In tropical areas termites and ants form the largest fraction of the animal biomass.

Systematics and phylogeny

The monophyly of Isoptera has never been disputed and is very well supported by numerous synapomorphies. Together with mantids and cockroaches the termites belong to the monophyletic Dictyoptera within modern pterygote insects (Pterygota: Neoptera). Termites are closely related to polyphagid cockroaches, and the sister group of Isoptera is the North American wood-feeding cockroach genus *Cryptocercus*. In addition to the general dictyopteran characters, *Cryptocercus* and primitive termites share a social behaviour, wood-feeding, the possession of intracellular endosymbiontic bacteria and protists (Lo *et al*., 2003), the specific structure of the proventriculus (Klass, 1997b), the mandibular dentition and the moniliform antennae (Grimaldi and Engel, 2005).

All fossil and Recent termites are classified within the seven Recent families Mastotermitidae, Hodotermitidae (including the extinct subfamily Carinatermitinae), Termopsidae (including the extinct subfamily Cretatermitinae), Kalotermitidae, Serritermitidae, Rhinotermitidae (including the extinct subfamily Archaeorhinotermitinae) and Termitidae. It is often assumed that these families are successively more closely related to the most modern and most derived family Termitidae. However, because of several very primitive characters of Termopsidae (long cerci with four to eight segments, vestige of fifth tarsal segment and one-piece nesting without a worker caste) and Kalotermitidae, I concur with Bohn (2003b: 248), who suggested the sequence Mastotermitidae, Termopsidae (?paraphyletic), Kalotermitidae and Hodotermitidae to be successively closely related to the clade of 'higher' termites formed by Termitidae and 'Rhinotermitidae'+Serritermitidae (the latter should instead be included as a subfamily within Rhinotermitidae because Rhinotermitidae is paraphyletic to Serritermitidae). Despite this, Mastotermitidae, Termopsidae, Hodotermitidae and Kalotermitidae all represent very basal and ancient lineages, and are the only taxa already present by the Lower Cretaceous.

The Australian relic species *Mastotermes darwinianus* (Mastotermitidae) is the most basal living termite and the only one to have retained certain blattarian characters like a larger size, a broader pronotum, an anal fan in the hind wings, tarsi with five distinct segments, vestige of ovipositor still present, deposition of eggs in pods (oothecae) and endosymbiontic bacteria.

The primitive families Hodotermitidae and Termopsidae have often been considered as closest relatives, but recent phylogenetic studies contradict this hypothesis (Grimaldi and Engel, 2005). The common presence of four or five cercal segments is only a symplesiomorphy of Hodotermitidae and Termopsidae that is actually absent in the most primitive Mastotermitidae. Furthermore, the reduction of the ocelli in Hodotermitidae and Termopsidae can hardly be considered as a convincing synapomorphy, as the ocelli are also reduced in other subordinate taxa within Isoptera, which in any case have a trend towards reduction of the eyes and ocelli.

Evolution

According to some early authors, Mantodea and Isoptera should have diverged during the Permian, a view supported by Krishna (1990). However, this hypothesis is now considered unlikely as it is neither supported by the fossil record nor by any modern phylogenetic analyses (Grimaldi and Engel, 2005). Living members of the most basal taxa Mastotermitidae and Hodotermitidae, even though they have retained a relatively primitive morphology, show a mixture of both primitive and derived traits in their social organization. The common presence of true workers and foraging behavior in the basal Mastotermitidae and Hodotermitidae as well as in the derived clade formed by Serritermitidae+Rhinotermitidae+Termitidae seems to support the so-called ancestral worker hypothesis, but from the viewpoint of evolutionary biology it is more probable that this is due to a triple parallel development, and that the one-piece nesting of Termopsidae and Kalotermitidae represents the ancestral condition for termite social organization (Thorne and Traniello, 2002). Nevertheless, currently it cannot be definitely decided if one-piece nesting (groups that consume only the wood in which they live and in which helpers have developmental flexibility) or organized foraging away from the nest (correlated with a true worker caste and soil nesting) represents the primitive state within termites.

Fossil record

The most recent systematic revision of all fossil termites was provided by Nel and Paicheler (1993), while Thorne *et al.* (2000), Belayeva (2002), Thorne and Traniello (2002) and Grimaldi and Engel (2005) summarized the current state of knowledge of their fossil record. Unfortunately, there is no fossil record of primitive proto-termites that could illustrate the evolutionary transition from blattarian ancestors to modern termites, which is suggested by a comparison of the Recent wood roach *Cryptocercus* and primitive Recent termites like *Mastotermes darwiniensis*. Except for *Meiatermes bertrani* from the lowermost Cretaceous of Spain, the fossil termites from the Crato limestones belong to the oldest known fossil termites of all. All alleged termites from the Upper Jurassic Solnhofen limestones of Bavaria in Germany are based on incorrect determinations (e.g. *Gigantotermes excelsus* is a lacewing) or on dubious specimens that have to be considered as indeterminable fossil problematica.

Several alleged fossil termite nests have been described from the Upper Triassic of North America (Hasiotis and Dubiel, 1995; Hasiotis *et al.*, 1997), the Lower Jurassic of South Africa (Bordy *et al.*, 2004) and the Upper Cretaceous of Texas (Rohr *et al.*, 1986).

The taxonomy and phylogenetic systematics of fossil termites requires urgent revision to better understand termite evolution. An example is *Valditermes* from the Cretaceous Weald Clay of England, which is still attributed to Hodotermitidae by Engel and Grimaldi (2005), as it was by Jarzembowski (1991), even though the well-developed anal area clearly excludes any position within the clade formed by all non-mastotermitid termite families. Jarzembowski (1991) even discussed this character and correctly stated that it is only a symplesiomorphy with Mastotermitidae, but ignored its phylogenetic implications. Likewise, the several fossil termite genera attributed to Hodotermitidae have five-segmented tarsi, which prohibits such a referral, and were mostly ignored or not considered in phylogenetic terms. The referral of *Carinatermes nascimbeni* from Upper Cretaceous New Jersey amber to Hodotermitidae must also be questioned, as it appears to have five-segmented tarsi, a broad pronotum and keeled fore coxae as in Mastotermitidae (Engel and Grimaldi, 2005: 246).

Palaeobiology and palaeoecology

About 1% of the several ten thousands of Crato insects so far discovered are termites. This small number actually represents several hundred specimens, indicating a high abundance in the hinterland, and indirect evidence for abundant woody plants and trees in the region, which is otherwise not well documented. Fossils of shrubby plants and herbs are common in the Crato Formation, but large logs of wood are very rare indeed. The biggest piece found was less than 1 m long. In fact, termites are more common than bits of wood over 10 cm in length. Maybe Crato termites foraged on smaller, stick-like plant material, which was provided by the abundant gnetaleans.

All fossil termites from this locality represent alate stages, except for one of the 21 specimens studied by Fontes and Vulcano (1998) that appears not to be a worker or soldier, but simply an alate stage with shed wings. This lack of workers and soldiers is odd considering that they occur frequently in Tertiary amber. Furthermore, the frequent occurrence of other flightless terrestrial arthropods (e.g. spiders or nymphs of bugs and cicadas) in the Crato Formation suggests that the absence of worker and soldier termites can hardly be attributed to biostratinomic processes. It may possibly hint at one-piece nesting behavior in the Crato termites, because the absence of foraging behavior would explain why only alate stages were likely to end up in the Crato lagoon. It is also quite obvious that Crato termites did not nest underground in the river valleys, because if they did, then whole nests would have been washed into the Crato lagoon during floods. So they must have nested in drier ground, above the floor of the river valleys.

Crato termites

Six termite species have been described from the Crato Formation (Krishna, 1990; Fontes and Vulcano, 1998; Martins-Neto *et al.*, 2006). Furthermore, images of Crato termites have been published (Maisey, 1991: 384; a specimen of *Mariconitermes talicei*; Bechly *et al.*, 2001a: figure 47, a specimen of *Nordestinatermes araripena*; and Fontes and Vulcano, 2004: figures 1 and 2, *Nordestinatermes araripena*; figure 3, *Mariconitermes talicei*).

Mastotermitidae

Diagnosis: short cerci with only two segments is the single autapomorphy for the group (at least in the Recent genus *Mastotermes*, convergent to all modern termites except Hodotermitidae and Termopsidae). The remaining characters are plesiomorphic: relatively large size; antennae long with more than 29–32 segments in alates; large compound eyes; ocelli present; fontanelle absent; pronotum distinctly broader than head capsule in alates; wings with complete venation with distinct and branched RS, M, and Cu; RS with anterior branches; anal fan of hind wing well developed; basal transverse suture absent in hind wings; five distinct tarsomeres; eggs produced in pods (homologous to the oothecae of Blattaria and Mantodea); eusocial with true worker caste and foraging behavior (probably convergent to Hodotermitidae and more modern termites).

Cratomastotermes gen. nov.

Type species: *Cratomastotermes wolfschwenningeri* sp. nov., by present designation.

Derivation of name: named after the Crato Formation and the Recent relic genus *Mastotermes*.

Diagnosis: same as type species, since it is monotypic.

Cratomastotermes wolfschwenningeri sp. nov.

Material: holotype SMNS 66186 (Figure 11.25a) and paratypes SMNS 66187 and SMNS 66188 (Figure 11.25b). A further but somewhat smaller specimen (SMNS 66189) with a body length of 11 mm and a wing length of 14 mm might also belong to this species.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after Dr Karin Wolf-Schwenninger for her invaluable help with my studies on fossil insects.

Diagnosis and description of alates (Figures 11.25a and b): body length 12–15 mm; compound eyes large; area of ocelli not preserved; pronotum broader than head (4–5 mm wide) and cockroach-like (plesiomorphy); legs and tarsi not preserved, thus number of tarsomeres unknown; forewings 17 mm, hind wings 16 mm long; SC long; veins RS, M and Cu in both pairs of wings well developed and richly branched; scales of wings not preserved; hind wing much broader than forewing with a well-developed anal fan; cerci not preserved, thus number of cercal segments unknown. The paratype specimen no. SMNS 66188 (Figure 11.25b) even shows soft-tissue preservation of abdominal internal organs including parts of the gut.

Comments: the comparably large size, the well-developed pronotal lobes, the complete wing venation, and the broad hind wings with anal fan strongly suggest referral to Mastotermitidae, even though this is based on symplesiomorphies. Although Mastotermitidae represents the most basal and most primitive family of termites (Grimaldi and Engel, 2005), which should be expected to be abundant among Mesozoic termites, this family is exceptionally rare in the Mesozoic. However, the occurrence of Mastotermitidae in the New World and in South America has previously been documented by four Tertiary species (Fontes and Vulcano, 1998: 280–281).

Termopsidae

Diagnosis: the following are apomorphies: ocelli absent (convergent to or synapomorphic with Hodotermitidae); antennae shorter with only 11–21 segments; pronotum flat (not saddle-shaped as in Hodotermitidae), usually less wide than head.

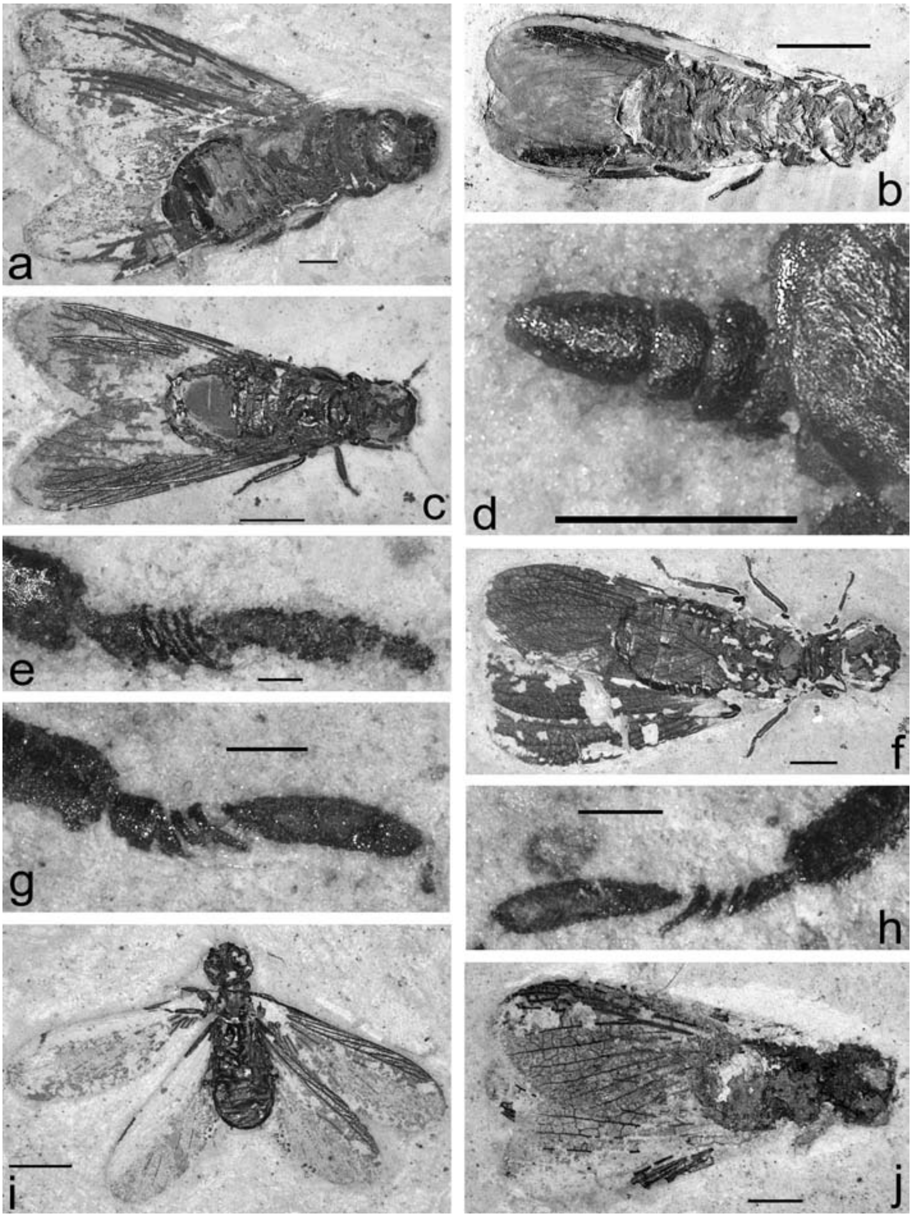

Fig. 11.25. Crato Formation Isoptera: (a) Mastotermitidae, *Cratomastotermes wolfschwenningeri* gen. et sp. nov., holotype, SMNS 66186; scale bar, 2 mm; (b) Mastotermitidae, *Cratomastotermes wolfschwenningeri* gen. et sp. nov., paratype, SMNS 66188; scale bar, 5 mm; (c) Termopsidae, *Nordestinatermes araripena*, SMNS 66190; scale bar, 2 mm; (d) Termopsidae, *Nordestinatermes araripena*, SMNS 66190, left cercus; scale bar, 1.4 mm; (e) Termopsidae, *Nordestinatermes araripena*, SMNS 66190, right hindtarsus; scale bar, 0.1 mm; (f) Termopsidae, *Mariconitermes talicei*, SMNS 66193; scale bar, 2 mm; (g) Termopsidae, *Mariconitermes talicei*, SMNS 66193, right midtarsus; scale bar, 0.25 mm; (h) Termopsidae, *Mariconitermes talicei*, SMNS 66193, left midtarsus; scale bar, 0.25 mm; (i) Kalotermitidae, *Cratokalotermes santanensis* gen. et sp. nov., holotype SMNS 66195 scale bar, 2 mm; (j) Rhinotermitidae, *Cretarhinotermes novaolindense* gen. et sp. nov., holotype SMNS 66196; scale bar, 2 mm.

The remaining characters are plesiomorphic: fontanelle absent; pronotum and width increasing from posterior to anterior side; wings with complete venation; Rs with anterior branches; anal fan of hind wing reduced (synapomorphy of all non-mastotermitid termites); scales of forewings shorter than those of hind wings; four or five tarsomeres (plesiomorphy of fossil members, in Recent members only a vestigial fifth segment); cerci with four to eight segments, usually with four or five segments (all Hodotermitidae have four cercal segments, all other termites only one or two segments); eusocial with pseudergates instead of a true worker caste and with one-piece nesting (otherwise only retained in Kalotermitidae).

Comments: the wing venational characters previously used to diagnose Termopsidae and Hodotermitidae are homoplastic and the arguments and attributions of different authors are consequently confusing and often conflicting. I therefore doubt the value of the wing-venation criteria employed by Krishna (1990) and Fontes and Vulcano (1998, 2004) to attribute Cretatermitinae to Hodotermitidae rather than Termopsidae.

Cretatermitinae

Nordestinatermes araripena (Krishna, 1990)

Material: three specimens: AMNH 43902 (holotype; Figure 11.26c), AMNH 43901 (paratype) and AMNH 43903 (paratype); in addition, 16 specimens with nos 580, 581, 582, 856, 1533, 1718, 2071, 2072, 2074, 2075, 2453, 5001, 5002, 5003, 5004 and 5008 in the Vulcano collection, Brazil, and three SMNS specimens (SMNS 66190 (Figures 11.25c–e), 66191 and 66192).

Diagnosis of alates: body length 7.0–8.5 mm; ocelli absent; pronotum about as broad as head or even slightly broader; tarsi five-segmented (Figure 11.25e); antennae with 18–22 segments; cerci definitely four-segmented (Figure 11.25d), not five-segmented as stated by Krishna (1990) and Fontes and Vulcano (1998); anal fan of hind wing reduced.

Comments: this species was transferred by Fontes and Vulcano (1998) from *Meiatermes* and the subfamily Hodotermitinae to *Cretatermes* and the subfamily †Cretatermitinae within Hodotermitidae. Martins-Neto *et al.* (2006) established a new genus *Nordestinatermes* which seems to be poorly defined, but is here accepted until a revision is available. However, referral to Hodotermitidae by Krishna (1990), Fontes and Vulcano (1998, 2004) and Martins-Neto *et al.* (2006) cannot be upheld: firstly, †Cretatermitinae was considered by all other authors to belong within Termopsidae rather than Hodotermitidae *sensu stricto*, and secondly, because five-segmented tarsi are absent in all termites (including all Recent Hodotermitidae) except Mastotermitidae and some Termopsidae. However, referral to

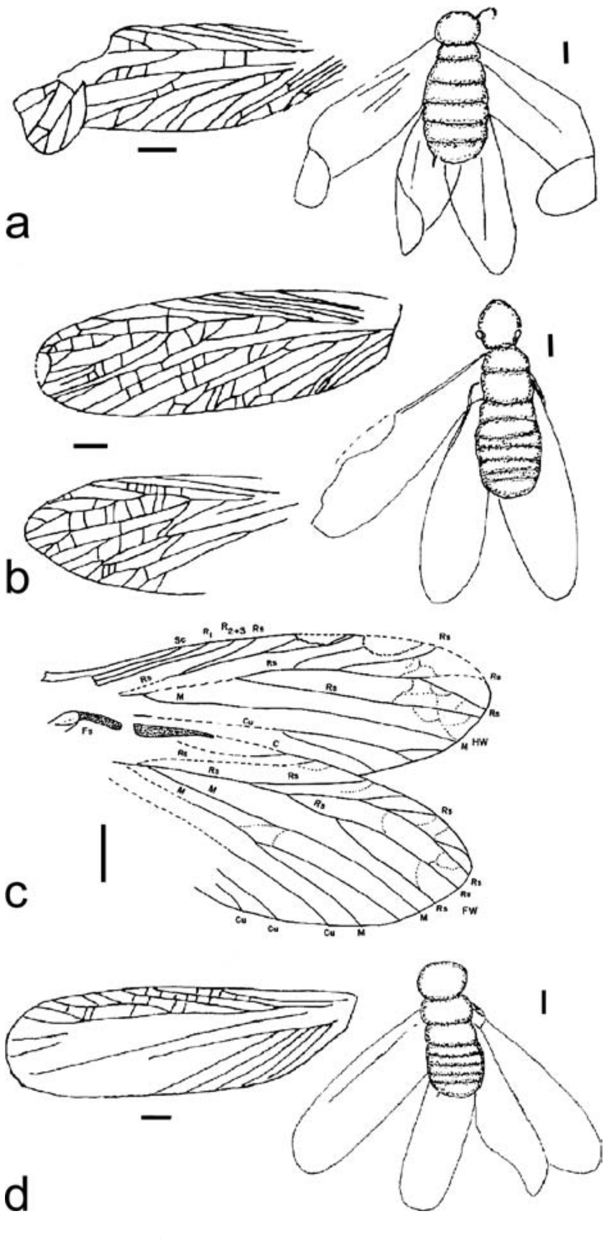

Fig. 11.26. Crato Formation Isoptera: (a) *Araripetermes nativa* Martins-Neto *et al*. 2006, habitus and wing venation; scale bars, 1 mm; **b**, *Caatingatermes megacephalus* Martins-Neto *et al*. 2006, habitus and fore- (below) and hind wing venation; (c) *Nordestinatermes araripena* (Krishna, 1990), holotype AMNH 43902, fore- and hind wings; (d) *Nordestinatermes obesa* Martins-Neto *et al*. 2006, habitus and forewing. Scale bars, 1 mm. (a,b,d) After Martins-Neto *et al*. 2006); (c) after Krishna (1990).

Mastotermitidae would be ill-founded on such a symplesiomorphy because all other characters show more modern states. *Termopsis heeri* from Baltic amber, the type species of *Termopsis* which is the type genus of Termopsinae, still has five-segmented tarsi (at least on the hind legs), while Recent Termopsinae rarely retain a vestigial fifth segment, which could suggest a more basal position within Isoptera than Hodotermitidae, that would correspond to their primitive social behavior (one-piece nesting). Either way, referral to Termopsidae-Cretatermitinae currently is best supported by the available characters. Also, the absence of a true worker caste and foraging behavior (suggested by the absence of non-alate stages among Crato termites) would be a symplesiomorphic similarity between *Nordestinatermes araripena* and Recent Termopsidae, while a fossil termite worker from the Lower Cretaceous of Spain (attributed to *Meiatermes bertrani*) seems to indicate that Hodotermitidae was already eusocial with a true worker caste in this early period of termite evolution.

It must also be noted that the figures of the wing venation of the original description (Krishna, 1990: figure 3) and the re-description (Fontes and Vulcano, 1998: figure 1) have little in common, so that it must be questioned if they indeed illustrate the same species. Furthermore, both figures are clearly incorrect, because they either show an impossible venation for Isoptera (Krishna, 1990), which always have separate stems for RS, M, and Cu, or the drawings differ from the venation seen in the photograph of the same specimen (Fontes and Vulcano, 1998: figures 1 and 11). All three specimens in the collection of SMNS, which can be clearly attributed to the present species, have a wing-venation pattern (especially of RS) that agrees with the original drawing of Krishna (1990) more than the confusing re-description of Fontes and Vulcano (1998). Obviously, all Cretatermitinae from the Crato Formation are in need of revision.

Nordestinatermes obesa Martins-Neto *et al.,* 2006

Material: holotype RGMN-T149 (Figure 11.26d), Martins-Neto collection, belonging to the Sociedade Brasileira de Paleoartropodologia.

Diagnosis: body length 6.3 mm and tegmen length 10.5 mm; body very robust. Otherwise the characters of the genus *Nordestinatermes*: head circular, pronotum about as long and wide as head, forewing with reduced number of R branches, origin of M close to wing base, M unbranched.

Cretatermes pereirai Fontes and Vulcano, 1998

Material: 2452 (holotype), 849 and 5005 (paratypes) in Vulcano collection, Brazil; specimen SMNS 66517, with a body length of 9 mm, may belong to this species.

Diagnosis of alates: body length 9.0–10.5 mm; otherwise more or less identical to *Cretatermes araripena.*

Comments: it appears very doubtful if *Cretatermes pereirai* is a good species at all, because there is only a very small size difference and other insignificant differences to *C. araripena* and the original description is flawed (see above). Nevertheless, the question of synonymy should be left open until a better and more detailed revision of Crato termites is available. This species was not discussed at all by Martins-Neto *et al.* (2006) and therefore might also belong to their new genus *Nordestinatermes*.

Termopsidae

Subfamilia *incertae sedis*

Mariconitermes Fontes and Vulcano, 1989

Mariconitermes talicei Fontes and Vulcano, 1998

Material: no. 5006 (holotype) and no. 5007 (paratype) in coll. Vulcano, Brazil; specimens SMNS 66193 (body length 12 mm, wing length 13 mm; Figures 11.25f–h) and SMNS 66194 (body length 8 mm, wing length 12 mm) are referred to this species.

Revised diagnosis of alates: body length 8–15 mm; ocelli apparently absent; pronotum of characteristic shape (typical for Termopsidae and Hodotermitidae), less wide than head, but with well-developed lateral lobes with concave margin; width of pronotum increasing from posterior to anterior side; tarsi five-segmented (Figures 11.25g and h); wings reticulated; cerci with five segments.

Comment: this taxon was placed in Hodotermitinae by Fontes and Vulcano (1998), but can now be referred to Termopsidae, because a new and very well-preserved specimen of this species in the in Stuttgart distinctly displays five tarsal segments on both mesotarsi. All Hodotermitidae possess only four tarsomeres like all other termites, except the most primitive Mastotermitidae and Termopsidae. The absence of a well-defined anal lobe on the hind wings and the five-segmented cerci excludes referral to Mastotermitidae. Likewise, all other so-called fossil Hodotermitidae with five-segmented tarsi (e.g. *Ulmeriella* spp.) must probably be transferred to Termopsidae.

Hodotermitidae?

Caatingatermitinae

Comment: this new subfamily was established within Hodotermitidae by Martins-Neto *et al.* (2006) and is distinguished from all other subfamilies of Termopsidae and Hodotermitidae by the origin of M very far from the wing base and distally fused to Cu. Unfortunately, Martins-*Neto et al.* (2006) did not describe the tarsus, so that no definite attribution to either Hodotermitidae or Termopsidae is presently possible. Martins-Neto (2005a, 2005b) erected two new taxa of Hodotermitidae as *nomina nuda* from the Crato Formation, which were formally described by Martins-Neto *et al.* (2006).

Caatingatermes megacephalus Martins-Neto *et al.*, 2006

Material: holotype RGMN-T147 (Figure 11.26b), Martins-Neto collection.

Diagnosis: body length 9 mm and tegmen length 11 mm, head pentagonal, longer than wide, eyes small and not prominent but displaced under the mid-length of head, pronotum trapezoidal and as wide as head base, size of pronotum about two-thirds of head size, forewing with the humeral suture well-defined, straight and perpendicular to costal margin, vein R secondarily branched with five long, pectinate anterior radial branches and five relatively short posterior radial branches that sometimes have secondary branches.

Araripetermes nativa Martins-Neto *et al.*, 2006

Material: holotype RGMN-T148 (Figure 11.26a), part and counterpart, Martins-Neto collection.

Diagnosis: body length 8 mm and tegmen length 10 mm, head ellipsoid, 20% wider than long, with rounded margins, forewing with sigmoidal M that is distally fused to Cu, origin of M distally of midwing position.

Kalotermitidae

Diagnosis: apomorphies include RS closely parallel to costal margin; antennae shorter with only 10–21 segments. The following features are plesiomorphic: small ocelli present in alates; fontanelle absent; pronotum flat and as broad or broader than head capsule; wings with less complete venation (synapomorphy with modern termites); RS with anterior branches, but the latter only short, oblique, and unforked or only weakly forked branches (apomorphy in the groundplan of modern termites, while the RS branches are completely reduced in Serritermitidae+Rhinotermitidae+Termitidae); anal fan of hind wing reduced (synapomorphy of all non-mastotermitid termites); scales of forewings much larger than those of hind wings; only four tarsomeres; cerci very short with only two (rarely three) segments (apomorphy of modern termites); eusocial with pseudergates instead of a true worker caste and with one-piece nesting (plesiomorphy, otherwise only retained in Termopsidae).

Cratokalotermes gen. nov.

Type species: *Cratokalotermes santanensis* sp. nov., by present designation.

Derivation of name: named after the Crato Formation and the Recent genus *Kalotermes*.

Diagnosis: as for type species, by monotypy.

Cratokalotermes santanensis sp. nov.

Material: only known by the holotype SMNS 66195 (Figure 11.25i).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: after the town of Santana do Cariri in the type area.

Diagnosis and description of alates: body length 6.1 mm; head very large and distinctly broader than pronotum (apomorphy); compound eyes small; area of ocelli not preserved; forewings 7.5 mm long and a maximum of 2.2 mm wide, hind wings 7.0 mm long and a maximum of 2.3 mm wide, thus wings not very elongate but rather broad; Sc very short; RS in both pairs of wings closely parallel to costal margin and with short, oblique, and five unforked or only weakly forked branches; M more closely parallel to Cu; area of M wider than that of RS or Cu; M and Cu branched and less strongly sclerotized than RS; scale of forewing much larger than in hind wing (the scales are well-preserved in the right pair of wings); cerci inconspicuous, extremely short and two-segmented.

Comments: this new taxon represents the first Mesozoic record and the first New World record of the Kalotermitidae. However, an undescribed kalotermitid has apparently been discovered in Lower Cretaceous Lebanese amber by André Nel (cited in Grimaldi and Engel, 2005: 247).

Rhinotermitidae

Diagnosis: apomorphies include antennae shorter with 14–22 segments; M weakly branched and area of M narrow; Cu terminating at wing apex, richly branched, occupying more than half of the wing; eusocial with a true worker caste. The following are plesimorphic: small ocelli present in alates; fontanelle present; pronotum more or less flat; wings with less complete venation (synapomorphy with modern termites); RS without distinct branches and closely parallel to costal margin (synapomorphy of Serritermitidae+Rhinotermitidae+Termitidae); anal fan of hind wing reduced (synapomorphy of all non-mastotermitid termites); wing venation distinctly reticulate (absent in Termitidae); scales of forewings much larger than those of hind wings; only three or four tarsomeres; cerci very short with only two segments (apomorphy of modern termites);

Cretarhinotermes gen. nov.

Type species: *Cretarhinotermes novaolindense* sp. nov., by present designation.

Derivation of name: after the Cretaceous age and the Recent genus *Rhinotermes*.

Diagnosis: as for type species, by monotypy.

Cretarhinotermes novaolindense sp. nov.

Material: holotype SMNS 66196 (Figure 11.25j); paratype SMNS 66197.

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: after the type locality.

Diagnosis and description of alates: body length 7.2–9.4 mm; head and thorax poorly preserved without details; legs and tarsi not preserved; wings about 12–13 mm long and rather broad (maximum width 4.2 mm) with a strongly reticulated venation; RS closely parallel to costal margin and apparently without long branches; M closely parallel to RS and apparently unbranched; Cu richly branched and apparently reaching the apex of the wing so that more than half of the wing is occupied by the Cu branches; cerci not preserved.

Comments: the wings are so different in shape and venation from other described species that there is no doubt that these two fossils represent an additional Crato taxon. Unfortunately, the bodies are very poorly preserved and the wings superimposed, so that it is difficult to recognize the precise venation. However, the visible parts of RS, M and Cu suggest that these two fossils constitute the oldest record of the modern family Rhinotermitidae and consequently also represent a *terminus post quem non* for the origin of the most derived clade within Isoptera that includes the Termitidae.

11.10 Chresmododea: fossil ‘water striders’

Günter Bechly

Chresmodids are large insects with a water-strider-like habitus that are only known as fossils. They have short, thick antennae and prognathous chewing mouthparts with strong mandibles. Their compound eyes are large and their legs are extremely prolonged with very long femora, shorter tibiae, and long, multi-segmented, flagellate tarsi with more than 40 tarsomeres, which is unique within Insecta (Nel *et al.*, 2004). The forelegs are usually directed anteriorly, while the middle and hind legs are directed latero-caudally. Female chresmodids have two pairs of membranous wings with a slender forewing with long and parallel longitudinal veins and a broad anal fan in the hind wings, but the males seem to be wingless. There are long, but only single-segmented, lanceolate cerci at the end of the abdomen (similar to Phasmatodea), and females have a prominent orthopteroid-like ovipositor. The nymphs are similar to the adults but are much smaller, with a distinctly shorter abdomen, and the absence of wings. Consequently their development was hemimetabolous as in orthopterans. Chresmodids probably lived on the water surface of lakes and lagoons (*contra* Baudoin, 1980, who did not know the true structure of the chresmodid legs), and fed on insects and other small animals at the water surface, just like the unrelated but morphologically similar modern Gerridae. The group is exclusively Mesozoic and may have suffered extinction during the catastrophic impact at the Cretaceous–Tertiary boundary.

Systematics, phylogeny and evolution

Contrary to Martynova (1962, 1991) here the Chresmododea are restricted to include only the family Chresmodidae, thus excluding the extinct families Aerophasmatidae, Necrophasmatidae and Aeroplanidae. However, this does not mean to say that these taxa (especially Aerophasmatidae) might not be more closely related to Chresmododea than to Orthoptera (see section 11.11), but currently there are no convincing arguments for such a relationship.

The phylogenetic relationship of chresmodids was long disputed and they have been attributed to Heteroptera-Gerromorpha, Grylloblattodea-Paraplecoptera, Mantodea, Orthoptera, Polyneoptera of uncertain affinity and most often to Phasmatodea. A sister-group relationship of Chresmododea and Phasmatodea is supported by the recent discovery of new fossil material with preserved fore- and hind wings (Martínez-Delclòs *et al.*, 2007).

Carpenter (1992) correctly recognized that fossil arthropods from the Lower Jurassic Solnhofen lithographic limestones, known under the name *Sternarthron zitteli*, are not Chelicerata-Pantopoda as previously believed, but clearly represent the nymphal stage of *Chresmoda obscura* from the same locality. A re-examination of the type specimens from the collection of the Bayerische Staatssammlung in Munich (BSPGM nos 1870 VII 45 and AS I 822) confirmed that the description and drawings of Haase (1890) are totally wrong (his drawings Figures 5 and 6 even appear to be manipulated to support his attribution) and the fossils clearly are hexapods with only three pairs of legs and structures that are very similar to adult *Chresmoda* (*contra* Bechly, 1999b: 9).

Carpenter (1992) retained the younger, and therefore junior, synonym *Propypolampis* Weyenbergh, 1874 as the valid name for the fossils previously known as *Chresmoda* Germar, 1839 and mentions a paper by himself (in press, 1992) that should allegedly reveal that the holotype of *Chresmoda* is a locust and was only later confused with the fossil ‘water striders’. Therefore, Carpenter (1992: 181) classified *Chresmoda* within Orthoptera-Caelifera as a ‘little-known genus probably related to Acrididae’, while he considered *Propygolampis* to be related to Phasmatodea. However, the cited paper of Carpenter that should have appeared in 1992 in the journal *Psyche* was never published (Furth, 1994) and the manuscript has to be considered as lost because it is neither archived at the intended publisher nor could it be found it in Carpenter’s archives in his laboratory at MCZ. These taxonomic problems will be discussed in detail in a future publication. Here the suggestion of Rasnitsyn (2002), to retain the oldest available generic name *Chresmoda* and the family name Chresmodidae as valid names for the fossil ‘water striders’, is followed, especially as the holotype of *Chresmoda obscura* is lost so that it is no longer possible to verify the taxonomic decisions of Carpenter (1992).

Fossil record

The history of this exclusively fossil taxon was discussed by Handlirsch (1906–1908), Esaki (1949), Ponomarenko (1986), Martínez-Delclòs (1989), Carpenter (1992), Rasnitsyn (2002), Nel *et al.* (2004) and Grimaldi and Engel (2005).

There are seven fossil species which range from the Upper Jurassic of Germany (*Chresmoda obscura* = *Propygolampis giganteus*), the Lower Cretaceous of Mongolia (*Chresmoda* sp. nov. and *Saurophthirodes mongolicus*, which could be a nymph of *Chresmoda*), China (*Chresmoda orientalis*), Brazil (*Chresmoda* sp. nov.) and Spain (*Chresmoda aquatica*), to the Upper Cretaceous of Lebanon (*Chresmoda libanica*).

Crato Formation chresmodids

Bechly (1998b: 155; 1999b: 9) was first to note the occurrence of chresmodids in the Crato Formation. Bechly *et al.* (2001a: 55, figure 44) discussed and figured a beautiful fossil *Chresmoda* from the Crato limestones. This female with ovipositor, seems to be the best preserved specimen from this locality of all (Plate 15d), and is deposited with preliminary no. 0134 (old number H56) at SMNS. Another example (AMNH specimen) was figured by Grimaldi and Engel (2005: figure 7.5), and four further specimens (e.g. specimen no. G88; Plate 15e) have been studied by the present author and will be described by Heads and Engel.

All six specimens of the new *Chresmoda* species from the Crato Formation are alate adults with long wings (wing length 27–28 mm). The body length from head (without antennae) to abdomen (without terminalia) is about 21–25 mm, and the mesofemora are about 20–22 mm long. The head has large globular compound eyes and large prognathous mandibles (similar to tiger beetles), and the antennae are 9–11 mm long. Distinct one-segmented cerci (3 mm long) and a prominent ovipositor are visible in one specimen. All other characters agree with the general diagnosis above.

Being surface striders on saline water that mainly fed on other insects that were trapped on the water surface, the chresmodids most probably represented the only autochthonous aquatic insects in the palaeohabitat of the Crato lagoon.

11.11 Orthopterida: grasshoppers, crickets, locusts and stick insects

Sam W. Heads and Rafael G. Martins-Neto

Phasmatodea: stick insects

The stick insects are an exclusively phytophagous group of orthopterids famous for their remarkable morphological and behavioural crypsis as mimics of sticks and leaves (Bedford, 1978; Key, 1991; Grimaldi and Engel, 2005). So extreme is the mimicry of Recent stick insects that it even extends to their eggs, which often resemble seeds (Sellick, 1997, 1998) and in some cases bear prominent capitula that, like the elaiosomes of many seeds, encourage their dispersal and burial by ants (Compton and Ware, 1991; Hughes and Westoby, 1992): a process known as myrmecochory.

Phasmatodea are rare as fossils, often occurring only as isolated wings (Gorochov and Rasnitsyn, 2002), with very few complete and articulated individuals recorded (e.g. Gorochov, 1994, 2000; Ren, 1997). Fossil stick-insect eggs are also rare but have been reported by Sellick (1994) and are distinguished by their unique detachable anterior operculum and distinctive mycropylar plate. Although the monophyly of Recent Phasmatodea is well established based on a suite of robust morphological characters, their relationship to fossil forms is somewhat controversial. Most workers recognize a number of Mesozoic families (e.g. Carpenter, 1992; Gorochov and Rasnitsyn, 2002; Willmann, 2003) but their assignment to Phasmatodea is questioned by others (notably Tilgner, 2000). However, it is generally accepted by most palaeoentomologists that the Mesozoic forms represent stem group stick insects (Willmann, 2003; Grimaldi and Engel, 2005), although a detailed phylogenetic analysis of Phasmatodea incorporating fossil forms is still lacking and is hindered by the paucity of their fossil record and the fragmentary nature of most specimens.

In the Crato Formation, Phasmatodea are represented by a single species, *Cretophasma araripensis* Martins-Neto, 1989b, known from a single forewing (Figure 11.27). *Cretophasma* was originally placed in its own family (Cretophasmatidae) by Sharov (1968) when he described *Cretophasma raggei* from the Early Cretaceous

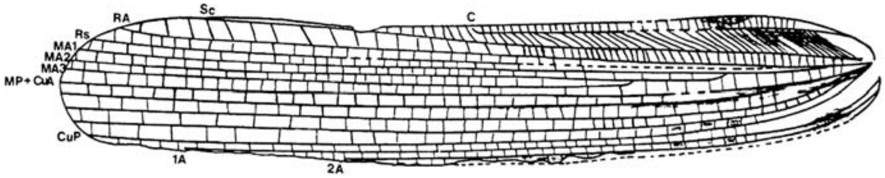

Fig. 11.27. Phasmatodea, Aerophasmatidae, Cretophasmatinae: *Cretophasma araripensis* Martins-Neto, 1989, holotype GP/IT-1623, forewing. After Martins-Neto (1989).

of Siberia and this was followed by Martins-Neto (1989b). However, the family was subsequently recognized as a subgroup of Aerophasmatidae by Gorochov (1992, 1994) and relegated to subfamily level (Cretophasmatinae). *Cretophasma araripensis* is very similar to *C. raggei* in the pattern of the main veins differing from the latter only in size (wing length 30 mm in *C. araripensis*; 42 mm in *C. raggei*) and in the costal vein being sharply curved distally.

Aerophasmatidae are known from the Early Jurassic of England and Germany (Chresmodellinae), the Late Jurassic of Kazakhstan (Aerophasmatinae) and the Early Cretaceous of England (Chresmodellinae). They have traditionally been allied with the Phasmatodea and this interpretation is followed here. However, a close relationship with Chresmododea cannot be ruled out (see Section 11.10). Cretophasmatinae are known from the Early Cretaceous of Baissa, Siberia (represented by the genera *Cretophasma* and *Baissophasma*), and the Crato Formation (represented only by *Cretophasma araripensis*). The apparent distribution of Aerophasmatidae is almost certainly Lagerstätten-controlled and the group was probably widespread during the Cretaceous.

Orthoptera: grasshoppers, crickets and locusts

Well known for their remarkable stridulation and jumping abilities, the Orthoptera constitute the most diverse group of Polyneoptera, comprising approximately 22,500 living species (Grimaldi and Engel, 2005) with many more undoubtedly awaiting discovery and description (Rentz and Su, 2003). The monophyly of Orthoptera is well established and supported by both morphological and molecular data (see Hennig, 1981; Kristensen, 1991; Flook and Rowell, 1997, 1998; Rowell and Flook, 1998; Flook *et al.*, 1999; Wheeler *et al.*, 2001; Gorochov and Rasnitsyn, 2002; Grimaldi and Engel, 2005). The order is defined by several distinctive morphological autapomorphies including large saltatorial (jumping) hind legs with a robust, muscular femur and straightened femoro-tibial articulation, the lateral development of the pronotum to form a cryptopleuron (the orthopteran 'saddle') and a reversal in the orientation of nymphal wing pads during development. Traditionally, the Orthoptera are divided into two monophyletic subgroups: the Ensifera (crickets, katydids and their allies) and the Caelifera (grasshoppers and locusts).

Orthopterans are famous for their songs, with calling behaviour playing a vital role in their reproductive biology and evolution. Indeed subtle differences in mating calls are critical in species recognition and are often used in systematic studies of living species (Marshall and Haes, 1988; Rentz, 1996; Grimaldi and Engel, 2005). Songs are produced differently in the two suborders. In Ensifera, sound is generated by the rubbing together of specialized stridulatory files on the forewings, with the resulting sound amplified by specialized membranous regions of the tegmina called 'mirrors'. In Caelifera sound is produced by rubbing the legs against the thickened edges of the forewings, although Cylindrachetidae (Caelifera: Tridactyloidea) stridulate using their mandibles (Grimaldi and Engel, 2005). Sounds are detected by means of auditory organs in the form of tympanal membranes situated on the protibia in ensiferans and abdominally in caeliferans. All orthopterans possess biting-chewing mouthparts and most species are phytophagous, feeding on leaves or roots. Many species are predaceous while a number feed on fungi and others are omnivorous. Some species are highly specialized, feeding only on seeds or on the pollen, nectar or flowers of specific plants (Rentz and Su, 2003). Many species are highly cryptic, often resembling the leaves, twigs or flowers of their host plants. Other anti-predation strategies include disruptive and aposematic colouration, gregarious behaviour, cryptic movement, catalepsy and repugnatorial secretions.

The orthopteran fauna of the Crato Formation is of worldwide importance, being the most diverse and well-preserved Mesozoic assemblage known (Martins-Neto, 1991a–d, 2003; Martins-Neto and Petrulevičius, 1998; Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). Among the fossils from the Crato Formation the orthopterans are the most abundant element, constituting approximately 27% of all fossil insects discovered. Both suborders are represented and have been extensively documented by Martins-Neto (1987–2003). However, a detailed revision of the fauna is required to establish the relationships of many of the described taxa and to evaluate possible synonymies.

Ensifera: crickets, katydids and their allies

The Ensifera (Figures 11.28–11.29, 11.33 and 11.30–11.31, 11.34) is the more ancient of the two orthopteran suborders, with putative forms recorded from as early as the Late Permian (Béthoux *et al.*, 2002). Monophyly of Ensifera has been supported by most recent phylogenetic studies and is based primarily on the long flagellate antennae (Flook and Rowell, 1997, 1998; Desutter-Grandcolas, 2003). The 10 Recent families are distributed in four superfamilies: Stenopelmatoidea, comprising the families Gryllacrididae (leaf-rolling crickets, tree crickets),

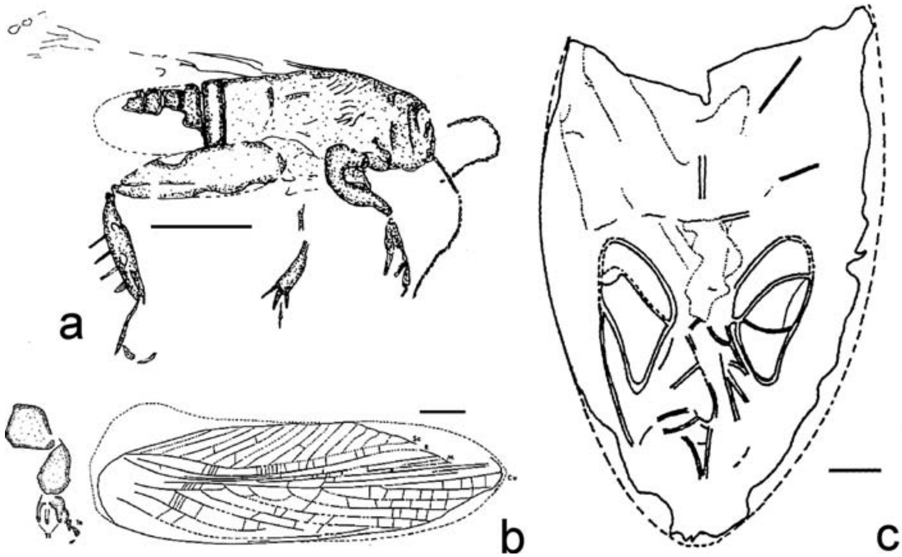

Fig. 11.28. Crato Formation Gryllotalpidae: (a) *Tetraspinus fossorius* Martins-Neto, 1995, holotype, UnG-035; scale bar, 5 mm; (b) *Palaeoscapteriscops cretacea* Martins-Neto, 1991a, tegmina and anterior appendage; scale bar, 2 mm; (c) *Archaeogryllotalpoides ornatus* Martins-Neto, 1991a, paired male tegmina; scale bar, 2 mm. a After Martins-Neto (1995), b and c after Martins-Neto (1991a).

Raphidophoridae (camel crickets, cave crickets and sand-treader crickets), Schizodactylidae (splay-footed crickets), Anostostomatidae (king crickets and wetas) and Stenopelmatidae (Jerusalem crickets); Tettigonioidea, comprising only Tettigoniidae (katydids and bush crickets); Hagloidea comprising the relict Haglidae (hump-winged crickets); and Grylloidea, comprised of Gryllidae (true crickets), Myrmecophilidae (ant crickets) and Gryllotalpidae (mole crickets). Of these superfamilies, only Grylloidea and Hagloidea are known from the Crato Formation. Grylloidea dominate the ensiferan assemblage in terms of diversity and are represented by Gryllidae and Gryllotalpidae along with the extinct Baissogryllidae. Hagloidea are represented by the †Prophalangopsidae. In addition to the taxa discussed below, Martins-Neto (1991a) erected *Phasmomimella*? *araripensis* (Figure 11.32a) within Phasmomimidae. However, the generic assignment of this highly fragmentary fossil is uncertain and it is here interpreted as Ensifera *incertae sedis*.

Baissogryllidae

The extinct grylloid family Baissogryllidae (Figures 11.29, 11.30 and 11.33) is represented by 19 species in six genera (Martins-Neto, 1998c): *Caririgryllus* Martins-Neto, 1991a, with five species; *Cearagryllus* Martins-Neto, 1991a, with eight species; *Santanagryllus* Martins-Neto, 1991a, and *Castillogryllus* Martins-Neto,

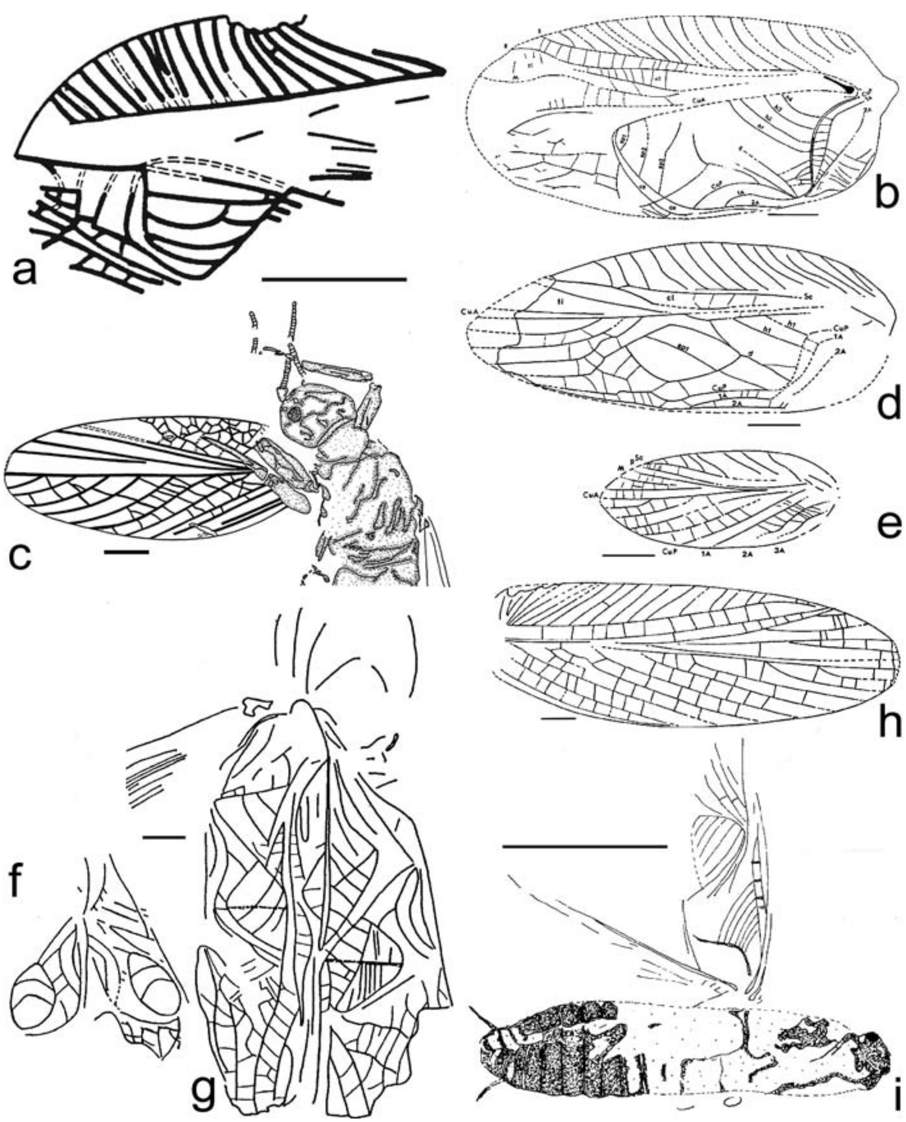

Fig. 11.29. Crato Formation Ensifera: (a) *Santanagryllus hesselae* Martins-Neto, 1991a, tegmina; scale bar, 2.5 mm; (b) *Brontogryllus excelsus* Martins-Neto, 1991a, tegmina; (c) *Caririgryllus arthaudi* Martins-Neto, 1991a, holotype, coll. Vulcano CV-1088, head, thorax and tegmina; scale bar, 2 mm; (d) *Caririgryllus elongatus* Martins-Neto, 1991a, tegmina; scale bar, 2 mm; (e) *Caririgryllus mesai* Martins-Neto, 1991a, tegmina; scale bar, 2 mm; (f) *Cratogryllus camposae* Martins-Neto, 1991a, tegmina; scale bar, 2 mm; (g) *Cratogryllus pentagonalis* Martins-Neto, 1991a, tegmina; scale bar, 2 mm; (h) *Caririgryllus pilosus* Martins-Neto, 1991a, tegmina; scale bar, 1 mm; (i) *Castillogryllus complicatus* Martins-Neto, 1995; scale bar, 5 mm. (a–h) After Martins-Neto (1991a), (i) after Martins-Neto (1995).

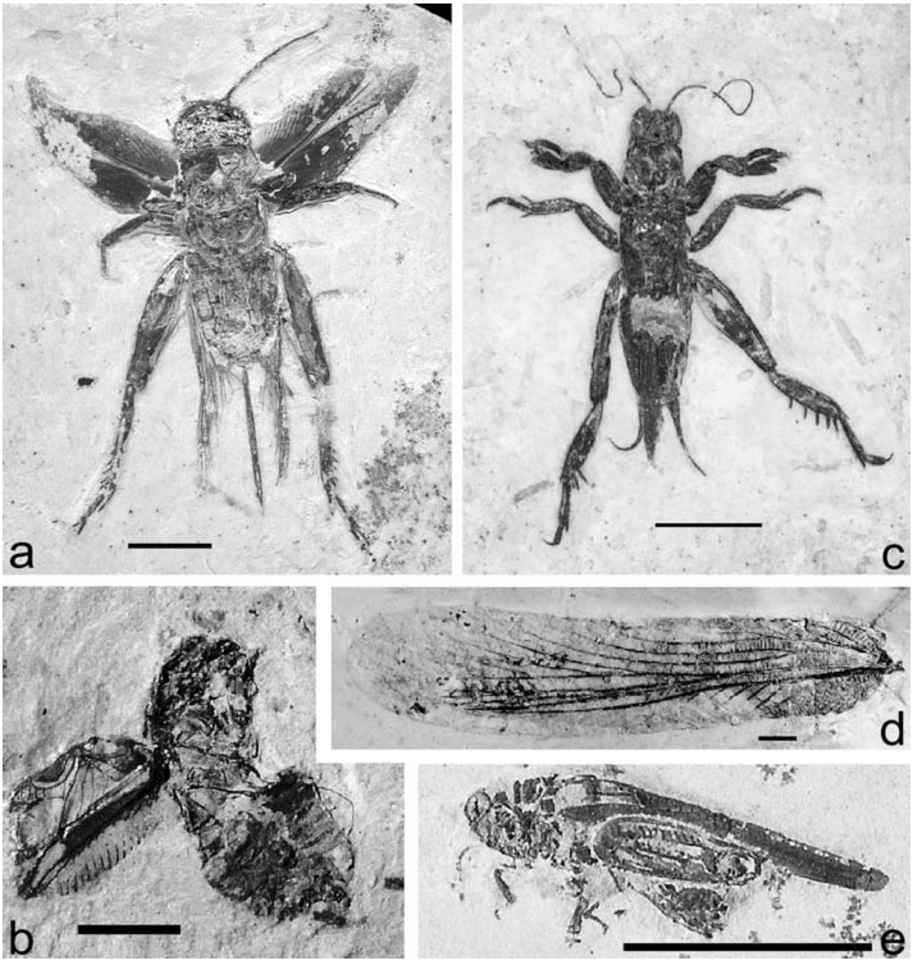

Fig. 11.30. Crato Formation Orthopterida: (a) Baissogryllidae, *Cearagryllus poliacanthus* Martins-Neto, 1991; (b) Gryllidae, *Araripegryllus camposae* Martins-Neto, 1987; (c) Gryllotalpidae, *Cratotetraspinus fossorius* (Martins-Neto, 1995), SMNK PAL 5477; (d) Hagloidea, Haglidae?, gen. et sp. indet. SMNS 66501; (e) Tetrigidae, gen. et sp. nov., SMNS prelim. no. 0160. Scale bars, 5 mm.

1991a, each with a single species; *Notocearagryllus* Martins-Neto, 1998b, and *Olindagryllus* Martins-Neto, 1998b, each with two species.

Gryllidae: true crickets

Gryllidae (Figures 11.29–11.31 and 11.33) constitute the principal family of the Grylloidea with more than 350 Recent genera encompassing over 3,000 species distributed world wide (Rentz and Su, 2003). Most classifications presently recognize about seven subfamilies. The true crickets are represented in the Crato Formation

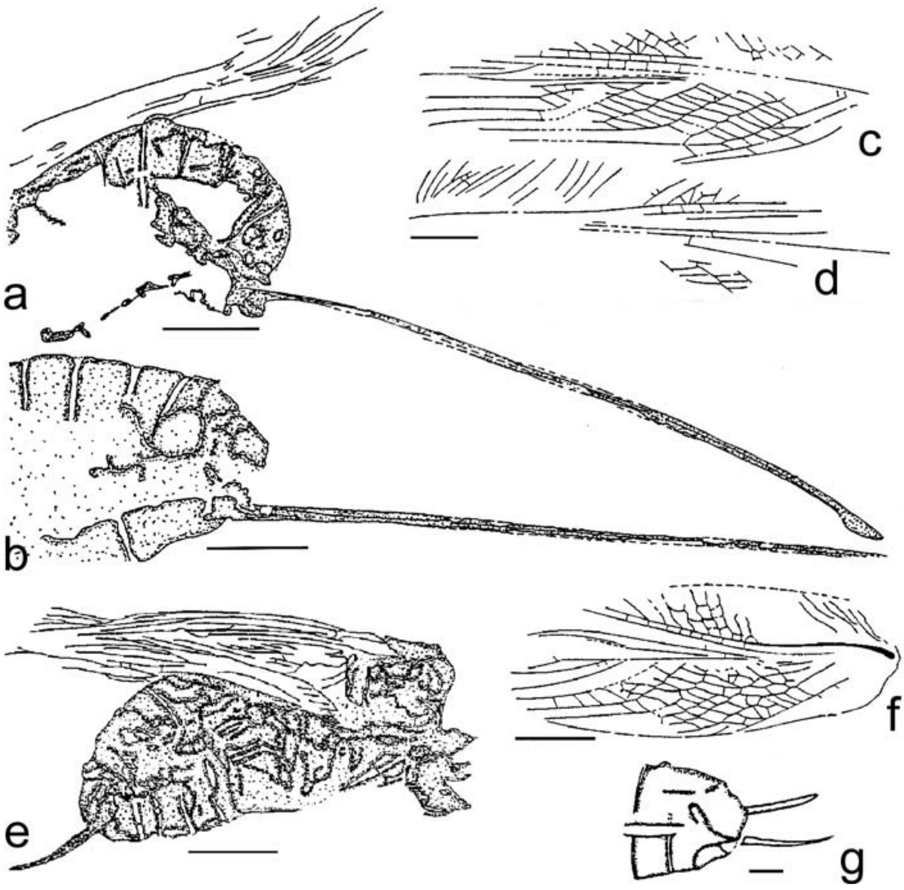

Fig. 11.31. Crato Formation Gryllidae: (a–d) *Cearagryllus perforatorius* Martins-Neto, 1991; (a–b) partial specimens with ovipositor; (c–d) tegmina, part and counterpart, CV-1699; (e, f) *Cearagryllus poliacanthus* Martins-Neto, 1991; (e) near-complete specimen with short ovipositor; (f) female tegmina, cv-1980; (g) *Cearagryllus gorochovi* Martins-Neto, 1991, male holotype, detail of cerci. Scale bar, 2 mm. All figures after Martins-Neto (1991).

by 11 species distributed in four genera: *Araripegryllus* Martins-Neto, 1987a, with six species; *Cratogryllus* Martins-Neto, 1991a, with three species; *Brontogryllus* Martins-Neto, 1991a, and *Nanoararipegryllus* Martins-Neto, 2002b, each with one species.

Gryllotalpidae: mole crickets

Gryllotalpidae, or mole crickets (Figures 11.28, 11.30 and 11.34), are an obscure group of grylloid crickets well known for their fossorial mode of life. They are characterized by their large, robust pronotum and their highly modified prothoracic legs

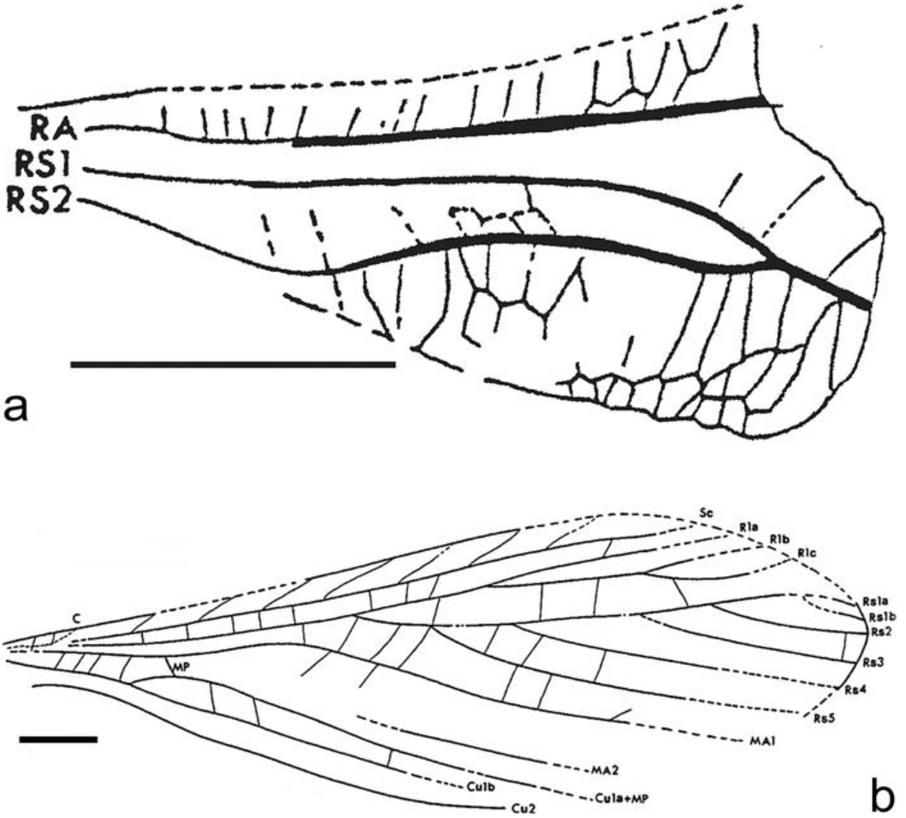

Fig. 11.32. Crato Formation Orthopteromorpha: (a) Orthopterida *incerta sedis*, *Phasmomimella*? *araripensis* Martins-Neto, 1991, forewing; scale bar, 5 mm; (b) Orthopterida *incerta sedis*, *Kevania araripensis* Martins-Neto, 1989, female forewing; scale bar, 2 mm.

which have a broad, spade-like tibia bearing numerous strong spines (tibial dactylar processes, or dactyls) used for digging. Gryllotalpidae are known from three monotypic genera in the Crato Formation: *Archaeogryllotalpoides ornatus* Martins-Neto, 1991a, *Palaeoscapteriscops cretacea* Martins-Neto, 1991a, and *Cratotetraspinus fossorius* (Martins-Neto, 1997b).

Hagloidea

Hagloidea (Figures 11.30d and 11.32b) are represented in the Crato Formation by two monotypic genera, *Kevania araripensis* Martins-Neto, 1991a and *Cratohaglopsis santanaensis* Martins-Neto, 1991a. Martins-Neto (1991a) placed both of these taxa in Prophalangopsidae, although this assignment may be erroneous. It is perhaps better to interpret them as Hagloidea *incertae sedis* until more complete material is studied.

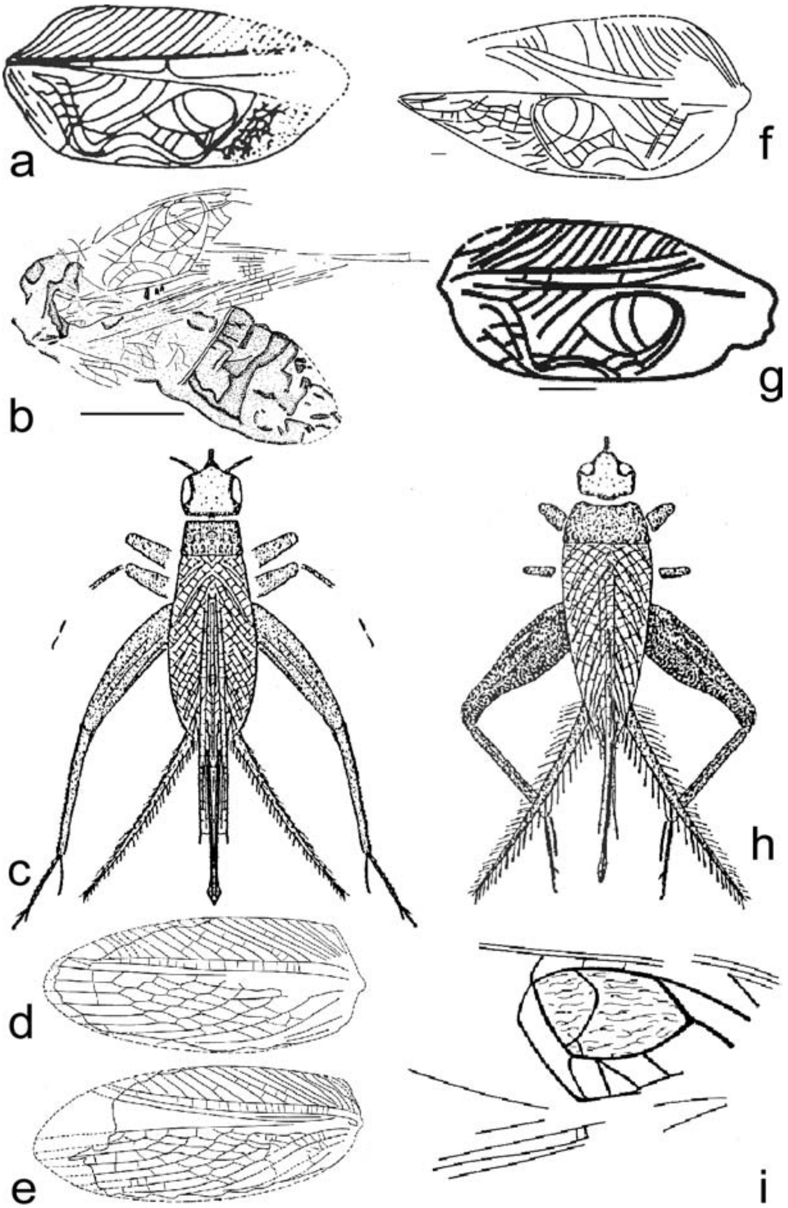

Fig. 11.33. Crato Formation Gryllidae and Baissogryllidae: (a and b) *Araripegryllus camposae* Martins-Neto, 1987, (a), tegmina; (b), habitus; (c) *Araripegryllus serrilhatus* Martins-Neto, 1991a, reconstructed habitus; (d, h) *Araripegryllus femininus* Martins-Neto, 1991a, (d) tegmina; (h) reconstructed habitus; (e) *Araripegryllus spinosus* Martins-Neto, 1991a, tegmina; (f) *Araripegryllus marianoi* Martins-Neto, 1991a, tegmina; (g) *Araripegryllus nanus* Martins-Neto, 1991a, tegmina; (i) *Cratogryllus cigueli* Martins-Neto, 1991b, partial wing. (a–h) After Martins-Neto (1991a), (i) after Martins-Neto (1991b).

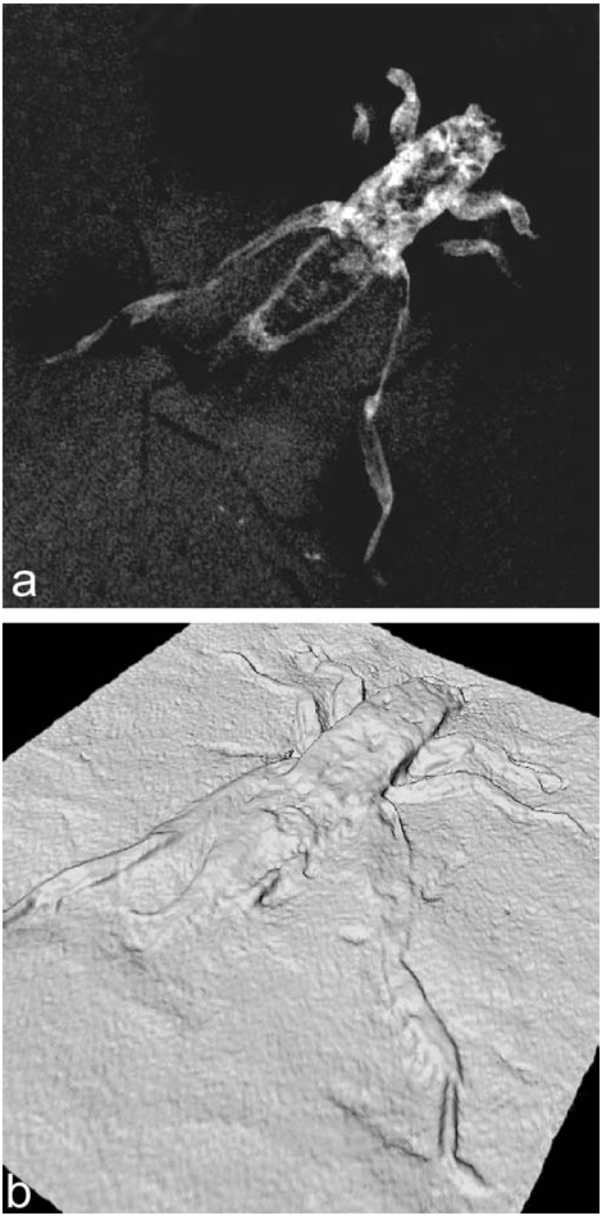

Fig. 11.34. Crato Formation Gryllotalpidae: (a) horizontal section produced by computed tomagraphy CT scanning of *Cratotetraspinus fossorius* revealing presence of internal structures in head and thorax, SMNK PAL 5477; (b) CT-scan-rendered three-dimensional image dorsal surface of same specimen. Body length, 17 mm. Images generated by Dr Sam MacDonald.

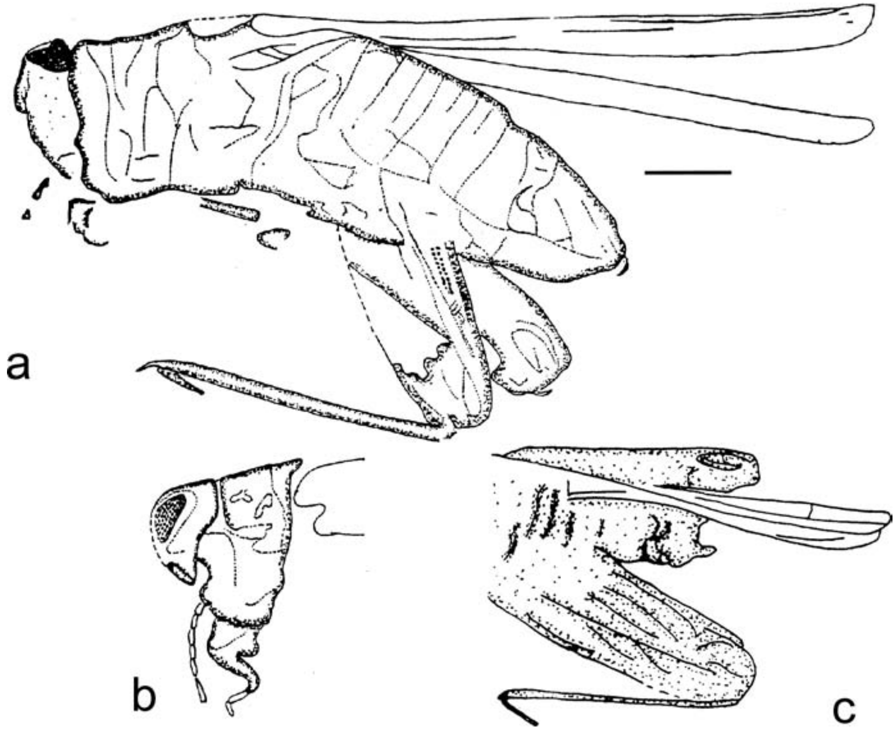

Fig. 11.35. Pigmy mole crickets, Tridactylidae: (a) *Cratodactylus ferreirai* Martins-Neto, 1990, holotype, GP/IT-1649; (b,c) *Cratodactylus kellneri* Martins-Neto, 1990; (a) holotype GP/IT-1649; (c) paratype CV-2037.

Caelifera: grasshoppers and locusts

The earliest true caeliferans are recorded from the Triassic and are thought to be derived from an elcanid-like stem group (Bethoux and Nel, 2002; Grimaldi and Engel, 2005). Monophyly of Caelifera is well supported by the reduced antennae and complete reduction of the ovipositor (Flook *et al.*, 2000; Grimaldi and Engel, 2005). The 20 Recent families are presently divided into eight superfamilies: Acridoidea, comprising the families Pamphagidae, Lentulidae, Pauliniidae (aquatic grasshoppers), Tristiridae (Andean wingless grasshoppers), Ommexechidae (toad-hoppers), Romaleidae (lubber grasshoppers), Lanthiceridae (gravel-hoppers), Pamphagodidae (twin-keeled grasshoppers) and Acrididae (locusts and true grasshoppers); Tanaoceroidea, Pyrgomorphoidea, Pneumoroidea and Tetrigoidea, each comprising a single family; Eumastacoidea, comprising the Eumastacidae (monkey grasshoppers) and Proscopiidae (stick grasshoppers); Trigonopterygoidea, comprising Trygonopterygidae (broad-leaf bush-hoppers) and Xyronotidae (razor-backed bush-hoppers); and Tridactyloidea comprising the Tridactylidae (pygmy mole crickets), Rhipipterygidae (mud crickets) and Cylindrachetidae

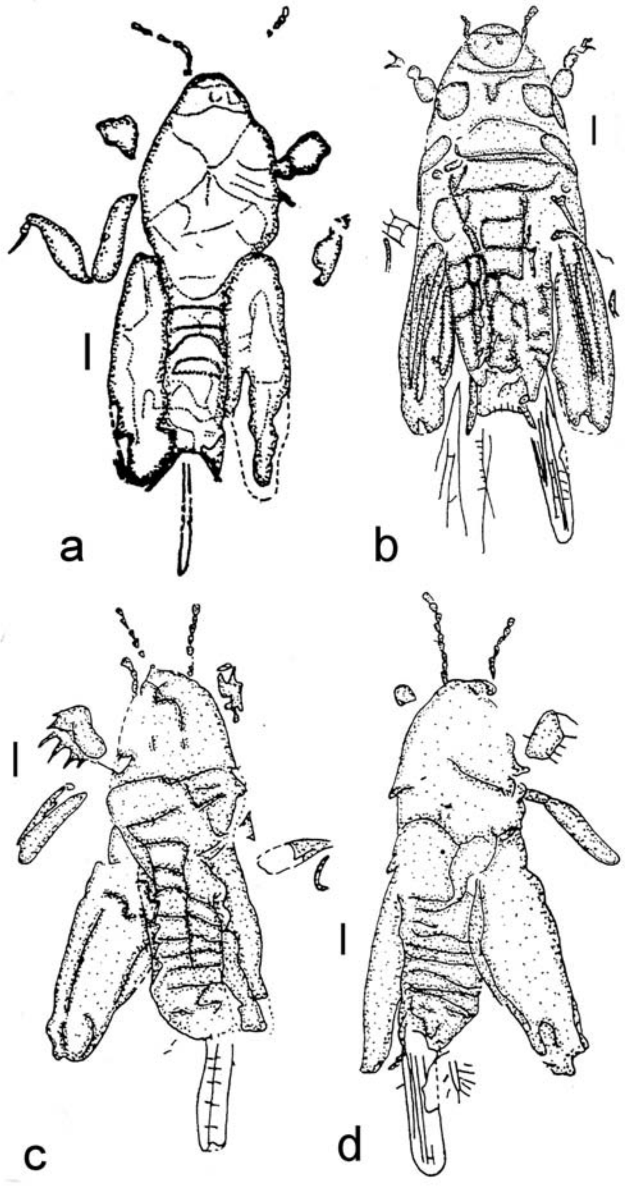

Fig. 11.36. Pigmy mole crickets, Tridactylidae: (a, b) *Cratodactylus ferreirai* Martins-Neto, 1990; (c, d) *Cratodactylus kellneri* Martins-Neto, 1990. Scale bars, 1 mm. After Martins-Neto (1990).

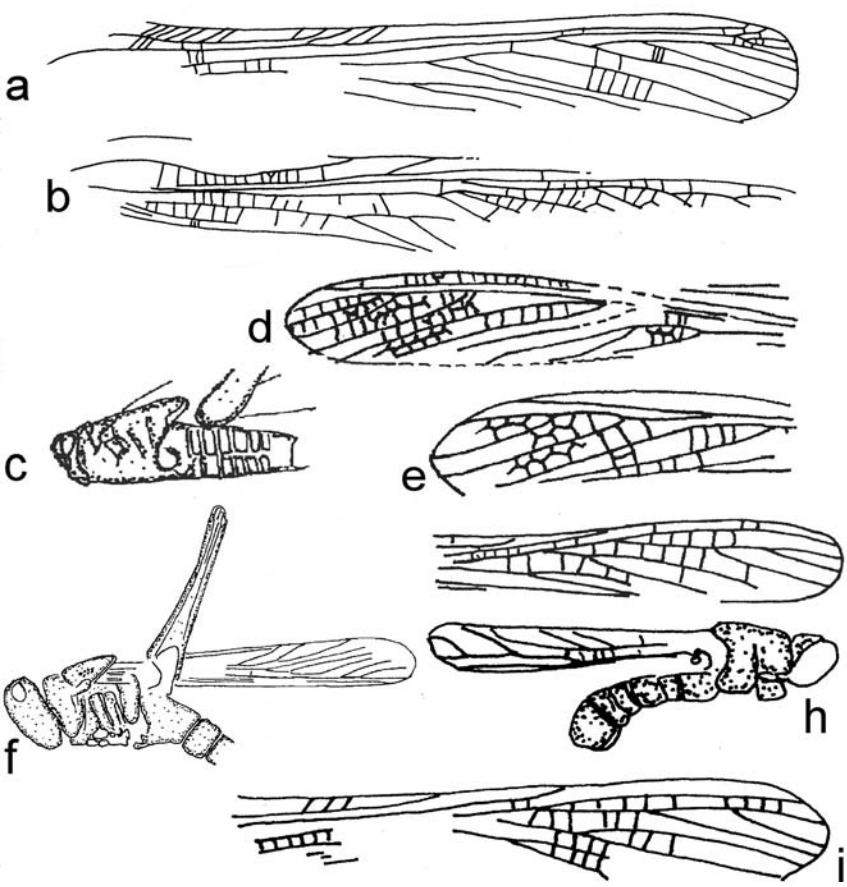

Fig. 11.37. Crato Formation Caelifera: (a) *Cratozeuneurella nervosa* Martins-Neto, 2003, holotype forewing, RGMN-T126; (b, e) *Cratozeuneurella godoii* Martins-Neto, 2003; (b), forewing holotype RGMN-T125; (c) body; (d) forewing; (e) hind wing of referred specimen AMNH 43868; (f) *Cratozeuneurella titanella* Martins-Neto, 2003, holotype RGMN-T127; (g, h) *Locustrix gallegoi* Martins-Neto, 2003, holotype RGMN-T128; (g) detail of forewing; (h) habitus; (i) *Locustrix audax* Martins-Neto, 2003, holotype forewing, RGMN-T129.

(sand gropers). The caeliferan fauna of the Crato Formation (Figures 11.35, 11.36, 11.37–11.38 and 11.39, 11.40) is dominated by extinct elcanid and 'locustopsoid' forms. Of the Recent superfamilies only Tridactyloidea have been formally described (represented by Tridactylidae). Bouretidae likely represent stem group Tetrigoidea and Tetrigidae *sensu stricto* are represented by a single, undescribed specimen in the collection at SMNS (Figure 11.30e). A first fossil record of Eumastacoidea was reported by Martins-Neto and Valarelli (1991). In addition, stem group Proscopiidae (Plate 11a) are represented by two specimens that are currently

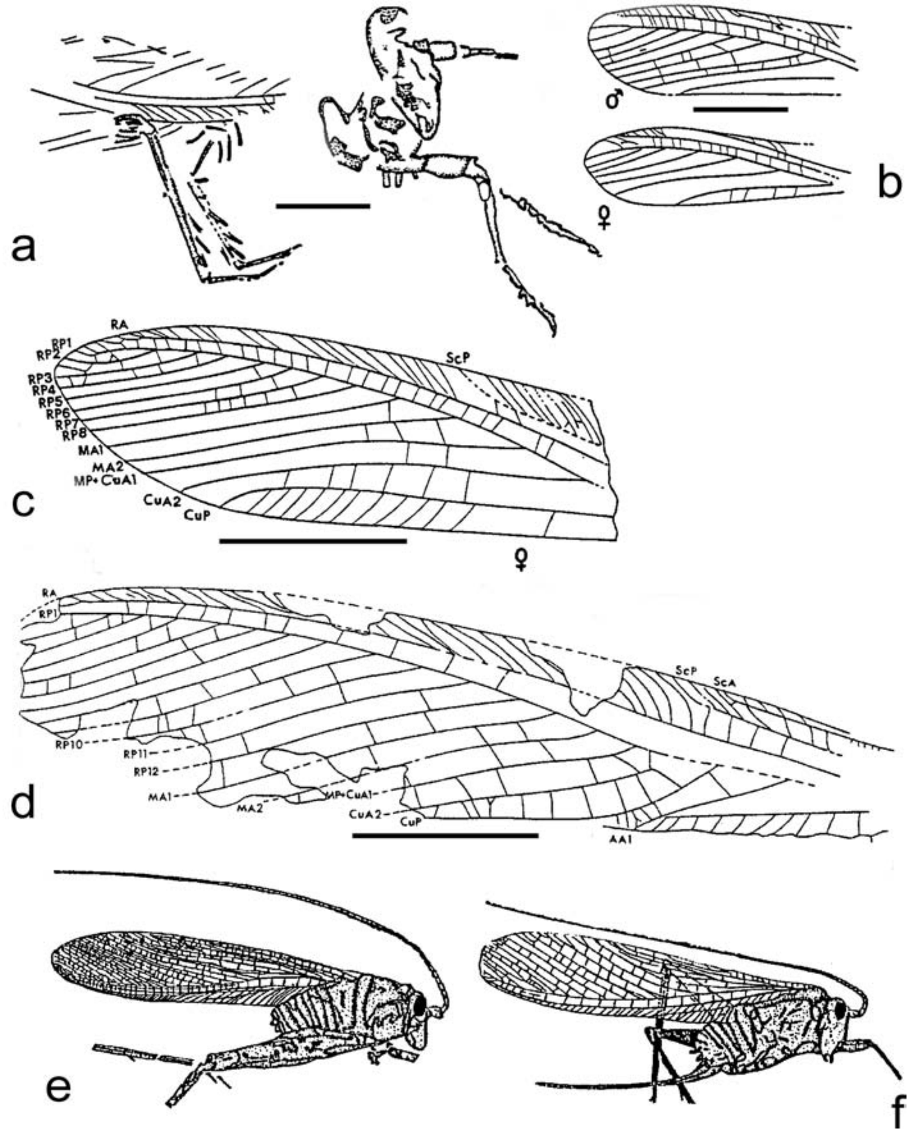

Fig. 11.38. Crato Formation Elcanidae: (a, b) *Cratoelcana damianii* Martins-Neto, 1991a; (a) head and thorax; (b) male and female wing venation; (c–f) *Cratoelcana zessini* Martins-Neto, 1991a; (c) reconstruction of wing venation; (d) entire wing; (e) reconstruction of male habitus; (f) reconstruction of female habitus. Scale bar, 5 mm. All figures from Martins-Neto (1991a).

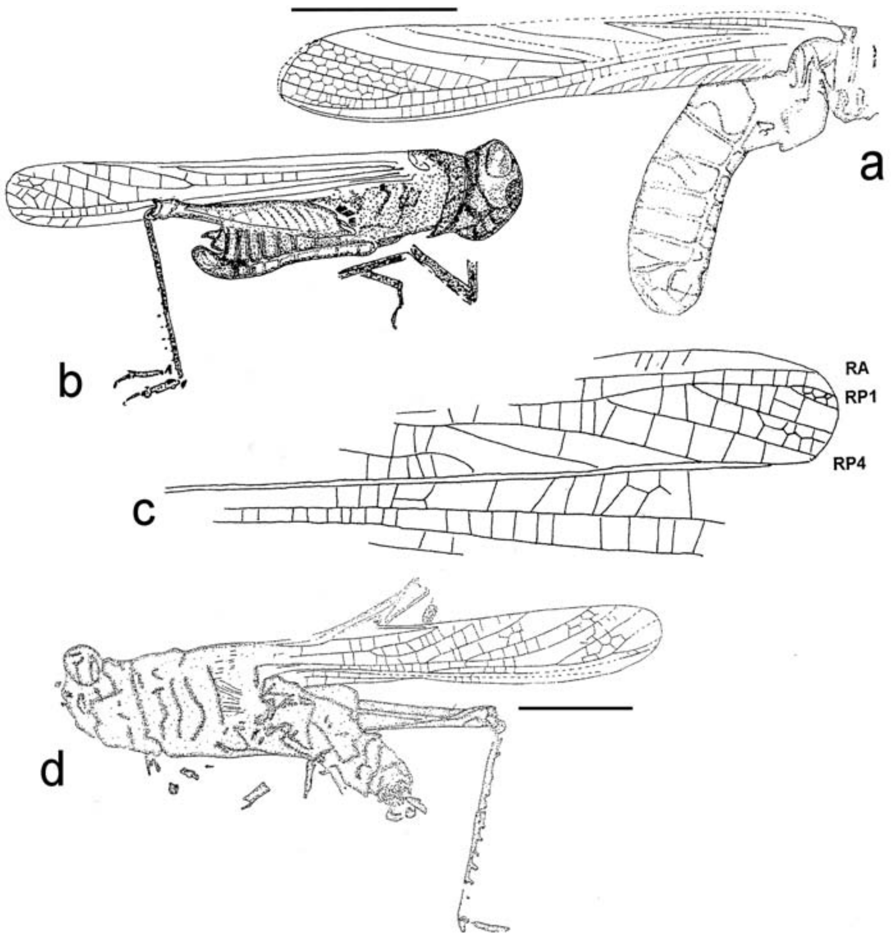

Fig. 11.39. Crato Formation Caelifera: (a) *Cratolocustopsis cretacea* (Martins-Neto, 1990), holotype GP/1T-1671; (b, c) *Cratolocustopsis contomax* Martins-Neto, 2003, holotype, RGMN-T113, habitus (b) and hind wing venation (c); (d) *Cratolocustopsis caririensis* (Martins-Neto, 1990), holotype, GP/1T-1672. Scale bars, 5 mm.

being described (Heads, 2008). The family Archaeopneumoridae that was mentioned together with Bouretidae as new family of Acridoidea from this locality by Martins-Neto (1987c) but apparently was never properly described and therefore still has to be considered as a *nomen nudum*.

Elcanidae

Although traditionally placed in Ensifera (Sharov, 1968; Martins-Neto, 1991a; Gorochov, 1995) the Elcanidae (Figure 11.38, Plates 11b and c) are now considered to represent either a paraphyletic assemblage of stem group caeliferans,

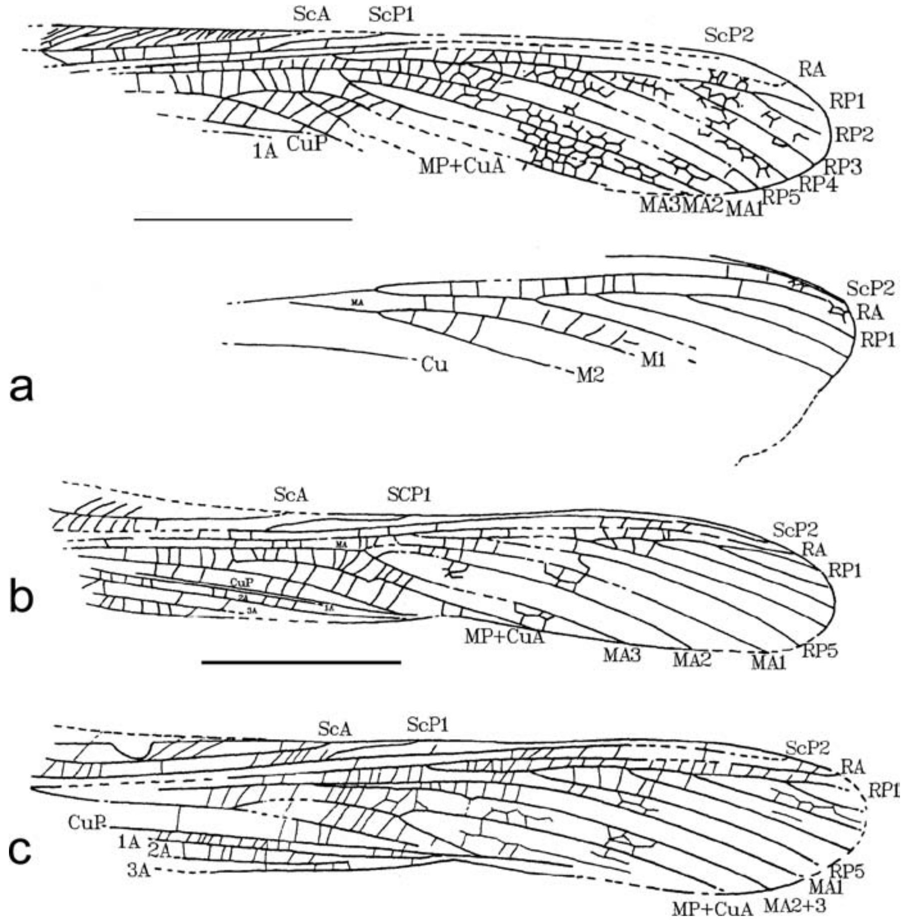

Fig. 11.40. Crato Formation Caelifera: (a) *Cratozeuneurella neotropica* Martins-Neto, 1998, holotype forewing (above) and hind wing, UnG-030; (b) *Cratozeuneurella amedegnatoi* Martins-Neto, 1998, holotype forewing CD-I-127; (c) *Cratozeuneurella nordestina* Martins-Neto, 1998, holotype forewing, UnG31. Scale bar, 5 mm.

or the sister group to Caelifera *sensu stricto* despite their long, filiform antennae (Béthoux and Nel, 2002; Grimaldi and Engel, 2005). Elcanidae appear to dominate the Crato Formation orthopteran fauna in terms of abundance despite only being represented by a single genus, *Cratoelcana* Martins-Neto, 1991a, with two species: *C. damianii* (perhaps the most abundant orthopteran in the fauna) and *C. zessini*.

Locustopseidae

The Locustopseidae (Figures 11.37, 11.40, 11.41 and 11.42, Plates 11d and e) are the most diverse group of Caelifera in the Crato Formation, known from 16

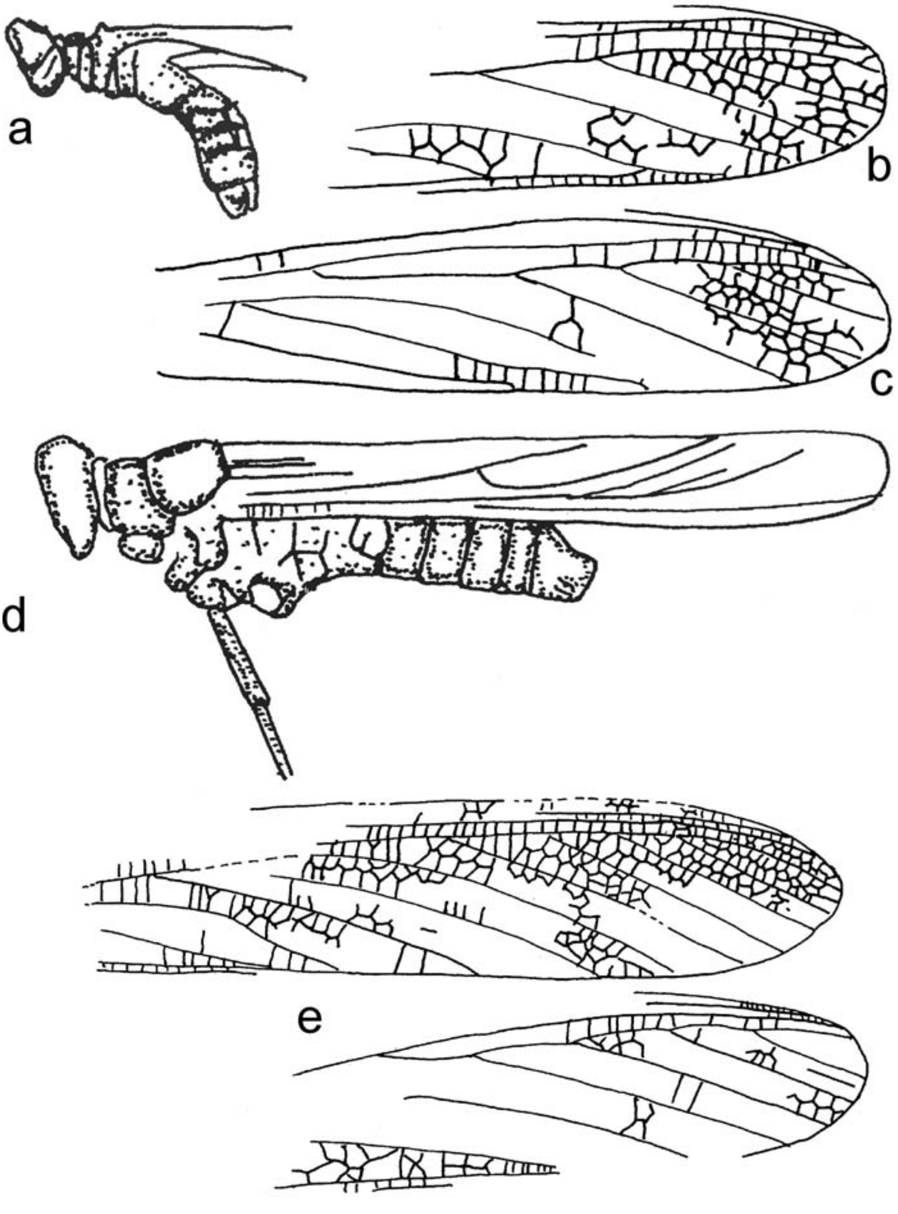

Fig. 11.41. Crato Formation Caelifera: (a–c) *Cratozeuneurella soaresi* Martins-Neto, 2003, holotype hind wing (b) RGMN-T118, and referred specimen CD-I-124, habitus (a) and hind wing (c); (d) *Zessinia petrulevicius* Martins-Neto, 2003, holotype RGMN-T116; (e) *Zessinia vikingi* Martins-Neto, 2003, holotype RGMN-T119, forewing (above) and hind wing (below).

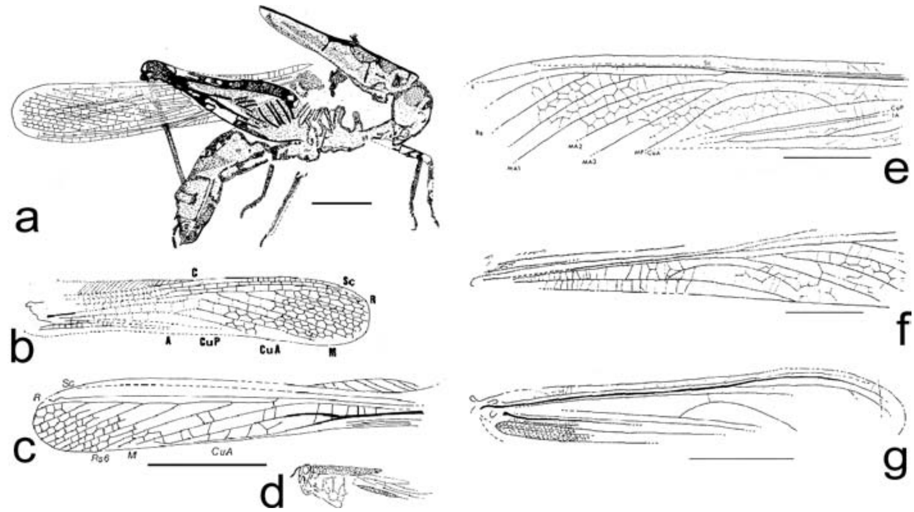

Fig. 11.42. Crato Formation Caelifera: (a, b) *Araripelocusta longinota* Martins-Neto, 1995, holotype, coll. Vulcano CV-1572; (c, d) *Araripelocusta brevis* Martins-Neto, 1995, wing, head and thorax; (e) *Zessinia caririensis* Martins-Neto, 1990, wing venation; (f) *Zessinia pulcherima* Martins-Neto, 1990, wing venation from holotype; (g) *Zessinia reticulata* Martins-Neto, 1990, wing venation. Scale bars, 5 mm. (a–d) After Martins-Neto (1995), (e–g) after Martins-Neto (1990).

species in four genera: *Zessinia* Martins-Neto, 1990c, with five species; *Cratozeunerella* Martins-Neto, 1998a, with six species; *Cratolocustopsis* Martins-Neto, 2003a, with three species; and *Locustrix* Martins-Neto, 2003a, with two species. The Locustopseidae are sometimes grouped together with the Locustavidae and Araripelocustidae in the extinct superfamily Locustopsoidea (Martins-Neto, 2003), which is almost certainly paraphyletic, with the individual families probably representing stem groups of modern clades.

Araripelocustidae

The extinct Araripelocustidae (Figure 11.42, Plates 11f and g) includes two species within the genus *Araripelocusta* Martins-Neto, 1995a: the type species *Araripelocusta longinota* and a second smaller species *Araripelocusta brevis*. The family is characterized by the very robust metathoracic femora and by the distinctive, strongly sclerotized posterior expansion of the pronotum and cryptopleuron to form a shield-like structure which, when the animal was at rest, would have covered the entire meso- and metathoraces as well as the base of the wings and possibly the first few abdominal segments.

Bouretidae

Bouretidae are a monotypic family erected by Martins-Neto (2001) for *Bouretia elegans*. Known only from a single poorly preserved specimen, the relationships of *Bouretia* are uncertain. Martins-Neto (1987c, 2001, 2003) placed Bouretidae within Locustopsoidea. However, there is little evidence to support this assignment and *Bouretia* shares several features in common with Tetrigidae (Tetrigoidea), including two-segmented pro- and mesothoracic tarsi, robust legs and an enlarged pronotum partly enclosing the abdomen. These features suggest a relationship with Tetrigidae, but until more complete and better-preserved material comes to light the relationships of this taxon will remain unresolved.

Tridactylidae: pygmy mole crickets

The Recent Tridactylidae (Figures 11.35 and 11.36, Plates 11h and i) or 'pygmy mole crickets', as they are commonly known, are generally small, often gregarious insects known from tropical and subtropical regions worldwide (Grimaldi and Engel, 2005). As their vernacular name would suggest, they superficially resemble the true mole crickets, with prothoracic legs modified for digging like those of Gryllotalpidae. In the Crato Formation, Tridactylidae are known from two species in the genus *Cratodactylus* Martins-Neto, 1990d: the type species *Cratodactylus ferreirai* and *Cratodactylus kellneri*.

11.12 Cicadomorpha: cicadas and relatives

Federica Menon, Sam W. Heads and Jacek Szwedo

Cicadomorpha is a suborder of the Hemiptera comprising the cicadas (Cicadoidea), froghoppers and spittle bugs (Cercopoidea), leafhoppers and treehoppers (Membracoidea), ground-dwelling leafhoppers (Myerslopioidea) and several extinct groups: Dysmorphoptiloidea, Hylicelloidea, Palaeontinoidea, Pereborioidea and Prosboloidea. Placement of paraphyletic Scytinopteroidea remains uncertain (Bourgoin and Campbell, 2002; Shcherbakov and Popov, 2002; Szwedo *et al.*, 2004). They are characterized by an enlarged postclypeus, small antennal pedicel, without conspicuous sensilla, aristiform flagellum, pronotum concealing bases of tegmina, punctate tegmina at least basally, a relatively long basicubital triangle on tegmina, short veins A_1+A_2 entering the claval apex and absence of the tegula at the base of tegmina, hind wings with an anal fold posterior of A_2, and the presence of an ambient vein running parallel to the margin in the hind wing, and small and narrowly separated middle coxae (Shcherbakov, 1996; Shcherbakov and Popov, 2002; Dietrich, 2005; Grimaldi and Engel, 2005).

Today they have a worldwide distribution, with the majority of species concentrated in warmer tropical areas. Cicadomorpha are rare in the Crato Formation and are represented by a low-diversity assemblage comprising the extinct families Palaeontinidae and Cercopionidae and the Recent families Cicadellidae, Myerslopiidae and Tettigarctidae. Some undescribed new taxa are present among the collections (Figures 11.43g and h).

Study of the Crato Formation Cicadomorpha began in the 1990s with Hamilton's (1990, 1996) largely descriptive treatment of the fauna. Hamilton (1990) recognized the presence of Cicadellidae, and erected the new family †Cercopionidae with the monotypic genus *Cercopion*. Hamilton also described taxa in the family Jascopidae, synonymized under Cicadellidae: Ledrinae (Shcherbakov, 1992). Subfamily Myerslopiinae mentioned by Hamilton (1990) with tribes Ovojassini and Hallicini was given familial status by Hamilton (1999). In the same paper, Hamilton related tribe Hallicini with Membracidae. In addition, Hamilton (1990) also erected the genus *Architettix* and placed it in Cicadoprosbolidae, which was subsequently recognized as a junior synonym of Tettigarctidae (see Menon, 2005). More recent studies by Ueda (1997), Martins-Neto (1998), Menon *et al.* (2005) and Menon and Heads (2005) have documented the occurrence of a diverse assemblage of Palaeontinidae.

Of 78 fossil cicadas from the Crato Formation studied by Szwedo and Bechly (2006, unpublished work), 55 specimens were Cicadomorpha (71%) and only 23 specimens were Fulgoromorpha (29%). Of the 56 Cicadomorpha specimens, 15 specimens (27%) belonged to the giant-cicada family Palaeontinidae.

†Palaeontinidae: giant cicadas

The †Palaeontinidae (Figures 11.43a–d, 11.44 and 11.45, Plate 12a) are an extinct stem group of Cicadomorpha well known from the Mesozoic of Europe and Asia (Handlirsch, 1906–1908; Becker-Migdisova, 1949; Gomez-Pallerola, 1984; Whalley and Jarzembowski, 1985; Shcherbakov, 1988; Zhang, 1997; Ren *et al.*, 1998a; Wang B. *et al.*, 2006a, b; Wang Y. and Ren, 2006; Wang Y. *et al.*, 2007a, b). The family was first recorded from the Crato Formation by Ueda (1997), who described *Parawonnacottella araripensis* from a single specimen. A year later, Martins-Neto (1998) erected *Cratocossus magnus* and described a second specimen of *Parawonnacottella araripensis*. Menon *et al.* (2005) and Menon and Heads (2005) subsequently described several new taxa from the Crato Formation and assessed the phylogenetic relationships and palaeobiogeography of the Brazilian fauna.

Parawonnacottella Ueda, 1997 (Figure 11.44c)

Parawonnacottella is known from two species in the Crato Formation: the type species *Parawonnacottella araripensis* Ueda, 1997 and *Parawonnacottella penneyi*

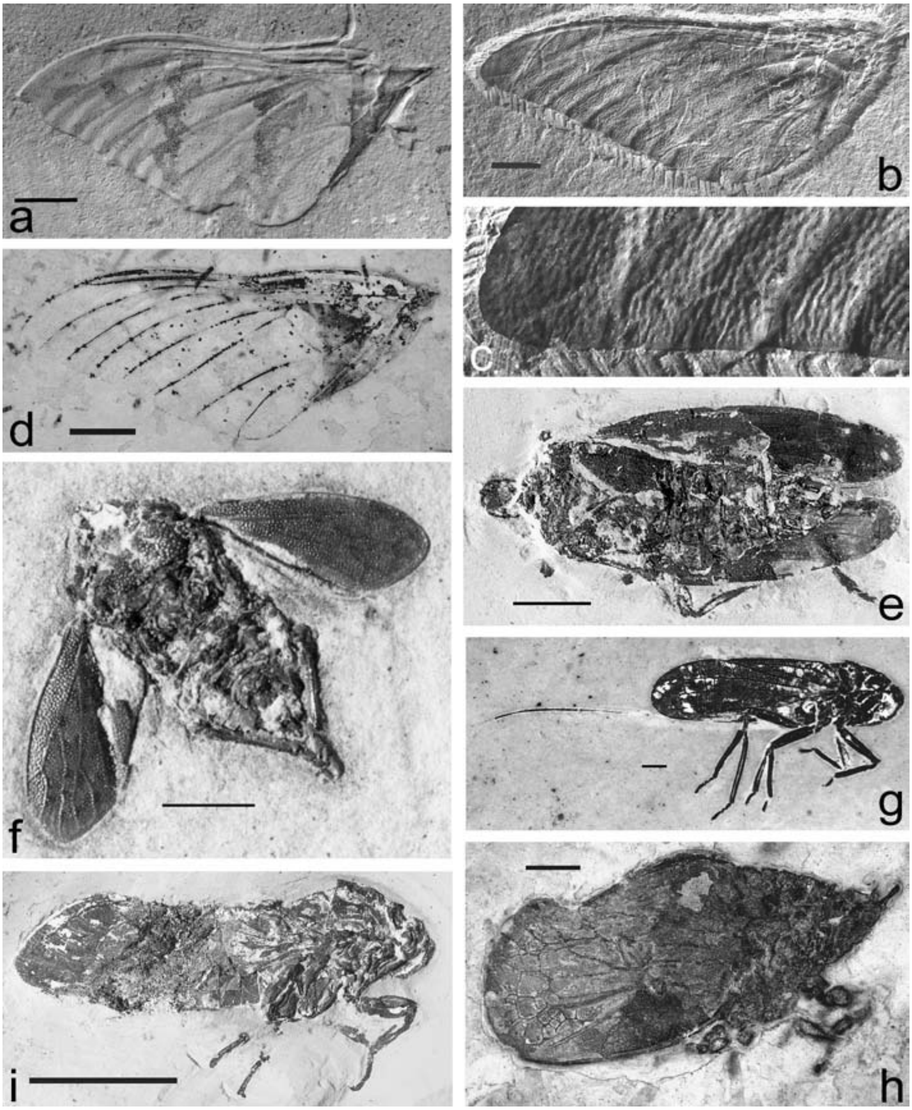

Fig. 11.43. Crato Formation Cicadomorpha: (a) *Colossocossus loveridgei*; (b) *Colossocossus giganticus* sp. nov., holotype MB.I 2103; (c) close-up of distal forewing margin of *C. giganticus*, holotype MB.I2103; (d) *Colossocossus bechlyi*; (e) Cercopionidae SMNS 66433b; (f) Myerslopiidae, Ovojassini, SMNS 66407; (g) Cicadomorpha fam. nov., R55 MSF; (h) new taxon, SMNS 66414; (i) Tettigarctidae, SMNS 66435. Scale bars: a–d, i, 10 mm; e–h, 2 mm.

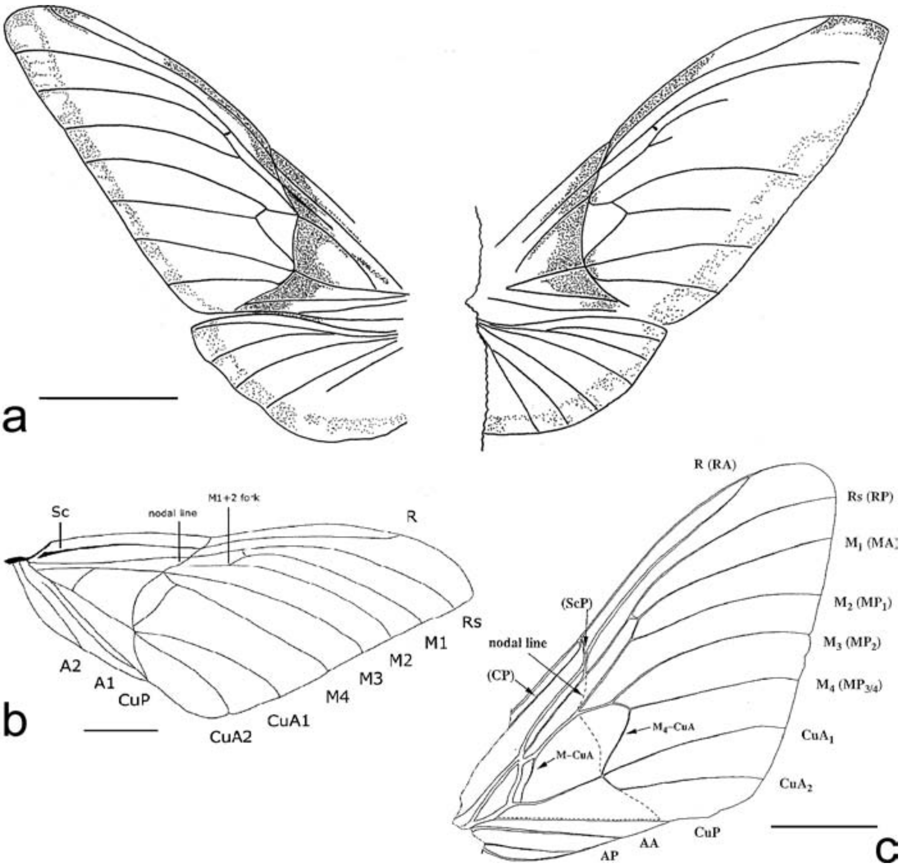

Fig. 11.44. Crato Formation Cicadomorpha (Palaeontinidae): (a) *Baeocossus fortunatus* Menon and Heads, 2005; (b) *Colossocossus bechlyi* Menon and Heads, 2005; (c) *Parawonnacottella araripensis* Ueda, 1997, holotype, KMNH IP 000,003. Scale bar, 10 mm. (a,b) Based on Menon and Heads (2005); (c) after Ueda (1997).

Menon *et al*., 2005. The venation of this genus is very similar to that of *Ilerdocossus* (= *Wonnacottella*) from the Valanginian–Berriasian of Montsec, Spain (Gomez-Pallerola, 1984; Whalley and Jarzembowski, 1985; Ueda, 1997). However, the general aspect of the forewing is notably different, having more rounded margins and a weak (or almost entirely absent) nodal indentation. This condition is characteristic of plesiomorphic forms from the Middle and Late Jurassic of central and eastern Asia (Becker-Migdisova, 1949; Shcherbakov, 1988; Carpenter, 1992) and may suggest a more basal phylogenetic position for *Parawonnacottella* than that presented by Menon *et al*. (2005).

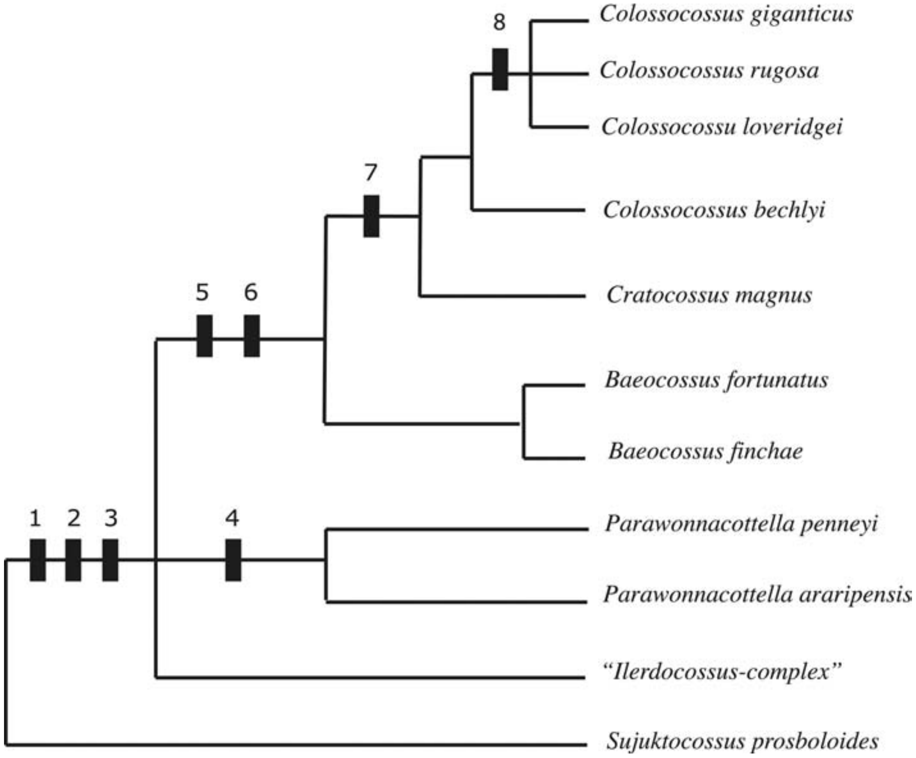

Fig. 11.45. Tree showing inferred phylogenetic relationships of the Brazilian Palaeontinidae. Character states: 1, increased narrowing of forewings; 2, reduced clavus; 3, migration of M-CuA fork basally; 4, costal margin without nodal indentations; 5, narrow forewing with pointed apex; 6, antenodal discal cell triangular; 7, postnodal discal cell lozenge-shaped; 8, antenodal region of discal cell not divided.

Cratocossus Martins-Neto, 1998f

Cratocossus is known from one species, *Cratocossus magnus* Martins-Neto, 1998f, based on a single poorly preserved specimen. The taxon has a markedly reduced postnodal discal region as in *Colossocossus* but differs from the later in the arrangement of the radial system and the unusual clavus (Menon *et al.*, 2005; Menon and Heads, 2005).

Baeocossus Menon *et al.*, 2005

Baeocossus (Figure 11.44a, Plate 12a) is known from two species: the type species *Baeocossus finchae* Menon *et al.*, 2005, and *Baeocossus fortunatus* Menon and Heads, 2005. Many well-preserved specimens are known from the Crato Formation, with preserved fore- and hind wings and body features (see Menon *et al.*, 2005;

Menon and Heads, 2005). One specimen from KMNH even has beautiful colour pattern preserved on the wings (Plate 12a). In this genus, the discal region is noticeably large in relation to the wing length. It can be distinguished from *Colossocossus* and *Cratocossus* by its comparatively smaller size and the quadrangular postnodal discal region (Menon *et al.*, 2005).

Colossocossus Menon *et al.*, 2005

Colossocossus (Figures 11.43a–d and 11.44b) is known from four species: the type species *Colossocossus loveridgei* Menon *et al.*, 2005, *Colossocossus rugosa* Menon *et al.*, 2005, *Colossocossus bechlyi* Menon and Heads, 2005, and *Colossocossus giganticus* sp. nov. described below.

Colossocossus giganticus Menon and Heads, sp. nov. (Figures 11.43b and c)

Holotype: MB.I 2103, single isolated forewing.

Derivation of name: from ‘gigantic’ in reference to the large size of this species.

Diagnosis: large *Colossocossus* (forewing 80 mm long); broad nodal indentation of costal margin; costal area expanded basally; discal cell relatively small (14% of total wing length) M_1+_2 branching at nodal line.

Description: single isolated forewing, 80 mm long, 33 mm wide at nodus, triangular in aspect; costal margin broadly indented at nodus and slightly curved at apex; posterior margin straight; anal margin incomplete, slightly curved; Sc apparently straight, but largely obscured by sediment; costal area widened basally, strongly sclerotized; R straight, origin at wing base; Rs origin not visible, probably from R near wing base; R curved apically, reaching the margin 20 mm from apex; Rs curved, reaching margin posteriorly of apex; origin of M+Cu not visible; M branching at nodal line; M_1+_2 straight, slightly undulated for 17 mm and branching 30 mm from wing base; M_1 almost straight, slightly curved distally; M_2 straight, curved near posterior margin; Rs-M_1 prominent, straight; M_3+M_4 fork at nodal line; M_3 and M_4 slightly curved posteriorly; M_4 reaches posterior margin at midwing; CuA slightly curved, forming the anal margin of antenodal discal region, branching at nodal line; CuA_1 straight; CuA_2 and CuA_3 sigmoidal; CuP not visible; anal area not preserved; discal cell 11 mm long (incomplete); antenodal region 9 mm long (incomplete); postnodal region 2 mm long; antenodal region probably triangular, although largely not preserved; postnodal region lozenge-shaped; M_4-CuA_1 6 mm long.

Remarks: *Colossocossus giganticus* sp. nov. differs from other species of *Colossocossus* most notably by its large size and the relatively minute discal cell. The lozenge-shaped postnodal discal region is characteristic of the genus, but the undivided antenodal region places *C. giganticus* closer to *C. loveridgei* and *C. rugosa* (Figure 11.45) than to the apparently plesiomorphic *C. bechlyi* (see Menon and

Heads, 2005). All species of *Colossocossus* appear to display a trend in decreasing discal cell size as the wing length increases. This is likely a consequence of the basal migration of the nodal line as the wings increase in size.

Phylogenetic significance of Brazilian Palaeontinidae

Menon *et al.* (2005) and Menon and Heads (2005) recently reviewed the phylogenetic relationships of the Crato Formation Palaeontinidae and found them to be closely related to the poorly defined "*Ilerdocossus*-complex" of Europe and Asia. The *Ilerdocossus* complex comprises a suite of taxa from the Early Cretaceous of Europe and Asia, including *Ilerdocossus* and *Wonnacottella* from Montsec, Spain and *Liaocossus* from the Jehol Biota of China. The latter two genera are both probable junior synonyms of *Ilerdocossus* (see Menon *et al.*, 2005). The preliminary assessment of relationships presented by Menon *et al.* (2005) places the Brazilian taxa in an unresolved clade with the *Ilerdocossus* complex (Figure 11.45), united by an increased narrowing of the forewing, a reduced clavus and the migration of the M-CuA fork towards the wing base. *Colossocossus*, *Cratocossus* and *Baeocossus* form a clade united by the triangular shape of the antenodal region of the discal cell. However, the positions of *Parawonnacottella* and the "*Ilerdocossus*-complex" with respect to this group remain unresolved (Menon and Heads, 2005). Future revision of the "*Ilerdocossus*-complex" will hopefully shed light on this problem and provide more data in order to resolve the trichotomy.

This group of Palaeontinidae was widespread by the Early Cretaceous, with representatives in eastern and central Asia (Shcherbakov, 1988; Ren *et al.*, 1998b; Wang B. *et al.*, 2006a, b; Wang Y. and Ren, 2006; Wang Y. *et al.*, 2007a, b) as well as Europe (Handlirsch, 1906–1908; Gomez-Pallerola, 1984; Whalley and Jarzembowski, 1985) and South America (Menon *et al.* 2005; Menon and Heads, 2005). Menon *et al.* (2005) suggested that the group might have originated in Asia sometime in the Middle–Late Jurassic before spreading westwards into Europe and South America. This hypothesis receives some support from the slightly older age of the European (Valanginian–Berriasian) and Asian (Hauterivian–Barremian) forms in comparison to the Brazilian taxa (Aptian). Furthermore, apparently plesiomorphic taxa such as *Palaeontinodes, Suljuktocossus* and *Pseudocossus* from the Jurassic of central Asia share many features in common with the Early Cretaceous taxa and may represent the sister group to the clade comprising the "*Ilerdocossus*-complex" and the Brazilian forms. Interestingly, the weak nodal indentation of these Jurassic taxa is very similar to the condition seen in *Parawonnacottella* and may suggest a more basal position for the genus. However, re-description of the Jurassic taxa is required along with a revision of the *Ilerdocossus* complex in order to fully resolve the relationships of these taxa.

Tettigarctidae: hairy cicadas

The Recent Tettigarctidae (hairy cicadas) (Figures 11.43i and 11.46a–d, Plate 12b) are a relict family known in the living fauna from two species (both in the genus *Tettigarcta* Distant, 1883; see also Distant, 1905) restricted to south-east Australia and Tasmania (Carver *et al.*, 1992; Grimaldi and Engel, 2005; Moulds, 2005). Cicadoprosbolidae Evans, 1956, is widely considered to be a junior synonym of Tettigarctidae (Becker-Migdisova, 1962a, 1962b; Shcherbakov, 1996; Nel, 1996; Nel *et al.*, 1998; Dietrich, 2002; Menon, 2005) and this view is upheld here. On the other hand, Boulard and Nel (1990) and D. E. Shcherbakov (personal communication) have divided the Tettigarctidae (one Recent and 14 fossil genera) into two subfamilies, the Tettigarctinae comprising the recent *Tettigarcta* and Cenozoic *Eotettigarcta* and *Meuniera*, and the Cicadoprosbolinae comprising all the Mesozoic genera (Moulds, 2005).

The fossil record of the family is poor but extends back to the Late Triassic (Popov *et al.*, 1994) where the family first appears in the latest Rhaetian of England (Whalley, 1983). Representatives are also known from Europe (Zeuner, 1944; Bode, 1953; Nel, 1996; Grimaldi and Engel, 2005), Asia (Becker-Migdisova, 1949; Shcherbakov, 1988; Hong, 1982; Moulds, 2005) and Africa (Nel *et al.*, 1998) as well as South America (Hamilton, 1990; Menon, 2005). This almost cosmopolitan ancient distribution is in stark contrast to the Recent distribution of the family.

Architettix Hamilton, 1990

Architettix (Figures 11.46a–d) is known from a single species, *Architettix compacta*, described by Hamilton (1990) and placed in the family Cicadoprosbolidae, now widely accepted as a junior synonym of Tettigarctidae (see Menon, 2005 for a review). The species is characterized by the inflated crown, large lateral ocelli, bulbous antennae and cicadellid-like tarsi (Hamilton, 1990). *Architettix* is known from several near complete specimens, including a nymph.

Tettagalma Menon, 2005

This genus is known from one near complete specimen (Plate 12b), lacking hind wings and poorly preserved upper body. The forewing venation, therefore, provides all the diagnostic characters: prominent costal margin, Rs with three branches, CuA strongly deflected anteriorly to nodal line (Menon, 2005) and wide marginal membrane with numerous, equally spaced striae. *Tettagalma* is somewhat similar to *Architettix*, but can be distinguished from the latter by the more basally placed

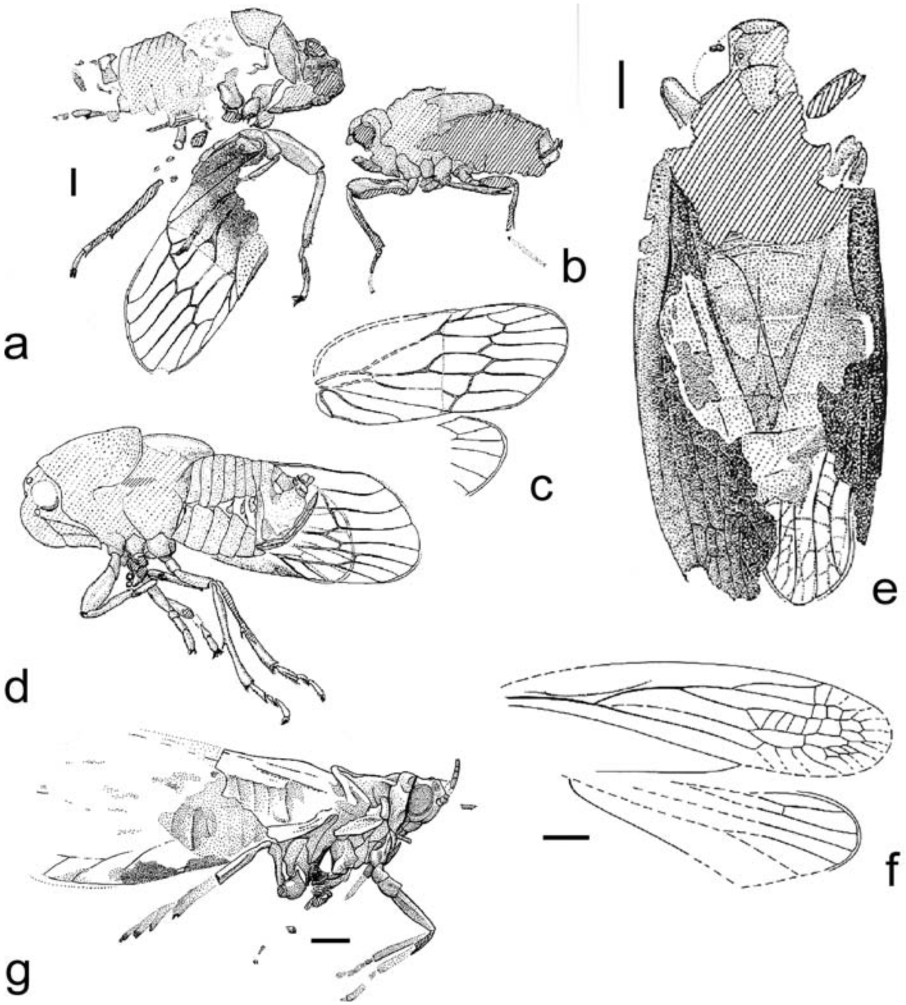

Fig. 11.46. Crato Formation Cicadomorpha (Tettigarctidae and Cercopionidae) and Fulgoromorpha: (a) Tettigarctidae, Cicadoprosbolinae, *Architettix compacta* Hamilton, 1990, holotype, AMNH43690; (b) *Architettix compacta* Hamilton, 1990, nymph, paratype, AMNH43683; (c) *Architettix compacta* restored venation; (d) *Architettix compacta* composite example based on AMNH 43600 and 43601; (e) Cercopionidae, *Cercopion reticulata* Hamilton, 1990, holotype, AMNH 43695; (f) *Cercopion reticulata* restored venation; (g) Fulgoromorpha, Fulgoroidea, *Megaleurodes megocellata* Hamilton, 1990, holotype, AMNH 43608. All after Hamilton (1990). Scale bars, 1 mm.

nodal line, wider costal space and elongated forewing. The wings had a characteristic colour pattern (Plate 12b).

Palaeobiogeography and palaeoecology of Tettigarctidae

Fossil Tettigarctidae are mainly known from the Northern Hemisphere (Becker-Migdisova, 1946, 1947; Popov *et al.*, 1994), making their recent discovery in Brazil noteworthy (Hamilton, 1990), demonstrating a more widespread Mesozoic distribution. This distribution is also interesting for its palaeoecological and palaeoenvironmental implications. The differences in habitat and perhaps feeding strategies between Recent and fossil representatives of the family is noticeable. Tettigarctidae are found today only in high altitude cold climates, in subalpine snowgum forests (Moulds, 1990) and can thrive in sub-zero temperatures. Many palaeoenvironmental reconstructions of the Crato settings refer instead to a tropical, possibly increasingly dry climate, supported by palaeontological and sedimentological data. In general, it appears that Mesozoic Tettigarctidae where euryecious. Other deposits, where fossil Tettigarctidae were recovered (i.e. Germany and Tunisia), are also found in between the limits of temperate regions (Nel, 1996; Nel *et al.*, 1998).

Shcherbakov (2004) suggests that the more specialized nymphal chaetotaxy and the nymphal labium position similar to that of Cicadidae (evaluated from the single known fossil tettigarctid nymph, *Tettigambra mouldsi* Shcherbakov) may indicate that the Cicadidae descended from the Cicadoprosbolinae rather than the Tettigarctinae, an idea also suggested by Becker-Migdisova (1947) based upon wing evidence (Moulds, 2005).

†Cercopionidae

This family (Figures 11.43e and 11.46e and f) was erected by Hamilton (1990) to accommodate his monotypic genus *Cercopion*. The primary diagnostic character is the simple, non-branching M in the hind wings with no connecting crossveins (Hamilton, 1990). The apical area of the forewings is characterized by the very busy cross-venation. *Cercopion reticulata* is the only species in this family and is known from only one near complete specimen with both fore- and hind wings. Hamilton (1990) diagnosed the species based on several features of the head and eyes, including head scarcely produced, ocelli between eyes, pronotum longer than crown.

Cicadellidae: leafhoppers

Cicadellidae, one of the largest insect families, comprises more than 25,000 described species currently grouped into 36 subfamilies (Oman *et al.*, 1990; Godoy

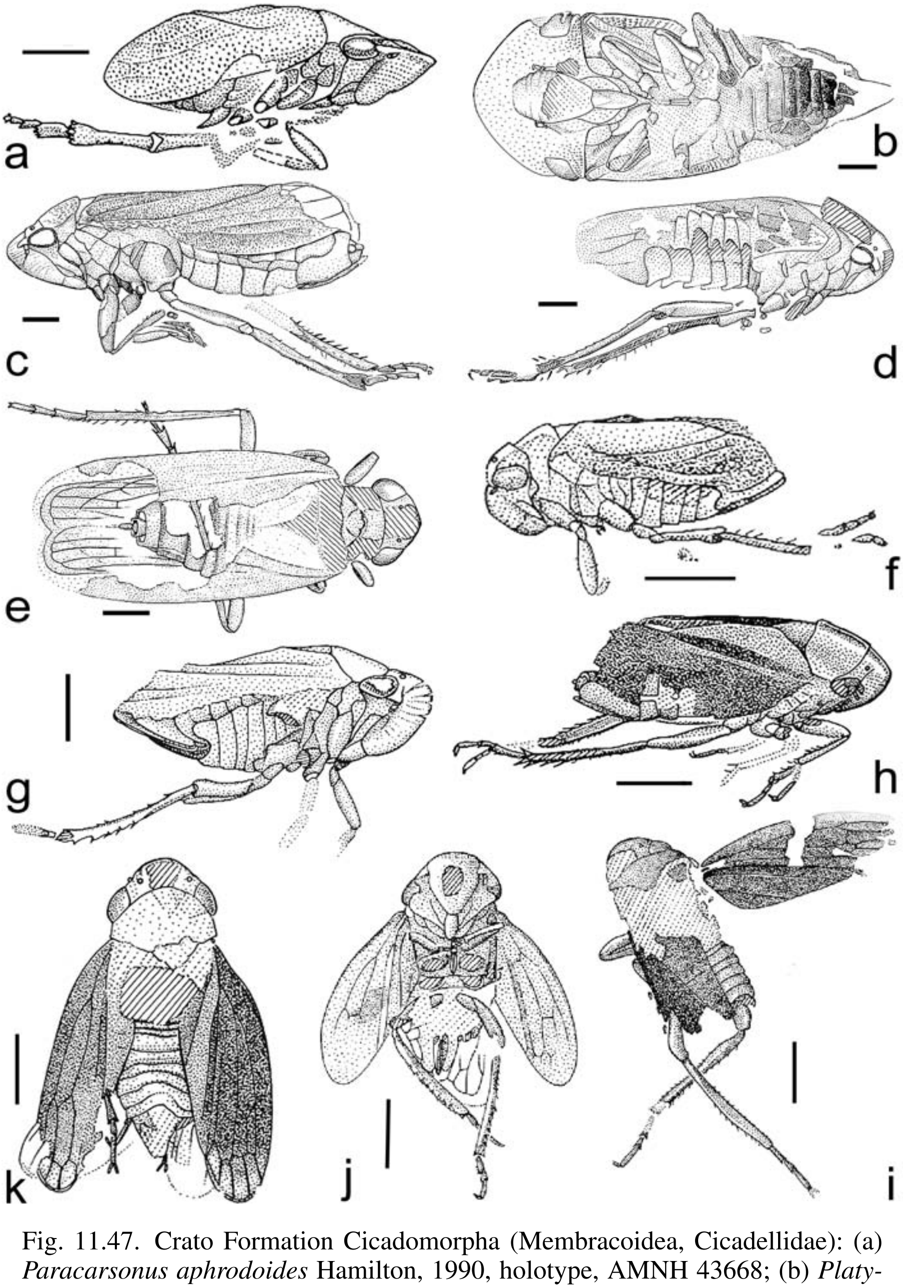

Fig. 11.47. Crato Formation Cicadomorpha (Membracoidea, Cicadellidae): (a) *Paracarsonus aphrodoides* Hamilton, 1990, holotype, AMNH 43668; (b) *Platyjassites inflatifrons* Hamilton, 1990, holotype AMNH 43693; (c) *Proerrhomus rugosus* Hamilton, 1990, holotype, AMNH 43612; (d) *Proerrhomus* sp. A of Hamilton (1990), AMNH 43630; (e) *Proerrhomus* sp. B of Hamilton (1990), AMNH 43613; (f) *Ovojassus minor* Hamilton, 1990, holotype, AMNH 43652; (g) *Ovojassus concavifer* Hamilton, 1990, holotype, AMNH 43660; (h) *Hallex xestocephalus* Hamilton, 1990, holotype, AMNH 43656; (i) *Hallex gongrogony* Hamilton, 1990, holotype, AMNH 43644; (j) *Hallex brevipes* Hamilton, 1990, holotype, AMNH 43645; (k) *Hallex gracilior* Hamilton, 1990, holotype, AMNH 43640. All after Hamilton (1990). Scale bars, 1 mm.

and Webb, 1994; Dietrich and Rakitov, 2002; Dietrich, 2005). Many of these subfamilies are poorly characterized morphologically, and phylogenetic analyses of morphological (Hamilton, 1983; Dietrich, 1999) and molecular (Dietrich *et al.*, 2001) data indicate that some, as traditionally defined (Oman *et al.*, 1990), are para- or polyphyletic.

Cicadellidae are medium-sized or small, of various types of habitus, more or less elongate cylindrical, with wide head, which is slightly narrower or slightly wider than pronotum, and hind tibiae furnished with numerous strong bristles. The boundaries of the frons, clypeus and vertex are indistinct or barely marked. The turn of face into the vertex is smooth, more rarely sharp; besides, the boundary between frons and vertex may be formed differently: ocelli are situated at the very boundary or on vertical surface. The head may be elongate; and the presence of processes and carinae on the head, disc of pronotum and scutellum are not typical. Bases of the antennae are inserted between the eyes. Wing dimorphism and a strong brachyptery is common. Fully developed tegmina is moderately consolidated; the degree of development of the peripheral membrane (so-called appendage of membrane) varies widely. The hind wings are mainly with a completely developed peripheral vein, but it is interrupted from apex up to the clavus in most Typhlocybinae. Hind coxae are seen with button fastening on contiguous medial surfaces. Tarsi are three-segmented (Anufriev and Emeljanov, 1988). Cicadellidae, descendants of Jurassic Karajassidae, first appear in the fossil record in the Lower Cretaceous (Shcherbakov, 1986; Hamilton, 1990, 1992). Cicadellidae are abundant in the Crato Formation, and well documented by Hamilton (1990).

Cicadellinae

Proerrhomini Hamilton, 1990

Proerrhomus Hamilton, 1990

Proerrhomus rugosus (Figures 11.47c–e) is the only species in this genus and is characterized by various aspects of the head morphology including a declivous crown, ocelli situated between the eyes and an inflated frons, and also by a strongly pitted tegmen (Hamilton, 1990). This genus is well known from complete and well-preserved adult specimens.

Ledrinae

Paracarsonini Hamilton, 1990

These leafhoppers (Figures 11.47a–b) were first recorded from the Crato Formation by Hamilton (1990), who erected two monotypic genera. *Paracarsonus aphrodoides*

(Figure 11.47a) is relatively small (4.5–5 mm long) with a carinate coronal margin (Hamilton, 1990) and is fairly abundant. *Platyjassites inflatifrons* (Figure 11.47b) can be distinguished from *Paracarsonus* by the enlarged frons and coronal margin extending beyond the eyes (Hamilton, 1990). Little is known of the wing venation of *Paracarsonus* and *Platyjassites*, but both genera were tentatively placed within the tribe Paracarsonini by Hamilton (1990) based on the morphology of the coronal margin. Paracarsonini were suggested to be placed among Cicadellidae: Ledrinae by Shcherbakov (1996), the action made by Shcherbakov and Popov (2002).

Hamilton (1990) placed Paracarsonini in family Jascopidae, which is a small extinct group of membracoid cicadomorphs, described from the Upper Cretaceous Canadian amber (Hamilton, 1971), and based on a nymph. Shcherbakov (1992) transferred *Jascopus notabilis* Hamilton to Cicadellidae: Ledrinae, and considers Jascopidae Hamilton, 1971 to belong to Membracoidea: Cicadellidae: Ledrinae. Shcherbakov and Popov (2002) supported the synonymy of Jascopidae under Cicadellidae *sensu lato*. In contrast, Hamilton (1992) interprets Jascopidae as a separate family, known from the Triassic, Jurassic and Cretaceous, with a few genera.

Clade Ulopidae+Aetalionidae+Melizoderidae+Membracidae

This monophyletic clade within Membracoidea was proposed by Hamilton (1999). The synapomorphies for the group are: frons bounded; sulci dorsal, but closer to ocelli than original margin of frons; tentorium pillar-like; tibiae broadest on outer face, narrower on inner face, nearly triangular in cross cection; hind basitarsomere no longer than apical tarsomere (convergent with cicadoidea); frons flattened (convergent with higher Cicadellidae). This clade is also partly supported by molecular research (Dietrich *et al.*, 2001; Cryan, 2005).

Hallicini

Hallex Hamilton, 1990

Hallex (Figures 11.47h–k) is the most abundant and diverse cicadellid in the Crato Formation and is characterized by the head having a strongly inflated frons and lacking a defined crown, and a reduced tegmen (Hamilton, 1990). Five species were described by Hamilton (1990): *Hallex xestocephalus* (the type species), *H. gongrogony*, *H. brevipes*, *H. laticeps* and *H. gracilior*. The various species are each distinguished based on aspects of their tarsal morphology.

Hamilton (1999) placed Hallicini near Ulopidae and Membracidae, based on the hind basitarsomere being shorter than the apical tarsomeres together. The relationship of Hallicini with Membracidae remains controversial. Fossil Membracidae are known from the Oligocene/Miocene, where they occur in Dominican amber (Shcherbakov, 1996), but are unknown in Baltic amber. Their presumed sister group, Aetalionidae, was reported from Oligocene/Miocene Mexican and Dominican ambers (Deitz and Dietrich, 1993; Szwedo and Webb, 1999).

Myerslopiidae

The Myerslopiidae (Figures 11.43f and 11.47f and g) are small cryptic insects, known as ground-dwelling leafhoppers. The head of recent Myerslopiidae is characterized by a foliaceous anterior margin, with humps on face and vertex. Pronotum with wing-like expansions, so-called paranota, tegmina coriaceous with distinct prominences and densely punctate, each puncture with a setiferous tubercle. Hind wings are lacking. Mesocoxae have a meral lobe produced. The hind femur has two apical macrosetae, but the internal one is usually very short. The hind tibiae are spinose. There are two rows of laterotergites on abdominal segments four to seven in adults. Encrusting particles of soil and litter cover the body. Adults and nymphs of Recent forms live in decomposing leaf litter and soil debris with high organic content in forest environments.

This group was elevated to family level by Hamilton (1999); formerly it was believed to be a member of Ulopidae. Recent Myerslopiidae comprise 21 species placed in the tribe Myerslopiini, divided among three genera: *Myerslopia* and *Pemmation* from New Zealand, and *Mapuchea* Szwedo, 2004, from Chile (Szwedo, 2004a, 2004b).

Ovojassini

Ovojassus Hamilton, 1990

This genus (Figures 11.47f and g) can be distinguished from other cicadellids by the small tarsal claws and the robust hind tibia. *Ovojassus* was placed by Hamilton (1990) in the modern subfamily Myerslopiinae and probably represents a somewhat primitive member of this ancient group. Two species are known: the type species *Ovojassus concavifer*, and *Ovojassus minor*, both represented by well-preserved and near-complete specimens.

The extinct tribe †Ovojassini (Figures 11.43f and 11.47f and g; which in fact lacks definitive synapomorphies with any particular leafhoppers lineage was postulated as supposed ancestors of Myerslopiidae (Hamilton, 1999; Szwedo, 2004a, 2004b). Myerslopiidae seems to be representatives of a monophyletic group lying at the base of the superfamily Membracoidea (Hamilton, 1999; Dietrich, 2002;

Szwedo, 2002). On the other hand, as illustrated by most recent analyses using combined morphological and molecular data (Dietrich *et al.*, 2001; Bourgoin and Campbell, 2002), the group seems to be related to Cicadoidea, and the process on the mesocoxal meron could be interpreted as a synapomorphy uniting Myerslopiidae with Cercopoidea (Hamilton, 1999). The most recent molecular data (Cryan, 2005) place Myerslopiidae as sister group to other recent Membracoidea, which is in agreement with postulated superfamilial rank (Szwedo *et al.*, 2004).

Distribution of Myerslopiidae and importance of Ovojassini

The question whether the Ovojassini were true ancestors of Myerslopiidae requires further research to collect more data on fossils from the Southern Hemisphere. If Ovojassini were indeed ancestral to Myerslopiidae, it seems reasonable to suppose that Myerslopiidae originated in Gondwana during the Mesozoic. It could be hypothesized that during Mesozoic–early Cenozoic times, Myerslopiidae had a wider distribution in the austral zone, but due to geological and climatic events they are now highly restricted in their distribution (Szwedo, 2004b).

11.13 Fulgoromorpha: planthoppers

Jacek Szwedo

Fulgoromorphs are a group of medium to large cicada-like insects characterized by a carina extending along the face, immobile hind coxae, ocelli and antenna base located below the eyes and a large antennal pedicel with sense organs on the first flagellomere (Shcherbakov, 1996: 32; Grimaldi and Engel, 2005: 304). They may have colourful wings, sometimes with striking patterns, including large ‘eye’ spots.

The earliest Fulgoromorpha, members of the Coleoscytidae, first appear in the Upper Permian (Shcherbakov, 2000). However, the Coleoscytoidea did not survive the biotic crisis at the Permian/Triassic boundary, but their relatives, the Surijokocixiidae, survived to the end of the Triassic, although they constituted only a minor element of the entomofauna. It is thought that the Surijokocixiidae gave rise to the Fulgoroidea: the modern lineage of Fulgoromorpha. Fulgorididae became common in the Jurassic, with over 130 species described in several genera from Western Europe and China (Szwedo *et al.*, 2004). Of the 24 recognized families of Fulgoroidea, the Fulgoridiidae, Lalacidae and Neazoniidae and Perforissidae are now extinct.

The taxonomic status of some units is not resolved. Achilixidae have been proposed to be included in Achilidae as the subfamilies Achilixinae and Bebaiotinae by Emeljanov (1991), and Kinnaridae seem to be a paraphyletic unit, and fall into the

Meenoplidae (Bourgoin, 1993). Monophyly of Cixiidae has also been challenged (Holzinger *et al.*, 2001). Gengidae have been proposed to unite with Eurybrachidae and Hypochtonellidae with Flatidae by O'Brien (2002). Issidae have been recently redefined, with Caliscelidae separated as a distinct family (Emeljanov, 1999). Acanaloniidae have been suppressed under Issidae (Fennah, 1954; O'Brien, 2002), but Emeljanov (1999) extended the range of the family, incorporating Tonginae and Trienopinae, formerly placed in Issidae, and placed Acanaloniidae as a sister or daughter group of Nogodinidae.

There is considerable disagreement between the different phylogenetic schemes for Fulgoromorpha (and Fulgoroidea) proposed on the basis of morphological evidence (Asche, 1988, Yang and Chang, 2000), molecular evidence (Bourgoin *et al.*, 1997) or combined data from molecular, morphological and palaeontological data (Bourgoin and Campbell, 2002).

Study of the Crato Formation fulgoroids began with the description of *Vulcanoia* by Martins-Neto (1988a) and in the following year by his description of *Fennahia* (Martins-Neto, 1989a). These preliminary studies were quickly followed by the extensive study of Hamilton (1990), who established a new family, Lalacidae to accommodate several highly variable Crato Formation insects, and noted the first occurrence of Achilidae in the Crato Formation.

Of 78 fossil cicada specimens from the Crato Formation studied by Szwedo and Bechly (2006, unpublished work), 55 were cicadomorphs (71%) and only 23 were fulgoromorphs (29%). Of these 23 specimens, only a single specimen could be referred to the Achilidae, five specimens to Fulgoridae and the remaining 17 specimens (27%) all belonged to different tribes within Lalacidae, which constitute 74% of all the fulgoromorphs.

Achilidae

The family Achilidae (Figures 11.48a and b and 11.52e) is one of these old families, lying near the basal stock of Recent Fulgoroidea, but still with unresolved taxonomic problems. Extant Achilidae are distributed world wide, and reach far north to the cold regions of the temperate zone in Northern Europe. Tegmina of Achilidae are characteristic of an open truncate clavus, with united claval veins entering the apex. The claval suture is sometimes traceable as a fold on the membrane. It is one of derivative characters of Achilidae, separating the family from Fulgoridiidae and most of the other Fulgoroidea, but shared with some Derbidae (Emeljanov, 1994; Szwedo and Stroinski, 2001). A single genus, *Acixiites* Hamilton, 1990, represents this family among Crato Formation fulgoroids. It seems it is the oldest record of the family; however, other taxa are recorded from Turonian/Cenomanian Burmese amber, such as *Niryasaburnia burmitina* (Cockerell, 1917), which proves the earlier

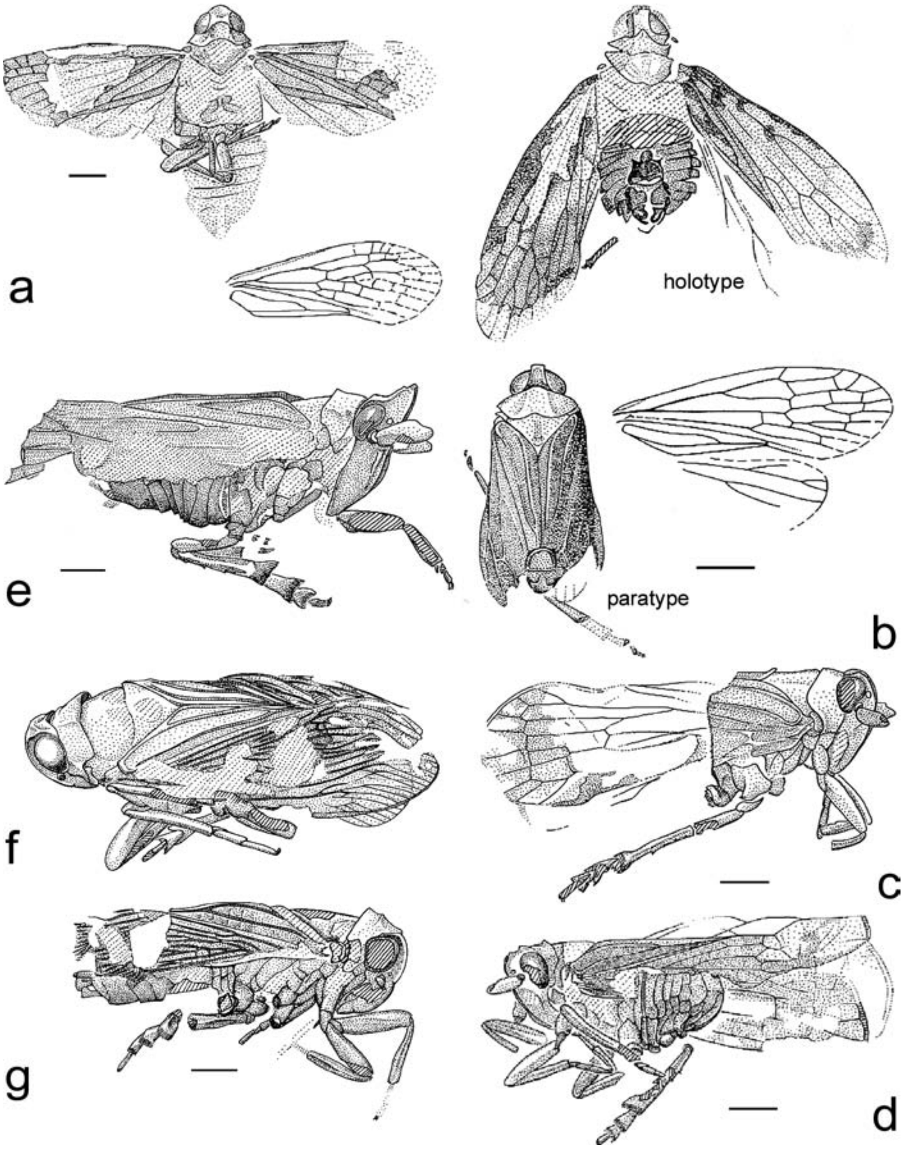

Fig. 11.48. Crato Formation Fulgoromorpha: (a) Achilidae, *Acixiites costalis* Hamilton, 1990, holotype, AMNH 43633; (b) Achilidae, *Acixiites immodesta* Hamilton, 1990, holotype, AMNH 43679, paratype AMNH 43632; (c) Lalacidae, *Protodelphax macroceps* Hamilton, 1990, holotype AMNH 43681; (d) Lalacidae, *Protodelphax miles* Hamilton, 1990, holotype AMNH 43624; (e) Lalacidae, *Protodelphax rhinion* Hamilton, 1990, holotype AMNH 43622; (f) Lalacidae, *Ancorale flaccidum* Hamilton, 1990, holotype, AMNH 43609; (g) Lalacidae, *Ancorale aschemon* Hamilton, 1990, holotype, AMNH 43625. Scale bars, 10 mm.

origin of the group. Any of these two extinct genera could be placed among recently recognized tribes (Szwedo, 2004c, 2006).

Acixiites Hamilton, 1990

Two species named *Acixiites immodesta* Hamilton, 1990 and *Acixiites costalis* Hamilton, 1990 (Figures 11.48a and b) are described from the Crato Formation (Hamilton, 1990). An open and truncate clavus, with fold traceable on the membrane is present in this genus, but *Acixiites* is lacking the perpendicular veinlet connecting the posterior branch of CuA with the tegmen margin, which is very characterstic for Achilidae. In this respect *Acixiites* resembles some Derbidae, as well as in the general pattern of tegmen venation. Also the vertex and pronotum structures and lack of subapical setae on the hind tarsomeres relate these fossils more with basal Derbidae than with Achilidae, so these fossils could be placed at the very point of separation of these two families. Simple venation, similar to some representatives of Derbidae and Achilidae tribe Plectoderini, but with a distinct transverse veinlet connecting CuA_2 and the margin, is also present in *Nirysaburnia burminitna* from Burmese amber. A very long rostrum, extending beyond the hind coxae near the apex of the hind femora, is another feature of *Acixiites*. It is worth noting that this character is also found among many specimens from Eocene Baltic amber and in ancestral Fulgoridiidae. *A. immodesta* was described based on a holotype male (AMNH 43679) and three paratype males (AMNH 43632, 43678 and 43761). The second species, *A. costalis* Hamilton, 1990, differs from the type species by a wider vertex and more veinlets on the tegmen, and is described on the basis of a holotype female (AMNH 43633) and paratype male (AMNH 43636). A few more specimens are preserved in various institutions (e.g. at SMNS).

Phylogenetic significance of fossil achilids

A number of fossil taxa attributed to Achilidae have been described, but some of them have limited validity and there is a call for revisionary studies (Szwedo *et al.*, 2004). The scheme of relationships among achilid tribes proposed by Emeljanov (1991, 1992) does not include fossil representatives of the family. The Crato Formation achilids present a lot of features common with Derbidae, a family that has been suggested as the sister group of Achilidae.

Supposed ancestors of Achilidae, Fulgoridiidae are characteristic of the 'typical' fulgoroidean head capsule, with the frons delimited laterally by a longitudinal carina and two carinae delimiting the frons from the vertex. Probably the median ocellus and median carina of the frons are still present, but lateral ocelli are placed slightly anteriad and at the level of the lower margin of the compound eye. It seems that the oldest Achilidae lost the median ocellus, and the vertex is delimited from the frons by a single transverse carina. In some extant taxa this margin is callused, with traceable lateroapical triangular excavations, which could be interpreted as remnants of the area between the transverse carinae of the achilid ancestor. In extant Achilidae the median carina of the vertex is frequently absent or incomplete, so it also could be interpreted as a reduction of the complete median carina of their ancestors. The rostrum was still long in the Cretaceous (including Crato Formation fossils) and Palaeogene Achilidae, and it is still long among Baltic amber inclusions, but Oligocene/Miocene Achilidae have a relatively short rostrum, as in Recent forms.

The claval suture extending to membrane, one of derivative characters of Achilidae, separates the family from Fulgoridiidae and most other Fulgoroidea, but it is shared with some Derbidae (Emeljanov, 1994; Szwedo and Stroinski, 2001). An open and truncate clavus, with a fold traceable on the membrane, is present in *Acixiites*, which resembles some Derbidae. The general pattern of tegmeninal venation of Crato fossils is also similar to some representatives of Derbidae. Also the vertex and pronotum structures and lack of subapical setae on hind tarsomeres relate Crato fossils more with basal Derbidae than with Achilidae, so these fossils could be placed at the very point of the separation of these two families.

Cixiidae

This family (Figure 11.49a) is represented in the Crato Formation by a single species, *Fennahia cretacea* Martins-Neto, 1988a. *Fennahia cretacea* was placed in Achilidae by Maisey (1991: 434), but this is incorrect, it clearly being a cixiid. An unnamed Crato specimen described and figured by Hamilton (1990: 97–98, figure 106: AMNH 43692) and assigned to Cixiidae very probably does not belong in this family.

Cretofennahia Martins-Neto and Szwedo, 2007

The original name *Fennahia* Martins-Neto, 1989a is preoccupied by the Recent cercopid *Fennahia* Sakakibara, 1979, so the replacement name *Cretofennahia* was offered by Martins-Neto and Szwedo (2007). However, here *Fennahia* Martins-Neto, 1989a is used rather than offering a replacement name. *Cretofennahia* is known from a single specimen in part and counterpart, housed in the Vulcano collection, São Paulo State, Brazil, no. CV-986. The diagnostic characters are: tegmen about 3.3 times as long as wide; costal margin very weakly curved, posterior margin elongately rounded; apex of clavus reaching 0.6 of tegmen length; pterostigma about twice as long as wide, vein Sc+R leaving basal cell slightly anteriad of vein M; forking of vein Sc+R slightly posteriad of claval veins junction, vein RA single, vein RP with three terminals; forking of vein M slightly posteriad of nodal line, anterior branch (M_1+_2) forked, posterior branch (M_3+_4) single, three terminals

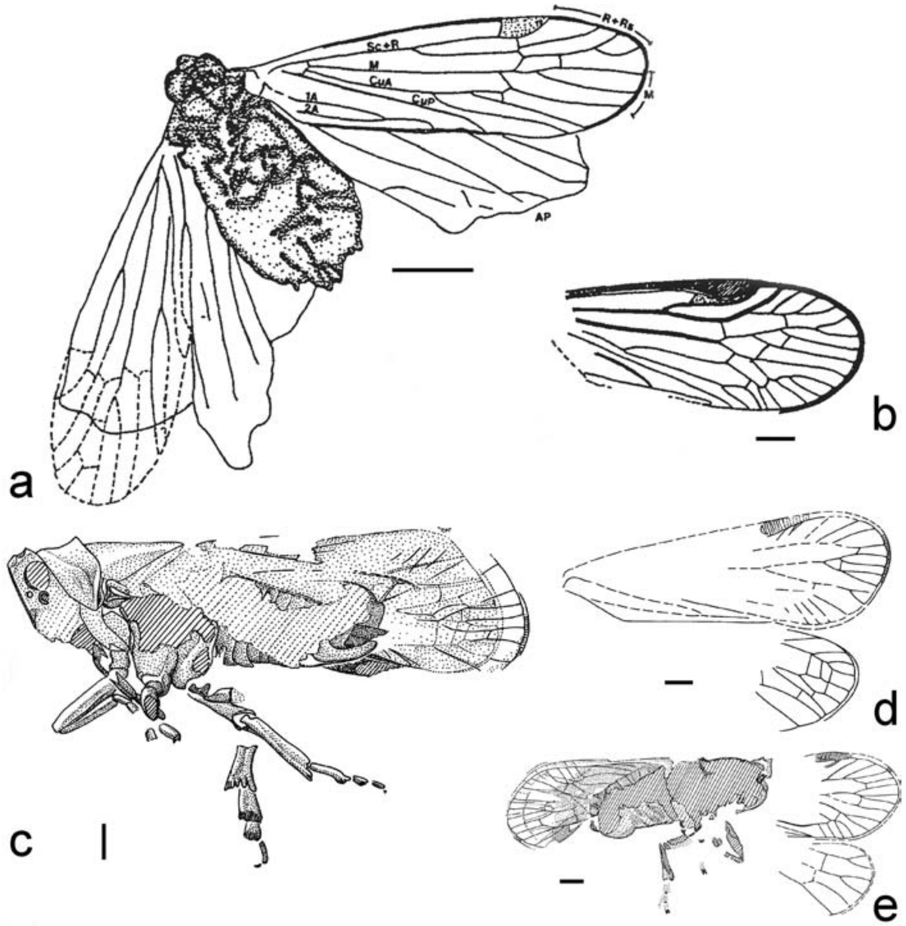

Fig. 11.49. Crato Formation Fulgoromorpha: (a) Cixiidae, *Cretofennahia cretacea* Martins-Neto, 1989, holotype, Vulcano coll. CV-986; (b) Lalacidae, *Vulcanoia membranosa* Martins-Neto, 1988; (c) Lalacidae, *Vulcanoia apicalis* Hamilton, 1990, holotype, AMNH 43603; (d) wing venation of *Vulcanoia apicalis* reconstructed; (e) Lalacidae, *Vulcanoia acuceps* Hamilton, 1990, holotype, AMNH 43689 with wing venation restored. Scale bars, 1 mm. (a,b) After Martins-Neto (1988); (c–e) after Hamilton (1990).

reaching margin of tegmen; vein CuA forked slightly posteriad of Sc+R forking, at level of connection of claval veins with margin, with two terminals; claval veins Pcu and A_1 fused at half of clavus length, at one-third of tegmen length; veinlets *ir*, *r-m* and *m-cu* slightly posteriad of nodal line.

Cretofennahia cretacea (Martins-Neto, 1989a) differs from other Cixiidae of similar age. From '*Cixius*' *petrinus* Fennah, 1961, from the Barremian Weald Clay Group of Surrey, England, it differs in details of venation and short subapical cell C_2.

It differs from *Karebopodoides aptianus* (Fennah, 1987) from Hauterivian–Aptian Lebanese amber by possession of a longer and narrower tegmen with straighter costal margin, distinctly shorter and wider pterostigma, distinctly more posteriad forking of veins Sc+R and CuA, forking of M posteriad of nodal line. It differs also in details of venation from undescribed cixiids from Aptian Burmese amber figured in Grimaldi *et al.* (2002: figures 23a and d). *Cretofennahia* cannot easily be placed in the recently recognized tribes of Cixiidae. The venation pattern resembles those found among some genera of Oecleini, but the short cell C_2 and only three terminals of M seem to be highly derivative characters of this fossil. Clearly this taxon requires reappraisal.

Phylogenetic significance of fossil cixiids

Fossil cixiids are known from the Late Jurassic (Shcherbakov and Popov, 2002) as probable descendants of the Jurassic family Fulgoridiidae which occur in England, Germany, Kyrgyzstan, Mongolia and China (Szwedo *et al.*, 2004).

Early Cretaceous occurrences of cixiids such as '*Cixius*' *petrinus* Fennah, 1961 in the Barremian of England and *Karebopodoides aptianus* (Fennah, 1987) from Hauterivian–Aptian Lebanese amber hint at an origin of the group in the Late Jurassic, or perhaps even earlier. Although a central Laurasian origin for the group was previously thought probable, the occurrence of South American cixiids in the Aptian Crato Formation now casts doubt on this hypothesis.

The Crato Formation cixiid presents a mixture of derived features with respect to the English and Lebanese genera, particularly the better-developed pterostigma, two terminal branches of CuA on the tegmen with a basal feature of the vein Sc+R leaving the basal cell separately and basad of vein M stem. Although *Cretofennahia* cannot be placed in the recently established tribes of Cixiidae, it may be close to Oecleini. This tribe is thought to lie in the most basal lineage of Cixiidae according to the scheme proposed by Emeljanov (2002). Representatives of this tribe are distributed worldwide today, with six genera and 12 species in the Neotropics (Holzinger *et al.*, 2002). Currently, the only fossil attributable to this tribe is *Oligocixia electrina* Gebicki and Wegierek, 1993 from Dominican amber (Gebicki and Wegierek, 1993).

Lalacidae

Lalacidae Hamilton, 1990 are diverse and abundant in the Crato Formation (Figures 11.48c–g, 11.49b–e, 11.50, 11.51 and 11.52a and b). The family was established by Hamilton (1990) and seems to be endemic for the Lower Cretaceous, although there may be Late Jurassic occurrences (see below). *Cretocixius*

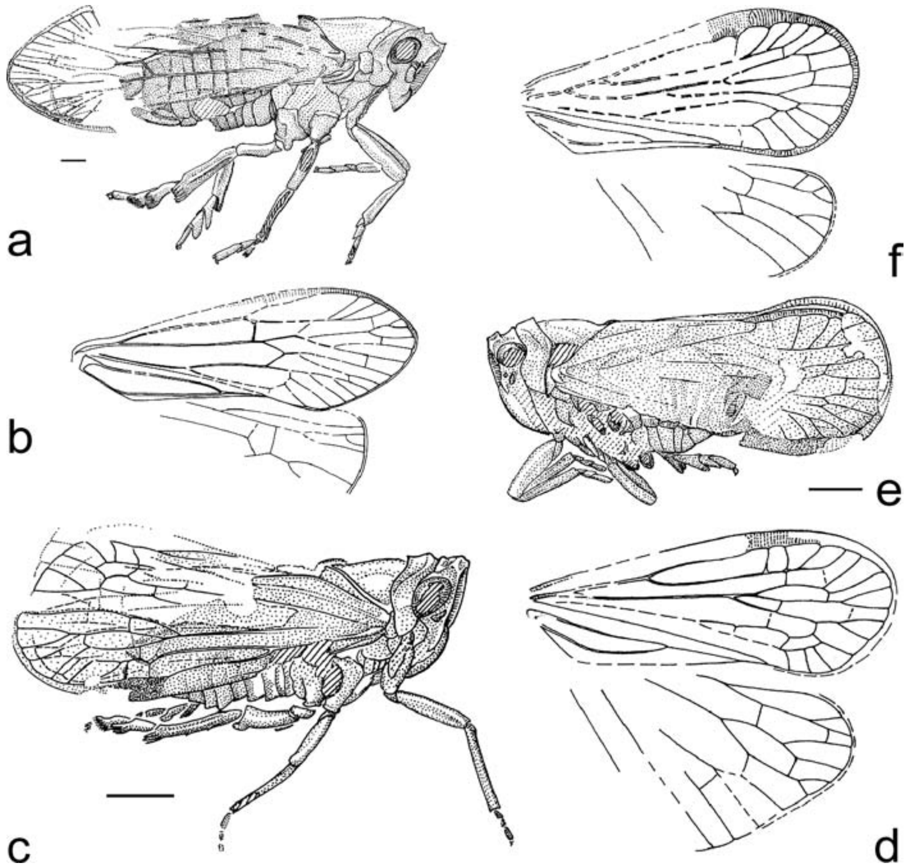

Fig. 11.50. Crato Formation Fulgoromorpha: (a) Lalacidae, *Carpopodus difficilis* Hamilton, 1990, holotype, AMNH 43604; (b) Lalacidae, *Carpopodus* reconstructed venation; (c, d) Lalacidae, *Psestocixius delphax* Hamilton, 1990, holotype, AMNH 43607, habitus and wing venation respectively; (e, f) Lalacidae, *Psestocixius fuscus* Hamilton, 1990, holotype, AMNH 43616, habitus and venation respectively. Scale bars, 10 mm. All figures after Hamilton (1990).

stigmatosus Zhang, 2002 from the Barremian Lushangfen Formation of China has been assigned to the Lalacidae (Zhang, 2002), while *Lapicixius decorus* Ren, Yin and Dou, 1998 from the Tithonian-Beriassian Yixian Formation (Smith *et al.*, 1995; Rasnitsyn *et al.*, 1998; Swisher *et al.*, 1999; Wang *et al.*, 2004, 2005) also seems to represent a lalacid, rather than a cixiid as originally thought (Szwedo *et al.*, 2004). Placement of *Yanducixius* Ren, Lu and Ji, 1995 from the Barremian Lushangfen Formation (Ren *et al.*, 1995; Rasnitsyn and Zherikhin, 2002) is ambiguous, but very probably it is a lalacid rather than a cixiid, as originally stated (Ren *et al.*, 1995). The presence of these lalacids in China again demonstrates the widespread distribution of fulgoromorphs in the Early Cretaceous.

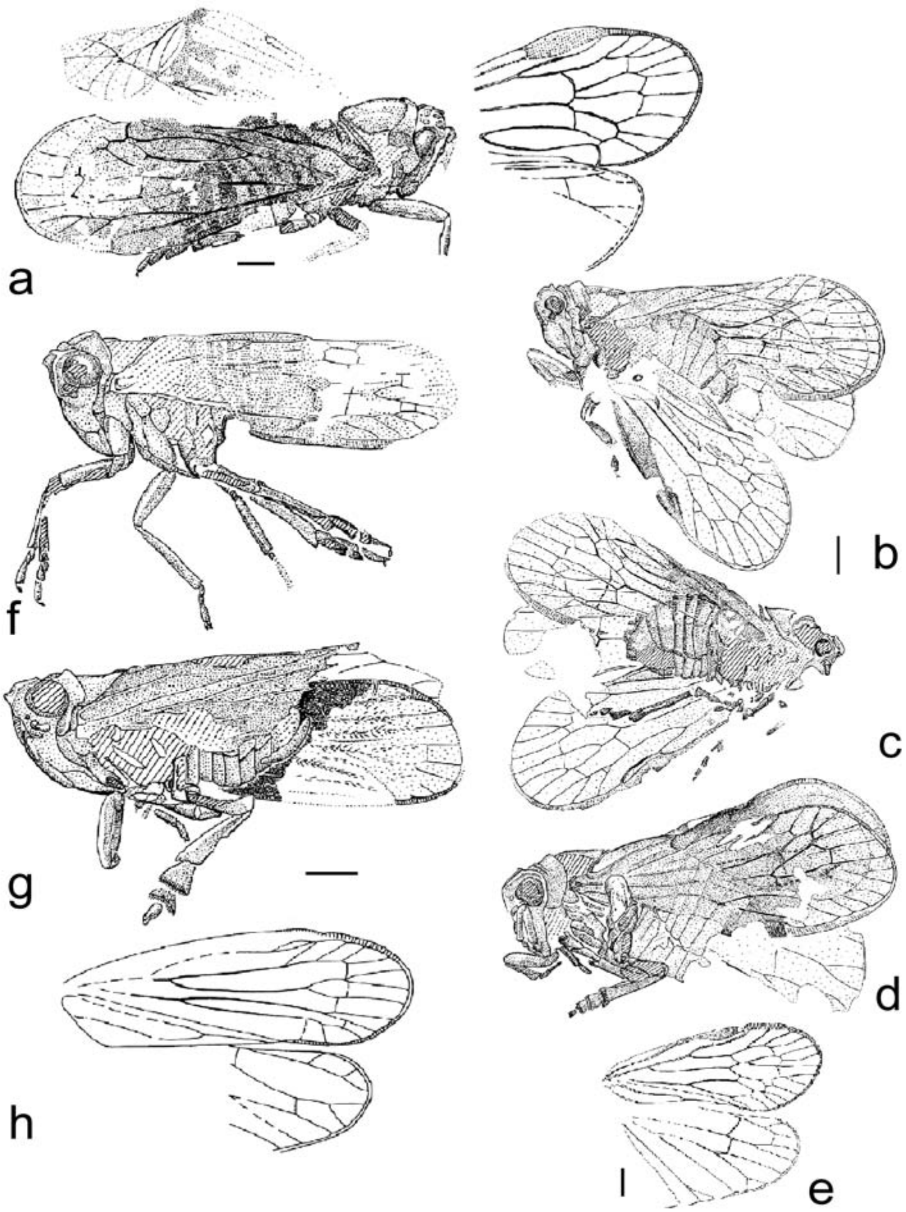

Fig. 11.51. Crato Formation Fulgoromorpha: (a) Lalacidae, *Kinnarocixius quassus* Hamilton, 1990, holotype, AMNH 43617 and reconstructed wing venation; (b–e) Lalacidae, *Lalax mutabilis* Hamilton, 1990; (b) holotype, AMNH 43658; (c) paratype AMNH 43685; (d) paratype AMNH 43684; (e) reconstructed venation; (f–h) Lalacidae; (f) *Patulopes myndoides*, male holotype, AMNH 43631; (g) *Patulopes setosa*, holotype, AMNH 43623, habitus; (h) *Patulopes myndoides*, female paratype, AMNH 43629, wing venation. Scale bars, 10 mm. All figures after Hamilton (1990).

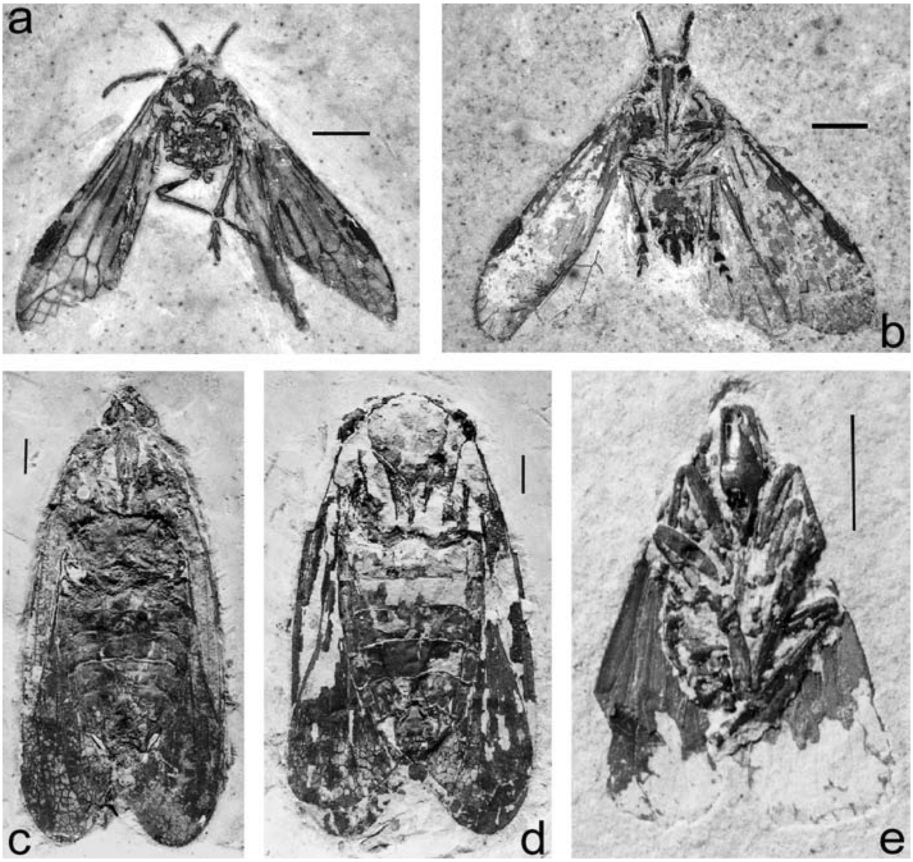

Fig. 11.52. Crato Formation Fulgoromorpha: (a) new Lalacidae, SMNS 66425; (b) new Lalacidae, SMNS 66415; (c) new Fulgoridae, SMNS 66413; (d) new Fulgoridae, SMNS 66428; (e) new Achilidae, SMNS 66440. Scale bars, 2 mm.

The genus *Vulcanoia* Martins-Neto, 1988a, described from the Crato Formation, and originally placed in Cixiidae (Martins-Neto, 1988a), was transferred to Lalacidae by Hamilton (1990).

The Lalacidae are characterized by the following: head narrow, bearing intermediate carinae, defining a pair of a shallow pits near the apex of the crown, and sometimes median pit as well; median ocellus close to frons, as in Cixiidae. Tegmina held tectiform, often steeply so; costal margin usually thickened, reinforced margin beyond ambient vein (appendix) narrow, with sclerous striations as in some Cixiidae, Kinnaridae and Meenopliidae; stigma absent or an extension of thickened margin forming stigmal area; appendix narrow on hind wings; venation similar to Kinnaridae and Cixiidae, with long *r-m* veinlet on tegmina and wings, but usually with more veinal branching. Hind tibia unarmed or armed with a few lateral spines. Hind tarsi similar to some Meenopliidae, but basal pair of tarsomeres (and sometimes also apex of tibia) of hind leg with row of teeth bearing subapical setae. Ovipositor short, strongly curved, ensiform with rounded tip. The family was divided by Hamilton (1990) into several subfamilies and tribes: Protodelphacinae (Protodelphacini), Ancoralinae (consisting of Ancoralini and Kinnarocixiini) and Lalacinae (comprising Lalacini and Carpopodini), and these are discussed below.

Protodelphacinae

Protodelphacini

Protodelphax Hamilton, 1990

Protodelphacini are planthoppers (Figures 11.48c–e) similar in habitus to some Delphacidae and Derbidae, with elongated antennae. Their tegminal venation is of a type found among other Lalacidae, with longitudinal veins not polymerized and stigmal area elongate and relatively narrow; apex of clavus slightly exceeding half of tegmen length. Tegminal subapical cell C_5 short, antenna with elongated scape. Hind tibia with three or four lateral spines, an apical row of 14 elongate teeth on the hind tibia with short subapical setae; hind basi- and midtarsomere similar, with 12–14 apical teeth, with short subapical setae, including external ones; hind leg basitarsomere about 1.5 times longer than mid tarsomere. The Crato Formation species are: *Protodelphax chamus*, *P. macroceps*, *P. miles* and *P. rhinion* (all species Hamilton, 1990). They differ from each other in their relative sizes, the structure of the head and the length of the face. *P. miles*, *P. macroceps* and *P. rhinion* are known only from holotypes (AMNH 43624, 43681 and 43622 respectively) and *P. chamus* is known from the holotype (AMNH 43621) and paratype (AMNH 43620). Another specimen (AMNH 43655) was not formally described due to its poor preservation.

Ancoralinae

Ancoralini

Ancorale Hamilton, 1990

Ancoralini are quite robust planthoppers with prominently raised veins on the upper surface of the tegmen. Their most characteristic feature is polymerization of longitudinal veins, particularly M, and veins with helical ridges. The apex of the clavus reaches nearly 0.6 of the tegmen length. Hind tibiae are relatively short, with a distinct row of 10–15 elongate apical teeth; apical teeth of hind tibia and hind basi- and midtarsomere with small subapical macrosetae; basitarsomere and mid tarsomere of hind leg of similar length. There are two species distinguishable by their size differences: *Ancorale flaccidum* Hamilton, 1990, known from the holotype (AMNH 43609) and three paratypes (AMNH 43626, 43680 and 43682) and *A. aschemon* Hamilton, 1990, known only from holotype (AMNH 43625; Figures 11.48f and g).

Kinnarocixiini

Kinnarocixius Hamilton, 1990

Kinnarocixiini are characterized by the following set of features. Head slightly produced, with well separated compound eyes, carinae of pronotum and mesonotum absent. Tegmen with veins strongly convex, narrow at base, widened apically, with costal margin slightly curved and apical margin rounded; stigmal area distinct, forming a bulla, apex of clavus exceeding 0.6 of tegmen length. Veins Sc+R and M with short common stem, vein CuA forked merely posteriad of claval veins junction; first veinlet *r-m* long; tegminal subapical cell C_5 long. Hind tibia stout with at least single lateral spine and 15 apical teeth, hind basi- and midtarsomere with 15 apical teeth with stout subapical setae, including external ones; basitarsomere slightly longer than midtarsomere. The tribe is monotypic on *Kinnarocixius quassus* Hamilton, 1999 (holotype AMNH 43617; paratype AMNH 44105; Figure 11.51a) from the Crato Formation. A specimen (AMNH 43614) referred by Hamilton (1990) to *Kinnarocixius* sp. very probably represents a distinct genus.

Lalacinae

Lalacini

Lalax Hamilton, 1990

This genus (Figures 11.51b–e) is characterized by narrow frons, delimited by distinctly elevated lateral carinae and inflated postclypeus; antennae slender; rostrum reaching mesocoxae. Postocular carinae of pronotum distinct. Tegmen narrow at base, distinctly widening apicad; costal margin curved at base then almost straight to level of stigmal area; apical margin rounded; clavus narrow, with apex reaching 0.6 length of tegmen, stigmal area distinct. Costal margin thickened, common stem of veins Sc+R and M relatively long; forking of veins Sc+RA and RP at same level as forking of vein CuA; vein M with forking of branch M_1+_2 basad of forking M_3+_4; claval veins united merely anteriad of vein CuA forking; tegminal subapical cell C_5 long. Hind tibia without lateral spines, apical row of eight elongate and scantly distributed teeth, bearing small and stout subapical setae; basitarsomere with 19 apical teeth, bearing subapical setae, excluding external ones, midtarsomere with 15 apical teeth bearing subapical setae, excluding external ones;

basitarsomere about as long as mid- and apical tarsomeres combined. Only a single species has been formally described, *Lalax mutabilis* Hamilton, 1990 (holotype AMNH 43685; paratypes AMNH 43615, 43618 and 43684) and a second, smaller species (AMNH 43628), was considered too poorly preserved for formal description (Hamilton, 1990).

Patulopes Hamilton, 1990

This genus (Figures 11.51f–h) differs from *Lalax* Hamilton, 1990 in several important characters: tegmen not distinctly wider on membrane than at base, apex of clavus exceeding 0.6 length of tegmen, stigmal area poorly defined. Postclypeus is not swollen; apex of rostrum reaching hind coxae. Pronotum with lateral carinae diverging posteriad. Hind tibia without lateral spines, apical row of teeth oblique, composed of six short and stout teeth lacking subapical setae. Basi- and midtarsomere broadly flared; basitarsomere with transverse row of 23 apical teeth with long and thick subapical setae, including external ones; midtarsomere with concave row of 18 apical teeth with long and thick subapical seatae, except external ones; basitarsomere about as long as combined length of mid- and apical tarsomere. Ovipositor short, ensiform, curved dorsad. Two species have been described: *Patulopes setosa* Hamilton, 1990, which is the the larger species, with tegminal veins outlined with short setae (holotype AMNH 43623), and *Patulopes myndoides* Hamilton, 1990, which is smaller, with distinct venation (holotype AMNH 43631; paratype AMNH 43629). Another specimen (AMNH 43610), representing a distinct species, is too poorly preserved for formal description (Hamilton, 1990).

Carpopodini

Carpopodini (Figures 11.49b–e and 11.50) are planthoppers characterized by possession of hind tibiae with six apical spines. Three genera included within the tribe.

Carpopodus Hamilton, 1990

Carpopodus Hamilton, 1990 (Figures 11.50a and b) is characterized by narrow frons with elevated lateral carinae, distinctly convex frontoclypeal suture, postclypeus convex; rostrum reaching hind coxae. Postocular carinae of pronotum nearly parallel to posterior margin. Tegmen narrow at base, then widening; costal margin thickened, apical margin acutely rounded; stigmal area weakly developed; apex of clavus not extending 0.6 of tegmen length. Common stem of veins Sc+R and M short, forking of veins Sc+RA and RP slightly basad of apex of clavus; forking of vein M at level of apex of clavus; forking of vein CuA basad of claval veins junction; claval veins Pcu and A_1 junction at three-quarters of clavus length; first veinlet *r-m* slightly basad of vein M forking. Hind tibia without lateral spines, apical row of six well-separated finger-like teeth, bearing tiny, rounded subapical setae. Hind basitarsus about 1.3 times longer than midtarsomere, with apical row of 16 teeth provided with short subapical setae; midtarsomere widening apically, apical margin slightly concave, with row of 22 apical teeth provided with short subapical setae. Apical tarsomere with tarsal claws of similar length as midtarsomere; tarsal claws distinct. Ovipositor ensiform, short, slightly exceeding length of pygofer, weakly curved with round apex.

Apart from the type species *Carpopodus difficilis* Hamilton, 1990, known only from the holotype (AMNH 43604), two additional specimens (AMNH 43602 and 43619) differ from *C. difficilis* and each other, designated *Carpopodus* sp. A and *Carpopodus* sp. B by Hamilton (1990), but they are too poorly preserved to allow formal description.

Psestocixius Hamilton, 1990

This genus (Figures 11.50c–f) is characterized by a broadened membrane of the tegmen, wide tegminal appendix and sclerified stigmal area of tegmen. Lateral carinae of frons diverging ventrad, frontoclypeal suture convex, postclypeus slightly convex. Rostrum exceeding hind coxae. Pronotum narrow, with weakly diverging lateral carinae. Costal margin of tegmen nearly straight, not strongly thickened, apical margin roundly broadened; stigmal area developed as a sclerotized widening of margin; apex of clavus at about 0.6 of tegmen length. Common stem of veins Sc+R and M short, vein Sc+R forked slightly anteriad of claval veins junction; vein M forked at level of apex of clavus, anterior branch M_{1+2} forked again in a short distance; vein CuA forked slightly posteriad of claval veins Pcu and A_1 junction; claval veins junction at about 0.6 of clavus length. Hind tibia with two small lateral spines and row of six apical teeth. Basitarsomere slightly longer than midtarsomere, both with high number of apical teeth provided with short subapical setae.

There are two species: *P. fuscus* Hamilton, 1990, known from the holotype and paratype (AMNH 43616, 43687 respectively), and *P. delphax* Hamilton, 1990 known only from holotype (AMNH 43607).

Vulcanoia Martins-Neto, 1988a

The genus *Vulcanoia* Martins-Neto, 1988a (Figures 11.49b–e) was originally placed in Cixiidae. Hamilton (1990) later transferred it to the new family Lalacidae and placed it in the Lalacinae: Carpopodini. *Vulcanoia* can be characterized by the following features: frons narrow, with lateral carinae elevated, subparallel; rostrum extending to hind coxae. Pronotum slightly longer than vertex. Costal margin of tegmen thickened, apical margin rounded, membrane slightly widened; stigmal area well delimited, slightly thickened; apex of clavus at level of 0.6 of tegmen length. Common stem of veins Sc+R and M short; vein Sc+R slightly thickened, forked slightly basad of claval veins junction; vein M slightly thickened, forked at level of apex of clavus; vein CuA forked basad of claval veins Pcu and A_1 junction and basad of veins Sc+R forking; claval veins junction at level of of clavus length. Hind tibia lacking lateral spines, apical row of six teeth without subapical setae; basitarsomere about 1.5 times as long as midtarsomere, basitarsomere and midtarsomere with a dozen or so apical teeth. Ovipositor ensiform, short, only slightly curved.

There are three species: first, *Vulcanoia membranosa* Martins-Neto, 1988a, known from the holotype deposited in the Vulcano collection, São Paulo State, Brazil. *Vulcanoia apicalis* Hamilton, 1990, known only from the holotype (AMNH 43603), differs from the other species in the genus by its narrower tegmina and longer pronotum. Finally, *Vulcanoia acuceps* Hamilton, 1990 is known from the male holotype (AMNH 43689) and female paratype (AMNH 43688). It differs from the type species of *Vulcanoia* by its larger size. Another specimen (AMNH 43611) assigned to *Vulcanoia* noted by Hamilton (1990) is too poorly preserved for formal description; however, Hamilton (1990) suggests it could be a male *V. apicalis*.

Palaeobiogeographic and phylogenetic significance of Lalacidae

Representatives of the Lalacidae are the most diverse and numerous fulgoromorphs in the Crato Formation. However, recently several taxa assigned to Lalacidae have been reported from China (Zhang, 2002; Szwedo *et al.*, 2004), where they come from strata slightly older (Beriassian and Barremian) than the Crato Formation, and differ morphologically from Crato Formation lalacids. *Cratocixius* Zhang, 2002 resembles in tegmental features and venation pattern *Psestocixius* Hamilton, 1990. These similarities include the shape of the tegmen, narrow at the base and widening apically, with a distinctly wider membrane, the costal margin thickened, the stigmal area developed as a sclerotized widening of the margin, with a wide appendix. Regarding the venation, the same pattern, with vein ScRA reaching the posterior margin of the stigmal area, veinlet *ir* reaching the stigmal area, a short common stem of veins Sc+R and M, and a short common stem of claval veins Pcu and A_1, is seen in both genera. *Lapicixius* Ren, Yin and Dou, 1998, from Tithonian-Berriasian of the Yixian Formation, differs from Crato Formation Lalacidae by having a vertex that is wider than long, distinctly more exposed occipital portion of the head capsule, the presence of median carinae on the frons and postclypeus, a nearly straight anterior margin and a convex posterior margin of the pronotum (which is exceptional among Fulgoroidea and may be a preservational artifact), with distinct median carina, and the mesonotum with five distinct carinae. Regarding venation, the most striking difference is the structure of the pterostigmal area, elongately triangular and reaching branch RA at short distance, and the presence of transverse veinlets connecting veins CuP and Pcu on the clavus. However, the hind tibia without lateral spines, but with a row of six apical teeth, the basitarsomere slightly longer than midtarsomere, both with row of 20 or so apical teeth, relates it with Lalacinae. *Yanducixius* Ren, Lu and Ji, 1995 from the Barremian Lushangfen Formation seems to be closely related to *Lapicixius*. These two genera appear, on the other hand, to be related to some Fulgoridiidae that are believed to be ancestral to other families of Fulgoroidea. Thus, it could be postulated that Lalacidae are descendants of Fulgoridiidae, widely distributed in the Early Cretaceous and highly differentiated. According to the scheme of relationships proposed by Bourgoin and Campbell (2002), Lalacidae are considered the sister group of the Achilidae+Achilixidae+Derbidae clade. On the other hand, certain Lalacidae are considered to be related to, or are compared with, Cixiidae, Delphacidae, Dictyopharidae, Kinnaridae and Meenoplidae (Martins-Neto, 1988a; Hamilton, 1990; Szwedo, 2002). The close relationships between Protodelphacinae and Delphacidae suggested by Hamilton (1990) remain uncertain. Delphacidae is sister group to Cixiidae according to the schemes of relationship proposed on the basis of morphology (Asche, 1988), molecular data (Bourgoin *et al.*, 1997; Yeh *et al.*, 2005) and combined morphological, palaeoentomological and molecular data (Bourgoin and Campbell, 2002). The exact placement of Lalacidae in a phylogenetic scheme of the Fulgoroidea needs further research and the question of whether Lalacidae are a blind branch or ancestral to Recent groups of Fulgoroidea remains unanswered.

Other Fulgoroidea

There are several other fulgoroids among Crato Formation fossils (Figures 11.46g and 11.52). Specimen AMNH 43692 figured by Hamilton (1990: figure 106) does not represent a cixiid. Newly available material includes several forms very close to it. These specimens represent the family Fulgoridae (Figures 11.52c and d) and it seems that these are the oldest representatives of the family.

Megaleurodes megocellata Hamilton, 1990 (Figure 11.46g) was tentatively assigned to the Permian family Boreoscytidae within the Aleyrodoidea by Hamilton (1990) but represents an as-yet-unidentified fulgoroid, because of the presence of lateral carinae of the frons, narrow, collar-like pronotum, tegulae, three-segmented tarsi, apex of tibia with row of apical teeth and basi- and midtarsomeres with a row of apical teeth. It was first suggested by Sorensen *et al.* (1995) that this fossil represents the postulated superfamily Fulgoridioidea. Later, Shcherbakov (2000) stated that this taxon is based on a poorly preserved planthopper, and has nothing in common with Boreoscytidae, a primitive group of Aphidodea or Aleyrodoidea. Consequently, there is no fossil record of Sternorrhyncha from the Crato Formation.

There are several specimens of Fulgoroidea from the Crato Formation in various collections (e.g. at SMNS), and among them a number of new species of Lalacidae (Figures 11.52a and b). There are also some specimens that could be attributed to other fulgoroid families, i.e. Fulgoridae (Figures 11.52c and d, Plate 12c) and very probably Derbidae and Achilidae (Figure 11.52e). These rich collections need further study as they could provide answers to a number of important phylogenetic and taxonomic questions.

11.14 Coleorrhyncha: moss bugs

Günter Bechly and Jacek Szwedo

Coleorrhyncha (also called Peloridiomorpha) are small, rarely medium sized (2–5.5 mm), insects with a mixture of cicadomorphan and bug-like characters, representing a separate suborder within the Hemiptera. The body is dorsoventrally flattened, with tegmina folding flat, their commissural margins and apices overlapping in repose. In macropterous forms the left tegmen is always over, so the postapical-area overlap in the underlying right tegmen is delimited better, with thinner veins, usually arranged in a somewhat different way than the left one. The head is opisthognathous, with a long rostrum directed caudad. The antennae are short and few-segmented, supra-antennal continuous from eye to eye. Macropters have three ocelli; the lateral ones are placed at anterior head margin, close to the compound eyes, and are untraceable in known fossils, and the median ocellus is placed above the ledge. The pronotum bears paranotal expansions and overlaps the mesonotum up to the apices of the parapsides. The scutellum is margined by grooves fixing the clavi in repose. Thoracal pro- and mesepisterna have anapleural clefts. The coxae are pagiopodous with exposed trochantines. Tarsi are two-segmented, with the first segment small; in jumping forms (extinct) hind tarsi are three-segmented, with the basitarsomere being the largest, armed as well as hind tibiae. The tegmina has a precostal carina, simple veins Rs and CuA_1, and vein M is three-branched, with crossvein-like CuA_2 and three crossveins (arculus, *r-m* and *m-cu*) and an ambient vein separating the appendix; sometimes venation is partly reticulate. The clavus with claval veins is in form of a letter Y, its stalk bearing a short interalar coupling lobe. The hind wing has simple venation and a straight anterior margin, the jugal lobe folding beneath in repose. The abdomen is flattened with laterotergites facing ventrad and bearing spiracles. The female seventh sternite is elongate, concealing the base of the cutting ovipositor. The pygofer (i.e. male ninth segment) is barrel-shaped, sometimes with lateral projections, parameres protruding and elbowed. The development is hemimetabolous with adult-like nymphal stages. Nymphs are flat, non-jumping, with antennae and legs short, broad paranota and long rostrum (Popov and Shcherbakov, 1991, 1996). Modern Coleorrhyncha – members of family Peloridiidae – are phytophagous and have a cryptic lifestyle on mosses in the wet and cool *Nothofagus* forests of southern South America, Australia, Tasmania, New Caledonia, Lord Howe Island and New Zealand. Such a circum-Antarctic relict distribution suggests an Early Cretaceous Gondwana origin of the crown group. Eskov (1984) and Eskov and Golovatch (1986) argued that Recent transoceanic disjunctive distributions of various taxa (including far-southern taxa) are merely remnants of a transpolar distribution in the geological past. However, this 'ousted relicts' hypothesis cannot be applied to the Peloridiidae, as it probably never existed in the Northern Hemisphere, even if it is applicable to Coleorrhyncha as a whole (Popov and Shcherbakov, 1996). Peloridiidae seems to be connected with *Nothofagus* forests. The history of *Nothofagus* is rather well documented by fossil pollen, leaves and wood (Romero, 1986; Tanai, 1986). Its biogeography was recently analysed by Linder and Crisp (1996) and the results discussed by Ladiges *et al.*, (1999). Extant Peloridiidae are usually found in damp moss, often on decaying mossy trunks and twigs of *Nothofagus* (in Southern Hemisphere), or still occasionally feed on moss rhizoids, or even on wood-destroying fungi or on lichens (Popov and Shcherbakov, 1996).

Systematics, phylogeny, evolution and fossil record

There are only 13 genera and 25 Recent species known, which are all classified in the single Recent family Peloridiidae (Evans, 1981; Burckhardt and Agosti, 1991; Burckhardt and Cekalovic, 2002). Coleorrhyncha have often been grouped together with Sternorrhyncha and 'Auchenorrhyncha' (i.e. suborders Fulgoromorpha and Cicadomorpha) in a paraphyletic taxon 'Homoptera', but since Schlee (1969) Peloridiidae are regarded as the sister group of Heteroptera, which was also confirmed by DNA studies (Ouvrard *et al.*, 2000) and comparative studies on male genital structures (Yang, 2002). Recent critics of this phylogenetic hypothesis are believed unfounded (see Grimaldi and Engel, 2005: 313) and are mainly based on typological reasoning. Schlee's (1969) proposal was criticized by Popov and Shcherbakov (1991, 1996; see Figure 11.53), who stated that synapomorphies of Coleorrhyncha and Heteroptera are at least dubious, and these two groups disagree in fundamental apomorphies. According to the latter authors, Coleorrhyncha and Heteroptera evolved from generalized 'Cicadomorpha' (a paraphyletic group) as independent stocks, acquired wing coupling of the same type and dorsoventrally flattened habitus with forewing overlap in parallel, and therefore are separated at subordinal level. Nevertheless, it must be emphasized that some autapomorphic differences and a putative parallelism in some of the potential synapomorphies does not invalidate the numerous other morphological and molecular synapomorphies of Coleorrhyncha and Heteroptera. The close relationship of Coleorrhyncha,

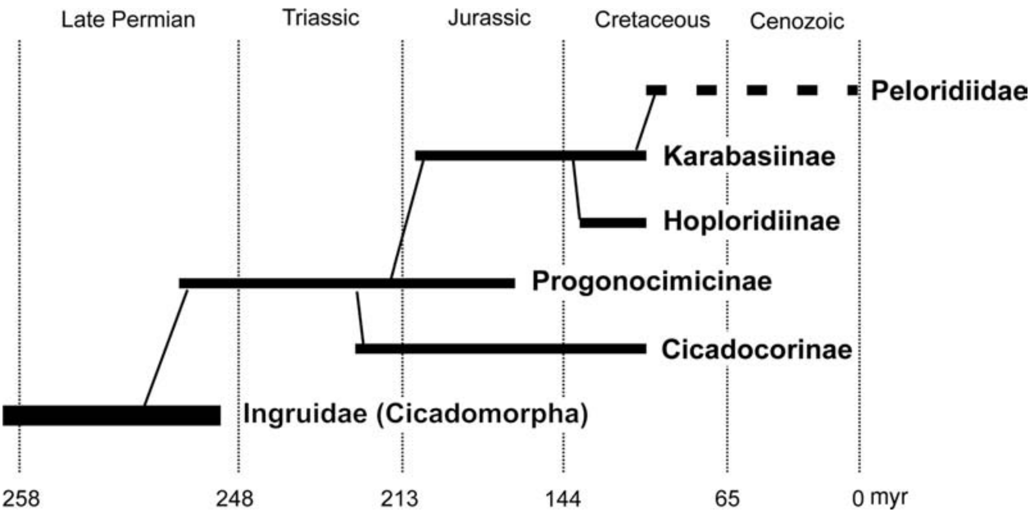

Fig. 11.53. Range chart for clades within the Coleorrhyncha.

Cicadomorpha and Heteroptera is supported by the presence of vibrational communication in these groups. Sweet (1996) hypothesized that large apodemes present at the posterior margin of the first and second abdominal dorsal sclerites in Peloridiidae are tymbal-like organs without a resonator. This assumption is supported by the recorded signals, hypothesized as disturbance calls or spontaneous calls in the context of initiating courtship, as has been observed in other hemipterans (Hoch *et al.*, 2006).

Recent Peloridiidae and †Karabasiidae are placed in the superfamily Peloridioidea, while the †Progonocimicidae are placed in their own superfamily, Progonocimicoidea (Popov and Shcherbakov, 1991). The Peloridiidae are not known from the fossil record, so that all fossil Coleorrhyncha belong to Progonocimicidae (comprising Progonocimicinae and Cicadocorinae) from the upper Permian and Triassic of Australia and from the Triassic, Jurassic and Lower Cretaceous of Eurasia, and to Karabasiidae (comprising Karabasiinae and Hoploridiinae) from the Late Jurassic and Early Cretaceous of Eurasia (Popov and Shcherbakov, 1991, 1996; Carpenter, 1992: 259–260).

Both fossil families are of doubtful monophyly (see Figure 11.53), and both are only stem group representatives of the Recent crown group Coleorrhyncha, because they still have a rather cicadoid wing venation (Grimaldi and Engel, 2005) and other plesiomorphies (see below). Furthermore, even the attribution to the stem group of Coleorrhyncha is not yet very strongly founded and they could also turn out to be stem group representatives of the clade formed by the sister groups Coleorrhyncha+Heteroptera.

Ingruidae, believed to constitute the earliest side branch of ‘Cicadomorpha’, evidently gave rise to both Coleorrhyncha and ‘Cicadomorpha’: Scytinopteroidea, the latter being ancestral to Heteroptera. The oldest Progonocimicinae (uppermost Permian) are very similar and easily derived from certain Ingruidae, and they retain numerous characters inherited from ancestral 'Cicadomorpha' or even from Archescytinoidea (Paleorrhyncha, ancestral to other Hemiptera). Earliest members of Coleorrhyncha, Progonocimicidae, would have been good jumpers, but already somewhat flattened. Their hind tibiae (at least in Cicadocorinae) have two lateral and sometimes apical movable spurs. Hind tarsi are three-segmented, with basitarsomere the largest, and basitarsomere and midtarsomere have apical pectens of macrosetae bearing teeth. They probably would have had non-jumping nymphs and have been phloem-feeders. Their descendants, the earliest Karabasiidae, became less vagile and acquired wing polymorphism, present also in Recent, relic Peloridiidae. Karabasiidae: Karabasiinae had the hind tarsi with basitarsomere and midtarsomere bearing lateroapical teeth. The nymphs were slow-moving, non-jumping, resembling corticicolous nymphs of Cicadellidae: Ledrinae and especially Phloeidae (Heteroptera: Pentatomoidea), probably living on relatively thick plant stems and were cryptic due to a cone-like shadowless habitus. Karabasiidae: Hoploridiinae were probably also corticicolous and convergently similar to Aradidae (nymphs and adults), jumping or non-jumping, with cryptic habitus and long rostrum, being bark-dwellers and associated with thick plant stems. They probably evolved due to retention of certain nymphal features at the adult stage resulting in the loss of jumping ability, flatness, wide paranota and somewhat reduced tegmina. Peloridiidae arose from Karabasiinae, constituting a blind offshoot of the peloridioid lineage. They acquired the uniform areolation of both the wide paranota and the precostal carinae, and a distinct terminal Sc. Peloridiidae lost the R stem in the hind wing, their nymphs became differently shaped, the dorsum being more flat and the anal tube invisible from above (Popov and Shcherbakov, 1991, 1996; Shcherbakov and Popov, 2002). Peloridiidae are found in damp moss, often on decaying mossy trunks and twigs of *Nothofagus*, and have retained a cryptic habitus as a non-functional heritage from corticicolous ancestors. It seems that Recent Peloridiidae, probably similar to their ancestors, are phloem-feeders, or occasionally feed on moss rhizoids, or even on wood-destroying fungi. Of course, the lifestyle of the modern Coleorrhyncha cannot be generalized easily to the fossil stem group representatives, so that the occurrence of such fossil coleorrhynchans does not provide any useful information about the palaeohabitat or the palaeoclimate.

Crato fossils

Several specimens of Progonocimicidae have been discovered among the Crato insect fossils but not yet described. They represent the first New World fossil records of the stem group of Coleorrhyncha. The presence of Peloridiomorpha was first mentioned by Maisey (1991: 434), and a very well-preserved specimen (AMNH SA45253) was figured by Grimaldi and Engel (2005: figure 8.55). Three specimens, SMNS 66408 and SMNS 66423 (Plate 15b), and SMNS 66431 (Plate 15c), are present in the SMNS collection. According to Ruf *et al.* (2005: 73) there are two monotypic families of Coleorrhyncha from the Crato Formation currently in the process of description by Martins-Neto. Martins-Neto (2005b: 479) lists three Crato Formation taxa, *Latiscutella santosi* Pinto and Ornellas, Martins-Neto and C., 1994, *Cratocoris schechenkoae* Martins-Neto, Popov and Zamb., 1999 and *Cratogocimex popovi* Martins-Neto, 2002, as belonging in Coleorrhyncha: Progonocimicidae, but there is no justification for these referrals of taxa, which had been previously described and unequivocally considered as Heteroptera (see below).

11.15 Heteroptera: bugs

Yuri A. Popov and Günter Bechly

Heteroptera, or true bugs, are one of the most diverse and important groups among both Recent and fossil insects. Their phylogeny was summarized by Schuh and Slater (1995) and Grimaldi and Engel (2005), and they are generally treated as a suborder of Hemiptera. The majority of over 75 accepted families occur everywhere except Antarctica. According to Schaefer (1996) there are approximately 37,000 described Recent species and perhaps approximately 25,000 species still awaiting description. So far nearly 1000 fossil heteropteran species belonging to various families have been described from Cenozoic of Western Europe (mainly in Germany, Spain, France, Czech Republic, Denmark and Baltic countries), China, and North (Oligocene of Florissant) and South America (Oligocene of São Paulo State, Brazil).

In contrast to the Mesozoic heteropteran fauna of Eurasia, that of South America is almost unknown and our knowledge is practically restricted to the Lower Cretaceous of Brazil (Crato Formation, Codo Formation and Areado Formation) and Argentina (La Cantera Formation). The majority of Cretaceous specimens are still undescribed.

The Early Cretaceous Heteroptera are quite similar to Late Jurassic assemblages which are mainly known from Eurasia. The transition from Jurassic to Cretaceous assemblages was marked by the appearance of such families as the semi-aquatic Hydrometridae or Veliidae, the phytophagous Tingidae and Aradidae, and the predatory Reduviidae: the latter still very rare in the Early Cretaceous. Some high-ranking taxa disappeared at this time, too, including the pleoid families Scaphocoridae (Late Jurassic) and Mesotrephidae (Early Cretaceous) of Kazakhstan, the water boatmen of Velocorixinae (Late Jurassic–Early Cretaceous of Mongolia and China), the belostomatid subfamily Stygeonepinae (Late Jurassic of Germany and Early Cretaceous of Spain), and the saldoid family Archegocimicidae, the lygaeoid family Pachymeridiidae and the aradoid family Kobdocoridae from the Early Cretaceous of Mongolia (Popov, 1986). The cimicomorphan plant bug family Miridae, which was rather abundant in the Late Jurassic of south-western Kazakhstan (Popov, 1968; Herczek and Popov, 2001), has not yet been recorded from any Lower Cretaceous localities at all, even though a cimicomorphan bug from the Crato Formation was recently figured by Grimaldi and Engel (2005: figure 8.79) and could belong to Miridae.

Some groups of terrestrial bugs became more abundant and more widespread during the Early Cretaceous, for example, the littoral saldoid Archegocimicidae and the terrestrial Pachymeridiidae as well as some Cydnidae (subfamily Amnestinae). Among cimicomorphan bugs three specimens of Reduviidae have been recognized. Aquatic bugs are also abundant in the Late Jurassic and the Early Cretaceous, mainly represented by the Recent families Corixidae (mostly subfamily Diaprepocorinae and Velocorixinae), Naucoridae, Notonectidae and Belostomatidae, and also two extinct families †Scaphocoridae and †Mesotrephidae (Popov, 1971).

In a short review of 73 bugs from the Crato Formation (Grimaldi and Maisey, 1990) Belostomatidae among water bugs and most terrestrial Pentatomomorpha (11 specimens) dominated. Some 30 specimens of undetermined Heteroptera mostly belonged to the lygaeoid Pachymeridiidae, including five species of Lygaeoidea. Judging from their figures (Grimaldi and Maisey, 1990: figures 1D, H, J, N and O) they are most probably the saldoid Archegocimicidae, and close to the extinct subfamily †Enicocorinae (Shcherbakov and Popov, 2002), one of the dominant saldid groups in the Early Cretaceous of the eastern part of East Siberia, Mongolia and China.

In the last 15 years new heteropteran material ($\approx$130 specimens) from the Crato Formation, collected under a collaborative programme with the Universidade Federal do Ceará, Departamento Nacional da Produção Mineral, Divisão de Crato, Centro de Pesquisas da Chapada do Araripe and, more recently, the Universidade Regional do Cariri, has added considerably to our knowledge of the heteropterofauna.

All of this new material can be referred to modern families, and although much of the material is awaiting formal description, the following aquatic bugs have been identified at familial level: Naucoridae (15 specimens), Notonectidae (three specimens), Corixidae (three specimens) and Belostomatidae (25 specimens), represented mostly by nymphs (belostomatids dominate the fossil bugs in many of the Crato collections).

There are also three specimens of semi-aquatic water striders *Cretaceometra brasiliensis* Popov and Nel (Hydrometridae), one specimen of amphibious

Veliidae and six specimens of saldoid leptopodomorphan bugs (Archegocimicidae). The remainder are terrestrial bugs belonging the lygaeoid family Pachymeridiidae (≈80 specimens), which are also the most common and widespread bugs in the Lower Cretaceous of Asia and America, and the Pentatomorpha (Cydnidae, three specimens; Aradidae, one specimen).

Crato bugs

Although several bug species have been described from the Crato Formation, Martins-Neto (2005b) lists only two species of Belostomatidae (*Araripebelostomum martinsnetoi* Nel and Paichler, 1994 and *Neponymphes godoii* Zamboni, 2001) in his compilation of fossil insects from the Crato Formation. Three further heteropteran taxa (*Latiscutella santosi* Pinto and Ornellas, Martins-Neto and C., 1994, *Cratocoris schechenkoae* Martins-Neto, Popov and Zamb., 1999 and *Cratogocimex popovi* Martins-Neto, 2002) are also listed in this publication, but are erroneously attributed by Martins-Neto (2005b) to Coleorrhyncha: Progonocimicidae.

The first Early Cretaceous bugs from Brazil were described by Pinto and Ornellas (1974) from the Codo Formation (Maranhao State): *Latiscutella santosi* and *Pricecoris beckerae*. They were originally placed in two monobasic families †Latiscutellidae and †Pricecoridae but were later transferred to the true burrower bugs of the Recent family Cydnidae (Popov and Pinto, 2000). Mesozoic representatives of this family (the subfamily Amnestinae) are most common and widespread in the Early Cretaceous of Asia (mainly in Siberia, Mongolia and China) and parts of South America. Later, *Latiscutella santosi* was also recorded from the Crato Formation (Martínez, 1982).

The amnestin cydnid *Clavicoris cretaceous* Popov and *Cretacoris gurvanicus* Popov from the lowest Lower Cretaceous of western Mongolia (Gurvan-Eren Formation) were described as the borrower bugs and assigned to the extinct subfamily †Clavicorinae (Popov, 1986). On account of the scutellum not being enlarged, the long and well-developed clavus forming a distinct claval commissure and the similar hind wing venation, these Early Cretaceous cydnids were considered to be related to the living Neotropical Amnestinae and were later included within this subfamily (Popov and Pinto, 2000).

After re-examining of the types of Early Cretaceous cydnids from Brazil and some of the abundant Cretaceous cydnids from Siberia and Mongolia we concluded that there are no cardinal external differences between all the Cretaceous Cydnidae. Mesozoic cydnids compared to some modern Amnestinae show the same ‘ground plan’ at the subfamily level, retaining the ancestral condition with a non-enlarged scutellum and opposite clavi touching to form a distinct claval commissure. The main external differences separating Mesozoic amnestines from the Recent ones are their longer claval commissure and larger average size.

These similarities are deemed sufficient to unite the Cretaceous and possibly even perhaps all Mesozoic Cydnidae, along with the Recent amnestines, into a single subfamily Amnestinae *sensu lato* (Popov and Pinto, 2000), including the Brazilian Early Cretaceous †Pricecoridae, †Latiscutellidae (Martins-Neto, 1987b) and Asiatic †Clavicorinae (Popov, 1986). Thus Amnestinae, now restricted to the Neotropical and Nearctic Regions, were widespread in the Mesozoic, especially the Early Cretaceous, in modern South America, Western Europe and Asia (East Siberia, Mongolia and China).

Suborder Nepomorpha (Hydrocorisae): water bugs

Belostomatidae: giant water bugs

The giant water bugs of the family Belostomatidae (Figures 11.54a–c) are one of the oldest, common and widespread aquatic heteropterans among all water bugs of the Late Jurassic and Early Cretaceous of Western Europe, Asia (Siberia, Kazakhstan, Mongolia and China), the USA and Brazil. The oldest belostomatids are from the Late Triassic of Virginia, USA (Grimaldi and Engel, 2005: figure 8.69). The stygeonepinous belostomatid *Iberonepa romerali* Martínez-Delclós, Nel and Popov, 1995 occurs frequently (mainly as nymphs) in the Lower Cretaceous of Las Hoyas, Spain, while *Mesobelostomum deperditum* (Germar) is frequent (mainly as adults) in the Upper Jurassic Solnhofen Formation in southern Germany (Popov, 1971). So far some 14 species in 13 genera belonging to two recent subfamilies Lethocerinae and Belostomatinae, and one extinct subfamily †Stygeonepinae, have been recorded from the Mesozoic.

Martins-Neto (1978b) first mentioned the belostomatids from the Lower Cretaceous of Brazil, where they appear to be abundant, mostly immature individuals, and most probably belong to the recent subfamily Belostomatinae. It is possible that they are related to the peculiar Recent monotypic Neotropical subfamily Horvathiniinae that is known mainly from Brazil. Two other Crato belostomatids were illustrated but not named or described by Grimaldi and Maisey (1990: figures 2F and H).

The first true belostomatid from the Crato Formation was described by Nel and Paicheler (1992). Named *Araripebelostomum martinsnetoi* it is considered to belong to the subfamily Belostomatinae. Zamboni (2001) described a late nymphal stage of a belostomatid from the Crato as *Neponymphes*, but it is probably congeneric with *Araripebelostomum* Nel and Paicheler, 1992 and is similar to the belostomatid figured by Grimaldi and Maisey (1990). Zamboni (2001) described a second belostomatid from the Crato Formation, *Paranoika placida* Zamboni,

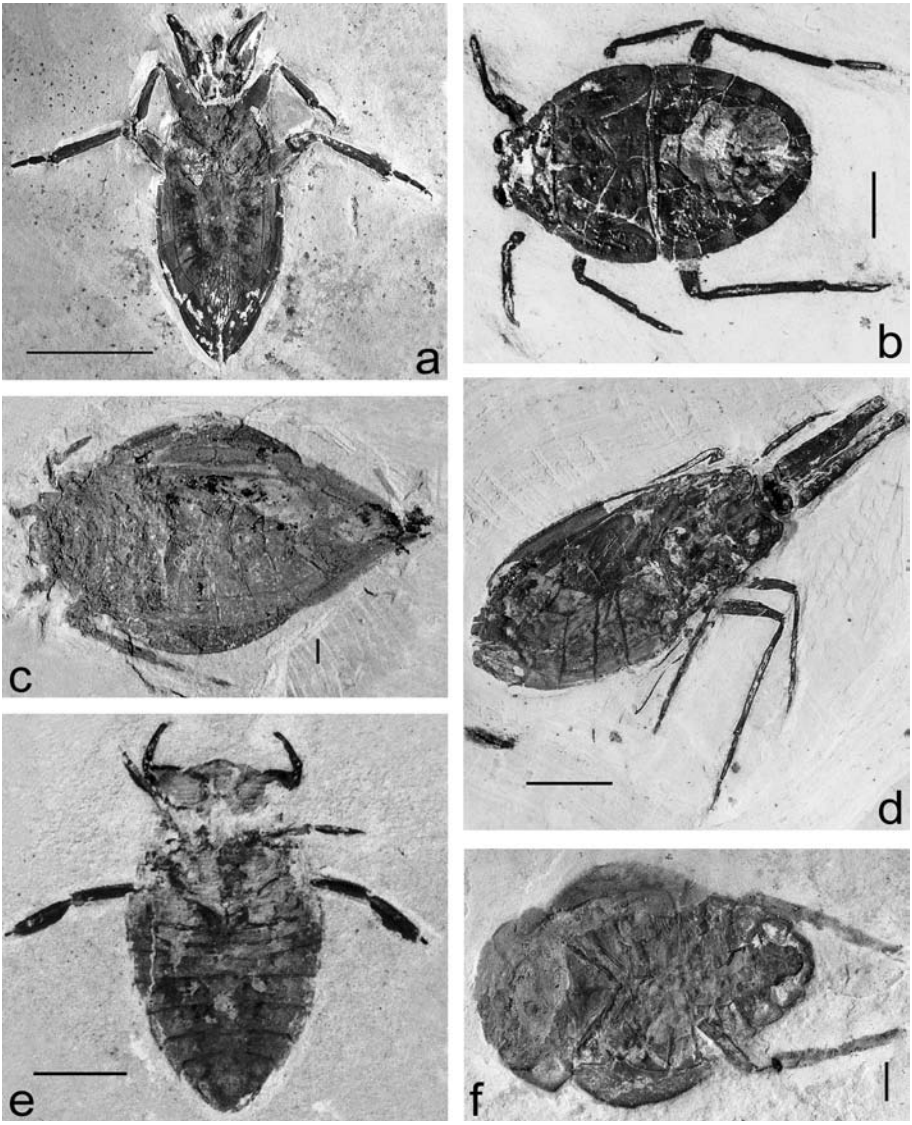

Fig. 11.54. Crato Formation Heteroptera: (a) Belostomatidae, B122 SMF; scale bar, 15 mm; (b) Belostomatidae larva, SMNS 66563; scale bar, 2 mm; (c) Belostomatidae, new species, F104/G81 coll. MSF; scale bar, 2 mm; (d) Nepidae, SMNS 66380; scale bar, 5 mm; (e) Naucoridae, G58 coll. MSF; scale bar, 5 mm; (f) Naucoridae, new species, SMNS 66377; scale bar, 5 mm.

Martins-Neto and Popov, and placed it in a new family †Paranoikidae. However, *Paranoika placida* clearly belongs with the Belostomatidae and should be placed in the subfamily Belostomatinae. Moreover, one cannot exclude that this belostomatid also belongs in *Araripebelostomum*. Consequently, the family Paranoikidae must be considered as a junior synonym of Belostomatidae. Just recently Nel and Waller

(2006) described *Lethocerus vetus* as one of the oldest representatives of the Recent subfamily Lethocerinae from the Crato Formation, which is also found in the Codo formation and seems to have been rather common.

Nepidae: waterscorpions

Several specimens of the family Nepidae have been found in the Crato Formation, for example in the collections of MNB and SMNS in Germany (Figure 11.54d), but none have been described yet.

Naucoridae: creeping water bugs

The Naucoridae (Figures 11.54e and f), like Belostomatidae, are also one of the oldest and widespread groups of water bugs. They appear first in the Upper Triassic deposits of Australia (Tillyard, 1922), North America (Olsen *et al.*, 1978), Central Asia (Kazakhstan and Kirghizia) and Eastern Europe (Ukraine), and can be among the most common water bugs in several Cretaceous sites (e.g. the Gurvan-eren Formation in West Mongolia contains abundant nymphs and adults of the naucoroid *Mongolonecta indistincta* Popov; 1986). Naucoroids account for about 80% of heteropteran specimens in the Lower Cretaceous Purbeck Limestone Group (southern England), although dominated by one or two common species (Popov *et al.*, 1994).

Santos (1971) described 11 specimens of naucoroid bugs from the Lower Cretaceous (Aptian) Areado Formation of Minas Gerais, Brazil, as *Saucrolus silvai* Santos, 1971, establishing for them a new monotypic family †Saucrolidae which was tentatively placed in Crustacea *incertae sedis*. The taxon was later transferred to the Coleoptera (Martins-Neto, 1999a) and then to the Heteroptera as superfamily Naucoroidea, family *incertae sedis* (Martins-Neto, 2001a). As a result of these systematic changes the †Saucrolidae can be considered as a synonym of Naucoridae. Later, two more naucorid bugs were described from the Crato Formation as *Cratocora crassa* (Figure 11.57c) and *Cratopelocoris carpinteroi* (Figure 11.57e) by Ruf *et al.* (2005).

Notonectidae: backswimmers

Notonectidae (Figure 11.55a), or backswimmers, from the Crato and Codo Formations can be assigned to the recent subfamily Notonectinae and are very similar to the notonectids *Canteronecta irajai* Mazoni, 1985, from the Lower Cretaceous of Argentina (La Cantero Formation; San Luis Province) and to species of the genus *Clypostemma*, which is widespread in the Lower Cretaceous of East Asia (East Siberia, Mongolia and China). This similarity of the notonectid from the Crato Formation and that from *C. irajai* Mazoni had previously been suggested by Grimaldi and Maisey (1990). Examining the photographs of type material of *C. irajai* (Mazzoni and Hünicken, 1984), one can notice that part of the type specimens seems to belong to Notonectidae and the other part to Naucoridae.

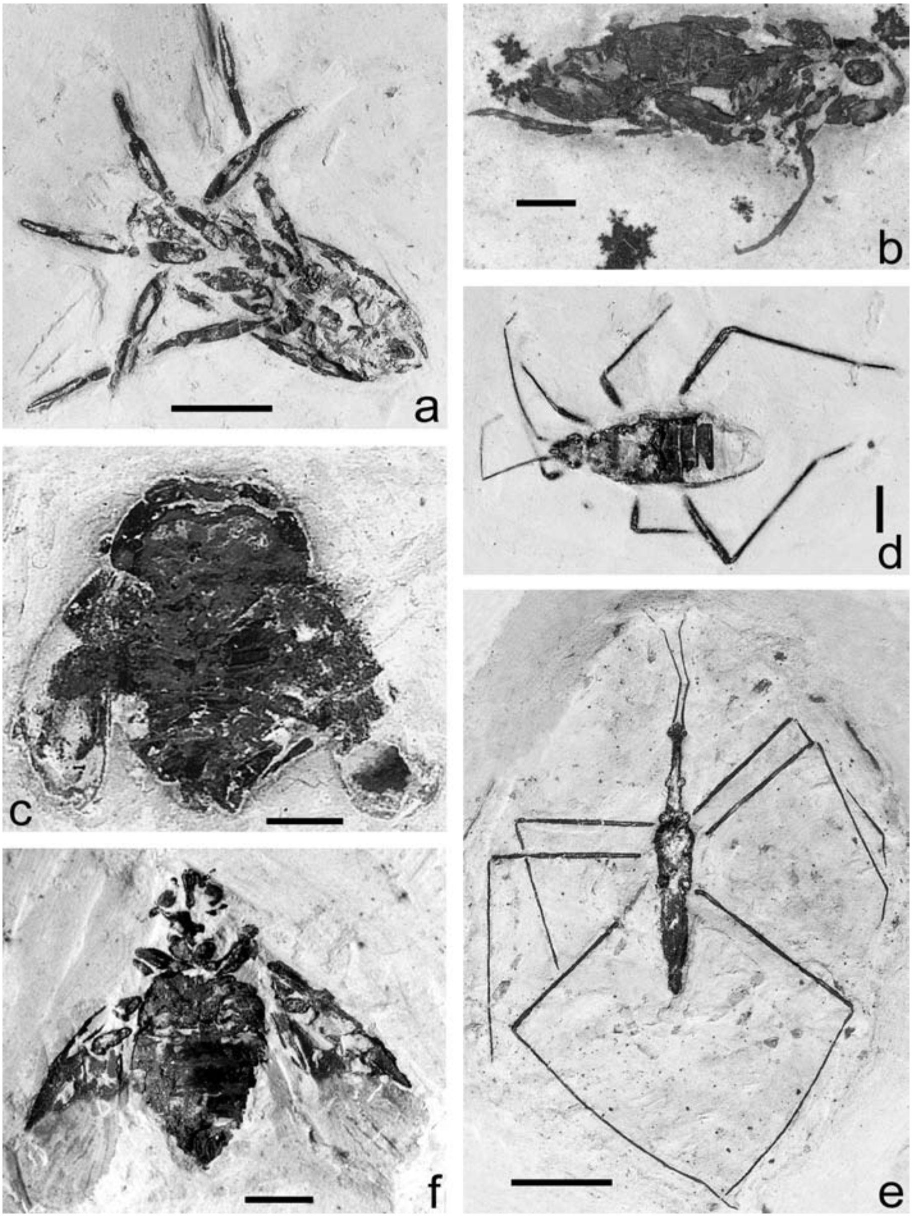

Fig. 11.55. Crato Formation Heteroptera: (a) Notonectidae, SMNS 66382; scale bar, 5mm; (b) Corixidae? (or Notonectidae or Cicadomorpha), SMNS 66436; scale bar, 1 mm; (c) Gelastocoridae, *Cratonerthra estevezae*, holotype SMNS 65416; scale bar, 2 mm; (d) Mesovellidae or Archegocimidae, SMNS 66371 scale bar, 2 mm; (e) Hydrometridae, SMNS 64654; scale bar, 5 mm; (f) Pachymerididae, SMNS 66359; scale bar, 2 mm.

Corixidae: water boatmen

Corixidae (Figure 11.55b), or water boatmen, are cicada-like water bugs that mostly feed on algae. They are quite rare in the Lower Cretaceous of Brazil with only a few (three or four) undescribed specimens known. Initial examination suggests that the Crato corixiids are similar to *Rhomboidella popovi* Mazzoni and Hünicken, 1987 from the Lower Cretaceous La Cantera Formation of Argentina. Elsewhere Corixidae are quite common among late Mesozoic entomofaunas, especially in Western Europe (mainly in Spain), Siberia, Mongolia and China, where they reach their greatest taxonomic diversity in the Late Jurassic to Lower Cretaceous.

Most late Mesozoic fossil corixids belong in the subfamily †Velocorixinae and the Recent plesiomorphic subfamily Diaprepocorinae, of which Recent representatives are only known from South Australia and New Zealand (Andersen and Weir, 2004). It is possible that some members of the Diaprepocorinae belong to the Recent subfamily Micronectinae, as the Recent Neotropical genus *Tenagobia* is widespread in the Western Hemisphere. Fossil micronectins are also known from the Oligocene Tremembé Formation, São Paulo State, Brazil (Martins-Neto, 1998e), and are similar to *Tenagobia*.

Gelastocoridae: toad bugs

Littoral nepomorphan bugs are represented in the Crato Formation by the Gelastocoridae, or toad bugs, which are quite typical, although never numerous, for the Lower Cretaceous of South America (Brazil and Argentina). Two species, *Cratonerthra corinthiana* (Figure 11.57d) and *Cratonerthra estevezae* (Figures 11.55c and 11.57f) were described by Ruf *et al.* (2005) and placed in the gelastocorid subfamily Nerthrinae. They also described the new genus and species *Pseudonerthra gigantea* for which they erected the new family †Pseudonerthridae that seems to be the sister group of Gelastocoridae.

Rumbucher (1995: 54–55, figure 6) copied from Maisey (1991) a figure of a fossil gelastocorid bug from the Crato Formation that he erroneously identified as myrmelionid ‘antlion’ larva.

Gerromorpha and Leptopodomorpha (Amphibicorisae): amphibic shore bugs

This is a relatively diverse group of bugs ($\approx$ 1,860 species in eight Recent families) that includes the well-known pond skaters. All inhabit aquatic environments, where they can often be found walking on the surface film. All are predatory, and some are found in marine environments (Grimaldi and Engel, 2005). Contrary to established opinion gerromorphan bugs are not so rare in the Mesozoic. *Engynabis tenuis*

Bode from the Lower Jurassic, Toarcian, Posidonia Shales of northern Germany is possibly the oldest representative, and is undoubtedly a member of Mesoveliidae.

Three of the Recent families occur in the Late Jurassic and Early Cretaceous; Hydrometridae (water measurers), Mesoveliidae (water treaders) and Veliidae (riffle bugs; Andersen, 1998). Mesoveliids are quite numerous in the Upper Jurassic of Kazakhstan, *Karanabis kititshenkoi* B.-M. (Becker-Migdisova and Popov, 1963) in the Lower Cretaceous of East Siberia and Mongolia, and in the Lower Cretaceous of Victoria (Australia), *Duncanovelia extensa* Jell and Dunc. (Jell and Duncan, 1986; Grimaldi and Engel, 2005: figure 8.65). Gerridae (water striders) are known from Tertiary amber, but are still completely unknown from the Mesozoic.

The first Gerromorpha to be formally described was the hydrometrid (three specimens), *Cretaceometra brasiliensis* Nel and Popov, 2000. A second Crato hydrometrid, *Incertametra santanensis* (four specimens; Figure 11.58), was described by Goodwyn (2002), who also figured three specimens as Hydrometridae *indet*. (gen. et sp. nor.; Figure 11.55e) and also one as *Cretaceometra* cf. *brasiliensis*. Most probably *Cretaceometra* and *Incertametra* are congeneric, the few small differences simply reflecting natural variation.

A specimen figured by Grimaldi and Maisey (1990: figure 1D), denoted as 'Gerromorpha?', appears to belong to the family Veliidae (riffle bugs), whose representatives are widespread elsewhere, including the Cretaceous of the Kazakhstan, Mongolia and China.

Fossil bugs very similar to the gerromorphan family Mesoveliidae and/or the leptopodomorphan family †Archegocimicidae (Figure 11.55d) occur frequently in the Crato Formation, but are still undescribed.

Suborders Pentatomomorpha and Cimicomorpha (Geocorisae): terrestrial bugs

The terrestrial Heteroptera are very diverse and numerous among true bugs. The lygaeoid family Pachymeridiidae (Figure 11.55f), presumably basal for the Pentatomomorpha, is one of the most abundant and widespread groups in Mesozoic faunas, especially in the Late Jurassic and Early Cretaceous. Most have been described from the Lower Cretaceous of Mongolia (Popov, 1986) and Siberia (Popov, 1990) but several have been reported from the Lower Jurassic of Germany (Handlirsch, 1925, 1939; Bode, 1953). However, the pentatomomorph bugs are one of the least-studied heteropterans of the Early Cretaceous of Brazil. A pachymeridiid was described from the Crato Formation, *Cratocoris shevchenkoae* Martins-Neto, Popov and Zamboni, 1999 (Figures 11.57a and b), and placed in the Coreoidea as family uncertain. Several specimens of the coreoid families Alydidae and Coreidae (*sensu lato*) have also been discovered in the Crato Formation (Figures 11.56a and b), but are as yet undescribed.

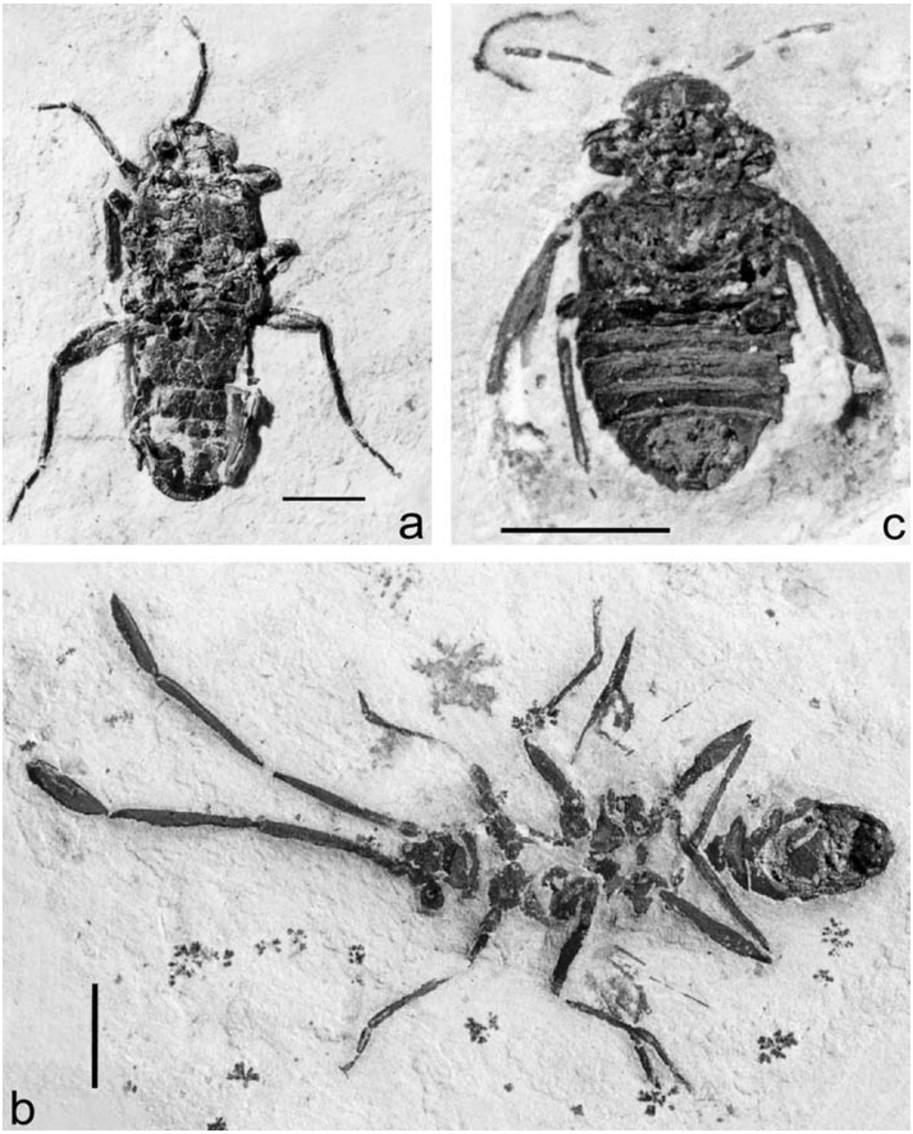

Fig. 11.56. Crato Formation Heteroptera: (a) Coreidae, SMNS 66360; (b) Coreidae, SMNS 66365; (c) Cydnoidea, SMNS 66357. Scale bars, 2 mm.

Another pentatomomorphan bug from the Crato Formation belongs to the peculiar Recent family Aradidae whose recent representatives are distributed all over the World and are mostly connected with tree bark. The Crato specimen appears to belong in the modern subfamily Mezirinae.

Most fossil aradids can be assigned to the recent genus *Aradu*s (Kormilev and Popov, 1989) and are known from the Late Jurassic of Kazakhstan, the later Early

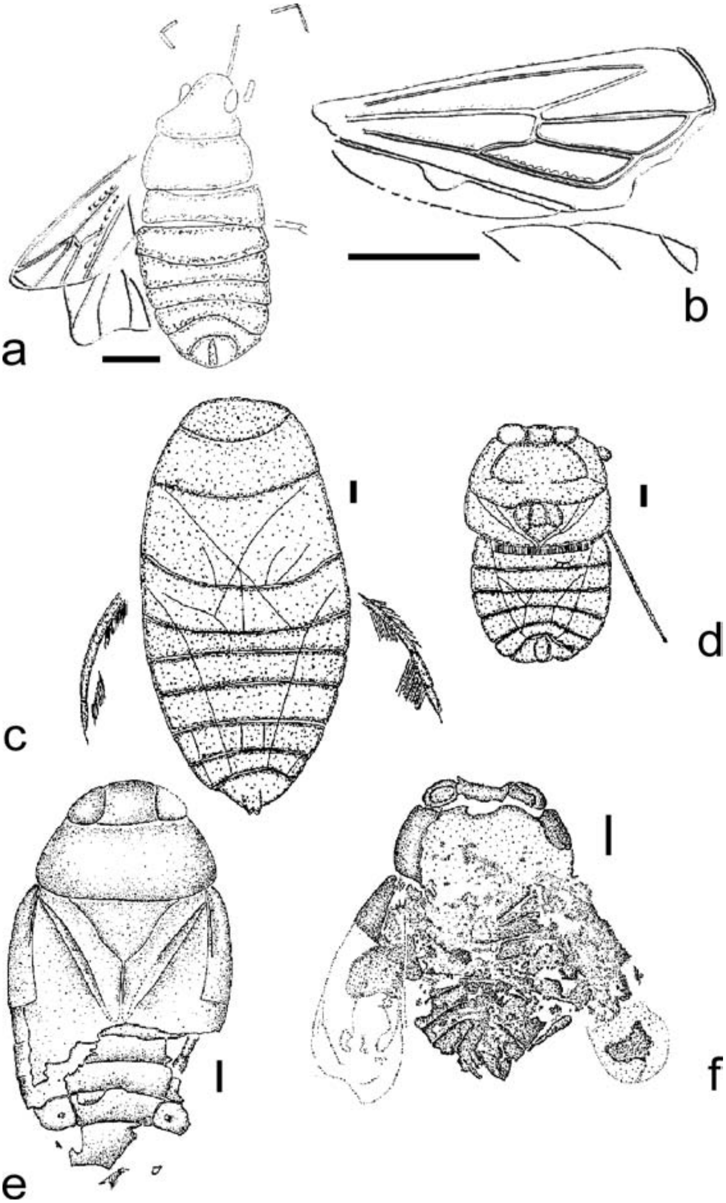

Fig. 11.57. Crato Formation Heteroptera: (a) *Cratocoris shevchenkoae* Martin-Neto, Popov and Zamboni, 1999, holotype, RGMN-T032; (b) hemi elytron of specimen in a; (c) *Cratocora crassa* Martins-Neto, 2005, holotype, MPFT-1–026; (d) *Cratonerthra corinthiana* Martins-Neto, 2005, holotype, MPFT-1–027; (e) *Cratopelocoris carpinteroi* Lopez Ruf and Perez Goodwyn, 2005, holotype, RGMN 499; (f) *Cratonerthra estevezae* Lopez Ruf and Perez Goodwyn, 2005, holotype, SMNS 65416. Scale bars, 1 mm. Illustrations (a, b) after Martin-Neto *et al.* (1999); (c–f) after Ruf *et al.* (2005).

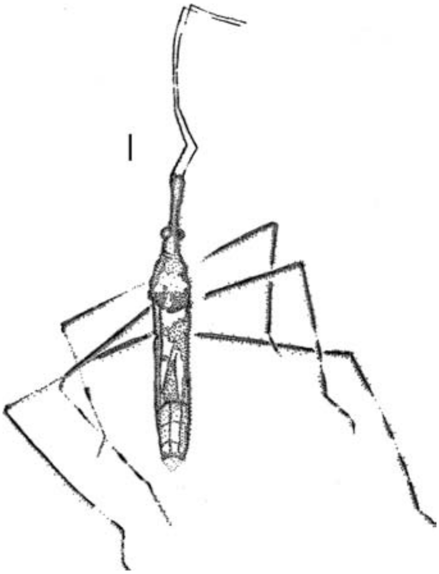

Fig. 11.58. Crato Formation Hydrometridae: *Incertametra santanensis* Goodwyn, 2002, holotype SMNS 64652; scale bar, 1 mm. After Goodwyn (2002).

Cretaceous of Central Mongolia (Aptian, Bon-Tsagan) Popov, 1986, and from the Late Cretaceous of north-east Siberia (Santonian, Magadan district). The Cydnoidea (Figure 11.56c) have already been discussed above. Unfortunately, a great number of terrestrial bugs from the Crato Formation have yet to be evaluated.

11.16 Neuropterida: snakeflies, dobsonflies and lacewings

Rafael G. Martins-Neto, Sam W. Heads and Günter Bechly

The Neuropterida, instantly recognizable by their proportionally large, hyaline wings and net-like venation, are one of the most basal groups of Holometabola and comprise the Raphidioptera (snakeflies), Megaloptera (dobsonflies and alderflies) and Neuroptera (lacewings and antlions). Aside from their typically busy venation, the Neuropterida are characterized by the fusion of the gonoplacs in the ovipositor, a medially divided metapostnotum, a proventriculus with an unpaired diverticulum and the first abdominal tergum having a caudally bifid longitudinal sulcus (Kristensen, 1991; Grimaldi and Engel, 2005). Although neuropterid monophyly is well established, the internal relationships of the group have proved difficult to resolve and remain controversial (Grimaldi and Engel, 2005). All three orders are represented in the Crato Formation, although many of the taxa (particularly the

Neuroptera) require extensive revision and re-description as undoubted synonymies exist.

Recently, the extraordinary new family Rafaelidae was described by Nel *et al.* (2005) with two new species *Rafaelia maxima* (Plate 14a) and *Rafaelia minima*. This family was only tentatively attributed to the neuripterid clade because the veins RP and MA have independent stems in Rafaelidae, but are fused in all known Neuropterida. Also, the other characters do not allow attribution to any of the neuropterid orders nor any other known insect order. The large compound eyes (head similar to libellulid Odonata), the distinct ovipositor and unusual wing venation (particularly the structure of Subcosta, Radius and Media) are unique characters within Neuropterida. Consequently, this family has to be considered as a new insect order, which we here give the new name Schwickertoptera Bechly, ordo. nov. (Plate 14a), in honour of Mr Michael Schwickert (Sulzbachtal, Germany) in recognition of his generous and ongoing support of numerous scientists and public natural history museums around the world.

Raphidioptera: snakeflies

Characterized by their elongate prothorax, the snake-like ‘neck’ from which the group takes its vernacular name, distinct venation and prominent ovipositor in females, the snakeflies constitute one of the least diverse holometabolous orders (Figures 11.59a–c and 11.69a, Plate 14e). Although monophyly of the order is not in doubt, compelling autapomorphies have never been immediately obvious. Traditionally the group has been characterized by the absence of a pretarsal arolium, the termination of Sc into the anterior wing margin and the bilobed third tarsomere (Kristensen, 1991; Grimaldi and Engel, 2005). In a recent reassessment Aspöck and Aspöck (2004: 16) added two further, apparently strong autapomorphies for the order; amalgamation of tergite and sternite of the ninth segment in the male to form a ring, and elongation of the ovipositor of the female. Interestingly, the ovipositor was discussed by Kristensen (1991) but was regarded as plesiomorphic following Mickoleit (1973). Following the classification of Engel (2002) the order is currently subdivided into two suborders: Priscaenigmatomorpha, including the single extinct family Priscaenigmatidae; and Raphidiomorpha, including the extinct families Baissopteridae, Mesoraphidiidae and Alloraphidiidae along with the two living families, Raphidiidae and Inocellidae.

In the Crato Formation, snakeflies are represented by four species in three genera that have undergone recent revisions by Willmann (1994) and Engel (2002) and represent the only Southern-Hemisphere occurrence of the order. Among the Baissopteridae, the genus *Austroraphidia* was erected by Willmann (1994) to accommodate *Raphidia brasiliensis* (Nel, Séméria and Martins-Neto, 1990). In addition,

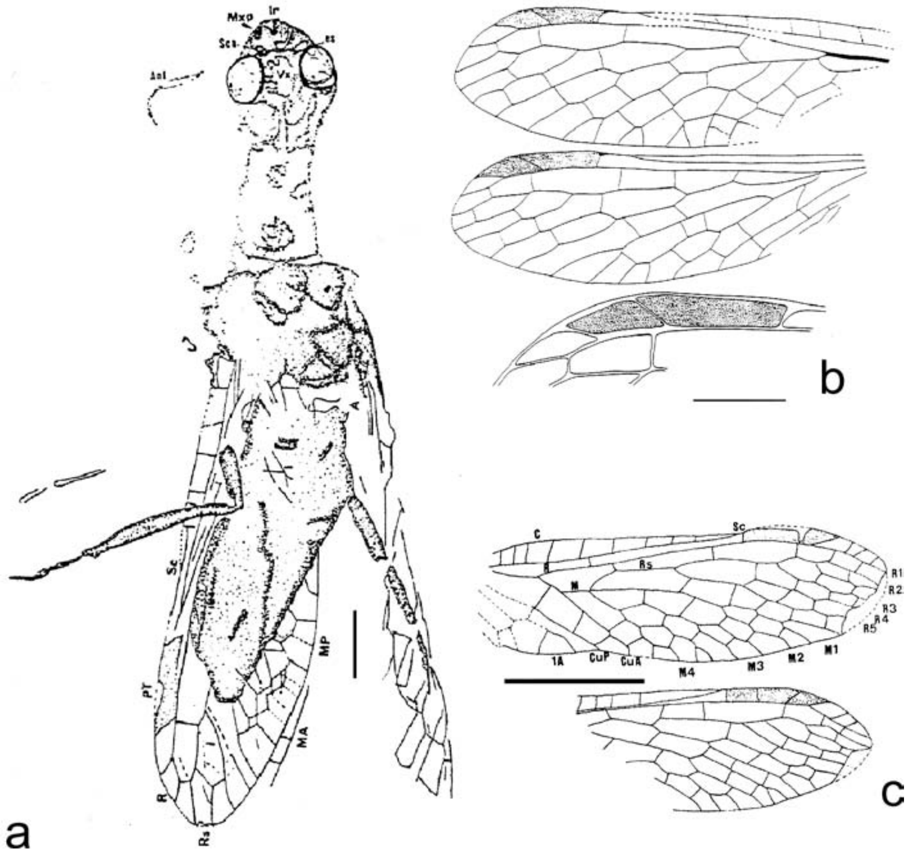

Fig. 11.59. Crato Formation Raphidioptera: (a) *Arariperaphidia rochai* Martins-Neto and Vulcano, 1990, holotype, CV-5010; (b) *Raphidia brasiliensis* Nel, Séméria and Martins-Neto, 1990, holotype MNHN IPM-R54102, forewing (above), hind wing (centre), detail of pterostigma; (c) *Cratoraphidia pulchra* Martins-Neto and Nel, 1993, holotype, GP/IT-1673, forewing (above), hind wing (below). Scale bars, 1 mm. (a) After Martins-Neto and Vulcano (1990); (b) after Nel, Séméria and Martins-Neto (1990); (c) after Martins-Neto and Nel (1993).

Cratoraphidia pulchra (Martins-Neto and Nel, 1992) was moved to the genus *Baissoptera* by Engel (2002). A second species, *B. brasiliensis* Oswald, 1990 is also known from the Crato Formation. In his catalogue, Engel (2002: 15) suggests that *Austroraphidia* may be a junior synonym of *Baissoptera* but notes several characters supporting a separate generic assignment. The monotypic *Arariperaphidia rochai* Martins-Neto and Vulcano, 1989a was the first snakefly to be reported from the Crato Formation, and in fact the first from South America, and was retained in Engel's (2002) catalogue as Raphidioptera *incertae sedis*.

Megaloptera: dobsonflies and alderflies

The Megaloptera (Figures 11.69b and c and 11.90f) are typically large insects that resemble Neuroptera but retain a broad anal region in the hind wing. The larvae are aquatic with lateral gills and lack the sucking mouthparts typical of neuropterans (Grimaldi and Engel, 2005). Like the Raphidioptera, compelling evidence for megalopteran monophyly is sparse and the order has been considered by some to be paraphyletic with respect to snakeflies (Achtelig, 1967; Afzelius and Dallai, 1988). Although traditionally considered a primitive trait, some authors now consider the aquatic lifestyle of megalopteran larvae as independently derived from that of basal Neuroptera. For example, Grimaldi and Engel (2005) suggest that an aquatic lifestyle and lateral gills in the larvae may be potential autapomorphies for the order. This, along with some evidence from molecular studies (Wheeler *et al.*, 2001), supports monophyly of the group. The order is currently subdivided into two families: Corydalidae, the dobsonflies; and Sailidae, the alderflies. Two extinct families have been described: the Parasailidae from the Permian of Russia (Ponomarenko, 1977, 2000); and the Euchauliodidae from the Triassic of South Africa (Riek, 1974). Although there have been no formal descriptions of Megaloptera from the Crato Formation, an adult specimen in a private collection was mentioned by Martins-Neto (1999a). In addition, several undescribed adult specimens in the collections at SMNS probably represent a new taxon. The fossil record of the order was recently reviewed by Grimaldi and Engel (2005) and although their rarity in the Crato Formation might seem surprising considering the aquatic lifestyle of their larvae, fossil Megaloptera are also rare elsewhere.

Neuroptera: lacewings and antlions

The predatory Neuroptera (Figures 11.60–11.68, 11.69d–i and 11.70) are among the most ancient members of the Holometabola and comprise the familiar lacewings and antlions. Readily identified by their complex venation the order is defined by the association of the ninth gonocoxites with the gonarcus and the unusual larval mouthparts in which the maxillae and mandibles form a sucking tube for liquid feeding (Aspöck *et al.*, 2001; Grimaldi and Engel, 2005). Although the internal phylogeny of the order is largely unresolved, most recent accounts recognize three distinct subgroups: the basal Nevrorthiformia, comprising the single Recent family Nevrorthidae; and the more diverse Myrmeleontiformia and Hemerobiiformia. Only the latter two groups have been recorded from the Crato Formation and have been documented extensively by Martins-Neto and Vulcano (1989b,c, 1990a,b, 1997) and Martins-Neto (1998b, 1990b, 1991d, 1992b, 1994, 1997a, 1998d, 2000, 2002a, 2005). Martins-Neto (2000) provided a key to all 11 families, 28 genera

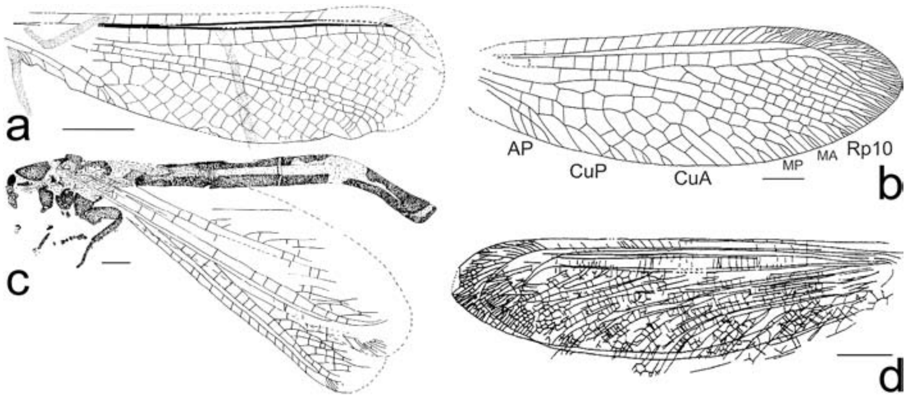

Fig. 11.60. Crato Formation Neuroptera: (a) *Cratoscalpha electroneura* Martins-Neto and Vulcano, 1997, holotype CV-2711, forewing venation; (b) *Olindanymphes makarkini* Martins-Neto, 2005, holotype forewing, MPFT-1–030; (c) *Neurastenyx gigas* Martins-Neto and Vulcano, 1997, holotype CV-2836; (d) *Neurastenyx polyhymnia* Martins-Neto, 1997, holotype AMNH 44412, forewing venation. Scale bars, 5 mm, except (b) 2 mm. (a) After Martins-Neto and Vulcano (1997); (b) after Martins-Neto (2005); d, after Martins-Neto (1997).

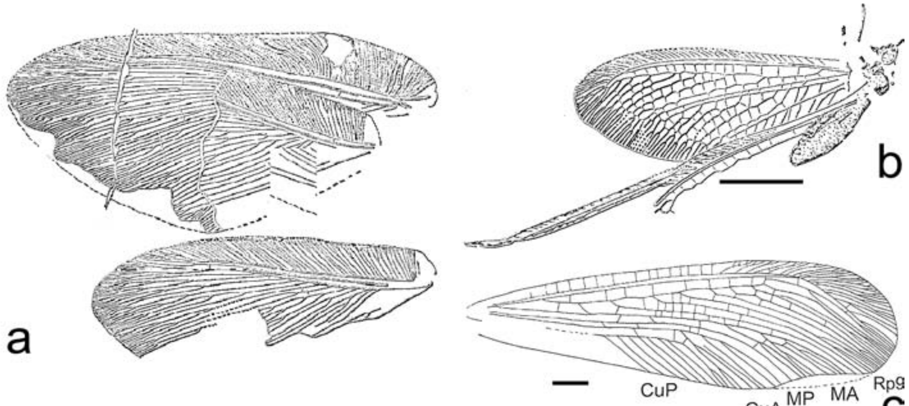

Fig. 11.61. Crato Formation Neuroptera: (a) *Pulchroptilonia espatiafata* Martins-Neto, 1997, holotype RGMN-T110, forewing (above) and hind wing (below); (b) *Roesleriana exotica* Martins-Neto and Vulcano, 1989, habitus; scale bar, 10 mm; (c) *Santananymphes ponomarenkoi* Martins-Neto, 2005, holotype MPFT-1-031, forewing, scale bar, 2 mm. (a) After Martins-Neto (1997); (b) after Martins-Neto and Vulcano (1989); (c) after Martins-Neto (2005).

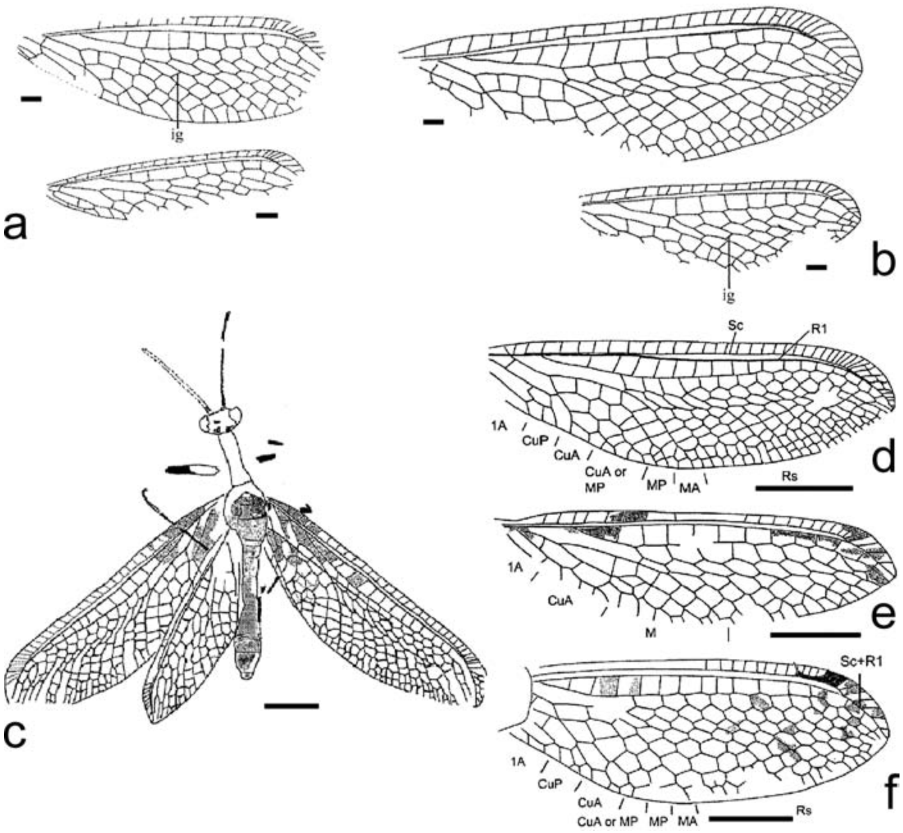

Fig. 11.62. Crato Formation Neuroptera: (a) *Armandochrysopa borschukewitzi* Nel, Delclo's and Hutin, 2005, forewing (above) and hind wing (below), holotype MNHN DHT-R55201, scale bar, 1 mm; (b) *Karenina breviptera* Martins-Neto, 1997, forewing (above) and hind wing (below); scale bars, 1 mm; (c–e) *Karenina longicollis* Makarkin and Menon, 2005, holotype, SMNS 65505; (c) complete specimen; (d) right forewing; (e) hind wing; (f) *Karenina leilana* Makarkin and Menon, 2005, holotype SMNS 66506, forewing. Scale bars: a, 1 mm; b–e, 5 mm. (a–b) After Nel and (2005); (c–f) after Makarkin and Menon (2005).

and 50 species of fossil Neuroptera described from the Crato Formation until then. Despite this, however, most forms described from the Crato Formation require redescription and a comprehensive revision of the fauna is still lacking. A complete list of the species and their current familial assignments is provided in the appendix.

Myrmeleontiformia

The Myrmeleontiformia includes some of the biggest and most impressive Neuroptera and comprises five Recent families: Psychopsidae (silky lacewings), Nemopteridae (spoon-winged and thread-winged lacewings; Plates 14c and d), Ascalaphidae (owlflies), Nymphidae (split-footed lacewings) and Myrmeleontidae

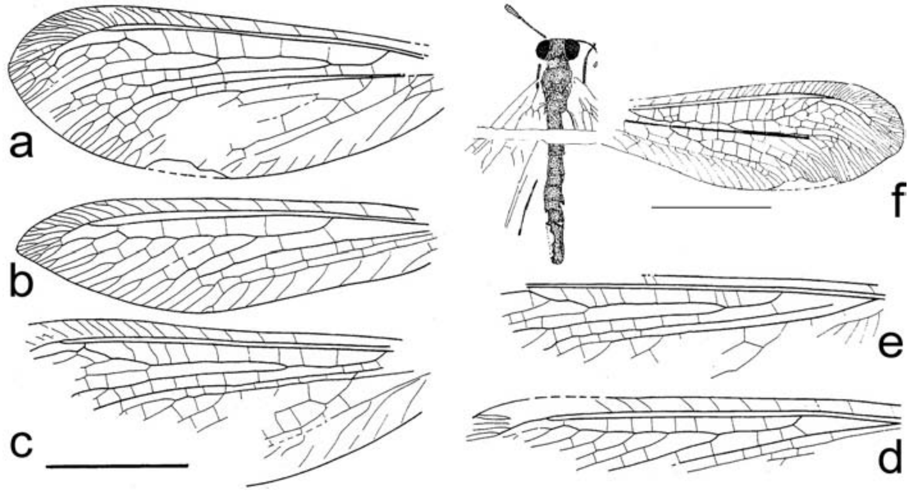

Fig. 11.63. Crato Formation Neuroptera: (a–b) *Caririneura regia* Martins-Neto and Vulcano, 1997, wing venation; (a) forewing; (b) hind wing; (c) *Caririneura crassatella* Martins-Neto and Vulcano, 1997, forewing of paratype, CV-995; (d, e) *Caririneura damianii* Martins-Neto, 1992, wing venation; (e) forewing; (d) hind wing; (f) *Paracaririneura priscila* Martins-Neto and Vulcano, 1997, holotype CV-6110. Scale bars, 5 mm. All figures after Martins-Neto and Vulcano (1997).

(antlions; Figure 11.69h). Of these, all but Psychopsidae are known from the Crato Formation, along with various extinct stem group 'myrmeleontoids' including Palaeoleontidae (Figure 11.69f, Plates 2e and 14b), Nymphitidae, Araripeneuridae, Babinskaiidae, Makarkiniidae, Brogniartiellidae and Kalligrammatidae. The assignment of *Pulchroptilonia espatifata* Martins-Neto, 1997a to Psychopsidae has to be reconsidered. Some 'families' described from the Crato Formation may be junior synonyms of crown group taxa (e.g. Roeslerianidae are without doubt plesiomorphic Nemopteridae and should at best be considered a subfamily of the latter) while others, such as Kalligrammatidae and Brogniartiellidae, likely represent stem groups to the Psychopsidae–Nemopteridae clade (Andersen, 2001; Grimaldi and Engel, 2005). The relationships of other groups are less clear. Palaeoleontidae are clearly 'myrmeleontoid' in general appearance (Heads *et al.*, 2005) and may be a subgroup of Myrmeleontidae or a paraphyletic stem group. Araripeneuridae and Babinskaiidae likely represent stem groups to the entire Nymphidae–Myrmeleontidae–Ascalaphidae clade. A single myrmeleontoid larva of the antlion-type is known from the Crato Formation (Figure 11.69d).

Hemerobiiformia

The Hemerobiiformia is the most diverse group of Neuroptera and comprises 11 Recent families: Polystoechotidae (giant lacewings), Ithonidae (moth lacewings),

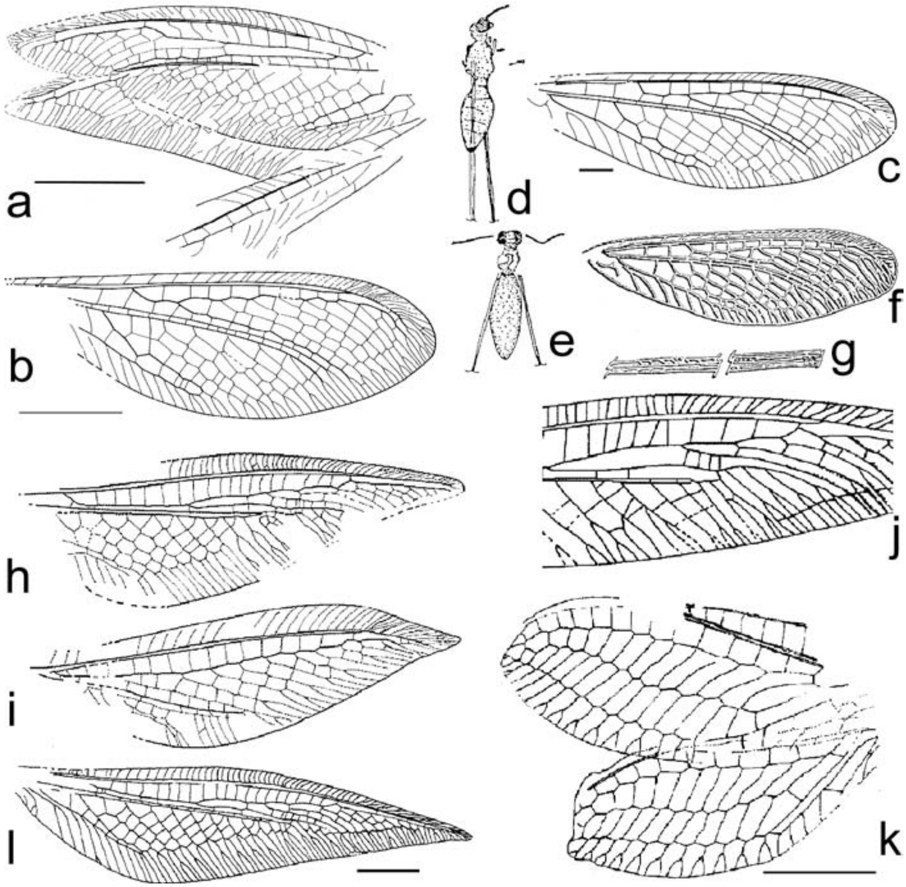

Fig. 11.64. Crato Formation Neuroptera: (a) *Cratoalloneura acuminata* Martins-Neto, 1992, CV-2712 fore- and hind wings; (b) *Cratonemopteryx speciosa* Martins-Neto and Vulcano, 1997, forewing; (c, d) *Cratonemopteryx audax* Martins-Neto, 1992, forewing and body respectively; (e–g) *Cratonemopteryx robusta* Martins-Neto, 1992, holotype, body, portion of forewing, portion of hind wing respectively; (h, i) *Cratoneura dividens* Martins-Neto, 1994 fore- and hind wings respectively; (j) *Cratoneura longissima* Martins-Neto, 1992; (k) *Mesypchrysa criptovenata* Martins-Neto, 1992, RGMN-T008, fore- and hind wings; (l) *Cratoneura dividens* Martins-Neto, 1994, forewing. (a–c, h–l) After Martins-Neto (1997); (d–f) after Martins-Neto (2000).

Osmylidae (osmylids), Chrysopidae (green lacewings), Hemerobiidae (brown lacewings), Coniopterygidae (dusty lacewings), Sisyridae (spongillaflies), Dilaridae (pleasing lacewings), Mantispidae (mantispids), Rachiberothidae (thorny lacewings) and Berothidae (beaded lacewings). Of the Recent hemerobiiforms, Osmylidae, Chrysopidae (Figure 11.69i), Hemerobiidae (Figure 11.70a), ?Sisyridae, Ithonidae (Figure 11.70b) and Berothidae are recorded from the Crato

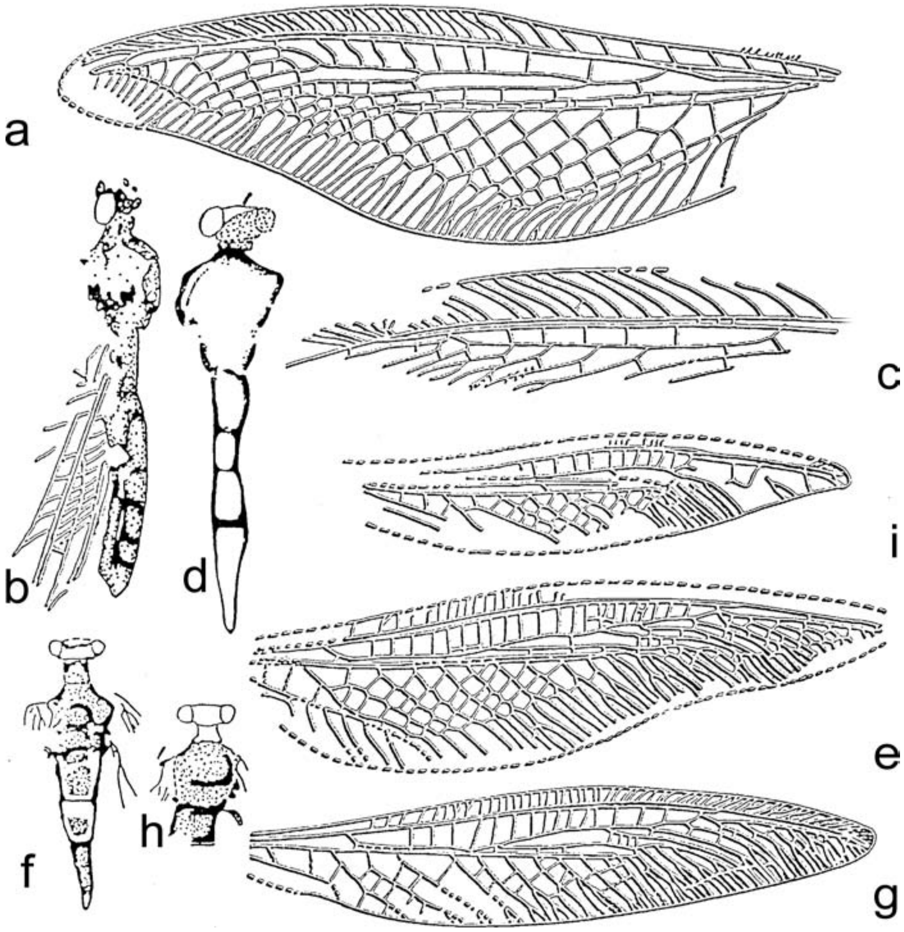

Fig. 11.65. Crato Formation Neuroptera: (a) *Cratoalloneura acuminata* Martins-Neto, 1992, forewing; (b) *Cratoalloneura acuminata* detail of body; (c) *Cratoalloneura acuminata* hind wing; (d) *Catoneura dividens* Martins-Neto, 1994, holotype body; (e) *Catoneura dividens* holotype forewing; (f) *Cratoneura longissima* Martins-Neto, 1992, holotype body; (g) *Cratoneura longissima* holotype forewing; (h) *Cratoneura pulchella* Martins-Neto, 1992, body of holotype; (i) *Cratoneura pulchella*, forewing of holotype. Based on Martins-Neto (2000).

Formation, along with the extinct chrysopoid families Mesochrysopidae (Figure 11.70c, Plate 15a), Limaiidae and Allopteridae (Figures 11.69e and g). Grimaldi and Engel (2005: 353) noted that *Cratosisyrops gonzagi* (Figure 11.66c), even though described by Martins-Neto (1997a) as earliest Sisyridae, has to be considered as *incertae sedis*. The Crato fauna is dominated by Chrysopoidea which have recently been revised by Nel *et al*. (2005).

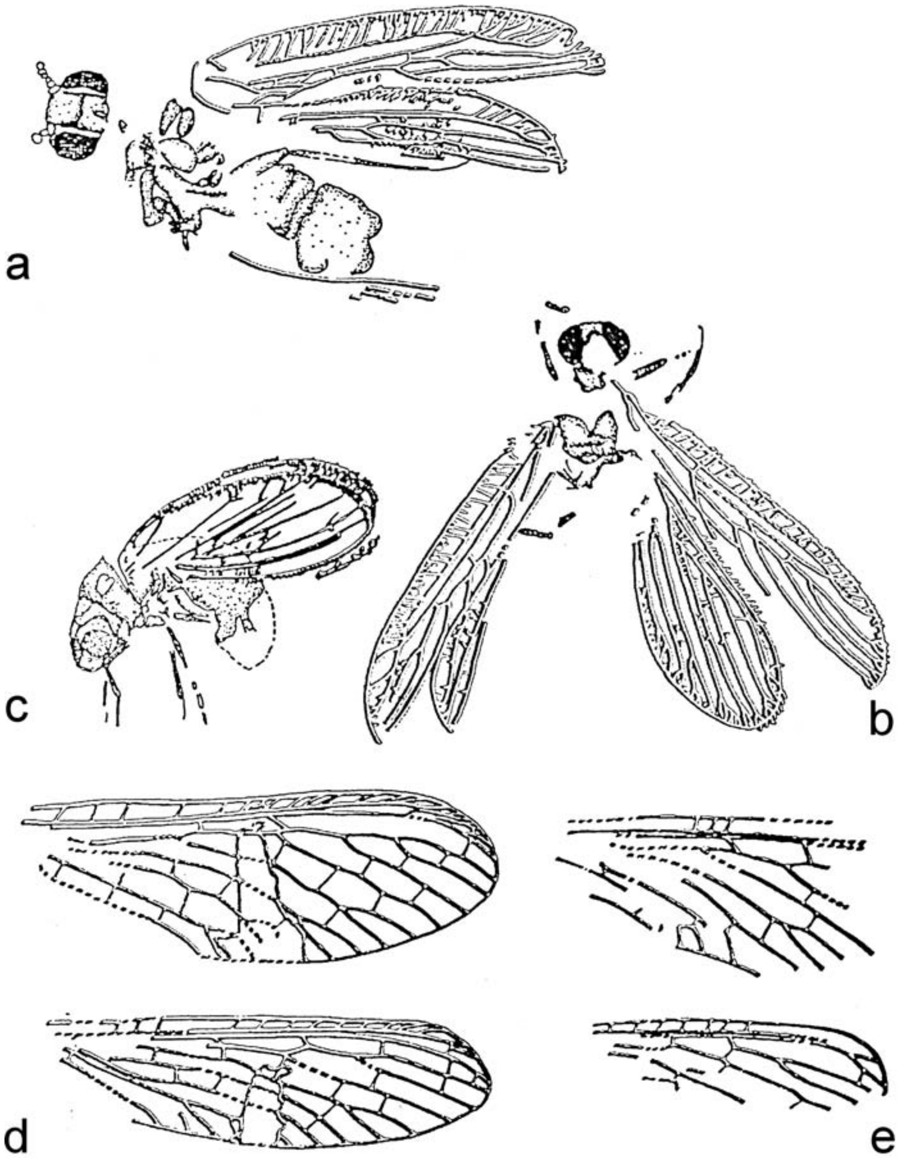

Fig. 11.66. Crato Formation Neuroptera: (a) *Caririberotha martinsi* Martins-Neto and Vulcano, 1990, holotype; (b) *Araripeberotha fairchildi* Martins-Neto and Vulcano, 1990, holotype; (c) *Cratosisyrops gonzagi* Martins-Neto, 1997, holotype, CV-1356; (d) *Cratochrysa wilmanni* Martins-Neto, 1997, forewing (above) and hind wing (below); (e) *Cratochrysa sublapsa* Martins-Neto, 1997, forewing (above) and hind wing (below). Figures based on Martins-Neto (2000).

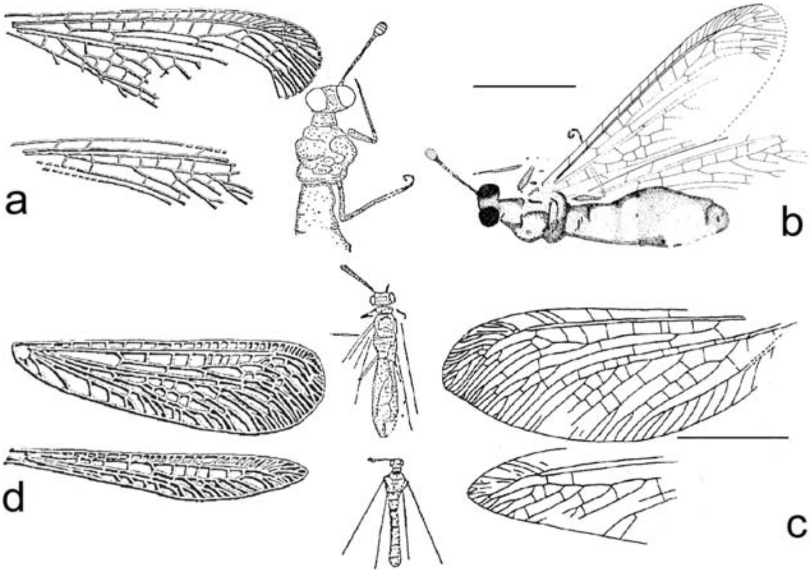

Fig. 11.67. Crato Formation Neuroptera: (a) *Caririneura crassatella* Martins-Neto and Vulcano, 1997, forewing (above), hind wing and body; (b) *Caririneura crassatella* Martins-Neto and Vulcano, 1997, holotype, CV-2461; scale bar, 5 mm; (c) *Caririneura damianii* Martins-Neto, 1992, forewing (above), hind wing and body, AMNH 43289; scale bar, 5 mm; (d) *Caririneura microcephala* Martins-Neto and Vulcano, 1989, forewing (above), hind wing and body. After Martins-Neto (2000) and Martins-Neto and Vulcano (1997).

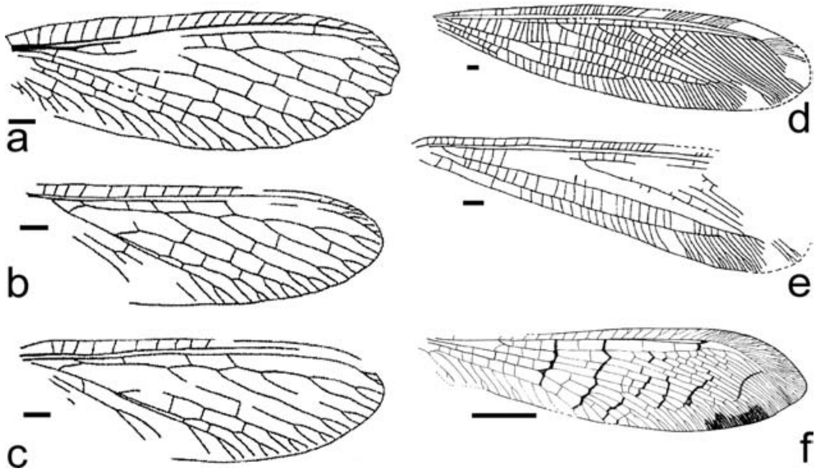

Fig. 11.68. Crato Formation Neuroptera: (a–c) Familia *incertae sedis*, *Cratochrysa martinsnetoi* Nel, Delclō's and Hutin, 2005; (a) holotype right forewing; (b) holotype right hind wing; (c) holotype left hind wing (reversed), MNHN-DHT R55224; (d, e) *Araripenymphes seldeni* Menon, Martins-Neto and Martill, 2005; (d), right forewing; (e) left hind wing (reversed); (f) *Blittersdorffia pulcherrina* Martins-Neto and Vulcano, 1997, holotype, coll. Vulcano no. CV-2080 m. Scale bars: a–e, 1 mm, f, 5 mm. (a–c) After Nel *et al.* (2005); (d,e) after Menon *et al.* (2005); (f) after Martins-Neto and Vulcano (1997).

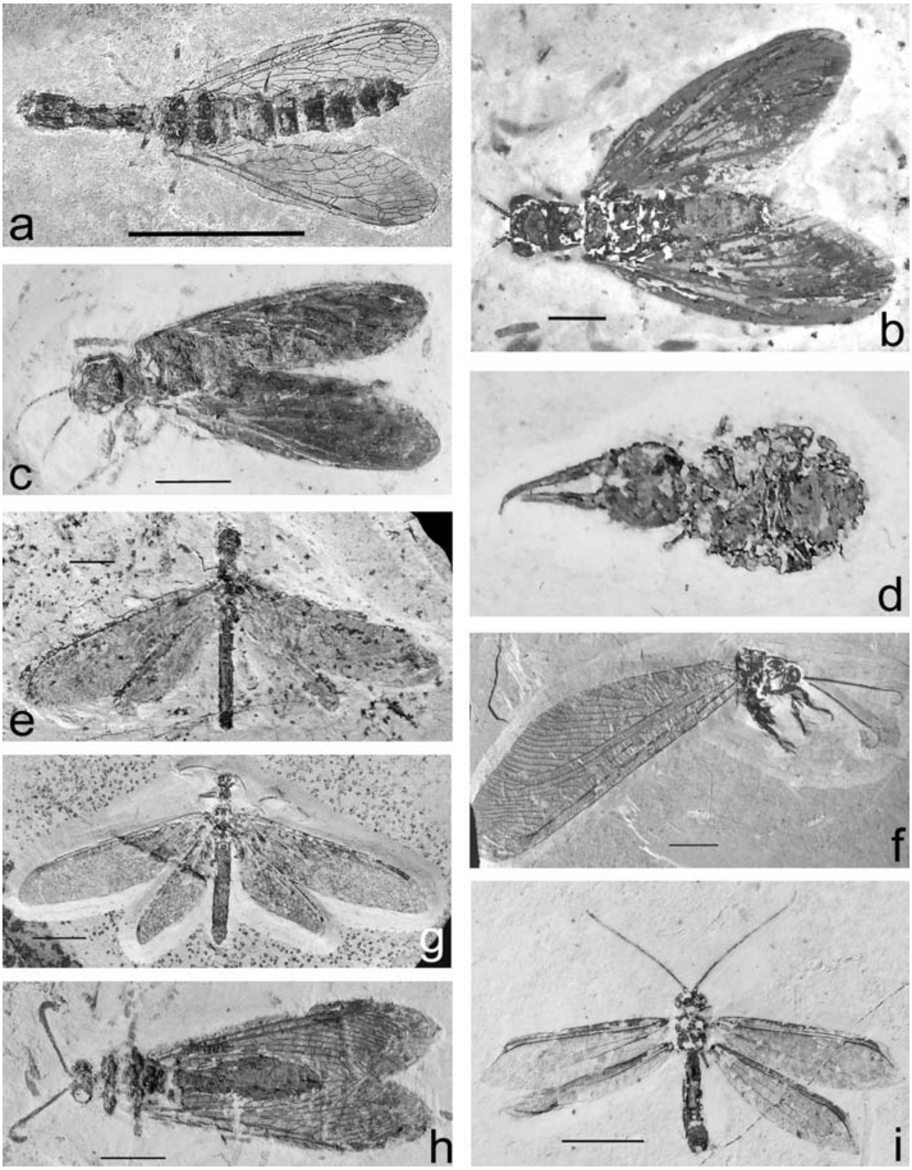

Fig. 11.69. Crato Formation Neuropterida: (a) Raphidioptera, Baissopteridae, *Baissoptera* sp.; scale bar, 10 mm; (b) Megaloptera gen. et sp. nov.; scale bar, 5 mm; (c) Megaloptera gen. et sp. nov.; scale bar, 5 mm; (d) Neuroptera, Myrmeleontiformia, Myrmeleontidae?, larva, MB coll.; (e) Neuroptera, Hemerobiiformia, Allopteridae, *Triangulochrysopa formosa*, SMNS coll.; (f) Neuroptera, Myrmeleontiformia, Palaeoleontidae, *Parapalaeoleon magnus*, holotype SMNS 66000-268; (g) Neuroptera, Hemerobiiformia, Allopteridae, *Triangulochrysopa formosa*, holotype SMNS 66000-271; (h) Neuroptera, Myrmeleontiformia, Myrmeleontidae, SMNS coll.; (i) Neuroptera, Hemerobiiformia, Chrysopidae, SMNS coll. Scale bars: b,c,e,h,i, 5 mm; a,f,g, 10 mm.

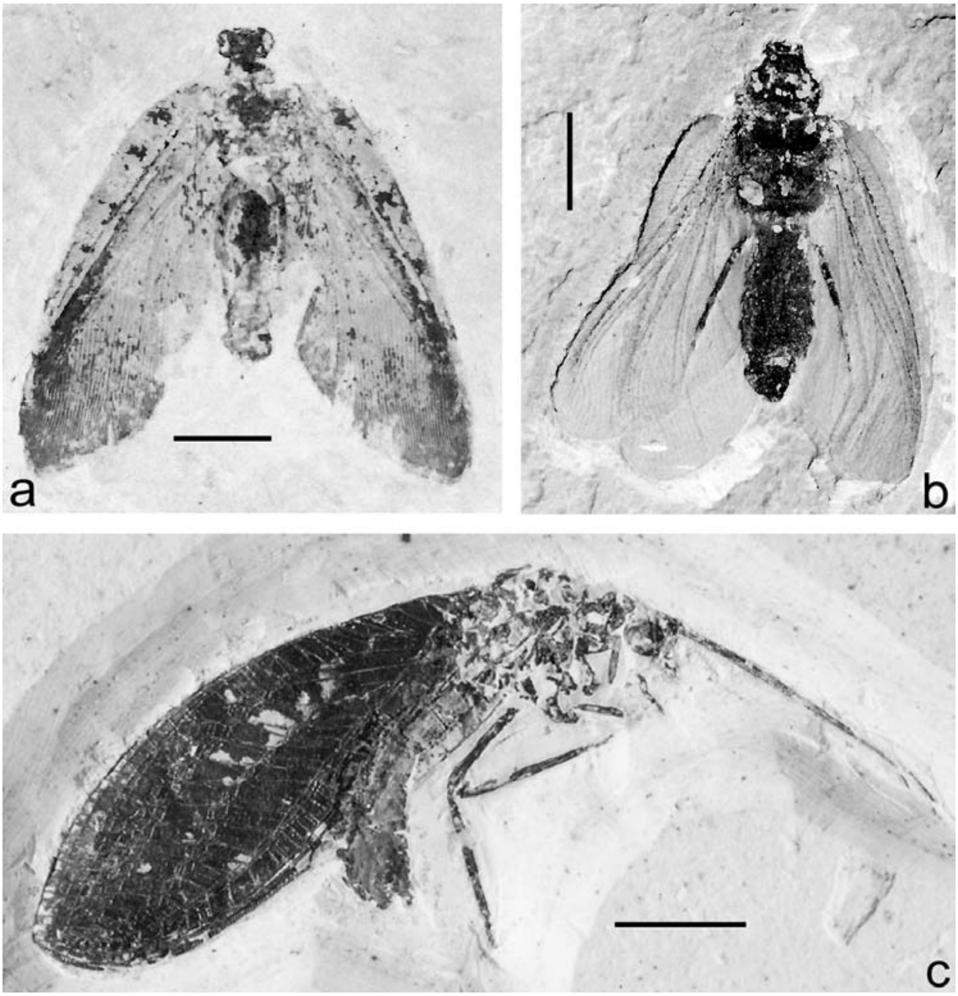

Fig. 11.70. Crato Formation Neuroptera, Hemerobiiformia: (a) Hemerobiidae gen et sp. undetermined, SMNS coll.; (b) Ithonidae *Principalia incerta* Makarkin and Menon, 2007, SMNK PAL 5352; (c) Mesochrysopidae undetermined, SMNS SMNK coll. Scale bars: a, 15 mm; b,c, 5 mm.

11.17 Coleoptera: beetles

Karin Wolf-Schwenninger and Wolfgang Schawaller

The Recent Coleoptera, with four suborders and 166 families (Lawrence and Newton, 1995), are probably the taxon with the highest number of species, not only among insects but also all other animals in general. Early estimates placed the figure at about 500,000 different species worldwide, but more recent studies on biodiversity, mainly in tropical rainforests, suggest a much higher number. Beetles possess a high ecological plasticity, occurring in all terrestrial and freshwater niches from the seashore up to 5,000 m altitude, in all forest types as well as in savannahs, steppes and even severely arid deserts, and are only absent from marine habitats and polar ice caps. The mode of life of larvae and adult beetles of the same species can be identical but might be also quite different.

Large collections of fossil beetles from all epochs and continents are summarized by Arnol'di *et al.* (1992) and Ponomarenko (2003). The oldest beetles recorded in the Old World are Tshekardocoleidae of the Archostemata from the Lower Permian of Moravia (Artinskian) and Chekarda, Ural (Kungurian; Ponomarenko, 2003). The oldest record for the New World is based on a single elytron from Lower Permian (Lower Artinskian) Wellington Formation of Oklahoma. The wing venation of this fossil differs from all other Permian beetles, and therefore is placed in Coleoptera without any familiar assignment (Lubkin and Engel, 2005).

An arboreal lifestyle is considered ancestral for Coleoptera (Crowson, 1981) and the oldest Lower Permian beetles are interpretated as bark-dwellers. Recent representatives of the basal suborder Archostemata (Cupedidae and Micromalthidae) are extremely similar in external appearance to their Mesozoic relatives and still live today under bark in tropical forests. Morphology of the mouthparts of Cupedidae additionally points to a life in arboreal habitats.

Archostemata: reticulated beetles

Archostemate beetles (Plates 13a and b) were common in the Mesozoic, with several fossil species recorded from Mongolia, Spain, North America and China (e.g. Ponomarenko, 1997; Ponomarenko and Martínez-Declòs, 2000; Lubkin, 2003; Tan *et al.*, 2005). Extinct species of the Recent genera *Omma* and *Tetraphalerus* (family Ommatidae) are known from the Lower Triassic to the Lower Cretaceous of Siberia, Central Asia and Western Europe. The few specimens from the Crato Formation probably belong to the Cupedidae (Plate 13a) and Ommatidae (Plate 13b).

Today, this group is quite poor in species. The genus *Omma* is represented by four Australian species, and *Tetraphalerus* by two species in South America (Brazil, Argentina and Bolivia; Neboiss, 1960; Vulcano and Pereira, 1975). Species of *Omma* occur in mature forests, but live also in more arid regions of open woodland and pastureland (Neboiss, 1960; Lawrence, 1999). Species of *Tetraphalerus* are known from arid parts of South America. From what is known of the ecology of other Archostemata (Cupedidae and Micromalthidae), it is assumed that ommatid larvae feed on dead, fungus-infested wood.

Adephaga

This suborder (Plate 13d) includes the terrestrial families Carabidae (including Paussinae and Cicindelinae), Rhysodidae, Trachypachidae and the aquatic families †Coptoclavidae, †Liadytidae, †Triaplidae, †Parahygrobiidae, Gyrinidae, Haliplidae, Hygrobiidae, Amphizoidae, Noteridae and Dytiscidae.

The first Adephagids are found in the Triassic, in which they are represented by many aquatic forms. Probably the earliest representatives of the adephagan lineage are the Triassic Shizophoridae (Archostemata; Beutel, 1995). During the Early Jurassic the diversity of Adephaga increased greatly, with at least the Recent families Carabidae and Trachypachidae being present by that time. In the Middle Jurassic they were the dominant group of beetles (Carpenter, 1992). The first aquatic beetles with adaptations for swimming in both the adult and larva appeared in the Cretaceous (Ponomarenko, 2003).

Coptoclavidae

The †Coptoclavidae are an extinct Mesozoic family composed of medium to large aquatic beetles with divided compound eyes (like modern Gyrinidae). The larvae had raptorial front legs and paddle-like mesothoracic and metathoracic legs (Maddison, 1995). The most common beetle during the Lower Cretaceous seemed to be *Coptoclava longipoda* Ping, 1928 because many thousands of larvae and hundreds of adults have been found in numerous localities in East Siberia, Mongolia and China (Ponomarenko, 2003).

A giant larva from the Crato Formation, described as *Conan barbarica* by Martins-Neto (1998c), was regarded as the first record of this group for the Southern Hemisphere. However, this fossil does not belong in Coleoptera: rather it is the larva of the giant dragonfly *Nothomacromia* (see Bechly, 1998c), which is quite common in the Crato Formation (Plate 13c). The long abdominal appendages are formed by the paraprocts and not by the cerci as was concluded by Martins-Neto. He also misinterpreted the spine-like epiproct as a paracercus. Consequently, Zamboni (2001) correctly concluded that the beetle family Coptoclavidae is not present in the New World and that *Conan barbarica* is a dragonfly nymph. Obviously based on Zamboni (2001), Martins-Neto (2005b: 475) lists '*Conan barbarica* Martins Neto, 1996' (*sic*) as Odonata – Aeschndiidae? *Conan barbarica* is designated by Bechly (see Section 11.5) a junior synonym of the dragonfly species *Nothomacromia sensibilis*.

Dytiscidae: diving beetles

Dytiscidae were comparatively rare in the Mesozoic and are only known from adults (Ponomarenko, 2003). The first fossil predaceous diving beetles from the Jurassic and Lower Cretaceous deposits in Asia were described by Ponomarenko (1987). A few alleged dytiscid specimens from the Crato Formation have been mentioned by Grimaldi and Maisey (1990: 7, figures 2f and h), but are still undescribed.

Carabidae: ground beetles and tiger beetles

The earliest fossil Carabidae is from the Late Triassic of Virginia (Grimaldi and Engel, 2005: 369, figure 10.16), but according to Ponomarenko (in Arnol'di *et al.*, 1992) the modern taxa first appear in the Cretaceous.

Grimaldi and Maisey (1990) were first to report on an unnamed carabid from the Crato Formation, and Grimaldi and Engel (2005: 370, figure 10.17) figure a beautiful but undescribed specimen that they attribute to an 'unusual caraboid' (but see below). The first species to be described from the Crato Formation is *Oxycheilopsis cretacicus* Cassola and Werner, 2004, which belongs to the subfamily Cicindelinae (Plate 13d), and is the oldest known fossil tiger beetle. The holotype is in possession of Mr Franz Wachtel (Öhnböck/Egling, Germany) and will be donated to the Zoologische Staatssammlung in Munich (ZSM), Germany. Adult cicindelids are characterized by large mandibles, prominent eyes and long legs: features that allow them to be very mobile and effective predators both on the soil surface and on plants.

Martins-Neto (2005b: 480) mentions *Alexcarabus megagnathus* Martins-Neto, 2002, but we could not locate this publication.

Polyphaga

Although the suborder Polyphaga (Plates 13e–p) represents the largest group of beetles today, it is often claimed that they did not make their appearance until the Early Jurassic. However, the undisputable record of Staphylinidae from the Upper Triassic (see below) demonstrates that the origin of Polyphaga must have been much older. In the Early Jurassic they still had a relatively low diversity which increased by the Mid Jurassic and was considerably enhanced by the end of the Jurassic, by when they had clearly become the dominant suborder, a position they still maintain. The Early Cretaceous species appear essentially like Cenozoic and modern species (Carpenter, 1992). Many examples of this group occur in the Crato Formation and are discussed in detail below.

Staphylinidae: rove beetles

The oldest staphylinid, more than 200 myr old, is from the Upper Triassic of Virginia, USA. Deposits from the Lower Jurassic to Middle Cretaceous in Eurasia have yielded specimens, most of which resemble members of modern subfamilies.

The Mesozoic Staphylinidae include the subfamilies Olisthaerinae, Omaliinae, Oxytelinae, Piestinae, Staphylininae, Tachyporinae and Trigonurinae, with Omalinae and Oxytelinae most frequently recorded (Herman, 2001). There are at least 10 genera of Middle Jurassic to Lower Cretaceous age that have been placed or probably belong in Omaliinae, some of which were compared with Recent genera of Omaliini or Anthophagini when described. The Recent members of Omaliini are trophically divers, including predators, pollen-feeders and probable saprophages and mycophages, found in forest litter, under bark and in fungi. Most genera are either northern temperate or southern temperate. The tribe Anthophagini is a very large and diverse Holarctic group. Species are predators or pollen-feeders, many of the former occurring along streams, especially in mountain areas, and some in forest litter (Newton and Thayer, 1995).

Archetypal staphylinids were probably saprophagous (scavengers). Saprophagy is still a major feeding mode in Piestinae. Mycophagy has evolved in some Tachyporinae. Phytophagy has evolved in some Oxytelinae. Saprophagy has evolved toward carnivory in many Tachyporinae and in the bulk of species in the family, so that it may be said that most Staphylinidae – tens of thousands of species – are facultative predators (Frank and Thomas, 2002).

The few staphylinids from the Crato Formation (six specimens known) remain undescribed (Plate 13e) or only poorly described. Martins-Neto (2005b: 480) mentions *Caririderma pilosa* Martins Neto, 1990a and *Cratophyllina minuscula* Martins Neto, 2002 and Grimaldi and Engel (2005: 376, figure 10.28) figure a nice example (see also Grimaldi and Maisey, 1990: 7, figure 2d and e).

Since species-level identification of present-day staphylinids normally requires dissection at least of the genitalia, the species descriptions of fossil specimens – where dissection is extremely difficult – have very limited value.

Scarabaeidae: dung beetles

The oldest scarabaeoid-like beetle, the small *Aphodiites* (5 mm long), comes from the Lower Jurassic of Switzerland. Nikolajev (1992) described several Upper Jurassic and Lower cretaceous species from Asia. Although based on only partially visible wing venation, the fossils described by Nikritin (see Arnol'di *et al.*,

1992) from the Lower Cretaceous of China resemble modern Geotrupinae and Hybosoridae (Scholtz and Chown, 1995).

According to Ponomarenko (2003) Lower Cretaceous scarabaeoids were most likely xylomycetophagous, rather than coprophagous. Evidence for beetle coprophagy (in dinosaurian dung) is only first known from the Upper Cretaceous (Chin and Gill, 1996). Fourteen specimens of Scarabaeidae have been examined from the Crato Formation (Plate 13f), 11 of which are probably referrable to Aphodiinae (Grimaldi and Maisey, 1990), and Grimaldi and Engel (2005: 380, figure 10.34) figure a nice example.

Hydrophilidae: water scavenger beetles

Recent hydrophilids, both as adults and as larvae, feed on plants or plant debris and are aquatic, usually inhabiting slow-running or standing fresh water and adjacent muddy habitats: or, they are coprophagous and occur in vertebrate excrement in various stages of decomposition. Several different genera and species of Hydrophilidae are described from the Cretaceous of Transbaikalia (Arnol'di *et al.*, 1992) and a well-preserved beetle larva from the Crato Formation (Plate 13g) shows the general shape of a hydrophilid larva of an indeterminate subfamily.

Buprestidae: jewel beetles

Buprestidae were very characteristic beetles of the end of the Lower Cretaceous (Ponomarenko, 2003). Several taxa of Mesozoic buprestids are described from Russia, Kazakhstan and Mongolia (Alexeev, 1993, 1996, 2000). These taxa could not be assigned to Recent subfamilies because taxonomically important features could not be studied; therefore, Alexeev (1994) created the new extinct subfamily †Parathyreinae to accommodate them. While many of the Asian fossil Buprestidae are only represented by isolated elytra, the Crato specimens are entire and fairly well preserved, and in one case even the aedeagus can be seen (Plate 13h).

Dryopidae

Adult dryopids and most of the larvae occur in leaf litter and soil, usually in wet or moist habitats. Some genera are aquatic as adults, and one genus (*Stygoparnus*) is truly aquatic as both larvae and adults. A single specimen which possibly belongs to this family is known from the Crato Formation and was figured by Grimaldi and Engel (2005: 381, figure 10.35).

Elateridae: click beetles

The elaterids, or click beetles, possess a prosternal process which slots into a groove in the mesosternum (Plate 13i) and allows the body to flex suddenly, thus producing the eponymous clicking sound. The biology of many Recent species remains unknown and the larval habits are highly varied. Larvae can be found under the bark of trees, in rotten wood or in the soil. Several species live in partially rotten wood where they feed on cerambycid beetle larvae. Other predaceous larvae hunt scarab beetle larvae in the soil, and the larvae of a Recent genus live in or adjacent to termite nests feeding on the inhabitants. The 'wire-worms' feed on plant roots and can be a pest.

The first occurrence of elateroid beetles dates back to the Early Jurassic (Dolin and Nel, 2002), and they are well represented in the fossil record from the Late Jurassic onwards. About 30 genera have been described, most from Karatau in Kazakhstan. A few specimens are known from the Crato Formation (Plate 13i; Grimaldi and Engel, 2005: 382, figure 10.38) but no species have been described.

Trogossitidae

Kirejtshuk and Ponomarenko (1990) described the new subfamily †Meligethiellinae within Peltidae, consisting of three genera with a couple of species from the Lower Cretaceous and Upper Jurassic of Transbaikalia and Kazhakstan. Lawrence and Newton (1995) considered Peltinae as a subfamily of Trogossitidae within the superfamily Cleroidea.

A single, as yet undescribed, fossil SMNS 66467 of the Crato Formation surely belongs to the Peltinae (Plate 13j). The flat body of the fossil by analogy with recent taxa mirrors an identical mode of life under rotten tree bark.

Nitidulidae: sap beetles

Fossil beetles interpreted as nitidulids (Kirejtshuk and Ponomarenko, 1990) appear first in the Lower Cretaceous, the oldest belonging to the subfamily Carpophilinae, while later species are placed in the Nitidulinae.

Recent nitidulids occupy a wide range of habitats and live under bark, within wood of various stages of decomposition, in the holes of other xylobiontic insects, in scattered wood sap, in decayed fruits and some taxa even live in flowers.

A specimen from the Crato Formation has been described as a nitidulid by Grimaldi and Maisey (1990), and another specimen figured here (SMNS 66470; Plate 13k) with clavate antennae and free tip of the abdomen is also assigned to this family.

Cucujidae *sensu lato*: flat bark beetles

Four Recent cucujoid families are commonly known as flat bark beetles: Cucujidae (*sensu stricto*), Laemophloeidae, Passandridae and Silvanidae. These mostly medium-sized, dorsoventrally compressed beetles are usually found under the bark of dead trees. The earliest records of Cucujidae occur in 100 myr old Burmese amber (Grimaldi and Engel, 2005), but two specimens (SMNS 66469, SMNS 66468; Plate 13l) from the slightly older Crato Formation ($\approx$120 myr old) demonstrate that cucujids had already appeared, and were widespread in the Early Cretaceous. In addition, Grimaldi and Engel (2005: 370, figure 10.17) illustrate an 'unusual caraboid beetle' from the Crato Formation which definitely does not belong to the carabids but resembles a cucujid. The specimen shows a great similarity to one of the two Crato cucujid fossils deposited at SMNS and might belong to the same species.

Tenebrionidae: darkling beetles

Recent Tenebrionidae are one of the most species-rich families of beetles, but surprisingly there are no Mesozoic records: the earliest fossil tenebrionids come from Tertiary deposits, such as the Eocene/Oligocene Florissant fossil beds of Colorado (Wickham, 1914) and the Middle Eocene Messel Formation of Germany (Hörnschemeyer, 1994). The first fossil tenebrionid from Dominican amber was described by Kaszab and Schawaller (1984).

Recent tenebrionids from different taxa belong roughly to two ecological groups, one consisting of dry and even arid-tolerant forms, the other, probably larger, group inhabiting decayed wood and fungi and could be considered as indicators of mature forests.

Although family characters cannot be seen, a single specimen SMNS 66472 (Plate 13m) with serrate antenna might point to the presence of Tenebrionidae in the Crato Formation. The compact body with short legs are characters of the tenebrionid forest dwellers (in contrast, slender bodies with longer legs indicate running behaviour in arid settings).

Pyrochroidae: fire-coloured beetles

A supposed pyrochroid beetle from the Crato Formation was described under the name *Cretaceimelittomoides cearensis* Vulcano and Pereira, 1987, and incorrectly listed by Martins-Neto (2005b: 480) as '*Cretaceomelittomoides araripensis* Vulcano and Pereira, 1987' as a member of the 'Pirochoidae' (sic). However, the publication Vulcano and Pereira (1987) appears only to be a congress abstract and no valid taxonomic description is provided, such that the name has to be considered as a *nomen nudum*. Thus, there is no definitive evidence for this group in the Crato Formation.

Chrysomelidae: leaf beetles

Eight Recent subfamilies of chrysomelids are represented in the Mesozoic: Sagrinae, Clytrinae, Cryptocephalinae, Chrysomelinae, Eumolpinae, Galerucinae, Alticinae and Cassidinae, most of which had already appeared by the Jurassic. Unfortunately, as a consequence of poor preservation of the diagnostic characters some of these fossil beetles may be incorrectly determined and several may not be Mesozoic chrysomelids at all (Santiago-Blay, 1994).

There are no fewer than 40,000 species worldwide today, but probably 100,000 species have existed since the Jurassic, when they first co-evolved with the Cycadoids and other primitive plant families. Subsequently their diversity increased rapidly with the Cretaceous radiation of the flowering plants. Pollen-feeding tends to be more common in the more primitive groups, but occurs commonly throughout all chrysomelids. Pollen as a food resource was available on conifers, cycads and precursors to angiosperms before the end of the Jurassic and its utilization as food possibly represents the initial step in the transition from other feeding modes to herbivory (Samuelson, 1994).

Feeding damage characteristic of hispine beetles on fossil angiosperms (Zingiberales from the latest Cretaceous) is documented. The subfamily Hispinae therefore evolved at least 20 myr earlier than suggested by insect body fossils (middle Eocene). This demonstrates the presence and trophic activity of derived, specialized, monocot-feeding chrysomelids near the time of the first appearances of present-day host groups (Wilf *et al.*, 2000).

Only two fossil chrysomelids are known from the Crato Formation. In respect of the few visible characters one (SMNS 66471; Plate 13n) might belong to the Eumolpinae, as it closely resembles the genus *Graphops* (tribe Scelodontini) from North America (L. Medvedev, personal communication). Larvae of this subfamily are primarily root-feeders, but adults commonly appear on the host plant.

Superfamily Curculionoidea: weevils

Although the Obrieniidae are often considered to be the oldest Curculionoidea, appearing in the Triassic (Ponomarenko, 2003), according to Kuschel (2003) there appears to be little reason for their inclusion in the superfamily of weevils, because the only character that would justify Obrieniidae within Curculionoidea is the presence of a head extended forward into a kind of rostrum. An extended head alone, however, does not define a curculionoid since this is also known in several other beetle groups. In the Late Jurassic the Curculionoidea became one of the most diverse and abundant groups among the Polyphaga (Arnol'di *et al.*, 1992). Early Cretaceous curculionid beetles have been found mainly in Asia but also in Europe (Gratshev and Zherikhin, 2000). Zherikhin and Gratshev (2004) studied fossil material from the Crato Formation (AMNH collection) and have described five new species in four new genera belonging to the following family group taxa:

- Nemonychidae: Rhinorhynchinae: Rhinorhynchini
  Cratomacer immerses
  Cratomacer ephippiger
- Belidae: ?Pachyurinae: ?Pachyurini
  Davidibelus cearensis
- ? Eccoparthridae
  Martinsnetoa dubia
- Brentidae: ?Eurhynchinae
  Axelrodiellus ruptus

In addition, the SMNS collection contains a weevil SMNS 66553 (Plate 13o) from the Crato Formation that resembles the belid subfamily Oxycoryninae (A. Riedel, personal communication).

Most Recent members of the Rhinorhynchinae, Belidae, Eccoparthridae and Eurhynchinae are distributed in the Southern Hemisphere. The Recent Rhinorhynchinae include the most morphologically plesiomorphic nemonychids, which are associated with strobili of Araucariaceae or Podocarpaceae in Chile, Argentina and Australia plus a single species living on Pinaceae in Colorado. Today the belid tribe Pachyurini comprises 13 genera associated with *Araucaria* and *Agathis* in Australia and New Zealand and a single genus associated with Podocarpaceae and Cupressaceae in Brazil (Farrell, 1998). The Recent New World taxa of Oxycoryninae live in association with either Araucariaceae or Cycads or root-parasitic Balanophoraceae and Hydnoraceae while the African and Asian members of this subfamily were collected in association with Celastraceae and Vitaceae or with palm flowers (Anderson, 2005). Araucariaceae are abundant in the Crato Formation (see Chapters 19 and 20).

Members of the family Attelabidae are known from the Lower Cretaceous of Asia but have not been recorded from the Crato site (Zherikhin and Gratshev, 2004). However, among the SMNS Crato fossils is one specimen SMNS 66449 (Plate 13p) which might belong to the subfamily Rhynchitinae (similar to *Auletes*, A. Riedel, personal communication). Rhynchitinae are generally associated with dead reproductive and other structures of a variety of plants (e.g. in decaying flower buds or fruits).

The most advanced family Curculionidae, appeared in the Early Cretaceous of Asia, but have yet to be found in the Crato Formation.

11.18 Hymenoptera: bees, wasps and ants

Till Osten

Hymenoptera is one of the most diverse Recent insect orders with at least 110,000 described species. The eusocial lifestyle and forming of complex societies with castes in some of the families (Formicidae, Vespidae and Apidae) also accounts for the fact that Hymenoptera are the most individual-rich insect group, which has conquered nearly all suitable biotopes. Consequently, the probability of fossilization should also be relatively high (Burnham, 1978). Nonetheless, the work of Darling and Sharkey (1990) and Martill (1993) documented comparatively few fossils of this group for the Crato Formation. In contrast to this, Rasnitsyn (1988; see also Grimaldi, 1990 and Grimaldi and Engel, 2005) presents a comprehensive summary of fossilized Hymenoptera from the Cretaceous from various other localities, which documents representatives from nearly all Recent families as well as several extinct families. Wasps from the group Parasitica are the most abundant elements, followed by Aculeata and comparatively few 'Symphyta'.

However, the Hymenoptera from the Crato Formation that were studied for this work show yet another grouping. The evolution, especially of the social Aculeata, had still not progressed far at this point in the Earth's history. The eusocial societies of the primitive Formicidae, Vespidae and Apidae consisted only of a few individuals; the separation into castes and therefore the increase of number of individuals had only just begun. Within the most primitive Formicidae ('Ponerinae', Myrmeciinae) this condition is still visible today (Wilson, 1971; Hölldobler and Wilson, 1990).

In most cases, the preservation of the fossils only allows a rough identification to familial level, and in some cases to subfamily or genus and even the description of new species. In contrast to amber inclusions, the specimens can usually only be examined from the single preserved side, and the important characters for confident determinations are often not visible.

Of special importance is the first record of a fossilized Sapygidae of the subfamily Fedtschenkiinae. However, some characteristics are unfortunately not visible in this specimen (shape of the compound eyes, toruli and the cleft between first and second sternum). Only the comparison with Recent material, and morphologically similar but unrelated representatives of the Vespoidea (Tiphiidae, Spyginae), allowed a determination and classification by successive exclusion of all other possibilities. The primitive aculeate Hymenoptera of the Lower Cretaceous were still very similar, and their group-defining characteristics were not as well developed or not developed at all compared with Recent representatives.

Only very vague conclusions about the habitat and the climate can be made on the basis of the fossil Hymenoptera assemblage of the Crato Formation. Overall, it seems that the habitat was very heterogeneous, with relatively humid biotopes with rather dense vegetation, as well as dry and relatively hot savannah and desert areas with sparse vegetation.

‘Symphyta’: sawflies

The Anaxyelidae–Syntexinae (Plates 15f and g) and Siricidae (Plate 15h) were the predominant groups in the Mesozoic. From the former family, the holotype (AMNH 43270) of *Prosyntexis gouleti* (Figure 11.76b) was described by Darling and Sharkey (1990), but Rasnitysn *et al.* (1998) transferred the genus *Prosyntexis* to the family Sepulcidae in the subfamily Trematothoracinae. Martins-Neto *et al.* (2007) described a second species, *Prosyntexis legitima*, in the family Sepulcidae. The family Siricidae (female specimen without number in coll. MURJ; Plate 15h) is reported here for the first time for the Crato Formation.

Apocrita/Parasitica: parasitic wasps

Cratephialtites kourios of the family Ephialtitidae is not rare in the Crato Formation. Darling and Sharkey (1990) had described the species as genus *Karatous* based on two specimens (AMNH 43269 and 43263; Figure 11.75d). A further specimen (AMNH 46321) was published by Grimaldi and Engel (2005: figure 11.11), and a similar, undescribed specimen has been studied by the author (SMNS 66296). However, a new specimen without number in coll. MURJ shows crucial new details of the legs and particularly the complete wing venation (Plates 15j and k). In the same collection, a possible representative of the Ichneumonoidea (Plate 15i) can be found which would be a first record of this group for the Crato Formation. Apart from these, only the families Proctotrupidae (*Protoprocto asodes*, AMNH 44101; Figure 11.76a) and Mesoserphidae (AMNH 43272; Figure 11.74) have been recorded by Darling and Sharkey (1990).

The parasitic larvae of the Apocrita prefer as hosts the adults, larvae and eggs of species of the orders Lepidoptera, Hymenoptera (‘Symphyta’), and Diptera.

Apocrita/Aculeata: stinging wasps

The Apoidea (Apidae+‘Sphecidae’) represent nearly 50% of the fossil aculeate Hymenoptera from this locality. Their abundance suggests a rich flower assemblage as a food resource for the adult animals, thus also a moderately dry and warm climate. Furthermore, a large and suitable contingent of food (spiders and insects such as Diptera, Hymenoptera, Orthoptera, Lepidoptera or Coleoptera and their larvae) must have been available for the larval development of the 'Sphecidae'. A sufficient amount of nectar and pollen must also have been available for the Apidae and their larvae.

The Vespoidea are represented by Scoliidae–Archaeoscoliinae (Figure 11.72c), some Tiphiidae (Rasnitsyn, 1986a; Figure 11.72a, Plates 15n and o), a single specimen of Sapygidae–Fedtschenkiinae (Figure 11.72b), and one questionable Mutillidae and Pompilidae (Plate 15l), as well as some Vespidae–Eumenidae (Carpenter and Rasnitsyn, 1990) (Plate 15p) and two specimens of the Formicidae–Myrmeciinae (Figure 11.77, Plate 15m; Wilson *et al.*, 1967; Wilson, 1985; Brandao *et al.*, 1989). These representatives of the Vespoidea rather suggest a dry, very warm, subtropical climate. Some areas might have had a savannah or desert-like type of vegetation (*Salicornia*-, *Salsola*- or *Arthemisia*-steppe for Fedtschenkiinae). These Vespoidea need other insects or spiders for the development of their larvae. Except for Formicidae, the adult animals are mostly visitors to flowers.

Mesorhopalosoma ceareae (holotype AMNH 44266, and two further specimens AMNH 43276 and 44109; Figures 11.75f and g), which was described by Darling and Sharkey (1990) as a species of Rhopalosomatidae, definitely does not belong to the Rhopalosomatidae or Pompilidae, but is more likely a further representative of the Angarosphecidae ('Sphecidae').

Pompilidae: spider wasps

Currently, only a single fossil that could be a possible representative of this family is known from the collection of MURJ (Plate 15l). This is even more surprising, as the Pompilidae are surely a very old subgroup of the Aculeata. This is already shown in their very limited prey spectrum, which the adults catch as food for their larvae: all Pompilidae exclusively hunt spiders, which explains their English vernacular name, spider wasps. Fossil spiders are relatively frequently found in the Crato Formation. The Pompilidae are cosmopolitan, but around 4,200 species populate tropical areas (Ceropalinae, Pepsinae, Pompilinae). The present fossil could belong to the subfamily Pompilinae due to its coiled antenna, the shape of the compound eyes, the pronotum, the wing venation (so far as can be seen), the comparatively short hind legs and the wide metasoma.

Formicidae: ants

The fossil record of ants (Figure 11.77, Plate 15m) is quite extensive (Grimaldi and Engel, 2005; for a review see Brandao *et al.*, 1989). Ants are, for example, very abundant in Tertiary Baltic and Dominican amber. However, the older the formation, the more sparse are the fossil records of ants. As mentioned above, this is probably due to the evolution of the eusocial societies, which consisted of very few individuals in the earlier stages, with hardly differentiated castes. Therefore, the first record of a fossilized ant (*Sphecomyrma freyi*) in the amber of the Upper Cretaceous of North America (Wilson *et al.*, 1967) was particularly interesting. Because of its primitive morphological structures, it was very difficult to classify the fossil in one of the Recent subfamilies. The authors therefore created the subfamily †Sphecomyrminae. Wilson (1985) described another species of *Sphecomyrma*, but at the same time also described some further Formicidae from the Eocene of Canada.

A real surprise was the record of a Formicidae from the Lower Cretaceous of the Crato Formation (Brandao *et al.*, 1989). However, the attribution of the specimen was at first not very confident at all, and is still disputed to this day (J. Rust, personal communication). The preservation of the holotype is relatively poor, with indistinct edges and incomplete cephalic area. Furthermore, it is not possible to see whether the specimen had wings or not. Subsequently, the animal has been mistaken for a representative of the Ampulicidae (‘Sphecidae’), which often have an extremely similar general habitus (Figure 11.72e). However, the structure of the petiolus indicates that the fossil indeed belongs to the Formicidae of the subfamily Myrmeciinae (bulldog ants), whose distribution is now limited to Australia. As it was not possible to attribute the new fossil species to the single Recent genus *Myrmecia*, it was named *Cariridris bipetiolata* Brandao *et al.*, 1989.

Two further specimens of *Cariridris* may have been discovered while examining fossil material for the present volume. There is no doubt that these two fossils also belong to the same genus and species *Cariridris bipetiolata* (Figure 11.77). The specimen SMNS 66565 (Plate 15m) is much better preserved than the holotype, and supports the attribution to Formicidae–Myrmeciinae (petiolus and head structures). The absence of wings in this specimen is of course no valid evidence against such an attribution.

Tiphiidae: flower wasps

With a worldwide distribution of 1,500 species, the family Tiphiidae (Figures 11.72a and 11.75e, Plates 15n and o) is a very heterogeneous subgroup of Aculeata. According to Kimsey (1991), they can be classified in seven subfamilies: Anthoboscinae, Tiphiinae, Brachycistidinae, Myzininae, Methochinae, Thynninae and Diamminae. Extreme sexual dimorphism is an often-occurring phenomenon in this family. The recognition of the conspecific status of both sexes is in most cases only possible if the animals are found in copula (e.g. in the case of Methochinae, Myzininae and Thynninae). This makes a proper classification of fossil representatives even more difficult or even impossible. Anthoboscinae and Tiphiinae present a less-marked

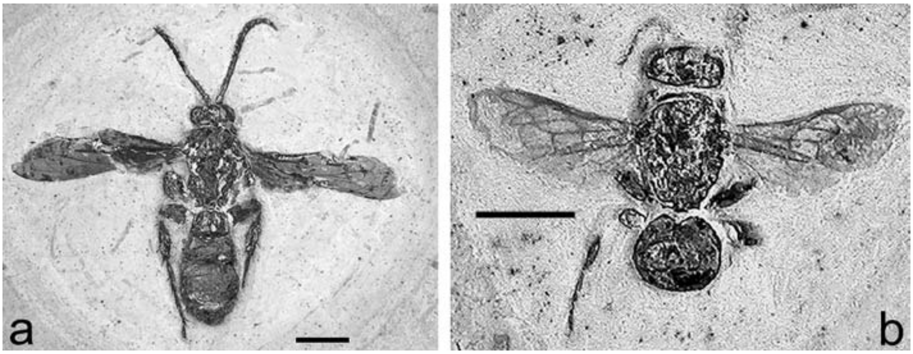

Fig. 11.71. Crato Formation Hymenoptera: (a) Angarosphecidae, *Cretobestiola* spec., SMNS 66297; scale bar, 5 mm; (b) Apidae, coll Murata; scale bar, 2 mm.

sexual dimorphism. All Tiphiidae are ectoparasitoids that feed on live beetle larvae living underground, except for the Australian Diamminae that feed on Gryllotalpidae. In terms of Earth history, they seem to represent a rather old group. Anthoboscinae are particularly distinguished by a high number of plesiomorphies (Brothers, 1975). A review of of fossil Tiphiidae was provided by Rasnitsyn (1986a).

Architiphia rasnitsyni was described as first fossil Tiphiidae (Anthoboscinae) from the Crato Formation by Darling and Sharkey (1990) based on a single holotype specimen (AMNH 43265), which was excellently preserved with clearly recognizable wing venation (Figure 11.75e). A further specimen of the same species was discovered by looking through the fossil material for the present work. The fossil is also preserved in ventral aspect and also shows legs and wing venation very clearly (Plate 15n). In addition, two undescribed specimens of putative Tiphiidae were found, for which a confident determination was not yet possible (Figure 11.72a, Plate 15o).

Sapygidae: club-horned wasps

Records of fossil Sapygidae (Figures 11.72b and 11.73a) are very rare (in Spahr, 1987: Gattung *Sapyga* von Brischke, 1886; Handlirsch, 1925). Therefore, the description of a fossil male sapygid from Middle Cretaceous Burmese amber by Bennet and Engel (2005) was of great importance. The Sapygidae have been classified in two subfamilies, Sapyginae and Fedtschenkiinae, by Pate (1947). Tobias (1965) elevated the taxonomic ranks without any plausible arguments to two families Sapygidae and Fetschenkiidae in a superfamily Sapygoidea. However, the recently discovered fossil exhibited so many morphological differences to the Recent Sapygidae (Sapyginae, Fedtschenkiinae), that Bennet and Engel (2005) decided to create a new subfamily †Cretosapyginae. The justification for the attribution of this amber fossil to the family Sapygidae is doubtful to the present

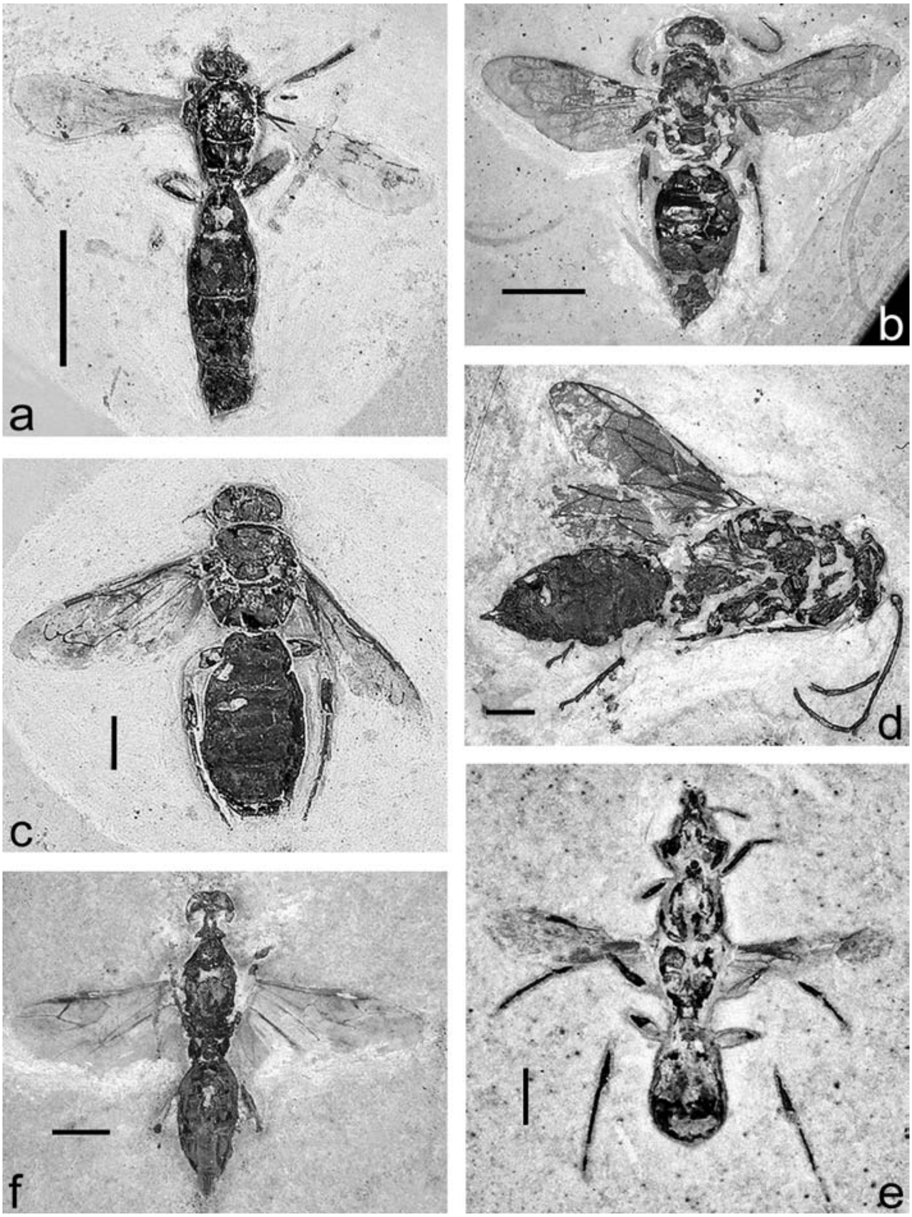

Fig. 11.72. Crato Formation Hymenoptera: (a) Tiphiidae, Tiphiinae?, coll Murata; (b) Sapygidae, *Cretofedtschenkia santanensis* gen. et sp. nov., holotype SMNS 66594; (c) Scoliidae, *Cretoscolia brasiliensis* sp. nov., holotype MURJ without number; (d) Angarosphecidae, *Cretosphex magnus*, F103 coll. MSF; (e) Ampulicidae, N69 coll. MSF; (f) Ampulicidae, SMNS 66291. Scale bar: a,b, 5 mm; c–f, 2 mm.

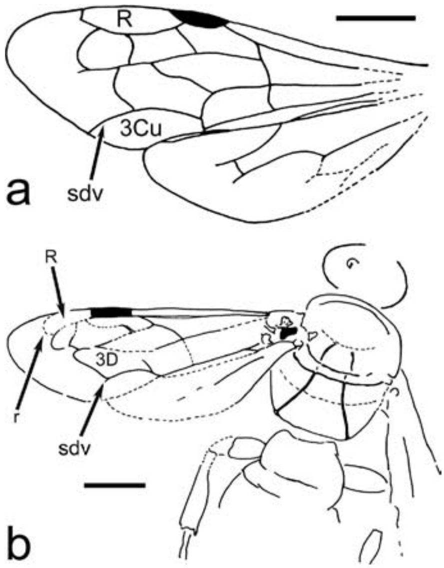

Fig. 11.73. Crato Formation Hymenoptera: (a) Sapygidae, *Cretofedtschenkia santanensis* gen. et sp. nov., holotype SMNS 66594, wings; (b) Scoliidae, *Cretoscolia brasiliensis* sp. nov., wings, holotype MURJ. Scale bar, 2 mm.

author: although the specimen is an amber fossil, which is much better preserved and shows many more details than those of the Crato Formation specimens, it simply lacks certain characteristics of the Sapygidae. Additionally, a referral to the sister group of the Sapygidae, the Mutillidae, could also be considered (Brothers, 1975).

The first record of a very well-preserved fossil Sapygidae, Fedtschenkiinae from the Lower Cretaceous Crato Formation of Brazil justifies a more exhaustive treatment of this taxon in the present work. The 80 Recent species are cleptoparasites or ectoparasitoids of Megachilidae, Apidae (Anthophorinae) and Eumeninae. The Recent representatives are widely distributed, except for the Australian region. A synapomorphy of all Sapygidae is the transformation of the sixth metasomal sternum of the female. It forms a cone at the metasomal apex from which the sting (or more precisely the ovipositor) extends. The strong sting of the Sapygidae does not only function as a defence device, but also still as an ovipositor, as in Chrysididae and Dryinidae. The rear edge of the pronotum is slightly concave, and its rounded sides reach the tegulae.

Due to the relative abundance of the Recent Sapyginae, much work has been done on their distribution, determination, systematics and biology (Bischoff, 1927; Pate, 1946, 1947; Bradley, 1955; Malyshev, 1968; Königsmann, 1976; Gauld and Bolton, 1988; Goulet and Huber, 1993; Gusenleitner, 1994, 1996, 1997; Yilderim and

Gusenleitner, 2001). In contrast to this, the living Fedtschenkiinae are comparatively rare, and show an extremely disjunctive distribution: *Fedtschenkia anthracina* Ashmead in the desert areas of California and Colorado, *F. grossa* Saussure in Turkey, Turkmenistan, Uzbekistan, Tajikistan and Iran, *F. indigotea* Radoszkowsky in Turkmenistan, *F. palaestinensis* Guiglia in Israel and *F. libanoi* Guiglia in Lebanon (Guiglia, 1955, 1969, 1972; Osten, 2004). According to Tobias (1965) and Y. Popov (personal communication), the relict-like distributional pattern of the Fedtschenkiinae suggest a Tertiary or even pre-Tertiary origin. The flower-visiting habit of *F. grossa*, which feeds on *Salsola subaphylla*, suggests an old desert flora as the ancestral biotope. It is remarkable that the very primitive genus *Crioscolia* (Scoliidae) shows an almost identical distribution to the Fedtschenkiinae (Osten, 2004).

The fossil Fedtschenkiinae from the Crato Formation, a complete female specimen, unfortunately does not exhibit all constituent characteristics of the group due to preservational circumstances. Particularly in the area of the head, the most important characters cannot be seen: the compound eyes are only weakly sinuate (reniform in Sapyginae), and the toruli are close together (widely separated in Sapyginae). The shape of the pronotum is visible. In the dorsal antero-lateral area it is rounded and flat (contrary to a very acute carina in Sapyginae). The wing venation is excellently preserved. It hardly differs from that of the Recent species. This wing venation is very primitive for Aculeata, and rather similar to other basal groups, for example within the Tiphiidae (Anthoboscinae or Tiphiinae). This restricts the value of the wing venation as a phylogenetic character. However, some peculiarities in the venation of the forewing allow a rather confident attribution to the Fedtschenkiinae: R truncated at the apical end (acute in Sapyginae), two *s-m* bulging (sigmoidal in Sapyginae). Tibiae of the hind legs are robust and thorned (burrowing devices; slim in Sapyginae). The metasoma is depressed and egg shaped (cylindrical in Sapyginae). Not visible in the fossil is the notch between sternum 1 and 2 (Sapyginae without notch). Clearly visible is the transformed sixth metasomal sternum with the protruding sting/ovipositor.

Eumeninae have been shown to be the hosts of the ectoparasitic larvae of the Recent species *Fedtschenkia anthracina*, while the cleptoparasitic larvae of the Sapyginae use Apidae as a food resource.

If fossil representatives of Sapygidae are compared with the very diverse groups of the Tiphiidae and Anthoboscidae, several similarities (symplesiomorphies and convergences) become apparent. The morphological differentiation of the basal representatives within the Vespoidea still had not progressed very far. For instance, the wing venation of certain representatives of Tiphiidae (Tiphiinae, Myzininae) and Anthoboscidae exhibits many symplesiomorphic similarities (Rasnitsyn, 1986), but a truncated radial cell can only be found in the Fedtschenkiinae as autapomorphy (Figure 11.73a). The shape of the pronotum is also very similar in the mentioned groups. The front edge of the pronotum is more or less straight in these groups, whereas it has a u-shape in the Fedtschenkiinae (Figure 11.72b). The females of Anthoboscidae and of some Tiphiidae have distinct pygidial plates, whereas the metasoma of the Fedtschenkiinae ends evenly conical without such a plate. In the females it ends in the characteristically protruding sting/ovipositor apparatus (Figure 11.72b). Despite many remarkable similarities, there are also sufficient characteristics that distinguish the Fedtschenkiinae from these other groups.

Fedtschenkiinae André, 1903

Cretofedtschenkia gen. nov.

Type species: *C. santanensis* sp. nov., by present designation.

Derivation of name: named after the Cretaceous age and the genus *Fedtschenkia*.

Diagnosis: as for type species, by monotypy.

C. santanensis sp. nov.

Material: holotype SMNS 66594 (Figures 11.72b and 11.73a).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member, of the Crato Formation.

Derivation of name: named after the town of Santana in the area of the type locality.

Diagnosis and description: the only specimen, a female, is characterized by the following features. The tibiae of the hind legs are robust and spinous, and suggestive of burrowing devices. The metasoma has an ovoid shape and extends in the visible sting/ovipositor apparatus. Tergites are partly finely dotted, but this is rather an artefact of preservation. The body length is 18 mm and forewing length is 10 mm. Radial cell of the forewing (R) is truncated at the apex. The subdiscoidal vein (sdv) reaches the outer forewing margin, so that there is a third closed cubital cell (3 Cu) developed.

Scoliidae: scoliid wasps

The Scoliidae (Figures 11.72c and 11.73b) form a comparatively small, monophyletic group within Vespoidea. Their sister group is the family Vespidae (Brothers, 1975; Carpenter, 1982). Approximately 570 Recent species of Scoliidae have been described to date (Osten, 2005). Their larvae develop as ectoparasitoids on beetle larvae, preferably Scarabaeidae. Based on the works of Rasnitsyn (1977), Day *et al.* (1981) and Osten (2001), they are classified in the subfamilies †Archaeoscoliinae (Rasnitsyn, 1993), Proscoliinae (Recent, one genus with two species; Osten, 1987, 1988, 1993) and the Scoliinae (tribes Campsomerini and Scoliini). The species of this family are morphologically very similar, which often makes a specific identification very difficult. The tribe Campsomerini shows in some species a very remarkable sexual dimorphism. Several species of the extinct subfamily †Archaeoscoliinae have been described by Rasnitsyn (1993), Rasnitsyn and Martínez-Delclòs (1999, 2000) and Zhang *et al.* (2002) from the Cretaceous localities in Asia (China, Siberia), Europe (Spain) and South America (Brazil).

Currently, there exists only one questionable record of a Proscoliinae: *Cretaproscolia josai* Rasnitsyn and Martinéz-Delclòs (1999) from the Crato Formation. Only the wing venation is preserved in the holotype specimen. Representatives of the †Archaeoscoliinae (*Archaeoscolia*, *Cretoscolia*, and *Protoscolia*) have not yet been found at this locality. The first fossil record of †Archaeoscoliinae, *Cretoscolia brasiliensis* sp. nov., from the Lower Cretaceous of Brazil is therefore quite remarkable. The female holotype specimen is relatively well preserved (Figure 11.72c). The complete habitus already suggests a Scoliidae. Unfortunately, some important characteristics of this group are not visible, such as the separated position of the metacoxae, due to the fact that the animal is preserved in the dorsal aspect. However, the elongate and tripartite propodeum and the venation of the frontal wing clearly support the attribution to Scoliidae (Figure 11.73b). The longitudinally wrinkled structure of the apical parts of the forewings, which is a characteristic of Recent Scoliidae, is still absent in the genera of *Archaeoscolia* and *Cretoscolia* (but not in *Cretaproscolia*). The slight constriction between the first and second metasomal tergite and sternum is a further evidence for the attribution to Scoliidae, especially in combination with the previously mentioned characters. As the wing venation is not fully preserved, the drawing (Figure 11.73b) of the holotype has been supplemented with a few slight hypothetical reconstructions, but they are all clearly marked with dotted lines. Problems of preservation are apparent particularly in the area of the radial cell (R) and the cubital cell.

The genus *Archaeoscolia* Rasnitsyn (1993) is characterized by the apex of the radial cell which hardly extends over the crossvein 3 *r-m*. For *Cretoscolia* the radial cell extends clearly over the crossvein. Unfortunately, the venation of the radial cell is not preserved in the holotype specimen. On the other hand, the long and slender third pair of legs (particularly the slim femur) suggests an attribution to the genus *Cretoscolia* (Figure 11.72c).

It could be argued that (if it is a male specimen) sexual dimorphism could be involved, because even the males of Recent Scoliidae do not possess the robust burrowing legs of the females. Only the females of the Recent Scoliidae species dig into the soil to either look for their hosts or to rest overnight. In contrast, the males rest on plants in the open. However, the wide head, the round metasoma and the lack of the three apical thorns in the holotype clearly show that it is a female specimen. The relatively slim and long hind legs of the genus *Cretoscolia* have to be considered a primitive character state (symplesiomorphy). Originally, Scoliidae attacked as hosts for their parasitoid larvae only larvae of the beetle family Scarabaeidae that live in or directly under the surface of rotten wood. Only during the course of evolution of the Scarabaeidae did these beetles also populate dry biotopes (Krell, 2000). To survive, deeper layers of soil in savannahs or deserts had to be chosen as habitat for the beetle larvae, instead of the original humid forests. The Scoliidae followed their hosts. To progress into the deeper soil, the hind legs developed into robust burrowing legs in the female sex, which also uses the mandibles for digging.

†Archaeoscoliinae Rasnitsyn 1993

Cretoscolia Rasnitsyn 1993

Type species: C. *promissiva* Rasnitsyn from the Late Cretaceous of north-east Siberia.

Diagnosis: see Rasnitsyn (1993).

Cretoscolia brasiliensis sp. nov.

Material: holotype specimen without number in coll. MURJ (Figures 11.72c and 11.73b).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: the species name is feminine and named after the country of the type locality.

Diagnosis and description: a single female holotype specimen. In contrast to the types of *Cretoscolia promissiva* Rasnitsyn and *C. patiens* Rasnitsyn, the specimen of *C. brasiliensis* is significantly better and more completely preserved. Neither body length nor sex is known for *C. patiens*. This makes a direct comparison of many morphological structures problematic. The wing venation of the holotype mostly agrees with that of the other two species. However, the third discoidal cell (3 D) is substantially shorter and wider in *C. brasiliensis*. There is also an indication of a subdiscoidal vein (sdv; Figure 11.73b). Body length is 13 mm and forewing length is 7.8 mm. The metasoma is wider than in *C. promissiva*.

Vespidae: wasps

Records of fossil Vespidae are extremely rare in the Lower Cretaceous (Carpenter and Rasnitsyn, 1990). Their Recent subfamilies (Euparagiinae, Masarinae, Eumeninae, Stenogastrinae, Vespinae and Polistinae; Carpenter, 1987) are distributed

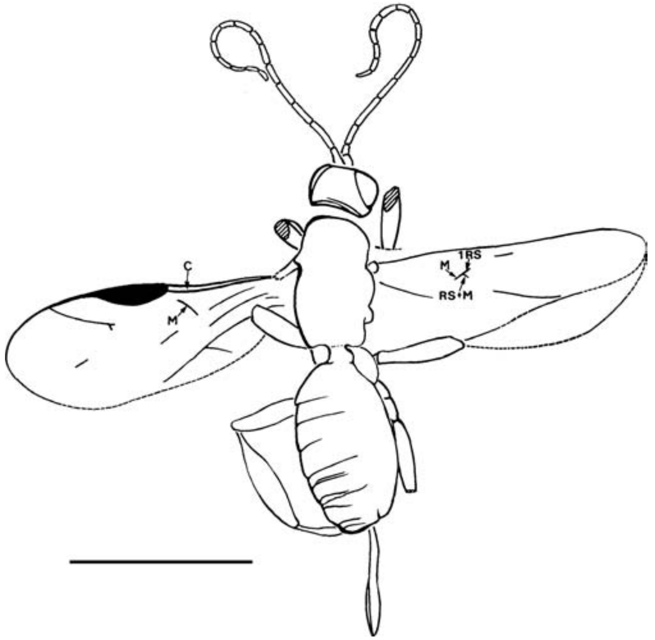

Fig. 11.74. Crato Formation Mesoserphidae: a mesoserphid hymenopteran with out-splayed wings, AMNH 43272; scale bar, 2 mm. After Darling and Sharkey, 1990: figure 5).

worldwide with approximately 4,000 species. These aculeate hymenopterans occur everywhere, not only because of the high number of species, but also based on the highly organized societies of the Vespinae and Polistinae. Their existence has substantial ecological significance (pollination, reduction of other insects as food for their larvae).

Although Carpenter and Rasnitsyn (1990) referred their described genera (*Curiosivespa* and *Priorvespa*) and species to the extinct subfamily †Priorvespinae (which is the sister group of all Recent crown group Vespidae), the newly discovered specimen SMNS 66295 could be referred to an Recent subgroup: based on its specific shape of the first metasomal segment, it could be classified as an Eumeninae (Plate 15p). Unfortunately the important shape of the compound eyes (reniform) is not visible in the fossil. The characteristic morphology of the forewing of Vespidae (longitudinal folding) is not visible in this fossil either. Therefore, better material and more work are needed before a formal taxonomic description is possible.

Apoidea: digger wasps and bees

Fossil Apoidea (Figures 11.71a and b, 11.72d–f and 11.75a–c) are of particular interest for the phylogeny of the Aculeata, but also associated with great problems of

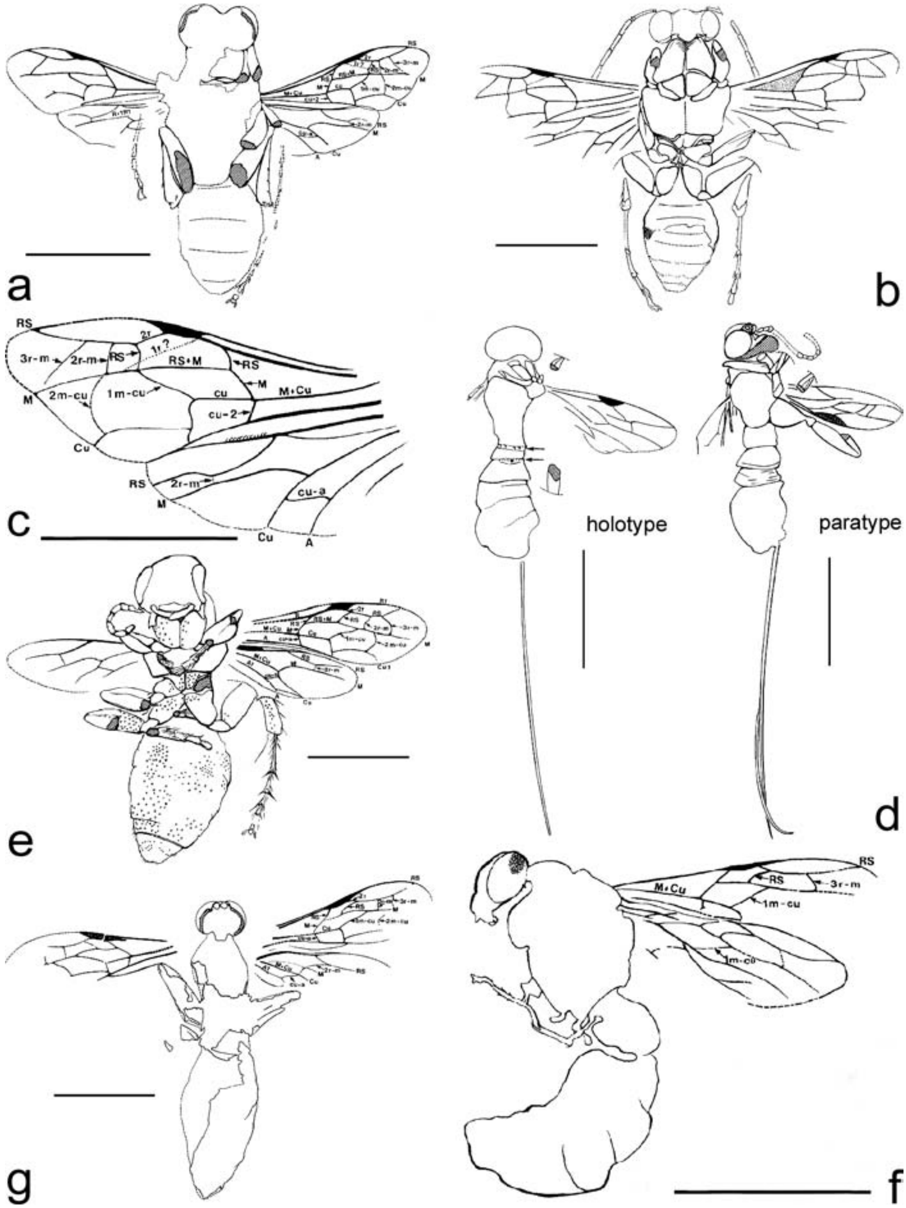

Fig. 11.75. Crato Formation Hymenoptera: (a) Sphecidae, *Cretosphex parvus* Darling, 1990, holotype, AMNH 43264; (b) *Cretosphex magnus* Darling, 1990, holotype, AMNH 44107; (c) *Cretosphex magnus* wing venation of paratype, AMNH 43267; (d) Ephialtitidae, *Cratephialtites kourios*, holotype, AMNH 43269 and paratype AMNH 43263; (e) Tiphiidae, *Architiphia rasnitsyni* Darling, and Sharkes 1990, holotype AMNH 43265; (f, g)?Angarosphecidae, *Mesorhopalosoma ceara* Darling, 1990; (f) paratype AMNH 44103; (g) holotype AMNH 43266. Scale bars, 5 mm. All illustrations after Darling and Sharkey (1990).

classification. According to more recent results (Bohart and Menke, 1976; Lomhold, 1982; O'Tool and Raw, 1991; Alexander, 1992; Ohl, 1995, 1996, 2000; Prentice, 1998; Melo, 1999; Michener, 2000; Engel, 2001), the traditional and still common division of Apoidea into 'Sphecidae' and Apidae cannot be upheld. The family 'Sphecidae' is non-monophyletic (at least in its wide definition), whereas the Apidae are clearly monophyletic. The sister group of the Apidae are the Crabronidae, and the 'Sphecidae' *sensu stricto* are the sister group of both of these taxa. The most primitive group within the Apoidea is the family Ampulicidae, which is also represented in the fossil material from the Crato Formation (Figures 11.72e and f).

The discovery of the Recent genus *Heterogyna* (Nagy, 1969) and the controversial discussion of the position of the Heterogynaidae in the system of the Apoidea has been fully discussed recently by Ohl and Bleidorn (2006): *Heterogyna* is either the sister group of the Crabronidae+Apidae (Alexander, 1992), or the sister group of all remaining Apoidea (Prentice, 1998), or only the sister group of the Ampulicidae (Prentice, 1998; Melo, 1999), or the sister group of the 'Sphecidae'+Crabronidae+Apidae (Melo, 1999). Different views concerning the phylogenetic relationships also prevail within these subgroups. These circumstances lead to particular difficulties with the classification of fossils: while fossils from the comparably young Dominican and Baltic amber (Engel, 2001) can clearly be classified in either Apidae or Sphecidae or any other hymenopteran subgroup, this attribution is much more problematic with primitive fossil representatives from Mesozoic outcrops like the Crato Formation.

Nevertheless a number of these fossils can be attributed to the extinct family †Angarosphecidae (Rasnitsyn *et al.*, 1999; Pulawski and Rasnitsyn, 2000; Grimaldi and Engel, 2005). This includes the two species *Cretosphex parvus* (Figure 11.75a) and *Cretosphex magnus* (Figures 11.72d and 11.75b and c) which, based on five specimens (*Cretosphex parvus*: AMNH 43264, 44106 and 44104; *C. magnus*: AMNH 44107 and 43267) were described by Darling and Sharkey (1990) as 'Sphecidae'. They belong to the most abundant fossil hymenopterans of the Crato Formation. It seems that the family of †Angarosphecidae had been rather common and widely distributed in the Lower Cretaceous. Specimen SMNS 66297 (Figure 11.71a) seems to represent a new species and first New World record of the angarosphecine genus *Cretobestiola* Pulawski and Rasnitsyn, 2000. Additionally, Ampulicidae (Figures 11.72e and f) are here recorded for the first time, as Darling and Sharkey (1990) only had a doubtful specimen of the Ampulicinae (AMNH 44108).

There are a number of fossil Hymenoptera from this locality that might be typologically identified as 'bees'. Only a very small number would really stand up to a more thorough and more critical examination. The difficulty or even impossibility of distinguishing primitive apids from primitive 'sphecids' has been mentioned

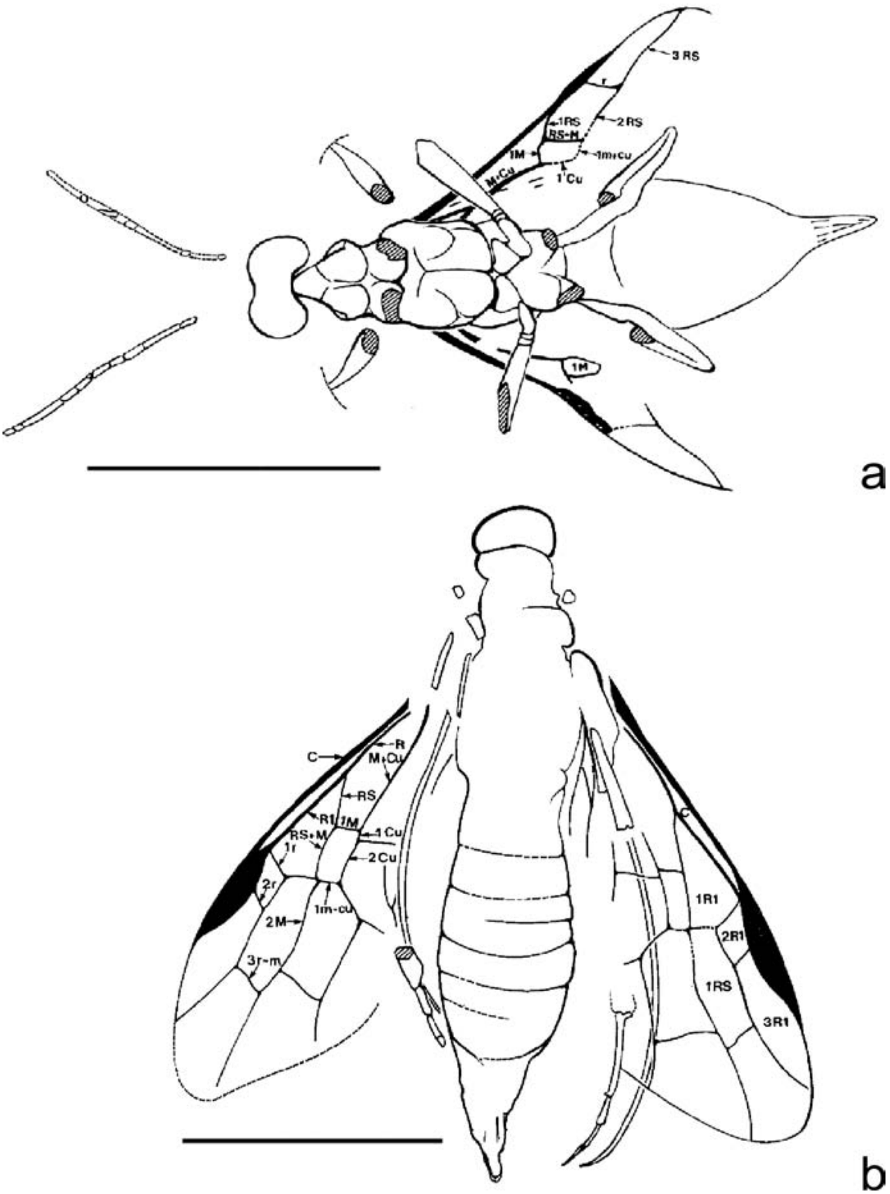

Fig. 11.76. Crato Formation Hymenoptera: (a) Proctotrupidae? *Protoprocto asodes* Sharkey, 1990, holotype, AMNH 44101; (b) Anaxyelidae, *Prosyntexis gouleti* Sharkey, 1990, holotype, AMNH 43270. Scale bars, 5 mm. After Darling and Sharkey (1990).

Fig. 11.77. A possible Crato Formation ant: *Cariridris bipetiolata* Brandao and Martins-Neto, 1989, holotype, private coll. Vulcano no. CV-293; scale bar, 2 mm. After Brandao *et al.* (1989).

above, and was already discussed in detail by Darling and Sharkey (1990). However, a very well-preserved bee-like fossil without number (Figure 11.71b) from coll. MURJ is very probably indeed a genuine apid, because it has a general habitus that is virtually unknown within the complete 'sphecid' grade. This specimen could therefore represent the oldest fossil record of bees, which are otherwise first known from the Upper Cretaceous amber of North America (however, just recently Poinar and Danforth, 2006, described the new fossil bee family Melittospecidae from the Lower Cretaceous amber of Burma). Further research and more material would of course be necessary to confirm and test this important discovery.

11.19 Mecoptera: scorpionflies

Günter Bechly

Mecopterans, the scorpion flies, are small-to-medium-sized (1.7–35 mm) insects, often with a fly-like habitus. Most of them have filiform antennae and orthognathous chewing mouthparts. In most taxa, anterior and lateral portions of the head and some of the mouthparts are more or less prolonged as a rostrum. The compound eyes are large and ocelli are either present or reduced. The legs have elongate coxae, long femora and tibiae, and five-segmented tarsi (except in Boreidae) with paired claws (except in Bittacidae). Two pairs of membranous wings of subequal size, similar shape and complete venation are usually present, except in a few apterous taxa and in the extinct Pseudopolycentropidae with much-reduced hind wings. The first abdominal tergum is fused to the metanotum. Males usually have a prominent genital apparatus which gave rise to their vernacular name. The abdominal cerci are relatively short with only one to three segments in the females and one segment in the males, but they are completely reduced in the males of the apterous Boreidae and Apteropanorpidae (but not in *Apterobittacus* and other wingless species). The development is holometabolous with a distinct eruciform or campodeiform larval stage with compound eyes, and an adult-like pupal stage. Mecoptera are either carnivorous, phytophagous, or saprophagous, and generally prefer moist habitats while only a few species are adapted to arid environments. Recent Mecoptera have a cosmopolitan distribution.

Systematics, phylogeny and evolution

There are about 600 extant species of Mecoptera and about 400 fossil species of 'mecopteroid taxa', but not all of the latter are necessarily members of the Mecoptera (see below). The extant species are classified in nine families, but the monophyly of extant Mecoptera is still under discussion, mainly because of a possibly more basal position of Nannochoristidae and a putative in-group position of Siphonaptera (Grimaldi and Engel, 2005). Together with the orders Siphonaptera, Diptera and possibly Strepsiptera (the relationship of Strepsiptera with Antliophora is still very disputed, but is apparently not only supported by molecular evidence, but as well by unpublished new morphological data (according to Mickoleit, personal communication), the order Mecoptera belongs to the clade Antliophora within Holometabola. Most probably Siphonaptera (fleas) represents either the sister group of Mecoptera or (more likely) the sister group of Boreidae within Mecoptera (see Willmann (1987, 1989) for a discussion of the internal phylogeny of Mecoptera). Nannochoristidae could be the sister group of only Boreidae+Siphonaptera or rather the sister group of all other Mecoptera (including Siphonaptera). The still three-segmented female cerci and the primary absence of a rostrum are plesiomorphies within Mecoptera (otherwise only present in the boreid genus *Caurinus*) that support the latter hypothesis, which also agrees with the oldest fossil occurrence. All other extant Mecoptera (except Nannochoristidae and Boreidae) belong to a clade Pistillifera that is diagnosed by the synapomorphic possession of a sperm pump in the male genital apparatus.

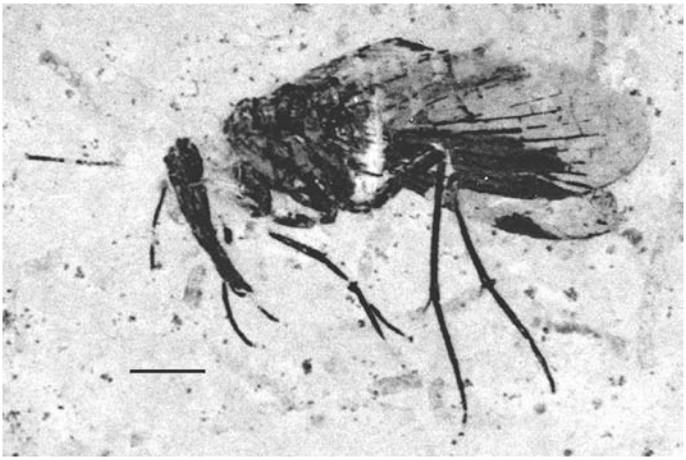

Fig. 11.78. Crato Formation Mecoptera: Familia indet., undescribed gen. et sp. nov., no. N72 at KMNH. Scale bar, 2 mm.

Fossil record

The fossil history of Mecoptera was discussed by Handlirsch (1906–1908), Willmann (1978), Carpenter (1992), Novokschonov (1997, 2002) and Grimaldi and Engel (2005). The oldest representatives of the crown group clade Mecoptera are fossil Nannochoristidae from the Upper Permian. Older fossil records are problematic because most fossils are isolated wings, and the wing venation of basal Mecoptera is hardly differentiated from the ancestral condition of Antliophora and Amphiesmenoptera (caddisflies and butterflies). Consequently, such Palaeozoic mecopteroid fossils could not only belong to the stem group of Mecoptera but could also belong to a mecopteroid grade of the stem group of Mecopteroidea (Antliophora+Amphiesmenoptera), Amphiesmenoptera, Antliophora or could represent still mecopteroid-like stem group representatives of Siphonaptera and/or Diptera.

Mecopterans are extremely rare in the Crato Formation, but are quite diverse and abundant in other Lower Cretaceous outcrops such as Liaoning (China), so that their rarity in the Crato Formation is somewhat unexpected and in need of explanation. Most likely, the arid conditions of the Crato habitat were unsuitable for Mecoptera. Therefore, their near absence or extreme rarity can be considered as a further corroboration of an arid environment of the Crato lagoon.

Crato fossils

Among the several tens of thousands of Crato insects there were no fleas at all (fossil fleas are extremely rare anyway) and only two specimens of Mecoptera (Figures 11.78 and 11.79).

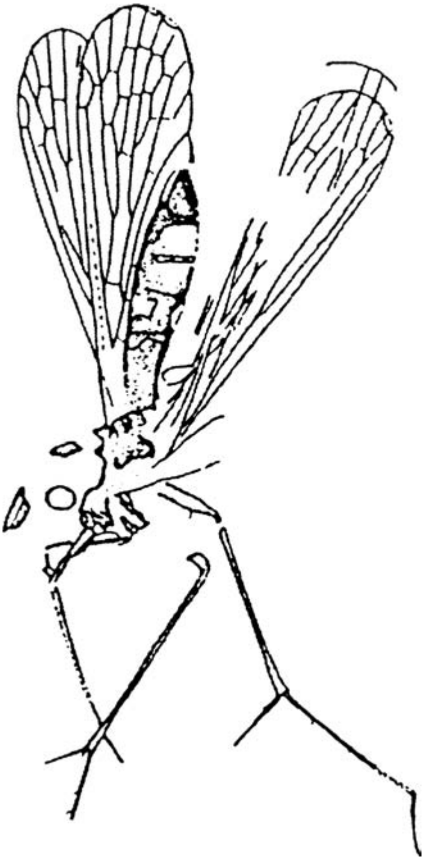

Fig. 11.79. Crato Formation Mecoptera: Bittacidae, gen. et sp. nov., coll Vulcano. Redrawn after Petrulevicius and Martins-Neto (2001: figure 1). Scale unknown.

Martins-Neto (2005b: 481) lists an undescribed mecopteran from the Crato Formation as 'Bittacidae Gen. et sp. n. Martins Neto, 1999'. However, this fossil from the private collection of Mrs Maria Aparecida Vulcano (São Paulo, Brazil) was briefly described and figured (Figure 11.79) as a putative new genus of Bittacidae, but not named, by Petrulevičius and Martins-Neto (2001). This fossil hangingfly was first mentioned by Petrulevičius (1998), and according to Willmann (personal communication) it is indeed a Bittacidae *sensu stricto*.

The second specimen (Figure 11.78) is still undescribed and figured here for the first time. It is deposited with no. 443 (old no. N72) at KMNH. It has a very long rostrum, short antennae and the wings are relatively broad with a dark colour pattern. According to Willmann (personal communication) it could be a stem group representative of Panorpini or Panorpoidea (first New World record) but, unfortunately, some important characters of the wing venation, like the structure of the

Media, are not clearly preserved. Most probably it is a new genus and species, but I here refrain from its formal description because it should be undertaken by a Mecoptera specialist.

11.20 Diptera: true flies, gnats, and crane flies

Jana Willkommen and David A. Grimaldi

Besides the Coleoptera (beetles) and Lepidoptera (butterflies) the order Diptera (true flies) is, with about 134,000 species, one of the most diverse insect groups (Gullan and Cranston, 2005). Their success is partly reflected by the diverse life histories and body forms. For example the largest fly has a body length of about 60 mm and wing span of 100 mm, which is the Neotropical *Mydas heros* Cole, 1969 (Mydidae–Brachycera). Among the smallest Diptera are certain gall midges (Cecidomyiidae) and biting midges (Ceratopogonidae): with about 0.5 mm body length and 1 mm wing span.

The Diptera inhabit nearly all aquatic and terrestrial habitats. Their larvae live in semi-aquatic or aquatic environments. The adults are predators, ectoparasites, saprophages, bloodsuckers or feed on nectar and pollen. The order has a worldwide distribution and can be found in all zoogeographic regions. They occur in humid and hot tropical regions, mountains and dry deserts, and in boreal regions flies are the dominant insect group (Hennig, 1973).

The Diptera are placed in the group Antliophora as sister group to the scorpionflies (Mecoptera, which are paraphyletic)+fleas (Siphonaptera). Diptera appear to have originated in the latest Permian or earliest Triassic and suddenly diversified into major living lineages (i.e. infraorders) some 20 myr later in the Late Triassic (Grimaldi and Engel, 2005; Blagoderov and Grimaldi, 2007). It was not until the Early to Mid Jurassic, approximately 200–175 mya, that the abundance of Diptera in palaeoecosystems approached the abundance and biomass we see today (Blagoderov and Grimaldi, 2007). This has been attributed to the diversification within the infraorders, especially of brachyceran flies (Krzeminski and Evenhuis, 2000; Blagoderov and Grimaldi, 2007), which took place in the Jurassic and later.

The Diptera have only one pair of fully developed wings in the body plan, with the hind wings reduced to club-like organs, the halteres, which maintain stability in flight as balance organs (McAlpine, 1981). The forewings are the functional flight organs, in which the narrow wing base allows the increased mobility of the wing. With halteres and other wing specializations Diptera are excellent flyers.

In compressed fossils the wing venation is very often the most important and consistent source of taxonomic characters.

Ground plans in dipteran wing venation are (Hennig, 1954):

- circumambient costal vein,
- four free radial sector veins,
- four free medial veins,
- closed discal cell,
- one free cubital vein,
- posterior cubitus and third anal vein are reduced.

The structure of the antennae and legs are further important taxonomic characters in compression fossils.

The Diptera have traditionally been divided into the ‘Nematocera’ (‘thread-horned’) and the Brachycera (‘short-horned’). The Nematocera include all true flies without the derived (apomorphic) characters of the Brachycera, and so nematocerans are paraphyletic with respect to the Brachycera. Nematocera are mostly slender insects with long legs and long antennae that have more than eight segments, generally 11–14 (flagellomeres). Short antennae with two to eight flagellomeres and more robust habitus are characteristic features of the Brachycera (Woodley, 1986). The suborder Brachycera is a monophyletic group.

Ground plans in brachyceran wing venation are, among others (Hennig, 1954):

- the radial sector contains only three free veins,
- the fork of R_4 and R_5 is short and their stem vein is distad of the cross vein *r-m*,
- veins CuA_2 and A_1 are closed together at the wing margin, or nearly so,
- vein A_2 is reduced and does not reach the wing margin.

Until now only a few fossil brachycerans were known from the Crato Formation of Brazil. Grimaldi (1990) reported three specimens of Asilidae: *Araripogon axelrodi* Grimaldi, 1990 and *Araripogon* sp. A further specimen of *Araripogon axelrodi* is figured in Grimaldi and Engel (2005). Another fossil of the Brachycera was described by Grimaldi (1990) that probably is a member of the family Therevidae. Martins-Neto (2003b) placed this fossil into Tabanidae (*Cratotabanus*) but in this fossil the crossvein *r-m* is located at about the middle of the discal-cell length, more as in Recent Therevidae than Recent Tabanidae. Mazzarolo and Amorim (2000) described a new family, the Cratomyiidae, for *Cratomyia macrorrhyncha* Mazzarolo and Amorim, 2000 (holotype, MZUSP; paratype FFCLRP, DBRP-0051). The family is placed as a sister group of the Xylomyidae and Stratiomyidae.

Crato dipterans

A relatively current catalogue of fossil Diptera is available on the worldwide web (http://hbs.bishopmuseum.org/fossilcat/). The dipteran fauna from the Crato

Formation is very distinctive compared to that of other diverse Cretaceous insect Konservat Lagerstätte, the most significant aspect being their relative rarity. The Diptera generally comprise 30–50% of all insect specimens in each of the major late-Mesozoic insect palaeofaunas, including both compression/impression and amber deposits (Blagoderov and Grimaldi, 2007), but Diptera from the Crato comprise merely 2% of all specimens in the AMNH collection, which is a proportion approximately similar in other collections of Crato fossils (e.g. at SMNS). Assuredly, there is bias in this figure, since diverse, small Diptera may be overlooked by quarry workers who excavate the material, but it is doubtful that such a bias could be so large. It is also doubtful that there is bias against preservation of small, delicate insects, since even delicate limoniid craneflies are preserved fully intact.

Other distinctive features of the Crato Formation Diptera are a unique abundance of Asilidae, a paucity of Rhagionidae and a complete absence of Empidoidea, Nemestrinidae and archaic taxa (i.e. extinct nematocerous families) common during the Early Cretaceous. As mentioned above, Asilidae are extremely rare in the Cretaceous (and even in Tertiary deposits), so the presence of a large series of robber flies (*Araripogon*) is exceptional. Conversely, Rhagionidae were one of the most diverse and abundant groups of Brachycera in the Mesozoic (Grimaldi and Cumming, 1999), but only one specimen is known thus far from the Crato Formation. Other groups that were abundant and diverse in the late Mesozoic include the dance flies and their relatives (superfamily Empidoidea; e.g. Grimaldi and Cumming, 1999), and the tangle-veined flies (family Nemestrinidae; e.g. Ren, 1998; Ansorge and Mostovski, 2000; Mostovski and Martínez-Delclòs, 2000), neither group of which is known thus far from the Crato Formation. Nemestrinidae, in particular, are denizens of similar arid environments inhabited by Asilidae, so their absence or rarity is taphonomically unusual. Archaic groups that extend from the Triassic or Jurassic to the Early Cretaceous and that are particularly common include *Architipula* (Limoniidae), Hennigmatidae, Eoptychopteridae, Procramptonomyiidae, Elliidae and various Mesozoic families of Bibionomorpha (Mesosciophilidae, Archizelmiridae, Eoditomyiidae and Protorhyphidae). None of these archaic groups are known to occur in the Crato Formation, so, taxonomically, the dipteran fauna of this formation is more similar in overall composition to that of Tertiary faunas than it is to the Early Cretaceous. Phylogenetically, the better-studied Brachyera from the Crato Formation are stem group taxa, reflecting nascent stages in the evolution of certain modern families.

All discovered fossil Brachycera of the Crato Formation belong to the more ancient group of the Brachycera: the 'basal brachyceran flies'. A new unidentified and still undescribed brachyceran is specimen SMNS 66199 (Figure 11.80).

Abundant fossil Diptera of the Crato Formation are species of the family Asilidae. Extant members of this family prefer arid and semi-arid environments with open

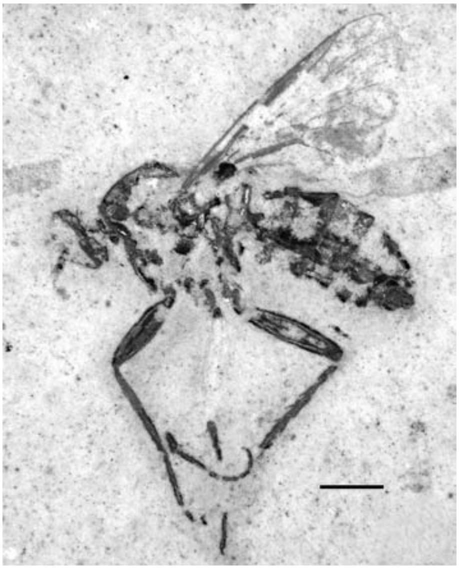

Fig. 11.80. Crato Formation Diptera: Brachycera, Familia *incertae sedis*, SMNS 66199. Scale bar, 1 mm.

vegetation. Like the Asilidae, Recent members of the Apioceridae and Mydidae are most diverse in semi-arid and arid habitats. The Recent members of the Stratiomyomorpha are found associated with wood and dead trees. This indicates that the environment was hot and dry – arid to semi-arid – with surrounding bushes and trees in the Cretaceous. The recorded Rhagionidae and Tabanidae might have been bloodsuckers on other invertebrates or cold-blooded animals.

Infraorder Tipulomorpha: crane flies

Limoniidae

With 11,000 Recent species, this is the largest family of Diptera. It is also among the most ancient, having existed from the Late Triassic and significantly diversified through the Mesozoic and Tertiary. There are some 300 named fossil species (reviewed by Evenhuis, 1994). The family is sometimes placed as a subfamily of the Tipulidae *sensu lato* ('craneflies'), or within a superfamily Tipuloidea. They are small (generally 3–10 mm long), gracile flies with very long, delicate legs, whose larvae breed in semi-aquatic habitats and wet or moist soils. Two species are named from the Crato Formation, both belonging to the extinct subfamily Eotipulinae Handlirsch, otherwise known only from the Mesozoic of Europe and

Asia. These species are *Cratotipula latialata* Ribeiro and Martins-Neto, 1999, and *Okrenomyia araripensis* Ribeiro and Krzemiski, 2000. The fossil tipulomorphs discussed and figured by Grimaldi (1990) also seem to belong to these two species (*C. latialata*: AMNH 43501; *O. araripensis*: AMNH 43500; Figures 11.84b, c and e). Thus, the Crato limoniids are the first Western Hemisphere records of this extinct subfamily.

Infraorder Culicomorpha
Culicoidea

Major families within this group include the bloodworms and midges (Chironomidae), the no-see-'ums (Ceratopogonidae) and mosquitoes (Culicidae). Primitive members of the first two families suck blood, as do most mosquitoes. The group is infamous for being the most serious vectors of epidemic diseases like malaria, yellow fever, encephalitides and many others. The earliest Culicoidea are from the Triassic, and by the Cretaceous Chironomidae were extremely abundant in lacustrine and amber deposits. Only two Cretaceous mosquitoes are known, both in amber (reviewed in Evenhuis, 1994; Grimaldi and Engel, 2005). The only Crato Formation record of the Culicomorpha is specimen AMNH 43503 (Figure 11.84a) by Grimaldi (1990: 166). The specimen is only partially preserved, and wing venation is not preserved, but the body proportions (long, slender legs; arched anterior portion of mesoscutum) and especially the large, brush antennae indicate this is a male culicoid. It is probably a chironomid since there appears to be no trace of a proboscis.

Simuliidae (?): black flies

These are the notorious black flies, of which swarms of blood-sucking females are scourges to warm-blooded vertebrates in boreal regions. Tropical species inhabit forests surrounding large river basins (where the larvae breed) and transmit diseases like river blindness (onchocerciasis). Mesozoic records were reviewed by Currie and Grimaldi (2000). The earliest definitive record is from the Jurassic–Cretaceous boundary, with very rare, isolated records from the Cretaceous (the exception being an abundant series of larvae from the Early Cretaceous of Australia, described by Jell and Duncan, 1986). A specimen in Late Cretaceous amber from New Jersey is an extinct sister group to the tribe Simuliini (Currie and Grimaldi, 2000), which is the more derived and speciose group of black flies. There is a single record of black flies from the Crato Formation, being *Cretaceosimulium araripense* Vulcano, 1985. The name was mentioned in an abstract, but is a *nomen nudum* since no type was designated nor a diagnosis given; moreover, the specimen is in a private collection and unavailable for study, so its identity is impossible to verify at present.

Infraorder Psychodomorpha
Psychodidae (?): moth flies

Among all infraorders of Diptera, monophyly of the Psychodomorpha is most problematic. The most recognizable and distinctive family of the group are the so-called moth flies, family Psychodidae, so named for the furry covering of hairs over the broad wings found in some groups. The family also includes notorious blood-sucking species in the subfamily Phlebotominae ('sand flies'), some of which transmit serious epidemic diseases like leishmaniasis ('kala azar'). The family originated in the Triassic (Blagoderov and Grimaldi, 2007), with modern (i.e. *Phlebotomus*-like forms) appearing by the Early Cretaceous. Psychodidae were diverse by the Cretaceous and Tertiary, though most fossil species are known from ambers. There is only one Crato Formation record, *Megapsychoda araripina* Azar and Nel, 2002, which was described on the basis of a well-preserved, unique specimen (no. SMNK 2363). This species is significantly larger than living psychodids, having a wing length of 4 mm. However, its venation (as well as the large size) is very similar to that of Tanyderidae (i.e. *Protanyderus*), which is a sister group to the Psychodidae. So, *Megapsychoda* may actually be a tanyderid. Larvae of Recent tanyderids breed in streams and rivers; those of psychodids breed in wet soils and even foul water.

Infraorder Bibionomorpha: march flies and fungus gnats

This infraorder is a large, diverse assemblage of families that are extremely different in adult and larval structure and habits. Bibionomorpha larvae are essentially terrestrial (feeding mainly on fungal mycelia), whereas larvae of other nematocerous lineages are aquatic or semi-aquatic. This life history reflects the relationships of Bibionomorpha as the sister group or stem group to the Brachycera (larvae of which are also mostly terrestrial). Only a few specimens of the group are known and have been reported by Grimaldi (1990), belonging to the Mycetophilidae–Macrocerinae? (AMNH 43502; Figure 11.86), Sciaridae or Sciaroidea (AMNH 43505 and 43506; Figure 11.84d) and the Bibionidae? (AMNH 43504; Figures 11.85c and d). Bibionids are well known in tropical and semi-tropical regions for the massive mating swarms that form near grassy swamps where they breed. The fossil record of the family is apparently Tertiary (only three of nearly 350 named species are from the Mesozoic), but this is a taxonomic artifact since some extinct Mesozoic 'families' like Protopleciidae appear to be paraphyletic stem groups to the Bibionidae.

Infraorder Stratiomyomorpha – soldier flies and wood soldier flies

Cratomyiidae Mazzarolo and Amorim, 2000

Diagnosis: antennae with flagellomeres barely differentiated, with at least six flagellomeres; proboscis long; abbreviated costal vein; cell m_3 closed; anal cell closed; petiole of M_1 and M_2 present, M_1 arched forward; fork of R_4+_5 short, R_5 ending at or before wing apex.

Type genus and species: *Cratomyia macrorrhyncha* Mazzarolo and Amorim, 2000.

Cratomyia Mazzarolo and Amorim, 2000

Type species: *C. macrorrhyncha* Mazzarolo and Amorim, 2000. By original designation.

Diagnosis: large species, approximately 24.0 mm body length, including approximately 7 mm long, jutting proboscis; eyes large, maxillary palp approximately one-quarter the length of proboscis. Distinguished from *Cratomyoides* gen. nov. by the relatively longer proboscis and longer discal cell.

Cratomyoides Wilkommen gen. nov.

Type species: *Cratomyoides cretacicus* sp. nov., by monotypy and present designation.

Derivation of name: named after the similar genus *Cratomyia*.

Diagnosis: distinguished from the Xylomyidae by short discal cell, the cell m_3 only slender, petiole of M_1 and M_2, long base of Rs, veins R_1 to R_5 ending before wing tip. Distinguished from *Cratomyia* Mazzarolo and Amorim, 2000 by the first-mentioned character and the shorter proboscis.

Cratomyoides cretacicus Wilkommen sp. nov.

Material: holotype SMNS 66179 (Figures 11.81a and 11.83a and b).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after Cretaceous type horizon.

Diagnosis: as for genus, by monotypy.

Description (Figures 11.81a and 11.83a and b): fossil about 9 mm long, body robust, wings relatively broad. Head about 1.3 mm long and antennae simple with no differentiation of flagellomeres; scape about twice as long as pedicel. Flagellum slender, with six to eight flagellomeres. Proboscis about as long as head. Wings 5.8 mm long, do not reach end of the abdomen in folded position. Costal vein ends

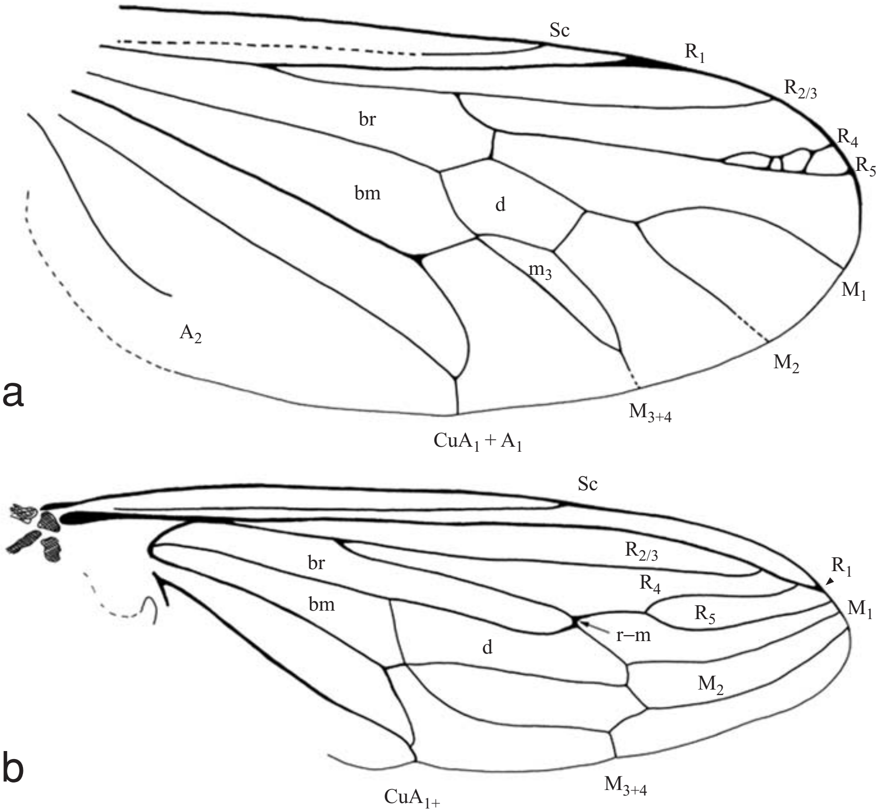

Fig. 11.81. Crato Formation Diptera: (a) Cratomyiidae, *Cratomyoides cretacicus* gen et sp. nov., holotype SMNS 66179, right wing; (b) Mydidae, *Cretomydas santanensis* gen. et sp. nov., holotype SMNS 66178, right wing. Without scale.

probably at apex of M_2. Subcostal vein meets wing margin after about two-thirds the wing length. Stem of radial sector is relatively long. All radial veins (R_1 to R_5) end before wing tip in wing margin, fork of R_4/R_5 short. Veins M_1 and M_2 with short petiole after discal cell. M_1 clearly arched anterior, meets wing margin after wing tip. Cell m_3 slender, closed before wing margin, veins CuA_1 and A_1 fused before wing margin. Basal cells br and bm about equal in length. Discal cell short, about twice as long as wide. Seven or eight abdominal tergites about 2.4 mm broad and 0.9 mm long.

Comment: the fossil belongs without a doubt to the Stratiomyomorpha and shows characters that are plesiomorphic to the Stratiomyidae, although some characters might be a derived state for the Xylomyidae. These characters are the short discal cell and the slender cell m_3 (probably shows the tendency to reduce the vein M_3 as is the case in Stratiomyidae). Furthermore, wing veins R_1 to R_5 end before the

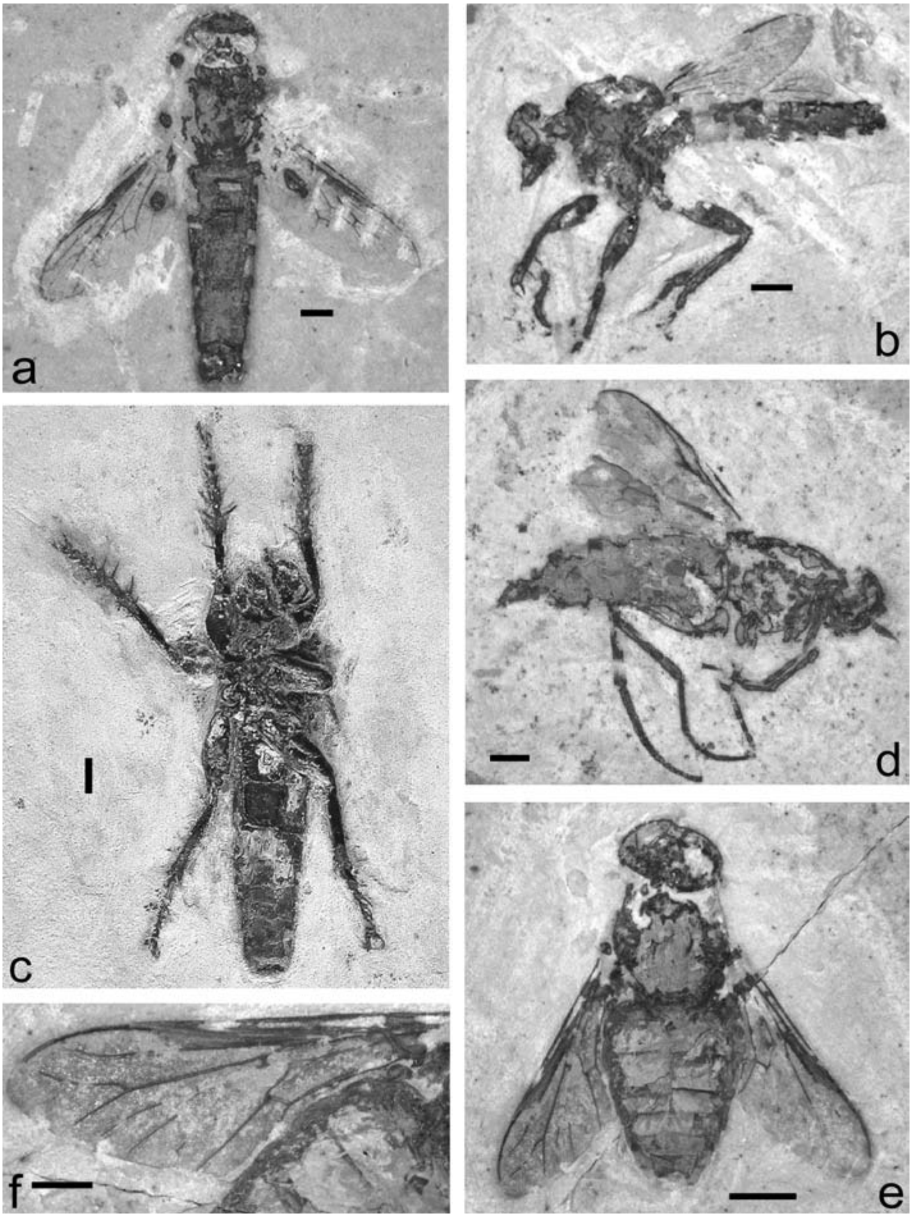

Fig. 11.82. Crato Formation Diptera: (a) Asilidae or Therevidae (?), seen in ventral view, legs not preserved, SMNS 66182; (b) Asilidae seen in lateral view, SMNS 66183; (c) *Araripogon* sp. Grimaldi 1990 in ventral view; (d) ?Rhagionidae, SMNS 66185; (e, f) Tabanidae, SMNS 66181; (e) habitus; (f) right wing. Scale bars, 1 mm, except e, 2 mm.

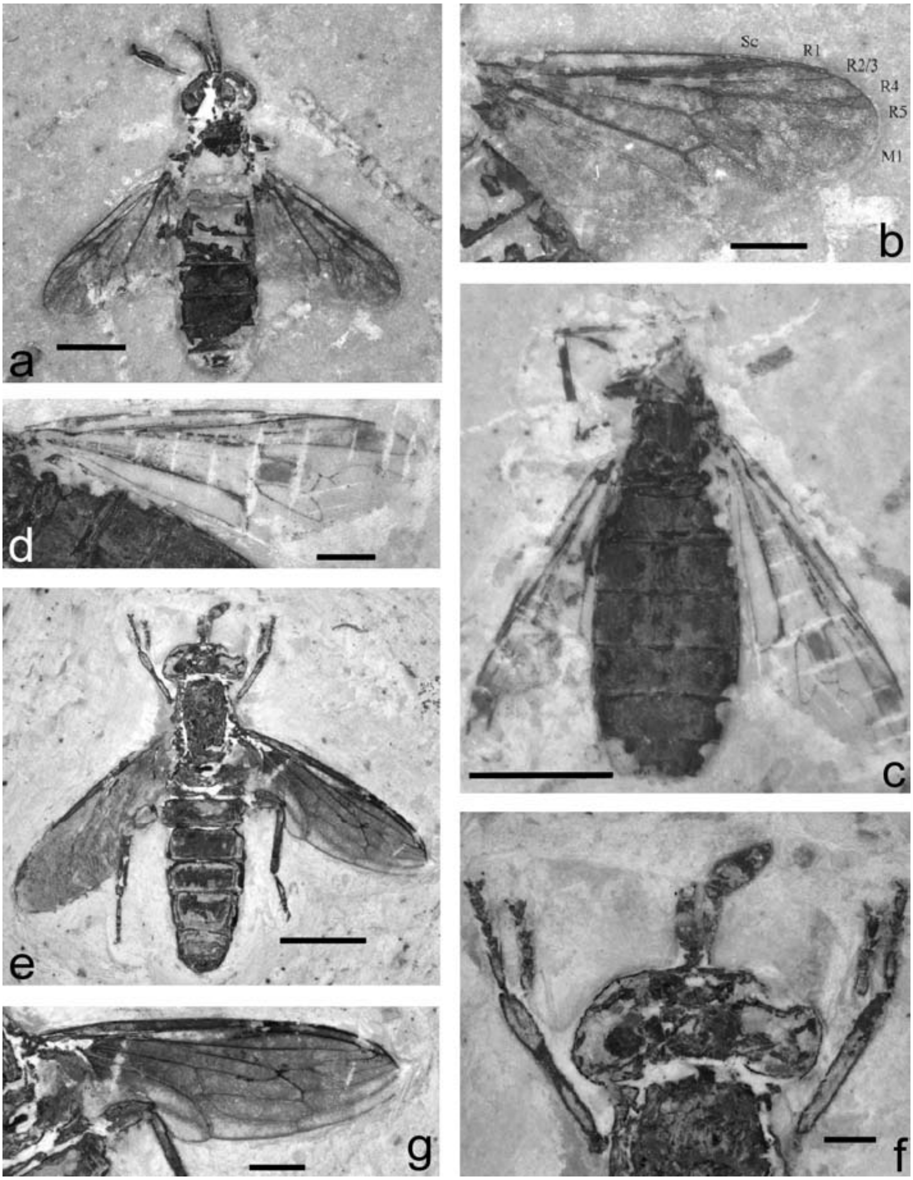

Fig. 11.83. Crato Formation Diptera: (a, b) Cratomyiidae, *Cratomyoides cretacicus* gen. et sp. nov., holotype SMNS 66179; (a) habitus; (b) right wing; (c, d) Cratomyiidae, SMNS 66180; (c) habitus; (d) right wing; (e–g) Mydidae, *Cretomydas santanensis* gen. et sp. nov., holotype, SMNS 66178; (e) habitus; (f) head with antennae and part of the forelegs; (g) right wing. Scale bars: b,f, 1 mm; a,d,g, 2 mm; c,e, 5 mm.

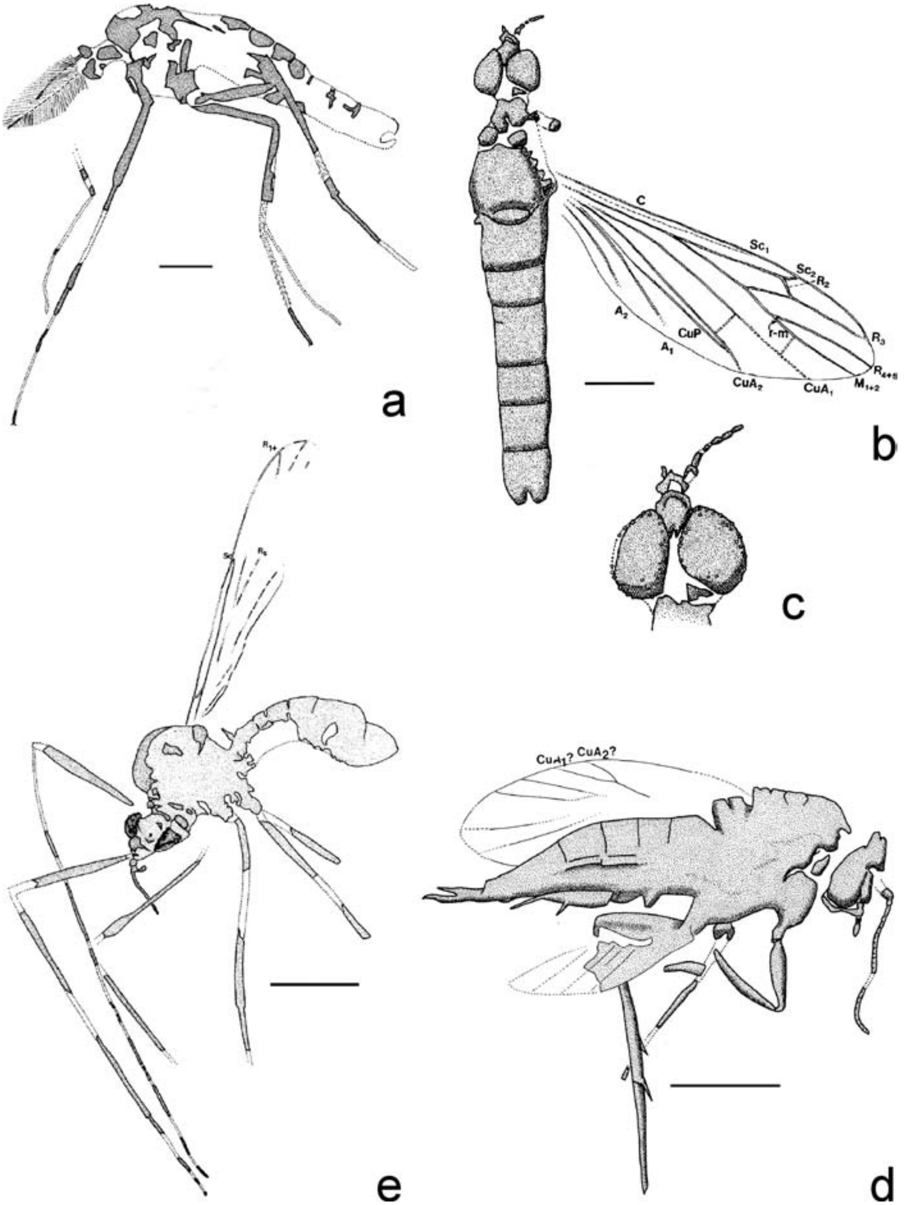

Fig. 11.84. Undescribed Crato Formation Diptera: (a) Chironomoidea, male, AMNH 43503; (b, c) Tipulidae, AMNH 43500; (d) Sciaroidea, AMNH 43506; (e) Tipulomorpha? AMNH 43501. Scale bars, 1 mm. All figures from Grimaldi (1990).

wing tip. Another fossil Cratomyiidae is specimen SMNS 66180 (Figures 11.83c and d) with a broad xylomyid abdomen and a wing venation typical of the family.

Zhangsolva cupressa, from the Early Cretaceous Laiyang Formation of China, has a wing venation that is nearly identical to that of Cratomyiidae. Very significantly, and apparently overlooked by the original (Mazzarolo and Amorim, 2000) and many subsequent authors, is that *Zhangsolva* is described as having '[a] proboscis (if so) conspicuously long' (Nagatomi and Yang, 1998: 140). Also, the antennal flagellum of Cratomyiidae Mazzarolo and Amorim, 2000 and of Zhangsolvidae Nagatomi and Yang, 1998 plesiomorphically has articles that are barely differentiated, though *Cratomyoides* has six to eight flagellomeres ('long' and 'multiarticulated' in *Cratomyia* (Mazzarolo and Amorim, 2000)), and *Zhangsolva* is reported to have 12. Eight flagellomeres are the ground-plan feature of Brachycera, so the number of flagellomeres in *Zhangsolva* should be carefully re-examined. It is very likely that *Zhangsolva* and Zhangsolvidae are senior synonyms of *Cratomyia* and Cratomyiidae, respectively, but this should be determined after *Z. cupressa* is re-studied.

The very close relationship between *Zhangsolva*, *Cratomyia* and *Cratomyoides* is highly significant. Phylogenetic relationships of these taxa within the anthophilous Stratiomyomorpha (Nagatomi and Yang, 1998; Mazzarola and Amorim, 2000), and their highly specialized proboscides, indicate they almost certainly foraged from flowers. Indeed, these are one of the few Early Cretaceous records of specialized anthophiles in the fossil record (Grimaldi, 1999; Grimaldi and Engel, 2005), and with Laurasian and Gondwanan records the group was apparently global in the Cretaceous. These flies may have had a significant impact on the pollination and thus diversification of Cretaceous angiosperms.

Mazzarolo and Amorim (2000) included *Cratomyia macrorrhyncha* in the Stratiomyomorpha, but basal to the Xylomyidae and Stratiomyidae because the base of the radial sector is long. *Cratomyoides cretacicus* is placed here into the Cratomyiidae but it is doubtful if this family is a basal clade to the Xylomyidae and Stratiomyidae because characters such as the anteriorly shifted R-veins, the short discal cell, and the slender cell m_3 could also be interpreted as a derived state to Xylomyidae.

Extant Xylomyidae and Stratiomyidae are distributed worldwide or nearly so. Only several immature stages of Xylomyidae are known. The larvae have been found associated with dead portions of trees and resemble those of the soldier flies (Stratiomyidae; Nagatomi and Rozkosny, 2000). Larvae of Stratiomyidae are found in rotten plant material, under bark, and in foul, wet substrates. The adults are probably nectar feeders (Rozkosny, 2000) and are often found on a variety of flowers. Derived characters of this family are the absence of spurs on fore and hind tibiae, the miniaturization of the discal cell and vein R_5 ending before the wing tip (James, 1981).

Mesozoic Xylomyidae and Stratiomyidae are rare and known entirely from the Cretaceous; they are more diverse and less rare in the Tertiary (Evenhuis, 1994). Only three known records exist for Cretaceous Xylomyidae: a putative one in Late Cretaceous Siberian amber (Evenhuis, 1994), an undescribed form in Early Cretaceous Spanish amber (Grimaldi *et al.*, unpublished work), and mention of an undescribed species 'near *Solva*' from the Crato Formation (Evenhuis, 1994). It is possible that the last report is of *Cratomyia*. Statiomyidae likewise have only three Cretaceous records: *Cretaceogaster pygmaeus* in Late Cretaceous Canadian amber, which is very primitive (Woodley, 1986; Grimaldi and Cumming, 1999); another primitive, but fragmentary and undescribed form in Late Cretaceous New Jersey amber (Grimaldi and Cumming, 1999), and, interestingly, an assemblage of abundant larvae in Early Cretaceous (Barremian-aged) limestone from Montsec, Spain (Gomez-Pallerola, 1986).

Infraorder Asilomorpha

Mydidae: mydas flies

Diagnosis: one- or two- segmented antennal flagellum; second flagellomere club-shaped; palp of a single segment or palp absent; Veins R_5, M_1 and M_2 join the wing margin before the wing tip; crossvein *r-m* is located at middle of the discal cell or close to the apex of discal cell; cell m_3 closed; anal cell closed.

Cretomydas Wilkommen gen. nov.

Type species: *Cretomydas santanensis* sp. nov., by present designation.

Derivation of name: named after Cretaceous type horizon and the first described genus of the family.

Diagnosis: distinguished from most Mydidae by both scape and first flagellomere short, and by wing venation, which resembles that of the Recent genus *Rhaphiomidas* (plesiomorphic mydid fly; Yeates and Irwin, 1996). End of vein M_2 is free, which is a plesiomorphic character within Mydidae found only in *Rhaphiomidas* and *Diochlistus*. Crossvein *r-m* is located close to the apex of discal cell, which is derived for Mydidae and also found in *Rhaphiomidas*. The hind basitarsomere is slightly less than five times longer than it is wide.

Cretomydas santanensis Wilkommen sp. nov.

Material: holotype SMNS 66178 (Figures 11.81b and 11.83e–g).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil.

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after the town Santana in the area of the type locality.

Diagnosis: as for genus, by monotypy.

Description (Figures 11.81b and 11.83e–g): body about 22 mm long, well preserved. Antennae are partially preserved and about twice as long as head. Scape and pedicel short, about equal in length; following element consists of only two flagellomeres. Right antenna well preserved and first flagellomere long and slender, three times longer than wide; second flagellomere club-shaped.

Wings are about 14 mm long. Costal vein is short, ending probably between vein R_5 and M_1. The subcostal vein ends at about two-thirds wing length. First radial vein fused with wing margin before wing tip. Veins R_2+_3 and R_4 fused with R_1. Last radial vein (R_5), meets the wing margin free. Branch of R_4 and R_5 located in proximal third of wing. Veins M_1 and M_2 ending separately at wing margin and before wing apex. Veins M_3 and M_4 fused before wing margin. Connection between cells m_3 and bm is short. Anal cell closed clearly before wing margin. Second cubital vein visible only as a fold near first cubital vein. Crossvein *r-m* short, located in distal fourth of discal cell (d), so basal cell br is very long. Hind basitarsomere a little less than five times longer than wide. Abdomen of fossil wider than thorax, second abdominal segment is broadest, with seven or eight tergites exposed.

Comments: the fossil is placed in the Mydidae because of the shape of the antennae and the wing venation. Furthermore, the hind basitarsomere is more than five times longer than the other tarsomeres of the hind leg in Apioceridae and as short as other tarsomeres of the hind leg in most Mydidae (the derived state found in apomorphic Mydidae, Yeates and Irwin, 1996). In the fossil the hind basitarsomere is longer than in apomorphic Mydidae but shorter than plesiomorphic Mydidae (i.e. *Rhaphiomidas*; after Yeates and Irwin, 1996) and in Apioceridae. So in the fossil this character shows the plesiomorphic state of the Mydidae (Yeates and Irwin, 1996).

This is the oldest known and only second described fossil mydid fly. Until now only one fossil mydid was known from the Tertiary (Evenhuis, 1994), which is *Mydas miocenicus* Cockerell, 1913, but he pictured neither the fossil nor its wing venation.

The Recent mydas flies are a worldwide family and can be found in all zoogeographic regions, with greatest diversity in South Africa and South America. Members of the family prefer arid to semi-arid environments with open vegetation; larvae are predators of other insect larvae. The majority of adult mydid flies are blossom visitors.

The flower-loving Apioceridae are also of worldwide distribution and prefer arid and semi-arid regions. They are most diverse in Australia and do not occur in the Palaearctic region and New Zealand. Their larvae are probably predators in the soil and the adults are blossom visitors. Even though they have relatively short wings they are excellent hoverers, which makes them efficient pollinators.

Therevidae (?): stiletto flies

A specimen (AMNH 43511) was discussed and figured by Grimaldi (1990), but it is too poorly preserved to allow a definite familial attribution (Figure 11.85e). The attribution to the tabanid *Cratotabanus* by Martins-Neto (2003b) has already been shown above to be very doubtful. Therefore, we tentatively still consider this fossil to represent a putative undescribed species of Therevidae.

Asilidae: robber flies

Araripogon Grimaldi, 1990

Type species: *Araripogon axelrodi* Grimaldi, 1990, by original designation. Holotype AMNH 43514 (Figure 11.85e), paratype AMNH 43507 (Figures 11.85a and b).

Diagnosis: an average-sized (≈c.11–13 mm long) asilid with relatively short wings (5–6 mm long); numerous, stout spines fore- and midleg; and a plesiomorphic wing venation, as follows: R_2+_3 free from R_1 and turned costad; R_4 turned slightly costad; veins M_1–M_3 arising separately from distal apex of discal cell.

Comment: specimen AMNH 43512 (Figure 11.85e) could be a second undescribed species of this genus according to Grimaldi (1990).

Unnamed new species

Material: SMNS 66182, Asilidae? (Therevidae?): body length about 12 mm; legs not preserved, wings about 7 mm long, R_1 long, end after about three-quarters of wing length and slightly turned costad, R_2+_3 long and turned costad, R_4 turned costad, second marginal cell bell-shaped, m_3 closed at wing margin, cross vein *r-m* at the middle of length of discal cell (Figure 11.82a); SMNS 66183: body length about 9 mm; legs with spines, R_1 long, end after about three-quarters of wing length, R_2+_3 long and turned costad, wing with marginal cell nearly closed, crossvein r-m at the middle of length of discal cell (Figure 11.82b); SMNS 66184 with nicely preserved wings; fossil Asilidae (stout spines on all legs, as in *Araripogon axelrodi* Grimaldi, 1990; Figure 11.82c).

The pictured fossils (Figures 11.82a–c) have wing venation characteristic of Recent robber flies and relatively short wings and are most probably members of this family. Although Therevidae have a similar plesiomorphic wing venation, vein R_1 is usually shorter in Therevidae, as in the fossil (SMNS 66182) and Recent Asilidae. The long radial vein R_1 runs parallel to the subcostal vein in

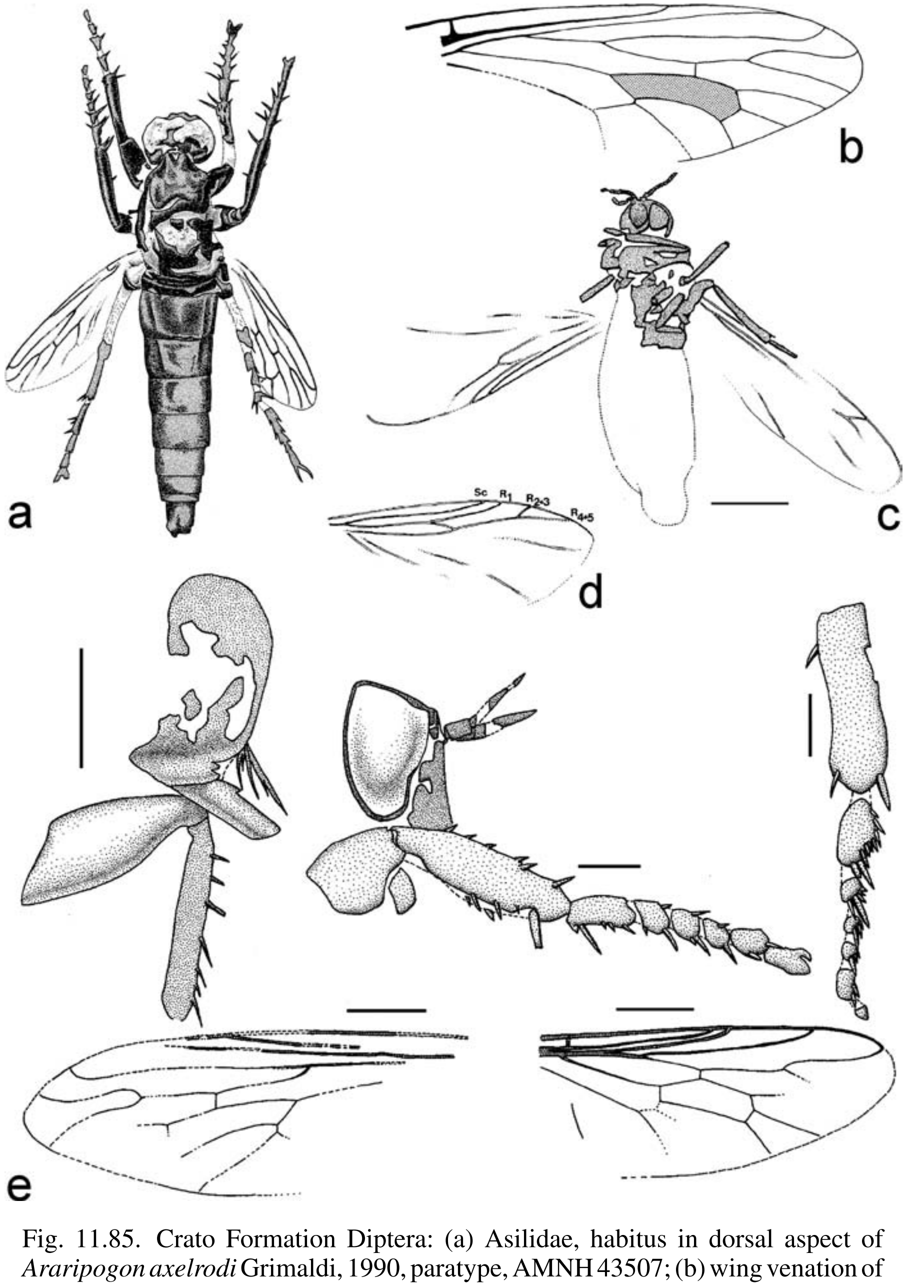

Fig. 11.85. Crato Formation Diptera: (a) Asilidae, habitus in dorsal aspect of *Araripogon axelrodi* Grimaldi, 1990, paratype, AMNH 43507; (b) wing venation of (a); (c) undescribed Bibionidae? AMNH 43504, ventral habitus; (d) wing venation of (c) reconstructed from both wings; (e) Asilidae, *Araripogon axelrodi* Grimaldi, 1990, holotype AMNH 43514 (left, head, left wing); *Araripogon* sp., AMNH 43512 (above right, head, foreleg, hind leg); ?Therevidae, AMNH 43511 (below left, right wing). Scale bars, 1 mm. Figures from Grimaldi (1990).

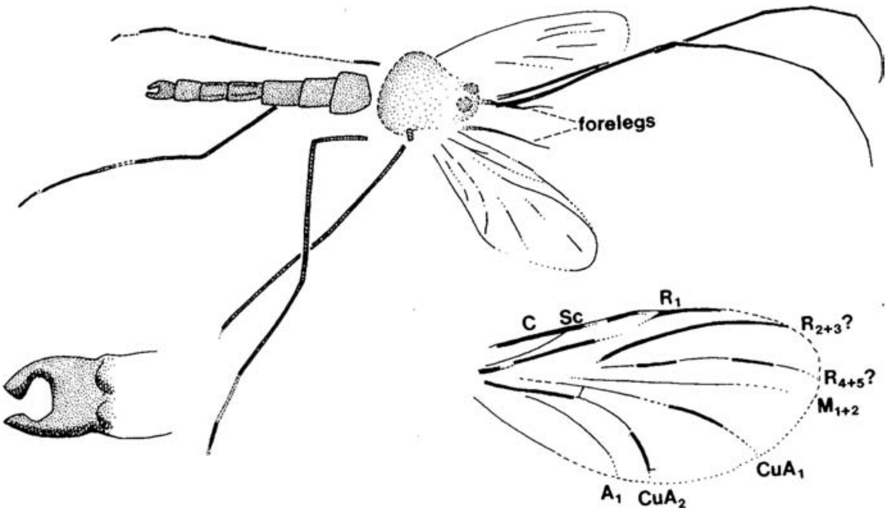

Fig. 11.86. Unidentified Mycetophilidae: habitus, reconstructed wing venation and male genitalia, AMNH 43502. After Grimaldi (1990).

Recent Asilidae, and veins R_2+_3 and R_4 run parallel and meet the wing margin nearly rectangularly. Crossvein *r-m* is located at about half the length of the arched discal cell, and the second submarginal cell is bell-shaped. In Recent robber flies the abdomen is longer than the wings in most cases and robber flies have characteristic stout spines on their legs as well as a jutting, rigid proboscis. The fossil robber fly *Araripogon axelrodi* shows the plesiomorphic characters of a free vein R_2+_3 and veins R_2+_3 and R_4 arched costad. The wings of *Araripogon axelrodi* are very short – shorter than the wings of the pictured fossils.

Asilidae are rare in the Cretaceous, which is the earliest period in which this family of some 7,000 Recent species appears. In fact, there are only two definitive Cretaceous records of Asilidae, one being a fragmentary specimen of a putative leptogastrine asilid in Late Cretaceous (Turonian) amber from New Jersey, USA (Grimaldi and Cumming, 1999), and the other records being the series of *Araripogon* specimens from the Crato Formation (Grimaldi, 1990; herein). The peculiar abundance of Asilidae in the Crato Formation may relate to an arid palaeoenvironment.

Tabanomorpha

Rhagionidae?: snipe flies

Material: single specimen SMNS 66185 (Figure 11.82d). Unnamed new species of Tabanoidea.

The fossil is about 5.5 mm long. The anntennal flagellum is tapered apicad but otherwise with little differentiation of flagellomeres, as the basal brachyceran type, which consists of at least six flagellomeres. The wing venation is simple, Sc end after less than two-thirds of the wing length, R_2+_3 slightly turned costad, R_5 end posterior to wing apex. It is not visible if cell m_3 is open or closed. Legs are preserved and spines are not visible.

Until now no fossil Rhagionidae have been known from the Crato Formation, even though it is a relatively old family common since the Upper Jurassic. Rhagionidae are the most diverse Recent family of Brachycera in the Mesozoic (reviewed by Evenhuis, 1994), particularly as compressions in rocks from central and South-East Asia (e.g. Nagatomi and Yang, 1998 review; Ren, 1998), as well as in Cretaceous ambers from Lebanon and New Jersey (Grimaldi and Cumming, 1999) and from Myanmar and Spain (Grimaldi *et al.*, unpublished work). This first record of putative Rhagionidae from the Crato Formation is significant because the only other Gondwanan records of the family include a species from the Early Cretaceous of Australia (Jell and Duncan, 1986) and the Early Jurassic of India (Mostovski and Jarzembowski, 2000). Unfortunately, the family as currently considered is polyphyletic (Stuckenberg, 2001), which has greatly complicated interpretation of fossils of this 'family'.

Females of several Recent genera of Rhagionidae are bloodsuckers, others are predatory or saprophagous; the larvae are presumed to be predators on other insects.

Tabanidae: horse flies and deer flies

Material: single specimen, SMNS 66181 (Figures 11.82e and f). Unnamed new species of Tabanoidea.

The fossil is about 5.5 mm long and shows a characteristic tabanid wing venation; R_2+_3 turned slightly costad, R_4 ends before wing apex, R_5 ends clearly after wing apex, cell m_3 open. Fossil also with typical tabanid habitus with large eyes and a robust body.

Martins-Neto (1994) described a fossil Tabanidae (*Cratotabanus stenomyomorphus* Martins-Neto and Santos, 1994) from the Crato Formation.

Like Asilidae, Cretaceous tabanids represent the earliest records of the family and these are rare. Isolated records include the Early Cretaceous of Liaoning, China (Ren, 1998), Baissa, Siberia and Dorset, England (Mostovski *et al.*, 2003), and an undescribed form in Late Cretaceous amber from New Jersey (Grimaldi, unpublished work). Thus, *Cratotabanus* is the only Gondwanan record of this important and cosmopolitan Recent family. Living species are notorious blood feeders, although some feed on nectar and pollen and even have long proboscides specialized for anthophily (particularly in the Pangoniinae). The larvae of most species prey on other invertebrates and annelids.

11.21 Trichoptera and Lepidoptera: caddisflies and butterflies

Günter Bechly

Caddisflies (Trichoptera) are inconspicuous, medium-sized, moth-like insects with aquatic larvae familiar because of their habit of constructing remarkable cases from small stones, shells or plant debris for protection. Butterflies and moths (Lepidoptera), hardly requiring introduction, are mostly medium-sized to large insects with four large wings that, in most species, are covered with microscopic, overlapping scales. The biggest difference between adult caddisflies and small butterflies of similar appearance is the presence of hairs on the wings instead of scales and the generally much longer filiform antennae. In Trichoptera the mouthparts are developed as a haustellum with reduced mandibles and maxillae, whereas in most butterflies (except the most basal taxa) the mouthparts (galeae) are developed as a long proboscis for feeding on nectar.

A further important difference, especially regarding their preservation potential as fossils, is that the larvae of butterflies and moths are nearly always terrestrial caterpillars whereas most caddisfly larvae are aquatic, and the few terrestrial forms certainly require very moist leaf litter to avoid dessication. Both groups have a holometabolous life cycle with true larvae that are very dissimilar from the adults followed by a distinct pupal stage. Both orders have a cosmopolitan distribution and are generally phytophagous.

About 11,500 species of Recent caddisflies and about 130,000 species of Recent butterflies have been described, and current views on their internal phylogeny have recently been summarized by Grimaldi and Engel (2005).

Fossil record

The fossil history of Trichoptera and Lepidoptera was first discussed by Handlirsch (1906–08), and more recently by Carpenter (1992), Ivanov and Sukatsheva (2002), Kozlov *et al.* (2002), and Grimaldi and Engel (2005). The attributions of Permian and Triassic taxa (e.g. ‘Necrotauliidae’) that have a trichopteran habitus is problematic and most likely belong to the common stem group of Amphiesmenoptera (Trichoptera+Lepidoptera). The oldest representative of crown group trichopterans is *Liadotaulius major* from the Lower Jurassic of Germany, while the oldest known crown group lepidopteran is *Archaeolepis mane* from the Lower Jurassic of

England. True butterflies (Rhopalocera) are still unknown from the Mesozoic and occur first in the Paleocene Fur Formation of Denmark.

Crato Trichoptera: caddisflies

Adult caddisflies (Figures 11.87a–d and 11.88a–b) are rare fossils in the Crato Formation, and no larvae have yet been discovered. The presence of the flying adults and the absence of their aquatic larvae is supporting evidence that most insects from the Crato Formation are of allochtonous origin. Only a few fossil caddisflies and butterflies from Crato have been described (Martins-Neto and Vulcano, 1989b: Martins-Neto, 1999b, 2001b).

Among Trichoptera the families Calamoceratidae, Leptoceridae and Rhyacophilidae were recorded by Martill *et al.* (1993) without further information and Bechly *et al.* (2001: 45, fig. 34) figured an undetermined small trichopteran from the Crato Formation. Martins-Neto (2001b) described the following seven new taxa (note: the original description is incorrectly cited as ‘Martins-Neto, 2002b’ by Martins-Neto, 2005b: 480–481).

- *Araripeleptocerus primaevus* (Figure 11.89b): earliest fossil record of the family Leptoceridae; body about 8.5 mm long; compound eyes large and prominent; antennae 1.5 times longer than wings and twice as long as body; tibial spur formula 2/2/2; forewing length 11 mm; distal fork formula 1/3/5; F_1 and F_3 with very long branches. Specimen SMNS 66281 (Figure 11.87a) is attributed to this species.
- *Raptortrichops sukatshevae* (Figure 11.89a): familia *incertae sedis*; body 11 mm long and robust; compound eyes very large; antennae slightly shorter than forewings and body; forewing length 11.5 mm; discoidal and median cell large and closed; distal fork formula 1/2/3/5. Specimen SMNS 66288 is a putative specimen of this species. Note, there are two original spellings of the genus name (*Raptortrichops* Martins-Neto, 2001b): 212 and *Raptortricops* Martins-Neto, 2001b: 224, figure 2) and of the species name (*sukatschevae* Martins-Neto, 2001b: 212 and *sukascheva* Martins-Neto, 2001b: 212).
- *Senka crassatella*: familia *incertae sedis*; body 13 mm long and robust; compound eyes large and prominent; antennae only 4.3 mm long; forewing length 14 mm; median cell closed and twice as long as the small and closed discoidal cell. Five specimens, SMNS 66284 (Figure 11.87b), SMNS 66283, SMNS 66285, SMNS 66286 and SMNS 66290, are identified as this species.
- Genus *Cratorella*: family Hydroptilidae (new attribution); small size; antennae distinctly shorter than forewing length; tibial spur formula 2–3/4/4; forewings broad in males and narrow in females; distal fork formula 1/2/3/4/5 in males and 1/3/5 in females; discoidal and median cells open; F_1 longer than F_2, F_3 and F_4 that are of similar size in males, while F_1 and F_3 are very small in females. The apparent ‘ovipositor’ described by Martins-Neto (2001b) for *C. feminina* is an extensible oviscapt, thus excluding its attribution to the Integripalpia. Indeed, it suggests instead affinities with the paraphyletic grade Spicipalpia

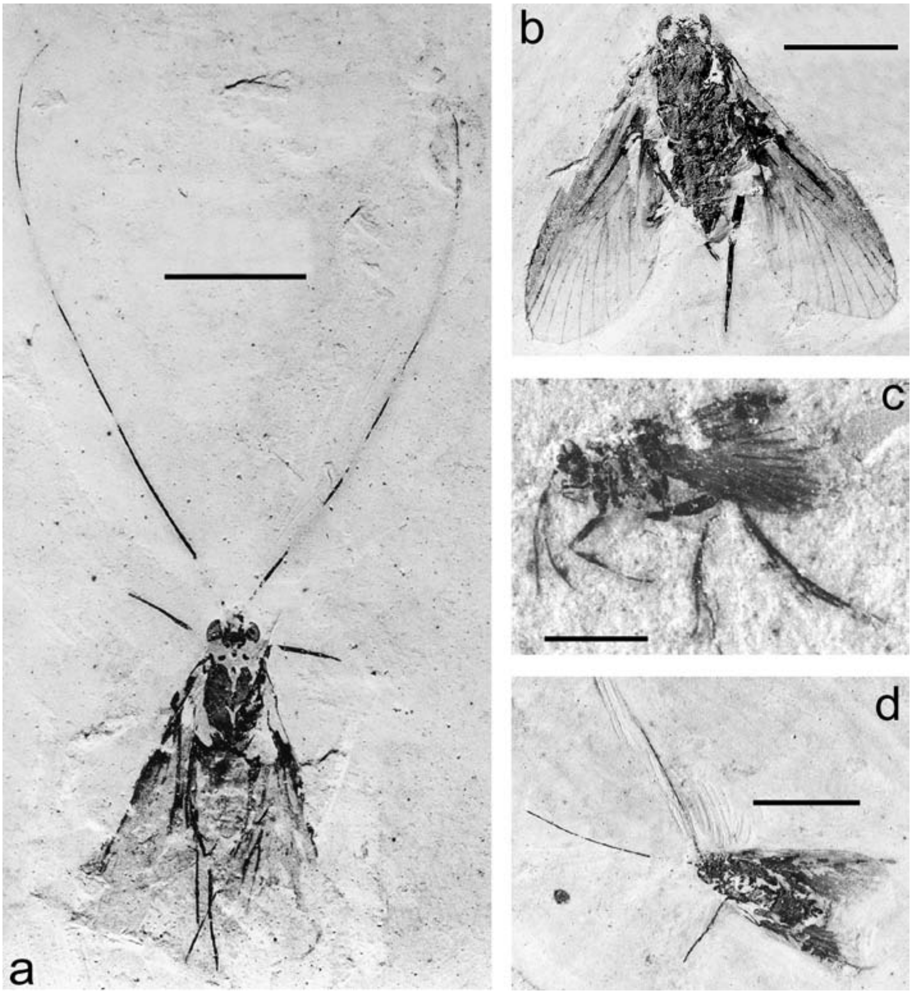

Fig. 11.87. Crato Formation Trichoptera: (a) Leptoceridae, *Araripeleptocerus primaevus*, SMNS 66281; (b) Familia *incertae sedis*, *Senka crassatella*, SMNS 66284; (c) Hydroptilidae, *Cratorella* cf. *media*, SMNS 66278; (d) undescribed gen. et sp. nov., SMNS 66282. Scale bars, 5 mm; except c, 1 mm.

(Rhyacophiloidea=Glossomatidae+Hydroptilidae+Rhyacophilidae+Hydrobiosidae), and is further supported by the five-segmented maxillary palps and the short antennae. Due to the small size of this species and its short antennae, it is probably allied with the micro-caddisflies Hydroptilidae rather than the Rhyacophilidae (contra Martins-Neto, 2001b), even though the longer basal segment of the maxillary palps and the tibial spur formula would exclude a position in crown group Hydroptilidae.

- *Cratorella magna*: body and forewing length approximately 7 mm; hind tibia 2.5 times length of hind femur. In the original description Martins-Neto (2001b) used the spelling '*C. maga*' (*sic*), but this is obviously an incorrect original spelling due to a *lapsus calami*,

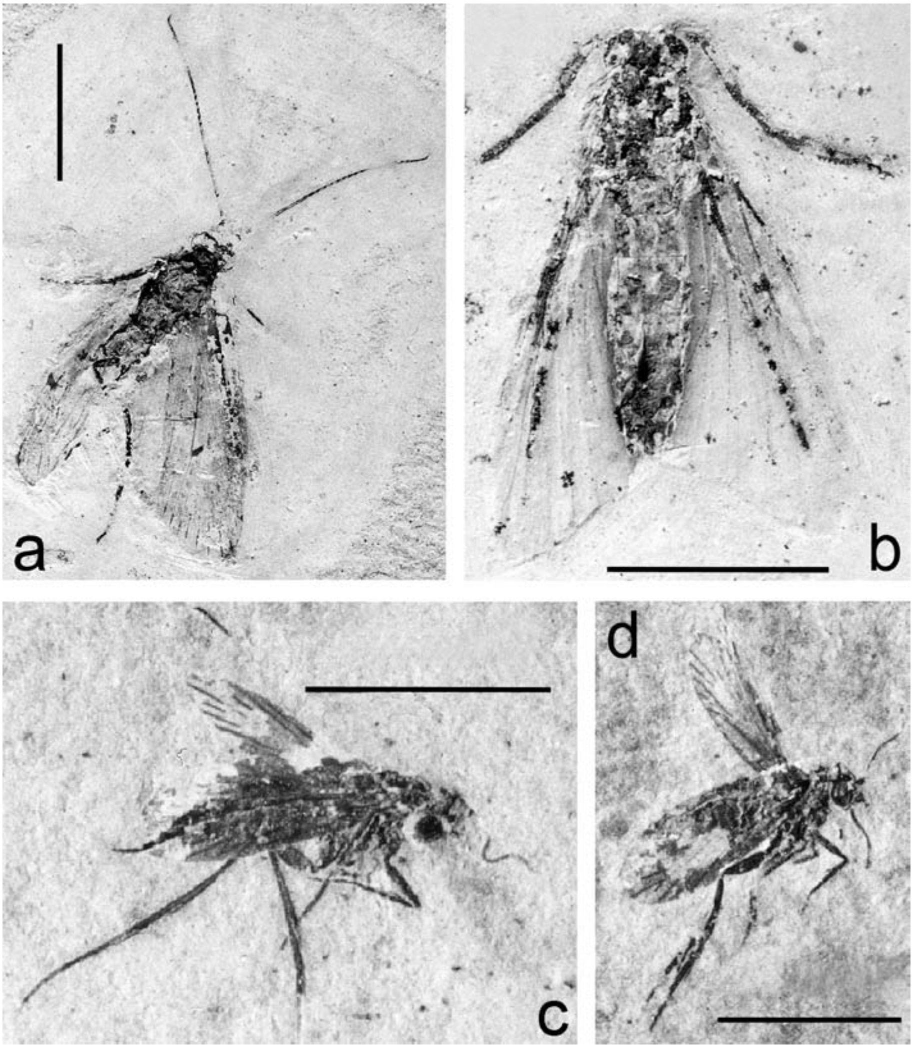

Fig. 11.88. Crato Formation Trichoptera and Lepidoptera: (a) Trichoptera, gen. et sp. nov. SMNS 66287; (b) Trichoptera, gen. et sp. nov., SMNS 66568; (c) Lepidoptera, Micropterygidae, *Parasabatanica caldasae*, SMNS 66279; (d) Lepidoptera, familia *incertae sedis*, *Gracilepterix pulchra*, SMNS 66277. Scale bars: a,b, 5 mm; c,d, 3 mm.

as is clearly documented by the derivation *nominis* and the further uses of this species name in the same publication. Consequently, the correct name of this species is *Cratorella magna*. Three specimens (SMNS 66280, 66561 and 66570) are identified as this species.

- *Cratorella media*: body and forewing length 3.4 mm; hind tibia two times length of hind femur. A single specimen (SMNS 66278) is similar to this species (Figure 11.87c) but it has a somewhat larger body length of 4.3 mm and could represent a new species.

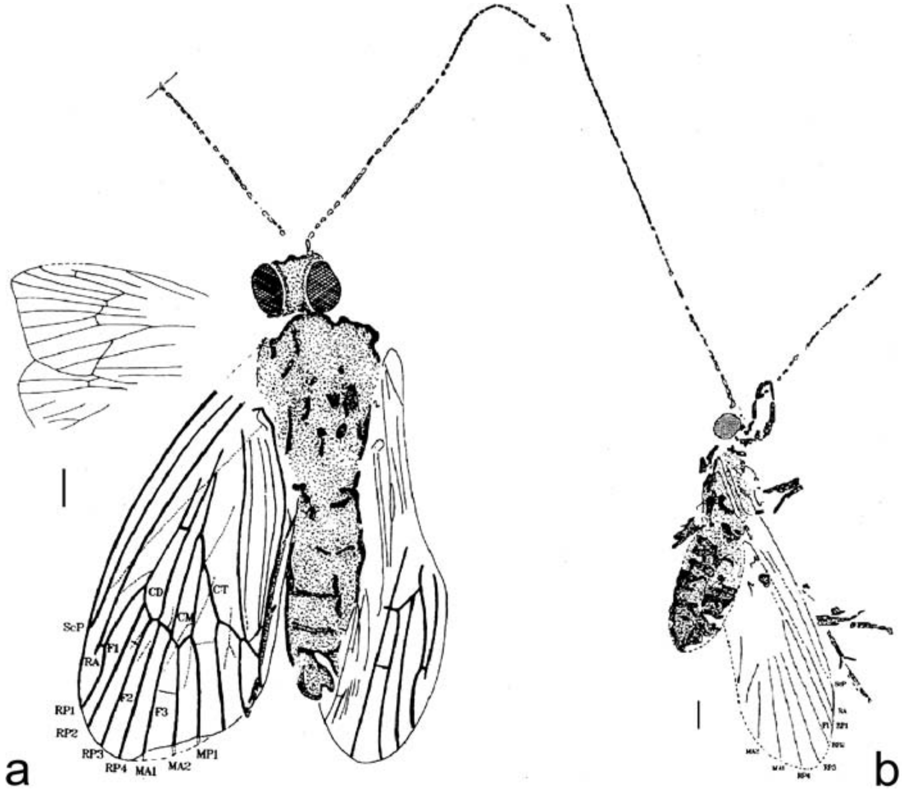

Fig. 11.89. Crato Formation Trichoptera: (a) *Raptortrichops sukatschevae* Martins-Neto, 2001, holotype, RGMN-T013; (b) *Araripeleptocercus primaevus* Martins-Neto, 2001, holotype, RGMN-T012. Scale bars, 2 mm. After Martins-Neto (2001).

- *Cratorella minuta*: body and forewing length 3 mm; hind tibia 1.5 times length of hind femur.
- *Cratorella feminina*: body length 2.6 mm; forewing length 3 mm; forewing narrow with very small F_1 and F_3 (female).

Many of the attributions and descriptions of Crato Formation Trichoptera require re-evaluation: the diagnosis of the monotypic genus *Raptotrichops* contradicts the description and figure of its type species concerning the length of the antennae; the figure and diagnosis of the monotypic genus *Araripeleptocerus* contradicts the statement of the antennal length in the description of the type species; the alleged sexual dimorphism (see above) within the genus *Cratorella* is insufficiently documented and it is unclear whether the features of *C. feminina* are dimorphic or taxonomic; the diagnosis of *Cratorella* provided by Martins-Neto (2001b) is a composite of the character patterns of four different species that might not even

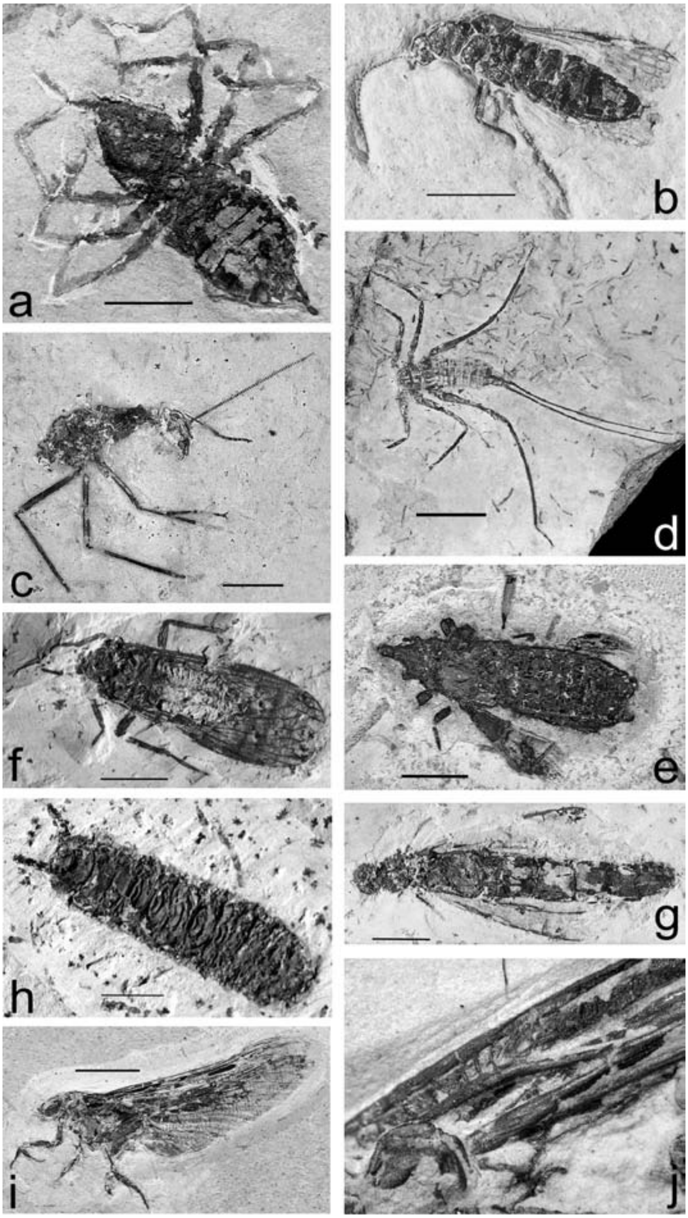

Fig. 11.90. Problematic arthropods: (a) unidentified arachnid, possibly Solifugae, Z21 coll. MSF; (b) Umenocoleidae, *Ponopterix* sp. preserved in lateral aspect, SMNS 66563; (c) Dictyoptera, possibly Raphidiomimidae, Z100 coll. MSF; (d) a large and weird-looking insect, probably Orthoptera, R29 coll. MSF; (e) a strange new Heteroptera, MURJ without number; (f) Holometabola, possibly Megaloptera, H80 coll. MSF; (g) Holometabola, putative ship-timber beetle, Coleoptera, Lymexylidae, SMNS 66534; (h) larva of unidentified holometabolous insect, H99 coll. MSF; (i) Ephemerida, undescribed stem group mayfly (not identical with *Cretereisma* gen. nov.), SMNS 66550, body size and structures of head and legs of this new taxon might even better correspond to the stem group mayfly larvae of the 'Ananas' type than the adults of *Cretereisma* described by Willmann in this volume (Section 11.3); (j) detail of same specimen SMNS 66550, costal brace like Permian Protereismatidae. Scale bars: 5 mm; except d, 20 mm; i, 10 mm.

belong to the same genus. A careful revision by a specialist on fossil Trichoptera would be very useful. Furthermore, there are several putative new genera and species to be described, such as specimens nos SMNS 66282 (Figure 11.87d), SMNS 66287 (Figure 11.88a) and SMNS 66568 (Figure 11.88b), which are clearly distinct from any described species.

Crato Lepidotera: moths and butterflies

Lepidoptera are extremely rare in the Crato Formation and only members of the microlepidopteran grade occur. Martins-Neto and Vulcano (1989b) and Martins-Neto (1999, 2001b) described the following five taxa.

- *Parasabatinca caldasae*: Micropterygidae; body length 3.5–5 mm; forewing length 3–3.5 mm; R_2 and R_3 ending near apex. Besides the holotype, a single specimen (SMNS 66279) has been identified as this species (Figure 11.87c).
- *Undopterix caririensis*: Undopterygidae; hind wing length 3.1 mm; M_1+M_2 fork slightly posterior to R_4+R_5 fork; CuA ending at anal margin near apex.
- *Gracilepterix pulchra*: in familia *incertae sedis*; similar to *Undopterix*; body length and forewing length about 3 mm; hind wing length 2.3 mm; R_1 forking anteriorly of R_2+R_3 and R_4+R_5 forks in forewings; Sc and R_1 unbranched in hind wings. One specimen of this species (SMNS 66277) has been identified (Figure 11.87d). This fossil butterfly was incorrectly listed as *Gracilepteryx* (*sic*) by Martins-Neto (2005b).
- *Xena nana* Martins-Neto, 1999b: Eolepidopterigidae. This taxon seems to be similar to *Eolepidopterix* and is said to be described by ‘Martins-Neto, 2000’ according to Martins-Neto (2005b), which seems to be a *lapsus* and should be ‘Martins-Neto, 1999b’.
- *Psamateia calipsa* Martins Neto, 2002: the present author could not locate the publication with this description, which is mentioned by Martins-Neto (2005b).

All the above species belong to the most primitive and most basal grade of Lepidoptera, and thus not within the Glossata, although Martins-Neto (2005b: 480) attributed all five species to the Eolepidopterigidae, but without explication. However, Grimaldi and Engel (2005: 562, figure 13.16) figured an unnamed primitive moth (AMNH SF 46441) with a piercing oviscapt similar to the Recent families Eriocraniidae and Acanthopteroctetidae that are indeed basal Glossata. This fossil could be the most derived Lower Cretaceous lepidopteran yet discovered, if it should not turn out to be just a small trichopteran like *Cratorella media*.

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Part III

The vertebrate fauna

12

The Crato Formation fish fauna

Paulo M. Brito

Introduction

Fossil fishes are abundant in the Nova Olinda Member of the Crato Formation, where the ichthyofauna is dominated by the gonorynchiform *Dastilbe crandalli* (Figures 12.1b, 12.3c, 12.4a–e). Fishes also occur, but more rarely, in the transition beds beneath the Nova Olinda Member at Cascata. Other fish taxa include the ophiopsid *Placidichthys bidorsalis*, the ichthyodectiform *Cladocyclus gardneri*, an undescribed amiiform, and rare occurrences of the semionotiform cf. *Araripelepidotes* sp. and the coelacanth *Axelrodichthys* sp. Except for *Dastilbe* and the amiiform, all the taxa cited above are well known and considerably more abundant in the slightly younger Romualdo Member of the Santana Formation of the same basin.

Recent collecting has yielded the semionotiform *Lepidotes* sp., a single specimen of the aspidorhynchiform *Vinctifer longirostris* and rare specimens of the tiny ostariophysan *Santanichthys* sp.

Many of the fishes occur as fully articulated skeletons with scales intact, and occasionally with *in situ* stomach contents. Partially articulated portions of fishes occur and may represent the relics of prey items, or portions from partially decomposed individuals. Isolated bones and scales also occur. Fishes are most frequently found preserved in left or right lateral view, with examples only rarely occurring in dorsal or ventral aspect. Bedding planes may contain several individuals of the same size (usually juveniles), suggestive of mass-mortality assemblages.

Systematic palaeontology

Actinopterygii Woodward, 1891

Neopterygii Regan, 1923

Holostei *sensu* Huxley, 1861

Semionotiformes Arambourg and Bertin, 1958

Semionotidae *sensu* Olsen and McCune, 1991

Genus *Lepidotes* Agassiz, 1823

Lepidotes sp.

Lepidotes is a geographically widespread genus with a temporal range from the mid Triassic to the Late Cretaceous. It occurs in both marine and fluvio-lacustrine strata in Europe, North America, Asia, Africa, South America and Cuba. In Brazil it is one of the most characteristic Mesozoic fishes, especially in the north-eastern basins, with a range from the Late Jurassic to Late Cretaceous, and with nine nominal species. The species display considerable morphological variations and are distinguished from each other principally by body size, shape of the hunchback (=pre-dorsal elevation), type of dentition (styliform marginal dentition or crushing dentition) and relative location of the fins (Gallo and Brito, 2004).

One species only is known in the Crato Formation (Figure 12.1a). It is a relatively small form, reaching about 250 mm standard length, having a moderate pre-dorsal elevation, scales lacking ornamentation and a moderately crushing dentition and resembling the species *Lepidotes wenzae* from the Santana Formation (Brito and Gallo, 2003). However, meristic features and the ornamentation of the skull bones suggest a new species.

Genus *Araripelepidotes* Santos, 1990

cf. *Araripelepidotes* sp.

Only one partially preserved example of cf. *Araripelepidotes* has been documented from the Crato Formation (Brito *et al.*, 1998). This taxon is relatively common in the Santana Formation, where it is known by a single species *Araripelepidotes temnurus* (Agassiz, 1841). Until recently it was considered a species of *Lepidotes*, but differs by possession of a weak, edentolous lower jaw composed of a single element; reduction of the coronoid process, and by separation of the dermopterotic and the frontal by the dermosphenotic. Other important features that can be used to differentiate *Araripelepidotes* from other western-Gondwana semionotids include the absence of pre-dorsal elevation; inconspicuous dorsal ridge scales, the relatively short size of the head and completely smooth dermal skull bones. *Araripelepidotes* appears to be endemic to the Araripe Basin.

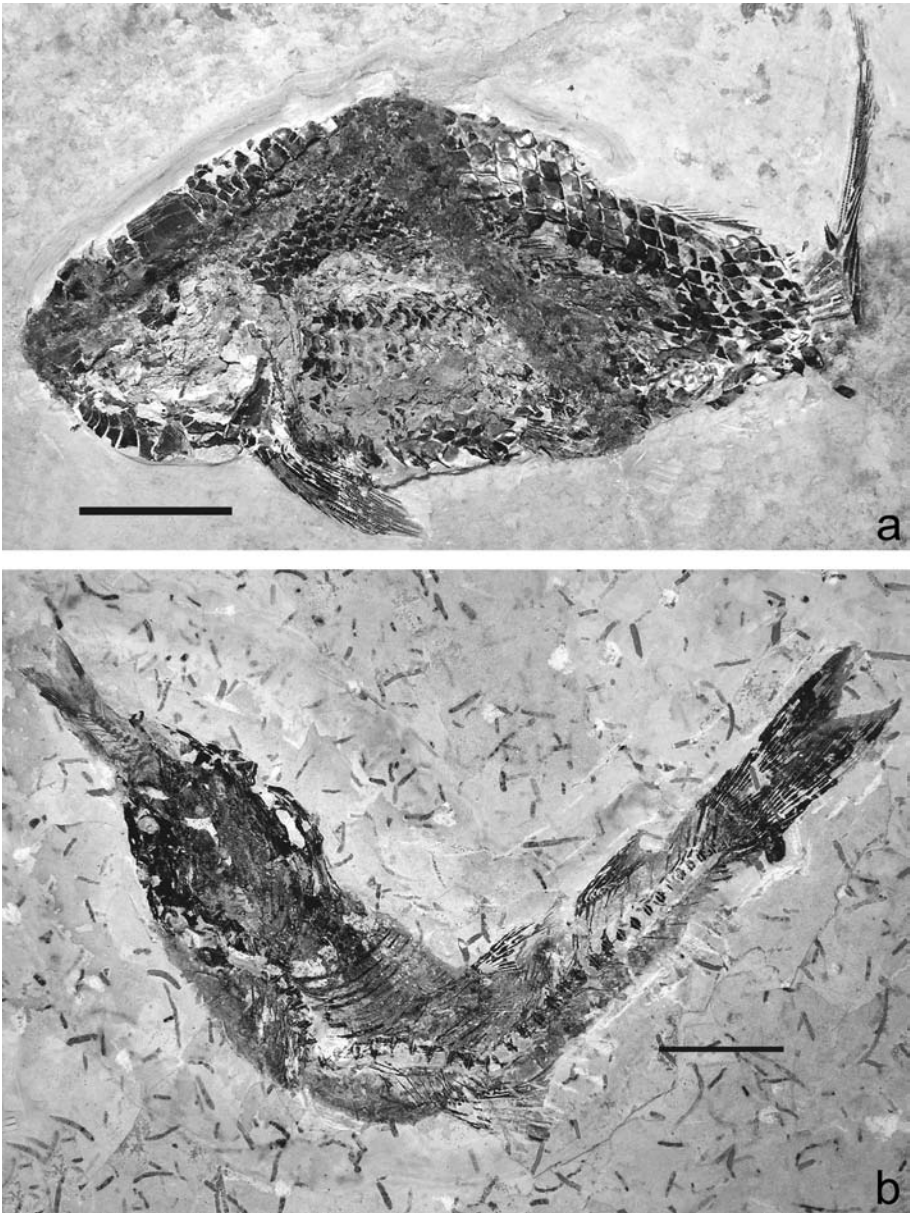

Fig. 12.1. Nova Olinda Member fishes: (a) cf. *Lepidotes* sp.; (b) *Dastilbe crandalli* swallowing a juvenile of the same species. Specimen in Museum of Paleontology, Santana do Cariri. Scale bars, 20 mm.

Halecomorphi Cope, 1872

Amiiformes Hay, 1929

Amiidae Bonaparte, 1838

Vidalamiinae Grande and Bemis, 1998

Today amiids are represented by a single species, the North American bowfin *Amia calva* found in the Mississippi drainage. However, in the past amiids had a world wide distribution and are known from all the major continents (Grande and Bemis, 1998) with the genus *Calamopleurus* occurring widely in the Cretaceous of Brazil.

Two species of *Calamopleurus* occur in South America. *C. mawsoni* occurs in the Barremian Ilhas Formation of Bahia while *C. cylindricus* (formerly *Enneles audax*) is common in the ?Albian Santana Formation of the Araripe Basin. In Africa *Calamopleurus* has been recorded from the Upper Cretaceous, Cenomanian Kem Kem beds of Morocco (Forey and Grande, 1998).

Amiids occur only rarely in the Crato Formation, the first record being that of Martill and Brito (2000), who described a partially preserved skull as *Calamopleurus* sp. Subsequent discoveries of somewhat better preserved specimens of this medium-sized fish, reaching approximately 700 mm standard length with, among other characters, a very long dorsal fin, identify it as Vidalamiinae (Plate 16).

Extant amiids are strictly freshwater fishes. If this was the case for Crato Formation forms, it may explain their rarity in the Crato Formation that has been interpreted by Martill (1993) as a saline lagoon, the rare examples perhaps representing stray fishes washed in from river systems.

Ionoscopiformes *sensu* Grande and Bemis, 1998

Ophiopsidae Bartram, 1975

Genus *Placidichthys* Brito, 2000

Placidichthys bidorsalis Brito, 2000

Ophiopsids are a common group in the Jurassic/Cretaceous of Europe, but in Brazil their presence has only been previously recorded by Santos and Valença (1968; cf. *Ophiopsis cretaceus* nomen dubium) for a specimen that unfortunately could not be diagnosed even to familial level. The discovery of *Placidichthys bidorsalis* (Figures 12.2b and c) by Brito (2000) in both the Crato and Santana Formations in the Araripe Basin demonstrated the presence of true ophiopsids in South America. *Placidichthys* is also known as a rare taxon in the Aptian Marizal Formation of Bahia.

Placidichthys is a small fish with a standard length of about 80 mm, and an elongate, fusiform body. It differs from other members of the family by possessing

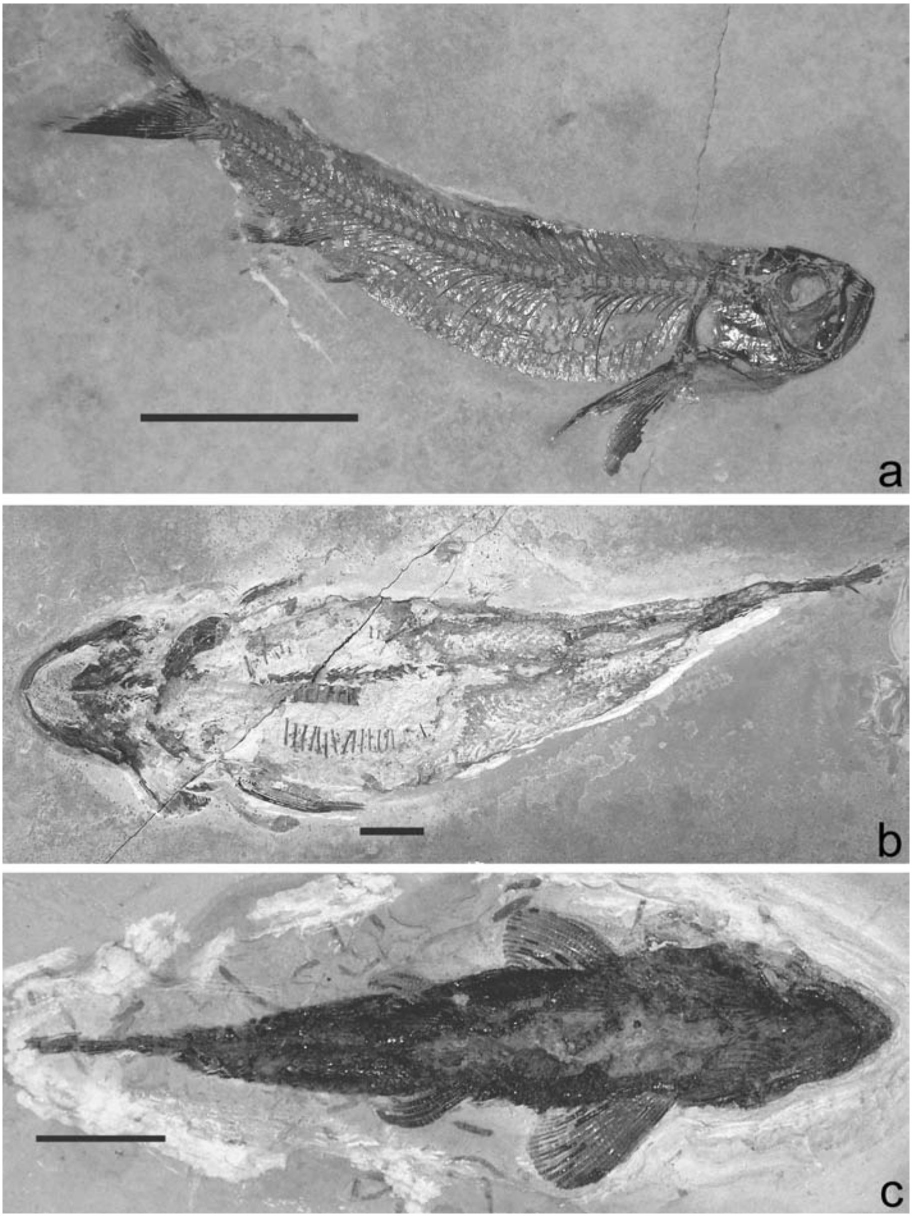

Fig. 12.2. Nova Olinda Member fishes: (a) juvenile, near-perfect example of *Cladocyclus gardneri* Agassiz, 1841; (b) Vidalamiinae gen et sp. nov in dorsal view; (c) *Placidichthys bidorsalis* in ventral view. Scale bars: a, 50 mm; b, c, 10 mm.

a distinctive dorsal fin divided in two. The cranial lobe of the dorsal fin contains about 14 rays, extending from about the 12th to the 23rd transverse scale row and the caudal-most lobe has about 13 rays between the 28th and the 36th scale rows.

Other diagnosable features of *Placidichthys* are that the deepest part of the body is between the head and the first dorsal fin with depth of the body decreasing strongly posteriorly towards the second dorsal fin; the presence of a massive lacrimal bone; small, thin, diamond-shaped ganoid scales distributed from the pectoral girdle to the base of the axial lobe of the caudal fin; the well-developed pectoral fin with its convex margin; and the caudal fin is deeply forked, with the upper lobe larger than the lower.

Teleostei Müller, 1846

Aspidorhynchidae Nicholson and Lydekker, 1889

Genus *Vinctifer* Jordan, 1919

Vinctifer longirostris Santos, 1990

Vinctifer, along with *Aspidorhynchus* and *Belonostomus*, comprise the Aspidorhynchidae, a widely distributed Mesozoic family of highly elongate predatory fishes. Aspidorhynchids are easily recognized by the presence of a long rostrum formed by the premaxillaries, the presence of a predentary on the lower jaw, deep elongate flank scales, and the posteriorly located dorsal and anal fins. *Vinctifer* is a typical southern Tethyan genus known from the Aptian–Albian of Brazil and Venezuela (Jordan, 1919; Santos, 1990; Maisey, 1991; Moody and Maisey, 1994; Brito, 1997), the Aptian of Colombia and Antarctica (Schultze and Stöhr, 1996; Brito, 1997), the Albian of Australia (Etheridge and Woodward, 1892) and Mexico (Applegate, 1996, Brito, 1997), and the Early Cretaceous of Rio Muni, central west Africa (Taverne, 1969).

Three nominal species are recognized: *Vinctifer comptoni*, the type species, is widely distributed and occurs in most of the Lower Cretaceous formations in north-eastern Brazil, as well as in Colombia, Venezuela and Mexico (Brito, 1997); *Vinctifer sweeti* occurs in Queensland, Australia, while *Vinctifer longirostris* is known only from the Tucano and the Araripe Basins, in north-eastern Brazil.

Aspidorhynchids are extremely rare in the Crato Formation, known from only a single specimen attributed to *V. longirostris* (Figure 12.3b). This is a medium-sized aspidorhynchid, reaching a maximum length of 450 mm. It differs from the other aspidorhynchids mainly by its relatively longer premaxillaries and lower jaws, the presence of teeth along the total length of the premaxillaries and smooth skull bones and scales.

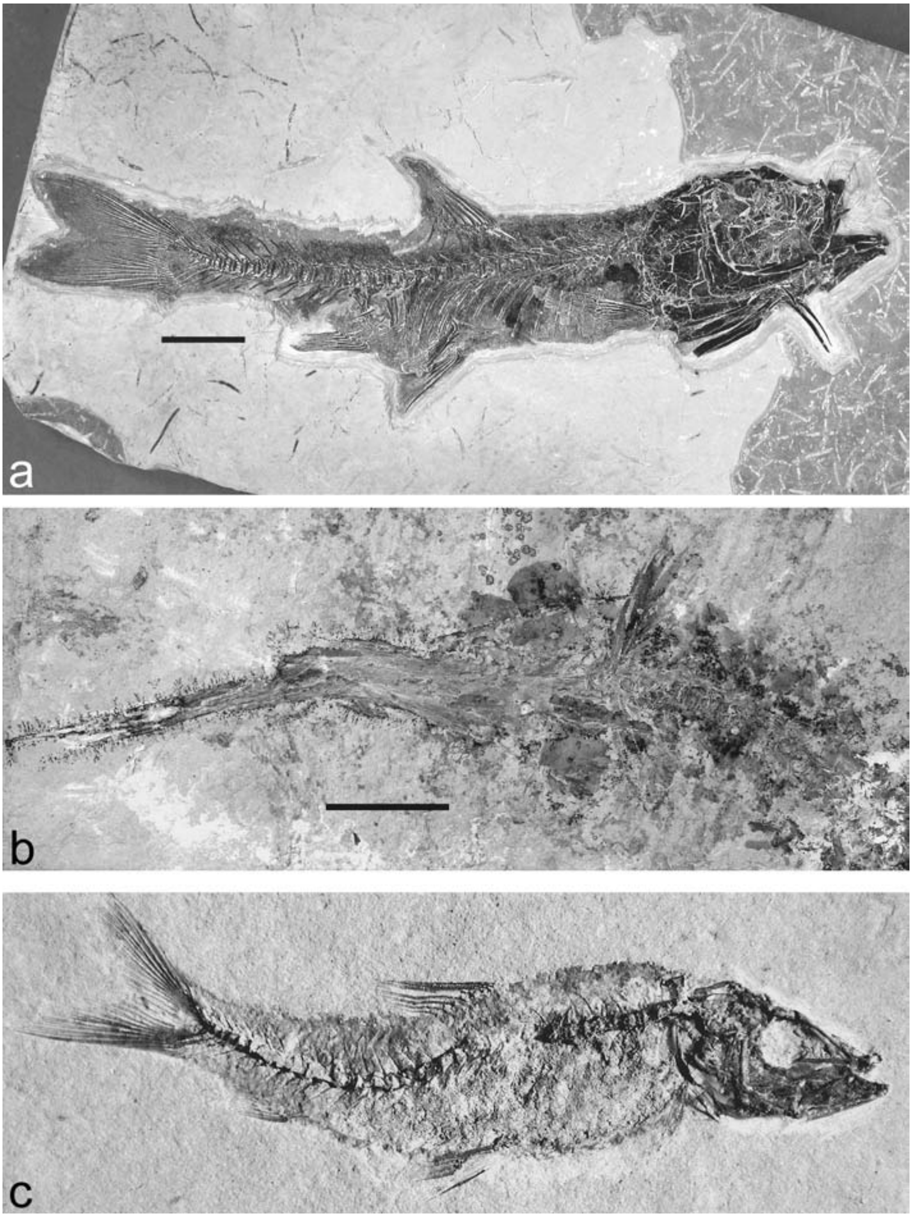

Fig. 12.3. Nova Olinda Member fishes: (a) *Dastilbe crandalli* Jordan, 1910; (b) only documented example of *Vinctifer longirostris* Santos, 1990 from the Crato Formation showing a somewhat disarticulated skull and anterior trunk; (c) *Santanichthys* sp. Scale bars, 20 mm.

V. longirostris occurs more commonly in the Aptian Marizal Formation of Bahia and in the lower part of the Santana Formation (black shales at Pedra Branca), considered as Aptian–Albian. In both of these horizons *V. longirostris* is known from small and young individuals as well as larger specimens with a standard length of 350 mm.

†Ichthyodectiformes Bardack and Sprinkle, 1969

†Ichthyodectoidei Romer, 1966

Cladocyclidae Maisey, 1991

Genus *Cladocyclus* Agassiz, 1841

Cladocyclus gardneri Agassiz, 1841

The †Ichthyodectiformes is an exclusively fossil group of teleosts represented by about 14 genera with a worldwide distribution and a temporal range from the Late Jurassic to Late Cretaceous (Leal and Brito, 2004).

Within †Ichthyodectiformes *Cladocyclus* is the most common genus in the Cretaceous of Brazil, and has been reported from most of the larger north-eastern basins (e.g. Parnaíba, Sergipe-Alagoas, Reconcavo, Tucano and Araripe Basins), being more abundant and better preserved in the Lower Cretaceous Araripe Basin, in both the laminated limestones of the Crato Formation and the carbonate concretions of the Santana Formation (Maisey, 1991; Leal and Brito, 2004).

Cladocyclus can reach a large size, attaining over 1 m standard length. It is easily recognized by its slender and laterally compressed body; large and oblique mouth opening upwards (Plate 18; Figure 12.2a), with a single series of conical, slender, pointed teeth; by the large orbital opening; the posterior position of the dorsal and anal fins; prominent cycloid scales; as well as the deeply forked caudal fin.

Agassiz (1841) first described *Cladocyclus gardneri* from specimens collected by George Gardner from the Santana Formation nodule beds near Jardim. Later, Santos (1950) identified a second species from the type locality which he named *Cladocyclus ferus*. Subsequently authors have attempted to distinguish specimens of *Cladocyclus* and allocate them to one or other of the two nominal species, but in all cases the results were that the majority of the specimens agreed with *C. gardneri*, fewer specimens agreed with *C. ferus*, while others seemed to be a chimaera with characters of both species (Patterson and Rosen, 1977). Thus it would appear that there is only a single species.

Cladocyclus was first recorded from the Crato Formation by Wenz and Campos (1985), who remarked that, although the geological age agreed with that of *Cladocyclus alagoensis* from the Aptian Muribeca Formation, Sergipe-Alagoas Basin, specimens from the Crato Formation bore a close resemblance to those of the Romualdo Member nodules of the Santana Formation. Maisey (1996) suggested that *Cladocyclus* from the Crato Formation represented a distinct freshwater species; however, Leal and Brito (2004), reviewing *Cladocyclus* from the Araripe Basin, showed that there was only one valid species in the Araripe Basin and that specimens from the Crato Formation represent young individuals of *C. gardneri*.

C. gardneri is frequently considered a marine taxon. While parts of the Santana Formation are considered to have been deposited in an epicontinental marine setting (Berthou, 1990; Martill, 1993), it cannot be ruled out that *Cladocyclus* could tolerate reduced salinities. In the Santana Formation, both juvenile and adult specimens of this species occur, but with strong prevalence of adult forms. In marked contrast, the majority of the specimens from the Crato Formation are juveniles, perhaps suggesting that *Cladocyclus* used the Crato lagoon as a nursery, as observed in many extant teleosts.

Ostariophysi *sensu* Rosen and Greenwood, 1970

Gonorynchiformes *sensu* Fink and Fink, 1981

Chanidae *sensu* Poyato-Ariza, 1996

Genus *Dastilbe* Jordan, 1910

Dastilbe crandalli Jordan, 1910

Dastilbe crandalli is by far the most abundant fish in the Crato Formation. The species is a Mesozoic member of the family Chanidae, whose living representative, the near globally distributed *Chanos chanos*, is sometimes referred to as the milk fish.

Four nominal species of *Dastilbe* have been described; *Dastilbe crandalli* Jordan, 1910, *D. elongatus* Santos, 1947, *D. moraesi* Santos, 1955 and *D. batai* Gayet, 1989. However, recent works argued for the validity of only a single nominal taxon, *Dastilbe crandalli* (see Davis and Martill, 1999; Dietz, 2007) whereas Dietz (2007) suggests that *D. batai* may belong within *Parachanos*. *Dastilbe* (Figures 12.1b, 12.3a and 12.4) is one of the most common fishes of Lower Cretaceous western-Gondwanan faunas, being very abundant principally in the north-eastern Brazilian basins (e.g. Parnaíba, Sergipe-Alagoas, Tucano and Araripe Basins), although there are also records for this taxon in south-eastern Brazil (Sanfranciscana Basin) and in Western Africa (Gabon Basin). The stratigraphical range of *D. crandalli* extends from the lower Aptian to the Aptian–Albian boundary.

D. crandalli is a medium-sized fish, up to about 210 mm standard length (Plate 17a), and is easily identified by its ovoid and smooth operculum expanded to about one-third to one-half of head length, and by the position of the anal fin, closer to the caudal than to the pelvics, as well as by its deeply forked caudal fin.

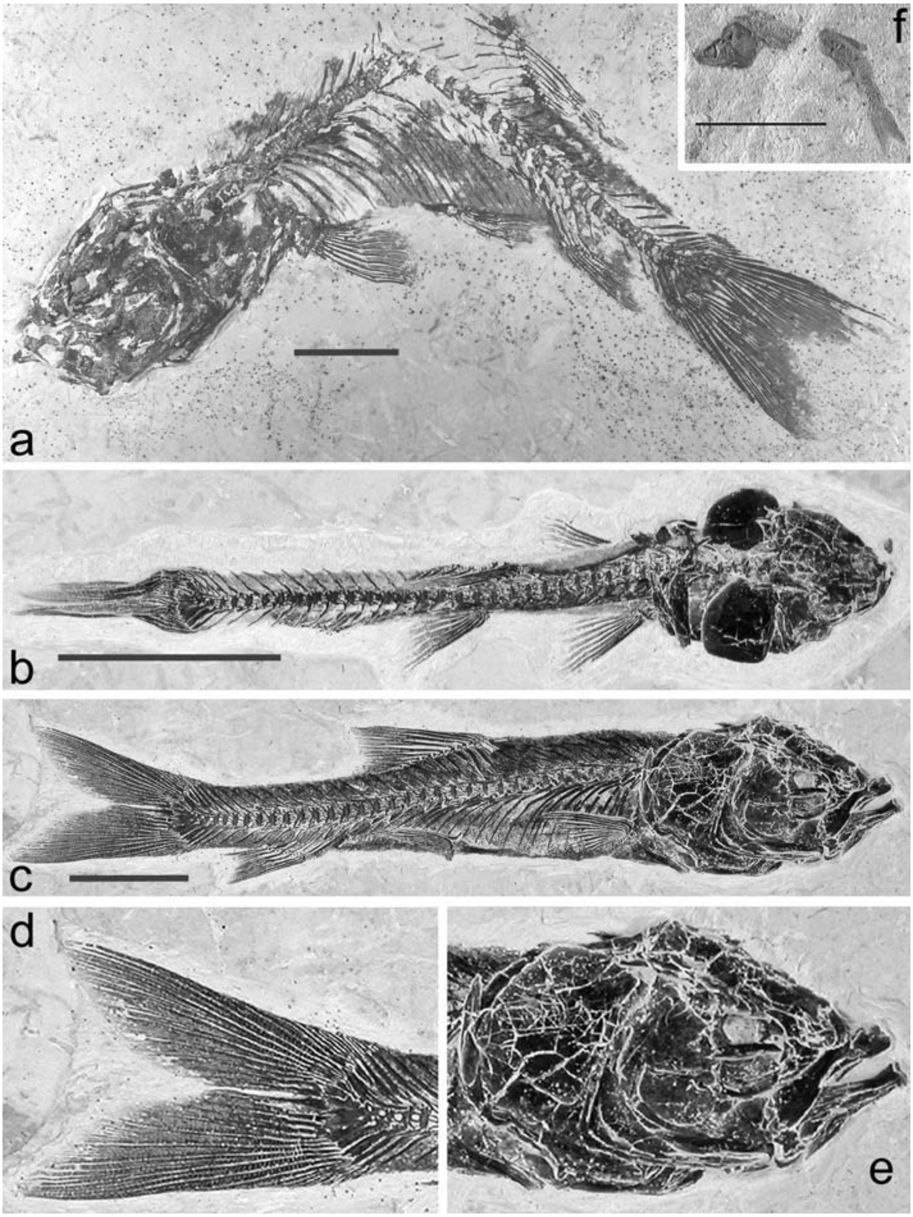

Fig. 12.4. *Dastilbe crandalli* Jordan, 1910: (a) example with broken vertebral column, typically only large individuals occur in this condition; (b) unusual example preserved in dorso-ventral attitude with 'butterfly' collapse of opercules; (c–e) a well-preserved example allowing many anatomical details; (f) juvenile. Scale bars: a–c, 20 mm; f, 5 mm.

Some characters, such as the shape of the dentary, vary with ontogeny and cannot be used to differentiate species. Similar variation is found for the relationship between the origin of pelvic and dorsal fins.

Othophysi *sensu* Rosen and Greenwood, 1970

Family *Incertae sedis*

Genus *Santanichthys* Santos, 1958

Santanichthys sp.

The recent discovery of three small specimens of *Santanichthys* in the Crato Formation adds to the number of taxa common to both the Crato and the Santana Formations. *Santanichthys* (Figure 12.3c) was originally described by Santos (1958) as a new species of leptolepid, *Leptolepis diasii*, from the nodules of the Santana Formation, but later (Santos, 1991) considered that it represents a distinct genus, which he called *Santanichthys*. Although he placed it within the clupeomorphs, the systematic position of this taxon is unclear. Recently, Filleul and Maisey (2004) re-described *Santanichthys*, considering it to be a stem group characiform. A detailed taxonomic or phylogenetic discussion regarding the position of *Santanichthys* is beyond the scope of this chapter, although *Santanichthys* is an othophysian, as it possesses a complete Weberian apparatus. However, it is probably premature to place it within Characiformes, but such a taxonomic position could imply a marine origin for this freshwater group.

Sarcopterygii Romer, 1955

Actinistia Cope, 1871

Family Mawsoniidae Schultze, 1993

Genus *Axelrodichthys* Maisey, 1986

Axelrodichthys sp.

Ever since the discovery of the living coelacanth *Latimeria chalumnae* in the late 1930s (Smith, 1939) this group of unusual fishes has been in the public domain. Considered as a living fossil, coelacanths gained prominence as they were often considered as a missing link between fishes and tetrapods. Coelacanth fossils are relatively common in western-Gondwanan basins where they are known by the very large (perhaps 2 m standard length) *Mawsonia* from the Lower Cretaceous of many north-eastern Brazilian basins, including the Barremian Missão Velha and the ?Albian Santana Formations of the Araripe Basin, as well as in the Lower Cretaceous of the Democratic Republic of Congo, Aptian–Albian of Niger and Cenomanian of Egypt and Morocco, and by *Axelrodichthys araripensis* from the Santana Formation nodules.

Brito and Martill (1999) described a single specimen of *Axelrodichthys* from the Crato Formation representing a small (70 mm total length) individual. The specimen (Plate 17c) has a very long epicaudal lobe, suggesting that it is a young individual rather than a small species.

Conclusions

Knowledge of the Crato ichthyofauna has increased considerably in the last 10 years, from an initial faunal list of just two species (*D. crandalli* and *C. gardneri*) to nine species. Of these nine only two seem to be endemic to the Crato Formation (*Lepidotes* sp. nov. and the vidalamine amiiform species). *Araripelepidotes* cf. *temnurus*, *P. bidorsalis, V. longirostris, C. gardneri, Santanichthys* cf. *diasii* and *Axelrodichthys* sp.) are all known from the slightly younger Santana Formation (black shales or Romualdo Member nodules) while *V. longirostris* is also known from the Marizal Formation of the Tucano Basin in Bahia.

D. crandalli is very abundant in many other Brazilian basins, such as the Parnaíba, Sergipe-Alagoas and Sanfranciscana Basins, although there is only a single, dubious record for this taxon in Equatorial Guinea.

It is difficult to draw palaeoecological conclusions from the nature of the Crato Formation fish assemblage. Partly this is due to the possibility that the rarer taxa are allochthonous, and have entered the Crato lagoon from adjacent water systems of unknown salinity, but most likely would have been freshwater river systems. Certain taxa do appear to be marine, such as *Vinctifer* and *Cladocyclus*, both genera of which are very common in the Santana Formation nodules but also in the upper part of the Santana Formation in where they are associated with echinoids. The presence of such fish suggests at least an intermittent connection of the Crato lagoon with marine waters, perhaps through a number of restricted channels that prevented wider circulation. Both *Vinctifer* and *Cladocyclus* appear to be surface- or near-surface-living fish, and it is notable that the benthic-dwelling fishes present in the Santana Formation nodules (e.g. the skates *Iansan* and the hybodont shark *Tribodus*) are absent from the Crato Formation. This might suggest that bottom waters were inhospitable, but that on occasion the upper water levels did allow for surface-dwelling fishes to enter the lagoon.

That many of the specimens from the Crato Formation are juveniles (e.g. *Placidichthys*, *Dastilbe*, *Santanichthys*, *Cladocyclus* and *Axelrodichthys*) suggests important palaeoecological implications related to the reproductive biology of these genera. Considering that the palaeoenvironmental conditions of the Crato Formation was that of a lagoonal system with probably fluctuating salinities (Martill, 1993) it is possible that marine forms entered the lagoon through one of the restricted links to the sea, perhaps for reproduction.

Fishes such as the Vidalamiinae amiiform were probably freshwater species and entered the Crato lagoon via river systems, in the same way as terrestrial plants, invertebrates (centipedes, scorpions and jaypygids) and rare vertebrates (lizards) were flushed into the lagoon.

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13

Anurans of the Crato Formation

Maria Eduarda C. Leal, David M. Martill and Paulo M. Brito

Introduction

The Anura – frogs and toads of common parlance – comprise about 5,250 extant species with a near world wide distribution, excluding only Antarctica, the highest latitudes of the Northern Hemisphere and the marine realm. Their unique morphology, physiology and behavioural adaptations allow anurans to inhabit a wide range of environments, from the arctic tundra to hot arid deserts. However, they achieve their maximum diversity in the Neotropical rainforests (Duellman and Trueb, 1994; Hofrichter, 2000), where they prefer moist environments. Most species are required to return to freshwater environments for the development of their larvae.

Their temporal range begins in the Triassic if the pro-anurans of Madagascar and Poland are considered anurans. True anurans are relatively scarce in the Mesozoic, only becoming common and diverse in the Cenozoic (Roček, 2000). The earliest occurrence of a true anuran is *Prosalirus bitis* Shubin and Jenkins, 1995, from the Lower Jurassic of Arizona. This taxon achieved the basic anuran body plan that has persisted without significant modification for approximately 200 myr. Of the present 33 anuran families, five have a fossil record extending to the Mesozoic (Leiopelmatidae, Discoglossidae, Pipidae, Pelobatidae and Leptodactylidae), and one family, †Palaeobatrachidae, is exclusively Mesozoic. All but the †Palaeobatrachidae occur in Gondwana (Roček, 2000; Gao and Chen, 2004).

Anurans were first reported in the Crato Formation by Kellner and Campos (1986), where they occur only in the Nova Olinda Member (see Maisey, 1991: 325 for figure). They are represented by several specimens belonging to a single species of Leptodactylidae (Leal and Brito, 2006; Figures 13.2a, b; 13.3) and a single specimen of an as-yet-undescribed pipoid (Figure 13.2c). They occur only

Fig. 13.1. Crato Formation frog: a beautiful example of unidentified frog with soft-tissue preservation of hindlimb integument and stomach contents; SMNK; scale bar, 10 mm. Photograph courtesy of Dr Dino Frey.

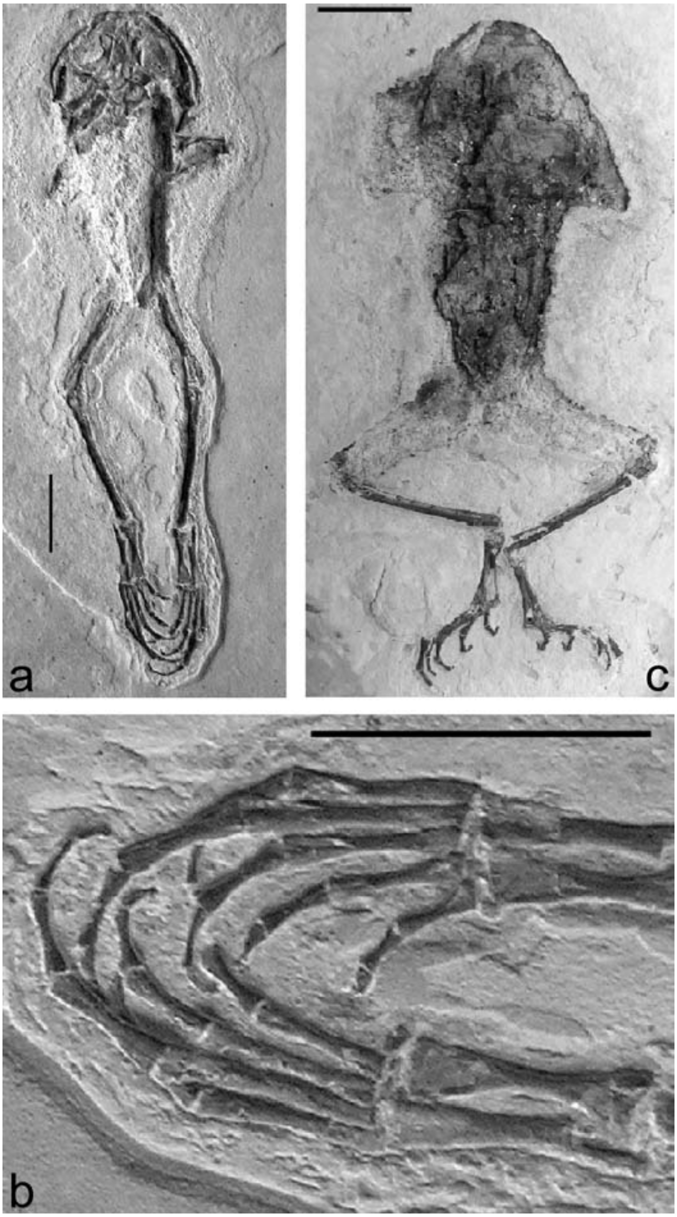

Fig. 13.2. Crato Formation frogs: (a, b) *Arariphrynus placidoi* Leal and Brito, 2006, paratype MPSC-Ap890; (c) possible pipoid. Scale bars, 10 mm.

infrequently, but are usually complete, fully articulated adult individuals of approximately 30–40 mm body length, and may show traces of soft-tissue preservation and, more rarely, the presence of gut contents (Figure 13.1). No tadpoles or spawn has been reported, probably as a consequence of the elevated salinity of the Crato Formation lagoons. In this respect, anurans in the Nova Olinda Member

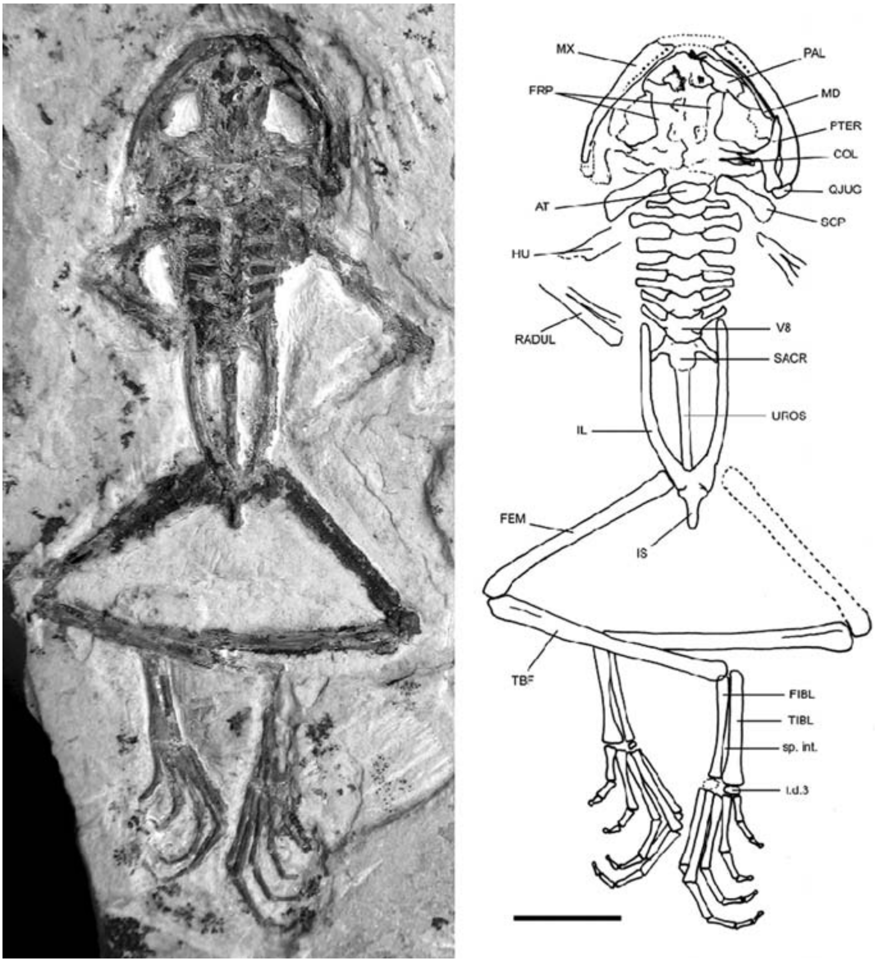

Fig. 13.3. Crato Formation frog: *Arariphyrnus placidoi* from the Nova Olinda Member: (a) holotype, MPSC-Ap 893 comprising a near-complete, articulated skeleton; (b) interpretative drawing. Scale bar, 10 mm.

are allochthonous, a possible explanation for their relative rarity (pterosaurs occur more frequently than frogs).

Systematic palaeontology

Amphibia

Salientia Laurenti, 1768

Anura Rafinesque, 1815

Leptodactylidae Werner, 1896

The Leptodactylidae is a neobatrachian frog clade occurring primarily in the neotropics, with a few representatives in temperate South and North America

(Lynch, 1971). It includes all non-myobatrachid bufonoids that lack synapomorphies regarded as indicative of family status, such as the intercalary cartilages (Hylidae, Pseudidae and Centrolenidae), or a Bidder's organ (Bufonidae). In the most recent phylogenetic analysis, leptodactylids are closest to centrolenids in a clade that is more basal than bufonids, etc. (Frost *et al.*, 2006).

Despite recent attempts to corroborate the family's monophyly, not a single synapomorphy has been identified to support the clade (Ford and Cannatella, 1993; Báez, 2000), which some authors claim to be paraphyletic (Dowling and Duellman, 1978; Ford, 1989) or polyphyletic (Ruvinsky and Maxson, 1996; Haas, 2003). Lynch (1971) recognizes four subfamilies within Leptodactylidae; Ceratophryinae, Hylodinae, Leptodactylinae and Telmatobiinae, of which Ceratophryinae and Hylodinae were hypothesized as monophyletic (Cannatella and Hillis, 1993).

Today the great majority of leptodactylids are Neotropical frogs, distributed all over South America, except for the high Andes, with a few representatives in southern North America and West Indies (Duellman and Trueb, 1994). Their fossil record is sparse, with five genera known only as fossils: †*Arariphrynus* from the Lower Cretaceous of Brazil, †*Estesiella* from the Paleocene of Bolivia, †*Wawelia* from the Miocene (Friasian) and †*Neoprocoela* from the Oligocene (Deseadean), both from Argentina, and †*Thaumastosaurus* from the Eocene (Bartonian-Priabonian) of France and England. A few extant genera (*Ceratophrys, Leptodactylus, Caudiverbera, Eupsophus* and *Eleutherodactylus*) are also known from Cenozoic South American strata (Sanchiz, 1998).

Arariphrynus **Leal and Brito, 2006**

Arariphrynus placidoi Leal and Brito, 2006

Arariphrynus placidoi, recently described by Leal and Brito (2006), is distinguished from all leptodactylids by the following combination of characters: premaxillae and maxillae with a single row of pedicellate teeth; premaxillae with short alary process rounded in its distal portion, directed posterodorsally; maxillary teeth from the articulation with the premaxillae to near the articulation with the anterior process of the pterygoid; quadratojugal contacting the maxillae and the posterior process of the pterygoid; eight procoelous presacral vertebrae; V1 and V2 not fused; atlas with cervical cotyles of type II; transverse processes of presacral vertebrae of uniform lengths, being distally widened in V2, V3 and V4; transverse processes of V2 and V3 inclined anteriorly, paralleled in V4, V5 and V6 and, directed anteriorly at an acute angle in V7 and V8; sacral diapophyses cylindrical, moderately expanded and posteriorly inclined; urostyle without transverse process; ribs absent; bicondylar sacral-coccygeal articulation; arched clavicle, strongly suggesting an arciferal pectoral girdle; clavicular articular surface of the scapula directed anteriorly; femur and tibiofibula with comparable lengths; tibiale and fibulare unfused; phalangeal formula of hind foot 2-2-3-4-3; knobbed terminal phalanges with crenulated distal surfaces (Figure 13.2b). Most anurans from the Nova Olinda Member can be assigned to this taxon, with only rare exceptions (see below).

Comments: Although there are records of leptodactylids from the Cretaceous (?Campanian) Los Alamitos Formation, of Argentina (Bonaparte, 1986; Báez, 1987, 1991; Gayet *et al.*, 1991; Roček, 2000) these are either undetermined or undescribed. Furthermore, the taxonomic assignment of various leptodactylids from the North American Mesozoic remain to be confirmed (Sanchiz, 1998). Thus the Brazilian †*Arariphrynus* from the Crato Formation, and †*Baurubatrachus pricei*, from the Marília Formation, Bauru Basin, (Upper Cretaceous, Santonian) are the only confirmed Mesozoic leptodactylid frogs (Báez and Peri, 1989; Leal and Brito, 2006), and *A. placidoi* represents the oldest member of the group.

Pipoidea Gray, 1825

A single specimen (Figure 13.2c) from the Crato Formation may be a representative of Pipoidea. The Pipoidea possess numerous synapomorphies, and is acknowledged as a monophyletic group in recent phylogenetic analysis including fossil as well as extant taxa (Frost *et al.*, 2006). The extant Pipoidea consists of the Rhinophrynidae and Pipidae, the latter being the only recent archaeobatrachian-grade anurans found in South America, (Cannatella and Trueb, 1988; Báez, 2000; Haas, 2003; Báez and Harrison, 2005; Roelants and Bossuyt, 2005).

Estimates of divergence times suggests a minimum age of 151 myr for the origin of Pipoidea, based on the fossil †*Rhadinosteus parvu*s (Roelants and Bossuyt, 2005). This fossil from the Late Jurassic (Kimmeridgian–Tithonian) of North America is the oldest representative of Pipoidea, being assigned to the family Rhinophrynidae (Henrici, 1998; Roček, 2000). The Crato Formation taxon, if confirmed as a pipoid, pre-dates the oldest known South American pipoid frog, *Avitabatrachus uliana* (Báez *et al.*, 2000), from the late Albian–early Cenomanian Candeleros Formation of north-western Patagonia, Argentina.

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14

Turtles of the Crato Formation

Darren Naish

Introduction

Turtles, properly called Testudines[1], are highly distinctive reptiles well represented in the Cretaceous fossil record, but known in the Crato Formation from just a few specimens (Fielding *et al.*, 2005; Oliveira and Kellner, 2005). Turtles make their earliest fossil appearance in the Norian of the Upper Triassic (Gaffney, 1990) and survive in the extant fauna as approximately 290 species. Uniquely, the turtle skeleton is encased within a bony shell, the dorsal component of which is termed the carapace, and the ventral component the plastron. Bones, variously termed neurals, costals and peripherals, form most of the shell (with a single nuchal bone at the anterior end of the midline, and a suprapygal and pygal at the posterior end), and in life these are covered by keratinous scutes. Members of a few groups, namely leatherback and softshell turtles, and the bizarre African pancake tortoise *Malacochersus tornieri*, have reduced both the bones that form the shell, and the scutes that cover it. Isolated shell bones are among the commonest turtle fossils, and the Crato Formation turtle fossils are unusual in that all specimens found so far are complete examples.

Although turtles might be regarded as constrained in diversity by way of the shell, they still include terrestrial, amphibious and fully aquatic species that, even today, occur worldwide with the exception of the polar regions. How turtles are related to other reptiles remains controversial. While they have conventionally been regarded as basal reptiles only distantly related to the other living reptile

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[1] Which taxonomic name should be used for turtles is controversial. The term used most often, Chelonia, should be abandoned as it is universally employed as the generic name for *Chelonia mydas*, the extant green turtle. A recent review concluded that the best available name for the turtle crown group is Testudines, and that the most inclusive clade incorporating Testudines might be termed Pantestudines (Joyce *et al.*, 2004).

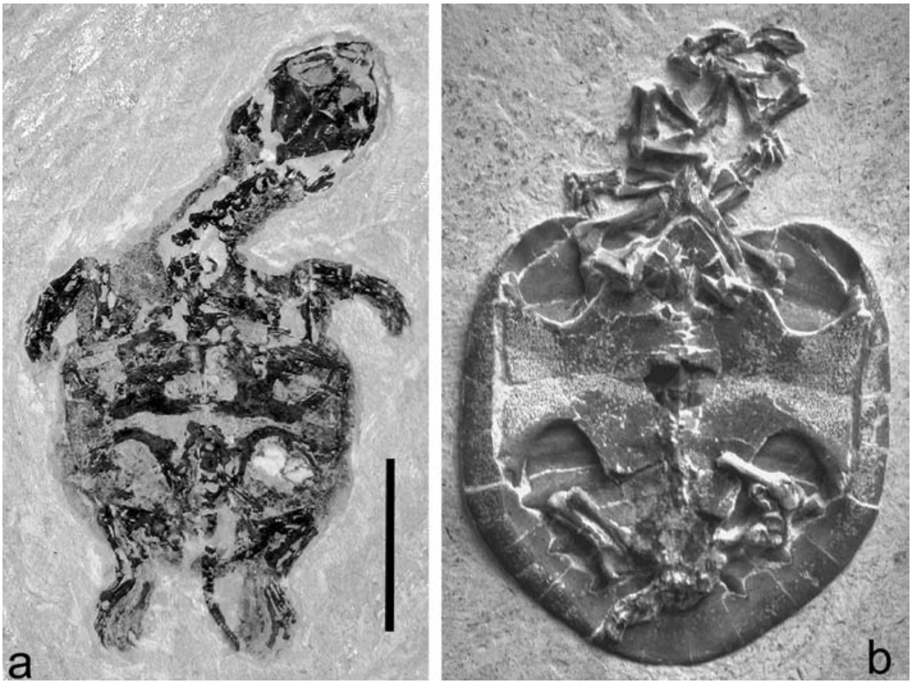

Fig. 14.1. Crato Formation turtles: (a) juvenile turtle gen. et sp. indet.; scale bar, 10 mm; (b) and undescribed example of *Araripemys barretoi*. Photographs courtesy of Dr D. Unwin.

groups, new molecular and morphological studies suggest instead that they are part of Diapsida, the reptile clade that includes lizards, snakes, crocodilians and others (Rieppel and Reisz, 1999).

Crown group turtles (Testudines) are best known for their two surviving clades, Cryptodira and Pleurodira. Conventionally these are divided according to how they retract their necks, with cryptodires performing retraction vertically, and pleurodires retracting horizontally. However, basal members of both clades were incapable of retraction, and other characters, predominantly those involving the jaw mechanism and basicranial architecture, have proved more useful in defining and differentiating the two groups (Gaffney and Meylan, 1988). Although pleurodires are successful today, with over 60 species in 25 genera, they are restricted to the Southern Hemisphere and, with one exception, to freshwater habitats (the exception, the South American snake-necked turtle *Hydromedusa tectifera*, sometimes enters brackish waters; Ernst and Barbour, 1989). Fossil pleurodires were more widespread, and occurred in North America, Europe and Asia as well as the southern continents, and were also more diverse ecologically, with several taxa known from nearshore marine sediments.

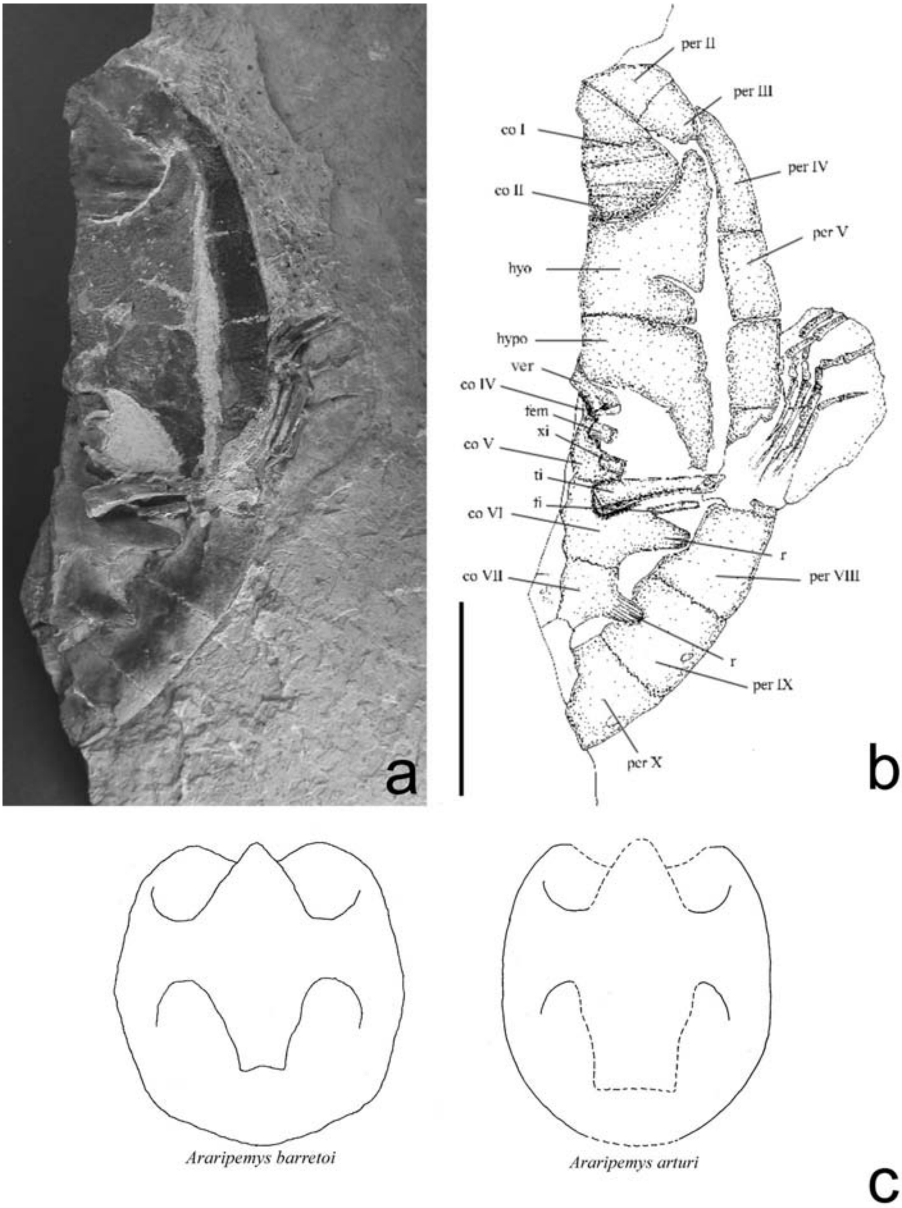

Fig. 14.2. Crato Formation turtles: (a) holotype of *Araripemys arturi* Fielding *et al*., 2005; scale bar, 50 mm; (b) interpretive diagram of *A. arturi*; (c) ventral outline highlighting difference between the two species in the shape of the posterior border.

In the Crato Formation, turtles are only known from the Nova Olinda Member, but are neither abundant nor taxonomically diverse. This contrasts with the Santana Formation of the same basin, where five named taxa, are known, and one of these, *Araripemys barretoi*, is known from multiple specimens. Four of the Santana turtles are pleurodires while the fifth, *Santanachelys gaffneyi* Hirayama, 1998, is a basal eucryptodire (Joyce, 2004). All the Crato Formation turtles are pleurodires: they consist of two species, both belonging to the genus *Araripemys* (Figures 14.1 and 14.2). *A. barretoi*, the commonest turtle of the Santana Formation nodule beds, was reported from the Crato Formation by Oliveira and Kellner (2006) while a second species, *Araripemys arturi* Fielding *et al.* (2005), is hitherto unknown in the Santana Formation.

Besides *A. arturi* and *A. barretoi*, the Nova Olinda Member has also yielded juveniles of an indeterminate pleurodire (Figure 14.1a). A complete specimen, preserving some soft tissues, was figured by Fielding *et al.* (2005). It may be a juvenile araripemydid, possibly referable to *Araripemys*, but this cannot be confirmed. Turtles have also been reported from the Missão Velha Formation that underlies the Crato Formation (Brito *et al.*, 1994).

Systematic palaeontology

Testudines Linnaeus, 1758

Pleurodira Cope, 1864

Pelomedusoides Cope, 1868

Araripemydidae Price, 1973

Araripemys Price, 1973

Araripemys was evected for *Araripemys barretoi* Price, 1973 from the Santana Formation, a distinctive long-necked pleurodire with a flat, sculptured carapace, reduced plastron bearing three mid-line fontanelles, and unusual ‘arrow-shaped’ unguals (Meylan and Gaffney, 1991; Meylan, 1996). Like some other Lower Cretaceous Brazilian taxa, *Araripemys* is not exclusively South American, having been reported from the Kem Kem Beds of Morocco and the Elrhaz Formation of Niger (Broin, 1980). Within Brazil, *A. barretoi* is also present in the Alcântara Formation; formerly known as the Itapecuru Formation (Batista, 2005).

Two other turtles have been classified within Araripemydidae: *Taquetochelys* Broin, 1980 from Lower Cretaceous Niger, and *Chelycarapookus* Warren, 1969 from Lower Cretaceous Australia. Meylan (1996) proposed that *Euraxemys* from the Santana Formation was also an araripemydid but this was not supported by Gaffney *et al.* (2006). Within Pleurodira, araripemydids are regarded as the most basal clade within Pelomedusoides, the other members of which are Pelomedusidae, Bothremydidae and Podocnemididae (Meylan, 1996; Gaffney *et al.*, 2006).

A. arturi Fielding *et al.*, 2005 is from the Nova Olinda Member of the Crato Formation, and is presently known only from the holotype. Consisting of a partial plastron and hindlimb, all preserved in ventral view, it exhibits the *Araripemys* characters of pitted plastral ornamentation, a contact between the first costal and the first peripheral, and the absence of mesoplastra. It lacks both the autapomorphic arrow-shaped unguals and distinct lateroposterior angle seen on the carapace of *A. barretoi*. Beyond these details it remains poorly known. The holotype is significant in preserving the external mould of the pes. The shape of this mould indicates that *A. arturi* had flipper-like feet resembling those of extant aquatic forms such as *Carettochelys*, the New Guinea pig-nosed turtle (Fielding *et al.*, 2005). Gaffney *et al.* (2006) argued that *A. arturi* should be provisionally synonymized with *A. barretoi* pending the discovery of better specimens.

Palaeobiology

In the Santana Formation, *A. barretoi* is preserved in association with marine fish and another turtle, *Santanachelys gaffneyi*. The latter is assumed to have been marine due to osteological evidence that it possessed large cranial salt glands (Hirayama, 1998). Consequently, *A. barretoi* may also have been a marine form (Kellner and Campos, 1999). This is supported by the presence of *A. arturi* in the Nova Olinda Member of the Crato Formation, a unit regarded by Martill and Wilby (1993) as having been deposited within a saline lagoon. Furthermore, Kischlat and Campos (1990) suggested that the scapulocoracoid and limb-bone morphology of *A. barretoi* were indicative of aquatic habits, and these observations are consistent with the discovery of a *Carettochelys*-like foot paddle in *A. arturi*. It seems that *Araripemys* was both more aquatic in habit than living pleurodires, and perhaps tolerant of euryhaline conditions. These observations are in agreement with the general picture that fossil pleurodires were far more diverse ecologically than extant members of the group, and that some may have inhabited brackish or marine environments. However, it should be noted that turtles are surprisingly rare in the Crato Formation, perhaps because the elevated salinity of the Crato lagoon made it a difficult environment to inhabit.

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15

Lizards of the Crato Formation

David M. Martill

Lizards, in the general sense of limbed Squamata, include iguanas, geckos, monitors, extinct mosasaurs, skinks and a wide number of other groups of usually long-tailed, sprawling-limbed diapsid reptiles. Snakes are also included within the Squamata as they are more closely related to lizards than to any other group of reptiles. As with most of the Crato palaeobiota, lizards appear to come only from the Nova Olinda Member laminated limestones of the Nova Olinda–Santana do Cariri region. Their remains are extremely rare and the described forms are of terrestrial groups, suggesting that the occurrences are largely allochthonous. The Crato Formation lizards are among the oldest known in South America (Candeiro, 2007) but, because of their rarity, any assessment of Crato lizard diversity is premature. Both described specimens appear to represent basal forms (Evans and Yabumoto, 1998; Bonfim, 2002).

In a number of specimens there is evidence of soft-tissue preservation, although the skeletons are not necessarily complete. They are usually articulated, but specimens may be missing distal regions of the tail (perhaps due to autotomy) and/or missing limbs. Perhaps such specimens, missing significant components of the skeleton, but otherwise well preserved, represent individuals dropped by volant predators.

Systematic palaeontology

Reptilia

Lepidosauria Heackel, 1866

Squamata, Oppel, 1811

Incertae sedis

Olindalacerta Evans and Yabumoto, 1998

Olindalacerta brasiliensis Evans and Yabumoto, 1998

This taxon is based on a single, certainly juvenile specimen, housed in the Kitakyushu Museum of Natural History & Human History in Japan, number KMNH VP

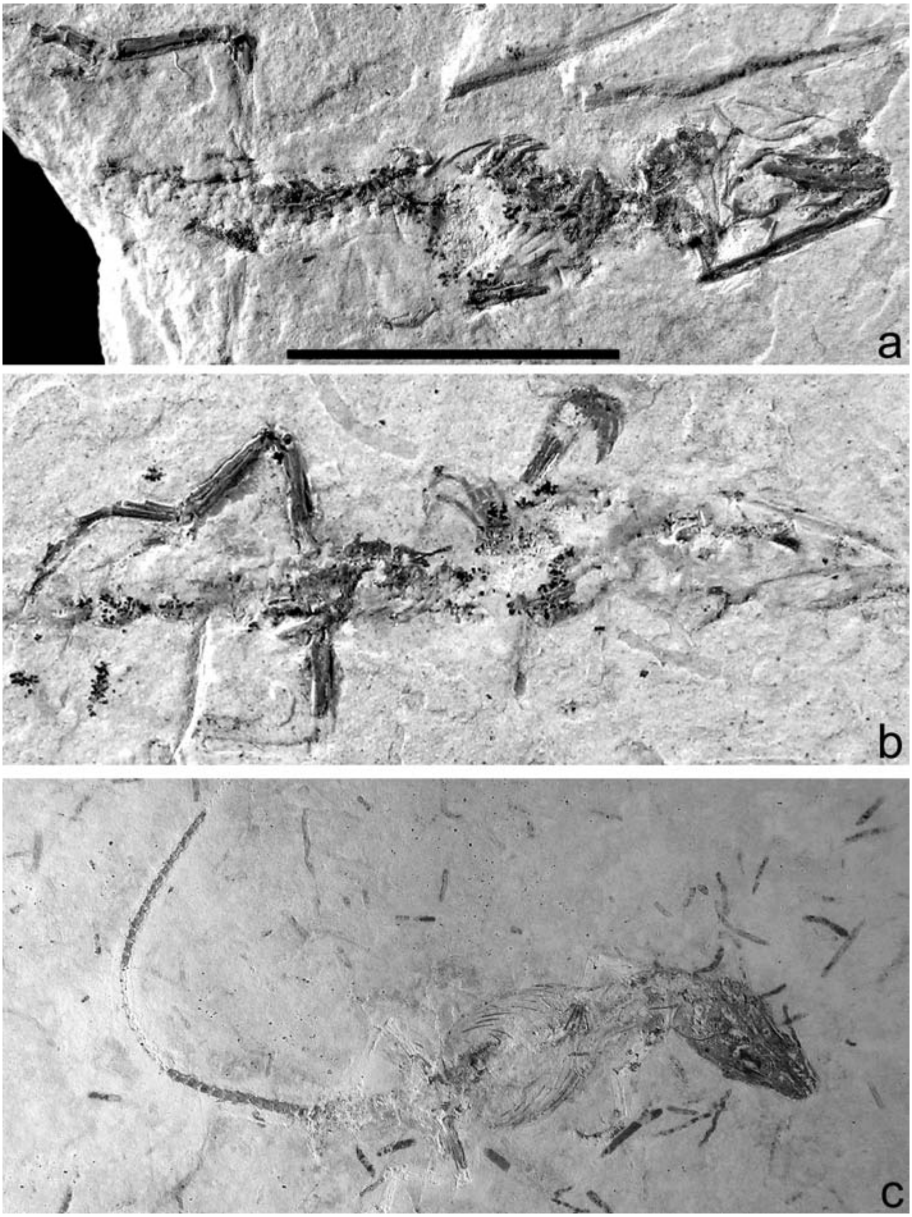

Fig. 15.1. Lizards from the Nova Olinda Member: (a, b), part and counterpart of holotype of the probable hatchling *Olindalacerta brasiliensis* Evans and Yabumoto, 1998 KMNH VP 400,001. Photographs courtesy of Dr Y. Yabumoto; (c), an unidentified lizard from a private collection. Scale bar in (a), 10 mm.

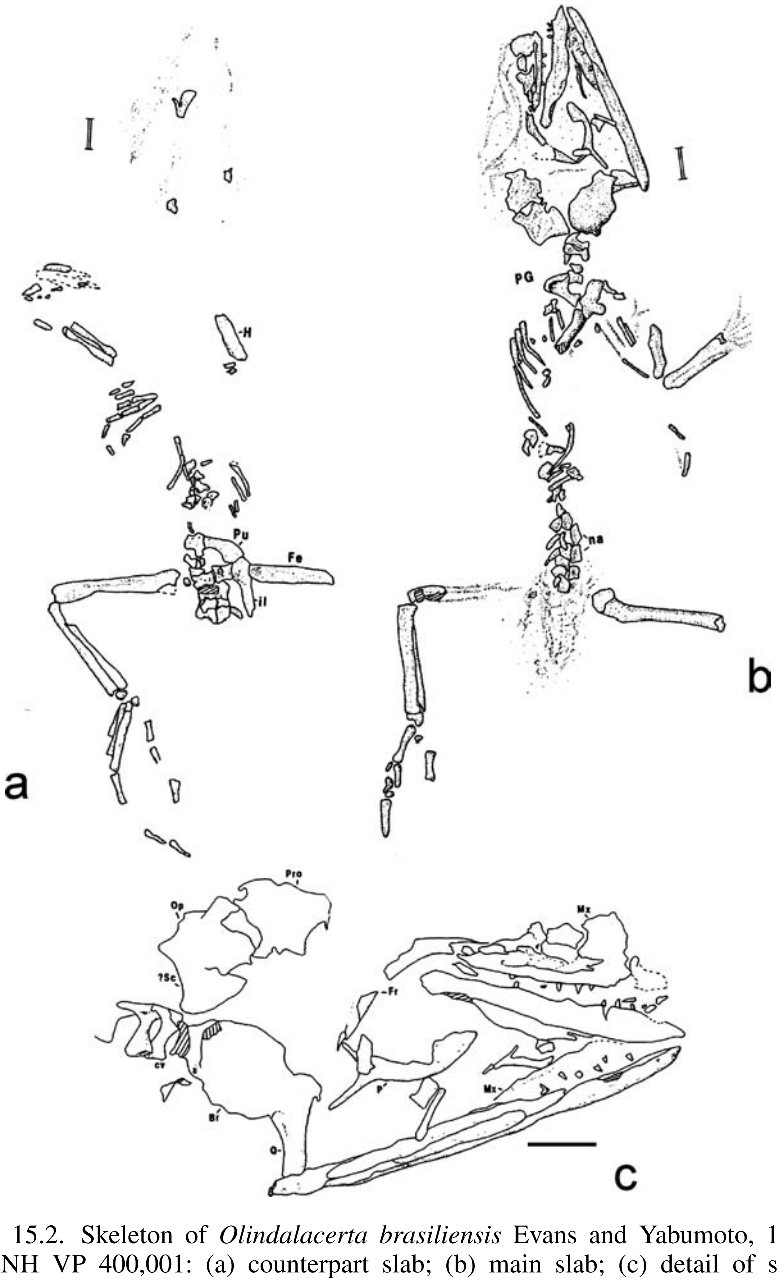

Fig. 15.2. Skeleton of *Olindalacerta brasiliensis* Evans and Yabumoto, 1998 KMNH VP 400,001: (a) counterpart slab; (b) main slab; (c) detail of skull elements. Scale bars, 1 mm. Based on Evans and Yabumoto (1998).

400,001, and comprises both the part and counterpart slabs (Figures 15.1a and b and 15.2). The specimen is not well preserved and is missing most of its tail, although this may have been present on the broken slab of Figure 15.1a. It is approximately 22 mm in length from the tip of the skull to the pelvis, and with many of the bones only weakly ossified, clearly represents a juvenile individual. Non-fusion of the neurocentral sutures suggest that it may represent a hatchling (Evans and Yabumoto, 1998). Such a young individual, in a rather poor state of preservation, prevents accurate identification, but the presence of a pleurodont dentition, a streptostylic quadrate, procoelous vertebrae and an emarginated scapulocoracoid clearly indicates it is a squamate. Although it is not possible to determine what type of lizard *Olindalacerta* is, it clearly is somewhat unusual in that it has particularly robust hindlimbs and a rather strange, elongate lower jaw that differs from all other lizard jaws.

***Tijubina* Bonfim Jr and Marques, 1997**

Tijubina pontei Bonfim Jr and Marques, 1997

Tijubina pontei Bonfim Jr and Marques, 1997 was the first lizard to be reported from the Crato Formation (Bonfim Jr, 1997a). Its discovery has been announced on several occasions in subsequent reports by Bonfim Jr (1997b, 2002), Bonfim Jr and Marques (1997a, 1997b, 1997c) and Bonfim Jr and Avilla (2002). Like *Olindalacerta*, this taxon is based on a single specimen preserved on a typical slab of Nova Olinda Member limestone. It is entire (total length 140 mm) and is preserved in a dorso-ventral orientation with the forelimbs pressed against its flanks and the rear limbs slightly splayed (Plate 19b). It lies on the bedding-plane surface and appears to have been split through the middle. Shortly after its formal description by Bonfim Jr and Marques (1997c), what appears to be the counterpart of the holotype was figured by Martill and Frey (1998). A sub-circular dark patch in the body region appears to be stomach contents and scales are preserved in the caudal region.

Reasonable evidence for the provenance of this specimen is that it was photographed by D.M.M. in Nova Olinda in a fossil ‘safe house’ prior to its disappearance into the murky world of commercial palaeontology in 1996.

Although originally described as belonging to Teiidae Gray, 1827, a subsequent analysis placed *Tijubina* in a more basal position outside of Teiidae and even more basal than Iguania (Bonfim Jr, 2002). An amended diagnosis of this taxon was presented as a poster display at a meeting in South America, but has yet to be published (Bonfim, Jr, 1997b).

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16

Crocodilians of the Crato Formation: evidence for enigmatic species

Eberhard 'Dino' Frey and Steven W. Salisbury

Crocodilians are extremely rare in the Crato Formation, and most of the material that has been collected is fragmentary or badly preserved. Only two species are represented, both of which are enigmatic concerning both their preservation and anatomy. Only one of these, *Susisuchus anatoceps* (Figures 16.1, 16.2 and 16.3; Plate 20), has been formally described (Salisbury *et al.*, 2003a) and, to our knowledge, is represented by a maximum of 10 specimens. The other species (Plate 21) is reported here for the first time. It is known from a single, almost complete skeleton with associated preserved soft tissues, and most likely represents a new species of *Araripesuchus*. Based on their extreme rarity, neither species is considered to have inhabited the Crato lagoon, but most likely lived in the surrounding hinterland.

Systematic palaeontology

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Neosuchia Benton and Clark, 1988

Susisuchidae Salisbury, Frey and Martill, 2003a

Genus *Susisuchus* Salisbury *et al.*, 2003a

Susisuchus anatoceps Salisbury *et al.,* 2003a

Remarks

Susisuchus anatoceps (Holotype: SMNK PAL 3804) is one of the oldest crocodilians with a dermal skeleton consistent with that seen in modern crocodilians (members of Eusuchia), comprising a dorsal shield with at least six longitudinal rows of osteoderms (Frey, 1988; Ortega and Buscalioni, 1995; Salisbury, 2001; Salisbury

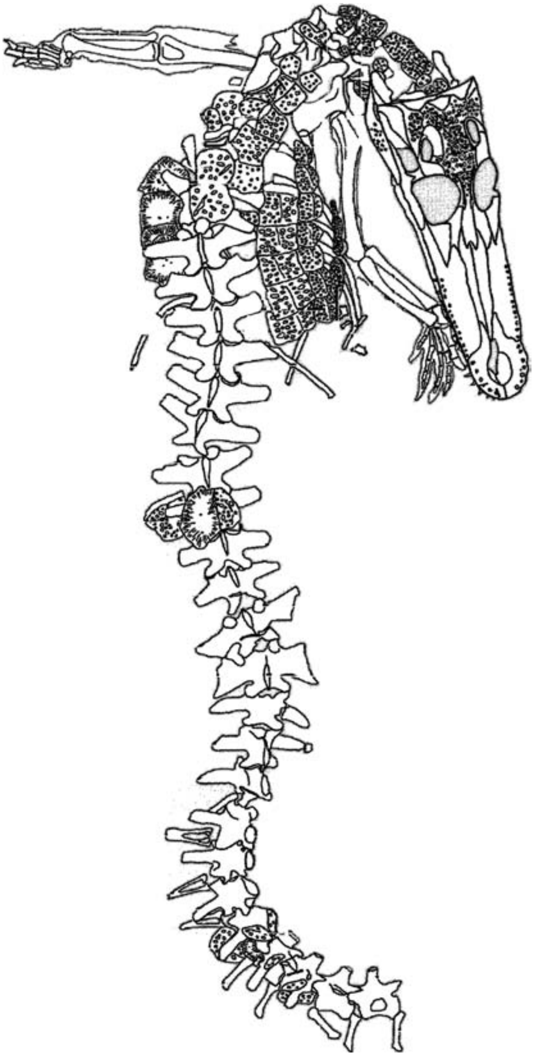

Fig. 16.1. Skeleton of *Susisuchus anatoceps*: After Salisbury *et al.* (2003a).

and Frey, 2001). The only other crocodilians of a comparable age with a similar type of dorsal shield are an as-yet-undescribed form from the Albian–Aptian Glen Rose Formation of north-central Texas, USA (Langston, 1974; Brochu, 1997b), and *Isisfordia duncani*, a basal eusuchian from the Albian–Cenomanian Winton Formation of central-western Queensland, Australia (Molnar and Willis, 1996; Salisbury *et al.*, 2006).

The most complete specimen of the Glen Rose crocodilian, USNM 42 7794, a partial skeleton, includes three thoracic vertebrae. As in eusuchians (including *Isisfordia*), some atoposaurids (Michard *et al.*, 1990; Salisbury, 2001; Salisbury

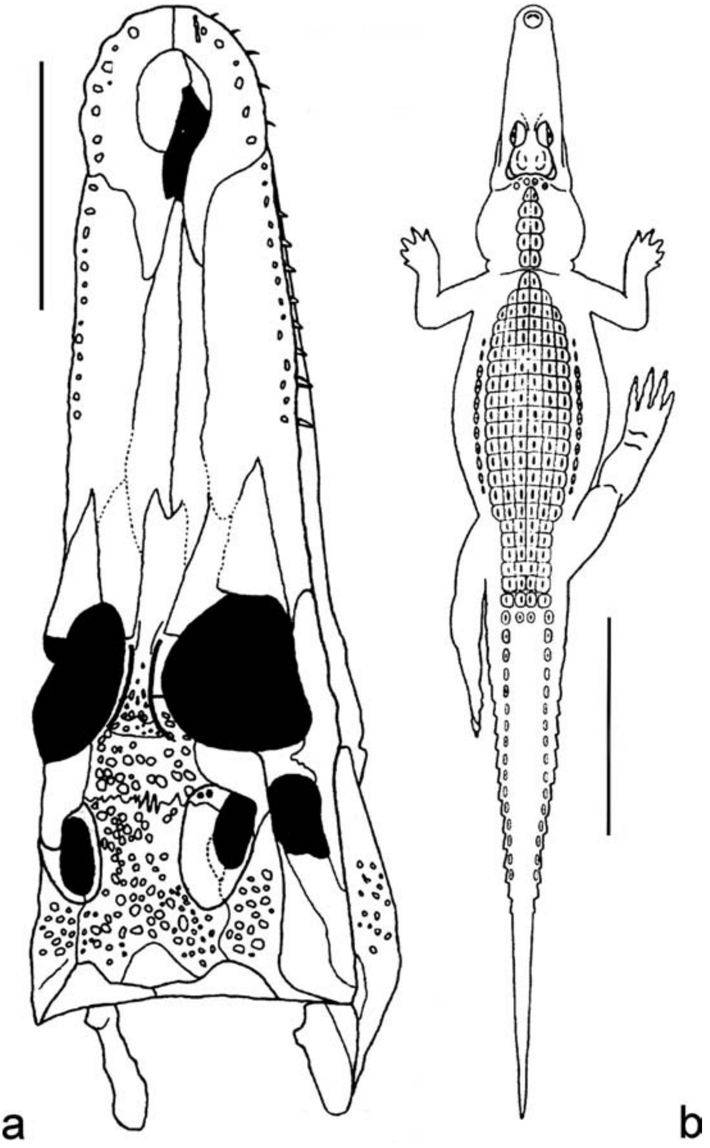

Fig. 16.2. *Susisuchus anatoceps*: (a) details of the skull, scale bar, 20 mm (b) reconstruction of dorsal osteoderm distribution, scale bar, 100 mm. Both after Salisbury *et al.* (2003a).

and Frey, 2001; Rogers, 2003) and the sphenosuchian *Junggarsuchus* (Clark *et al.*, 2004), these vertebrae have been described as being procoelous (Clark, 1986; Norell and Clark, 1990; Clark and Norell, 1992; Brochu, 1997a, 1997b, 1999). In *Susisuchus*, however, the vertebrae are amphicoelous, a condition typical of mesoeucrocodylians. The configuration of the dorsal shield of *Isisfordia* is very

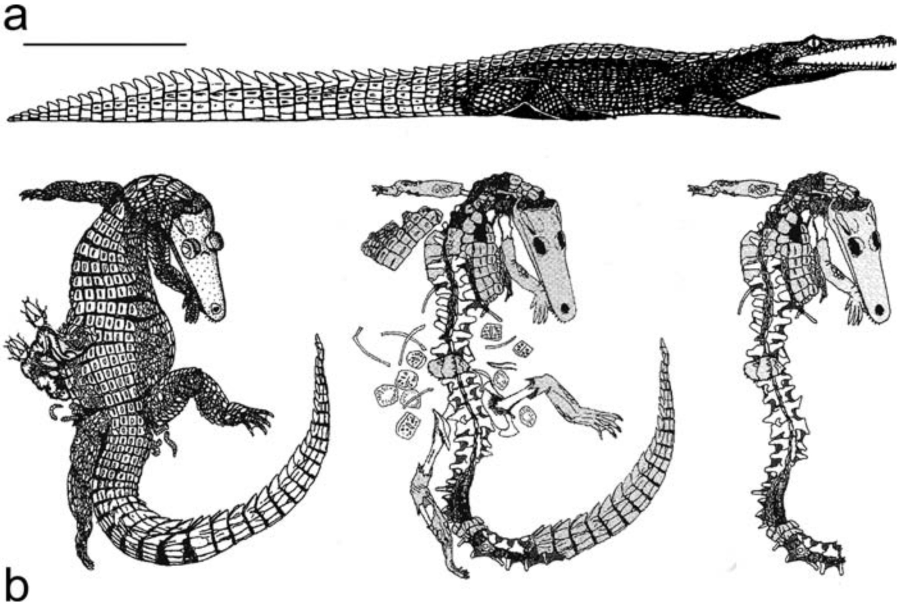

Fig. 16.3. *Susisuchus anatoceps*: (a) life restoration, scale bar, 100 mm; (b) decay sequence of *Susisuchus* holotype specimen (from left): carcass is disrupted by small scavengers followed by dessication, perhaps on river bank; disrupted carcass sheds many skeltal elements, but dehydrated ligaments keep part of axial skeleton, skull, forelimbs and a few osteoderms together; final drifting phase into Crato lagoon as disrupted, desiccated carcass with some hardened integument. After Salisbury *et al.* (2003a).

similar to that of *Susisuchus*, but unlike *Susisuchus*, the vertebrae of this taxon are weakly procoelous.

The unique combination of amphicoelous vertebrae with a eusuchian-type dorsal shield lead Salisbury *et al*. (2003a) to consider *Susisuchus* representative of a phase of crocodilian evolution very close to the origin of Eusuchia. This view has been supported by the phylogenetic analysis of Salisbury *et al*. (2006), which firmly places *Susisuchus* as the sister taxon to Eusuchia. In addition to the configuration of its dorsal shield, aspects of *Susisuchus*' osteology that align it with Eusuchia include the modest indentation in the dorsal margin of its iliac blade, its caudodorsally projecting retroarticular process, the smooth rostromedial corner to its supratemporal foramen, and the small boss medial to the paroccipital process on its exoccipital (Salisbury *et al*., 2006).

Biogeography

Material that may be referable to susisuchid neosuchians has been identified in the Early Cretaceous (Aptian–Albian) Eumerella Formation of southern Victoria, Australia (Salisbury *et al.*, 2003b). During the Early Cretaceous, South America was connected to Australia via Antarctica (Frakes *et al.*, 1987). This situation persisted until the earliest Paleocene, after which time only a small chain of islands linked the current Antarctic Peninsula with Cape Horn (Veevers, 1991; Lawver *et al.*, 1992; Shen, 1995; Livermore and Hunter, 1996). During Aptian and Albian times, susisuchids could therefore have dispersed between South America and Australia, either through inland fluvial systems or, though less likely, along the Atlantic coastline of Antarctica. Such a distribution assumes that these crocodilians were present on all landmasses between South America and Australia during (and perhaps beyond) the latest Early Cretaceous, including Antarctica, the Indian subcontinent, Madagascar and probably also Africa (Salisbury *et al.*, 2003a, 2003b). This distribution, coupled with the occurrence of primitive eusuchians in the early Mid Cretaceous of Australia (Molnar, 1980; Salisbury *et al.*, 2006) strongly suggests that the rise of modern crocodilians occurred on Gondwana (Salisbury *et al.*, 2006).

Lifestyle and inferred habitat

In life, the holotype specimen *Susisuchus* would have had a total length of approximately 0.5 m. The dense pitting of the skull roof bones and osteoderms, combined with the slender outline of the upper skull openings, indicates that this individual was most likely a sub-adult when it died (Salisbury *et al.*, 2003a). Presumably, adults of this species did not grow much longer than 1 m. The rostrum, which is about three times longer than wide at its base, flat and parallel-sided (Figure 16.2a), resembles the bill of a duck. With its minute, conical, widely spaced teeth and the flat rostrum lacking any buttresses, *Susisuchus* could seize only small prey items, such as tiny fishes, insects, molluscs, worms and soft-shelled crustaceans. The flat rostrum would also have been useful to stir through muddy or sandy sediments in search of prey, in the manner of some ducks, platypus or North American alligators.

Compared with the head and body, the forelimbs of *Susisuchus* were long and slender. The well-mineralized tetraserial dorsal shield indicates a bracing system that stabilized the vaulted body during high-walking (Salisbury, 2001; Salisbury and Frey, 2001). Therefore, *Susisuchus* was probably capable of the same terrestrial locomotor modes employed by extant crocodilians (Salisbury, 2001), but it could also use its long legs for pushing through water plants or for walking on the bottom of its aquatic environment.

Given its hypersaline nature, it is unlikely that *Susisuchus* frequented the Crato lagoon for extended periods. For its mass, the small body would have offered a relatively large surface area to the salty water. Furthermore, the coastline of the lagoon was probably bare of plants and thus, in or out of the water, this small crocodilian would probably have died rapidly from dehydration. Therefore, *Susisuchus* most likely lived upstream from the Crato lagoon in a freshwater river or stream, where it hunted in the sheltered shallow waters along the banks or among nearby oxbows.

Taphonomy of the holotype

The preservation of the holotype specimen of *Susisuchus* (SMNK PAL 3804; Figure 16.1) is highly unusual for a crocodilian. While the skull, forelimbs and thorax are perfectly preserved in articulation, the hindlimbs and most of the tail are missing, as is the dermal armour from the abdomen and the tail base. The left forelimb lies perpendicular to the shoulder, while the right is in a relaxed position alongside the thorax. The neck is strongly curved to the right with the tip of the snout facing backward. On these parts, remnants of the skin with scales are preserved as an orange-red goethite stain.

Following death, perhaps during a flood, it appears likely that the animal was washed upon a sand island in the river mouth close to the lagoon. The head and right arm were pushed up by small waves, while the right arm was pulled away, when the water level fell. Large scavengers did not touch the carcass, but there is evidence that micro-scavengers, such as insects and their larvae, played a role during the early stages of decay (Figure 16.3b). The skin of crocodilians is too tough for micro-scavengers; they invade the body through the vent and mouth. This was accompanied by desiccation. The slender end of the tail, the hands and feet, the head, neck and the front part of the chest were the first parts that mummified. Slowly, the desiccation began to enclose the parts of the body being devoured by micro-scavengers. The gut and the large muscles of the tail base would have remained soft and humid longest, and were probably the only parts of the carcass that began to decay.

Finally, the remnants of *Susisuchus* were completely dry. At some later stage the carcass was returned to the river, probably by a flood, and was washed into the lagoon. It is during this time that the end of the tail, the legs and loose flakes of the skin probably detached, while the torso continued drifting a short time, probably due to air trapped in its thorax. This air must have escaped before the desiccated muscles and ligaments became softened in the water and caused sinking (Salisbury *et al.*, 2003a).

A new Crato Formation araripesuchid

The Cretaceous crocodilian *Araripesuchus* is represented by four species, three of which come from South America: *Araripesuchus gomesii* (?Albian, Araripe Basin, north-eastern Brazil; Price, 1959); *Araripesuchus patagonicus* (Cenomanian-Turonian, Neuquén Province, Argentina; Ortega *et al.*, 2000); and *Araripesuchus buitreraensis* (Cenomanian, Rio Negro Province, Argentina; Pol and Apesteguia, 2005). The fourth species – which is yet to be named – is from the Late Cretaceous of Madagascar (Buckley *et al.*, 1997; Sereno *et al.*, 2004; Turner, 2004). *Araripesuchus wegeneri* from the Aptian of Niger (Buffetaut 1981) may represent a fifth species, but its referral to *Araripesuchus* has been doubted by Ortega *et al.* (2000). Two more possible araripesuchids have been reported from Cameroon (Barremian–Aptian) and Malawi (Aptian; Colins and Jacobs, 1990). The most beautiful specimens of *Araripesuchus* come from the north-east Brazilian Santana Formation nodules, where several complete and fully articulated specimens of *A. gomesi* have been discovered (Maisey, 1991).

Here we provide a preliminary account of a new araripesuchid from the Crato Formation. A full description of this specimen is beyond the scope of this chapter, but is currently being undertaken and will be published shortly.

Systematic palaeontology

Crocodyliformes Hay, 1930

Mesoeucrocodylia Wetstone and Whybrow, 1983

Notosuchia Gasparini, 1971

Araripesuchidae Price, 1959

cf. *Araripesuchus* Price, 1959

Preservation

The specimen (SMNK PAL 6404) is an associated skeleton preserved in loose articulation (Plate 21a). The skull and mandible lie in occlusion and are exposed in ventrolateral aspect (Plate 21b). The lateral wall of the right mandibular ramus and the right side of the maxillary rostrum are exposed, while the left side is obscured by sediment. The two pairs of nuchal osteoderms lie *in situ* between the jaw articulations, with the median suture in line with the occipital condyle. Only the internal surface of the nuchal shield is visible. The dorsal and caudal shields complete and articulated, but separated from the nuchal shield. Only the left row of dorsal osteoderms is visible on the trunk and the medial margin of the left row of osteoderms is visible at the base of the tail. Towards the tip of the tail, torsion of the axial skeleton and associated osteodermal casing increases, so that the dorsal surface of each osteoderm is visible. The entire dorsal and caudal shield is dorsally vaulted near the tip of the tail, forming a sigmoidal curve. The vertebral column is only visible in the tail, but is displaced ventrally with respect to the dorsal and caudal shield. All the vertebrae are exposed on their left side. The haemal arches in the mid-part of the tail are still in place. The pelvic girdle is preserved *in situ* with the left hip joint exposed. Of the right part of the pelvis only the dorsal crest of the ilium is protruding beyond the osteoderms. The lateral face of the left side of the pelvic girdle is obscured by a cluster of gastral ribs, along with bones that may come from the left foot.

Only two thoracic ribs are preserved, but an external mould of the entire trunk, lined with manganese dendrites, is visible. Inside this external mould a rough and weathered surface indicates that most of the skeleton must have been preserved on the counter slab, but was probably lost due to weathering or damaged during extraction.

The left arm is the only limb preserved (Plate 21c). The humerus, radius and ulna are almost in natural articulation, but the entire arm is reversed with the elbow facing cranially. The hand lies at 90° to the radius and ulna in a cranial direction, and is exposed in palmar aspect. The carpals are disarticulated but still in place.

Referral to cf. *Araripesuchus*

SMNK PAL 6404 is preliminarily referred to *Araripesuchus* based on the combined possession of the following osteological features listed in Ortega *et al.* (2000) and Pol and Apesteguia (2005): massive skull with divided, rostrolaterally oriented nares; deep, laterally compressed rostrum with vertical lateral maxillary walls; maxilla laterally convex at the enlarged third maxillary tooth and markedly concave caudal to this point; lateral outline of the premaxillae concave, forming a sharp tip rostrally; proportionately thick, transversely oval osteoderms with a longitudinal keel that cranially forms a blunt process. The latter process is part of an interosteodermal peg-and-groove articulation. Medial to the sagittal keel, the osteoderms are deeply pitted. Lateral to the keel, the osteoderms are slightly angled ventrally with a finely pitted or smooth surface. The osteoderms form a biserial dorsal shield. The nuchal shield consists of two pairs of osteoderms, which are longitudinally oval and separated from the dorsal series by a gap. The dorsal shield continues onto the tail base. From the mid-part of the tail towards its tip, the width of the shield tapers, while the length of the segments remain nearly constant. In the terminal third of the tail, the keels on the osteoderms become prominent and continue over the caudal margin in a sharp process, that overlaps the caudally following osteoderm. Such an arrangement of the dermal skeleton is typical for *Araripesuchus*. The deep mandibular symphysis is formed by one-quarter of the splenials.

The Crato specimen represents the oldest araripesuchid and differs from other species of *Araripesuchus* by the proportions of skull (less than one-quarter the length of the body) and its forelimbs (longer than body). In addition, the manus has remarkably long metacarpals, and long, strongly curved linguals terminating the medial three digits, and the nuchal shield is separate from the dorsal shield (a feature shared with eusuchians and the atoposaurid *Brillanceausuchus babouriensis*).

Lifestyle and inferred habitat

The Crato araripesuchid was characterized by a rigid body and tail, with its flexibility restricted by the dorsal and caudal shields. Lateral undulation of the trunk was most likely limited, but dorsoventral flexion was possible, which indicates a poor swimming capacity. Of the total length of 750 mm, 170 mm belong to the massive head with its laterally compressed, stubby snout. Based on the length of the lower arm and carpus, the head and cranial part of the body would have been held more than 150 mm off the ground during high-walking, such that the animal must have resembled a dog or a small hyaena. The dentition shows a pair of fangs in the front third of the rostrum. The teeth in front of these fangs are short and conical. The teeth in the back of the jaws show blunt globular crowns.

Given these morphological characteristics, the Crato araripesuchid was most likely a terrestrial crocodilian that roamed the hinterland of the Crato lagoon. With its long legs and stiff body and tail it could rapidly walk, run or even gallop. The dentition could be used to eat almost everything. It is likely that this crocodilian was capable of actively hunting down all kinds of animals. Large prey could be held down with the powerful long-clawed hand and ripped into pieces with a powerful bite, which is indicated by the large adductor muscle arcades above the pterygoids. The (possibly) detached nuchal shield may be indicative of reduced segmentation of the dorsal epaxial muscles in the neck. As in living crocodiles and alligators, this feature is characteristic of increased flexibility of the neck, as well as the flexibility of the head against the neck (Salisbury, 2001; Salisbury and Frey, 2004a). Presumably it also scavenged carcasses. Even large bodies with thick skins (dinosaurs?) could be opened with a strong bite. With its blunt cheek teeth, bones as well as shells of crabs and small turtles could have been crushed and processed in the back of the mouth prior to swallowing. Given the dentition, the Crato araripesuchid may also have been partly herbivorous, as has been suggested for other mesoeucrocodylians (e.g. Buckley *et al.*, 2000). Thus foods such as fruit may have been an option, which would not be unusual given recent reports of frugivory in extant crocodilians (Brito *et al.*, 2002).

That only one araripesuchid specimen is known from the Crato limestone indicates that these terrestrial crocodilians probably avoided the vicinity of the lagoon, and made their living in the forests of the surrounding uplands.

Taphonomy

The almost perfectly preserved dorsal shield indicates that, during life, this element was the limiting factor for body movements, and was most likely integrated with the underlying epaxial muscles (Salisbury and Frey, 2004b). During decomposition, the dorsal shield remained intact, while other elements underwent decay. It can be assumed that the carcass arrived on the floor of the lagoon when most muscles and ligaments were already disintegrated, thus allowing the vertebral column to move inside the skin sack. The right arm and the hindlimbs were lost shortly before sinking or on the way down, because the left arm was still hanging loosely in the shoulder joint.

It is possible that this presumably predominately terrestrial crocodilian came to the shore of the Crato lagoon to scavenge after a flood or, like *Susisuchus*, may have been caught by a high flood of a river and washed into the lagoon. After death, the body must have been exposed to decay for some time, but likely did not desiccate, as shown by the loose joints. The cause of its death, however, will remain a secret.

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17

Pterosaurs of the Crato Formation

David M. Unwin and David M. Martill

Introduction

The first significant account of a pterosaur from the Crato Formation was published over a decade ago (Frey and Martill, 1994). In the short intervening period between then and now, more than 30 individuals have come to light. This is a modest total, especially when compared to the 1000+ individuals recovered, for example, from the Solnhofen Limestones of southern Germany or the Niobrara Chalk of Kansas. Still, several finds notable for their completeness, or for the exceptional preservation of soft-tissue structures, such as extensions to cranial crests or of the integument associated with the foot, have already demonstrated the importance of this lagerstätte for our understanding of pterosaur palaeobiology (Frey and Martill, 1994; Campos and Kellner, 1997; Frey and Tischlinger, 2000; Frey *et al.*, 2003c). The Crato pterosaur assemblage also contains a number of genera (e.g. *Arthurdactylus*, *Ludodactylus*, *Ingridia* gen. nov.) that are unique to this deposit (Frey and Martill, 1994; Frey *et al.*, 2003b; this chapter). They represent several Lower Cretaceous pterosaur lineages and throw some much-needed light on the ecology, palaeobiogeography and evolutionary history of pterosaurs during an interval when they appear to have reached their highest levels of global diversity (Unwin, 2005).

Fragments of several limb bones from the Upper-Triassic Caturrita Formation of southern Brazil (Bonaparte *et al.*, 2006) may represent the earliest occurrence of pterosaurs in South America. So far, however, the oldest certain records of pterosaurs from this continent consist of remains of at least two different non-pterodactyloids (rhamphorhynchoids) from the Jurassic (Callovian) Cañadon Asfalto Formation (Rauhut *et al.*, 2002; Unwin *et al.*, 2004) of Chubut, Argentina. Other fragmentary records of Jurassic pterosaurs have been reported from several localities in Argentina (see Gasparini *et al.*, 1987; Codorniú *et al.*, 2006; Codorniú and Gasparini, 2007).

More complete remains are known from Cretaceous sequences, most importantly the Santana Formation of Brazil, which has yielded superbly preserved fossils of ctenochasmatoids, an ornithocheiroid and azhdarchoids (reviewed in Kellner, 1991; Wellnhofer, 1991a, 1991b; Martill, 1993; Kellner and Tomida, 2000; Veldmeijer, 2003; Unwin, 2005), and the slightly older Crato Formation, which has produced a similar, albeit smaller, assemblage (Frey and Martill, 1994; Campos and Kellner, 1996, 1997; Martill and Frey, 1998, 1999; Sayão and Kellner, 1998, 2000, 2006; Frey and Tischlinger, 2000; Nuvens *et al.*, 2002; Sayão, 2003; Frey *et al.*, 2003a, 2003b, 2003c). In addition, the Lower Cretaceous Lagarcito Formation of Argentina has yielded hundreds of individuals, including neonates and an embryo, of the filter feeding ctenochasmatoid *Pterodaustro* (Bonaparte, 1970; Chiappe *et al.*, 1998, 2000, 2004; Codorniú and Chiappe, 2002). Calvo and Lockley (2002) recently described the first pterosaur tracks from South America and further fragmentary remains of Cretaceous pterosaurs have been reported from Argentina (Montanelli, 1987; Kellner *et al.*, 2003; Codorniú and Gasparini, 2007), Brazil (Price, 1953), Chile (Bell and Padian, 1995; Martill *et al.*, 2000, 2006; Rubilar *et al.*, 2002), Venezuela (Kellner and Moody, 2003) and Peru (Bennett, 1989).

Preservation

At the time of writing, remains of 32 pterosaurs, five of which are noted here for the first time, have been reported from the Crato Formation, although further, as-yet-undescribed, remains are known (the most important of these, an almost complete, fully articulated pterosaur skeleton, illustrated in Figure 17.15, was offered for sale on a website in 2005 and is now in a private collection). Most specimens seem to have been recovered from the Nova Olinda Member (Martill and Wilby, 1993) of the Crato Formation, from the area between Nova Olinda, Santana do Cariri and Tatajuba, in southern Ceará (Martill and Frey, 1998; Frey *et al.*, 2003b).

Not one of the 32 reported individuals is complete (Figure 17.1); each consists either of an isolated, complete or incomplete skull, or post-cranial skeleton varying in completeness from almost intact (for example, as in the holotype of *Arthurdactylus conandoylei*; Figures 17.2 and 17.3), to just a few bones in the case of SMNK PAL 2342 (e.g. Figures 17.1 and 17.17), or even isolated bones and teeth (Martill and Frey, 1998; Nuvens *et al.*, 2002). In many cases (e.g. SMNK PAL 3828, SMNK PAL 2342) incompleteness can be attributed to careless collection and the original remains were almost certainly more complete. At the same time, isolated bones suggest that decay and/or scavenging during prolonged post-mortem drifting also played a significant role in modifying carcasses before their final deposition.

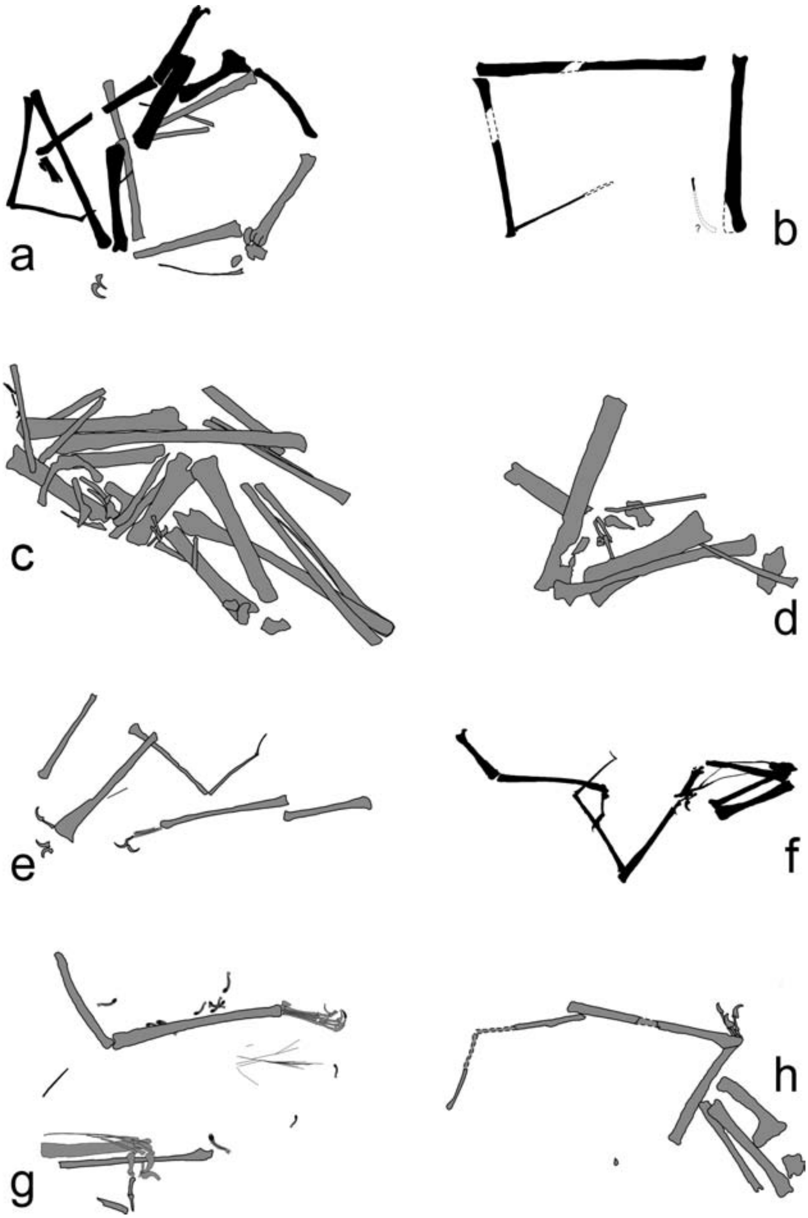

Fig. 17.1. Pterosaurs from the Nova Olinda Member: diagrams of the skeletal elements of eight individuals illustrating aspects of the taphonomy of Crato Formation pterosaurs. (a) Tapejaridae gen. et sp. indet., SMNK PAL 3900; (b) Tapejaridae gen. et sp. indet., SMNK PAL 2342; (c) *Arthurdactylus conandoylei* SMNK PAL 1132; (d) SMNK PAL 3842; (e) azhdarchoid, SMNK PAL 6409; (f) 'tupuxuarid' SMNK PAL 3855; (g) Tapejaridae gen. et sp. indet., SMNK PAL 3830; (h) Tapejaridae gen. et sp. indet., Santana do Cariri Museum specimen.

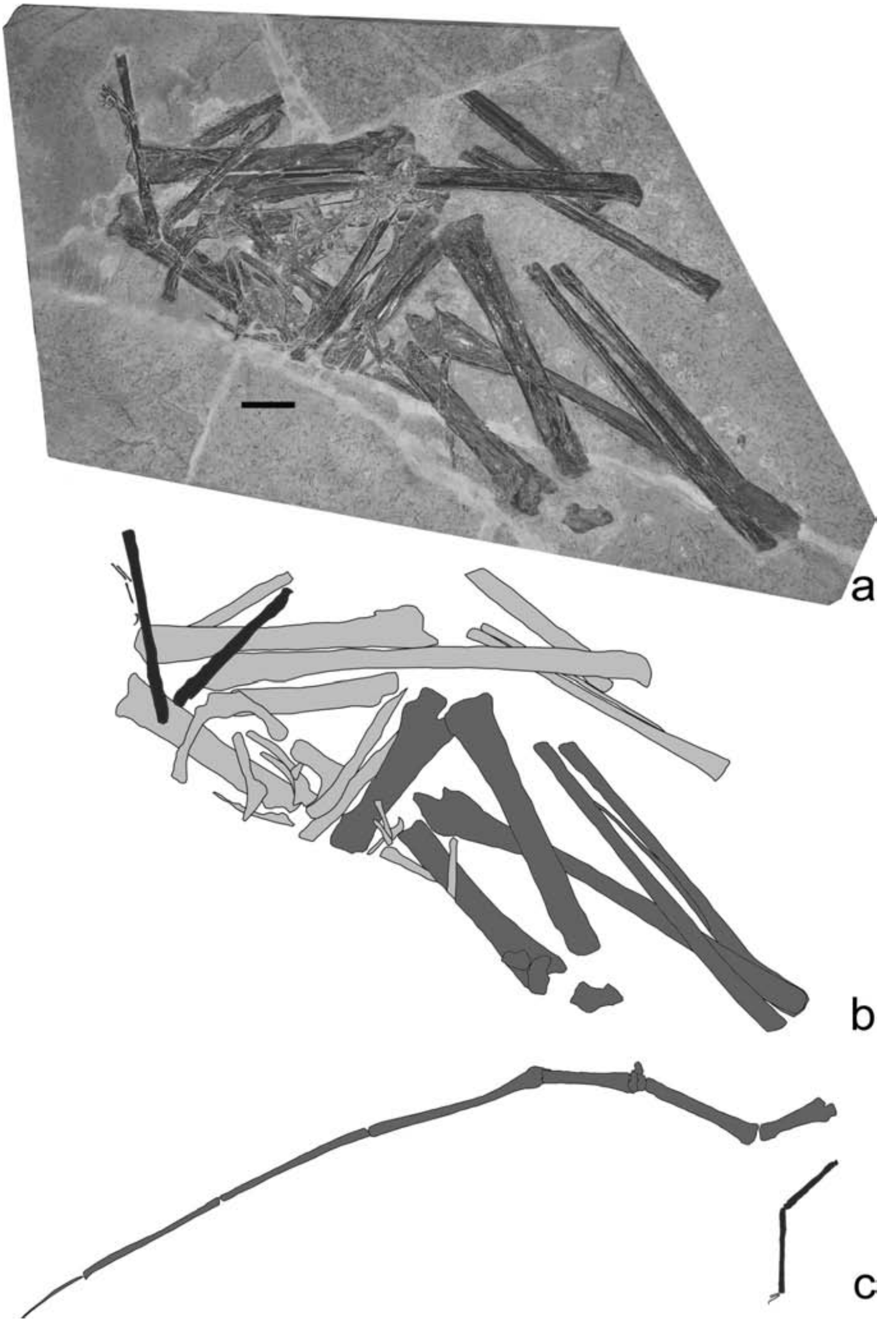

Fig. 17.2. Pterosaurs from the Nova Olinda Member: (a) the holotype (SMNK PAL 1132) and only known example of *Arthurdactylus conandoylei* Frey and Martill, 1994; (b) principal skeletal elements of *Arthurdactylus conandoylei* shaded for ease of recognition; black, hindlimb; dark grey, left wing; (c) the same elements manipulated with the aid of computer graphics to reconstruct wing and hindlimb proportions. Scale bar, 50 mm.

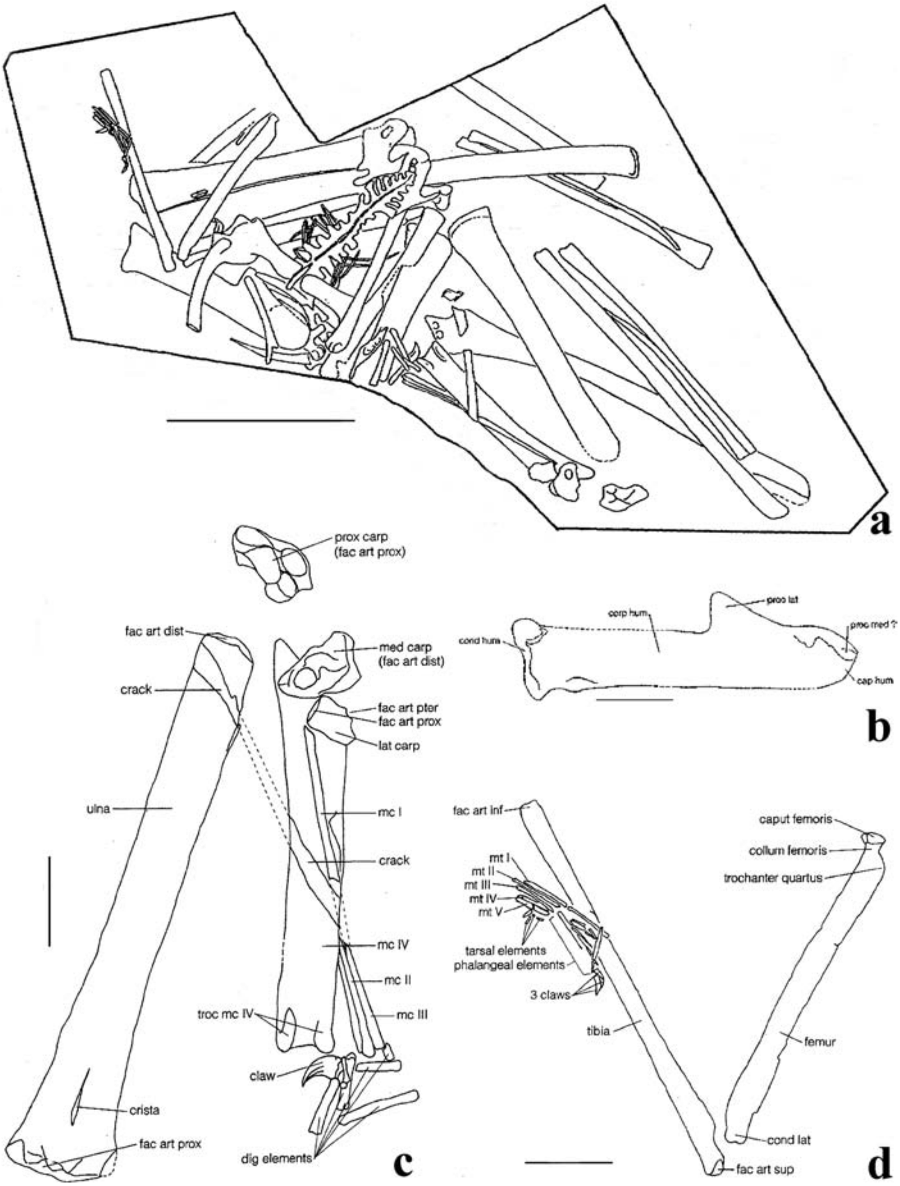

Fig. 17.3. Pterosaurs from the Nova Olinda Member: *Arthurdactylus conandoylei* SMNK PAL 1132 skeletal anatomy; (a) outline of holotype skeleton; scale bar, 200 mm; (b) humerus; scale bar, 50 mm; (c) ulna, carpals, metacarpals and elements of the manus; scale bar, 50 mm; (d) hindlimb and pes; scale bar, 50 mm; (e) restored scapulocoracoid; (f) restored pelvic girdle; scale bar, 50 mm; (g) restored synsacrum in dorsal aspect; scale bar, 50 mm; (h) axial skeleton; scale bar, 50 mm. All figures after Frey and Martill (1994).

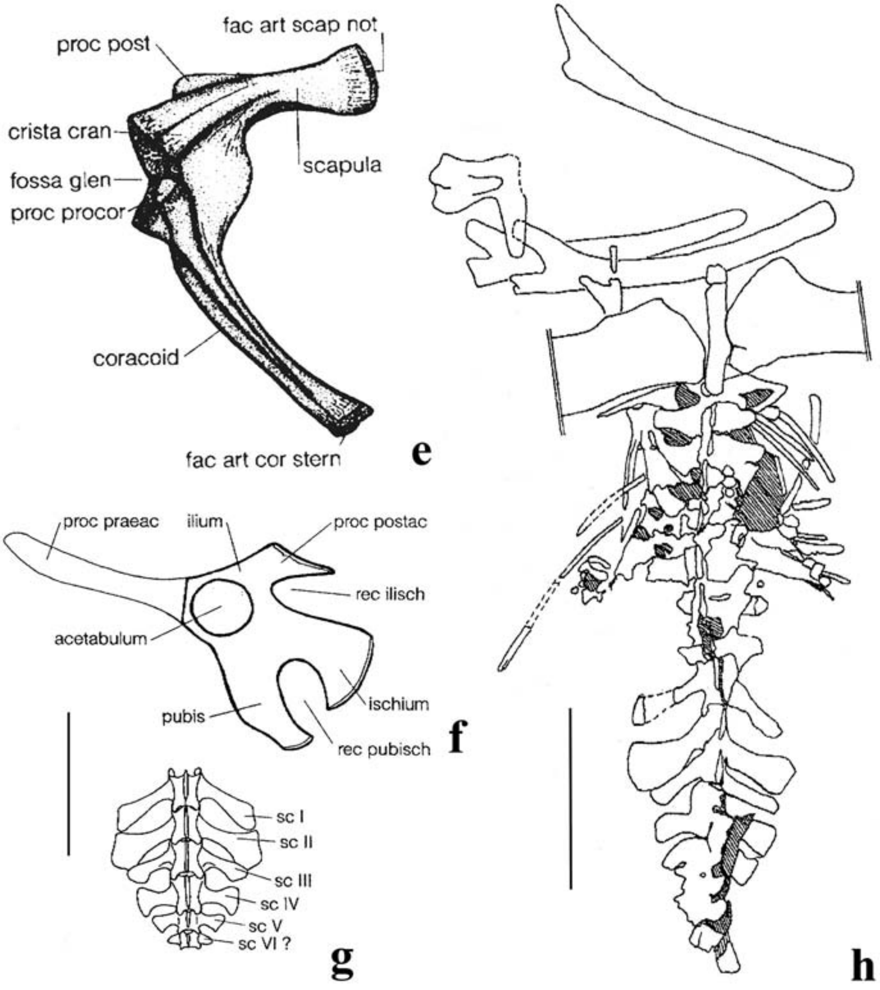

Fig. 17.3. (*cont.*)

Unlike the well-preserved, uncrushed, three-dimensional bones found in the Santana Formation nodules, the skeletal remains are usually somewhat crushed, reflecting the compaction that the original sediments of the Crato Formation must have undergone. The degree of compression is variable, however, and partial three-dimensional characteristics are often observed in regions such as the articulatory ends of robustly constructed limb bones; for example, in SMNK PAL 2342 (Figure 17.13), which still preserves the shape of the cross-section of the wing phalanges (Martill and Frey, 1999). Apart from crushing, bones, which usually have a shiny, dark brown appearance, are well preserved and skeletons seem to have been relatively unaffected by diagenesis, unlike, for example, those from

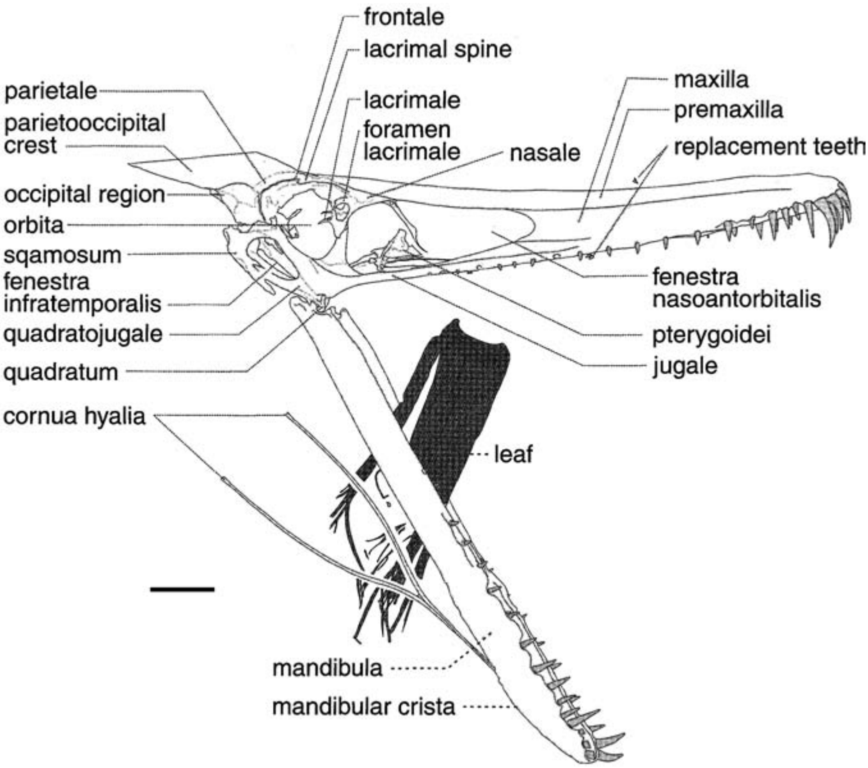

Fig. 17.4. Pterosaurs from the Nova Olinda Member: *Ludodactylus sibbicki* Frey, Martill and Buchy, 2003 (SMNK PAL 3828) detailing the elements of the skull. Scale bar, 50 mm.

Solnhofen where diagenetic calcite often obscures the articular ends of limb bones. Consequently, the skeletal details of the bones are often well preserved.

The degree of articulation is variable. No complete naturally articulated skeletons have been described so far, but there is at least one example, SMNK PAL 3830 (Figure 17.11), wherein part of the skeleton, in this case the wing and the legs including the feet, are more or less naturally articulated (Frey *et al.*, 2003c). In *Arthurdactylus conandoylei* the vertebral column remains in articulation, but the limbs are partially disarticulated. This is also true of other individuals represented by post-cranial remains where, as a rule, while bones are associated they are no longer in natural articulation. Martill and Frey (1998) attributed this to gravitational collapse and/or microbial degradation and later suggested (Martill and Frey, 1999) in the case of a partial wing (SMNK PAL 2342) that this may also reflect desiccation of tendons. Most of the skulls lack the lower jaws, except in the case of *L. sibbicki* (Figure 17.4; Plate 22) where, although fully depressed, they appear to be naturally articulated. Notably, in the toothed skulls the sockets retain all their teeth. This is in sharp contrast to toothed pterosaurs from other localities such as the Santana Formation, where tooth sockets are frequently empty.

An important feature of the Crato pterosaurs is the occurrence of high-quality soft-tissue preservation, examples of which are found in at least six specimens. The commonest structure to be preserved is the cranial crest of tapejarids, and a rhamphotheca covering the beak has also been described. In addition, wing membranes and wing fibres, claw sheaths, foot webs and a heel pad have also been reported (Frey *et al.*, 2003c). Soft parts are preserved as internal or external moulds, picked out by mineralized replacements of a rusty-looking reddish-brown colour that appears to be the hydrated iron oxide goethite, most probably the product of oxidization of an original pyrite mineralization. This mineralization appears to mimic the general outlines of soft tissues and occasionally replicates some details of internal structures, for example in the cranial crests or the wing membranes. Three-dimensionality is sometimes evident, as for example in the cranial crests of some tapejarids (Frey *et al.*, 2003a, 2003c), but usually preservation is two-dimensional.

Aspects of the preservation of the Crato pterosaurs permit some inferences regarding the main taphonomic events that seem to have affected most individuals. Generally, the reason for death is unknown, although some kind of event such as a storm seems reasonable. However, in one particular case, *Ludodactylus sibbicki*, a plausible explanation of death has been advanced (Frey *et al.*, 2003b). It has been suggested that a leaf of the gnetalean *Welwitschiella* became trapped between the left mandibular ramus and the tongue, having been caught by the pterosaur in the mistaken assumption that it was a fish (Figure 17.4; Plate 22). The frayed edge of the leaf beneath the mandibles (Plate 22b) suggests that the pterosaur unsuccessfully attempted to dislodge the leaf by rubbing it against the ground. Impeded by the leaf and unable to eat, Frey *et al.* (2003b) propose that this individual eventually succumbed to starvation and possibly by sepsis of the wound.

Following death and arrival into the Crato lagoon, either directly from the air or by transport in water flow, most pterosaur carcasses appear to have spent some time drifting in the water column, buoyed up by their air-sac system, during which time major elements such as the skull and or mandible became detached (e.g. Figure 17.10) and arrived separately at the bottom of the lagoon. In some cases burial may have taken place fairly rapidly, but often the disarticulated nature of the skeleton suggests that carcasses spent some time on the lagoon floor, possibly at or near neutral buoyancy, during which time elements of the skeleton became disarticulated although, as a rule, remaining in the vicinity of the carcass. Gas escape appears to have disrupted the rib cage in the case of *A. conandoylei* (Frey and Martill, 1994) and most of the joints in this specimen have been bent beyond their normal range of articulation, suggesting that cartilaginous capsules had reached an advanced state of decay. Any bottom currents must have been very light or non-existent in that, for example, there is no preferred orientation of elements, or fish, on the *Arthurdactylus* slab (Frey and Martill, 1994).

During this period relatively labile soft tissue such as the internal organs rapidly decayed, but tougher structures, such as wing membranes, cranial crests, claws and foot webs (probably extensively keratinized or composed of relatively robust material such as collagen in the case of the wing fibres), survived long enough to become buried and mineralized. Following burial, skeletons were compressed by compaction of the sediment and were further modified by erosion, action of plant roots and through collection practices such as trimming of the slabs by quarry workers which led, for example, to the loss of the apex of the crest in *Ludodactylus sibbicki*.

Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Ornithocheiroidea Seeley, 1870

Ornithocheiridae Seeley, 1870

As detailed by Unwin (2001), Ornithocheiridae was originally founded upon *Ornithocheirus*, the type species of which is *Ornithocheirus simus* (Seeley, 1869). The holotype of *Ornithocheirus simus* is CAMSM B54.428, a highly distinctive jaw fragment originally described and figured by Owen (1861) under the name *Pterodactylus simus*. Unfortunately, in the mistaken belief that a type species was still needed, several authors have attempted to establish a new type species, among them Khozatskii and Yur'ev (1964), Kuhn (1967) and most recently Wellnhofer (1978), who erroneously proposed that *Pterodactylus compressirostris* Owen, 1851, be used as the type species, even though this name was not mentioned by Seeley in his original proposal of *Ornithocheirus* in 1869. Despite the attention that has been drawn to this problem (Unwin, 2001: 194), several recent works (Kellner, 2003, 2004; Wang *et al.*, 2005; Veldmeijer, 2006; Veldmeijer *et al.*, 2006) have perpetuated this error. Junior synonyms of Ornithocheiridae include 'Anhangueridae' Campos and Kellner, 1985 and 'Criorhynchidae' Hooley, 1914.

Arthurdactylus Frey and Martill, 1994

Arthurdactylus conandoylei Frey and Martill, 1994

This pterosaur, the first to be described from the Crato Formation (Frey and Martill, 1994), is represented by a single, largely complete post-cranial skeleton (SMNK PAL 1132) consisting of an almost continuous (although poorly preserved) series of dorsal, sacral and proximal caudal vertebrae, the shoulder girdles and pelvis and the essentially complete fore- and hind-limbs (Figures 17.2 and 17.3). Although the bones are somewhat compressed this is one of the most complete skeletons known for any large pterodactyloid and provides important information on the body and wing proportions of ornithocheirid pterosaurs.

A. conandoylei appears to have had a remarkably short body, approximately 0.22 m from the base of the neck to the base of the tail, relatively long forelimbs (each forelimb = 2.2 m) and slender, gracile hindlimbs, each just over 0.5 m in length. An estimated wing span of 4.6 m makes this the largest pterosaur yet known from the Crato Formation. The holotype and only known individual (SMNK PAL 1132) seems to have reached adulthood, or near adulthood, because the extensor tendon process is fused to the proximal end of wing-phalanx one (Frey and Martill, 1998), and many other composite skeletal structures, including the notarium, shoulder girdles, syncarpals and elements contributing to the pelvic plates, are co-ossified (Bennett, 1993). By contrast, the sacral vertebrae are not fused to one another, nor are the distal ends of the sacral ribs fused to the pelvis. While this might indicate that full osteological maturity had not been attained (Kellner and Tomida, 2000) there is another possible explanation, that this lack of fusion might be related to sexual dimorphism, as discussed below.

The preserved portion of the vertebral column (Figure 17.3h) contains 19 vertebrae. The first, a prenotarial dorsal, is the largest. Subsequently, the vertebrae steadily decrease in size, with the last preserved, a second caudal, being the smallest. The notarium is composed of three dorsals, their neural spines fused into a single bar of bone, and is followed by seven free dorsals. The sacrum (Figure 17.3g) contains six vertebrae, the first of which appears to have been incorporated from the dorsal series, while the last is apparently a modified caudal (Frey and Martill, 1994). Unusually, the sacrals show no co-ossification. The first pair of sacral ribs are rather slender and directed outwards and backwards, while the second pair are the largest and most massive of all the ribs, and have strongly expanded distal terminations. Subsequent pairs of ribs show a rapid decline in size.

The scapula is relatively short and stout with an expanded distal end that articulated with the notarium. The coracoid is almost half as long again as the scapula and has a long, slender shaft. Proximally it is fused to the scapula, forming a massive glenoid that, as in other ornithocheiroids, is supported posteriorly by a well-developed buttress of bone. The scapulocoracoids appear to lie in their natural position on either side of the notarium, the notarial plate sandwiched between their distal ends (Figure 17.3h). The long axis of each scapula is perpendicular to the notarium (which is aligned with the sagittal plane), a position that is typical for ornithocheiroids, but not for other pterosaurs (e.g. dsungaripterids, 'tupuxuarids' and azhdarchids) where the scapulae are relatively longer and slant forwards and outwards from their contact with the notarium. The arrangement in ornithocheiroids has been characterized as 'top-decker', in reference to aeroplanes that have the wings attached above the centre of gravity, a construction that supposedly confers increased flight stability (Frey *et al.*, 2003d).

The humerus was relatively robust, with a large deltopectoral crest that curves around the proximal end of this bone. The ulna is more than double the width of the radius, but at only 1.36 times the length of the humerus it is relatively short compared to other pterodactyloids. Each syncarpal is fully fused and all three carpal elements compare closely with those of ornithocheirids such as *Coloborhynchus*. Thus, for example, in proximal view the proximal syncarpal has a distinctive elongate pentagonal outline with a prominent ventral notch while, in distal view, the distal syncarpal has a rounded profile and dorsal and ventral articular facets of similar size (cf. Unwin, 2003: figure 18). The pteroid is relatively long and slender, reaching at least 70% the length of the humerus.

The wing-metacarpal is robust, but relatively short compared to that of most other pterodactyloids, not even reaching the length of the humerus. The proximal extension of the thin, rod-like third metacarpal seems to have articulated with the carpus, but metacarpals one and two appear to have lost this contact. The wing-finger is unusual in that it formed a greater proportion of the total forelimb length (65%) than in almost any other pterodactyloid where, typically, this value is 58–60% (as is plesiomorphic for pterosaurs) or less. The four wing-finger phalanges contribute to 31, 28, 22 and 19% of the wing-finger respectively. This steady decrease in length distally is plesiomorphic for pterodactyloids and clearly distinguishes *Arthurdactylus* from azhdarchoids where typically the first phalange occupies more than 40% of the wing-finger while the last forms less than 10%.

The pelvic elements are completely fused to one another and their general morphology, especially the large circular acetabulum and rearward directed pubis and ischium, corresponds closely to that seen in ornithocheirids from the Santana Formation (Frey and Martill, 1994; Kellner and Tomida, 2000). The ilia were not fused to the sacral ribs, and nor were the pelvic plates fused ventrally. This condition might reflect osteological immaturity, but is inconsistent with the extensive degree of fusion seen elsewhere. Alternatively, the possibility of a small degree of lateral mobility of each plate would have allowed the pelvis to widen, perhaps to facilitate the passage of an egg. In this case SMNK PAL 1132 would appear to have been a female.

The hindlimbs are gracile, lightly built and relatively short (Figure 17.3d). Unlike most pterosaurs, where the head of the femur is angled somewhat inward at about 135–140°, the caput is directed terminally and the collum is almost straight. The tibia is a slender element and, at only 1.23 times the length of the femur, relatively short. The fibula was either extremely reduced or completely absent. The foot was remarkably small and slender. The metatarsals reached only 26% the length of the humerus, while the pes claws were less than half the size of those in the hand.

There has been some uncertainty concerning the relationship of *Arthurdactylus* to other pterosaurs. Frey and Martill (1994) were of the opinion that *Arthurdactylus* might be an ornithocheirid, an idea that was supported by Unwin (2001, 2003) and Steel *et al.* (2005), while Kellner and Tomida (2000) assigned it to the Pteranodontoidea (a junior synonym of Ornithocheiroidea; see Unwin 2003: 161) and presumed a close relationship with 'Anhangueridae'.

Arthurdactylus is undoubtedly a pterodactyloid and can be assigned with confidence to the Ornithocheiroidea since it exhibits numerous apomorphies of this distinctive taxon: a scapula that is shorter than the coracoid, oriented perpendicular to the spinal column and articulated with a notarium; relatively long forelimb more than five times the length of the femur+tibia; warped deltopectoral crest of the humerus; radius half the diameter of the ulna; ornithocheiroid carpus; loss of contact between the first two metacarpals and the wrist; and femur with stout neck and steeply directed caput (Unwin, 2003).

Arthurdactylus exhibits several apomorphies of the Ornithocheiridae. Among pterodactyloids a relatively elongate wing-finger, more than 60% of total forelimb length, is only found in ornithocheirids (although also present in several non-pterodactyloids). In addition, the extremely reduced or absent fibula and remarkably short metatarsus (only one-quarter the length of the humerus) are unique features of ornithocheirids. Bolstering this conclusion, *Arthurdactylus* lacks derived characters of other ornithocheiroids. Thus, the relatively low humerus/ulna ratio and relatively short wing-metacarpal differ from the much higher values found in istiodactylids, while pteranodontians (Pteranodontidae+Nyctosauridae) have wing-metacarpals that are twice the length of the humerus (Unwin, 2003).

As noted by Frey and Martill (1994) unique features of the shoulder girdle and pelvis appear to distinguish *Arthurdactylus* from other ornithocheirids. The development of an articulation between the distal end of the scapula and two neural processes of the dorsal vertebra (Frey and Martill 1994: figure 4a) seems to be unique to *Arthurdactylus*, since in other ornithocheirids contact is only with one vertebra or shows just a slight overlap with preceding or succeeding vertebrae. In addition, as Kellner and Tomida (2000) note, the short, pointed postacetabular process of the ilium, and the large, deep, rounded opening between the ischium and pubis (Figure 17.3f) also seem to be unique to *Arthurdactylus*, although the pelvis is only known in relatively few ornithocheirids, principally *Coloborhynchus robustus*.

Ludodactylus **Frey** ***et al.,*** **2003b**

Ludodactylus sibbicki Frey *et al.,* 2003b

This species is known from a single skull complete with lower jaw (SMNK PAL 3828), but lacking the distal termination of a large cranial crest, preserved on a slab with examples of the fish *Dastilbe* (Figure 17.4; Plate 22). First mentioned by Frey and Tischlinger (2000) and later described and named by Frey *et al.* (2003b; see also Viohl, 2000; Unwin, 2005), this pterosaur, nicknamed the tree-biter, has a leaf preserved between the left and right mandibular rami that may have been responsible for the death of this particular individual (see above).

Ludodactylus sibbicki was a large pterosaur, with a skull length (tip of jaw to rear margin of occiput) of almost 0.5 m. When compared to other, more complete ornithocheirids such as *Coloborhynchus* this indicates a wingspan in the region of 4 m.

The skull (Figure 17.4) was remarkably elongate, with a long, attenuate snout region and an elongate nasoantorbital opening that is relatively straight, rather than concave as in many ornithocheirids and into which projected a long, narrow, nasal process. The rostrum lacked a premaxillary crest, distinguishing *Ludodactylus* from other ornithocheirids, with the exception of *Brasileodactylus*, which also lacks such a crest (Kellner, 1984). The orbit is large and pear-shaped, its long axis sloping from posterodorsal to anteroventral. There is a well-developed lacrimal foramen, as is typical for ornithocheirids, but *L. sibbicki* is distinguished from other members of this clade by the rounded triangular shape of the foramen and by the development of a distinctive sharp-pointed lacrimal spine that projects caudally into the orbit (Frey *et al*., 2003b). Moreover, with the exception of *Caulkicephalus* (Steel *et al*., 2005), *Ludodactylus* is the only known ornithocheirid with a prominent, well-developed, narrow (1.5 mm thick) blade-like cranial crest that sweeps upward and backward from the frontoparietal margin of the cranium and that is largely formed by the parietals. The mandibles bear a low ventral crest, and have a symphysis that occupies 40% the length of the entire lower jaw. The hyoids are well developed and shaped rather like a tuning fork.

The dentition consisted of 23 tooth pairs in the upper jaw and 17 in the lower jaw. The teeth are simple, slightly recurved, elongate and generally sharply pointed. Almost all stand vertically in the jaw, except for the first three pairs which increasingly slant forward and downward (rostrum), or upward (mandible), the first pair oriented at almost 45° to the long axis of the jaw. Tooth size is variable. In the upper jaw tooth size increases from the first to the third position, the latter being the most robust tooth of the entire dentition. Subsequently, tooth size declines, that in the fifth position being particularly small, but then increases again up to the seventh or eighth pair, which are almost as large as the first pair. Tooth size then

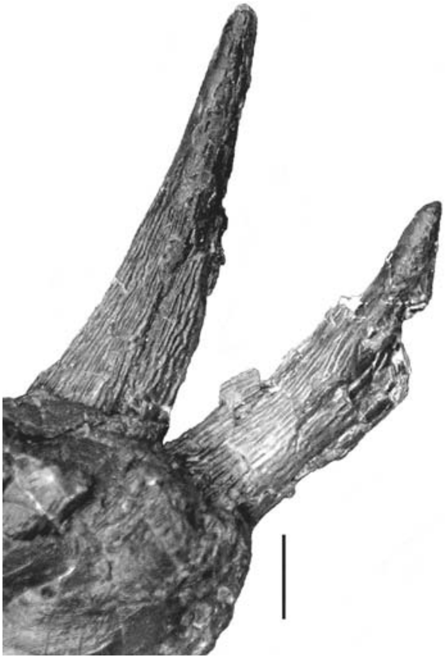

Fig. 17.5. Pterosaurs from the Nova Olinda Member: *Ludodactylus sibbicki* (SMNK PAL 3828) anterior-most teeth of mandible; notice the robust, slightly crenulate ribbing. Scale bar, 5 mm.

rapidly decreases and the last nine pairs are relatively small and widely spaced. The mandibular dentition exhibits a similar pattern except that there are fewer teeth and the tooth row terminates further rostrally. The anterior-most teeth have slightly crenulate ribbing (Figure 17.5)

Ludodactylus was included in the Ornithocheiridae by Frey *et al*. (2003b) because it exhibits a pattern of variation in tooth size that is diagnostic for this family (e.g. Unwin, 2001, 2003) and this assignment has been supported by other studies (Lü and Ji, 2005; Steel *et al*., 2005). The general morphology of the skull of *Ludodactylus* corresponds well to that of other ornithocheirids such as *Coloborhynchus* and *Ornithocheirus*, and exhibits several apomorphies of Euornithocheira: concave margin of the nasoantorbital opening, infilling of the ventral region of the orbit and extension of the maxillary process of the jugal to the rostral end of the nasoantorbital opening (Unwin, 2003). Moreover, the development of a large blade-like fronto-parietal crest is only found in ornithocheiroids (*Caulkicephalus*, pteranodontids, nyctosaurids) although its exact homology within this clade is still unclear.

Apart from *L. sibbicki*, two other ornithocheirids, *A. conandoylei* and *Brasileodactylus* sp. indet., are also known from the Crato Formation. There is a distinct possibility that the isolated skull of *L. sibbicki* might belong to the same taxon as the post-cranial skeleton described under the name *A. conandoylei*, but, as noted by Frey *et al.* (2003b), more complete remains are required before this possibility can be resolved. Significantly, the corresponding portions of *L. conandoylei* and the fragmentary jaws assigned to *Brasileodactylus* are, in almost all respects, practically identical (Veldmeijer, 2006). This observation and its implications are discussed in more detail below.

While there can be little doubt that *L. sibbicki* is an ornithocheirid, its relationships to other members of the Ornithocheiridae are unclear. Insofar as they are known, most ornithocheirids, including *Ornithocheirus*, *Coloborhynchus*, *Haopterus* and *Boreopterus*, lack a prominent fronto-parietal crest. By contrast, such a structure is present in a new ornithocheirid, *Caulkicephalus*, from the Wessex Formation of the Isle of Wight, England (Steel *et al.*, 2005), and might be used to suggest a closer relationship between these taxa than to other ornithocheirids. On the other hand, the absence of crests on the jaws of *Ludodactylus* and their general similarity in almost all respects to the jaws of *Brasileodactylus* (see also below) might encourage the alternative view of a close relationship between these taxa. However, it would be premature to argue for either of these relationships or any other pairings within Ornithocheiridae until the distribution and biological significance of crests is better understood and a detailed systematic revision of ornithocheirid pterosaurs is carried out.

The remarkable similarity between the cranial crest of *Ludodactylus* and this structure in *Pteranodon* (Bennett, 1994, 2001) further supports the view that ornithocheirids and pteranodontians are closely related (Unwin, 2003), but until the interrelationships of ornithocheirids are better understood the exact significance of this observation cannot be fully established.

Brasileodactylus sp. indet. Sãyao and Kellner, 2000

At present this taxon is represented in the Crato Formation by a single individual (MN 4797-V) consisting of the anterior ends of the upper and lower jaws and an intact dentition (Figure 17.6). The specimen was first figured by Frey and Martill (1994: figure 19), mentioned by them again in Martill and Frey (1998) and finally described in detail by Sãyao and Kellner (2000). The preserved portion of the upper jaw is 136 mm long while that of the lower jaw, which is slightly more complete, reaches 184 mm. Compared with other ornithocheirids this suggests an original skull length of approximately 0.4–0.45 m and general anatomical dimensions similar to those of the single known individuals of *Arthurdactylus* and *Ludodactylus*.

The upper jaw is long and low, tapering to a rounded tip and with no evidence of a crest. The lower jaw is similar in form, but is a little deeper than the upper jaw, and has a blunter tip. Although it too is supposedly crestless, the ventral margin

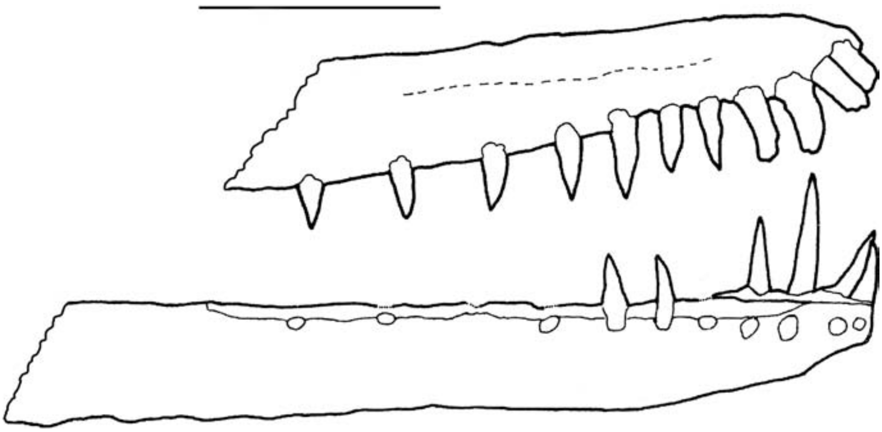

Fig. 17.6. Pterosaurs from the Nova Olinda Member: *Brasileodactylus* sp. Anterior ends of rostrum and mandibular symphysis in right lateral view. Scale bar, 50 mm. Redrawn from Sayão and Kellner (2000).

extending from a point below the third tooth as far back as the eight tooth seems to be slightly inflated and flange-like, possibly representing an incipient crest.

The dentition, consisting of stout, slightly recurved, sharp-pointed teeth, is typically ornithocheirid. In the upper jaw tooth size initially increases, the third and fourth positions containing the largest preserved teeth. This is followed by a sharp decrease in size, with a relatively small tooth at the fifth position, and then an increase in size again caudally, the largest tooth being the seventh. Beyond this tooth size rapidly decreases. There is a similar pattern of size variation in the lower jaw, except that the largest teeth in this case are the second, and sixth/seventh. In the upper jaw most of the teeth erupt perpendicularly to the palatal margin, but from the fourth tooth forwards teeth become increasingly procumbent, the first pair directed forward and downward at about 45° to the long axis of the jaw. In the lower jaw only the first pair are noticeably procumbent, directed forward and upward at about 70° to the lower-jaw long axis.

There can be little doubt that MN 4797-V is an ornithocheirid since details of the dentition match very closely those of other ornithocheirids and form a clear and unambiguous apomorphy of this clade (Unwin, 2003). Sãyao and Kellner (2000) assigned the jaw to *Brasileodactylus*, primarily because it appears to lack any cranial crests, at least, upon the jaws. The difficulty with this is that at least one other ornithocheirid, *Ludodactylus*, also lacks crests upon the jaws and there is a further complication in that the development of crests is probably related to sexual dimorphism (Bennett, 1992, 2002; Unwin, 2005), and thus the presence/absence of crests per se may not be a reliable guide to taxonomic affinity (although, pronounced differences in the position or shape of crests may be). Other proposed apomorphies of *Brasileodactylus*, such as the expanded end of the lower jaw, and the development of a medial groove that starts at the anterior tip of the palatal surface of the symphysis and widens caudally are also problematic because they are found in other ornithocheirids such as *Coloborhynchus*. For the present, the assignment of MN 4797-V to *Brasileodactylus* is retained, but this and other aspects of ornithocheirid systematics clearly require revision.

Comparison of MN 4797-V with the holotype of *L. sibbicki* (Frey *et al*., 2003b) shows that the two are remarkably similar, in terms of both jaw shape and details of the dentition. The only distinctive difference concerns the significantly greater depth of the mandibles compared to the rostrum in MN 4797-V. By contrast, in *L. sibbicki*, the upper and lower jaws are of approximately the same depth anterior to the nasopreorbital opening. The significance of this distinction is unclear, and it might be related, at least in part, to the degree to which the Crato specimens have been crushed. It seems likely, therefore, that MN 4797-V and SMNK PAL 3828 belong either to the same species, or at the least to two closely related taxa. Further investigation is needed to resolve this issue and the more general problem of the validity and distinction of *Brasileodactylus*.

Other ornithocheirids

A further six, as-yet-undescribed, specimens can be assigned to the Ornithocheiridae. These include jaw remains (Figure 17.7) that show some similarities to *Brasileodactylus*, a jaw fragment (Figure 17.8) currently in a private collection, and perhaps referable to *Anhanguera*, a tooth, MN 4798-V (Sayão and Kellner, 2000), and a virtually complete postcranial skeleton, SMNK PAL 3854 (Frey *et al*., 2003c). An incomplete left wing, MPSC R-739, with an estimated original length of 1.5 m, was identified by Nuvens *et al*. (2002) as tapejarid. However, the relative shortness of the wing-metacarpal compared to other forelimb elements and the small disparity in the lengths of wing-finger phalanges one and two demonstrate that it is ornithocheirid. The same applies to MPSC R-779, also represented by an incomplete forelimb belonging to a slightly smaller individual (estimated forelimb length, 1.1 m) that exhibits several features of osteological immaturity including an extensor tendon process that is not fused to the main body of the wing-phalanx one (Frey and Martill, 1998) and unfused syncarpals (Nuvens *et al*., 2002).

Lophocratia Unwin, 2003

Only recently recognized, this taxon, the name of which refers to the prominent cranial crest borne by many of its members (Unwin, 2003), essentially groups together the non-ornithocheiroid pterodactyloids: Ctenochasmatoidea, Dsungaripteroidea and Azhdarchoidea.

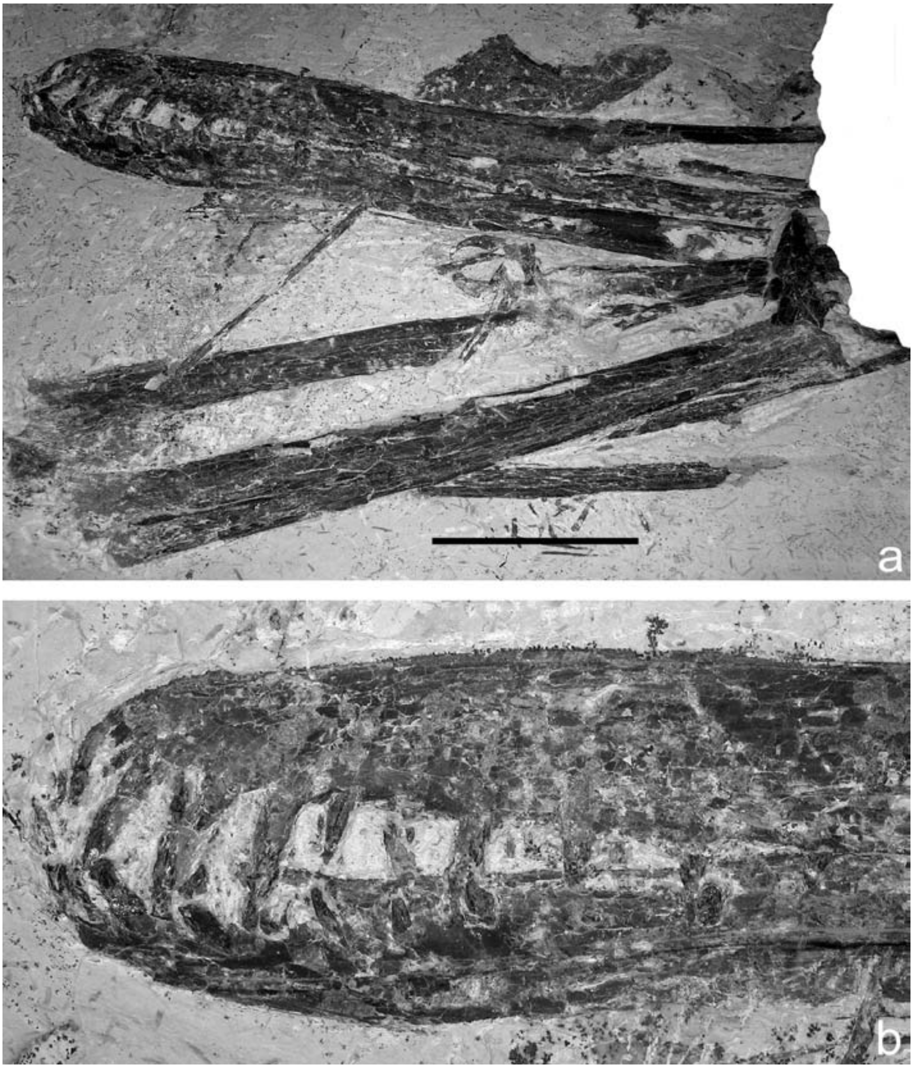

Fig. 17.7. Pterosaurs from the Nova Olinda Member: another example, possibly referable to *Brasileodactylus* sp.; (a) specimen comprising part of the rostrum with nasoantorbital fenestra, dentary and several postcranial elements; (b) detail of the premaxilla and anterior dentary. Specimen in coll. of Museum of Paleontology, Santana do Cariri, Ceará.

Azhdarchoidea Nesov, 1984

When first proposed this clade united all long-necked pterodactyloids including *Pterodactylus*, ctenochasmatids, *Lonchodectes* and azhdarchids (Unwin, 1992). Subsequently, it was argued that ctenochasmatoids, including *Lonchodectes*, formed a distinct clade and the content of Azhdarchoidea was modified to include

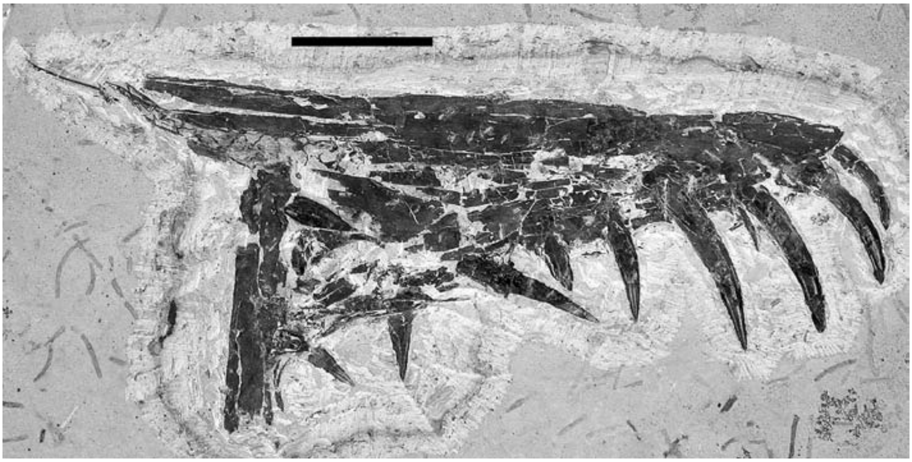

Fig. 17.8. Pterosaurs from the Nova Olinda Member: evidence for an additional toothed pterosaur taxon from the Crato Formation. This specimen, now in a private collection, exhibits a much greater angle between the presumed dorsal margin of the premaxilla and the dental border than in *Ludodactylus* or *Brasileodactylus*. In this respect it resembles *Anhanguera* sp. Scale bar, 20 mm.

just Tapejaridae and Azhdarchidae (Unwin, 1995a; Kellner, 1996). Further investigations of the interrelationships of azhdarchoids and a huge increase in our knowledge of the anatomy of several key genera (thanks to the discovery of relatively complete skeletons in the Santana Formation of Brazil and the Jehol Group of China) has led to the suggestion that Tapejaridae is paraphyletic (Unwin and Lu, 1997; Unwin, 2003; Lü *et al.*, 2006; Martill and Naish, 2006). Originally formulated to include tapejarids and 'tupuxuarids', it now seems that the latter are more closely related to azhdarchids than they are to tapejarids (Unwin, 2003; Martill and Naish, 2006), consequently Tapejaridae is restricted here to *Sinopterus*, *Huaxiapterus* and *Tapejara* and a new genus composed of two species (*T. imperator* and *T. navigans*) originally included in *Tapejara* (see also Lü *et al.*, 2006).

Tapejaridae Kellner, 1989

Ingridia gen. nov.

Type species: *Tapejara imperator* Campos and Kellner, 1997.
Included species: *Tapejara navigans* Frey *et al.*, 2003a.

Derivation of name: in memory of Ingrid Wellnhofer, wife of Peter Wellnhofer, the leading authority on pterosaurs for much of the last four decades.

Diagnosis: Tapejarid with a very large premaxillary crest associated with vertical spine-like supra-premaxillary ossification and a relatively elongate preorbital rostrum bearing a stout and relatively sharply down-turned jaw tip.

Distribution: *Ingridia* is known only from the Lower Cretaceous (Aptian) Crato Formation of Brazil.

Comments: *Ingridia* is proposed as a new genus that incorporates the two named tapejarids, *Tapejara imperator* Campos and Kellner, 1997 and *Tapejara navigans* Frey, Martill and Buchy, 2003, from the Crato Formation. These species, and the new genus to which they are assigned, are clearly distinguished from other species of *Tapejara* by their relatively elongate skull, a nasoantorbital opening with a length that is more than twice its height (only 1.6 in *Tapejara wellnhoferi*), a relatively higher position of the orbit (in *T. wellnhoferi* it lies well below the level of the dorsal margin of the nasoantorbital opening), and, uniquely, the presence of a supra-premaxillary ossification. *Ingridia* is distinguished from both Chinese tapejarids, *Sinopterus* and *Huaxiapterus*, by the presence of a large premaxillary crest and supra-premaxillary ossification. *Sinopterus* appears to lack any significant development dorsally of the bony crest and in *Huaxiapterus* this development is small and flange-like. Moreover, in both the Chinese tapejarids the anterior end of the rostrum appears to be longer and more slender than that of *Ingridia* and is flexed downwards at a lower angle.

Ingridia imperator (Campos and Kellner, 1997)

Synonym: Tapejara imperator Campos and Kellner, 1997.

This species of *Ingridia* is represented by three skulls: DNPM MCT 1622-R, the holotype, consisting of an almost complete cranium, but lacking the mandibles (Campos and Kellner, 1996, 1997); SMNK PAL 2839, a cranium lacking the anterior part of the rostrum and the mandibles (Frey *et al.*, 2003c: figure 13); and a near-complete skull in a private collection (Figure 17.9). The holotype, apparently an adult since most bone sutures are obliterated (Campos and Kellner, 1997), is 420 mm in length from the tip of the rostrum to the rear margin of the occiput, and approximately 800 mm high, measured from the ventral margin to the tip of the cranial crest. The second specimen is of similar size. Comparison with the holotype of *Sinopterus dongi* (Wang and Zhou, 2002), one of the most completely preserved tapejarid skeletons, suggests a wing span in the region of 3 m.

I. imperator has a highly distinctive skull morphology (Figure 17.9) with several typical azhdarchoid characters including the absence of teeth, a very large nasoantorbital fenestra occupying almost 60% of the skull length, a pear-shaped orbit located below the dorsal margin of the nasoantorbital opening and extension of the frontal anterior to the lacrimal-jugal bar (Unwin, 2003). Tapejarid features include a

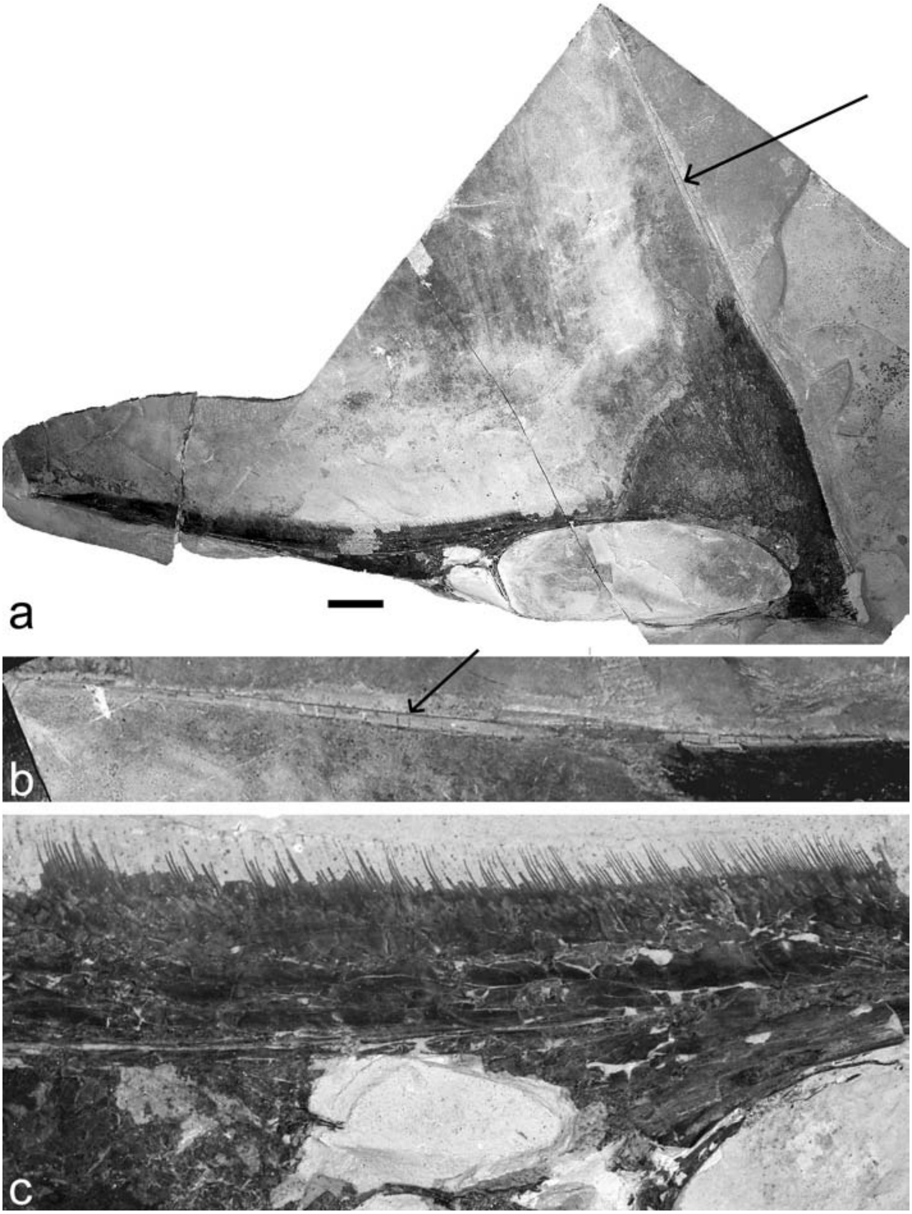

Fig. 17.9. *Ingridia imperator* (Campos and Kellner, 1997): (a) near-complete skull currently in a private collection; scale bar, 100 mm; (b) anterodorsal ossification (arrow) that formed the leading edge of the soft-tissue crest; (c) dorsal margin of caudal process of the ?premaxilla with 'comb-like' bone extensions that entered into and presumably anchored the soft-tissue crest.

down-turned rostrum anterior to the nasoantorbital fenestra, and a large vertically oriented cranial crest primarily based on the premaxillae (Lü *et al.*, 2006). The basal portion of the crest is fully ossified and the anterior portion almost triangular in shape. The upper, main part of the crest is formed from soft tissues.

I. imperator appears to be distinguished from the other species in this genus, and indeed from all other tapejarids, by the presence of a remarkably elongate bony rod that extends backward and upwards from the posterodorsal apex of the skull. Presumably, this rod was composed of the parietals and possibly the supraoccipitals (Campos and Kellner, 1997). As demonstrated in SMNK PAL 2839, it also supported the rearward extension of the cranial crest, more details of which are given below.

Ingridia navigans (Frey *et al.*, 2003a)

Synonym: Tapejara navigans (Frey *et al.*, 2003a).

The second species of *Ingridia*, this taxon is also represented by two specimens. The holotype (SMNK PAL 2344), a cranium lacking the mandibles (Plate 23), is almost complete, but lacks the dorsal tip of the cranial crest. A second example (SMNK PAL 2343) is slightly larger, but less well preserved (Figure 17.10). It too lacks the mandibles, the jugal-lacrimal bar and parts of the occiput, and only the lower regions of the cranial crest are preserved. The holotype is 375 mm long from the tip of the rostrum to the rear edge of the occiput, while the second specimen is about 13% larger and thus almost exactly the same size as the holotype of *I. imperator*.

The cranium of *I. navigans* is similar in general shape to that of *I. imperator*: edentulous, with a large nasoantorbital opening, a rostrum that is flexed ventrally at about 24° and a pear-shaped orbit that lies below the level of the naso antorbital opening. There are, however, two notable differences. First *I. navigans* lacks the long bony rod extending from the posterodorsal apex of the skull. Second, the cranial crest of *I. navigans* stands much more vertically than that of *I. imperator* with an almost vertical anterior margin rather than sloping backwards as in *I. imperator*, and with a straight rather than arcuate caudal margin (Martill and Frey, 1998). In addition, the dorsal extent of the striated bone lamina supporting the cranial crest is much greater in *I. imperator* than in *I. navigans*. Moreover, since known specimens are of rather similar dimensions, these distinctions cannot be explained away as age- or size-related. Frey *et al.* (2003a) also proposed that the caudal process of the jugal was twice as broad as in other tapejarids, but this does not seem to be the case for *I. imperator*.

Several soft-tissue structures are preserved in association with the skull of *I. navigans*. Patches of soft tissues preserved within the nasoantorbital opening

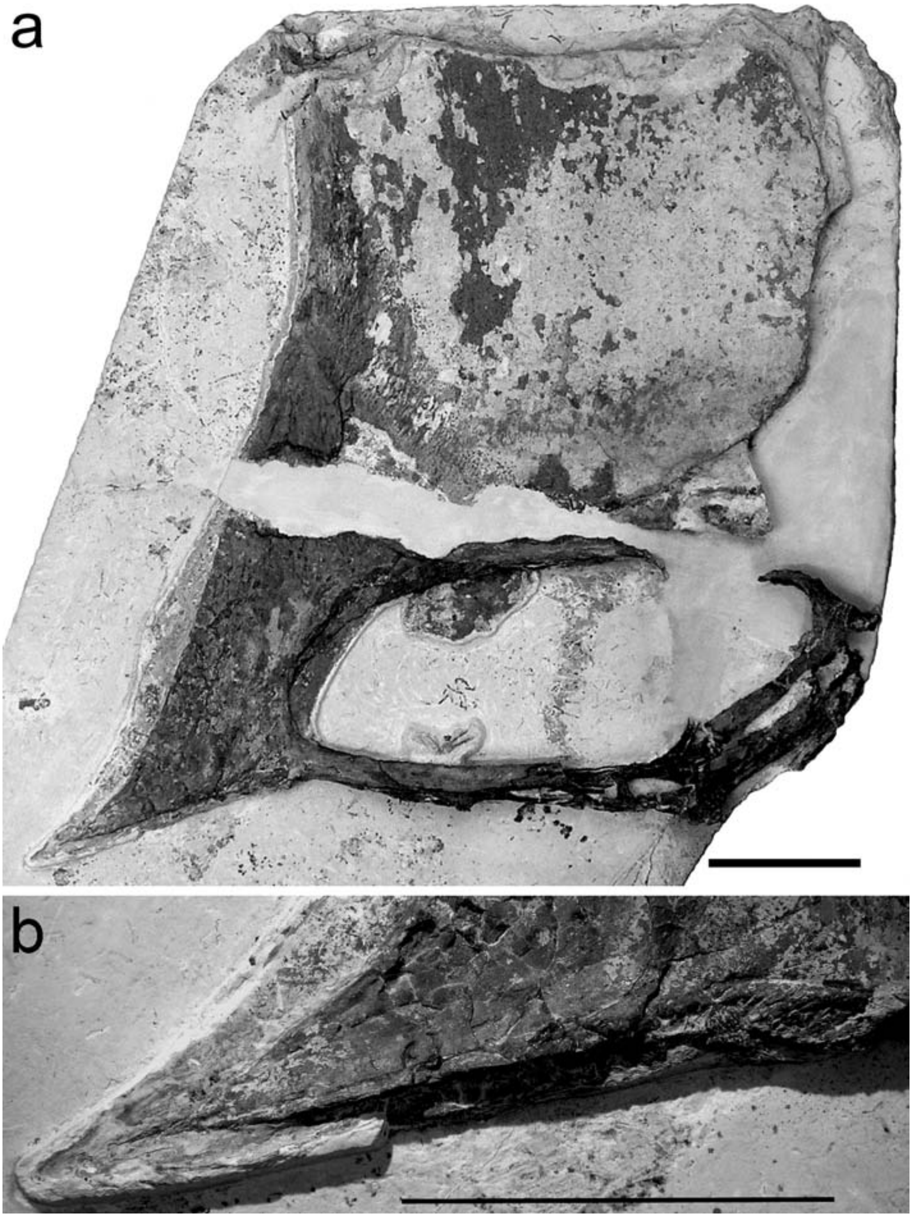

Fig. 17.10. Pterosaurs from the Nova Olinda Member: *Ingridia navigans* (Frey, Martill and Buchy, 2003), SMNK PAL 2343; (a) skull with soft-tissue head crest in left lateral aspect; (b) detail of anterior rostrum showing rhamphotheca. Scale bars, 50 mm.

(Figure 17.10a) were interpreted by Frey *et al.* (2003c) as the remains of an internasal septum which, if correct, is the first record of this structure in any pterosaur. Remains of what appears to have been a keratinous rhamphotheca, consisting of a blade-like sheath whose outline closely matches that of the rostrum, are preserved on the anterior and ventral margins of the premaxillae (Figure 17.10b). The rhamphotheca, which presumably covered and protected the rostrum in life, appears to have had sharp ventrolateral edges and a slender, pointed tip. Assuming that the mandibles matched this morphology, in life *Ingridia* was equipped with tweezer-like jaw tips that, according to Frey *et al.* (2003c), were well adapted for collecting and manipulating even tiny food items.

The most notable feature of *I. navigans*, and also of *I. imperator*, is the presence of a large and spectacular cranial crest. The lower region of the crest is supported anteriorly by ossified extensions of the premaxillae and, presumably, the frontals and parietals posteriorly. The upper regions of the crest appear to have been composed of soft tissues (Figure 17.10; Plate 23), presumably keratin, supported and stiffened internally by fine, vertically oriented fibres, possibly made of collagen or cartilage and anteriorly by an ossified supra-premaxillary spine (Frey *et al.*, 2003c; Figure 17.9a). The surface of the crest seems to have been smooth and in cross-section appears to have been shaped like a symmetrical aerofoil. In *I. imperator* the crest reached a point that was as much as four or five times the height of the skull at the occiput, and its lateral surface area was as much as six times that of the skull (Figure 17.9a). In *I. navigans* the crest may have reached a similar height (Frey *et al.* 2003a), but was narrower from front to back and had a surface area that was about three times that of the skull (Plate 23). These finds confirm suggestions that in other pterosaurs, including ctenochasmatoids and dsungaripteroids, 'unfinished' crests with jagged edges also had extensions composed of soft tissues, as has been reported for *Germanodactylus* (Bennett, 2002).

The function of the cranial crest of *Ingridia* is unclear. Frey *et al.* (2003c) have suggested that in *I. imperator* the crest may have functioned rather like a weather vane and could be used for steering, since the area of the crest caudal to the occipital joint is approximately the same as that anterior to the joint. However, in *I. navigans* the area of crest posterior to the occipital joint is relatively small and a weather-vane function seems unlikely. In this case it is supposed that the crest might have functioned rather like a thrust-generating wind-surfing sail, although lateral drift is likely to have been a problem. This might have been counteracted by the webbed feet, if they were held vertically, or by movements of the wings. Additionally, it has been proposed that the pterosaur could have maintained course by trailing its webbed feet in the water, although this option must have been severely limited and the interpretation seems, at best, unlikely.

The difficulty with all mechanical explanations of crests is that they fail to explain diversity in crest shape, size and position. The alternative, that crests were used for display purposes (Bennett, 1992; Campos and Kellner, 1997; Unwin, 2005), does satisfy this requirement. In order for crests to function in this respect it is only necessary that they be visible and all crests meet this demand. Moreover, one corollary of this explanation is that crests of different species that lived at the same time in the same area should have differed to some degree (Figure 17.19). This accords well with the small but significant differences in the crests of *I. imperator* and *I. navigans*. Moreover, the same pattern is seen, for example, in the Santana Formation pterosaurs, where crests also differ from species to species. Undoubtedly, crests also generated aerodynamic forces, but whether these were helpful or disadvantageous has yet to be established.

Tapejaridae gen. et sp. indet. SMNK 3830 PAL

This individual, with an estimated wingspan of about 2.8 m, consists of parts of a left forelimb and the complete hindlimbs, associated with extensive preservation of the wing membranes and soft tissue associated with the foot (Frey and Tischlinger, 2000; Frey *et al.*, 2003c; Figure 17.11; Plate 24). The claw digits of the left hand and their supporting metacarpals are well preserved and largely articulated, although slightly displaced from their position in life. The wing-phalanx one, however, is displaced distal to the wing-metacarpal. The hindlimbs are complete and naturally articulated except for the right ankle, where the distal tarsals are slightly displaced.

The presence of an elongate wing-metacarpal that is longer than the humerus and the loss of the fifth toe demonstrate that SMNK PAL 3830 is pterodactyloid (Kellner, 2003; Unwin, 2003), while the absence of any anatomical features typical of ornithocheiroids show that it is a lophocratian. The proportions of the wing-finger phalanges: 46, 29, 19 and 7%, in particular the elongate wing-phalanx one and short-wing phalanx four, are unique to azhdarchoids, as is the femur/humerus ratio of >1.25 (Unwin, 2003). Two further proportions, the ratio of the metatarsal to the rest of the leg (11%) and of the forelimb to the hindlimb (2.93), are also typical of azhdarchoids, although not unique to this clade, since a short metatarsal is also typical of ornithocheirids and a wing/leg ratio of less than 3.00 can also be found in some species of *Pterodactylus* (Wellnhofer, 1970).

The absence of azhdarchid apomorphies, such as a T-shaped cross-section of wing-finger phalanges two and three, a highly elongate wing-metacarpal (longer than wing-phalanx one) and a wing-finger that forms less than 50% of total forelimb length, demonstrate that SMNK PAL 3830 is a basal azhdarchoid and does not belong within the Azhdarchidae. Comparison with basal azhdarchoids is complicated by our incomplete knowledge of the post-cranial skeleton in several tapejarids (*Tapejara* and *Ingridia*) and the difficulty of discriminating between those taxa (*Sinopterus*, *Huaxiapterus* and ‘*Tupuxuara*’) where such information is available. In terms of the proportions of the limb bones, SMNK PAL 3830 shows

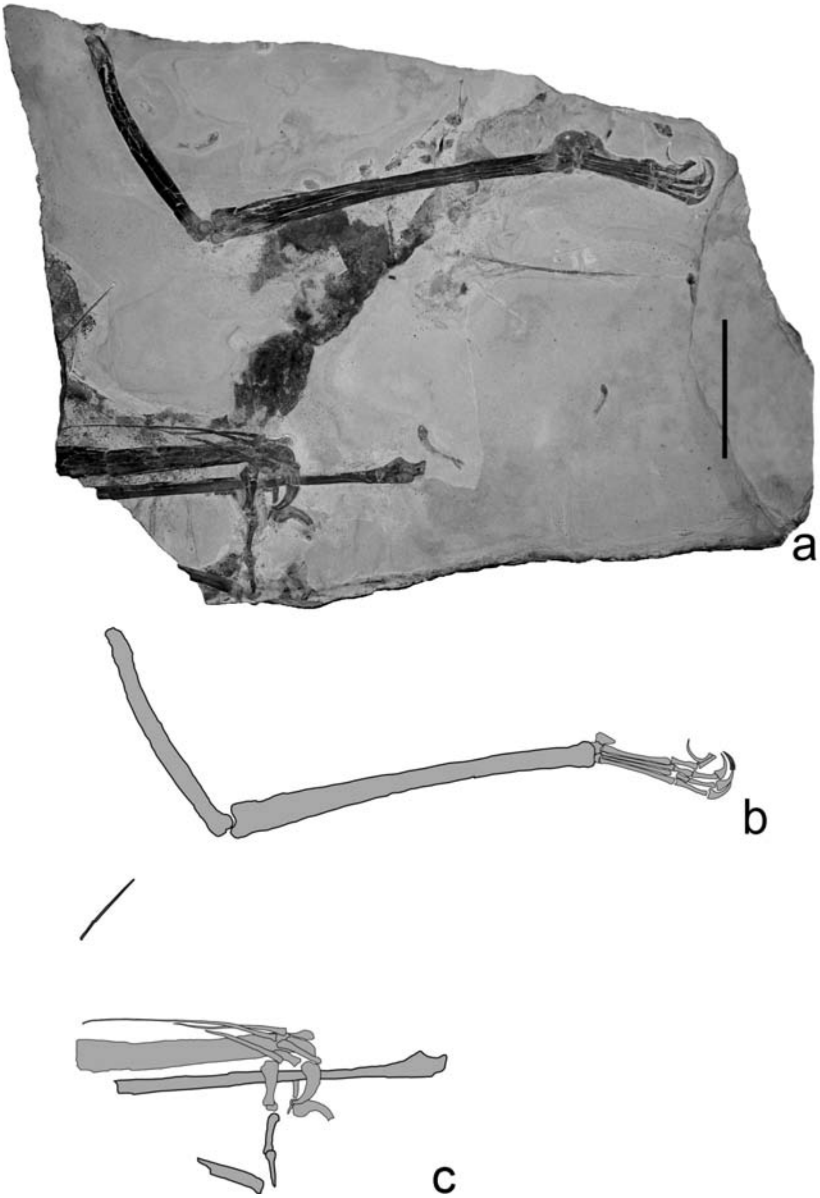

Fig. 17.11. Pterosaurs from the Nova Olinda Member: Tapejaridae gen. et sp. indet., SMNK PAL 3830: (a) slab bearing parts of the left forelimb and the complete left hindlimb. Note the well-preserved remains of the cheiropatagium extending from the manus to the lower leg; (b) the hindlimb bones; (c) the manus with associated distal metacarpals and wing-phalanx one. Scale bar, 100 mm.

closest similarity to the holotype of *Sinopterus dongi*, only differing in the relatively short wing-metacarpal and relatively elongate wing-phalanx one. This suggests that SMNK PAL 3830 is most probably tapejarid, and not 'tupuxuarid', the proportions of which are rather different (like azhdarchids, '*Tupuxuara*' has a relatively long wing-metacarpal and relatively short wing-finger). In that all tapejarid skulls so far recovered from the Crato Formation belong to *Ingridia* it would not be unreasonable to assume that SMNK PAL 3830 may also belong to this taxon, an idea that is supported by the close similarity in size of SMNK PAL 3830 to the predicted dimensions of the post-cranial skeleton of the two known examples of *Ingridia imperator*.

The key feature of this specimen is the extensive and excellent preservation of several types of soft tissue, including wing membranes, heel pads, foot webs and claw sheaths (Plate 24). The latter are associated with the terminal unguals of digits one to three of the manus and one to four of each pes. In each case these remarkably large, sickle-shaped, keratinous sheaths almost double the length of the claw, continuing its curve round a greater part of a circle, resulting in highly curved, sharp-pointed claws both in the hand and on the foot. The shape of the claw appears well suited for gripping, while their narrow, blade-like shape and slender needle-pointed tip suggests a role in climbing rather than in predation (Feduccia, 1993).

Webbing, picked out as a goethitic film, is preserved between all four digits of each foot and the same film is also seen flanking the metatarsals. Presumably, this represents remains of the integument, although no structure is seen within the webbing, unlike an exceptionally well preserved example of *Pterodactylus* where a similar webbing contains fine elongate fibres (Frey and Tischlinger, 2000). The heel pad, reported by Frey *et al.* (2003c) for the first time in pterosaurs, is very well developed on both feet and consists of a rounded area immediately behind the ankle region and enclosing metatarsal five. The external relief of this pad is composed of fine, subcircular, convex scales 1–2 mm in diameter (Plate 24c and d). The discovery of these soft-tissue structures in the feet of pterosaurs is matched by reports of exactly the same features in impressions of pterosaur feet found in Upper Jurassic sequences in both Spain (Garcia-Ramos *et al.*, 2002) and France (Mazin *et al.*, 1995). Foot webs, in particular, seem to have been common and possibly even universal in pterosaurs, since they are evident in many pteraichnites (Unwin, 2005), and are most likely to have served as vertical flaps that were used for trimming and steering during flight (Frey *et al.*, 2003c).

An extensive portion of the main flight membrane, the cheiropatagium, is preserved between the carpal region of the left forelimb and the left hindlimb, extending as far as the ankle (Plate 24a; Figure 17.11). This demonstrates that, as in other pterosaurs (e.g. Unwin and Bakhurina, 1994), the cheiropatagium linked together the fore- and hindlimbs. Parts of this flight membrane are well preserved and show folds and long, fine striations up to 180 mm long and 0.1 mm thick, that represent the remains of wing fibres (aktinofibrillae).

Patches of goethitic staining are also to be seen flanking the three short digits of the left hand (Plate 24e). This has been interpreted by Frey *et al.* (2003c) as evidence that the propatagium extended distal to the wrist and incorporated the first three digits as far as the base of the claws. This idea, in which the propatagium extended well in front of the forelimb, supported by a forward-directed pteroid articulated at the wrist, is controversial, but has recently received further support from both fossil evidence (Unwin, 2005) and aerodynamic analyses (Wilkinson, 2002; Wilkinson *et al.*, 2006).

?Tapejaridae gen. et sp. indet. MN 6527-V

In a study detailing the histology of Lower Cretaceous pterosaurs, Sãyao (2003: figures 2 and 6) illustrated an associated, but disarticulated, set of fore- and hindlimb bones consisting of: an incomplete humerus; radius and ulna; carpal elements; a pteroid; an incomplete wing-metacarpal; two wing-phalanges; part of the femur; and an incomplete tibia (Figure 17.12). According to Sayão (2003) the carpals are unfused, although in her figure 2 they are illustrated as fully fused. Thin sections of the humerus revealed reticulo-fibrolamellar tissue indicative of fast growth from which the author concluded that MN 6527-V was a young animal still in the process of growing.

Sayão (2003) stated that MN 6527-V was an azhdarchoid, based on the proportions of the distal end of the wing-metacarpal relative to its total length, but did not provide any further comments on the taxonomic affinities of this specimen. The relatively elongate wing-metacarpal indicates that MN 6527-V is a pterodactyloid and anatomical details of the carpals confirm that it is a lophocratian. Published details are not sufficient to demonstrate any unique azhdarchoid characters, but the proportions of the preserved limb bones generally correspond to those of *Sinopterus* (Wang and Zhou, 2002; Li *et al.*, 2003); thus it seems likely that MN 6527-V is a basal azhdarchoid. Comparison with SMNK PAL 3830 reveals some distinct differences: notably the humerus/wing-phalanx one ratio is 2.48 in SMNK PAL 3830, but only 1.56 in MN 6527-V. While these and other differences, for example in the humerus/ulna ratio, do not exclude MN 6527-V from the Azhdarchoidea, at the same time they do not encourage the idea that these individuals originally belonged to the same species. It is possible that they represent the two species of *Ingridia* known from the Crato Formation, although exactly which post-cranial remains belong to which species cannot yet be established.

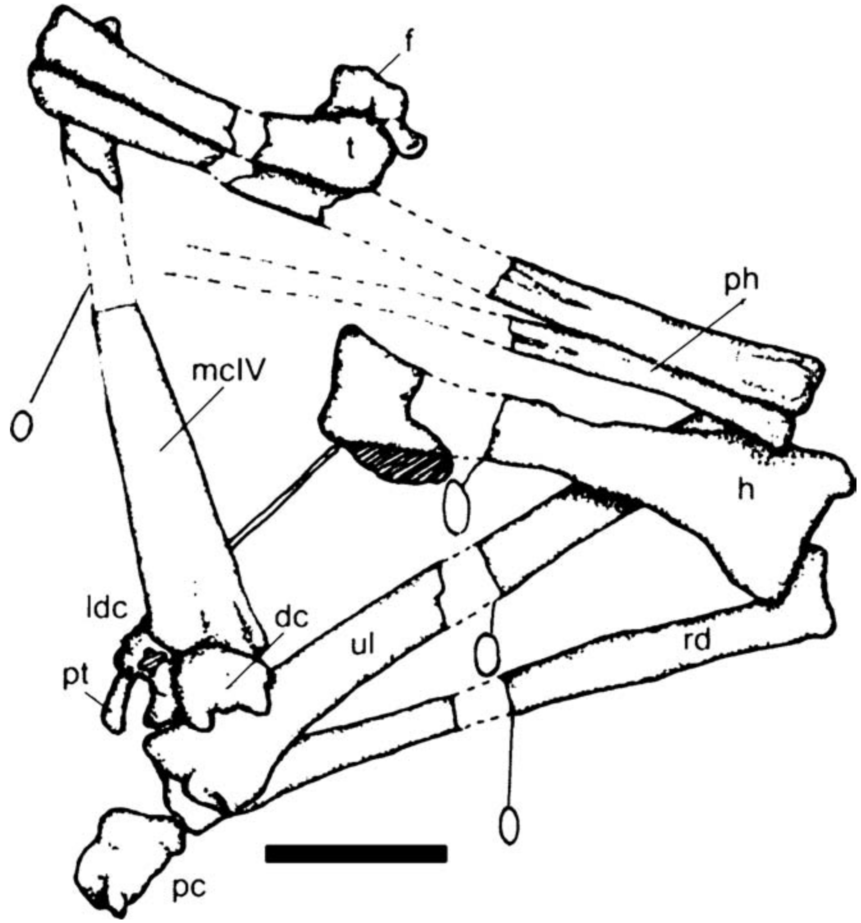

Fig. 17.12. Pterosaurs from the Nova Olinda Member: sketch of a partial postcranial skeleton of ?Tapejaridae gen. et sp. indet (MN 6527-V). Scale bar, 150 mm. Redrawn from Sayão (2003).

?Tapejaridae gen. et sp. indet. SMNK PAL 2342

This individual is represented by part of the left forelimb and comprises a complete wing-metacarpal, wing-phalanges one and two, an incomplete wing-phalanx three and the terminal portion of what may be an incomplete metacarpal (Martill and Frey, 1998: figure 4; Martill and Frey, 1999: figures 2 and 3; Figure 17.13). The bones, some of which project beyond the edges of the slab, indicating that this individual was originally more complete, are preserved in association, but not in natural articulation. Comparison with the holotype of *Sinopterus dongi* (Wang and Zhou, 2002) the proportions of which are almost identical to those of SMNK PAL 2342, permits the wingspan of the latter to be estimated at 2.2 m.

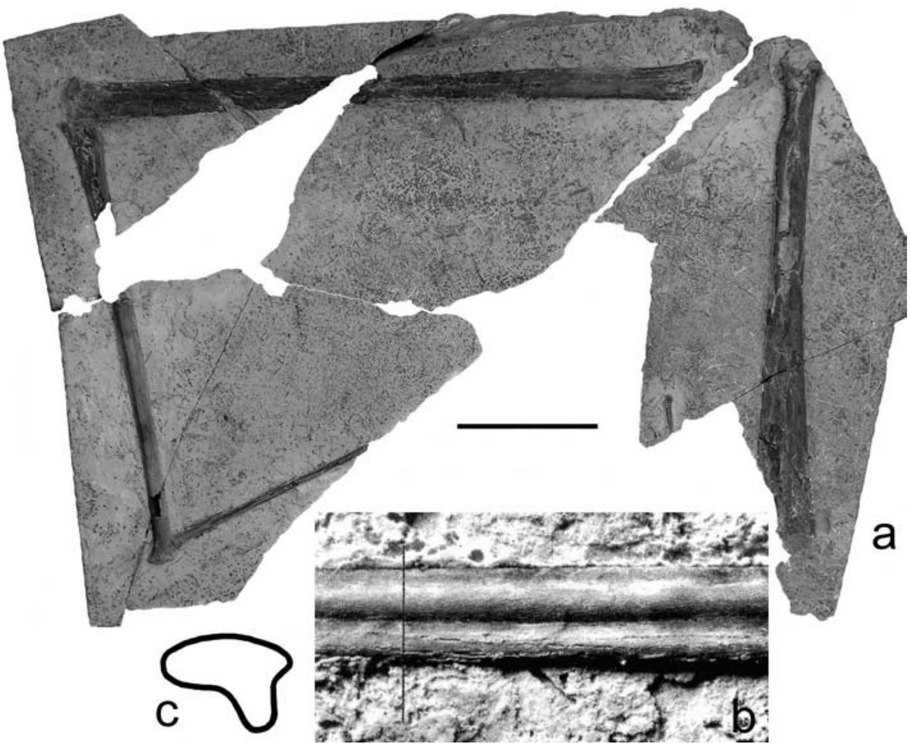

Fig. 17.13. Pterosaurs from the Nova Olinda Member: ?Tapejaridae gen. et sp. indet. (SMNK PAL 2342): (a) slab bearing the wing-metacarpal and part of the wing-finger; (b) detail of the T-shaped wing-phalanx two; (c) cross-sectional shape of wing-phalanx two. Scale bar, 50 mm.

Martill and Frey (1998, 1999) tentatively assigned this specimen to the Azhdarchidae (see also Frey *et al.*, 2003c) on the basis of a single character: the presence, in wing phalanges two and three, of a T-shaped cross-section (Figure 17.13b and c). At present this type of cross-sectional shape has only been demonstrated in azhdarchids (e.g. Unwin, 2003), which appears to confirm Martill and Frey's taxonomic assignment. The issue may, however, be more complex. The shape of the cross-section in SMNK PAL 2342 is somewhat different from that illustrated for *Quetzalcoatlus*, or observed, for example, in *Azhdarcho*. Moreover, Kellner (2004: 527) claims that this type of cross-section is also present in tapejarids, although no particular taxon was specified and *Tapejara wellnhoferi*, at least, lacks this feature (Martill and Frey, 1998).

In addition, the wing-metacarpal of SMNK PAL 2342 is substantially shorter than wing-phalanx one, while in all azhdarchids where this proportion can be established (*Zhejiangopterus*, *Quetzalcoatlus*) the wing-metacarpal is significantly longer than the first wing-phalanx. Indeed, as mentioned, the proportions of the complete limb bones of SMNK PAL 2342 correspond closely to the values for *Sinopterus dongi* (Wang and Zhou, 2002) and are similar to the condition in other Chinese tapejarids such as *Huaxiapterus jii* (Lü and Yuan, 2005; Lü *et al.*, 2006). Moreover, in so far as comparisons can be made, SMNK PAL 2342 also compares closely with MN 6527-V, identified here as probably tapejarid. The most parsimonious conclusion that can be drawn from these observations is that SMNK PAL 2342 is an azhdarchoid and possibly a tapejarid.

Other ?tapejarid remains

An incomplete somewhat disarticulated postcranial skeleton (MPSC R-868; Nuvens *et al.*, 2002) was illustrated by Martill and Frey (1998: figure 7) and also featured in an issue of *National Geographic* magazine (May 2001, p. 91). The proportions of the bones such as the wing-finger phalanges one and two, and the femur and tibia, correspond fairly closely to those of SMNK PAL 3830. It seems likely that this individual is an azhdarchoid and possibly a tapejarid. Comparison with SMNK PAL 3830 suggests that this was a relatively small individual with a wingspan of about 1.6 m.

Nuvens *et al.* (2002) mention a large pterosaur (MPSC R-771) in the collections of the Museum of Paleontology Santana do Cariri. Identifiable bones including the radius and ulna, wing-metacarpal, wing-finger phalanges one–three, femur and tibia compare closely in their dimensions with the corresponding elements of SMNK PAL 3830. Consequently it seems that MPSC R-771 is almost certainly an azhdarchoid, probably tapejarid and may represent another example of *Ingridia*.

Other azhdarchoids

A complete left forelimb associated with well-preserved patches of fossilized flight membrane (MN 4729-V) was briefly described by Sãyao and Kellner (1998, 1999). The skeletal material consists of a fused scapulocoracoid (indicating that the individual was osteologically mature, or nearly mature), humerus, radius/ulna, parts of the wrist and metacarpus and the complete wing-finger. The wingspan can be fairly accurately estimated at two metres. The cheiropatagium is preserved in the vicinity of the radius, wing-metacarpal and wing-phalanx one and contains fine parallel lines indicating the presence of wing fibres (Sayão and Kellner, 1998, 1999).

The relatively elongate wing-metacarpal (exceeding the length of the ulna) demonstrates that MN 4729-V is a pterodactyloid and the coracoid is shorter than the scapula, indicating that MN 4729-V is a lophocratian (Unwin, 2003). A comparison of the relative lengths of the main forelimb elements reveals two azhdarchoid apomorphies: the wing-finger forms only 55% of total forelimb length, and wing-phalanx one makes up well over 40% of the total length of the wing-finger (Kellner, 2004). The presence of a large ventral process on the coracoid may be another azhdarchoid apomorphy (Sayão and Kellner, 1999), although such a structure is also found in some dsungaripterids.

Sayão and Kellner (1998, 1999) suggested that MN 4729-V might be tapejarid, but pointed out that comparison with *Ingridia imperator* was impossible because the latter is only known from cranial material. Inclusion in Tapejaridae is doubtful, however, because the relative lengths of the main forelimb bones of MN 4729-V are quite different from those of typical tapejarids such as *Tapejara*, *Sinopterus* and *Huaxiapterus*. In particular, the humerus/ulna ratio is only 1.23 compared to values of 1.4–1.5 in tapejarids, and wing-phalanx one is one and a half times the length of wing-phalanx two, compared to values of less than 1.4 for tapejarids.

By contrast, the proportions of MN 4729-V show a striking similarity to those of an almost-complete skeleton of a large basal azhdarchoid, IMCF 1052, that is currently assigned to '*Tupuxuara longicristatus*' (Unwin, 2003; Kellner, 2004; Martill and Naish, 2006). Indeed, the proportions of MN 4729-V to the latter are almost identical, the only exception being the relative greater length, in IMCF 1052, of the wing-phalanx one compared to wing-phalanx two. This may be attributable to the far greater size of the latter, which is almost twice that of MN 4729-V.

(In light of the description by Veldmeijer *et al.* (2005) of new material that they assign to *Thalassodromeus sethi* and the probability that this species is not a junior synonym of '*Tupuxuara longicristatus*' (see Martill and Naish, 2006), we note that, where determinable, supposedly diagnostic features of the latter (see Kellner and Campos 1988, 1994; Kellner, 2003, 2004; Unwin, 2003; Martill and Naish, 2006) are also present in *Thalassodromeus sethi*. Moreover, we were unable to identify other features of the holotype material (MN 6591-V) of '*Tupuxuara longicristatus*' that might be used to diagnose this taxon, raising the possibility that ' *Tupuxuara*' and ' *T. longricristatus*' are *nomina dubia*. To indicate this uncertainty these taxa, and derivative terms such as 'tupuxuarid', are cited in quotation marks.)

At present, 'tupuxuarids', in which we would include ' *Tupuxuara*', *Thalassodromeus* and possibly TMM 42489–2 (see Kellner, 2004; Martill and Naish, 2006), are primarily identified on the basis of cranial characters, and since such material is lacking for MN 4729-V an unequivocal assignment to this group is impossible. It is widely accepted, however, that the relative proportions of the main elements of the fore- and hindlimbs can be diagnostic for particular clades (Unwin, 2003). In this respect the association of a relatively low humerus/ulna ratio with a relatively short wing-finger and relatively elongate wing-phalanx one could be considered an apomorphy of 'tupuxuarids'. The presence of this derived condition in MN 4729-V is considered sufficient here to warrant assignment of this individual to this group. More complete remains will be needed, however, to determine whether this Crato

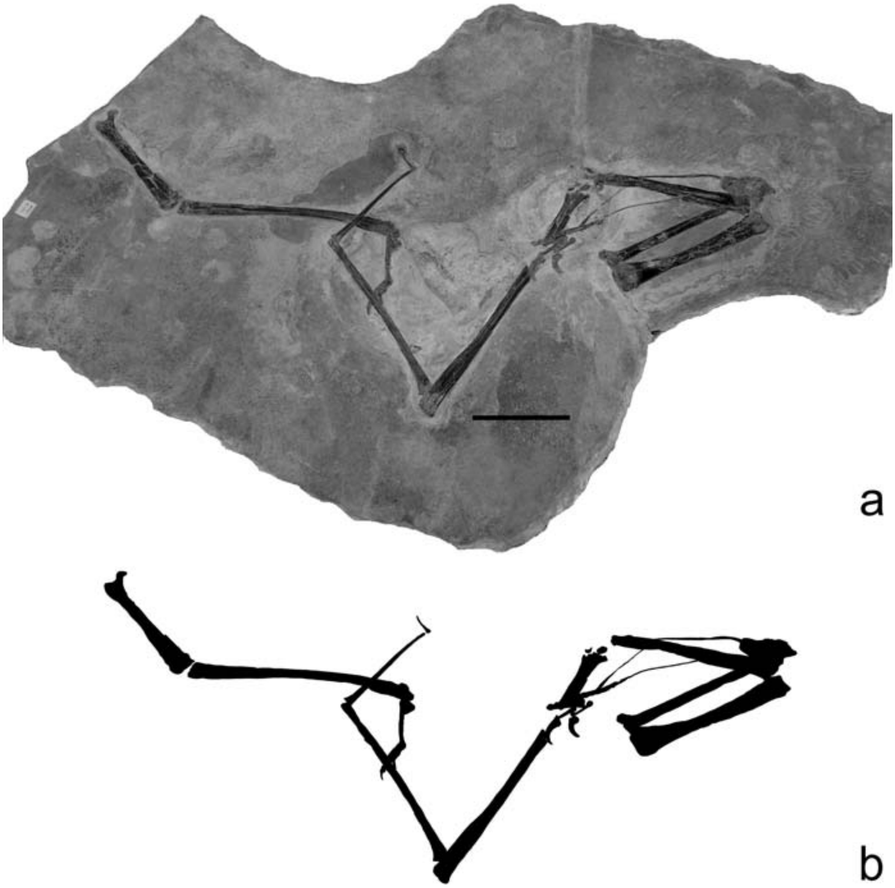

Fig. 17.14. Pterosaurs from the Nova Olinda Member: 'tupuxuarid' (SMNK PAL 3855): (a) complete hindlimb and wing missing only the humerus; (b) computer-generated diagram highlighting skeletal elements. Note the highly reduced terminal phalanx. Scale bar, 100 mm.

'tupuxuarid' can be assigned to one of the two named genera (both known from the Santana Formation) or represents a distinct taxon.

An as-yet-undescribed, incomplete post-cranial skeleton (SMNK PAL 3855) mentioned by Frey *et al.* (2003c) and referred to by these authors as 'probably a tapejarid' might also be 'tupuxuarid'. This individual (Figure 17.14) is about 33% larger than MN 4729-V but, where comparable, has relative bone lengths of almost exactly the same proportions.

Confirmation of the presence of 'tupuxarids' in the Crato limestone is provided by an almost complete skeleton, with skull (Figure 17.15), that is strikingly similar, both in terms of skeletal morphology and the relative lengths of limb elements, to IMCF 1052.

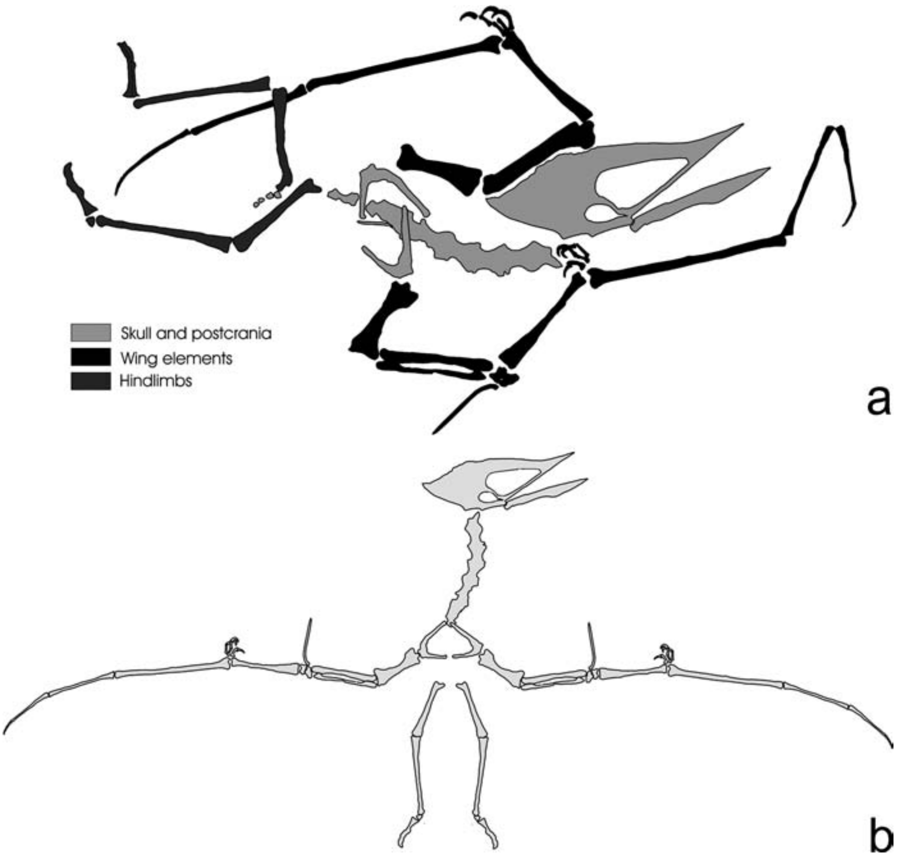

Fig. 17.15. Pterosaurs from the Nova Olinda Member: (a) skeleton as seen on limestone slab; (b) reconstruction of skeleton. Drawings made from an image of a pterosaur offered for sale on the Internet and now housed in a museum somewhere in the Far East according to the website's administrator. This specimen would appear to represent a new taxon close to *Tupuxuara*. It is also the most complete pterosaur to be recovered from the Crato Formation. The vendor was less than helpful and unwilling to authorize reproduction of photographic evidence.

In 2006 Sayão and Kellner briefly described an incomplete pterosaur (MN 6588-V) represented by part of the spinal column (consisting of the last cervical, a complete dorsal and sacral series and the first three caudals), the shoulder girdles, pelvis, including prepubes, some ribs and gastralia. Comparison with more complete remains suggests a wingspan of about 2.4 m. Fusion of the scapulocoracoid and the development of a notarium and synsacrum suggest that this individual was osteologically mature. The relatively elongate scapula, presence of a tubercle on the posteroventral margin of the coracoid and pelvis morphology suggest that MN 6588-V is an azhdarchoid and, according to Sayão and Kellner (2006, 2007), belongs within Tapejaridae. Tapejarids seem to lack a notarium (Unwin, 2003), but this structure is present in neoazhdarchians (Unwin, 2003; Martill and Naish, 2006), represented in the Crato Formation by at least one tupuxuarid (see above) and to which this individual might also belong.

Other Crato pterosaurs

There are several specimens that have not yet been described or figured and whose taxonomic relationships have not been resolved beyond an identification as pterosaurian. These are as follows. An isolated humerus was reported by Sayão and Kellner (2000) in the collections of the AMNH. In addition to the specimens described earlier, the collections of the Staatliches Museum für Naturkunde Karlsruhe also contain the rostrum of a large edentulous azhdarchoid SMNK PAL 4325 (M. Witton, personal communication), the complete wing and hindlimb of a tapejarid (SMNK PAL coll.; Figures 17.1a and 17.16), an incomplete forelimb (SMNK PAL coll.; Figures 17.1d and 17.17), the associated wing-finger and hindlimb of an azhdarchoid (SMNK PAL coll.; Figure 17.1e) and the almost complete forelimb of a tapejarid (SMNK PAL coll.; Figure 17.1h). A humerus (MPSC R-869), the posterior part of a skull (MPSC R-931) and an incomplete postcranial skeleton associated with fossilized soft tissues (MPSC R-932) have been noted by Sayão and Kellner (2000) and Nuvens *et al.* (2002) in the collections of the Museum of Paleontology Santana do Cariri.

Taxonomic composition of the Crato pterosaur assemblage

To date, 32 fossil pterosaurs have been reported from the Crato Formation. It is conceivable that two or more sets of these remains belong to the same skeleton, but the circumstances of preservation render this highly improbable. Consequently, it can be assumed that the minimum number of individuals recorded so far stands at 32.

Three individuals (SMNK PAL 3828, MN 4797-V and SMNK PAL 1132) undoubtedly belong to the Ornithocheiridae. At present each is assigned to a different genus and species but, although this cannot yet be satisfactorily demonstrated, it is probable that they represent a single (or at most two) species of ornithocheirid. Further undescribed remains including two jaw fragments, an isolated tooth (MN 4798-V), and three individuals represented by incomplete post-cranial skeletons (SMNK PAL 3854, MPSC R-739, MPSC R-779) are also most likely ornithocheirid and may well belong to the one or more species mentioned above.

Five individuals represented by skulls (DNPM MCT 1622-R, SMNK PAL 2839, SMNK PAL 2343 and SMNK PAL 2344: Figure 17.10) can be confidently assigned to the Tapejaridae and appear to represent two different but closely related species assigned to a new genus, *Ingridia*. A further five individuals (SMNK PAL 3830,

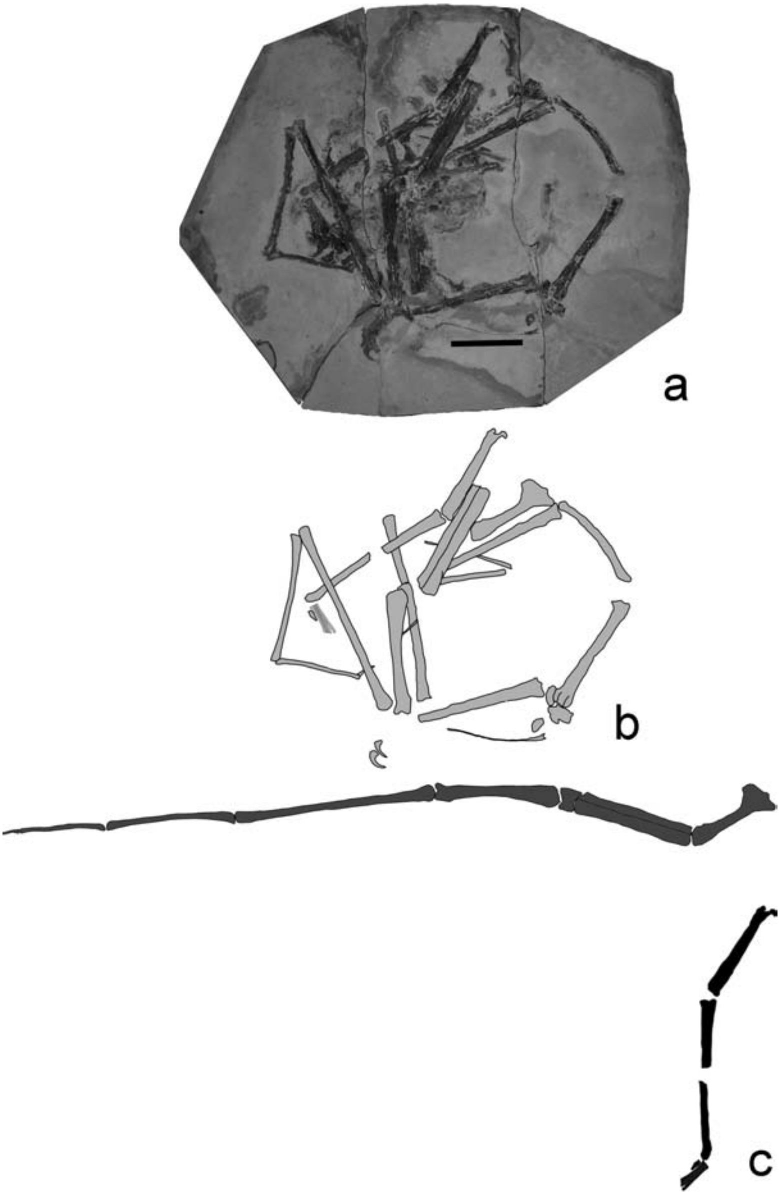

Fig. 17.16. Pterosaurs from the Nova Olinda Member: Tapejaridae gen. et sp. indet., SMNK specimen; (a) slab with partial skeleton comprising complete wing and hindlimb; (b) diagram highlighting skeletal elements; (c) reconstructed wing and hindlimb. All to same scale; scale bar, 100 mm.

Fig. 17.17. Pterosaurs from the Nova Olinda Member: disarticulated partial wing skeleton of unidentified pterosaur, SMNK PAL 3842.

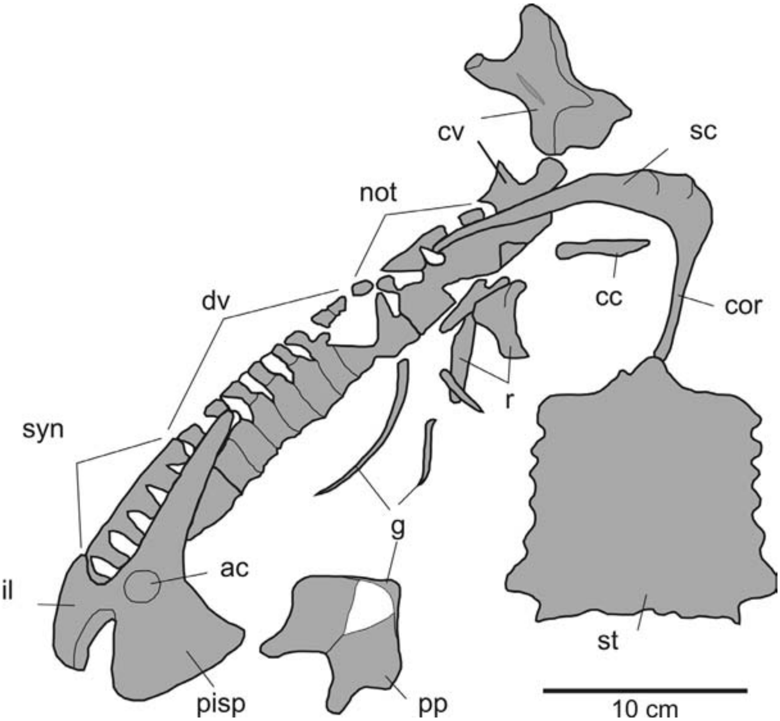

Fig. 17.18. Pterosaurs from the Nova Olinda Member: Neoazhdarchia gen. et sp. indet., articulated, partial post cranial skeleton MN 6588-V referred to Tapejaridae by Sayão and Kellner (2007), but the presence of a notarium is more suggestive of Neoazhdarchia. Redrawn from Sayão and Kellner (2007); ac acetabulum, cc cervical rib, cor coracoid, cv cervical vertebrae, dv dorsal vertebrae, g gastralia, il ilium, pisp ischio pubis, pp pre-pubes, r ribs, sc scapula, st sternum, syn synsacrum. Scale bar = 10 cm.

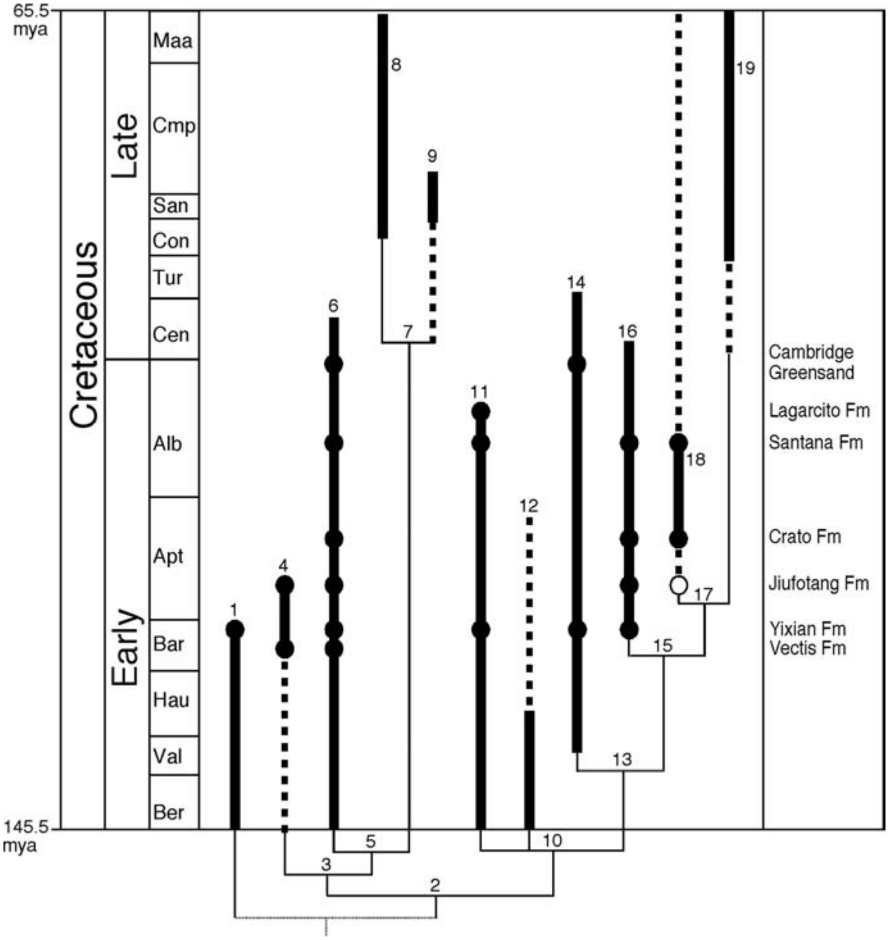

Fig. 17.19. Pterosaur evolution in the Cretaceous. Relationships of main clades based on Unwin (2003, 2005). Clades: 1, Anurognathidae; 2, Pterodactyloidea; 3, Ornithocheiroidea; 4, Istiodactylidae; 5, Euornithocheira; 6, Ornithocheiridae; 7, Pteranodontia; 8, Nyctosauridae; 9, Pteranodontidae; 10, Lophocratia; 11, Ctenochasmatoidea; 12, Dsungaripteroidea; 13, unnamed clade; 14, Lonchodectidae; 15, Azhdarchoidea; 16, Tapejaridae; 17, Neoazhdarchia; 18, 'tupuxuarids'; 19, Azhdarchidae. Timescale based on Gradstein *et al.*, 2005. Large solid circle, confirmed record of this clade from the relevant stratigraphic unit to the right; open circle, unconfirmed record of this clade from the stratigraphic unit to the right; thick solid line, known temporal range of a particular clade; thin solid line, clade inferred to exist on the basis of phylogenetic interrelationships; thick dashed line, range extension of clade on the basis of an unconfirmed record, or uncertain dating of last occurrence. Alb, Albian; Apt, Aptian; Bar, Barremian; Ber, Berriasian; Cen, Cenomanian; Cmp, Campanian; Con, Coniacian; Hau, Hauterivian, Maa, Maastrichtian; San, Santonian; Tur, Turonian; Val, Valanginian.

SMNK PAL 2342, MN 6527-V, MPSC R-771 and MPSC R-868), known only from post-cranial remains, are assignable to the Tapejaridae and in most, if not all cases, probably represent species of *Ingridia*.

Three individuals (MN 4729-V, SMNK PAL 3855; Figure 17.15), two of which are represented by incomplete post-cranial remains, are identified as 'tupuxuarids' and possibly represent a genus distinct from known forms. A putative neoazhdarchian (MN 6588V) may also belong to this taxon.

A further nine individuals, not yet described or figured and not examined in this study, are known, but their taxonomic status has yet to be established. That notwithstanding, it seems likely that among these remains there is material representing at least one new taxon, distinct from any of those mentioned previously.

Apart from ornithocheirids, tapejarids and 'tupuxuarids', several additional pterodactyloid lineages are known, or can be inferred, to have existed (Figure 17.19) in the Aptian. These include istiodactylids, pteranodontians, ctenochasmatids, lonchodectids, azhdarchids and possibly dsungaripterids (if they survived that late into the Cretaceous). So far, no remains belonging to these lineages have been found in the Crato pterosaur assemblage. Moreover, their cranial characters and, in many cases, proportions of their post-cranial skeleton, are highly distinctive, so it is rather unlikely that any of the fossils studied so far might eventually prove to belong to one of these taxa. Consequently their absence so far from the Crato Formation can be accepted with confidence.

Ecology of the Crato pterosaurs

Several contrasting factors need to be considered to gain insights into the ecology of the Crato pterosaur assemblage. The most important of these include the absolute size, ontogenetic status, likely diet and possible flight styles of the pterosaurs themselves. Other aspects, such as associated fauna and flora and the likely geography, must also be factored into this analysis.

Predominantly, Crato ornithocheirids are represented by large, subadult or adult individuals of 4–5 m in wingspan. Smaller individuals such as MPSC R-779 and MPSC R-739, with estimated wingspans of 2.4 and 3.3 m respectively, show evidence of osteological immaturity and are probably juveniles. It is widely thought that ornithocheirids caught their prey during flight, using the well-developed 'tooth grab' at the anterior end of the dentition to snatch up fish from the water surface (Wellnhofer, 1987, 1991a; Unwin, 2005: Figure 17.20d). Skeletal remains from the Crato limestone and elsewhere show that in terms of their flight apparatus, these pterosaurs were 'top-deckers'; that is, the shoulder joint was located at a relatively high level with regard to the centre of mass (Frey *et al.*, 2003d). This is likely to have conferred aerodynamic stability, perhaps at the expense of manoeuverability,

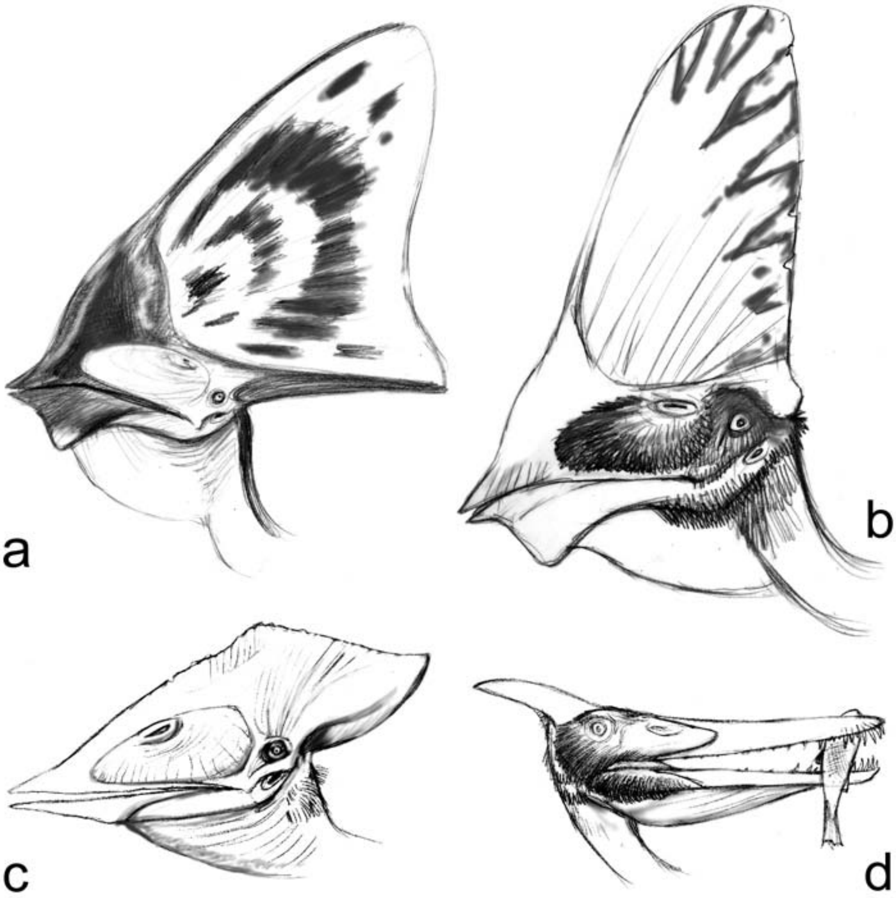

Fig. 17.20. Life restorations of Crato Formation pterosaurs by Luis Rey: (a) *Tapejara imperator*; (b) *Tapejara navigans*; (c) a pterosaur close to *Tupuxuara*; (d) *Ludodactylus*.

but may have aided long-distance soaring. This type of flight style is consistent with the relatively long, pointed wings of ornithocheirids which, even assuming that the main wing membrane attached to the hindlimbs, must have had a relatively high aspect ratio (Wilkinson, 2002; Chatterjee and Templin, 2004). The hindlimbs, by contrast, are relatively small and slender and it seems likely that ornithocheirids had relatively poor terrestrial ability.

Tapejarids make up more than one-third of all identifiable pterosaur remains in the Crato Formation (Figures 17.20a and b). Most individuals appear to have been in the region of 3 m in wingspan and show osteological evidence of maturity. A couple of specimens, SMNK PAL 2342 and MPSC R-868, are somewhat smaller, with estimated wingspans of 2.2 and 1.6 m respectively. The ontogenetic status of these individuals has yet to be precisely established, but surface features of the bones (see Bennett, 1993) suggest that they were in the later stages of the rapid growth phase.

The diet of tapejarids is uncertain. It has been argued that they were frugivores since the morphology of the jaws shows some similarity to that of extant parrots (Wellnhofer and Kellner, 1991). Moreover, the relatively long and robust hindlimbs suggest a more competent terrestrial ability than, for example, ornithocheirids, while the well-developed claws on the manus and pes hint at an effective climbing capability which, doubtless, would have been advantageous for a frugivore. Alternatively, tapejarids might have been piscivorous, feeding on smaller prey such as *Dastilbe*, which is found in great abundance in the Crato limestones (see Chapter 12).

With a wing/leg ratio of less than 3.0 (compared to 5.2 for *Arthurdactylus*) the Crato tapejarids had relatively short, broad wings and a much lower aspect ratio than the ornithocheirids. Moreover, the proportions of the shoulder girdle indicates that they were probably ‘middle-deckers’, and perhaps more manoeuverable than ornithocheirids. Thus, although the exact aerodynamic characters have yet to be established it seems likely that the tapejarid flight style was different from that of the ornithocheirids.

‘Tupuxuarids’ are represented by three, or possibly four, individuals that, although only 2–2.5 m in wingspan, and thus markedly smaller than ‘tupuxuarids’ from the Santana Formation, appear to have been osteologically mature (Figure 17.19c). The feeding ecology of ‘tupuxuarids’ is uncertain, not least because details of the mandibular symphysis of ‘*Tupuxuara*’ and *Thalassodromeus* appear to differ (Kellner and Campos, 2002), perhaps hinting at different feeding styles. It has been suggested by Kellner and Campos (2002) that *Thalassodromeus* may have fed in a skimmer-like fashion, using the supposedly blade-like mandibular symphysis to cut through the water, although this idea has been challenged (Williams, 2002) and is probably erroneous. Another possibility is that with their relatively long and robust hindlimbs (a typical feature of azhdarchoids) ‘tupuxuarids’ may have had a relatively effective terrestrial capability, and might have fed in a manner similar to that of storks. Only more complete fossils and detailed functional analyses will resolve these issues.

The Crato pterosaur assemblage is distinct in two other ways: there are few juveniles and perinatal individuals, such as found, for example, in the Loma del *Pterodaustro* (Codorniú and Chiappe, 2002; Chiappe *et al.*, 2004) and Solnhofen limestone assemblages (Bennett, 1995, 1996; Unwin, 1995b), and there are no small pterosaurs of less than 1.5 m in wingspan. This is in sharp contrast to Jurassic assemblages where the vast majority of individuals have wingspans of no more than 1–1.5 m (Wellnhofer, 1991a; Unwin, 2005). It is possible that a preservational filter was operating that excluded the preservation of small individuals (i.e. small adults, or the young of larger species), even though they were present in this region of South America in the Aptian. This seems unlikely, however, because many small animals including invertebrates, fish, turtles and small crocodilians are preserved in the same rocks (see Chapters 8–16). The most plausible explanation is that: (a) small species of pterosaur were rare in the Lower Cretaceous, which is borne out by the almost complete absence of such finds in other localities, and (b) perinatal and juvenile individuals were rarely present in the region of the Crato lagoons.

A tentative conclusion that can be drawn from these several ecological aspects is that the tapejarids and 'tupuxuarids' may have been indigenous or at least partially indigenous to the Crato lagoon area. Tapejarids may have been specialist feeders on the shoals of *Dastilbe* that appear to have been common in the lagoon. The 'tupuxuarid' may also have fed upon *Dastilbe* perhaps by wading in the shallower margins of the lagoon. The ornithocheirid(s) by contrast, with their well-developed soaring ability, almost certainly had a much greater feeding range, and were not necessarily indigenous to this area. They may have preyed on large individuals of *Dastilbe* (which reached 300 mm in length) or other sizeable fish in the Crato lagoon. Alternatively, they might represent individuals, as for example in the case of *Ludodactylus*, that ended up in the lagoon by accident.

Evolutionary significance of the Crato pterosaurs

Comparisons with other mid-Lower- to mid-Upper Cretaceous fossil localities that have produced pterosaurs (Figure 17.19) reveal that in terms of its taxonomic composition the Crato Formation assemblage shows greatest similarity to the somewhat younger pterosaur assemblage from the Santana Formation of Brazil. In general terms, the Crato and Santana pterosaur assemblages are strikingly similar. Both contain ornithocheirids, tapejarids and 'tupuxuarids' and, even though it cannot yet be demonstrated with any statistical rigor, even the relative abundances of these taxa appear similar: ornithocheirids and tapejarids are common, while 'tupuxuarids' seem to be rare.

The principal taxonomic differences concern the presence of a ctenochasmatid (*Cearadactylus*) in the Santana Formation (although this taxon is known from only one, possibly two individuals; Unwin, 2002), and the greater taxonomic diversity of the pterosaurs from the latter, which include several ornithocheirid genera, two 'tupuxuarids' and two species of *Tapejara*. These differences may, in part, be attributable to the much larger sample from the Santana Formation which, according to Sãyao and Kellner (1999), has yielded more than 350 individuals.

A different view has been advanced by Campos and Kellner (1997) and Martill and Frey (1999), who have argued that the Crato and Santana pterosaur assemblages are distinct from one another. Indeed, close comparison of taxa at the generic and specific levels reveals dissimilarities. The Crato ornithocheirid is remarkably similar in size and, so far as comparisons can be made, morphology, to the holotype of *Brasileodactylus* from the Santana Formation, but while these two may well be congeneric, minor variations in dental details and the shape of the rostrum and mandible suggests that they are probably not conspecific. Moreover, *Ingridia*, with its longer, lower skull, is clearly distinct from and apparently less derived than *Tapejara*, while the Crato 'tupuxuarid' seems to be smaller and quite distinct from either '*Tupuxuara*' or *Thalassodromeus*. These differences are not surprising. The Crato Formation is some 10 myr older than the Santana Formation; consequently the less-derived nature of *Ingridia* and smaller size of the Crato 'tupuxuarid' are both predictable and consistent with the age of the assemblages.

The Crato pterosaur assemblage is also similar, in a general way, to that from the almost coeval Jiufotang Formation of China (Wang *et al.*, 2005). The latter has yielded several tapejarids including *Sinopterus* and *Huaxiapterus*, a large ornithocheirid (*Liaoningopterus*) and what may be a 'tupuxuarid' (*Chaoyangopterus*). However, the Jiufotang assemblage also includes an istiodactylid (*Liaoxipterus*/*Nurhachius*) and several basal azhdarchoids (*Jidapterus*, *Eoazhdarcho* and *Eopteranodon*) of uncertain status (Lü and Ji, 2006; Unwin, 2006). Irrespective of the exact number and identity of taxa in the Jiufotang Formation, it is clear that this assemblage is more diverse than the Crato assemblage and, again, close taxonomic comparison shows that they share no species or even genera in common.

Other Lower Cretaceous pterosaur assemblages have a different taxonomic composition. Remaining in South America, the Lagarcito Formation of Argentina, now dated as Albian, has yielded hundreds of individuals of the ctenochasmatid *Pterodaustro*, but no other pterosaurs (Chiappe *et al.*, 1998, 2000). This assemblage is completely different from that found in the Crato or Santana formations and demonstrates that there was ecological heterogeneity in pterosaur communities. Elsewhere, in Europe, for example, Barremian–Aptian pterosaurs from the Isle of Wight include an istiodactylid, *Istiodactylus* (Howse *et al.*, 2001), and an ornithocheirid, *Caulkicephalus* (Steel *et al.*, 2005), an assemblage that shows clear affinities with that from the Jiufotang Formation. By contrast, the late Albian pterosaur assemblage from the Cambridge Greensand of eastern England is dominated by ornithocheirids, including *Ornithocheirus* and *Coloborhynchus* (Unwin, 2001). The only other taxon certainly recorded from this deposit is *Lonchodectes*, which is so far unknown from South America.

The picture that emerges if we try to combine these observations with other records of Lower Cretaceous pterosaurs suggests a rather complex evolutionary history for the group during this interval (Figure 17.19). The main determinant for the patterns of distribution evident at present would appear to be ecological. That is, the kinds of pterosaurs found in a particular assemblage was primarily determined by the local ecology, as it is today for avian communities. Thus, the presence of shallow lakes with opportunities for filter feeding attracted flocks of *Pterodaustro* to their shores. By contrast, the diverse and complex terrestrial communities of north-east China provided many different opportunities for pterosaurs, which is reflected in the unparalleled systematic diversity found in the Jiufotang and Yixian formations (Wang *et al.*, 2005; Unwin, 2006). By contrast, marginal marine localities with dense populations of fish, such as the Crato lagoon, were frequented by tapejarids and the undoubtedly piscivorous ornithocheirids.

In most cases, well-developed flight ability and the distribution of the land masses probably provided little or no hindrance to the widespread dispersal of most pterosaur lineages. This is emphasized by the broad distribution of many Lower Cretaceous groups such as ctenochasmatids, ornithocheirids and tapejarids. On the other hand, some clades such as the Istiodactylidae and Lonchodectidae seem to be restricted to Laurasia, perhaps hinting at some regionalization. It should be emphasized, however, that the sample sizes upon which these ideas are based are highly variable and in many cases the numbers reported, so far, are still modest. Still, some general patterns are beginning to emerge, but further finds, and detailed assessments of the systematics of the Crato and other pterosaur assemblages, are needed to test their validity.

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18

Birds of the Crato Formation

Darren Naish, David M. Martill and Ian Merrick

Introduction

Remains of possible birds are extremely rare in the Crato Formation and have so far only been reported from the Nova Olinda Member. The first report was of an isolated probable remex (Figure 18.1a) described by Martins-Neto and Kellner (1988), and subsequently refigured by Kellner *et al.* (1991) and Kellner (2002). Martill and Filgueira (1994) later described a semiplume, while Kellner *et al.* (1994) reported the occurrence of an isolated down feather. Several other feathers have since been reported from the Crato Formation (Kellner, 2002). Avian skeletal remains, although known from anecdotal accounts and personal observations, have yet to be reported in the literature and two examples are figured here for the first time (Plate 25d, Plate 26).

Isolated feathers occur in both the weathered, buff-coloured laminated limestone as goethite pseudomorphs, and as carbonaceous replicas in the unweathered limestones. Specimens preserved as carbonaceous replicas may be represented by bacterial autolithifications (Martill and Frey, 1995), and in this respect the preservation mirrors that of the famous soft-tissue fossils of the Eocene Messel Formation of Germany (Wuttke, 1983). As in the case of the Crato Formation insects, fine details may be preserved in the feathers, despite the bacterial autolithification. In some cases colour patterns appear to have been preserved; in most instances as dark and light transverse bands (Plate 25).

Although it has been possible to categorize these isolated feathers by comparison with modern feather morphotypes, it has not been possible to assign them to any particular taxon. Indeed, it cannot be determined if they are from birds, or from any of the non-avian theropod clades now known to possess true feathers, such as Oviraptorosauria, Troodontidae or Dromaeosauridae. Furthermore, it is quite possible that Crato Formation feathers are derived from several different and disparate taxa, so while some may be true avian feathers, others might be of non-avian identity. Skeletal remains do not assist in resolving this, as Crato Formation theropod remains are all but unknown. Theropods are known from the slightly younger Santana Formation: they include the possible tyrannosauroid *Santanaraptor* (Kellner, 1999), the compsognathid *Mirischia* (Naish *et al.*, 2004), the spinosaurid *Irritator* and an indeterminate specimen described as a possible oviraptorosaur by Frey and Martill (1995). On the basis of analogy with related taxa from elsewhere in the world (Chen *et al.*, 1998; Xu *et al.*, 2004), *Santanaraptor* and *Mirischia* would most likely have possessed simple quill-like integumentary structures rather than true feathers. If the 'possible oviraptorosaur' really is a member of Oviraptorosauria (which is doubtful), it would presumably have possessed true feathers, including remiges and rectrices, such as those known from the Chinese oviraptorosaur *Caudipteryx* (Ji *et al.*, 1998; Zhou *et al.* 2000).

All of the feathers recovered from the Nova Olinda Member so far are relatively small, with sizes ranging from as little as 10 mm to a maximum of 85 mm measured from the base of the calamus to the distal tip of the rachis.

Feathers

Asymmetrical remex

An isolated asymmetrical feather typical of modern avian primary remiges was described by Martins-Neto and Kellner (1988). The specimen, in the Institute of Geosciences, São Paulo University, Brazil, number GP/2T-136, is 64 mm long and 8 mm wide at its widest point (Figure 18.1a). A similar feather, associated with two or three smaller feathers and with some indeterminate bones, is described below.

Elongate symmetrical feathers

A number of feather morphs are symmetrical, or nearly so, including rectrices, semiplumes and some contour feathers. A single isolated feather with a symmetrical vane was described by Martill and Davis (2001). Superficially resembling the rectrices of archaeopterygids (de Beer, 1954; Christiansen and Bonde, 2004), it has a maximum length of 85 mm (of which 66 mm is the vane) and is the longest feather known from the Crato Formation. For much of the vane's length the width is around 11 mm. Slight asymmetry is present, but this is possibly an artefact caused by damage to the vane margins.

Of particular note is the occurrence on this feather of possible parasite eggs (Martill and Davis, 1998, 2001). Several tens of small (68–75 µm) spherical or sub-spherical bodies are attached to the feather's barbs (Figures 18.1b and c).

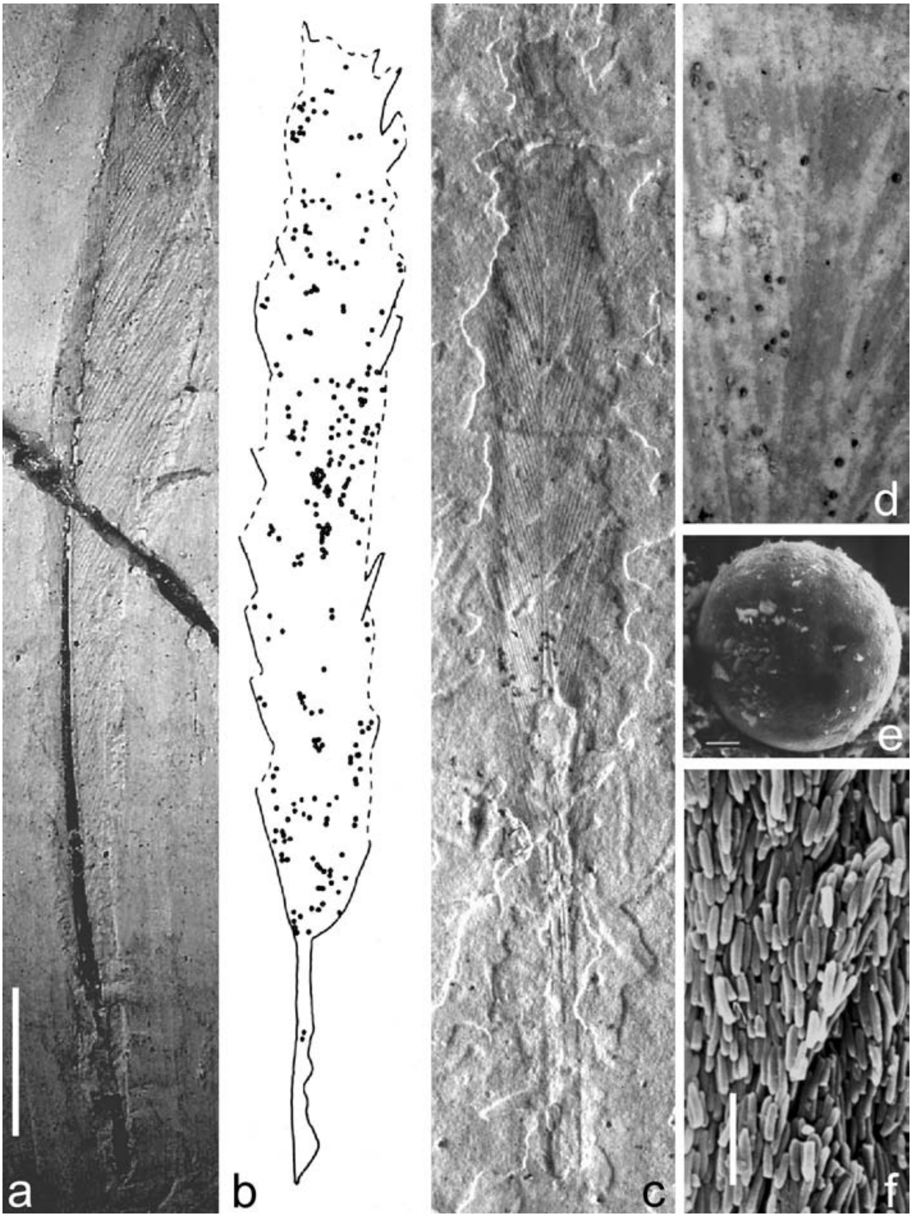

Fig. 18.1. Feathers from the Nova Olinda Member: (a) isolated asymmetrical flight feather, scale bar, 10 mm (photograph courtesy of R. G. Martins-Neto); (b, c) isolated symmetrical feather with adherent eggs of possible parasite; (d) portion of feather at higher magnification showing random scatter of eggs; (e) single egg; scale bar, 100 µm; (f) scanning electron micrograph of a down feather showing autolithified bacteria; scale bar, 2µm. The original feather was 85 mm long.

Several of the eggs possess a sub-circular aperture, perhaps showing that they had hatched. On the basis of size and general morphology, the eggs were attributed to parasitic Acari, but derivation from some other parasite could not be ruled out (Martill and Davis, 1998). Proctor (2003) suggested that the eggs might be those of ostracods, as some members of this group are known to lay their eggs on detritus. While ostracods are not recorded from the Nova Olinda Member, they are abundant in strata immediately beneath (see Chapter 10).

Semiplumes

Semiplumes have been reported from the Crato Formation by Martill and Filgueira (1994) and by Kellner *et al.* (1994). Such feathers occur frequently in the Crato Formation: we examined some 20 or more specimens during the course of this study (Plate 25), compared to only one possible remex and two or three symmetrical rectrices. Most are small with lengths of between 10 and 20 mm, but some larger examples occur, with one measuring 22 mm.

Osteological remains

At least two cases where skeletal remains are associated with feathers from the Nova Olinda Member have come to our attention, neither of which have been formally described, and we here present only preliminary descriptions. Plate 25d shows an unaccessioned specimen in the Senckenberg Museum, Frankfurt, in which three asymmetrical feathers are preserved in association with several presumed carpal bones. The longest feather measures 81 mm, while the smallest is 14 mm in length.

A second specimen, held in private collection MURJ in Japan, consists of a partial skeleton with associated feathers (Plate 26). It is a poorly preserved, somewhat crushed, partially articulated specimen with many bones represented only by external moulds. An incomplete skull is preserved in palatal view, and while a braincase, mid-line palatal elements and possible rod-like jugal bar of 18 mm in length are discernible, it is not possible to identify or distinguish individual bones from the photographs. There are approximately 25 vertebrae preserved, including cervical, dorsal and caudal vertebrae. Several of the cervical vertebrae are preserved in ventral view. They possess elongate centra that have gently concave lateral margins and thin cervical ribs that appear to extend for the length of the entire centrum. It is not possible to be confident about the number of dorsal vertebrae.

The neural spines of the specimen's dorsal vertebrae are distinctive, being longer at their apices than they are at mid-height. In this respect they differ from the neural spines of basal enantiornithines and many other basal birds but strongly resemble those of euenantiornithines such as *Sinornis santensis*. The centra of the dorsal vertebrae appear to bear lateral excavations that, on some of the centra, extend for most of the centrum's length. While lateral fossae on dorsal centra are widespread in basal birds (they are present in archaeopterygids, confuciusornithids, enantiornithines and *Ichthyornis*), the shape and extent of the fossae in the Crato Formation bird invites comparison with euenantiornithines, as antero-posteriorly elongate fossae of this form are seen in members of this group (Chiappe and Walker, 2002). Some of the dorsal vertebrae appear to possess a lateral projection mid way along their length, presumably the parapophysis. If this interpretation is correct then this feature confirms a euenantiornithine identity for the specimen as only members of this group possess parapophyses in this unusual position (Chiappe and Walker, 2002).

At least three complete caudal vertebrae are preserved, two of which are articulated, and fragments of other caudal vertebrae are also present. Incomplete transverse processes are present and the most proximal vertebra appears to possess two sub-rounded concavities on its lateral surface. These may be autapomorphies of this taxon. If a pygostyle was present (as it presumably was) it is not preserved. A chevron is present ventral to the two articulated vertebrae. It appears proportionally large and laterally compressed, and therefore similar to the chevrons known for the basal enantiornithine *Iberomesornis romerali* (Sanz *et al.*, 2002).

A partial ilium and a possible ischium have been tentatively identified. The best-preserved part of the specimen, however, is the ?left hindlimb which comprises the femur (≈40 mm), tibiotarsus (≈39 mm), tarsometatarsus (≈31 mm) and hallux (11 mm). The hallux appears proportionally large and fully reversed and its ungual still retains its claw sheath.

The total length of the specimen from the rostral-most preserved tip of the skull to the last preserved caudal vertebra is 156 mm: about the size of the chaffinch *Fringilla coelebs*. The specimen therefore falls within the size range of Lower Cretaceous enantiornithines including *Iberomesornis*, *Eoalulavis* and *Sinornis*.

Impressions of feathers are preserved alongside the tarsometatarsus and adjacent to the femur. The presence of tarsometatarsal feathering has been reported for a number of basal birds (Christiansen and Bonde, 2004; Zhang and Zhou, 2004) and non-avian maniraptorans (Norell *et al.*, 2002; Xu *et al.*, 2003; Xu and Zhang, 2005) and is likely to be a plesiomorphic character for maniraptoran theropods (Christiansen and Bonde, 2004).

If this specimen does represent a basal bird, it is the oldest Gondwanan avian fossil known from skeletal remains.

Comparisons with other deposits

Although several Mesozoic deposits are known to have yielded fossil feathers in association with skeletal remains, such occurrences are extremely rare, and the Crato Formation represents the only such occurrence in South America where feathers occur frequently. Furthermore, the Crato Formation represents one of only a handful of Mesozoic bird-bearing localities in Gondwana (Chiappe, 1995, 1996; Dalla Vechia and Chiappe, 2002).

Elsewhere in Gondwana, isolated feathers have been recorded from the Lower Cretaceous Korumburra Group of Koonwara, Australia (Waldman, 1970), but no skeletal material has been reported. Postcranial skeletal remains of a taxon initially described as a basal bird, *Rahonavis*, have been reported from the Upper Cretaceous of Madagascar (Forster *et al.*, 1998), and while this specimen preserves keratinous claw sheaths, its feathers were not preserved. While *Rahonavis* was clearly a bird-like maniraptoran, it may not belong to Aves. A recent study concluded that it and several other Gondwanan maniraptorans form a dromaeosaurid clade termed Unenlagiinae (Makovicky *et al.*, 2005). However, the Upper Cretaceous of Madagascar has also yielded the basal ornithuromorphan *Vorona berivotrensis* as well as at least three additional avian taxa, none of which have yet been described (Forster *et al.*, 2002).

Gondwanan birds have also been reported from the Cretaceous of Africa: an isolated avian vertebra was reported from the Cenomanian of Morocco (Riff *et al.*, 2004). South America has a diverse Cretaceous avifauna, with several enantiornithines (Chiappe and Walker, 2002), the flightless basal ornithuromorphan *Patagopteryx deferrariisi* (Chiappe, 2002), and neornithines such as the gaviiform *Neogaeornis* (Olson, 1992) and a possible charadriiform (Hope, 2002). Enantiornithines, a diverse basal bird clade now known to have had a virtually global distribution in the Cretaceous, were first described from the Maastrichtian Lecho Formation of Argentina (Walker, 1981) and the first good, associated specimens were also Argentinian (Chiappe, 1991, 1996). Finally, Antarctica has also yielded Cretaceous birds: Case and Tambussi (1999) reported a probable charadriiform tarsometatarsus, Chatterjee (2002) reported the gaviiform *Polarornis* (though see Mayr, 2004) and Clarke *et al.* (2005) described the anseriform *Vegavis*.

Conclusions

Although bird remains are generally rare in Mesozoic deposits, isolated feathers occur regularly in the Nova Olinda Member of the Crato Formation, making it one of the richest Mesozoic feather localities, excluding the Yixian Formation of China where complete birds with feathers occur commonly. The occurrence of colour-pattern preservation, rare associations with possible parasites and a variety of feather morphs add further importance to the locality. The presence of what are apparently small, volant birds in the Crato Formation provides evidence of the earliest avian remains in South America. These birds may have been responsible for predation marks present on some Nova Olinda Member insects.

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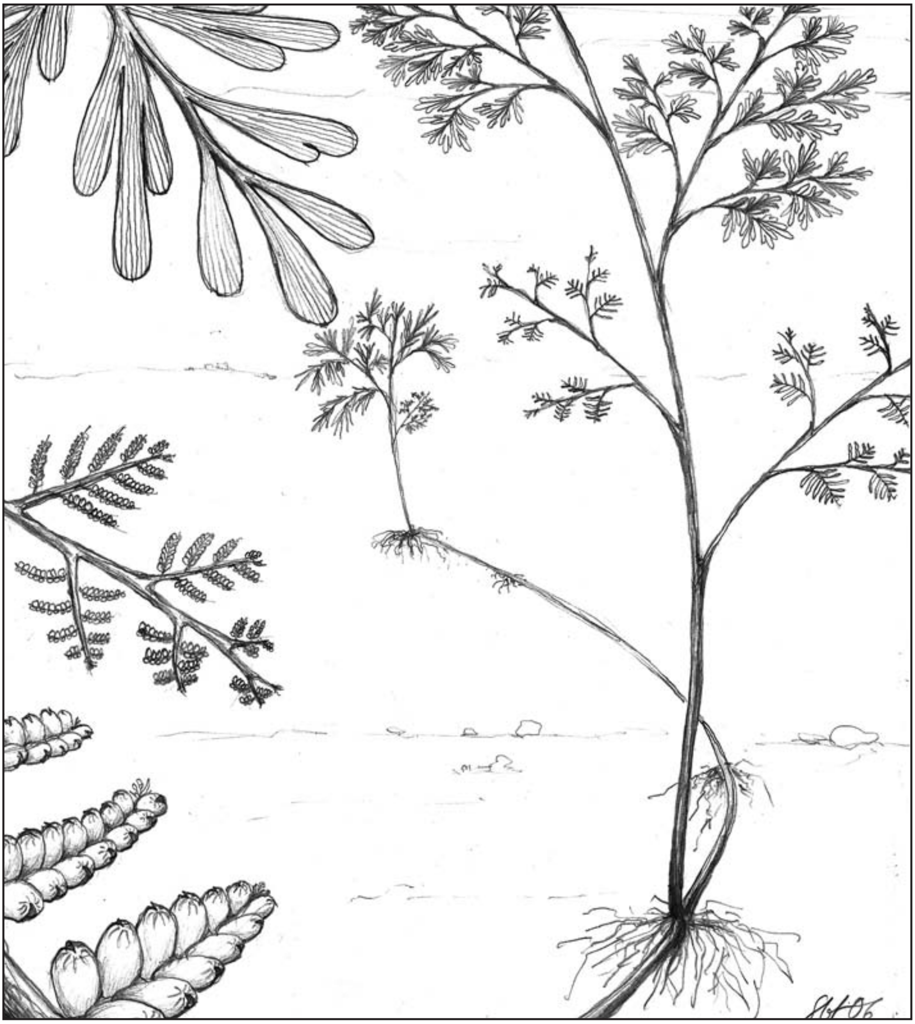
Part IV

The flora



19

The macrophyte flora of the Crato Formation

Barbara A. R. Mohr, Mary E. C. Bernardes-de-Oliveira
and Robert F. Loveridge

Introduction

Plant fossils from the Crato Formation are not only remarkable because of their beauty, but equally because of their scientific value, being on the cusp of the gymnosperm decline and the angiosperm radiation. Many of these fossils are preserved more or less entire, often with roots, stems, leaves, sporangia and flowering structures attached; there is also palaeosoil present in some specimens (Figure 19.1). The more or less complete fossils are not only attractive, but are of immense importance to the palaeobotanist, who often has to deal with dispersed organs, of which the natural connection remains unknown, until a more complete specimen is found.

The original organic material of the Crato plant fossils is generally covered or replaced by goethite, a hydrated iron oxide, which causes the rusty, conspicuous colouring of the weathered fossils. Often, they are very weathered, poorly preserved and can only be seen as reddish brown impressions on the light yellowish slabs. In rare cases, mainly in specimens coming from layers at the base of the section, black organic material with cellular structures can be preserved. Then, fine details, even of reproductive organs – the most indicative parts concerning the taxonomic evaluation of a plant – may be observed three-dimensionally with scanning electron microscopy (SEM).

The palaeoflora is known to be relatively diverse, but has not been fully described. It is now being investigated by an international team of researchers from various Brazilian and European institutions (FAPESP/Fundaçao de Amparo à Pesquisa do Estado de São Paulo). The flora includes several spore-bearing plants, but is dominated by seed plants including gymnosperms (such as conifers, cycadophytes and gnetophytes) and angiosperms, the flowering plants. Early studies (Lima, 1978, 1979, 1980, 1989; Pons *et al.*, 1996; Arai *et al.*, 2001) on dispersed pollen and spores

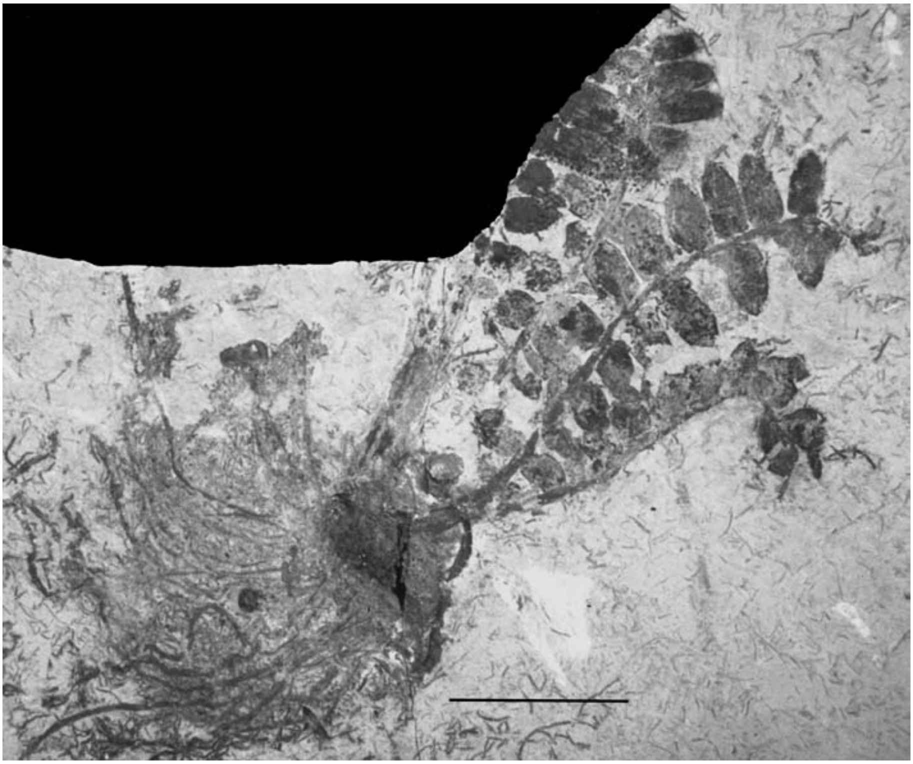


Fig. 19.1. Complete plant with roots, stems and leaves, notable for the inclusion of a sample of sandy palaeosoil in the root ball. Scale bar, 100 mm.

from the Crato and Santana Formations provided the first reasonably accurate age estimation of these strata, generally considered to be late Aptian or early Albian. They also indirectly provided indications of a species-rich flora, including all of the major plant groups of the Mesozoic. Macrofossil remains belonging to ferns, conifers and angiosperms were reported during the 1980s and 1990s (Duarte, 1985, 1993; Crane, 1991; Oliveira-Babinsky and Lima, 1991; Bernardes-de-Oliveira *et al.*, 1993; Martill, 1993; Barreto *et al.*, 2000). With the discovery of organically preserved specimens a second phase of palaeobotanical research began (Mohr and Friis, 2000; Kunzmann *et al.*, 2004; Mohr and Bernardes-de-Oliveira, 2004) that opened not only a window to the understanding of the vegetation in Early Cretaceous palaeoequatorial South America, but also increased our knowledge of the evolution of the most important plant group today, the angiosperms.

Species richness of the Crato flora is relatively high, with more than 80 taxa, excluding pollen- and spore-based genera. Besides a few putative algal remains, all major groups of tracheophytes, typical for the Early to mid Cretaceous, are present. Spore-bearing plants comprise approximately 10% of the diversity, while gymnosperms are dominant, at about 60%. Nearly 30% of the total diversity may be angiosperms, although their macrophyte remains seem to be rare.

Pteridophytes

Spore-bearing tracheophytes of the Crato Formation include horsetails (Equisetales), members of lycophytes, the quillworts (Isoetales) and ferns (Filicales). Remains of horsetails with their typical articulated stems are rare and fragmentary. They include possibly rhizomes and pieces of stems of the genus *Equisetites*, globally common during the Mesozoic. Although the Crato quillwort closely resembles extant *Isoetes*, for Mesozoic quillworts the genus name *Isoetites* is generally used. Crato *Isoetites* exhibits a short, unbranched corm about 3–4 cm long. Attached to the corm are dichotomously branching roots and a dozen or more elongated, flattened leafy sporophylls, reaching a length of 20 cm or more and a width of 0.5 cm (Figure 19.2a). Crato *Isoetites* morphologically resembles *Isoetites choffati* from the Early Cretaceous of Portugal (Teixeira, 1948).

Ferns are among the most common plant fossils of the Crato Formation (Figures 19.2b and c and 19.3a), but belong mostly to one taxon of the Schizaeaceae, *Ruffordia goeppertii*; the habit is reconstructed for this extinct fern (Figure 19.2d). A few more fern taxa, proven by either poorly preserved specimens (Figure 19.2b) or a single pinnule (Figure 19.2c), are recorded. The latter also most likely a member of the Schizaeaceae, resembling the extant *Anemia mexicana* (Figure 19.3b). This contrasts with the palynological record, where the presence of a variety of Schizaeaceae, with typical trilete, striate and reticulate spores (e.g. *Cicatricosisporites* and *Klukisporites*) and additional fern families, including Gleicheniaceae, have been demonstrated from the Crato and Santana Formations (Lima, 1978, 1979).

R. goeppertii, a rather small fern with creeping rhizomes and an upright habit, bears partially dimorphic, partially sterile, triangularly shaped fronds of up to 60 cm high. Distichous petioles are about 12–15 cm long. The rachis is imparipinnate, alternate, approximately ascending, gradually decreasing from the base to the apex. The pinnules are normally catadromic, highly dissected, ultimate segments subrhombic, with a simple dichotomizing venation pattern (Figure 19.3a). When fronds are fertile, the fertile segments usually sit at the base of the rachis, comprising up to six fertile pinnae. The sporangia sit on reduced segments with schizaeoid sporangia, containing trilete spores. *R. goeppertii*, known from many Mesozoic rocks by macro- and microfossils (*Cicatricosisporites* sp.; van Konijnenburg-van Cittert, 1991; Dettmann and Clifford, 1992), is close in appearance to extant *Anemia*, especially to *Anemia adiantifolia* (Figure 19.3c), the pine fern of the Americas (Tryon and Tryon, 1982), where it grows in dry, partially sandy soils. However, *R. goeppertii* differs from *A. adiantifolia* in that the fertile segments are more or

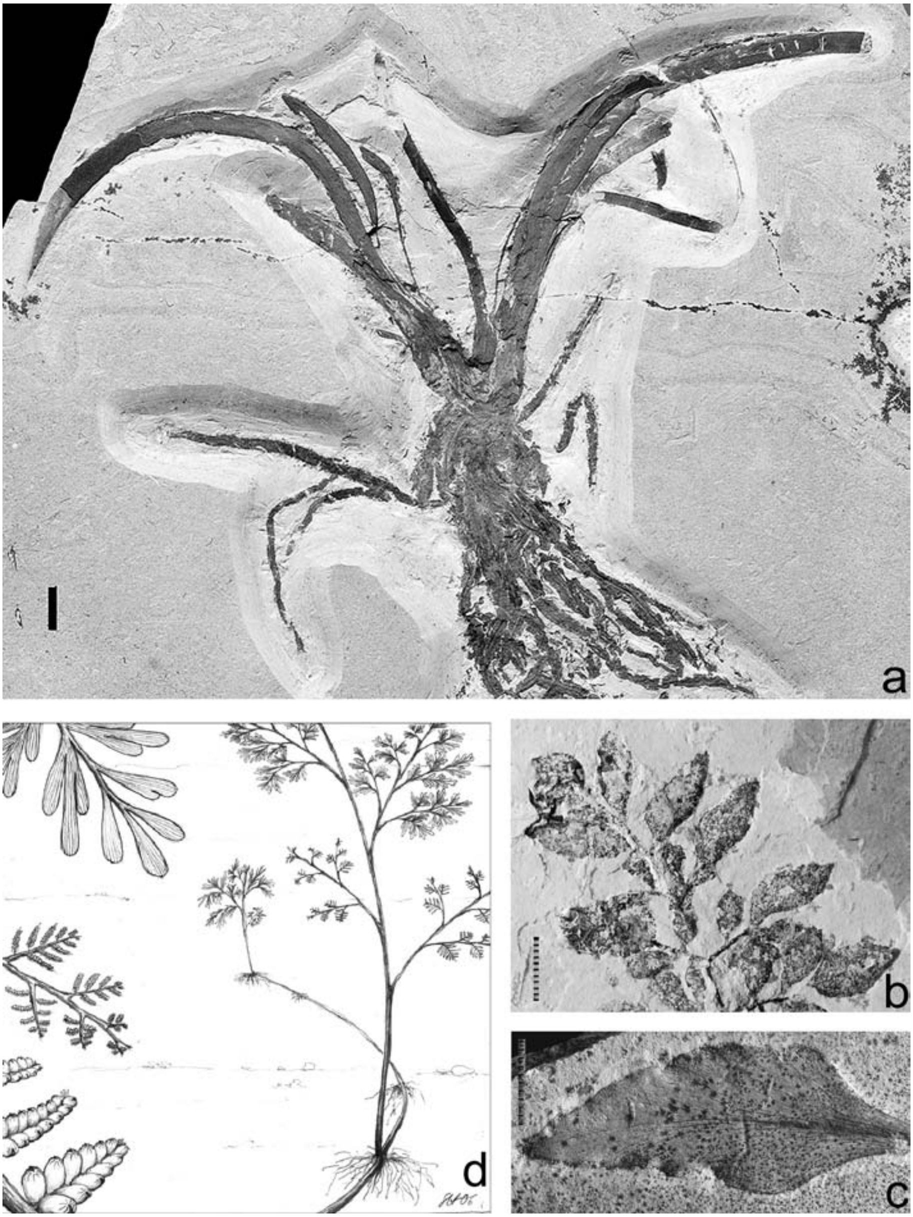


Fig. 19.2. Spore-bearing plants: (a) quillwort *Isoetites* sp. similar to the recent *Isoetes*, entire plant, MB 2002–854; (b) portion of fern frond; (c) single fern pinnule; (d) reconstruction of the extinct fern *Ruffordia*. Scale bars, 10 mm.

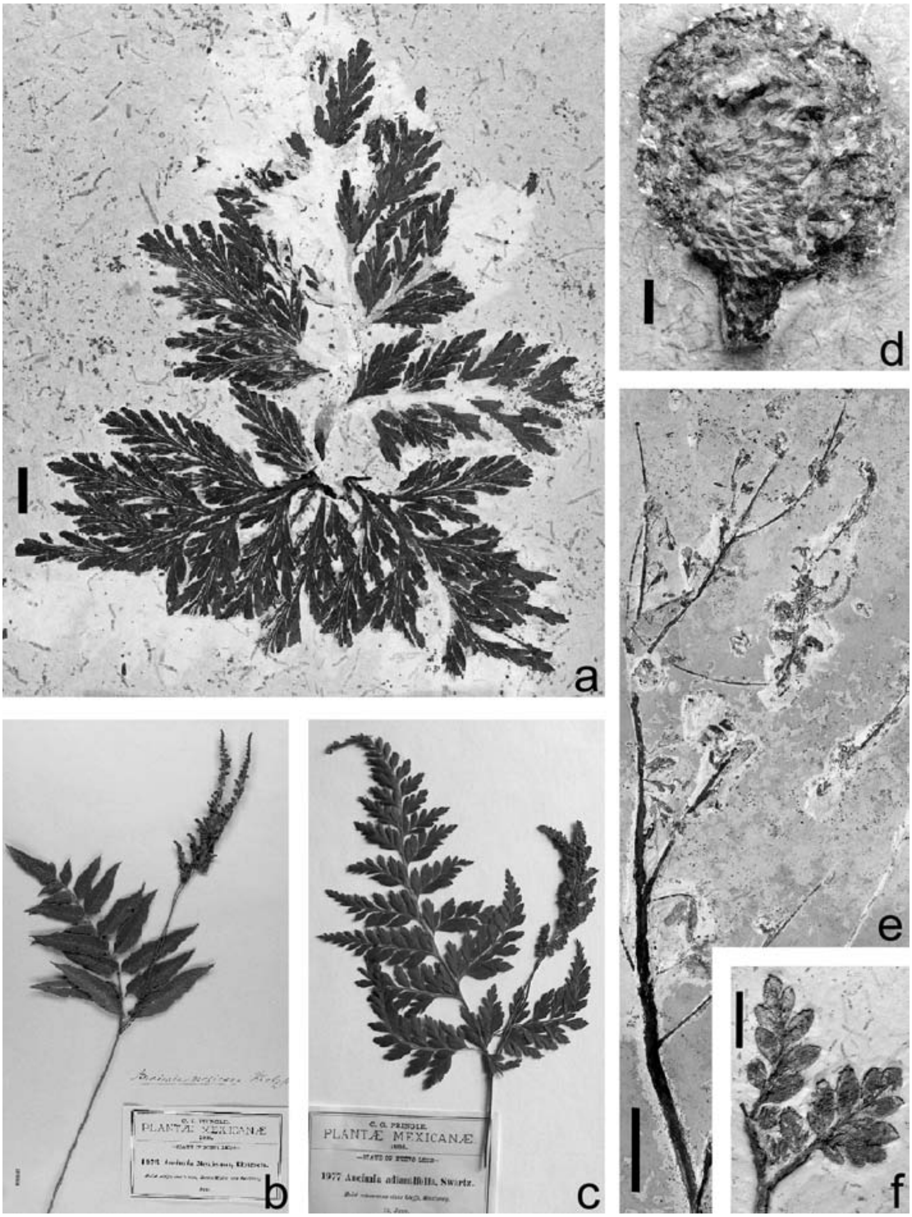


Fig. 19.3. Crato Formation fern, seed fern and bennettitalean; (a) fronds of the extinct schizaeacean fern *Ruffordia* sp., BM 2000–1456; (b) herbarium specimen of extant schizaeacean fern *Anemia mexicana*; (c) herbarium specimen of extant schizaeacean fern *Anemia adiantifolia*; (d) ovulate cone of bennettitalean? (e) large seed fern; (f) portion of frond from seed fern. All scale bars, 10 mm; except (e), 5 mm.

less as long as the sterile ones, whereas *Anemia* stipes of the fertile segments equal or exceed the sterile ones (Duek, 1980). This may be a character for this group of ferns that evolved after the Early Cretaceous.

Gymnospermae

During the early Mesozoic gymnosperms were the most dominant component of the flora. This changed with the rise of the angiosperms during the mid Cretaceous. Early to mid Cretaceous gymnosperms included seed ferns, cycadophytes, bennettitaleans (Figure 19.3d), gnetophytes, ginkgos and conifers. Ginkgophytes, though, seem to be absent in palaeoequatorial South America, possibly for ecological reasons. Remains of Bennettitales and/or Cycadales are rare. Bennettitalean ovulate cones of up to 8 cm in length and about 6 cm in diameter in the Crato Formation, may be referable to *Williamsonia*.

During the Cretaceous seed ferns were not as diverse, or as common, as they were in the late Palaeozoic, disappearing with the rise of angiosperms during the mid to Late Cretaceous. Several late Mesozoic South American seed ferns have been described from Argentina, including *Mesodescolea*, *Ticoa* (Archangelsky, 1963, 1966) and *Ruflorinia* (Villar de Seoane, 2000), and considered to belong to Caytoniales. However, none of these fronds are comparable with seed ferns from the Crato Formation, which has up to 70-cm-high axes that are bifurcate, or often more or less trifurcate (Figure 19.3e) and bear highly variable pinnule-like leaves with a reticulate venation pattern. This plant is very striking, with its up to 1-mm-long trichomes that cover axes as well as leaves (Figure 19.3f). Its female, ovule-bearing structures contain several multi-ovulate cupules, up to 0.8 mm wide. Each cupule with a lip-like projection near the point of attachment is nearly circular in outline and encloses several seeds of up to 3–4 mm long, characters typical for *Caytonia*. Thus, this Crato Formation seed fern is most likely a member of the Caytoniales.

Several conifer taxa occur in the Crato Formation, among which are members of families still growing in South America today, such as the Araucariaceae and the Podocarpaceae, the latter known only from the pollen record (de Lima, 1979). However, there are also members of extinct families including the Cheirolepidiaceae, and taxa of unknown affinity (Kunzmann *et al.*, 2004), such as *Lindleycladus*, most likely also a conifer of araucarian affinity, with relatively large lanceolate, parallel-nerved leaves (Figure 19.4a and b). *Lindleycladus* is known from the Northern Hemisphere in Europe, possibly China and perhaps Colombia (Van Waveren *et al.*, 2002).

Sterile araucariacean foliage, known as *Brachyphyllum obesum*, is among the most common plant remains in these strata (Figures 19.4c and d). Its leaves, partly preserved with cuticles and seed cones of *Araucaria* and isolated cone scales, most likely belonging to the same genus, have been described in detail by Kunzmann

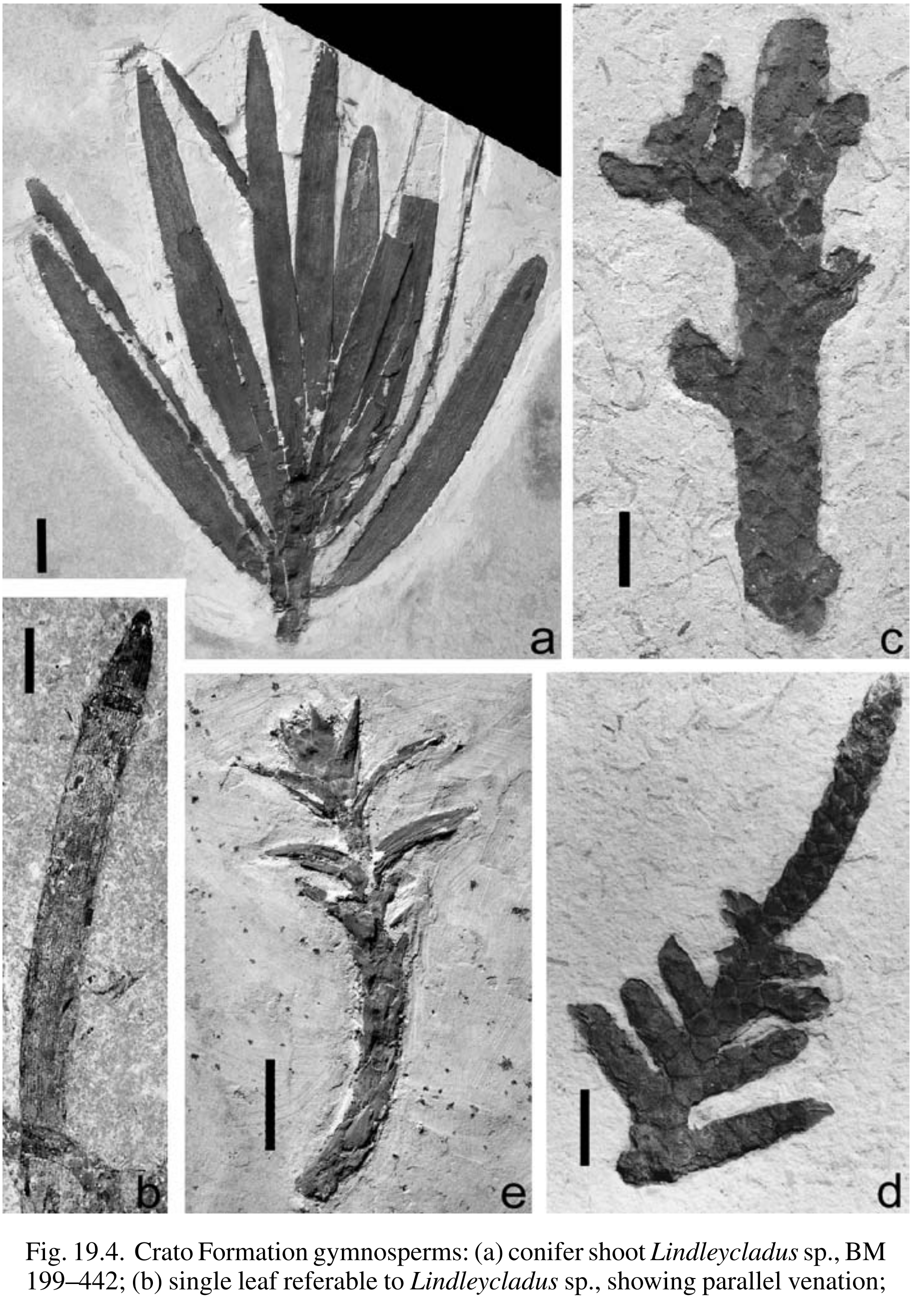


Fig. 19.4. Crato Formation gymnosperms: (a) conifer shoot *Lindleycladus* sp., BM 199–442; (b) single leaf referable to *Lindleycladus* sp., showing parallel venation; (c, d) shoots of the conifer *Brachyphyllum obesum*; (e) shoot of *Tomaxellia* sp., a rare cheirolepid dimorphic conifer, BM 1998–484. Scale bars, 10 mm.

et al. (2004). Amber, most likely produced by various Araucariaceae, had been recently analyzed by Martill *et al.* (2005).

Cheirolepidiaceae are present, but not common. Sterile foliage of frenelopsid conifers occurs in various stages of preservation, sometimes with several orders of branching, more often only the last-order twigs with their typical habit of nodes, cylindrical internodes and sheaths with one or two free leaf tips. Remains are rare of the cheirolepid *Tomaxellia*, a dimorphic conifer (Figure 19.4e) with characteristic cuticle and cone structures, previously known from the Cretaceous of Argentina (Archangelsky, 1968). Its leaves, which have the stomata scattered over the leaf surface, reach up to 1.8 cm in length in the Crato specimens (Kunzmann *et al.*, 2006). A conifer of unknown affinity, *Brachyphyllum castilhoi*, previously described only from the Santana Formation (Duarte, 1985), seems to be very rare, in contrast to *B. obesum*. Axes seem to have been rather thick, even last-order branches. Side branches are short and club-shaped. Sterile foliage is very characteristic in that these shoots bear many small leaves that are arranged helically (Figure 19.5a).

Members of Czekanowskiales, an isolated Mesozoic gymnosperm group (Harris and Miller, 1974), may be represented by twigs with clusters of needle-like leaves 10 cm long and 1.5 mm wide. A seed plant of unknown affinity, most likely belonging to the gymnosperms, has been described as *Novaolindia* (Kunzmann *et al.*, 2007). The most complete specimen, close to 20 cm long, with an approximately 0.5-cm-wide axis and several side branches, bears foliage as well as flattened globose capsules, characteristic for the genus (Figure 19.5b). The leaves of this specimen are simple or trifurcate, elongate, decurrent, decussate and up to 1 cm long. Several, more or less rounded to heart-shaped, capsules at the top of the axis, 2 mm in diameter, appear immature. Each capsule consists of two valves; the outer margin of the valve is relatively thick (Figure 19.5c).

Gnetophytes from the Crato Formation are very common and diverse. Three extant relic genera are recognized – *Gnetum* (Gnetaceae), *Ephedra* (Ephedraceae) and *Welwitschia* (Welwitschiaceae) – each with very distinct morphologies and differing ecological requirements. These comprise a monophyletic group, the gnetophytes, of which the latter two families are certainly represented in the Brazilian Early Cretaceous.

The relationship between gnetophytes and other seed-plant groups has been discussed extensively over the last 10 years and has proved highly controversial (for earlier discussions see Friedman, 1996). During the mid-to-late 1990s Gnetales were considered to represent a possible sister group of angiosperms, together with Bennettitales and Pentoxylales (Doyle, 1996, 1998), belonging to an 'Anthophyte clade'. Goremykin *et al.* (1996), Chaw *et al.* (2000) and Bowe *et al.* (2000)

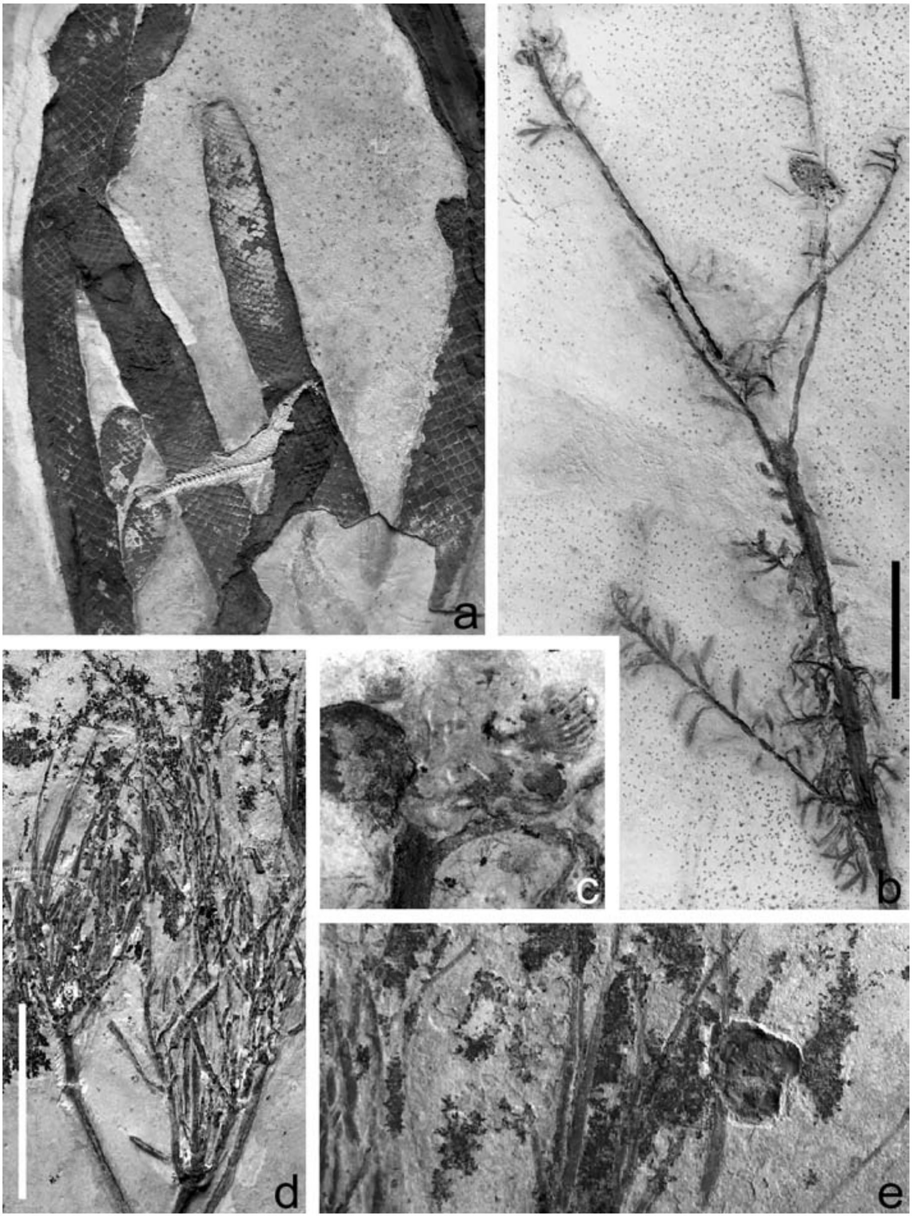


Fig. 19.5. Crato Formation gymnosperms and gnetaleans: (a) a rare example of *Brachyphyllum castilhoi* Duarte, 1985; (b) shoot of a gymnosperm?; scale bar, 10 mm; (c) close-up of fertile parts; (d, e) ephedroid gnetalean taxon A; (d) plant; scale bar, 10 mm; (e) detail of ephedroid taxon A with strobili.

questioned this model and placed the gnetophytes within the conifers, based on molecular studies. Rydin *et al.* (2002) and Magallon and Sanderson (2002) found conflicts within and between molecular data, which indicate that seed-plant phylogeny is poorly understood. One reason for these difficulties could be the influence of gene flux from a variety of sources (Won and Renner, 2003). However, considering the difficulties in judging the position of extant Gnetales, the study of macrofossils with a mosaic of characters might add new insights to this problem.

Cretaceous gnetalean fossils are somewhat more common and geographically widespread (Crane, 1996) than earlier accounts might imply, but are in some cases rather fragmentary. *Ephedrites*, a relatively small plant with several female organs attached to the tender stems, from the Liaoning Province in China lacks organic preservation. *Gurvanella* is known from Siberia, Mongolia and China (Krassilov, 1982; Duan, 1998; Sun *et al.*, 2001). Coalified seeds with anatomical preservation from Portugal and China (Rydin *et al.*, 2004; Yang *et al.*, 2005; Rydin *et al.*, 2006) document that characters and pollination mechanisms unique to *Ephedra* have been retained for about 120 myr or more. One of the best documented fossil gnetophytes is *Drewria* from North America. The presence of relatively broad leaves with parallel venation and secondary Y-shaped arches, and microsporangiate strobili containing ephedroid/welwitschioid pollen (Crane and Upchurch 1987), indicate that it may be related to *Welwitschia*.

In South America a mid-Cretaceous abundance of gnetalean pollen was documented by Lima (1980), while ultrastructural studies on pollen (Osborn *et al.*, 1993) revealed their unequivocal relationship to gnetophytes. Pons *et al.* (1992), Rydin *et al.* (2003) and Dilcher *et al.* (2005a, 2005b) discussed several gnetalean macrofossils from the Crato Formation belonging either to Ephedraceae or Welwitschiaceae.

The following gnetalean taxa are probably closely related to Ephedraceae or to Welwitschiaceae. Several gnetophyte genera might even belong to undescribed, now extinct families, since their character combination does not exist among the three living families. Among the Ephedraceae the genus *Ephedra sensu stricto* was most likely present (taxon A; Figure 19.5d). This, more than 25-cm-high taxon was a much-branched, erect, small shrub that shares the general habit of all Ephedraceae: it has longitudinally grooved, rigid jointed axes and is branched at the nodes. Several branches diverge from these nodes at a relatively narrow angle. Branch diameters range from about 5 mm at the base to about 1.5–2 mm in diameter at the tips. Leaves are not clearly visible, but possibly marked as small triangularly shaped thickenings at the nodes. Three strobili are closely attached to last order branches, of which two of them grow together for about 1 cm (double strobili). One strobilus seems to comprise possibly up to eight whorls of broadly elliptical, about 1.5 mm long and 2–3 mm broad, slightly ribbed cone bracts (Figure 19.5e). Micro- or megasporangia are not observed, but according to the general habit, these are most likely male strobili. Extant species of *Ephedra* may have up to eight pairs of bracts.

Additional taxa with ephedroid characters comprise male and female plants of one particular, relatively common, dioecious taxon (taxon B). It bears highly reduced leaves and exhibits a specific opposite branching mode with succeeding branch lengths being approximately half that of the previous lengths (Figures 19.6a and b). These plants reach a height of at least 60 cm. The female plant has reduced female strobili attached exclusively at the tip of the axes, with cup-shaped bracts containing one seed only (Figure 19.6c); in male plants the strobili are small, bearing many non-fused microsporangia, containing the typical elongated striate pollen of Ephedraceae (Figure 19.6d–f).

A third ephedroid (taxon C) may be partly comparable with fossil *Liaoxia* (*Ephedrites*), from the Early Cretaceous Yixian Formation in western Liaoning, north-east China (Cao *et al.*, 1998; Sun *et al.*, 2001; Guo and Wu, 2000). It is relatively delicately built, and has many fine, almost hair-like, leaves attached to its nodes (Figure 19.7a). This genus produces female strobili containing up to five ovules, but more commonly three. Their bracts are reduced, appear to be split into hair-like fibres and thus give a 'fuzzy' impression. It is not clear what the male strobili of this genus looked like.

Another type of ephedroid had extremely elongated (male) strobili, containing up to 15 pairs of bracts (taxon D; Figure 19.7b). Taxa B–D share several characters that differ from those of extant *Ephedra*. These are, highly modified female and elongated male strobili, with more pairs of bracts than in extant *Ephedra*. When preserved, the fossil microsporangia do not appear to be fused as in recent *Ephedra*, leading to antherophores. Thus taxa B–D may be a sister group to recent *Ephedra*, called 'unnamed group' in a gnetophyte cladogram (Figure 19.8).

Two clearly welwitschioid taxa are found in the Crato Formation. One taxon, based on a seedling (Figure 19.7c) with cotyledons and roots, *Cratonia cotyledon* (Rydin *et al.*, 2003), resembles seedlings of recent *Welwitschia*. The cotyledons exhibit a venation pattern unique to extant seedlings of *Welwitschia*, with a Y-shaped venation between larger parallel veins. This seedling may belong to an as-yet-unnamed plant (taxon E), with characters typical of Gnetales, such as a sturdy stem and rigid jointed branches. It has parallel-veined leaves up to 4 cm wide, with a pointed tip and along the margin extends a well-developed vein. This plant produces small male strobili attached to side branches, subtended by relatively small pointed leaves (Figure 19.7d). These strobili contain tiny anthers with *in situ* pollen of the *Welwitschia* type.

Another dioecious gnetophyte of larger size is relatively common (taxon F); its creeping-to-erect articulated axes reach about 8 mm in diameter (Plate 27b). The ovate-to-obovate-shaped leaves exhibit a characteristic venation pattern. Small

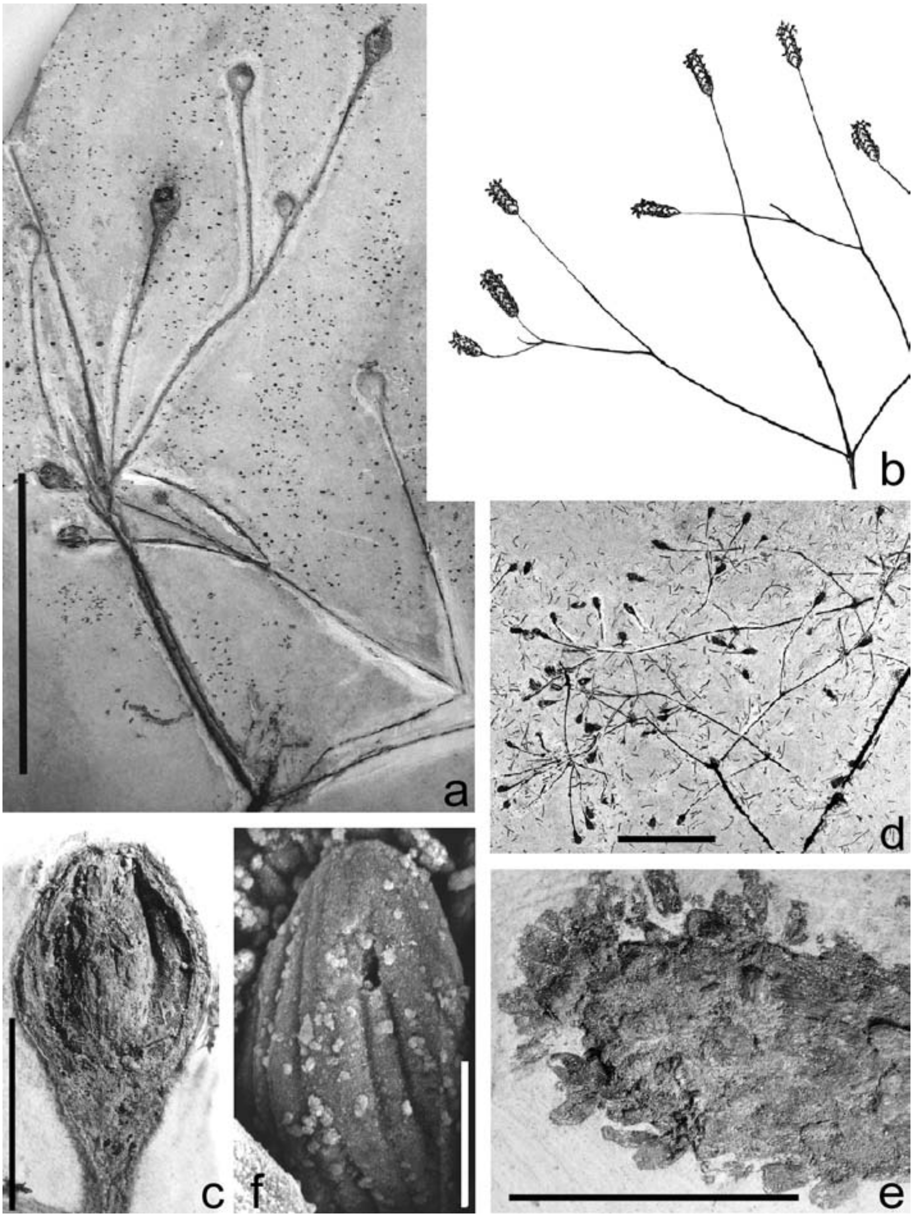


Fig. 19.6. Crato Formation gnetaleans: (a) ephedroid taxon B; (b) drawing of male plant of ephedroid taxon B; (c) seed of ephedroid taxon B; (d) ephedroid taxon B showing male stobili, MB 1999–398; (e) ephedroid taxon B, detail of male strobilus; (f) scanning electron micrograph of striate ephedroid pollen. Scale bars: a,d, 50 mm; c,e, 5 mm; f, 10 μm.

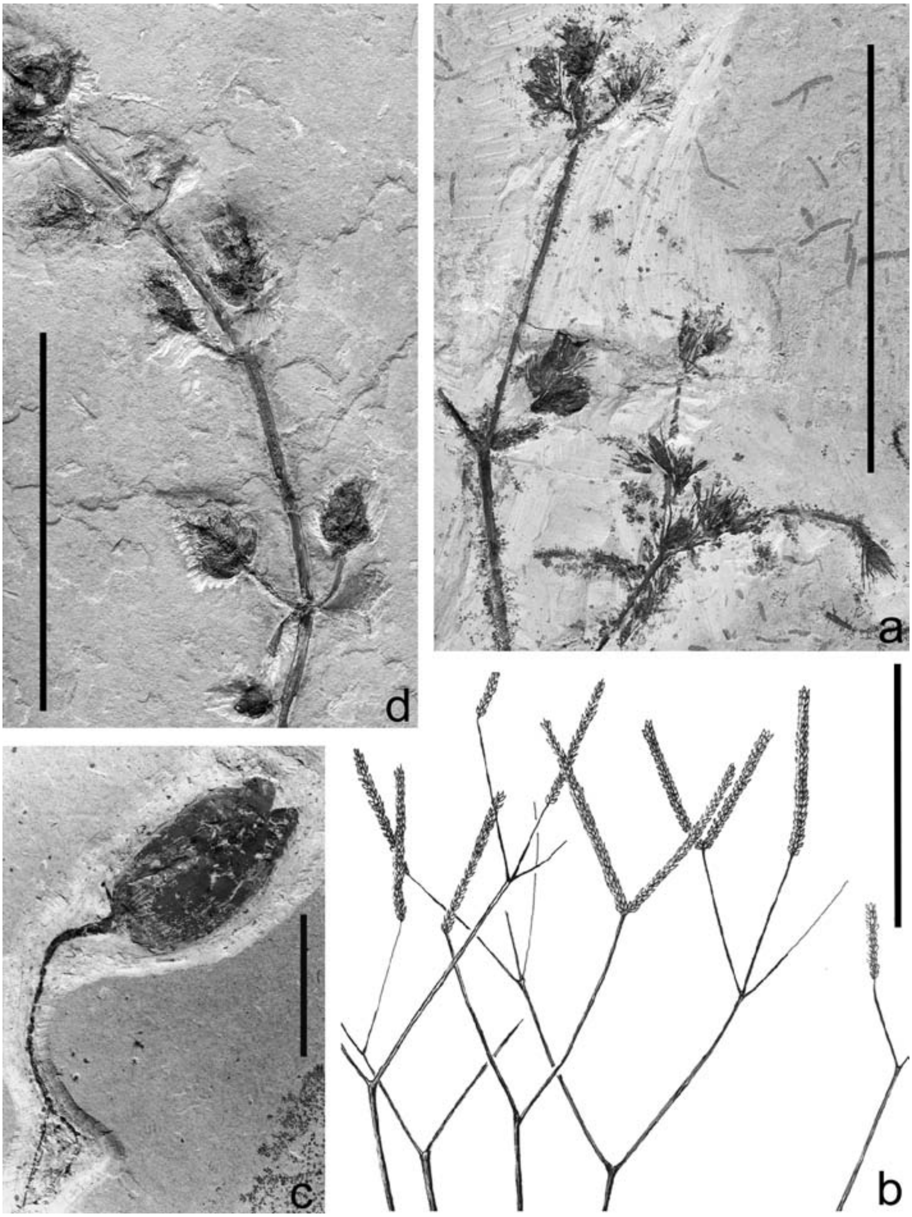


Fig. 19.7. Crato Formation gnetaleans: (a) ephedroid taxon C showing female characters, 1999–521; (b) drawing of male taxon D; (c) Welwitschioid seedling *Cratonia cotyledon*; (d) a plant with welwitschioid affinities, MB 2002–1051 (taxon E). Scale bars: a,b,d, 50 mm; c, 20 mm.

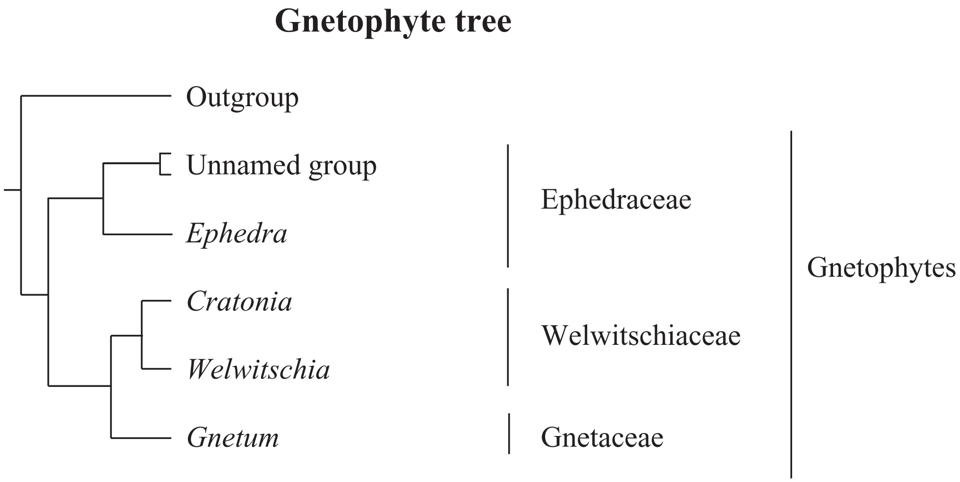


Fig. 19.8. Cladogram demonstrating relationships between gnetophyte higher taxa.

crossveins are developed between more or less flabellate to parallel veins of the first order, resulting in an almost reticulate pattern. Male strobili seem to be terminal, slightly elongated when young, becoming more globose, with a decussate pattern of paired, broadly oval bracts and non-fused stamens. Female strobili are elongate and contain more than 12 whorls of bracts that have an acute apex. *In situ* seeds are small and resemble those of extant *Ephedra*. Dilcher *et al.* (2005a, 2005b) compared these strobili to those of extant *Welwitschia* and named this taxon *Welwitschiostrobus murili*. The combination of characters not observed today in any of the three families may require the erection of a new, now extinct, gnetophyte family (Plate 27e).

Several taxa remain enigmatic, but may belong to gnetophytes. A small plant, around 25 cm in height (taxon G), the articulated stem with a diameter of approximately 1–1.5 mm, contains two small, ear-shaped leaves per whorl. These leaves do not reach more than 5 mm in length and exhibit a close to parallel, nearly flabellate venation pattern. Small strobili, up to 10 mm in length, are either attached to the tips of the axes or to short side axes. These plants were sometimes transported in lumps of several specimens, with their roots still attached. This gives the impression that this taxon G may have been part of a dense ground cover (Plate 27a).

Large coriaceous leaves, reaching more than 120 cm in length and 9 cm in width at the base, are rather common as isolated leaves in the Crato Formation. They have been interpreted by Dilcher *et al.*, (2005a) as welwitschioid remains (Plates 27c and d) and, accordingly, the name *Welwitschiophyllum* has been erected for them. Another of these remains of uncertain origin, called originally *Welwitschiella* and later renamed *Priscowelwitschia* (Dilcher *et al.*, 2005b), has been interpreted as a seedling of a welwitschioid plant based on the possible occurrence of Y-shaped venation. However, none of the specimens shown in the publication, nor those

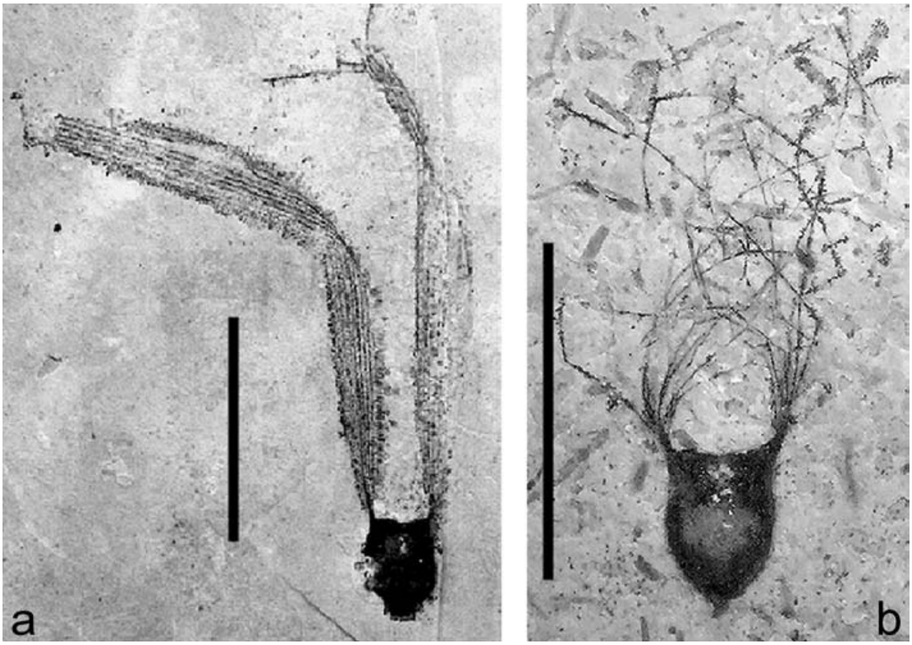


Fig. 19.9. Enigmatic seedlings of *Priscowelwitschia*: (a) seedling with parallel veined ‘leaves’; (b) degraded ‘leaves’ with only main veins preserved. Scale bars, 50 mm.

observed by the authors of this paper, have any signs of roots, crucial to validate the latter assumption. Thus this genus remains enigmatic (Figure 19.9).

A third plant (taxon H), is more than 50 cm high and produces short articulated side branches at the nodes, from which grow about four to six relatively elongated leaves, with five to six parallel main veins. Second-order venation is poorly preserved. Female plants produce strobili and or reproductive bodies with up to seven ovulate structures that seem to comprise possible bracts, and bracteoles (Plate 28a). Better-preserved material is needed to determine taxonomic affinities.

Angiospermae

Angiosperms are not as common as gymnosperms in the Crato Formation, usually occurring as isolated leaves, fruits and seeds. A variety of leaf types have been described, demonstrating moderate diversity of angiosperms at the palaeoequatorial region during this time (Mohr and Friis, 2000), indicating significantly higher diversity than at contemporaneous localities from southern high latitudes (Crane and Litgard, 1989). These isolated leaves or leaves attached to axes comprise mostly small-to-medium sized specimens, ranging from about 0.5 cm to around 10 cm in length (Plate 29). Leaf shape is variable, including obovate to elliptical leaves, but also lobed and reniforme to peltate types which may exceed 15 cm in diameter. In several taxa, the petioles are either not developed, or only weakly developed, the leaves being strongly decurrent (Plate 29c). When isolated from the axis, typically the leaf base is disrupted. The leaf margins appear to be mostly entire, but serrate and lobed leaves are also present. The venation is usually rather disorganized, with pinnate or more rarely palmate primary venation and remnants of ethereal oil cells are often observed. Thus, leaf morphology and architecture conform to the level of complexity known from other late Early Cretaceous strata, such as the Potomac flora of North America (Upchurch, 1984), and indicate that most of the angiosperm component might have been members of basal clades. Compound leaves may have been at a very early stage of development at this time (Plate 29a). The habit of the Crato angiosperms was partly woody, partly herbaceous, with the latter including water lilies and additional taxa of unknown affinity.

An approximately 15-cm-high fragment of a young plant, with primary roots attached, most likely belongs to the herbaceous taxa. Its leaves are highly characteristic with relatively long petioles (≈ 2 cm). The spatulate, approximately 3.5 cm leaf blade with a very narrow base shows several palmate (main) veins and higher-order disorganized crossveins. The main axis of this young plant is broken off at a height of about 10 cm and exhibits several strands. When cut transversally a central pit, now filled with sediment, and several concentrically arranged strands are recognized (Plate 30a).

A second young flowering plant has, by contrast, a very extensive root system and a relatively sturdy stem/axis and may thus represent a woody species (Plate 30b) of shrubby or arboreal growth. It is possible that vines were also present.

Most of the angiosperms seem to have been dicotyledons, while monocotyledons considered to be nested within the basal angiosperm clades (Soltis *et al.*, 2005) might also have been present (Figure 19.10). Isolated fruits and seeds often consist of single carpels (Barreto *et al.*, 2000), or groups of carpels (Plate 30c) with *in situ* ovules/seeds (Mohr and Friis, 2000). In most of these pluricarpellate structures the carpels were clearly free, with rare cases exhibiting syncarpy. Thus it can be assumed that most of the angiosperms belong to basal taxa (magnoliids), with only a few being eudicotyledons.

Basal angiosperms

Remains of one of the most basal and oldest angiosperm clades (Friis *et al.*, 2001), the Nymphaeales, are among the most common and completely preserved angiosperm remains of the Crato Formation. At least two taxa of water plants with nymphaealean features are recognized, all of them characterized by creeping rhizomes and relatively large, peltate leaves (Mohr *et al.*, 2005). A rhizomatous

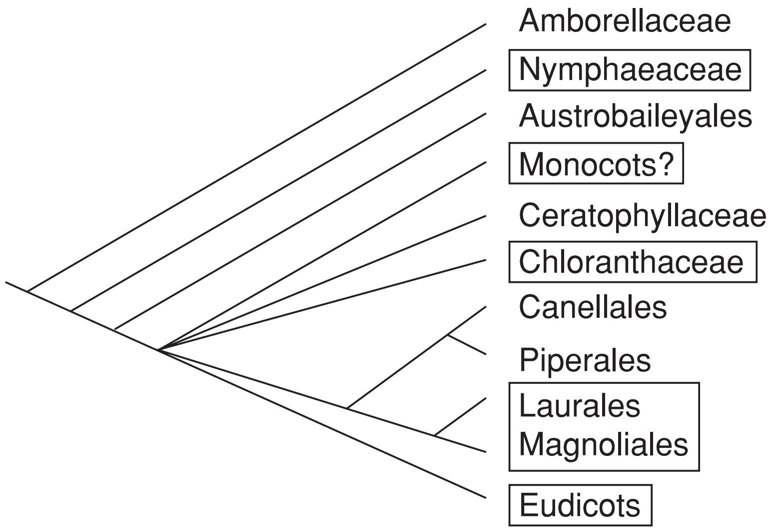


Fig. 19.10. Cladogram showing relationship of major angiosperm groups. Those families most likely present in the Crato Formation are boxed.

taxon bears thin ovate peltate, small leaves (1–2.5 cm) borne on long petioles. The leaf blades show a highly disorganized actinodromous venation pattern (Plate 30d). Several solitary flowering structures on peduncles are also derived from the rhizome. One flower is preserved in an early stage of development and shows possibly ovate tepals and several young follicles. The more mature flowers contain up to 12 apocarpous carpels that are spirally attached to the flat receptacle. These carpels reach up to 1 cm in length and contain several small (up to 1.2-mm-long) ovoid seeds with a hilum. The general habit, as well as the carpel arrangement and seeds, show similarity with the Cabombaceae but there are also several differences when compared with extant *Brasenia* and *Cabomba* (Mohr *et al.*, 2005).

A second taxon is known from several dispersed leaves and from two nearly complete specimens with rhizomes, attached roots and petiolate leaves. Its leaves are nearly orbicular, crenate to sinuate, up to about 7 cm in length and exhibit an actinodromous primary venation. The leaf petioles and possibly also the blades appear to be covered with fine prickles. Although floral features are as yet unknown in this taxon, its general habit, as well as the leaf venation pattern is close to that of extant Nymphaeaceae (Figure 19.11a).

Another specimen, perhaps belonging to Nymphaeales or possibly to the Nelumbonales (a group of basal eudicots), is also characterized by a horizontal rhizome with roots. It bears relatively large petiolate peltate leaves, more than 10 cm in length, with an entire to slightly sinuate margin and an actinodromous venation pattern. One solitary flowering structure sits on a long, thick peduncle of

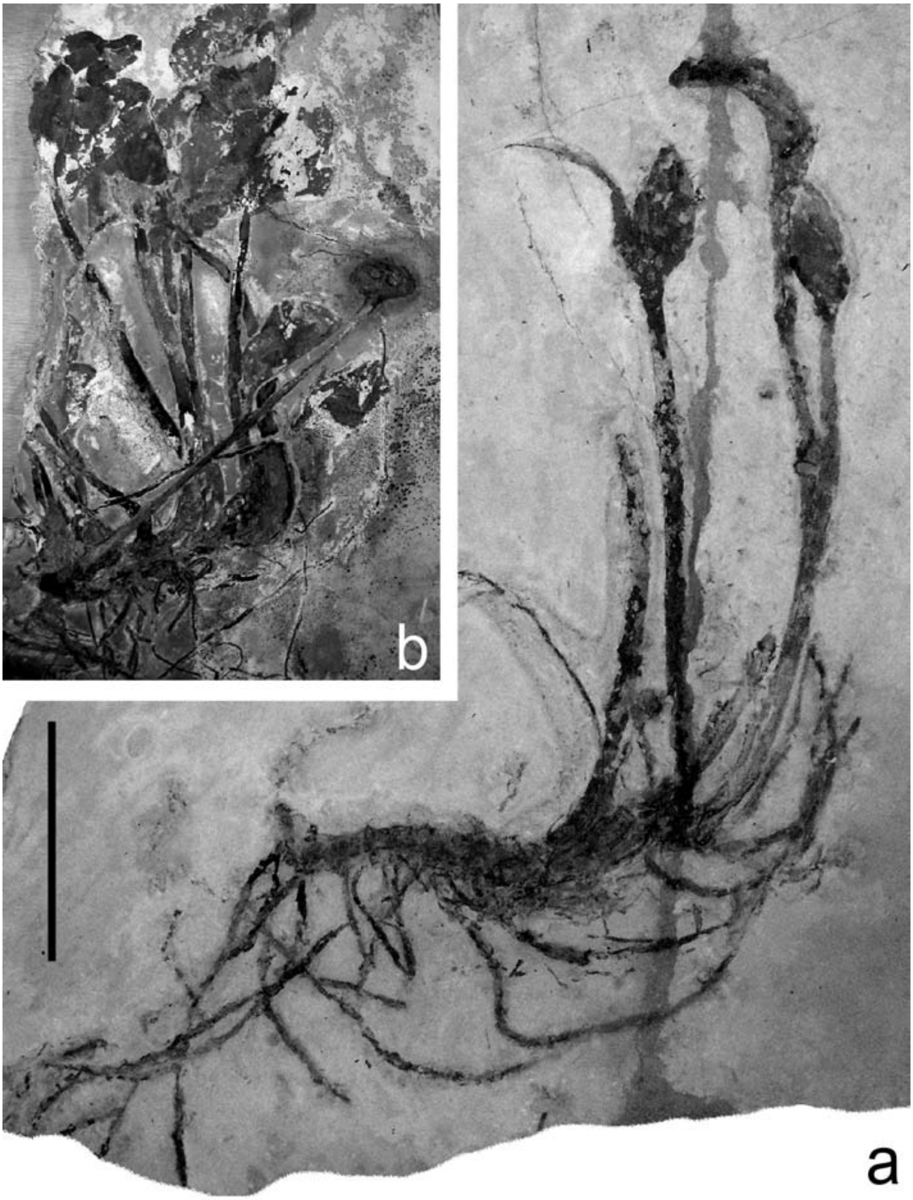


Fig. 19.11. Crato Formation angiosperms: (a) plant with possible affinities to Nymphaeales; scale bar, 50 mm; (b) plant with possible affinites to Nelumbonales.

which the anatomical features are preserved (Figure 19.11b). The actinomorphic multipartite flower, more than 3 cm wide, is not actually preserved, only the imprints of the flowering structure, and therefore its taxonomic relationship cannot be determined with confidence.

The Early Cretaceous record of monocotyledons is generally rather poor (Gandolfo *et al.*, 2000), but they seem to be at least as old as Aptian (Friis *et al.*, 2004). One possible monocotyledon, *Klitzschophyllites* (Plate 31a), is present in the Crato Formation. Previously described as *Trifurcatia* (Mohr and Rydin, 2002; Mohr *et al.*, 2006), it is known from Portugal, North Africa and from two localities in Brazil. This plant is known from shoot fragments, leaves and a possible multi-stemmed basal structure (Plate 31c). The stems are jointed, with trifurcate axes (Plate 31a) and bear on each axis a single amplexicaul serrate leaf at the apex. These flabellate leaves, with an acrodromous to parallelodromous venation pattern, exhibit several primary, secondary and higher-order crossveins and glands between their teeth (Plate 31b).

A small twig with attached sheathing narrowly ovate leaves – two alternating leaves per node – may also be a monocotyledon. The leaves exhibit several features of the venation that are typically observed in monocotyledons, but are not sufficient to differentiate this group entirely: the parallel primary veins are of different sizes (Plate 28b), finer crossvenation connects the longitudinal veins which converge and fuse towards the apex. A detailed analysis of stomata may be possible and would certainly help to understand the fossil's affinities. Leme *et al.*, (2005) reported monocotyledon flowering structures, possibly related to a new family close to Bromeliaceae.

Magnoliid angiosperms include several genera most likely belonging to calycanthoid and magnolialean taxa. A twig with lobed leaves and several reproductive structures, two nearly mature and six immature flowering buds, exhibits characters unique to the fossil *Araripia florifera* (Mohr and Eklund, 2003). Variable leaf shape and ethereal oil cells plus hairs were observed on the leaf blades. The flowers are characterized by a deep, cup-shaped hypanthium, combined with many helically arranged floral organs, today present in Calycanthaceae. These features suggest that the fossil may represent an extinct member of the Laurales, or a member of the lauralean stem lineage to Laurales, or it may be even more basal and part of a stem lineage leading to Magnoliales and Laurales.

Endressinia brasiliana (Mohr and Bernardes-de-Oliveira, 2004), a magnolialean angiosperm – so far the oldest unequivocal report – with relatively small entire leaves with ethereal oil cells, exhibits even more details of its reproductive structures (Plate 31d). Its three-dimensionally preserved flowers allow detailed studies of the flower organs. The hermaphrodite flowers contain many helically arranged apocarpous carpels and broad staminodes with glands, interpreted as odour-producing organs that might have played a crucial role in the pollination process. Flowers with similar features are seen in extant Eupomatiaceae (Endress, 1993) and thus *Endressinia* might be sister to Eupomatiaceae. It might, however, represent an extinct lineage with convergent staminode morphology.

An unnamed magnolialean angiosperm (Angiosperm A) shares several characters of the vegetative and reproductive structures of *Endressinia*: small multipartite flowering structures are attached to the tip of thin axes. Its simple cauline, opposite, decussately(?) arranged, undivided leaves have entire margins and its branches and leaves are densely covered with ethereal oil cells. The flowering structures of less than 10 mm in diameter show several to many spirally arranged simple elongate pistils in their centre, with broadly roundish tepals covering several staminodes or stamens (Plate 31e).

Angiosperm B exhibits features similar to the previously described taxon. Twigs of up to 30 cm in length, with completely preserved leaves, bear single hermaphroditic(?) flowers of slightly more than 1 cm in diameter at the tip of the axes. The leaves are identical with those described as dispersed leaves (Plate 29d), 'Type 6' of Mohr and Friis (2000). These leaves are usually broken at the base, because they sit in an alternate to subopposite arrangement with the petioles sheathing the stem, enclosing more or less completely the axis. The single flowers consist of an apocarpous gynoecium and a slightly cup-shaped hypanthium, with the arrangement of many stamens or staminodes unclear (Figure 19.12a).

Eudicotyledons

Eudicotyledons were certainly present in the Araripe Basin. Angiosperm C seems to be of an overall small size and is possibly herbaceous. The small, less-than-1-cm-long leaves are compound, petiolate and incised. The flowers, in contrast, must have been relatively large, more than 3 cm in diameter (Figure 19.12b). The fossil bears a rather mature flowering structure that consists of several, most likely fully grown free follicles, up to 2.5 cm long, with distinct transverse veins; ovules have not been observed. This taxon may have affinities to Ranunculales, a group that might have already been present at this time (von Balthazar *et al.*, 2005).

One, so-far-unnamed fossil, consisting of two branching axes, is most likely a herbaceous plant. These axes bear more than 20 small, sessile clusters of flowering structures, which are globose inflorescences of many closely packed flowers with small follicles. Structures interpreted as spatulate tepals are present at the outer margin of one of the clusters (Mohr and Friis, 2000). Similar structures have been observed in *Platanocarpus* (Friis *et al.*, 1988) and thus we assume that this as-yet-unnamed fossil might be linked to the Proteales. Nelumbonaceae, also considered to belong to the Proteales, might have been present as well (Figure 19.11b). Several tricolpate dispersed pollen taxa from the Crato Formation (Pons *et al.*, 1996) confirm the assumption that Eudicotyledons had aready reached a degree of diversity.

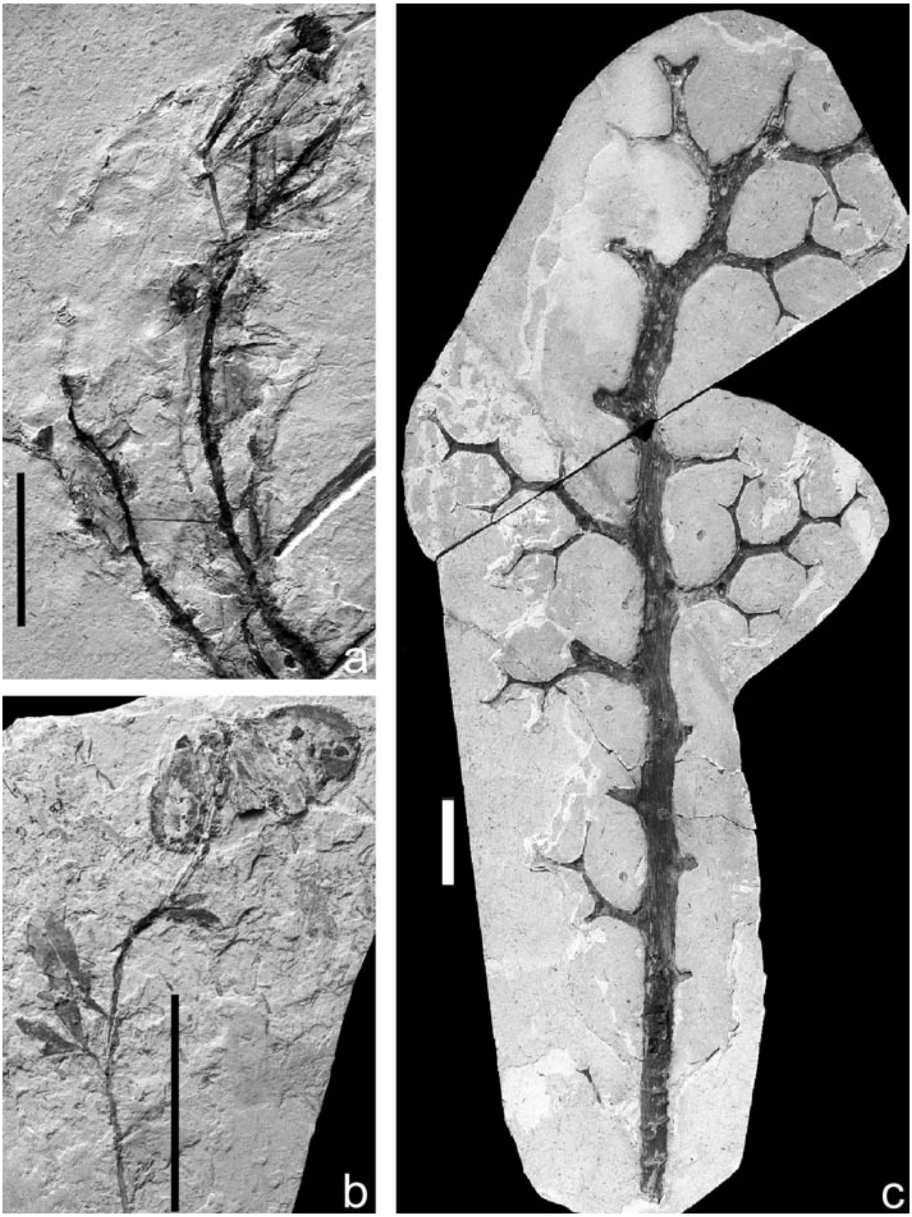


Fig. 19.12. Crato Formation angiosperms and gymnosperms: (a) unidentified angiosperm B; (b) unidentified angiosperm C, a possible eudicotyledon; (**c**) woody, multi-branched gymnosperm of unknown affinity. Scale bars, 50 mm.

Possible pollination mechanisms of Crato angiosperms

Animal–plant interaction can be on different levels and has been demonstrated from the early Palaeozoic (Trewin, 2001). The increase of insect diversity during the Mesozoic, especially during the Early Cretaceous, is most likely intimately linked with the rise and diversification of angiosperms that delivered nutrition to these insect groups. Of special interest here are palynophagous insects that are advantageous in the pollination of flowers.

Not only angiosperms, but also several groups of gymnosperms, have adaptations facilitating insect pollination. Among extant gnetophytes *Ephedra* develops a pollination drop and is pollinated by dipterans (Bino *et al.*, 1984). *Welwitschia* also produces nectar-like drops, the apex of the ovule is expanded into a prominent funnel, male flowers are clustered in an erect and visually prominent group and flowers of yellow-brown colour and distinctive odour (Crane and Hult, 1988), probably pollinated by a fire bug (Coleoptera; Raven *et al.*, 2001, figure 20.43) or by Dermaptera, Hymenoptera and/or Diptera (Endress, 1996).

Insect pollination has been suggested in the past, based on the presence of fecal pellets in fossil bennettitalean strobili and ephedralean and conifer pollen in the gut contents of fossil insects (Labandeira, 2002). Sometimes a fossil gymnosperm pollen/plant is exclusively known from the gut contents of insects, as is the case for the Lower Cretaceous *Vitimipollis* from Transbaikalia, found inside a xyelid hymenopteran (Krassilov *et al.*, 2003).

Extant basal flowers of angiosperms share several important features that often include a high and variable number of floral parts, spiral phylotaxis and a lack of perfect syncarpy. However, today many of these flowers have developed complex pollination mechanisms. Among these are thermogenesis (biochemical reactions in flowers that produce heat), floral odours and protogyny. The most common pollination today is by insect vectors – Coleoptera, Diptera, Hymenoptera, Thripidae and Micropterigidae – and, more rarely, by wind pollination (Thien *et al.*, 2000).

Thermogenesis has been observed in nine living angiosperm families, partly among monocotyledons (Araceae, Arecaceae and Cyclanthaceae) and the basal dicotyledon families Nymphaeaceae, Illiaceae, Magnoliaceae, Annonaceae and Aristolochiaceae, and the eudicotyledon family Nelumbonaceae. In these families thermogenesis is nearly always combined with the production of strong floral fragrances and protogyny. Active beetles often prefer the temperature ranges in these flowers.

Most Crato angiosperms have flowers with these basal features: small-to-medium-sized, spirally arranged multiparted apocarpous flowering structures. Nymphaeales, one of the most basal angiosperm clades, was certainly present and might have already established a relationship with one group of scarab beetles, the

Cyclocephalini, a relationship hypothesized as having originated at least 100 mya (Ervik and Knudsen, 2003). *Endressinia*'s flower morphology is considered to be very similar to extant *Eupomatia*. Both species of *Eupomatia* are pollinated by curculionid beetles (weevils) of the genus *Elleschodes* (Endress, 1993), most likely attracted by the emission of fruity scents produced by the flowers.

General features of the flora: ecological and climatic implications

Land plants exhibit various physiological adaptations to the environments in which they live. These can be adaptations to aridity, elevated salinity, moisture, etc., and may involve anatomical characteristics of the stems, leaves and fertile parts, such as specializations in the vascular tissues, in the epidermis and/or flowers, fruits and seeds. The climatic and ecological implications drawn from Crato plant fossils have varied in the past. Interpretations by Lima (1983) were based on pollen spectra, while those of Mohr *et al.* (2006) were based on interpretations of selected northern Gondwana plants and assumed a semi-dry to seasonally dry climate, with possibly sudden heavy rains. Dilcher *et al.* (2005a), by contrast, hypothesized warm, but not dry conditions for the Crato environment. Arguments for the assumption that episodic torrential floods had occurred are also suggested by the unusual preservation, in that complete plants, including roots, were ripped out of the ground and transported quickly to the place of sedimentation. Unstable environments were also hypothesized for early angiosperm habitats (Feild *et al.*, 2003, 2004).

The presence of certain insects and arachnids, such as camel spiders (Dunlop and Martill, 2004), usually living today in arid environments, suggest at least semi-arid conditions in the nearby hinterland and is in accordance with global climate reconstructions for this region (Skelton, 2003).

Many of the plant taxa, including wood of unknown affinity, ferns, seed ferns, conifers and angiosperms, seem to exhibit adaptations to at least partially dry conditions.

A branch more than 80 cm in length belonging to a hitherto unknown gymnosperm displays a unique growth mode. Its scalariform fibres and tracheids with bordered pits suggest it represents a new wood taxon. Branches and twigs of higher order are bifurcating, but the growth of the (main?) axis is suppressed. This growth mode and the density of the wood suggest an extreme environment where this plant grew (Figure 19.12c).

Ferns, usually very diverse under warm and moist conditions, are represented almost exclusively by a few schizaeacean taxa (spores and megafossils) and gleicheniacean spores. However, the morphologically closest living relatives, certain species of *Anemia*, often live in dry sunny habitats and *Gleichenia* belongs to pioneer vegetation on devastated areas. Several gymnosperms also seem to have been adapted to either physical or physiological drought and include seed ferns as well as conifers. Among the seed ferns one taxon is densely covered with up-to-1mm-long trichomes. Cheirolepid conifers, especially frenelopsids with their highly reduced leaves and deeply sunken and covered stoma-apparatus, are considered by many authors to be at least partially drought-adapted and/or salt-tolerant, forming coastal forests (e.g. Jung, 1974; Alvin, 1982). The presence of several welwitschioid and ephedroid taxa, the latter with highly reduced leaves, may be interpreted similarly.

Also several of the angiosperms seem to exhibit characters that are interpreted as adaptations to seasonal drought. *Klitzschophyllites*, for example, has a reduced leaf surface, relative thick lamina with spines and possibly trichomes. Also most of the other flowering plants of the Crato Formation show features seen today as adaptations to drought: small, coriaceous leaves, oil cells in the sterile and fertile parts and a more or less dense cover of trichomes. These characters point to an unfavourably dry climate with rare and/or periodic rainfall and perhaps to the existence of larger areas with at least seasonal hypersaline conditions, an assumption that is in agreement with sedimentological characteristics of the Crato limestones that contain many idiomorphs of salt crystals up to 2 cm in size.

Concluding remarks

Even though many plant taxa of this unusual lagerstätte are now understood, unique material still awaits detailed descriptions. This comes at a time when discussions about seed-plant evolution and phylogeny seem to have come to certain halt, because molecular data, combined with morphological data of extant members, fail to provide conclusive answers to understanding their phylogeny. In this case, fossils with a new mosaic of characters might help to solve these open questions. Thus, in the future Crato plants may prove to be vitally important for understanding major aspects of seed-plant evolution.

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20

Spores and pollen from the Crato Formation: biostratigraphic and palaeoenvironmental implications

David J. Batten

Well over 150 spore and pollen taxa have been recorded in the literature from the Crato Formation and other slightly older and younger formations in the Chapada do Araripe, but detailed information on stratigraphic occurrences and relative abundances is mostly lacking. As a result, it is difficult to draw precise biostratigraphic and palaeoenvironmental conclusions, and impossible to recognize any changes in climate and depositional conditions upwards through the succession on the basis of the published record of these plant microfossils. By a process of elimination it is reasonable to suggest an age range of late Aptian to early Albian for the formation from the data presented. It may also be inferred that during the time it accumulated much of the surrounding vegetation was adapted to semi-arid conditions, although there must also have been some habitats that were able to sustain moisture-loving and aquatic plants. The latter is emphasized by the palynological composition of two samples examined specifically for consideration in this chapter, which are unequivocally from the Crato Formation. The assemblages recovered also suggest that the formation is more likely to be late Aptian than early Albian in age. In addition, evidence of reworking of Devonian deposits is apparent. A few of the spores and pollen grains recovered are illustrated (Figure 20.1 and Plate 32).

Background

The great variety and exquisite preservation of insect, fish, plant and other macrofossil remains in the Crato Formation is not obviously matched by similarly abundant and well-preserved palynomorphs (plant microfossils), despite the large number of forms that have been recorded. This is owing to a combination of the sedimentary conditions prevalent at the time of deposition of the formation and the effects of present-day weathering, which has not been conducive to their preservation. The

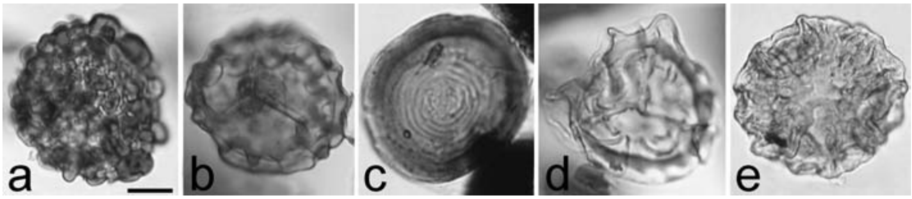

Fig. 20.1. Crato Formation palynomorphs: (a) *Leptolepidites* sp.; (b) *Klukisporites* sp.; (c) *Chomotriletes minor* Pocock; (d) *Retitriletes* sp.; (e) *Callialasporites dampieri* (Balme). Scale bar, 10 μm.

plants are mostly preserved as compressions but little, if any, of the original organic material remains (see Chapter 19). Instead they are largely limonite replications; even the parts most resistant to decay, the cuticles (outer protective wall layers) of stems and leaves, are seldom encountered.

Although the exines (outer walls) of most spores and pollen grains are generally more resistant to decay than cuticles (indeed, they are among the most resistant of all forms of organic matter), the mode of preservation of the macrofossils does not bode well for the recovery of the minute organs associated with the reproduction of the plants concerned. Oxidizing and alkaline conditions are usually the main causes of poor, or a lack of, preservation in fine-grained lithologies. In addition, the coarser the grain size, the lower the chances of recovering palynomorphs.

Nevertheless, they have been recovered from some of the limestones and mudstones, the latter generally yielding better-preserved specimens and larger amounts of non-palynomorph organic matter in association. Although numerous genera and species have been recorded by Lima (1978, 1979, 1980, 1989), Lima and Perinotto (1984), Pons *et al.* (1990, 1996) and others, most of the studies have been based on samples that were not precisely located stratigraphically. This has rendered determinations of the age of the formation vague and open to question. Such biostratigraphic blurring is most unfortunate because satisfactory assessment of the data presented and conclusions drawn is impossible; lists of taxa with minimal or no reference to sampling horizons are of little value except in a general way. The fact that these are not only based on occurrences in the Crato Formation but also presumed to be at least partly from samples taken from the formations stratigraphically above (Ipubi and Santana formations) and a little below (Batateiras Formation) is a major problem, especially if the succession reflects deposition during several million years, which is quite likely. The numerous changes that have been made to the lithostratigraphical nomenclature and what the Crato, Santana and other formations actually represent do not help.

Hence, a reliable age determination for the formation must await a rigorous biostratigraphic analysis of all of the deposits of the Crato–Santana group. Nevertheless, following a discussion of the possibilities and a brief assessment of the criteria that can be applied to restrict the age range of the Crato Formation, the composition of the palynomorph assemblages recovered from the two samples mentioned above is used here to suggest that it can probably be constrained more precisely than has commonly been stated.

A scarcity of stratigraphic precision and details of sedimentological relationships also hinders palaeoenvironmental analyses. The composition of the vegetation as implied by the palynomorphs that have been reported from the Crato Formation can be discussed in a general way but any changes through time cannot be recognized. Again, it is possible to add to what may be inferred from the confusing literature by commenting on the environmental implications of the two samples examined.

Assemblage composition and age implications

The assemblages described by Lima in the papers cited above are thought to be based on samples taken from the lowest part of the Crato Formation and the upper part of the underlying Batateiras Formation (Berthou *et al.*, 1994), but may also come from younger deposits (Santana Formation). A large number of taxa with straight or twisted ridges were assigned to the polyplicate genera *Equisetosporites* and *Gnetaceaepollenites*. Species of the former have nothing to do with the 'horsetail' order Equisetales, which the name implies; rather, in common with *Gnetaceaepollenites*, they are referable to the younger Gnetales (*Cratonia*, *Ephedra*, *Gnetum*, *Welwitschia*; e.g. Osborn *et al.*, 1993; Rydin *et al.*, 2003, 2004; Dilcher *et al.*, 2005), most records of which are not older than Barremian. Other taxa recorded by de Lima and, for example, by Pons *et al.* (1990) and Neumann (2003), include several species of *Araucariacites*, *Cicatricosisporites*, *Classopollis*, *Cyathidites*, *Deltoidospora*, *Inaperturopollenites*, *Leptolepidites*, *Singhia* and *Steevesipollenites*, one, two or three species of many other genera, and a few megaspores.

As is typical of many palynological preparations, some of the components are long-ranging and of no biostratigraphic value, some have ranges that are close to their beginning or end during the period of deposition represented by the succession being investigated, which in this case may be assumed to be not older than Barremian or younger than Cenomanian, and some have short ranges and can, therefore, usually be relied upon for reasonably precise age determinations. Among the second and third categories recorded in the literature are *Appendicisporites tricornitatus* Weyland and Greifeld, *Balmeisporites minutus* Brenner, *Crybelosporites striatus* (Cookson and Dettmann), *Distaltriangulisporites perplexus* (Singh), *Galeacornea causea* Stover, *Gnetaceaepollenites rectangularis* Lima, *Sergipea naviformis* Regali, Uesugui and Santos, *Sergipea variverrucata* (Regali, Uesugui and Santos), *Singhia reyrei* Lima and *Steevesipollenites binodosus* Stover, which together suggest that the Crato Formation is likely to be younger than not only Barremian but also early Aptian.

The question is, do these biostratigraphically useful species occur throughout the Crato Formation or only towards the top of it, or in overlying formations? The data in the rather numerous, mostly short papers by de Lima, Regali and others published after 1980 that refer to the Crato, Santana and other formations help to narrow down the options to some extent, but several of the observations made are biostratigraphically confusing.

The limited representation of flowering plants, both numerically and morphologically, is typical of Aptian and, to a lesser extent, early Albian deposits in middle and low Cretaceous latitudes. Taxa recorded include species of the monocolpate (monosulcate) *Clavatipollenites*, *Retimonocolpites* (*Brenneripollis*) and *Stellatopollis*, indicating the presence of monocotyledons or early (magnoliid) dicotyledons, the tricolpate *Striatopollis* and *Tricolpites*, which are considered to be diagnostic of non-magnoliid dicotyledons (Doyle *et al*., 1982), and the zonasulcate *Afropollis*. On the other hand, the absence of monosulcate *Tucanopollis* (*Transitoripollis*), a pollen grain with a sculptured, sometimes circular aperture (Regali, 1989), suggests that the Crato Formation is younger than early Aptian. The presence of *Galeacornea causea*, if recorded from the formation, confuses the picture somewhat in that its earliest occurrence is usually reported to be middle Albian.

The lack of certain forms that are typical of middle or late Albian and early Cenomanian assemblages in the West African–South American palynofloral province of the North Gondwanan Realm, such as the elaterates *Elaterocolpites*, *Elateroplicites*, *Elaterosporites*, *Senegalosporites* and *Sofrepites* (e.g. Herngreen, 1975, 1998; Herngreen and Chlonova, 1981; Batten, 1984; Batten and Li, 1987; Regali and Viana, 1989) and the polyporate angiospermous *Cretacaeiporites*, suggests that the maximum age range for the Crato Formation is late Aptian–early Albian. However, if the characteristics of the assemblages of spores and pollen grains recovered from the two Crato samples mentioned above are typical of the formation as a whole (see below) then an early Albian age is less likely. This conclusion ties in with other data and observations in some of the literature of the past decade (e.g. Pons *et al*., 1996; Arai *et al*., 2001; Coimbra *et al*., 2002) including those of Regali (2001), who considered the younger Santana, Arajara and Exu formations to be referable to her *Complicatisaccus cearensis* Zone and late Aptian in age, hence implying that the Crato Formation is also no older than late Aptian.

Palaeoenvironmental implications

The considerable mix of spore and pollen taxa suggests that they are derived from plants that colonized both wet and dry habitats. It is quite possible that these co-existed, but whether wetter and drier climatic periods are represented upwards through the formation cannot be determined from the available data. Indicators of wet habitats and standing water include the megaspores *Balmeisporites minutus* and *Paxillitriletes* (recorded as *Thomsonia*), and the small spore *Crybelosporites striatus*, all of whose affinities are known to lie with heterosporous plants (those that produce both megaspores and microspores), and at least some of the fern spores. Drier conditions are indicated by the species of, for example, common *Araucariacites*, *Classopollis* (*sensu lato*; i.e. including *Circulina* and *Corollina*), *Ephedripites*, *Equisetosporites*, *Gnetaceaepollenites* and *Steevesipollenites*, and also *Galeacornea causea* and *Sergipea naviformis*. The first of these is considered to represent the extant coniferalean family Araucariaceae and the second, the extinct family Cheirolepidiaceae, and in common with the other genera, both are typical of low-latitude mid Cretaceous palynofloras. Macrofossil remains of probable araucariacean and cheirolepidiacean affinity have been recorded from the Crato Formation (Crane and Maisey, 1991), as have plants of gnetalean affinity that presumably yielded the ephedroid pollen grains (*Ephedripites*, *Galeacornea*, *Gnetaceaepollenites* and others), other non-angiospermous seed plants (probable representatives of the Cycadales and/or Bennettitales), angiosperms (Mohr and Friis, 2000), horsetails and ferns, the last of these including representatives of the Schizaeaceae with which the dispersed spore *Cicatricosisporites* is associated. Possibly not only drier but also cooler conditions are indicated by the saccate pollen taxa (e.g. *Alisporites*, *Callialasporites*, *Podocarpidites* and *Protopinus*), which appear to be uncommon and of low diversity, and may reflect more distant, higher-altitude vegetation.

One of the Crato samples examined for this chapter was a limestone, the other a silty mudstone. Both yielded brown wood fragments, cuticles (including small pieces of bennettitalean origin) and other tissues, and tracheidal debris, but amorphous organic matter is proportionally more abundant in the limestone. The latter proved to contain much less organic matter than the mudstone and an impoverished palynomorph assemblage dominated by a species of *Crybelosporites* (Plate 32, figure 15). Only a small number of other spores and even fewer gymnosperm pollen grains occur in association, including species of *Cicatricosisporites* and *Deltoidospora*, and *Araucariacites* respectively, along with representatives of the freshwater alga *Ovoidites* (Plate 32, figure 13) and a minor reworked component consisting of Devonian algal bodies, including *Maranhites* (Plate 32, figure 20; see also Brito and Quadros, 1995).

The large quantity of organic matter recovered from the mudstone is not only rich in plant debris but also contains many spores and pollen grains. The most abundant taxon is *Classopollis*, some in tetrad configuration. Species of *Cicatricosisporites*, *Ephedripites*, *Gnetaceaepollenites* and the angiosperm pollen

Afropollis and *Penetetrapites* are among the more common subordinate taxa. Other forms recorded include species of the triradiate spores *Converrucosisporites*, *Crybelosporites*, *Deltoidospora*, *Densoisporites*, *Foveotriletes*, *Interulobites*, *Klukisporites*, *Leptolepidites* and *Verrucosisporites*, the gymnosperm pollen grains *Araucariacites*, *Callialasporites*, *Eucommidiites*, *Exesipollenites* and *Vitreisporites*, the angiospermous *Stellatopollis* and the freshwater alga *Chomotriletes* (for examples of some of these and other taxa, see Plate 32, figures 1–12, 14, 16–19, 21–24; Figure 20.1).

The composition of the two palynofacies suggests that not only depositional conditions differed but also a range of plant habitats is represented. Climatic differences might also be indicated, but these cannot be determined on the basis of palynological data from only two samples. The assemblage yielding common *Crybelosporites* implies derivation from a possible water-fern community in close proximity to the depositional site. The comparatively varied assemblage of spores recovered from the mudstone coupled with common *Classopollis* and, to a lesser extent, ephedroid pollen grains suggests that plant communities favouring, respectively, generally moist and seasonally dry conditions are represented.

Conclusions

Approaches to palaeopalynology have changed substantially since the potential of spores and pollen grains recorded from sediments and sedimentary rocks for resolving pre-Quaternary biostratigraphic and palaeoenvironmental problems was first recognized. Before they could be used they had to be described. As a result, many publications during the first three decades of widespread palynological study, from the mid-1950s to the mid-1980s, contained large numbers of not necessarily very well-described, illustrated and satisfactorily differentiated new species, along with varying amounts of (frequently minimal) biostratigraphic data, and commonly brief notes on supposed botanical affinities. Unfortunately, most of those on the palynology of the Cretaceous formations of the Chapada do Araripe fall into this category. Although there has been some improvement in recent years, a new comprehensive study of the succession is now required, which should include a reassessment of all of the taxa that have been recorded previously; hence my reluctance here to identify most to species level. Also necessary are determinations of relative abundances throughout the succession and an analysis of the non-palynomorph organic matter with which they are associated based on samples for which there are detailed lithological descriptions and accurate stratigraphic records. Only then will the biostratigraphic and palaeoenvironmental potential of the spores and pollen grains preserved be fully realized. The organic composition of the two samples examined prior to writing this chapter and the recent work of Neumann *et al.* (2003) suggest that there is much still to learn about the palynology of the Crato Formation and the under- and overlying rocks, and its palaeoenvironmental implications.

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Part V

Miscellanea

21

Miscellaneous biota

David M. Martill

The Crato Formation yields a number of fossils and other, possibly fossil, objects that are somewhat puzzling. The most conspicuous of these are the small (usually 5–10 mm in length) pellet-like structures that often cover the bedding surfaces. Others are less mysterious, but their presence in the formation is hard to explain, such as the isolated occurrence of pieces of amber. Below is a review of some of these objects with possible explanations for their occurrence and identity.

Pelleted bedding planes

A characteristic of many bedding surfaces in the Nova Olinda Member is the super-abundance of evenly distributed pellet-like structures (Figure 21.1). On fresh surfaces they appear to be black or dark grey, but are usually brown or orange on weathered surfaces. When found in early diagenetic concretions they are clearly cylindrical. Most are straight, or only slightly curved, they never bifurcate and lengths may vary from 2 to 15 mm while the diameter is usually between 0.5 and 1.5 mm. Hydrofluoric acid extraction of unweathered specimens showed that they can contain high concentrations of palynomorphs. Their occurrence within larger coprolites that also contain bones is puzzling. Their pellet-like morphology suggests that they are just that: faecal pellets. Their size and super-abundance would suggest that they were generated by young individuals of the fish *Dastilbe*. The high abundance of palynomorphs within the pellets is then easily explained as a consequence of the filter-feeding activities of young *Dastilbe*.

An alternative explanation for their origin was proposed by Neumann *et al.* (2003), who suggested that they are the remains of isolated branchlets of a cheirolepidiaceous conifer. Arguments against such an origin include the lack of internal structure when viewed under the microscope and their unusual distribution, being

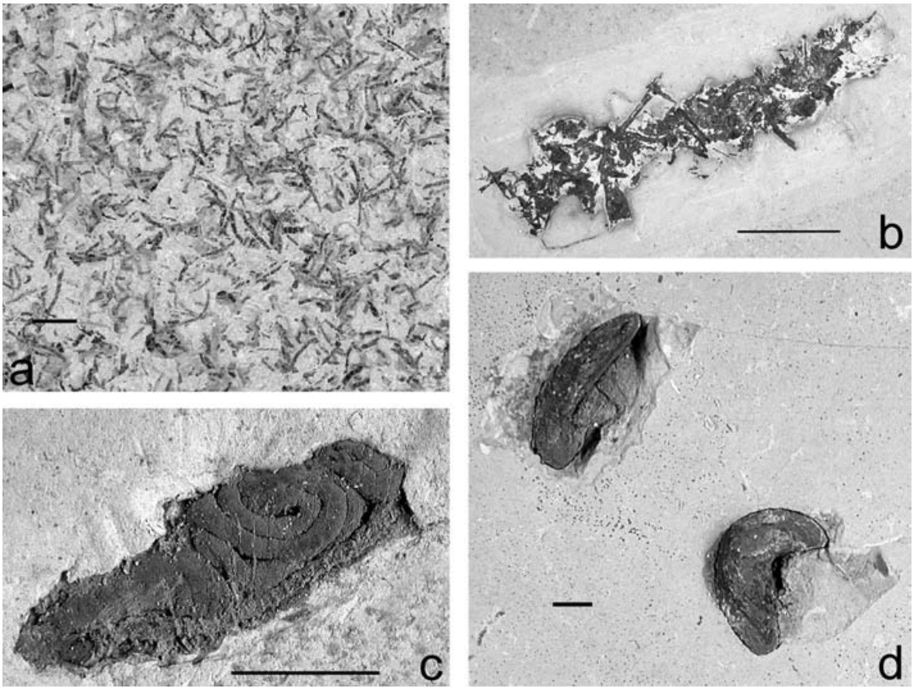

Fig. 21.1. Coprolites and pellets: (a) typical bedding plane of Nova Olinda Member laminite covered with carbonaceous pellets; (b) aggregate of small fish bones that may represent a regurgitate; (c) vermiform coprolite with inclusion of *Dastilbe* sp.; (d) unidentified seed-like objects. Scale bars: a,b, 10 mm; c,d, 5 mm.

scattered evenly on most bedding planes. As a cheirolepidiaceous branchlet, they would be allochthonous, and it is therefore difficult to conceive of how they would become so evenly distributed. Furthermore, no macrophyte with such branchlets *in situ* has been recorded for the Crato Formation.

Mucous membranes

Tangled mats of somewhat structureless, filamentous material occur frequently as discreet entities on bedding surfaces (Figures 21.2c and d). They show no internal structure that permits easy identification, and are usually assumed to be filamentous algae, although no analysis exists. They are usually comprised of a series of looped or tangled aggregations and appear to represent diaphanous sheets that split and recombine. Their size varies from patches of just 30–50 mm across to larger specimens reaching 20 cm or more in diameter. Examples occur in which insect remains are included, often in high numbers, and some specimens have been found containing discreet aggregates of sphalerite crystals. This latter occurrence is assumed to be diagenetic, but its origin is unknown. Although an algal origin is perhaps the

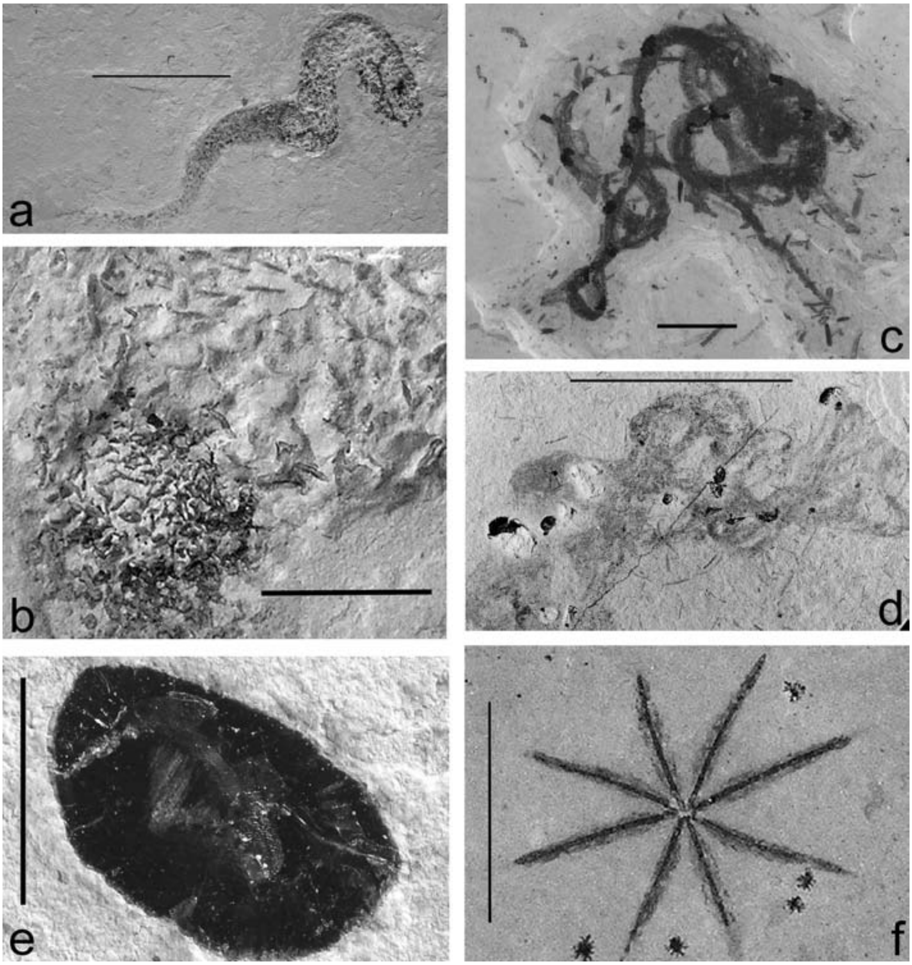

Fig. 21.2. Enigmatic fossils: (a, b) a worm-like organism; (a) with various types of spicules; (b) in the integument; (c) filamentous 'algal' mat with adherent euhedral sphalerite (ZnS) crystals (dark spots); (d) a similar 'algal' mat with entrapped insects; (e) a pebble of fossil resin; (f) unidentified fossil, perhaps a 'feathered' seed. Scale bars: a,d, 50 mm; b, 25 mm; c, e, f, 10 mm.

most parsimonious, there is no proof that this is so, and other origins cannot be ruled out, including mucous-like excreta from vertebrates (guano), degraded frog-spawn jelly or bacterial mucilage.

Phosphatic coprolites

Typical phosphatic coprolites do occur in the Nova Olinda Member limestone, but they are not as common as in other laminated lagerstätten such as the Santana Formation nodules or the Eocene Green River Formation, both of which are famous for the diversity and abundance of predatory fishes (Grande, 1983). Their scarcity in the Nova Olinda Member is most likely a reflection of the rarity of larger, predatory fishes. Crato coprolites are usually small, being just a few millimetres in length and just 1–2 mm in diameter, light-to-dark brown, but weathering white, and are most commonly seen on the cut edges of slabs of the limestone.

Larger coprolites may occasionally contain isolated bones, and at least one specimen is known that contains an articulated fish (Figure 21.1c). Such examples may not represent true coprolites, but coelolites.

Amorphous brown patches

Patches of irregular, amorphous brown material with a microgranular or earthy texture occur occasionally. The boundaries are sharp and the material has depth, but is usually little more than 2 mm thick. Its origin is unknown, but may be coprolitic, perhaps representing larger coprolites that have been highly compacted. However, the irregular shape does not seem entirely compatible with this explanation.

Amber

Small (5–30 mm diameter) grains of resinous material, interpreted as amber by Martill *et al.* (2005), occur infrequently in both the weathered and unweathered laminated limestone (Figure 21.2). Varying in colour from dark brown to almost black when *in situ*, once extracted it is amber yellow or even ruby red. The amber pieces are uncompacted but do contain numerous microfractures. Possible inclusions of micro-organism have been noted, but no insect inclusions have yet been reported.

Other mysterious objects

A number of possible fossils have proved difficult to identify. Figure 21.1d depicts two ‘bean-like’ structures that may represent a hitherto unknown seed, while Figure 21.2f shows a feathered star which is also thought to be a possible unknown seed.

Among mystery objects that may have an animal origin is a spicule-coated, worm-like entity in the Museum of Paleontology in Santana do Cariri (Figures 21.2a and b). A tangled mass of fine bones (Figure 21.1b) is thought to be an unusual coprolite or regurgitate.

References

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Neumann, V. H., Borrego, A. G., Cabrera, L. and Dino, R. 2003. Organic matter composition and distribution through the Aptian-Albian lacustrine sequences of the Araripe Basin, northeastern Brazil. *International Journal of Coal Geology* **54**: 21–40.

Appendix: species list for the Crato Formation

David M. Martill, Günter Bechly and Sam W. Heads

Arachnida

Araneae

Araneomorphae
Araneoidea
Familia *incertae sedis*
  Cretaraneus Selden, 1990
  Cretaraneus martinsnetoi Mesquita, 1996
Mygalomorphae
Dipluridae
  Diplurinae
    Cretadiplura ceara Selden in Selden *et al.*, 2006
    Dinodiplura ambulacra Selden in Selden *et al.*, 2006

Chelonethi = Scorpiones

Chactoidea
Chactidae
  Araripescorpius ligabuei Campos, 1986
Scorpionoidea
Hemiscorpiidae
  Hormurinae
    Protoischnurus axelrodorum Carvalho and Lourenço, 2001

Acari

Parasitengona
Erythraeoidea
?Erythraeidae
    Pararainbowia martilli Dunlop, 2007

Solifugae

Ceromidae
    Cratosolpuga wunderlichi Selden in Selden and Shear, 1996

Uropygi/Thelyphonida

?Thelyphonidae
    ?Mastigoproctinae
        Mesoproctus rowlandi Dunlop, 1998

Amblypygi

Neoamblypygi
?Phrynidae
    Britopygus weygoldti Dunlop and Martill, 2002

Crustacea

Decapoda

Caridea
Familia *incertae sedis*
    Beurlenia araripensis Martins-Neto and Mezzalira, 1991

Ostracoda

Theriosynoecum silvai (Silva, 1978)
Theriosynoecum munizi (Silva, 1978)
Theriosynoecum quadrinodosa (Silva, 1978)
Harbinia micropapillosa (Bate, 1972)
Harbinia angulata angulata (Krömmelbein and Weber, 1971)
Darwinula martinsi Silva, 1978
Cyrpridea araripensis Silva, 1978
Brasacypris sp.
Candona sp.
Zonocypris(?) sp.

Conchostraca

Cyzicus codoensis (Cardoso, 1962)
Cyzicus brauni (Cardoso, 1962)
Cyzicus pricei (Cardoso, 1966)

Chilopoda

Scolopendromorpha

- Scolopendridae
  - Sterropristinae
    - cf. *Rhysida*
  - Subfamilia *incertae sedis*
    - *Cratoraricus oberlii* Wilson, 2003
    - *Velocipede bettimari* Martill and Barker, 1998

Scutigeromorpha

- Scutigeridae
  - *Fulmenocursor tenax* Wilson, 2001

Hexapoda = insecta

'APTERYGOTA'

Diplura

- Japygoidea
- Familia *incertae sedis*
  - *Ferrojapyx vivax* Wilson and Martill, 2001

Zygentoma

- Lepismatidae
  - *Lepismatidae* gen. spec. 'Araripe' Sturm, 1998

Pterygota

Stem group Ephemeroptera

- Panephemeroptera
- Ephemerontoidea
- Ephemeronta
- Reticulata

Heptabranchia

Cretereismatidae fam. nov.

(diagnosis as type genus since monotypic; see description in this volume)

Cretereisma antiqua Willmann, this volume

Cretereisma schwickertorum Willmann, this volume

Ephemeroptera

†Hexagenitidae

Protoligoneuria limai Demoulin, 1955

Cratohexagenites longicercus Staniczek, this volume

Cratohexagenites minor Staniczek, this volume

Oligoneuriidae

Colocrus indivicum McCafferty, 1990

Colocrus? magnum Staniczek, this volume

Ephemeroidea (*sensu* McCafferty, 1991)

Potamanthidae?

Olindinella gracilis Martins-Neto and Caldas, 1990

Euthyplociidae

Pristiplocia rupestris McCafferty, 1990

Gen. et sp. nov.

Ephemeridae

Australiephemera revelata McCafferty, 1990

Microephemera neotropica McCafferty, 1990

Cratonympha microcelata Martins-Neto and Caldas, 1990

Polymitarcyidae?

Caririnympha mandibulata Martins-Neto and Caldas, 1990

Baetiscidae

Protobaetisca bechlyi Staniczek, this volume

+several as-yet-unnamed genera and species

Ephemeroptera *incertae sedis*

Costalimella nordestina Martins-Neto, 1996

Costalimella zuechii Zamboni, 2001

Insecta *incertae sedis*

Cariephemera marquesi Zamboni, 2001

Odonata

Zygoptera

Familia *incertae sedis* (probably Hemiphlebiidae)

Cretarchistigma? essweini Bechly, 1998

Hemiphlebiidae Tillyard, 1926

- *Parahemiphlebia cretacica* Jarzembowski *et al.*, 1998
- *Parahemiphlebia mickoleiti* Bechly, 1998
- *Parahemiphlebia* spec. nov. (?) Bechly, 1998

Protoneuridae
- Isostictinae
- †Eoprotoneurini
  - *Eoprotoneura hyperstigma* Carle and Wighton, 1990

Thaumatoneuridae
- Thaumatoneurinae
- †Euarchistigmatini
  - *Euarchistigma atrophium* Carle and Wighton, 1990
  - *Euarchistigma marialuiseae* Bechly, this volume

'Anisozygoptera'

†Stenophlebioptera

†Stenophlebiidae
- *Cratostenophlebia schwickerti* Bechly, this volume

Anisoptera

†Nothomacromiidae Carle, 1995 (stat. rest.)
- *Nothomacromia sensibilis* (Carle and Wighton, 1990)

†Aeschnidiidae
- *Wightonia araripina* Carle in Carle and Wighton, 1990
- *Santanoptera gabotti* Martill and Nel, 1996

†Cretapetaluridae
- *Cretapetalura brasiliensis* Nel *et al.*, 1998
- *Eotanypteryx paradoxa* Bechly, this volume

†Liupanshaniidae
- *Paramesuropetala gigantea* Bechly *et al.*, 2001
- *Araripeliupanshania annesuseae* Bechly *et al.*, 2001

Gomphaeschnidae
- †Gomphaeschnaoidinae
  - *Gomphaeschnaoides obliquus* (Wighton, 1987)
  - *Gomphaeschnaoides petersi* Bechly *et al.*, 2001
  - *Gomphaeschnaoides betoreti* Bechly *et al.*, 2001
  - *Gomphaeschnaoides magnus* Bechly *et al.*, 2001
  - *Progomphaeschnaoides ursulae* Bechly *et al.*, 2001
  - *Progomphaeschnaoides staniczeki* Bechly *et al.*, 2001
  - *Paramorbaeschna araripensis* Bechly *et al.*, 2001
  - *Anomalaeschna berndschusteri* Bechly *et al.*, 2001

†Araripegomphidae
- *Araripegomphus cretacicus* Nel and Paicheler, 1994
- *Araripegomphus andreneli* Bechly, 1998
- *Araripegomphus hanseggeri* Bechly, 2000
- *Araripegomphus* sp. nov. (?) Bechly, 1998

†Proterogomphidae

- †Cordulagomphinae
    - *Cordulagomphus tuberculatus* Carle and Wighton, 1990
    - *Cordulagomphus fenestratus* Carle and Wighton, 1990
    - *Cordulagomphus winkelhoferi* Bechly, this volume
    - *Cordulagomphus hanneloreae* Bechly, this volume
    - Subgenus *Procordulagomphus* Nel and Escuillié, 1994
    - *Cordulagomphus (Procordulagomphus) xavieri* Nel and Escuillié, 1994
    - *Cordulagomphus (Procordulagomphus) senckenbergi* Bechly, 1998
    - *Cordulagomphus (Procordulagomphus) primaerensis* Petrulevicius and Martins-Neto, 2006
    - *Cordulagomphus (Procordulagomphus) michaeli* Bechly, this volume

Lindeniidae
- Lindeniinae
    - *Cratolindenia knuepfae* Bechly, 2000

†Araripephlebiidae
- *Araripephlebia mirabilis* Bechly, 1998

†Araripechlorogomphidae
- *Araripechlorogomphus muratai* Bechly and Ueda, 2002

†Araripelibellulidae
- †Araripelibellulinae
    - *Araripelibellula martinsnetoi* Nel and Paicheler, 1994
    - *Cratocordulia borschukewitzi* Bechly, 1998

+ eight undescribed genera and species of uncertain familial affinity

Dermaptera

Forficulina
Anisolabididae
- *Cratoborellia gorbi* Haas, this volume

Labiduridae
- *Caririlabia berghoffi* Haas, this volume
- *Caririlabia brandaoi* Martins-Neto, 1990

Eudermaptera
Spongiphoridae
- *Cretolabia cearae* Popham, 1990
- *Kotejalabis haeuseri* Haas, this volume
- *Kotejalabis goethitica* Engel and Chatzimanolis, 2005

Dictyoptera

Mantodea

Santanmantis axelrodi Grimaldi, 2003
+ an unnamed species

‘Blattaria’

†Mesoblattinidae
    Undescribed sp of? Mesoblattina
†Raphidiomimidae
    Undescribed sp.
†Umenocoleoidea
†Cratovitismidae fam. nov.
    Cratovitisma oldreadi Bechly, this volume
†Umenocoleidae
    Ponopterix axelrodi Vršanský and Grimaldi in Vršanský, 1999a
    Ponopterix maxima Bechly, this volume
†Blattulidae
    Elisama americana Vršanský, 2002
Blattellidae
    ‘*Mesoblattina*’ *limai* Pinto and Purper, 1986
    Undescribed gen. et sp. nov. A
Blattidae
    Mesoblattinopsis schneideri Pinto, 1989
Familia *incertae sedis*
    Undescribed gen. et sp. nov. B

Isoptera

Mastotermitidae
    Cratomastotermes wolfschwenningeri Bechly, this volume
Termopsidae
    Cretatermitinae
        Nordestinatermes araripena (Krishna, 1990)
        Nordestinatermes obesa Martins-Neto *et al.*, 2006
        Cretatermes pereirai Fontes and Vulcano, 1998
    Subfamilia *incertae sedis*
        Mariconitermes talicei Fontes and Vulcano, 1998

Hodotermitidae?
    Caatingatermitinae
        Caatingatermes megacephalus Martins-Neto *et al.*, 2006
        Araripetermes nativa Martins-Neto *et al.*, 2006
Kalotermitidae
    Cratokalotermes santanensis Bechly, this volume
Rhinotermitidae
    Cretarhinotermes novaolindense Bechly, this volume

Orthopterida

Chresmododea

Chresmoda sp. nov.

Phasmatodea

Aerophasmatidae
Cretophasmatinae
    Cretophasma araripensis Martins-Neto, 1989

Orthoptera

Ensifera
Baissogryllidae
    Caririgryllus elongatus Martins-Neto, 1991
    Caririgryllus pilosus Martins-Neto, 1991
    Caririgryllus arthaudi Martins-Neto, 1991
    Caririgryllus mesai Martins-Neto, 1991
    Caririgryllus brevipterus Martins-Neto, 2002
    Cearagryllus monstruosus Martins-Neto, 1991
    Cearagryllus robustus Martins-Neto, 1991
    Cearagryllus gorochovi Martins-Neto, 1991
    Cearagryllus perforatorius Martins-Neto, 1991
    Cearagryllus poliacanthus Martins-Neto, 1991
    Cearagryllus microcephalus Martins-Neto, 1991
    Cearagryllus revelatus Martins-Neto, 1998
    Cearagryllus previstus Martins-Neto, 1998
    Santanagryllus hesselae Martins-Neto, 1991
    Castillogryllus complicatus Martins-Neto, 1995
    Notocearagryllus dutrae Martins-Neto, 1998
    Notocearagryllus leipnitzi Martins-Neto, 2002
    Olindagryllus obliteratus Martins-Neto, 1998
    Olindagryllus rotundus Martins-Neto, 1998
Gryllidae
    Araripegryllus caposae Martins-Neto, 1987
    Araripegryllus femininus Martins-Neto, 1991
    Araripegryllus marianoi Martins-Neto, 1991
    Araripegryllus nanus Martins-Neto, 1991
    Araripegryllus serrilhatus Martins-Neto, 1991
    Araripegryllus spinosus Martins-Neto, 1991
    Brontogryllus excelsus Martins-Neto, 1991
    Cratogryllus pentagonalis Martins-Neto, 1991

Cratogryllus guimaraesae Martins-Neto, 1991
Cratogryllus ciguelli Martins-Neto, 1991
Nanoararipegryllus pigamaeus Martins-Neto, 2002
Gryllotalpidae
Archaeogryllotalpoides ornatus Martins-Neto, 1991
Palaeoscapteriscops cretacea Martins-Neto, 1991
Cratotetraspinus fossorius (Martins-Neto, 1995)
Hagloidea *incertae sedis*
Cratohaglopsis santanaensis Martins-Neto, 1991
Kevania araripensis Martins-Neto, 1991
Ensifera *incertae sedis*
Phasmomimella? araripensis Martins-Neto, 1991
Caelifera
Elcanidae
Cratoelcana damianii Martins-Neto, 1991
Cratoelcana zessini Martins-Neto, 1991
Locustopseidae
Cratozeunerella neotropica Martins-Neto, 1998
Cratozeunerella amedegnatoi Martins-Neto, 1998
Cratozeunerella godoii Martins-Neto, 2003
Cratozeunerella nervosa Martins-Neto, 2003
Cratozeunerella soaresi Martins-Neto, 2003
Cratozeunerella titanella Martins-Neto, 2003
Cratolocustopsis cretacea Martins-Neto, 2003
Cratolocustopsis araripensis Martins-Neto, 2003
Cratolocustopsis contumax Martins-Neto, 2003
Zessinia pulcherrima Martins-Neto, 1990
Zessinia caririensis Martins-Neto, 1990
Zessinia reticulata Martins-Neto, 1990
Zessinia petruleviciusi Martins-Neto, 2003
Zessinia vikingi Martins-Neto, 2003
Locustrix gallegoi Martins-Neto, 2003
Locustrix audax Martins-Neto, 2003
Bouretidae (possible junior synonym of Tetrigidae)
Bouretia elegans Martins-Neto, 2001
Araripelocustidae
Araripelocusta longinota Martins-Neto, 1995
Araripelocusta brevis Martins-Neto, 1995
Tridactylidae
Cratodactylus ferreirai Martins-Neto, 1990
Cratodactylus kellneri Martins-Neto, 1990
Proscopiidae
Gen. et sp. nov. Heads, 2008

Hemiptera

Cicadomorpha

- †Palaeontinidae
  - *Parawonnacottella araripensis* Ueda, 1997
  - *Parawonnacottella penneyi* Menon *et al.*, 2005
  - *Cratocossus magnus* Martins-Neto, 1998
  - *Baeocossus fortunatus* Menon and Heads, 2005
  - *Colossocossus loveridgei* Menon *et al.*, 2005
  - *Colossocossus rugosa* Menon *et al.*, 2005
  - *Colossocossus bechlyi* Menon and Heads, 2005
  - *Colossocossus giganticus* Menon and Heads, this volume
- Tettigarctidae
  - Cicadoprosbolinae
    - *Architettix compacta* Hamilton, 1990
    - *Tettagalma striata* Menon, 2005
- †Cercopionidae
  - *Cercopion reticulata* Hamilton, 1990
- Cicadellidae
  - Cicadellinae
  - Proerrhomini Hamilton, 1990
    - *Proerrhomus rugosus* Hamilton, 1990
  - Ledrinae
  - Paracarsonini Hamilton, 1990
    - *Paracarsonus aphrodoides* Hamilton, 1990
    - *Platyjassites inflatifrons* Hamilton, 1990
- Lineage Ulopidae+Aetalionidae+Melizoderidae+Membracidae
  - Hallicini
    - *Hallex xestocephalus* Hamilton, 1990
    - *Hallex gongrogony* Hamilton, 1990
    - *Hallex brevipes* Hamilton, 1990
    - *Hallex laticeps* Hamilton, 1990
    - *Hallex gracilior* Hamilton, 1990
- Myerslopiidae
  - Ovojassini
    - *Ovojassus concavifer* Hamilton, 1990
    - *Ovojassus minor* Hamilton, 1990

Fulgoromorpha

- Achilidae
  - *Acixiites immodesta* Hamilton, 1990
  - *Acixiites costalis* Hamilton, 1990
- Cixiidae

- *Cretofennahia cretacea* (Martins-Neto, 1988)

Lalacidae
- Protodelphacinae
- Protodelphacini
  - *Protodelphax chamus* Hamilton, 1990
  - *Protodelphax macroceps* Hamilton, 1990
  - *Protodelphax miles* Hamilton, 1990
  - *Protodelphax rhinion* Hamilton, 1990
- Ancoralinae
- Ancoralini
  - *Ancorale flaccidum* Hamilton, 1990
  - *Ancorale aschemon* Hamilton
- Kinnarocixiini
  - *Kinnarocixius quassus* Hamilton, 1999
  - *Kinnarocixius* sp. (probably a distinct genus)
- Lalacinae
- Lalacini
  - *Lalax mutabilis* Hamilton, 1990
  - *Patulopes setosa* Hamilton, 1990
  - *Patulopes myndoides* Hamilton, 1990
- Carpopodini
  - *Carpopodus difficilis* Hamilton, 1990
  - *Carpopodus* sp. A Hamilton, 1990
  - *Carpopodus* sp. B Hamilton, 1990
  - *Psestocixius fuscus* Hamilton, 1990
  - *Psestocixius delphax* Hamilton, 1990
  - *Vulcanoia membranosa* Martins-Neto, 1988
  - *Vulcanoia apicalis* Hamilton, 1990
  - *Vulcanoia acuceps* Hamilton, 1990

Familia *incertae sedis* (Boreoscytidae?)
- *Megaleurodes megocellata* Hamilton, 1990

Coleorrhyncha

Peloridioidea
†Progonocimicidae
- Undescribed spp.

Heteroptera

Nepomorpha (Hydrocorisae)
Belostomatidae

- Belostomatinae
    - *Araripebelostomum martinsnetoi* Nel and Paicheler, 1992
    - *Neponymphes godoii* Zamboni, 2001 (probably a nymph of *Araripebelostomum*)
    - *Paranoika placida* Zamboni, Martins-Neto and Popov, 2002
- Lethocerinae
    - *Lethocerus vetus* Nel and Waller, 2006

Nepidae
- Undescribed spp.

Naucoridae
- *Cratocora crassa* Ruf *et al*., 2005
- *Cratopelocoris carpinteroi* Ruf *et al*., 2005

Notonectidae
- Notonectinae
    - ?*Canteronecta* sp.

Corixidae
- †Velocorixinae
    - sp. with aff. *Rhomboidella*

Gelastocoridae
- Nerthrinae
    - *Cratonerthra corinthiana* Ruf *et al*., 2005
    - *Cratonerthra estevezae* Ruf *et al*., 2005

†Pseudonerthridae
- *Pseudonerthra gigantea* Ruf *et al*., 2005

Gerromorpha (Amphibicorisae)

Hydrometridae
- *Cretaceometra brasiliensis* Nel and Popov, 2000
- *Incertametra santanensis* Goodwyn, 2002

Veliidae
- Undescribed sp.

Mesoveliidae
- Undescribed sp.

Leptopodomorpha

Archegocimicidae?
- Undescribed sp.

Pentatomomorpha

Pachymeridiidae
- *Cratocoris shevchenkoae* Martins-Neto, Popov and Zamb, 1999
- Undescribed sp.

Alydidae
- Undescribed spp.

Coreidae
- Undescribed spp.

Aradidae

Mezirinae
    Undescribed sp.
Cydnidae
Amnestinae?
    Latiscutella santosi Pinto and Ornellas, Martins Neto and C., 1994
Cimicomorpha
Familia *incertae sedis*
    Undescribed sp.
Heteroptera *incertae sedis*
    Cratogocimex popovi Martins Neto, 2002
+ several undescribed genera and species of bugs

Holometabola

Neuropterida

Schwickertoptera Bechly, this volume

Rafaelidae
    Rafaelia maxima Nel *et al.* 2005
    Rafaelia minima Nel *et al.* 2005

Raphidioptera

Raphidiomorpha
Baissopteridae
    Austroraphidia brasiliensis (Nel, Séméria and Martins-Neto, 1990)
    Baissoptera pulchra (Martins-Neto and Nel, 1992)
    Baissoptera brasiliensis Oswald, 1990
Familia *incertae sedis*
    Arariperaphidia rochai Martins-Neto and Vulcano, 1989

Megaloptera

Undescribed spp.

Neuroptera/Planipennia

Myrmeleontiformia
Psychopsidae
    Pulchroptilonia espatifata Martins-Neto, 1997 (family assignment doubtful)
Nemopteridae

- *Roesleriana exotica* Martins-Neto and Vulcano, 1989
- *Cratonemopteryx robusta* Martins-Neto and Vulcano, 1989
- *Cratonemopteryx audax* Martins-Neto, 1995
- *Cratonemopteryx speciosa* Martins-Neto and Vulcano, 1997
- *Krila pilosa* Martins-Neto, 1992

Ascalaphidae
- *Cratoscalapha electroneura* Martins-Neto and Vulcano, 1997

Myrmeleontidae
- *Pseudonymphes araripensis* Martins-Neto and Vulcano, 1989
- *Pseudonymphes ponomarenkoi* Martins-Neto, 1995
- *Pseudonymphes brunherottae* Martins-Neto, 1994
- *Pseudonymphes zambonii* Martins-Neto, 1998

Araripeneuridae
- *Araripeneura regia* Martins-Neto and Vulcano, 1989
- *Araripeneura gracilis* Martins-Neto and Vulcano, 1989
- *Blittersdorfia pleoneura* Martins-Neto and Vulcano, 1989
- *Blittersdorfia volkheimeri* Martins-Neto and Vulcano, 1989
- *Blittersdorfia dicotomica* Martins-Neto, 1990
- *Blittersdorfia polyplusia* Martins-Neto, 1997
- *Blittersdorfia pulcherrima* Martins-Neto and Vulcano, 1997
- *Caldasia cretacea* Martins-Neto and Vulcano, 1989
- *Caririneura microcephala* Martins-Neto and Vulcano, 1989
- *Caririneura damianii* Martins-Neto, 1992
- *Caririneura crassatella* Martins-Neto, 1992
- *Caririneura nemopteroides* Martins-Neto, 2002
- *Cratoalloneura acuminata* Martins-Neto, 1992
- *Cratoneura longissima* Martins-Neto, 1992
- *Cratoneura pulchella* Martins-Neto, 1992
- *Cratoneura dividens* Martins-Neto, 1994
- *Paracaririneura priscila* Martins-Neto and Vulcano, 1997
- *Cratopteryx robertosantosi* Martins-Neto and Vulcano, 1989
- *Bleyeria nordestina* Martins-Neto, 1995

Makarkiniidae
- *Makarkinia adamsi* Martins-Neto, 1995

Babinskaiidae
- *Babinskia pulchra* Martins-Neto and Vulcano, 1989
- *Babinskia formosa* Martins-Neto and Vulcano, 1989
- *Neliana maculata* Martins-Neto, 1992
- *Neliana impolluta* Martins-Neto, 1997

Palaeoleontidae
- *Baisopardus araripensis* Martins-Neto, 1992
- *Baisopardus polyhymnia* Martins-Neto, 1997
- *Baisopardus gigas* Martins-Neto and Vulcano, 1997

Baisopardus cryptohymen Heads *et al.*, 2005
Paraneurastenyx ascalaphix Martins-Neto, 1995
Parapalaeoleon magnus Menon and Makarkin, 2008
Hemerobiiformia
Ithonidae
Principiala incerta Makarkin and Menon, 2007
Osmylidae
Nuddsia longiantennata Menon and Makarkin, 2008
Sisyridae
Cratosysirops gonzagai Martins-Neto, 1997
Berothidae
Araripeberotha martinsi Martins-Neto and Vulcano, 1990
Caririberotha fairchildi Martins-Neto and Vulcano, 1990
Allopteridae
Kareninia breviptera Martins-Neto, 1997
Armandochrysopa borschukewitzi Nel *et al.*, 2005
Triangulochrysopa formosa Menon and Makarkin, 2008
Limaiidae
Limaia conspicua Martins-Neto and Vulcano, 1989
Limaia adicotomica Martins-Neto, 1997
Mesypochrysa criptovenata Martins-Neto and Vulcano, 1989
Mesypochrysa confusa Martins-Neto and Vulcano, 1989
Araripechrysa magnifica Martins-Neto and Vulcano, 1989
Cratochrysa willmanni Martins-Neto, 1994
Cratochrysa sublapsa Martins-Neto, 1997
Cratochrysa martinsnetoi Nel *et al.*, 2005

Coleoptera

Archostemata
cf. Ommatidae
Undescribed sp.
cf. Cupedidae
Undescribed sp.
Adephaga
Dytiscidae
Undecribed spp.
Carabidae
Cicindelinae
Oxycheilopsis cretacicus Cassola and Werner, 2004
Subfamilia *incertae sedis*
Alexcarabus megagnathus Martins-Neto, 2002

Polyphaga
Staphylinidae
  Caririderma pilosa Martins-Neto, 1990
  Cratophyllina minuscula Martins-Neto, 2002
  +undescribed spp.
Scarabaeidae
  Aphodiinae
    Undescribed spp.
  Subfamilia *incertae sedis*
    Undescribed spp.
Hydrophilidae
  Undescribed larva
Buprestidae
  Undescribed spp.
Dryopidae
  Undescribed sp.
Elateridae
  Undescribed spp.
Trogossitidae
  ?Peltinae
    Undescribed sp.
Nitidulidae
  Undescribed spp.
Cucujidae
  Undescribed sp.
Tenebrionidae
  Possible undescribed sp.
?Pyrochroidae
  Cretaceimelittomoides cearensis Vulcano and Pereira, 1987 (probably *nomen nudum*)
Chrysomelidae
  ?Eumolpinae
    Undescribed sp.
  Subfamilia *incertae sedis*
    Undescribed sp.
Curculionoidea
Nemonychidae
  Rhinorhynchinae
  Rhinorhynchini
    Cratomacer immerses Zherikhin and Gratschev, 2004
    Cratomacer ephippiger Zherikhin and Gratschev, 2004
Belidae
  ?Pachyurinae
  ?Pachyurini

    Davidibelus cearensis Zherikhin and Gratschev, 2004
  ?Oxycoryninae
    Undescribed sp.
?Eccoparthridae
  Martinsnetoa dubia Zherikhin and Gratschev, 2004
Brentidae?
  Eurhynchinae
    Axelrodiellus ruptus Zherikhin and Gratschev, 2004

Hymenoptera

'Symphyta'
Anaxyelidae (or Sepulcidae?)
  Syntexinae
    Prosyntexis gouleti Darling and Sharkey, 1990
    Prosyntexis legitima Martins-Neto, Melo and Prezoto, 2007
Siricidae
  Undescribed sp.
Apocrita/Parasitica
Ephialtitidae
  Cratephialtites kourios (originally described in the genus *Karatous*)
*?*Ichneumonoidea
  Undescribed sp.
Proctotrupidae
  Protoprocto asode
Mesoserphidae
  Undescribed sp.
Apocrita/Aculeata
Pompilidae
  ?Pompilinae
    Undescribed sp.
Formicidae
  Myrmeciinae
    Cariridris bipetiolata Brandao *et al.*, 1989
Tiphiidae
  Architiphia rasnitsyni Darling and Sharkey, 1990
Sapygidae
  Fedtschenkiinae André, 1903
    Cretofedtschenkia santanensis Osten, this volume
Vespoidea
Scoliidae
  ?Proscoliinae

        - *Cretaproscolia josai* Rasnitsyn and Martinéz-Delclòs, 1999
    - †Archaeoscoliinae Rasnitsyn, 1993
        - *Cretoscolia brasiliensis* Osten, this volume
- Vespidae
    - Undescribed sp.
- Apoidea
- †Angarosphecidae
    - *Cretosphex parvus* Darling and Sharkey, 1990
    - *Cretosphex magnus* Darling and Sharkey, 1990
    - *Mesorhopalosoma ceareae* Darling and Sharkey, 1990
    - *Cretobestiola* sp. nov.
- Ampulicidae
    - Undescribed sp.
- Apidae?
    - Undescribed sp.

Mecoptera

- Panorpoidea?
    - Undescribed sp.
- Bittacidae
    - Undescribed sp.

Diptera

- Tipulomorpha
- Limoniidae
    - *Cratotipula latialata* Ribeiro and Martins-Neto, 1999
    - *Okrenomyia araripensis* Ribeiro and Krzemiski, 2000
- Culicomorpha
- Culicoidea
- ?Chironomidae
    - Undescribed sp.
- ?Simuliidae
    - *Cretaceosimulium araripense* Vulcano, 1985 (probably nomen nudum)
- Psychodomorpha
- Tanyderidae?
    - *Megapsychoda araripina* Azar and Nel, 2002
- Bibionomorpha
- Mycetophilidae
    - Macrocerinae?
        - Undescribed sp.

Sciaridae or Sciaroidea
  Undescribed sp.
Bibionidae?
  Undescribed sp.
Stratiomyomorpha
Cratomyiidae
  Cratomyia macrorrhyncha Mazzarolo and Amorim, 2000
  Cratomyoides cretacicus Willkommen, this volume
Asilomorpha
Mydidae
  Cretomydas santanensis Willkommen, this volume
Therevidae (?)
  Cratotabanus stenomyomorphus Martins-Neto and Santos, 2004
Asilidae
  Araripogon axelrodi Grimaldi, 1990
  Unnamed new species (possibly Therevidae?)
Tabanomorpha
Tabanoidea
Rhagionidae?
  Undescribed sp.
Tabanidae
  Cratotabanus stenomyomorphus Martins-Neto and Santos, 1994
  Undescribed sp.

Trichoptera

Leptoceridae
  Araripeleptocerus primaevus Martins-Neto, 2001
Familia *incertae sedis*
  Raptortrichops sukatsheva Martins-Neto, 2001
  Senka crassatella Martins-Neto, 2001
'Spicipalpia'
Hydroptilidae
  Cratorella magna Martins-Neto, 2001
  Cratorella media Martins-Neto, 2001
  Cratorella minuta Martins-Neto, 2001
  Cratorella feminina Martins-Neto, 2001

Lepidoptera

Micropterygidae
  Parasabatinca caldasae Martins-Neto and Vulcano, 1989
Undopterygidae
  Undopterix caririensis Martins-Neto and Vulcano, 1989

Familia *incertae sedis*
Gracilepterix pulchra Martins-Neto and Vulcano, 1989
Eolepidopterigidae
Xena nana Martins-Neto, 1999
Psamateia calipsa Martins Neto, 2002

Vertebrata

Actinopterygii

Neopterygii
Holostei
Semionotiformes
Semionotidae
Lepidotes sp.
Araripelepidotes sp.
Halecomorphi
Amiiformes
Amiidae
Vidalaminae
Gen et sp. nov.
Ionoscopiformes
Ophiopsidae
Placidichthys bidorsalis Brito, 2000
Teleostei
Aspidorhynchidae
Vinctifer longirostris Santos, 1990
Ichthyodectiformes
Ichthyodectoidei
Cladocyclidae
Cladocyclus gardneri Agassiz, 1841
Ostariophysi
Gonorynchiformes
Chanidae
Dastilbe crandalli Jordan, 1910
Othophysi
Familia *incertae sedis*
Santanichthys sp.

Sarcopterygii

Actinistia
Mawsoniidae
Axelrodichthys sp.

Lissamphibia

Salientia
Anura
Leptodactylidae
    Araripehrynus placidoi Leal and Brito, 2006
Pipoidea Gray, 1825
    Gen et sp. nov.

‘Reptilia’

Testudines

Pleurodira
Pelomedusoides
Araripemydidae
    Araripemys barretoi Price, 1973
    Araripemys arturi Fielding, Martill and Naish, 2005
Diapsida

Lepidosauria

Squamata
Familia *incertae sedis*
    Olindalacerta brasiliensis Evans and Yabumoto, 1998
    Tijubina pontei Bonfim Jr and Marques, 1997

Archosauria

Crocodyliformes

Mesoeucrocodylia
Neosuchia
Susisuchidae
    Susisuchus anatoceps Salisbury, Frey and Martill, 2003
Notosuchia
Araripesuchidae
    cf. *Araripesuchus* Price, 1959

Pterosauria

Pterodactyloidea
Ornithocheiroidea

Ornithocheiridae
  Arthurdactylus conandoylei Frey and Martill, 1994
  Ludodactylus sibbicki Frey *et al.*, 2003
  Brasileodactylus sp.
Lophocratia
Azhdarchoidea
Tapejaridae
  Ingridia imperator (Campos and Kellner, 1997)
  Ingridia navigans (Frey *et al.*, 2003a)
?Tupuxuaridae
  ‘*Tupuxuara*’ sp. nov.

Dinosauria

Theropoda
?Spinosauroidea
  Isolated tooth

Aves

?Euenantiornithiformes
  Undescribed sp. and numerous feathers

Flora

Algae

Botryoccocus sp.

Dinoflagellata

Subtilisphaera senegalensis

Vascular plants

Taxa based on macrophytes.

Pteridospermae

Equisetales
  Equisetum sp.
Isoetales

Isoetites cf. *choffati*

Filicales

Schizaeaceae

Ruffordia goepperti Seward, 1961

Gymnospermae

Cycadales

Undescribed spp.

Bennettitales

cf. *Williamsonia*

Caytoniales

Undescribed sp.

Araucariaceae

Brachyphyllum castilhoi Duarte, 1985

Brachyphyllum obesum Heer, 1875

Araucaria sp.

Resin

Cheirolepidiaceae

Lindleycladus

Tomaxellia sp.

Czekanowskiales

?Gymnospermae

Novaolindia dubia Kunzmann, Mohr and Bernardes-de-Oliveira, 2007

Gnetales

Welwitschiaceae

Welwitschiella austroamericana Dilcher, Bernardes-de-Oliveira, Pons and Lott, 2005

Welwitschiophyllum brasiliense Dilcher, Bernardes-de-Oliveira, Pons and Lott, 2005

Welwitschiostrobus murili Dilcher, Bernardes-de-Oliveira, Pons and Lott, 2005

Priscowelwitschia Dilcher, Bernardes-de-Oliveira, Pons and Lott, 2005

Ephedraceae

Taxon A

Taxon B

Taxon C

Taxon D

Taxon E

Taxon F

Taxon G

Taxon H

Angiospermae

Monocotyledons
  Araripia florifera Mohr and Eklund, 2003
  Klitzschophyllites flabellata (Mohr and Rydin, 2002)
  Cratonia cotyledon Rydin, Mohr and Friis, 2003
  Trifurcatia flabellata Mohr and Rydin, 2002
  Endressinia brasiliana Mohr and Bernardes-de-Oliveira, 2004
Dicotyledons
?Nymphaeales
Magnolialea
  Angiosperm A
  Angiosperm B
Eudicots
?Proteales
  Angiosperm C

Plant taxa based on pollen and spores (listed alphabetically).

Spores

Appendicisporites sp.
Baculatisporites sp.
Balmeisporites sp.
Bellisporites pallescens (Bolkhovitina, 1956) Pocock, 1970
Boseisporites sp. Lima, 1979
Bullasporis aequatorialis Krutzch, 1959
Ceratosporites parvus Brenner, 1963
Cicatricosisporites breavilaesuratus (Couper, 1958) Kemp, 1970
Cicatricosisporites orbiculatus Singh, 1964
Cicatricosisporites subrotundus Brenner, 1963
Cicatricosisporites venustus Déak, 1963
Cingulatisportes psilatus Groot and Penny, 1960
Collarisporites fuscus Déak, 1964
Concavissimisporites punctatus (Delcourt and Sprumont, 1955) Brenner, 1963
Converrucosisporites platyverrucosus Brenner, 1963
Crybelosporites pannuceus (Brenner, 1963) Srivastava, 1975
Cyathidites minor Couper, 1953
Deltoidospora sp.
Densoisporites velatus (Weyland and Krieger, 1953) Krasnova, 1961
Distaltriangulisporites sp.
Dictyophyllidites sp.
Foveotriletes subtriangularis Brenner, 1963
Granulatisporites sp.

Intervlobites sp.
Klukisporites sp.
Leptolepidites verrucatus Couper, 1953
Lycopodiumsporites sp. 1
Lycopodiumsporites sp. 2
Matonisporites equiexinus Couper, 1958
Matonisporites silvai Lima, 1979
Paxillitriletes sp.
Reticulisporites sp.
Retitriletes sp.
Sergipea variverrucata (Regali, Uesugui and Santos, 1974) Regali, 1987
Sergipea sp.
Trilobosporites humilis Delcourt and Sprumont, 1955
Uvaesporites glomeratus Döring, 1965
Verrucosisporites sp.

Pollen

Afropollis aff. *jardinus* Doyle *et al.*, 1982
Alisporites sp.
Applanopsis dampieri (Balme, 1957) Döring, 1961
Applanopsis segmentatus (Balme, 1957) Pons, 1988
Applanopsis trilobatus (Balme, 1957) Döring, 1961
Applanopsis trubatus (Balme, 1957) Dörhöffer, 1977
Araucariacites australis Cookson, 1947
Bennettitaepollenites sp. Lima, 1978
Callialasporites sp.
Classopollis noeli Reyre, 1970
Clavatipollenites hughesii Couper, 1958
Cretacaeiporites sp.
Cycadopites sp.
Elaterocolpites sp.
Elateroplicites sp.
Elaterosporites sp.
Ephedripites sp.
Equisetosporites ambiguus (Hedlund, 1966) Singh, 1983
Equisetosporites reyrei Lima, 1980
Equisetosporites subcircularis Lima, 1980
Eucommiidites sp. Kemp, 1970
Exesipollenites tumulus Balme, 1957
Foveotricolpites sp.
Galeacornea sp.

Gnetaceaepollenites barghoornii (Pocock, 1964) Lima, 1980
Gnetaceaepollenites boltenhagenii Dejax, 1985
Inaperturopollenites dubius (Potonie and Venitz, 1934) Pflug and Thompson 1953
Penetetrapites mollis Hedlund and Norris, 1968
cf. *Penetetrapites incipiens* Lima, 1978
Podocarpidites sp.
Protopinus sp.
Psilatricolpites psilatus Pierce, 1961
Psilatricolpites sp.
Retimonocolpites dividuus Pierce, 1961
cf. *Retimonocolpites* sp. 2 Doyle *et al.*, 1977
Rousea sp.
Senegalosporites sp.
Sergipea sp.
Singhia sp.
Sofrepites sp.
Spheripollenites scabratus (Couper, 1958) Pocock, 1970
Steevesipollenites sp.
Stellatopollis araripensisdensiornatus (Lima 1976) Lima 1978
Stellatopollis barghoornii Doyle, 1975
Striatopollis sp.
Tetracolpites sp.
Tricolpites micromunus (Groot and Pennt, 1960) Singh, 1971
Tricolpites sp.
Tucanopollis sp.
Vitreisporites sp.

Algae

Chomotriletes sp.
Maranhites sp.
Ovoidites sp.

Systematic index

Plate 1. The Chapada do Araripe. (a) View looking south from Santana do Cariri towards the spring-line village of Cancau with the escarpment of the Chapada do Araripe in the background. The Crato Formation crops out on the lower flanks of the chapada in this region. (b) A typical stone quarry in the Nova Olinda Member of the Crato Formation between Nova Olinda and Santana do Cariri with the Chapada do Araripe escarpment in the background.

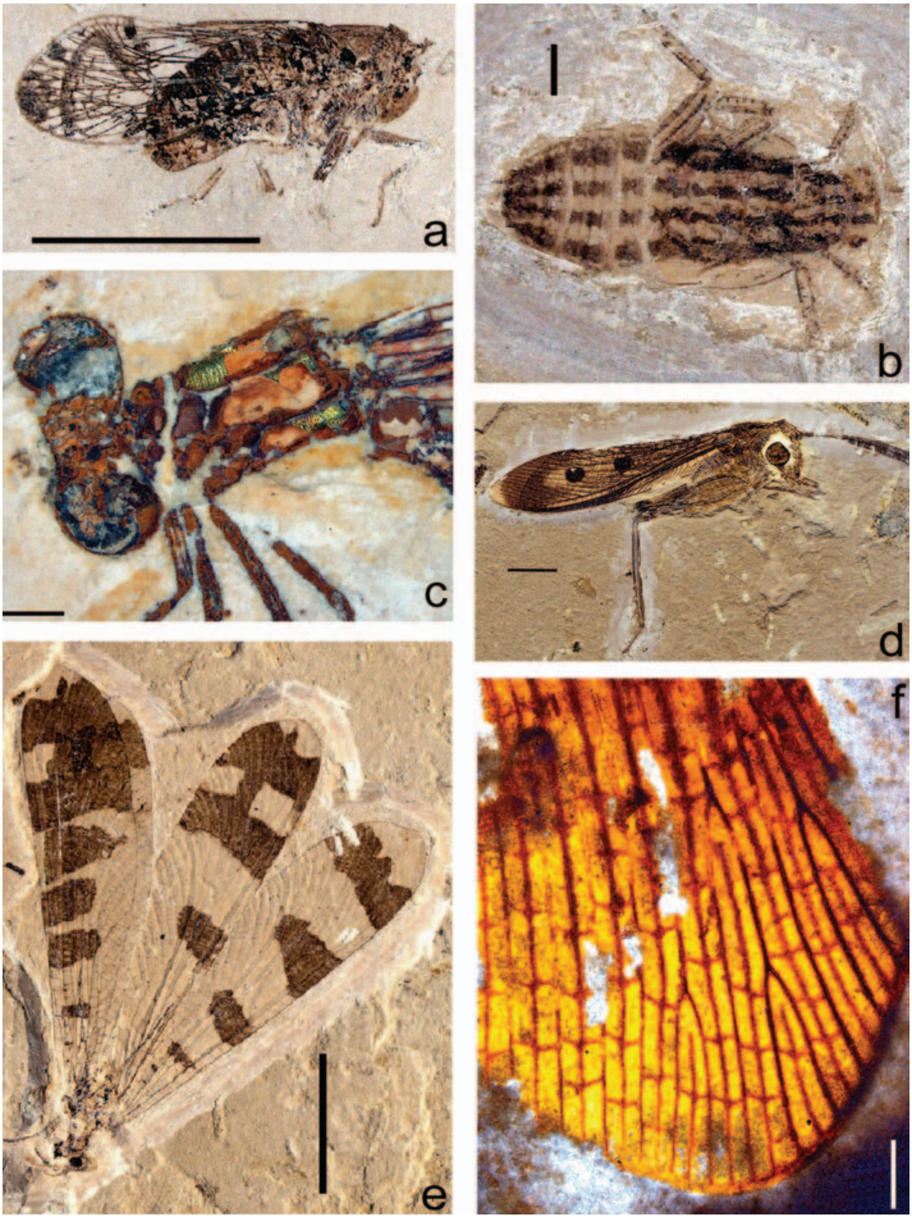

Plate 2. Colour preservation in Crato Formation insects. (a) Spots on the wings of a cicadomorph; scale bar, 10 mm. (b) Stripes on the body of a probable cockroach larva, scale bar, 2 mm. (c) Metallic green colour preserved on thorax of the odonatan *Cretarchistigma* (?) *essweini*, SMNS 66393; scale bar, 1 mm (this is the oldest fossil record of preserved interference colours!). (d) Spots and anterior wing stripe on an orthopteran; scale bar, 5 mm. (e) Spots on the wings of the neuropteran *Baisopardus cryptohymen*, holotype SMNS 65470. (f) A roach wing, acid-prepared from both sides and embedded in synthetic resin; scale bar, 0.5 mm.

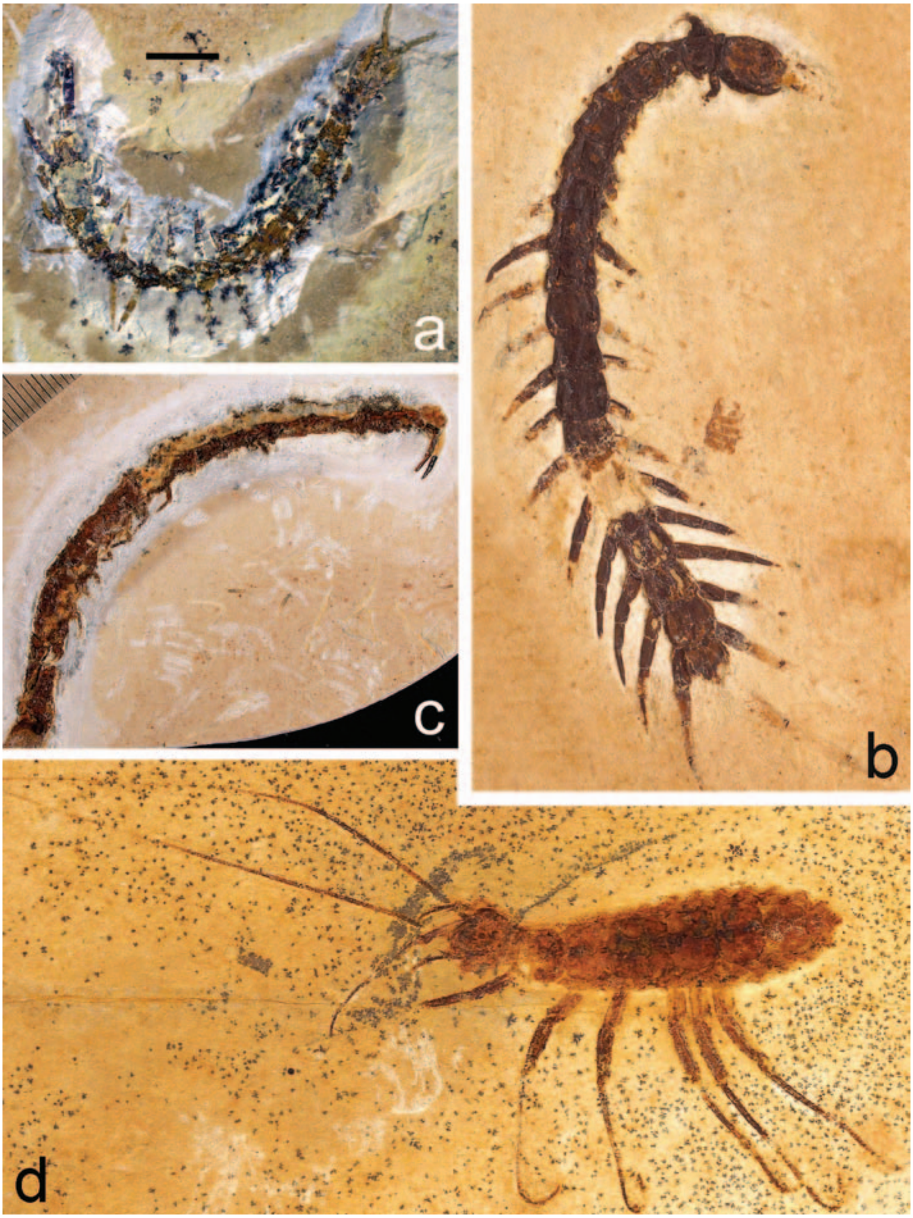

Plate 3. Crato centipedes: (a) *Velocipede betimari* (Martill and Barker, 1998), SMNK 2345; (b) *Cratoraricrus oberlii* (Wilson, 2003), holotype specimen SMNS 64431; (c) undetermined centipede, MURJ; (d) *Fulmenocursor tenax* (Wilson, 2001), holotype SMNS 64275. Scale bars, 10 mm.

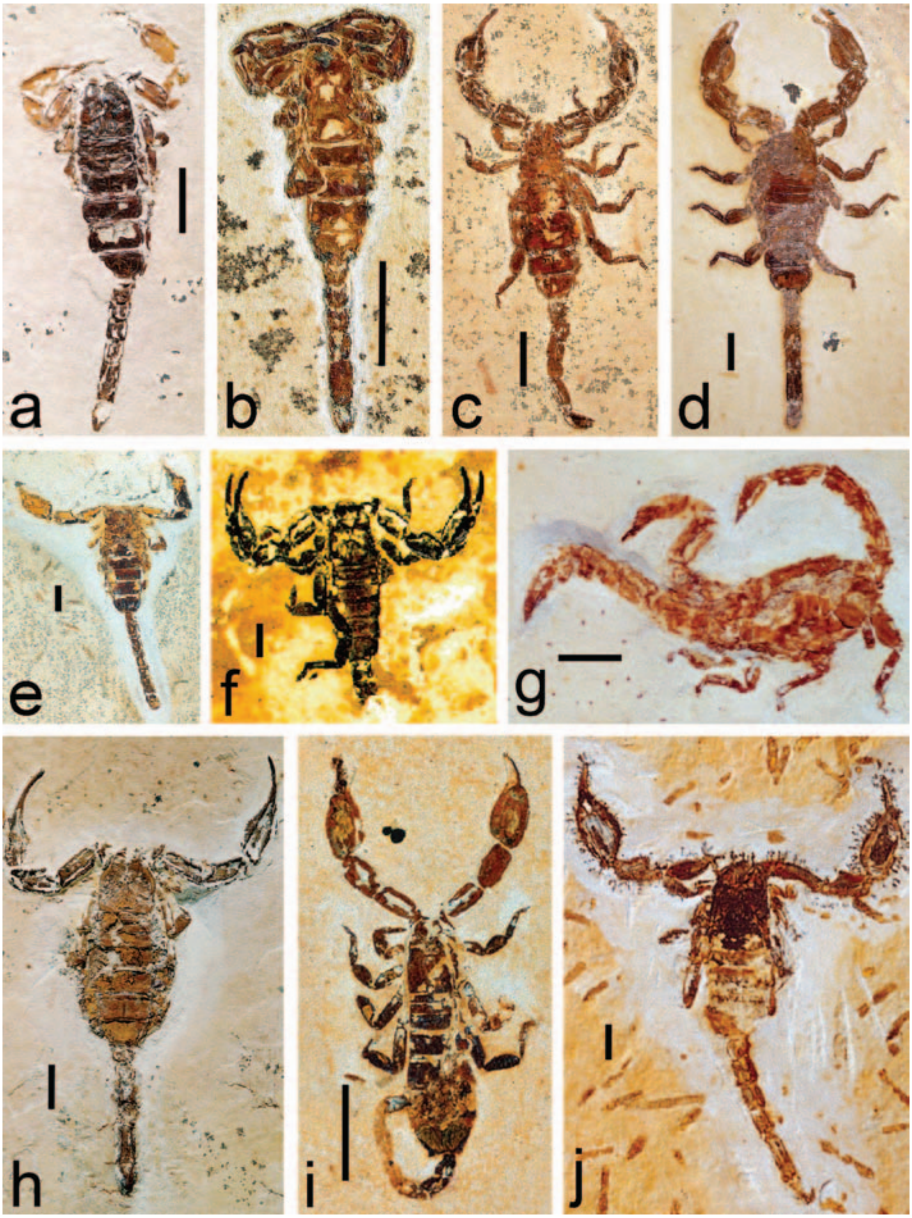

Plate 4. Crato scorpions: (a–f, i, j) *Protoischnurus axelrodorum* Carvalho and Lourenço, 2001; (g) Scorpionidae indet.; (h) *Araripescorpius ligabuei* Campos, 1986. Scale bars, 10 mm.

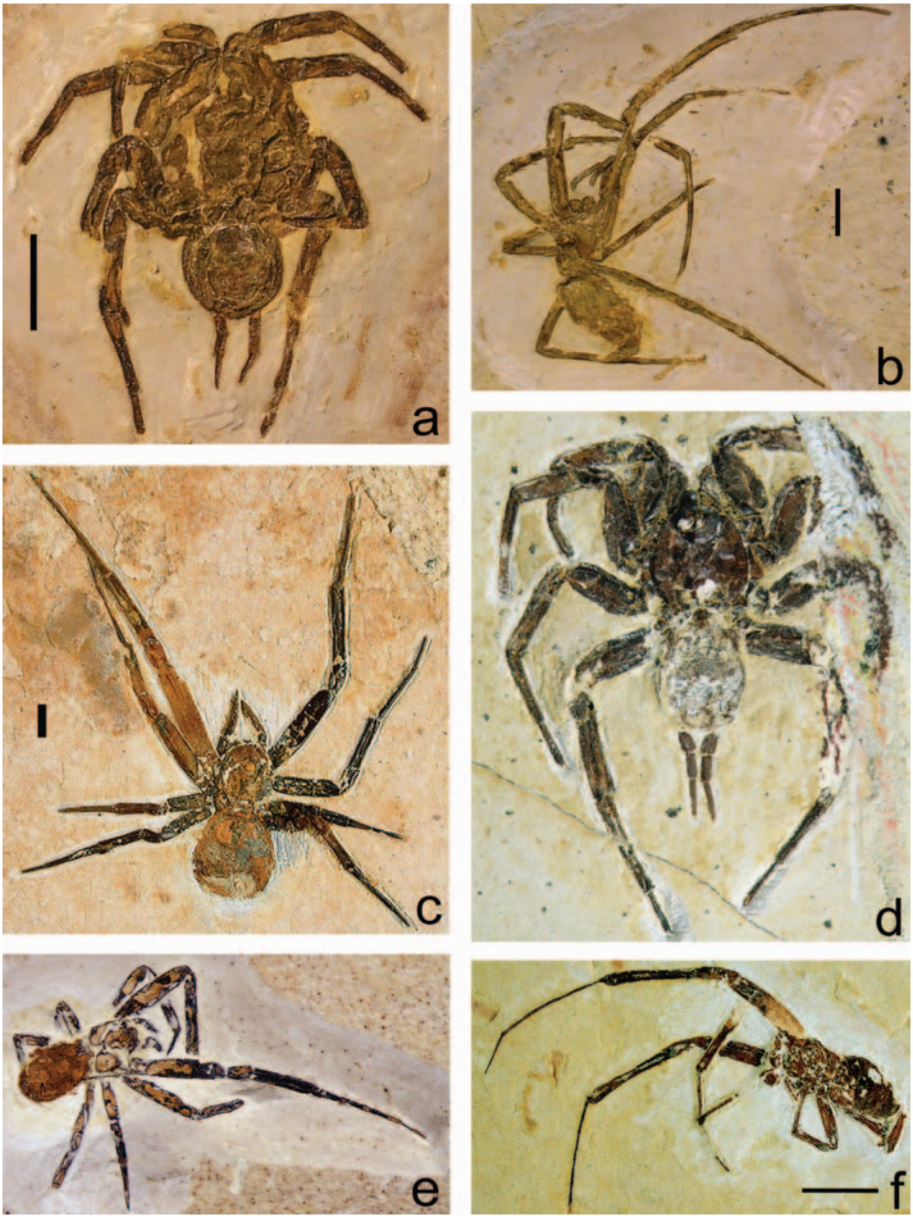

Plate 5. Crato spiders: (a) *Dinodiplura ambulacra* Selden, 2006; (b, c, e, f) *Cretaraneus martinsnetoi* Mesquita, 1996; (d) *Cretadiplura ceara* Selden, in Selden *et al.*, 2006. Scale bars, 5 mm (a, b, f), 1 mm (c).

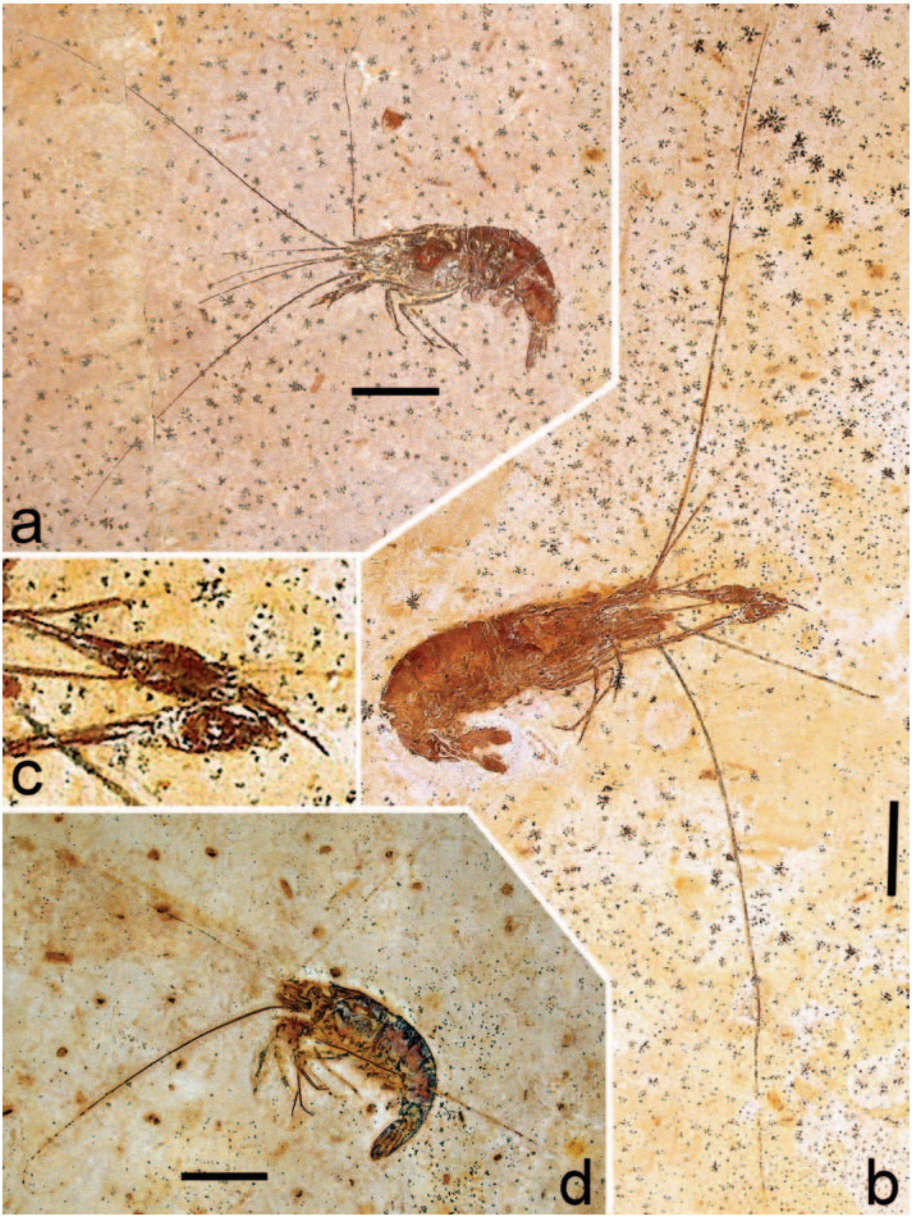

Plate 6. Crato shrimp *Beurlenia araripensis* Martins-Neto and Mezzalira, 1991. (a) MURJ. Length of specimen from tip of the rostrum to the end of the tail fan, measured along the dorsal line, is 37 mm. (b) A well-preserved example, MURJ. (c) Detail of terminal anterior appendages. (d) Moult with preserved rostrum but lacking some appendages, MSF; length of specimen approximately 23 mm. Scale bars, 10 mm.

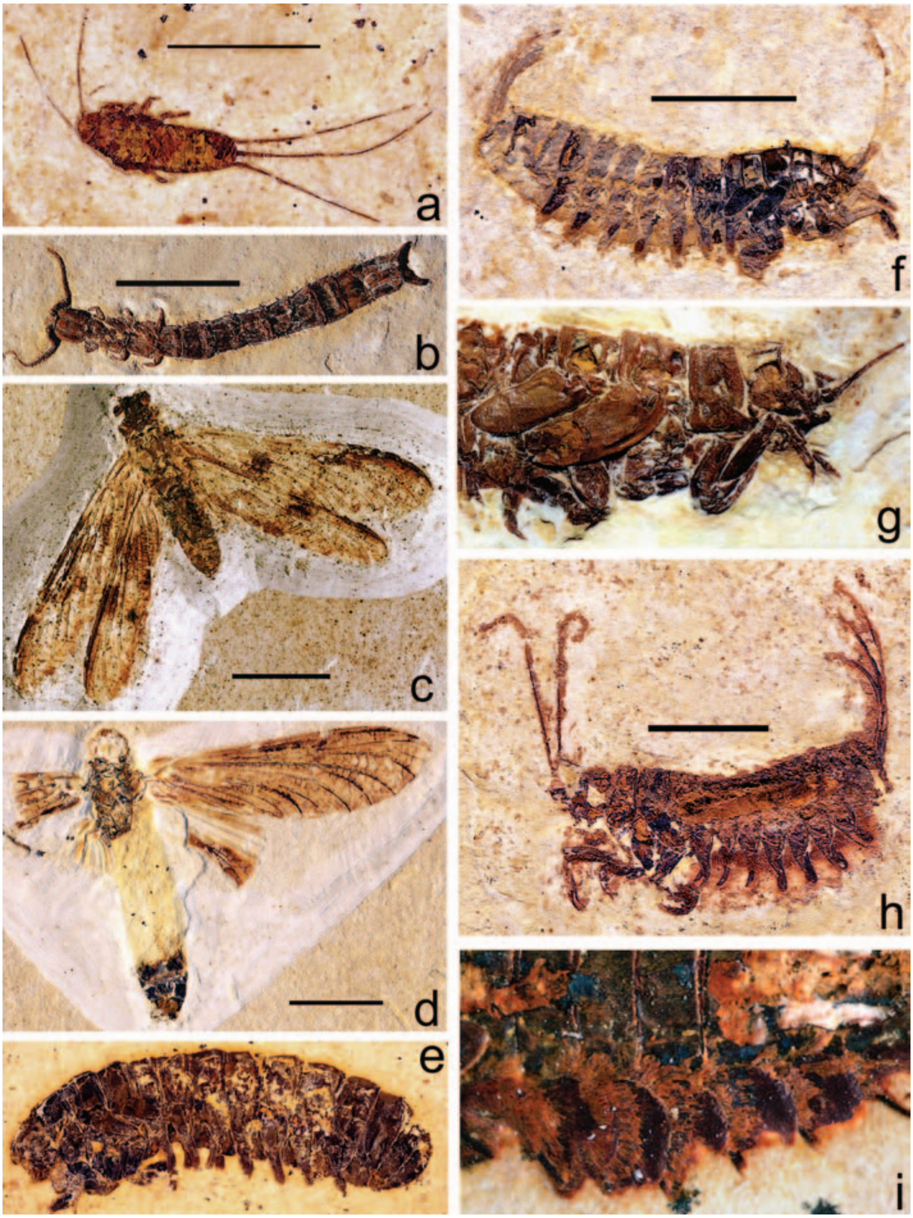

Plate 7. Crato insects: (a) Zygentoma, Lepismatidae gen. et sp. nov., SMNS 66535; (b) Diplura, Japygoidea, *Ferrojapyx vivax* Wilson and Martill, holotype, SMNS 64276; (c) *Cretereisma antiqua* sp. nov., holotype SMNS 66546 (Photo B. Schuster); (d) *Cretereisma schwickertorum* sp. nov., holotype SMNS 66598, ventral aspect; (e) *Cretereisma* sp., nymph, SMNS 66673; (f) *Cretereisma* sp., nymph, SMNS 66547; (g) *Cretereisma* sp., nymph no. 512 MURJ; (h) *Cretereisma* sp., nymph, SMNS 66599; (i) Ephemeroptera, Hexagenitidae, *Protoligoneuria limai*, larval gills with tufts, MSF Q4. Scale bars, 10 mm.

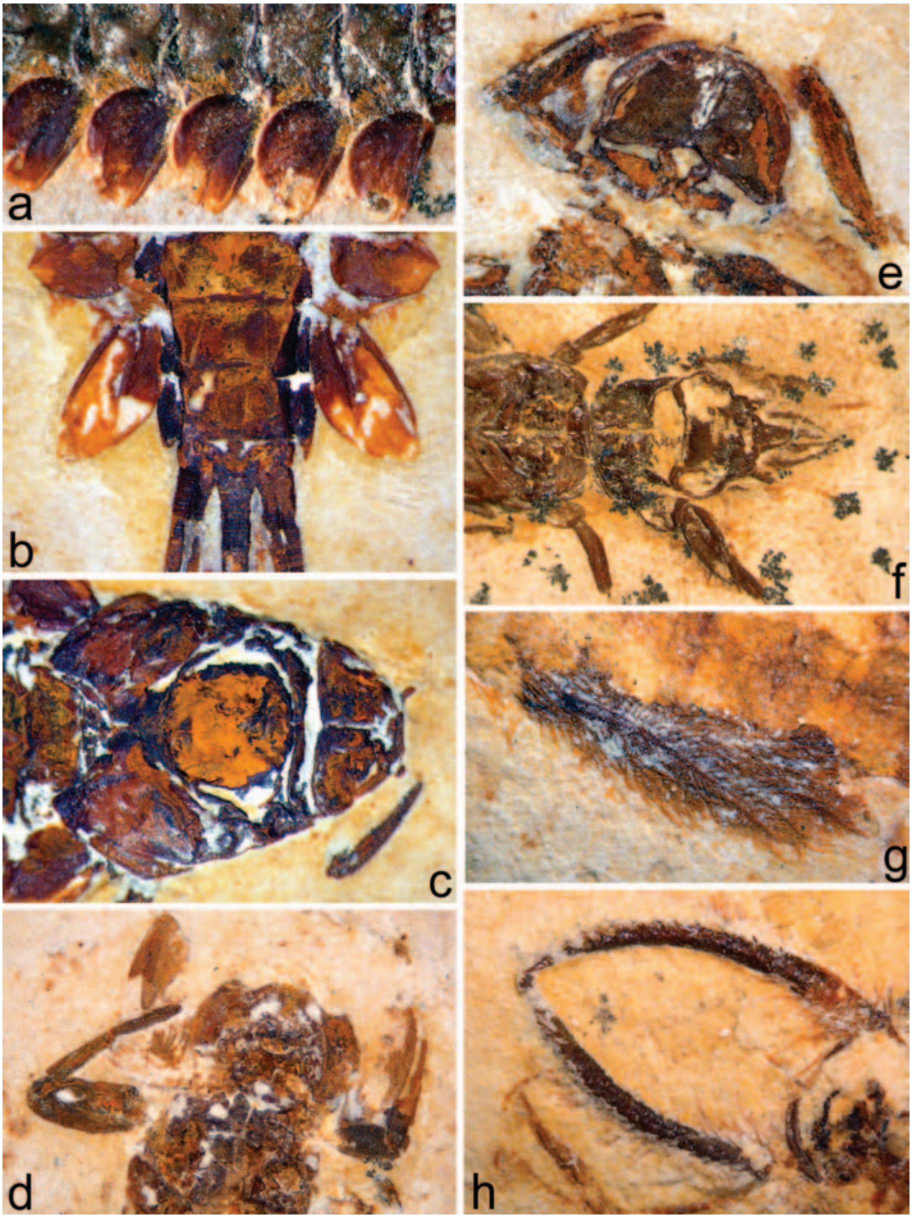

Plate 8. Crato mayfly larvae: (a) *Protoligoneuria limai*, larval gills with tufts, MSF Q9; (b) *Protoligoneuria limai* larval seventh gill plates, SMNS 66537; (c) *Protoligoneuria limai*, larval head and thorax with fusion of wing pads, SMNS 66537; (d) *Colocrus indivicum*, larval filter apparatus, SMNS 66538; (e) *Colocrus indivicum*, larval head with labial plate, SMNS 66619; (f) Ephemeroidea indet., larval head, SMNS 66630; (g) Euthyplocidae, *Pristiplocia* sp., larval gills, SMNS 66621; (h) Euthyplocidae, *Pristiplocia* sp., larval mandibles, SMNS 66621. Without scale bars.

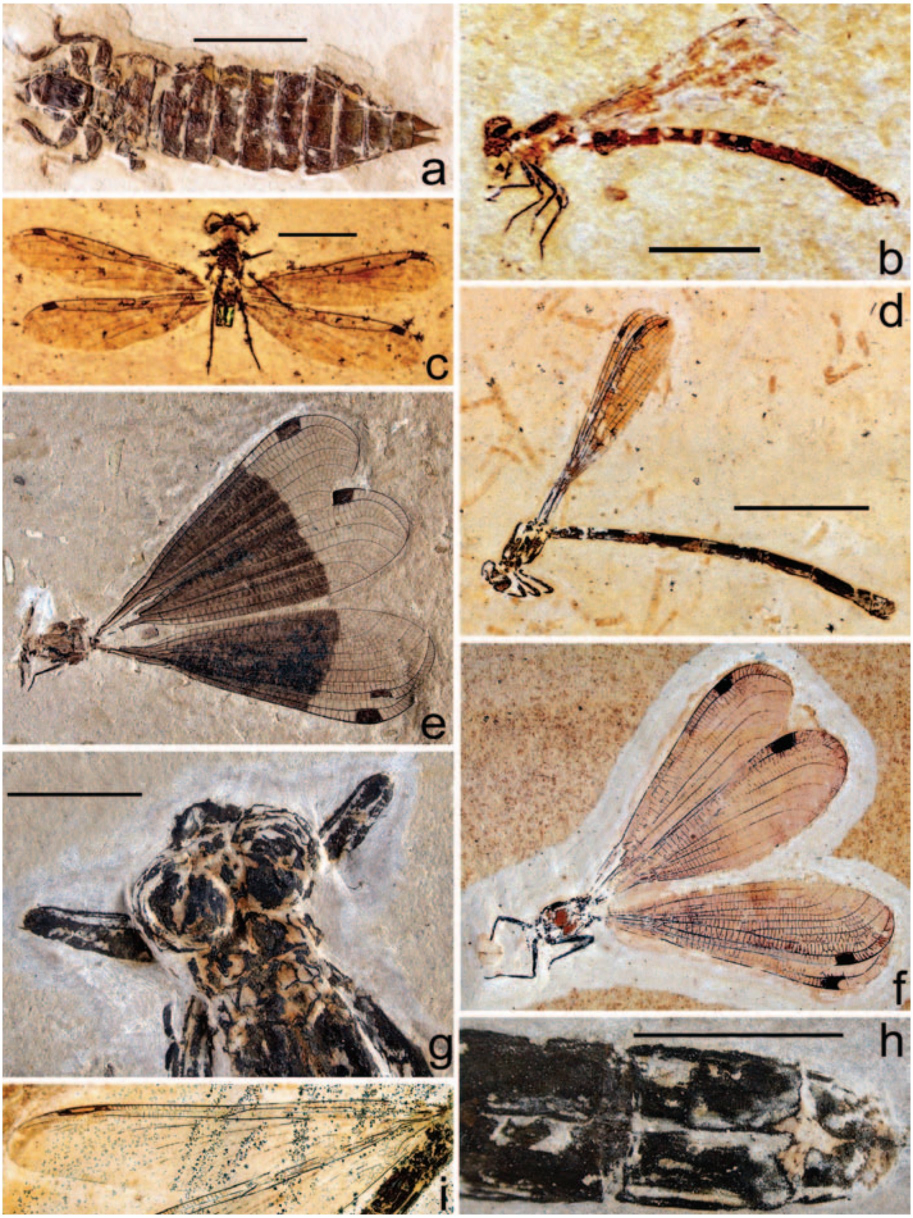

Plate 9. Crato Odonata: (a) gomphid larva with mask, SMNS 66402; (b) Hemiphlebidae?, *Cretarchistigma essweini*, male with anal appendages, MSF G3; (c) *Parahemiphlebia cretacica* with preserved green metallic colour on first abdominal segment, MSF 39; (d) *Eoprotoneura hyperstigma*, female with ovipositor, MSF O6; (e) *Euarchistigma atrophium* with colour pattern, SMF Q55; (f) *Euarchistigma marialuiseae* sp. nov., holotype SMF Q56; (g) *Cratostenophlebia schwickerti* gen. et sp. nov., male head, holotype SMNS Z109; (h) *Cratostenophlebia schwickerti* gen. et sp. nov., male anal appendages, holotype SMNS Z109; (i) *Cratostenophlebia schwickerti* gen. et sp. nov., female, left forewing, paratype and allotype SMNS Z110. Scale bars, 10 mm, except (a), 5 mm.

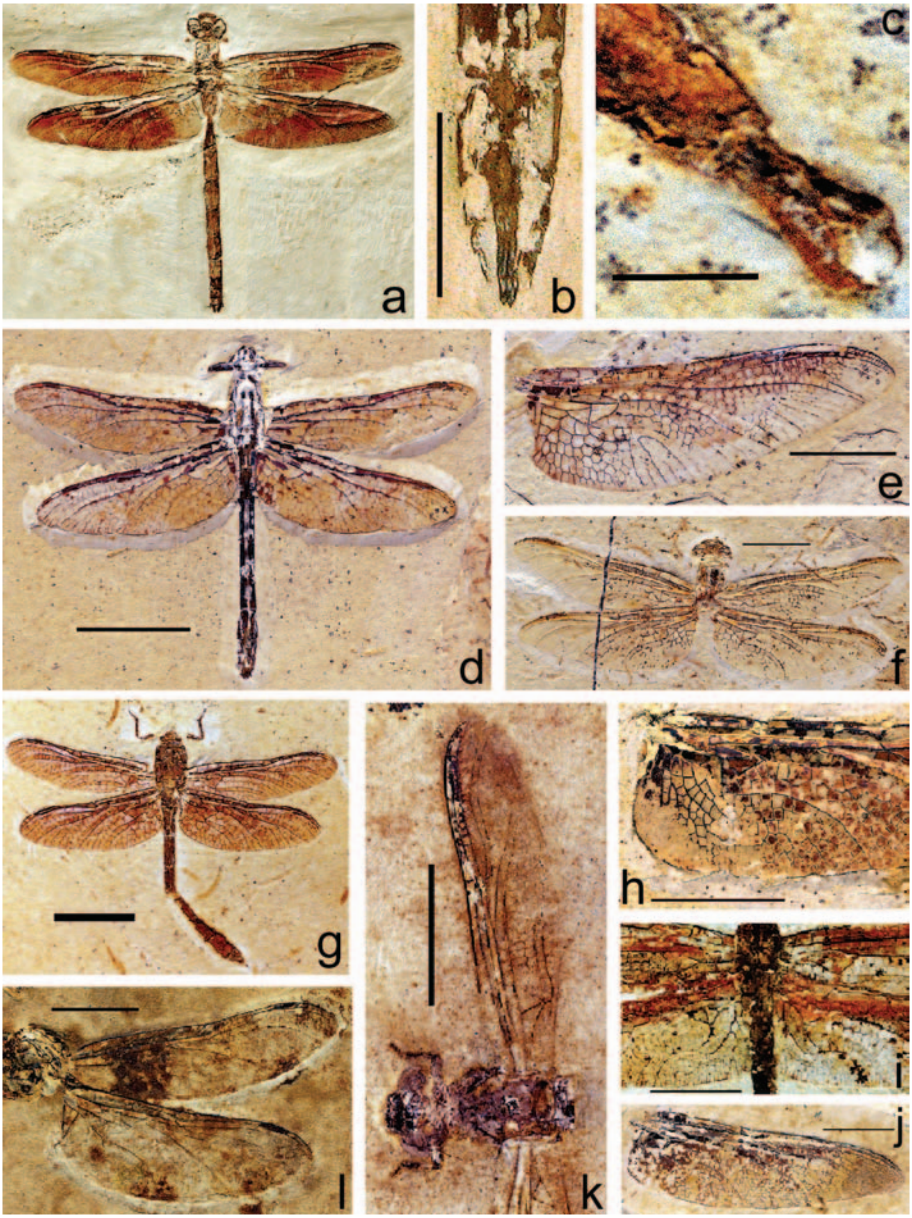

Plate 10. Crato Odonata: (a) *Araripeliupanshania annesuseae*, male, holotype MB. 1999.3 MB.I.2047; (b) *Araripegomphus andreneli*, female, ovipositor, SMNS 66392; (c) *Araripegomphus andreneli* male, anal appendages, MSF G10; (d) *Cordulagomphus* cf. *tuberculatus*, female, SMNS 64361; (e) *Cordulagomphus winkelhoferi* sp. nov., male, holotype SMNS 66607; (f) *Cordulagomphus hanneloreae* sp. nov., female, holotype SMNS 66591; (g) *Procordulagomphus michaeli* sp. nov., male, holotype MURJ no 514; (h) *Araripephlebia mirabilis*, female?, right hind wing, SMNS 66618; (i) *Araripephlebia mirabilis*, female?, wing bases, MSF G16; (j) Odonata, Anisoptera, gen. et sp. nov., female, SMNS 66567; (k) Odonata, Anisoptera, gen. et sp. nov., SMNS 66608; (l) Odonata, Anisoptera, gen. et sp. nov., male, SMNS 66614. Scale bars: (b), 5 mm; (c), 3 mm; (d, f, j, k), 15 mm; (e, g, h, i, l), 10 mm.

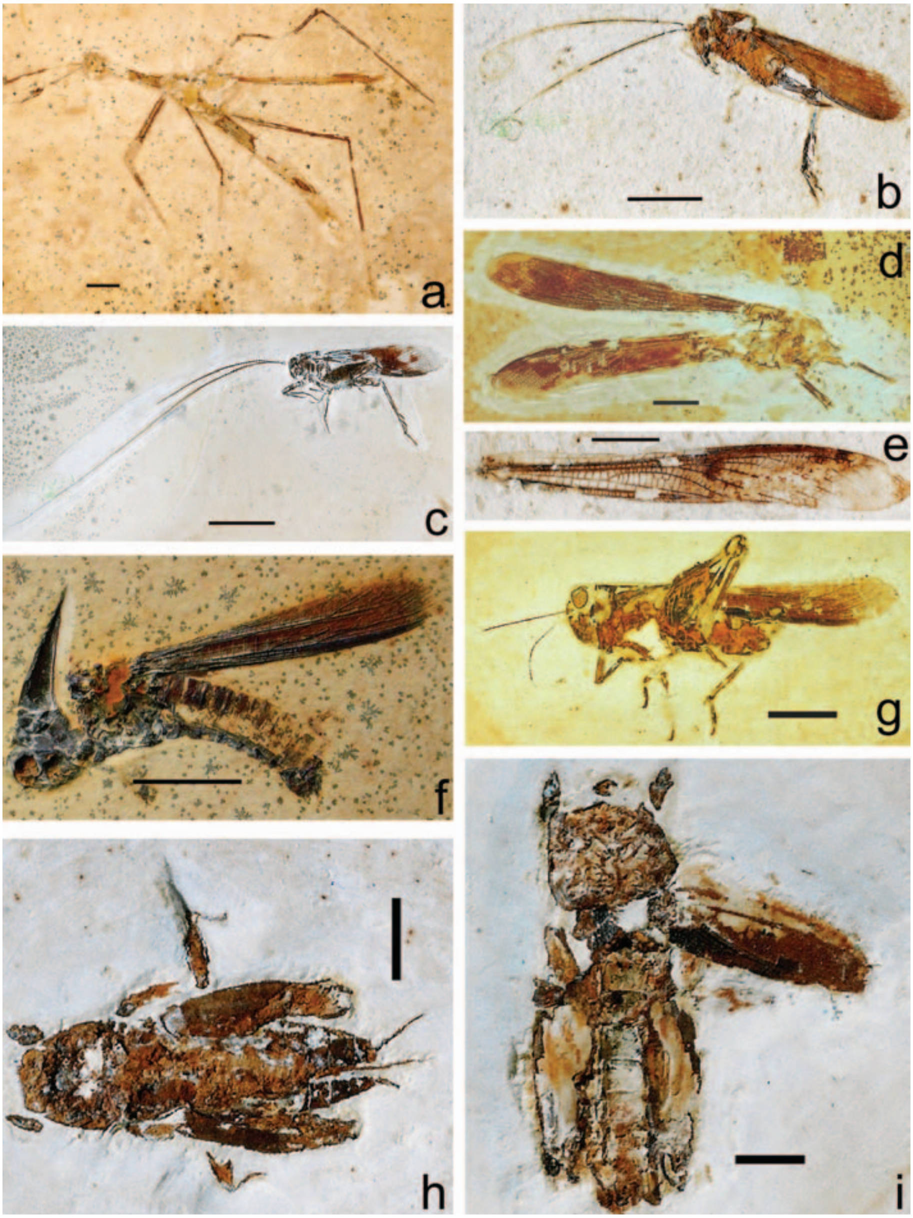

Plate 11. Crato Orthoptera: (a) Proscopiidae gen. et sp. nov. SMNS 66000–135; (b) Elcanidae, *Cratoelcana damianii* Martins-Neto, 1991a, SMNS 66498; (c) *Cratoelcana zessini* Martins-Neto, 1991a, SMNS 66566; (d) Locustopseidae, *Zessinia pulcherrima* Martins-Neto, 1990, priv. coll.; (e) Locustopseidae gen. nov., SMNS 66499; (f) Araripelocustidae, *Araripelocusta longinota* Martins-Neto, 1995, koshny coll.; (g) *Araripelocusta brevis* Martins-Neto, 1995, priv. coll.; (h) Tridactylidae, *Cratodactylus ferreirai* Martins-Neto, 1990, SMNS 66495; (i) *Cratodactylus ferreirai* Martins-Neto, 1990, SMNS 66489. Scale bars, 5 mm except h and i, 2 mm.

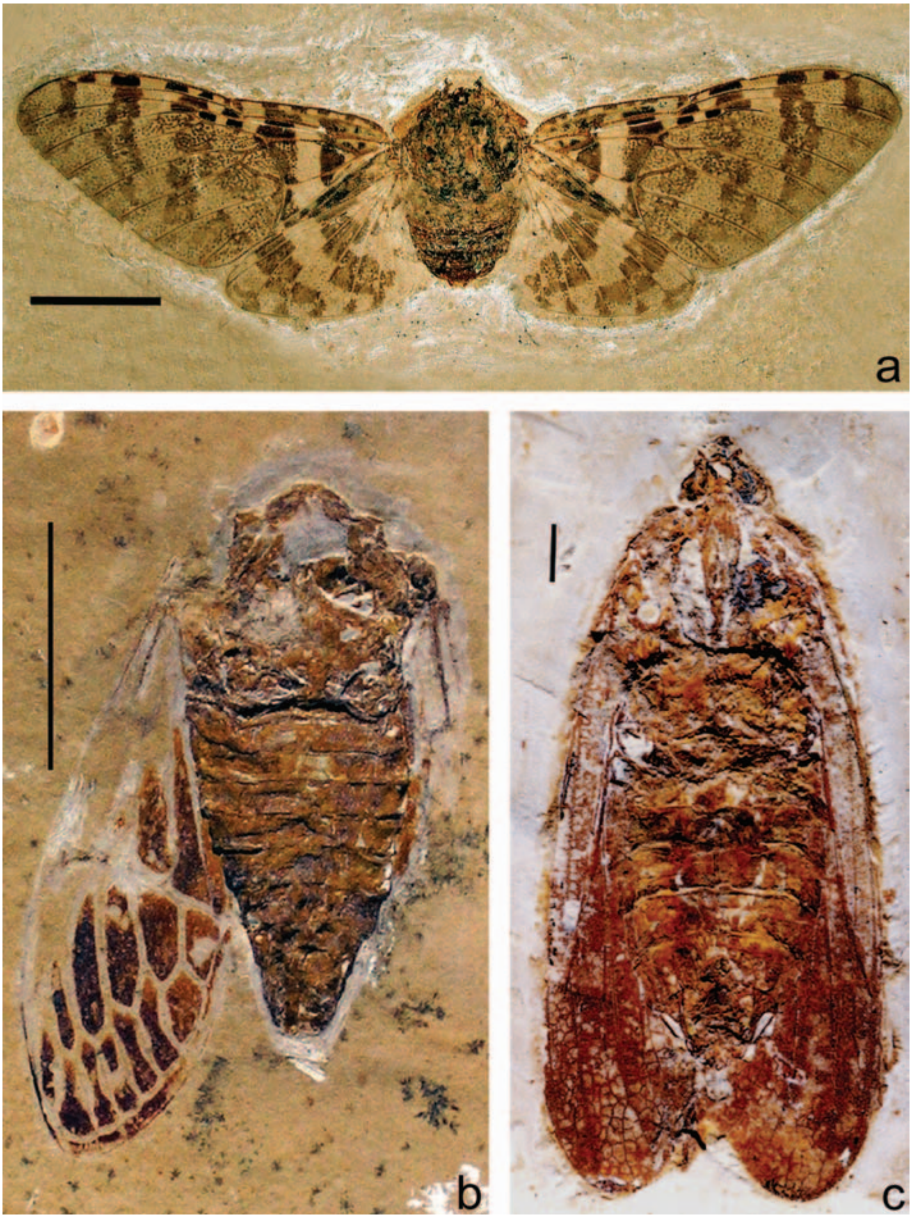

Plate 12. Crato Cicadomorpha and Fulgoromorpha: (a) fine example of palaeontinid cicadomorph *Baeocossus* cf. *fortunatus* Menon and Heads, 2005, with colour pattern preservation, KMNH without number; (b) Tettigarctidae *Tettagalma striata* Menon, 2005 with colour pattern preservation, SMNS 66507; (c) Fulgoromorpha, Fulgoridae, gen. et sp. nov., SMNS 66413, ventral aspect. Scale bars: a, b, 1 mm; c, 2 mm.

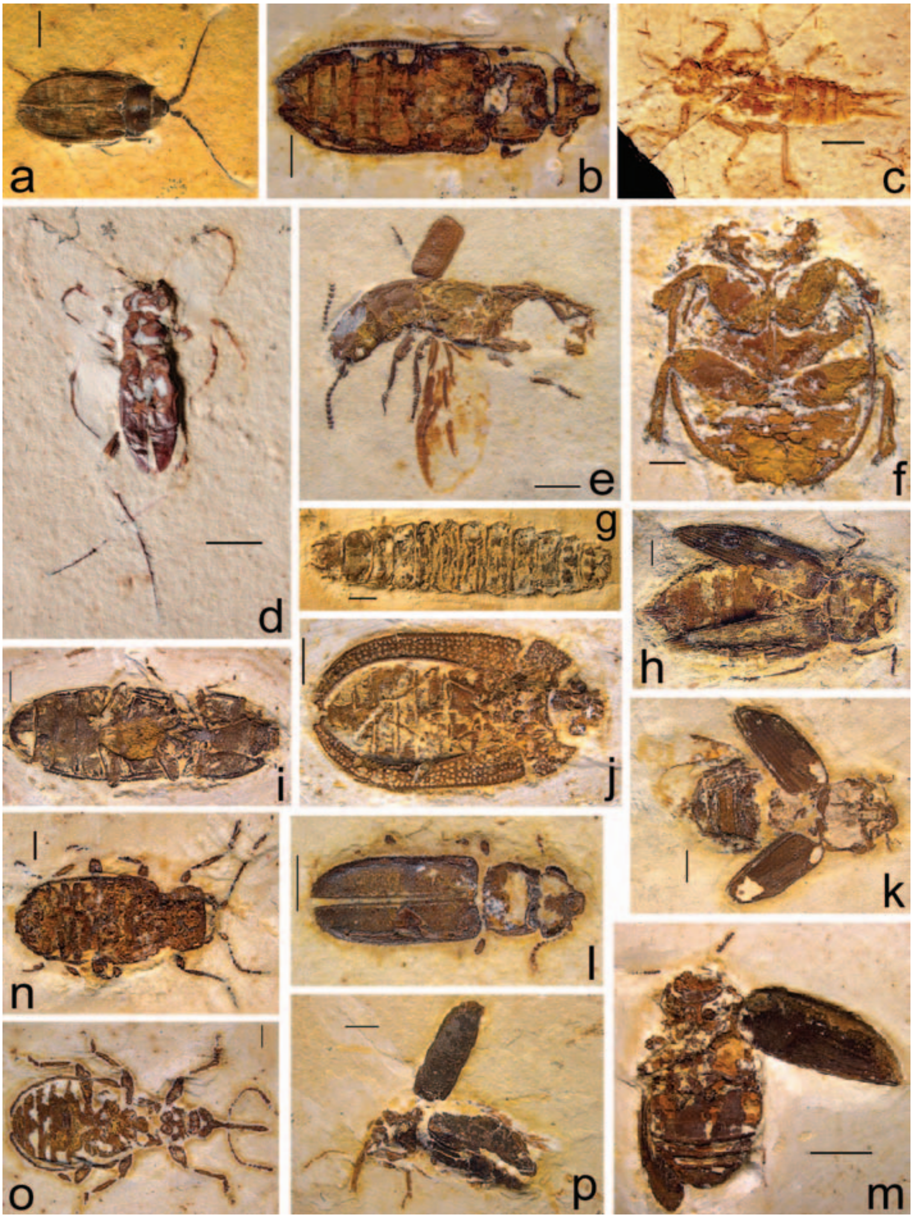

Plate 13. Crato beetles: (a) Archostemata, probably Cupedidae, SMNS 66552; scale bar, 2 mm; (b) Archostemata, probably Ommatidae, SMNS 66456; scale bar 2 mm; (c) Odonata dragonfly larva *Nothomacromia sensibilis*, originally described as a possible coptoclavid beetle named *Conan barbarica* by Martins-Neto (1998); scale bar, 10 mm; (d) Carabidae, Cicindelinae, *Oxycheilopsis cretacicus* Cassola and Werner, 2004, holotype ZSM without number; scale bar, 2 mm (photograph courtesy of Karl Werner); (e) Staphylinidae, SMNS 66452; scale bar, 1 mm; (f) Scarabaeidae, SMNS 66458; scale bar, 1 mm; (g) Hydrophilidae, larva, SMNS 66446; scale bar, 1 mm; (h) Buprestidae, SMNS 66461; scale bar, 2 mm; (i) Elateridae, SMNS 66465; scale bar, 2 mm; (j) Trogossitidae, Peltinae, SMNS 66467; scale bar, 2 mm; (k) Nitidulidae, SMNS 66470; scale bar, 1 mm; (l) Cucujidae, SMNS 66468; scale bar, 1 mm; (m) probably Tenebrionidae, SMNS 66472; scale bar, 5 mm; (n) Chrysomelidae, probably Eumolpinae, SMNS 66471; scale bar, 1 mm; (o) Curculionoidea, probably Belidae,?Oxycoryninae, SMNS 66553; scale bar, 1 mm; (p) Curculionoidea, Attelabidae, probably Rhynchitinae, SMNS 66449; scale bar, 2 mm.

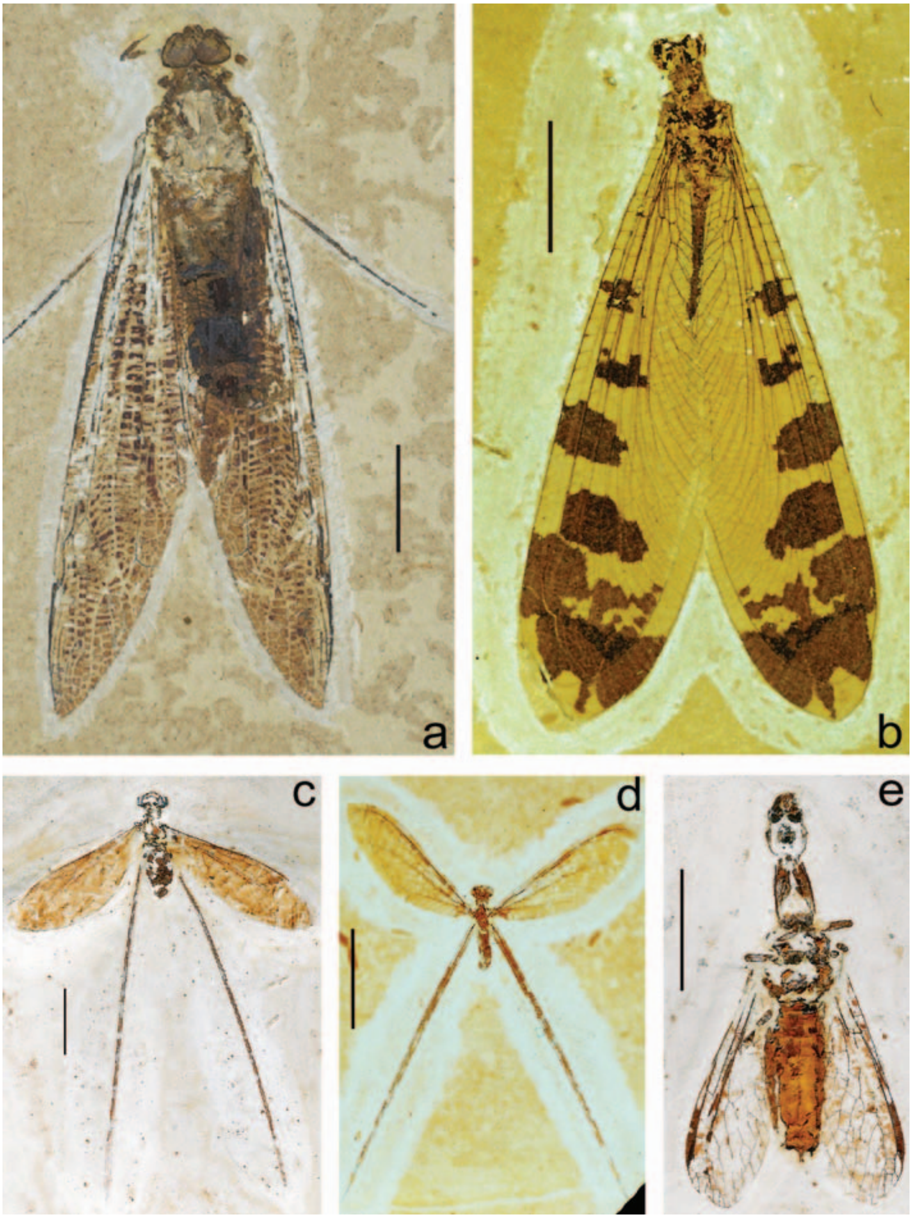

Plate 14. Crato Neuropterida: (a) Schwickertoptera Bechly ord. nov., *Rafaelia maxima* Nel *et al*. 2005, SMNS coll.; (b) Myrmeleontiformia, Palaeoleontidae, SMNS coll.; (c) Myrmeleontiformia, Nemopteridae sp. 2, SMNS 66000/260; (d) Myrmeleontiformia, Nemopteridae sp. 1, priv. coll.; (e) Raphidioptera, *Baissoptera* sp. Scale bars, 10 mm, except (e), 5 mm.

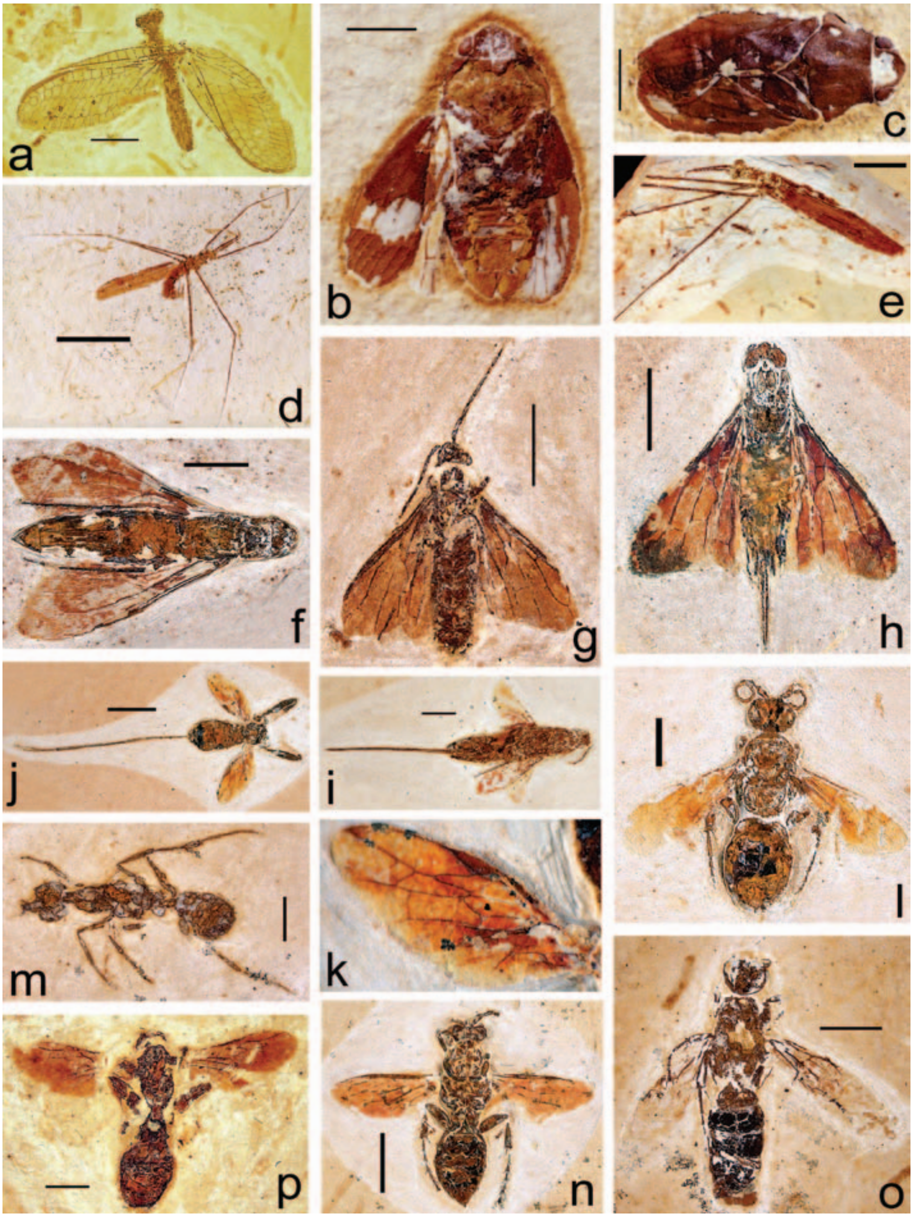

Plate 15. Crato insects: (a) Neuroptera, Hemerobiiformia, Mesochrysopidae gen. et sp. nov., priv. coll.; scale bar, 5 mm; (b) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66423; scale bar, 2 mm; (c) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66431; scale bar, 2 mm; (d) Chresmododea, Chresmodidae, *Chresmoda* sp. nov., SMNS prelim. no. 0134 (old no. H56), scale bar = 20 mm; (e) Chresmododea, Chresmodidae, *Chresmoda* sp. nov., ex MSF coll G88; scale bar, 10 mm; (f) Hymenoptera, Anaxyelidae, MURJ without number; scale bar, 5 mm; (g) Anaxyelidae, *Protsyntexis* sp., SMNS 66304; scale bar, 5 mm; (h) Siricidae, MURJ without number; scale bar, 5 mm; (i)?Ichneumonoidea, MURJ without number; scale bar, 5 mm; (j) Ephialtitidae, *Cretephialtites kourios*, MURJ without number; scale bar, 5 mm; (k) Ephialtitidae, *Cretephialtites kourios*, right wings, MURJ without number, without scale; (l) ?Pompilidae, MURJ without number; scale bar, 2 mm; (m) Formicidae, Mymeciinae, *Cariridris bipetiolata*, SMNS 66565; scale bar, 2 mm; (n) Tiphiidae, *Architiphia rasnitsyni*, MURJ without number; scale bar, 5 mm; (o) Tiphiidae,?Myzininae, SMNS 66303; scale bar, 5 mm; (p) Vespidae, ?Eumeninae, SMNS 66295; scale bar, 2 mm.

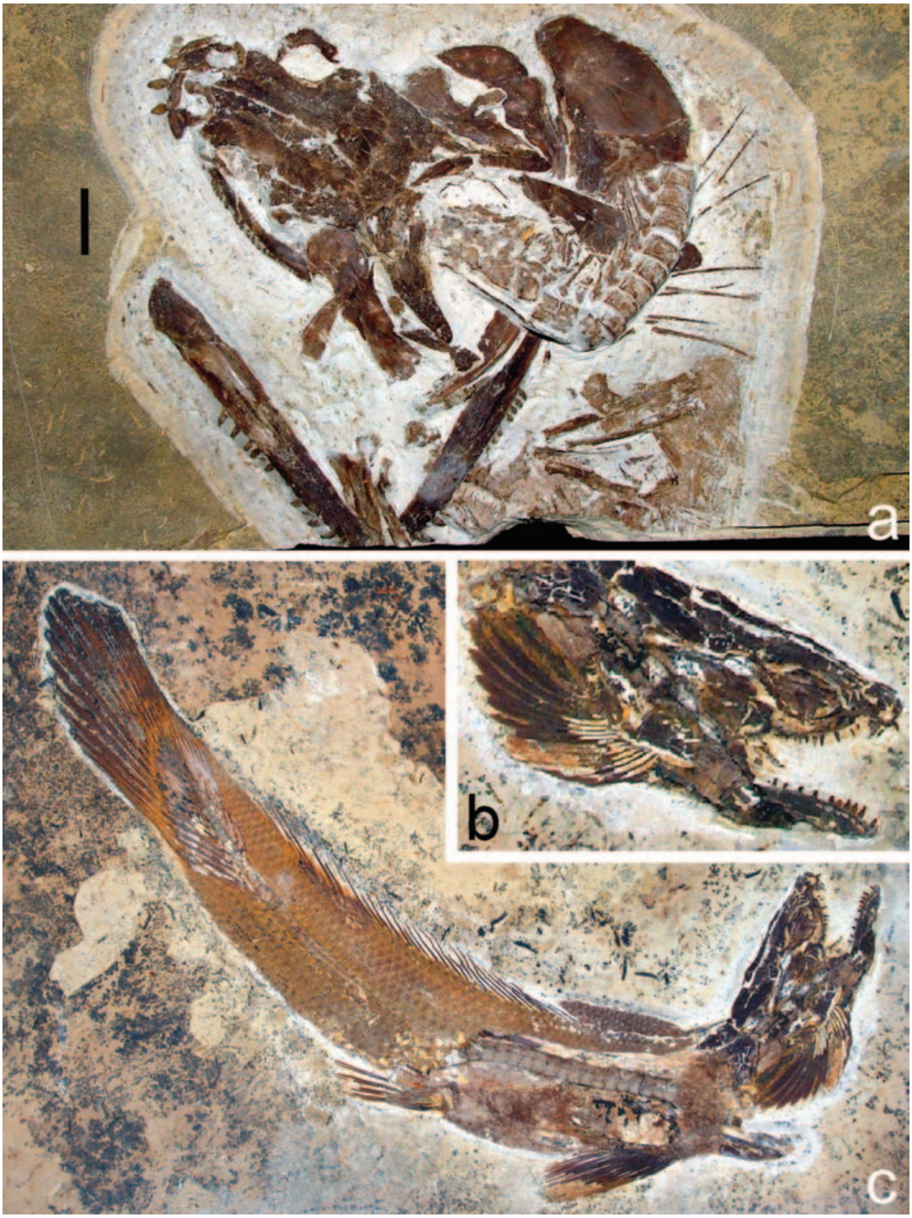

Plate 16. Crato Amiiformes: (a) disarticulated skull of unidentified Amiidae, possibly Vidalamiinae; scale bar, 10 mm; (b, c) rare example of a complete Crato Fm. Amiidae, MURJ coll.

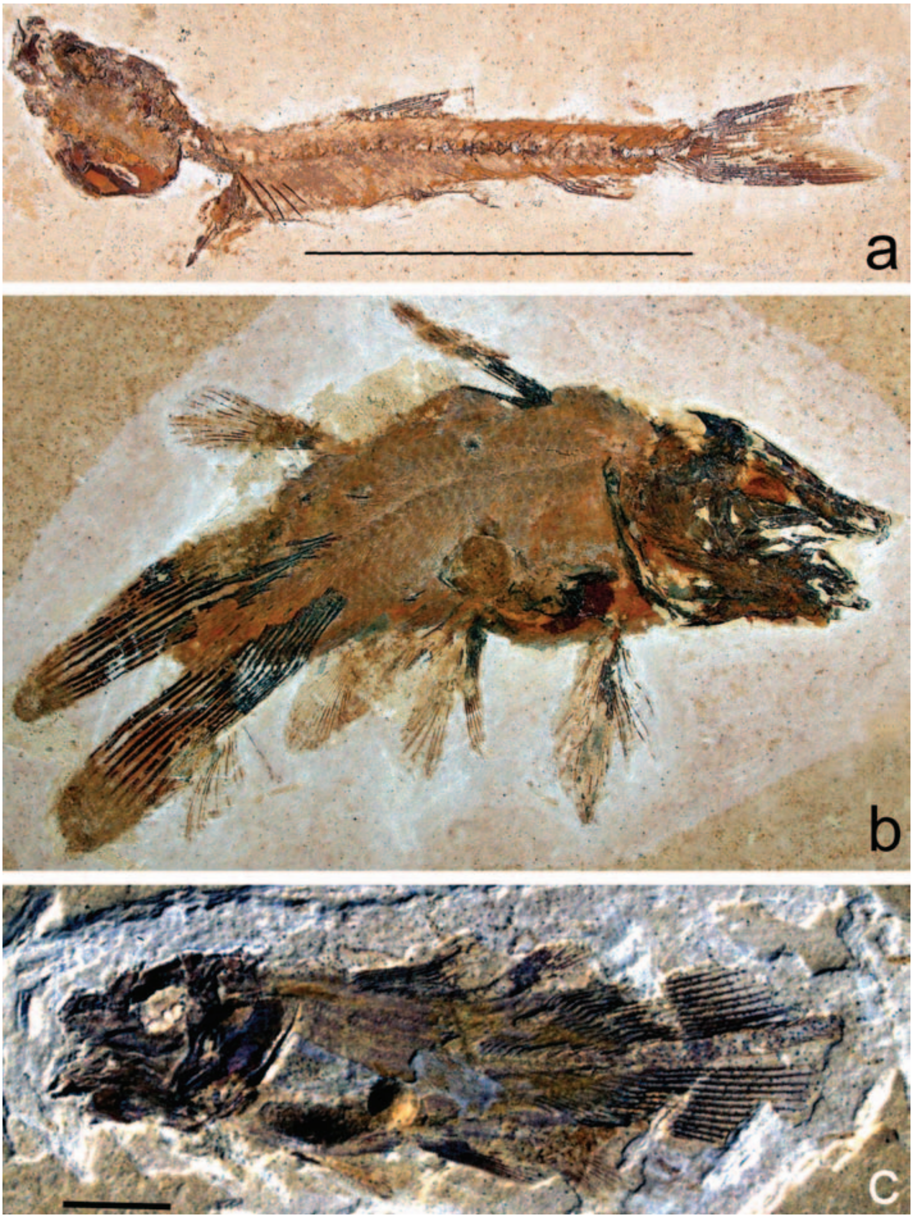

Plate 17. Crato fish: (a) *Dastilbe crandalli* Jordan, 1910, young example with partially detached skull; (b, c) two examples of juvenile coelacanth *Axelrodichthys* sp. The distal lobes of the caudal fin in (b) are a fabrication executed by the fossil collectors of Nova Olinda.

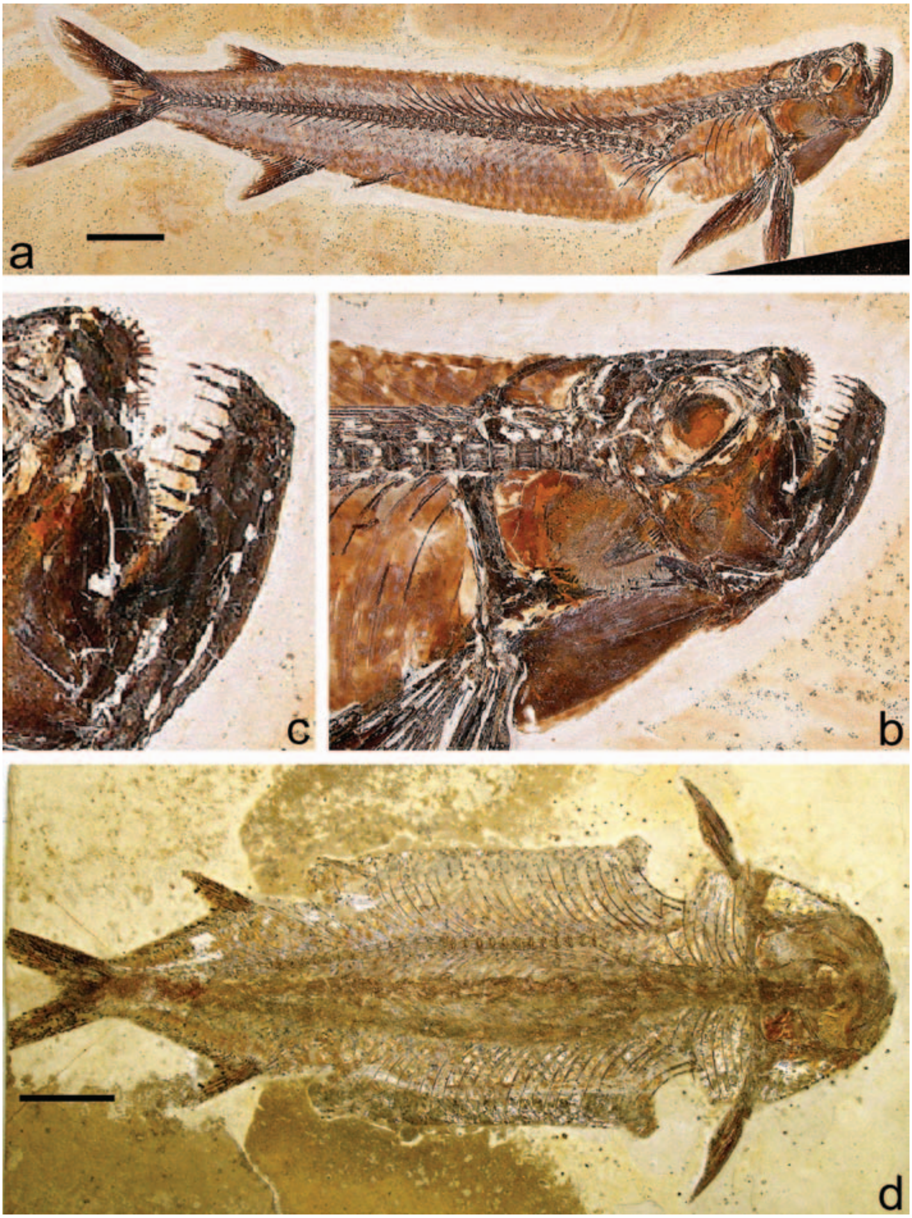

Plate 18. Examples of the ichthyodectid *Cladocyclus gardneri* Agassiz, 1841: (a) near-complete example in almost perfect condition, excepting disrupted vertebral column just above stomach region; (b) skull of same specimen highlighting the dorsally directed mouth opening; (c) dentition of same specimen showing the semi-circular dental border of the premaxilla and needle-like teeth of the dentary; (d) a ‘filleted’ example. Unusually, this specimen appears to have split along its ventral border. Scale bars, 20 mm.

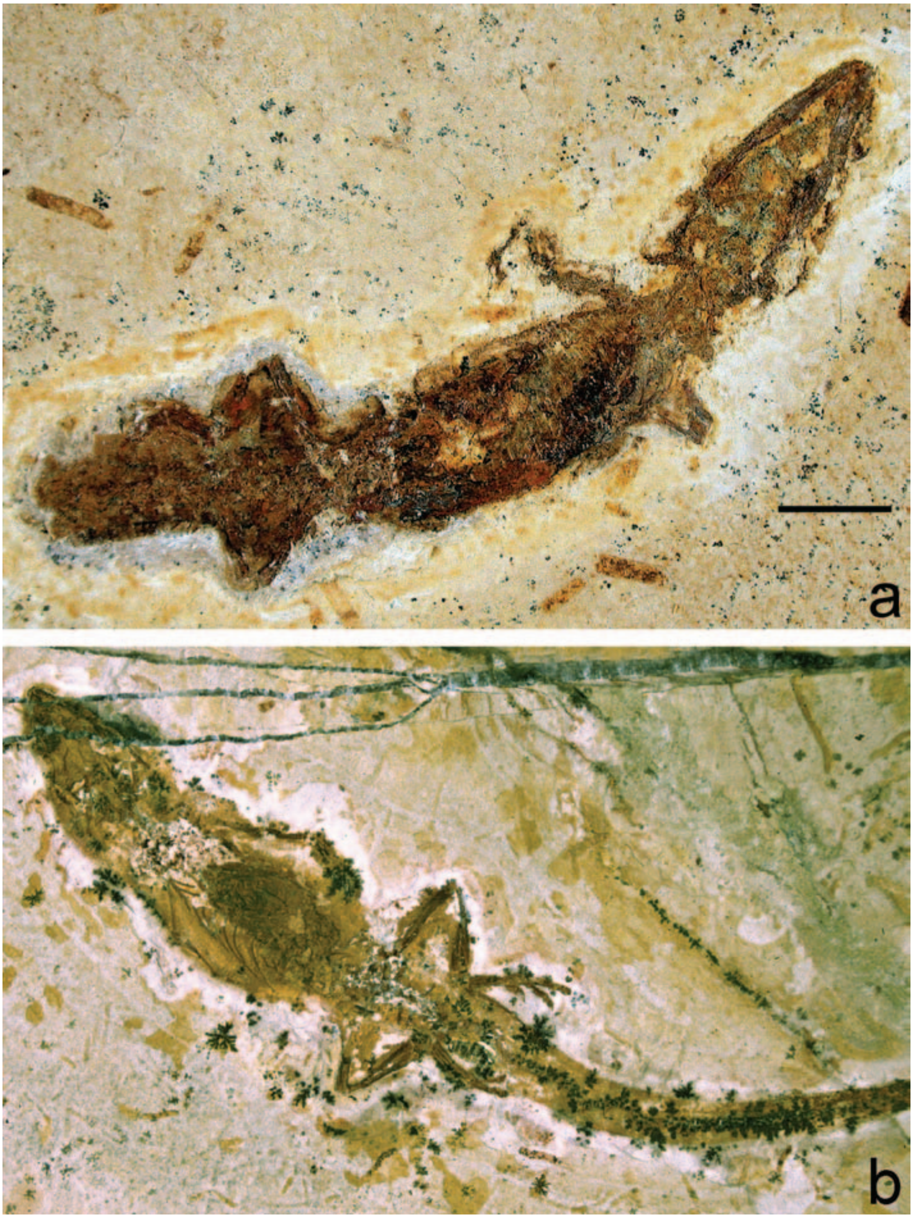

Plate 19. Crato lizards: (a) undescribed lizard missing its tail; the dark area just behind the forelimbs is the stomach contents; SMNK; (b) *Tijubina pontei* Bonfim Jr and Marques, 1997, counterpart to the holotype, current whereabouts unknown. Scale bar, 5 mm.

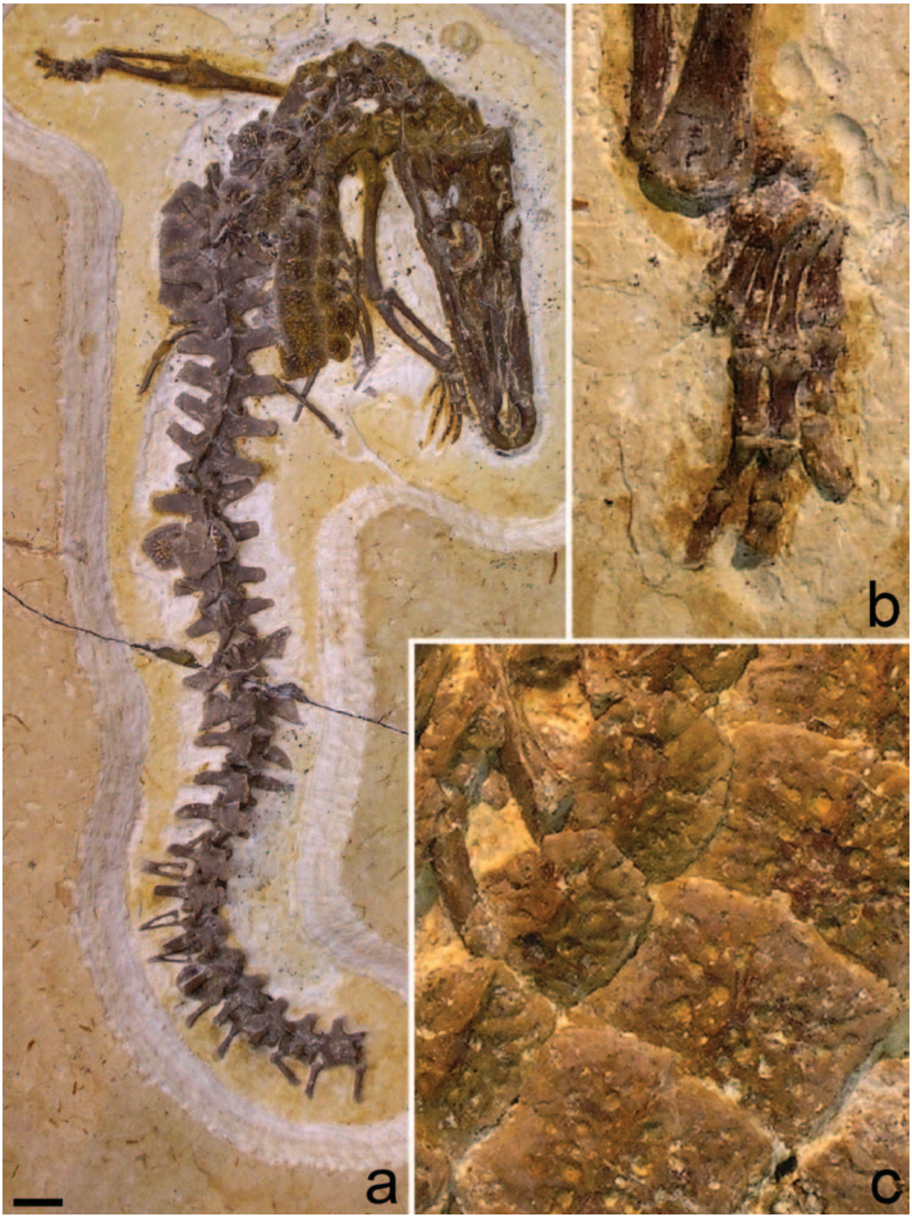

Plate 20. Crato crocodilian *Susisuchus anatoceps* Salisbury, Frey and Martill, 2003, holotype SMNK PAL 3804: (a) partial skeleton with complete skull, both forelimbs and partial vertebral column wanting distal-most caudals, and cranial-most dermal skeleton; (b) detail of left manus; (c) detail of osteoderms. Scale bar, 10 mm.

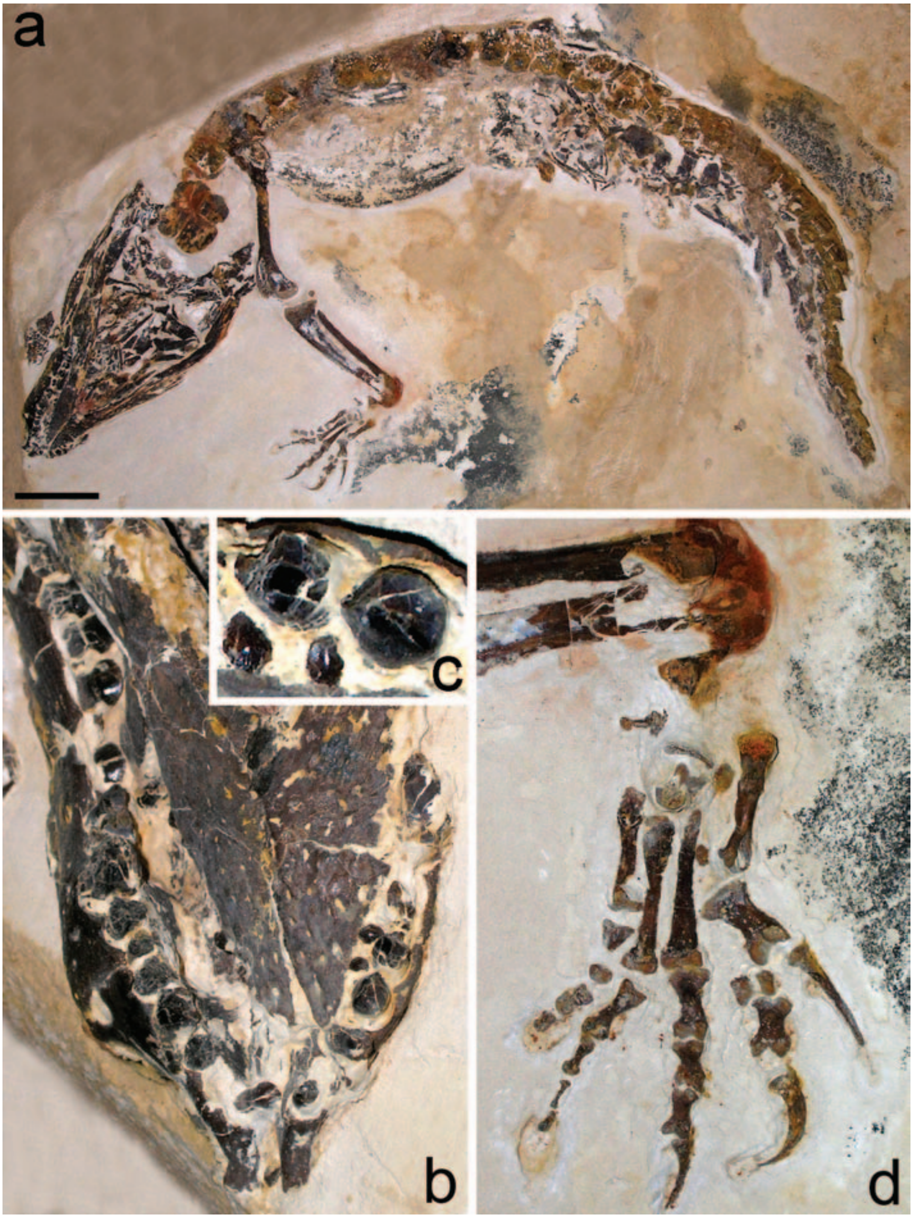

Plate 21. New araripesuchid crocodilian: (a) partial skeleton SMNK PAL 6404 with complete skull, left forelimb and axial skeleton with associated osteoderms; (b) detail of lower jaw symphysis and occlusal surface of premaxillae with exposed dentition; (c) detail of dentition; (d) detail of left manus. Scale bar, 50 mm.

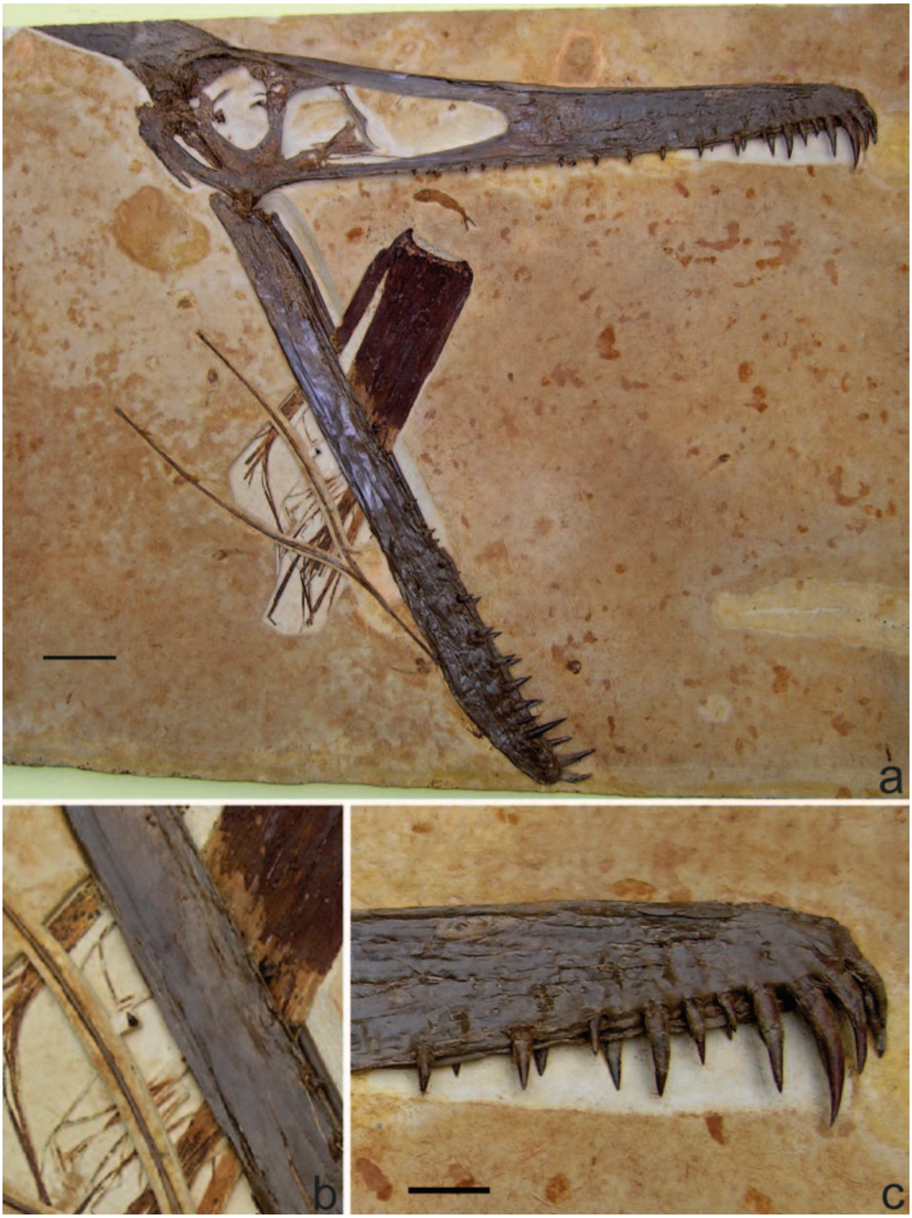

Plate 22. Skull of the Crato pterosaur *Ludodactylus sibbicki*, SMNK PAL 3828: (a) in right lateral view; (b) detail of the leaf lodged between the mandibular rami illustrating its frayed end; (c) detail of premaxillary dentition. Scale bars: a, 50 mm; c, 20 mm.

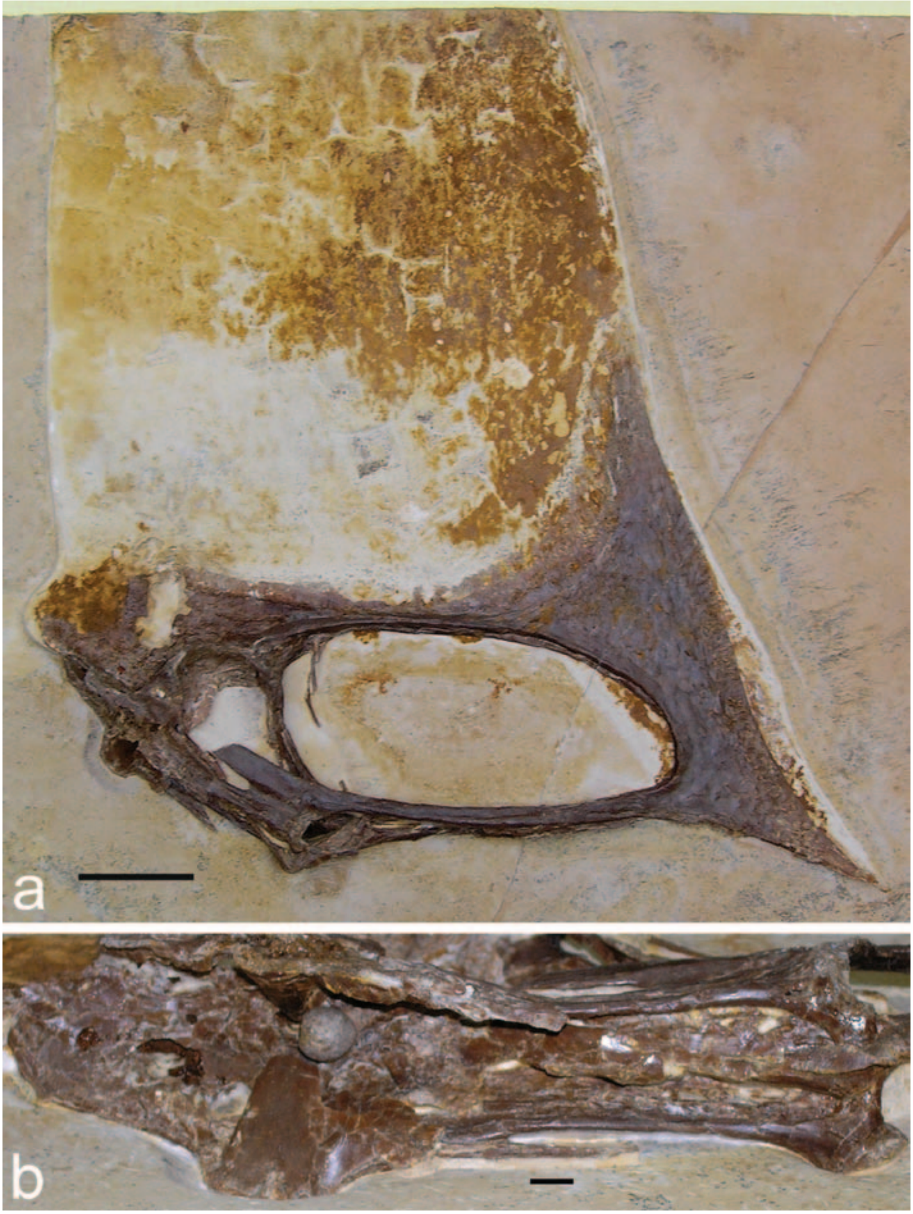

Plate 23. Skull of the Crato pterosaur *Ingridia navigans* (Frey, Martill and Buchy, 2003), SMNK PAL 2344. (a) Holotype skull in right lateral view as preserved; scale bar, 50 mm. (b) Caudal view of skull of same specimen showing occipital condyle and quadrates; scale bar, 5 mm.

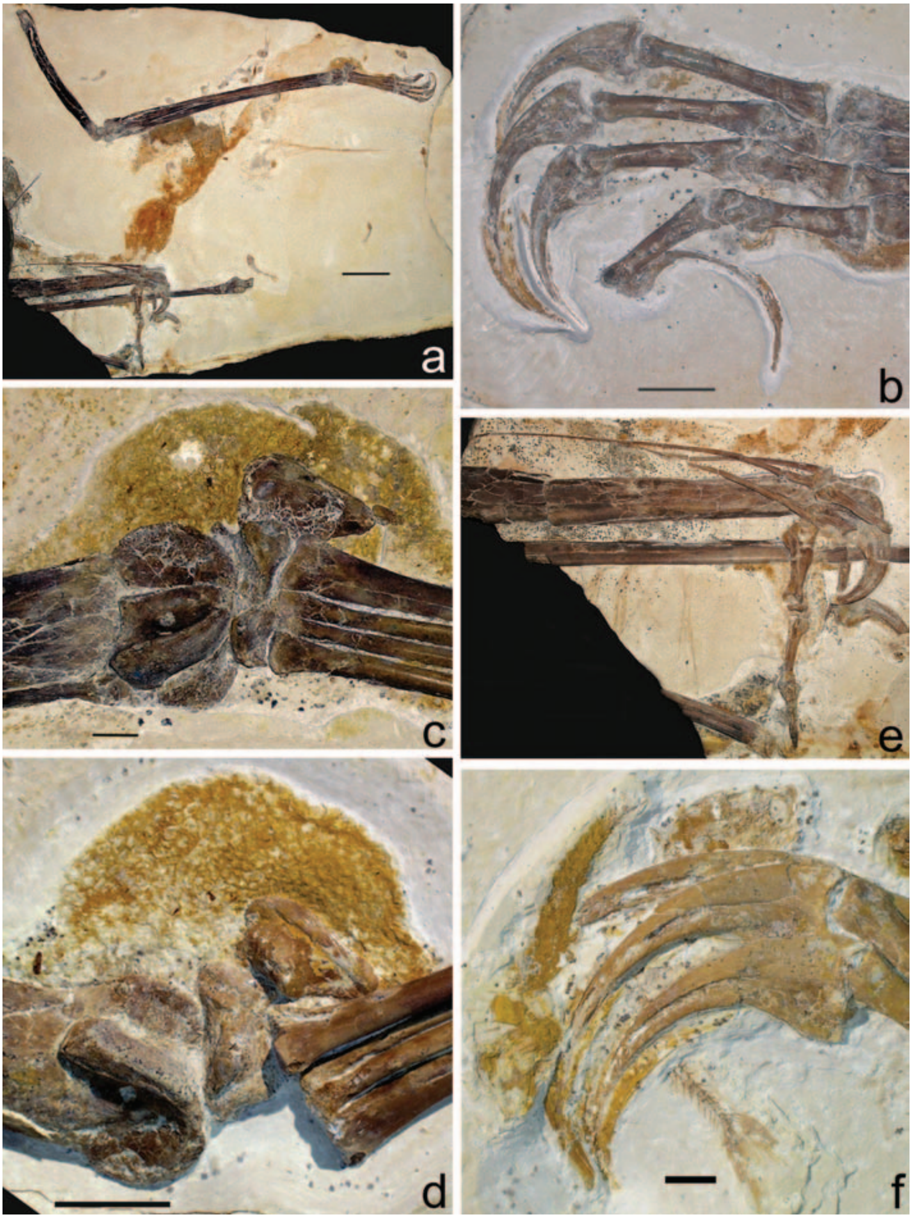

Plate 24. Tapejaridae gen. et sp. indet., SMNK PAL 3830: (a) slab bearing parts of the left forelimb and the complete left hindlimb, with a well-preserved cheiropatagium extending from the manus to the left lower leg; scale bar, 100 mm; (b) pes of same specimen with claw sheaths preserved; scale bar, 10 mm; (c, d) heel pad with scales; scale bars, 10 mm; (e) manus of same specimen showing associated soft tissues; (f) pedal phalanges with claw sheaths showing extension well beyond the unguals; scale bars, 5 mm.

Plate 25. Crato feathers: (a–c) isolated down feathers; (d) partial 'wing' comprising single large asymmetric 'primary' flight feather, five smaller asymmetric feathers and two unidentifiable bones, non-accessioned specimen in SMF; (e) small down feather with pattern of transverse bands; (f) single elongate down feather; (g) feather with pattern of fine, diagonally arranged banding; (h) elongate symmetrical feather with pattern of offset bands. Scale bar in e, 5 mm.

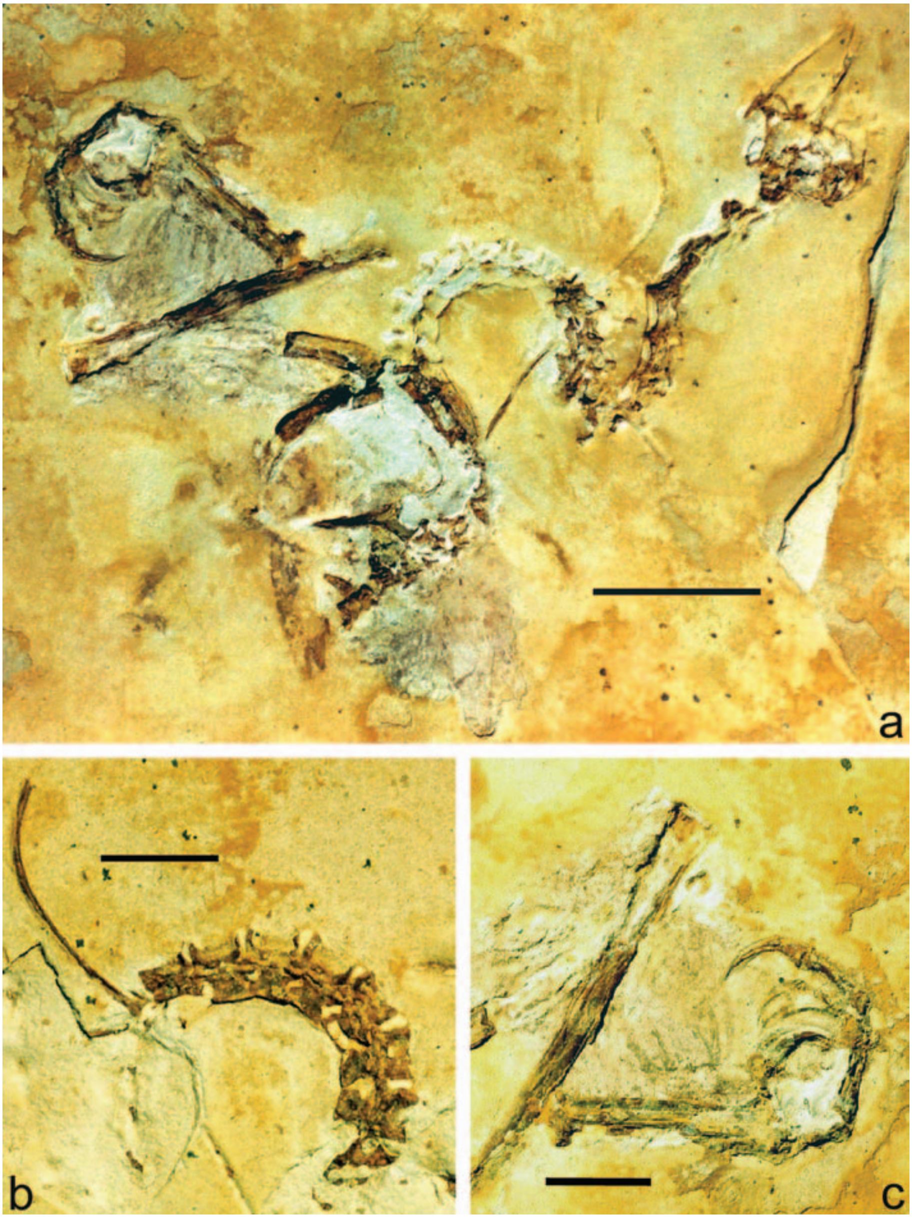

Plate 26. Crato bird: (a) partial skeleton a of probable enantiornithine bird; (b) dorsal vertebrae from counterpart slab; (c) pes showing fully reversed hallux. MURJ. Scale bars: a, 20 mm; b, c, 10 mm.

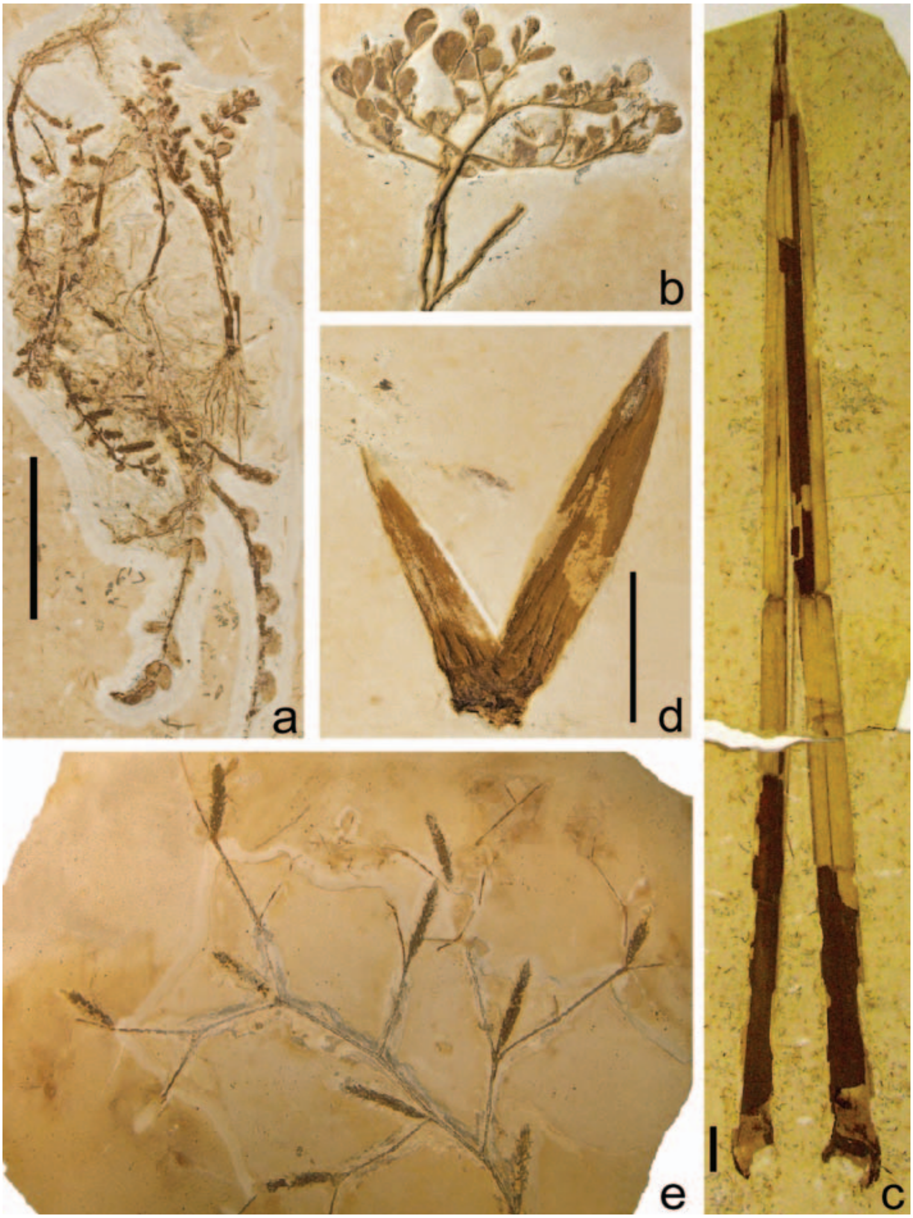

Plate 27. Crato plants: (a) Gnetophyte taxon G, small plant; (b) Gnetophyte taxon F, male plant; (c) large example of *Welwitschiophyllum* leaf; (d) an unusual example of *Welwitschiophyllum* sp. with two leaves; (e) Gnetophyte, *Welwitschiostrobus murili* Dilcher *et al*., 2005. Scale bars: a, c, d, 50 mm.

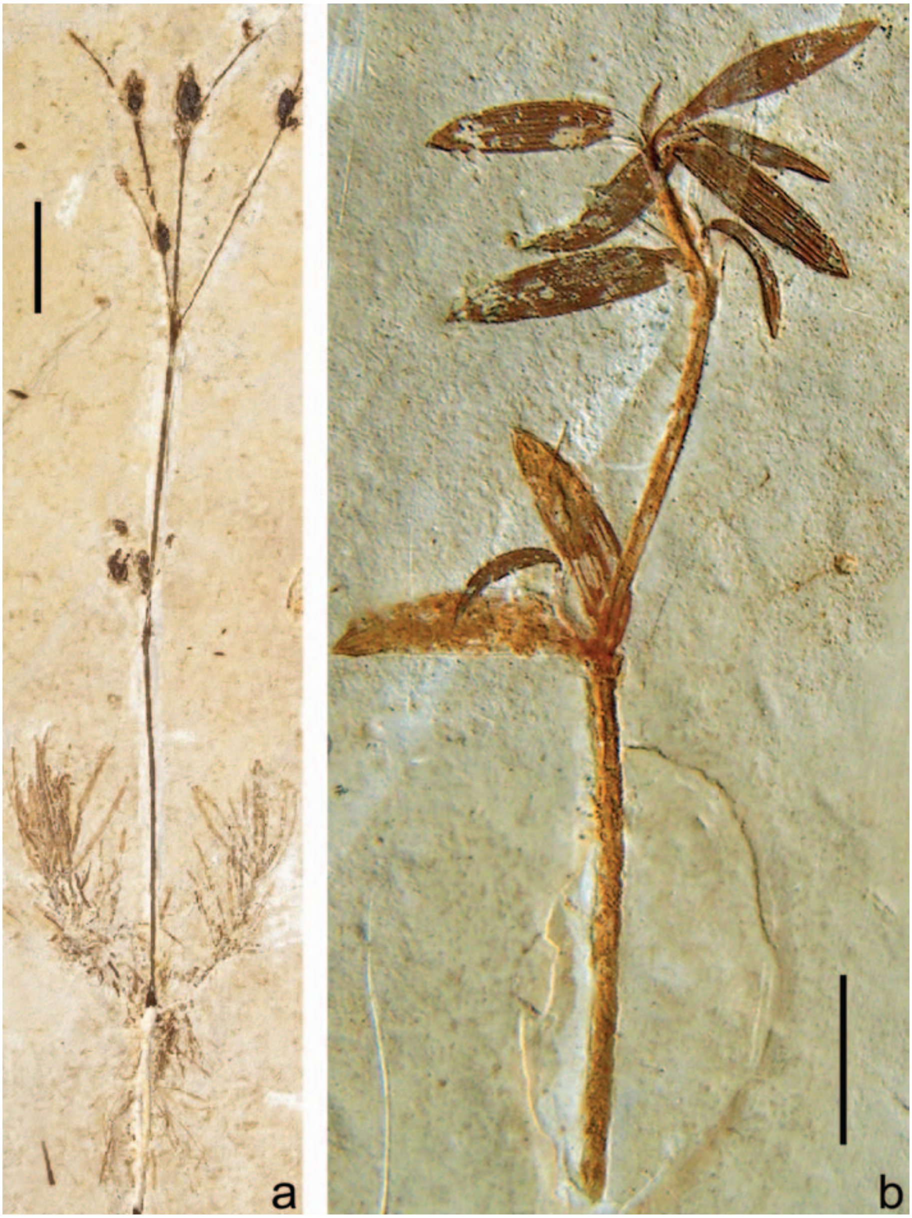

Plate 28. Crato plants: (a) gnetophyte taxon H, a large plant with short articulated side branches; scale bar, 50 mm; (b) monocotyledon, unnamed taxon. Scale bar, 10 mm.

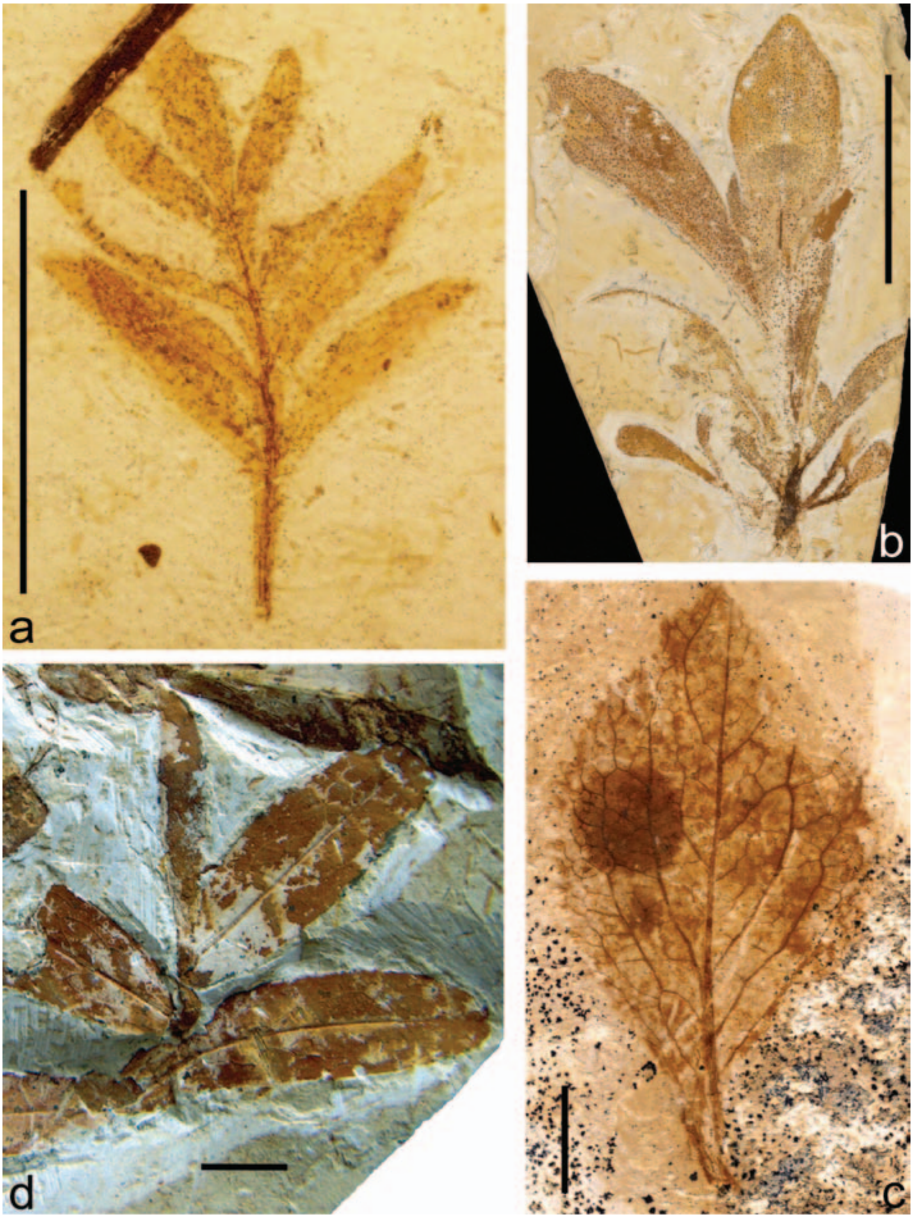

Plate 29. Crato angiosperms: (a) complex leaf of undescribed angiosperm; (b) large leaves of undescribed angiosperm; (c) chloranthacean leaf; (d) leaves of an undescribed angiosperm type B. Scale bars: a, b, 50 mm; c, d, 10 mm.

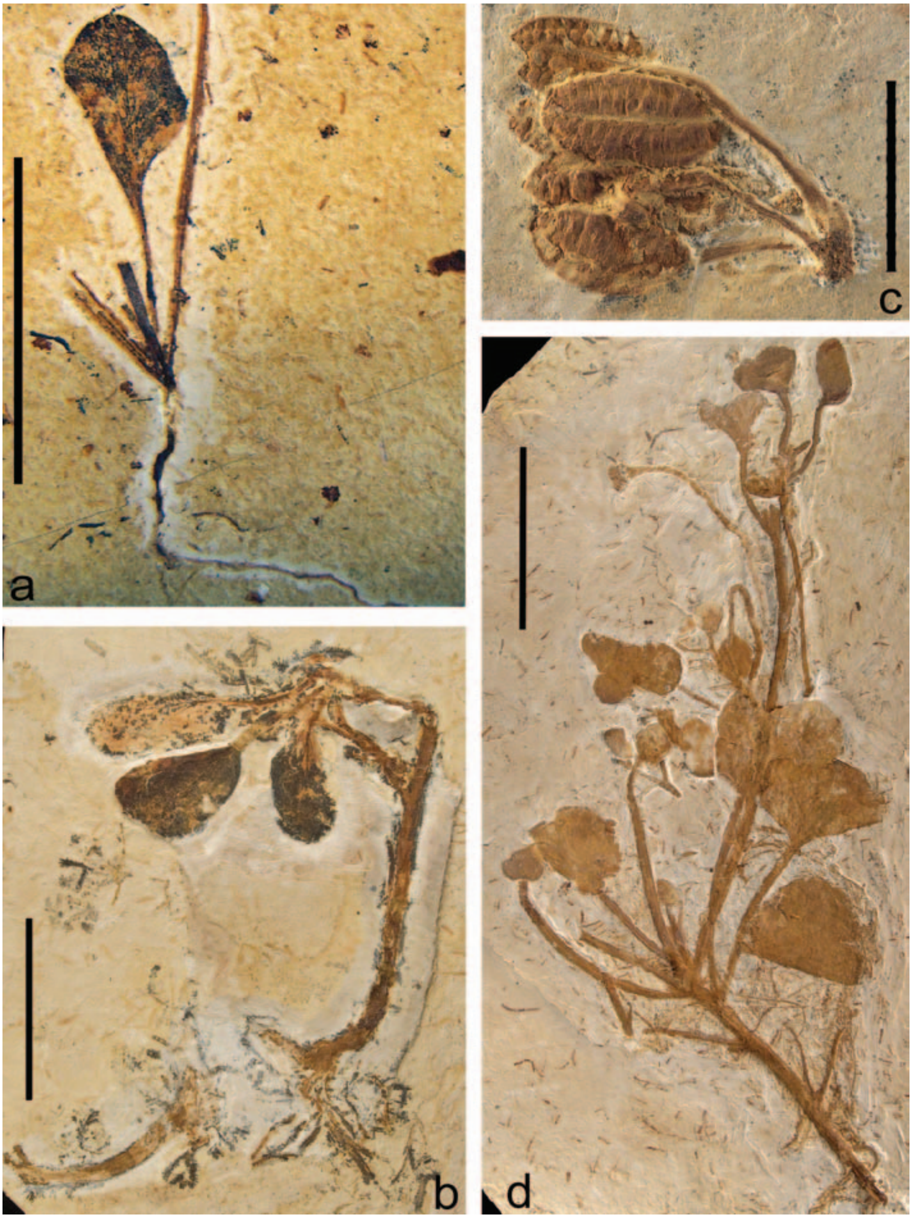

Plate 30. Crato plants: (a) young herbaceous plant with possible primary root; (b) young herbaceous angiosperm with extensive root system; (c) group of isolated angiospermous carpels; (d) possible nymphaealean cabombacean. Scale bars: a–c, 50 mm; d, 10 mm.

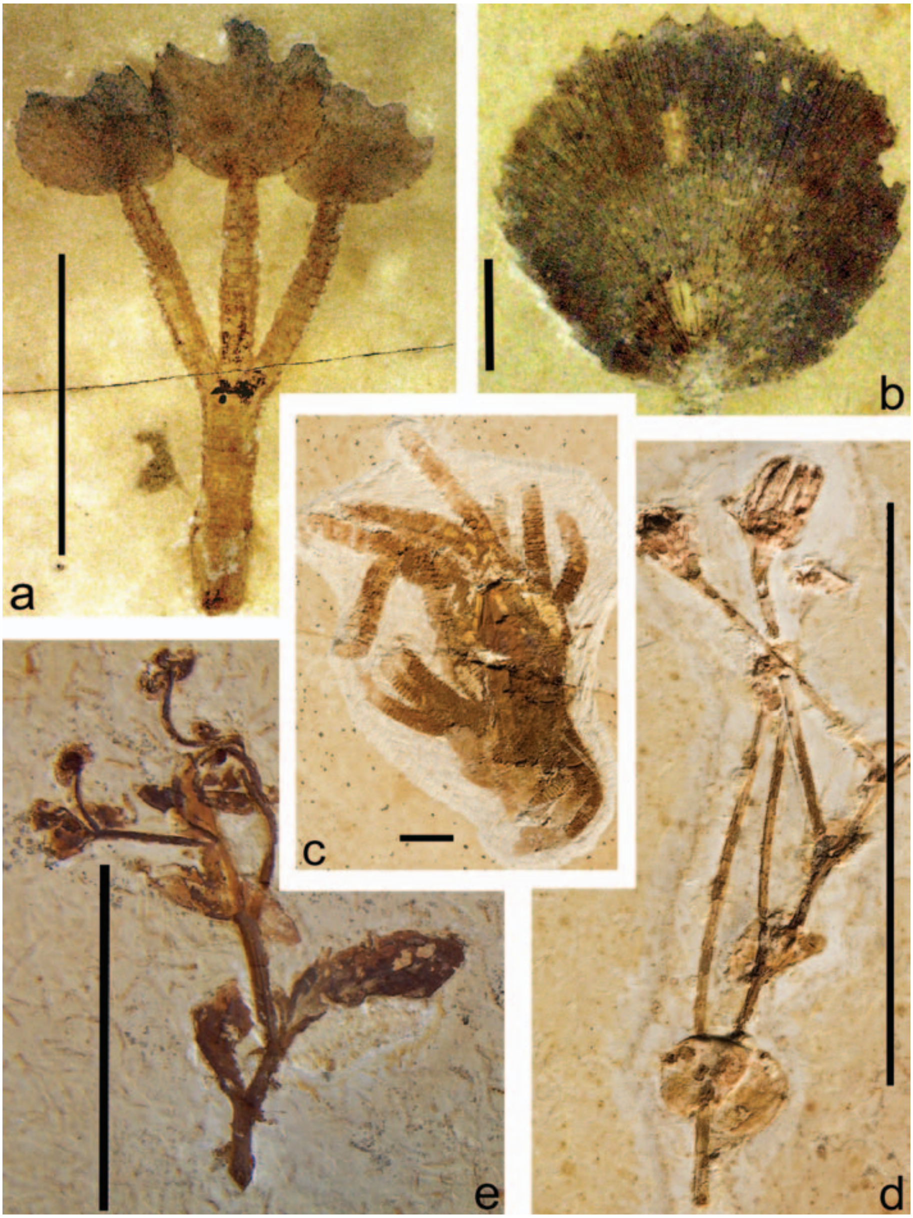

Plate 31. Crato monocotyledon plants: (a) *Klitzschophyllites flabellata* showing the typical trifurcate branching pattern; (b) *Klitzschophyllites* single leaf showing venation and terminal glands; scale bar, 10 mm; (c) basal complex of a possible multi-stemmed example of *Klitzschophyllites*; (d) *Endressinia brasiliana* with leaves and flowers; (e) small, undescribed angiosperm type A. Scale bars. a, c, d, e, 50 mm.

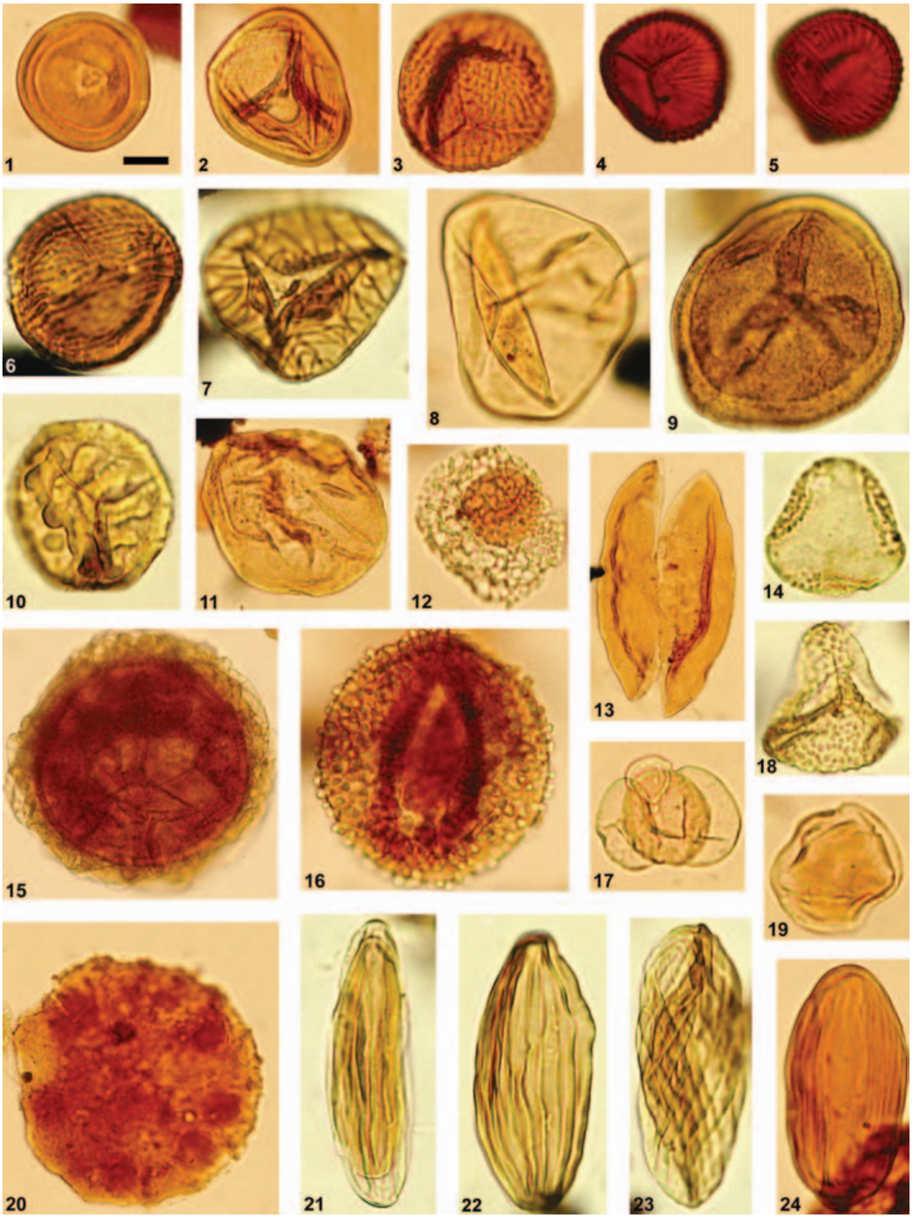

Plate 32. Crato palynomorphs: (1–2) *Classopollis* spp.; (3–7) *Cicatricosisporites* spp.; (8) *Deltoidospora* sp.; (9) *Densoisporites microgranulatus* Brenner; (10) *Interulobites* sp.; (11) *Araucariacites australis* Cookson; (12) *Afropollis jardinus* (Brenner); (13) *Ovoidites parvus* (Cookson and Dettmann); (14) *Penetetrapites mollis* Hedlund and Norris; (15) *Crybelosporites* sp.; (16) *Stellatopollis* sp.; (17) *Vitreisporites* sp.; (18) *Foveotriletes* sp.; (19) *Exesipollenites tumulus* Balme; (20) *Maranhites mosesii* (Sommer); (21–24) ephedroid pollen grains. Scale bar in 1 represents 10 μm and applies to all apart from 8, 11, 13, 15 and 20, the maximum dimensions of which are 66, 65, 160, 91 and 93 μm respectively.