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Pleistocene Amphibians and Reptiles in Britain and Europe

J. ALAN HOLMAN

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J. Alan Holman

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PREFACE

The Pleistocene epoch, or Ice Age, an extended period of advancing and retreating continental ice sheets, is characterized by striking climatic oscillations and sea level fluctuations. This age saw the rise and spread of humans and a great extinction of large mammals by the end of the epoch. In fact, the world today is essentially the product of dramatic changes that took place in the Pleistocene. Major works have dealt with Pleistocene mammals in North America and Europe and the ''why'' of the worldwide mammalian extinction. Moreover, a recent book (Holman, 1995c) has dealt with North American Ice Age amphibians and reptiles. Yet no comparable work deals with British and European Pleistocene herpetofaunas. This book attempts to address this situation by focusing on the Pleistocene amphibians and reptiles in Britain and the European continent eastward through Poland, the Czech Republic, Hungary, Yugoslavia, and Greece.

The book begins with an overview of the Pleistocene epoch and its significance, followed by a general discussion of the Pleistocene in Britain and Europe in Chapter 2, with emphasis on regional terms used to define Pleistocene chronological events. Chapter 3 looks at the pre-Pleistocene herpetofauna of the study area to set the stage for a discussion of the Pleistocene herpetofauna. A large portion of the book consists of a ''Bestiary'' (Chapter 4), a series of annotated taxonomic accounts of Pleistocene herpetological taxa from the region. Illustrations of bones that are especially useful in the identification of Pleistocene herpetological species are included in many of these accounts, along with a discussion of important characters used in the identification of Pleistocene species. A list of locality numbers for each taxon in the Bestiary correlates with those of localities detailed in Chapter 5. These accounts contain lists of herpetological species, literature references, and when appropriate, remarks about the site.

Following this is the interpretive section. It begins with a discussion of herpetological species as paleoenvironmental indicators in Chapter 6. Next, Chapter 7 analyzes herpetological population adjustments to Pleistocene events in Britain and Europe. Chapter 8 follows with a discussion of extinction patterns in the region, including a dialogue about the apparent evolutionary stasis of the Pleistocene herpetofauna compared with avian and mammalian populations. Finally, Chapter 9 discusses the differences and similarities between Pleistocene herpetological events in Britain and Europe and North America.

This book is meant to be a college-level introduction to the study of Pleistocene amphibians and reptiles of Britain and Europe and a companion volume to *Pleistocene Amphibians and Reptiles in North America* (Holman, 1995c). It does not pretend to be a definitive taxonomic revision of Pleistocene herpetological taxa or claim to cite every reference for each Pleistocene herpetological species found in the vast area covered by the book. It should, however, be a standard reference for anyone interested in Pleistocene flora or fauna as well as Pleistocene events in general. It should be especially useful for modern herpetologists, ecologists, and evolutionary biologists. I have tried to keep the approach to the subject simple and direct and have purposely tried not to get involved in esoteric and convoluted arguments about Pleistocene events and patterns.

East Lansing, Mich. J.A.H.

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CONTENTS

PLEISTOCENE AMPHIBIANS AND REPTILES IN BRITAIN AND EUROPE

1

INTRODUCTION

There is disagreement about the time of the beginning of the Pleistocene. For instance, Repenning (1987), a North American, puts the beginning date at 1.9 million ybp. On the other hand, some modern Europeans studying the subject (e.g., Gibbard et al., 1991; Kolfschoten and Meulen, 1986; Roebroeks and Kolfschoten, 1995; Zagwijn, 1985, 1992) consider the epoch to have begun about 2.3 million ybp. The system used here, however, follows Sanchiz (in press), who accepts the official usage of Harland et al. (1990), who put the beginning of the Pleistocene at 1.64 million ybp. Evidence that the Pleistocene ended about 10,000 ybp (Meltzer and Mead, 1983) is widely accepted. This ending date correlates very closely with the terminal extinction of many large land mammal species.

The Pleistocene is characterized by climatic oscillations and a series of glacial and interglacial events where great continental ice sheets advanced and retreated many times. The ice sheets were massive forces, sculpting the topography of the land and carrying much sedimentary material, including huge boulders and even megablocks of land up to 4 km in diameter, as far as 250 km in the Canadian prairies (MacStalker, 1977). In Britain and Europe, as well as in North America, the advance and retreat of ice sheets had a marked effect on the distribution of plant and animal life. Huge tracts of habitat were alternately obliterated and reopened several times, but other effects perhaps are not so well known. For instance, during glacial times, so much atmospheric water was tied up in the formation of the ice that sea levels worldwide lowered markedly. On the other hand, sea levels rose during interglacial times when water was melting off the ice sheets.

The most interesting and controversial biological event that took place in the Pleistocene was the sudden, almost worldwide, extinction of large land mammals, and to a lesser extent birds, that took place by the end of the epoch 10,000 years ago. At least 200 mammalian genera became extinct, among them large herbivores, the carnivores that preyed on them, and the scavengers that fed on the remains of both groups. Some of the striking kinds of mammals that became extinct in Britain and Europe in the late Pleistocene (Stuart, 1991) were the cave bear (*Ursus spelaeus*); the spotted hyena (*Crocuta crocuta*), which presently survives elsewhere; the wooly mammoth (*Mammuthus primigenius*); the straight-tusked elephant (*Palaeoloxodon antiquus*); one or two species of extinct nonwooly rhinoceroses of the genus *Dicerorhinus*; the wooly rhinoceros (*Coelodonta antiquitatis*); one or two species of horses of the genus *Equus*; the hippopotamus (*Hippopotamus amphibius*), which presently survives elsewhere; the giant deer (*Megaloceros giganteus*); and an extinct bison (*Bison priscus*).

Much discussion and debate concerning the extinction of the "mammalian megafauna" has taken place over the past decades (e.g., Martin and Wright, 1967; Martin and Klein, 1984; Stuart, 1991), with the main issue being whether the rise of human big game hunters or changing environmental conditions were the major causes. But suprisingly few works have addressed the other vertebrate classes and their role in the complex events of the Pleistocene, and no summary works have been written about the Pleistocene herpetofauna of Britain and Europe. This book, then, deals with a discussion of the Pleistocene herpetofauna of the British Islands and the European continent east through Poland, the Czech Republic, Hungary, Yugoslavia, and Greece. This study area includes the fol-

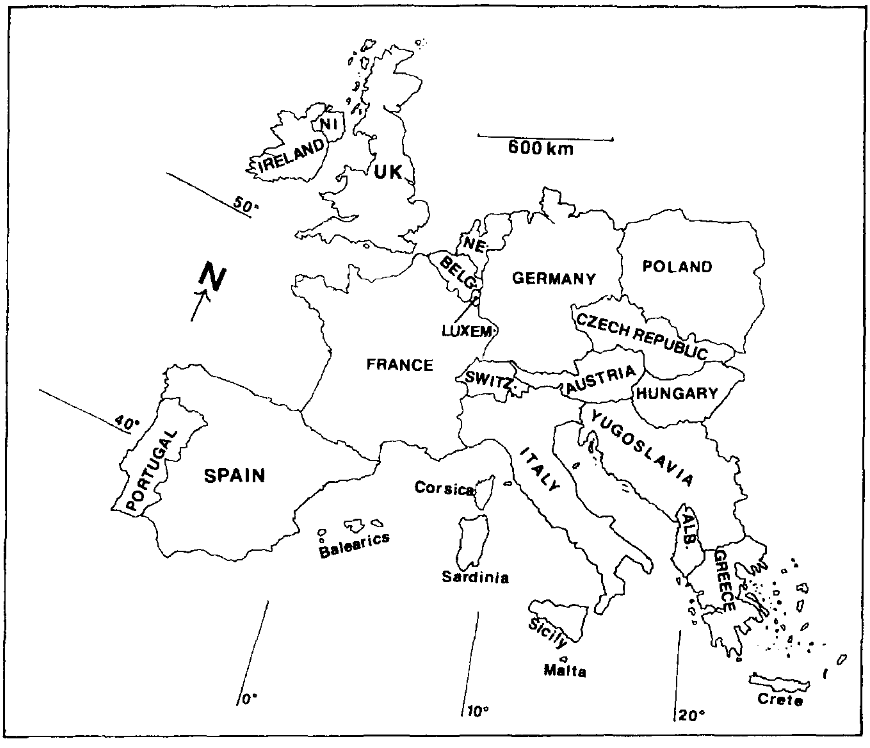

FIGURE I. Map of the region covered by this book (except for the Spanish Canary Islands).

lowing political entities: Ireland, Great Britain, France and its oceanic islands, Monaco, Spain and its oceanic islands, the Netherlands, Belgium, Luxembourg, Germany, Austria, Switzerland, Poland, Czech Republic, Italy and its oceanic islands (as well as Malta), Hungary, Yugoslavia (Croatia, Bosnia, Serbia), and Greece and its oceanic islands (Fig. 1).

The fact that the terms ''Britain'' and ''Europe'' are used as separate entities in the title of this book, rather than merely referring to ''Pleistocene amphibians and reptiles in Europe,'' is meant to reflect the unique position of the British Islands in the Pleistocene and early Holocene. These islands represent a large land mass that was connected to continental Europe during much of the Pleistocene, only to become separated from the larger land mass soon after the end of the epoch.

As it happens, the herpetofauna of Britain and Europe was quite stable during the Pleistocene compared to the mammalian fauna, which suffered familial, generic, and specific extinction (Stuart, 1991). A compelling question, then, is ''What attributes have allowed the herpetofauna to survive the stresses that caused dramatic extinctions in the mammalian fauna of the Pleistocene?'' This question is addressed after a review of the British and European Pleistocene herpetofauna, and a consideration of herpetological range adjustments and extinction patterns in the Pleistocene. Finally, herpetological events in Britain and Europe and North America are compared. The following chapter is a discussion of the Pleistocene in Britain and Europe with an emphasis on terms that are presently used to designate Pleistocene chronological events in the area (Fig. 1) covered by this book.

2

THE PLEISTOCENE IN BRITAIN AND EUROPE

A general introduction to the Pleistocene with an emphasis on herpetological remains was presented in the companion volume *Pleistocene Amphibians and Reptiles in North America* (Holman, 1995c). For a general introduction to the Pleistocene that gives much attention to Britain and Europe, the reader is referred to Sutcliffe (1985). A detailed account of Pleistocene mammals in Britain is given by Stuart (1982), and a general account of Pleistocene mammals in Europe is given by Kurtén (1968). The present chapter deals mainly with chronological divisions of the Pleistocene in Britain and Europe.

Early geologists recognized that glacial deposits and land forms existed far south of existing glaciated areas, and they correctly reasoned that these features indicated not only the presence of ice sheets but the onset of cold climates, as well. As these features were mapped and stratigraphic studies were made, it was found that some sections contained weathered zones of organic soils and plant remains between layers of glacially derived sediments. It was suggested that these organic zones represented nonglacial environments and that ice sheets must have advanced and retreated several times.

In Europe, before studies of deep sea sediments were made, Pleistocene chronological events were determined on the basis of piecemeal evidence from terrestrial sediments. The earliest widely accepted chronology of climatic Pleistocene intervals was the classic fourfold subdivision of Pleistocene glacial events in the Alps by Penck and Brückner (1909). These glacial stage names, from oldest to youngest, are Günz glacial, Mindel glacial, Riss glacial, and Würm glacial. Between the glacial stages, interglacial stages were designated by compound names based on the underlying and overlying glacial stages (e.g., The Günz–Mindel interglacial stage lies between the Günz and Mindel glacial stages). These Alpine glacial stages have been widely used, and one still finds references to them (especially the younger stages) in the recent literature (e.g., Fritz, 1995).

Other local chronologies were set up in other regions and continents (e.g., Table 1), and for a time it appeared that the fourfold subdivision of the Alpine

Table 1. Pleistocene Stage Names

Dutch/European	Alps	Britain	North America
1. Weichselian G	Würm G	Devensian G	Wisconsinan G
2. Eemian I	Riss–Würm I	Ipswichian I	Sangamonian I
3. Saalian G	Riss G	Wolstonian G	Illinoian G
4. Holsteinian I	Mindel–Riss I	Hoxnian I	Yarmouthian I
5. Elsterian G	Mindel G	Anglian G	Kansan G
6. Cromerian I	Günz-Mindel I	Cromerian I	Aftonian I
7.	Günz G	Beestonian G	Nebraskan G

Note: Stages below 2 do not necessarily correlate laterally. G=Glacial, I=Interglacial.

system could be matched in other areas. But through the years it became apparent that exact correlation of temporal units, especially older ones, could not be accomplished in different regions. Then, as more time elapsed, it became obvious that the continental chronologies were far too simple. Evidence from deep sea sediments, correlated with paleomagnetic-dated loess sequences in Europe, indicated that the classical sequence of four glacial–interglacial stages in the Alps covered at least eight stages, going back only to a marine stage dated at about 800,000 ybp (Kukla, 1970, 1977). Moreover, it was found that the supposed interglacial stages actually represented periods of crustal movement and not climatic events. Kukla (1977) argued that the classical Alpine terminology should be abandoned in interregional correlations, which he suggested should be based on the oxygen isotope dates in the deep sea sediments. Thus, at present, there is a tendency for more and more Quaternary paleontologists to try to correlate the terrestrial evidence with the paleomagnetically dated chronology of the deep sea cores.

Yet the use of chronological terminology originally based on the classic concept of glacial and interglacial events is still very much alive. Three sets of stage names, the Alpine, the Dutch/European, and the British Isles system (Table 1) continue to be used by European vertebrate paleontologists, with the Dutch/European and British chronologies most frequently used. In the three systems, the Upper Pleistocene last glacial–interglacial stage sequences correlate fairly well. The last interglacial stages (Alpine: Riss–Würm; Dutch/European: Eemian; British Islands: Ipswichian) began approximately 120,000 ybp and ended approximately 110,000 ybp. The last glacial stages (Alpine: Würm; Dutch/European: Weichselian; British Island: Devensian) began approximately 110,000 ybp and ended 10,000 ybp at the end of the Pleistocene (Stuart, 1982, 1988).

It has been suggested that glacial ages are usually of much longer duration than interglacial ages. In fact, paleoclimatologists point out that the present temperate age has continued for 10,000 years, and that if the frequency of previous glacial–interglacial cycles is a model for future events, the earth could go into another glacial cycle very quickly (see references in Sutcliffe, 1985, pp. 213–214). This would have tremendous ramifications for the herpetofauna in the northern latitudes, not to mention human and other mammalian populations!

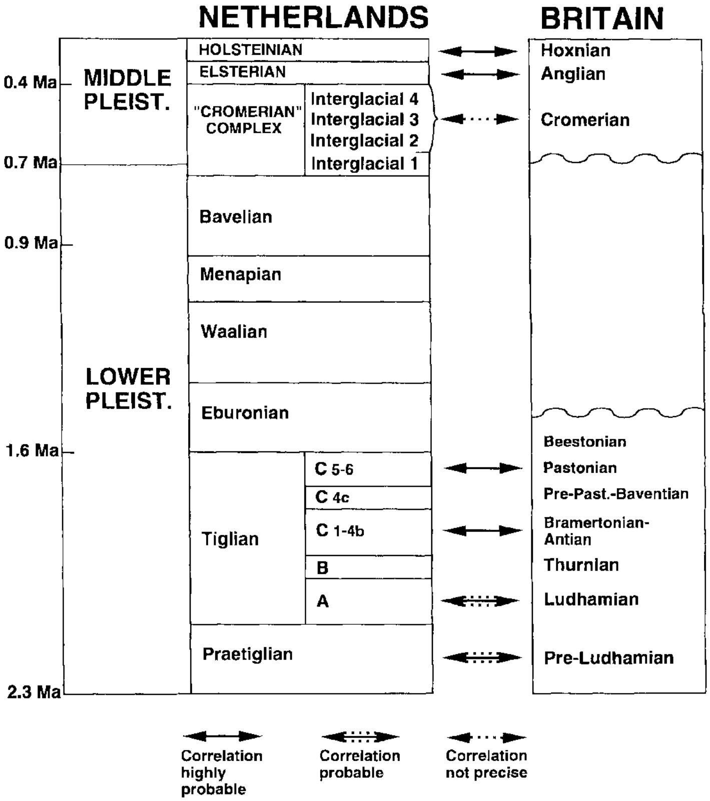

FIGURE 2. Correlation of Lower and Middle Pleistocene beds in Britain (East Anglia) and The Netherlands. [Interpretations are from Gibbard et al., 1991]

Since it has been very difficult to accurately correlate the earlier (Lower and Middle Pleistocene) chronological units in Europe, a team of British and Dutch scientists met in Norwich, England, in 1988 to discuss establishing correlations of Lower and Middle Pleistocene stages across the southern North Sea. These correlations were attempted on the basis of floral, faunal, and paleoclimatic data. The results of this meeting were recently published (Gibbard et al., 1991). This scheme (Fig. 2) has the Pleistocene beginning much earlier than the one used here, which considers the Lower Pleistocene to begin at about the base of the Netherlands Eburonian and the British Beestonian. Nevertheless, the Middle Pleistocene correlations in Figure 2 are of considerable interest. Note that the type section of the British Cromerian interglacial stage roughly correlates with the upper three interglacial stages of the continental "Cromerian Complex." Later works (e.g., Kolfschoten and Turner, 1996) have shown that specific British "Cromerian" localities specifically correlate with specific "Cromerian Complex" localities in the Netherlands, and these studies continue. It is highly probable that the British Anglian glacial stage correlates with the Netherlands

Table 2. Time span of the Lower, Middle, and Upper Pleistocene Used in This Book

Time Period	Years before Present (ybp)
Lower Pleistocene	1.64 million to 700,000 ybp
Middle Pleistocene	700,00–127,000 ybp
Upper Pleistocene	127,000–10,000 ybp

Note: Time designations are based on Sanchiz (in press).

(=Dutch/European) Elsterian glacial stage and that the British Hoxnian interglacial stage correlates with the Netherlands (=Dutch/European) Holsteinian interglacial stage.

Roberts et al. (1995), based in part on the proceedings of the European Science Foundation Workshop at Tautavel, France, in 1993 on the earliest occupation of Europe by humans, correlated several British Cromerian sites (including two important herpetological sites, the Boxgrove and Westbury–Sub-Mendip) with the Cromerian IV interglacial of the Dutch/European sequence. Also important, they point out that the stratigraphic record in Britain between the Anglian and Ipswichian (see Table 1) has been oversimplified, mainly because of too much reliance on palynological studies. In reality, there are probably at least two temperate stages rather than the present single Hoxnian stage in this interval. British Pleistocene herpetological sites have been important in some of these interpretations.

Sutcliffe (1985) astutely points out that ''glacials and interglacials have tended to become rigid 'boxes' into which all climatic events have to be fitted'' (p. 61). In the Netherlands, for instance, 36 major and minor climatic cycles have been recorded in the Pleistocene, with seven cycles being observed in the last (Weichselian) glacial sequence alone (Kolfschoten and Turner, 1996). The reader should be alerted that in the herpetological literature some assignments of European Pleistocene herpetological sites to traditional glacial and interglacial stages may have been oversimplified.

This book follows Sanchiz (in press) in arranging herpetological sites under ''Lower Pleistocene,'' ''Middle Pleistocene,'' and ''Upper Pleistocene'' headings (Table 2), with some sites merely being listed as ''Pleistocene Undesignated.'' More restrictive chronological divisions are pointed out in remarks on some of the sites in Chapter 5. Sanchiz followed the official usage of Harland et al. (1990). The reader should be reminded again that other publications (e.g., Repenning, 1987; Gibbard et al., 1991) indicate an earlier beginning of the Pleistocene.

3

THE EUROPEAN HERPETOFAUNA
Paleocene Through Pliocene

In both Europe and North America, modern herpetological families and genera became established quite early in the Cenozoic, and modern species occurred as early as the Miocene. Because of deteriorating climates that began late in the Eocene, a marked decrease in herpetological diversity occurred in the Oligocene in both continents. However, both areas became herpetologically enriched in the Miocene. In post-Miocene times Europe was isolated from Africa and warm areas in the east by the Mediterranean Sea and eastern mountain ranges, and a depauperate herpetofauna developed there that continued into recent times. In North America, however, with its vast, accessible southern land mass, the richness of the Miocene herpetofauna (with the exception of several archaic colubrid genera [Parmley and Holman, 1995] that became extinct in the the Miocene) persisted into modern times.

The following discussion of changes in the European herpetofauna in the Cenozoic era has been synthesized from Auge (1986), Bailón (1991a), Bailón et al. (1988), Barbadillo et al. (1997), Crochet et al. (1981), Estes (1981, 1982, 1983), Fritz (1995), Holman (1995c), Milner (1986), Milner et al. (1982), Młynarski (1976), Rage (1984a, 1984c, 1986, 1993), Rage and Auge (1993), Rage and Ford (1980), Roček (1994), Sanchiz (1977b, in press), Sanchiz and Młynarski (1979), Sanchiz and Roček (1996), Špinar (1972), Szyndlar (1984, 1991b, 1991c), and Szyndlar and Böhme (1993).

Because of the high probability that herpetological fossils have been identified correctly at the family level, herpetological families are used here to reflect the taxonomic diversity of the European herpetofauna from the Paleocene through the Pliocene. In a following section, the earliest appearance of herpetological genera and species in the European Tertiary are discussed. Extinct families are prefixed with an asterisk (*). Families that became extinct in Europe in the Cenozoic but presently occur elsewhere are prefixed with a number sign (#).

Epochal Occurrences of Families

Salamander Families

Two primitive, extinct, presumably permanently aquatic salamander families, the *Albanerpetontidae and *Batrachosauroididae (the latter also known from the Tertiary of North America) made limited appearances in the Cenozoic of Europe. The *Albanerpetontidae occurred only in the Middle Miocene (having reappeared from the Cretaceous), and the *Batrachosauroididae occurred from the Upper Paleocene to the Lower Eocene. The primitive, permanently aquatic, very large hellbenders of the family #Cryptobranchidae (also known from the Tertiary and modern fauna of North America) occurred from the Upper Oligocene to the Lower Pliocene in Europe.

The extant North American giant salamander family #Dicamptodontidae, a group with a terrestrial adult stage, made a brief appearance in Europe, occurring in the Upper Paleocene and again in the Middle Miocene. The mainly New World lungless salamander family Plethodontidae has been recorded in the Lower Pliocene of Europe but has not been reported as a Pleistocene fossil. The Plethodontidae presently has a very restricted distribution in southern Europe. The neotenic aquatic water dog and olm family Proteidae is presently widespread in the United States (water dogs) but has a very restricted occurrence in the modern fauna of southern Europe (olms). The Proteidae occurred in the Lower and Middle Miocene and Pliocene of Europe, and there is a questionable record of *Proteus* from the Pleistocene of Germany. Finally, the newt and salamander family Salamandridae, a group of species that are mainly terrestrial in the adult stage, occurred in all of the Cenozoic epochs of Europe. The salamandrids dominate the present European salamander fauna.

In summary, three families of salamanders, one extinct (*Batrachosauroididae) and two modern (#Dicamptodontidae and Salamandridae) occurred in the Paleocene of Europe. Although the Eocene is a much longer epoch, only two salamander families, *Batrachosauroididae and Salamandridae, have been recorded there. Only two Oligocene salamander families, the #Cryptobranchidae and Salamandridae, have been reported. The Miocene had the most salamander families that ever existed in Europe. Five families, *Albanerpetontidae (a reappearance from the Cretaceous!), #Cryptobranchidae, #Dicamptodontidae, Proteidae, and Salamandridae occurred in that epoch. The Pliocene was also rich in salamander families, as the #Cryptobranchidae, Plethodontidae, Proteidae, and Salamandridae were present. Thus, three salamander families occurred in the Paleocene and only two in the Eocene and Oligocene. But five salamander families occurred the Miocene and four in the Pliocene. The Pleistocene sediments have yielded only two families, the Proteidae (a questionable record according to some) and the Salamandridae. Three families, Plethodontidae (rare), Proteidae (rare), and Salamandridae (abundant), occur in modern Europe.

Anuran Families

Only one family of anurans, the *Palaeobatrachidae, is extinct (Roček, 1995). This was an aquatic group that is thought to have been adaptively similar to the modern clawed frog, *Xenopus*. The *Palaeobatrachidae occurred continuously throughout the Tertiary of Europe and persisted into the Pleistocene before becoming extinct. This family also occurred in the early Tertiary of the United States.

The primitive painted frog family Discoglossidae had a continuous distribution through the Cenozoic in Europe and persisted into modern times, but the three discoglossid subfamilies had somewhat different temporal distributions. The Discoglossinae (painted frogs) occurred in Europe from Paleocene to modern times. But the Bombinatorinae (firebelly toads) did not appear until the Lower Miocene, and the Alytinae (midwife toads) did not appear until the Upper Miocene. Both subfamilies survived into modern times. The spadefoot family Pelobatidae, another primitive anuran group, occurred continuously in Europe from the Lower Eocene to modern times. But the closely related parsley frog family Pelodytidae had a discontinuous Cenozoic distribution. The Pelodytidae occurred in the Lower Eocene and again in the early Upper Eocene. It was absent from the later part of the Upper Eocene and the entire Oligocene, but reappeared in the Lower Miocene, continuing into modern times.

The remaining anuran familes are considered to be advanced groups. The tropical frog group #Leptodactylidae, a huge family that currently lives mainly in Central and South America, occurred briefly in Europe in the Middle and Upper Eocene. The true frogs of the family Ranidae occurred continuously in Europe from Middle Eocene to modern times. The true toads of the family Bufonidae occurred from the Lower Miocene to the present, and the treefrogs of the family Hylidae occurred from the Upper Miocene to modern times. The advanced, extralimital anuran families #Rhachophoridae (flying frogs) and #Microhylidae (narrowmouth toads) made spotty appearances in the European fossil record; the #Rhacophoridae occurred in the Upper Eocene and again in the Upper Pliocene, and the #Microhylidae occurred only in the Upper Eocene.

In summary, two families of anurans, one extinct (*Palaeobatrachidae) and one modern (Discoglossidae), occurred in the Paleocene of Europe. In the Eocene the anuran fauna of Europe was greatly enriched, as eight families, the *Palaeobatrachidae, Discoglossidae, Pelobatidae, Pelodytidae, #Leptodactylidae, Ranidae, #Rhacophoridae, and #Microhylidae were present. The extralimital #Leptodactylidae and #Microhylidae were restricted to this epoch. The Oligocene saw a plunge in European anuran diversity, as only four families (*Palaeobatrachidae, Discoglossidae, Pelobatidae, and Ranidae) were present. The diversity of anuran families rebounded in the European Miocene as seven families, the *Palaeobatrachidae, Discoglossidae, Pelobatidae, Pelodytidae, Bufonidae, Hylidae, and Ranidae, occurred there. This marked the first appearance of the Bufonidae and Hylidae in Europe. All of the Miocene anuran families continued into the Pliocene, and the #Rhacophoridae reappeared from the Upper Eocene.

Thus, we see only two anuran families in the Paleocene, but an enriched anuran fauna with eight anuran families in the Eocene. Anuran family diversity dropped in half in the Oligocene, as only four families have been reported. The diversity of anuran families shot up again in the Miocene, as seven are known, and the important families Bufonidae and Hylidae first appeared. The Pliocene saw the same high level of family diversity as the Eocene, as eight anuran families have been recorded. The European Pleistocene is actually richer in anuran families than the modern fauna, as all of the modern families are known (Discoglossidae, Pelobatidae, Pelodytidae, Bufonidae, Hylidae, and Ranidae) as well as the the extinct family *Palaeobatrachidae.

Turtle Families

Only two nonmarine turtle families are known from the Cenozic of Europe: the pond turtles, family Emydidae, and the tortoises, family Testudinidae. Both of these families are known from the Lower Eocene and have a rather continuous occurrence through the epochs of the Tertiary into Pleistocene and modern times.

Lizard Families

The chisel-toothed lizards of the family Agamidae occurred from the Lower Eocene of Europe rather continuously through the Oligocene and Miocene into the Pliocene. They are not known from the Pleistocene, but occur in the modern fauna of Greece and adjacent islands. The chameleons of the family Chamaeleontidae are reported from the Lower and Middle Miocene and Upper Pliocene of Europe. Chameleons are unknown in the Pleistocene of Europe but have a limited modern distribution in southwestern Spain and on Crete. The geckos of the family Gekkonidae appeared in Europe in the Lower Eocene and had a rather continuous occurrence through the Oligocene, Miocene, and Pliocene. They are poorly known from the Pleistocene but are found in the modern fauna of the Mediterranean region in Europe. Lacertid lizards of the family Lacertidae are presently the dominant lizards in Europe. They were first recorded from the Paleocene and occurred continuously through the Eocene, Oligocene, Miocene, and Pliocene. They are very well known from the Pleistocene of Europe.

Two families, the skinks of the family Scincidae and the African extralimital girdle-tailed lizards of the family #Cordylidae, have a fragmentary record in the Cenozoic of Europe. The Scincidae occurred in the Lower Miocene and again in the Middle Miocene and Upper Pliocene. They had a very restricted occurrence in the Pleistocene of Europe, but are known in the modern fauna of eastern

Europe most of Iberia, and the Mediterranean region. The #Cordylidae are known only from the Middle and Upper Eocene and the Upper Oligocene of Europe. They presently occur only in southern Africa and Madagascar.

The anguid lizards of the family Anguidae are represented by two subfamilies that are important in the European fossil record. The extinct glyptosaurs of the subfamily *Glyptosaurinae occurred continuously from the Lower Eocene to the early part of the Lower Oligocene. This subfamily was also important in the early Tertiary of North America. The extant lateral fold lizards of the subfamily Anguinae occurred continuously from the Lower Eocene into the modern fauna of Europe. Both modern European genera have been reported from the Pleistocene.

The extinct necrosaurid lizards of the family *Necrosauridae appeared in the Paleocene and occurred continuously through the Eocene, becoming extinct at the end of that epoch. The extralimital North American beaded lizards of the family #Helodermatidae are known from the Lower Eocene to the Lower Oligocene of Europe. The group is also found in the Tertiary of North America, where it persisted into the modern fauna and is represented by two large, poisonous species of the genus *Heloderma*, one occurring in the southwestern United States and both occurring in Mexico. The extralimital monitor lizards of the tropical family #Varanidae were first recorded from the Lower Eocene of Europe. They were absent during the Oligocene but appeared again in the late part of the Lower Miocene and were also present in the Pliocene. There is an extremely doubtful varanid record from the Pleistocene of Europe. The family is unknown in the modern fauna of the area.

In summary, only two families, the extinct *Necrosauridae and the extant Lacertidae, are known from the Paleocene of Europe. The Eocene, however, was rich in lizard families, as eight, possibly nine families have been recorded: Agamidae, Gekkonidae, Lacertidae, #Cordylidae (questionably the odd family *Dorsetisauridae, not previously discussed), Anguidae, *Necrosauridae, #Helodermatidae, and #Varanidae. A drop in lizard family diversity occurred in the Oligocene, where six families (Agamidae, Gekkonidae, Lacertidae, #Cordylidae, Anguidae, and #Helodermatidae) occurred. In the Miocene and Pliocene seven lizard families are known: Agamidae, Chamaeleontidae, Gekkonidae, Lacertidae, Scincidae, Anguidae, and #Varanidae.

Thus, only two lizard families occurred in the Paleocene, but a great enrichment of families occurred in the Eocene, where eight and possibly nine families are known. This was the height of lizard diversity in the Cenozoic of Europe. The number of lizard families dropped to six in the Oligocene but rebounded to seven in the Miocene and Pliocene. Moreover, with the exception of the Agamidae and probably the #Varanidae (an extremely doubtful Pleistocene record is present), the same Miocene and Pliocene families occur in the Pleistocene of Europe. The modern fauna contains all of the Miocene and Pliocene families with the exception of the #Varanidae.

Amphisbaenian Families

The worm lizards of the family Amphisbaenidae are first known from the Eocene and occurred continuously through the Cenozoic into the modern fauna of Europe.

Snake Families

Snakes of the very primitive suborder Scolecophidia (Anomalepididae, Leptotyphlopidae, Typhlopidae, and Uropeltidae) are represented in the European fossil record only by vertebrae. Scolecophidian vertebrae are so simple and uniform in structure (see Fig. 27a) that it is usually difficult or impossible to identify them to the familial level. Scolecophidians are known from the European Eocene, Miocene, and Pliocene but have not been found in the Oligocene. The primitive, extralimital South American and Southeast Asian pipesnakes of the family #Aniliidae are known from the Middle and Upper Eocene and the Oligocene of Europe. They were absent in the Miocene but occurred again in the Pliocene before becoming extinct in the region.

The primitive boid snakes of the family Boidae occurred from the Paleocene through the Pleistocene into modern times. In the Pliocene and Pleistocene they were represented only by the small sand boas of the subfamily Erycinae. #Nonerycine boids of other subfamilies occurred from the Paleocene to the Middle Miocene in the region. The extinct, giant marine snakes of the family *Palaeopheidae occurred abundantly in some European deposits in the Eocene, but they became extinct in the region in the middle of that epoch. Extralimital Central and South American tropidopheid snakes of the family #Tropidopheidae occurred rather continuously from the Lower Eocene to the Upper Oligocene of Europe, when they become extinct in the region. These primitive snakes resemble advanced snakes in several features.

Three extinct snake families that are intermediate between primitive and advanced snake families occurred in the Tertiary of Europe. These families are the *Anomalopheidae and the *Nigeropheidae that occurred only in the Lower Eocene, and the *Russellopheidae that occurred in the Lower and Middle Eocene and and became extinct in the Upper Eocene.

The advanced families of snakes, the Colubridae, Elapidae, and Viperidae, occurred later in Europe than any of the previous groups of snakes. The giant family Colubridae appeared in the Lower Oligocene and occurred continuously into the Pleistocene and modern fauna of Europe, where it is presently the dominant snake group. The extralimital front-fanged poisonous family #Elapidae appeared in the Lower Miocene of Europe and occurred continuously there until it became extinct in the region at the end of the Pliocene. The poisonous vipers of the family Viperidae appeared in the Lower Miocene and occurred continuously into the Pleistocene and modern fauna of the region.

In summary, the only snakes known from the European Paleocene are #nonerycine boids of the family Boidae. But at least eight families, all primitive groups, are recorded from the Eocene: undetermined scolecophidians, #Aniliidae, Boidae (both erycine and #nonerycine taxa), #Tropidopheidae, *Palaeopheidae, *Nigeropheidae, *Anomalopheidae, and *Russellopheidae. In the Oligocene, however, the number of snake families dropped to at most one half of those found in the Eocene, as only the #Aniliidae, Boidae (both erycine and #nonerycine taxa), #Tropidopheidae, and Colubridae were present. The most important Oligocene herpetological event in Europe was the first appearance of the modern snake family Colubridae in the early part of the epoch.

The Miocene was a time of modernization of the snake fauna in Europe, as the three modern snake families, Colubridae, Elapidae, and Viperidae, became dominant. The only primitive Miocene snake groups were undesignated scolecophidian remains and boids (both erycine and #nonerycine taxa). This was the last appearance of the #nonerycine boids in Europe. In the Pliocene the only primitive snake groups in Europe consisted of undetermined scolecophidian material and the families Boidae (erycines only) and #Aniliidae (an aniliid reappearance from the Oligocene and its last appearance in Europe). The advanced families Colubridae, Elapidae, and Viperidae became very modern in the Pliocene, and the Colubridae dominated not only Pliocene herpetofanas but Pleistocene and modern ones, as well.

Early Occurrences of Cenozoic Genera and Species

This section focuses on the earliest occurrences of European Tertiary and Quaternary genera and species.

Salamander Genera and Species

In the family Salamandridae, vertebrae and unspecified material assigned to cf. *Salamandra* was reported from the Upper Paleocene of France and the Lower Eocene of Belgium. A definitive occurrence of *Salamandra* was recorded from the Upper Eocene of Britain. The earliest occurrence of the Pleistocene and modern European species *Salamandra salamandra* was reported from the Pliocene of Poland. Another salamandrid genus, *Triturus*, was reported as cf. *Triturus* from the Lower Eocene of Belgium on the basis of unspecified material. A definitive occurrence of the genus was reported from the Upper Eocene of Britain. The Pleistocene and modern species *Triturus marmoratus* was reported as *Tritutus* cf. *Triturus marmoratus* from several Lower Miocene localities in western Europe, and the Pleistocene and modern *Triturus cristatus* was reported from the Middle Pliocene of Hungary.

Anuran Genera and Species

Alytes of the family Discoglossidae has been questionably reported from the Miocene of Spain and from the Upper Pliocene of Germany. Another discoglossid, *Bombina*, occurred in the Miocene of Germany. The Pleistocene and modern species *Bombina bombina* has been reported from the Lower Pliocene of Russia. Another Pleistocene and modern species, *Bombina variegata*, was questionably reported from the Upper Pliocene of central Europe. Finally, the discoglossid genus *Discoglossus* was reported from the Miocene of Mediterranean Europe.

Pliobatrachus langhae*, the longest surviving species of the extinct family *Palaeobatrachidae, appeared in the Lower Pliocene of Romania and made its last appearance in the Pleistocene of Germany and Poland (Pliobatrachus* cf. *Pliobatrachus langhae*). *Pelobates* of the family Pelobatidae was recorded from the Oligocene–Miocene boundary in Germany, and the Pleistocene and modern species *Pelobates fuscus* occurred in the the Pliocene of Europe. *Pelodytes* of the family Pelodytidae was reported from the Miocene of Spain and the Pleistocene, and modern species *Pelodytes punctatus* was questionably reported from the Pliocene of that country.

The genus *Bufo* of the family Bufonidae occurred from the Miocene to the recent in Europe. The Pleistocene and modern species *Bufo viridis* occurred in the Upper Miocene of Europe, and the Pleistocene and modern species *Bufo bufo* and *Bufo calamita* have been reported from the Pliocene. *Hyla* of the family Hylidae appeared in the Miocene of Europe. These remains are most similar to the *Hyla arborea* complex of species. The genus *Rana* of the family Ranidae appeared in Europe in the Lower Oligocene. In fact, the Pleistocene and modern *Rana ridibunda* species group (water frog group) has also been reported from the Lower Oligocene of Europe. The Pleistocene and modern species *Rana arvalis* and *Rana temporaria* appeared in Europe in the Pliocene. The Pleistocene and modern species *Rana latastei* was questionably reported from the Upper Pliocene of Italy.

Turtle Genera and Species

The genus *Mauremys* of the pond turtle family Emydidae has been reported in the Upper Oligocene of Europe, and the Pleistocene and modern species *Mauremys leprosa* is known from the Lower Pliocene of France. *Emys orbicularis*, a modern emydid species with an extensive Pleistocene record, appeared in the Upper Pliocene of Poland. *Testudo* of the land tortoise family Testudinidae appeared in Europe in the Lower Oligocene of France. The Pleistocene and modern species *Testudo hermanni* has been recorded at the Pliocene/Pleistocene boundary in Europe.

Lizard Genera and Species

The genus *Agama* of the family Agamidae has been reported from the Upper Miocene of France, but fossils questionably assigned to this genus are known from the Upper Eocene or Lower Oligocene of France. *Lacerta* of the family Lacertidae has been reported from the Oligocene, and the Pleistocene and modern species *Lacerta viridis* appeared in the Upper Pliocene of Hungary and Poland. *Anguis* of the family Anguidae appeared in the Lower Oligocene of Belgium, whereas the Pleistocene and modern species *Anguis fragilis* has been reported from the Upper Pliocene of the Czech Republic. Also in the family Anguidae, *Ophisaurus* has been reported from the Lower Eocene of Britain. The modern species *Ophisaurus apodus* (=''**Ophisaurus pannonicus*'') appeared in the Upper Pliocene of central Europe.

Amphisbaenian Genera and Species

Blanus of the Amphisbaenidae may have appeared as early as the Upper Eocene of England, and the Pleistocene and modern species *Blanus cinereus* is known from the Upper Pliocene of Spain.

Snake Genera and Species

The genus *Eryx*, of the family Boidae (subfamily Erycinae), has been reported from the Upper Miocene of the Ukraine. It seems odd that species of this genus do not appear in the Pliocene of eastern and central Europe.

Coronella (subfamily undesignated) of the family Colubridae appeared in the Upper Pliocene of Moldavia, and the colubrine genus *Coluber* appeared in the Middle Oligocene of France. *Coluber caspius* has been reported from the Upper Miocene of Hungary, *Coluber gemonensis* from the Middle Pliocene of Moldavia and the Ukraine, and *Coluber viridiflavus* from the Pliocene of Poland and the Ukraine.

The colubrine genus *Elaphe* has been reported from the Upper Miocene of Austria and Hungary. It is probable that it also occurred in the Upper Miocene of the Ukraine. Modern species of *Elaphe* are known from the Pliocene. *Elaphe longissima* has been reported from the Upper Pliocene of Hungary, and remains assigned to cf. *Elaphe longissima* have been reported from the Middle Pliocene of Moldavia. *Elaphe quatuorlineata* remains are known from the Upper Pliocene of Austria. Material that probably represents the colubrine genus *Malpolon* has been reported from the Upper Pliocene of Greece. A doubtful record of this genus is from the Upper Miocene of Hungary.

The natricine genus *Natrix* (water snakes and grass snakes) appeared in the Oligocene in Europe. The grass snake species *Natrix natrix*, known from many Pleistocene records and widely distributed in the modern fauna of Europe, has been reported from the uppermost Miocene of Hungary. The water snake species

Natrix tesselata also appeared in the uppermost Miocene of Hungary. The genus *Vipera* of the poisonous snake family Viperidae appeared in the Lower Miocene of the Czech Republic. Two Pleistocene and modern species, reported as *Vipera* cf. *Vipera ammodytes* and *Vipera* cf. *Vipera aspis* of the *Vipera aspis* species complex, occurred in the Upper Miocene of Hungary. Specifically unidentified remains of the *Vipera berus* complex of species occurred the Upper Miocene of the Ukraine.

Summary

Based on the epochal occurrence of families in Europe, the Paleocene herpetofauna was depauperate, but there was a remarkable expansion of herpetological families in the Eocene. Because of a deteriorating climate in the late Eocene and Oligocene, there was a marked reduction in both amphibian and reptile families in the Oligocene. The Miocene saw an enriched herpetofauna again, but deteriorating climates and European isolation from southern land masses in the latter part of the Neogene led to the depauperate European herpetofauna of Pleistocene and Holocene times. The Cenozoic herpetofauna of Europe was enriched from time to time by immigration of herpetological groups from South America, North America, Africa, and Asia, but many of these families became extinct in the area during Neogene times. Turning to the lower taxonomic groups, a few modern herpetological genera were established by Oligocene times, and by the end of the Miocene several modern European herpetological genera were present, as well as a few modern species. Probably all modern genera and most modern species were established by the end of the Pliocene.

4

A BESTIARY

This chapter consists of annotated taxonomic accounts of Pleistocene amphibians and reptiles recorded from the study area (see Fig. 1). General external characters, habits, and distributional patterns of modern taxa of amphibians and reptiles that occur in the British and European Pleistocene in this and following chapters are from the author's unpublished field notes and photographs as well as the following sources: Arnold and Burton (1978), Ballasina (1984), Beebee (1983), Berger et al. (1969), Duellman (1993), Duellman and Trueb (1986), Engelmann et al. (1986), Ernst and Barbour (1989), Escriva (1987), Estes (1981, 1983), Frazer (1983), Frost (1985), Günther (1996), Halliday and Adler (1986), Hellmich (1962), Hvass (1972), King and Burke (1989), Matz (1983), Noble (1931), Smith (1964), Sparreboom (1981), and Zug (1993).

The reader is cautioned *not to attempt to identify Pleistocene amphibian and reptile fossils solely on the basis of skeletal characters discussed or skeletal figures presented* in this book—or in other publications. To identify Pleistocene amphibian and reptile fossils accurately, it is necessary to compare them with adequate modern and fossil skeletal material.

Pleistocene locality numbers below correspond with locality numbers in Chapter 5.

Order Caudata Scopeli, 1977: Salamanders and Newts

Pleistocene caudate amphibians are usually identified on the basis of individual trunk vertebrae (see Holman, 1995c, p. 83). Figure 3 illustrates the important features of a trunk vertebra of *Triturus cristatus* from the Middle Pleistocene of Cudmore Grove, Essex, England.

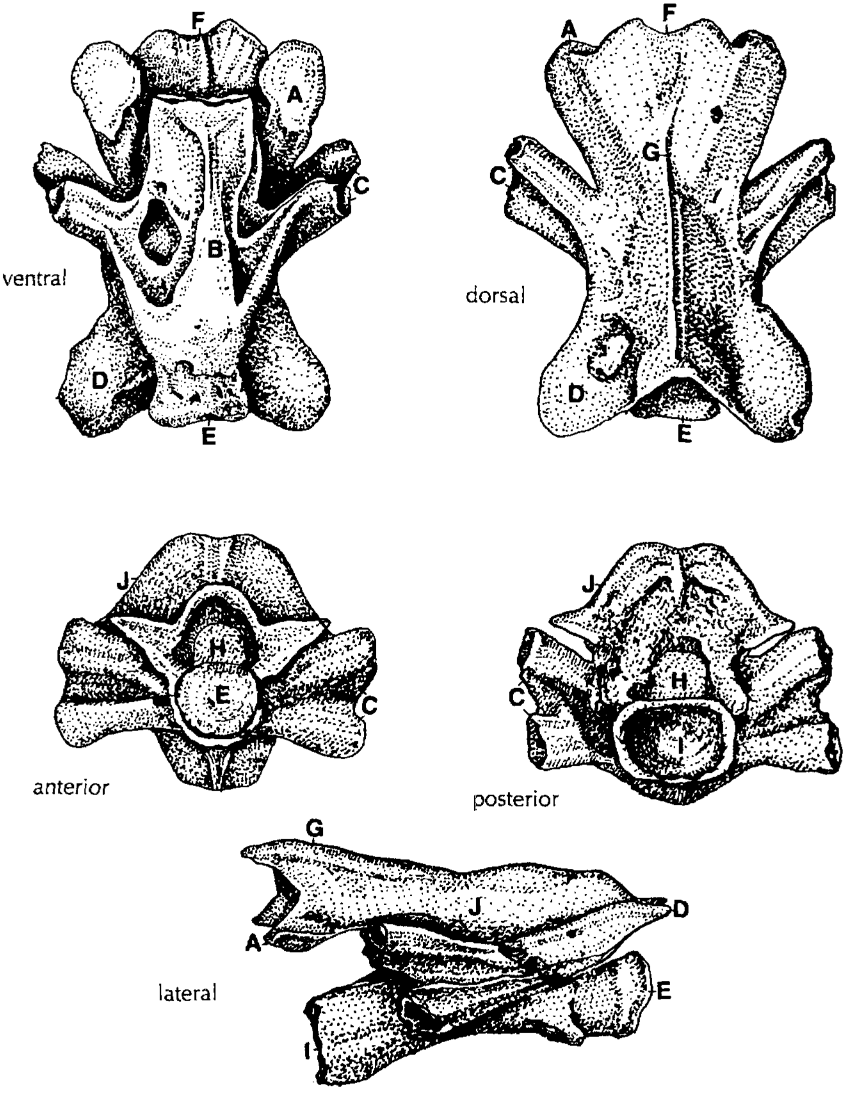

FIGURE 3. Trunk vertebra of *Triturus cristatus* (Salamandridae) from the Middle Pleistocene of the Cudmore Grove Site, Essex, England, indicating important taxonomic characters. (A) Postzygapophyses; (B) keel on centrum; (C) rib-bearing processes; (D) prezygapophyses; (E) condyle; (F) posterior end of neural arch; (G) neural spine; (H) neural canal; (I) cotyle; (J) lateral wall of neural arch. [Drawing by Rosemarie Attilio in Holman et al., 1990; terminology is from Holman, 1995c]

Caudata undesignated: Unidentified Salamander or Newt Material

Pleistocene Localities
Germany: Middle Pleistocene—10.
Hungary: Middle and Upper Pleistocene—1; Upper Pleistocene—4.

Family Proteidae Hogg, 1838

Olms and Water Dogs

The proteids are paedomorphic salamanders with broad, flattened heads and persistent gills. There are two living and two fossil genera (Estes, 1981; Frost, 1985; Duellman, 1993) One of the two modern genera, *Proteus*, is a cave species that occurs only along the northeast border of the Adriatic Sea. The other modern genus, *Necturus*, is a surface water form that has a wide range in eastern North America.

Proteids are unique among salamanders in that they lack a maxillary bone. Derived skeletal characteristics of the family include ossification in the columellar portion of the squamosal bones as well as a parasphenoid that extends posteriorly almost to the level of the occipital condyles. The presence of an opisthotic bone in this family is considered to be a primitive character (Estes, 1981).

Genus *Proteus* Laurenti, 1768: Olms

The genus *Proteus* is composed of a single modern species, a very elongate, paedomorphic salamander that appears white because of a lack of pigment. It retains three pairs of gills. The eyes are so reduced that the animal is essentially blind. The limbs are reduced, with three digits on the front feet and two on the hind feet.

The species occurs in the lightless zones in caverns along the northeast Adriatic Seaboard as far north as the Istrian region and as far south as Montenegro. An isolated population exists in northern Italy. *Proteus anguinus* lives in cold water ranging from about 40°F to 50°F and remains active throughout the year.

Skeletal characters of *Proteus anguinus* are: frontals moderately divergent laterally and separated by parietals; opisthotic bone separated from other skull bones; and 37 presacral vertebrae, all with forked neural spines and single-headed rib bearers (Estes, 1981).

Proteus sp. indet.: Olm

Pleistocene Locality
Germany: Upper Pleistocene—30.

This alleged *Proteus* specimen (Brunner, 1956) was found in cave sediments in Bavaria. If the Bavarian record is correct, it indicates a more widespread occurrence of this species in Europe in the Pleistocene than at present, as the fossil locality is about 350 km northwest of the nearest modern populations.

Problematic Taxa

Proteus bavaricus Brunner 1956 was described on the basis of a single parasphenoid bone that was recovered from the Teufelshöhle (Devil's Cave; Germany: Upper Pleistocene Site 30). The parasphenoid resembles that of *Proteus* based on its elongated shape (Estes, 1981). But a figure of the bone (Brunner, 1956, plate 7, fig. 1) does not show the differences between "*Proteus bavaricus*" and *P. anguinus* pointed out by Brunner (1956). I cautiously refer this specimen to *Proteus* sp. indet. Böhme (1996) is also not convinced that the German specimen actually represents *Proteus*.

Family Salamandridae Goldfuss, 1820

Fire Salamanders and Newts

Salamandrids have a primitive-type salamander body that is moderately long with a rather slender tail. Salamandrids are rough skinned except during the aquatic phase. They may have patches of bright pigment either dorsally or ventrally consisting of green, yellow, red, or orange. The family differs from related ones in that it lacks vertical grooves on the body called rib or costal grooves. The front feet have four digits and the hind feet have either four or five.

The family is composed of 15 modern genera (Frost, 1985; Duellman, 1993) and eight extinct ones (Estes, 1981). None of the extinct genera occur in the Pleistocene. The modern distribution of salamandrids is from the British Isles and Scandanavia eastward to the Ural Mountains, then southward into Iberia and Asia; north-central India and China to northern Vietnam; extreme northwest Africa; southern Canada and the United States to northern Mexico.

Salamandrids sometimes have an aquatic newt and a terrestrial eft stage. The time spent in the newt or eft stage is variable and may differ between species or individual populations of the same species.

Selected derived skeletal characters of the Salamandridae are: palatal tooth row extended posteriorly by lateral extension of vomer; vomerine teeth replaced from medial side; angular, lacrymal, septomaxillary, and second epibranchial elements absent; columella fused; and frontal-squamosal arches often present (Estes, 1981). The vertebrae are opisthocoelous, in that an anterior ball or condyle occurs at the anterior end of the centrum, and a concavity or cotyle occurs at the posterior end.

Two modern genera, *Salamandra* and *Triturus*, are known from the Pleistocene of Britain (*Triturus*) and Europe (*Salamandra* and *Triturus*).

Salamandridae indet.: Fire Salamander or Newt

Pleistocene Locality
Spain: Upper Pleistocene—15.

Genus *Euproctus* Gene, 1838: European Mountain Salamanders

Salamanders of the genus *Euproctus* (Fig. 4A) are rather small, relatively robust animals with roughened or somewhat roughened skins. Three modern species are recognized (Frost, 1985; Duellman, 1993). The genus presently occurs in the Pyrenees Mountains of Spain and France and on the islands of Sardinia and Corsica. They are usually found in or near cold, running water at relatively high altitudes.

Osteological characters are: premaxillae fused; maxilla ends anterior to posterior border of eye; nasals separated; operculum unossified; second basibranchial and epibranchials rarely present; ribs not of the protruding type; and caudosacral ribs absent (Wake and Özeti, 1969).

Euproctus sp. indet.: European Mountain Salamander

Pleistocene Locality
Spain: Upper Pleistocene—11.

Genus *Salamandra* Laurenti, 1768: Fire Salamanders

This genus contains moderately large, mainly terrestrial salamanders with a smooth skin and no costal grooves. Newt (aquatic) and eft (terrestrial) morphs do not occur. Two species, *Salamandra atra* Laurenti, 1768 and *Salamandra salamandra* [Linnaeus, 1758], are recognized (Frost, 1985; Duellman, 1993).

The genus occurs today in middle and southern Europe, northwest Africa, and western Asia. *Salamandra* species are terrestrial and dwell in moist woodlands in hilly to mountainous country and tend to hide by day under logs or stones or in rocky crevices. Poisonous secretions protect them from various small predators.

Skeletal characters of the genus are: frontal-squamosal arch absent; operculum unossified; caudosacral ribs absent; maxillopterygoid joint absent; vertebrae opisthocoelous with wide, low neural arches; and low neural spine (in part from Wake and Özeti, 1969). Only one of the two modern species, *Salamandra salamandra*, occurs in the Pleistocene of Europe. No members of the genus *Salamandra* occur in the Pleistocene of Britain.

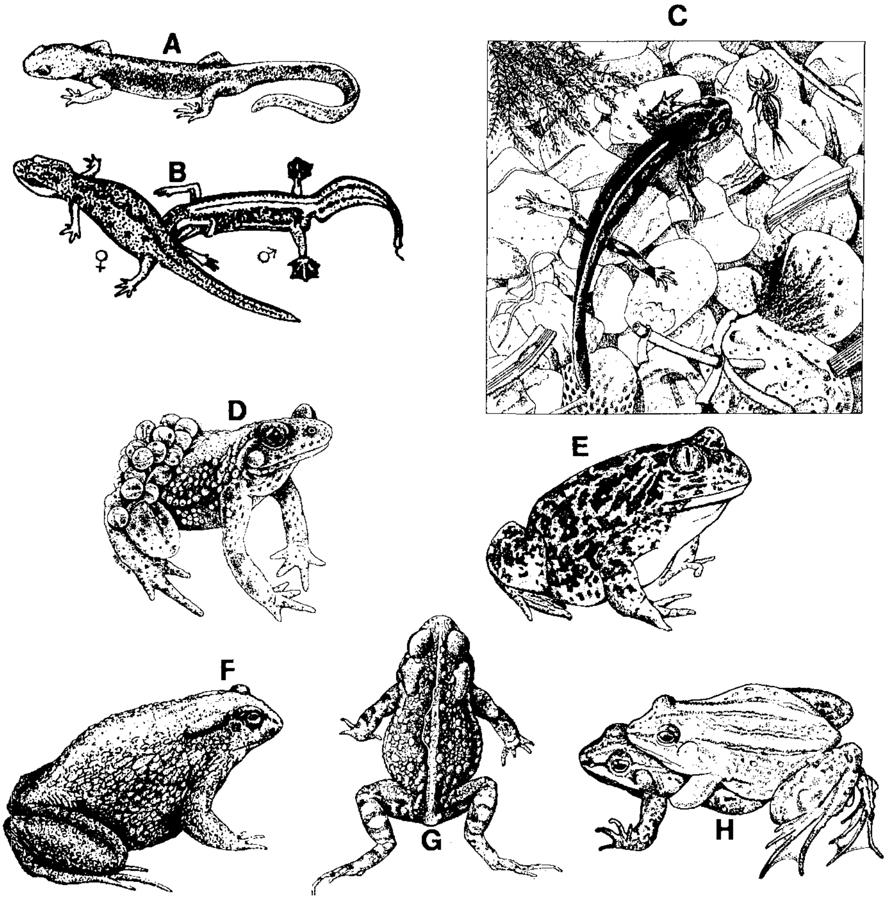

FIGURE 4. Examples of modern amphibian taxa that occurred in the Pleistocene of Britain and Europe. (A) *Euproctus* (Salamandridae), Europe only. (B) *Triturus helveticus* (Salamandridae), Britain and Europe. (C) *Salamandra salamandra* larva (Salamandridae), Europe only. (D) *Alytes obstetricans* (Discoglossidae), Europe only. (E) *Pelobates syriacus* (Pelobatidae), Europe only. (F) *Bufo bufo* (Bufonidae), Britain and Europe. (G) *Bufo calamita* (Bufonidae), Britain and Europe. (H) *Rana arvalis* (Ranidae), Britain and Europe. [A and G from Noble, 1931; C, D, and F from covers of *Herpetological Journal*, reprinted with permission; E and H from *Herpetological Review*, reprinted with permission]

Problematic Taxa

A parasphenoid from the Breitenberg Cave near Gössweinstein (Germany: Middle Pleistocene site 2) was described as the fossil species **Salamandra perversa* Brunner, 1957. This bone is probably the broken parasphenoid of a fish (Estes, 1981) and thus is presently recognized as a *nomen dubium*.

Salamandra sp. indet.: Fire Salamander

Pleistocene Localities

France: Middle Pleistocene—1, 6, 7; Upper Pleistocene—5; Pleistocene undesignated—2.

Salamandra salamandra [Linnaeus, 1758]: European Fire Salamander

Pleistocene Localities

Spain: Upper Pleistocene—7, 11, 12, 15, 18.
Germany: Middle Pleistocene—2; Upper Pleistocene 3, 10, 16.
Hungary: Upper Pleistocene—8.
Serbia: Upper Pleistocene and Holocene—1.

The fire salamander is large and colorful with a robust body and a moderately short tail. It has large paratoid glands that emit tiny jets of toxic fluid when the animal is disturbed. It normally has bright yellow, orange, or reddish spots or stripes on a black background. This species presently occurs in western, central, and southern Europe, northwest Africa, and southwestern Asia as far as the Iraq–Iran border.

Salamandra salamandra occurs mainly in damp woods, usually in hilly country or in mountains up to about 2000 m in the southern part of its range. In the Alps, it is said to be most common under about 800 m. It seldom wanders far from water and hides under logs or rocks or in rock crevices by day.

Indentification of Pleistocene Fossils

Salamandra salamandra has been identified from the Pleistocene of Europe on the basis of parasphenoids, vertebrae, and ribs. Vertebrae from the middle part of the body (Fig. 5A) appear to be diagnostic. They are procoelous with robust condyles that are separated from the centrum by a neck region. The vertebrae are of a simple form with a wide, flattened neural arch and a low neural spine. The prezygapophyseal articular surfaces are large and ovaloid, as are those of the postzygapophyseal articular surfaces. The rib bearers are robust, fused, and directed posteriorly. The posterior border of the neural arch ends anterior to the posterior extent of the postzygapophyses.

In ventral view, the centrum is smooth and unkeeled, is constricted medially, and flares posteriorly in the cotylar area. The posterior end of the centrum ends anterior to the posterior end of the neural arch. A typical vertebra has a greatest length (measured through the tips of prezygapophyseal and postzygapophyseal articular surfaces) of about 5 mm.

In Pleistocene sites, the trunk vertebrae of *Triturus cristatus* (Figs. 3 and 5B) are often as large as those of *Salamandra salamandra* (Fig. 5A). *Salamandra salamandra* trunk vertebrae, however, are shorter and wider and have a much more depressed neural arch than those of *Triturus cristatus*. Moreover, the trunk

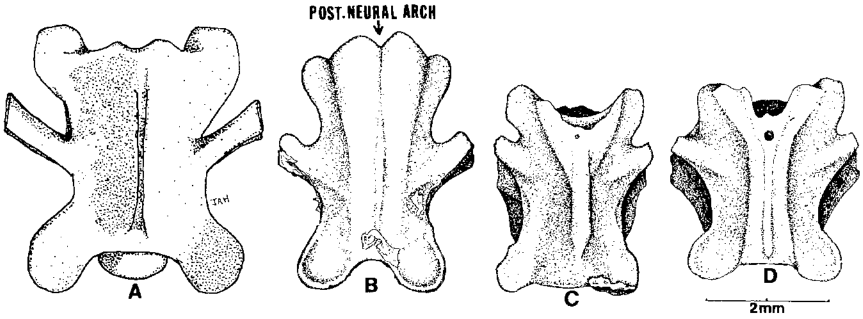

FIGURE 5. Trunk vertebrae of modern Salamandridae. (A) *Salamandra salamandra*; (B) *Triturus cristatus*; (C) *Triturus helveticus*; (D) *Triturus vulgaris*. The scale bar applies to all figures. [A, drawing by the author; B–D, drawings by Lisa Hallock and Teresa Petersen in Holman and Stuart, 1991]

vertebrae of *Triturus cristatus* taper markedly from the posterior to the anterior end, unlike the mainly straight-sided vertebrae of *Salamandra salamandra*.

Problematic Taxa.

Among fossils described by Brunner (1957) from the Breitenberg Cave near Gössweinstein (Germany: Middle Pleistocene Site 2) was material described as **Salamandra mimula* Brunner, 1957. This taxon was relegated to the synonymy of *Salamandra salamandra* by Estes (1981).

Salamandra cf. *Salamandra salamandra:*
Probable European Fire Salamander

Pleistocene Localities

Germany: Upper Pleistocene—25.
Hungary: Lower Pleistocene—2.

Genus *Triturus* Rafinesque, 1815: Alpine Newts

This genus contains small to moderately large salamanders that generally have two distinct phases or morphs. The eft morph is terrestrial with a roughened skin: it lacks a crest or "tail fin," and the feet are not elongated, fringed, or webbed. The newt morph is aquatic, has a smooth skin and a crest on the tail or sometimes on the body and the tail; a lateral line may develop, and the feet may become elongated, fringed, or webbed; costal grooves are lacking.

Twelve modern species of *Triturus* are recognized (Frost, 1985; Duellman, 1993). Several extinct species of *Triturus* have been recognized from sites predating the Pleistocene, but the material on which these species were described has often been poorly preserved or inadequate for diagnosis (Estes, 1981). The genus presently occurs in England, Scandanavia, continental Europe, and Asia

Minor around the Black Sea and to the western part of the Caspian Sea eastward to the Ural Mountains.

Some newt populations stay in the water most of the year, and in a few cases, mainly in deep water or at high altitudes, larvae may grow to large size and are able to breed. On land, species of *Triturus* tend to be quite secretive and spend most of their time under rocks, logs, or piles of leaves.

Two species groups of *Triturus* are recognized: the *Triturus cristatus* group and the *Triturus vulgaris* group (Frost, 1985). Both groups occur in Britain and Europe as Pleistocene fossils.

Some important skeletal characters of the genus are: maxilla ending behind posterior margin of eye; nasals not in contact; operculum cartilaginous; caudosacral ribs and second basibranchial absent; and second ceratobranchial cartilaginous (Wake and Özeti, 1969).

Five extant species of *Triturus* occur in the Pleistocene of Britain and Europe: *Triturus cristatus* group—*T. cristatus* and *T. marmoratus*; *Triturus vulgaris* group—*T. alpestris*, *T. helveticus*, and *T. vulgaris*.

Triturus sp. indet.: Newts

Pleistocene Localities

Britain: Middle Pleistocene—2, 3, 4, 5, 11; Upper Pleistocene—13; Latest Pleistocene or earliest Holocene—1.
Spain: Upper Pleistocene—11.
Germany: Middle Pleistocene—2; Upper Pleistocene—11, 30.
Czech Republic: Lower Pleistocene—1.
Hungary: Lower Pleistocene—2.
Greece: Pleistocene undesignated—2.

***Triturus cristatus* Group**

Triturus cristatus Laurenti, 1758: Crested Newt

Once again the name *Triturus carnifex* (Laurenti, 1768) has reappeared in some of the literature and has been applied to populations of crested newts that occur from the Alpine district of Austria northward to Salzburg and to the Donau of Linz, Vienna Woods, northern Yugoslavia, Istrian Peninsula, southern Alps, and Apennine Peninsula, Italy (Frost, 1985, pp. 614–615). We shall use the conventional name *Triturus cristatus* for these populations.

Pleistocene Localities

Britain: Middle Pleistocene—4, 5; Upper Pleistocene—13.
Germany: Middle Pleistocene—3, 9, 13, 14; Upper Pleistocene—3, 7, 27, 32; Upper Pleistocene and Holocene—4.
Czech Republic: Upper Pliocene and Lower Pleistocene—1.
Italy: Upper Pleistocene—3.
Hungary: Upper Pliocene or Lower Pleistocene—1.

The crested newt is large, rough-skinned species and is usually brownish or grayish above with black spots. It lacks the green coloration of its close relative *Triturus marmoratus*. At present, *Triturus cristatus* is absent in Ireland but occurs in Great Britain and from Europe eastward to the central part of the former Soviet Union. The warty newt favors still or very slow flowing water where there is ample aquatic vegetation. On land, the species usually stays near the breeding ponds and hides beneath rocks and logs and other flattened objects.

Identification of Pleistocene Fossils

Triturus cristatus has been identified from the Pleistocene on the basis of skulls, trunk vertebrae, humeri, and femora. The relationship of the frontal bone to the squamosal bone in the skull is important in the identification of *Triturus* species (Arnold and Burton, 1978, fig. p. 241). When the frontal and the squamosal bones have projections that extend toward or meet each other, the condition is termed the frontal-squamosal arch. The skull of *Triturus cristatus* may be separated from *Triturus helveticus*, *T. marmoratus*, and *T. vulgaris* in that *T. cristatus* lacks the frontal-squamosal arch, as no frontal or squamosal projections occur.

The trunk vertebrae of *Triturus cristatus* (Figs. 3 and 5B) are separable from those of *Salamandra salamandra* (Fig. 5A) on the basis that they are longer and narrower and have a much less depressed neural arch. Moreover, the trunk vertebrae of *Triturus cristatus* taper from the posterior to the anterior end.

The trunk vertebrae of *Triturus cristatus* differ from those of *Salamandra* and *Triturus marmoratus* in that the posterior end of the neural arch (Fig. 5B) extends well beyond the ends of the postzygapophyses. In *Salamandra salamandra* and *Triturus marmoratus* the posterior end of the neural arch ends well in front of the ends of the postzygapophyses.

The trunk vertebrae of *Triturus cristatus* (Figs. 3 and 5B) are larger with a much lower neural spine than in *T. alpestris*, *T. helveticus* (Fig. 5C) or *T. vulgaris* (Fig. 5D). Moreover, in *T. cristatus* the posterior end of the neural arch extends posterior to the ends of the postzygapophyses and has a V-shaped notch; the posterior end of the neural arch ends anterior to the postzygapophyses and has a U-shaped notch in *T. alpestris*, *T. helveticus*, and *T. vulgaris*.

The humeri of *Triturus cristatus* (Fig. 6A) have a more elongate crista ventralis (terminology of Duellman and Trueb, 1986) and a thicker shaft than in *T. helveticus* (Fig. 6B) and *T. vulgaris*. The femora of *T. cristatus* (Fig. 6C) have the tibial end more widely flared, the medial part of the shaft wider, and the area between the trochanter and the femoral end more elongate than in *T. helveticus* and *T. vulgaris* (Fig. 6D,E).

Triturus cf. *Triturus cristatus*: Probable Crested Newt

Pleistocene Locality

Germany: Upper Pleistocene—4.

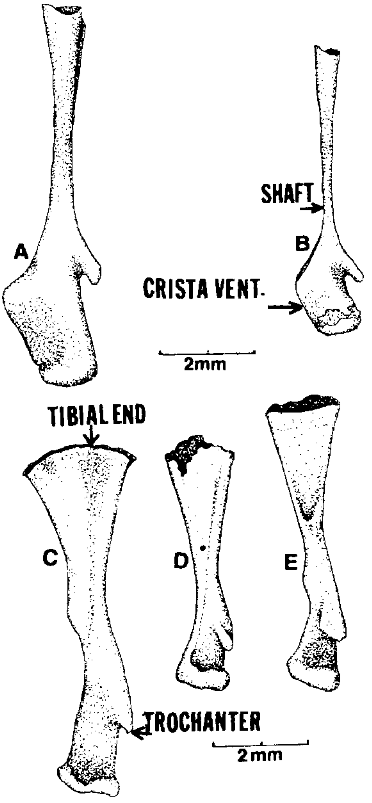

FIGURE 6. Right humeri (upper) and right femora (lower) of modern *Triturus*. (A) *Triturus cristatus*; (B) *Triturus helveticus*; (C) *Triturus cristatus*; (D) *Triturus helveticus*; (E) *Triturus vulgaris*. Upper scale bar applies to A and B; the lower scale bar applies to C–E. "Crista vent." in B = crista ventralis. [Drawings by Lisa Hallock and Teresa Petersen in Holman and Stuart, 1991]

Triturus marmoratus (Latreille, 1800): Marbled Newt

Pleistocene Localities

Spain: Middle Pleistocene—11; Upper Pleistocene—7, 11.

The marbled newt is a large, bright green newt that is mottled with black above. During the breeding season the males develop a dorsal crest with a smooth edge rather than an irregular one as in *Triturus cristatus*. At present, *Triturus marmoratus* occurs only in Iberia and in southern and western France.

The habits of *Triturus marmoratus* are similar to those of *T. cristatus* but it is not as aquatic. Moreover, it does not always inhabit damp woodlands and may sometimes be found in dry woods and heathlands. When aquatic, *Triturus marmoratus* prefers situations with abundant vegetation. *Triturus marmoratus* is restricted to lower altitudes than is *T. cristatus*.

Identification of Pleistocene Fossils

Triturus cristatus has no trace of a frontal-squamosal arch. *Triturus marmoratus* has this arch, but it is very reduced and restricted to only a small posterior projection of the frontal bone. Indicating the close relationship of the two species, the trunk vertebrae of *Triturus marmoratus* are more similar to those of *T. cristatus* than to any other European salamander. However, *Triturus marmoratus* trunk vertebrae may be distinguished from those of *T. cristatus* on the basis that the posterior end of the neural arch ends well in front of the ends of the postzygapophyses, whereas in *T. cristatus* the posterior end of the neural arch extends well beyond the ends of the postzygapophyses (Fig. 5B).

Triturus vulgaris Group

Triturus alpestris (Laurenti, 1768): Alpine Newt

Pleistocene Localities

Spain: Upper Pleistocene—11.
Germany: Middle Pleistocene—7.

The alpine newt is a medium-sized newt that is dark dorsally but has a uniformly colored dark yellow to red venter. At present it occurs from westernmost Russia to southern Denmark, northern and eastern France, Belgium, the Netherlands, northern Italy, and central Greece, with an isolated population in northern Spain. This is a very aquatic newt that is usually found in or near water. It occurs in a variety of habitats in northern Europe, but in the south it is found only in the mountains.

The presence of this species in the Pleistocene of Spain (Spain: Upper Pleistocene Site 11) has been noted by Martín and Sanchiz (1990) in reference to an unpublished paper by Sanchiz and Martín.

Triturus helveticus (Razoumowsky, 1789): Palmate Newt

Pleistocene Localities

Britain: Middle Pleistocene—5; latest Pleistocene or earliest Holocene—1.
Spain: Upper Pleistocene—15. Netherlands: Middle Pleistocene—2.

The palmate newt (Fig. 4B) is a small newt that may be distinguished by the dark, strongly webbed hind feet. It is smooth skinned, and the male has a very low tail crest. Sometimes *Triturus helveticus* is confused with the smooth newt, *T. vulgaris*, but *T. helveticus* has fewer and smaller spots on the belly and lacks the chin spots of *T. vulgaris*.

At present, the palmate newt is absent from Ireland but occurs in Great Britain, continental western Europe from northern Germany to southern France and northern Iberia, and east to Poland and the Czech Republic.

Triturus helveticus is more terrestrial than *T. cristatus* or *T. marmoratus*, but is more aquatic than *T. vulgaris*. *Triturus helveticus* tends to be ubiquitous in its choice of breeding places, which include temporary puddles, woodland and heathland ponds, edges of lakes at high elevations, and even brackish water near the sea. It is said to prefer clearer, more acidic water than *T. vulgaris*. The palmate newt occurs up to about 1000 m in the Alps and up to about 2000 m in the Pyrenees.

Identification of Pleistocene Fossils

The skull of *Triturus helveticus* has the frontal-squamosal arch completely closed and bony, forming lateral fenestrae on each side of the posterior portion of the skull. The only other European newt with this condition is Bosca's newt, *Triturus boscai*, whose modern range is restricted to the western part of the Iberian Peninsula.

Holman and Stuart (1991) found that the trunk vertebrae of *Triturus helveticus* (see Fig. 5) were diagnostic, but they could not find characters to distinguish the humeri and femora of *T. helveticus* from those of *T. vulgaris*. Trunk vertebrae of *T. helveticus* may be separated from those of *T. cristatus* and *T. marmortus* in being smaller, shorter, and wider and in having a much higher neural spine. *Triturus helveticus* trunk vertebrae have the terminal notch in the posterior end of the neural arch broadly U-shaped (Fig. 5C), whereas this notch is narrowly U-shaped in *T. vulgaris* (Fig. 5D).

Triturus helveticus or *Triturus vulgaris*:
Palmate or Smooth Newt

Pleistocene Localities

Britain: Middle Pleistocene—3.
Germany: Middle Pleistocene—9, 10, 13.

These remains could be identified as belonging to either *Triturus helveticus* or *Triturus vulgaris* but were too fragmentary to identify to species.

Triturus vulgaris (Linnaeus, 1758): Smooth Newt

Pleistocene Localities

Britain: Middle Pleistocene—3, 4, 5, 11; Upper Pleistocene—10; latest Pleistocene or earliest Holocene—1.
Netherlands: Middle Pleistocene—2.
Germany: Middle Pleistocene—3, 13, 14; Upper Pleistocene—3, 4, 27.
Czech Republic: Upper Pliocene and Lower Pleistocene—1.
Italy: Middle Pleistocene—6.

Triturus vulgaris is a small, smooth-skinned newt. The male has a high, undulating crest and fringed toes during the breeding season. Sometimes, outside of the breeding season, *Triturus vulgaris* is confused with *T. helveticus*, but *T. vulgaris* has larger spots on the belly and has chin spots. Chin spots are absent in *T. helveticus*. At present, the smooth newt occurs in Ireland and Great Britain, almost all of Europe, and the western part of Asia.

The smooth newt is more terrestrial than most other species of European newts and tends to be a lowland form that lives in a wide variety of moist habitats. It usually breeds in still, shallow, well-vegetated bodies of water. Smooth newts are the most common salamanders found in the Pleistocene of Britain. On the continent, many Pleistocene remains identified as *Triturus* sp. probably represent smooth newts.

Identification of Pleistocene Fossils

The skull of *Triturus vulgaris* has an interrupted frontal-squamosal arch with no closed fenestrae. This skull condition is shared only with the Italian newt, *Triturus italicus.*

Holman and Stuart (1991) show that the trunk vertebrae of *Triturus vulgaris* may be distinguished from those of *T. helveticus* in that the terminal notch at the end of the neural arch is narrowly U-shaped (Fig. 5D) rather than broadly U-shaped as in *T. helveticus* (Fig. 5C).

Triturus cf. *Triturus vulgaris*: Probable Smooth Newt

Pleistocene Locality

Germany: Upper Pleistocene—2, 7, 9.

Order Anura Rafinesque, 1815: Frogs and Toads

Pleistocene anurans may be identified on the basis of a number of individual skeletal elements, but the ilium is the most important of these (see Holman, 1995c, p. 85). Figure 7 shows important features of individual anuran bones.

Anura indet.: Unidentified Anuran Material

Pleistocene Localities

Britain: Middle Pleistocene—10; Upper Pleistocene—16.
Spain: Upper Pleistocene—15.
Germany: Upper Pleistocene—17; Upper Pleistocene/Holocene boundary.
Hungary: Upper Pleistocene and Holocene—1.

Family Discoglossidae Günther, 1859 "1858"

Disk-Tongued Toads

The Discoglossidae comprises a heterogeneous group of primitive anurans with disk-shaped tongues. Some are brightly colored, but others are rather drab and toadlike. The family has five living and eight extinct genera (Duellman, 1993; Sanchiz, in press). At present the group occurs in Europe, North Africa, Israel, Turkey, western and eastern portions of the former Soviet Union, China, Korea, and southeast Asia, including the Philippines. Several discoglossid species have unique reproductive and behavioral patterns.

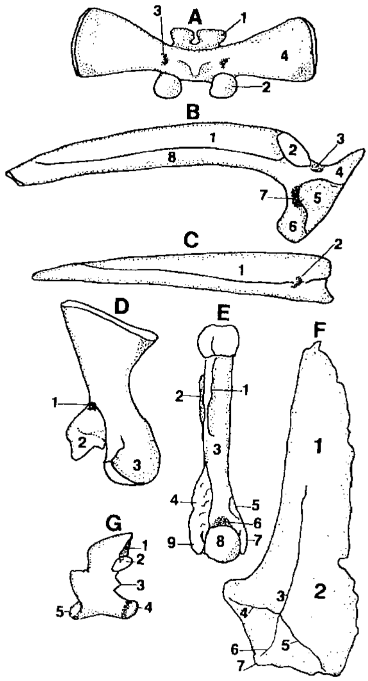

FIGURE 7. Bones of a typical *Rana* indicating important taxonomic structures of anurans. (A) Sacral vertebra in dorsal view: (1) condyle, (2) prezygapophyseal articular surface, (3) dorsal fossa, (4) sacral diapophysis. (B) Left ilium in lateral view: (1) dorsal crest (or vexillum), (2) dorsal prominence (or tuber superior), (3) supra-acetabular fossa, (4) dorsal acetabular expansion (or pars ascendens ilii), (5) acetabulum (or acetabular cup), (6) ventral acetabular expansion (or pars descendens ilii), (7) preacetabular fossa, (8) ilial shaft (or ala, or pars cylindriformis). (C) Urostyle in lateral view: (1) dorsal crest, (2) lateral foramen. (D) Right scapula: (1) supraglenoid fossa, (2) glenoid process, (3) acromial process. (E) Left humerus of male in ventral view: (1) ventral crest, (2) paraventral crest, (3) humeral shaft, (4) mesial crest (this flared mesial crest is a sexually dimorphic male character), (5) radial crest, (6) cubital fossa, (7) radial epicondyle, (8) distal condyle, (9) ulnar epicondyle. (F) Left frontoparietal in dorsal view: (1) frontal region, (2) parietal region, (3) medial line, (4) prootic line, (5) transverse line, (6) occipital line, (7) occipital process. (G) Atlas in lateral view: (1) suprazygapophyseal cavity, (2) postzygapophysis, (3) subzygapophyseal tubercle, (4) condyle, (5) cotyle. [Drawings by the author; terminology is mainly from Bailón, 1986; Böhme, 1977; Duellman and Trueb, 1986; Holman, 1995c]

Osteological characters of the family modified from Duellman and Trueb (1986) are: palatines absent; parahyoid bone (or bones) present; cricoid ring complete; teeth present on both maxillary and premaxillary; eight stegochordal, opisthocoelous presacral vertebrae with imbricate neural arches present; free ribs present on presacrals II through IV; sacrum with expanded sacral diapophyses; two condyles that articulate with urostyle (except for *Barbourula* with a single condyle); pectoral girdle arciferal with cartilaginous omosternum and sternum; ilia simple (Fig. 8D); astragulus and calcaneum fused only proximally and distally; and phalangeal formula normal.

Three genera, *Alytes*, *Bombina*, and *Discoglossus*, are found in the Pleistocene of Europe. The family has not yet been recorded in the Pleistocene of Britain.

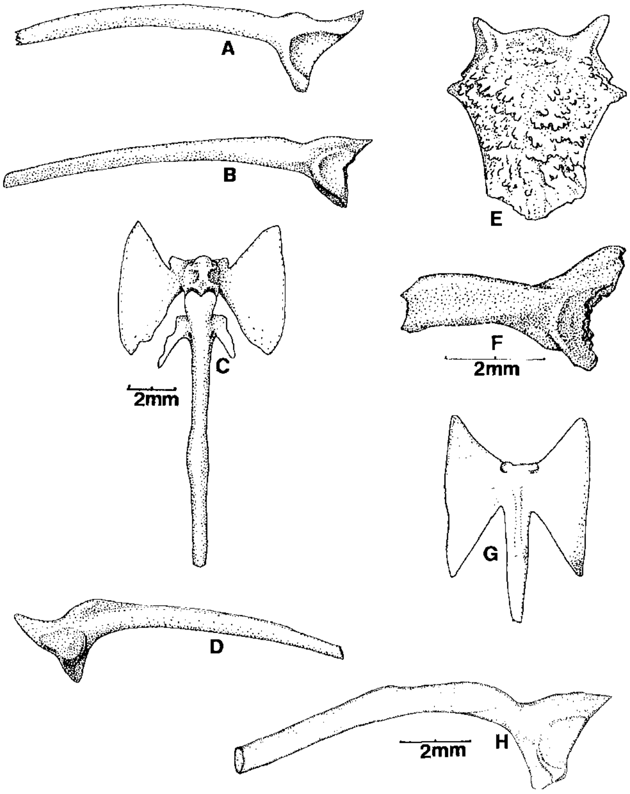

Figure 8. Bones of primitive anuran genera. (A) Left ilium of modern *Alytes obstetricans*; (B) left ilium of modern *Bombina bombina*; (C) sacrum and partially fused urostyle of modern *Bombina bombina* in ventral view; (D) right ilium of modern *Discoglossus pictus*; (E) frontoparietal of modern *Pelobates fuscus* in dorsal view; (F) left ilium of *Pelobates fuscus* from the Middle Pleistocene Boxgrove Site, West Sussex, England; (G) sacrum and fused urostyle of modern *Pelobates fuscus*; (H) left ilium of *Pelodytes punctatus* from the Middle Pleistocene Westbury–Sub-Mendip Site, Somerset, England. The scale bar on the left applies to A–D. No scale is available for E and G. [Drawings are by Teresa Petersen; F from Holman, 1992b; H from Holman, 1993c]

Discoglossidae indet.: Indeterminate Disk-Tongued Toad

Pleistocene Localities
Italy: Lower Pleistocene—1, 4.

Genus *Alytes* Wagler, 1829: Midwife Toads

The midwife toads of the genus *Alytes* (Fig. 4D) are plump, drab, and warty and characterized by their unique reproductive habits in which the males carry fertilized eggs about on the posterior part of their bodies. Three species are currently recognized (Duellman, 1993). At present, the genus occurs in Europe, with the exception of the northern and eastern parts, and in northwestern Africa. Species of *Alytes* are mainly secretive and nocturnal. Burrows are dug with the forelimbs in most species.

Osteological characters are: frontoparietal narrow and deeply notched; sphenethmoid with an extensive U-shaped dorsal indentation; ilium (Fig. 8A) lacking a dorsal crest (vexillum) with an elongate, sharply pointed dorsal acetabular expansion (pars ascendens ilii); and sacrum with moderately expanded sacral diapophyses.

Two extant *Alytes* species, *Alytes obstetricans* and *Alytes muletensis*, occur in the Pleistocene of Europe. The genus has not been recorded from the Pleistocene of Britain.

Alytes sp. indet.: Indeterminate Midwife Toad

Pleistocene Localities

Spain: Pliocene/Pleistocene boundary—1; Pleistocene undesignated—1.

cf. *Alytes*: Probable Midwife Toad

Pleistocene Localities

Spain: Middle Pleistocene—1, 3; Middle and Upper Pleistocene—1; Upper Pleistocene—2.

Alytes muletensis (Sanchiz and Adrover, 1979, ''1977''): Balearic Island Midwife Toad

Pleistocene Localities

Spain: Middle Pleistocene—12; Upper Pleistocene—3, 22; Upper Pleistocene and Holocene—1.

The Balearic Island midwife toad is a very small, brownish anuran that is usually less than 40 mm in snout-to-vent length. It is presently found only in the Balearic Islands of Spain. It is less fossorial than the other species of *Alytes* and inhabits rapid streams.

Of considerable interest is the fact that the species was first described as a fossil from the Pleistocene of Majorca Island (Sanchiz and Adrover, 1977) and later discovered as a living inhabitant of the Balearics. Mayol and Alcover (1981) discuss the biology of the living species.

Identification of Pleistocene Fossils

The skeleton of *Alytes muletensis* differs from those of other *Alytes* species in several respects (Sanchiz, in press). It has a wider pars dentalis and shorter medial synthesis in the premaxillae, which also bear more teeth (14–16). The maxilla is lower, and the lateral margin of the nasal is longer and has an indistinct posterior margin. The sphenethmoid is not completely ossified. The frontoparietal is less ossified than in the other *Alytes* species and is without medial contact, except at the posterior end. The prootic process is poorly developed. The humerus lacks fossorial modifications.

Alytes obstetricans (Laurenti, 1768): Common Midwife Toad

Pleistocene Localities

France: Upper Pleistocene—3, 13; Upper Pleistocene or Holocene—1, 2.
Spain: Middle Pleistocene—5; Upper Pleistocene—7, 10, 11, 15.

The midwife toad, *Alytes obstetricans* (Fig. 4D), is a small greenish or brownish anuran with three tubercles on the front foot. It ranges up to about 50 mm in snout-to-vent length. At present this species occurs mainly in western Europe and Morocco. In western Europe the northern limit of this species is in the southern Netherlands, and its eastern limit is in Germany, Switzerland, and southeastern France. It occupies a wide variety of habitats, including woodlands, quarries, and rock slides as well as farmlands and gardens, and occurs up to 2000 m in the southern part of its range.

Identification of Pleistocene Fossils

Osteological characters that distinguish this species from the other known Pleistocene species (*A. muletensis*) are given in the preceding account.

Genus *Bombina* Oken, 1816: Firebelly Toads

Species of *Bombina* are depressed, toadlike animals, dull colored and warty above but variegated below, with bright colors such as red, white, orange, or yellow mixed with black. Five species of *Bombina* are currently recognized (Duellman, 1993). At present, the genus occurs in Europe, Turkey, disjunctly in the western and eastern parts of the former Soviet Union, China, Korea, and Vietnam. These animals are usually found in low-energy aquatic situations.

Osteological characters for the genus are: frontoparietal narrow and weakly notched; sphenethmoid with a moderately extensive, rounded, dorsal excavation; ilium (Fig. 8B) lacking a dorsal crest (vexillum) but with a long, low, relatively smooth dorsal prominence (tuber superior); dorsal acetabular expansion (pars ascendens ilii) relatively short; ventral acetabular expansion (pars ascendens ilii) obsolete or absent, at least in most *Bombina bombina*; and sacrum with greatly expanded sacral diapophyses (Fig. 8C).

Two extant species of *Bombina*, *Bombina bombina* and *Bombina variegata* have been identified from the Pleistocene of Europe. The genus has not been reported as a Pleistocene fossil from Britain.

Bombina sp. indet.: Indeterminate Firebelly Toad

Pleistocene Localities

Germany: Upper Pleistocene—18, 30.
Poland: Upper Pleistocene and Holocene—1.
Hungary: Lower Pleistocene—5; Upper Pleistocene—4.
Croatia: Upper Pleistocene—6.

cf. *Bombina*: Probable Firebelly Toad

Pleistocene Locality

Hungary: Lower Pleistocene—3.

Bombina bombina (Linnaeus, 1761): Firebelly Toad

Pleistocene Localities

Germany: Upper Pleistocene and Holocene—4.
Poland: Lower Pleistocene—3.

Bombina bombina is a flattened, warty anuran with a brightly colored underside of red or reddish-orange markings on a black background. This species presently occurs in central and eastern Europe from Denmark and western Germany east to the Ural Mountains and south to the Caucasus Mountains and in the north to the Gulf of Finland. It also is found in Turkey. Specimens identified from Sweden were probably introduced (Frost, 1985). Firebelly toads are found in a variety of shallow, low-energy aquatic situations, usually in lowlands.

Identification of Pleistocene Fossils

Sanchiz (in press) points out that the European species of *Bombina* are very similar osteologically and that hybrids are found in places where species come together. He also points out that the available criteria for the identification of fossil *Bombina* species (e.g., Hodrová, 1985) are only effective in specific fossil assemblages.

Bombina cf. *Bombina bombina*: Probable Firebelly Toad

Pleistocene Locality

Czech Republic: Late Pliocene and Lower Pleistocene—1.

Bombina variegata (Linnaeus, 1758): Yellowbelly Toad

Pleistocene Locality

Serbia: Upper Pleistocene and Holocene—1.

Bombina variegata is a flattened, warty anuran with a brightly colored underside of yellow or yellowish-orange markings on a black background. This species is found in central and southern Europe (excluding the Iberian Peninsula, northwestern France, and Britain) southeast to the Carpathian Mountains. This species is found in a variety of shallow, low-energy aquatic situations. It occurs in lowlands as well as mountainous and hilly areas, especially in areas where it is sympatric with *Bombina bombina*.

Identification of Pleistocene Fossils

It has been pointed out in the preceding account that identification of *Bombina* skeletal elements to the specific level is very difficult.

Bombina cf. *Bombina variegata*: Probable Yellowbelly Toad

Pleistocene Localities

Germany: Upper Pleistocene—27.
Hungary: Upper Pliocene or Lower Pleistocene—1.

Genus Discoglossus Otth, 1837: Painted Frogs

Species of *Discoglossus* are medium-sized, froglike anurans with plumpish, shiny bodies. They are readily distinguished from the typical frogs of the genus *Rana* by their disk-shaped tongue, their round or triangular rather than vertical pupil, and their inconspicuous tympanum. Six modern species of *Discoglossus* occur (Duellman, 1993), and an extinct, undescribed species from the Pliocene–Pleistocene boundary of the Balearic Islands is under study (Sanchiz, in press). At present the genus occurs in southern Europe, northwestern Africa, Israel, and questionably, Syria. This is an aquatic group of frogs that prefers shallow pools, streams, and the edges of rivers.

Osteological characters of the genus are: frontoparietal broad and unnotched; sphenethmoid with a very extensive dorsal notch; ilium (Fig. 8D) with an obsolete dorsal crest (vexillum), with a long, rounded dorsal protuberance (tuber superior), and a moderately long, pointed dorsal acetabular expansion (pars ascendens ilii); and sacrum with moderately expanded sacral diapophyses.

Frost (1985) recognized three species of *Discoglossus*, but Duellman (1993) now recognizes six. An osteological cladistic analysis of the genus was done by Clarke (1988). Four of the six modern *Discoglossus* species (*D. galganoi*, *D.* cf. *D. jeanneae*, *D. pictus*, and *D. sardus*) have been identified from the Pleistocene of Europe. The genus has not been identified from the Pleistocene of Britain.

Discoglossus sp. indet.: Painted Frog

Pleistocene Localities

France: Upper Pleistocene—10, 14; Middle Pleistocene—1.
Spain: Pliocene/Pleistocene Boundary—1; Lower Pleistocene—1, 3, 5; Middle or Upper Pleistocene—1; Pleistocene undesignated—1.
Italy: Lower Pleistocene—7, 5; Middle Pleistocene—2, 5; Upper Pleistocene—20; Pleistocene undesignated—6.
Croatia: Upper Pleistocene—5.
Greece: Lower Pleistocene—3; Middle Pleistocene—2.

Discoglossus galganoi Capula, Nascetti, Lanza, Bullini and Crespo, 1985: Portugal Painted Frog

Pleistocene Localities

Spain: Middle Pleistocene—2, 3.

This recently described species is presently known only from Portugal and southwestern Spain (Duellman, 1993).

Discoglossus cf. *Discoglossus jeanneae* Busack, 1986: Spanish Painted Frog

Pleistocene Localities

Spain: Middle Pleistocene—8; Middle and Upper Pleistocene—1.

This recently described species is known only from southern Cádiz Province, Spain (Duellman, 1993).

Discoglossus pictus Otth, 1837: Common Painted Frog

Pleistocene Locality

Italy: Middle Pleistocene—1.

This species is quite variable in coloration and may be gray, olive, yellowish, or even reddish color above, with darker, light-edged spots. At present, it occurs in the Iberian Peninsula, except the northeastern part, and in the eastern Pyrenees. It also occurs north of the Sahara in Tunisia, Algeria, and Morocco as well as in Sicily and Malta. Painted frogs are usually found in or near either still or running water.

Discoglossus cf. *Discoglossus pictus*: Probable Common Painted Frog

Pleistocene Localities
Italy: Middle Pleistocene—9; Upper Pleistocene—6.

Discoglossus sardus Tschudi, 1837: Sardinian Painted Frog

Pleistocene Locality
Italy: Upper Pleistocene and Holocene—1.

This frog is very similar to the preceding species but tends to be a more robust form with a broader head. It is presently known from Sardinia, Corsica, Giglio, Monte Cristo, and Iles d'Hyéres.

Discoglossus cf. *Discoglossus sardus*: Probable Sardinian Painted Frog

Pleistocene Localities
Italy: Upper Pleistocene—7, 15; Upper Pleistocene or Holocene—2.

Family *Palaeobatrachidae Cope, 1865

Palaeobatrachid Frogs

This is the only extinct family of anurans (Roček, 1995). It is composed of highly aquatic *Xenopus*-like frogs. Four genera are currently recognized (Sanchiz, in press). Osteologically the family is apparently the sister group of the modern family Pipidae, differing in having procoelous rather than opisthocoelous vertebrae and an extra phalynx on the fifth toe (Estes and Reig, 1973).

Important osteological characters of the family, modified from Sanchiz (in press) and Špinar (1972), are: orbits large and anterior on the skull; teeth present on both the premaxillary and maxillary; frontoparietal single; parasphenoid dagger-shaped and lacking lateral wings; vertebrae procoelous; two posterior vertebrae involved in sacrum; sacrum with dilated diapophyses; two cotyles articulating with the urostyle; pectoral girdle arciferal with a short, undivided scapula and a coracoid that is axe shaped medially; and ilium lacking a dorsal crest (vexillum), but with a long, well-developed dorsal protuberance (tuber superior).

The genus **Pliobatrachus* lingered into the Pleistocene of Europe.

Genus **Pliobatrachus* Féjeváry, 1917: Pliobatrachid Frogs

The genus **Pliobatrachus* is known from the Pliocene and Pleistocene of central and eastern Europe on the basis of a single species, **Pliobatrachus langhae*, the last member of the *Palaeobatrachidae. A diagnosis of **Pliobatrachus langhae* is modified from Sanchiz (in press). It is a large species with the frontoparietal having a U-shaped dorsal groove in its middle portion and a trifurcate anterior end that overlies the sphenethmoid. Teeth are present on both the premaxillary and maxillary bones, but the number of teeth is reduced. The teeth are not inserted in a pleurodont manner, but occur as osseous knobs that alternate with alveoli. The mandibular coronoid process forms a medially depressed, round tubercle. The ilium has a well-developed interiliac process.

**Pliobatrachus* cf. *Pliobatrachus langhae* Fejéváry, 1917: Langha's Pliobatrachid Frog

Pleistocene Localities

Germany: Middle Pleistocene—20.
Poland: Lower Pleistocene—3, 5.

Family Pelobatidae Bonaparte, 1850

Spadefoot Toads

The family Pelobatidae comprises a group of primitive anurans with short-legged, plump bodies, and large eyes with vertical pupils. Pelobatids are divided into Holarctic and Oriental subfamilies (Pelobatinae and Megaphryinae), with three extant Holarctic and eight extant Oriental genera currently recognized (Duellman, 1993).

The distribution of the family is Pakistan east to the Indo-Australian Archipelago and the Phillipines; Europe, western Asia, and northern Africa; and southwestern Canada and eastern United States to southern Mexico. The Holarctic pelobatids (Pelobatinae) are smooth-skined fossorial species with a spadelike metatarsal tubercle that is used for digging. The Oriental pelobatids (Megaphryinae) are more diverse in general appearance, some with dorsolateral folds and/or odd processes on the head.

Osteological characters of the family, modified from Duellman and Trueb (1986), are: eight presacral vertebrae with imbricate neural arches present; ossified intervertebral disks fused with centrum to form a procoelous condition (except in the Oriental forms, where the disks remain free); ribs absent; sacrum (Fig. 8G) with very broadly expanded sacral diapophyses; sacrum firmly fused to urostyle; pectoral girdle arciferal; parahyoid absent; cricoid ring incomplete dorsally; teeth present on premaxillary and maxillary; and ilium (Fig. 8F) lacking dorsal crest (vexillum), with dorsal prominence (tuber superior) usually obsolete or absent.

Genus *Pelobates* Wagler, 1830: European Spadefoots

European spadefoots superficially resemble the true toads of the genus *Bufo* but have vertical pupils, have a sharp metatarsal tubercle on the hind foot for digging, and lack paratoid glands. Four living species of *Pelobates* are recognized (Duellman, 1993). At present the genus occurs in Europe, western Asia, and northwestern Africa. European spadefoots are generally found in areas with sandy soils where they dig burrows with the hind feet. They normally occupy these burrows during the daytime and come out of them at night to feed.

Some important osteological characters of *Pelobates* are: frontoparietals (Fig. 8E) fused and with a sculptured dorsal surface; sphenethmoid normally longer than wide, with relatively narrow lateral processes, and a relatively shallow U-shaped dorsal excavation; ilium (Fig. 8F) lacking a dorsal crest (vexillum), with dorsal prominence (tuber superior) either obsolete or absent, and with dorsal border of dorsal acetabular expansion (pars ascendens ilii) slightly concave (Fig. 8F); and sacrum (Fig. 8G) fused to urostyle, with sacral diapophyses greatly expanded and usually perforated ventrally.

Three living taxa, *Pelobates cultipres*, *P. fuscus*, and *Pelobates* cf. *P. syriacus* have been identified from the Pleistocene of Europe. Only *Pelobates fuscus* has been recorded from the Pleistocene of Britain.

Pelobates sp. indet: Indeterminate European Spadefoot

Pleistocene Localities

France: Lower Pleistocene—1; Middle Pleistocene—1; Upper Pleistocene—8.
Spain: Middle Pleistocene—5.
Poland: Lower Pleistocene—3.
Hungary: Middle and Upper Pleistocene—1; Upper Pleistocene—4.
Croatia: Upper Pleistocene—5, 6.
Greece: Middle Pleistocene—1; Pleistocene undesiganted—1.

Pelobates cultipres (Cuvier, 1829): Western Spadefoot

Pleistocene Localities

Spain: Middle Pleistocene—2, 3, 4; Upper Pleistocene—2, 14.

The western spadefoot is larger and lacks the prominent lumplike dome on the top of the head that occurs in the common spadefoot (*Pelobates fuscus*). *Pelobates cultipres* presently occurs in the Iberian Peninsula and in southern France. This species is common in sandy coastal areas but also occurs in some open wetland situations. It is sometimes more diurnal than *Pelobates fuscus*.

Identification of Pleistocene Fossils

Böhme (1977, pp. 289, 292) illustrates frontoparietals and sphenethmoids that have characters that appear to separate *Pelobates cultipres* from *P. fuscus* and

P. syriacus. In *Pelobates cultipres* the occipital processes of the frontoparietals are wide at the base and taper rapidly to a point. In the other two species the occipital processes of the frontoparietals are narrower at the base, are more uniform in width throughout their length, and have more rounded ends. In *Pelobates cultipres* the sphenethmoid is much longer than wide, and its lateral processes are somewhat anteriorly directed. In the other two species the sphenethmoid is slightly longer than wide, and the lateral processes emerge at right angles to the long axis of the bone. It should be pointed out that all of these characters may be subject to individual variation.

Pelobates cf. *Pelobates cultipres*: Probable Western Spadefoot

Pleistocene Localities

France: Lower Pleistocene—4.
Spain: Lower Pleistocene—6.

Pelobates fuscus (Laurenti, 1768): Common Spadefoot

Pleistocene Localities

Britain: Middle Pleistocene—3.
France: Upper Pleistocene—7.
Luxembourg: Pleistocene undesignated—1.
Germany: Upper Pleistocene—2, 3, 15, 18, 27; Pleistocene undesignated—4, 8; Upper Pleistocene and Holocene—4.
Austria: Lower and Middle Pleistocene—1; Pleistocene undesignated—2.
Poland: Lower Pleistocene—3, 5; Upper Pleistocene and Holocene—1.
Czech Republic: Lower Pleistocene—2.
Hungary: Lower Pleistocene—3; Middle Pleistocene—1; Upper Pleistocene—2; Upper Pleistocene and Holocene—6.
Serbia: Upper Pleistocene and Holocene—1.

The common spadefoot has a well-developed dome on the top of the head that easily separates it from *P. cultipres* described above and *P. syriacus* described below. The present distribution of *Pelobates fuscus* is in France, Belgium, Netherlands, Denmark, southeastern Sweden, and northern Italy east to southern Siberia, western Kazakhstan, and the northern Caucasus. The extralimital occurrence of this species in the Middle Pleistocene of England is addressed in Chapter 7. This species also spends most of the daylight hours in its burrow, emerging to forage at night. The common spadefoot may be found in cultivated as well as in natural sandy areas.

Identification of Pleistocene Fossils

Figures in Böhme (1977, p. 289) indicate that the frontoparietal of *Pelobates fuscus* may be separated from those of *P. cultipres* on the basis that the occipital processes are not as wide at the base and are more uniformly narrow throughout their extent than in *P. cultipres*. Moreover, the ventral excavation in the frontoparietals of *Pelobates fuscus* appear to be much more extensive than in either *P. cultipres* or *P. syriacus*. The sphenethmoid of *Pelobates fuscus* (Böhme, 1977, fig. p. 292) appears to be distingishable from that of *P. cultipres* and *P. syriacus* in having its anterior portion with a constricted neck region. This region is flared in both of the other species. The ilium of *Pelobates fuscus* (Böhme, 1977, fig. p. 294) has an obsolete dorsal protuberance (tuber superior) present, whereas *P. syriacus* has none. It should be pointed out that all of these characters may be subject to individual variation.

Pelobates cf. *Pelobates fuscus*: Probable Common Spadefoot

Pleistocene Localities

Germany: Upper Pleistocene—32; Pleistocene undesignated—5; Upper Pleistocene or Holocene—1.
Hungary: Lower Pleistocene—5.

Pelobates cf. *Pelobates syriacus* Boettger, 1889: Probable Eastern Spadefoot

Pleistocene Localities

Czech Republic: Late Pliocene and Lower Pleistocene—1.
Greece: Middle Pleistocene—3, 4.

The eastern spadefoot (Fig. 4E) may be externally distinguished from the two *Pelobates* species described above in lacking a dome on the head, having a pale metatarsal tubercle on the hind foot, and having indented webbing on the hind foot. *Pelobates syriacus* presently occurs in northern Israel, Lebanon, northern Syria, northern Iraq, Turkey, Caspian Iran, eastern Transcaucasia, and the Balkan Peninsula north to southern Yugoslavia and Romania. The habits of the eastern spadefoot are, in general, similar to those of the two *Pelobates* species described above.

Identification of Pleistocene Fossils

The frontoparietal of *Pelobates syriacus* (Böhme, 1977, fig. p. 289) may be separated from that of *P. fuscus* on the basis of the lesser excavation on the ventral surface of the bone and from *P. cultipres* on the basis of having occipital processes that are narrower at the base and of more uniform width throughout their extent. The sphenethmoid of *Pelobates syriacus* (Böhme, 1977, fig. p. 292) is shorter and wider than in either of the two other species. The ilium of *Pelobates syriacus* (Böhme, 1977, fig. p. 294) has no evidence of a dorsal prominence (tuber superior), while that of *Pelobates fuscus* bears an obsolete dorsal prominence. It should be pointed out that all of these characters may be subject to individual variation.

Family Pelodytidae Hogg, 1838

Parsley Frogs

The Pelodytidae are closely related to and sometimes included with the Pelobatidae. Pelodytid frogs are small, agile anurans with long legs, and they rather resemble true frogs of the genus *Rana*. Only one living genus, *Pelodytes*, is recognized (Duellman, 1993). The present distribution of the Pelodytidae is in southwestern Europe and the Caucasus region. These anurans are mainly nocturnal terrestrial forms that are usually found in rather moist, vegetated situations.

This family is osteologically similar to the Pelobatidae, but they have the derived skeletal characters of an elongate pterygoid, a scapula with an anterior tubercle, and a fused tibiale and fibulare (Henrici, 1994).

Genus *Pelodytes* Bonaparte, 1838: Parsley Frogs

The genus has but two species, *Pelodytes punctatus* and *Pelodytes caucasicus* (Frost, 1985, Duellman, 1993). Only the former species is known as a Pleistocene fossil. Some important skeletal characters of the genus are: frontoparietals unfused and lacking hornlike occipital processes; and ilia (Fig. 8H) generally similar to Pelobatidae except the dorsal edge of the dorsal acetabular expansion (pars ascendens illi) is slightly convex rather than slightly concave. This last character appears to be remarkably consistent.

Pelodytes sp.: Parsley Frog

Pleistocene Locality

Poland: Lower Pleistocene—4.

Pelodytes punctatus (Daudin, 1802): Common Parsley Frog

Pleistocene Localities

Britain: Middle Pleistocene—12.
Spain: Middle Pleistocene—2, 5; Upper Pleistocene—2.
Germany: Middle Pleistocene—16.

Pelodytes punctatus is a small, agile frog with a flat head and large eyes. This taxon might possibly be mistaken for a small species of true frog of the genus *Rana*. The common parsley frog presently occurs in Belgium through France to Spain and extreme northwestern Italy. The extralimital occurrence of this species in the Middle Pleistocene of England is addressed in Chapter 7. The species is principally a nocturnal, terrestrial form that prefers somewhat damp and rather well-vegetated habitats.

Identification of Pleistocene Fossils

Böhme (1977, fig. p. 294) indicates that the ilium of *Pelodytes punctatus* may be separated from the only other species in the genus, *Pelodytes caucasicus*, on the basis of having a more flattened surface in the posterior part of the dorsal rim of the dorsal acetabular expansion (pars ascendens ilii) and a shallow, cuplike indentation between the dorsal acetabular expansion and the ilial shaft. These characters, however, may be individually variable.

Pelodytes cf. *Pelodytes punctatus: Probable Common Parsley Frog*

Pleistocene Localities

France: Lower Pleistocene—4; Middle Pleistocene—1, 4, 9; Upper Pleistocene—7, 16; Pleistocene undesignated—4.

Family Bufonidae Gray, 1825

True Toads

Bufonids are usually short-legged animals with thick, glandular, often warty skins. Many genera have large, paired paratoid glands on the body just back of the head, and others have conspicuous glands on the legs. Most species have well-ossified skulls that are co-ossified with the skin of the head. Thirty-one living genera of the Bufonidae are currently recognized (Duellman, 1993). At present, bufonids are mainly cosmopolitan except for the Australian and Madagascaran regions. Most species are terrestrial and some are fossorial.

The Bufonidae form a large and diverse group that is diffcult to define osteologically. Nevertheless, some important osteological characters (mainly modified from Duellman and Trueb, 1986) are: usually eight holochordal presacral vertebrae present (fusion of presacrals leads to a lesser number in some genera); ribs absent; sacrum with dilated, but not greatly expanded sacral diapophyses; sacrum not fused to urostyle in majority of genera, including *Bufo*; pectoral girdle arciferal or pseudofirmisternal; palatines almost always present; teeth present on premaxillary and maxillary; and ilium usually lacking dorsal crest (vexillum), but usually bearing a more or less prominent dorsal prominence (tuber superior).

Only two genera of Bufonidae are known as fossils, and both of these (*Bufo* and *Peltophryne*) are presently living (Sanchiz, in press).

Bufo sp. or *Rana* sp.: Indeterminate True Toad or True Frog

Pleistocene Localities

Britain: Middle Pleistocene—6, 8, 10; Upper Pleistocene—3, 7, 18.

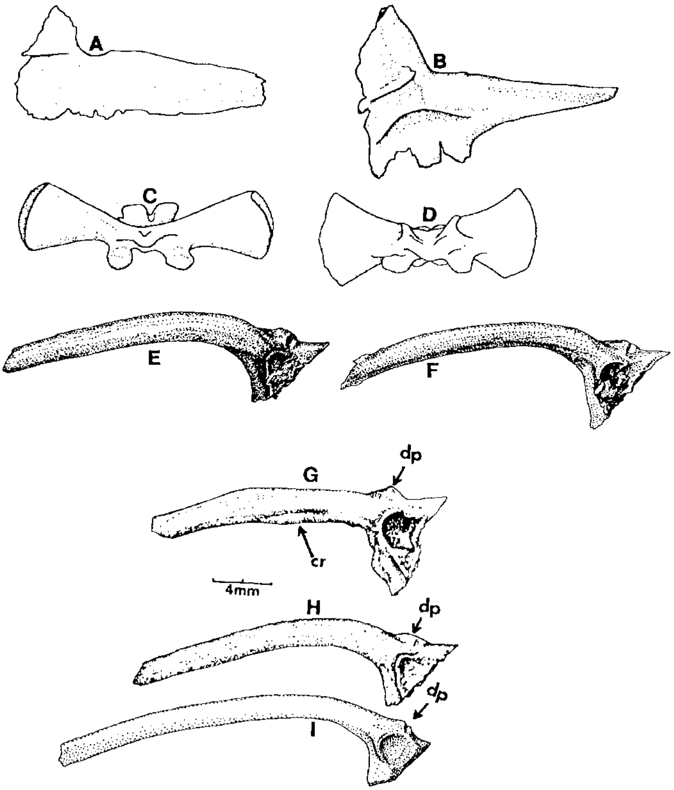

FIGURE 9. Bones of modern *Bufo*. (A) left frontoparietal of *Bufo bufo*; (B) left frontoparietal of *Bufo calamita*; (C) dorsal view of sacrum of *Bufo bufo*; (D) dorsal view of sacrum of *Bufo calamita*; (E) left ilium of *Bufo bufo* with rounded dorsal prominence; (F) left ilium of *Bufo bufo* with bladelike dorsal prominence; (G) left ilium of *Bufo calamita* indicating dorsal prominence (dp) and "*calamita* ridge" or groove (cr); (H) left ilium of *Bufo bufo* showing low, rounded dorsal prominence and lack of "*clamita* ridge" or groove; (I) left ilium of *Bufo viridis* indicating two-lobed dorsal prominence. [A–D are drawings by Lisa Hallock from Holman, 1988; E–H are drawings by Rosemarie Attilio; G and H from Holman, 1988; I is a drawing by Teresa Petersen] The scale bar applies to G, H, and I only.

Genus *Bufo* Laurenti, 1768: True Toads

The huge genus *Bufo* is composed of plump-bodied, warty, short-legged anurans with a pair of conspicuous paratoid glands behind the head on the back. The eyes have horizontal pupils. Two hundred and eleven living species are recognized (Duellman, 1993). Some rather suspect extinct Tertiary forms have been named in North America (see Holman, 1995c; Sanchiz, in press). At present the genus is cosmopolitan except for Arctic regions, New Guinea, and Australia and nearby islands. The living forms are mainly terrestrial, and some are semifossorial.

Some important osteological characters of European *Bufo* are: frontoparietals unfused and with prominent prootic processes (Figs. 9A–B); indentation on ventral surface of sphenethmoid broadly U-shaped and limited to posterior half of the bone; ilium (Fig. 9 E–I) lacking dorsal crest (vexillum) with prominent dorsal prominence (tuber superior) occurring at top of the bone; sacral diapophyses dilated (Fig. 9C), but not as expanded as in several more primitive anuran groups; and sacrum not fused to urostyle.

All three modern European species of *Bufo* (*B. bufo*, *B. calamita*, and *B. viridis*) have been identified from the Pleistocene of both Britain and Europe.

Bufo sp.: Indeterminate True Toad

Pleistocene Localities

Britain: Middle Pleistocene—3, 5, 7, 11; Upper Pleistocene—6, 9, 13; Pleistocene and Holocene—2; Latest Pleistocene or Earliest Holocene—1.
France: Upper Pleistocene—9; Middle Pleistocene—1; Pleistocene undesignated—2, 3; latest Pleistocene and earliest Holocene—1.
Spain: Middle Pleistocene—9, 14, 15; Upper Pleistocene—20.
Netherlands: Middle Pleistocene—1.
Germany: Middle Pleistocene—6, 8, 9, 13, 18, 20; Upper Pleistocene—26; Pleistocene undesignated—1, 4, 8, 11; Upper Pleistocene/Holocene boundary—1.
Poland: Lower Pleistocene—1, 4, 6; Upper Pleistocene—15; Upper Pleistocene and Holocene—1.
Italy: Lower Pleistocene—1; Middle Pleistocene—1, 3; Middle or Upper Pleistocene—1.
Hungary: Lower Pleistocene—2, 3, 4, 5; Middle and Upper Pleistocene—1; Upper Pleistocene—8, 9; Upper Pleistocene and Holocene—1.
Croatia: Middle Pleistocene—1; Upper Pleistocene—4.
Greece: Upper Pleistocene—4; Pleistocene undesignated—2.

cf. *Bufo*: Probable True Toad

Pleistocene Localities

Germany: Pleistocene undesignated—16.
Hungary: Upper Pliocene or Lower Pleistocene—2.

Bufo bufo (Linnaeus, 1758): Common European Toad

Pleistocene Localities

Britain: Middle Pleistocene—1, 3, 4, 5, 7, 5; Upper Pleistocene—4, 6, 9, 10, 14, 15; Pleistocene undesignated—2, 4; Pleistocene and Holocene—1, 2; latest Pleistocene or earliest Holocene—1.
France: Lower Pleistocene—2; Middle Pleistocene—1, 4, 5, 6, 9; Upper Pleistocene—3, 4, 5, 6, 7, 8, 13, 15, 17; Pleistocene undesignated—4; Upper Pleistocene or Holocene—1.

Spain: Lower Pleistocene—2; Middle Pleistocene—2, 3, 4, 5, 6, 8, 13, 15; Middle and Upper Pleistocene—1; Upper Pleistocene—1, 2, 4, 7, 8, 9, 10, 11, 12, 13, 14, 15, 19.
Netherlands: Middle Pleistocene—2.
Belgium: Upper Pleistocene—1.
Germany: Middle Pleistocene—1, 2, 3, 7, 9, 13, 14, 15; Upper Pleistocene—2, 3, 7, 10, 11, 18, 19, 22, 25, 27, 28, 29, 30; Pleistocene undesignated—2, 3, 6, 7; Upper Pleistocene and Holocene—4.
Poland: Lower Pleistocene—2, 3, 4, 5; Upper Pleistocene—13.
Czech Republic: Late Pliocene and Lower Pleistocene—1; Lower Pleistocene—2; Lower or Middle Pleistocene—1; Pleistocene undesignated—2, 3.
Italy: Lower or Middle Pleistocene—1: Upper Pleistocene—8, 9, 10, 12, 13, 14, 16, 18, 19; Pleistocene undesignated—2, 5; Upper Pleistocene or Holocene—1, 3.
Hungary: Lower Pleistocene—5; Upper Pleistocene—4; Upper Pleistocene and Holocene—3, 6.
Croatia: Middle Pleistocene—4; Upper Pleistocene—3, 5, 6; Upper Pleistocene and Holocene—2.
Serbia: Upper Pleistocene and Holocene—1.

Bufo bufo (Fig. 4F) is the largest toad in modern Britain and Europe. Very large specimens occur in southern Europe. The common toad tends to be uniformly brownish in color and lacks the bright yellow stripe down the middle of the back of *Bufo calamita* described below. At present, *Bufo bufo* is found in Europe (except for Ireland and some of the Mediterranean islands) east to Lake Baikal in southern Siberia; the Caucasus; northern Asia Minor and northern Iran. It also occurs in northwestern Africa. The common toad is found in a wider variety of habitats than most British and European amphibian species and sometimes is found in surprisingly dry situations. It is mainly nocturnal and tends to retire to the same hiding place each day.

Identification of Pleistocene Fossil Bufo Species

Several authors (e.g., Bailón, 1986; Böhme, 1977; Holman, 1989b; Rage, 1974; Sanchiz, 1977b) have discussed the identification of Pleistocene bones of the three British/European species of *Bufo*. Several individual bones appear to be useful in the separation of these species, but the reader is cautioned that one needs to examine series of modern skeletons to determine that any characters used, published or not, are not individually variable.

Böhme (1977, fig. p. 290) indicates that the frontoparietal of *Bufo calamita* has an elongate, sharply pointed frontal portion that separates it from both *B. bufo* and *B. viridis*; and that *Bufo bufo* may in turn be separated from *B. viridis* on the basis of having a cup-shaped indentation on the lateral surface of the frontoparietal just anterior to the prootic process.

Böhme (1977, fig. p. 293) shows that the sphenethmoid of *Bufo bufo* is much shorter and wider that in *B. calamita* and *B. viridis* and has the posterior indentation of its ventral surface much more broadly U-shaped. *Bufo viridis* apparently may be distinguished from *B. bufo* and *B. calamita* on the basis of the presence of a pair of anterolateral ossified processes of the sphenethmoid that are separated from the main body of the bone.

The ilium appears to be the best element to distinguish the three *Bufo* species (e.g., Holman, 1989b). *Bufo calamita* (Fig. 9G) has a triangular dorsal prominence (tuber superior) and a prominent ridge and/or groove on the posteroventral portion of the ilial shaft just anterior to the ventral acetabular expansion (pars descendens ilii). This feature is sometimes referred to as "the *calamita* ridge." Both *Bufo bufo* and *Bufo viridis* lack this ridge and/or groove, at least a prominent one, in this area. Moreover, *Bufo bufo* has a low, rounded, sometimes roughened, or very occasionally, a somewhat bladelike dorsal prominence (Fig. 9 E,F), and *Bufo viridis* has a rather low, bilobate dorsal prominence (Fig. 9I).

Bufo cf. *Bufo bufo*: Probable Common European Toad

Pleistocene Localities

France: Upper Pleistocene—8.
Netherlands: Middle Pleistocene—1.
Germany: Upper Pleistocene—9.
Austria: Lower and Middle Pleistocene—1.
Poland: Upper Pleistocene—2, 3, 7.

Bufo calamita Laurenti, 1768: Natterjack Toad

Pleistocene Localities

Britain: Middle Pleistocene—3, 5; Upper Pleistocene—9, 10, 15; Pleistocene and Holocene—1; latest Pleistocene or earliest Holocene—1.
France: Lower Pleistocene—4; Middle Pleistocene—1, 4; Upper Pleistocene—3, 4, 7, 6, 7, 8, 9, 16; Pleistocene undesignated—4.
Spain: Middle Pleistocene—2, 5, 8, 14; Middle and Upper Pleistocene—1; Upper Pleistocene—2, 5, 11, 19.
Netherlands: Middle Pleistocene—2.
Germany: Pleistocene undesignated—3; Upper Pleistocene and Holocene—4.
Czech Republic: Lower Pleistocene—2.

Modern *Bufo calamita* (Fig. 4G) may be distinguished from *B. bufo* and *B. viridis* on the basis of the bright yellow stripe that runs down the middle of the back. The species tends to move about by making mouselike dashes, rather than walking or hopping, and is sometimes referred to as a "running toad." At present, the natterjack toad occurs in western and northern Europe as far east as western Russia and including parts of England and Ireland. In England it is an endangered species. In the northern part of its range *Bufo calamita* is usually found in sandy areas including dunes by the sea. In other parts of its range, however, the natterjack toad occurs in a wider variety of habitats, including the mountains in Iberia.

Identification of Pleistocene Fossils

Characters for the identification of selected skeletal elements of *Bufo calamita* are given above under *Bufo bufo*.

Bufo cf. *Bufo calamita*: Probable Natterjack Toad

Pleistocene Localities

France: Upper Pleistocene—15.
Belgium: Upper Pleistocene—1.

Bufo viridis Laurenti, 1768: European Green Toad

Pleistocene Localities

Britain: Middle Pleistocene—5.
France: Middle Pleistocene—9; Upper Pleistocene—14.
Spain: Upper Pleistocene and Holocene—1.
Germany: Middle Pleistocene—3, 16; Upper Pleistocene—2, 3, 15, 30, 32.
Poland: Upper Pleistocene—14.
Czech Republic: Lower Pleistocene—2.
Italy: Middle Pleistocene—6; Upper Pleistocene—7, 17; Pleistocene undesignated—2; Upper Pleistocene and Holocene—1; Upper Pleistocene or Holocene—3.
Hungary: Upper Pliocene or Lower Pleistocene—1; Lower Pleistocene—2; Upper Pleistocene—4, 10; Upper Pleistocene and Holocene—3.
Croatia: Upper Pleistocene—3, 5, 6; Upper Pleistocene and Holocene—1.
Bosnia: Upper Pleistocene—1, 2.
Serbia: Upper Pleistocene and Holocene—1.
Greece: Middle Pleistocene—3, 4; Pleistocene undesignated—1.

Bufo viridis has a much more contrasting dorsal color pattern than the two species described above. This pattern includes well-defined green markings. The green toad may have a weak middorsal stripe, but it is normally not the bright yellow color found in *Bufo calamita.* At present *Bufo viridis* occurs in Europe (including the southern tip of Sweden, but excluding the rest of Fenno-Skandia and the British Islands and western Europe west of the Rhine River) east to Kazakhstan and the Altai mountains, Mongolia, and extreme western China; it also occurs in parts of the northern coast of Africa. The green toad is essentially a lowland species that often lives in dry, sandy areas but is not restricted to such situations.

Identification of Pleistocene Fossils

Characters for the identification of selected *Bufo viridis* elements are described above under *Bufo bufo.*

Bufo cf. *Bufo viridis*: Probable European Green Toad

Pleistocene Localities

Italy: Lower to Middle Pleistocene—1; Middle Pleistocene—9.
Hungary: Upper Pleistocene—2.
Greece: Middle Pleistocene—1; Upper Pleistocene—1; Pleistocene undesignated—3.

Family Hylidae Rafinesque, 1815:
Treefrogs

Although hylids are quite variable in external appearance, they usually may be distinguished by their prominent, disklike toe pads. The Hylidae is another huge anuran family and has 33 recognized genera (Duellman, 1993). This family occurs in North and South America, the West Indies, and the Australian-Papuan region; one species group of the genus *Hyla* occurs in temperate Eurasia, including extreme northern Africa and the Japanese Archipelago.

Osteological characters modified from Duellman and Trueb (1986) are: eight holochordal, procoelous presacral vertebrae bearing nonimbricate neural arches present; ribs absent; sacrum with dilated diapophyses (except for a few species that have round ones); pectoral girdle arciferal; palatines normally present; parahyoid absent; cricoid ring complete; and ilium usually lacking dorsal crest (vexillum), with dorsal prominence (tuber superior) usually laterally placed (Fig. 10). All of the fossil genera that have been identified thus far are presently living (Sanchiz, in press).

Genus *Hyla* Laurenti, 1768: Common Treefrogs

The huge genus *Hyla* consists mainly of arboreal frogs with prominent disk-like toe pads. Two hundred and eighty-one species are recognized by Duellman (1993). The fact that 258 species were recognized by Frost (1985) is an indication of the rate at which new species of *Hyla* are being described. At present the genus occurs in central and southern Europe; eastern Asia; northwestern

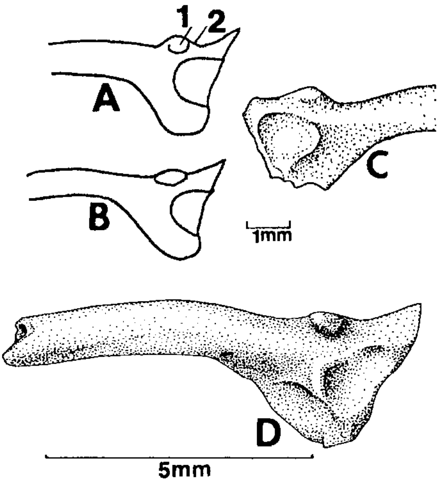

FIGURE 10. Ilia of *Hyla*. (A) Camera lucida drawing of modern *Hyla meridionalis* showing important distinguishing characters: (1) dorsal protuberance; (2) dorsal prominence. (B) Camera lucida drawing of *Hyla arborea*. (C) Right ilium of *Hyla meridionalis* from the Upper Pleistocene Itteringham Pit Site, Norfolk, England. (D) Left ilium of *Hyla arborea* from the Middle Pleistocene East Farm, Barnham Site, Suffolk, England. The upper scale bar applies to A–C. [A and B are drawings by the author, and C is a drawing by Lisa Hallock, all in Holman, 1992d; D is a drawing by Teresa Petersen]

Africa; North, Central, and South America; and the Greater Antilles of the West Indes.

Some important osteological characters of European *Hyla* are: frontoparietals unfused, slender, and of rather uniform width throughout their length; sphenethmoid wider than long, with U-shaped excavation on its ventral surface encroaching about the posterior half of the bone; ilium lacking a dorsal crest (vexillum), with rounded dorsal prominence (tuber superior) produced laterally (Fig. 10) rather than dorsally as in *Bufo* (Fig. 9E–I); sacral diapophyses dilated, but not as expanded much as in several primitive groups of anurans; and sacrum free from urostyle.

Three modern species of *Hyla* (*H. arborea*, *H. meridionalis*, and *H. sarda*) have been identified as Pleistocene fossils within the area covered by this book. *Hyla arborea* and *H. meridionalis* have been recorded from Britain, *H. arborea* from the continent, and *H. sarda* from Corsica and Sardinia.

Hyla sp. indet.: Indeterminate Common Treefrog

Pleistocene Localities

Britain: Middle Pleistocene—4;
France: Middle Pleistocene—1, 4; Upper Pleistocene—6.
Spain: Middle Pleistocene—2, 3.
Italy: Lower Pleistocene—1.

cf. *Hyla*: Probable Common Treefrog

Pleistocene Locality

Spain: Upper Pleistocene—2.

Hyla arborea (Linnaeus, 1758): Common European Treefrog

Pleistocene Localities

Britain: Middle Pleistocene—5, 11.
Germany: Middle Pleistocene—3; Upper Pleistocene—2, 7; Upper Pleistocene and Holocene—4.
Croatia: Upper Pleistocene—3.
Serbia: Upper Pleistocene and Holocene—1.

Hyla arborea is a small treefrog with long legs, a smooth skin, and disklike toe pads. It is normally green, but can change its color pattern to shades of brown or gray. A dark stripe runs through the eye and tympanum through the flanks to the groin. At present the common treefrog occurs from central and southern Europe east to the Caucasus. It also occurs in the northwest coast of Africa and in Turkey. The extralimital occurrence of the common treefrog in the Pleistocene of Britain is addressed in Chapter 7. *Hyla arborea* is mainly nocturnal and occurs in habitats with abundant vegetation.

Identification of Pleistocene Fossils

Holman (1992d) was able to separate fossil *Hyla arborea* from *Hyla meridionalis* on the basis of the structure of the dorsal prominence (tuber superior) of the ilium. In *Hyla arborea* the dorsal prominence does not have a raised triangular portion, is lower on the shaft, and is usually ovaloid in shape (Fig. 10B,D). In *Hyla meridionalis* the dorsal prominence has a raised triangular portion with a rounded protuberance near its apex (Fig. 10A,C).

Hyla cf. *Hyla arborea*: Probable Common European Treefrog

Pleistocene Locality

Italy: Middle Pleistocene—9.

Hyla (*arborea*) sp.: Indeterminate Treefrog of the *Hyla arborea* Group

Pleistocene Localities

Poland: Lower Pleistocene—3.
Croatia: Upper Pleistocene—5.
Greece: Pleistocene undesignated—2.

Hyla meridionalis Boettger, 1874: Stripeless Treefrog

Pleistocene Locality

Britain: Upper Pleistocene—6.

Hyla meridionalis is also a small treefrog and is externally similar to *Hyla arborea* except that it lacks a clear stripe on the flanks. At present the stripeless treefrog occurs in northwestern Africa and southwestern Europe, including Portugal (Madeira), southern and eastern Spain, southern France, and the Balearic and Canary Islands. The extralimital occurrence of this species in the late Pleistocene of East Anglia in England is of considerable interest and is addressed in Chapter 7. The habits of the stripeless treefrog are similar to those of *Hyla arborea*, but when the two species occur together, *Hyla meridionalis* tends to occur at lower altitudes.

Identification of Pleistocene Fossils

Ilial characters that separate *Hyla meridionalis* from *Hyla arborea* are described above under *Hyla arborea*.

Hyla sarda De Betta, 1853: Sardinean Treefrog

Pleistocene Locality
France: Upper Pleistocene—14.

Hyla sarda, previously considered a subspecies of *Hyla arborea*, differs externally from *Hyla arborea* in that it is smaller, has a shorter rostrum, and has a flank stripe that is poorly developed and lacks an upward-extending branch. At present, this species is known to occur in Sardinia, Corsica, and nearby Islands in the Tyrrhenian Sea.

Hyla cf. *Hyla sarda*: Probable Sardinean Treefrog

Pleistocene Locality
Italy: Upper Pleistocene—7.

Family Ranidae Rafinesque-Schmaltz, 1814
True Frogs

The Ranidae is the most generically diverse family of anurans covered in this book, with 46 living genera recognized (Duellman, 1993). Ranid taxa are extremely variable in external appearances and size, ranging from about 30 to 300 mm in snout-to-vent length. All of the fossil forms belong to extant genera (Sanchiz, in press). The family Ranidae is cosmopolitan except for southern South America and most of Australia. Ranids may be lake, pond, mountain stream, or woodland species; and long-legged, toadlike, arboreal, and fossorial taxa occur.

Osteological characters, modified from Duellman and Trueb (1986), are: eight holochordal presacral vertebrae present, usually with nonimbricate neural arches; sacrum with an anterior, broadened, convex articular surface (condyle), as well as two posterior, rounded, convex articular surfaces (condyles); sacral diapophyses cylindrical; pectoral girdle firmisternal (except for a few species of *Rana* that have the arciferal condition); palatines present; parahyoid absent, cricoid ring complete; teeth present on premaxillary and maxillary in most groups; and ilia (Figs. 11–13) usually with dorsal crest or vexillum (crest present in all of the Holarctic species), with many species having an elongate, compressed dorsal prominence (tuber superior).

Genus *Rana* Linnaeus, 1758: True Frogs

Members of the extremely large genus *Rana* are typically long-legged frogs with smooth skins, webbed feet, and prominent tympanni. Two-hundred and twenty-two living species of *Rana* are recognized (Duellman, 1993). Most fossil species have been poorly defined. The genus *Rana* has essentially the same distribution in the modern world as the family Ranidae.

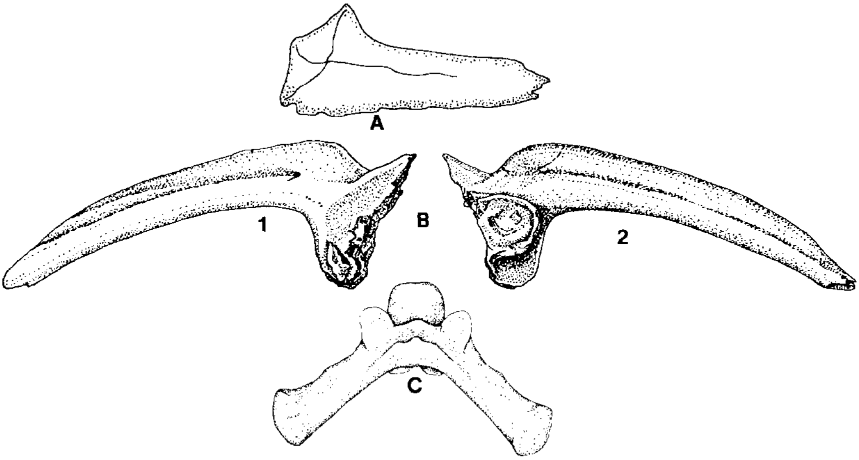

FIGURE 11. Some taxonomically important bones of *Rana*. (A) Left frontoparietal; (B) right ilium: (1) medial view, (2) lateral view; (C) sacral vertebra in dorsal view. [Drawing A by the author, B by Rosemarie Attilio, C by Lisa Hallock]

In the Holarctic the genus *Rana* contains species referred to as "water frogs" that are mainly aquatic and often have green or olive in their color pattern and "brown frogs" that are more terrestrial, brownish in color, and often have a face mask. Examples of water frog species are the green frog (*Rana clamitans*) and its relatives in North America and the marsh or lake frog (*Rana ridibunda*) and its relatives in Europe. Examples of brown frog species are the wood frog (*Rana sylvatica*) in North America and common frog (*Rana temporaria*) and its relatives in Britain and Europe.

Some important osteological characters of the genus that especially apply to the British and European species are: frontoparietals unfused, with a prominent prootic process (Fig. 11A), but generally not as large as in *Bufo* (Fig. 9A,B); sphenethmoid longer than wide, its ventral surface encroached to about one-half its length by a narrowly U-shaped excavation; ilium with well-developed dorsal crest or vexillum (weakly developed in *Rana temporaria*) and elongate, depressed, dorsal prominence or tuber superior (Fig. 11B); sometimes roughened in *Rana temporaria*; and sacrum free from urostyle and having cylindrical diapophyses and one anterior and two posterior condyles (Fig. 11C). Eleven species of *Rana*, all presently living, have been identified from the Pleistocene of the area covered by this book.

Problematic Taxa

A Pleistocene form, obviously similar to *Rana temporaria*, but of generally larger size than the modern species, was named **Rana mehelyi* Bolkay, 1912. This form has also be cited as **Rana temporaria mehelyi*. These taxa are pres-

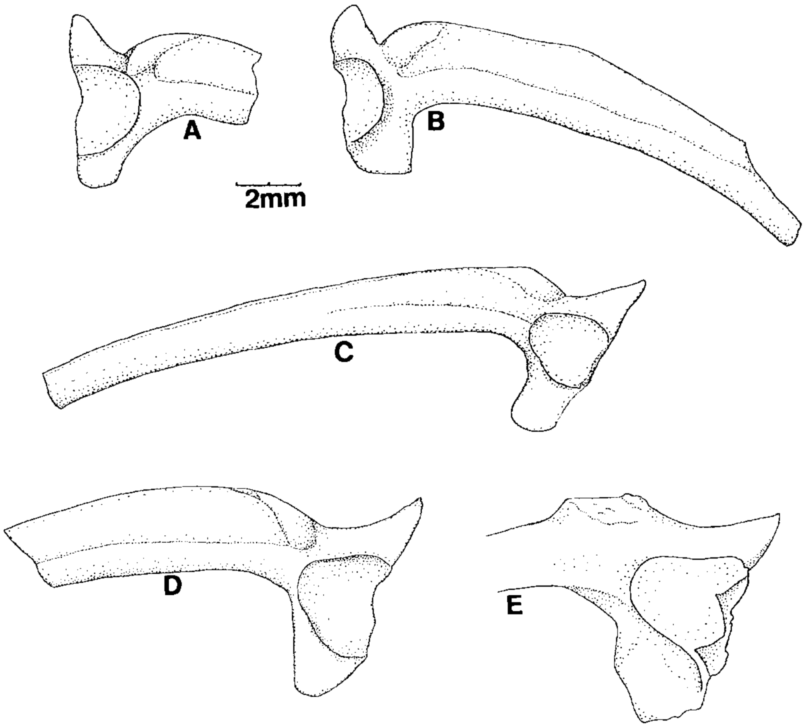

FIGURE 12. Ilia of modern brown frogs. (A) Right ilium of female *Rana arvalis* from the Czech Republic; (B) right ilium of *Rana dalmatina* from Russia; (C) left ilium of female *Rana graeca* from Greece; (D) left ilium of female *Rana iberica* from Spain; (E) left ilium of *Rana temporaria* from England. The scale bar applies only to A–C. [From camera lucida drawings by the author]

ently considered synonyms of *Rana temporaria* (e.g., Bailón and Rage, 1992; Sanchiz, in press).

Another problematic form is a humerus that was named **Rana robusta* by Brunner (1956). The type humerus is lost, and based on the original description and figure, Sanchiz (in press), suggests that it may represent a male *Bufo bufo*.

Another problematic situation in the genus *Rana* in Britain and Europe is the identification of water frog species. Not only are these frogs osteologically very similar, but natural hybrids (see the water frogs *Rana esculenta* and *Rana perezi* described below) occur. Moreover, because of the absence of osteological studies on newly described modern water frog species, it is not possible to distinguish these new taxa in the Pleistocene.

Sanchiz (in press) uses the term "*Rana* (*ridibunda*) sp." for most water frogs previously identified from the Pleistocene. This term indicates that the fossil belongs to a species of the *Rana ridibunda* European water frog group, mainly

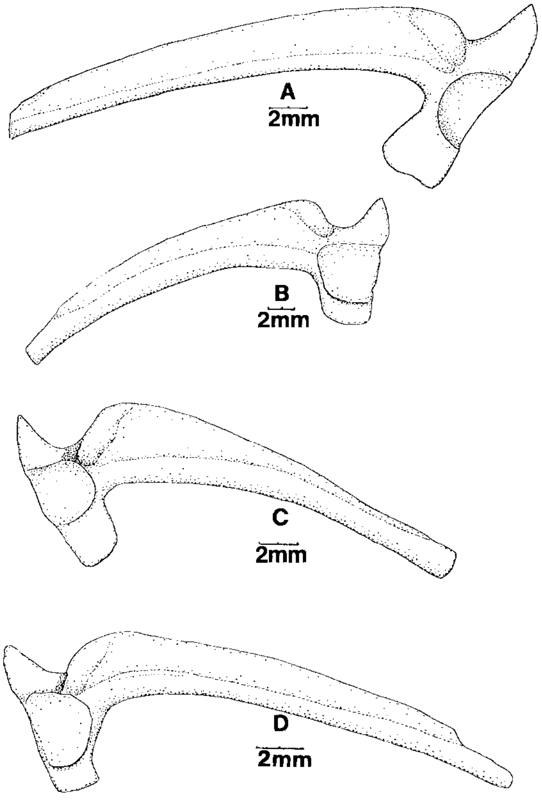

FIGURE 13. Ilia of modern water frogs. (A) Left ilium of female *Rana* "*esculenta*" from Denmark; (B) left ilium of *Rana lessonae*; (C) right ilium of female *Rana perezi* from Spain; (D) right ilium of *Rana ridibunda* from the Czech Republic. [From camera lucida drawings by the author]

either *Rana lessonae* or *Rana ridibunda* or the natural hybrid between the two species *Rana* "*esculenta.*" Osteological studies of water frogs include Böhme and Günther (1979), Böhme (1983a) and Sanchiz et al. (1993).

Rana sp. indet.: Indeterminate True Frogs

Pleistocene Localities

Britain: Middle Pleistocene—2, 3, 4, 5, 9, 11, 12; Upper Pleistocene—1, 4, 6, 7, 9, 10, 11, 13, 14; Pleistocene and Holocene—2; latest Pleistocene or earliest Holocene—1.
France: Middle Pleistocene—6; Upper Pleistocene—9; Pleistocene undesignated—2.
Spain: Lower Pleistocene—5; Middle Plestocene—5, 14; Upper Pleistocene—1, 2, 4, 9; Upper Pleistocene or Holocene—1.
Netherlands: Middle Pleistocene—2.
Germany: Middle Pleistocene—4, 6, 13, 19, 20; Middle and Upper Pleistocene—2, 19, 23; Upper Pleistocene—4, 7, 25, 26, 30; Pleistocene undesignated—2, 11.
Poland: Lower Pleistocene—1, 2, 3, 4, 6; Upper Pleistocene—4, 8, 15; Upper Pleistocene and Holocene—1.
Czech Republic: Lower Pleistocene—1; Lower or Middle Pleistocene—1; Pleistocene undesignated—2, 3.

Italy: Middle Pleistocene—1; Middle or Upper Pleistocene—1; Upper Pleistocene—18.
Hungary: Lower Pleistocene—2, 4, 5; Middle and Upper Pleistocene—1; Upper Pleistocene—8; Upper Pleistocene and Holocene—6.
Croatia: Upper Pleistocene—4.
Greece: Lower Pleistocene—1; Upper Pleistocene—4.

Brown Frog Group

Rana arvalis Nilsson, 1842: Moor Frog

Pleistocene Localities

Britain: Middle Pleistocene—4, 5, 9, 10, 11; Upper Pleistocene—4, 10, 14.
France: Middle Pleistocene—1.
Netherlands: Middle Pleistocene—2.
Germany: Middle Pleistocene—3, 7, 13; Upper Pleistocene—2, 3, 29, 30; Upper Pleistocene/Holocene boundary—1; Upper Pleistocene and Holocene—4.
Poland: Upper Pleistocene—14.
Bosnia: Upper Pleistocene—1, 2.
Serbia: Upper Pleistocene and Holocene—1.

The moor frog, *Rana arvalis* (Fig. 4H), a brown frog species with a face mask, has relatively short legs, a pointed rostrum, and a large, often sharp, metatarsal tubercle. The present distribution of the species is in northeastern France, Belgium, Netherlands, Germany, Denmark, Sweden, Finland south to the Alps, northern Yugoslavia, northern Romania, and east to Siberia. The species is found in moist meadows and fields and in some wetland areas such as bogs and fens. The extralimital occurrence of *Rana arvalis* in several localities in Britain is addressed in Chapter 7. *Rana arvalis* tends to occupy damper habitats than *Rana temporaria* when the two species occur together.

Identification of Pleistocene Fossils

Ilia are the best individual skeletal elements on which to base specific identifications of European and North American *Rana*, although these ilial identifications may be difficult in closely related species. In general, in *Rana arvalis*, an important ilial character is that the dorsal crest (vexillum) tends to slope downward from a point anterior to the anterior edge of the dorsal prominence (tuber superior Fig. 12A).

Rana cf. *Rana arvalis*: Probable Moor Frog

Pleistocene Localities

Germany: Lower Pleistocene—1; Middle Pleistocene—7; Upper Pleistocene—2, 7.
Poland: Upper Pleistocene—1.
Czech Republic: Late Pliocene and Lower Pleistocene—1.

Rana dalmatina Fitzinger in Bonaparte, 1838: Agile Frog

Pleistocene Localities

Germany: Upper Pleistocene and Holocene—4.
Italy: Lower Pleistocene—5; Middle Pleistocene—6; Upper Pleistocene—3.
Croatia: Upper Pleistocene 5, 6; Upper Pleistocene and Holocene—2.

The agile frog, *Rana dalmatina*, is a species of the brown frog group that has long limbs and a delicate, almost translucent skin. At present, *Rana dalmatina* occupies northern France and extreme southern Sweden to northeastern Spain, Sicily, Greece, the Carpathian Ukraine, and western Turkey. This species prefers moist woodlands, fields, and meadows. It is capable of long jumps to evade its predators.

Identification of Pleistocene Fossils

The ilium of *Rana dalmatina* (Fig. 12B) is rather similar to that of the brown frog species *Rana arvalis* (Fig. 12A), except that the dorsal crest (vexillum) tends not to slope downward as much anterior to the edge of the dorsal prominence (tuber superior).

Rana cf. *Rana dalmatina*: Probable Agile Frog

Pleistocene Localities

France: Middle Pleistocene—2.
Spain: Upper Pleistocene—10.
Czech Republic: Late Pliocene and Lower Pleistocene—1.
Croatia: Upper Pleistocene—1.

Rana graeca Boulenger, 1891: Stream Frog

Pleistocene Localities

Croatia: Upper Pleistocene—3, 5.
Bosnia: Upper Pleistocene—1, 2.

The stream frog (*Rana graeca*) is a member of the brown frog group that has rather long legs, a somewhat rounded rostrum (rounder than in *Rana dalmatina*), and a dark gular area with a light median stripe. At present this species occurs in the Balkan peninsula from central Yugoslavia and southern Bulgaria south, and in Italy. This frog is normally found in mountainous areas near streams.

Identification of Pleistocene Fossils

The ilium of *Rana graeca* (Fig. 12C) is similar to *Rana temporaria* (Fig. 12E) in the reduction of the dorsal crest (vexillum), but the dorsal crest of *Rana graeca* usually extends farther down the ilial shaft than in *R. temporaria*.

Rana cf. *Rana graeca*: Probable Stream Frog

Pleistocene Locality
Greece: Pleistocene undesignated—2.

Rana iberica Boulenger, 1879: Iberian Frog

Pleistocene Localities
Spain: Upper Pleistocene—7, 16.

Rana iberica, a member of the brown frog group, somewhat resembles the common frog (*Rana temporaria*) externally but may be distinguished from the common frog by its well-separated dorsolateral folds and longer legs. At present the Iberian frog is known only from Portugal and northwestern and central Spain. *Rana iberica* occurs in mountainous regions near streams as well as in woodlands, meadows, and moors.

Identification of Pleistocene Fossils
Esteban and Sanchiz (1990) have done a detailed morphometric analysis of the ilium of several brown frog species that enabled them to detect the presence of *Rana iberica* in the Middle Pleistocene deposit at Millan Cave, Burgos Province, Spain. New ilial measurements were proposed in the Esteban and Sanchiz (1990) study. An ilium of *Rana iberica* is illustrated in Figure 12D.

Rana temporaria Linnaeus, 1758: Common Frog

Pleistocene Localities
Britain: Middle Pleistocene—3, 5, 11, 12; Upper Pleistocene—1, 3, 4, 6, 10, 11, 14, 15, 16, 17; Pleistocene undesignated—2, 4; Pleistocene and Holocene—1, 2; latest Pleistocene or earliest Holocene—1.
Ireland: Pleistocene undesignated—1, 2, 3, 4.
France: Middle Pleistocene—1, 4, 6, 8; Upper Pleistocene—4, 5, 6, 7, 9, 11, 13, 15, 16, 17; Upper Pleistocene or Holocene—1.
Spain: Middle Pleistocene—5; Upper Pleistocene—1, 7, 8, 9, 10, 11, 15, 17, 19.
Netherlands: Middle Pleistocene—1, 2.
Belgium: Upper Pleistocene—1.
Germany: Lower Pleistocene—2; Middle Pleistocene—2, 3, 7, 13, 14, 16; Upper Pleistocene; 2, 3, 5, 7, 10, 11, 13, 15, 16, 18, 19, 22, 24, 27, 28, 29, 31, 32; Pleistocene undesignated—1, 4, 7, 8, 9; Upper Pleistocene and Holocene—4.
Austria: Pleistocene undesignated—2.
Poland: Lower Pleistocene—3, 5; Upper Pleistocene—6, 9, 14; Upper Pleistocene and Holocene—2, 3.
Czech Republic: Lower Pleistocene—2.
Italy: Upper Pleistocene—10.

Hungary: Upper Pliocene or Lower Pleistocene—1; Middle Pleistocene—2; Middle and Upper Pleistocene—1; Upper Pleistocene—1, 3, 4, 5, 6, 7, 8, 9, 11; Pleistocene undesignated—1; Upper Pleistocene and Holocene—1, 2, 3, 4, 5.
Croatia: Middle Pleistocene—4; Upper Pleistocene—6.
Serbia: Upper Pleistocene and Holocene—1.

Rana temporaria, the common frog, is presently the most widespread anuran in Britain and Europe and is often the most common anuran in moist terrestrial habitats, especially in central and northern Europe. This brown frog has a face mask and has a small, soft metatarsal tubercle that separates it from *Rana arvalis*, which has a large, hard, sometimes bladelike metatarsal tubercle. The present distribution of *Rana temporaria* is throughout Britain and Europe east to the Urals, but excluding most of Iberia, much of Italy, and the southern Balkans. It is the only herpetological species definitely recorded from the Pleistocene of Ireland and is among the very few herpetological species that occur in glacial-age deposits in Britain. Moreover, it is often the only herpetological species that occurs in continental sites that represent maximum glacial conditions.

This is probably the most terrestrial of all of the British and European *Rana* species and very often is found in water only during the breeding season. It may occur in almost every moist habitat throughout its range. It lives at very high latitudes and altitudes and is one of the most cold-tolerant herpetological species in Britain and Europe.

Identification of Pleistocene Fossils

Pleistocene *Rana temporaria* are readily identified on the basis of ilia (Fig. 12E), although other skeletal elements also appear to be diagnostic (e.g., Böhme, 1977). The ilia of *Rana temporaria* have a poorly developed dorsal crest (vexillum) that is only prominent anteriorly. The dorsal prominence (tuber superior) may be either smooth or roughened (Fig. 12E).

Rana cf. *Rana temporaria*: Probable Common Frog

Pleistocene Localities

Britain: Pleistocene undesignated—3.
France: Middle Pleistocene—9.
Poland: Upper Pleistocene—1, 2, 3, 7, 12.

Water Frog Group

The ilia of water frog species may usually be rather easily separated from those of brown frog species on the basis of the much steeper slope of the dorsal edge of the dorsal prominence (tuber superior) area into the dorsal acetabular expansion in the water frogs. For example, compare the ilium of *Rana perezi* (Fig. 13C) with that of *Rana iberica* (Fig. 12D). The same differences may be seen between the ilia of North American water frogs and brown frogs. For instance, in Holman (1995c), compare the ilium of the water frog *Rana catesbeiana* (Fig. 20A) with that of the brown frog *Rana sylvatica* (Fig. 20E).

Rana cf. *Rana bedriagae* Camerano, 1882: "Probable" Bedriaga's Syrian Frog

This taxon is not recognized in the standard world lists of Frost (1985) and Duellman (1993).

Pleistocene Locality
Greece: Middle Pleistocene—1.

This water frog of the *Rana* (*ridibunda*) group has been questionably identified from the Pleistocene of Chios Island, Greece (Sanchiz, in press).

Rana cf. *Rana cretensis* Beerli, Hotz, Heppich and Uzzell, 1994; Probable Cretian Frog

Pleistocene Localities
Greece: Middle Pleistocene—2; Upper Pleistocene—5.

This water frog of the *Rana ridibunda* group has been tentatively identified from the Middle and Upper Pleistocene of Crete. Sanchiz (in press) points out that no osteological studies have yet been made on this recently described insular species.

Rana "esculenta" Linnaeus, 1758: Edible Frog

Pleistocene Locality
Germany: Upper Pleistocene and Holocene—4.

Rana "esculenta", referred to as "*Rana* synklepton *esculenta*" by Sanchiz (in press), has seldom been identified as a fossil. *Rana "esculenta"* is a natural hybrid between the water frogs *Rana lessonae* and *Rana ridibunda*, two closely related species. An ilium of *Rana "esculenta"* is illustrated in Figure 13A.

Rana lessonae Camerano, 1882, "1881": Pool Frog

Pleistocene Locality
Germany: Upper Pleistocene and Holocene—4.

Rana lessonae, the pool frog, is a moderately large water frog species that is usually green or brown in coloration. The pool frog is similar to the marsh or lake frog (*Rana ridibunda*) but is usually smaller and has a relatively larger metatarsal tubercle. At present *Rana lessonae* occurs in France and southern

Sweden to the Volga River basin in Russia. It also occurs in Italy and the northern Balkans. The pool frog is usually found around small, low-energy bodies of water. When it is not breeding, it sometimes wanders rather far away from aquatic situations.

Identification of Pleistocene Fossils

Difficulties in the osteological identification of water frog species are discussed in the genus *Rana* section. An ilium of *Rana lessonae* is illustrated in Figure 13B.

Rana perezi Seone, 1885: Southern Marsh Frog

Pleistocene Localities

Spain: Lower Pleistocene—5; Middle Pleistocene—2, 3, 4, 8; Upper Pleistocene or Holocene—3.

Rana perezi is closely related in apprearance and habits to *Rana ridibunda* (described below). In fact, hybrids between *Rana perezi* and *Rana ridibunda* have been reported several times in southern France and northern Spain (e.g., Begoña et al., 1994; Graf et al., 1977; Uzzell and Tunner, 1983). *Rana perezi* presently occurs in southern France, Iberia, and northwestern Africa and has been introduced on the Azores and Canary Islands.

Identification of Pleistocene Fossils

Although the skeletons of *Rana perezi* and *Rana ridibunda* are very similar (see Sanchiz et al., 1993, table 1, for comparisons of ilia), *Rana perezi* is recognized from several Pleistocene deposits in Spain, all within the present range of the species. An ilium of *Rana perezi* is illustrated in Figure 13C.

Rana cf. *Rana perezi*: Probable Southern Marsh Frog

Pleistocene Localities

Spain: Middle Pleistocene—13; Middle and Upper Pleistocene—1.

Rana ridibunda Pallas, 1771: Marsh Frog

Pleistocene Locality

Germany: Upper Pleistocene and Holocene—4.

Rana ridibunda is the largest native European anuran, reaching a snout-to-vent length of about 150 mm. It is a robust, often warty frog with a pointed snout and frequently has some green or olive color on the back. Dark spots are almost always present. The metatarsal tubercle is relatively small. At present the marsh frog is found in central Europe east of northwestern France, north to the southern shore of the Baltic Sea, south to northern Italy and the Balkans. It is found in southwestern Asia east to about 81°E in the Asiatic portion of the former USSR and Xinjiang, China, south to Afghanistan and Pakistan. This is a very aquatic frog that occurs in many different types of aquatic situations and is often observed with its head protruding from mats of aquatic vegetation or sunning itself on lily pads.

Identification of Pleistocene Fossils

The difficulty in the identification of water frog species of the genus *Rana* is discussed in the genus *Rana* section. Taxa designated below as ''*Rana* (*ridibunda*) sp.'' (following Sanchiz, in press) could belong to any of the European water frog species. An ilium of *Rana ridibunda* is illustrated in Figure 13D.

Rana (*ridibunda*) sp.: European Waterfrog Species

Pleistocene Localities

Britain: Middle Pleistocene—4, 5, 11; Upper Pleistocene—6, 10.
France: Middle Pleistocene—1, 4; Upper Pleistocene—7, 15; Pleistocene undesignated—5.
Spain: Upper Pleistocene—18.
Netherlands: Middle Pleistocene—2.
Belgium: Upper Pleistocene—1.
Germany: Middle Pleistocene—13; Upper Pleistocene—2, 3, 15, 19, 25, 27; Pleistocene undesignated—3.
Poland: Lower Pleistocene—3.
Czech Republic: Lower Pleistocene—2.
Italy: Middle Pleistocene—6; Upper Pleistocene—3; Pleistocene undesignated-5; Upper Pleistocene or Holocene—1.
Hungary: Upper Pliocene or Lower Pleistocene—1; Upper Pleistocene—3, 4, 8; Upper Pleistocene and Holocene—1.
Croatia: Upper Pleistocene—6; Upper Pleistocene and Holocene—2.
Greece: Middle Pleistocene—3, 4; Upper Pleistocene—4; Pleistocene undesignated—1.

The extralimital occurrence of water frogs in Britian is addressed in Chapter 7.

CLASS REPTILIA LAURENTI, 1768: REPTILES

Order Testudines Batsch, 1788: Turtles and Tortoises

Pleistocene turtles and tortoises are identified mainly on the basis of partial shells or individual shell bones. The shell bones of a typical emydid turtle are illustrated in Figure 14.

Testudines Undesignated: Unidentified Turtle Material

Pleistocene Locality

Hungary: Middle Pleistocene—1.

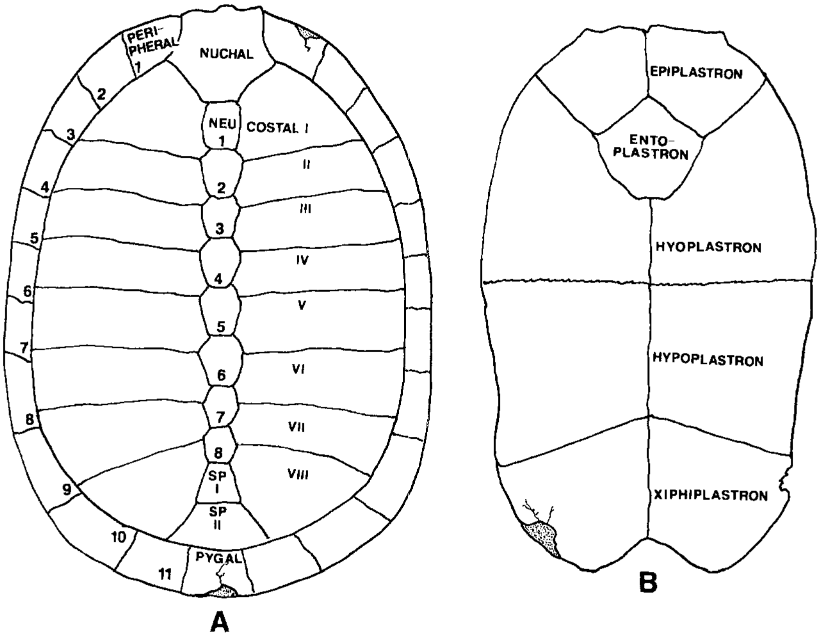

FIGURE 14. Shell bones of a typical emydid turtle. (A) Carapacial bones; (B) plastral bones. NEU = neural bones 1–8; SP = suprapygal bones I and II. [Drawing by the author]

Family Emydidae Lydekker, 1889 in Nicholson and Lydekker

Pond Turtles

The Emydidae mainly have flattened shells and the limbs are not modified as stumplike legs, as in the Testudinidae, or as flippers, as in sea turtles. The feet usually have partially to strongly webbed toes. The Emydidae is the most diverse turtle family in the world, with 33 modern genera recognized (King and Burke, 1989). At least 10 extinct genera have been described, but some of these have been rather poorly defined (Młynarski, 1976).

The family occurs in the temperate parts of the Holarctic, southeast Asia, the Japanese Archipelago, northwestern Africa, Central America and the West Indies, and in parts of northern and southern South America. Emydids are typically semiaquatic, but there are aquatic forms that come on land only to lay eggs or to seek new aquatic situations during dry times, and there are a few genera that are mainly terrestrial. Several species have a single hinge on the plastron.

Important osteological characters of the Emydidae are: mesoplastral bones absent on plastron, which is composed of the following dermal bones from anterior to posterior—paired epiplastra, an unpaired entoplastron, and paired hyoplastra, hypoplastra, and xiphiplastra (Fig. 14B); carapace and plastron usually joined by a broad bony bridge, often differently shaped than in the Testudinidae; carapace sometimes with median or lateral keels; skulls relatively small in comparison with shell; temporal region emarginated posteriorly, preventing contact of squamosals and parietals; postorbital wider than in the Testudinidae; frontal bone takes part in formation of orbit; maxilla separated from quadratojugal; quadrate exposed posteriorly; and premaxillae usually not meeting to form hooklike beak.

Genus *Emys* Dumeril, 1806: European Pond Turtles

The genus *Emys* consists of semiaquatic turtles with a single weakly developed plastral hinge. A single living species, *Emys orbicularis*, is known and three extinct Tertiary species are recognized (Fritz, 1995). *Emys orbicularis* occurs in the western Mediterranean coast of Africa and through much of central and southern Europe to central Kazakhstan.

The following remarks apply to the living species, Emys orbicularis. The European pond turtle has yellowish spots and streaks on the head and carapace. A single, transverse hinge allows the front portion of the plastron to move up and down to a limited extent, but some specimens have a rigid plastron. *Emys orbicularis* usually occurs in permanent, low-energy aquatic situations with abundant aquatic vegetation. It tends to be a basking species that often lies on stones, logs (see Fig. 40), or mats of aquatic vegetation. It is sensitive to pollution.

Emys orbicularis (Linnaeus, 1758): European Pond Turtle

Pleistocene Localities

Britain: Middle Pleistocene—4, 5, 8, 9, 12; Upper Pleistocene—2, 4, 6, 8, 9, 10, 12, 14.
France: Lower Pleistocene—3; Middle Pleistocene—6; Upper Pleistocene—1, 12; Pleistocene undesignated—7.
Monaco: Upper Pleistocene—1.
Spain: Middle Pleistocene—3; Upper Pleistocene—16.
Netherlands: Middle Pleistocene—2, 3.
Belgium: Upper Pleistocene—2, 3.
Germany: Middle Pleistocene—3, 5, 11, 12, 15, 17, 19; Middle and Upper Pleistocene—1; Upper Pleistocene—2, 6, 11, 12, 14, 20, 21, 22, 23, 25, 28, 33; Upper Pleistocene and Holocene—4.
Austria: Middle or Upper Pleistocene—1; Pleistocene undesignated—1.
Switzerland: Middle Pleistocene—1.
Czech Republic: Middle Pleistocene—1, 2; Upper Pleistocene—1; Pleistocene undesignated—1.
Italy: Lower Pleistocene—2, 4; Lower or Middle Pleistocene—1; Middle Pleistocene—7, 10; Upper Pleistocene—1, 4, 15, 18, 19, 20, 22; Pleistocene undesignated—1; Upper Pleistocene or Holocene—3.
Hungary: Middle to Upper Pleistocene—1.
Croatia: Upper Pleistocene—2, 5, 6; Upper Pleistocene and Holocene—1.

Serbia: Upper Pleistocene and Holocene—2.
Greece: Pleistocene/Holocene boundary—1.

Because turtle shell bones fossilize readily and *Emys orbicularis* elements are easily recognized in fossil assemblages, there is an extensive Pleistocene record of the species in Britain and Europe (e.g., Fritz, 1995; Stuart, 1979). The extralimital Pleistocene occurrence of *Emys orbicularis* in the area has significant climatic implications that are addressed in Chapter 6.

Identification of Pleistocene Fossils

Mauremys caspica and the very closely related *Mauremys leprosa* are the only other modern and Pleistocene emydid turtles in Britain and Europe. Holman (1995b) has given characteristic of carapacial and plastral bones (Figs. 15–17) that enable one to distinguish *Emys orbicularis* from *Mauremys leprosa* as follows.

Carapacial Bones. In dorsal view, the nuchal bone of *Emys orbicularis* is wider than long, isanteriorly truncated, and has a cervical scute impression that is less than one third the length of the bone (Fig. 15A). In *Mauremys leprosa* the nuchal bone is about as wide as long, is not anteriorly truncated, and has a cervical scute impression that is more than one third the length of the bone (Fig. 15B).

In dorsal view, the third neural bone of *Emys orbicularis* is crossed horizontally by the edge of the vertebral scute impression very near the posterior edge of the bone (Fig. 15C). In *Mauremys leprosa* it is crossed horizontally by the edge of the vertebral scute at about the middle of the bone (Fig. 15D). In *Emys*

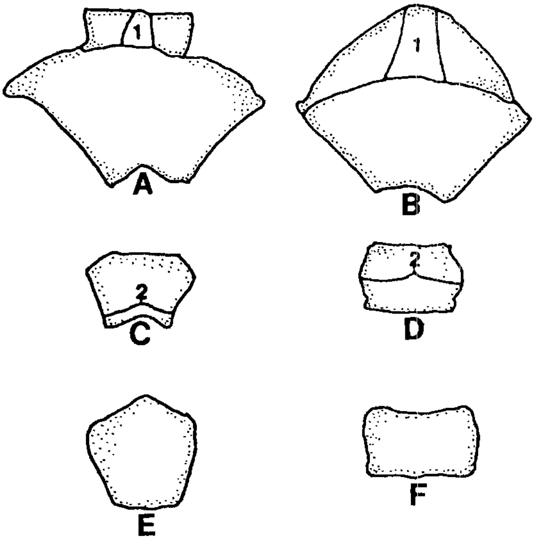

FIGURE 15. Carapacial bones (in dorsal view) of *Emys orbicularis* and *Mauremys leprosa*. A, C, and E: *Emys orbicularis*; B, D, and F: *Mauremys leprosa*. A and B: nuchal bone; C and D: third neural bone; E and F: fourth neural bone. 1 = cervical scute impression; 2 = edge of vertebral scute impression. [From camera lucida drawings by the author]

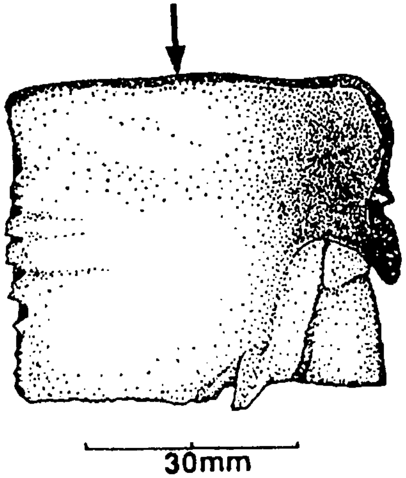

FIGURE 16. Right hypoplastral bone (in dorsal view) of *Emys orbicularis* from the Upper Pleistocene of Shropham, Norfolk, England, showing the smooth, slightly grooved surface along the hinge line (end of arrow). [Drawing by Teresa Petersen in Holman, 1996]

orbicularis the fourth neural bone is longer than wide (Fig. 15E). In *Mauremys leprosa* the fourth neural bone is wider than long (Fig. 15F).

In dorsal view, the pygal and suprapygal bones of *Emys orbicularis* are smooth. In *Mauremys leprosa* the suprapygal and pygal bones have a wide, irregular keel.

Plastral Bones. A plastral hinge occurs in *Emys orbicularis* (Fig. 16) and is lacking in *Mauremys leprosa*. Evidence of this hinge may be seen in both the hyo- and hypoplastral bones of *Emys orbicularis*, which are smooth and slightly grooved along the hinge line rather than having dove-tailed sutures as in *Mauremys leprosa.*

In dorsal view, the epiplastral tubercle of *Emys orbicularis* (Fig. 17A) is more weakly developed than that of *Mauremys leprosa* (Fig. 17B). Also in dorsal view, the entoplastron of *Emys orbicularis* is rounded and has a long, posteriorly extending spike (Fig. 17C). In *Mauremys leprosa* the spike is very short and is exposed only on the dorsal surface of the bone (Fig. 17D).

In dorsal view, the hypoplastron of *Emys orbicularis* has the inguinal scute impression wide and subtriangular (Fig. 17E), whereas in *Mauremys leprosa* it is elongate and narrow (Fig. 17F). Moreover, in *Emys orbicularis* the articulated xiphiplastra form a shallow xiphiplastral notch (Fig. 17G), whereas the articulated xiphiplastra form a deeper notch in *Mauremys leprosa* (Fig. 17H).

Genus *Mauremys* Gray, 1869: Stripeneck Terrapins

The genus *Mauremys* comprises four modern species of stripenecked aquatic turtles with a composite range including northwestern Africa, southern Europe, and the Middle East and Asia to Japan. The two European species are brown-colored taxa that are easily distinguished from *Emys orbicularis* on the basis of the distinct stripes on their necks and the prominent mid-dorsal keel on the

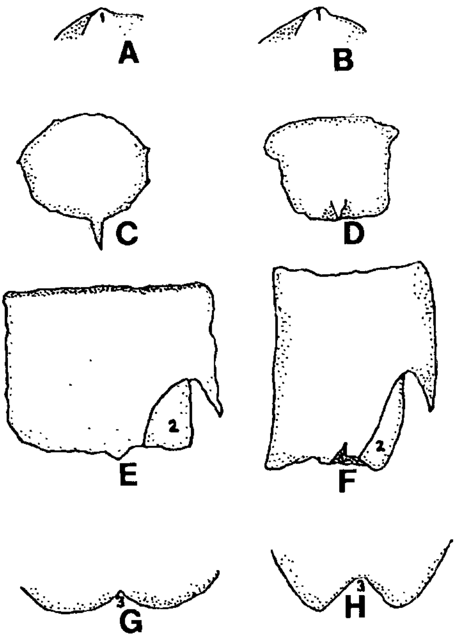

FIGURE 17. Plastral bones (in dorsal view) of *Emys orbicularis* and *Mauremys leprosa*. A, C, E, and G: *Emys orbicularis*; B, D, F, and H: *Mauremys leprosa*. A and B: tubercular portion of left epiplastron; C and D: entoplastron; E and F: right hypoplastron; G and H: posterior end of fused xiphiplastra. 1 = epiplastral tubercle; 2 = inguinal scute impression; 3 = xiphiplastral notch. [From camera lucida drawings by the author]

carapace. The European species include two that were long considered to be subspecies of the taxon *Mauremys caspica*: a western form, *Mauremys leprosa*, and an eastern form, *Mauremys caspica*. These species are presently separated by a wide gap between southeastern Spain and Yugoslavia.

Mauremys leprosa occupies the western end of the Mediterranean region from Iberia to western Libia, Tunisia, Algeria, Morocco, and around northwestern Africa to Senegal, Dahomey, and Niger. *Mauremys caspica* ranges from the southwestern part of the former Soviet Union and central Iran to Saudi Arabia and Israel, northward through Turkey to Bulgaria, and through Cyprus, Crete, and the Ionian Peninsula to Yugoslavia.

Mauremys sp. indet.: Indeterminate Stripeneck Terrapin

Pleistocene Locality
Italy: Middle Pleistocene—4.

Mauremys cf. *Mauremys caspica* (Gmelin, 1774): Probable Caspian Terrapin

Pleistocene Locality
Italy: Upper Pleistocene—15.

The probable presence of *Mauremys caspica* on the island of Sardinia (Italy: Upper Pleistocene Site 15) is of interest, as it is presently absent from this island (Caloi et al., 1981) as well as continental Italy.

Mauremys leprosa (Schweigger, 1812): Mediterranean Terrapin

Pleistocene Locality
Spain: Upper Pleistocene and Holocene—2.

Living *Mauremys leprosa* may be distinguished from *Mauremys caspica* on the basis of a round yellow or orange spot that lies between its eye and tympanum. No such spot exists in *Mauremys caspica*. At present, *Mauremys leprosa* occurs in almost every type of available aquatic habitat and occupies brackish waters. Unlike *Emys orbicularis*, *Mauremys leprosa* is remarkably tolerant of pollution.

Family Testudinidae Gray, 1827

Tortoises

The land tortoises of the family Testudinidae usually have domed shells. They have stumplike, webless hindfeet, and the front feet (also webless) are sometimes modified for digging. Twelve living genera are recognized (King and Burke, 1989). Several extinct genera of fossil tortoises have been named, but some of these are of questionable status and need to be redefined. At present the distribution of tortoises is generally worldwide (with the exception of Australia) in temperate and tropical terrestrial habitats. Tortoises are terrestrial vegetarians that usually prefer relatively dry habitats.

Although the shells of the Testudinidae are usually more domed than those of the Emydidae, they are similar in having the same series of plastral bones (see Emydidae account above) and in lacking mesoplastral bones. On the other hand, the structure of the bony bridge between the carapace and plastron is usually differently shaped in the two families. Moreover, median keels, often present on the carapaces of the Emydidae, are absent in all adult tortoises.

Gaffney (1979) points out that the relatively short and wide skulls of the Testudinidae differ from the Emydidae in several ways. Among these differences are the fact that the postorbital bone is narrow, the frontal bone is restricted from the orbit (in some taxa), the quadrate is closed posteriorly and completely surrounds the stapes, and the premaxillae meet dorsally to form a hooklike beak.

Problematic Taxa
The tortoise genus *Geochelone* is listed without discussion or references from the Pleistocene "Alcomo Travertines" of Sicily (Bonfiglio and Insacco, 1992, Table 2). As far as I am able to determine, previous reports of "*Geochelone*" from Europe, namely, from Aegean islands and from Malta, either were from

Pliocene sites (Auffenberg, 1974) or were actually bones of *Testudo* (Savona Ventura, 1984).

Genus *Testudo* Linnaeus, 1758: Palearctic Tortoises

The genus *Testudo* is composed of relatively small, dome-shelled tortoises. Five living species are recognized (King and Burke, 1989). Six extinct fossil species of *Testudo* were discussed by Młynarski (1976), and at least one of them is probably invalid. At present the species of *Testudo* are found mainly around the Mediterranean, but some forms range through the Middle East to the Caspian Sea, Afghanistan, and Pakistan.

Important osteological characters of the genus are: shell domed; posterior border of carapace sometimes flared or serrated; narrow cervical scute present on nuchal bone (Fig. 18A); anterior neural bones alternatively four-sided or octagonal; usually a single suprapygal; suprapygal and pygals may (Fig. 18b) or may not have a median scute impression, depending on whether one or two supracaudal scutes occur; plastron with weak hinge between hyo- and hypoplatron in four of the five species; entoplastron usually anterior to humeropectoral scute impression; maxillae separate from palate palate; temporal arch weak; prootics usually covered anteriorly and dorsally by parietal; and quadrate usually encloses stapes.

Three living species, *Testudo graeca*, *Testudo hermanni*, and *Testudo marginata*, occur in the Pleistocene of Britain and Europe.

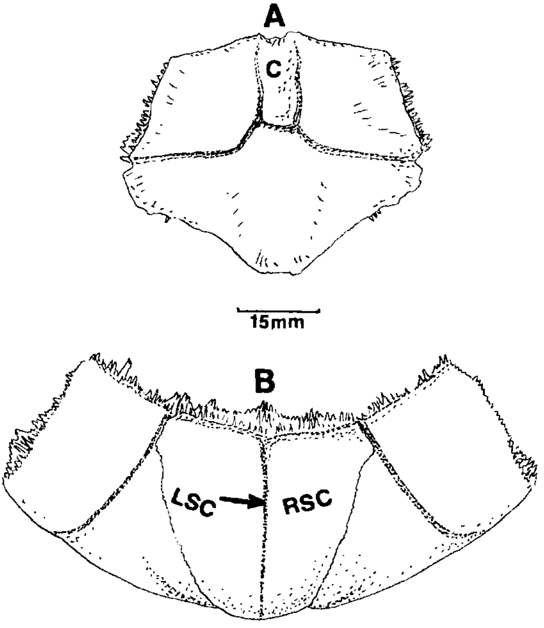

FIGURE 18. Carapacial elements of *Testudo hermanni*. (A) Nuchal bone showing the impression of the cervical scute (C); (B) posterior portion of carapace showing the division (arrow) between the left (LSC) and the right (RSC) supracaudal scutes. Scute impressions are indicated by the dotted lines. [Drawing by Teresa Petersen]

Testudo sp. indet.: Indeterminate Tortoise

Pleistocene Localities

France: Upper Pleistocene—8.
Italy: Middle Pleistocene—1, 5; Upper Pleistocene—17.
Hungary: Upper Pleistocene. 10.
Croatia: Middle Pleistocene—2.
Serbia: Upper Pleistocene—1.

Testudo graeca Linnaeus, 1758: Spur-Thighed Tortoise

Pleistocene Localities

France: Pleistocene undesignated—6.
Italy: Upper Pleistocene or Holocene—3.
Hungary: Upper Pleistocene—10.
Croatia: Upper Pleistocene—5.
Serbia: Upper Pleistocene—1.

The spur-thighed tortoise has a dome-shaped shell that may reach a carapacial length of over 250 mm. Externally, *Testudo graeca* may be separated from the closely related *Testudo hermanni* on the basis of the prominent spurs on the thighs and by usually having one rather than two supracaudal scutes. *Testudo graeca* presently occurs in southern Spain and the Balearic islands, in southern Italy and Sicily, in the eastern Balkans south of the Danube to Macedonia, European Turkey, and some Aegean islands; also in North Africa, Asia Minor, and the Middle East to Iran.

At present, the spur-thighed tortoise lives on dry, open steppes, barren hillsides, and wastelands where vegetation may vary from sea dune grasses to scrubby thorn bushes, or dry woodlands. The species occurs from sea level up to about 3000 m.

Identification of Pleistocene Fossils

If the posterior part of a carapace is available, *Testudo graeca* may be distinguished from the closely related *T. hermanni* on the basis that the suprapygal and pygal bones usually lack the median scute impression that usually occurs in *T. hermanni* (Fig. 18B). Moreover, the posterior rim of the carapace is flared, sometimes markedly so, in *Testudo graeca*, whereas it is downturned in *T. hermanni* (Fig. 18B)

If neural and costal carapacial bones are available, these bones have smooth dorsal surfaces in *Testudo graeca*, whereas these bones are often lumpy in *T. hermanni*. Moreover, the 4th and 5th vertebral scute impressions differ in their relation to the neural and costal bones in the two species.

Testudo cf. *Testudo graeca*: Probable Mediterranean Spur-thighed Tortoise

Pleistocene Locality

Spain: Middle and Upper Pleistocene—1.

Testudo hermanni Gmelin, 1789 in Linnaeus: Hermann's Tortoise

Pleistocene Localities

France: Middle Pleistocene—1.
Germany: Pleistocene undesignated—10.
Italy: Middle Pleistocene—9: Middle and Upper Pleistocene—1, 2, 3; Upper Pleistocene—18; Pleistocene undesignated—4.
Bosnia: Middle Pleistocene—1.
Serbia: Upper Pleistocene—1.

Hermann's tortoise is a dome-shelled form that rarely exceeds 200 mm in carapacial length. Externally, it may be separated from *Testudo graeca* on the basis of lacking prominent spines on the thighs, and in that it usually has two supracaudal scutes rather than one as in *T. graeca. Testudo hermanni* presently occurs in the Balkans mainly south of the Danube, the Ionian islands, southeastern and western Italy, Sicily, Elba, Pianosa, Corsica, Sardinia, the Balearics, and southern France. *Testudo hermanni* lives in dry meadows, scrubby hillsides, and rocky slopes. It prefers dense vegetation but avoids moist places.

Identification of Pleistocene Fossils

Characters that separate the shells of *Testudo hermanni* and *Testudo graeca* were presented in the preceding account of *Testudo graeca.*

Testudo cf. *Testudo hermanni*: Probable Hermann's Tortoise

Pleistocene Locality

Italy: Lower or Middle Pleistocene—1.

Testudo marginata Schoepff, 1792: Marginated Tortoise

Pleistocene Localities

Greece: Upper Pliocene to lowermost Pleistocene—1; Upper Pleistocene—1.

Testudo marginata has an elongate shell with the posterior margin of the carapace distinctly flared and thus may easily be distinguished from *T. graeca* and *T. hermanni*, which have more domelike shells and lack the distinctly flared posterior margin of the carapace. *Testudo marginata* may reach a shell length of up to 300 mm. At present, *Testudo marginata* occurs in Greece from Mount Olympus southward and some small Greek islands. It has been introduced into

Sardinia. The marginated tortoise is typically found in dry, scrubby areas and often occurs on rocky hillsides.

Identification of Pleistocene Fossils

If entire fossil shells are available, *Testudo marginata* has a more elongated shell than either *T. graeca* or *T. hermanni*. Moreover, the posterior margin of the carapace is much more flared in *Testudo marginata* than in either of the other two European tortoises.

Order Sauria McCartney, 1802: Lizards

Pleistocene lizards are most often identified on the basis of individual dentary bones (Fig. 19), although in the family Anguidae, vertebrae (see Figs. 22 and 24) and even osteoderms (see Fig. 23) may be diagnostic.

Sauria Undesignated: Unidentified Lizard Material

Pleistocene Localities

Hungary: Middle Pleistocene—1; Upper Pleistocene—10; Upper Pleistocene and Holocene—5.

Family Gekkonidae Gray, 1825

Geckos

The family Gekkonidae forms a huge and variable group of lizards with soft skins and immovable eyelids that are fused to form a transparent window. There are upwards of 80 genera and more than 850 species in the group (Zug, 1993). Three extinct fossil genera are recognized (Estes, 1983). Gekkonids vary from terrestrial to arboreal forms, and some species are legless. The true geckos differ from the eyelid geckos (family Eublepharidae) in usually lacking angular and supratemporal bones (Zug, 1993). Indeterminate gekkonid remains have been recorded from the Middle Pleistocene of Spain.

Bailón et al. (1988) report that *Hemidactylus turcicus* occurs in the Middle Pleistocene of France based on the personal observations of Salvador Bailón. Unfortunately, no locality was given.

Family Gekkonidae indet.: Indeterminate Gekkonid

Pleistocene Locality

Spain: Middle Pleistocene—10.

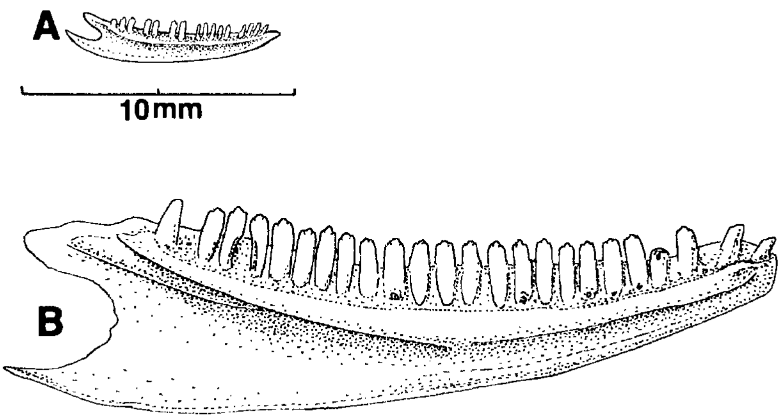

FIGURE 19. Left dentary bones, in lingual view, of a small and a large modern species of *Lacerta*. (A) female *Lacerta vivipara* from England with a snout–vent length of 70 mm. (B) *Lacerta lepida* from a captive specimen at the Brookfield Zoo, Chicago. *Lacerta lepida* is presently the largest *Lacerta* on the European continent. The scale bar applies to both specimens. [Drawing by Teresa Petersen]

Family Lacertidae Bonaparte, 1831

Lacertid Lizards

Lacertids are elongated lizards with conical heads, a well-developed neck, long trunk, long tails, and well-developed limbs. They have large head scales, and granular dorsal scales, and their ventral scales are wide and enlarged. About 20 genera and more than 200 species are presently known (Zug, 1993). Six extinct fossil genera of lacertids are known from the Tertiary (Estes, 1983). At present, the family occurs in most of Eurasia except for the northernmost parts and from almost all of Africa. They are absent from Madagascar. Lacertids inhabit a wide range of habitats, including forests, grasslands, scrub, and desert regions.

Important osteological characters of the family, modified from Estes (1983), are: supertemporal fenestra partially or completely filled in by postfrontal, which may fuse with postorbital; frontals fused; supratemporal either small or fused with parietal; interpterygoid vacuities usually narrow; coronoid overlapping dentary labially; and osteoderms, when present, are limited to skull.

Genus *Lacerta* Linnaeus, 1758: Common Eurasian Lizards

The lizards of the genus *Lacerta* might well be called the "typical" lizards of the family Lacertidae in that they have all of the usual general characteristics of the family (see family account above). Forty-three living species of *Lacerta* are recognized by Frank and Ramus (1995). Some extinct Tertiary and Quaternary species of *Lacerta* are questionable, but three extinct Pleistocene species from southern oceanic islands near Europe are valid (Estes, 1983).

At present, the genus is known from most of the Palearctic except for very cold areas. *Lacerta* species are typically active, diurnal insectivores. They are often divided into two groups, the larger, more robust "green lizards" that tend to occur in areas with dense vegetation, and the "small lacertas" that tend to be ubiquitous in their habits.

Important osteological characters of the genus, modified from Estes (1983), are: parietal foramen present on posterodorsal part of skull; frontals always paired; postorbitals and postfrontals almost always separated; clavicle cruciform with its lateral portions not strongly directed forward; oval sternal fontanelle almost always present; ribs present on all presacral vertebrae except first three; vertebrae usually A or B type of Etheridge (1967).

More Pleistocene species of *Lacerta* have been identified than in any other genus of lizard in Briain and Europe. Following Estes (1983), we shall combine the genus "*Podarcis*" (commonly called wall lizards) with the genus *Lacerta*, as on external morphological and osteological grounds, wall lizards are extremely similar to many small species of *Lacerta*.

Problematic Taxa

**Lacerta castellanensis* de Gregorio 1925 from the Upper Pleistocene of Castellana, Sicily, Italy, (Italy: Upper Pleistocene Site 5) is not a *Lacerta* (Kotsakis, 1977b). **Lacerta fossilis* Pomel 1853 from the Upper Pleistocene of Brèche de Coudes and Neschers, Auvergne, France, (France: Upper Pleistocene Site 2) was not adequately described, no figure was given, and the type material is unknown. Thus, this taxon is a *nomum dubium* (Estes, 1983).

?*Lacerta*: Questionable *Lacerta*

Pleistocene Locality

Germany: Upper Pleistocene—30.

Lacerta sp. indet: Indeterminate Common Eurasian Lizard

Pleistocene Localities

Britain: Middle Pleistocene—4, 5.
France: Middle Pleistocene—1, 6; Upper Pleistocene—8, 9.
Spain: Lower Pleistocene—1; Middle Pleistocene—3, 4, 8; Upper Pleistocene—15, 19; Pleistocene undesignated—1.
Germany: Middle Pleistocene—2, 6, 9, 13; Upper Pleistocene—1, 2, 7; Pleistocene undesignated—3.
Poland: Lower Pleistocene—1, 4.
Czech Republic: Lower Pleistocene—1, 2, 3.
Italy: Middle Pleistocene—1, 9; Upper Pleistocene—11; Pleistocene undesignated—3.

Hungary: Lower Pleistocene—2, 3, 5; Middle and Upper Pleistocene—1; Upper Pleistocene—2, 4, 8, 10.
Croatia: Middle Pleistocene—1, 4; Pleistocene undesignated—1.
Greece: Middle Pleistocene—1.

Lacerta agilis Linnaeus, 1758: Sand Lizard

Pleistocene Localities

Germany: Middle Pleistocene—7, 9; Upper Pleistocene—3, 10, 27; Upper Pleistocene and Holocene—4.
Poland: Lower Pleistocene—2, 3, 5.
Croatia: Middle Pleistocene—4; Upper Pleistocene—5.
Serbia: Upper Pleistocene and Holocene—1.

The sand lizard is a robust, short-limbed form with a short, stocky head. The species is quite variable in coloration but usually has a dark band or series of dark markings down the middle of the back. The species pressently occurs in most of Europe north to southern and northwestern England and southern Scandanavia. It is rare or absent in parts of western and southern France and is absent from Italy, the southern Balkans, and most of Iberia. Sand lizards also occur eastward to central Asia.

The sand lizard is a ground lizard of diurnal habits that occurs in several kinds of dry habitats, including ones that are more open than these occupied by other ''green lizard'' species in Europe. In England and in the northern part of its range, the sand lizard is restricted mainly to coastal dunes and sandy heathland. But in southern Europe it occurs in a wider variety of habitats up to about 2,000 m.

Identification of Pleistocene Fossils

Holman and Kolfschoten (1997b) give characters that separate the dentary of *Lacerta agilis* from some other British and European lacertids. Some of these include the following: The dentary (Fig. 20A) of *Lacerta agilis* is smaller and has fewer teeth than in *Lacerta lepida* (21 in *L. agilis*, 27–28 in *L. lepida*) and lacks tricuspid teeth (tricuspids present in *L. lepida* and *L. viridis*).

The dentary differs from the small lacertid species *Lacerta* (''*Podarcis*'') *muralis* and *Lacerta vivipara* in being larger (tooth row 5.6 mm in *L. agilis*, usually less than 5.0 mm in *L. muralis* and *L. vivipara*), in having the anterior teeth less pointed and recurved, and in having the Meckelian groove with more robust borders.

Lacerta cf. *Lacerta agilis: Probable Sand Lizard*

Pleistocene Locality

Germany: Upper Pleistocene—7.

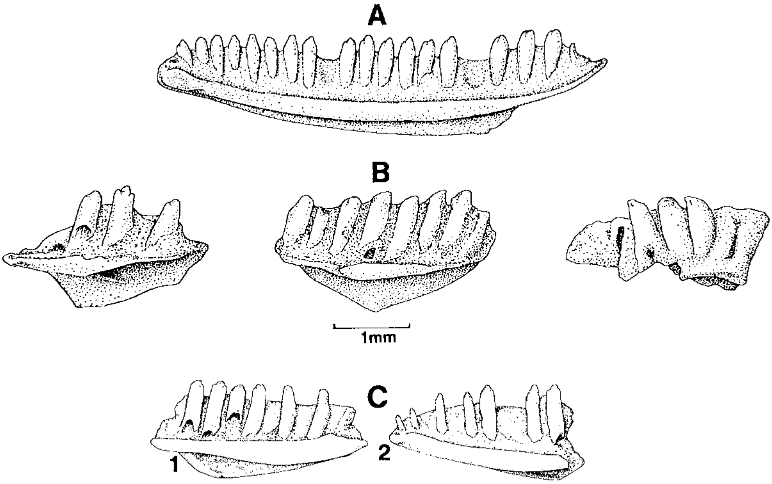

FIGURE 20. *Lacerta* fossils from the Middle Pleistocene Kärlich G Site, Germany. (A) Right dentary of *Lacerta agilis*; (B) three maxillary fragments of *Lacerta* sp. (a large form); (C) a left (1) and a right (2) dentary fragment of *Lacerta vivipara*. The scale bar applies to all specimens. [Drawing by Teresa Petersen]

Lacerta cf. *Lacerta* (''*Podarcis*'') *erhardii* Bedriaga, 1882: Probable Erhard's *Lacerta*

Pleistocene Locality

Greece: Upper Pleistocene—1.

Erhard's *Lacerta* is a medium-sized wall lizard that has a variable but basically striped pattern. It occurs from the southern Balkans north to Albania, Macedonia, and southern Bulgaria and south to Peloponnese. It also occurs in many Aegean islands. It is a lizard of dry rocky or stony habitats. Fossil specimens reported by Kotsakis (1977a) from Bate Cave, Rethymnon Crete, Greece, were referred to as *Lacerta* cf. *L. erhardii* by Estes (1983). The identification was made on the basis of a dentary which Kotsakis (1977a) noted did not differ from modern specimens of the species.

**Lacerta goliath* Mertens, 1942: Canary Islands Giant *Lacerta*

Pleistocene Locality

Spain: Upper Pleistocene or Holocene—2.

**Lacerta goliath* is twice the size of *Lacerta lepida*, the largest modern European *Lacerta* species. It is known from Upper Pleistocene or Holocene beds from the Martianez beds of Tenerife and La Palma in the Canary Islands (Spain: Upper Pleistocene or Holocene Site 2). It is known on the basis of a maxilla (holotype), articular, angular, surangular (same individual as the holotype), maxilla, dentary, lower jaw fragments, pterygoid, postfrontal, parietals, postfrontal-squamosal, vertebrae, and other miscellaneous elements.

The diagnosis is: a *Lacerta* reaching 90–100 cm in total length and close to the similar Canary Islands form *L. simonyi*; differing from the latter in having 28 maxillary teeth, 18 pterygoid teeth arranged in a V pattern, and a closed parietal foramen (Mertens, 1942).

A description of the skull based on the Canary Island remains modified from Estes (1983) is as follows: The skull is not strongly curved in the preorbital region. The type maxilla is 55.3 m. long, and the tooth row is not bent. The teeth are bicuspid, and tricuspid, and some even have four cusps. The head scalation is typical of that of *Lacerta*.

The vertebrae of **Lacerta goliath* are up to 13.6 mm in length and are robust and well ossified. Gasc (1971) pointed out that the great development of spongy bone tissue in the vertebrae suggested a pathologic gigantism in this species. Another interesting vertebral character is that the neural canal was almost obscured by ossification (Estes, 1983).

Lacerta lepida Daudin, 1802: Ocellated Lizard

Pleistocene Localities

France: Middle Pleistocne—5.
Spain: Middle Pleistocene—4, 8; Middle and Upper Pleistocene—1.

Lacerta lepida is a very large (often 200 mm snout-to-vent or larger), spectacular lizard with prominent blue spots on the sides. Males have massive heads. At present, ocellated lizards occur in Iberia, southern France, northwestern Italy, and northwestern Africa. These lizards prefer rather dry habitats and often retreat into thorny bushes when they are disturbed. They occur from sea level up to about 2000 m.

Identification of Pleistocene Fossils

Size alone is helpful in the identification of this species as a fossil. As an example, the dentary tooth row of an adult sand lizard, *Lacerta agilis*, certainly not a small form, is about 6 mm long. On the other hand, a modern adult *Lacerta lepida* in the Michigan State University Collections (MSU 1643, Fig. 19B) has a tooth row 22.0 mm long. Moreover, *Lacerta lepida* has a large number of dentary teeth (27–28 in two individuals), and the teeth are relatively swollen. Also, the great posterior depth of the dentary is usually a good character (Fig. 19B). Bailón (1986) also gives characters for the identification of this species.

Lacerta aff *Lacerta lepida*: Possible Ocellated Lizard

Pleistocene Locality

Spain: Middle Pleistocene—3.

Lacerta (''*Podarcis*'') *lilfordi* Gunther, 1874: Lilford's Wall Lizard

Pleistocene Localities

Spain: Middle Pleistocene—12; Upper Pleistocene—3, 5, 6, 22; Upper Pleistocene and Holocene—1.

Lacerta lilfordi is rather robust for a small *Lacerta*. It tends to have a basically green back with lines along the back and sides that are composed of interrupted spots. The scales are smooth. This species presently occurs only on the Balearic islands of Majorca and Minorca and nearby small islands and rocks. This hardy lizard can exist in hostile environments in areas with limited amounts of vegetation.

Lacerta aff *Lacerta* (''*Podarcis*'') *lilfordi*: Possible Lilford's Wall Lizard

Pleistocene Locality

Spain: Pliocene/Pleistocene boundary—1.

**Lacerta maxima* Bravo, 1953: Tenerife *Lacerta*

Pleistocene Locality

Spain: Upper Pleistocene or Holocene—2.

**Lacerta maxima* was described from the Martianez beds, Tenerife, Canary Islands, on the basis of a partial skull and numerous other bones from the type locality. This is another huge oceanic island *Lacerta*, as it reached a length of 120–125 cm. The diagnosis of the specimen is as follows: A species of *Lacerta* reaching 120–125 cm; differing from *L. goliath* in having 36 dentary and 33 maxillary teeth; pterygoid teeth more than 50, arranged in an arc in three of four rows on a bony concretion; parietal foramen open (Bravo, 1953).

Bravo (1953) reported that **Lacerta maxima* was similar to **Lacerta goliath*, but that it consistently differed from it in features noted in the diagnosis. He also stated that it occurred in fossil deposits earlier than **Lacerta goliath*. The fact that this taxon had an open parietal foramen indicates it was a more primitive species than **Lacerta goliath*. Moreover, the fact that the teeth of **Lacerta maxima* were multicuspate probably indicates that it had a diet different from that of the other giant species.

Lacerta cf. *Lacerta* (''*Podarcis*'') *sicula* Rafinesque, 1810: Probable Italian Wall Lizard

Pleistocene Locality

Germany: Middle Pleistocene—2.

These variably colored lizards may be green, yellowish, or brownish above and usually have no spots on the lightish belly. The main range of the species is in Italy, Sicily, Minorca, southeastern Spain, the eastern Adriatic coast, European Turkey, and many small islands in the Tyrrhenian and Adriatic seas. It has also established colonies on the coast of Africa, Philadelphia, Pennsylvania, and probably other locations. The Italian wall lizard is an opportunistic ''weed species'' that often occurs in disturbed habitats and can exist in close proximity to humans.

**Lacerta siculimelitensis* Böhme and Zammit-Maempel, 1982: Malta Tooth-expanded *Lacerta*

Pleistocene Localities

Italy: Middle Pleistocene—9; Upper Pleistocene—21 (Malta).

The third-Quaternary very large *Lacerta* that is considered a valid extinct species by Estes (1983) is also an oceanic island form. **Lacerta siculimelitensis* was described on the basis of a dentary from the Upper Pleistocene Wied Incita Quarry, near Attard, central Malta (Italy: Upper Pleistocene Site 21). Referred specimens from the Middle Pleistocene Spinagallo Cave, Siracusa, Sicily, consist of a dentary, maxillae, vertebrae, and pelves (Estes, 1983).

This *Lacerta* species had a total length that was estimated to have been about 700–750 mm. The key diagnostic character is the fact that the dentary bears expanded, molariform teeth, and that the last few dentary teeth are very reduced in size. This is the only *Lacerta* species in which tooth expansion occurs, thus it is certainly a distinctive Pleistocene taxon.

Lacerta viridis Laurenti, 1768: Green Lizard

Pleistocene Localities

Monaco: Upper Pleistocene—1.
Italy: Upper Pliocene or Lower Pleistocene—1; Middle Pleistocene—9; Upper Pleistocene—17.
Hungary: Upper Pliocene or Lower Pleistocene—1.
Croatia: Middle Pleistocene—3; Upper Pleistocene—5, 6.
Serbia: Upper Pleistocene and Holocene—1, 2.

Lacerta viridis is a large (up to about 135 mm snout–vent) green lizard with a short, deep head and a long tail. Males are more brilliantly green than females, which usually have some darker pigments on the body. The green lizard occurs widely in Europe, where it ranges northward to the Channel Islands. It occurs in the Czech Republic and southwestern Russia, extending southward into northern Spain, Sicily, and Greece. It is present on scattered oceanic islands. *Lacerta viridis* is a sun-loving lizard that usually occurs near dense vegetation. It may be found in mountains in the southern portion of its range and has been found in brushy heathlands in the north.

Identification of Pleistocene Fossils

Lacerta viridis differs from *L. agilis* in having tricuspid teeth in the maxillae. Tricuspid teeth are apparently lacking in the maxillae of *Lacerta agilis* (Fig. 20A). *Lacerta viridis* has much smaller maxillae and less robust maxillary teeth than in *Lacerta lepida*.

Lacerta cf. *Lacerta viridis*: Probable Green Lizard

Pleistocene Localities

Poland: Lower Pleistocene—3.
Hungary: Lower Pleistocene—5; Middle and Upper Pleistocene—1.

Lacerta vivipara Jaquin, 1887: Viviparous Lizard

Pleistocene Locality

Britain: Upper Pleistocene—15; Pleistocene and Holocene—1.
Netherlands: Middle Pleistocene—2.
Germany: Middle Pleistocene—9; Upper Pleistocene—3, 19, 27; Upper Pleistocene and Holocene—4.
Poland: Upper Pleistocene—9.

The viviparous lizard, a small *Lacerta*, is unique in the genus in that it gives birth to living young, although some southern populations are egg-laying. It is a short-legged lizard with a rounded head that is not distinct from the neck. *Lacerta vivipara* is usually a rather dull brownish color and normally has interrupted lines down the back and sides.

The most widespread lizard in the Palaearctic, the viviparous lizard occurs from northern Scandinavia, Ireland, and Britain south to northern Spain, northern Italy, and southern Yugoslavia and Bulgaria, and then eastward across much of Asia to the Pacific coast. The viviparous lizard is one of the most cold-tolerant reptiles of the northern hemisphere and enters the Arctic Circle in localities in northern Europe. Moreover, it is one of only two reptiles reported from Pleistocene glacial sites in Britain.

The habitus of *Lacerta vivipara* is not typical of the genus. The viviparous lizard requires a rather moist environment, even though it occupies a wide variety of habitats, ranging from heathlands in the north to Alpine meadows in the south. I have noticed that the movements and feeding activities of this species are more similar to those of small northern Nearctic skink species (*Eumeces*) than they are to typical *Lacerta* species. *Lacerta vivipara* is also one of the few lizards that avidly devours earthworms.

Identification of Pleistocene Fossils

Holman and Kolfschoten (1997b) made these remarks relative to the identification of *Lacerta vivipara* from the Middle Pleistocene of the Karlich G site in northwestern Germany. The dentaries (Fig. 20C; see also Fig. 19A) differ strongly from *L. agilis*, *L.. lepida*, and *L. viridis* in (1) being smaller (much smaller than in *L. lepida* and *L. viridis*); (2) having the dentary teeth much more gracile, with the anterior teeth more pointed and usually more recurved; and (3) having borders of the Meckelian groove that are much less swollen and robust. The dentaries differ from *L.* (''*Podarcis*'') *muralis* in having several tricuspid teeth in each of the dentary bones, whereas *L.* (''*Podarcis*'') *muralis* has all of its teeth in the dentary unicuspid or bicuspid.

The maxillary bones of *Lacerta vivipara* are also smaller and the teeth more gracile than in *L. agilis*, *L. lepida*, and *L. viridis*. The maxillary bones further differ from *L. agilis* and *L.* (''*Podarcis*'') *muralis* in bearing tricuspid teeth. A vertebra from the Cudmore Grove Middle Pleistocene Site in Essex, England (Fig. 21), that was identified merely as *Lacerta* sp. probably represents *Lacerta vivipara.*

Lacerta cf. *Lacerta vivipara*: Probable Viviparous Lizard

Pleistocene Localities

Britain: Middle Pleistocene—3; Upper Pleistocene—10.
Germany: Middle Pleistocene—10; Upper Pleistocene—2, 32.
Poland: Upper Pleistocene and Holocene—1.

aff ''*Podarcis*'' (= wall lizard section of *Lacerta*): Possible Wall Lizard

Pleistocene Locality

Spain: Upper and Middle Pleistocene—1.

Family Scincidae Gray, 1825

Skinks

The skinks comprise a very large family of lizards that is considered by most herpetologists to form a monophyletic group. Most skinks have cylindrical bodies, conical heads, robust tails, and shiny scales that overlie compound bony osteoderms. There are about 100 modern genera and over 1,000 species recognized (Zug, 1993).

Three questionable extinct fossil genera of skinks are recognized, and some extinct species of the modern genus *Eumeces* are known (Estes, 1983). At present, the family is distributed essentially worldwide except for very cold areas and a large coastal area west of the Andes in South America. Skinks occupy a

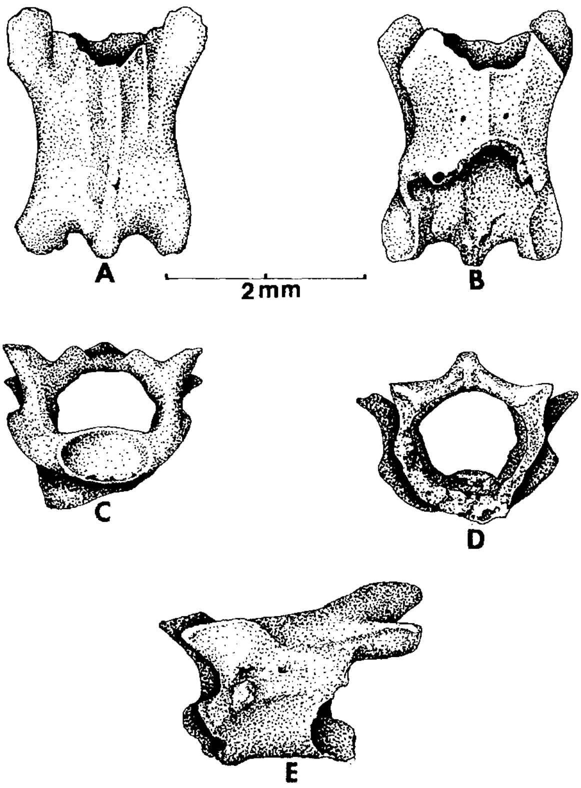

FIGURE 21. Vertebra of *Lacerta* sp. (probably *Lacerta vivipara*) from the Middle Pleistocene Cudmore Grove Site, Essex, England. (A) Dorsal; (B) ventral; (C) anterior; (D) posterior; (E) lateral. The scale bar applies to all views. [Drawing by Rosemarie Attilio in Holman et al., 1990]

wide variety of habitats and range from forms with strong limbs to limbless forms. The general tendency in skink evolution is that the more reduced the limbs become, the more elongate and snakelike the body becomes. The *Lygosoma* group of skinks has species with rather well-developed legs, species with poorly developed legs, and legless species!

Some important skeletal characters, mainly modified from Estes (1983), are: supratemporal fenestra roofed mainly by posterior growth of prefrontal except in Acontinae; some development of secondary bony palate always occurs; palatines and pterygoids meet on midline; palate usually toothless; prominent fingerlike processes project ventrally from parietal; compound, cycloid osteoderms underly scales; and tooth crowns striated distally and concave lingually.

Genus *Chalcides* Linnaeus, 1758: Cylindrical Skinks

The genus *Chalcides* contains forms with chunky bodies, short legs, and short, fat tails, as well as elongate, striped, snakelike forms with tiny legs. European *Chalcides* have species with both body forms. All European *Chalcides* give birth to living young. About 17 modern species and no extinct fossil species have been described (Estes, 1983). The genus occurs in the Iberian Peninsula, the Mediterranean region and many of its associated islands, and eastward into southwestern Asia. Important osteological characters of the genus, modified from Boulenger (1885) and Estes (1983), are: palatines not meeting on ventral midline; palate toothless; and teeth often with obtuse crowns.

Chalcides sp. indet: Indeterminate Cylindrical Skink

Pleistocene Locality

Spain: Pleistocene undesignated—1.

The one fossil record of *Chalcides* is of considerable interest. Dentary and maxillary fragments from Pleistocene cave breccia from Menorca in the Balearic Islands were identified as *Chalcides* sp. by Boulenger (in Bate, 1919). The genus does not occur on Menorca today. Estes (1983) compared these fossils with skeletons of several modern species of the genus and confirmed the generic identification of Boulenger. Alcover et al. (1980) also noted these specimens. Additional investigations to determine the specific identity of these specimens is desirable.

Family Anguidae Gray, 1825

Anguid Lizards

The family Anguidae includes elongate lizards that have relatively small limbs or are limbless. All living species have large, rectangular osteoderms that underlie the scales and that provide a form of body armor. Usually, a longitudinal dorsolateral fold on each side of the body separates the dorsal and ventral portions of this armor, allowing the body to expand for breathing or for swallowing prey. Fourteen genera and numerous species are presently recognized (Frank and Remus, 1995).

The Anguidae have an exceptional fossil record, especially in the Tertiary of North America, where many valid genera have been described on the basis of excellent material. Anguids presently occur in the midwestern, southeastern, and Pacific coastal area of the United States and extreme southwestern Canada, south through Central America (excluding the Yucatan Peninsula) to northern South America. They also occur in southeastern South America, Europe, and southwestern and southeastern Asia. Living anguids are mainly terrestrial animals with semifossorial habits. They occur in both moist and dry habitats. They are all carnivores and are mainly insectivores, except that the larger species may eat small vertebrates. They may be either live-bearing or egg-laying.

Osteological characters of the family, largely modified from Estes (1983), are: temporal arch as well as supratemporal fenestra reduced in size; mandible very characteristic, with ventral margin of surangular process of dentary fitting into posterodorsal groove on lateral side of surangular; surangular extending to internal mental canal of dentary; angular process of dentary reduced; dentary with flat, obovate retroarticular process; apices of teeth often recurved and chisel-shaped; caudal vertebrae all with fracture planes that allow autonomous shedding of tail; and osteoderms deeply imbricate anteroposteriorly but only moderately imbricate laterally.

Only two genera, *Anguis* and *Ophisaurus*, both limbless forms, are known from the Pleistocene of Britain and Europe.

Genus *Anguis* Linnaeus, 1758: Slow Worms

?*Anguis* sp.: Possible Slow Worm Species

Pleistocene Locality

Czech Republic: Lower Pleistocene—1.

Anguis sp. indet.: Indeterminate Slow Worm Species

Pleistocene Locality

Hungary: Middle and Upper Pleistocene—1.

Anguis fragilis Linnaeus, 1758: Slow Worm

Pleistocene Localities

Britain: Middle Pleistocene—2, 3, 4, 5, 11, 12; Upper Pleistocene—4, 15; Pleistocene and Holocene—1.
France: Upper Pleistocene—5, 17; Pleistocene undesignated—2.
Spain: Upper Pleistocene—15, 19.
Netherlands: Middle Pleistocene—2.
Germany: Middle Pleistocene—3, 7, 9, 10, 13, 14, 16; Upper Pleistocene—2, 3, 4, 7, 9, 10, 16, 22, 25, 27, 28, 30; Pleistocene undesignated—6; Upper Pleistocene and Holocene—1, 2, 3, 4, 5.
Poland: Lower Pleistocene—3, 4, 5; Upper Pleistocene and Holocene—1.
Czech Republic: Lower Pleistocene—2.
Hungary: Upper Pleistocene—4, 8, 10; Upper Pleistocene and Holocene—1.
Serbia: Upper Pleistocene and Holocene—1.

Anguis fragilis is the only modern species in the genus *Anguis*. The slow worm is a very smooth-scaled, legless lizard that has a tail that is often somewhat longer than the body, except in cases where it has been broken off and regenerated. The color is usually a brownish gray and males may have attractive blue spots on the body.

Anguis fragilis occurs almost all over the European continent except for Ireland, southern Iberia, and far northern areas. It occurs in Britain and east to the Urals and Caucasus, and parts of southwestern Asia as well as in northwestern Africa. The slow worm prefers rather moist habitats with ample vegetation. It is a semifossorial form that is usually found beneath various objects. When it moves about on the surface (often after rain showers), it is very slow and deliberate.

Identification of Pleistocene Fossils

The most common *Anguis fragilis* fossils found in the Pleistocene of Britain and Europe are vertebrae (Fig. 22) and osteoderms (Fig. 23). The trunk vertebrae of *Anguis fragilis* and the other European anguid genus, *Ophisaurus apodus*, are very simply constructed, with the bottom of the centrum flat, keelless, and smooth. Moreover, the osteoderms of both species are rectangular in shape. Vertebrae of *Anguis fragilis*, however (Fig. 22), are normally much smaller than those of *Ophisaurus apodus* (Fig. 24). Estes (1983) states that the vertebrae of *Anguis* may be distinguished from those of *Ophisaurus* on the basis of having a more rounded ventral surface bordered laterally by parallel inferior margins. I have found that the neural spines of *Anguis fragilis* (Fig. 22) tend to be lower

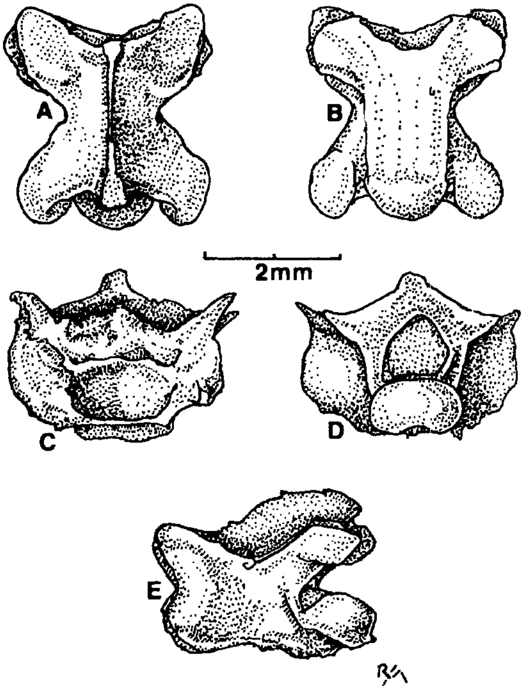

FIGURE 22. Trunk vertebra of modern *Anguis fragilis* from Sussex, England. (A) Dorsal; (B) ventral; (C) anterior; (D) posterior; (E) lateral. The scale bar applies to all views. Drawing by Rosemarie Attilio.

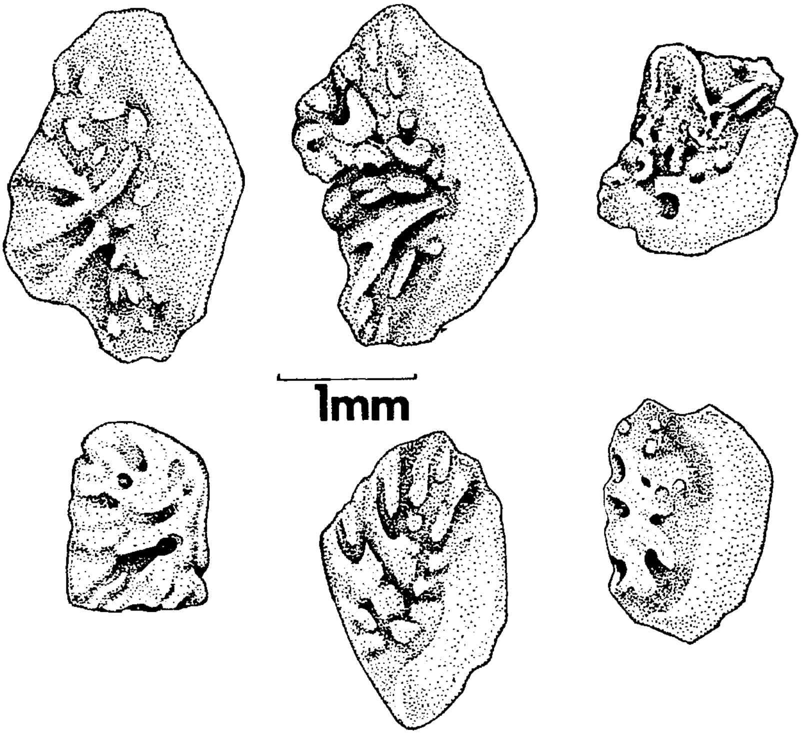

FIGURE 23. Osteoderms of *Anguis fragilis* from the Middle Pleistocene Boxgrove Site, West Sussex, England. The scale bar applies to all figures. [Drawing by Teresa Petersen in Holman, 1992b]

than *Ophisaurus apodus* (Fig. 24) and have a convex rather than a concave anterior edge. The osteoderms of *Anguis fragilis* (Fig. 23) are smaller and thinner than those of *Ophisaurus apodus*.

Problematic Taxa

**Anguis stammeri* Brunner, 1954 was described from the Middle Pleistocene of Fuchsloch, Siegmannsbrunn, Bavaria, Germany (Germany: Middle Pleistocene Site 6) on the basis of a dentary. Other remains from the Middle Pleistocene Breitenberg Cave, Gössweinstein, Bavaria, Germany (dentaries), and the Upper Pleistocene Devil's Cave Site near Pottenstein, Germany (dentary, mandibles, palatine), were also referred to this species.

**Anguis stammeri* is distinguished from *Anguis fragilis* on the basis of having much more robust teeth, especially in the anterior region of the jaw. A description of the dentary and palatine of **Anguis stammeri* is provided by Estes (1983): "Dentary with about 10 teeth; teeth robust, recurved, sharply pointed;

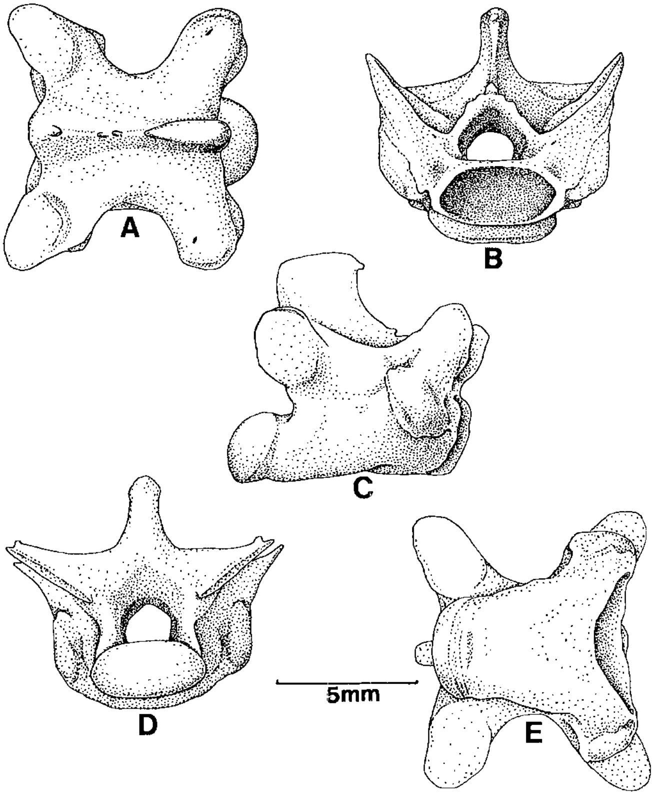

FIGURE 24. Trunk vertebra of modern *Ophisaurus apodus* from the Balkans. (A) Dorsal; (B) anterior; (C) lateral; (D) posterior; (E) ventral. The scale bar applies to all figures. [Drawing by Teresa Petersen.]

anterior teeth large, robust, not much smaller than posterior teeth; referred palatine broader than long'' (p. 135).

Unfortunately, Estes was unable to compare the specimens of **Anguis stammeri* with other related lizard species, yet he expressed the view that the fossil might be a valid species in that *Anguis fragilis* usually has smaller teeth.

On the other hand, Młynarski (1962) suggested that **Anguis stammeri* is actually an *Ophisaurus*, as some *Ophisaurus* now limited to the Oriental region (but that have not occurred in Europe since the Miocene) have similar robust, acuminate teeth. I observed a complete, very large *Anguis fragilis* specimen from the Ightham fissures near Sevenoaks, Kent, England (Holman, 1985), that approached *Ophisaurus apodus* in size. This fossil, which could be from a few hundred to a few thousand years old, had very robust teeth. I suggest that **Anguis stammeri* is merely a robust variant of *Anguis fragilis*. This has also been suggested by other workers (most recently Böhme, 1996).

Anguis cf. *Anguis fragilis: Probable Slow Worm*

Pleistocene Locality

France: Middle Pleistocene—7

Genus *Ophisaurus* Daudin, 1803: Glass Lizards

Glass lizards of the genus *Ophisaurus* are moderately large to large, elongate, legless lizards, with shiny scales and long fragile tails. About 14 species are currently recognized (Frank and Ramus, 1995). About 11 species have been described from Tertiary and Quaternary deposits, some of which are of doubtful validity (see Estes, 1983; Sullivan, 1987). At present the genus occurs in the midwestern and southeastern United States south to Veracruz in eastern Mexico. It also occurs in Morocco, southeastern Europe into Afghanistan, southeastern Asia, Borneo, and Sumatra.

These lizards are generally semifossorial, or at least secretive. They are generally insectivores, although the larger forms will occasionally feed on small vertebrate species. They are often crepuscular in their foraging habits, but some species forage in full daylight. All of these animals have brittle tails that are usually readily shed when the animal is seized by a predator. They usually have distinct fracture planes in the middle of their caudal vertebrae.

Skeletal features, modified from Estes (1983), are: skull long and narrow and of generally of primitive anguid type; limb skeletons absent or reduced to bony remnants of pelvic skeleton; osteoderms thickened, subangular, with gliding surface continuous as a lateral bevel; and trunk vertebrae simple and keeless.

Problematic Taxa

**Ophisaurus pannonicus* Kormos, 1911 differs from the very large modern southeastern European species *Ophisaurus apodus* mainly in characters that correlate with the even larger size of **Ophisaurus pannonicus* (maximum skull length about 90–100 mm). **Ophisaurus pannonicus* has a more massively built skeleton with greater development of crests for muscle attachment, thicker tubercles, and thicker osteoderms. Moreover, even in young specimens, the parietal is broader, with the axes separating the interparietal, parietal, and occipital scutes being nearly perpendicular (see Bolkay, 1913, plate 12m, fig. 1).

Młynarski (1964), however, stated that Upper Pliocene specimens of **Ophisaurus pannonicus* from Poland could not be distinguished from extant individuals of *Ophisaurus apodus* from the Balkan Peninsula, and Estes (1983) suggested that **Ophisaurus pannonicus* may have been merely a large northern race of *O. apodus*. I consider **Ophisaurus pannonicus* to be merely a large form of *O. apodus*. Most of the following Pleistocene references to *Ophisaurus apodus* have been previously published as **Ophisaurus pannonicus*.

Ophisaurus sp. indet.: Indeterminate Glass Lizard Species

Pleistocene Locality
Croatia: Upper Pleistocene—5.

Ophisaurus apodus Pallas, 1775: European Glass Lizard

Pleistocene Localities
Poland: Lower Pleistocene—1, 4.
Hungary: Upper Pliocene and Lower Pleistocene—2; Lower Pleistocene—1, 5; Pleistocene Undesignated—1, 2, 3.
Serbia: Upper Pleistocene and Holocene—1.

These spectacular legless lizards may be 60 mm thick and have been described as looking like a ''giant slow worm'' (*Anguis fragilis*). On the other hand, the ones I have seen have been much more active than *A. fragilis*. The European glass lizard presently ranges in the Balkans as far north as the Istrian region and northeastern Bulgaria. It also occurs in Crimea, the Caucusus, and parts of southwestern and central Asia. They are usually found in dry habitats such as rocky hillsides and embankments. They are able to feed on small terrestrial vertebrate prey such as young mice and small snakes and lizards. The northern extralimital occurrence of *Ophisaurus apodus* (=''**Ophisaurus pannonicus*'') in Poland is addressed in Chapter 7.

Family Varanidae Gray, 1827

Monitors

Living varanid lizards contain two very different groups, the earless monitors (Lanthanotinae), slender, semiaquatic forms; and the monitors of a single genus, *Varanus* (Varaninae), that are powerful lizards with long necks, robust bodies and limbs, and long, powerful tails. The largest living lizard is *Varanus komodoensis*, which reaches a weight of 250 kg and occurs in the East Indies islands of Komodo, Flores, and Padar. At present varanids are widely distributed in the Old World from Africa to southern Asia, the Indo-Australian Archipelago, the Phillipines, New Guinea, and Australia. Most varanids are carnivores, and *Varanus komodoensis* is able to bring down large vertebrate prey.

Problematic Record
**Varanus marathonensis* Weithofer, 1888 was described from the Pliocene of Germany and occurs in other Pliocene localities in Greece, Hungary, and Turkey (Estes, 1983). It has also been reported from the Upper Pleistocene of Arene Candide Cave, Italy by Morelli (1891). Since no other Pleistocene varanids have been reported from southern Europe since 1891, the record appears very doubtful, and Estes (1983) states that the Italian record requires confirmation.

Order Amphisbaenia Gray, 1844: Worm Lizards

Family Amphisbaenidae Gray, 1865

Tropical Worm Lizards

All tropical worm lizards of the family Amphisbaenidae lack limbs and limb girdles and, like worm lizards of the three other amphisbaenian families, have a very compact skull modified for digging, no external ears, an elongate body with a very short tail, and circular rings around the body and develop only a right lung. The Amphisbaenidae have blunt-headed species, spade-snouted species, and species with compressed heads, all of which burrow in different ways. At least 17 genera are currently recognized (Frank and Ramus, 1995).

At present, the family occurs in Spain, the Mediterranean area, Africa, South America, Panama, and the West Indies. The amphisbaenid worm lizards are fossorial and are very seldom seen on the surface. The bullet-headed forms move through the soil by head-ramming and some circular motions of the head and are considered to be the most generalized group. The spade-snouted taxa burrow by moving the head up and down, and the laterally compressed-head taxa burrow by swinging the head from side to side. The family is considered to be primitive, and there appear to be no skeletal characters that are unique to the group. The vertebrae of amphisbaenids are generally simple and flattened with low neural arches and are ventrally unkeeled.

Genus *Blanus* Wagler, 1830: Mediterranean Worm Lizards

The genus *Blanus* contains primitive members of the family with a bullet-shaped head and minute eyes. Two modern species occur in Europe, *Blanus cinerus*, which occurs in Iberia, Morocco, and Algeria, and *Blanus strauchi*, which lives in Turkey and Greece. These species tend to occur in sandy soils or soils that have a high humus content.

Blanus cinereus Vandelli, 1797: Mediterranean Worm Lizard

Pleistocene Locality

Spain: Middle Pleistocene—7, 8; Upper Pleistocene—21.

cf. *Blanus cinereus*: Probable Mediterranean Worm Lizard

Pleistocene Locality

Spain: Middle Pleistocene—10.

Blanus cf. *Blanus strauchi* (Bedriaga, 1884): Probable Turkish Worm Lizard

Pleistocene Locality
Italy: Lower Pleistocene—3.

This species does not presently occur in Italy, and this Pleistocene occurrence in Italy is addressed in Chapter 7.

Order Serpentes Linnaeus, 1758: Snakes

Pleistocene snakes are mainly identified on the basis of individual vertebrae. Important nomenclature associated with snake vertebrate is given in Figures 25 and 26.

Serpentes undesignated: Undesignated snake material

Pleistocene Localities
Germany: Upper Pleistocene—27.
Hungary: Upper Pliocene or Lower Pleistocene—2; Lower Pleistocene—2, 3, 5; Middle Pleistocene—1; Middle and Upper Pleistocene—1; Upper Pleistocene—2, 4, 8, 9, 10, 11; Upper Pleistocene and Holocene—1, 3.

cf. Family Typhlopidae Gray, 1825

Probable Blind Worm Snakes

Vertebrae of the primitive snakes of the suborder Scolecophidia (Fig. 27A) are so simple (e.g., neural spines and hemals keels are absent) that it is difficult to identify families, genera, and species. But Szyndlar (1991b) states that vertebrae from the Middle Pleistocene of Greece do not differ from one another or from the living European species *Typhlops vermicularis* of the family Typhlopidae. Thus, on the basis of parsimony, I suggest that the family Typhlopidae and *Typhlops vermicularis* are probably represented by the Greek fossils.

The typhlopids are slender, cylindrical snakes with short tails. Their eyes are reduced and lie beneath large scales. They have tooth-bearing, movable maxillae, but the dentaries are toothless. There are about 200 species in the family (Zug, 1993). Typhlopids are primarily tropicolitan but range into parts of temperate Eurasia and Australia. They are fossorial snakes that feed mainly on termites.

cf. *Typhlops* Oppel, 1811: Probable Common Worm Snakes

This genus has about 125 species that occur throughout the tropic of the world (Zug, 1993).

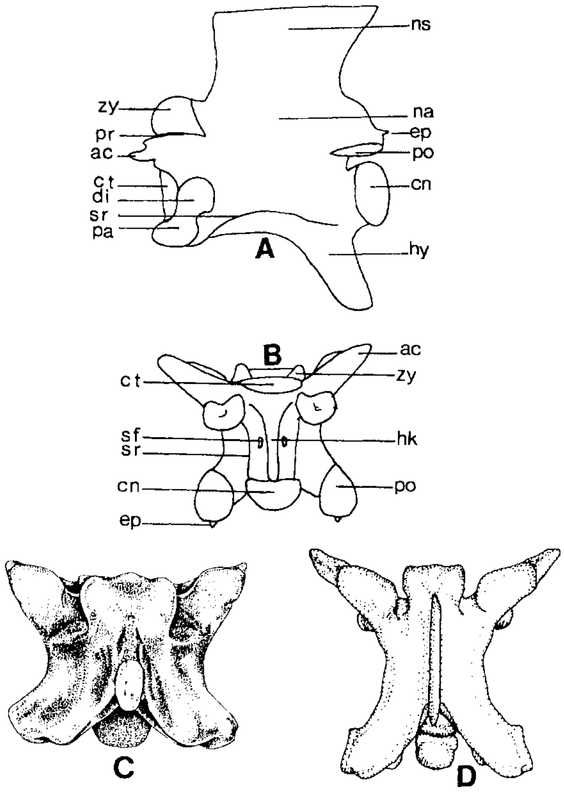

FIGURE 25. Snake trunk vertebrae. (A) Natricine (Colubridae) trunk vertebra in lateral view. Abbreviations (starting at the top left): zy = zygosphene; pr = prezygapophyseal articular facet; ac = prezygapophyseal accessory process; ct = cotyle; di = diapophyseal portion of synapophysis; sr = subcentral ridge; pa = parapophyseal portion of synapophysis; ns = neural spine; na = neural arch; ep = epizygapophyseal spine; po = postzygapophyseal articular facet; cn = condyle; hy = hypapophysis. (B) Colubrine (Colubridae) trunk vertebra in ventral view. Abbreviations not listed in A: sf = subcentral foramen; hk = hemal keel. (C) Generalized erycinine (Boidae) trunk vertebra in dorsal view. (D) Genralized colubrine (Colubridae) trunk vertebra in dorsal view. [All from Holman, 1995c: A and B, drawings by the author; C, drawing by Donna Holman; D, drawing by Rosemarie Attilio]

cf. *Typhlops vermicularis* Merrem, 1820: Probable Worm Snake

Pleistocene Localities

Greece: Middle Pleistocene—3, 4.

Typhlops vermicularis presently occurs in Albania, southern Yugoslavia, southern Bulgaria, and some Greek islands as well as in southwestern Asia, the Caucasas, and northeastern Egypt.

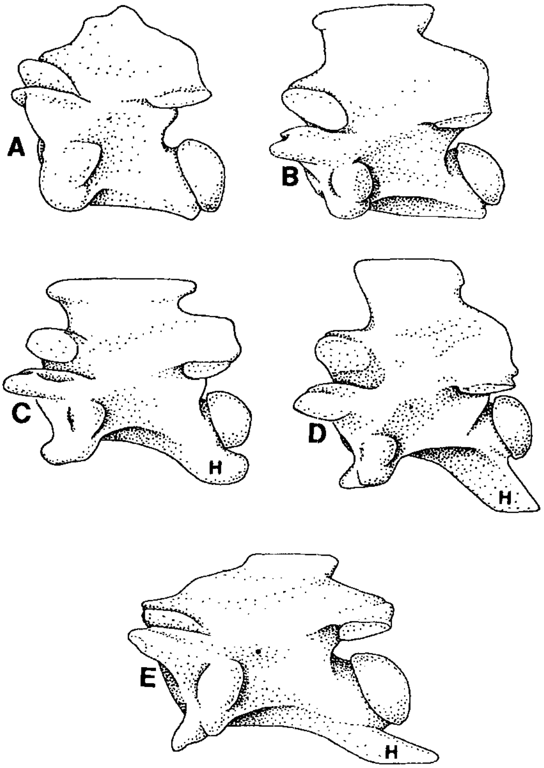

FIGURE 26. Presence or absence of hypapophyses in trunk vertebrae of British and European snake families and subfamilies. Hypapophyses are absent in the trunk vertebrae of European Boidae (A, *Eryx jaculus*) and the subfamily Colubrinae of the Colubridae (B, *Elaphe longissima*). Hypapophyses are present in the trunk vertebrae of the subfamily Natricinae of the Colubridae (C, *Natrix natrix*; D, *Natrix tesellata*) and in the Viperidae (E, *Vipera berus*). Cervical (neck) vertebrae of all of these groups, however, bear hypapophyses. H = hypapophysis. [Redrawn by Teresa Petersen from drawings by Z. Szyndlar, 1991b, 1991c, with his kind permission]

Family Boidae Gray, 1825

Boas and Pythons

Snakes of the family Boidae (pythons are included in this group) are relatively primitive, constricting serpents, some of which are presently the world's largest snakes. There are at least 20 living genera, and several fossil genera have been described (Rage, 1984c). The family is widely distributed at present, mainly in semitropical and tropical regions. Boids occur in Africa, Madagascar, Australia, the Pacific islands, southern Asia, southeastern Europe, western North America, and Central and South America. They range from fossorial or secretive forms that feed on small vertebrates to large aquatic and arboreal forms that are able

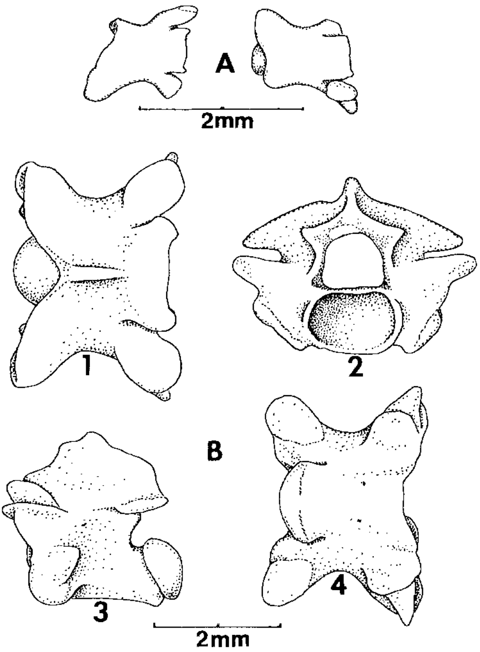

FIGURE 27. Trunk vertebrae of primitive snakes. (A) Two vertebrae of Scolecophidia indet. (probably *Typhlops vermiculatus*) in dorsal view from the Middle Pleistocene Tourkobounia 2 Site, Greece (left) and the Middle Pleistocene Tourkobounia 5 Site, Greece (right). The scale bar applies to both vertebrae. (B) Trunk vertebra of *Eryx jaculus* (Boidae, Erycinae) from the Upper Quaternary of the Pili B Site, Greece: (1) dorsal, (2) anterior, (3) lateral, (4) ventral. The scale bar applies to all views. [Redrawn by Teresa Petersen from drawings by Z. Szyndlar, 1991b, with his kind permission]

to kill and devour large vertebrates and, very occasionally, humans. All of them kill their prey by constriction.

Important osteological characters of the Boidae, modified from Rage (1984c), are: maximum width of braincase occurs at anterior level of parietal, except in a few species where otic region is as wide as anterior part of parietal; supratemporal projects caudally behind reduced paroccipital process; length of supratemporal variable; quadrate vertical, either short, or moderately elongate; postfrontal absent; optic foramen occurs between frontal and parietal; vomerine process of premaxilla reduced and either separate from vomers or only in loose contact; ascending process of maxilla absent; coronoid usually present; vertebrae (Figs. 25C and 27B) short, wide, and massive, with hypapophyses usually limited to cervical vertebrae; and bony vestiges of pelvic girdle almost always present in males, frequently absent in females.

Only one Pleistocene boid species, *Eryx jaculus*, is known from Europe.

Genus *Eryx* Daudin, 1803: Sand Boas

Snakes of the genus *Eryx* are very small boids with short, blunt tails. These snakes are adapted to dry and even desert conditions. Ten living species are recognized (Frank and Ramus, 1995), and no extinct fossil species have been described (Rage, 1984c). At present the genus is found in southeastern Europe, southwestern Asia, and North Africa. Sand boas are mainly fossorial, spending their time in rodent excavations or loose soil. They occasionally venture to the surface at night. Their food consists mainly of small rodents, but other small vertebrates are occasionally eaten.

The vertebrae (Figs. 26A and 27B) of the boid subfamily Erycinae and the genus *Eryx* are quite distinctive. The neural arch is depressed, and the neural spines of trunk vertebrae are usually low (high in most other nonerycine boids). The neural spines of caudal vertebrae (except for the modern genus *Lichanura* and the fossil genus *Albaneryx*) are characteristically very swollen. Only a single species, *Eryx jaculus*, is known from the Pleistocene of Europe.

Eryx jaculus Linnaeus, 1758: Caucasian Sand Boa

Pleistocene Localities

Greece: Middle Pleistocene—1; "Upper Quaternary"—1.

Eryx jaculus is a stout snake with a short, blunt tail. The pointed head is not distinct from the neck and has a protruding, chisel-shaped rostrum. Presently the species occurs in the southern Balkans north to southern Albania and Yugoslavia, southern Bulgaria, and southeastern Romania, as well as on several Greek oceanic islands. It also occurs in North Africa and in southwestern Asia.

This sand boa is found in dry areas where the soil is either light or sandy. It characteristically moves about in rodent tunnels or burrows in loose soil, sometimes moving to the surface at night. The staple diet of *Eryx jaculus* is rodents, but it may feed on lizards and other small vertebrates. Constriction is usually employed when larger prey is eaten.

Identification of Pleistocene Fossils

The vertebrae of *Eryx* are distinguishable from the related genus *Charina* on the basis that the trunk and caudal vertebrae have lower neural spines than in *Charina* (Rage, 1984c).

Family Colubridae Oppel, 1811

Advanced Snakes

The family Colubridae contains such a wide variety of snakes that it is an especially difficult vertebrate group to define. About 290 genera and 560 species of colubrid snakes are presently recognized (Halliday and Adler, 1986). Moreover, the family continues to be broken up and rearranged taxonomically.

Typical colubrids have distinct heads and a tapering body with a relatively long tail. They also have a characteristic pattern of scales on the head as well as hemipenes that are ornamented with spines.

Several extinct Tertiary genera, termed "archaic colubrid genera," have been described in North America (e.g., Holman, 1979; Parmley and Holman, 1995; Sullivan and Holman, 1996). At present the Colubridae occur throughout the world except for very cold areas, most of Australia, and from some rather large islands such as Ireland.

Within the Colubridae one can find burrowing species, very fast terrestrial taxa, climbing snakes, aquatic species, and taxa adapted for killing their prey by constriction. Other adaptations include forms with grooved teeth that introduce poisonous saliva into the bodies of their prey, as well as harmless species that mimic deadly poisonous ones of other families. Many colubrids have become specialized for a single item of diet.

Because of its heterogeneous content, the Colubridae is difficult or impossible to define osteologically, other than as an osteologically advanced group that lacks tubular poisonous fangs. On the other hand, fossil snakes usually may be readily identified as colubrids on the basis of their trunk vertebrae (Fig. 25B,D). Characters are: vertebrae lightly built, usually longer than wide or about as long as wide; neural spine relatively thin, often longer than high or about as high as long; centrum usually with prominent subcentral ridges and a relatively thin ventral keel; trunk vertebrae lacking hypapophyses (Fig. 26B) in most subfamilies (Natricinae, Fig. 26C,D, being a notable exception); and distinct excavations or pits usually occurring on either side of cotyle and on the bottom of centrum.

Colubrid Subfamily Undesignated: Smooth Snakes

It is possible that the genus *Coronella* will eventually be placed in its own colubrid subfamily for a variety of reasons, including its hemipenial, maxillary, and vertebral structure.

Genus *Cornella* Laurenti, 1768: Smooth Snakes

The genus *Coronella* consists of rather small smooth-scaled snakes with a rounded body and a head that is not distinct from the neck. The eyes are small. The two modern species both occur as Pleistocene fossils. The present range of the genus is defined in the accounts of the two modern species below. Both species are rather secretive, and they tend to be slow moving when they leave their resting or hiding places. Both taxa are said to feed mainly on lizards.

Coronella sp. indet.: Indeterminate Smooth Snake

Pleistocene Localities

France: Lower Pleistocene—4; Middle Pleistocene—1, 6.

cf. *Coronella* sp.: Probable Smooth Snake

Pleistocene Locality

Poland: Lower Pleistocene—4.
Greece: Middle Pleistocene—3; "Upper Quaternary"—1.

Coronella austriaca Laurenti, 1768: Smooth Snake

Pleistocene Localities

Britain: Middle Pleistocene—12.
Germany: Middle Pleistocene—3; Upper Pleistocene—2, 3, 4, 7, 27, 31; Pleistocene Undesignated—6; Upper Pleistocene and Holocene—1, 2, 3, 4, 5.
Poland: Lower Pleistocene—1, 2, 3, 4, 5; Upper Pleistocene—7.
Serbia: Upper Pleistocene and Holocene—1.

This small snake is separable from the only other species of the genus, *Coronella girondica*, in having a dark stripe that runs from the nostril to the eye (this stripe is usually lacking in *C. girondica*), and in having a darkish belly with light specks (belly with rows of bold black black spots in *C. girondica*). At present *Coronella austriaca* occurs in southern England, France, and northern Iberia, east to southern Scandanavia and Russia, and south to Italy, Sicily, and Greece. It also occurs in northern Asia Minor north to Iran. The smooth snake is a secretive animal, but it tends to be active during the daylight hours. It prefers dry, sunny habitats, and in the southern part of its range it tends to occur in mountains.

Identification of Pleistocene Fossils

Unlike snakes in the colubrid subfamiliy Natricinae and in the Viperidae (Fig. 26C–E), the trunk vertebrae of *Coronella austriaca* (Fig. 28) and *Coronella girondica* lack the prominent ventral structures called hypapophyses that project from the bottom of the centrum. Other diagnostic characters include a low but not obsolete neural spine, a depressed neural arch, and a broad, nondistinct hemal keel.

Szyndlar (1984, 1991b) gives characters that separate the vertebrae of *Coronella austriaca* (Fig. 28) from *Coronella girondica*, including the observation that the basal portion of the prezygapophyses is more strongly built and the parapophyses are longer in *Coronella austriaca*. More differences between these species were detected on several cranial elements (Szyndlar, 1984).

Coronella cf. *Coronella austriaca*: Probable Smooth Snake

Pleistocene Localities

France: Middle Pleistocene—4, 7, 9; Upper Pleistocene—8.

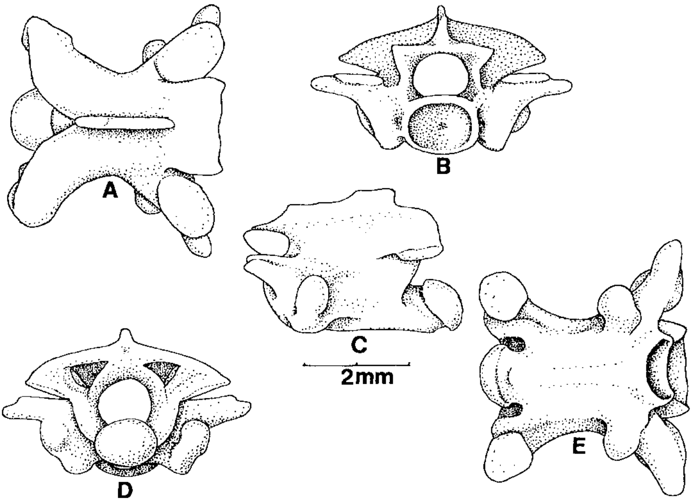

FIGURE 28. Trunk vertebra of *Coronella austriaca* from the Middle Pleistocene Kozi Grzbiet Site, Poland. (A) Dorsal; (B) anterior; (C) lateral; (D) posterior; (E) ventral. The scale bar applies to all views. [Redrawn by Teresa Petersen from a drawing by Z. Szyndlar, 1991b, with his kind permission.

?*Coronella* aff *Coronella austriaca*: Possible Smooth Snake

Pleistocene Localities

Czech Republic: Lower Pleistocene—2, 3.

Coronella girondica (Daudin, 1803): Southern Smooth Snake

Pleistocene Locality

Spain: Middle and Upper Pleistocene—1.

External and osteological characters that differentiate *Coronella girondica* from *Coronella austriaca* are given in the *Coronella austriaca* account above. At present, *Coronella girondica* has a more southern range than *Coronella austriaca*, occurring in Iberia, southern France, Italy, Sicily, and northwestern Africa. The habits of the two species differ in that *Coronella girondica* tends to be active in the evening rather than in the daytime. This may be because it feeds on nocturnal geckos.

Coronella cf. *Coronella girondica*: Probable Southern Smooth Snake

Pleistocene Localities

France: Middle Pleistocene—4.
Spain: Middle Pleistocene—8.

Subfamily Colubrinae Cope, 1895

Holarctic Terrestrial and Arboreal Snakes

The Colubrinae (colubrine snakes) form an exceedingly large group of Holarctic terrestrial and arboreal snakes that has at least once been divided into six tribes (Dowling and Duellman, 1974-1978). Colubrine snakes (and *Coronella*) lack the prominent ventral structures called hypapophyses that project from the bottom of the centrum of the trunk vertebrae that are present in the Colubridae subfamily Natricinae and in the family Viperidae (Fig. 26).

Colubrinae indet.: Indeterminate Holarctic Terrestrial or Arboreal Colubrid Snakes

Pleistocene Localities

Spain: Upper Pleistocene—15.
Poland: Upper Pleistocene—5.
Greece: Middle Pleistocene—1, 3, 4; "Upper Quaternary"—1.

Genus *Coluber* Linnaeus, 1758: Whipsnakes and Racers

Snakes of the genus *Coluber* are slender, active, diurnal snakes that do not constrict their prey, although some species immobilize the animals that they are swallowing with a loop of the body. About 26 species are currently recognized (Frank and Ramus, 1995). Several extinct species of the genus *Coluber* have been named from the Tertiary and Pleistocene of Europe, and several of these are invalid.

At present the genus occurs from southern Canada south to Guatemala and in southern Europe, North Africa, and parts of Asia. These snakes are usually able to move very rapidly, have large eyes, and have the appearance of being very alert. They eat small mammals and birds as well as a variety of ectothermic vertebrates including other snakes, lizards, frogs, and toads. Insects are also a part of the diet of many species. Many of them are partially arboreal, climbing into bushes, shrubs, and low trees.

It is difficult to define the genus *Coluber* on the basis of osteology, for many skeletal characters overlap with those of other colubrid genera such as *Elaphe*, *Lampropeltis*, *Opheodrys*, *Salvadora*, and especially *Masticophis*, which some authors include as part of the genus *Coluber*. In fact, it is often difficult or impossible to distinguish the trunk vertebrae of the New World genera *Coluber* and *Masticophis* (Holman, 1981).

In comparing North American and European *Coluber*, one finds that the vertebrae of all North American *Coluber* are elongate and gracile, with slender neural spines and a slender median keel (hemal keel) on the bottom of the centrum. In Europe, however, the vertebrae of some species of *Coluber* is shorter and not as gracile, with thicker neural spines and a thicker median keel (hemal keel) on the bottom of the centrum than in the North American taxa. In fact, the vertebral type of these European *Coluber* are more similar to North American *Elaphe* (rat snakes) than they are to North American *Coluber*!

Problematic Taxa

**Coluber fossilis* Pomel, 1853 is only known from the Middle Pleistocene of Coudes, Puy-de-Dome, France (France: Middle Pleistocene Site 3). The syntypes, one parietal and one compound bone, are lost (Rage, 1984c). Although the description was inadequate, it satisfies the provisions of the International Code of Zoological Nomenclature to the extent that **Coluber fossilis* is considered a *nomen dubium* (Rage, 1984c). It appears very likely that **Coluber fossilis* actually belongs to the modern species *Coluber viridiflavus*, which has been found at the type locality.

**Coluber freybergi* Brunner, 1954 was described on the basis of one maxilla, one palatine, two fragmentary compound bones, and one dentary from the Middle Pleistocene locality of Fuchsloch, Siegmannsbrunn, Bavaria, Germany (Germany: Middle Pleistocene Site 6). The species is similar to the living species *Coluber viridiflavus* except that the maxillary teeth may be more numerous (Rage, 1984c). Since the number of maxillary teeth is variable within modern species of *Coluber*, it is probable that **Coluber freybergi* actually represents *Coluber viridiflavus*.

**Coluber gervaisii* Pomel, 1853 was named on the basis of syntypic material (one parietal and one parabasisphenoid) from the Middle Pleistocene of Coudes, Puy-de-Dome, France (France: Middle Pleistocene Site 3). The syntypes are lost, and Pomel's original description was inadequate. Nevertheless, the description satisfies the International Code of Zoological to the extent that **Coluber gervaisii* is considered a *nomen dubium* (Rage, 1984c). Since vertebrae clearly definable as *Coluber viridiflavus* occur at the sole locality of **Coluber gervaisii*, I would strongly suggest that **Coluber gervaisii* actually represents *Coluber viridiflavus*.

To summerize these accounts: three supposedly extinct Pleistocene species of *Coluber*—**Coluber freybergi* from the Middle Pleistocene of Germany and **Coluber fossilis* and **Coluber gervaisii* from a single Middle Pleistocene locality in France—probably represent the modern species *Coluber viridiflavus*.

Coluber and/or *Elaphe*: Whipsnake or Racer and or Ratsnake

Pleistocene Locality
Spain: Middle Pleistocene—8.

?*Coluber*: Possible Whipsnake or Racer

Pleistocene Localities
Italy: Lower Pleistocene—4; Middle Pleistocene—8.

Coluber sp. indet.: Indeterminate Whipsnake or Racer

Pleistocene Localities
France: Middle Pleistocene—4; Upper Pleistocene—4, 5.
Czech Republic: Lower Pleistocene—2, 3.
Italy: Upper Pleistocene—7, 15.
Croatia: Middle Pleistocene—1.

Coluber caspius Gmelin, 1789: Large Whip Snake

Pleistocene Localities
Austria: Middle Pleistocene—1, 2.
Czech Republic: Lower Pleistocene—2.

I am here following Szyndlar (1991b) in using the name *Coluber caspius* Gmelin, 1789 for the large whip snake (vernacular name used by Arnold and Burton, 1978) rather than *Coluber jugularis*, a name that has been commonly used in the recent literature.

Coluber caspius is the largest European snake (Szyndlar, 1991b) and may reach a total length of about 200 cm. It is an elongate snake with a head that is moderately distinct from the body, smooth scales, and rather prominent eyes. It is usually olive or yellowish brown in color with weak light stripes on the top of the body. The belly is usually pinkish or yellowish. At present the species occurs in the southern and eastern Balkans north to the southwestern part of the former Soviet Union, Romania, Hungary, and parts of Yugoslavia. It occurs on many Aegean islands and in southwestern Asia. The large whip snake is a very fast, active, terrestrial snake that prefers open, dry habitats with adequate ground cover. It hunts during the day and mainly feeds on small mammalian prey.

The extralimital occurrence of this species in the Middle Pleistocene of Austria is discussed in Chapter 7.

Identification of Pleistocene Fossils

The trunk vertebrae of *Coluber caspius* (Fig. 29) differ from those of other large-sized European colubrines (Szyndlar, 1991b). The following remarks are modified from Szyndlar's account of these differences. The vertebrae are longer than wide, and the zygosphene, even in smaller specimens, is concave in dorsal view. The hemal keel is well produced from the bottom of the centrum and is sharp throughout most of its length. The height of the hemal keel diminishes immediately behind the cotylar rim, and the keel becomes wider and flatted just anterior to the condyle.

Detailed morphological descriptions of the skull of modern *Coluber caspius* have been provided by Rabeder (1977) and Szunyoghy (1932), while Szyndlar (1984) provided illustrations of of all of the individual bones of the skull of this snake.

Coluber gemonensis (Laurenti, 1768): Balkan Whip Snake

Pleistocene Localities

Austria: Middle Pleistocene—1, 2.
Italy: Middle and Upper Pleistocene—4.

The Balkan whip snake is a slender snake with a well-defined head and rather large eyes. This species reaches a length of about 100 cm. Other than its smaller size, it may be separated from the large whip snake, *Coluber caspius*, on the basis of having dark blotches on the top and sides of the body. At present *Coluber gemonensis* occupies the eastern Adriatic coast and adjacent islands and Greece. It also occurs on Gioura island in the Cyclades. The Balkan whip snake prefers relatively dry habitats, such as scrub areas or open woods, where it forages for lizards and sometimes small mammals and large insects. It is a nervous, very active snake. The extralimital occurrence of this species in Austria is addressed in Chapter 7.

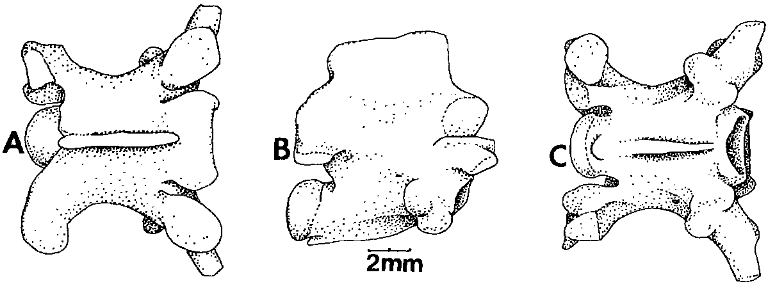

FIGURE 29. Trunk vertebra of *Coluber caspius* from the Middle Pleistocene of Varbeshnitsa, Bulgaria. (A) Dorsal; (B) lateral; (C) ventral. The scale bar applies to all views. [Redrawn by Teresa Petersen from a drawing by Z. Szyndlar, 1991b, with his kind permission]

Identification of Pleistocene Fossils

Diagnostic characters of the trunk vertebrae of *Coluber gemonensis* (Fig. 30) are modified from Szyndlar (1991b). The trunk vertebrae of *Coluber gemonensis* are characterized by having a very slightly convex anterior border of the zygosphene in dorsal view and prezygapophyseal processes that are long and sharply pointed. These are supposedly the only vertebral characters that differentiate *Coluber gemonensis* from other small colubrines. Szyndlar (1991b) also points out that the character he used in Szyndlar (1984), namely, that the hemal keel of *Coluber gemonensis* is better developed than other in small European colubrines, is not a useful one. A detailed description of the skull of *Coluber gemonensis* was provided by Szunyoghy (1932).

Coluber cf. *Coluber gemonensis*: Probable Balkan Whip Snale

Pleistocene Locality

Greece: Upper Pleistocene—1.

?*Coluber* aff *Coluber gemonensis*: Possible Balkan Whip Snake

Pleistocene Locality

Czech Republic: Lower Pleistocene—2.

Coluber hippocrepis Linnaeus, 1758: Horseshoe Whip Snake

Pleistocene Locality

Spain: Middle and Upper Pleistocene—1.

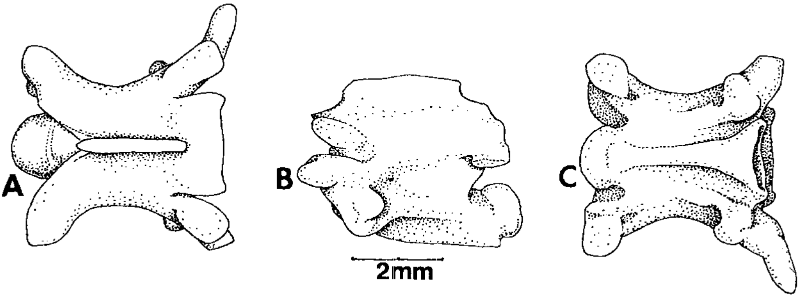

FIGURE 30. Trunk vertebra of cf. *Coluber gemonensis* from the Upper Pleistocene of Stoilovo, Bulgaria. (A) Dorsal; (B) lateral; (C) ventral. The scale bar applies to all views. [Redrawn by Teresa Petersen from a drawing by Z. Szyndlar, 1991b, with his kind permission]

The horseshoe whip snake is another long, slender whip snake, that reaches a length of about 130–140 cm but is occasionally larger. It may be distinguished by a striking pattern of dark blotches on the back and sides that ranges from reddish brown to almost black. There is often a horseshoe-shaped or V-shaped mark on the back of the head. At present *Coluber hippocrepis* occurs in Iberia, particularly in the southwest and along the eastern Mediterranean coast; southern Sardinia; Pantellaria; and northwestern Africa. This is another fast, diurnal whip snake that prefers dry landscapes, especially rocky or shrubby ones.

Identification of Pleistocene Fossils

The author was able to study the skeleton of a single skeleton of *Coluber hippocrepis* from an individual with a total length of 82 cm from Villarreal de San Carlos, Caseres, Spain. The trunk vertebrae were very similar to those of the North American genus *Sonora*, which are themselves similar to those of North American *Coluber* and *Masticophis* in having delicate vertebral processes but with a shorter vertebral form and lacking epizygapophyseal spines.

In *Coluber hippocrepis* the trunk vertebrae are about as long as wide. The neural spine is very thin and is longer than high. The hemal spine is straight and distinct, as are the sides of the centrum in ventral view. The prezygapophyseal processes are very long and pointed. Epizygapophyseal processes are absent.

Coluber viridiflavus Lacépède, 1789: Western Whip Snake

Pleistocene Localities

France: Middle Pleistocene—3, 7; Upper Pleistocene—6.
Germany: Middle Pleistocene—2.
Austria: Middle Pleistocene—2.
Italy: Middle Pleistocene—9; Pleistocene undesignated—6.

Coluber viridiflavus is a slender whip snake, with a well-defined head, smooth scales, and relatively prominent eyes. Adults may be recognized by the striking yellow and black markings on the anterior part of the body or by the body being entirely black above. They reach a total length of about 130–140 cm, but occasionally individuals may be found that are much larger.

At present the species occurs in extreme southern Spain, southern France, southern Switzerland, northwestern Yugoslavia, and south to Sicily and Malta. They also occur on islands in the Adriatic and Tyrrhenian Seas. The western whip snake is found in mainly dry lanscapes with significant amounts of vegetation. It is largely terrestrial, but it is able to climb well among bushes and rocky outcrops. Its food includes lizards, other snakes, and small mammals. The extralimital Pleistocene occurrences of *Coluber viridiflavus* in Europe are addressed Chapter 7.

Identification of Pleistocene Fossils

Diagnostic characters for the trunk vertebrae of *Coluber viridiflavus* (Fig. 31) are modified from Szyndlar (1991b). The trunk vertebrae of *Coluber viridiflavus* may be distinguished from those of other large European colubrines on the basis of the distinctly flattened hemal keel that widens posteriorly and by the fact that the anterior edge of the zygosphene is straight in dorsal view. However, Szyndlar cautions that the anterior edge of the zygosphene may be concave in dorsal view in very large snakes. The prezygapophyseal processes are almost as long as the prezygapophyseal facets and are acutely pointed. The neural spine is slightly longer than high.

Coluber cf. *Coluber viridiflavus*: Probable Western Whip Snake

Pleistocene Locality

Czech Republic: Lower Pleistocene—3.

Coluber aff *Coluber viridiflavus*: Possible Western Whip Snake

Pleistocene Locality

Spain: Middle and Upper Pleistocene—1.

Genus *Elaphe* Fitzinger, 1833: Rat Snakes

The snakes of the genus *Elaphe* have a distinct head and large eyes like the whip snakes, but they are less slender and are more powerfully built. They have a glossy scalation, and a very flat belly is characteristic of the genus. About 40 species are currently recognized (Frank and Ramus, 1995). Extinct species are recognized from the late Tertiary of Europe and North America (Rage, 1984c). The genus occurs both in the western and eastern portions of the Northern Hemisphere and ranges from the temperate latitudes to the tropics.

All rat snakes are able to climb, and species range from essentially ground-dwelling to ones that spend considerable time in trees. The main food item of most species is rodents, but some eat reptiles and one species specializes in anurans.

It is difficult to define the genus *Elaphe* on the basis of osteology because of the basic similarity of the skeletons of *Elaphe* and several genera of large colubrine snakes. For instance, in Europe it is difficult to distinguish the vertebrae of some species of *Coluber* from some species of *Elaphe* (not so in North America). In general, on a worldwide basis, the vertebrae of *Elaphe* are somewhat shorter and less gracile than those of whipsnakes and racers of the genus *Coluber*, but not as robustly built as several ground-dwelling, constricting genera such as *Lampropeltis* (kingsnakes).

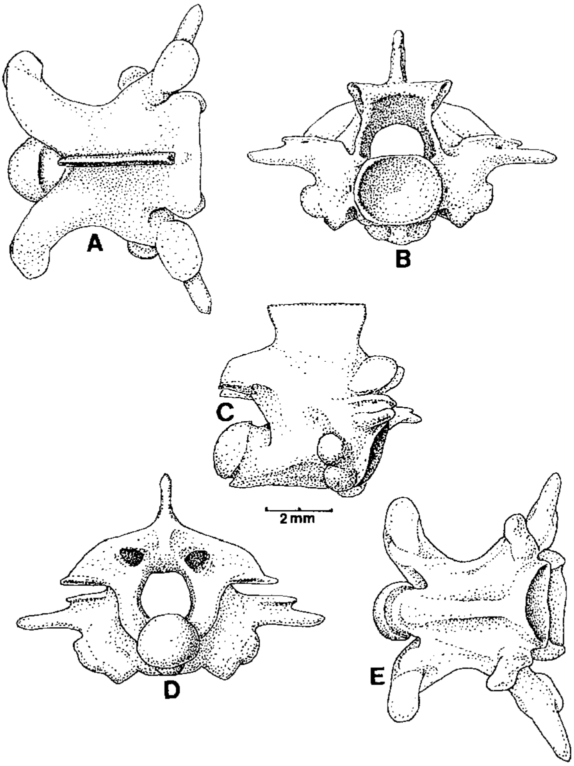

FIGURE 31. Trunk vertebra of modern male *Coluber viridiflavus* from southwestern Europe. (A) Dorsal; (B) anterior; (C) lateral; (D) posterior; (E) ventral. The scale bar applies to all views. [Drawing by Teresa Petersen]

Problematic Taxa

**Elaphe lobsingensis* (Heller, 1960) was described on the basis of a parietal and an articulated parabasisphenoid from the Upper Pleistocene Eemian interglacial site at Lobsing in Bavaria, western Germany (Germany: Upper Pleistocene Site 17). Rage (1984c) reported that the hooked retroarticular process of the mandible, thought to be an important character of the new species by Heller (1960), was merely an interspecific variation. I agree with Rage (1984c) in this matter, as I have found the shape of the end of the retroarticular process to be variable within species of colubrid snakes. The parietal of **Elaphe lobsingensis* has a somewhat more pointed posterior end than that of the living species *Elaphe quatuorlineata*, but is otherwise similar. Rage (1984c) states "*E. lobsingensis* is perhaps a valid species," (p. 48), but Szyndlar (1984) came to the conclusion that the fossils represented the living species *Elaphe longissima*, and this was supported by Böhme (1996), who considers **Elaphe lobsingensis* to be a synonym of *Elaphe longissima*. I concur with Szyndlar and Böhme.

Elaphe sp. indet.: Indeterminate Rat Snake

Pleistocene Localities
Spain: Middle and Upper Pleistocene—1.
Austria: Middle Pleistocene—1.
Croatia: Upper Pleistocene—5.

cf. *Elaphe* sp.: Probable *Elaphe* species

Pleistocene Locality
France: Middle Pleistocene—6.

Elaphe longissima (Laurenti, 1768): Aesculapian Snake

Pleistocene Localities
Britain: Middle Pleistocene—2, 4, 5.
France: Middle Pleistocene—9.
Germany: Middle Pleistocene—3, 16; Upper Pleistocene—2, 3, 10, 17, 22, 25, 28; Pleistocene undesignated—6; Upper Pleistocene and Holocene—2, 3, 4.
Austria: Middle Pleistocene—2.
Poland: Lower Pleistocene—1, 3, 4, 5, 6; Upper Pleistocene—2, 7, 10, 11, 15: Upper Pleistocene and Holocene—1.
Czech Republic: Lower Pleistocene—2, 3.
Croatia: Upper Pleistocene—5.
Serbia: Upper Pleistocene and Holocene—1.
Greece: Middle Pleistocene—4.

The Aesculapian snake is a narrow-headed rat snake with smooth scales. It tends to be olive above and yellowish to whitish below. Vague dark lines often occur down the body. At present the species occurs in central France, southern Switzerland, southern Austria, the Czech Republic, southern Poland, and the southwestern portion of the former Soviet Union; and then south to extreme northeastern Spain, Sicily, and southern Greece. The species also occurs in Sardinia, a few isolated localities in Germany that are north of most of the range of the species, and Turkey and northern Iran.

Legend has it that *Elaphe longissima* was brought into central Europe by the Romans to be kept in temples erected to Aesculapius, the god of medicine, and that the isolated northern records of this species in Germany reflected these introductions. The fossil record, however, shows that during the warmer periods of the Quaternary, *Elaphe longissima* invaded areas far north of its present range on the European continent and in Britain (e.g., Holman, 1994; Szyndlar, 1984). Thus, the modern northern colonies of *Elaphe longissima* are best regarded as remnants from past warmer climates rather than as Roman introductions. The extralimital occurrence of the species in the Pleistocene of Britain and Europe is addressed in Chapter 7.

The typical habitat of *Elaphe longissima* is in dry, sunny, rather open situations with shrubby vegetation or in dry, open woodlands. The food consists mainly of small rodents, which are killed by constriction. The animal is a very good climber and may ascend trees from time to time.

Identification of Pleistocene Fossils

Diagnostic characters of the trunk vertebrae of *Elaphe longissima*, modified from Szyndlar (1991b), are as follows. The trunk vertebrae (Figs. 26B and 32) have a distinct, spatulate hemal keel. This keel is usually rounded rather than being sharp or flattened. The anterior edge of the zygosphene has three distinct lobes, but is more or less straight in dorsal view in large individuals. The prezygapophyseal processes are somewhat shorter than the prezygapophyseal facets. The

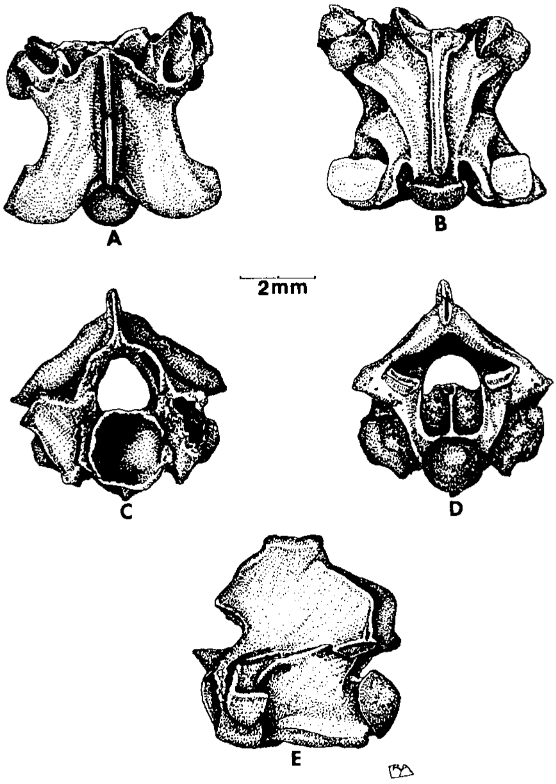

FIGURE 32. Trunk vertebra of *Elaphe longissima* from the Middle Pleistocene Cudmore Grove Site, Essex, England. (A) Dorsal; (B) ventral; (C) anterior; (D) posterior; (E) lateral. The scale bar applies to all views. [Drawing by Rosemarie Attilio in Holman et al., 1990]

neural spine is almost as high as long. The skull morphology of this species was figured and described in detail by Szunyoghy (1932).

Elaphe cf. *Elaphe longissima*: Probable Aesculapian Snake

Pleistocene Localities
France: Middle Pleistocene—4; Upper Pleistocene—4.
Croatia: Upper Pleistocene—6.

cf. *Elaphe longissima*: Probable Aesculapian Snake

Pleistocene Localities
Greece: Middle Pleistocene—3; Upper Pleistocene—2; ''Upper Quaternary''—1.

Elaphe aff *Elaphe longissima*: Possible Aesculapian Snake

Pleistocene Locality
France: Middle Pleistocene—7.

Elaphe quatuorlineata (Lacépède, 1789): Four-Lined Snake

Pleistocene Localities
Austria: Middle Pleistocene—1, 2.
Czech Republic: Lower Pleistocene—2.
Hungary: Lower Pleistocene—1.
Croatia: Upper Pleistocene—6.
Greece: Middle Pleistocene—4.

The four-lined snake is a large rat snake (up to about 200 cm in total length) with keeled scales that give it a less shiny appearance than the smooth-scaled species of *Elaphe*. It is a robust snake, that in the western part of its range has four dark stripes along the back and sides but in the eastern part of its range has blotches on the back and sides. At present the four-lined snake occurs in southeastern Europe north to Istria and southwestern portions of the former Soviet Union as well as many islands in the Aegean, central and southern Italy, Sicily, and parts of southwestern Asia.

Elaphe quatuorlineata is a slow-moving constrictor that prefers somewhat moister habitats than other whip snakes and rat snakes and may be observed near marshy situations or ponds and streams. It is a good climber, but it occasionally may be seen swimming. The food consists mainly of small mammals up to about rat size. The extralimital occurrence of this species in the Czech Republic is addressed in Chapter 7.

Identification of Pleistocene Fossils

Diagnostic vertebral characters for *Elaphe quatuorlineata*, modified from Szyndlar (1991b), are as follows. The hemal keel (Fig. 33C) is strongly flattened and is not widened anterior to the condyle. The zygosphene has its anterior edge strongly concave. The prezygapophyseal processes are acutely pointed and quite short. In fact, they are only half as long as the prezygopophyseal facets. The vertebrae are the shortest and widest of all the European colubrines. The hypapophyses of the cervical vertebrae of *Elaphe quatuorlineata* are directed forward rather than backward as in other European snakes.

Elaphe cf. *Elaphe quatuorlineata*: Probable Four-Lined Snake

Pleistocene Locality

Croatia: Upper Pleistocene—5.

Elaphe cf. *Elaphe scalaris* Schinz, 1822: Probable Ladder Snake

Pleistocene Localities

France: Middle Pleistocene—4.
Spain: Middle Pleistocene—3.

The ladder snake is a large, somewhat robust snake with an overhanging rostrum and a rather short tail. The young of this species have a prominent, dorsal ladderlike pattern that becomes two longitudinal stripes in the adult. The ladder snake presently occurs in Iberia, the Mediterranean coast of France, and Minorca and Iles d'Heyéres. The snake is typically found in dry, bushy habitats. The adults usually feed on rodents and birds, which are killed by constriction.

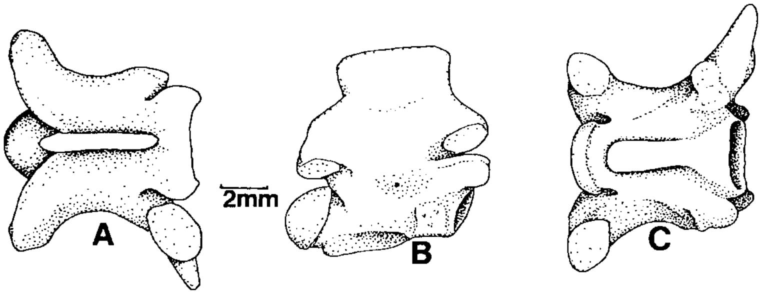

FIGURE 33. Trunk vertebra of *Elaphe quatuorlineata* from the Middle Pleistocene Tourkobounia 2 Site, Greece. (A) Dorsal; (B) lateral; (C) ventral. The scale bar applies to all views. [Redrawn by Teresa Petersen from a drawing by Z. Szyndlar, 1991b, with his kind permission]

Identification of Pleistocene Fossils

The trunk vertebrae (Fig. 34) of *Elaphe scalaris* appear to be diagnostic. In dorsal view the vertebra is wider than long. The prezygapophyseal processes are very well developed. In anterior and posterior views the neural arch is only moderately vaulted. In lateral view the neural spine is longer than high and the dorsal border of the neural spine has an overhanging posterior edge. In ventral view the hemal keel is slender and straight.

cf. *Elaphe situla* (Linnaeus, 1758): Probable Leopard Snake

Pleistocene Localities

Greece: Middle Pleistocene—3; Upper Pleistocene—1, 3, ; “Upper Quaternary”—1.

The leopard snake is a relatively small-sized, rather slender rat snake with a pattern of dark-edged blotches of brown to reddish-brown that remind one of

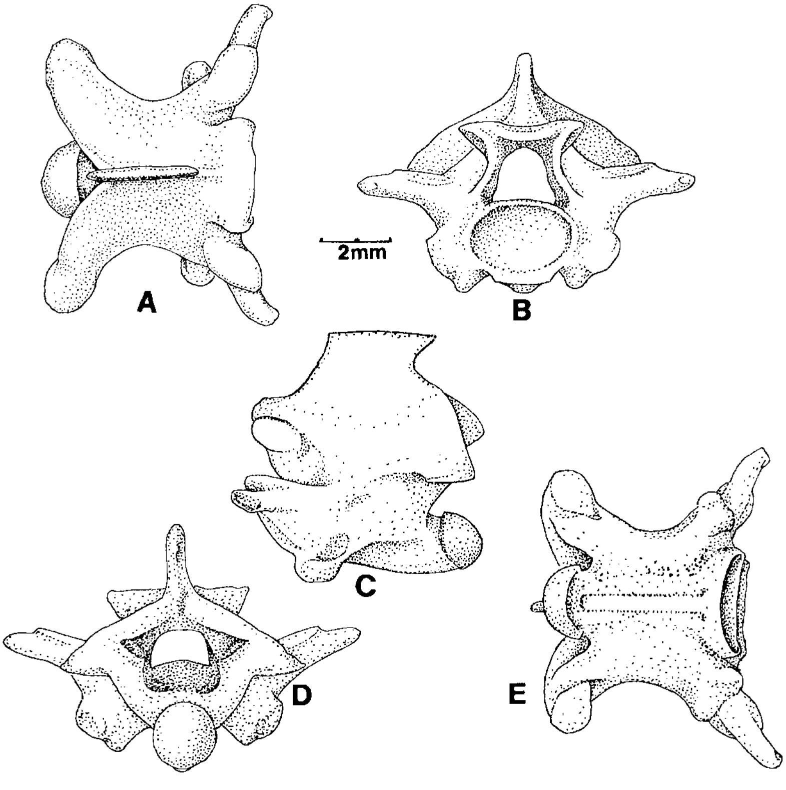

FIGURE 34. Trunk vertebra of modern *Elaphe scalaris* from Europe. (A) Dorsal; (B) anterior; (C) lateral; (D) posterior; (E) ventral. The scale bar applies to all views. [Drawing by Teresa Petersen]

the American corn snake (*Elaphe guttata*). *Elaphe situla* presently occurs in the southern and western Balkans, southern Italy, parts of Sicily, some Aegean islands, Malta, and into southern Crimea, Asia Minor, and the Caucasus. The leopard snake is mainly a ground snake that is often found in sunny, edge situations but that occasionally is found near marshes or streams. Its food consists mainly of small rodents, which it kills by constriction.

Identification of Pleistocene Fossils

Diagnostic vertebral characters for *Elaphe situla*, modified from Szyndlar (1991b), are as follows. The main differences between the vertebrae of *Elaphe situla* and those of other small-sized European colubrines are that the prezygapophyseal processes of *Elaphe situla* are very short and sharply pointed and that the central lobe of the anterior edge of the zygosphene is triangle shaped. Moreover, the trunk vertebrae are shorter (Szyndlar, 1991b, fig. 20) in *Elaphe situla* than in other small European colubrine snakes.

Genus *Malpolon* Fitzinger, 1826: Montpellier Snakes

The genus *Malpolon* is considered monotypic here; thus, the description of the genus here applies to the single species *Malpolon monspessulanus*. A second species, *Malpolen moilensis*, from Africa, has sometimes been recognized, but Szyndlar (1991b) reports that this form shows a completely different morphology in its skull and vertebrae and most likely does not represent the genus *Malpolon*. Montpellier snakes are very large (some reach about 200 cm in total length), distinctive, smooth-scaled snakes that tend to have a uniform body color, often olive-gray, and distinctive ridges over the eyes. At present they occur in most of Iberia and the Mediterranean coast of France, are absent from most of peninsular Italy, and pick up their distribution in the eastern Adriatic coast and the southern Balkans; they also occur on some Greek islands. They occur in the western Caspian region and in southwestern Asia.

This snake is a swift terrestrial species that is usually found in warm, dry habitats with shrubby plant growth, where it may retreat. Its food is said to consist mainly of lizards, with small mammals being taken up to the size of young rabbits. Montpellier snakes have well-developed rear fangs that they use to kill their prey. For this to occur, the prey must be taken so that the venom can be worked into the prey from the back of the snake's mouth.

Problematic Taxa

**Palaeomalpolon borealis* Szyndlar, 1981 was described from the Middle Pleistocene Kozi Grzbiet site in Poland (Poland: Lower Pleistocene Site 3). It was described on the basis of a parasphenoid that had its basispterygoid processes strongly projecting laterally and widely separated from each other. Moreover, the medial part of the basipterygoid process was directed posteriorly and lacked a median-ventral ridge. By 1984 Szyndlar thought this genus should be relegated to the genus *Natrix* (Rage, 1984c), but Rage cautioned that the orientation of the basisterygoid process might support recognition at the generic level and that the generic status of the taxon was open to question. I have found that such characters on the basispterygoid are often quite variable within species of the Colubridae, and I suggest that the type material belongs to a living colubrid taxon. Nevertheless, I am not able to judge whether it represents *Malpolon* or some other living genus.

Identification of Pleistocene Fossils

Diagnostic vertebral characters of *Malpolon monspessulanus*, modified from Szyndlar (1991b), are as follows. The vertebrae may be distinguished from other large western palearctic colubrines on the basis of having a thin and sharp hemal keel (Fig. 35C) that only weakly widens anterior to the condyle. In adults, the anterior edge of the zygosphene is usually straight. The trunk vertebrae are longer than any other large-sized colubrine except *Coluber caspius*.

Malpolon monspessulanus (Hermann, 1804): Montpellier Snake

Pleistocene Localities

France: Middle Pleistocene—4; Upper Pleistocene—8; Pleistocene undesignated—1.
Spain: Middle Pleistocene—8.

Malpolon cf. *Malpolon monspessulanus*: Probable Montpellier Snake

Pleistocene Localities

France: Middle Pleistocene—9.

Subfamily Natricinae Bonaparte, 1840

Water Snakes and Allies

All of the trunk vertebrae of the subfamily Natricinae have prominent structures called hypapophyses (Fig. 26C,D) that project ventrally from the bottom of the centrum. Hypapophyses occur in the family Viperidae and Elapidae but are lacking in *Coronella* and the subfamily Colubrinae.

Genus *Natrix* Laurenti, 1768: Grass Snakes and Water Snakes

The genus *Natrix* contains a group of moderately stout-bodied snakes with strongly keeled scales. Three modern species, *Natrix maura*, *Natrix tesselata*, and *Natrix natrix*, all presently living within the area covered by this book, are recognized. The genus is widely distributed in Europe and southwestern and central Asia and also occurs in North Africa. Two species of the genus, *N. maura* and *N. tesselata* are aquatic, and the third, *N. natrix*, spends most of its time on land.

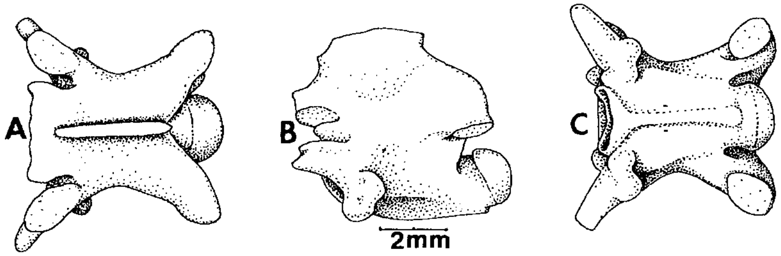

FIGURE 35. Trunk vertebra of *Malpolon* sp. from the Upper Pliocene of Tourkobounia 1 Site, Greece. (A) Dorsal; (B) lateral; (C) ventral. The scale bar applies to all views. [Redrawn by Teresa Petersen from a drawing by Z. Szyndlar, 1991b, with his kind permission]

The trunk vertebrae of all three species of *Natrix* may be distinguished from those of species of *Vipera* (another snake genus that bears hypapophyses on its trunk vertebrae; see Fig. 26E) on the basis that the vertebrae of *Natrix* (Fig. 26C,D) have shorter, more robust hypapophyses.

Problematic Taxa

**Natrix rusticus* Brunner, 1957 was described on the basis of an incomplete dentary from Breitenberg Cave near Gössweinstein, Bavaria, Germany (Germany: Middle Pleistocene Site 2). According to Brunner (1957), the teeth of *Natrix rusticus* were stouter than those of *Natrix natrix*. This character is a very poor one on which to base the naming of a new species. In fact, Młynarski (1961) stated that the teeth of **Natrix rusticus* are identical to those of several living Colubridae. Rage (1984c) considers **Natrix rusticus* to be a *nomen dubium*. I suggest that the dentary merely be listed as "Colubridae indeterminate" in future publications.

Natrix sp. indet.: Indeterminate Grass or Water Snake

Pleistocene Localities

Britain: Middle Pleistocene—3, 4, 5, 7, 12; Upper Pleistocene—10.
France: Middle Pleistocene—4; Upper Pleistocene—4, 11.
Spain: Middle Pleistocene—2.
Germany: Middle Pleistocene—13; Upper Pleistocene—6; Upper Pleistocene and Holocene—2.
Poland: Lower Pleistocene—4.
Czech Republic: Lower Pleistocene—2, 3.
Italy: Middle Pleistocene—9; Upper Pleistocene—7.
Croatia: Upper Pleistocene—5.
Greece: Lower Pleistocene—2; Middle Pleistocene—2, 3, 4; Upper Pleistocene—5; "Upper Quaternary"—1.

Natrix maura (Linnaeus, 1758): Viperine Snake

Pleistocene Locality

France: Upper Pleistocene—5.

Natrix maura is an aquatic snake that inhabits western Europe, whereas *Natrix tesselata*, another aquatic species, occurs in eastern Europe into central Asia. *Natrix maura* is a medium-sized snake with a robust body and two rows of dark blotches down the back. Its head is boldly marked with bars and blotches, in contrast to the mainly unmarked head of *Natrix tesselata*. At present, *Natrix maura* occurs in Iberia, southern France, southwestern Sweden, northwestern Italy, the Balearic Islands, Sardinia, and northwestern Africa. *Natrix maura* prefers ponds and streams with ample aquatic vegetation and feeds mainly on amphibians.

Identification of Pleistocene Fossils

It is very difficult to distinguish *Natrix maura* (Fig. 36E) from *Natrix tesselata* (Fig. 26D) on the basis of individual vertebrae, but Szyndlar (1984) has shown that both of these species may be separated from the grass snake, *Natrix natrix*, on the basis of individual trunk vertebrae. In both *Natrix maura* (Fig. 36E) and *Natrix tesselata* (Fig. 26D), the hypapophysis is pointed at the distal end and the parapophyseal processes are slender, whereas in *Natrix natrix* (Figs. 26C and 36C) the parapophyseal processes are strongly built and the hypapophysis is usually obtuse distally, I have added the word "usually" in the sentence above as I have found some variation of this character in *Natrix natrix*.

Natrix maura (Linnaeus, 1758) or *Natrix tesselata* (Laurenti, 1768): Viperine Snake or Dice Snake

Pleistocene Localities

Britain: Middle Pleistocene—4, 5; Upper Pleistocene—10.

The extralimital occurrence of aquatic *Natrix* in Britain is addressed in Chapter 7.

Natrix tesselata (Laurenti, 1768): Dice Snake

Pleistocene Localities

Germany: Upper Pleistocene and Holocene—2, 3, 45.
Croatia: Upper Pleistocene—5.

The dice snake has a more eastern distribution than the viperine snake, *Natrix maura*, occurring mainly in the Balkans and Italy north to southern Switzerland, eastern Austria, the Czech Republic, and eastward into southwestern and central Asia. The dice snake is more aquatic than the viperine snake, *N. maura*, and may stay submerged for long periods of time. It mainly feeds on fishes.

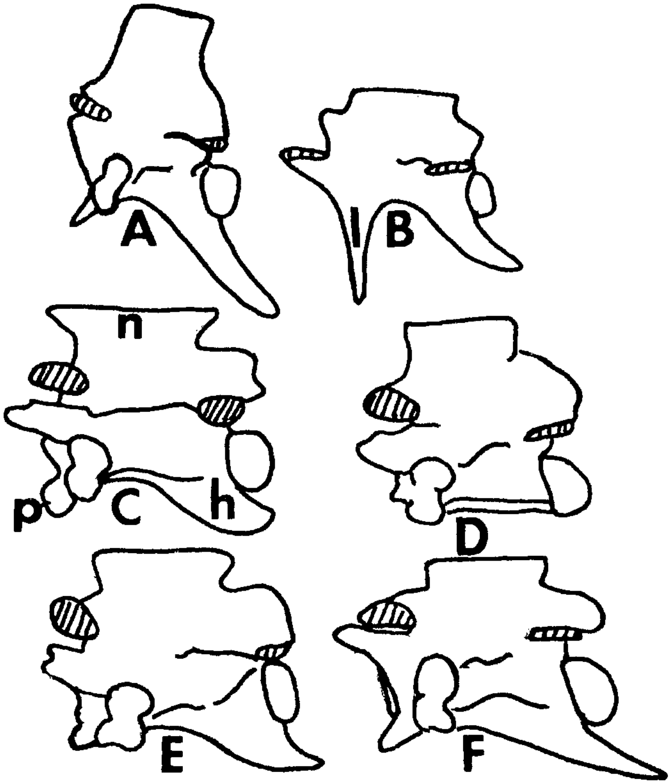

FIGURE 36. Outline drawings of various snake vertebrae in lateral view. (A) generalized cervical vertebra; (B) generalized caudal vertebra; (C) trunk vertebra of *Natrix natrix*; (D) trunk vertebra of *Elaphe longissima*; (E) trunk vertebra of *Natrix maura*; (F) trunk vertebra of *Vipera berus*. h = hypapophysis; l = lymphopophysis; p = parapophyseal process. [Drawings by the author]

Natrix cf. *Natrix tesselata*: Probable Dice Snake

Pleistocene Localities

Poland: Lower Pleistocene—4.
Czech Republic: Lower Pleistocene—3.
Greece: Middle Pleistocene—3; Upper Pleistocene—2.

Natrix natrix (Linnaeus, 1758): Grass Snake

Pleistocene Localities

Britain: Middle Pleistocene—3, 4, 5, 7, 8, 9, 10, 12; Upper Pleistocene—6, 9, 10, 11, 14; Pleistocene undesignated—1, 4.
Netherlands: Middle Pleistocene—2.

Germany: Middle Pleistocene—1, 3, 13, 14; Upper Pleistocene—2, 3, 10, 25; Upper Pleistocene and Holocene—1, 2, 3, 4, 5.
Austria: Middle Pleistocene—1, 2.
Poland: Lower Pleistocene—1, 2, 3, 4, 5; Upper Pleistocene—8, 10, 14; Upper Pleistocene and Holocene—1.
Czech Republic: Lower Pleistocene—2, 3.
Croatia: Upper Pleistocene—5.
Serbia: Upper Pleistocene and Holocene—1.

The grass snake (see Fig. 40) is a rather large, thick-bodied snake with keeled scales. The color of these snakes is quite variable, but there is usually a yellow collar with a black border that occurs just behind the head. This snake occurs in nearly all of Europe, ranging north to near the arctic circle in Scandinavia and extending eastward to Lake Baikal. It also occurs in northwestern Africa. This snake is diurnal and largely terrestrial, although it is sometimes seen swimming in the water. It normally prefers moist habitats over dry ones, as its main food consists of frogs and toads. *Natrix natrix* is the only snake that has been found in a Pleistocene glacial site in Britain.

Identification of Pleistocene Fossils

The trunk vertebrae of *Natrix natrix* are robust and rather elongate (Figs. 26C and 37). They have a relatively low, long, neural spines and the neural arch is moderately depressed. The hypapophysis is relatively short and robust and tends to have its tip obtuse or truncated, rather than pointed as in *Natrix maura* and *Natrix tesselata*. The synapophyses are prominent, and the parapophyseal process is strongly built rather than somewhat weakly built as in *N. maura* and *N. tesselata*. Szyndlor (1991a) has provided some cranial characters of *Natrix natrix*.

Natrix cf. *Natrix natrix*: Probable Grass Snake

Pleistocene Localities

Britain: Upper Pleistocene—4.
France: Middle Pleistocene—6, 7.
Germany: Upper Pleistocene—4, 7, 9, 27; Middle Pleistocene—20; Pleistocene undesignated—3.

cf. *Natrix natrix*: Probable Grass Snake

Pleistocene Locality

Britain: Middle Pleistocene—10.

(?) Family Elapidae Boie, 1827
Elapid Snakes

Elapid snakes are deadly poisonous snakes with permanently erect fangs that occur on the ends of the maxillary bones. All of them have hypapophyses on the trunk vertebrae. At present, they have a very wide distribution in both the

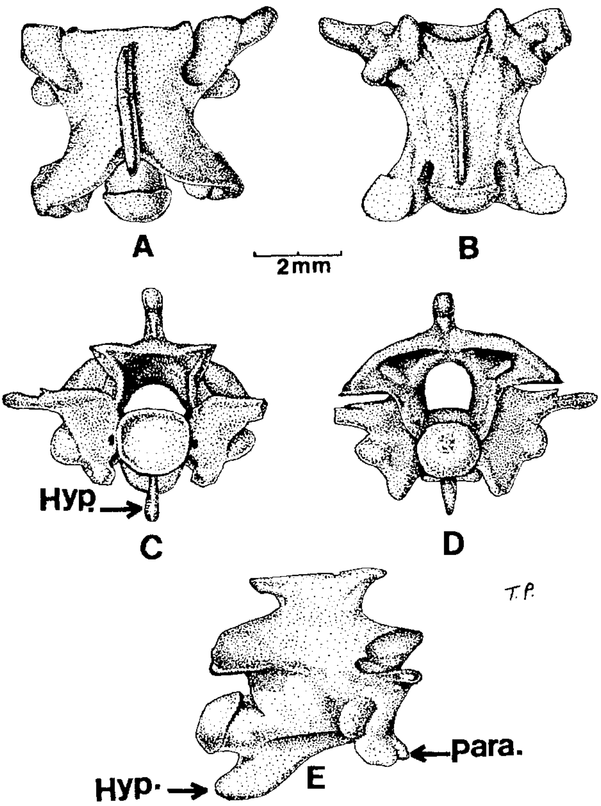

FIGURE 37. Trunk vertebra of *Natrix natrix* from the Upper Pleistocene Shropham (interglacial stratum) Site, Norfolk, England. (A) Dorsal; (B) ventral; (C) anterior; (D) posterior; (E) lateral. Hyp. = hypapophysis; Para. = parapophyseal process. [Drawing by Teresa Petersen in Holman, 1996]

Old and the New World, mainly in warm and tropical areas, but none of them occur in Britain and Europe. Invalid Pleistocene records of the cobra genus *Naja* occur within the region.

Genus *Naja* Laurenti, 1768: Cobras

Problematic Taxa

**Naja sauvagei* Rochebrune, 1880 was described on the basis of an anterior trunk vertebra from the Middle Pleistocene of Coudes, Puy-de-Dome, France (France Middle Pleistocene Site 3). Hoffstetter (1938) stated that *Naja sauvagei* was uncontestably a colubrid, and Rage (1984c) examined the type specimen and found that it belonged to that of a recent colubrid snake. It is difficult to assign this vertebra to any living genus of Colubridae because the specimen came from a juvenile individual. Nevertheless, Rage (1984c) suggests that it perhaps represents the genus *Natrix*.

"*Naja*" sp.: ?Natricine

Pleistocene Locality
Greece: Middle Pleistocene—1.

Schneider (1975) reported vertebrae of *Naja* sp. from the Middle Pleistocene of the island of Chios, Greece. Szyndlar (1991c) states that the description does not demonstrate that these vertebrae belong to *Naja* and that the trunk vertebra figured by Schneider (1975, fig. 3b) displays natricine rather than elapid morphology. I suggest that this record be referred to as cf. Natricinae indet. in future publications until the material is reexamined.

Family Viperidae Oppel, 1811

Vipers

Viperids are deadly poisonous snakes that often have triangular heads and are characterized by the fact that each of the shortened, square-shaped maxillary bones bears a single functional, tubular fang (with replacement teeth behind). The elongated ectopterygoid bone acts as a lever to erect or depress these fangs. The trunk vertebrae of viperids have very well-developed hypapophyses (Fig. 26E). There are more than 20 genera and more than 150 species currently recognized (Zug, 1993). All of the fossil species of the Viperidae belong to living genera. Viperids are generally worldwide in distribution except for very cold areas and occur on all of the continents but Australia. There are also no viperids on the island of Madagascar.

In general, viperids are very stout-bodied snakes that use their potent venom to kill warm-blooded prey. They are mainly terrestrial ground-dwelling forms, but some arboreal vipers occur in the New World tropics.

Osteological characters for the family, modified from Rage (1984c), are: maxilla shortened anteroposteriorly and elongate dorsoventrally, bearing only tubular teeth and hinged so that fangs may be erected and depressed; ectopterygoid elongate and slanting posteriorly; and hypapophyses present on all trunk vertebrae, all of which have quite large cotyles and condyles.

Genus *Vipera* Laurenti, 1768: Sand Vipers

The vipers of the genus *Vipera* are, in general, heavy-bodied snakes with a triangular head. The dorsal body scales are strongly keeled. About 20 modern species are recognized (Frank and Ramus, 1995). Several extinct Miocene and Pliocene species of *Vipera* are recognized (Rage, 1984c; Szyndlar, 1991c). Snakes of the genus *Vipera* occur in Europe and into Asia except for very cold places; they also range south into Africa. They are absent from Ireland. The species of the genus *Vipera* are mainly ground-dwelling forms that feed on small, warm-blooded prey. Several species occur in very sandy areas.

Szyndlar (1991c) has discussed the identification of isolated vertebrae of *Vipera*. He reports that the identification of isolated vertebrae to particular species complexes of the genus is usually easily accomplished. Vertebrae of the so-called Oriental vipers are larger and shorter than those of the European species. Of the European vipers, the *Vipera berus* group (*V. berus* and *V. ursinii*) may be differentiated from the *Vipera aspis* group (*V. ammodytes*, *V. aspis*, and *V. latastei*) on the basis of having longer cervical vertebrae (Fig. 38) with with lower neural spines and shorter hypapophyses.

Vipera sp. indet.: Indeterminate Sand Vipers

Pleistocene Localities

France: Lower Pleistocene—4; Middle Pleistocene—1; Upper Pleistocene—5, 8, 9.
Spain: Middle Pleistocene—8.
Germany : Middle Pleistocene—16; Pleistocene undesignated—6; Upper Pleistocene and Holocene—3.
Czech Republic: Lower Pleistocene—2, 3.
Croatia: Middle Pleistocene—1.

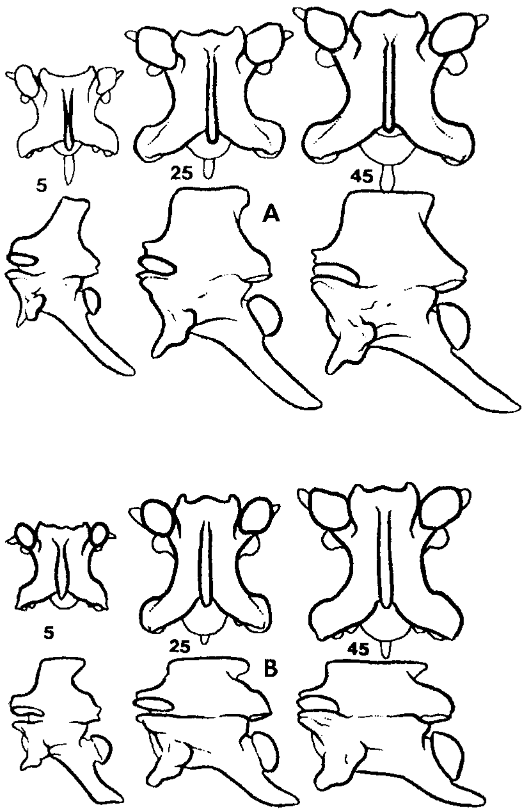

FIGURE 38. Cervical vertebrae 5, 25, and 45 in *Vipera ammodytes* (A) compared with those of *Vipera berus* (B). In both A and B the upper rows of vertebrae are in dorsal view and the lower rows are in lateral view. [From Z. Szyndlar, 1984, used with his kind permission]

Oriental Viper Group

Vipera sp.: Oriental Viper Group Indeterminate Species

Pleistocene Locality
Greece: Middle Pleistocene—1.

The extralimital occurrence of an Oriental viper in Greece is noteworthy.

Vipera aspis Group

Vipera (*aspis*) sp.: *Vipera aspis* Species Group Member Indeterminate

Pleistocene Localities
France: Middle Pleistocene—4; Upper Pleistocene—4, 5.

Vipera ammodytes (Linnaeus, 1758): Eastern Nose-Horned Viper

Pleistocene Localities
Czech Republic: Lower Pleistocene—2.
Serbia: Upper Pleistocene and Holocene—1.

Vipera ammodytes is a rather stout-bodied snake with a distinct nose horn. The species presently occurs in eastern Europe. *Vipera latastei*, another nose-horned viper, presently occurs in western Europe and is separated from *Vipera ammodytes* by a wide geographic gap. *Vipera ammodytes* presently occurs mainly in the Balkans and north to northeastern Italy, southern Austria, and southwestern and southeastern Romainia; it also extends into southwestern Asia. Its favorite habitat appears to be rocky areas exposed to the sun. The extralimital occurrence of this species in the Pleistocene of the Czech Republic is addressed in Chapter 7.

Identification of Pleistocene Fossils
Vipera ammodytes is in the *Vipera aspis* group of vipers; thus, it has shorter cervical vertebrae (Fig. 38A) with higher neural spines and longer hypapophyses than in the *Vipera berus* group (Fig. 38B). *Vipera ammodytes* may easily be separated from *V. aspis* on the basis that *Vipera ammodytes* has cervical vertebrae (Fig. 38A) with much longer neural spines and much higher hypapophyses than in *V. aspis*. But it is difficult to distinguish between the trunk vertebrae of the two species (Szyndlar, 1984).

Vipera cf. *Vipera ammodytes*: Probable Eastern Nose-Horned Viper

Pleistocene Localities

Czech Republic: Lower Pleistocene—3.
Greece: Middle Pleistocene—3.

Vipera cf. *Vipera aspis* (Linnaeus, 1758): Probable Asp Viper

Pleistocene Locality

France: Middle Pleistocene—4.

Vipera aspis is quite variable in coloration and pattern but may be identified in that, though it has an upturned rostrum, it lacks a nose horn. At present this species occurs in western and central Europe east into southwestern Germany, Switzerland, and Italy south to Sicily. The asp viper presently occurs in dry habitats, especially on open hillsides.

Identification of Pleistocene Fossils

See the account of *Vipera ammodytes* above.

Vipera latastei Bosca, 1878: Lataste's Western Nose-Horned Viper

Pleistocene Locality

Spain: Middle and Upper Pleistocene—1.

Vipera latastei, another nose-horned viper, currently occurs in western Europe and is geographically separated from *Vipera ammodytes* by a wide gap. The range of *Vipera latastei* presently comprises the Iberian Peninsula except for the extreme northern part as well as northwestern Africa. This species occurs in rather dry, open, sometimes sandy areas, where it mainly feeds on small mammals.

Identification of Pleistocene Fossils

Vipera latastei is also in the *Vipera aspis* group of vipers and thus may be separated from the *Vipera berus* group on the basis of having shorter vertebrae with higher neural spines and longer hypapophyses. I am not aware of any detailed studies that distinguish *Vipera latastei* from other species in the *Vipera aspis* group.

Vipera berus Group

Vipera berus (Linnaeus, 1758): Adder

Pleistocene Localities

Britain: Middle Pleistocene—4, 5, 11, 12; Pleistocene and Holocene—1.
Germany: Middle Pleistocene—3; Upper Pleistocene—2, 3, 11; Upper Pleistocene and Holocene—1, 3, 4, 5.
Austria: Middle Pleistocene—2.
Poland: Lower Pleistocene—1, 2, 3, 4, 5; Upper Pleistocene—2, 7, 8; Upper Pleistocene and Holocene—1.
Czech Republic: Lower Pleistocene—2.
Serbia: Upper Pleistocene and Holocene—1.

The adder, *Vipera berus*, lacks a nose horn, usually has several large scales on the top of the head, and usually has a clearly visible zigzag stripe down the back. At present the adder occurs in much of Europe, where it extends north to beyond the arctic circle and southward to northwestern Spain, northern Italy, and much of the northern Balkans; it extends across the former Soviet Union to the Pacific coast. Adders occur in a very wide variety of habitats and extend up to about 3000 m in the Alps. The food consists mainly of small mammals.

Identification of Pleistocene Fossils

Characters that differentiate the vertebrae of the *Vipera berus* group from the *Vipera aspis* group are given in the genus *Vipera* account. Szyndlar (1984), who gives a detailed account of the morphology of the vertebrae of *Vipera berus*, reports that the precaudal of *Vipera berus* and the closely related *Vipera ursinii* are very similar, but some minor differences were found in the caudal vertebrae. A vertebra of *Vipera berus* from the Middle Pleistocene of the Cudmore Grove Site, Essex, England is illustrated in Figure 39.

Vipera cf. *Vipera berus*: Probable Adder

Pleistocene Localities

Germany: Middle Pleistocene—7; Upper Pleistocene—27.

Vipera cf. *Vipera ursinii*: Probable Orsini's Viper

Pleistocene Localities

France: Middle Pleistocene—4.
Czech Republic: Lower Pleistocene—3.

Vipera ursinii of the *Vipera berus* species group is the smallest European viper and often has a roughened appearance. It lacks the upturned snout of the

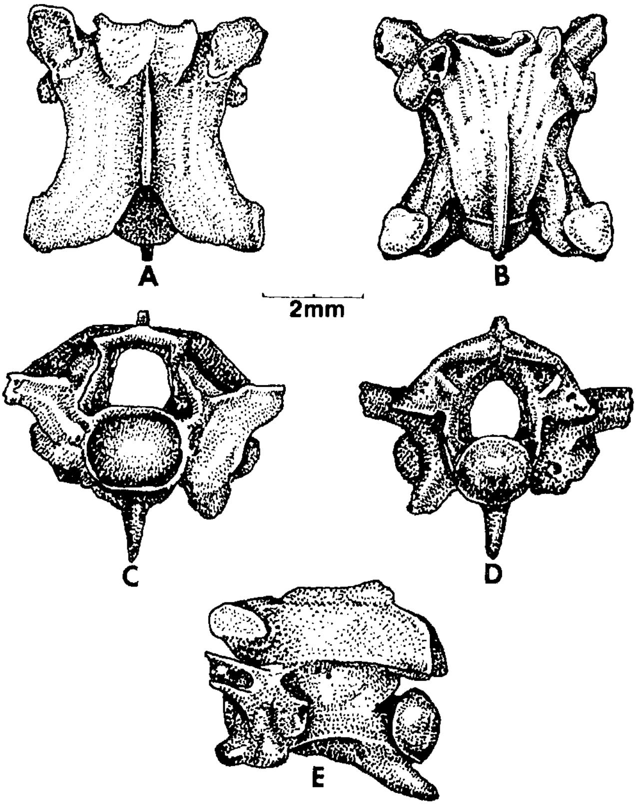

FIGURE 39. Trunk vertebra of *Vipera berus* from the Middle Pleistocene Cudmore Grove Site, Essex, England. (A) Dorsal; (B) ventral; (C) anterior; (D) posterior; (E) lateral. The scale bar applies to all views. [Drawing by Rosemarie Attilio in Holman et al., 1990]

Vipera aspis species group and differs from its close relative *Vipera berus* in having a narrower head and a more tapering rostrum. At present *Vipera ursinii* occurs in isolated areas in southeastern France as well as in central Italy, eastern Austria, the Balkan countries, and into Asia Minor and Iran. In some areas in Europe this species is principally a montane species, while in other areas it may inhabit lowland meadows or marshes. The extralimital occurrence of this species in the Czech Republic is addressed in Chapter 7.

Identification of Pleistocene Fossils

See the account of *Vipera berus* above.

Vipera (*berus*) sp.: *Vipera berus* Species Group Member Indeterminate

Pleistocene Localities
France: Middle Pleistocene—4, 7.
Greece: Lower Pleistocene—1, 2; Middle Pleistocene—3.

5

PLEISTOCENE HERPETOLOGICAL LOCALITIES

Localities in countries in the Geographic Divisions below are numbered to correspond with those in the taxonomic accounts in Chapter 4. Figure 40 is an artists concept of some Pleistocene herpetological species and extinct mammals at the Shropham Pit Locality (Interglacial Component), Norfolk, England (Britain: Upper Pleistocene Site 10).

Geographic Divisions

Countries are arranged in divisions from west to east, and from north to south when possible. Oceanic islands are listed under the country to which they belong. Malta is included with Italy because of its important Pleistocene herpetofauna and proximity to Sicily and Italy.

I. Northwest Division: Ireland and Britain, p. 130
II. French Division: France and Monaco, p. 142
III. Southwest Division: Spain, p. 149
IV. Northcentral Division: Netherlands, Belgium, Luxembourg, Germany, Austria, and Switzerland, p. 157
V. Northeast Division: Poland and the Czech Republic, p. 175
VI. Southeast Division: Italy, Hungary, Yugoslavia: (Croatia, Bosnia, Serbia), and Greece, p. 182

Division I: Ireland and Britain

Ireland

Pleistocene herpetofaunal records in Ireland are rare and consist mainly of records of *Rana temporaria*. More work needs to be done in this critical area for

FIGURE 40. Artist's concept of the quiet pool that existed at the Shropham Site, Norfolk, England during the Upper Pleistocene (Ipswichian) last interglacial age. A grass snake (*Natrix natrix*) is in the lower left corner. A common frog (*Rana temporaria*) sits in front of the snake. A European pond tortoise (*Emys orbicularis*) basks on a log in the right corner. A hippopotamus is in the water in the upper left, and a hyaena lurks on the shore in the upper right. [Drawing by Teresa Petersen in Holman, 1996]

the study of the fragmentation of ranges of herpetological species in the Pleistocene.

Pleistocene Undesignated

1. Alice and Gwendoline Caves, County Clare, Ireland

Taxon. *Rana temporaria.*

References. Sanchiz (in press), Scharff (1904).

2. Edenvale Catacombs, County Clare, Ireland

Taxon. *Rana temporaria.*

References. Sanchiz (in press), Scharff (1904), Sutcliffe and Kowalski (1976).

3. Kesh Cave, County Sligo, Ireland

Taxon. *Rana temporaria.*

References. Sanchiz (in press), Scharff et al. (1903), Sutcliffe and Kowalski (1976).

4. Newhall-Barntick, County Clare, Ireland

Taxon. *Rana temporaria.*

References. Sanchiz (in press), Scharff (1904).

Britain

The Pleistocene herpetofauna of Great Britain, which is known almost entirely on the basis of sites in England, has become moderately well documented by studies that began in the early 1980's. Only Middle and Upper Pleistocene herpetological localities are documented. Figure 41 indicates the location of important Pleistocene herpetological sites in Britain.

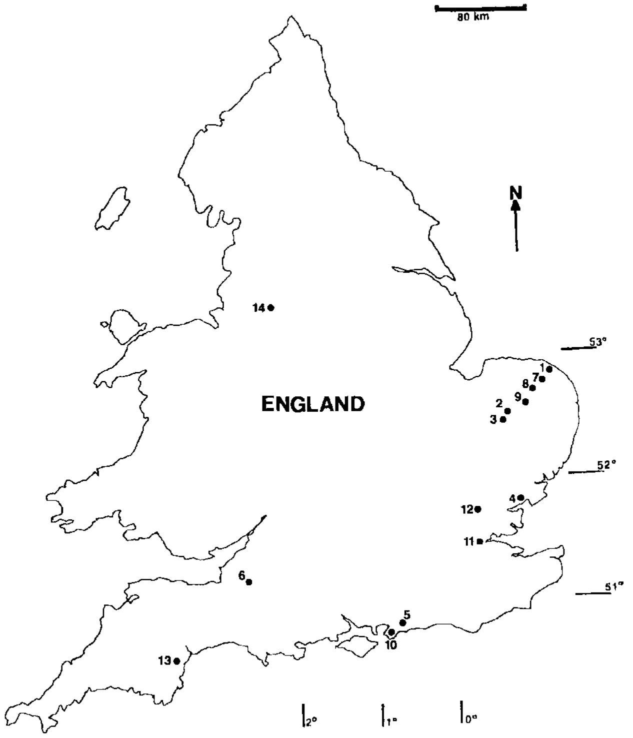

FIGURE 41. Location map of important Pleistocene herpetological sites in Britain. Middle Pleistocene Temperate: (1) West Runton, Norfolk; (2) East Farm, Barnham, Suffolk; (3) Beeches Pit, Suffolk; (4) Cudmore Grove, Essex; (5) Boxgrove, West Sussex; (6) Westbury–Sub-Mendip, Somerset. Upper Pleistocene Temperate: (7) Itteringham Pit, Norfolk; (8) Swanton Morely, Norfolk; (9) Shropham (interglacial beds), Norfolk; (10) Selsey, West Sussex. Upper Pleistocene Glacial: (9) Shropham (Devensian pocket), Norfolk; (11) Baker's Hole, Kent; (12) Nazeing, Essex; (13) Tornewton Cave, Devon. Pleistocene/Holocene Boundary: (14) Whitemoor Channel, West Cheshire.

Middle Pleistocene

1. Barnfield Pit, Swanscombe, Kent, England

Taxon. *Bufo bufo*..

References. Bridgland (1994), Holman (1987a), Kerney (1971), Roberts et al. (1995).

Remarks. The Barnfield Pit, Swanscombe, Kent, is the best known of all British Palaeolithic sites (Roberts et al., 1995). It has been shown that the Swanscombe sediments represent a single, gross upward fining sedimentary fill that terminates in periglacial sedimentation and that the lower sediments of the site represent the first warm event after the Anglian Glacial (Bridgland, 1994). Thus, the site is considered to belong to the Hoxnian stage and to be equivalent to the Dutch/European Holsteinian Sequence (Roberts et al., 1995).

The site is best known for its refitted human skull that was recovered from the Upper Middle Gravel layer. The skull is believed to be a female and has two features that indicate Neanderthal affinities.

Holman (1987a) reported the occurrence of a common toad (*Bufo bufo*) at the site. The specimen consisted of the posterior portion of an appendicular skeleton embedded in sand and was not placed in specific context within the sediments.

The habits of the common toad, *Bufo bufo*, are so ubiquitous that it is difficult to suggest any specific habitat based on this fossil occurrence, except that the presence of a low-energy aquatic situation would be necessary for the toad to breed. An aquatic situation at the site is suggested by the presence of pike (*Esox lucius*), shoveler (*Anas clypeata*), and red-breasted merganser (*Mergus serrator*); Stuart (1982).

2. Beeches Pit, West Stow, Suffolk, England

Taxa. *Triturus* sp., *Rana* sp., *Anguis fragilis*, *Elaphe longissima*.

References. Holman (1994), Preece et al. (1991), Roberts et al. (1995).

Remarks. The Beeches Pit lies in an abandoned brickyard near West Stow, Suffolk. A preliminary report (Preece et al., 1991) discussed its remarkable mollusk faunas as well as its fishes and 12 species of mammals. Both the mollusks and mammals suggest a late Middle Pleistocene age and a temperate climate. The site is considered to represent the Hoxnian interglacial stage and to be equivalent to the Dutch/European Holsteinian sequence (Roberts et al., 1995).

The most important herpetological record from this site is that of the extralimital species *Elaphe longissima*, which suggests not only a temperate climate but, based on the present habits of the snake, also the presence of a rather dry, sunny habitat near the locality.

3. Boxgrove, West Sussex, England

Taxa. *Triturus helveticus* or *vulgaris*, *Triturus vulgaris*, *Triturus* sp., *Pelobates fuscus*, *Bufo bufo*, *Bufo calamita*, *Bufo* sp., *Rana arvalis*, *Rana temporaria*, *Rana* sp. *Anguis fragilis*, *Lacerta* cf. *Lacerta vivipara*, *Natrix natrix*, *Natrix* sp.

References: Holman (1992b, 1993a), Kolfschoten and Turner (1996), Roberts et al. (1995).

Remarks. The Boxgrove site occurs at Amey's Eartham Pit, Boxgrove, West Sussex, and is a Middle Pleistocene site that is correlated with the Interglacial IV stage of the Cromerian Complex of the Dutch/European sequence (Roberts et al., 1995). Kolfschoten and Turner (1996) correlated the Boxgrove site with the Miesenheim I Site in Germany, a locality that is discussed further below.

Boxgrove is one of the most interesting Pleistocene sites in the British and European area because human artifacts and skeletal material suggest that it is the earliest human occupational site in Europe (Roberts et al., 1995) and that this occupation occurred about 500,000 years ago. Based on osteological material, the early colonizers are provisionally assigned to *Homo* cf. *Homo heidelbergensis*.

All of the herpetological species are extant forms, and seven of the nine occur natively in Britain today. Two amphibians, *Pelobates fuscus* and *Rana arvalis*, are extralimital continental forms. The presently endangered species *Bufo calamita* is another important taxon recorded from the site.

Most of the herpetological species of the Boxgrove site are so small that procuring them for food might have been a waste of energy for ancient humans. The species most likely to have been eaten from time to time are probably the common frog, *Rana temporaria*, and perhaps the moor frog, *Rana arvalis*. These species could have been caught in large numbers during the breeding season.

4. Cudmore Grove, Mersea Island, Essex, England

Taxa. *Triturus cristatus*, *Triturus vulgaris*, *Triturus* sp., *Bufo bufo*, *Hyla* sp., *Rana arvalis*, *Rana* (*ridibunda*) sp., *Rana* sp., *Emys orbicularis*, *Lacerta* sp., *Anguis fragilis*, *Elaphe longissima*, *Natrix maura* or *tesselata*, *Natrix natrix*, *Natrix* sp., *Vipera berus*.

References. Holman (1991, 1993a), Holman et al. (1990).

Remarks. The Cudmore Grove Site, Mersea Island, Essex, has yielded the second largest Pleistocene herpetofauna in England and one of the largest in the geographic area covered by this book. The deposit is of freshwater, estuarine origin and was palynologically dated to Hoxnian Interglacial Substage Ho IIIb (Holman et al., 1990). The reader is advised that Roberts et al. (1995) cautioned that there may have been an overreliance on palynological dates in chronological studies on British Pleistocene sites in the past.

All of the 13 taxa identified at Cudmore Grove are extant. Six of the 13 do not presently occur natively in Britain but are found in continental Europe. These forms are *Hyla* sp., *Rana arvalis*, *Rana* (*ridibunda*) sp., *Emys orbicularis*, *Elaphe longissima*, and *Natrix maura* or *tesselata*. It should be pointed out that *Rana* "*esculenta*" or *ridibunda* and *Rana lessonae*, originally reported from this site (Holman et al., 1990), are here combined under the designation *Rana* (*ridibunda*) sp.

The herpetological taxa suggest a fairly wide range of habitats in the general vicinity of the fossil site. A permanent, fairly large, low-energy body of water is indicated, as well as surrounding damp terrestrial habitats with ample groundcover and at least patches of dense vegetation. *Elaphe longissima* indicates the presence of dry, shrubby or woodland habitats in the vicinity of the site, and

Emys orbicularis, *Elaphe longissima*, and *Natirx maura* or *tesselata* indicate a warmer climate than presently occurs in the area.

5. East Farm, Barnham, Suffolk, England

Taxa. *Triturus cristatus*, *Triturus helveticus*, *Triturus vulgaris*, *Triturus* sp., *Bufo bufo*, *Bufo calamita*, *Bufo viridis*, *Bufo* sp., *Hyla arborea*, *Rana arvalis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Rana* sp., *Emys orbicularis*, *Lacerta* sp., *Anguis fragilis*, *Elaphe longissima*, *Natrix maura* or *tesselata*, *Natrix natrix*, *Natrix* sp., *Vipera berus*.

References. Ashton et al. (1994), Holman (1997), Roberts et al. (1995).

Remarks. The East Farm Barnham site, Suffolk, has yielded by far the largest Pleistocene herpetofauna in Britain and one of the largest known from Europe. Roberts et al. (1995) assigned the East Farm Barnham site to the Hoxnian interglacial stage, which correlates with the Dutch/European Holsteinian sequence. The sediments at Barnham were laid down in a postglacial river system that flowed in a channel that ran through glacial outwash gravel.

The site is important because Acheulian and Clactonian stone biface tools were found in the same context; thus, the Clactonian Industry cannot continue to be viewed as an earlier stratigraphic event than the Acheulian Industry.

Seventeen taxa of amphibians and reptiles were found in silt deposits of the site, along with rich fish and mammalian faunas. All of the species represent living taxa, but seven are extralimital and presently found on the European continent. These are *Bufo viridis*, *Hyla arborea*, *Rana arvalis*, *Rana* (*ridibunda*) sp., *Emys orbicularis*, *Elaphe longissima*, and *Natrix maura* or *tesselata*. The green toad, *Bufo viridis*, is recorded for the first time as a British fossil at this site, and this is the first record *Bufo calamita*, a presently endangered species in Britain, from the Hoxnian. This inland fossil record of the natterjack toad is of considerable interest in that most modern British records of this species are from coastal dunes (Holman and Stuart, 1991). *Hyla arborea* is known only at one other locality in Britain, the West Runton Freshwater Bed Cromerian site (Parfitt, 1997).

This complex of fossil amphibian and reptiles species indicates a rather wide range of habitats. A body of still or slowly moving water, wetlands, damp habitats with low bushes, and finally dry, open habitats are suggested by segments of the herpetofauna.

That wetter habitats gave way to drier ones as sedimentation progressed at the East Farm Barnham site is indicated by the composition of herpetological species at different stratigraphic levels. Moreover, a warmer climate than presently occurs in East Anglia is strongly suggested by several species (e.g., *Bufo viridis*, *Emys orbicularis*, and *Elaphe longissima*).

In contrast to the older Sugworth and West Runton Middle Pleistocene sites (described below in this section), the East Farm Barnham site produced extralimital continental forms of presently more southern latitudes (e.g., *Bufo viridis*, *Emys orbicularis*, *Elaphe longissima*).

6. Halls Pit, Oxfordshire, England

Taxon. *Bufo* sp. or *Rana* sp.

References. Holman (1990a), Stuart (1982).

Remarks. Halls Pit, near Benton, Oxfordshire, England, represents the Anglian cold stage of the Middle Pleistocene. Northern mammals were associated with these anuran remains.

7. Hoxne, Suffolk, England

Taxa. *Bufo bufo*, *Bufo* sp., *Natrix natrix*, *Natrix* sp.

References. Holman (1993b), Roberts et al. (1995).

Remarks. This site (pronounced "Hoxen") is the type site for the Middle Pleistocene Hoxnian interglacial stage of the British Pleistocene, yet Roberts et al. (1995, table 1, p. 166) assigned it questionably to presently unrecognized stages that lie between the Wolstonian cold stage and the Ipswichian warm stage of the Upper Pleistocene. In this book it is included with the Middle Pleistocene, as there is still some evidence that it might represent the conventional Hoxnian interglacial stage (see discussion in Roberts et al., 1995, p. 179).

Holman (1993b) identified *Bufo bufo* and *Natrix natrix* from the Hoxne site, but these species have such ubiquitous habits and such a wide range in Europe today that they do not add much ecological information other than that *Bufo bufo* would need quiet water in which to breed and *Natrix natrix* often hunts for amphibian prey near or in aquatic situations.

8. Ingress Vale, Swanscombe, Kent, England

Taxa. *Bufo* sp. or *Rana* sp., *Emys orbicularis*, *Natrix natrix*.

References. Holman (1987a, 1991), Roberts et al. (1995), Sanchiz (in press), Stuart (1974, 1979, 1982).

Remarks. The Ingress Vale locality at Swanscombe, Kent, represents the Hoxnian interglacial stage and is equivalent to the Dutch/European Holsteinian sequence (Roberts et al., 1995). Stuart (1982) recognizes this as a locality separate from Barnfield Pit at Swanscombe. The most important herpetological fossil at this site is *Emys orbicularis*, an extralimital continental form that indicates a mild climate at the time of the deposition of the bones.

9. Little Oakley, Essex, England

Taxa. *Rana arvalis*, *Rana* sp., *Emys orbicularis*, *Natrix natrix*.

References. Holman (1991, 1993a), Lister et al. (1990).

Remarks. The Little Oakley site is considered temporally equivalent to the Boxgrove and Westbury sites (Holman, 1993a) and thus belongs in the late Cromerian interglacial stage (Cromerian IV of the Dutch/European sequence). The presence of *Emys orbicularis* indicates a permanent, low-energy body of water with an abundance of aquatic vegetation. *Rana arvalis* and *Natrix natrix* indicate a moist terrestrial habitat.

10. Sugworth, Near Oxford, Berkshire, England

Taxa. Anura indet., *Bufo* sp. or *Rana* sp., *Rana arvalis*, *Rana* sp., cf. *Natrix natrix*.

References. Holman (1987c, 1991, 1993a), Stuart (1980), Kolfschoten and Turner (1996).

Remarks. The Sugworth site is thought to be temporally equivalent to the West Runton Freshwater Bed (Holman, 1993a) and thus to represent the British Cromerian interglacial age that correlates with the Dutch/European Cromerian

II sequence (Kolfschoten and Turner, 1996). *Rana arvalis* is an extralimital member of the fauna that presently occurs on the European continent.

11. West Runton Freshwater Bed, West Runton, Norfolk, England

Taxa. *Triturus vulgaris*, *Triturus* sp., *Bufo bufo*, *Bufo* sp., *Hyla arborea*, *Rana arvalis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Rana* sp., *Anguis fragilis*, *Natrix natrix*, *Vipera berus*.

References. Holman (1989a, 1991, 1993a), Holman et al. (1988), Kolfschoten and Turner (1996), Newton (1982a, 1982b), Parfitt (1997).

Remarks. The West Runton Freshwater Bed site, at West Runton, near Cromer, England, is the type locality for the classic British Cromerian interglacial age (Holman et al., 1988). It is presently considered to be temporally equivalent to the Sugworth, England, site and thus correlates with the Dutch/European Cromerian II sequence (Kolfschoten and Turner, 1996).

This locality contains a large mammalian fauna, and the herpetofauna is rather small in the light of the intensive collecting that has been done at the site over the years. Three anurans, *Hyla arborea* (only the second record from the British Pleistocene), *Rana arvalis*, and *Rana* (*ridibunda*) sp., are extralimital forms that now occur on the European continent. Since these anurans presently occur on the continent at the same latitude as West Runton, they do not particularly suggest a warmer climate at the site during the time of the deposition of the bones.

12. Westbury–Sub-Mendip Cave, Somerset, England

Taxa. *Pelodytes punctatus*, *Rana temporaria*, *Rana* sp., *Emys orbicularis*, *Anguis fragilis*, *Coronella austriaca*, *Natrix natrix*, *Natrix* sp., *Vipera berus*.

References. Andrews (1990), Holman (1993c), Roberts et al. (1995), Stuart (1979, 1982).

Remarks. The Westbury–Sub-Mendip Cave site in Somerset is considered to be temporally equivalent to the Boxgrove, England, site and thus to represent the British Cromerian interglacial age that correlates with Cromerian IV of the Dutch/European sequence (Roberts et al., 1995).

This is a classic site for the study of small mammalian paleoecology (Andrews, 1990). Compared to the thousands of small mammal bones were excavated at the site, herpetological remains are rare. The individual herpetological fossils came from separate stratigraphic units within the cave.

In contrast to the older Cromerian Sugworth and West Runton British sites, the Westbury site has yielded *Emys orbicularis*, an extralimital continental form that Stuart (1979, 1982) considers to indicate milder climates than the present one in Britain. The Westbury site has yielded the only British record of the extralimital continental form *Pelodytes punctatus*.

Upper Pleistocene

1. Baker's Hole Pit, Northfleet, Kent, England

Taxa. *Rana temporaria*, *Rana* sp.

References. Holman (1995d), Stuart (1982).

Remarks. Bakers Hole Pit, Northfleet, Kent, contains periglacial deposits representing the Wolstonian cold stage of the Upper Pleistocene. Remains of large mammals as well as human artifacts have been found at the site (Stuart, 1982). These animals are believed to have lived near the ice margin in a periglacial environment. At least two individuals of *Rana temporaria* and three individuals of *Rana* sp. are represented.

Rana temporaria occurs today north of the Arctic Circle, reaching the northern tip of Norway, Sweden, and Finland and occurring throughout the Kola Peninsula (Frazer, 1983). Thus, it is not be surprising that this species existed near the ice margin in glaciated Britain. Moreover, its presence in such a cold environment, where it lived with the wooly rhino and mammoth, may indicate that *Rana temporaria* existed in parts of southern England during all full glacial times and must have been one of the first, if not the first amphibian, to reinvade recently deglaciated areas in Britain and the continent.

2. Bobbitshole, East Suffolk, England

Taxon. *Emys orbicularis*.

References. Holman (1993a), Stuart (1979), Roberts et al. (1995).

Remarks. Bobbitshole represents the Ipswichian temperate stage (last interglacial of the Pleistocene) and is correlated with Eemian of the Dutch/European sequence (Roberts et al., 1995). The presence of *Emys orbicularis* at Bobbitshole indicates a milder climate than presently occurs in the area.

3. Coston, Norfolk, England

Taxa. *Bufo* sp. or *Rana* sp., *Rana temporaria*.

References. Holman (1990a), Lightwing (1983), Sanchiz (in press), Stuart (1982).

Remarks. The Coston, Norfolk, site is considered to represent the early part of the Devensian cold stage (last cold stage of the British Pleistocene). The presence of *Rana temporaria* reported by Lightwing (1983) and Sanchiz (in press) is therefore not surprising (see remarks under Baker's Hole Pit, above).

4. Greenlands Pit, Purfleet, Essex, England

Taxa. *Bufo bufo*, *Rana arvalis*, *Rana temporaria*, *Rana* sp., *Anguis fragilis*, *Natrix* cf. *Natrix natrix*.

References. Holman (1991, 1993a), Holman and Clayden (1988).

Remarks. This site may belong to one of the unrecognized British temperate stage sites (see Holman and Clayden, 1988; Roberts et al., 1995, table 1, p. 166). Neither a very warm nor a very cold stage is indicated by this assemblage. A rather moist terrestrial habitat is indicated by the herpetofauna.

5. Harkstead, Suffolk, England

Taxon. *Emys orbicularis*.

References. Holman (1993a), Stuart (1979, 1982).

Remarks. This is another site that represents the Ipswichian (last interglacial) stage of the British Pleistocene, possibly the latter part of the stage (Stuart, 1982). The presence of *Emys orbicularis* indicates a milder climate than presently occurs in the area. Nevertheless, the wooly mammoth occurs in the same deposit (Stuart, 1982, table 7.4, pp. 126–127).

6. Itteringham Pit, Norfolk, England

Taxa. *Bufo bufo*, *Bufo* sp., *Hyla meridionalis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Rana* sp., *Emys orbicularis*, *Natrix natrix*.

References. Hallock et al. (1990), Holman (1991, 1992d, 1993a).

Remarks. The Itteringham Pit fauna represents a temperate stage of the British Pleistocene, and Hallock et al. (1990) suggested that it represented the Ipswichian (last British interglacial stage) based on mammals collected here by J. D. Clayden.

The pit contains the extralimital continental taxa *Rana* (*ridibunda*) sp., *Hyla meridionalis*, (the only British Pleistocene record), and *Emys orbicularis*. A detailed analysis of the entire faunal composition of the site is needed. Unfortunately, a pollen study cannot be made, as the pit is now a commercial fishing pond.

7. Levaton, near Newton Abbott, South Devonshire, England

Taxon. *Bufo* sp. or *Rana* sp.

References. Carreck (1957–1958), Sanchiz (in press), Sutcliffe and Kowalski (1976).

8. Mundesley, Norfolk, England

Taxa. *Emys orbicularis*.

References. Holman (1993a), Stuart (1979, 1982).

Remarks. The Mundesley, Norfolk, site represents the early part of the Ipswichian (last interglacial stage). Here an *Emys orbicularis* was found in association with a straight-tusked elephant (*Palaeoloxodon antiquus*). Evidently, no other vertebrates have been listed from this locality (Stuart, 1982, table 4, pp. 126–127).

9. Selsey, West Sussex, England

Taxa. *Bufo bufo*, *Bufo calamita*, *Bufo* sp., *Rana* sp., *Emys orbicularis*, *Natrix natrix*.

References. Holman (1992c), Stuart (1979, 1982).

Remarks. The Selsey, West Sussex, site is also thought to represent the early part of the Ipswichian interglacial stage. The two most significant herpetological species are *Bufo calamita*, an endangered British species, and *Emys orbicularis*, which indicates a milder climate than presently exists in the area. Human artifacts as well as a straight-tusked elephant and an extinct rhino were also collected at the site (Stuart, 1982).

10. Shropham Pit (Interglacial Component), Norfolk, England

Taxa. *Triturus vulgaris*, *Bufo bufo*, *Bufo calamita*, *Rana arvalis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Rana* sp., *Emys orbicularis*, *Lacerta* cf. *Lacerta vivipara*, *Natrix maura* or *tesselata*, *Natrix natrix*, *Natrix* sp.

References. Holman (1991, 1993a, 1996), Holman and Clayden (1990).

Remarks. The Shropham Pit contains both a Devensian cold stage (last cold stage) and an interglacial (probably Ipswichian) component. The Devensian component contains mainly large mammals, but the interglacial one contains smaller vertebrates, including herpetological species. The most significant herpetological species from the interglacial sediments at Shropham are *Emys or-*

bicularis and *Natrix maura* or *tesselata*, extralimital continental forms that suggest that the Shropham area was warmer during the time of the deposition of the bones than it is at present. This Upper Pleistocene record of the British endangered species *Bufo calamita* is also noteworthy. Staff of the Castle Museum, Norfolk, Norwich, England, are presently studying the mammalian remains. Hopefully, pollen and other studies will help reveal the specific age of the interglacial component.

11. Shropham Pit (Devensian Pocket), Norfolk, England

Taxa. *Rana temporaria*, *Rana* sp., *Natrix natrix*.

References. Holman (1990a, 1992a, 1993a, 1996).

Remarks. Among the massive, large-mammal-bearing sediments at the Shropham site is an isolated pocket that has yielded small vertebrates including herpetological remains. The most significant find from the pocket is the remains of the grass snake, *Natrix natrix*, as this is the only record of a snake from a cold-stage fauna in Britain. The presence of the cold-tolerant *Rana temporaria* is not unexpected.

12. Stoke Tunnel, East Sussex, England

Taxon. *Emys orbicularis*.

References. Holman (1993a), Stuart (1979, 1982).

Remarks. The Stoke Tunnel site is questionably referred to the latest part of the Ipswichian interglacial stage (Stuart, 1982, table 7.4, pp. 126–127). Here *Emys orbicularis* occurs with 11 species of mammals, including the extinct cold-adapted wooly mammoth (*Mammuthus primigenius*).

13. Stonehouse Lane, Purfleet, Essex, England

Taxa. *Triturus cristatus*, *Triturus* sp., *Bufo* sp., *Rana* sp.

References. Holman (1995a), Roberts et al. (1995).

Remarks. This site at Purfleet may well represent one of the unrecognized temperate stages that lies between the Wolstonian cold stage and the Ipswichian interglacial stage (Roberts et al., 1995), or it may represent the Ipswichian itself. This is the only British record of *Triturus cristatus* from an Upper Pleistocene site.

14. Swanton Morley, Norfolk, England

Taxa. *Bufo bufo*, *Rana arvalis*, *Rana temporaria*, *Rana* sp., *Emys orbicularis*, *Natrix natrix*.

References. Holman (1987b), Stuart (1982).

Remarks. This site is considered to represent an early part of the Ipswichian interglacial age (Stuart, 1982, table 7.4, pp. 126–127). Here there are two extralimital continental forms, *Rana arvalis* and *Emys orbicularis*. *Emys orbicularis* indicates a warmer climate than presently occurs in the area.

15. Torbryon Caves (Broken Cavern and Three Holes Cave), Devonshire, England

Taxa. *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Lacerta vivipara*, *Anguis fragilis*.

Reference. Gleed-Owen (1997).

Remarks. Both of these cave faunas are said to represent the late Devensian, but a radio-carbon accelerator date of 11,080 ± 222 ybp was obtained from

Broken Cavern only. This is said to be the first evidence of *Bufo calamita* recolonization of Britain during any glacial stage (Gleed-Owen, 1997).

Unfortunately, the author did not make it clear whether all of the herpetological species listed were present in each cave or that it was composite list from both caves, nor did he give osteological characters or references used for the identification of any of the species except *Bufo calamita.*

16. Tornewton Cave, Devonshire, England

Taxa. indeterminate anuran, *Rana temporaria.*

References. Holman (1990a, 1993a), Stuart (1982).

Remarks. The fossil Rana temporaria is believed by Holman (1990a) to be from the Wolstonain cold stage part of Tornewton Cave (see Stuart, 1982, fig. 7.11, and pp. 129, 146–147). This record of the cold-tolerant *Rana temporaria* is not surprising.

17. Upton Warren, Worcestershire, England

Taxon. *Rana temporaria.*

References. Coope et al. (1961), Holman (1990a), Stuart (1982).

Remarks. The Upton Warren site has been radiocarbon dated at 42,000 ybp and thus represents the middle part of the Devensian cold stage (see Stuart, 1982, table 8.2, pp. 148–149). Again, the presence of the cold-tolerant frog *Rana temporaria*, is not surprising in this cold-stage fauna.

18. Waterhall Farm, Hertfordshire, England

Taxon. *Bufo* sp. or *Rana* sp.

References. Holman (1990a), Stuart (1982).

Remarks. The Waterhall Farm site represents the Wolstonian cold stage (Stuart, 1982, table 8.1, p. 144).

Pleistocene Undesignated

1. Grays Thurrock, Essex, England

Taxon. *Natrix natrix.*

References. Hinton (1901).

Remarks. Hinton states that these sites come from ''Pleistocene Brick Earths,''; thus, it is probable that the Ipswichian (last interglacial age) is represented.

2. Hoe-Grange Quarry, Longcliffe near Brassington, Derbyshire England

Taxa. *Bufo bufo, Rana temporaria.*

References. Arnold-Bemrose and Newton (1905), Sanchiz (in press).

3. Sidestrand, England

Taxon. *Rana* cf. *Rana temporaria.*

References. Sanchiz (in press), Woodward and Sherborn (1890).

4. Westbury-on-Severn, England

Taxa. *Bufo bufo, Rana temporaria, Natrix natrix.*

Reference: Hinton (1901).

Remarks. Hinton (1901) stated that this was a ''Forest Bed equivalent,'' which, if true, would mean that it was some part of the Cromerian sequence.

Pleistocene and Holocene

1. Cow Cave, Chudleigh, Devonshire, England

Taxa. *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Anguis fragilis*, *Vipera berus.*

References. Holman (1988, 1993a), Holman and Stuart (1991).

Remarks. This site probably is a composite of Devensian and Holocene fossils. *Bufo calamita* from this site may be of Holocene origin (Holman and Stuart, 1991).

2. Nazeing III, Essex, England

Taxa. *Bufo bufo*, *Bufo* sp., *Rana temporaria*, *Rana* sp., *Lacerta vivipara.*

References. Allison et al. (1952), Holman (1990a, 1993a), Sanchiz (in press), Stuart (1982).

Remarks. Stuart (1982, table 8.2, pp. 148–149) estimates the age of the Nazeing Site at between about 10,413 and 9,800 ybp on the basis of pollen zones. I am not convinced that this site does not represent the Holocene, at least in part, as there are no extinct Pleistocene mammals known from Nazeing III.

Latest Pleistocene or Earliest Holocene

1. Whitemoor Channel, near Bosley, East Cheshire, England

Taxa. *Triturus helveticus*, *Triturus vulgaris*, *Triturus* sp., *Bufo bufo*, *Bufo calamita*, *Bufo* sp., *Rana temporaria*, *Rana* sp.

References. Gleed-Owen (1997), Holman (1993a), Holman and Stuart (1991), Sanchiz (in press).

Remarks. The fossils of the Whitemoor Channel site came from a lacustrine *Chara* marl that has an estimated date of ca. 10,000–8,800 ybp based on pollen. The identification of *Bufo calamita* from the site by Holman and Stuart (1991) is not recognized as valid by Gleed-Owen (1997) but is accepted by Sanchiz (in press).

Division II: France and Monaco

France

Unlike Ireland and Britain, France has Lower Pleistocene herpetological sites as well as those of Middle and Upper Pleistocene age.

Lower Pleistocene

1. Chagny, near Beaune, Cote-D'Or, eastern central France

Taxon. *Pelobates* sp.

References. Sanchiz (in press), Vergnaud-Grazzini (1970).

Remarks. One might expect that this record represents *Pelobates fuscus*, the only species of the genus that presently lives in the area. The western spadefoot, *Pelobates cultipres*, presently occurs only in southern and western France.

2. Dufort, Gard, central Mediterranean basin, France

Taxon. *Bufo bufo*.

References. Gervais (1877), Isle (1877), Piveteau (1927), Rage (1974), Sanchiz (in press).

Remarks. This site has been questionably assigned to the Lower Pleistocene (Sanchiz, in press). *Bufo bufo* is so ubiquitous in its habits that it is not a good indicator of specific ecological conditions, other than that it needs still water in which to breed.

3. La Rochelambert, Haute Loire, central southern France

Taxon. *Emys orbicularis*.

References. Cheylan (1981), Fritz (1995).

Remarks. *Emys orbicularis* currently occurs in the general area of the site and indicates the presence of a permanent, low-energy, well-vegetated body of water.

4. Mas Rambault, Mediterranean basin, France

Taxa. *Pelobates* cf. *Pelobates cultipres*, *Pelodytes* cf. *Pelodytes punctatus*, *Bufo calamita*, *Coronella* sp., *Vipera* sp.

References. Bailón (1991a), Sanchiz (in press).

Remarks: The anurans indicate the presence of a rather moist, bushy area, and *Coronella* probably occupied a somewhat dryer terrestrial situation.

Middle Pleistocene

1. Abîmes de la Fage, Correze, northern portion of southwestern France

Taxa. *Salamandra* sp., *Discoglossus* sp., *Pelobates* sp., *Pelodytes* cf. *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, *Bufo* sp., *Hyla* sp., *Rana arvalis*, *Rana dalmatina*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Testudo hermanni*, *Lacerta* sp., *Coronella* sp., *Vipera* sp.

References. Bailón and Rage (1992), Rage (1972a), Sanchiz (in press).

Remarks. The Middle Pleistocene site at Abîmes de la Fage has yielded a particularly interesting herpetofauna. The site contains a complex mixture of extralimital species as well as taxa that presently occur in the area. *Discoglossus* sp. presently occurs nearest the site in the western part of the Mediterranean basin. *Rana arvalis*, on the other hand, is nearest the site in northeastern France. Currently, *Rana temporaria* is absent from the site area, but occurs in moister areas in France. The nearest *Testudo hermanni* to the site occurs about 300 km to the southeast on the Mediterranean coast.

The specific occurrence and abundance of herpetofaunal species changes from the bottom to the top of the site. A lower bed indicates a wet climate (e.g., *Rana temporaria*), but the upper beds indicate a dryer climate (e.g., *Discoglossus* sp. and *Testudo hermanni*). At one level, *Discoglossus* sp. and *Rana arvalis* occur together, possibly indicating a transitional climate.

The herpetofauna at Abîmes de la Fage is similar to that of the East Farm, Barnham Middle Pleistocene herpetofauna from Suffolk in East Anglia, England (Britain: Middle Pleistocene Site 5), in that both sites have extralimital forms with southern affinities as well as species indicating a change to dryer conditions in the upper levels of the deposit.

2. Balaruc O, Mediterranean basin, France

Taxon. *Rana* cf. *Rana dalmatina.*

References. Bailón (1991a), Sanchiz (in press).

Remaers: This site is questionably assigned to the Middle Pleistocene (Sanchiz, in press).

3. Coudes, Puy-de-Dome, southern central France

Taxa. **Coluber fossilis*, **Coluber gervaisii*, *Coluber viridiflavus*, **Naja sauvagei.*

References. Hoffstetter (1938), Młynarski (1961), Rage (1984c).

Remarks. Three of the taxa from the Coudes site are problematic forms. **Coluber fossilis* and **Coluber gervaisii* are considered *nomina dubia* and probably represent *Coluber viridiflavus* (see Chapter 4), and **Naja sauvagei* should be considered a recent colubrid snake (Hoffstetter, 1938; Rage, 1984c, p. 54). *Coluber viridiflavus* is a modern taxon that occurs in the area. In the future I suggest that *Coluber viridiflavus* be the only snake recognized from this site.

4. Lazaret C, Alpes Maritimes, extreme southeastern Mediterranean area

Taxa. *Pelodytes* cf. *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, *Hyla* sp., *Rana* (*ridibunda*) sp., *Rana temporaria*, *Coronella* cf. *Coronella austriaca*, *Coronella* cf. *Coronella girondica*, *Coluber* sp., *Elaphe* cf. *Elaphe longissima*, *Elaphe* cf. *Elaphe scalaris*, *Malpolon monspessulanus*, *Natrix* sp., *Vipera* cf. *Vipera aspis*, *Vipera* cf. *Vipera ursinii*, *Vipera* (*aspis*) sp., *Vipera* (*berus*) sp.

References. Bailón (1991a, 1991b), Rage (1969), Sanchiz (in press).

Remarks. This is an Acheulian archaeological site. The presence of *Rana* (*ridibunda*) sp. indicates a permanent, low-energy aquatic habitat at the site, which could have provided a breeding place for the other anurans. A moist terrestrial habitat is indicated by *Pelodytes* cf. *Pelodytes punctatus* and *Rana temporaria.* The snakes, in general, indicate the presence of a dry, shrubby terrestrial habitat. All of the herpetological species currently occur in or near the area of the fossil locality, suggesting a paleoclimate similar to the modern one.

5. Lunel-Viel Cave, southern France

Taxa. *Bufo bufo*, *Lacerta lepida.*

References. Bailón (1991a), Bailón and Rage (1992), Boule (1919), Brocchi (1879), Estes (1983), Sanchiz (in press).

Remarks. Based on the presence of *Lacerta lepida* and the ubiquitous *Bufo bufo*, a dry scrubby or open woodland habitat is suggested.

6. Montoussé 3, Hautes Pyrenees, French/Spanish border

Taxa. *Salamandra* sp., *Pelobates* sp., *Bufo bufo*, *Rana temporaria*, *Rana* sp., *Emys orbicularis*, *Lacerta* sp., *Coronella* sp., cf. *Elaphe*, *Natrix* cf. *Natrix natrix.*

References. Bailón (1991a), Bailón et al. (1988), Clot et al. (1976b), Fritz (1995), Sanchiz (in press).

Remarks. This site has yielded amphibian and reptile taxa that all currently occur in the area. *Emys orbicularis* indicates the presence of a permanent, low-energy body of water with ample aquatic vegetation. The other species indicate a moist terrestrial habitat nearby (e.g., *Rana temporaria* and *Natrix* cf. *Natrix natrix*) that perhaps gave way to a somewhat dryer terrestrial situation (e.g., *Bufo bufo* and *Lacerta* sp.).

7. Montoussé 4 and 5, Hautes Pyrenees, French/Spanish border

Taxa. *Salamandra* sp., *Anguis* cf. *Anguis fragilis Coronella* cf. *Coronella austriaca*, *Coluber viridiflavus*, *Elaphe* aff *Elaphe longissima*, *Natrix* cf. *Natrix natrix*, *Vipera* (*aspis*) sp., *Vipera* (*berus*) sp.

References. Bailón (1991a), Clot et al. (1976a), Estes (1981, 1983).

Remarks. All of the species identified currently occur in the area. A moist woodland grading into a dryer upland area would support the species in this fossil herpetofauna.

8. Nestier, France

Taxon. *Rana temporaria.*

References. Rage (1977), Sanchiz (in press).

9. Terra Amata, Alpes Maritimes, extreme southeastern Mediterranean area

Taxa. *Pelodytes* cf. *Pelodytes punctatus*, *Bufo bufo*, *Bufo viridis*, *Rana* cf. *Rana temporaria*, *Coronella* cf. *Coronella austriaca*, *Elaphe longissima*, *Malpolon* cf. *Malpolon monspessulanus*.

References. Bailón (1991a, 1991b), Sanchiz (in press).

Remarks. These animals together indicate a rather moist terrestrial habitat grading into a dryer upland area. All of these taxa presently occur in the area.

Upper Pleistocene

1. Basse Cave, near Entrechaux, southern central France

Taxon. *Emys orbicularis.*

References. Cheylan (1981), Fritz (1995).

Remarks. This site is said to represent either the Riss II–Würm I interglacial or the Würm I–II interstadial event (Fritz, 1995). The presence of *Emys orbicularis* again indicates a permanent, low-energy body of water with ample aquatic vegetation.

2. Brèche de Coudes and Neschers, Auvergne, southern central France

Taxa. **Lacerta fossilis.*

References. Estes (1983), Pomel (1853).

Remarks. **Lacerta fossilis* is a problematic taxon that is discussed in Chapter 4 (see *Lacerta* section). It is considered to be a *nomen dubium*, and the whereabouts of the type is unknown (Estes, 1983).

3. Brette 2, French/Spanish border

Taxa. *Alytes obstetricans*, *Bufo bufo*, *Bufo calamita.*

References. Bailón (1991a), Sanchiz (in press).

4. Cantet Cave, Espeche, Hautes Pyrenees, French/Spanish border

Taxa. *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Coluber* sp., *Elaphe* cf. *Elaphe longissima*, *Natrix* sp., *Vipera* (*aspis*) sp.

References. Bailón (1991a), Clot et al. (1984), Sanchiz (in press).

Remarks. All of these species presently occur in the area. These taxa indicate a moist terrestrial habitat (*Rana temporaria*) as well as a dryer upland area (*Elaphe* cf. *Elaphe longissima* and *Vipera* (*aspis*) sp.).

5. Carrière Cave, a Gerde, Hautes Pyrenees, French/Spanish border

Taxa. *Salamandra* sp., *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Anguis fragilis*, *Coluber* sp., *Natrix maura*, *Vipera* (*aspis*) sp.

References. Bailón (1991a), Estes (1981, 1983), Rage (1977), Sanchiz (in press).

Remarks. All of these taxa may currently be found in the area. A permanent aquatic situation is indicated by the presence of *Natrix maura*. A moist terrestrial situation is suggested by *Salamandra* sp., *Rana temporaria*, and *Anguis fragilis*. *Bufo calamita* indicates a somewhat dryer terrestrial situation.

6. Citoyenne, French/Spanish border

Taxa. *Bufo bufo*, *Bufo calamita*, *Hyla* sp., *Rana temporaria*, *Coluber viridiflavus*.

References. Bailón (1991a), Sanchiz (1997)

Remarks. These taxa presently occur in the area. Anurans (e.g., *Hyla* sp., *Rana temporaria*) indicate the presence of a moist terrestrial habitat, whereas other taxa (e.g., *Bufo bufo*, *Bufo calamita*, and *Coluber viridiflavus*) indicate a dryer upland situation.

7. Combe Grenal, southwestern France

Taxa. *Pelobates fuscus*, *Pelodytes* cf. *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Coronella* cf. *Coronella austriaca*.

References. Bailón (1991a), Sanchiz (in press).

Remarks. *Rana* (*ridibunda*) sp. indicates the presence of a permanent, low-energy aquatic situation. *Paloclytes* cf. *P. punctatus* and *Rana temporaria* indicate a moist area nearby, and the other forms suggest somewhat dryer, upland habitats.

8. Hortus Cave, Herault, central Mediterranean basin, France

Taxa. *Pelobates* sp., *Bufo bufo*, *Bufo* cf. *Bufo bufo*, *Bufo calamita*, *Testudo* sp., *Lacerta* sp., *Malpolon monspessulanus*, *Vipera* sp.

References. Bailón (1991b), Estes (1983), Rage (1972b).

Remarks. The locality represents Würmian II (Rage, 1972b). These taxa are presently found in the area and mainly indicate a dry, terrestrial situation. A small and a very large *Lacerta* species were present.

9. Jaurens Cave, Nespouls, Correze, northeren portion of southwestern France

Taxa. *Bufo calamita*, *Bufo* sp., *Rana temporaria*, *Rana* sp., *Lacerta* sp., *Vipera* sp.

References. Rage (1979), Sanchiz (in press).

Remarks. These species could have existed in a moist habitat giving way to a dryer terrestrial situation.

10. Macinaggio Cave, Corsica Island, France

Taxon. *Discoglossus* sp.

References. Gasc (1961), Lanza et al. (1986), Sanchiz (in press).

Remarks. At present, *Discoglossus sardus* is the only species of the genus that occurs on the island of Corsica.

11. Malarode Cave, French/Spanish border

Taxa. *Rana temporaria*, *Natrix* sp.

Reference. Bailón (1991a), Sanchiz (in press).

Remarks. The presence of a moist, terrestrial habitat is indicated by *Rana temporaria.*

12. Mas d' Azil, southwestern France

Taxon. *Emys orbicularis.*

References. Fritz (1995), Parent (1972).

Remarks. This locality represents a late Würm glacial interval, and it is probable that the presence of *Emys* indicates the return of warmer temperatures at the end of the interval. The fossil turtle bone had been made into a graver tool by Pleistocene humans (Parent, 1972).

13. Noisetier, France

Taxa. *Alytes obstetricans*, *Bufo bufo*, *Rana temporaria.*

References. Bailón (1991a), Sanchiz (in press).

14. Oletta, Corsica Island, France

Taxa. *Discoglossus* sp., *Bufo viridis*, *Hyla sarda.*

References. Ferrandini and Salotti (1995), Sanchiz (in press).

Remarks. All of these taxa presently occur on the island of Corsica.

15. Padirac, France

Taxa. *Bufo bufo*, *Bufo* cf. *Bufo calamita*, *Rana dalmatina*, *Rana* (*ridibunda*) sp., *Rana temporaria.*

References. Guerin (1993), Sanchiz (in press)

Remarks. *Rana* (*ridibunda*) sp. indicates the presence of a permanent body of still or slowly flowing water. *Rana dalmatina* and *Rana temporaria* indicate a moist, terrestrial habitat, whereas *Bufo bufo* and *Bufo* cf. *Bufo calamita* suggest a somewhat dryer upland situation.

16. Roche-Cotard, France

Taxa. *Pelodytes* cf. *Pelodytes punctatus*, *Bufo calamita*, *Rana temporaria.*

References. Bailón (1991a), Rage (1984b), Sanchiz (in press).

Remarks. A rather moist habitat is indicated by the presence of *Pelodytes* cf. *Pelodytes punctatus* and *Rana temporaria*, whereas *Bufo calamita* indicates a dryer upland area.

17. Siréjol, Lot, southwestern France

Taxa. *Bufo bufo*, *Rana dalmatina*, *Rana temporaria*, *Anguis fragilis.*

References. Philippe (1975), Sanchiz (in press)

Remarks. All of these anurans may currently be found in the area. *Rana dalmatina* and *Rana temporaria* indicate a moist, terrestrial habitat. *Bufo bufo* could have existed in a somewhat dryer situation.

Pleistocene Undesignated

1. Breches de la Vallette, Herault, central Mediterranean basin, France

Taxon. *Malpolon monspessulanus.*

Reference: Bailón (1991b).

Remarks. This species suggests a warm, dry terrestrial habitat.

2. Chilleurs-aux-Bois, Loiret, northern central France

Taxa. *Salamandra* sp., *Bufo* sp., *Rana* sp., *Anguis fragilis.*

References. Chaline (1960), Sanchiz (in press).

Remarks. These species together suggest a moist terrestrial habitat.

3. Corscia Island (only designation), France

Taxon. *Bufo* sp.

Reference. Sanchiz (1984a).

4. Pierres Blanches, France

Taxa. *Pelodytes* cf. *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita.*

References. Bailón (1991a), Sanchiz (in press).

Remarks. *Pelodytes* cf. *Pelodytes punctatus* indicates the presence of a rather moist habitat, whereas *Bufo bufo* and *Bufo calamita* could have occurred in dryer situations.

5. Valerots, Nuits-Saint-Georges, France

Taxon. *Rana* (*ridibunda*) sp.

References. Chaline (1976), Sanchiz (in press).

Remarks. The presence of a permanent, low-energy body of water is indicated by the presence of *Rana* (*ridibunda*) sp.

6. Vallée de Fontechevade, Charente, northern part of southwestern France

Taxon. *Testudo graeca.*

References. Auffenberg (1974), Henri-Martin (1946), Młynarski (1976).

Remarks. At present, *Testudo graeca* gets no closer to France than extreme southern Spain, whereas *Testudo hermanni* occurs in the Mediterranean coastal area of France. This *Testudo* material should be restudied to confirm the specific identification. Nevertheless, the record marks a northern range extension for *Testudo* in the Pleistocene and indicates a warmer, dryer climate for the area at the time.

7. Vosges, northeastern France

Taxon. *Emys orbicularis.*

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks: This occurrence indicates that a rather moderate paleoclimate existed in the area. The designation of this site as Pleistocene is not positive (Fritz, 1995).

Upper Pleistocene or Holocene

1. Arthez d' Asson PH3, France.

Taxa. *Alytes obstetricans*, *Bufo bufo*, *Rana temporaria.*

References. Bailón (1991a), Sanchiz (in press).

Remarks. *Rana temporaria* indicates a moist terrestrial habitat, whereas *Alytes obstetricans* indicates a dryer terrestrial situation.

2. Chinchon, Vaucluse, France

Taxon. *Alytes obstetricans*.

References. Poulain (1977), Sanchiz (in press).

Monaco

Upper Pleistocene

1. Grimaldi Cave, Monaco.

Taxa. *Emys orbicularis*, *Lacerta viridis*.

References. Boule (1906, 1919), Cheylan (1981), Estes (1983), Fritz (1995), Lumley-Woodyear (1969).

Remarks. Both of these species currently occur in the area. *Emys orbicularis* indicates the presence of a permanent low-energy body of water with ample aquatic vegetation. *Lacerta viridis* would have occurred in an area of thick vegetation with exposure to the sun. The site has been relegated to the Riss II–Würm I interglacial sequence.

Division III: Spain

Spain has produced many Pleistocene herpetological localities ranging from the Pliocene-Pleistocene boundary to the Pleistocene-Holocene boundary. Pleistocene caves, Palaeolithic archaeological sites, and oceanic islands have yielded important herpetological material.

Pliocene-Pleistocene Boundary

1. Pedrera de s'Onix, Majorca Island, Spain

Taxa. *Alytes* sp., *Discoglossus* sp., *Lacerta* aff *Lacerta* (''*Podarcis*'') *lilfordi*.

References. Alcover and Mayol (1981), Alcover et al. (1984), Alomar et al. (1983), Gallemí (1988), Kotsakis (1981b), Sanchiz (in press).

Remarks. *Alytes* in the form of *Alytes muletensis* presently occurs on the island of Majorca, but *Discoglossus* does not.

Lower Pleistocene

1. Binigaus, Majorca Island, Spain

Taxa. *Discoglossus* sp., *Lacerta* sp.

References. Alcover et al. (1980), Kotsakis (1981b), Lanza et al. (1986), Sanchiz (in press).

Remarks. *Discoglossus* does not presently occur on the island of Majorca. The *Lacerta* is probably a wall lizard (''*Podarcis*'') species (Kotsakis, 1981b).

2. Castelldefels, Barcelona Province, northeastern Mediterranean area, Spain

Taxon. *Bufo bufo.*

References. Sanchiz (1977a, in press), Villalta and Crusafont (1950).

3. Loma Quemada, Granada Province, southwestern Mediterranean area, Spain

Taxon. *Discoglossus* sp.

References. Bailón (1991a), Sanchiz (in press).

4. Orce 1 and 4, Granada Province, southwestern Mediterranean area, Spain

Taxa. *Rana* cf. *Rana perezi.*

References. Felix and Montori (1987), Sanchiz (in press).

Remarks. *Rana perezi* currently occurs in the area.

5. Venta Micena 1, Granada Province, southwestern Mediterranean area, Spain

Taxa. *Discoglossus* sp., *Rana perezi*, *Rana* sp.

References. Bailón (1991a), Felix and Montori (1987), Raposo and Santonja (1995), Sanchiz (in press).

Remarks. The Venta Micena sites have produced questionable evidence of Lower Pleistocene homonids (Raposo and Santonja 1995). *Rana perezi* indicates a permanent, low-energy aquatic situation existed in the area.

Middle Pleistocene

1. Agua, Granada Province, southwestern Mediterranean area, Spain

Taxon. cf. *Alytes.*

References. Lopez and Ruiz (1977), Sanchiz (in press), Sevilla (1988).

2. Ambrona, Soria Province, northeastern Spain

Taxa. *Discoglossus galganoi*, *Pelobates cultipres*, *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, *Hyla* sp., *Rana perezi*, *Natrix* sp.

References. Aguirre and Fuentes (1969), Raposo and Santonja (1995), Sanchiz (1977a, 1990, in press).

Remarks. The lower levels of the Ambrona site have produced questionable evidence of the presence of homonids (Raposo and Santonja, 1995).

Discoglossus galganoi is an extralimital species that presently occurs in Portugal and southwestern Spain All of the other species currently occur in Soria Province. *Rana perezi*, the western equivalent of the marsh or lake frog, *Rana ridibunda*, indicates a permanent, low-energy aquatic habitat near the site at the time of the deposition of the fossils. Other forms such as *Discoglossus galgoni*, *Pelobates cultipres*, *Pelodytes punctatus*, *Hyla* sp., and possibly *Natrix* sp. occurred in moist habitats near the permanent aquatic situation. *Bufo bufo* and *Bufo calamita* could have ranged into dryer situations.

3. Aridos 1, Arganda, Madrid Province, central Spain

Taxa. cf. *Alytes*, *Discoglossus galganoi*, *Pelobates cultipres*, *Bufo bufo*, *Hyla* sp., *Rana perezi*, *Emys orbicularis*, *Lacerta* cf. *Lacerta lepida*, *Lacerta* sp., *Elaphe* cf. *Elaphe scalaris*.

References. Estes (1983), Fritz (1995), Jimenéz Fuentes (1980), Sanchiz (1977a, in press), Sanchiz and Sanz (1980), Raposo and Santonja (1995), Sanz and Sanchiz (1980).

Remarks. The Aridos site has produced evidence of the presence of homonids and represents the late part of the Middle Pleistocene (Raposo and Sontanja, 1995).

Discoglossus galganoi is an extralimital species that presently occurs in Portugal and southwestern Spain. (Duellman, 1993). All of the other taxa presently occur in Madrid Province, Spain. The presence of a permanent, low-energy, well-vegetated body of water is indicated by *Emys orbicularis*. The anurans mainly suggest a moist, terrestrial habitat. *Lacerta lepida* and *Elaphe* cf. *Elaphe scalaris* suggest a dry, bushy or shrubby situation.

4. Arriaga, Madrid Province, central Spain

Taxa. *Pelobates cultipres*, *Bufo bufo*, *Rana perezi*, *Lacerta lepida*, *Lacerta* sp.

References. Gamazo (1982), Sanchiz (1990, in press).

Remarks. This herpetofauna indicates habitats similar to the Aridos 1 herpetofauna above, namely, a permanent, low-energy body of water (*Rana perezi*), a moist, terrestrial habitat (*Pelobates cultipres*), and a dry bushy or shrubby situation (*Lacerta lepida*).

5. Atapuerca, Burgos Province, central northern Spain

Taxa. *Alytes obstetricans*, *Pelobates* sp., *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Rana* sp.

References. Raposo and Santonja (1995) Sanchiz (1977a, 1987, in press).

Remarks. The Atapuerca sites are important archaeological features that have yielded remains of ancient homonids (Aguirre, 1990; Raposo and Santonja, 1995) in the lower part of the Middle Pleistocene. All of the amphibians presently occur in the area, with the possible exception of *Rana temporaria*, which appears to be very near the southern edge of its range in northcentral Spain (see Escriva, 1987, map 23, p. 556; Raposo and Santonja, 1995, fig. 1, p. 10). *Pelodytes punctatus* and *Rana temporaria* indicate a moist, terrestrial habitat. The other anurans indicate a somewhat dryer terrestrial situation.

6. Bagur 2, Gerona Province, extreme northeastern Spain

Taxa. *Pelobates* cf. *Pelobates cultipres*, *Bufo bufo*.

References. Sanchiz (1977a, in press).

Remarks. Both of these anuran species currently occur in the area.

7. Culler de Baza I-E, southeastern Spain

Taxa. *Blanus cinereus*.

References. Barbadillo (1989), Delfino (1995).

Remarks. This species presently occurs in the area.

8. Grajas Cave, Malaga Province, southwestern Mediterranean area, Spain

Taxa. *Discoglossus* cf. *Discoglossus jeanneae*, *Bufo bufo*, *Bufo calamita*, *Rana perezi*, *Lacerta lepida*, *Lacerta* sp., *Blanus cinereus*, *Coluber* and/or *Elaphe*, *Coronella* cf. *Coronella girondica*, *Malpolon monspessulanus*, *Vipera* sp.

References. Sanchiz (1990, in press).

Remarks. At present, *Discoglossus jeanneae* occurs only in southern Cádiz Province, Spain (Duellman, 1993), the province directly west of Malaga. Whether this represents a difference in the range of this species in the Pleistocene or merely the failure to collect modern specimens in the area is problematic.

This herpetofauna indicates a permanent, low-energy body of water (*Rana perezi*), a rather moist area (e.g., *Discoglossus* and *Blanus cinereus*), and a sunny, dry, scrubby area (e.g., *Lacerta lepida*, *Coronella girondica*, and *Malpolon monspessulanus*).

9. Higuerón, Malaga Province, southwestern Mediterranean area, Spain

Taxon. *Bufo* sp.

References. Montes (1992), Sanchiz (1977a, in press).

10. Pontón, Madrid Province, central Spain

Taxa. Indeterminate Gekkonidae, cf. *Blanus cinereus*.

Reference. Sanchiz (1990).

Remarks. The geckko *Tarentola mauritica* and *Blanus cinereus*. currently occur in Madrid Province, Spain.

11. Sarrión-Cerro de los Espejos, Teruel Province, central eastern Spain

Taxon. *Triturus marmoratus*.

References. Estes (1981), Sanchiz (1977a).

Remarks. *Triturus marmoratus* presently occurs in the area. Estes (1981) identified these remains as *Triturus* cf. *Triturus marmoratus*, but I accept the identification of Sanchiz (1977a) on the basis of zoogeographic grounds (see Escriva, 1987, maps 5 and 6, p. 546).

12. Son Bauçá, Majorca Island, Spain

Taxa. *Alytes muletensis*, *Lacerta* (*"Podarcis"*) *lilfordi*.

References. Alcover and Mayol (1981), Alcover et al. (1984), Alomar et al. (1983), Gallemí (1988), Sanchiz (1977a, in press), Sanchiz and Adrover (1977).

13. Unión, Spain

Taxa. *Bufo bufo*, *Rana* cf. *Rana perezi*.

References. Sanchiz (1977a, in press).

14. Villacastín, Segovia Province, central Spain

Taxa. *Bufo calamita*, *Bufo* sp., *Rana* sp.

References. Arribas (1995), Sanchiz (in press).

Remarks. These taxa presently occur in the area.

15. Yedras Cave, Granada Province, southwestern Mediterranean area, Spain

Taxa. *Bufo bufo*, *Bufo* sp.

References. Lopez and Ruiz (1977), Ruiz (1978), Sanchiz (in press).

Middle and Upper Pleistocene

1. Horá Cave, Granada Province, southwestern Mediterranean area, Spain

Taxa. cf. *Alytes*, *Discoglossus* cf. *Discoglossus jeanneae*, *Bufo bufo*, *Bufo calamita*, *Rana* cf. *Rana perezi*, *Testudo* cf. *Testudo graeca*, *Lacerta lepida*, aff "*Podarcis*," *Coluber hippocrepis*, *Coluber* aff *Coluber viridiflavus*, *Coronella girondica*, *Elaphe* sp., *Vipera latastei*.

References. Bailón (1986), Fuentes and Meijide (1975), Sanchiz (in press).

Remarks. Based on lithic industries at the site, the Hora Cave accumulation ranges from about 150,000 to 35,000 ybp. Again, *Discoglossus jeanneae* is recorded in the Pleistocene out of its modern range in southern Cádiz Province (Duellman, 1993). Whether this represents a difference in the range of this species in the Pleistocene or merely the failure to collect modern specimens in the area is problematic. A definite extralimital species, *Coluber viridiflavus*, barely reaches the extreme northeastern corner of Spain at present (see Escriva, 1987, map 70, p. 576). The other taxa currently occur in the area.

The presence of *Rana perezi* indicates a permanent, low-energy aquatic situation, but the remainder of the fauna mainly represents a typical Mediterranean scrub fauna with abundant warm, sunny days during many months of the year. Nevertheless, one must remember that this assemblage represents a long sequence of accumulation and probably contains species from both the Late Middle and the Upper Pleistocene.

Middle or Upper Pleistocene

1. Solana del Zamborina, Grenada Province, southwestern Mediterranean area, Spain

Taxa. *Discoglossus* sp., *Coronella* cf. *Coronella girondica*.

References. Bailón (1991a), Sanchiz (in press).

Upper Pleistocene

1. Aitzbitarte 4, Guipuzcoa Province, northeastern Spain

Taxa. *Bufo bufo*, *Rana temporaria*, *Rana* sp.

References. Sanchiz (1977a, 1984b, in press).

Remarks. Several archaeological levels are represented in this deposit. Both species presently occur in this province.

2. Arbreda, Northeast Catalunya District, Spain

Taxa. cf. *Alytes*, *Pelobates cultipres*, *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, cf. *Hyla*, *Rana* sp.

References. Felix (1985), Sanchiz (in press).

Remarks. These anurans are species that prefer rather moist habitats as well as those that range into somewhat dryer situations.

3. Barxa Cave, Majorca Island, Spain

Taxa. *Alytes muletensis*, *Lacerta ("Podarcis") lilfordi.*

References. Alcovar et al. (1984), Alomar et al. (1983), Gallemí (1988), Sanchiz (in press).

4. Chufín Cave, Santander Province, central Bay of Biscay area, Spain

Taxa. *Bufo bufo*, *Rana* sp.

References. Sanchiz (1977a, in press).

5. Cova de Llenaire, Majorca Island, Spain

Taxon. *Lacerta ("Podarcis") lilfordi.*

Reference. Kotsakis (1981b).

6. Cova des Pilar, Majorca Island, Spain

Taxon. *Lacerta ("Podarcis") lilfordi.*

Reference. Kotsakis (1981b).

7. Cova Rosa, Asturias Province, extreme northwestern Spain

Taxa. *Salamandra salamandra*, *Triturus marmoratus*, *Alytes obstetricans*, *Bufo bufo*, *Bufo calamita*, *Rana iberica*, *Rana temporaria.*

References. Esteban and Sanchiz (1990), Sanchiz (1977a, 1982, in press).

Remarks. This cave site contains several archaeological industrial levels. All of the herpetological species presently occur in Asturias Province, Spain, but it may be questionable whether *Rana iberica* is found in the immediate vicinity of the fossil site (see Escriva, 1987, map 22, p. 556).

6. Cueto de la Mina, Asturias Province, extreme northwestern Spain

Taxa. *Bufo bufo*, *Rana temporaria.*

References. Sanchiz (1977a, in press).

Remarks. These species currently occur in the area.

9. Ekain, Deba, Guipuzcoa Province, extreme northeastern Spain

Taxa. *Bufo bufo*, *Rana temporaria*, *Rana* sp.

References. Sanchiz (1977a, 1984b, in press).

Remarks. This is an Upper Palaeolithic site. Anuran remains were found in sites ranging from ca. 21,000 ybp to ca. 12,000 ybp. Both of these anuran species presently occur in the area. A previous record of *Rana* cf. *Rana dalmatina* at the site was removed by Sanchiz (in press).

10. Erralla, Guipuzcoa Province, extreme northeastern Spain

Taxa. *Alytes obstetricans*, *Bufo bufo*, *Rana* cf. *Rana dalmatina*, *Rana temporaria.*

References. Esteban (1990), Esteban and Sanchiz (1985), Sanchiz (in press).

Remarks. This site dates from ca, 16,500 to 15,400 ybp (Esteban and Sanchiz, 1985). A previous record of *Bufo calamita* from the site was removed by Sanchiz (in press). All of these anuran species presently occur in the area.

11. Hienas Cave, Asturias Province, extreme northwestern Spain

Taxa. *Euproctus* sp., *Salamandra salamandra*, *Triturus alpestris*, *Triturus marmoratus*, *Triturus* sp., *Alytes obstetricans*, *Bufo bufo*, *Bufo calamita*, *Rana temporaria.*

References. Martín and Sanchiz (1990), Sanchiz (1977a, in press).

Remarks. This large amphibian fauna occurs in the Las Caldas area of the Province and the Pleistocene interval represented by the sampled sediments ranges from 90,000 to 40,000 ybp. All of these amphibian taxa are found in the area at present, with the exception of *Euproctus* sp. The nearest *Euproctus* currently occurs to the site is in extreme northeastern Spain, where *Euproctus asper* may be found (Escriva, 1987, map 4, p. 545).

12. Huesos Cave, Asturias Province, extreme northwestern Spain

Taxa. *Salamandra salamandra, Bufo bufo.*

References. Sanchiz (1977a, in press).

Remarks. Both of these species presently occur in the area.

13. Jarama 2, Valdesotos, Guadalajara Province, eastern central Spain

Taxon. *Bufo bufo.*

References. Adán et al. (1995), Sanchiz (in press).

Remarks. This species presently occurs in the area.

14. Jarama 6, Valdesotos, Guadalajara Province, eastern central Spain

Taxa. *Pelobates cultipres, Bufo bufo.*

References. Adán et al. (1995), Sanchiz (in press).

Remarks. Both of these anurans currently inhabit the area.

15. Laminak Cave II, Berriatua, Vizkaya Province, northeastern Spain

Taxa. *Salamandra salamandra, Triturus helveticus*, Salamandridae indeterminate, *Alytes obstetricans, Bufo bufo, Rana temporaria*, Anura indeterminate, *Lacerta* sp., *Anguis fragilis*, Colubrinae indeterminate.

References. Arribas and Berganza (1989), Sanchiz (in press), Sanchiz and Esteban (1994).

Remarks. This site in Basque Country in northeastern Spain has been dated at ca. 11,000 ybp. All of the taxa identified from this fauna may be currently found in the area. In general, this herpetofauna indicates a rather moist terrestrial situation.

16. Millán Cave, Burgos Province, northern central Spain

Taxon. *Rana iberica.*

References. Esteban and Sanchiz (1990), Sanchiz (in press).

Remarks. This site has been dated at about 37,000 ybp. (Esteban and Sanchiz, 1990). *Rana iberica* was identified on the basis of sophisticated biometric methods (see *Rana iberica* account, Chapter 4). The nearest this extralimital species presently occurs to the fossil site is in extreme northern Madrid Province.

17. Mortero, Santander Province, central Bay of Biscay area, Spain

Taxon. *Rana temporaria.*

References. Bailón (1991a), Sanchiz (1977a, in press).

Remarks. This species presently occurs in the area.

18. Oscura Cave, Asturias Province, extreme northwestern Spain

Taxa. *Salamandra salamandra, Rana* (*ridibunda*) sp.

Reference: Sanchiz (1977a).

Remarks. *Rana (ridibunda)* sp. indicates the presence of a permanent, low-energy body of water. *Salamandra salamandra* suggests a moist terrestrial situation.

19. Paloma Cave, Asturias Province, extreme northwestern Spain

Taxa. *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Anguis fragilis*, *Lacerta* sp.

References. Estes (1983), Sanchiz (1977a, 1980, in press).

Remarks. *Rana temporaria* and *Anguis fragilis* indicate a rather moist terrestrial habitat. *Bufo calamita* indicates a dryer situation.

20. Pedraza, Soria Province, northeastern Spain

Taxon. *Bufo* sp.

References. Sanchiz (1977a, in press).

21. Pontones, Jaen Province, central southern Spain

Taxon. *Blanus cinereus.*

References. Delfino (1995), Lopez-Martinez and Sanchiz (1981).

Remarks. This species currently occurs in the area.

22. Son Maiol, Majorca Island, Spain

Taxa. *Alytes muletensis*, *Lacerta ("Podarcis") lilfordi.*

References. Alomar et al. (1983), Alcover et al. (1984), Gallemí (1988), Sanchiz (in press).

Pleistocene Undesignated

1. Majorca Island (no other designation), Spain

Taxa. *Alytes* sp., *Discoglossus* sp., *Lacerta* sp., *Chalcides* sp.

References. Alcover et al. (1980), Boulenger in Bate (1919), Estes (1983).

Remarks. These records are very likely not from the same sites. *Discoglossus* and *Chalcides* are not presently known from Majorca Island.

Upper Pleistocene and Holocene

1. Muleta Cave, Majorca Island, Spain

Taxa. *Alytes muletensis*, *Bufo viridis*, *Lacerta ("Podarcis") lilfordi.*

References. Alcover and Mayol (1981), Alcover et al. (1984), Alomar et al. (1983), Arntzen and García-París (1995), Sanchiz (1977a, in press), Sanchiz and Adrover (1977).

Remarks. This is the type locality for *Alytes muletensis*, a modern species that was first discovered as a fossil (Sanchiz and Adrover, 1977).

2. Nerja Cave, Malaga Province, southwestern Mediterranean area, Spain

Taxa. *Emys orbicularis*, *Mauremys leprosa.*

References. Fritz (1995), Jiminéz-Fuentes (1986).

Remarks. This site ranges in age from ca 15,000 to 8000 ybp (Jiminéz Fuentes, 1986). Both species presently occur in the area.

Upper Pleistocene or Holocene

1. Congosto Cave, Guadalajara, central Spain

Taxon. *Rana* sp.

References. Sanchiz (1977a, in press).

2. Martianez Beds, Tenerife and La Palma, Canary Islands Spain

Taxa. **Lacerta goliath*, **Lacerta maxima*.

References. Bravo (1953), Estes (1983), Gasc (1971), Kuhn (1963), Mertens (1942).

Remarks. These distinctive, extinct ''giant'' lacertids are recognized as valid species by Estes (1983).

3. Rincón de la Victoria, Spain

Taxon. *Rana perezi*.

References. Sanchiz (1977a, in press).

Division IV: Netherlands, Belgium, Luxembourg, Germany, Austria, Switzerland

Netherlands

Unfortunately, published Pleistocene herpetofaunas are few in the Netherlands.

Middle Pleistocene

1. Maastricht-Belvédère 3, southern Limburg, Netherlands

Taxa. *Bufo* cf. *Bufo bufo*, *Rana temporaria*.

References. Holman and Kolfschoten (1997c), Kolfschoten (1992), Kolfschoten et al. (1993).

Remarks. The Maastricht-Belvédère 3 site represents the Saalian stage of the Middle Pleistocene and lies below the Maastricht-Belvédère 4 site that follows. Both of the site 3 anurans may be presently found in the area, but they are so ubiquitous in their habits and tolerate such a wide range of temperatures on the continent that they do not allow a fine-tuned interpretation of either Pleistocene habitats or climates.

2. Maastricht-Belvédère 4, southern Limburg, Netherlands

Taxa. *Triturus helveticus*, *Triturus vulgaris*, *Bufo bufo*, *Bufo calamita*, *Bufo* sp., *Rana arvalis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Rana* sp., *Emys orbicularis*, *Lacerta vivipara*, *Anguis fragilis*, *Natrix natrix*.

References. Fritz (1995), Holman and Kolfschoten (1997c), Kolfschoten (1985).

Remarks. The Maastricht-Belvédère 4 site in southern Limburg is considered to represent the late Middle Pleistocene and an interstadial part of the Saalian stage. All of the amphibians and reptiles found at the site may be found in the area at present or have been recorded there during historic times (see maps in Sparreboom, 1981).

The presence of such a well-developed herpetofauna and the occurrence of *Emys orbicularis* at the site are consistent with an interstadial climate. In fact, the herpetofauna is one that might be expected if an undisturbed landscape presently existed in the area. A permanent, low-energy body of water with ample aquatic vegetation is indicated by *Emys orbicularis* and *Rana* (*ridibunda*) sp. *Triturus helveticus*, *Triturus vulgaris*, *Rana arvalis*, *Rana temporaria*, *Lacerta vivipara*, *Anguis fragilis*, and *Natrix natrix* indicate a rather moist terrestrial habitat. *Bufo bufo* and *Bufo calamita* could have lived in a somewhat dryer situation.

3. Maasvlakte Lake, near Rotterdam, Netherlands

Taxon. *Emys orbicularis*.

References. Fritz (1995), Kerkhoff (1986, 1987).

Remarks. Historic records of *Emys orbicularis* exist in the Rotterdam area (Sparreboom, 1981), but the species evidently no longer occurs there.

Belgium

Belgium also has only a few sites where Pleistocene amphibians or reptiles have been recorded.

Upper Pleistocene

1. Marie-Jeanne, Hastière-Lavaux, Belgium

Taxa. *Bufo bufo*, *Bufo* cf. *Bufo calamita*, *Rana* (*ridibunda*) sp., *Rana temporaria*.

References. Ballmann et al. (1980), Sanchiz (in press).

Remarks. All of these species currently occur in Belgium. As a whole the fauna is not a strong indicator of climate. *Rana* (*ridibunda*) sp. indicates the presence of a permanent, low-energy aquatic situation. *Rana temporaria* suggests a moist terrestrial habitat, whereas *Bufo calamita* could have existed in a dryer upland area.

2. Namur, Grand Malades area, Namur Province, Belgium

Taxon. *Emys orbicularis*.

References. Fritz (1995), Parent (1979), Schreuder (1946).

Remarks. This site has been questionably suggested to be an anaglacial phase of the Würm I stage of the Upper Pleistocene (Fritz, 1995). Certainly the presence of *Emys orbicularis* indicates a temperate rather than a full glacial climate. This species has been recently recorded in the general region (see Sparreboom, 1981, map, p. 252).

3. Trou Félix Cave, near Dinant, Belgium

Taxon. *Emys orbicularis*.

References. Fritz (1995), Parent (1979), Schreuder (1946), Ullrich and Młynarski (1978).

Remarks. Again, the presence of *Emys orbicularis* indicates a temperate rather than a glacial climate.

Luxembourg

Few Pleistocene herpetological remains are known from Luxembourg.

Peistocene Undesignated

1. Oetrange, Luxembourg

Taxon. *Pelobates fuscus.*

References. Ferrant and Friant (1940), Sanchiz (in press).

Remarks. Although *Pelobates fuscus* presently occurs in the Netherlands and Belgium, there are apparently no records of this species in the modern fauna of Luxembourg (Sparreboom, 1981, map, p. 242).

Germany

Germany is enriched with many interesting Pleistocene herpetological sites. Unfortunately, material of several supposedly extinct Pleistocene species is lost or has been poorly described. There are many records of *Emys orbicularis* in the Pleistocene of Germany. This species indicates the presence of a permanent, low-energy body of water with abundant aquatic vegetation. *Emys orbicularis* together with with several other species is indicative of climatic optimum warm periods in the German Pleistocene (Böhme, 1996). Most of the German Pleistocene records of *Elaphe longissima* are either extralimital or at least extralocal as the species presently occurs only in isolated areas in southwestern Germany near Frankfort and Mannhiem and in the extreme southeastern part of the country. Figure 42 indicates the location of important Pleistocene herpetological sites in Germany.

Lower Pleistocene

1. Hohensulzen, southern Rheinhessen, (Hessia), Germany

Taxon. *Rana* cf. *Rana arvalis.*

References. Sanchiz (in press), Weiler (1952).

Remarks. This species indicates the presence of a moist terrestrial habitat.

2. Wilhelma-Bäerengehege, Stuttgart, southwestern Germany

Taxon. *Rana temporaria.*

References. Böttcher (1994), Sanchiz (in press).

Remarks. A rich, well-preserved fish fauna was an important feature of this site (Böttcher, 1994). *Rana temporaria* indicates the presence of a moist terrestrial habitat near the aquatic one.

FIGURE 42. Location map of some important Pleistocene herpetological sites in Germany. (1) Kärlich Middle Pleisteocene sites and Miesenheim Middle and Upper Pleistocene sites; (2) Steinheim on the Murr Upper Pleistocene site; (3) Steinbrüche Hass und Lauster and Steinbruch Schmid Middle Pleistocene sites and Villa Seckendorff Upper Pleistocene site; (4) Hunas near Hartmannshof Middle Pleistocene site and Teufelshöhle Upper Pleistocene site; (5) Teufelsbrücke Upper Pleistocene site; (6) Lobsing Upper Pleistocene site; (7) Ehringsdorf Middle and Upper Pleistocene site and Parkhöhlen and Taubach Upper Pleistocene sites; (8) Bad Langensalza, Burgtonna, and Gräfentonna Upper Pleistocene sites; (9) Muehlhausen Middle Pleistocene site; (10) Bilzingsleben Middle Pleistocene site; (11) Schönfeld near Cottbus Upper Pleistocene site; (12) Pisede near Malchin Upper Pleistocene and Holocene site.

Middle Pleistocene

1. Bilzingsleben, north of Erfurt, Thuringia, central Germany

Taxa. *Bufo bufo*, *Natrix natrix*.

References. Böhme (1989), Koenigswald (1995), Kolfschoten (1992), Sanchiz (in press).

Remarks. The Bilzingsleben site represents the Holsteinian interglacial stage of the Middle Pleistocene (Kolfschoten, 1992). This is a well-known hunting site of *Homo erectus* (Koenigswald, 1995). The presence of *Bufo bufo* and *Natrix natrix* indicates that a somewhat moist terrestrial area was probably some-where near the site, but these two species tolerate such a wide range of temperatures that it is difficult to suggest a specific paleoclimate.

2. Breitenburg Cave, near Gössweinstein, Bavaria, Germany

Taxa. *Salamandra salamandra*, *Triturus* sp., *Bufo bufo*, *Rana temporaria*, *Lacerta* cf. *Lacerta* (''*Podarcis*'') *sicula*, *Lacerta* sp., *Anguis fragilis*, *Coluber viridiflavus*, **Natrix rusticus*.

References. Brunner (1938, 1953, 1957, 1958b, 1959), Estes (1981, 1983), Młynarski (1961, 1962, 1964), Rage (1984c), Sanchiz (in press), Sanchiz and Schleich (1986), Szyndlar and Böhme (1993).

Remarks. The taxonomy of this herpetofauna has been revised by several authors, and the snakes are presently under revision by M. Ivanov of Brno, Czech Republic. A previous report of the Mediterranean species *Elaphe situla* on the basis of fragmentary tooth-bearing bones (Brunner, 1957) is probably invalid (Szyndlar and Böhme, (1993). *Coluber viridiflavus* reported by Brunner (1958b) is included here, although Szyndlar and Böhme (1993) state the record is probable but not convincing. Both *Coluber viridiflavus* and *Lacerta* (''*Podarcis*'') *sicula* are extralimital southern species that now occur nearest the site in Switzerland.

Anguis fragilis is the robust form referred to by some previous authors as ''**Anguis stammeri*.'' **Natrix rusticus* is a nomen dubium (Rage (1984c) and probably represents some living colubrid species. If all of the present specific identifications are correct, a warmer climate than presently exists in the area is suggested. In this light, the restudy of the numerous snake fossils is quite important.

3. Ehringsdorf Site Complex, Middle Pleistocene Lower Travertine Unit, near Weimar, Thuringia, central Germany

Taxa. Lower Section of the Lower Travertine Unit: *Rana arvalis*, *Emys orbicularis*, *Elaphe longissima*, *Natrix natrix*. Upper Section of the Lower Travertine Unit: *Triturus cristatus*, *Triturus vulgaris*, *Bufo bufo*, *Bufo viridis*, *Hyla arborea*, *Rana temporaria*, *Anguis fragilis*, *Coronella austriaca*, *Natrix natrix*, *Vipera berus*. Pocket in the Lower Travertine Unit: *Bufo bufo*, *Rana temporaria*, *Anguis fragilis*, *Coronella austriaca*, *Natrix natrix*, *Vipera berus*.

References. Böhme (1989, 1997), Heinrich (1981), Koenigswald (1995), Młynarski and Ullrich (1975).

Remarks. The complex Ehringsdorf site transcends Middle and Upper Pleistocene time and has been repeatedly occupied by an ancient form of *Homo sapiens*. The Lower Travertine Unit appears to represent the Middle Pleistocene Saalian glacial sequence (Kahlke in Koenigswald, 1995). The Lower Section of the Lower Travertine Unit represents a mild climate based on the presence of *Emys orbicularis* and *Elaphe longissima*. The Upper Section of the Lower Travertine Unit and the Pocket in the Lower Travertine Unit probably represent the return of cooler times. The seemingly unlikely occurrence of *Emys orbicularis* in association with the wooly mammoth (*Mammuthus primegenius*) in the site (Kahlke in Koenigswald, 1995) might indicate a transitional climate.

4. Erpfingen, Germany

Taxon. *Rana* sp.

References. Heller (1936), Sanchiz (in press).

Remarks. This site was considered to be equivalent to the type Cromerian section at West Runton, Norfolk, England, by Heller (1936); thus, the locality could represent one of the Cromerian complex interglacial sequences presently recognized in Europe (see Fig. 2).

5. Federsee, southwestern Germany

Taxon. *Emys orbicularis.*

Reference. Fritz (1995).

Remarks. This site is questionably referred to the Holsteinian interglacial stage (Fritz, 1995).

6. Fuchsloch, Siegmannsbrunn, Bavaria, Germany

Taxa. *Bufo* sp., *Rana* sp., *Anguis fragilis*, **Coluber freybergi.*

References. Brunner (1954), Estes (1983), Rage (1984c), Sanchiz (in press), Szyndlar and Böhme (1993).

Remarks. This is the type locality of **Coluber freybergi* (see Chapter 4) that is probably a synonym of the modern species *Coluber viridiflavus*, a southern form that occurs nearest the site in Switzerland. *Anguis fragilis* is the robust "**Anguis stammeri*" form, also originally described from Fuchsloch.

7. Hunas near Hartmannshof, Erlangen area, Bavaria, Germany

Taxa. *Triturus alpestris*, *Bufo bufo*, *Rana arvalis*, *Rana temporaria*, *Lacerta agilis*, *Anguis fragilis*, *Vipera* cf. *Vipera berus.*

References. Böhme (in press), Brunner (1936), Groiss (1983), Heller (1983), Koenigswald (1995), Stadie (1983).

Remarks. The Hunas site represents the ruins of an ancient cave filling that contains human artifacts as well as vertebrate faunal remains. An analysis of the herpetofauna was done by Böhme (in press), who suggests the ancient cave sediments are of late Middle Pleistocene age. The herpetofauna could have existed in a relatively cool, moist climate. The herpetofauna represents a rather moist terrestrial habitat as well as a somewhat dryer area (*Bufo bufo* and *Lacerta agilis*).

8. Kärlich E, near Koblenz, southwestern Germany

Taxa. Anuran indet., *Bufo* sp.

References. Holman and Kolfschoten (1997b), Kolfschoten and Turner (1996).

Remarks. The Kärlich E site represents the Dutch/European Cromerian complex stage II of the Middle Pleistocene (Kolfschoten and Turner, 1996).

9. Kärlich G, near Koblenz, southwestern Germany

Taxa. *Triturus cristatus*, *Triturus helveticus* or *vulgaris*, *Triturus vulgaris*, *Bufo bufo*, *Bufo* sp., *Lacerta agilis*, *Lacerta vivipara*, *Lacerta* sp., *Anguis fragilis.*

References. Holman and Kolfschoten (1997b), Koenigswald (1995), Kolfschoten and Turner (1996), Urban (1983).

Remarks. The Kärlich G site represents Dutch/European Cromerian complex stage III of the Middle Pleistocene (Kolfschoten and Turner, 1996). In reference to well-known British herpetofaunas, this site would be older than the Boxgrove and Westbury–Sub-Mendip herpetofaunas that are thought to represent the Dutch/European Cromerian complex stage IV and younger than the West Runton herpetofauna that represents stage II.

Based on the Kärlich G herpetofauna, there is no indication that the paleoclimate was either warmer or cooler than it is at present. A moist terrestrial habitat is indicated by the newt species as well as by *Lacerta vivipara* and *Anguis fragilis*. *Lacerta agilis* indicates the presence of a dryer terrestrial situation.

10. Kärlich H, near Koblenz, southwestern Germany

Taxa. *Triturus helveticus* or *vulgaris*, *Lacerta* cf. *Lacerta vivipara*, *Anguis fragilis*.

References. Holman and Kolfschoten (1997b), Kolfschoten and Turner (1996).

Remarks. The Kärlich H site is considered to represent the Holsteinian interglacial stage of the Middle Pleistocene (Kolfschoten and Turner, 1996). All of these species presently occur in the area. The assemblage is indicative of a moist terrestrial habitat.

11. Klinge near Cottbus, Lusatian Area, eastern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This site is questionably referred to the Holsteinian interglacial stage of the Middle Pleistocene (Fritz, 1995).

12. Köchstedt, near Hamburg, northern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Toepfer (1963).

Remarks. This site is referred to the Holsteinian interglacial stage of the Middle Pleistocene (Fritz, 1995). This locality, and the several Pleistocene localities near Hamburg that follow, are in the vicinity of the northern limits of the historical distribution of *Emys orbicularis* in Germany.

13. Miesenheim I, Neuwied Basin, southwestern Germany

Taxa. *Triturus cristatus*, *Triturus vulgaris*, *Triturus helveticus* or *vulgaris*, *Bufo bufo*, *Bufo* sp., *Rana arvalis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Rana* sp., *Lacerta* sp., *Anguis fragilis*, *Natrix natrix*, *Natrix* sp.

References. Holman and Kolfschoten (1997d), Koenigswald (1995), Kolfschoten and Turner (1996).

Remarks. The Miesenheim I site represents Dutch/European Cromerian interglacial stage IV and thus is thought to be equivalent in age to the Boxgrove and Westbury–Sub-Mendip sites in Britain (Kolfschoten and Turner, 1996).

This herpetofauna does not indicate that the Pleistocene climate of the area was either warmer or cooler than it is at present. All of the herpetological species presently currently occur in the area except for *Rana arvalis* which occurs east and southeast of the site near Limburg and Wiesbaden. *Rana* (*ridibunda*) sp. indicates the presence of a permanent, low-energy body of water. *Triturus cristatus*, *Triturus vulgaris*, *Rana arvalis*, *Rana temporaria*, *Anguis fragilis*, and *Natrix natrix* would have occurred in a moist habitat nearby.

14. Muehlhausen, Thuringia, central Germany

Taxa. *Triturus cristatus*, *Triturus vulgaris*, *Bufo bufo*, *Rana temporaria*, *Anguis fragilis*, *Natrix natrix*.

Reference: Böhme (1989).

Remarks. This Saalian glacial site herpetofauna indicates the presence of a moist terrestrial habitat.

15. Steinbrüche Hass and Lauster, Stuttgart, Southwestern Germany

Taxa. *Bufo bufo*, *Emys orbicularis*.

References. Böttcher (1994), Sanchiz (in press).

Remarks. A permanent low-energy aquatic situation with a nearby terrestrial habitat is indicated.

16. Steinbruch Schmid, Stuttgart, southwestern Germany

Taxa. *Pelodytes punctatus*, *Bufo viridis*, *Rana temporaria*, *Anguis fragilis*, *Elaphe longissima*, *Vipera* sp.

References. Böttcher (1994), Sanchiz (in press).

Remarks. These species could have ranged from a moist, terrestrial habitat (*Pelodytes punctatus*, *Rana temporaria*, and *Anguis fragilis*) to a somewhat dryer, shrubby one (*Bufo viridis* and *Elaphe longissima*). *Pelodytes punctatus* presently occurs west of the site in France and *Elaphe longissima* is extralocal.

17. Stuttgart-Bad, Cannstatt, southwestern Germany

Taxon. *Emys orbicularis*.

Reference: Fritz (1995).

Remarks. This site has been referred to the Holsteinian interglacial stage of the Middle Pleistocene (Fritz, 1995).

18. Sudmer-Berg 2, Harz Mountains area, central Germany

Taxon. *Bufo* sp.

References. Koenigswald (1972), Sanchiz (in press).

19. Sulzerrain, Stuttgart, southwestern Germany

Taxa. *Rana* sp., *Emys orbicularis*, *Natrix* cf. *Natrix natrix*.

References. Böttcher (1994), Sanchiz (in press).

Remarks. A permanent, low-energy aquatic situation (*Emys orbicularis*) and a moist terrestrial habitat (*Natrix* cf. *Natrix natrix*) are indicated.

20. Voigtstedt, Thuringia, central Germany

Taxa. **Pliobatrachus* cf. *Pliobatrachus langhae*, *Bufo* sp., *Rana* sp.

References. Kretzoi (1965), Sanchiz (in press).

Remarks. This is one of the latest occurrences of this extinct genus of palaeobatrachid frog.

Middle or Upper Pleistocene

1. Gräfentonna, near Hamburg, northern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Karl (1984), Ullrich (1956).

Middle and Upper Pleistocene

1. Köenigslutter, near Hamburg, northern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Ullrich and Młynarski (1978).

2. Wildscheuer, Germany

Taxon. *Rana* sp.

References. Éhik (1920–21), Sanchiz (in press).

Upper Pleistocene

1. Bad Langensalza, near Erfurt, Thuringia, Germany

Taxon. *Lacerta* sp.

Reference: Estes (1983).

2. Burgtonna, northwest of Erfurt, Thuringia, central Germany

Taxa. Travertine Unit: *Emys orbicularis*, *Elaphe longissima*. *Hystrix* Horizon: *Triturus* cf. *Triturus vulgaris*, *Bufo bufo*, *Rana* cf. *Rana arvalis*, *Rana temporaria*, *Anguis fragilis*, *Lacerta* sp. *Vipera berus*. Laminated Horizon (Deckschichten): *Pelobates fuscus*, *Bufo bufo*, *Bufo viridis*, *Hyla arborea*, *Rana arvalis*, *Rana temporaria*, *Rana* (*ridibunda*) sp., *Lacerta* cf. *Lacerta vivipara*, *Natrix natrix*, *Vipera berus*.

References. Böhme (1989, 1997), Fritz (1995), Heinrich and Jäger (1978), Karl (1984), Koenigswald (1995), Maul (1994), Młynarski et al. (1978), Sanchiz (in press), Szyndlar and Böhme (1993), Ullrich and Młynarski (1978).

Remarks. The Burgtonna site represents the Eemian (last) interglacial into early Weichselian glacial times (Koenigswald, 1995). *Emys orbicularis* and *Elaphe longissima* of the Travertine Unit indicate an optimum warm phase for that depositional sequence. The late Eemian *Hystrix* Horizon herpetofauna dominated by *Rana temporaria* indicates a return to cooler conditions. The Laminated Horizon (Deckschichten) contains a *Rana temporaria*–dominated herpetofauna that indicates a continuation of cooler times, but it also contains a steppe component (*Pelobates fuscus* and *Bufo viridis*). The fauna of the Laminated Horizon probably represents the early Weichselian (last glacial) sequence (see Mania, Heinrich, and Maul references in Koenigswald, 1995).

3. Ehringsdorf Site Complex, Upper Pleistocene Units, near Weimar, Thuringia, central Germany

Taxa. Pariser Unit: *Salamandra salmandra*, *Triturus cristatus*, *Triturus vulgaris*, *Pelobates fuscus*, *Bufo bufo*, *Rana arvalis*, *Rana temporaria*, *Rana* (*ridibunda*) sp., *Lacerta agilis*, *Anguis fragilis*, *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*. Upper Travertine Unit: *Anguis fragilis*, *Coronella austriaca*, *Natrix natrix*. Black Colluvial Unit: *Triturus vulgaris*, *Bufo bufo*, *Bufo viridis*, *Rana arvalis*, *Rana temporaria*, *Lacerta vivipara*, *Anguis fragilis*, *Vipera berus*.

References. Böhme (1997), Böhme and Heinrich (1994), Heinrich (1994), Koenigswald (1995), Młynarski and Ullrich (1975), Schäfer (1986).

Remarks. The Upper Units of the complex Ehringsdorf Site, near Weimar, represent the Upper Pleistocene. The Pariser Unit is a loosely cohesive muddy sediment up to 2 m thick that forms a continuous horizon that covers the Lower Travertine Unit discussed in the German Middle Pleistocene accounts above. The Pariser is thought to represent the Eemian (last) interglacial sequence of the Upper Pleistocene.

The rich Pariser herpetofauna contains the robust form of *Anguis fragilis* ("**Anguis stammeri*" of Brunner, 1954) and the extralimital southern form *Elaphe longissima*, and is thought to indicate a warmer climate than presently exists in the area. The three herpetological species in the Upper Travertine Unit currently occur in the area and much farther north as well. The dominance of *Rana temporaria* and *Vipera berus* in the Black Colluvial Unit, as well as the presence of *Lacerta vivipara*, is thought to indicate a return to a cooler climate.

4. Gamsenberg near Oppung, Thuringia, central Germany

Taxa. *Triturus* cf. *Triturus cristatus, Rana* sp., *Anguis fragilis, Coronella austriaca, Natrix* cf. *Natrix natrix.*

Reference: Schäfer et al. (1991).

Remarks. It has been suggested that this Palaeolithic archaeological site represents a full glacial part of the Weichselian glacial age (Schäfer et al., 1991). The herpetofauna, however, is more likely to indicate a moderately cool climate.

5. Geissenklosterle near Blaubeuren, Germany

Taxon. *Rana temporaria.*

References. Böhme (1982), Sanchiz (in press).

6. Godenstedt, near Hamburg, northern Germany

Taxon. *Emys orbicularis.*

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This site is referred to the Eemian interglacial stage of the Upper Pleistocene (Fritz, 1995).

7. Grabschütz, Gräfenhainichen, Germany

Taxa. *Triturus cristatus, Triturus* cf. *Triturus vulgaris, Bufo bufo, Hyla arborea, Rana* cf. *Rana arvalis, Rana temporaria, Rana* sp., *Lacerta* cf. *Lacerta agilis, Lacerta* sp., *Anguis fragilis, Natrix* cf. *Natrix natrix.*

Reference. Benecke et al. (1990).

Remarks. "*Rana* sp." designates unidentified water frog and brown frog species. The water frog indicates the presence of a permanent, low-energy, aquatic situation, and the remainder of the herpetofauna mainly indicates a moist terrestrial habitat.

8. Gräfentonna Travertine, near Erfurt, Thuringia, central Germany

Taxon. *Coronella austriaca.*

References. Böhme (1989), Ullrich and Młynarski (1978).

9. Gröbern, Delitzsch, Germany

Taxa. *Triturus* cf. *Triturus vulgaris, Bufo* cf. *Bufo bufo, Anguis fragilis, Natrix* cf. *Natrix natrix.*

Reference. Benecke et al. (1990).

Remarks. This herpetofauna indicates a rather moist terrestrial habitat.

10. Grundfelsen Cave near Gaisheim, Nuremberg area, southeastern Germany

Taxa. *Salamandra salamandra, Bufo bufo, Rana temporaria, Lacerta agilis, Anguis fragilis, Elaphe longissima, Natrix natrix.*

References. Brunner (1942–1943), Sanchiz (in press), Szyndlar and Böhme (1993).

Remarks. The amphibians, as well as *Anguis fragilis* and *Natrix natrix*, indicate a rather moist terrestrial habitat. *Lacerta agilis* and *Elaphe longissima* indicate a dryer terrestrial situation. *Elaphe longisima* is an extralimital form that presently occurs nearest the site in extreme southeastern Germany.

11. Günthersthaler Lake near Velden, Nuremberg area, southeastern Germany

Taxa. *Triturus* sp., *Bufo bufo*, *Rana temporaria*, *Emys orbicularis*, *Vipera berus*.

References. Brunner (1950), Szyndlar and Böhme (1993).

Remarks. These taxa indicate the presence of a pond and a rather moist terrestrial habitat as well as a temperate climate. *Coluber hippocrepis*, a snake that presently occurs in the Mediterranean region, was reported from this site on the basis of a fragmentary toothed bone by Brunner (1950). This identification is thought to be invalid by Szyndlar and Böhme (1993), so the species is not included in the taxonomic list.

12. Honerdingen, near Hamburg, northern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This site is referred to the Eeemian interglacial stage of the Upper Pleistocene (Fritz, 1995).

13. Kemathen Cave, Germany

Taxon. *Rana temporaria*.

References. Böhme (1982), Sanchiz (in press).

14. Klein-Lieskow near Cottbus, Lusatian area, eastern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Striegler (1991).

15. Lehmgrube Biedensteg (Biedensteg Clay Pit), Germany

Taxa. *Pelobates fuscus*, *Bufo viridis*, *Rana* (*ridibunda*) sp., *Rana temporaria*.

References. Jacobshagen (1963), Sanchiz (in press).

Remarks. *Rana* (*ridibunda*) sp. indicates the presence of a permanent, low-energy body of water. *Rana temporaria* indicates a moist terrestrial habitat, whereas *Pelobates fuscus* and *Bufo viridis* indicate a dryer terrestrial habitat.

16. Llisenhöhle (Llisen Cave), Ranis, Thuringia, central Germany

Taxa. *Salamandra salamandra*, *Rana temporaria*, *Anguis fragilis*.

References. Böhme (1997), Hülle (1977).

Remarks. This Palaeolithic herpetofauna indicates a moist terrestrial habitat.

17. Lobsing, near Neustadt/Donau, Bavaria, Germany

Taxa. Indeterminate Anurans, *Elaphe longissima*.

References. Böhme (1997, in press), Heller (1960), Rage (1984c), Szyndlar and Böhme (1993).

Remarks. This Eemian site is the type locality of **Elaphe lobsingensis* (Heller, 1960). This taxon has been synonymized with *Elaphe longissima* (discussed in the *Elaphe* account, Chapter 4).

18. Michelfeld, Oberfalz, Germany

Taxa. *Bombina* sp., *Pelobates fuscus*, *Bufo bufo*, *Rana temporaria*.

References. Brunner (1958a), Sanchiz (in press).

Remarks. Both modern species of *Bombina* are often found in shallow water situations. *Rana temporaria* would be found in moist areas near the aquatic situation, and *Pelobates fuscus* and *Bufo bufo* indicate a dryer terrestrial habitat.

19. Miesenheim II, Neuwied Basin, southwestern Germany

Taxa. *Bufo bufo*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Lacerta vivipara*.

References. Holman and Kolfschoten (1997d).

Remarks. This site was radiocarbon-dated at about 11,000 ybp and thus represents very late Weichselian glacial time. All of these taxa presently occur in the area. *Rana* (*ridibunda*) sp. indicates the presence of a permanent, low-energy body of water. *Bufo bufo*, *Rana temporaria*, and *Lacerta vivipara* could have existed in a rather moist, terrestrial situation near the aquatic habitat. The herpetofauna may indicate cool conditions but probably not a full glacial climate.

20. Nedder-Aversbergen, near Hamburg, northern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This deposit is considered to represent the Eemian interglacial stage of the Upper Pleistocene (Fritz, 1995).

21. Osterode am Fallstein, Kreis-Halberstadt, near Hamburg, northern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This site is also considered to represent the Eemian interglacial stage of the Upper Pleistocene (Fritz, 1995).

22. Parkhöhlen (Park Cave) Travertine, Weimar, Thuringia, central Germany

Taxa. *Bufo bufo*, *Rana temporaria*, *Emys orbicularis*, *Anguis fragilis*, *Elaphe longissima*.

References. Böhme (1989, 1997).

Remarks. This Eemian interglacial site has produced *Emys orbicularis* and *Elaphe longissima*, species that indicate an optimal warm climate (Böhme, 1996).

23. Rabutz, near Hamburg, northern Germany

Taxon. *Emys orbicularis*.

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This is yet another site in the Hamburg region that is referred to the Eemian interglacial stage of the Upper Pleistocene (Fritz, 1995).

24. Rübeland, Harz Mountain area, northern central Germany

Taxon. *Rana temporaria*.

Reference: Arnold et al. (1982).

Remarks. This cave site has a vertebrate fauna that contains arctic and boreal birds and mammals that indicate a Weichselian full glacial climate. The fact that only one herpetological species, the very cold-tolerant *Rana temporaria*, occurs at the site follows the model of Böhme (1996).

25. Schönfeld near Cottbus, Lusatian area, eastern Germany

Taxa. *Salamandra* cf. *Salamandra salamandra*, *Bufo bufo*, *Rana.* (*ridibunda*) sp., *Rana* sp., *Emys orbicularis*, *Anguis fragilis*, *Elaphe longissima*, *Natrix natrix.*

References. Böhme (1991), Fritz (1995), Striegler (1991), Striegler and Striegler (1983), Ullrich (1984).

Remarks. The Schönfeld site is referred to the Eemian interglacial of the Upper Pleistocene. The presence of *Emys orbicularis* and *Elaphe longissima* suggests an optimal warm climate. The *Rana* sp. designation indicates a specifically unidentified brown frog. This is a northern extralimital record for *Elaphe longissima* which presently occurs nearest the site in extreme southeastern Germany.

26. Sirgenstein, Germany

Taxa. *Bufo* sp., *Rana* sp.

Reference: Sanchiz (in press).

27. Steinheim on the Murr, north of Stuttgart, southwestern Germany

Taxa. *Triturus cristatus*, *Triturus vulgaris*, *Bombina* cf. *Bombina variegata*, *Pelobates fuscus*, *Bufo bufo*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Lacerta agilis*, *Lacerta vivipara*, *Anguis fragilis*, *Coronella austriaca*, *Natrix* cf. *Natrix natrix*, *Vipera* cf. *Vipera berus.*

References. Bloos et al. (1991), Koenigswald (1995), Sanchiz (in press), Szyndlar and Böhme (1993), Ziegler (1989).

Remarks. This site is believed to represent the transition time between the Eemian and Weichselian stages of the Upper Pleistocene. The bones resulted from animals hibernating in the cave as well as from badger dung and owl pellets.

A permanent, low-energy body water is indicated by the presence of *Rana* (*ridibunda*) sp. and *Bombina* cf. *Bombina variegata.* A moist terrestrial habitat is indicated by the newts, as well as by *Rana temporaria*, *Anguis fragilis*, and *Natrix* cf. *Natrix natrix.* The other amphibians and reptiles indicate a somewhat dryer terrestrial situation.

28. Taubach near Weimar, Thuringia, central Germany

Taxa. *Bufo bufo*, *Rana temporaria*, *Emys orbicularis*, *Anguis fragilis*, *Elaphe longissima.*

References. Böhme (1989, 1997), Fritz (1995) Młynarski and Ullrich (1977), Sanchiz (in press). Szyndlar and Böhme (1993), Tatarinov (1984), Wolterstorff (1896).

Remarks. This site is referred to the Eemian interglacial stage of the Upper Pleistocene. The presence of *Emys orbicularis*, *Elaphe longissima*, and the robust form of *Anguis fragilis* (= "**Anguis stammeri*") is consistent with an optimal warm climate.

29. Teufelsbrücke (Devil's Bridge) near Saalfeld, Thuringia, central Germany

Taxa. *Bufo bufo*, *Rana arvalis*, *Rana temporaria.*

References. Böhme (1980, 1991). Sanchiz (in press).

Remarks. This archaeological site represents the end of the Dryas II settlement period and had a moderately cool to subarctic climate at the time of the deposition of the bones (Böhme, 1980). This anuran fauna would be most consistent with a cool climate.

30. Teufelshöhle (Devil's Cave), Pottenstein, northeast of Erlangen, Bavaria, Germany

Taxa. *Proteus* sp., *Triturus* sp., *Bombina* sp., *Bufo bufo*, *Bufo viridis*, *Rana arvalis*, *Rana temporaria*, *Rana* sp., ?*Lacerta* sp., *Anguis fragilis*, (snakes under revision).

References. Brunner (1938, 1951, 1956), Estes (1981), Koenigswald (1995), Sanchiz (in press), Szyndlar and Böhme (1993).

Remarks. This site is considered to represent the Weichselian glacial age of the Upper Pleistocene (Koenigswald, 1995). The dominant member of the fauna is the cave bear (*Ursus spelaeus*). The faunal list has been greatly revised since the early papers of Brunner (see references listed), and the fossil snakes from this site are presently under revision by M. Ivanoff of Brno, Czech Republic.

A somewhat doubtful record is that of the neotenic cave salamander, *Proteus*, that reaches the northernmost part of its present range just north of the Adriatic Sea. The fauna definitely does not represent a full glacial climatic part of the Weichselian glacial stage, as it contains *Bombina* and the robust form of *Anguis fragilis* (= "**Anguis stammeri*").

31. Thuisbrunn, Germany

Taxon. *Rana temporaria*.

Reference. Sanchiz (in press).

32. Villa Seckendorff, Stuttgart, southwestern Germany

Taxa. *Triturus cristatus*, *Pelobates* cf. *Pelobates fuscus*, *Bufo viridis*, *Rana temporaria*, *Lacerta* cf. *Lacerta vivipara*, *Coronella austriaca*.

References. Böttcher (1994), Sanchiz (in press).

Remarks. This fauna suggests a moist terrestrial situation (*Triturus cristatus*, *Rana temporaria*, and *Lacerta* cf. *Lacerta vivipara*) as well as a dryer terrestrial habitat (*Pelobates* cf. *Pelobates fuscus* and *Bufo viridis*).

33. Weimar Travertines, Thuringia, central Germany

Taxon. *Emys orbicularis*.

Reference. Ullrich (1984).

Remarks. These Eemian travertines yielded a total of 17 individual *Emys orbicularis* and one clutch of eggs of this species (Ullrich, 1984).

Pleistocene Undesignated

1. Sackdillinger Cave, Oberpfalz, Germany

Taxa. *Bufo* sp., *Rana temporaria*.

References. Dely (1955a), Heller (1930), Sanchiz (in press).

2. Schmiedberg-Abri near Hirschbach, Oberpfalz, Germany

Taxa. *Bufo bufo*, *Rana* sp.

References. Brunner (1959), Sanchiz (in press).

3. Steinbruch Biedermann, Stuttgart, southwestern Germany

Taxa. *Bufo bufo*, *Bufo calamita*, *Rana* (*ridibunda*) sp., *Lacerta* sp., *Natrix* cf. *Natrix natrix*.

References. Böttcher (1994), Sanchiz (in press).

Remarks. A permanent, shallow, low-energy body of water is indicated by *Rana* (*ridibunda*) sp. *Natrix* cf. *Natrix natrix* suggests a moist terrestrial situation. *Bufo bufo* and *Bufo calamita* suggest a somewhat dryer habitat.

4. Thiede, Germany

Taxa. *Pelobates fuscus*, *Bufo* sp., *Rana temporaria*.

References. Kuhn (1971), Sanchiz (in press).

Remarks. *Rana temporaia* indicates a moist terrestrial situation, and *Pelobates fuscus* suggests a somewhat dryer terrestrial habitat.

5. Thiele, Germany

Taxon. *Pelobates* cf. *Pelobates fuscus*.

References. Kuhn (1971), Sanchiz (in press).

6. Viadukt, Stuttgart, southwestern Germany

Taxa. *Bufo bufo*, *Anguis fragilis*, *Coronella austriaca*, *Elaphe longissima*, *Vipera* sp.

References. Böttcher (1994), Sanchiz (in press).

Remarks. A moist terrestrial habitat (*Anguis fragilis*) as well and dryer terrestrial situation (*Elaphe longissima*) are suggested.

7. Weimar-Stadtgebiet, Germany

Taxa. *Bufo bufo*, *Rana temporaria*.

References. Böhme (1989), Wolterstorff (1896), Sanchiz (in press).

8. Westeregeln, Germany

Taxa. *Pelobates fuscus*, *Bufo* sp., *Rana temporaria*.

Reference. Sanchiz (in press).

Remarks. *Rana temporaria* indicates a moist terrestrial situation, and *Pelobates fuscus* indicates the presence of a dryer habitat.

9. Wuerzburg, southwestern Germany

Taxa. *Rana temporaria*.

References. Sanchiz (in press), Sandberger (1870–1875).

10. Württemburg (only), southwestern Germany

Taxon. *Testudo hermanni*.

References. Auffenberg (1974), Młynarski (1976), Plieninger (1847).

Remarks. The nearest this species presently occurs to the Württemburg district of Germany is the Mediterranean basin of France. This material should be restudied, and the precise age of the fauna should be established.

11. Zuzlawitz, Germany

Taxa. cf. *Bufo*, *Rana* sp.

References. Sanchiz (in press), Woldrich (1881), Wolterstorff (1885, 1886).

Upper Pleistocene/Holocene Boundary

1. Bedburg-Königshoven, near Nordrhein, Westfalen, Germany

Taxa. *Bufo* sp., *Rana arvalis*, Anuran indeterminate.

References. Holman and Kolfschoten (1997a), Kolfschoten (1994).

Remarks. This site has been dated from 9,600 to 9,700 ybp (Kolfschoten, 1994).

Upper Pleistocene or Holocene

1. Magdeburg, northeastern Germany.

Taxon. *Pelobates* cf. *Pelobates fuscus.*

References. Gislen (1936), Sanchiz (in press).

Upper Pleistocene and Holocene

1. Dietfurt near Sigmaringen, Germany

Taxa. *Anguis fragilis*, *Coronella austriaca*, *Natrix natrix*, *Vipera berus.*

References. Markert (1976), Szyndlar and Böhme (1993).

Remarks. A somewhat moist terrestrial habitat is suggested by this small herpetofauna.

2. Euerwanger Bühl, near Greding, Nuremberg area, southeastern Germany

Taxa. *Anguis fragilis*, *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*, *Natrix tesselata*, *Natrix* sp.

References. Markert (1975, 1976), Szyndlar and Böhme (1993).

Remarks. The presence of a low-energy aquatic situation is indicated by the presence of *Natrix tesselata*, a very aquatic species. A rather moist terrestrial habitat (e.g., *Anguis fragilis* and *Natrix natrix*) and a dryer upland situation (*Elaphe longissima*) are also indicated. *Elaphe longissima* presently occurs south of the site in extreme southeastern Germany, while *Natrix tesselata* is currently found in three isolated populations in the Rhineland and Palatinate districts of southwestern Germany.

3. Malerfels near Greding, Nuremberg area, southeastern Germany

Taxa. *Anguis fragilis*, *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*, *Natrix tesselata*, *Vipera berus*, *Vipera* sp.

Reference: Markert (1976).

Remarks. This small reptile fauna indicates the same type of habitats as the Euerwanger Bühl fauna described above and it also contains the extralimital taxa *Elaphe longissima* and *Natrix tesselata.*

4. Pisede near Malchin, Neubrandenberg, northeastern Germany

Taxa. *Triturus cristatus*, *Triturus vulgaris*, *Bombina bombina*, *Pelobates fuscus*, *Bufo bufo*, *Bufo calamita*, *Hyla arborea*, *Rana arvalis*, *Rana dalmatina*, *Rana "esculenta,"* *Rana lessonae*, *Rana ridibunda*, *Rana temporaria*, *Emys orbicularis*, *Lacerta agilis*, *Lacerta vivipara*, *Anguis fragilis*, *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*, *Vipera berus.*

References. Böhme (1979, 1983b), Böhme and Günther (1979), Estes (1981), Heinrich et al. (1983), Ippen and Heinrich (1977), Markert (1976), Peters (1977a, 1997b), Sanchiz (in press).

Remarks. This large herpetofauna has been well studied, and the amphibian fauna has been most recently reviewed by Sanchiz (in press). A system of small mammal burrows covering more than 10,000 years was significant in the accumulation of the vertebrate bones (Heinrich et al., 1983). Two extralimital species occur in the Pisede fauna. *Elaphe longissima* presently occurs well south of the fossil site in extreme southeastern Germany. *Rana dalmatina* is another extralimital species that is presently absent from most of northeastern Germany.

This is a very noteworthy locality as *Rana lessonae* and *Rana ridibunda* have been recorded as well as the hybrid between these two species, *Rana* ''*esculenta*.'' These taxa as well as *Bombina bombina* indicate the presence of a permanent, low-energy body of water. Species that indicate a moist, terrestrial habitat include *Triturus cristatus*, *Triturus vulgaris*, *Hyla arborea*, *Rana arvalis*, *Rana dalmatina*, *Rana temporaria*, *Anguis fragilis*, and *Natrix natrix*. Species that indicate a dryer, terrestrial situation include *Pelobates fuscus*, *Bufo bufo*, *Bufo calamita*, *Lacerta agilis*, *Coronella austriaca*, and *Elaphe longissima*.

5. Spitzbubenhöhle (Cave) near Eselburg, Germany

Taxa. *Anguis fragilis*, *Coronella austriaca*, *Natrix natrix*, *Natrix tesselata*, *Vipera berus*.

References. Markert (1976), Szyndlar and Böhme (1993).

Remarks. *Natrix tesselata* indicates the presence of a permanent aquatic situation. *Anguis fragilis* and *Natrix natrix* suggest a moist terrestrial habitat. *Coronella austriaca* and *Vipera berus* indicate a somewhat dryer terrestrial situation. *Natrix tesselata* presently exists in three isolated populations in the Rhineland and Palatinate districts of southwestern Germany.

Austria

Austria has relatively few Pleistocene sites that have yielded significant herpetological remains.

Lower and Middle Pleistocene

1. Hundsheim, Austria

Taxa. *Pelobates fuscus*, *Bufo* cf. *Bufo bufo*.

References. Freudenberg (1914), Sanchiz (in press).

Middle Pleistocene

1. Bad Deutsch, Altenberg 2, northeastern Austria

Taxa. *Coluber caspius*, *Coluber gemonensis*, *Elaphe quatuorlineata*, *Elaphe* sp., *Natrix natrix*.

References. Rabeder (1974), Szyndlar (1991b, 1991c), Szyndlar and Böhme (1993).

Remarks. *Coluber caspius* (*Coluber jugularis* of some authors), *Coluber gemonensis*, and *Elaphe quatuorlineata* are all extralimital southern species that presently occur nearest to the site in northern Yugoslavia. These three taxa indicate a warm, dry, shrubby habitat. *Natrix natrix*, however, indicates a moister terrestrial habitat.

2. St. Margarethen, near Hainburg, northeastern Austria

Taxa. *Coluber caspius*, *Coluber gemonensis*, *Coluber viridiflavus*, *Elaphe longissima*, *Elaphe quatuorlineata*, *Natrix natrix*, *Vipera berus*.

References. Rabeder (1977), Szyndlar (1991b, 1991c), Szyndlar and Böhme (1993).

Remarks. Three extralimital snakes characteristic of the Balkans and eastward are present in the St. Margarethen fauna. These are *Coluber caspius*, *Coluber gemonensis*, and *Elaphe quatuorlineata*, all presently occurring nearest the site in northern Yugoslavia. The other snakes presently occur in the area. *Natrix natrix* and *Vipera berus* indicate rather moist habitats, but the extralimital snakes indicate a warm, dry, shrubby habitat.

Middle and Upper Pleistocene

1. Vienna, Austria

Taxon. *Emys orbicularis*.

References. Fritz (1995), Siebenrock (1916), Ullrich and Młynarski (1978).

Remarks. *Emys orbicularis*, which presently occurs in the area of Vienna, would indicate the presence of a permanent, low-energy body of water with abundant aquatic vegetation.

Pleistocene Undesignated

1. "Austria" (only)

Taxon. *Emys orbicularis*.

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. See Middle and Upper Pleistocene Account 1 above.

2. Merkenstein Cave, Austria

Taxa. *Pelobates fuscus*, *Rana temporaria*.

References. Sanchiz (in press), Wettstein-Westersheimb and Mühlhofer (1938).

Remarks. *Rana temporaria* suggests a rather moist terrestrial habitat, whereas *Peolobates fuscus* indicates a somewhat dryer terrestrial situation.

Switzerland

Middle Pleistocene

1. Gondiswil-Zell, Switzerland

Taxon. *Emys orbicularis.*

References. Fritz (1995), Heschler and Kuhn (1949), Studer in Baumberger et al. (1923).

Remarks. This site may represent an interstadial of the Riss glacial stage (Fritz, 1995). This species currently occurs in the area. It indicates the presence of a permanent, low-energy body of water with abundant aquatic vegetation.

Division V: Poland and the Czech Republic

Poland

Poland has a moderate number of Pleistocene sites that have yielded herpetological remains. Figure 43 indicates the location of important Pleistocene herpetological localities in Poland.

Lower Pleistocene

1. Kamyk, central southern Poland

Taxa. *Bufo* sp., *Rana* sp., *Lacerta* sp., *Ophisaurus apodus*, *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*, *Vipera berus.*

References. Bosák et al. (1982), Estes (1983), Młynarski (1961, 1962), Młynarski and Szyndlar (1989), Sanchiz (in press), Szyndlar (1984).

Remarks. The Kamyk site represents the early Biharian sequence of the continental stages of the Lower Pleistocene (Młynarski and Szyndlar, 1989). *Natrix natrix* and *Vipera berus* indicate a rather moist terrestrial habitat, whereas *Ophisaurus apodus* (=*"*Ophisaurus pannonicus*") and *Elaphe longissima* suggest a dryer terrestrial situation. *Ophisaurus apodus* is a southern extralimital form that presently occurs nearest Poland in northern Yugoslavia.

2. Kielniki 3A, central southern Poland

Taxa. *Bufo bufo*, *Rana* sp., *Lacerta agilis*, *Coronella austriaca*, *Natrix natrix*, *Vipera berus.*

References. Młynarski (1977), Młynarski and Szyndlar (1989), Sanchiz (in press), Stworzewicz (1981), Szyndlar (1984).

Remarks. The Kielniki 3A site represents the early part of the Biharian sequence of the Lower Pleistocene (Młynarski and Szyndlar, 1989). All the above herpetological species listed presently occur in the area. *Natrix natrix* and *Vipera berus* suggest a rather moist terrestrial habitat, whereas a dryer situation is suggested by *Lacerta agilis.*

FIGURE 43. Location of important Pleistocene herpetological sites in Poland. Lower Pleistocene: (1) Kamyk Site and Kielniki 3A Site; (2) Kozi Grzbiet Site; (3) Żabia Cave Site; (4) Zalesiaki A Site. Upper Pleistocene: (5) Ciasna Cave Site, Niedostępna Cave Site, Neitoperzowa Cave Site, and Zytnia Skala Cave Site; (6) Wierzbica Site; (7) Rząśnik Site; (8) Zdrody Site.

3. Kozi Grazbiet, southern central Poland

Taxa. **Pliobatrachus* cf. *Pliobatrachus langhae*, *Bombina bombina*, *Pelobates fuscus*, *Pelodytes* sp., *Bufo bufo*, *Hyla* (*arborea*) sp., *Rana* (*ridibunda*) sp., *Rana temporaria*, *Rana* sp., *Lacerta agilis*, *Lacerta* cf. *Lacerta viridis*, *Anguis fragilis*, *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*, *Vipera berus*.

References. Głazek et al. (1977), Kowalski (1989), Lang (1989), Młynarski (1977), Młynarski and Szyndlar (1989), Sanchiz (in press), Sanchiz and Szyndlar (1984), Stworzewicz (1981), Szyndlar (1981, 1984, 1991b, 1991c).

Remarks. This is one of the largest Pleistocene herpetofaunas in Europe. The Kozi Grzbiet site is considered to represent the late part of the Biharian sequence of the continental stages of the Lower Pleistocene. This is one of the latest occurrences of **Pliobatrachus* cf. *Pliobatrachus langhae*, an extinct genus and species of the extinct anuran family *Palaeobatrachidae. *Pelodytes* sp. is an extralimital taxon that presently occurs in western Europe and Iberia, ranging nearest the site in France in the form of *Pelodytes punctatus*. This is an odd occurrence considering that the rest of the extant fauna would presently be rather typical of the area.

Bombina bombina, **Pliobatrachus* cf. *Pliobatrachus langhae*, and *Rana* (*ridibunda*) sp. indicate a permanent, low-energy body of water. Other taxa indicate a moist terrestrial habitat (*Pelodytes* sp., *Rana temporaria*, *Anguis fragilis*, *Natrix natrix*, and *Vipera berus*). A dryer upland situation is suggested by *Lacerta agilis*, *Lacerta* cf. *Lacerta viridis*, and *Elaphe longissima*. *Natrix natrix* comprises 98.5% of the snake remains (Szyndlar, 1984).

4. Żabia Cave, central southern Poland

Taxa. *Bufo bufo*, *Bufo* sp., *Rana* sp., *Lacerta* sp., *Anguis fragilis*, *Ophisaurus apodus*, *Coronella austriaca*, cf. *Coronella* sp., *Elaphe longissima*, *Natrix natrix*, *Natrix* cf. *Natrix tesselata*, *Natrix* sp., *Vipera berus*.

References. Bosák et al. (1982), Ivanov (1997), Kowalski (1989), Młynarski and Szyndlar (1989), Sanchiz (in press), Szyndlar (1984, 1991b, 1991c).

Remarks. This Polish site represents the early part of the Biharian sequence of the Lower Pleistocene. It is also a site that has yielded the large, extralimital glass lizard *Ophisaurus apodus* (=''**Ophisaurus pannonicus*'') that presently occurs closest to Poland in northern Yugoslavia. This is the northernmost European fossil record of *Natrix tesselata* (Ivanov, 1997).

A permanent, low-energy aquatic situation is indicated by *Natrix* cf. *Natrix tesselata*. A moist terrestrial habitat is suggested by *Natrix natrix*, *Anguis fragilis*, and *Vipera berus*. *Ophisaurus apodus* and *Elaphe longissima* indicate a dryer terrestrial situation. Stratigraphic differences in the abundance of reptiles, especially snake species, suggested that these ectothermic forms were more sensitive to minor climatic changes than were the small mammals (Ivanov, 1997).

5. Zalesiaki A, central southern Poland

Taxa. **Pliobatrachus* cf. *Pliobatrachus langhae*, *Pelobates Fuscus*, *Bufo bufo*, *Rana temporaria*, *Lacerta agilis*, *Anguis fragilis*, *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*, *Vipera berus*.

References. Młynarski (1977), Młynarski and Szyndlar (1989), Sanchiz (in press), Szyndlar (1984).

Remarks. The Zalesiaki A site also represents the Biharian sequence of the Lower Pleistocene (Młynarski and Szyndlar, 1989). Another late occurrence of the extinct genus **Pliobatrachus* cf. *Pliobatrachus langhae* is recorded at Zalesiaki A. The other taxa form a herpetological assemblage that could have occurred in the area in historic times. Essentially, the same habitats are suggested by the Zalesiaki A herpetofauna that were indicated by the Żabia Cave fauna above.

6. Zamkowa Dolna Cave, Poland

Taxa. *Bufo* sp., *Rana* sp., *Elaphe longissima*.

References. Młynarski and Szyndlar (1989), Sanchiz (in press), Szyndlar (1984).

Remarks. This site was first assigned to the Upper Pleistocene Weichselian sequence by Szyndlar (1984) and then reassigned to the late part of the Biharian sequence of the Lower Pleistocene (Młynarski and Szyndlar, 1989).

Upper Pleistocene

1. Bramka, Poland

Taxa. *Rana* cf. *Rana arvalis*, *Rana* cf. *Rana temporaria*.

References. Madeyska (1981), Nadachowski (1988), Sanchiz (in press).

2. Ciasna Cave, Layers 6 and 7, central southern Poland

Taxa. *Bufo* cf. *Bufo bufo*, *Rana* cf. *Rana temporaria*, *Elaphe longissima*, *Vipera berus*.

References. Młynarski and Szyndlar (1989), Nadachowski (1988), Sanchiz (in press), Szyndlar (1984).

Remarks. Layers 6 and 7 of this cave represent the Dutch/European Weichselian glacial stage of the Upper Pleistocene. All of these amphibians and reptiles could have occurred in the area during historic times. These species occur in moist habitats (e.g., *Rana temporaria*) as well as relatively dry ones (e.g., *Elaphe longissima*).

3. Jaskinia Niedostępna, Poland

Taxa. *Bufo* cf. *Bufo bufo*, *Rana* cf. *Rana temporaria*.

References. Madeyska (1981), Sanchiz (in press).

4. Koziarnia, Poland

Taxon. *Rana* sp.

References. Madeyska (1981), Sanchiz (in press).

5. Mała Cave, central southern Poland

Taxon. Colubrinae indet.

References. Głazek and Szynkiewicz (1987), Szyndlar (1991b).

6. Nad Mosurem Starym Duza Cave, Layer 5, central southern Poland

Taxon. *Rana temporaria*.

Reference. Nadachowski et al. (1989).

Remarks. Layer 5 was deposited in a cold, moderately humid climate.

7. Niedostępna Cave, central southern Poland

Taxa. *Bufo* cf. *Bufo bufo*, *Rana* cf. *Rana temporaria*, *Coronella austriaca*, *Vipera berus*.

References. Młynarski and Szyndlar (1989), Nadachowski (1988), Sanchiz (in press), Szyndlar (1984).

Remarks. This herpetofauna could have existed in a moderately cool Upper Pleistocene climate. A rather moist terrestrial situation is indicated.

8. Nietoperzowa Cave, southern central Poland

Taxa. *Rana* sp., *Natrix natrix*, *Vipera berus*.

References. Madeyska (1981), Młynarski and Szyndlar (1989), Sanchiz (in press), Szyndlar (1984).

Remarks. This site is referred to the Dutch/European Weichselian glacial stage of the Upper Pleistocene (Szyndlar, 1984).

9. Oblazowa 2, Poland

Taxa. *Rana temporaria*, *Lacerta vivipara*.

Reference. Nadachowski et al. (1993).

Remarks. This site has been radiocarbon-dated at 33,430 ± minus 1,230 ybp (Nadachowski et al., 1993); thus, it is referable to the middle part of the Dutch/European Weichselian glacial stage of the Upper Pleistocene. Both of these species would probably be able to exist in ice-free areas during glacial times.

10. Rząśnik, near Warsaw, Poland

Taxa. *Elaphe longissima*, *Natrix natrix*.

Reference. Szyndlar (1984).

Remarks. This site is provisionally assigned to the Dutch/European Eemian interglacial stage of the Upper Pleistocene (Szyndlar, 1984). The occurrence of the southern extralimital form *Elaphe longissima* in the site would be consistent with a warm interglacial climate.

11. Wierzbica I, west of Warsaw, Poland

Taxon. *Elaphe longissima*.

Reference. Szyndlar (1984).

Remarks. This site is also provisionally relegated to the Dutch/European Eemian interglacial stage of the Upper Pleistocene (Szyndlar, 1984). The occurrence of the extralimital southern species *Elaphe longissima* would again be consistent with a warm interglacial climate.

12. Zachodnia, Poland

Taxon. *Rana* cf. *Rana temporaria*.

References. Nadachowski (1988), Sanchiz (in press).

13. Zalas, Poland

Taxon. *Bufo bufo*.

References. Bocheński et al. (1983). Sanchiz (in press).

14. Zdrody, northeastern Poland

Taxa. *Bufo viridis*, *Rana arvalis*, *Rana temporaria*, *Natrix natrix*.

References. Bałuk et al. (1979), Młynarski and Szyndlar (1989), Sanchiz (in press), Szyndlar (1984).

Remarks. This site is questionably assigned to the Dutch/European Eemian interglacial stage of the continental Upper Pleistocene (Młynarski and Szyndlar, 1989). On the other hand, the herpetofauna seems typical of a rather cool climate. A moist terrestrial habitat is indicated by *Rana arvalis*, *Rana temporaria*, and *Natrix natrix*. *Bufo viridis* could have existed in a somewhat dryer terrestrial situation.

15. Żytnia Skala, central southern Poland

Taxa. *Bufo* sp., *Rana* sp., *Elaphe longissima*.

References. Kowalski et al. (1967), Młynarski and Szyndlar (1989), Szyndlar (1984).

Remarks. This site is assigned to the Dutch/European Weichselian glacial stage of the Upper Pleistocene (Szyndlar, 1984), but the presence of *Elaphe longissima* at the site would argue against a glacial climate at the time of the deposition of the bones.

Upper Pleistocene and Holocene

1. Raj Cave, central southern Poland

Taxa. *Bombina* sp., *Pelobates fuscus*, *Bufo* sp., *Rana* sp., *Lacerta* cf. *Lacerta vivipara*, *Anguis fragilis*, *Elaphe longissima*, *Natrix natrix*, *Vipera berus*.

References. Madeyska (1981), Młynarski and Szyndlar (1989), Sanchiz (in press), Szyndlar (1984).

Remarks. This site contains both Weichselian and Holocene sediments. All of these taxa could have existed in the area in historic times. *Bombina* sp. indicates a shallow, low-energy aquatic habitat. *Lacerta* cf. *Lacerta vivipara*, *Anguis fragilis*, and *Natrix natrix* suggest a rather moist terrestrial situation. *Pelobates fuscus* and *Elaphe longissima* indicate a dryer terrestrial habitat.

2. Mamutowa Cave, central southern Poland

Taxon. *Rana temporaria.*

References. Nadachowski (1976), Sanchiz (in press).

3. Zawalna Cave, central southern Poland.

Taxon. *Rana temporaria.*

References. Alexandrowicz et al. (1992), Sanchiz (in press).

Czech Republic

The Czech Republic, rich in very ancient amphibian remains, has relatively few published Pleistocene herpetological sites.

Upper Pliocene and Lower Pleistocene

1. Včeláre, near Trebišav, eastern Czech Republic

Taxa. *Triturus cristatus*, *Triturus vulgaris*, *Bombina* cf. *Bombina bombina*, *Pelobates* cf. *Pelobates syriacus*, *Bufo bufo*, *Rana* cf. *Rana arvalis*, *Rana* cf. *Rana dalmatina.*

References. Hodrová (1985), Lang (1989), Roček (1988), Sanchiz (in press).

Remarks. All of these anurans may presently be found in the area of the site, with the exception of *Pelobates syriacus*, which is currently found in the southern Balkans. *Bombina* cf. *Bombina bombina* suggests a shallow, low-energy body of water. The other amphibians together indicate a rather moist terrestrial habitat.

Lower Pleistocene

1. Holštejn, Mähren, Czech Republic.

Taxa. *Triturus* sp., *Rana* sp., *Lacerta* sp., ?*Anguis* sp.

References. Musil (1966), Sanchiz (in press).

2. Malá Dohoda Quarry, Moravian Karst Area, Central Czech Republic

Taxa. *Lacerta* sp., *Anguis fragilis*, *Coluber caspius*, ?*Coluber* aff *Coluber gemonensis*, *Coluber* sp., ?*Coronella* aff *Coronella austriaca*, *Elaphe longissima*, *Elaphe. quatuorlineata*, *Natrix natrix*, *Natrix* sp., *Vipera ammodytes*, *Vipera berus*, *Vipera* sp.

Reference: Ivanov (1994).

Remarks. The fossils from this karst cavity represent the late Biharian part of the Lower Pleistocene. *Coluber caspius*, ?*Coluber* aff *Coluber gemonensis*, *Elaphe quatuorlineata*, and *Vipera ammodytes* represent a distinctive, extralimital "Mediterranean" component of this reptile fauna (Ivanov, 1994), and warmer, dryer conditions than presently occur in the area are indicated. The other taxa presently live in the area.

3. Stránzá Skála Hill near Brno, central southern Czech Republic

Taxa. *Pelobates fuscus*, *Bufo bufo*, *Bufo calamita*, *Bufo viridis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Lacerta* sp., ?*Coronella* aff *Coronella austriaca*, *Coluber* cf. *Coluber viridiflavus*, *Coluber* sp., *Elaphe longissima*, *Natrix natrix*, *Natrix* cf. *Natrix tesselata*, *Natrix* sp., *Vipera* cf. *Vipera ammodytes*, *Vipera* cf. *Vipera ursinii*, *Vipera* sp.

References. Ivanov (1995), Němec (1972), Roček (1988), Sanchiz (in press).

Remarks. This site also represents the late Biharian part of the Lower Pleistocene. *Coluber viridiflavus* presently occurs nearest to the site in Switzerland and northern Yugoslavia. *Vipera ammodytes* and *Vipera ursinii* are also southern extralimital species that currently occur no closer to the fossil locality than northern Hungary.

A permanent, still or slowly flowing body of water is indicated by the presence of *Rana* (*ridibunda*) sp. and *Natrix* cf. *Natrix tesselata.* Other species such as *Rana temporaria* and *Natrix natrix* suggest a moist terrestrial habitat. A warmer, dryer situation is indicated by *Coluber* cf. *Coluber viridiflavus*, *Elaphe longissima*, and *Vipera* cf. *Vipera ammodytes.* Alternating warmer and cooler Pleistocene climates are indicated by the stratigraphic distribution of the herpetological species of this site.

Lower or Middle Pleistocene

1. Zechovice, Czech Republic

Taxa. *Bufo bufo*, *Rana* sp.

References. Němec (1974), Sanchiz (in press).

Middle Pleistocene

1. Předletice, near Prague, Czech Republic

Taxon. *Emys orbicularis.*

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. The site is referred to the "Cromerian" sequence by Fritz (1995). The presence of this species indicates a permanent, low-energy body of water with ample aquatic vegetation.

2. Zlatý Kůň, near Koněprusy, Czech Republic

Taxon. *Emys orbicularis.*

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This site is also referred to the "Cromerian" sequence by Fritz (1995).

Upper Pleistocene

1. Gánovce, Slovakia, Czech Republic

Taxon. *Emys orbicularis.*

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This site is referred to the Dutch/European Eemian interglacial stage by Fritz (1995).

Pleistocene Undesignated

1. Bojnice, Slovakia, Czech Republic

Taxon. *Emys orbicularis.*

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. This site is questionably assigned to the Pleistocene, as dating methods were not definitive (Fritz, 1995).

2. Dekansky Vrch, Czech Republic

Taxa. *Bufo bufo*, *Rana* sp.

References. Němec (1974), Sanchiz (in press).

3. Malenice, Czech Republic

Taxa. *Bufo bufo*, *Rana* sp.

References. Němec (1974), Sanchiz (in press).

Division VI: Italy, Hungary, Yugoslavia (Croatia, Bosnia, Serbia), Greece

Italy

Italy has a wealth of Pleistocene herpetological localities. Malta is included with Italy here because of its proximity to Sicily and Italy.

Upper Pliocene or Lower Pleistocene

1. Monte Pellegrino, Italy

Taxon. *Lacerta viridis.*

References. Estes (1983), Kotsakis (1980a), Pasa (1948).

Lower Pleistocene

1. Baullino, Italy

Taxa. Discoglossidae indet., *Bufo* sp., *Hyla* sp.

References. Fondi (1972), Sanchiz (in press).

Remarks. Relative to the undetermined discoglossid material, *Alytes* and *Discoglossus* are absent in the modern fauna of the Italian peninsula. *Bombina variegata*, however, presently occurs there and may be the species represented.

2. Capena, Rome, Italy

Taxon. *Emys orbicularis.*

References. Fritz (1995), Kotsakis (1981a).

Remarks. *Emys orbicularis* indicates the presence of a permanent, low-energy body of water with an abundance of aquatic vegetation.

3. Cava Dell'Erba Apricena, Foggia, southern Italy

Taxon. *Blanus* cf. *Blanus stauchi.*

Reference. Delfino (1995).

Remarks. This species occurs in the islands of Rhodes and Kos, Asia Minor, Syria, and north Mesopotamia, but it does not presently occur on the Italian peninsula, nor does the western form *Blanus cinereus.*

4. Nuraghe Su Casteddu, Sardinia Island, Italy

Taxa. Discoglossidae indet., *Emys orbicularis*, ?*Coluber.*

References. Fritz (1995), Esu and Kotsakis (1980), Kotsakis (1980b), Kotsakis and Palombo (1979), Sanchiz (in press).

5. Scoppito, Italy

Taxa. *Discoglossus* sp., *Rana dalmatina.*

References. Kotsakis (1982b), Lanza et al. (1986), Sanchiz (in press).

Remarks. *Discoglossus* does not occur on the Italian peninsula at present, but it does occur on the islands of Corsica, Sardinia, Sicily, and Malta.

Lower to Middle Pleistocene

1. Loreto di Venosa, Potenza, Basilicata Province, southern Italy

Taxa. *Bufo bufo*, *Bufo* cf. *Bufo viridis*, *Emys orbicularis*, *Testudo* cf. *Testudo hermanni.*

References. Fritz (1995), Kotsakis (1980d), Sanchiz (in press).

Remarks. All of these species live in the area at present. A permanent, low-energy aquatic situation with abundant vegetation is indicated by *Emys orbicularis. Testudo* cf. *Testudo hermanni*, however, indicates a warm, dry, shrubby habitat.

Middle Pleistocene

1. Comiso, southeast Sicily Italy

Taxa. *Discoglossus pictus*, *Bufo* sp., *Rana* sp., *Emys orbicularis*, *Testudo* sp., *Lacerta* sp.

References. Bonfiglio and Insacco (1992), Sanchiz (in press).

Remarks. These taxa presently occur on Sicily. *Emys orbicularis* indicates the presence of a permanent, low-energy body of water with an abundance of aquatic vegetation. *Testudo* and perhaps *Lacerta* sp. would indicate a dry, shrubby habitat.

2. Montagnola Senese, Italy

Taxon. *Discoglossus* sp.

References. Fondi (1972), Lanza et al. (1986), Sanchiz (in press).

Remarks. *Discoglossus* does not presently occur on the Italian peninsula, but it does occur on the islands of Corsica, Sardinia, Sicily, and Malta.

3. Monte-Cros, Italy

Taxon. *Bufo* sp.

References. Jeannet (1979), Sanchiz (in press).

4. Ponte Salario, Rome, Italy

Taxon. *Mauremys* sp.

Reference: Kotsakis (1981a).

Remarks. The specimen consists of an entire plastron. The genus does not currently occur in Italy or its islands. The closest modern populations are in the southern Balkans, where *Mauremys caspica* presently occurs.

5. Ragusa, Sicily, Italy

Taxa. *Discoglossus* sp., *Testudo* sp.

References. Bonfiglio and Insacco (1992), Sanchiz (in press).

Remarks. *Discoglossus pictus* presently occurs on the island of Sicily and indicates the presence of a low-energy aquatic situation near the site. *Testudo* suggests the presence of a dry, shrubby habitat.

6. Riano Flaminio, Rome, Italy

Taxa. *Triturus vulgaris*, *Bufo viridis*, *Rana dalmatina*, *Rana.* (*ridibunda*) sp.

References. Bottali (1975), Kotsakis (1981a), Mastrorilli (1965), Sanchiz (in press).

Remarks. All of these anurans presently occur in the Rome area of Italy. The presence of *Rana* (*ridibunda*) sp. indicates a permanent, low-energy body of water. *Triturus vulgaris* and *Rana dalmatina* live in damp, terrestrial habitats. *Bufo viridis* may indicate a somewhat dryer terrestrial situation.

7. San Cosimato, Rome, Italy

Taxon. *Emys orbicularis.*

References. Fritz (1995), Kotsakis (1981a).

Remarks. See Italian Lower Pleistocene Site 2, for the habitat indicated by *Emys orbicularis.*

8. Sedio del Diavolo, Rome, Italy

Taxon. ?*Coluber* sp.

Reference: Kotsakis (1981a).

7. Spinagallo Cave, Siracusa, Sicily, Italy

Taxa. *Discoglossus* cf. *Discoglossus pictus*, *Bufo* cf. *Bufo viridis*, *Hyla* cf. *Hyla arborea*, *Testudo hermanni*, **Lacerta siculimelitensis*, *Lacerta viridis*, *Lacerta* sp., *Coluber* cf. *Coluber viridiflavus*, *Natrix* sp.

References. Böhme and Zammit-Maempel (1982), Bonfiglio and Insacco (1992), Kotsakis (1977b), Lanza et al. (1986), Sanchiz (in press).

Remarks. **Lacerta siculimelitensis* is an extinct species with uniquely expanded teeth (see account in Chapter 4). *Discoglossus pictus* presently occurs on Sicily, but it does not occur on the Italian peninsula (nor do any other *Discoglossus* species). The other amphibians and reptiles are currently found on Sicily. Although a permanent, low-energy body of water is indicated by *Discoglossus* cf. *Discoglossus pictus*, the other members of the herpetofauna mainly indicate a dry, shrubby terrestrial habitat.

8. Vittoria, Sicily, Italy

Taxon. *Emys orbicularis.*

References. Conti et al. (1979), Fritz (1995).

Remarks. *Emys orbicularis* presently occurs in Sicily.

Middle and Upper Pleistocene

1. Caprine, Rome, Italy

Taxon. *Testudo hermanni.*

Reference. Kotsakis (1981a).

Remarks. This tortoise presently occurs in the area.

2. Palombara Marcellina, Rome, Italy

Taxon. *Testudo hermanni.*

Reference. Kotsakis (1981a).

3. Tarquina, Rome, Italy

Taxon. *Testudo hermanni.*

Reference. Kotsakis (1981a).

4. Volpe Cave, near Verona, Italy

Taxon. *Coluber gemonensis.*

References. Kotsakis (1980a), Pasa (1948–1949).

Remarks. This extralimital species presently occurs along the eastern Adriatic coast and Greece, including Crete and many smaller islands.

Middle or Upper Pleistocene

1. Monte Delle Gioie Bone Cave, Rome, Italy

Taxa. *Bufo* sp., *Rana* sp.

References. Indes (1869), Kotsakis (1981a), Sanchiz (in press).

Upper Pleistocene

1. Acque Caje, Viterbo, northwest of Rome, Italy

Taxon. *Emys orbicularis.*

References. Fritz (1995), Kotsakis (1981a).

Remarks. *Emys orbicularis* presently occurs in the area. The habitat indicated by this turtle is discussed above under the Italian Lower Pleistocene, Site 2.

2. Arene Candide Cave, Italy

Taxon. **Varanus marathonensis.*

References. Estes (1983), Morelli (1891).

Remarks. This sole European record for this Pliocene taxon is very doubtful and requires confirmation (see chap. 4).

3. Baccano, Basilicata, Rome, Italy

Taxa. *Triturus cristatus*, *Rana dalmatina*, *Rana* (*ridibunda*) sp.

References. Kotsakis (1981a), Sanchiz (in press).

Remarks. All of these taxa are presently found in the area. A permanent, low-energy aquatic situation is suggested by *Rana* (*ridibunda*) sp. *Triturus cristatus* and *Rana dalmatina* indicate a moist terrestrial habitat.

4. Basilica di San Paolo, near Rome, Italy

Taxon. *Emys orbicularis.*

References. Fritz (1995), Kotsakis (1981a).

5. Castellana, Sicily, Italy

Taxon. **Lacerta castellanensis*.

References. Estes (1983), Kotsakis (1977b)

Remarks. This taxon is not a *Lacerta* (Kotsakis, 1977b) and should be removed from Pleistocene lists until the fossil is restudied.

6. Castello, Sicily, Italy

Taxon. *Discoglossus* cf. *Discoglossus pictus*.

References. Caloi et al. (1988), Sanchiz (in press).

Remarks. This taxon presently occurs on Sicily.

7. Dragonara, Cappo Caccia, Sardinia, Italy

Taxa. *Discoglossus* cf. *Discoglossus sardus*, *Bufo viridis*, *Hyla* cf. *Hyla sarda*, *Coluber* sp., *Natrix* sp.

References. Kotsakis (1977a, 1980b, 1980c), Sanchiz (in press).

Remarks. All of these species presently occur on Sardinia.

8. Finocchione, Lazio, central Italy

Taxon. *Bufo bufo*.

References. Kotsakis (1981a), Sanchiz (in press), Segre (1956a, 1956b).

9. Grimaldi Cave, Baousse-Rousse, Italy

Taxon. *Bufo bufo*.

References. Boule (1919), Kotsakis (1980d), Sanchiz (in press).

10. Menton Cave, Italy

Taxa. *Bufo bufo*, *Rana temporaria*.

References. Boule (1919), Brocchi (1879), Rivière (1886), Sanchiz (in press).

11. Monte Pellegrino, Sicily, Italy

Taxon. *Lacerta* sp.

Reference: Estes (1983).

12. Pedagaggi, Sicily, Italy

Taxon. *Bufo bufo*.

References. Gliozzi and Kotsakis (1986), Sanchiz (in press).

13. Polesini Cave, Rome, Italy

Taxon. *Bufo bufo*.

References. Kotsakis (1981a), Sanchiz (in press).

14. San Agostino Cave, Gaeta, Latina, Italy

Taxon. *Bufo bufo*.

References. Kotsakis (1981a), Sanchiz (in press).

15. San Giovanni, Sinis, Oristano, western Sardinia, Italy

Taxa. *Discoglossus* cf. *Discoglossus sardus*, *Emys orbicularis*, *Mauremys* cf. *Mauremys caspica*, *Coluber* sp.

References. Caloi et al. (1981), Fritz (1995), Sanchiz (in press).

Remarks. These taxa occur in brackish beds of Tyrrhenian age that lie just below aeolian Würmian dune deposits. The presence of *Mauremys* cf. *Mauremys caspica* is of special interest as it is presently absent in the herpetofauna of the island (Caloi et al., 1981). The nearest modern occurrence of this species is in the southern Balkans.

16. San Teodoro Cave, Acuedolci, Sicily, Italy

Taxon. *Bufo bufo.*

References. Burgio and Patti (1990), Sanchiz (in press).

17. Sternatia, Lecce, Apulia, Italy

Taxa. *Bufo viridis, Testudo* sp., *Lacerta viridis.*

References. Rustioni et al. (1994), Sanchiz (in press).

Remarks. This fauna comes from a karstic fissure of Würmian age, possibly the second part of the early Pleniglacial (Rustioni et al., 1994). This small herpetofauna suggests a relatively dry habitat.

18. Torre del Pagliaccetto, Rome, Italy

Taxa. *Bufo bufo, Rana* sp., *Emys orbicularis, Testudo hermanni.*

References. Caloi and Palombo (1978), Fritz (1995), Kotsakis (1981a), Sanchiz (in press).

Remarks. This site has been referred to the Dutch/European Eemian interglacial stage of the Upper Pleistocene (Fritz, 1995).

19. Val Radice, Frosinone, southeast of Rome, Italy

Taxa. *Bufo bufo, Emys orbicularis.*

References. Bidditu et al. (1967), Fritz (1995), Kotsakis (1981a), Sanchiz (in press).

20. Vitinia, Rome, Italy

Taxa. *Discoglossus* sp., *Emys orbicularis.*

References. Fritz (1995), Kotsakis (1981a), Lanza et al. (1986), Sanchiz (in press).

Remarks. *Discoglossus* does not presently occur on the Italian peninsula. The nearest modern *Discoglossus* occurs to continental Italy is on the islands of Corsica, Sardinia, Sicily, and Malta.

21. Wied Incita Quarry near Attard, central Malta

Taxon. **Lacerta siculimelitensis.*

References. Böhme and Zammit-Maempel (1982), Estes (1983).

Remarks. This is the type locality for **Lacerta siculimelitensis*, which is a large species and the only *Lacerta* that has tooth expansion (Estes, 1983).

22. Zandobbio, Bergamo, northeastern Italy

Taxon. *Emys orbicularis.*

References. Fritz (1995), Vialli (1956).

Remarks. This site has been relegated to the Dutch/European Eemian interglacial age of the Upper Pleistocene (Fritz, 1995).

Pleistocene Undesignated

1. Agrigento, Sicily, Italy

Taxon. *Emys orbicularis.*

References. Fritz (1995), Kotsakis (1977b).

Remarks. This site has been questionably referred to the Pleistocene (Kotsakis, 1977b). Habitat indicated by *Emys orbicularis* is given above under Italian Lower Pleistocene, Site 2. The species currently occurs in Sicily.

2. Cucigliana Cave, Monti Pisani, Italy

Taxa. *Bufo bufo*, *Bufo viridis*.

References. Campana (1912), Sanchiz (in press).

3. Malta (caves undesignated)

Taxon. *Lacerta* sp.

References. Adams (1877), Estes (1983), Kotsakis (1977b).

4. Monsummano, Italy

Taxon. *Testudo hermanni*.

References. Auffenberg (1974), Campana (1917), Młynarski (1976).

5. Monte Peglia, Italy

Taxa. *Bufo bufo*, *Rana* (*ridibunda*) sp.

Reference: Sanchiz (in press).

6. Monte Tignoso, Toscana, Italy

Taxon. *Coluber viridiflavus*.

Reference: Kotsakis (1980a).

Remarks. This species is presently found in the area.

7. Siniscola 2, Sardinia, Italy

Taxon. *Discoglossus* sp.

Reference: Sanchiz (in press).

Remarks. This genus currently occurs on the island of Sardinia.

Upper Pleistocene and Holocene

1. Corbeddu Cave, Sardinia, Italy

Taxa. *Discoglossus sardus*, *Bufo viridis*.

References. Lanza et al. (1986), Sondaar et al. (1984, 1988), Sanchiz (in press).

Remarks. These species presently occur on the island of Sardinia.

Upper Pleistocene or Holocene

1. Arene Candide Cave, Italy

Taxa. *Bufo bufo*, *Rana* (*ridibunda*) sp.

References. Morelli (1891), Sanchiz (in press).

Remarks. A permanent, low-energy body of water with an adjacent terrestrial situation is indicated by these two species.

2. Silanus, Sardinia, Italy

Taxon. *Discoglossus* cf. *Discoglossus sardus*.

References. Kotsakis (1980c), Sanchiz (1979, in press).

Remarks. This species presently occurs on the island of Sardinia.

3. Zebbug and Ghar Dalam Cave deposits, Malta

Taxa. *Bufo bufo*, *Bufo viridis*, *Emys orbicularis*, *Testudo graeca*.

Reference: Savona Ventura (1984).

Remarks. These remains may be partly or entirely associated with human cultural remains. *Testudo graeca* does not presently occur on Malta, although humans have introduced it into Sicily.

Hungary

Hungary is well represented by herpetological Pleistocene localities, which consist of Lower, Middle, and Upper Pleistocene sites, all of which are in caves, depressions, or rock shelters on karst plateaus. In general, the reptile material has been poorly studied, especially the snakes.

Upper Pliocene or Lower Pleistocene

1. Brassó, Hungary

Taxa. *Triturus cristatus*, *Bombina* cf. *Bombina variegata*, *Bufo viridis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Lacerta viridis*.

References. Bolkay (1913), Estes (1981, 1983), Sanchiz (in press).

Remarks. A permanent, low-energy aquatic situation is indicated by the presence of *Bombina* cf. *Bombina variegata* and *Rana* (*ridibunda*) sp. A moist terrestrial habitat is suggested by *Rana temporaria*. A somewhat dryer situation is indicated by *Bufo viridis* and *Lacerta viridis*.

2. Villány 7, Villány Mountains region, southwestern Hungary

Taxa. cf. *Bufo*, *Ophisaurus apodus*, serpentes undesignated.

References. Jánossy (1986), Kretzoi (1956), Sanchiz (in press).

Remarks. *Ophisaurus apodus* was previously listed as "**Ophisaurus intermedius*" (="**Ophisaurus pannonicus*") by Jánossy (1986). *Ophisaurus apodus* presently reaches the northernmost extent of its range in northern Yugoslavia, west of the fossil locality.

Lower Pleistocene

1. Csarnóta 4, Villány Mountains region, southwestern Hungary

Taxa. *Bufo viridis*, *Ophisaurus apodus*, *Elaphe quatuorlineata*.

References. Kretzoi (1956), Sanchiz (in press), Szyndlar (1991b).

Remarks. *Ophisaurus apodus* and *Elaphe quatuorlineata* presently occur somewhat west of the fossil locality in northern Yugoslavia. Together, these species indicate a somewhat dry, open habitat.

2. Kövesvarád, Bükk Mountain region, northeastern Hungary

Taxa. *Salamandra* cf. *Salamandra salamandra*, *Triturus* sp., *Bufo* sp., *Rana* sp., *Lacerta* sp., Serpentes undesignated.

References. Jánossy (1986), Sanchiz (in press).

Remarks. In general, this herpetofauna indicates moist, terrestrial conditions.

3. Nagyharsányhegy 3 and 6, Villány Mountains region, southwestern Hungary

Taxa. cf. *Bombina* sp., *Pelobates fuscus*, *Bufo* sp., *Lacerta* sp., Serpentes undesignated.

References. Jánossy (1976, 1986), Kretzoi (1956), Sanchiz (in press).

4. Ürömhegy, Budapest, Hungary

Taxa. *Bufo* sp., *Rana* sp.

References. Jánossy (1986), Sanchiz (in press).

5. Villány 5 and 8, Villány Mountains region, southwestern Hungary

Taxa. *Bombina* sp., *Pelobates* cf. *Pelobates fuscus*, *Bufo. bufo*, *Bufo* sp., *Rana* sp., *Lacerta* sp., *Lacerta* cf. *Lacerta viridis*, *Ophisaurus apodus*, Serpentes undesignated.

References. Bolkay (1913), Estes (1983), Jánossy (1986), Kretzoi (1956), Sanchiz (in press).

Remarks. *Ophisaurus apodus* was previously listed as "**Ophisaurus intermedius*" (="**Ophisaurus pannonicus*") by Jánossy (1986). *Ophisaurus apodus* presently occurs somewhat west of the fossil locality in northern Yugoslavia. "**Monitor deserticolis*" listed from the site by Jánossy (1986) also must represent *Ophisaurus apodus* (see Estes, 1983, pp. 141–142). *Bombina* sp. indicates the presence of a shallow, low-energy aquatic situation. The other species suggest a rather dry terrestrial habitat.

Middle Pleistocene

1. Burgberg-Hilton, Budapest, Hungary

Taxa. *Pelobates fuscus*, Testudines undesignated, Sauria undesignated, Serpentes undesignated.

References. Jánossy (1976, 1986), Sanchiz (in press).

2. Fortyogohegy, Hungary

Taxon. *Rana temporaria*.

References. Dely (1955a), Sanchiz (in press).

Middle to Upper Pleistocene

1. Budapest (only), Hungary

Taxon. *Emys orbicularis*.

References. Fritz (1995), Ullrich and Młynarski (1978).

Remarks. *Emys orbicularis* indicates the presence of a permanent, low-energy body of water with abundant aquatic vegetation.

Middle and Upper Pleistocene

1. Tarkő, Bükk Mountains region, northeastern Hungary

Taxa. Caudata undesignated, *Pelobates* sp., *Bufo* sp., *Rana temporaria*, *Rana* sp., *Lacerta* sp., *Lacerta* cf. *Lacerta viridis*, *Anguis* sp., Serpentes undesignated.

References. Jánossy (1974, 1986), Sanchiz (in press).

Remarks. *Rana temporaria* and *Anguis* sp. indicate a rather moist, terrestrial habitat. *Pelobates* sp. and *Lacerta* cf. *Lacerta viridis* indicate a dryer terrestrial situation.

Upper Pleistocene

1. Balla Cave, Bükk Mountains Region, northeastern Hungary

Taxon. *Rana temporaria.*

References. Dely (1955b), Féjerváry (1916), Sanchiz (in press).

2. Érd, Hungary

Taxa. *Pelobates fuscus*, *Bufo* cf. *Bufo viridis*, *Lacerta* sp., Serpentes undesignated.

References. Jánossy (1986), Sanchiz (in press).

3. Istállóskő, Bükk Mountains region, northeastern Hungary

Taxa. *Rana* (*ridibunda*) sp., *Rana temporaria.*

References. Dely (1955a, 1955b, 1955c), Jánossy (1986), Sanchiz (in press).

4. Kálmán Lambrecht Cave, Bükk Mountains region, northeastern Hungary

Taxa. Caudata undesignated, *Bombina* sp., *Pelobates* sp., *Bufo bufo*, *Bufo viridis*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Lacerta* sp., *Anguis fragilis*, Serpentes undesignated.

References. Dely (1955a, 1955c), Jánossy (1986), Sanchiz (in press).

Remarks. *Bombina* sp. and *Rana* (*ridibunda*) sp. indicate the presence of a permanent, low-energy body of water. A moist terrestrial habitat is indicated by *Rana temporaria* and *Anguis fragilis*. *Pelobates* and *Bufo virids* suggest a dryer upland area.

5. Novi, Hungary

Taxon. *Rana temporaria.*

References. Dely (1955a), Sanchiz (in press).

6. Palffy, Hungary

Taxon. *Rana temporaria.*

References. Dely (1955a), Fejérváry (1916), Sanchiz (in press).

7. Peskő, Hungary

Taxon. *Rana temporaria.*

References. Dely (1955a), Sanchiz (in press).

8. Rejtek 1, Bükk Mountains region, northeastern Hungary

Taxa. *Salamandra salamandra*, *Bufo* sp., *Rana* (*ridibunda*) sp., *Rana temporaria*, *Rana* sp., *Lacerta* sp., *Anguis fragilis*, Serpentes undesignated.

References. Jánossy (1986), Jánossy and Kordos (1976), Sanchiz (in press).

Remarks. *Rana* (*ridibunda*) sp. indicates the presence of a permanent, low-energy aquatic situation. Together, the other herpetological species indicate a rather moist terrestrial habitat.

9. Seybold Stone Quarry, Kőszeg, western Hungary

Taxa. *Bufo* sp., *Rana temporaria*, Serpentes indet.

References. Dely (1955a), Féjerváry (1916), Kordos (1979), Sanchiz (in press).

Remarks. Arctic rodents as well as those found in more temperate situations occur in this faunal assemblage (Kordos, 1979).

10. Süttő Upper Pleistocene strata, Gerecse Mountains region, northwestern Hungary

Taxa. *Bufo viridis*, *Testudo* sp., *Testudo graeca*, Sauria undesignated, *Lacerta* sp., *Anguis fragilis*, Serpentes undesignated.

References. Jánossy (1986), Sanchiz (in press).

Remarks. The extralimital presence of *Testudo* sp. and *Testudo graeca* is of considerable interest. At present the nearest that *Testudo graeca* occurs to the site is in the eastern Balkans south of the Danube. *Testudo hermanni* reaches the northern part of Yugoslavia, west of the site. This *Testudo* material probably should be reexamined.

11. Tokod-Nagyberek, Hungary

Taxa. *Rana temporaria*, Serpentes undesignated.

References. Jánossy (1986), Sanchiz (in press).

Pleistocene Undesignated

1. Beremend, Villány Mountains region, southwestern Hungary

Taxon. *Ophisaurus apodus*.

References. Estes (1983), Jánossy (1986), Kretzoi (1956).

Remarks. *Ophisaurus apodus* (= "**Ophisaurus pannonicus*") presently occurs somewhat west of the fossil locality in northern Yugoslavia. Estes (1983) merely indicated that this site was Pleistocene and did not relate which Beremend locality the specimen came from. It may have come from Locality 11(see Jánossy, 1986, p. 30), which is Lower Pleistocene.

2. Köpecz, Villány Mountains region, southwestern Hungary

Taxon. *Ophisaurus apodus*.

References. Estes (1983), Kretzoi (1956).

Remarks. The same remarks in Site 1 above apply to this fossil record of *Ophisaurus apodus* (= "**Ophisaurus pannonicus*").

3. Miskolć, Bükk Mountains region, northeastern Hungary

Taxon. *Rana temporaria*.

References. Boda (1964), Bolkay (1911), Dely (1955a), Féjerváry (1916), Sanchiz (in press).

Upper Pleistocene and Holocene

1. Függő-Kő Cave, northern Hungary

Taxa. Caudata indet., Anuran indet. *Bufo* sp., *Rana* (*ridibunda*) sp., *Rana temporaria*, Serpentes indet., *Lacerta* sp., *Anguis fragilis*.

References. Jánossy et al. (1982-1983), (Sanchiz, in press).

Remarks. These species indicate the presence of a permanent, low-energy body of water [*Rana* (*ridibunda*) sp.] as well as a rather moist terrestrial situation (remaining taxa).

2. O-Ruzsin, Hungary

Taxon. *Rana temporaria*.

References. Bolkay (1911), Sanchiz (in press).

3. Petényi Cave, Bükk Mountains region, northeastern Hungary

Taxa. *Bufo bufo*, *Bufo viridis*, *Rana temporaria*, *Lacerta* sp., Serpentes indet.

References. Dely (1957), Jánossy and Kordos (1976), Sanchiz (in press).

Remarks. This small herpetofauna indicates a moist terrestrial habitat (*Rana temporaria*) as well as a somewhat dryer one (remaining taxa).

4. Pilisszántó 1, near Budapest, Hungary

Taxon. *Rana temporaria.*

References. Dely (1955a), Fejérváry (1916), Jánossy (1986), Sanchiz (in press).

5. Remetehegy, northwest of Budapest, Hungary

Taxa. *Rana temporaria*, Sauria undesignated.

References. Dely (1955a), Jánossy (1986), Sanchiz (in press).

6. Tekeresvölgy, western Hungary

Taxa. *Pelobates fuscus*, *Bufo bufo*, *Rana* sp.

Reference: Sanchiz (in press).

Yugoslavia
(Croatia, Bosnia, Serbia)

Yugoslavia has a moderate number of Pleistocene herpetological sites. Figure 44 indicates the location of important Pleistocene herpetological localities in Yugoslavia.

FIGURE 44. Location of Pleistocene herpetological sites in Yugoslavia. Middle Pleistocene: (1) Dubci; (2) Marjan; (3) Podumci; (4) Potočka Zijalka. Upper Pleistocene: (5) Crvena Stijena Cave; (6) Zelena Cave; (7) Bijambarska Cave; (8) Šandalja; (9) Romualdova Cave; (10) Klek Cave; (11) Velika Cave. Upper Pleistocene and Holocene: (12) Veternica.

Croatia

Middle Pleistocene

1. Dubci, Croatia

Taxa. *Bufo* sp., *Lacerta* sp., *Coluber* sp., *Vipera* sp.

References. Paunović (1983b, 1984b), Sanchiz (in press).

Remarks. The site is said to be in the "Cromerian" sequence (Paunović, 1984b).

2. Marjan, Croatia

Taxon. *Testudo* sp.

Reference: Paunović (1983b, 1984a).

Remarks. This site is also referred to the "Cromerian" sequence (Paunović, 1983b).

3. Podumci, Croatia

Taxa. *Lacerta viridis*, *Lacerta* sp.

References. Paunović (1983b, 1984b).

Remarks. This is another site referred to the "Cromerian" sequence (Paunović, 1983b).

4. Potočka Zijalka, Croatia

Taxa. *Bufo bufo*, *Rana temporaria*, *Lacerta agilis*.

References. Malez (1963), Paunović (1983b), Sanchiz (in press).

Remarks. This site is referred to the Riss glacial age (Paunović, 1983b).

Upper Pleistocene

1. Klek Cave, Croatia

Taxon. *Rana* cf. *Rana dalmatina*.

References. Malez et al. (1975), Paunović (1983b, 1984b), Sanchiz (in press).

Remarks. This species presently occurs in the area.

2. Krapina, Croatia

Taxon. *Emys orbicularis*.

References. Fritz (1995), Paunović (1983b, 1984b), Ullrich and Młynarski (1978).

Remarks. This site represents an interstadial event in the Dutch/European Weichselian glacial stage. *Emys orbicularis* indicates the presence of a permanent, low-energy aquatic situation with abundant aquatic vegetation. This species presently occurs in the area.

3. Pećine U Brini, Dalmatia, Croatia

Taxa. *Bufo bufo*, *Bufo viridis*, *Hyla arborea*, *Rana graeca*.

References. Malez (1963), Paunović (1988b), Sanchiz (in press).

Remarks. These species all currently occur in the area. *Rana graeca* is almost always associated with cool running water. The other anuran species could be found near the stream in moist to relatively dry areas.

4. Romualdova Cave, Croatia

Taxa. *Bufo* sp., *Rana* sp.

References. Malez (1963, 1968), Paunović (1983b, 1984b), Sanchiz (in press).

Remarks. The Romualdova site is a Paleolithic locality.

5. Šandalja, near Pula, Istrian Peninsula, extreme northwestern Croatia

Taxa. *Discoglossus* sp., *Pelobates* sp., *Bufo bufo*, *Bufo viridis*, *Hyla* (*arborea*) sp., *Rana dalmatina*, *Rana graeca*, *Rana temporaria*, *Emys orbicularis*, *Testudo graeca*, *Lacerta agilis*, *Lacerta viridis*, *Ophisaurus* sp., *Elaphe longissima*, *Elaphe* cf. *Elaphe quatuorlineata*, *Elaphe* sp., *Natrix natrix*, *Natrix tesselata*, *Natrix* sp.

References. Malez (1972), Paunović (1983b, 1984a, 1984b), Sanchiz (in press).

Remarks. This is one of the largest and most significant Pleistocene herpetofaunas in Europe. At present, the nearest that *Discoglossus* occurs to the Istrian Peninusla of Croatia is on the islands of Sardinia, Corsica, and Elba across the Italian Peninsula in the Tyrrhenian Sea. This recalls the situation in the Italian peninsula, where *Discoglossus* sp. is found in the Pleistocene but is absent in the modern fauna. *Rana graeca*, a form presently adapted to cool streams, is also extralimital, presently occurring southeast of the site in central Yugoslavia.

Another extralimital species is *Testudo graeca*, which presently occurs nearest the site in southeastern Yugoslavia and in Bulgaria. *Lacerta agilis* and *Lacerta vivipara* barely enter the Istrian Peninsula north of Pula. The other members of the herpetofauna presently occur in the area.

Paunović (1984b) assigns this fauna to the Würmian sequence, but this rich herpetofauna, with extralimital southern and island species present, indicates a warm phase of the interval.

A wide variety of habitats is indicated by the Šandalja herpetofauna. *Emys orbicularis* indicates the presence of a permanent, low-energy body of water with an abundance of aquatic vegetation. This habitat could be shared by *Natrix tesselata*. On the other hand, *Rana graeca* is adapted for cool, running water. A moist terrestrial habitat is indicated by several species (e.g., *Rana dalmatina*, *Rana temporaria*, and *Natrix natrix*), whereas a dry, shrubby area would support *Testudo graeca*, *Ophisaurus* sp., *Elaphe* cf. *Elaphe quatuorlineata*, and *Elaphe longissima*.

6. Velika Cave, Croatia

Taxa. *Bombina* sp., *Pelobates* sp., *Bufo bufo*, *Bufo viridis*, *Rana dalmatina*, *Rana* (*ridibunda*) sp., *Rana temporaria*, *Emys orbicularis*, *Lacerta viridis*, *Elaphe* cf. *Elaphe longissima*, *Elaphe quatuorlineata*.

References. Malez (1967), Paunović (1984b), Lenardić (1990), Sanchiz (in press).

Remarks. Paunović (1984b) suggests this is a postglacial fauna. The presence of *Rana* (*ridibunda*) sp. and *Emys orbicularis* indicates a permanent, low-energy body of water. A moist terrestrial situation is indicated by species such as *Rana dalmatina* and *Rana temporaria*, and a dryer upland situation by *Lacerta viridis*, *Elaphe* cf. *Elaphe longissima*, and *Elaphe quatuorlineata*.

Pleistocene Undesignated

1. Unisic, Dalmatian area, Croatia

Taxa. *Lacerta* sp., Serpentes undesignated.

References. Estes (1983), Kormos (1931).

Remarks. Kormos (1931) designated this site as a''Forestbed-Fauna''; thus, it may be a part of the ''Cromerian'' sequence. Estes (1983), however, did not give a specific Pleistocene designation to the site.

Upper Pleistocene and Holocene

1. Kličevica Cave, near Benkovac, Dalmatia, Croatia

Taxa. *Bufo viridis*, *Emys orbicularis*.

Reference: Paunović (1990).

2. Veternica Cave, Croatia

Taxa. *Bufo bufo*, *Rana dalmatina*, *Rana* (*ridibunda*) sp.

References. Malez (1963, 1965), Paunović (1983b, 1984b), Sanchiz (in press).

Remarks. *Rana* (*ridibunda*) sp. indicates the presence of a permanent, low-energy body of water. *Rana dalmatina* could have lived in an adjacent, somewhat moist terrestrial situation.

Bosnia

Upper Pleistocene

1. Bijambarska Cave, southwest of Olovo, middle Bosnia

Taxa. *Bufo viridis*, *Rana arvalis*, *Rana graeca*.

References. Paunović (1983b, 1986, 1988a), Sanchiz (in press).

Remarks. *Rana graeca* indicates the presence of a cool stream. The other anuran species indicate a moist (*Rana arvalis*) to a somewhat dryer (*Bufo viridis*) terrestrial situation.

2. Zelena Cave, Bosnia and Hercegovina

Taxa. *Bufo viridis*, *Rana arvalis*, *Rana graeca*.

References. Malez (1973), Paunović (1983b, 1987, 1988a), Sanchiz (in press).

Remarks. These species indicate the same habitats as the Bijambarska Cave assemblage described above.

Serbia

Upper Pleistocene

1. Crvene Stijena (Red Rock) Cave, Petrovica, Montenegro, Serbia

Taxa. *Testudo graeca*, *Testudo hermanni*, *Testudo* sp.

Reference: Paunović (1983a).

Remarks. Paunović (1983a) indicates that this is a Riss glacial deposit, but the tortoise species indicate a warm, dry Mediterranean interstadial climate. This attests to the dramatic climatic fluctuations that occurred within the so-called glacial ages.

Upper Pleistocene and Holocene

1. Smolučka Cave, near Novi Pazar, southwestern Serbia

Taxa. *Salamandra salamandra, Bombina variegata, Pelobates fuscus, Bufo bufo, Bufo viridis, Hyla arborea, Rana arvalis, Rana temporaria, Lacerta agilis, Lacerta viridis, Anguis fragilis, Ophisaurus apodus, Coronella austriaca, Elaphe longissima, Natrix natrix, Vipera ammodytes, Vipera berus.*

References. Paunović and Dimitrijević (1990), Sanchiz (in press).

Remarks. This deposit consists of glacial and overlying Holocene deposits. The only species in the glacial deposits were *Rana temporaria* and *Vipera berus* (Paunović and Dimitrijević, 1990). *Rana esculenta* was listed in this fauna by Paunović and Dimitrijević (1990) but was not included in the fauna by Sanchiz (in press). *Ophisaurus apodus* was listed as ''**Ophisaurus pannonicus*'' by Paunović and Dimitrijević (1990).

2. Trebjesi Cave, Crna Gora, Serbia

Taxa. *Lacerta viridis, Emys orbicularis.*

Reference: Lenardić (1990).

Greece

Greece has a moderate number of Pleistocene herpetological sites, the most interesting of which are on oceanic islands.

Upper Pliocene to Lowermost Pleistocene

1. Lakonia, southeast Peloponnes, Greece

Taxon. *Testudo marginata.*

Reference. Schleich (1982).

Remarks. This is possibly the earliest recorded occurrence of *Testudo marginata* (Schleich, 1982).

Lower Pleistocene

1. Laghada A, Island of Kos, Greece

Taxa. *Rana* sp., *Vipera* (*berus*) sp.

References. Sanchiz (1984a, in press), Szyndlar (1991c).

2. Laghada B, Island of Kos, Greece

Taxa. *Natrix* sp., *Vipera* (*berus*) sp.

References. Sanchiz (1984a, in press), Szyndlar (1991c).

3. Sitia-Psilokefalo, Crete, Greece

Taxon. *Discoglossus* sp.

References. Kotsakis (1982b), Sanchiz (in press).

Remarks. *Discoglossus* does not presently occur in Greece or on the island of Crete. Its nearest present occurrence to the site is on Sicily and Malta in the form of *Discoglossus pictus*.

Middle Pleistocene

1. Chios Island, Greece

Taxa. *Pelobates* sp., *Bufo* cf. *Bufo viridis*, *Rana* cf. *Rana bedriagae*, *Lacerta* sp., *Eryx jaculus*, Colubrinae indet., (?)*Naja* sp., *Vipera* (Oriental viper) sp.

References. Kotsakis et al. (1979), Sanchiz (in press), Schneider (1975), Storch (1975), Szyndlar (1991b, 1991c).

Remarks. The (?)*Naja* record is probably invalid (see Chapter 4). The occurrence of an extralimital Oriental viper of the genus *Vipera* on the island is of considerable interest. The Sanchiz (in press) anuran records were recorded from a site called "Latomi 1."

2. Sitia 1, Island of Crete, Greece

Taxa. *Discoglossus* sp., *Rana* cf. *Rana cretensis*, *Natrix* sp.

References. Caloi et al. (1988), Kotsakis (1982b), Sanchiz (in press).

Remarks. *Discoglossus* does not presently occur on Crete, the nearest modern occurrence being in Sicily and Malta in the form of *Discoglossus pictus*.

3. Tourkobounia 2, Greece

Taxa. *Pelobates* cf. *Pelobates syriacus*, *Bufo viridis*, *Rana* (*ridibunda*) sp., aff *Typhlops vermiculatus*, cf. *Coronella*, cf. *Elaphe longissima*, cf. *Elaphe situla*, Colubrinae indet., *Natrix* cf. *Natrix tesselata*, *Natrix* sp., *Vipera* cf. *Vipera ammodytes*, *Vipera* (*berus*) sp.

References. Sanchiz (in press), Szyndlar (1991b, 1991c).

Remarks. *Rana* (*ridibunda*) sp. and *Natrix* cf. *Natrix tesselata* indicate the presence of a permanent aquatic situation. The other species could exist in a relatively dry terrestrial situation.

4. Tourkobounia 5, Greece

Taxa. *Pelobates* cf. *Pelobates syriacus*, *Bufo viridis*, *Rana* (*ridibunda*) sp., *Elaphe longissima*, *Elaphe*. *quatuorlineata*, Colubrinae indet., *Natrix* sp.

References. Sanchiz (in press), Szyndlar (1991b, 1991c).

Remarks. In general, these taxa indicate the same type of habitat situation as the Tourkobounia 2 Site described above.

Upper Pleistocene

1. Bate Cave, Rethymnon, Island of Crete, Greece

Taxa. *Bufo* cf. *Bufo viridis*, *Testudo marginata*, *Lacerta* cf. *Lacerta* ("*Podarcis*") *erhardii*, *Coluber* cf. *Coluber* cf. *gemonensis*, cf. *Elaphe situla*.

References. Estes (1983), Kotsakis (1977a), Kotsakis et al. (1979), Sanchiz (in press), Szyndlar (1991b).

Remarks. *Testudo* does not occur on Crete today, although the other members of the herpetofauna do occur there. Kotsakis (1977a) reports that the fauna indicates a hot Mediterranean bush climate such as presently occurs on the island.

2. Gerani 1, Island of Crete, Greece

Taxa. aff *Typhlops vermiculatus*, cf. *Elaphe longissima*, *Natrix* cf. *Natrix tesselata*.

References. Szyndlar (1991b, 1991c).

Remarks. *Elaphe longissima* does not presently occur on the island of Crete, but it does occur on mainland Greece.

3. Gerani 4, Island of Crete, Greece

Taxon. cf. *Elaphe situla*.

Reference: Szyndlar (1991b).

Remarks. This species presently occurs on Crete as well as on mainland Greece.

4. Liko B, Greece

Taxa. *Bufo* sp., *Rana* (*ridibunda*) sp., *Rana* sp.

Reference: Sanchiz (in press).

5. Sitia 2, Island of Crete, Greece

Taxa. *Rana* cf. *Rana cretensis*, *Natrix* sp.

References. Sanchiz (1984a, in press), Szyndlar (1991c).

Pleistocene Undesignated

1. Arnissa, Greece

Taxa. *Pelobates* sp., *Bufo viridis*, *Rana* (*ridibunda*) sp.

Reference: Sanchiz (in press).

2. Kaiafa, Greece

Taxa. *Triturus* sp., *Bufo* sp., *Hyla* (*arborea*) sp., *Rana* cf. *Rana graeca*.

References. Estes (1981), Sanchiz (1977a, in press).

Remarks. *Rana graeca* usually indicates the presence of a cool stream. The other taxa indicate a moist terrestrial situation.

3. Mavromouri, Island of Crete, Greece

Taxon. *Bufo* cf. *Bufo viridis*.

References. Caloi et al. (1988), Sanchiz (in press).

Pleistocene/Holocene Boundary

1. Vraona Cave, Greece

Taxon. *Emys orbicularis*.

References. Fritz (1995), Symeonidis et al. (1979).

Remarks. The presence of *Emys orbicularis* indicates a permanent, low-energy body of water with abundant aquatic vegetation.

"Upper Quaternary"

1. Pili B, Island of Kos, Greece

Taxa. *Eryx jaculus*, cf. *Coronella*, cf. *Elaphe longissima*, cf. *Elaphe situla*, Colubrinae indet., *Natrix* sp.

References. Szyndlar (1991b, 1991c).

Remarks. *Elaphe longissima* does not presently occur on the island of Kos, or in Greece or other Greek islands, but the other taxa are currently found there.

6

HERPETOLOGICAL SPECIES AS PALEOENVIRONMENTAL INDICATORS

In Chapter 5 we have seen that Pleistocene herpetofaunas are often used to suggest paleoenvironmental conditions. The present chapter discusses the validity of this use.

With the exception of behavioral responses (and a few quasi-physiological adaptations in reptiles), herpetological species are poorly adapted to resist temperature changes. Or, to put it another way, amphibians and reptiles lack the complex internal physiological mechanisms that interact to regulate temperature in endotherms. This has led to the assumption by many that herpetological species, because of their supposed greater sensitivity to temperature changes, are much better indicators of local thermal conditions than are birds and mammals.

Moreover, most Quaternary amphibians and reptiles represent extant species whose ecological tolerances and habitat preferences are well known, whereas many Pleistocene endotherms, especially large mammals, are extinct species whose ecological traits and specific habitat requirements are not totally understood. This suggests that Pleistocene herpetofaunas should give more refined information about specific habitats than endothermic faunas. Also, it can be argued that most amphibian and reptile species are more spatially confined than endothermic ones (especially birds and large mammals) and that Pleistocene herpetological species indicate paleoenvironmental conditions of more restricted areas.

Bailón and Rage (1992) address this subject in the light of their European experience: "They [amphibians and reptiles] are unable to compensate for large climatic variations as endotherms (birds and mammals) can; therefore each amphibian and reptile species can live only in a definite climate." (p. 95). Moreover,

> Amphibians and reptiles present another advantage: whereas endotherm vertebrates are represented in Quaternary fossiliferous localities by a not negligible percentage of extinct species, practically all fossil amphibians and reptiles of that age belong to extant species. If a species is extinct its ecological requirements cannot be

> known with certainty and are open to speculation whereas living species present in fossiliferous assemblages afford accurate information. (p. 95)

They also state that the size of reptile home ranges is small, and that as these species are not the preferred prey of predaceous birds, they are probably not an admixture of species that live in a wide area around the locality. Let us examine these assumptions.

Temperature Effects

Although some European herpetological species are restricted to areas where relatively warm temperatures occur (e.g., many southern European and Mediterranean reptile species), several herpetological taxa have very broad ranges in Europe and are able to exist in warm as well as very cold climates (e.g., *Rana arvalis*, *Rana temporaria*, *Lacerta vivipara*, and *Vipera berus*). On the other hand, the presence of certain Pleistocene reptiles, particularly those that require an extended period of warm weather for the hatching of their eggs (e.g., turtle species and certain egg-laying lizards and snakes), should at least reflect the warmth of the summer season.

For instance, the critical time in the life cycle of a northern-hemisphere turtle is the number of warm days in the summer for egg incubation (Graham et al., 1983). A mean July temperature in excess of 18°C appears necessary for the European pond tortoise, *Emys orbicularis*, to breed successfully in Europe (Stuart, 1979). *Emys orbicularis* presently does not occur in England, although the species was common there during warm intervals in the Pleistocene. Although England presently has an equable climate, *Emys orbicularis* cannot survive there because the daily summer temperatures are not warm enough for the successful hatching of its eggs.

As we have seen in Chapter 4, almost all Pleistocene herpetological species in Europe (with the notable exception of some large lizards on oceanic islands) represent extant species. The parsimonious assumption is that extant Pleistocene species have the same ecological preferences and requirements of their present-day counterparts. Some paleontologists have suggested, mainly verbally, that Pleistocene herpetological species could have rather rapidly adapted to climatic changes in the Pleistocene, and thus would not be particularly good indicators of paleoclimates.

I generally doubt this assumption, especially relative to any rapid genetic adjustments in turtles, lizards, or snakes that would allow for the maturation of embryos in eggs in the cool or cold summers of glacial Britain and Europe. Some North American turtles such as *Chrysemys picta* have young that can survive winter freezing in nests above the frost line (DePari, 1996). But even North American turtle species that can survive winter freezing are limited in their northern distribution by the lack of summer warmth for the hatching of their eggs.

On the other hand, in the Great Basin desert area of southwestern North America, pollen studies made at Pleistocene sites containing reptiles showed that typical desert reptile species were able to adjust to Pleistocene changes from desert to pinyon-juniper assocation woodland situations (see Holman, 1995c, and references therein). One could question, however, whether this adaption evolved during the Pleistocene or was present within the range of tolerances already present in the animals. In the case of the Great Basin Pleistocene reptiles, it has been demonstrated that a more equable Pleistocene climate, with cooler summers and warmer winters than at present, existed in the area and that this is why the reptiles stayed in place rather than migrating southward to desert refugia.

Turning to the amphibians, one could argue that some species acquired or at least sharpened some of their physiological adaptations for cold tolerances in the Pleistocene. Four North American frogs (*Pseudacris crucifer*, *Pseduacris triseriata*, *Hyla versicolor*, and *Rana sylvatica*) are tolerant of freezing between −6 and −10°C (Hochachka and Guppy, 1987). These frozen frogs have stiff limbs and opaque eyes. They do not breathe and have no heartbeat, and no bleeding occurs when the aorta is severed. These animals hibernate in the soil above the frost line, and when spring comes they thaw out and begin the breeding cycle. Moreover, animals experimentally frozen in amplexus by K. Storey (personal communication, 1996) continued breeding when thawed out! The American toad, *Bufo americanus*, however, must burrow below the frost line to survive freezing temperatures, and most North American salamanders enter mammal burrows to avoid freezing.

I am not aware of any published literature that indicates European frogs successfully freeze during the winter. One might wonder if such adaptations occur in species like *Rana arvalis* and *Rana temporaria* that live north of the Arctic Circle, and if such adaptions might have been selected for during Pleistocene climatic changes. Nevertheless, K. Storey (personal communication, January 9, 1997) reports that he has been unable to successfully freeze *Rana temporaria* in the laboratory.

Certainly, more Pleistocene herpetological studies should be combined with physiological studies of temperature tolerances in modern amphibians and reptiles. Obviously, the role of Pleistocene climatic changes in the selection of temperature tolerance in all ectothermic animals is a compelling scientific problem.

Size of Habitat Indicated

Let us now turn to the assumption that amphibians and reptiles in the Pleistocene had smaller home ranges than those of birds and mammals. This certainly seems like a parsimonious suggestion based on the rather limited home ranges of most modern herpetological species. But the other assumtion made by Bailón and Rage (1992), namely, that amphibians and reptiles are not the preferred prey of predaceous birds and were not transported from afar by these birds, needs some discussion.

Martín and López (1990) published an exhaustive study that showed that many amphibians and reptiles in southwestern Europe were eaten by birds of prey. Even amphibian species with noxious secretions were eaten. *Bufo bufo* was eaten by 16 species, including herons, many hawks and owls, and seagulls. A presumably less noxious species, *Rana temporaria*, was eaten by 23 species. The very noxious *Salamandra salamandra* was eaten by *Buteo buteo*, *Gallus gallus*, *Strix aluco*, and even *Turdus torquatus*! Perhaps more surprising is that the salamander *Pleurodeles walti*, an animal that bristles with extruded poisonous ribs, was preyed on by 11 species of birds!

North American great horned owl pellets may be packed with salamander remains (Holman, 1976), and the largest North American Pleistocene herpetofauna (Reddick, Florida; Holman, 1995c) consists mainly of species derived from owl pellets. I would suggest that many Pleistocene amphibian and reptile assemblages, especially from cave sites, might have been brought there from a wide variety of habitats by avian raptors.

Oddly, the Pleistocene Westbury-Sub-Mendip site in England (British Middle Pleistocene Site 12) yielded few herpetological bones (Holman, 1993c), even though thousands of small mammal remains were found there as the result of at least 13 avian predators (Andrews, 1990).

A Central European Model

Böhme (1996) has listed certain herpetological species or assemblages of species that are characteristic of portions of Quaternary climatic cycles in central Europe:

I. *Rana temporaria* tends to be the only species present in ice-free areas during full cold stages.
II. Early invaders during the latter part of a cold stage are *Bufo bufo*, *Rana arvalis*, and *Vipera berus*.
III. Invaders during the early part of a warm stage are *Rana dalmatina*, *Rana lessonae*, *Triturus cristatus*, *Triturus vulgaris*, *Anguis fragilis*, *Lacerta agilis*, *Coronella austriaca*, and *Natrix natrix*.
IV. Species characteristic of warm climatic optima are *Salamandra salamandra*, *Bombina bombina*, *Hyla arborea*, *Pelobates fuscus*, *Rana ridibunda*, *Lacerta viridis*, *Elaphe longisimma*, and *Emys orbicularis*
V. First invaders of the latter part of a warm stage are *Bufo calamita* and *Bufo viridis*.
VI. Species characteristic of an outgoing warm stage and the beginning of a cold stage are *Rana temporaria*, *Bufo viridis*, *Lacerta vivipara*, and *Vipera berus*.

This model is based on a large number of detailed Pleistocene herpetofaunal studies by G. Böhme (see the references section), and it will be interesting to see if the model stands the test of time in light of the many ongoing studies of

European Pleistocene herpetofaunas. Thus far, the model appears to fit well in Britain, especially concerning such species as *Rana temporaria*, *Hyla arborea*, *Emys orbicularis*, and *Elaphe longissima*.

Skeletochronology

Thus far, attempts to obtain paleoclimatic data on the basis of skeletochronological studies on Pleistocene amphibians in Europe have met with somewhat mixed results (e.g., Esteban and Sanchiz, 1985; Esteban, 1990). Assumptions are that bone tissue growth is time dependent and that bone ceases to grow at excessively low (or high) temperatures. Thus, growth pause lines should allow measurements that reflect the length of the growing season as well as the nongrowing (hibernating or aestivating) season. Moreover, comparison of known age classes from different fossil sites could allow estimates of climate-related size changes.

Size of Individuals in Pleistocene Populations Related to Paleoecological Factors

The relationship of body size in Pleistocene herpetological species to paleoecological factors has never been thoroughly addressed, even though it is well known that Pleistocene amphibians and reptile species are sometimes larger than their modern equivalents. In Europe, several of these large forms have been named as fossil species (see Chapters 4 and 8).

On the continent, ''*Rana mehelyi*'' is merely a large form of the common frog, *Rana temporaria*, and ''*Anguis stammeri*'' and ''*Ophisaurus pannonicus*'' are thought to be merely robust forms of the slow worm, *Anguis fragilis*, and the European glass lizard, *Ophisaurus apodus*. An oversimplified explanation for the large size of these taxa in the Pleistocene is that they have responded to the so-called ''reversed Bergmann's rule,'' in other words, that these forms have become larger in response to the warmer climates of Pleistocene interglacial times. But the problem is obviously more complex than this, and other factors such as the unwarranted predation and destruction of habitats by invading humans could have been important.

The ''giant'' endemic *Lacertas* (*Lacerta goliath*, *Lacerta maxima*, and *Lacerta siculimelitensis*) from several oceanic islands near Europe are definitely extinct species and may have been driven to extinction by the invasion of humans and their plant and animal introductions.

Large-sized North American continental Pleistocene species are not uncommon and include anurans (e.g., *Rana catesbeiana*), turtles and land tortoises (e.g., *Emydoidea blandingii*, *Terrapene carolina*, and *Geochelone crassiscutata*), and diamondback rattlesnakes (*Crotalus adamanteus*; Holman, 1995c).

Populations made up of small-sized Pleistocene amphibians and reptiles are seldom, if ever, reported (e.g., Holman, 1995c). In one instance, however, Kerkhoff (1994) studied a series of *Emys orbicularis* shells from various Tegelen late Pliocene sites and concluded that these turtles were smaller than their modern equivalents. I know of no reports on populations of small-sized British or European Pleistocene amphibians and reptiles.

Are Pleistocene Herpetological Species Stratigraphically Important?

Because herpetological taxa have evolved so slowly, and since the Pleistocene herpetofauna of Britain and Europe has essentially remained in evolutionary stasis through the epoch, it might appear that herpetological species have no stratigraphic importance in Pleistocene studies. The G. Böhme model above, however, shows that certain herpetological assemblages appear to indicate certain phases of Pleistocene cycles.

Thus, if the cold-tolerant *Rana temporaria* is the only herpetological species in a large Pleistocene vertebrate fauna that contains boreal and arctic mammalian species, one must admit that *Rana temporaria* helps support the interpretation that the fauna represents a cold stage of the Pleistocene. Moreover, if *Emys orbicularis* and *Elaphe longissima* occur far north of their present range in Europe in the Pleistocene, there is little doubt that a warm stage is represented by the site. Herpetological species may not determine the chronological age of a Pleistocene deposit, but they certainly are of great use in determining the *type* of stage (warm or cold) and, considering the central European model above, in determining even the specific *phase* of that stage (e.g., late warm, early cold, etc.).

7

HERPETOLOGICAL RANGE ADJUSTMENTS IN THE PLEISTOCENE OF BRITAIN AND EUROPE

Compared to herpetological population adjustment patterns in North America (see Holman, 1995c), the patterns in Britain and central and northern Europe seem to be rather straightforward. Basically, (1) very few herpetological species were present in ice-free areas during full glacial times, and (2) formerly glaciated areas were reinvaded by species from the south during warming cycles. Moreover, during climatic optimal warm times, several southern species existed well north of their present ranges. The invasion of southern Europe by northern populations in cold times is taken for granted (e.g., Roček, 1995), although, as addressed in this chapter, it is difficult to document this in the fossil record.

Northwest Division: Ireland and Britain

As indicated by geological and fossil evidence, the British Islands were connected to continental Europe during much of the Pleistocene. Although sea level changes in the British late Pleistocene are a subject of some controversy (Stuart, 1982), it is generally agreed that Britain first separated from Ireland and then from the continent early in the Holocene. The classic idea is that the very depauperate British heretofauna of the cold part of the Devensian (last glacial stage) became somewhat, but not fully enriched by herpetological species during a warming trend that began about 10,000 ybp and lasted until about 8,500 ybp.

The fact that Ireland has a much poorer modern herpetofauna (*Triturus vulgaris*, the rare *Bufo calamita*, *Rana temporaria*, and *Lacerta vivipara*) than Britain, which has six native species of amphibians and six native species of reptiles (Frazer, 1983; Smith, 1964), is attributed to Ireland's early separation from Britain. The Irish herpetofauna suggests that this separation occurred rather soon after the final withdrawal of the Devensian (last glacial) ice sheet.

One of the most common questions asked about snakes, especially near St. Patrick's Day, is, "Have there ever been any snakes in Ireland?" No fossil snakes have ever been found in Ireland. But since Ireland lacks a terrestrial fossil record during most of the time that snakes have existed, it would seem that snakes could have lived in Ireland during some part of geological time.

As far as I am aware, the few Pleistocene deposits containing herpetological remains in Ireland represent very late Devensian (last glacial) times. Moreover, it appears that the only herpetological species that has been recovered from these deposits (most of which are from caves) is the very cold-tolerant common frog, *Rana temporaria*. One might suspect that the tiny bones of *Triturus vulgaris* and *Lacerta vivipara* and the somewhat larger bones of *Bufo calamita* have been missed by fossil collectors. Additional Pleistocene herpetofaunal studies in Ireland are badly needed.

Great Britain has a much better Pleistocene herpetological record than Ireland. In Britain, Pleistocene sites, in combination, contain all of the present herpetofauna except the sand lizard, *Lacerta agilis*. Moreover, many temperate sites have yielded continental taxa that do not presently occur natively in Britain.

But British cold-stage sites, in combination, have yielded only four taxa: *Bufo* sp., *Rana temporaria*, *Lacerta vivipara*, and *Natrix natrix*. Moreover, *Lacerta vivipara* and *Natrix natrix* are known from only one site each (see Chapter 5). At present, *Rana temporaria* is probably the most cold-tolerant amphibian in Europe and *Lacerta vivipara* is probably the most cold-tolerant reptile. Of great interest is the fact that without the single record of *Natrix natrix*, the cold-stage herpetofauna of Britain very much resembles the modern fauna of Ireland!

Temperate or warm-stage exotic continental taxa in the Pleistocene of Britain are listed below. Ilia of "water frogs," *Rana* (*ridibunda*) sp., have reportedly been identified from a Bronze-age site in Cambridgeshire and from Saxon sites in Norfolk and Lincolnshire (Inns, 1995). If this is true, it is possible that an isolated colony of *Rana lessonae* in East Anglia in Britain has not been recently introduced as has been previously believed.

British Middle Pleistocene Sites

Pelobates fuscus: Boxgrove, West Sussex.

Pelodytes punctatus: Westbury–Sub-Mendip, Somerset.

Hyla arborea: East Farm, Barnham, Suffolk; West Runton, Norfolk.

Hyla sp.: Cudmore Grove, Essex.

Bufo viridis: East Farm, Barnham, Suffolk.

Rana arvalis: Boxgrove, West Sussex; Cudmore Grove, Essex; East Farm, Barnham, Suffolk; Sugworth, Berkshire; West Runton, Norfolk.

Rana (*ridibunda*) sp.: Cudmore Grove, Essex; East Farm, Barnham, Suffolk; West Runton, Norfolk.

Emys orbicularis: Cudmore Grove, Essex; East Farm, Barnham, Suffolk; Ingress Vale, Kent; Westbury–Sub-Mendip, Somerset.

Elaphe longissima: Beeches Pit, Suffolk; Cudmore Grove, Essex; East Farm, Barnham, Suffolk.
Natrix maura or *Natrix tesselata*: Cudmore Grove, Essex; East Farm, Barnham, Suffolk.

British Upper Pleistocene Sites

Hyla meridionalis: Itteringham Pit, Norfolk.

Rana arvalis: Greenlands Pit, Purfleet, Essex; Shropham Pit, Norfolk; Swanton Morley, Norfolk.

Rana (*ridibunda*) sp.: Itteringham Pit, Norfolk; Shropham Pit, Norfolk.

Emys orbicularis: Bobbitshole, Suffolk; Harkstead, Suffolk; Itteringham Pit, Norfolk; Mundesley, Norfolk; Selsey, West Sussex; Shropham Pit, Norfolk; Stoke Tunnel, Sussex; Swanton Morley, Norfolk.

Natrix maura or *Natrix tesselata*: Shropham Pit, Norfolk.

Summary

It appears that *Rana temporaria* is the only herpetological species known from Pleistocene sites in Ireland, and it is the only common species found in cold-stage faunas in Britain. In this light, it is interesting to note that Böhme (1996) indicates that *Rana pipiens* tends to be the only herpetological species found in ice-free areas in full cold-stage faunas in central Europe.

Middle Pleistocene warm-stage British Pleistocene sites, in combination, have produced at least nine herpetological species that presently occur in continental Europe but are absent in the modern native fauna of Britain. Four of these—*Hyla arborea*, *Pelobates fuscus*, *Emys orbicularis*, and *Elaphe longissima*—are considered to be among the eight herpetological species characteristic of warm climatic optimal peaks in central Europe (Böhme, 1996). Several British Middle Pleistocene warm-stage sites have two or more of the species listed above (see Chapter 5).

British Upper Pleistocene sites have yielded five exotic continental species, four fewer than yielded by Middle Pleistocene sites. Five exotic species found in British Middle Pleistocene sites that are absent in British Upper Pleistocene sites are *Pelobates fuscus*, *Pelodytes punctatus*, *Bufo viridis*, *Hyla arborea*, and *Elaphe longissima*. On the other hand, the Mediterranean species *Hyla meridionalis* occurs only in the Upper Pleistocene Itteringham Pit, Norfolk, Ipswichian (last interglacial) site, and records of *Emys orbicularis* are more common in the Upper Pleistocene than in the Middle Pleistocene.

Nevertheless, there are no faunas in the British Upper Pleistocene that have yielded such rich herpetofaunas with such a large number of exotic continental species as occur in the East Farm, Barnham, Suffolk, and the Cudmore Grove, Essex, sites.

Comment

As we turn to the continent, we obviously see a more expanded range of Pleistocene climates than occured in Britain. In northern and central Europe, herpetological range adjustment patterns were generally simlar to those in Britain. A single herpetological species, *Rana temporaria*, tends to be the only one that has been recorded from ice-free areas during full glacial times. On the other hand, during optimal warm times, modern local species as well as southern invaders were present.

In southern Europe, Mediterranean species sometimes extended their ranges northward. On other occasions, some species adjusted their ranges in response to alternating wet and dry conditions. In other cases, extralimital mainland species were found on oceanic islands and vice versa.

Northern herpetological immigrants into southern faunas, however, are difficult to document in the Pleistocene fossil record in Europe as well as in North America (Holman, 1995c). This is because ''northern'' herpetological species have such broad ecological tolerances that they are able to exist in both northern and southern latitudes. In Europe, taxa such as *Bufo bufo*, *Rana arvalis*, *Rana temporaria*, *Lacerta vivipara*, and *Vipera berus* are very widely distributed in both the north and the south. Thus, fossils representing northern animals pushed southward by glacial advances are not distinguishable from those of the resident populations.

French Division: France and Monaco

In France, the extralimital occurrence of *Rana arvalis* and *Rana temporaria* was detected in a fauna due to alternating wet and dry conditions in the Middle Pleistocene. The Âbimes de la Fage site in the Department of Correze in the northern part of southwest France lies where the present climate is too dry to support populations of *Rana arvalis* and *Rana temporaria*. But moister climates existed in the area during Middle Pleistocene times, and both *Rana arvalis* and *Rana temporaria* were found in the lower deposits of the site (Rage, 1972a). On the other hand, the upper beds of the site yielded the extralimital Mediterranean taxa *Discoglossus* sp. and *Testudo hermanni*, indicating a warmer, dryer climate. Enigmatically, however, at one level, *Discoglossus* sp. and *Rana arvalis* occur together, a difficult situation to interpret.

Another record of an extralimital Mediterranean tortoise in the Pleistocene of France is reported from the Pleistocene site at Vallée de Fontechevade (stage undesignated) in the Department of Charente in the northern part of southwestern France near the Bay of Biscay. The tortoise was identified as *Testudo graeca* (Henri-Martin, 1946), but at present this species gets no closer to France than extreme southern Spain and the Balearic Islands. As *Testudo hermanni* presently occurs in the western Mediterranean basin of France, it would seem more likely that this is the species that was represented. This tortoise material should be reexamined to verify the specific identification. Nevertheless, this record marks a northern range extension for *Testudo* in the Pleistocene and indicates a warmer, dryer climate for the area.

Southwest Division: Spain

Pleistocene paleoherpetological studies in Spain have produced several interesting records of extralimital species. Hienas Cave, an Upper Pleistocene site in Asturias Province in extreme northwestern Spain, has yielded *Euproctus* sp. (Martín and Sanchiz, 1990). The nearest this genus presently occurs to the site is along the French border in northeastern Spain, where the species *Euproctus asper* occurs. This species normally occurs in or near cool mountain streams or lakes.

The painted frog genus, *Discoglossus* sp., has been reported from the Balearic Island of Majorca, Spain. The genus is not found in the Balearic Islands at present. The nearest that modern *Discoglossus* gets to Majorca Island is in the form of *Discoglossus pictus*, which presently reaches the southern coast of Spain. The Majorcan fossil *Discoglossus* remains were yielded by the Pliocene/Pleistocene Pedrera de s'Onix site, the Lower Pleistocene Binigaus site, and a Pleistocene (stage undesignated) site with no specific locality given.

The extant species *Discoglossus galganoi* that presently occurs in Portugal and southwestern Spain was a southern extralimital immigrant in two Middle Pleistocene sites, the Ambrona, Soria Province, site in northeastern Spain, and the Aridos 1, Arganda, Madrid Province, site in central Spain.

The extant species *Discoglossus jeanneae*, which presently occurs only in southern Cádiz Province, Spain, across from Morocco (Duellman, 1993), has been identified as *Discoglossus* cf. *Discoglossus jeanneae* in the Pleistocene of two provinces to the east of Cádiz Province: the Middle Pleistocene Grajas Cave Site in Malaga and the Middle and Upper Pleistocene Horá Cave site in Granada. However, it is possible that modern herpetologists may yet collect the species in the two provinces.

Rana iberica has been recorded from the Upper Pleistocene Millán Cave site in Burgos Province in northern central Spain. It is a somewhat extralimital Pleistocene species that presently occurs nearest to the fossil site in the northern part of Madrid Province in central Spain.

The skink genus *Chalcides* is presently represented by species in southern Spain and the Canary Islands, but it is absent from the Balearic Islands. A single record of *Chalcides* is known from a Majorca Island Pleistocene site whose specific location and age are undesignated.

Coluber viridiflavus presently occurs only in the northeastern corner of Spain. Therefore, a record of *Coluber* aff *Coluber viridiflavus* (if correct) from the Middle and Upper Pleistocene site of Horá Cave, Granada Province, in the southwestern Mediterranean area represents quite a southern range extension for this species in Spain. *Coluber viridiflavus* does, however, presently occur in other southern Mediterranean area localities in Sardinia, Sicily, and southern Italy.

Northcentral Division: Netherlands, Belgium, Luxembourg, Germany, Austria, Switzerland

Extralimital herpetological species in the Pleistocene of the Northcentral Division mainly consist of southern taxa that moved northward during warm climatic times. Several extralocal records of Pleistocene amphibians and reptiles in the Northcentral Division are not discussed here (e.g., records of *Elaphe longissima* from the Lobsing and Euerwanger Bühl sites in Germany; see Szyndlar, 1984, pp. 100–101) because it is probable that these taxa became extirpated during historic times. Extralimital Pleistocene species of the Northcentral Division follow.

A somewhat questionable record of the neotenic cave salamander, *Proteus* sp., has been reported from the Upper Pleistocene Teufelshöhle (Devil's Cave) site, Pottenstein, northeast of Erlangen, Bavaria, Germany. This taxon presently reaches the northernmost part of its range just north of the Adriatic Sea. The identification was based on a single parasphenoid bone; thus, more remains are needed to confirm the record.

Pelodytes punctatus that presently occurs west of Germany in France has been recorded from the Middle Pleistocene Steinbruch Schmid site, Stuttgart, whereas *Rana arvalis* is extralocal at the Middle Pleistocene Meisenheim I site in the Neuwied Basin.

Testudo hermanni has been reported from early literature records (see Chapter 5) from the Pleistocene (stage undesignated) of the Württemburg district in southwestern Germany. No definite locality was given. The nearest this species presently occurs to the area is in the Mediterranean basin of France. The material should be restudied, and the precise age of the site should be established.

Lacerta cf. *Lacerta* (''*Podarcis*'') *sicula* has been reported from the Middle Pleistocene of Breitenburg Cave, near Gössweinstein, Bavaria, Germany. The nearest that this southern extralimital species presently occurs to the site is in Switzerland.

Coluber caspius (*Coluber jugularis* of some authors) has been reported from two Middle Pleistocene sites in northeastern Austria. The nearest that this species presently occurs to these sites is in northern Yugoslavia. The Austrian sites are (1) Bad Deutsch, Altenberg 2, and (2) St. Margarethen, near Hainburg.

Coluber gemonensis has been reported from the same two sites as *Coluber caspius* in the above account. *Coluber gemonensis* also presently occurs nearest to these sites in northern Yugoslavia.

Coluber viridiflavus, a southern extralimital species, has been found in two Middle Pleistocene sites in southwestern Germany. These sites are (1) Breitenburg Cave, near Gössweinstein, Bavaria, and (2) Fuchsloch, Siegmannsbrunn, Bavaria. The nearest that this species presently gets to Germany is in localities in Switzerland. The Seigmannsbrunn occurrence was first reported as **Coluber freybergi*, a taxon that is now considered to be a synonym of *Coluber viridiflavus* (see Chapter 4).

Elaphe longissima has been found well north of its present range in Germany in the following sites. There are other extralocal records in the country (See Germany section, Chapter 5).

Middle Pleistocene: Ehringsdorf Site Complex, near Weimar, Thuringia, central Germany.
Upper Pleistocene: (1) Burgtonna, near Erfurt, Thuringia, central Germany. (2) Ehringsdorf Site Complex, near Weimar, Thuringia, central Germany. (3) Parkhöhlen Travertine, Weimar, Thuringia, central Germany. (4) Schönfeld near Cottbus, Lusatian area, eastern Germany. (5) Taubach, near Weimar, Thuringia, central Germany.
Upper Pleistocene and Holocene: Pisede near Malchin, Neubrandenberg area, northeastern Germany.

Elaphe quatuorlineata remains have been recovered from two Middle Pleistocene sites in northeastern Austria. At present, the nearest this species occurs to the Austrian sites is in northern Yugoslavia. The two Austrian sites are (1) Bad Deutsch, Altenberg 2, and (2) St. Margarethen, near Hainburg.

Natrix tesselata has been found in the Upper Pleistocene and Holocene sites at Malerfels and Euerwanger Bühl near Greding in the Nuremberg area of southeastern Germany. These occurrences lie between the present range of the species in the eastern Czech Republic and three isolated populations in southwestern Germany.

Northeastern Division: Poland and the Czech Republic

As in the Northcentral Division, most of the extralimtal species represent southern taxa that moved north of their present ranges during warm-stages of the Pleistocene. Several extralocal Pleistocene records of *Elaphe longissima* in southern Poland are near a nineteenth-century record of the species and an existing isolated population in southeastern Poland (see Szyndlar, 1984, pp. 100–101). These Pleistocene records are not addressed here because they probably represent populations that became extirpated during historic times.

Pelodytes sp. was recognized in material from the Lower Pleistocene Kozi Grzbiet site in southern central Poland. *Pelodytes* is presently a western European genus whose nearest occurrence to the site is in France in the form of the species *Pelodytes punctatus*.

Ophisaurus apodus (=**Ophisaurus* ''*pannonicus*'') has been identified from two Lower Pleistocene sites (Kamyk and Żabia Cave) in central southern Poland. The nearest that *Ophisaurus apodus* presently gets to these Polish Pleistocene sites is in northern Yugoslavia.

Coluber caspius (*Coluber jugularis* of some authors) has been reported from the Lower Pleistocene Malá Dohoda Quarry in the central part of the Czech

Republic. The closest this species presently gets to the fossil site is in northwestern Hungary.

?*Coluber* aff *Coluber gemonensis* has also been reported from the Lower Pleistocene Malá Dohoda Quarry. This species presently occurs nearest the fossil site in northern Yugoslavia.

Coluber cf. *Coluber viridiflavus* has been identified from the Lower Pleistocene Stránzá Skála Hill site, near Brno in the central southern part of the Czech Republic. This southern European taxon presently gets no closer to the site than Switzerland and northern Yugoslavia.

Elaphe longissima has been identified from two Upper Pleistocene sites (Rząśnik and Wierzbica 1) in the vicinity of Warsaw in central Poland. The nearest that the species presently occurs to these sites is in an isolated population in southeastern Poland, although an isolated nineteenth-century record exists in central southern Poland. Numerous possible extralocal Pleistocene records of *Elaphe longissima* exist in southern Poland (see Chapter 5).

Elaphe quatuorlineata has been identified from the Lower Pleistocene Malá Dohoda Quarry in the central part of the Czech Republic. The nearest that the species presently gets to the site is in northern Yugoslavia.

Vipera cf. *Vipera ammodytes* and *Vipera* cf. *Vipera ursinii* have been identified from the Lower Pleistocene Stránzá Skála Hill site near Brno in the central southern portion of the Czech Republic. These species presently get no closer to the fossil locality than northern Hungary.

Southeastern Division: Italy, Hungary, Yugoslavia (Croatia, Bosnia, Serbia), Greece

Pleistocene herpetological population adjustments in the Southeastern Division consisted of the extinction of Pleistocene Oceanic island species that are presently found on the mainland and vice versa, as well as mainland adjustments, including northward movement of southern species.

Pleistocene records of *Discoglossus* sp. on the mainland of Italy and Croatia are of special interest, as the only modern occurrences of this genus in the eastern Mediterranean region are on the islands of Corsica and Sardinia, where *Discoglossus sardus* is found, and Sicily and Malta, where *Discoglossus pictus* is found.

A Lower Pleistocene record of *Discoglossus* sp. from Scoppito, Italy, exists. Moreover, a Middle Pleistocene record from Montagnolla, Senese, Italy, occurs as well as an Upper Pleistocene record from Vitinia, Rome. *Discoglossus* sp. was also reported from the Upper Pleistocene Šandalja site near Pula on the Istrian Peninsula in extreme northwestern Croatia.

On the other hand, *Discoglossus* sp. was recorded from two Pleistocene sites on the Island of Crete, Greece, which is the only large island in the eastern Mediterranean area where the genus does not presently occur. These sites are the Lower Pleistocene Sitia-Psilokefalo site and the Middle Pleistocene Sitia 1 site.

Rana graeca, a form that is presently adapted to cool streams, is an extralimital southern form that was reported from the Upper Pleistocene Šandalja site near Pula on the Istrian Peninsula of extreme northwestern Croatia. In the Balkan states, this species presently reaches its northern limits in central Yugoslavia.

Mauremys cf. *Mauremys caspica*, a freshwater turtle, was reported from the Upper Pleistocene San Giovanni site, Sinis, Oristano, in the western part of Sardinia Island. This species is presently absent from all of Italy and its islands, the closest occurrence being in the southern Balkans. Of additional interest is that *Mauremys* sp. has been recorded from the Middle Pleistocene Ponte Salario site, Rome, Italy.

Testudo graeca, a tortoise with a spotty distribution in the Mediterranean region at present, has been recorded extralimitally from the Zebbug Cave and Ghar Dalam Cave deposits in Malta. These sites both represent the Upper Pleistocene or Holocene. The *Testudo graeca* remains are partly or entirely associated with human cultural artifacts. This species does not presently occur on Malta, but it has been introduced into Sicily by humans.

Testudo graeca has also been recorded from the Upper Pleistocene Šandalja site near Pula in the Istrian Peninsula in extreme northwestern Yugoslavia. The closest that this tortoise presently occurs to the area is in southeastern Yugoslavia and Bulgaria.

Moreover, remains of *Testudo* sp. and *Testudo graeca* from the Upper Pleistocene strata of the Süttő site in northwest Hungary are very extralimital, and the material should probably be reexamined. *Testudo hermanni* presently reaches northern Yugoslavia west of the site, but *Testudo graeca* is currently very far from the site, occurring in southern Italy and the southern and eastern Balkans.

The genus *Testudo* does not presently occur on Crete, but there is an Upper Pleistocene record of *Testudo marginata* at the Bate Cave, Rethymnon, site on the island. The other taxa in the Bate Cave herpetofauna presently occur on Crete.

Again we turn to the large glass lizard *Ophisaurus apodus* (=**Ophisaurus* ''*pannonicus*''). *Ophisaurus apodus* occurs in the Upper Pliocene or Lower Pleistocene Villány 7 site and the Lower Pleistocene Csarnóta 4 and Villány 5 and 8 Sites, all in southwestern Hungary. These sites are somewhat east of the present range of the the species in northern Yugoslavia. Two other records of *Ophisaurus apodus* are from Pleistocene (stage undesignated) sites in Beremend and Köpecz, Hungary, also somewhat east of the present range of the species.

The worm lizard species *Blanus* cf. *Blanus strauchi* has been identified from the Lower Pleistocene Cava Dell'Erba site, Apricena, Foggia, southern Italy. At present this species occurs on the islands of Rhodes and Kos, Asia Minor, Syria, and north Mesopotamia. This species does not presently occur on the Italian peninsula, nor does the western species *Blanus cinereus*.

Coluber gemonensis has been reported from the Middle and Upper Pleistocene Volpe Cave site near Verona, Italy. This extralimital species presently occurs along the eastern Adriatic coast into Greece, including Crete and many smaller islands.

A probable occurrence, cf. *Elaphe longissima*, has been recorded from the Upper Pleistocene Gerani 1 site on the island of Crete and from the "Upper Quaternary" Pili B site on Kos Island. *Elaphe longissima* presently does not occur in Greece or on Greek islands.

Elaphe quatuorlineata has been identified from the Lower Pleistocene Csarnóta 4 site, southwestern Hungary. This site is somewhat east of the present occurrence of the species in northern Yugoslavia.

Finally, extralimital Oriental vipers of the genus *Vipera* (not identified to species) have been found in the Middle Pleistocene of the Greek island of Chios.

8

EXTINCTION PATTERNS IN THE HERPETOFAUNA OF THE PLEISTOCENE OF BRITAIN AND EUROPE

As we have seen in Chapter 4, many invalid European Pleistocene amphibian and reptile species were named on the basis of insufficient and inadequately described fossils (e.g., Estes, 1981, 1983; Rage, 1984c; Sanchiz, in press). Some of these forms have been synonymized with modern species, but others are in taxonomic limbo because of the international rules of zoological nomenclature.

We now turn to a consideration of the few European Pleistocene fossil herpetological species that have been recognized as valid in recent years. These taxa fit into three catagories: (1) an extinct Pliocene anuran taxon that extended into the Pleistocene, (2) large *Lacerta* species that lived on oceanic islands, and (3) Pleistocene species that are probably morphological variants of living forms. All of the following taxa are addressed in Chapter 4.

Order Caudata

No extinct species of Pleistocene salamanders are currently recognized in Britain or Europe.

Order Anura

Family *Palaeobatrachidae

Pliobatrachus* cf. *Pliobatrachus langhae

The genus **Pliobatrachus* from the Pliocene of eastern Europe extended into the Lower Pleistocene of Poland and the Middle Pleistocene of Germany in the form of **Pliobatrachus* cf. *Pliobatrachus langhae*. The **Palaeobatrachidae*, the only family in the history of the Anura that became totally extinct (Roček, 1995), represents the *only* extinct herpetological family known in the Pleistocene of

Britain and Europe, and **Pliobatrachus* represents the *only* extinct herpetologcal genus known in the Pleistocene of the region.

Roček (1995) suggested that the *Palaeobatrachidae did not survive the Pleistocene cooling because of their prevailingly aquatic mode of life, unlike, for instance, the Ranidae and Bufonidae that were able to withdraw from ice-obliterated areas and return when climatic conditions improved.

Order Sauria

Family Lacertidae

**Lacerta goliath*

**Lacerta goliath* is a Pleistocene or Holocene species that is known only from two localities in the Canary islands (see Chapters 4 and 5). It is twice the size of *Lacerta lepida*, the largest modern European *Lacerta.*

**Lacerta maxima*

**Lacerta maxima* is another very large Pleistocene or Holocene *Lacerta* that is endemic to the Canary Islands. This species is known from a single fossil locality (see Chapters 4 and 5) and is differentiated from **Lacerta goliath* on the basis of several trenchant osteological characters.

**Lacerta siculimelitensis*

**Lacerta siculimelitensis* is a third large, extinct, endemic, oceanic island *Lacerta*. It also is a well-differentiated Pleistocene species; among other characters, it is the only *Lacerta* in which tooth expansion occurs. **Lacerta siculimelitensis* has been found in the Middle Pleistocene of Sicily and the Upper Pleistocene of Malta (see Chapters 4 and 5).

Family Anguidae

*"*Anguis stammeri"*

"**Anguis stammeri*" is a very doubtful Middle and Upper Pleistocene species from central Europe. It is distinguished from the modern European *Anguis fragilis* based mainly on the more robust and more sharply pointed teeth of the fossil form. Estes (1983) was unable to compare specimens of "**Anguis stammeri*" to other related lizard species but expressed the view that it might be a valid species. Młynarski (1962) suggested "**Anguis stammeri*" might be an *Ophisaurus* (see Chapter 4). I have seen fossil specimens of *Anguis fragilis* of very large size and with very robust teeth from a Holocene deposit in England (see Chapter 4), and I consider "**Anguis stammeri*" to be merely a robust variant of *Anguis fragilis.*

''*Ophisaurus pannonicus''

''*Ophisaurus pannonicus'' is a taxon that appeared in the Pliocene and has been found in the Pleistocene of eastern and central Europe. This form differs from the very large southeastern European modern species, *Ophisaurus apodus*, in its even larger size and more robust osteology. Młynarski (1964) suggested that even the Upper Pliocene fossils of ''*Ophisaurus pannonicus*'' could not be distinguished from extant individuals of *Ophisaurus apodus* from the Balkan Peninsula; thus, Estes (1983) thought the extinct *Ophisaurus* might have been a large northern race of *Ophisaurus apodus*. Large Pleistocene variants of modern herpetological species are not uncommon (Holman, 1995c), and I consider ''*Ophisaurus pannonicus*'' to be merely a large variant of *Ophisaurus apodus*.

Order Serpentes

Family Colubridae

I suggest that three supposed Pleistocene fossil species of European *Coluber* (''*Coluber fossilis*,'' ''*Coluber freybergi*,'' and ''*Coluber gervaisii*'') represent the modern species *Coluber viridiflavus* (see Chapter 4).

Summary

In good conscience, I consider only four herpetological taxa in the area covered by this book to be unquestionably valid extinct Pleistocene species. These are (1) **Pliobatrachus* cf. *Pliobatrachus langhae*, (2) **Lacerta goliath*, (3) **Lacerta maxima*, and (4) **Lacerta siculimelitensis*.

The extinct aquatic frog **Pliobatrachus* cf. *Pliobatrachus langhae* is a carryover from Pliocene times and represents the only extinct European Pleistocene herpetological family and genus. The three extinct ''giant'' lizard species are all oceanic island endemics. **Lacerta goliath* and **Lacerta maxima* probably survived into at least the early Holocene.

The "Why" of Pleistocene Herpetofaunal Stability

A debate has raged for decades about the cause of the worldwide extinction of large mammalian species (and to a lesser extent the birds) in the late Pleistocene. The two general hypotheses are that this faunal revolution was caused either by human big game hunters or by environmental changes at the end of the epoch (e.g., Martin and Wright, 1967; Kurtén, 1968; Kurtén and Anderson, 1980; Martin and Klein, 1984).

In northern Eurasia alone several large mammalian genera, all of which greatly impacted the ecosystem, became extinct in the late Pleistocene. These include the cave bear (*Ursus spelaeus*), spotted hyena (*Crocuta crocuta*) that presently survives elsewhere, wooly mammoth (*Mammuthus primigenius*), straight-tusked elephant (*Palaeoloxodon antiquus*), extinct rhino (*Dicerorhinus hemitoechus*), wooly rhino (*Coelodonta antiquitatis*), hippo (*Hippopotamus amphibius*) that presently survives elsewhere; and giant deer (*Megaloceros giganteus*; Stuart, 1991). Several important smaller European mammalian taxa also became extinct (e.g., Kurtén, 1968; Stuart, 1982) in the late Pleistocene.

In North America, extinction at the generic level was even more devastating, as 33 of 45 (73%) large mammals as well as many species of smaller mammals died out in the late Pleistocene (Kurtén and Anderson, 1980; Stuart, 1991). On the other hand, the North American herpetofauna, with the exception of the extinction of a few taxa, has essentially been in evolutionary stasis since the onset of the Pleistocene.

We now turn to a consideration of the situation in Britain and Europe (Table 3). Of the 28 Pleistocene amphibian and reptile genera reported here, only one of 28 (3.6%) is extinct. This compares with 7 of 24 (29%) large late Pleistocene mammalian genera in northern Eurasia and 33 of 45 (73%) in North America (Stuart, 1991).

Of the 76 amphibian and reptile species reported here, only four (5.3%) are unquestionably extinct (Table 3). Note that these taxa consist of (1) the extinct

Table 3. Extinction in the Pleistocene Herpetofauna of Britain and Europe

Living	Extinct (%)	
Salamanders		
Families	2	0 (0.0)
Genera	4	0 (0.0)
Species	6	0 (0.0)
Anurans		
Families	6	1 (16.7)
Genera	9	1 (11.1)
Species	29	1 (3.4)
Turtles		
Families	2	0 (0.0)
Genera	3	0 (0.0)
Species	6	0 (0.0)
Lizards and Amphisbaenians		
Families	6	0 (0.0)
Genera	5	0 (0.0)
Species	14	3 (21.4)
Snakes		
Families	4	0 (0.0)
Genera	7	0 (0.0)
Species	21	0 (0.0)

Note: Four of 76 total species are extinct (5.3%). **Anguis stammeri* is considered to be a large variant of *Anguis fragilis*, and **Ophisaurus pannonicus* is considered to be a large variant of *Ophisaurus apodus*.

frog **Pliobatrachus* cf. *Pliobatrachus langhae* and (2) three species of oceanic island lizards. Thus, in the area covered by this book, only one mainland form is considered to be an unquestionably valid extinct Pleistocene species!

It should be noted here that although valid extinct Pleistocene herpetological species (other than tortoises) are rare in mainland North America (Holman, 1995c), several extinct Pleistocene anurans, tortoises, and lizards (including large forms) have been reported from late Pleistocene sites in the oceanic West Indes islands (e.g., Auffenberg 1958, 1974; Etheridge, 1965, 1966; Pregill, 1981).

It is difficult to compare extinct species of Pleistocene amphibians and reptiles with the many described extinct species of Pleistocene small mammals and birds because so many small, extinct endothermic taxa are considered to be of dubious validity (mammals: Stuart, 1991; birds: Carroll, 1988). Nevertheless, the British and European herpetofauna appears to have been in remarkable stasis since the onset of the Pleistocene, in other words, virtually unchanged for the last 1.64 million years!

The most stunning aspect of this is that an industrialized, environmentally exploitive human society has apparently placed hundreds of amphibian species (and who knows how many reptilian species) in jeopardy in a mere instant of geological time.

The most compelling question raised by the North American Pleistocene herpetofauna (Holman, 1995c), and now raised again by that of Britain and Europe, is what attributes have allowed the herpetofauna to survive the stresses that have caused dramatic extinctions in other classes during the Pleistocene?. But to remain scientifically objective, before we speculate about the "why" of the apparent evolutionary stasis in the Pleistocene herpetofaunas of North America and Europe, some possible modifications of the concept should be considered.

Because of the information loss that occurs during the death and preservation of most herpetological fossils, the majority of Pleistocene amphibians and reptiles are represented by fragmentary individual bones rather than by complete skeletons. Some of the most important of these elements are vertebrae in salamanders, ilia in anurans, portions of shells in turtles, dentaries in lizards, and vertebrae in amphisbaenians and snakes.

Thus, one of the most frustrating problems is that undoubtedly extinct species have gone unrecognized. For instance, water frogs of the *Rana ridibunda* complex of species are distinct on the basis of external morphology but are extremely difficult to distinguish osteologically. The same is true of the water snakes *Natrix maura* and *Natrix tesselata*. How, then, would one recognize an extinct water frog or water snake on the basis of an isolated ilium or vertebra?

Cryptic species are also a problem. In North America, cryptic species such as the gray treefrogs *Hyla versicolor* and *Hyla chrysoscelis* have identical skeletons as far as I can determine, and cryptic forms undoubtedly occurred in the Pleistocene of both North America and Europe.

Another problem for paleoherpetologists is that often when complete skeletons of Pleistocene amphibians and reptiles such as frogs or snakes are available, they are so embedded in matrix that they present only a two-dimensional view, and usually have obscure bony processes and muscle scars. Often, a single frog ilium or snake vertebra, unbroken and free from matrix, will be a much more diagnostic piece that an entire frog or snake embedded in rock.

A problem that is difficult to resolve is the ingrained idea among some paleoherpetologists is that all Pleistocene herpetological material other than ''giant'' lizards on oceanic islands or extinct tortoises in North America must belong to modern species. This bias has undoubtedly grown out of the negative reaction of the ''new'' generation of paleoherpetologists of the 1950s to the overzealous naming of Pleistocene species by their predecessors. It is evident in the present paleoherpetological community that anyone who attempts to name a Pleistocene amphibian or reptile species is immediately the recipient of intense scrutiny by his or her colleagues, but one who identifies modern species on the basis of an isolated bone is likely not to be questioned.

It appears that this bias can only be changed by intense studies of osteological variation in modern and fossil amphibian species. But serious limitations exist. Seldom does one get an adequate sample of fossil amphibian or reptile species, and considering modern conservation ethics and laws, procuring a modern comparative skeleton collection that is adequate for variational studies may be extremely difficult.

All this having been said, however, there is still no doubt that the herpetofaunas of the British Islands, the European continent, and North America have been strikingly more stable since the beginning of the Pleistocene than the endothermic faunas there. Moreover, this has been documented by hundreds of Pleistocene sites.

The Direction of Future Studies

Answers to the question of the ''why'' of Pleistocene herpetofaunal stasis will be obtained by additional modern and fossil studies. It is a given that ectothermic animals with low metabolic rates that can aestivate or hibernate (brumate) would have had advantages over endothermic birds and mammals during climatic oscillations. The fact that several species of frogs are able to freeze solid regularly in the winter and thaw out in the spring with no harmful effects (e.g., Layne and Lee, 1995), and that some North American turtle hatchlings freeze in the nests during the winter with no ill effects (e.g., DePari, 1996), certainly would have benefited these species in the Pleistocene ice ages. Continuing studies of aestivation and hibernation (brumation) rhythms in amphibians and reptiles should be important in establishing parameters for estimating their Pleistocene adjustments.

The small body size of most northern temperate amphibians and reptiles would appear to be advantageous to them in the face of Pleistocene habitat shrinkage, particularly compared with the larger endotherms, particularly the megaherbivores (Owen-Smith, 1987) that need large tracts of land to exist.

A compelling possibility exists that few Pleistocene amphibians and reptiles depended directly on the megaherbivores that became extinct during the Pleistocene, either as predators, scavengers, or commensals. In North America, at the well-documented Pleistocene site at Rancho La Brea in California, the scavenging or commensal birds and the dung beetles that depended on the large herbivorous mammals became extinct along with these mammals (Harris and Jefferson, 1985). On the other hand, all of the amphibian and reptile species survived into the present.

But in Australia, the giant monitor lizard *Megalania* and the huge snake *Wonambi* (Murray, 1984) were top predators and became extinct during the Pleistocene probably because so many large marsupial herbivores died out. For some reason, few suggestions have been made in Pleistocene studies about the possible ecological relationships of the amphibians and reptiles to the large extinct mammals in either Britain and Europe or North America. It certainly might be that herpetological species existed well outside of the interactions that took place between the large mammalian herbivores and their predators and scavengers. Studies of how small amphibians and reptiles tie into the food web in African communities that support large herbivorous mammals may be interesting in the light of the differential Pleistocene extinctions.

Parenting in endothermic birds and mammals is obviously part of the reproductive stress syndrome and would appear to be a considerable drain on their energy during times of climatic change. Of course, parenting, at least in the sense of birds and mammals, is lacking in amphibians and non-crocodilian reptiles.

For decades the hypothesis of human overkill has been promoted as a most important factor in the Pleistocene extinction of the large herbivorous mammals (e.g., Martin and Wright, 1967; Martin and Klein, 1984). Holman (1959) compared extinction percentages of amphibians and reptiles to mammals in a Pleistocene fauna in Florida and suggested that the rise of humans might have been an important factor in the differential extinction of the herpetological and mammalian components of the fauna. This might reflect the less desirable aspect of most amphibian and reptile species as a food resource compared with the large mammalian herbivores. Obviously, the huge land tortoises of the genus *Geochelone* would have been an easily obtained source of food for humans (e.g., at the Little Salt Spring site in Florida; Clausen et al., 1979), and this might have been a major cause for the extinction of the large tortoise species in the North American Pleistocene.

In summary, further studies of many modern aspects of amphibian and reptile physiology and ecology will directly bear on the ''why'' of the general stasis of the herpetofauna in Britain, Europe, and North America in the face of climatic and environmental changes. These will include studies of physiological responses to environmental changes such as cryobiology. Moreover, further study of the place of amphibians and reptiles in the Pleistocene food web as well as modern studies of this subject, especially in megaherbivore-dominated communities such as occur in Africa, should also provide additional insights. Finally, paleolithic studies in Britain and Europe, as well as postglacial Pleistocene studies in North America, may eventually provide information about the importance of Pleistocene amphibians and reptiles as a Pleistocene food resource for humans.

9

PLEISTOCENE HERPETOFAUNAS OF BRITAIN AND EUROPE AND NORTH AMERICA COMPARED

This last chapter deals with differences and similarities between British and European and North American Pleistocene herpetofaunas.

Compared with North America, Britain and Europe had a depauperate Pleistocene herpetofauna, which has carried over into modern times. For instance, the large, ''warm'' country of Spain, which by European standards has a rich modern herpetofauna, has only 13 species of snakes and four species of nonmarine turtles (Engelmann et al., 1986). On the other hand, Michigan, a northern border state with cold winters, has 17 species of snakes and 11 species of turtles (Holman et al., 1989; Harding and Holman, 1990). Indiana, just south of Michigan, has 31 species of snakes and 15 species of turtles (Minton, 1972; Brown, 1996; Conant and Collins, 1991). The southern coastal state of Florida has 45 species of snakes and 20 species of nonmarine turtles (Conant and Collins, 1991). This is almost twice as many snakes and more than three times as many nonmarine turtles as occur in Britain and Europe.

In the Pleistocene, British or European herpetofaunas are considered to be rich when they contain 10 species. In North America, Pleistocene herptofaunas with more than 20 species are common, and sites with more than 40 herpetological species are known (Holman, 1995c).

The reasons for these differences are as follows. Both North America and Europe became herpetologically enriched in the Miocene. But the climatic deterioration at the end of the Miocene caused a depletion of the herpetofauna in Europe. Because Europe was mainly isolated from Africa by the Mediterranean Sea and from warm areas to the east by mountain ranges and seas, its depauperate herpetofauna persisted into modern times. Ireland and Britain have even more depauperate modern herpetofaunas than the continent because these islands were cut off from the mainland before they could be reinvaded by all of the species displaced by the last glaciation (Fig. 45).

In North America, however, with a vast, accessible southern land mass, and equable Pleistocene climates south of the periglacial regions (Lundelius et al.,

FIGURE 45. Approximate distribution of the ice (areas enclosed by broken line) during the time of the Devensian glacial expansion about 18,000 ybp. Britain and Ireland appear as they are at present. [Drawing by Teresa Petersen in Holman, 1993a]

1983), the richness of the Miocene herpetofauna persisted into Pleistocene and modern times.

Because of greater contrast between glacial and interglacial climates in Europe than in North America, Pleistocene herpetological events differed markedly in the two regions. In Britain and northwestern Europe, in full glacial times, land masses as well as the surrounding seas froze over (Fig. 45), causing bitterly cold climates in ice-free areas. Moreover, glaciated mountains occurred in Spain, France, eastern-central Europe, and even the Balkans.

In North America, however, even though the continental ice sheet extended south as far as central Illinois, Indiana, and Ohio in the last full glacial episode (Fig. 46), and even farther south in a previous glacial stage, warm air masses from the Gulf Coast contributed to an equable climate in areas as near as 150 km from the ice front (Holman and Richards, 1993).

The huge, accessable, unglaciated land mass in North America thus provided an equable refugium for herpetological species when ice sheets advanced; and when the glaciers withdrew, rich herpetofaunas were able to recolonize formerly glaciated areas.

For instance, Michigan (Fig. 46), a northern border state, presently has 11 modern species of turtles (Harding and Holman, 1990), whereas the entirety of

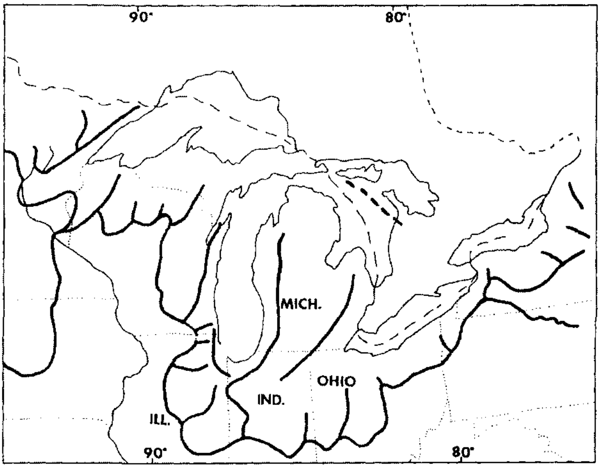

FIGURE 46. Maximum extent of the Laurentide Ice Sheet in the late Wisconsinan in North America showing the principle lobes and sublobes 21,000–20,000 ybp. [From Holman, 1995c]

Britain and Europe has only six species of modern nonmarine turtles (Arnold and Burton, 1978). The comparatively rich Michigan turtle fauna reflects the fact that a relatively warm, equable climate, able to sustain a rich turtle fauna, existed only 150 km south of the ice front (Holman and Richards, 1993) at the time of the last maximum glaciation. At least four species of turtles had reoccupied central southern Michigan area by about 6,000 ybp (Holman, 1990b). Northwestern Ohio (Fig. 46) was covered by the last ice sheet until about 14,800 ybp, but 18 herpetological species (one salamander, seven anurans, three turtles, and seven snakes) sucessfully reinvaded the area by about 11,700 ybp (Holman, 1997). Based on data from Pleistocene sites in Indiana and Ohio, Holman (in press) calculated that four species of frogs (*Rana catesbeiana*, *R. clamitans*, *R. pipiens*, and *R. sylvatica*) moved northward into unglaciated territory at a rate of about 100 km per 1,000 years.

However, south of the periglacial areas in North America, the herpetofaunas tended to stay in place in both glacial and interglacial times. In fact, Pleistocene herpetofaunas in all regions in eastern North America from northern Ohio and southern Pennsylvania southward tended to be composed mainly of species that presently live in the fossil site areas (Holman, 1995c). This is believed to be due to the equable climate in North America that existed south of the periglacial ice-free areas in both glacial and interglacial times (Lundelius et al., 1983).

In Britain and northwestern Europe, however, the glacial climates were so severe that often the very cold-tolerant *Rana temporaria* was the only herpetological species present in ice-free areas during full glacial times. Moreover, contrasting with North America, many of the interglacial herpetofaunas became much more enriched than they are today (e.g., Middle and Upper Pleistocene interglacial faunas in Britain, Chapter 5).

In summary, because of factors discussed above, (1) the herpetofauna of Britain and Europe has been much less rich than in North America since the climatic deterioration at the end of the Miocene, and (2) the herpetofaunas of Britain and northwestern Europe became much more depleated in glacial times and much more enriched in interglacial times than those south of the periglacial areas in North America.

The one notable similarity between North America and British and European Pleistocene herpetofaunas is that when one compares extinctions in *mainland* Europe (Britain included) with North America, one finds that only one out of 73 identified species in Europe (1.4%) is an unquestioned extinct species. In mainland North America 10 out of 229 identified species (4.37%) are considered to be extinct (Holman, 1995c). These extinct species percentages are very low (below 5%) in each region. Moreover, I suspect that in years to come some of the North American Pleistocene species will be synonymized with living taxa.

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GENERAL INDEX

This index relates to the chapters in the book other than Chapters 4 and 5, which are covered in the taxonomic and site indices.

TAXONOMIC INDEX

This generic index leads the reader to find taxa in Chapter 4 that may be traced to Pleistocene sites in Chapter 5.

SITE INDEX

British and European Pleistocene herpetological sites are listed by country alphabetically. Abbreviations: LP=Lower Pleistocene, MP=Middle Pleistocene, UP=Upper Pleistocene, PU=Pleistocene sites undesignated temporally, or representing mixed or transgressive periods of Pleistocene time.