New herpetological records from the Middle Pleistocene Boxgrove Hominid Site, England

J. Alan Holman

Summary

Additional herpetological material from the Middle Pleistocene Boxgrove hominid site, West Sussex, England, has provided the first records from the site of two salamanders (crested newt, *Triturus cristatus*, and palmate newt, *Triturus helveticus*), two anurans (common parsley frog, *Pelodytes punctatus*, and water frog (*Rana* [ridibunda] sp.), and one snake (smooth snake, *Coronella austriaca*); as well as additional records of the nine previously reported herpetological species by Holman (1999). The total Boxgrove herpetofauna now consists of three salamanders, seven anurans, two lizards, and two snakes, forming one of the largest Pleistocene herpetofaunas in the British Isles. All 14 herpetological species from Boxgrove are presently living, but three species: spadefoot, *Pelobates fuscus*; common parsley frog, *Pelodytes punctatus*; and moor frog, *Rana arvalis* are continental species that do not presently occur in Britain. As a whole, the herpetofauna indicates a climate that is similar to the present one in the Boxgrove area. The herpetological species indicate the presence of a shallow pond; a wet or damp grassy area; a moderately moist, well-vegetated, terrestrial area; and a rather open, sandy habitat.

Samenvatting

Nieuw herpetologisch materiaal van de Midden Pleistocene Boxgrove hominid site in West Sussex, Engeland, heeft nog twee watersalamanders (kamsalamander *Triturus cristatus*, en zwemvoetsalamander *Triturus helveticus*), twee kikkers (de modderspringer of groengestipte kikker *Pelodytes punctatus* en de groene waterkikker *Rana* [ridibunda] sp.), en een slang (gladde slang *Coronella austriaca*) opgeleverd. Verder zijn er nog een aantal stukken aangetroffen van de negen al eerder door Holman (1999) gerapporteerde soorten. De complete herpetofauna van Boxgrove bestaat nu uit drie salamanders, zeven kikkers, twee hagedissen, en twee slangen, en vormt zo één van de grootste Pleistocene herpetofauna's van de Britse eilanden. Alle veertien herpetologische soorten van Boxgrove komen tegenwoordig nog voor; drie soorten echter (Europese knoflookpad *Pelobates fuscus*, groengestipte kikker *Pelodytes punctatus*, heikikker *Rana arvalis*) zijn continentale soorten die tegenwoordig niet in het Verenigd Koninkrijk voorkomen. Als geheel wijst de herpetofauna op een klimaat dat overeenkomt met het huidige klimaat van het gebied rond Boxgrove. De herpetologische soorten tonen de aanwezigheid aan van een ondiep water, een nat of vochtig grasland, een tamelijk vochtig, dicht-begroeid hoger gelegen land en een vrij open, zanderig gebied.

Introduction

The Middle Pleistocene homonid locality (fig. l) at Eartham Quarry, Boxgrove, West Sussex, England, British National Grid Reference Number SU920085, is one of the most publicized Quaternary sites in the Old World because the human artifacts and skeletal material suggest that it is the earliest human occupational site in Europe (e.g. Roberts et al., 1995; Roberts & Parfitt, 1999). Boxgrove is correlated with the Interglacial IV stage of the Cromerian Complex of the Dutch/European sequence (Roberts et al., 1995). In a narrower sense, the Boxgrove site is correlated with the Miesenheim I Site in Germany (Kolfschoten & Turner, 1996), an important continental herpetological site (Holman, 1998). Roberts & Parfitt (1999) have provided the latest information (previous to the present report) on the fauna of Boxgrove.

Holman (1992, 1998, 1999) previously published reports on the Boxgrove herpetofauna from material collected up to 1992. These fossils represent at one species of salamander, five anurans, two lizards, and one snake. Since that time, much additional herpetological material has been collected at Boxgrove, and this has provided records of two salamanders, two anurans, and one snake that are new to the fauna; as well as additional material of previously reported Boxgrove amphibians and reptiles.

This paper provides (1) a systematic annotated list of the new herpetological material from Boxgrove, (2) a checklist of the entire herpetofauna as it is known at present, and (3) some comments on the significance of the herpetofauna.

Fossil elements are listed by bulk sample number, the contextual details of which are in Parfitt (1999).

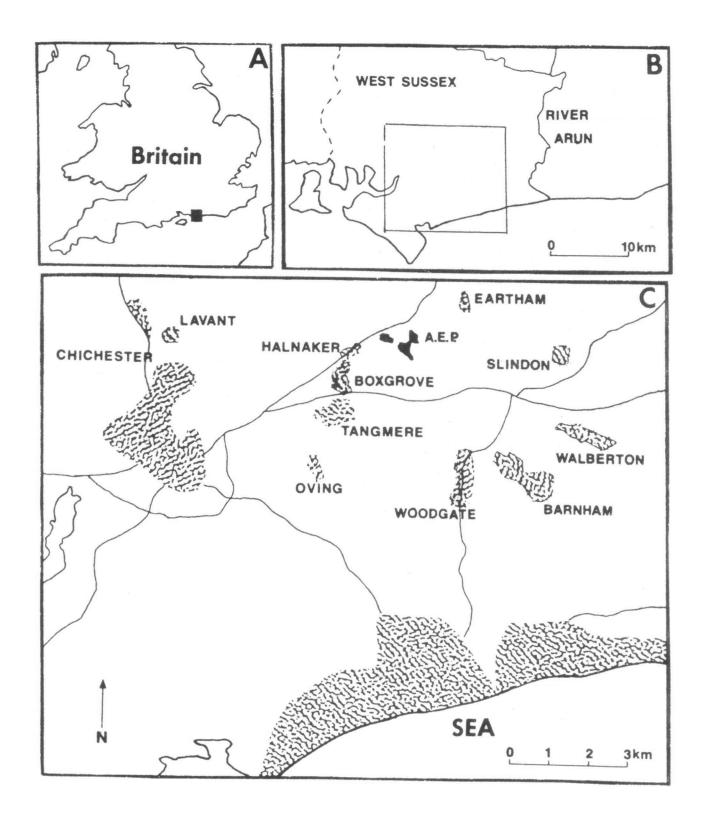


Fig. 1 Location map of Amey's Eartham Pit (A.E.P) where the Boxgrove herpetofauna was collected Plattegrond van Amey's Eartham Pit (A.E.P), waar de Boxgrove herpetofauna verzameld is

Annotated list of the new Boxgrove herpetological material

Order Caudata Scopeli, 1977

Family Salamandridae Goldfuss, 1820 Genus *Triturus* Rafinesque, 1815 Alpine Newts

This genus contains salamanders of small or moderately small size that usually have two distinct phases: an eft phase that is terrestrial, has a rough skin, and lacks a dorsal crest or "tail fin"; and a newt phase that is aquatic, has a smooth skin, and has a crest and sometimes a "tail fin." The genus presently occurs in England, Scandanavia, continental Europe, and Asia Minor around the Black Sea and to the westward part of the Caspian Sea eastward to the Ural Mountains.

Two species groups of *Triturus* are presently recognized: the *Triturus cristatus* group and the *T. vulgaris* group (Frost, 1985). Osteologically, these groups are so different that they could easily be separated into two distinct genera. Both groups have been recorded from the Pleistocene of Europe (Holman, 1998). All of the three modern species that presently occur in Britain have now been recorded from the Boxgrove Site.

Species group undesignated *Triturus* sp. Alpine newt

Damaged elements that cannot be referred with certainty to either the *Triturus cristatus* or the *T. vulgaris* group are included here. Holman (1992, 1998) previously reported *Triturus* sp. from the Boxgrove Site. New material: jaw fragment (182), partial femur (621), eight fragmental vertebrae (235, 238, 278, 281, 663, and 741-743).

Triturus cristatus Group Triturus cristatus Laurenti, 1758 Crested Newt

New species record from the site. The crested newt is a large rough-skinned taxon that is presently absent in Ireland but occurs in Great Britain and from Europe eastward to the central part of the former Soviet Union. The crested newt favors quiet or very slow flowing water where there is abundant vegetation. The terrestrial form usually stays near the breeding pond where it hides under rocks or other flattened objects. Holman (1998) gave characters of the skull, humeri, and vertebrae that separate *T. cristatus* from other species of European newts. This is the

first record of the species from Boxgrove and only the fourth record from the Pleistocene of Britain (Gleed-Owen, 1999; Holman, 1998). New material: two trunk vertebrae (54 and 690).

Triturus vulgaris Group Triturus helveticus or vulgaris Palmate Newt or Smooth Newt

These small newt fossils do not belong to the *T. cristatus* group, but they are fragmentary enough so that they lack the characters that enable one to identify them as either *T. helveticus* or *T. vulgaris*. Holman (1992, 1998) previously identified "*T. helveticus* or *T. vulgaris*" from the Boxgrove Site. New material: five vertebrae (40, 78, 485, 590, and 773).

Triturus vulgaris Group Triturus helveticus (Razoumowsky, 1789) Palmate Newt

New species record from the site. The palmate newt is a small species that is smooth skinned and has dark, strongly webbed hind feet. The palmate newt is presently absent from Ireland but it 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, but it is more aquatic than T. vulgaris. It is rather ubiquitous in its choice of breeding places. Holman (1998) gave vertebral characters to separate T. helveticus from T. cristatus and T. vulgaris. This is the first unequivocal record of this species from the Boxgrove Site and only the second record for the Pleistocene of Britain (Gleed-Owen, 1999). New material: two trunk vertebrae (679 and 741).

Triturus vulgaris Group Triturus vulgaris (Linnaeus, 1758) Smooth Newt

The smooth newt is small, smooth-skinned newt that lacks the webbed hind feet of *T. helveticus*. *Triturus vulgaris* presently occurs in Ireland, Great Britain, almost all of Europe, and the western part of Asia. The smooth newt is more terrestrial than most other species of European *Triturus* and tends to be a lowland species that lives in a wide variety of moist habitats. It normally breeds in still, shallow water with an abundance of aquatic vegetation. Holman (1998) gave vertebral characters that separate *Triturus vulgaris* from *T. cristatus* and *T. helveticus*. This newt has previously been reported from the Boxgrove Site (Holman, 1992, 1998) and has been

rather frequently reported from the Pleistocene and Holocene of Britain (Gleed-Owen, 1999; Holman, 1998). New material: six trunk vertebrae (53, 91, 228, 297, 635, and 735).

Family Pelodytidae Hogg, 1838 Genus *Pelodytes* Bonaparte, 1838 Parsley Frog

The genus bears only two species, *Pelodytes punctatus* and *Pelodytes caucasicus* (Frost, 1985; Duellman, 1993). Only the former species is known as a Pleistocene fossil. The ilium of this genus is generally similar to *Pelobates fuscus* of the family Pelobatidae except that the edge of the dorsal acetabular expansion is slightly convex rather than slightly concave. This character appears to be remarkably constant.

Pelodytes punctatus (Daudin, 1802) Common Parsley Frog

New species from the site. This species is a small, agile frog with a flat head and big eyes. The common parsley frog presently occurs in Belgium through France to Spain and extreme northwestern Italy. This taxon is principally a nocturnal, terrestrial form that prefers rather damp, well-vegetated habitats. Holman (1998) discussed the separation of *Pelobates punctatus* from the only other species in the genus, P. caucasicus on the base of ilial characters. This is only the second record of this species from the fossil record of England, the first record being from the early Middle Pleistocene site at Westbury-Sub-Mendip Cave, Somerset, England (Gleed-Owen, 1999; Holman, 1993, 1998). New material: left ilium (131), two right ilia (434 and 778).

Family Bufonidae Gray, 1825 Genus *Bufo* Laurenti True Toads

The very large genus *Bufo* consists of plump, warty, short-legged anurans that have a pair of pronounced paratoid glands behind the head. Two hundred and eleven living species are recognized (Duellman, 1993). The genus is presently cosmopolitan except for the arctic regions, New Guinea, and Australia and nearby islands. The modern forms are mainly terrestrial, although some are fossorial. The three modern European species have all been identified from the Pleistocene of the region.

Bufo sp. True Toads New material: two right scapulae (772), right scapula (774), two scapulae from among samples 428-434, three more scapulae (286, 456, and 698), two left humeri (429), three left humeri (280, 672, and 735), right humerus (799), five humeri (106, 159, 428, 741, and 773), three left ilia (110, 122, and 279), and seven sacra (270, 434, 735, 742, 744, 749, and 772). New material of probable true toad (cf. *Bufo* sp.): two humeri (73 and 78), and a tibiofibular fragment (361).

Bufo bufo (Linnaeus, 1758) Common European Toad

Bufo bufo is the largest and most common of the three European species of true toads. This taxon tends to be uniformly brownish in color. Bufo bufo is found in Europe (except for Ireland and some of the Mediterranean islands) east to Lake Baikal in southern Siberia; in the Caucasus; northern Asia Minor and northern Iran. It also occurs in northwestern Africa. This species is found in a wider variety of habitats than other European toads. It has previously been recorded from the Boxgrove Site (Holman, 1992, 1998). Characters for distinguishing the ilia of *B. bufo* from the other European species are given in Holman (1998). New material: left ilium (from among samples 428-434), nine left ilia (44, 238, 428, 438, 442, 476, 593, 639, and 741), right ilium (from among samples 428-434), ten more right ilia (215, 428, 434, 476, 548, 581, 656, 665, 695, and 739).

Bufo calamita Laurenti, 1768 Natterjack Toad

Modern natterjack toads may be distinguished from *B. bufo* on the basis of the bright yellow stripe that runs down the middle of the back. *Bufo calamita* tends to move about by making mouselike dashes rather than merely walking or hopping as in other European toads. Presently the natterjack occurs in western and northern Europe as far east as western Russia and including parts of England and Ireland. In the northern part of its range this species is usually found in sandy areas including dunes by the sea. In other parts of its range it is more ubiquitous in its habits. It has previously been recorded from Boxgrove (Gleed-Owen, 1999; Holman, 1992, 1998). New material: left ilium (221).

Family Ranidae Rafinesque-Schmaltz, 1814 Genus *Rana* Linnaeus, 1758 True Frogs

The genus *Rana* is another extremely large taxon. They are typically long-legged frogs with smooth skins, webbed feet, and prominent tympanni.

Two-hundred and twenty-three living species are recognized (Duellman, 1993). The genus *Rana* is presently cosmopolitan except for southern South America and most of Australia. In Europe 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 dark face mask. Some important osteological characteristics of the genus *Rana* were given in Holman (1998).

cf. Rana sp.
Probable True Frog
New material: partial femur (79).

Rana sp. indet. True Frog

It is not known whether these elements represent water frogs or brown frogs. New material: scapula (from among samples 428-434), two scapulae (670 and 809), six left humeri (72, 75, 112, 118, 129, and 696), five right humeri (75, 129, 156, 773, and 805), two left ilia (582), two right ilia (45), fourteen left ilia (46, 77, 82, 91, 95, 157, 193, 200, 287, 349, 578, 603, 662, and 841), eighteen right ilia (126, 218, 226, 246, 251, 263, 271, 358, 373, 476, 548, 593, 596, 628-629, 679, 695, and 809), and three sacra (141, 415, and 584).

Water Frog Species Group

Waterfrogs are very difficult to identify to species (Sanchiz, 1998) and I have not been able to determine the waterfrog species represented at the Boxgrove Site. Sanchiz (1998) refers to these indeterminate water frogs as follows.

Rana (ridibunda) sp. Indeterminate European Water Frog

New *Rana* species group from the site. Holman (1998) has indicated how the ilia of European water frogs usually differ from those of brown frogs. Normally, one would expect that the presence of water frogs would indicate the presence of a permanent body of freshwater near the fossil site. Water frogs as such have not previously been reported from the Boxgrove Site. New material: four left ilia (35, 91, 250, and 580), and two right ilia (519 and 644).

Brown Frog Species Group

Rana arvalis Nilsson, 1842 Moor Frog

Moor frogs are a brown frogs with a face mask. This taxon has relatively short legs and a pointed

rostrum. The present distribution of the moor frog is in northeastern France, Belgium, Netherlands, Germany, Denmark, Sweden, Finland south to the Alps, northern Yugoslavia, northern Romania, and east to Siberia. *Rana arvalis* is found in moist meadows and fields and in wetland areas such as bogs and fens. Holman (1992, 1998) has previously identified *R. arvalis* from the Boxgrove Site. Holman (1998) pointed out a diagnostic character on the ilium of *Rana arvalis*. New material: right ilium (717).

Rana cf. Rana arvalis Nilsson, 1842 Probable Moor Frog New material: two right ilia (78 and 263).

Rana temporaria Linnaeus, 1758 Common Frog

The common frog is the most widespread anuran in Britain and Europe today and is often the most abundant anuran in moist, terrestrial habitats in central and northern Europe. This brown frog has a face mask and a small, soft metatarsal tubercle that distinguishes it from the moor frog (Rana arvalis) which has a large, hard, and often bladelike tubercle. Presently, Rana temporaria occurs throughout Britain and Europe east to the Urals, but excluding most of Iberia, much of Italy, and the southern Balkans. It is probably the most terrestrial of all of the European Rana species and in many areas is found in water only during the breeding season. It is one of the most cold-tolerant species in Europe. The common frog has previously been identified from the Boxgrove Site (Gleed-Owen, 1999; Holman, 1992, 1998). Holman (1998) gives ilial characters for the identification of Rana temporaria. New material: two left ilia (476 and 772), three right ilia (68, 112, and 672).

Order Squamata Oppel, 1811

Family Lacertidae Bonaparte, 1831 Genus *Lacerta* Linnaeus, 1758 Common Eurasian Lizards

This genus has about 43 living species (Frank & Ramus, 1995) and has most of the general characters of the family. *Lacerta* is known from most of the Palearctic except for very cold areas. Estes (1983) has given important osteological characters for the genus. Species of the genus *Lacerta* are often divided into two groups, the larger, more robust "green lizards" that tend to live in areas with dense vegetation and the "small lacertas" (including the genus *Podarcis*) that tend to be ubiquitous in their habits.

Lacerta vivipara Jaquin, 1887 Viviparous Lizard

New positive identification. The viviparous lizard, a small *Lacerta*, is unique in the genus in that it gives birth to living young, although some populations in the South lay eggs. It is a short-legged form with a rounded head that is not particularly distinct from the neck and has a rather dull brownish color normally with interrupted lines down the back and sides. This species is the most widespread lizard in the Palearctic, occurring from northern Scandinavia, Ireland, and Britain south to northern Spain, northern Italy, southern Yugoslavia and Bulgaria, and then eastward across much of Asia to the Pacific coast.

It is one of the most cold-tolerant reptiles of the northern hemisphere and enters the Arctic Circle in localities in northern Europe. Unlike most lizards of the genus Lacerta, the viviparous lizard requires a rather moist environment and is one of the few lizards that avidly eats earthworms. It occupies a wide variety of habitats, ranging from heathlands to Alpine meadows in the south. This viviparous lizard was previously tentatively identified from Boxgrove as Lacerta cf. Lacerta vivipara by Holman (1998). A partial right dentary with four relatively slender teeth, including one tricuspid tooth, enables a positive identification (see Holman, 1998: 85) of Lacerta viridis to be made from the Boxgrove Site. New material: partial right dentary with 4 teeth (188).

Family Anguidae Gray, 1825 Genus Anguis Linnaeus, 1758 Anguis fragilis Linnaeus, 1758 Slow Worm

Anguis fragilis is the only modern species in the genus. This taxon is a very smooth-scaled, legless lizard with a tail that is often longer than the body, except when the tail has been broken off and regenerated. The color is usually brownish grey and males often have blue spots on the body. This species occurs almost all over Europe except for Ireland, southern Iberia, and the far north. 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 semifossorial and has very slow and deliberate movements. Holman (1998) gives characters for the identification of Pleistocene fossils of this species which has previously been reported from the Boxgrove Site (Gleed-Owen, 1999; Holman, 1992, 1998). New material: five trunk vertebrae (32, 44, 79, 330 and 672), ten caudal vertebrae (53,

188, 286, 476, 634, 672, 741, 743, 787, and 809), six fragmentary vertebrae (91, 126, 287, 591, 654, and 683), and three osteoscutes (471, 485, and 624).

Family Colubridae Oppel, 1811 Genus Coronella Laurenti, 1768 Coronella austriaca Laurenti, 1768 Smooth Snake

New species record from the site. The genus Coronella consists of rather small, smooth-scaled snakes with a round body and an indistinct head. Both living species of the genus are secretive and slow-moving. Both taxa are said to feed principally on lizards. The small C. austriaca differs from the other snake in 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. Presently C. 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. This snake is secretive, but it tends to be active in the daylight hours, preferring dry and sunny habitats. Holman (1998) gives characters for the identification of fossil vertebrae of Coronella austriaca. This is the first record of this genus and species from the Boxgrove Site. It is only the second record of C. austriaca from the Pleistocene of Britain, the first one being from the Early Middle Pleistocene of the Westbury-Sub-Mendip Cave Site in Somerset. New Material: trunk vertebra (484).

Genus *Natrix* Laurenti, 1768 Water Snakes

This genus contains moderately stout snakes with strongly keeled scales. The genus is widely distributed in Europe and southwestern and central Asia, also occurring in Africa. In Europe, two species of the genus, *N. maura* and *N. tesselata* are aquatic, and the third, *N. natrix*, spends most of the time on land.

cf. Natrix sp.

Probable Water Snake Species New material: fragmentary vertebra (112)

Natrix natrix (Linnaeus, 1758) Grass Snake

The grass snake is a rather large, thick-bodied snake with keeled scales. The color is variable, but there is usually a yellow collar with a black border that occurs just behind the head. This species occurs in nearly all of Europe, ranging north to near the Arctic Circle in Scandanavia and extending eastward to Lake Baikal. It also ocurs in northwestern Africa. This taxon is diurnal and mainly terrestrial, although it is sometimes seen swimming in the water. It prefers moist, grassy habitats over dry ones. Holman (1998) gave characters for the identification of fossil *Natrix natrix* vertebrae. This species has previously been reported from the Boxgrove Site (Gleed-Owen, 1999; Holman, 1992, 1998). New material: partial vertebra with complete hypapophysis (286). Probable grass snake *Natrix* cf. *Natrix natrix*: new material: partial vertebra (651).

Checklist of the Boxgrove herpetofauna

Following is an updated checklist of the amphibians and reptiles of the Boxgrove site that takes into account the new herpetological records from the site reported in the present paper.

Newts

Triturus sp. (alpine newt, species group undetermined)

Triturus cristatus (crested newt) - new record Triturus helveticus or vulgaris (palmate or smooth newt)

Triturus helveticus (palmate newt) - new record Triturus vulgaris (smooth newt)

Anurans

Pelobates fuscus (common spadefoot)

Pelodytes punctatus (common parsley frog) - new record

cf. Bufo sp. (probable true toad)

Bufo sp. (true toad)

Bufo bufo (common European toad)

Bufo calamita (natterjack toad)

cf. Rana sp. (probable true frog)

Rana sp. (true frog)

Rana (ridibunda) sp. (European water frog) - new record

Rana arvalis (moor frog)

Rana cf. Rana arvalis (probable moore frog

Rana temporaria (common frog)

Squamates

Lacerta vivipara (viviparous lizard) - new positive identification

Lacerta cf. Lacerta vivipara (probable viviparous lizard)

Anguis fragilis (slow worm)

Coronella austriaca (smooth snake) - new record

cf. Natrix (probable grass or water snake)

Natrix sp. (grass or water snake)

Natrix natrix (grass snake) Natrix cf. Natrix natrix (probable grass snake)

As far as can be determined, all of the Boxgrove amphibian and reptiles are presently living. This is in contrast to the temporally equivalent Miesenheim 1 herpetofauna of the Neuwied Basin of Germany where Pliobatrachus cf. Pliobatrachus langhae Féjèvary, 1917 has been identified. This permanently aquatic frog represents an extinct family, genus, and species, and in fact represents the only extinct anuran family ever described. Pliobatrachus has been identified from other Middle Pleistocene localities in Central and Eastern Europe (see Holman, 1998; Ratnikov, 1997); thus one wonders, considering the large British Pleistocene herpetofaunas known from Boxgrove, Cudmore Grove, and East Farm, Barnham, whether Pliobatrachus ever occurred in the British Pleistocene, or for that matter, in the Pleistocene of Western Europe.

Although no extinct amphibians and reptiles are known from the Boxgrove site, three extralimital species are known that are presently absent from Britain, but occur at rather similar latitudes on the continent (see Arnold & Burton, 1978). These taxa are: *Pelobates fuscus* (common spadefoot), *Pelodytes punctatus* (common parsley frog), and *Rana arvalis* (moor frog).

Paleoclimatically, there are no herpetological species that indicate that the climate in the Boxgrove area at the time of the deposition of the bones was much different than it is at present. The lack of such forms as *Emys orbicularis* (European pond turtle) and *Elaphe longissima* (Aesculapian snake), species that are said to indicate warmer climates than at present at other British and continental sites (e.g. Stuart, 1979; Holman, 1998; Böhme, 1996), are conspicuously absent at the intensively studied Boxgrove Site.

The Boxgrove amphibians and reptiles are yet to be analyzed, if this is possible, on a microstratigraphic basis. Nevertheless, as a whole, the herpetofauna generally indicates ponding and adjacent moist habitats. All of the newt species prefer moist habitats and need at least temporary water in which to breed. Among the anurans, water frogs (Rana [ridibunda] sp.) prefer permanent aquatic situations. Parsley frogs (Pelodytes punctatus) prefer moist, well-vegetated areas. Both moor frogs (Rana arvalis) and common frogs (Rana temporaria) prefer marshy or damp grassy areas. Common toads (Bufo bufo) are rather ubiquitous in their habits, but always must return

to water to breed. Both the spadefoot (*Pelobates fuscus*) and natterjack (*Bufo calamita*), both represented by relatively few elements at Boxgrove, are more partial to sandy areas, but both need water in which to breed.

Among the reptiles, both the viviparous lizard (Lacerta vivipara) and the slow worm (Anguis fragilis) prefer moist, at least moderately well-vegetated areas. The grass snake (Natrix natrix), as its name implies, is usually most common in moist grassy areas, usually fairly near an aquatic situation. The smooth snake (Coronella austriaca), represented by only one vertebra from Boxgrove, prefers dry, sunny habitats.

Acknowledgements

I am deeply grateful to Mark Roberts and Simon Parfitt for the opportunity to study the previous and new Boxgrove herpetofaunal material. Teresa Peterson made the location map of the Boxgrove Site.

Adress of the author

J. Alan Holman Michigan State University East Lansing Michigan USA 48824-1045

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