Cranium, jrg. 10, no. 2, pag 87-96, augustus 1993

Pleistocene Herpetofauna of Westbury-Sub-Mendip Cave, England

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SUMMARY

Herpetofauna were identified from six of 15 Side Chamber Units in the Middle Pleistocene cave deposits at Westbury-Sub-Mendip, Somerset, England. Taxa identified include *Pelodytes punctatus* (parsley frog), *Rana temporaria* (common frog), *Rana* sp. (frog), *Emys orbicularis* (European pond tortoise), *Anguis fragilis* (slow worm lizard), *Coronella austriaca* (smooth snake), *Natrix natrix* (grass snake), *Natrix* sp. (natricine snake), and *Vipera berus* (adder). All of these species represent living taxa, but *Pelodytes punctatus* and *Emys orbicularis* are exotic to Britain today and occur on the European continent. The record of *Pelodytes fuscus* is the first record of the family, genus, and species in the native fauna of Britain. The herpetofauna from the Westbury site does not differ significantly from those of the other important British Middle Pleistocene pre-Anglian Sites at West Runton or Boxgrove in either species diversity or in number of exotic species. But it does differ from the Middle Pleistocene post-Anglian Interglacial herpetofauna at Cudmore Grove in both of these areas. The occurence of *Emys orbicularis* and *Coronella austriaca* in the basal layer of the cave fauna indicates a somewhat warmer climate than occurs in the area today. The occurrence of *Pelodytes punctatus* in intermediate Units 12 and 13 may indicate a slightly warmer climate than occurs in the area today.

The Westbury-Sub-Mendip Cave near Bristol, England, (Fig. 1) has produced one of the most spectacular Middle Pleistocene mammalian faunas known. These mammalian fossils have been intensively studied systematically (BISHOP, 1982) and taphonomically (ANDREWS, 1990) and the birds have been analyzed by HARRISON (1987). But other than reports on the occurence of the European pond tortoise, *Emys orbicularis* (STUART 1979, 1982; ANDREWS, 1990), the amphibians and reptiles have not been identified and published. The present paper is concerned with the identification of the Westbury-Sub-Mendip Cave herpetofauna with comments on its paleogeographic, stratigraphic, and paleoecological relationships.

SAMENVATTING

In de grot Westbury-Sub-Mendip bij Bristol (Engeland) zijn zeer spectaculaire Midden Pleistocene zoogdierfaunas verzameld. De zoogdierresten zijn uitgebreid bestudeerd zowel systematisch (BISHOP, 1982) als taphonomisch (ANDREWS, 1990). De vogelresten zijn door HARISSON (1987) geanalyseerd. Van de reptielen en de amphibiëen was weinig bekend. Het voorkomen van de Europese moerrasschildpad *Emys orbicularis* werd genoemd door STUART (1979, 1982) en ANDREWS (1990). In dit artikel worden ook overblijfselen van andere reptielen en amphibiëen beschreven en op basis van de aanwezigheid van deze dieren worden paleogeografische, stratigrafische en paleo-oecologische conclusies getrokken.

De fossiele reptielen en amphibiëen van Westbury-Sub-Mendip zijn afkomstig uit zes van de in totaal 15 stratigrafische eenheden. Tot de aanwezige soorten behoren: *Pelodytes punctatus* (moddersprinqer), *Rana temporaria* (bruine kikker), *Rana* sp. (kikker), *Emys orbicularis* (Europese moerasschildpad), *Anguis fragilis* (hazelworm), *Coronella austriaca* (gladde slang), *Natrix natrix* (ringslang), *Natrix* sp. (een andere soort ringslangachtige), en *Vipera berus* (adder). Al deze soorten komen tegenwoordig in Europa voor, *Pelodytes punctatus* en *Emys orbicularis* leven alleen op het Europese continent en niet in Groot Britanië. De knoflookpad (*Pelodytes fuscus*) is tot op heden de enige vertegenwoordiger van de familie van de knoflookpadden, de Pelobatidae, in de britse fauna.De herpetofauna van Westbury verschilt nauwelijks wat betreft de diversiteit als het aantal exotische soorten van andere belangrijke Middenpleistocene vindplaatsen met een pre-Anglian (=pre-Elsterien) ouderdom zoals West Runton en Boxgrove. De fauna verschilt wel van die van Cudmore Grove, een jongere post-Anglian (post-Elsterien) interglaciale fauna.

Het voorkomen van *Emys orbicularis* en *Coronella austriaca* in de basale lagen van de grot toont aan dat het tijdens de afzetting van die laag iets warmer was dan tegenwoordig. Dat geldt, op grond van het voorkomen van *Pelodytes punctatus*, ook voor de periode waarin de Units 12 en 13 zijn afgezet.

The Cave Site

The Westbury-Sub-Mendip Cave Site (Fig. 1) occurs in an limestone quarry on the southeast side of the Mendip Hills in Somerset, England, about 28 km south of Bristol and 1.75 km NNE of Westbury-Sub-Mendip Village, Somerset, England (ST508504 [51 degrees 15'N., 42' W.] 210-245 km m O.D.). The Mendip Hills trend southeast to northwest in the form of a flattened plateau that contains many caves cut into the Clifton Down Limestone (FORD and STANTON, 1968).

The Westbury-Cave formed during the early Pleistocene over one million years BP and gathered sediments during the Middle Pleistocene about 350,000 to 400,000 BP (ANDREWS, 1990). The sediments consist of mainly of silts and cave breccias which came from mixtures of rocks and soils from outside of the cave and eroded

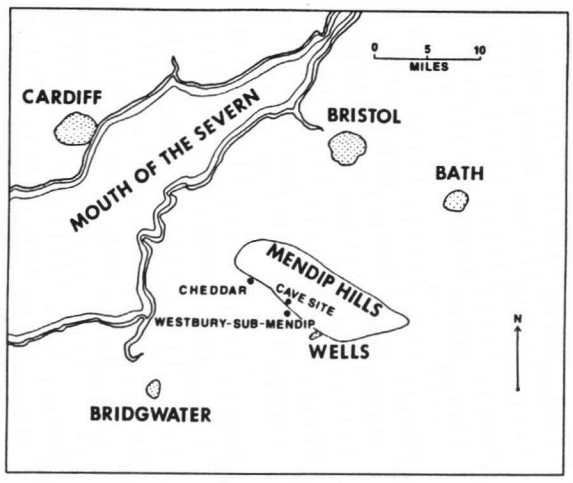

Fig. 1: Location of Westbury-Sub-Mendip Cave Site, Somerset, England (Modified from ANDREWS, 1990).

Fig. 1: Ligging van Westbury-Sub-Mendip Cave in Somerset, Engeland (naar ANDREWS, 1990).

limestone products from inside the structure. Vertebrate fossils were first discovered during quarrying operations in 1969. As the quarry continued to be worked, a large cavern was exposed and its sediments proved to be exceedingly rich in additional fossil vertebrates. Earlier papers by HEAL (1970), STANTON (1973), and BISHOP (1974, 1982) indicated how complex and faunally rich the deposit was. Recently, ANDREWS (1990) has done an exhaustive account of the taphonomy of the small mammals of the cave. Moreover, the cave has been mentioned many times in the more general literature (e.g. STUART, 1982,1988; SUTCLIFFE, 1985).

Today, the Westbury cave system (Fig. 2) is exposed as a horizontally oriented structure called the main chamber and a vertically oriented chamber called the side chamber; with indications of a third chamber beneath the side chamber. The main chamber is about 70 m long and 30 m high. It has been determined that it runs along the strike of the limestone and such strike caverns tend to have large entrances of gentile relief (ANDREWS, 1990). These kinds of entrances allow massive amounts of sedimentary inflow. They also allow vertebrates of all

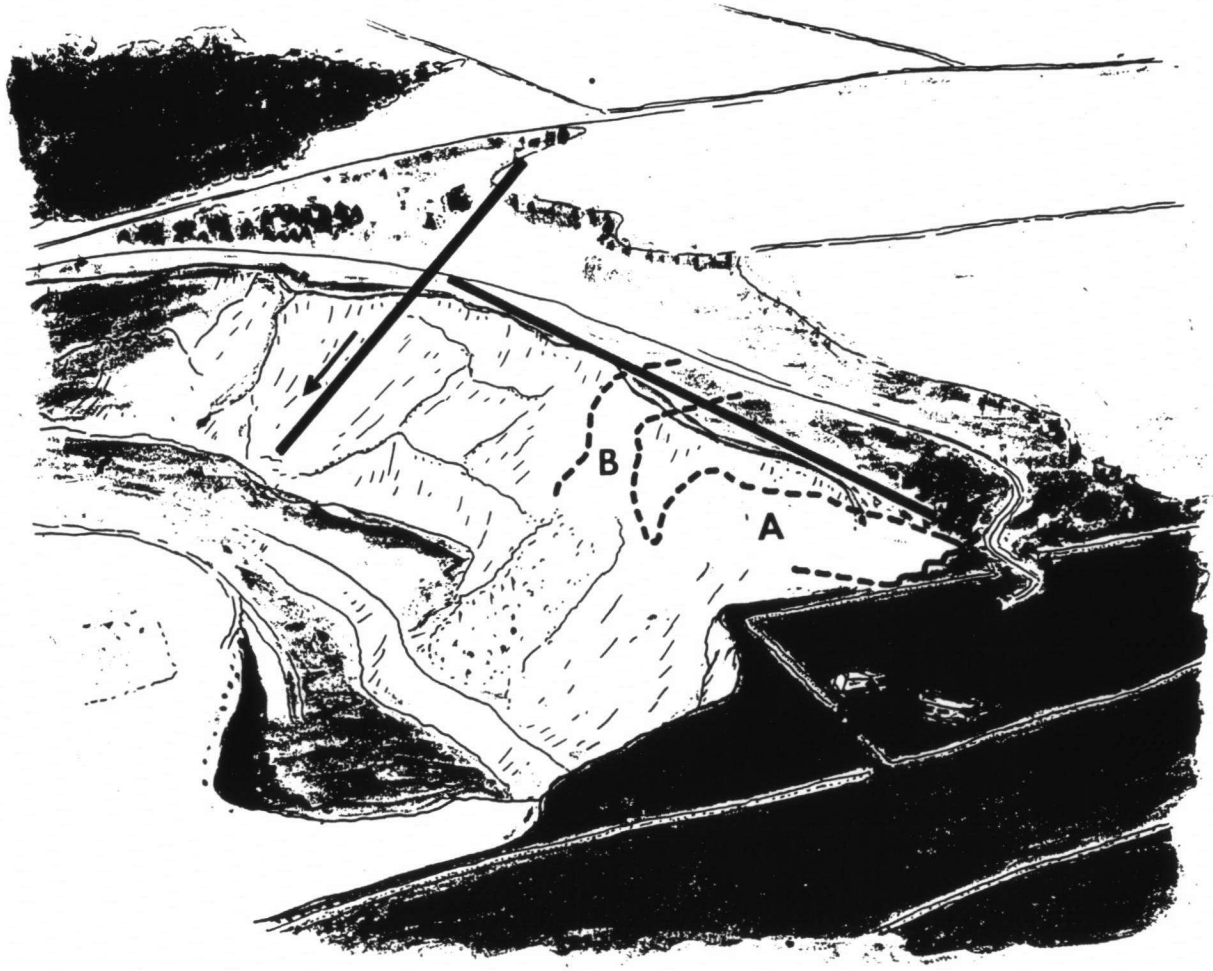

Fig. 2: Location of the Main Chamber (A) and Side Chamber (B) of the Westbury-Sub-Mendip Cave Site, Somerset, England. The strike of the limestone is indicated by the arrow and its dip by the perpendular line (drawn from an aerial photograph from ANDREWS, 1990).

Fig. 2: Ligging van de Main Chamber (A) en Side Chamber (B) van de Westbury-Sub-Mendip Cave, Somerset, Engeland. De kalksteen is aangegeven door de pijl en de helling ervan door de lijn loodrecht erop. (getekend naar een luchtfoto van ANDREWS, 1990).

sizes to either find shelter near the entrance or to move deep into the cave. Northwest of the main chamber is the smaller side chamber. This chamber runs downward along the dip of the limestone. Its total area is unknown because most of it remains underground, but magnetometer surveys suggested that it may extend as much as 40 to 50 m back from the face of its present exposure (ANDREWS, 1990). The side chamber is much narrower and steeper than the main chamber and it is believed that it had a narrow opening at the top. Therefore, access for both animals and sediments was limited, although one might expect that the side chamber acted as a natural trap.

All of the amphibians and reptiles of this report were collected from the side chamber. A system for designating excavation localities within the side chamber has been presented by ANDREWS (1990). In this system all of the locality numbers are preceeded by a "W" indicating the Westbury Cave. Three localities W9, W2 and W3 as well as W2/9 repesenting an interface between W2 and W9, yielded the fossil herpetological material of this study. All of the excavation localities of this side chamber have the stratigraphy shown in Figure 3. These sedimentary units are numbered from 1 to 15 from bottom to top. Thus, an amphibian or a reptile bone from "W2/15" would be from Excavation Locality 2 and from Unit 15 (Upper Red Breccia) of the side chamber (Fig. 3). The following is a synopsis of all of the stratigraphic units (from ANDREWS, 1990) that yielded fossil amphibian and reptile bones.

Sites W2/9 and W3, Unit 8 (The Red Silt).

--The Red Silt Unit is the lowest of the side chamber sequence of units (Fig. 3) that contained the bones of small mammals (ANDREWS, 1990). Large mammalian fossils were also very abundant in this part of the cave. The main component of this unit is yellowish red silt. The gravel and the sand grain components of this unit are heavily stained with manganese dioxide and tere is evidence of corrosion. It has been shown that the fauna from this unit has been transported, either from inside or from outside of the cave, and it has been suggested that the fauna from this unit is "mixed" (ANDREWS, 1990). It has been suggested that the climate at Westbury may have been warmer than today at the time of the Red Silt fauna (ANDREWS, 1990). Herpetological records from the Red Silt are *Emys orbicularis* (European pond tortoise) and *Coronella austriaca* (smooth snake).

Site W2, Unit 11 (Pink Breccia).

--The Pink Breccia is the lowest fossil-bearing unit of the upper part of the side chamber (Fig. 3). It lies as a distinct light unit on top of the Unit 10 Yellow Silty Breccia which is almost completely unfossiliferous.

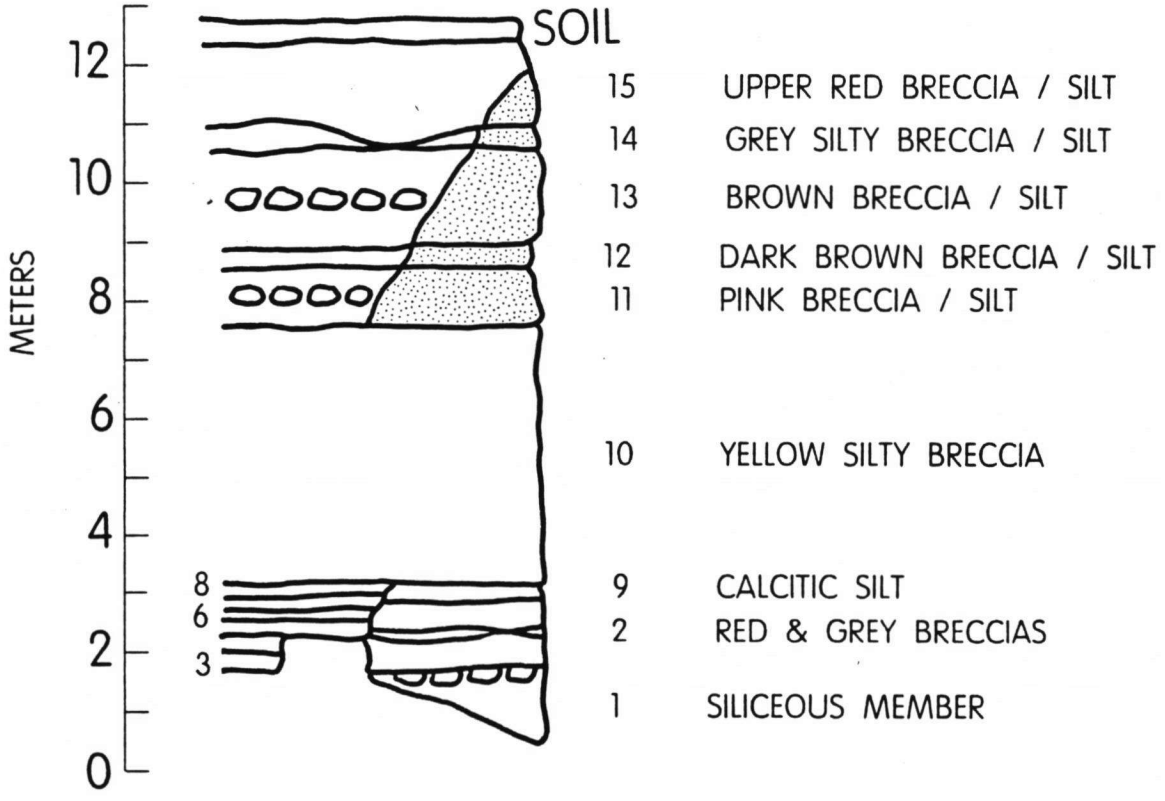

Fig. 3: Stratigraphic units of the Side Chamber of Westbury-Sub-Mendip Cave Site, Somerset, England (modified from ANDREWS, 1990).
Fig. 3: Stratigrafische eenheden van de Side Chamber van Westbury-Sub Mendip Cave (gewijzigde versie van ANDREWS, 1990).

The Pink Breccia not only has some lithological differences, but was divided into faunal subunits by ANDREWS (1990).The Pink Breccia contain a high diversity of small mammals and some birds, many in pellet-like structures that accumulated through the activities of predators; one of which most certainly was the European eagle owl. Based on the fauna in the Pink Breccia, ANDREWS (1990) concluded "... that the Pink Breccia was laid down during peak interglacial conditions and the vegetation in the area around Westbury Cave consisted largely of deciduous woodland with abundant ground vegetation". Herpetological records from the Pink Breccia are *Pelodytes punctatus* (parsley frog), *Rana temporaria* (common frog) and *Rana* sp.

Site W2, Unit 12 (Dark Brown Breccia).

-- The Dark Brown Breccia rests conformably on the Pink Breccia and differs from it mainly in the greater amounts of manganese staining which gives it a darker reddish-brown color. The Dark Brown Breccia Unit has not produced the abundance of bone found in the Pink Breccia and lacks the pellet-like structures. The Dark Brown Breccia fauna, however, also indicates temperate deciduous woodland conditions, and that few changes in climate or habitat had occurred since the time Pink Breccia was deposited. Herpetological records from the Dark-Brown Breccia are *Rana temporaria* (common frog), *Rana* sp. and *Vipera berus* (adder).

Sites W2, W2/9 and W9, Unit 13 (Brown Breccia).

--The Brown Breccia is said to be the most mixed and least stratified of the sequences at Westbury (ANDREWS, 1990). It varies in color from dark brown to reddish brown. The main difference between it and the other units is the large number of limestone clasts whichtogether from a matrix partially filled with finer sediments. The mammalian fauna of the Brown Breccia unit is complex and has been subdivided into three faunal groups that are distinguished from one another on the basis of differences in preservation. A continental climate is indicated with the vegetation intermediate between deciduous and boreal forest, said to be similar to the situation that occurs in southern Sweden today (ANDREWS, 1990). Herpetological records from the Brown Breccia are *Pelodytes punctatus* (parsley frog), *Rana temporaria* (common frog), *Rana* sp., *Natrix natrix* (grass snake), and *Natrix* sp.

Site W9, Unit 14 (Grey Silty Breccia).

-- The Grey Silty Breccia is said to be a discontinuous unit that formed around a small roof collapse. The color of this unit may be greyish brown, yellowish brown, olive brown or even dark brown. Small mammal bones are present throughout Unit 14. It was concluded that the Grey Silty Breccia accumulated during a cold phase where a dry continental climate occured that supported a vegetation that was a mixture of deciduous and boreal woodlands with more open areas present. Herpetological records from Unit 14 are *Natrix natrix* (grass snake) and *Natrix* sp.

Site W2 and W2/9, Unit 15 (Red Breccia).

--This is a very complex unit that occurs at the top of the cave sequence (Fig. 3). It has been divided into three subunits. One of these subunits contains a layer called the "rodent earth" which contains about 40% by weight of bone. Other parts of Unit 15 are much less fossiliferous. These subunits have been interpreted as having a climate ranging from somewhat temperate to one that was rather dry and cold. Herpetological records from Unit 15 include *Rana* sp. *Anguis fragilis* (slow worm lizard), *Natrix natrix* (grass snake), *Natrix* sp., and *Vipera berus* (adder).

Systematic Paleontology

Scientific nomenclature follows FROST (1985) for Amphibia, MLYNARSKI (1976) for Testudines, ESTES (1983) for Sauria and RAGE (1984) for Serpentes. All measurements are in mm. All specimen numbers are those of the Palaeontological Collections of the Natural History Museum, London - BM (NM)R-.

Class Amphibia Linnaeus, 1758
Order Anura Rafinesque, 1815
Family Pelodytidae Bonaparte, 1838
Genus *Pelodytes* Bonaparte, 1838
Pelodytes punctatus (Daudin, 1802)
Parsley Frog

Material.-- Locality W2: Unit 11 (Pink Breccia, Lower Shelf), right ilium BM (NM) R-12226 (Fig. 4a). Locality W2: Unit 11 (Pink Breccia, Bulk Sample), left ilium R-12227 (Fig. 4b), right ilium R-12228 (Fig. 4c); a small left and right ilium very possibly from the same young individual R-12229. Locality W2: Unit 13 (Brown Breccia), right ilium R-12230.

Remarks.-- The ilia of modern *Pelodytes punctatus* are distinctive elements. They are readily seperated from ilia of the species of *Rana* in that they lack a dorsal ilial blade (vexillum of BOHME, 1977). They are distinct from all other European genera but *Pelobates* in lacking a distinct dorsal prominence or protuberance. *Pelodytes punctatus* may be seperated from *Pelobates* on the basis of the former species in having a much more gracile ilial shaft and in having the dorsal acetabular expansion convex than concave (compare Figs. 4a,b,c, this paper and Fig. 7/5 of RAGE [1974] with Fig. 7/4 of RAGE [1974]). This is the first record of the natural occurrence of the family, genus and species in Britain. Today, the Parsley Frog is distributed from Belgium through France to Spain and extreme northwestern Italy (FROST, 1985; ARNOLD and BURTON, 1978, map 30).

Family Ranidae Gray, 1825
Genus *Rana* Linnaeus, 1758
Rana temporaria Linnaeus, 1758
Common Frog

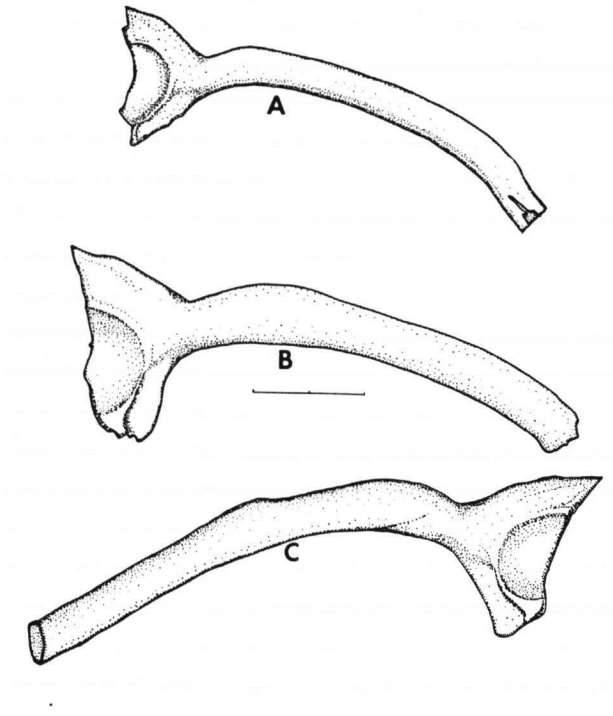

Fig. 4: Ilia of *Pelodytes punctatus* from the Westbury-Sub-Mendip Cave Site, Somerset, England. A, right ilium BM(NM)R-12226; B, right ilium BM(NM)R-12228; C, left ilium BM(NM)R-12227. The line equals 2 mm and applies to all figures.

Fig. 4: Ilia (=onderdeel bekken) van *Pelodytes punctatus* van de Westbury-Sub-Mendip Cave. A= rechter ilium BM(NM)R-12226; B= rechter ilium BM(NM)R-12228; C= linker ilium BM(NM)R-12227.Het streepje is in werkelijkheid 2 mm en geldt voor alle figuren.

Material.--Locality W2: Unit 11 (Pink Breccia), right ilium BM (NM) R-12232 (Fig. 5a). Locality W2: Unit 11 (Pink Breccia), right ilium R-12235. Locality W2: Unit 11 (Pink Breccia, Lower Shelf), left ilium R-12237. Locality W2: Unit 11 (Pink Breccia, Bulk Sample), two left and one right ilia R-12233. Locality W2: Unit 12 (Dark Brown Breccia), one sacrum and two left and one right ilia R-12236. Locality W2/9: Unit 13 (Brown Breccia), five left and five right ilia R-12234. Locality W9: Unit 13 (Brown Breccia), right ilium R-12231.

Remarks.--The ilia of modern *Rana temporaria* are also distinctive elements. They may be assigned to the genus *Rana* on the basis of having a dorsal blade present (vexillum of BOHME, 1977), but they are distinct from all other European species of *Rana* in having this blade depressed anterior to the dorsal prominence (tuber superior of BOHME, 1977). This common modern British species (FRAZER, 1983) is also a common British Pleistocene interglacial fossil and has been sparingly found in British Pleistocene glacial sites (HOLMAN, 1990).

Rana sp. indet.

Material.-- Locality W2: Unit 11 (Pink Breccia, Lower Shelf), right ilium BM (NM) R-12238. Locality W2: Unit 12 (Dark Brown Breccia), one left and one right

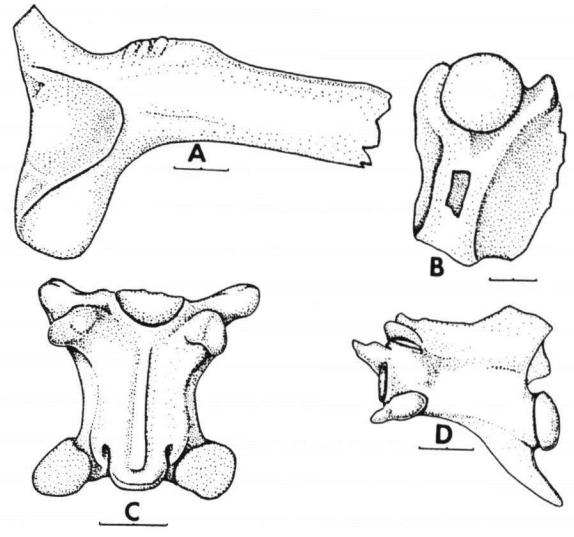

Fig. 5: Anuran and snake fossils from the Westbury-Sub-Mendip Cave Site, Somerset, England. A right ilium of *Rana temporaria* BM(NM)R12232. B, distal left humerus of *Rana* sp. BM(NM)R-12240. C, ventral view of trunk vertebra of *Coronella austriaca* BM(NM)R-12249. D, lateral view of trunk vertebra of *Vipera berus* BM(NM)R-12256. All lines equal 2 mm.

Fig. 5: Kikvorsachtige en slangefossielen van Westbury-Sub-Mendip Cave. A= rechter ilium van *Rana temporaria* BM(NM)R-12232; B= distale eind van een linker humerus van *Rana* sp. BM(NM)R-12240; C= buikzijde van een wervel van *Coronella austriaca* BM(NM)R-12249; D= zijaanzicht van een wervel van *Vipera berus* BM(NM)R-12256. Streepjes = 2 mm.

scapulae, fragmentary sacral vertebra R-12239. Locality W2: Unit 13 (Brown Breccia), right distal humerus of male R-12242. Locality W2: Unit 13 (Red Breccia, Dark Red Brown above Light Red Brown), left distal humerus of male R-122240 (Fig. 5b). Locality W2/9: Unit 13 (Dark Brown Breccia), left distal of male R-12241.

Remarks.--HALLOCK et al. (1990) discussed characters of the scapula and humerus that allow one to identify the genus *Rana*. These criteria were used here. I have been unable to use these elements to make specific identifications of this genus.

Class Reptilia Laurenti, 1768
Order Testudines Batsch, 1870
Family Emydidae Gray, 1826
Genus *Emys* (Linnaeus, 1758)
Emys orbicularis (Linnaeus, 1758)
European Pond Tortoise

Material.-- Locality W3: Unit 8 (Red Silt), skeletal elements (museum numbers not available).

Remarks.-- The presence of European Pond Tortoise (*Emys orbicularis*) remains at the Westbury-Sub-Mendip Cave Site was reported by STUART (1979, 1982, 1988), but no specific information was given. ANDREWS (1990) supplied the specific locality and unit from which this species was recovered, but did not supply the na-

mes or museum number or numbers of the individual bones (presumably, at least shell elements). I have not been able to observe the specimens. This species is not native to modern Britain, although it has been reported from all of the British interglacial stages and the Flandrian (STUART, 1979). Today the range of *Emys orbicularis* in Western Continental Europe includes all of Portugal and Spain, thence through southern France, southern Germany and all of Italy including Sardinia and Corsica (ARNOLD and BURTON, 1978, Map 48).

Order Sauria McCartney, 1802
Family Anguidae Gray, 1825
Genus *Anguis* Linnaeus, 1758
Anguis fragilis Linnaeus, 1758
Slow worm

Material.-- Locality W2: Unit 15 (Red Breccia, Mole Layer), partial right dentary with five complete teeth BM (NM) R-12244. Locality W2: Unit 15 (Red Breccia, Dark Red Brown above Light Red Brown), four trunk vertebrae R-12243. Locality W2: Unit 15 (Red Breccia, Dark Red Brown above Light Red Brown), a large trunk vertebra with a greatest length of 4.7 mm R-12247. Locality W2/9: Unit 15 (Red Breccia, Yellow Brown), trunk vertebra R-12245. Locality W2/9: Unit 15 (Red Breccia, Red Silt with Weathered Limestone), three trunk vertebrae R-12246. Locality W2/9: Unit 15 (Red Breccia), trunk vertebra R-12248.

Remarks.--HOLMAN (1985) reported that *Anguis fragilis* skeletal elements including skull bones, lower jaw bones, vertebrae, osteoderms, and even ribs are distinguishable from the bones of other British and European reptiles, mainly due to adaptations for a limbless fossorial condition. SMITH (1973, fig. 58) provides an illustration of an *Anguis fragilis* skull in three views, and another of *Anguis fragilis* mid-caudal vertebrae compared to those of *Lacerta vivipara*. All of the Westbury-Sub-Mendip *Anguis* elements appear to be identical to those in modern skeletons of the species. This rather common modern British species (FRAZER, 1983) is also a rather common British Pleistocene interglacial fossil, but has never been reported from a British Pleistocene glacial site (HOLMAN, 1990).

Order Serpentes Linnaeus, 1758
Family Colubridae Oppel, 1811
Genus *Coronella* Laurenti, 1768
Coronella autriaca Laurenti, 1768
Smooth Snake

Material.-- Locality W2/9: Unit 8 (Red Silt and Weathered Limestone Blocks), trunk vertebra BM (NM) R-12249 (Fig. 5c).

Remarks.-- The trunk vertebrae of *Coronella austriaca* are diagnostic, and identifications of this species have been recently made on the basis of isolated vertebrae by SZYNDLAR (1984) and HOLMAN (1985). Trunk vertebrae of *Coronella austriaca* differ from those of species of *Natrix* and *Vipera* in lacking a hypapophysis. They differ from European species of *Elaphe* on the basis of being smaller; having a neural spine that is much longer than high; having a more depressed neural arch; and having a haemal keel that is somewhat wider posteriorly than anteriorly and that is somewhat flattened. Today, *Coronella austriaca* is an endangered species in Britain and is only found in southern England where it ranges now from Dorset to Surrey in isolated populations (FRAZER, 1983) and possibly occurs in isolated spots in Berkshire. This is only the second fossil record of the smooth snake from Britain, the first being a Flandrian record from the Ightham Fissures near Sevenoaks, Kent (HOLMAN, 1985).

Genus *Natrix* (Linnaeus, 1758)
Natrix natrix (Linnaeus, 1758)
Grass Snake

Material.-- Locality W2/9: Unit 13 (Brown Breccia), one trunk vertrebra BM (NM) R-12252. Locality W2/9: Unit 15 (Red Breccia), one trunk vertebra R-12253. Locality W2/9: Unit 15 (Red Breccia), two trunk vertebrae R-12255. Locality W2/9: Unit 15 (Red Breccia and Weathered Limestone), one trunk vertebra R-12251. Locality W9: Unit 13 (Brown Breccia), one trunk vertebra R-12250. Locality W9: Unit 14 (Grey Silt Breccia), one trunk vertebra R-12254.

Remarks.-- The trunk vertebrae of *Natrix natrix* may be distinguished from European colubrine genera (eg. *Coluber,Coronella, Elaphe*) on the basis of having a long, ventral hypapophysis. Trunk vertebrae of European adders (*Vipera*) also have hypapophyses, but they are longer and more gracile. Moreover, the vertebrae of European adders have a less rounded neural arch (as viewed posteriorly) and the anterior and posterior borders of the neural spines are much less undercut (as viewed laterally). *Natrix natrix* may be distinguished from the other European species of the genus (*Natrix maura* and *Natrix tessellata*) on the basis of having its hypapophysis more rounded distally and its parapophyseal processes more massive. *Natrix natrix* is a moderately common snake in Britain today (FRAZER, 1983) and has been reported from more Pleistocene localities than any other snake in Britain (HOLMAN, 1991a).

Natrix sp. indet.

Material.-- Locality W2: Unit 15 (Red Breccia, Dark Red Brown above Light Red Brown), four fragmentary trunk vertebrae BM (NM) R-12260. Locality W2: Unit 15 (Red Breccia , Dark Red Brown above Light Red Brown), one eroded trunk vertebra R-12265. Locality W2/9: Unit 15 (Red Breccia), two eroded trunk vertebrae R-12264. Locality W2/9: Unit 15 (Red Breccia), three fragmentary trunk vertebrae R-12266. Locality W2/9: Unit 15 (Red Breccia, Red Silt and Weathered Limestone Blocks), one fragmentary trunk vertebra R-12261. Locality W2/9: Unit 15 (Red Breccia, Red Silt with Weathered Limestone), two trunk vertebrae with

essential processes worn R-12263. Locality W2/9: Unit 15 (Red Breccia, Yellow Brown), five fragmentary trunk vertebrae R-12262. Locality W9: Unit 13 (Brown Breccia), small fragmentary vertebra R-12268. Locality W9: Unit 14 (Grey Silty Breccia), two fragmentary trunk vertebrae R-12267.

Remarks.-- These vertebrae are all too worn or incomplete for specific identification.

Family Viperidae
Genus *Vipera* (Linnaeus, 1758)
Vipera berus (Linnaeus, 1758)
Adder

Material.-- Locality W2: Unit 12 (Dark Brown Breccia), one trunk vertebra BM (NM) R-12257. Locality W2/9: Unit 15 (Red Breccia), two trunk vertebrae R-12259. Locality W2/9: Unit 15 (Red Breccia and Weathered Limestone Blocks), trunk vertebra R-12256 (Fig. 5d). Locality W2/9: Unit 15 (Red Breccia and Weathered Limestone Blocks), one vertebra R-12258.

Remarks.-- *Vipera berus* have hypapophyses on their trunk vertebrae as do *Natrix natrix*, but the adder may be distinghuised from the latter in that its neural spine is lower and has its anterior and posterior borders less undercut; and in that its hypapophyses are longer and more gracile.

Discussion

In this discussion the herpetofaunas from all of the Westbury-Sub-Mendip Cave stratigraphic zones will be considered together as an unit.

Paleogeographic Comments

The Westbury-Sub-Mendip Cave herpetofauna consists of at least seven species, including two amphibians and five reptiles. All of these species are living today and five of the seven live in Britain today. The two exotic species in the fauna are *Pelodytes punctates* and *Emys orbicularis*. *Pelodytes punctatus* (parsley Frog) occurs across the English Channel in northwestern France (ARNOLD and BURTON, 1978, map 30). This is the first record of this family, genus, and species in the native fauna of Britain. *Emys orbicularis* (European pond tortoise) presently occurs nearest to Britain in the Rennes-Laval-Le Mans area in northwestern France (ARNOLD and BURTON, 1978, map 48). Taken together, all of the Westbury species would be typical of the central part of Western Europe today.

The absence of *Pelodytes punctates* in the modern herpetofauna of Britain probably reflects the elimination of this species from southwestern England during the Devensian or Anglian Glacial Stages (Table 1) and the subsequent failure of the species to reinvade Britain after its geological seperation from the European continent in the early part of the Flandrian. *Emys orbicularis* did, however, reinvade Britain during the early Flandrian (STUART, 1979, 1982), but probably became extinct when the climate cooled to its present state. STUART (1979, 1982) convinsingly points out that the present equable but cool climate of Britain probably does not provide enough warm days for the eggs of this species to hatch.

The record of *Coronella austriaca* (Smooth Snake) is the first from pre-Flandrian sites in Britain and is only the second fossil record of this taxon in Britain. The previous record is from the Ightham Fissures Site, Sevenoaks, Kent (HOLMAN, 1985). At present, the natural range of this endangered species is confined to a few localities in Dorset and Surrey, and perhaps in Berkshire (FRAZER, 1983). Thus, the fossil record of specimens from Kent and Somerset indicates that the snake might have had a wider distribution in southern England during the temperate intervals of the Pleistocene.

Stratigraphic Comments

The modern herpetofauna in North Temperate areas was mainly established by the early part of the Pleistocene (HOLMAN, 1991b).

Thus, most herpetological species (unlike several mammalian taxa) are not good stratigraphic indicators in Quaternary deposits. Nevertheless, certain patterns in Pleistocene assemblages such as species composition, diversity, or even numbers of exotic species present, might have stratigraphic implications.

In Britain, there is uncertainty about the contemporaneity of early Middle Pleistocene sites. It has been suggested that the type of the Cromerian (first glacial stage of the Pleistocene, Table 1) at West Runton, Norfolk, is older than the Boxgrove, West Sussex, or the Westbury Site (STUART, 1982; KOLFSCHOTEN, 1985, 1990) of the early Middle Pleistocene (Fig. 6). It has even been suggested that the Boxgrove and Westbury sites represent an unnamed interglacial stage between the Cromerian and the following Anglian Glacial Stage. The composition of the Westbury mammalian fauna broadly correlates with the Cromerian Interglacial mammalian faunas. In fact, 15 of the 23 small mammal species present at Westbury occur at the Type Cromerian Fauna at West Runton (ANDREWS, 1990).

Many of these small mammalian taxa (e.g. *Sorex runtonensis*, *Sorex savini* and *Neomys newtoni*) have a very limited time range (BISHOP, 1982). Nevertheless, there are two differences from the West Runton mammalian fauna that indicate that the Westbury site is younger. First, the microtine *Arvicola* is present in all of the Westbury strata, and *Arvicola* is considered to be a descendant of *Mimomys* which occurs at West Runton. Second, several Westbury species are larger than those found at West Runton. This has led BISHOP (1982) to suggest that the Westbury fauna represents an interglacial stage that intervened between the Cromerian and the Hoxnian interglacial stages.

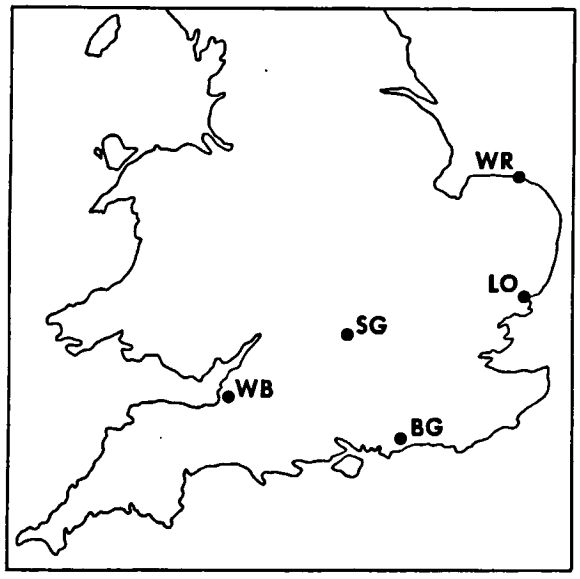

Fig. 6: Location of Middle Pleistocene pre-Anglian Interglacial Sites with herpetofauna in Britain. WR, West Runton, Norfolk; LO, Little Oakley, Essex; SG; Sugworth, Berkshire; BG, Boxgrove, West Sussex; and WB, Westbury-Sub-Mendip, Somerset. WR, BG, and WB are the important Middle Pleistocene pre-Anglian Interglacial herpetofaunal sites discussed in this paper.

Fig. 6: Ligging van middenpleistocene pre-Anglian vindplaatsen met een kruipende fauna in Engeland.

Table 2 compares the herpetofaunas of the West Runton, Boxgrove, and Westbury sites with each other and with the Cudmore Grove, Essex, herpetofauna of the Hoxnian Interglacial Stage (last interglacial stage of the Pleistocene). No different patterns of species composition, diversity, or number of exotic species are apparant in any of these three sites. Nevertheless, taken together, these three herpetofaunas differ from the Cudmore Grove Hoxnian herpetofauna in (1) having less species diversity and (2) many fewer less exotic continental species (see totals of number of species and number of exotic species for each fauna at end of Table 2). This may, of course, be due to paleontological sampling error. Nevertheless, this can only be determined by the collection of new herpetological material from these established sites as well as from new sites.

In summary, the herpetological evidence does not indicate that the three early Middle Pleistocene sites are more different from one another. But there is some indication of differences in herpetofaunal and number of exotic species between the early Middle Pleistocene Interglacial and the later Cudmore Grove Middle Pleistocene Interglacial sites.

Paleoecological Comments

The Westbury-Sub-Mendip herpetofauna came from six of 15 units identified from the Side Chamber of the cave. This Side Chamber sequence has been interpreted by ANDREWS (1990) as indicating a climatic oscillation sequence of warm-cool-warm-cold. Unfortunately the herpetological remains at Westbury are few and scattered compared with the very abundant small mammalian remains studied by Andrews. Of the six units that had herpetological content (Table 3), only two had as many as three species represented and the average number of species represented for the six units was only 2.17.

Nevertheless, the two species confined to Unit 8, *Pelodytes punctatus* and *Emys orbicularis*, together would indicate warm conditions, in fact, somewhat warmer conditions than occur in Westbury today. STUART (1979,1982) convincingly argues that the reason *Emys orbicularis* cannot maintain populations in southern England today is because there are not enough total warm days for the eggs to hatch. Moreover, *Coronolla austriacus* is presently restricted to a few counties in extreme southern England (FRAZER, 1983) where it prefers dry, sunny habitats. The above records supplement the comment made about Unit 8 by ANDREWS (1990) who stated "The indications are, therefore, that the climate at Westbury at the time of the unit 8 fauna may have been warmer than today, but the data are not sufficient to be any more positive than that".

Pelodytes punctatus is the second exotic species of the Westbury Cave herpetofauna. It occurs across the English Channel from England in northwestern France (ARNOLD and BURTON, 1978, Map 30) where it prefers slightly damp habitats and low vegetation. This species has only been found in Units 12 and 13 at Westbury. The presence of the parsley frog might indicate a slightly warmer climate than occurs at Westbury today, or perhaps a more continental type of climate.

All of the remaining herpetological species found at Westbury (*Rana temporaria*, *Anguis fragilis*, *Natrix natrix*, and *Vipera berus*) are quite wide-ranging in their distribution in Britain and central-western Europe today and do not indicate either warmer or cooler climates for the Westbury area.

Acknowledgments

Sandra Chapman and Andrew Currant kindly provided access for my study of the Westbury herpetofauna at the Natural History Museum, London. John Clayden and David Harrison provided new fossil material for my study of the West Runton herpetofauna. Teresa Petersen rendered some of the figures that were drawn by the author in London. A grant from the National Geographic Society (4545-91) supported my work in England in 1991.

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Table 1: British and North American Glacial and Interglacial Stages Referred to in the Text. (G equals Glacial, I equals Interglacial).

Tabel 1: Engelse en Amerikaanse termen voor glacialen en interglacialen, zoals gebruikt in de tekst (G = glaciaal; I = interglaciaal).

BRITISH NAMES	NORTH AMERICAN NAMES	YEARS AGO AT STAGE BEGINNING
Flandrian Postglacial	Holocene Postglacial	10,000
Devensian (G) Last Cold Stage	Wisconsinan (G) Last Cold Stage	ca 110,000
Ipswichian (I) Last Interglacial	Sangamonian (I) Last Interglacial	ca 120,000
Wolstonian (G)	?	
Hoxnian (I)	?	? 200-250,000
Anglian (G)	?	
Cromerian (I)	?	? 350-500,000

Table 2: Herpetofaunas of British Middle Pleistocene sites. PRA indicates pre-Anglian sites, POA indicates post-Anglian sites. An asterisk (*) indicates an exotic continental species.

Tabel 2: Kruipende fauna's van Britse middenpleistocene vindplaatsen.

WEST RUNTON (PRA)	BOX GROVE (PRA)	WESTBURY (PRA)	CUDMORE GROVE (POA)
Triturus vulgaris	*Triturus vulgaris*	----------	*Triturus vulgaris*
----------	----------	----------	*Triturus cristatus*
	**Pelobates fuscus*	----------	----------
----------	----------	**Pelodytes punctatus*	----------
Bufo bufo	*Bufo bufo*	----------	*Bufo bufo*
----------	*Bufo calamita*	----------	----------
----------	----------	----------	**Hyla* sp.
**Rana arvalis*	**Rana arvalis*	----------	**Rana arvalis*
**Rana esculenta or ridibunda*			**Rana esculenta or ridibunda*
Rana temporaria	*Rana temporaria*	*Rana temporaria*	----------
----------	----------	----------	**Rana lessonae*
----------	----------	**Emys orbicularis*	**Emys orbicularis*
Anguis fragilis	*Anguis fragilis*	*Anguis fragilis*	*Anguis fragilis*
----------	*Lacerta* cf *vivipara*	----------	*Lacerta* sp.
----------	----------	*Coronella austriaca*	----------
----------	----------	----------	**Elaphe longissima*
----------	----------	----------	**Natrix maura or tessellata*
Natrix natrix	*Natrix natrix*	*Natrix natrix*	*Natrix natrix*
Vipera berus	----------	*Vipera berus*	*Vipera berus*
TOTAL	TOTAL	TOTAL	TOTAL
8 species	9 species	7 species	14 species
2 exotics	2 exotics	2 exotics	7 exotics

Table 3: Distribution of Westbury-Sub-Mendip Cave Herpetofauna on the basis of Side Chamber Units.
Tabel 3: Verspreiding van de Westbury-Sub-Mendip Cave fauna gebaseerd op de Side Chamber Units.

Unit 8	Unit 11	Unit 12
Emys orbicularis	*Pelodytes punctatus*	*Rana temporaria*
Coronella autriaca	*Rana temporaria*	*Rana* sp.
	Rana sp.	*Vipera berus*
Unit 13	**Unit 14**	**Unit 15**
Pelodytes punctatus	*Natrix natrix*	*Anguis fragilis*
Rana temporaria	*Natrix* sp.	*Natrix natrix*
Rana sp.		*Natrix* sp.
Natrix natrix		*Vipera berus*
Natrix sp.		

References:

ANDREWS, P. 1990. Owls, Caves and Fossils. Chicago: University of Chicago Press.

ARNOLD, E.E. & BURTON, J.A. 1978. A Field Guide to the Reptiles and Amphibians of Britain and Europe. London: Collins.

BISHOP, M. J. 1974. A preliminary report on the middle Pleistocene mammal bearing deposits of Westbury-Sub-Mendip, Somerset. Proceedings of the University of Bristol Speleological Society 13, 301-318.

BISHOP, M. J. 1982. The mammalian fauna of the early middle Pleistocene bearing deposits of Westbury-Sub-Mendip, Somerset. Paleontological Association Special Papers 28, 1-108.

BOHME, G. 1977. Zur bestimmung quartärer Anuran Europas an hand von Skelettelementen. Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematik-Naturwissenschaft 26, 283-300.

ESTES, R. 1983. Sauria Terrestria, Amphisbaenia. Part 10-A. Handbuch der Paläoherpetologie Stuttgart and New York: Fischer Verlag.

FORD, D. C. & STANTON, W. I. 1968. The geomorphology of the South-Central Mendip Hills. Proceedings of the Geological Association 79, 401-427.

FRAZER, D. 1983. Reptiles and Amphibians in Britain. London: Collins. FROST D, R. ed. 1985. Amphibian Species of the World. Lawrence: Allen Press.

HALLOCK, L. A., HOLMAN, J. A. & WARREN, M. R. 1990. Herpetofauna of the Ipswichian Interglacial Bed (Late Pleistocene) of the Itteringham Gravel Pit, Norfolk, England. Journal of Herpetology 24, 33-39.

HARRISON, C. J. O. 1987. Pleistocene and prehistoric birds of south-west Britain. Proceedings of the University of Bristol Speleological Society 18, 81-104.

HEAL, G. J. 1970. A new Pleistocene mammal site, Mendip Hills, Somerset. Proceedings of the University of Bristol Speleological Society 12, 125-136.

HOLMAN, J.A. 1985. Herpetofauna of the late Pleistocene fissures near Ightham, Kent. Herpetological Journal 1, 26-32.

HOLMAN, J. A. 1990. New records and comments on British Peistocene cold-stage amphibians and reptiles. British Herpetological Society Bulletin 34, 39-41.

HOLMAN, J. A. 1991a. Fossil history of the grass snake (*Natrix natrix*) with emphasis on the British fossil record. British Herpetological Society Bulletin 36, 8-13.

HOLMAN, J. A. 1991b. North American Pleistocene herpetofaunal stability and its impact on the interpretation of modern herpetofaunas, an overview. Illinois State Museum Scientific Papers 23, 227-235.

KOLFSCHOTEN, T. VAN 1985. The Middle Pleistocene (Saalien) and Late Pleistocene (Weichselian) mammal faunas from Maastricht-Belvédère, Southern Limburg, The Netherlands. Mededelingen Rijks Geologische Dienst 39-1, 45-74.

KOLFSCHOTEN, T. VAN 1990. The evolution of the mammal fauna in the Netherlands and the middle Rhine area (Western Germany) during the Late Middle Pleistocene. Mededelingen Rijks Geologische Dienst 43-3, 1-69.

MLYNARSKI, M. 1976. Testudines Part 7. Handbuch der Paläoherpetologie, Stuttgart and New York: Fischer Verlag.

RAGE, J. C. 1974. Les batraciens des gisements quaternaires européens détermination ostéologique. Extrait Bulletin Mensuel de la Societé Linnéenne de Lyon 43, 276-289.

RAGE, J. C. 1984. Serpentes. Part 11. Handbuch der Paläoherpetologie. Stuttgart and New York: Fischer Verlag.

SMITH, M. 1973. The British Amphibians and Reptiles. London: Collins.

STANTON, W. I. 1973. Notes on the geology and geomorphology of the Westbury bone fissure. Wessex Cave Club Journal. 1973: 289-293.

STUART, A. J. 1979. Pleistocene occurences of the European pond tortoise (*Emys orbicularis* L.) in Britain. Boreas 8, 359-371.

STUART, A. J. 1982. Pleistocene Vertebrates in the British Isles. London and New York: Longman.

STUART, A. J. 1988. Life in the Ice Age. Aylesbury: Shire Publications.

SUTCLIFFE, A. J. 1985. On the Track of Ice Age Mammals. Dorchester: Dorset Press.

SZYNDLAR, Z. 1984. Fossil snakes from Poland. Acta Zoologica Cracoviensa 28, 1-156.