Cranium, jrg. 13, no. 2, pag. 131-138, november 1996

Amphibians and reptiles from Late Pleistocene Glacial and Interglacial age deposits near Shropham, Norfolk, England

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SUMMARY

Amphibians and reptiles were identified from Late Pleistocene sediments in a gravel pit in the interior of East Anglia near Shropham, Norfolk, England (National Grid Reference TM005938). The herpetofauna came from small pockets within course sediments of Devensian Glacial Age at the top of the site as well as from finer underlying sediments of Ipswichian Interglacial Age.

At least ten species, six amphibians and four reptiles, were identified from the Ipswichian. Four exotic species, moor frog (*Rana arvalis*), a specifically indeterminate water frog (*Rana* sp. indet.), European pond tortoise (*Emys orbicularis*), and a water snake (*Natrix maura* or *tessellata*) were found in the interglacial sediments. This percentage of exotic species (40%) compares well with eight other Ipswichian faunas in Britain, which in combination have a total of 45.5% exotic species. All of the exotic herpetological species may be found in the western or southwestern part of continental Europe today. The Shropham interglacial herpetofauna presents an ecological picture of a well-vegetated pool bordered by grassy meadows and shrubby or wooded habitats. The occurrence of the presently endangered natterjack toad (*Bufo calamita*) in the interior of East Anglia supports other evidence that the natterjack toad may have been more widespread in Britain during Pleistocene interglacial ages than it is today.

The Shropham Devensian Glacial Age fauna includes only two species, the cold-tolerant common frog (*Rana temporaria*) and the grass snake (*Natrix natrix*). This is the only record of a snake from any of the British Pleistocene cold-stage faunas.

SAMENVATTING

Verscheidene amfibieën en reptielen zijn gevonden in Laat Pleistocene sedimenten in een grindgroeve in East Anglia nabij Shropham in Norfolk, Engeland. De fauna is zowel afkomstig uit kleine lenzen in het grove sediment van het Devensien glaciaal [Red.:Weichselien], dat aan de top van de groeve ligt, als uit de fijnere onderliggende sedimenten van het Ipswichien [Red.: Eemien]. In de interglaciale fauna werden vier exoten aangetroffen, de heikikker (*Rana arvalis*), en niet nader te determineren kikkersoort (*Rana* sp. indet.), de moerasschildpad (*Emys orbicularis*), en een adderringslang of dobbelsteenslang (*Natrix maura* of *tessellata*). Dit percentage exoten (40%) komt goed overeen met dat van acht andere Britse Ipswichien fauna's (totaal 45,5 %). Alle exoten leven vandaag de dag nog in het westen of zuidwesten van het Europese continent. De interglaciale herpetofauna van Shropham duidt op een vegetatierijk water met daaromheen zowel velden als struikgewas. De aanwezigheid van de momenteel bedreigde rugstreeppad (*Bufo calamita*) bevestigt dat deze soort tijdens interglacialen in Engeland algemener was dan tegenwoordig.

De Devensien fauna van Shropham bestaat uit slechts twee soorten, de koude-bestendige bruine kikker (*Rana temporaria*) en de ringslang (*Natrix natrix*). Dit is tot dusver de enige slang die ooit in een Engelse glaciale fauna is gevonden.

The Shropham Gravel Pit Site

In 1983 John D. Clayden discovered Pleistocene vertebrate fossils in a gravel pit owned by the Minn's Aggregates Company in the interior of East Anglia near Shropham (fig. 1), Norfolk, England (National Grid Reference TM 005938). Since then the deposit has been visited by J. D. Clayden and associates, Martin Warren of the Cromer Museum, Norfolk, and A. J. Stuart and associates of the Castle Museum, Norwich, Norfolk. J. A. Holman made several trips to the site with J. D. Clayden in 1989, and soon after began a study of the Pleistocene herpetofauna. A. J. Stuart is presently engaged in a comprehensive study of the mammalian fauna at Shropham.

The Pleistocene vertebrates of the Shropham pit come from two major units (1) Devensian Glacial Age gravels and muds at the top of the site and (2) Ipswichian Interglacial Age detritus muds below. The stratigraphy (bot-

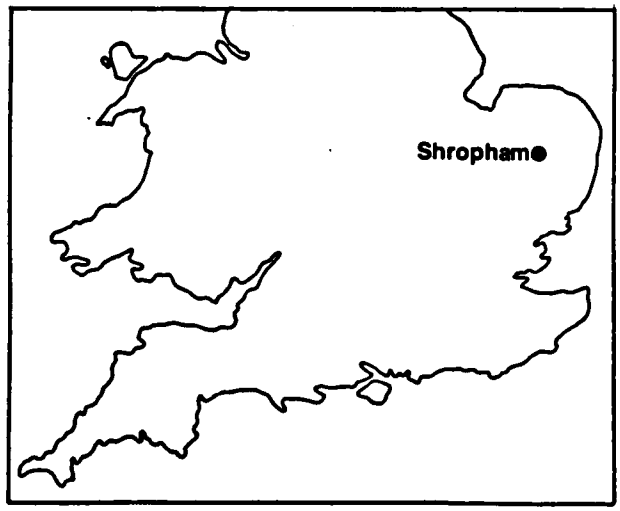

Fig. 1: Location of the Shropham Site in the interior of East Anglia, Norfolk, England.

Fig.1: Locatie van de vindplaats Shropham in East Anglia, Norfolk, Engeland.

tom to top) in the part of the pit where J. D. Clayden and J. A. Holman collected vertebrate fossils in 1989 consisted of (1) an undetermined thickness of Cretaceous chalk, (2) a chalky, pebbly gravel about one metre thick, (3) a fossiliferous layer of detritus mud containing a late Pleistocene interglacial fauna, mainly of smaller bones and (4) Devensian gravels and muds at the top of the site, containing large vertebrate bones and forming a layer about eight metres thick. This is typical of other fossiliferous localities within the Shropham site.

The Devensian gravels and muds of the Shropham site have yielded fossil brown bear (*Ursus arctos*), wolf (*Canis lupus*), lion (*Panthera leo*), wooly rhino (*Coelodonta antiquitatis*), extinct bison (*Bison* sp.), red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*) and mammoth (*Mammuthus primigenius*) collected by J.D.Clayden (HOLMAN and CLAYDEN 1990). Pockets of finer sediments within the Devensian portion of the site have produced a few fossil amphibians and a snake that are detailed below.

The Ipswichian detritus muds below the Devensian deposits yielded the amphibians and reptiles reported below, but also produced water chestnut fruits and chewed hazel nuts, a rich molluscan and beetle fauna, bird bones and bird egg fragments as well as the following mammalian species collected by J. D. Clayden: extint water vole (*Arvicola cantiana*), bank vole (*Clethrionomys glareolus*), field vole (*Microtus agrestis*), northern vole (*Microtus oeconomus*), beaver (*Castor fiber*), pigmy shrew (*Sorex minutus*), water shrew (*Neomys* sp.), extinct bison (*Bison* sp.), and hippopotamus (*Hippopotamus amphibius*) (HOLMAN and CLAYDEN, 1990). The presence of this mammalian fauna along with the European pond tortoise (*Emys orbicularis*) indicates an Ipswichian age for the detritus muds of the site (see Ipswichian faunal lists in STUART, 1982).

Systematic Palaeontology

The amphibian and reptile fossils discussed in this report come from four sources.

(1) Amphibians and reptiles collected from the interglacial detritus muds by J. D. Clayden and his associates from 1983 through 1989. These collections are from two localities within the muds designated Locality NP and Locality JC (HOLMAN and CLAYDEN, 1990). Specimen numbers from these localities are prefaced by the abbreviation JCSHR followed either by NP or JC (John Clayden Collection - Shropham - Locality NP or JC)

(2) Amphibians and reptiles collected from the interglacial units by J. D. Clayden and his associate Rickey Green after 1989 and donated to the Michigan State University Museum by J. D. Clayden. These fossils came from two localities within the interglacial sediments designated Section U and Section H4 by Clayden. Numbers for specimens from these sites are prefaced by MSUVP (Michigan State University Vertebrate Paleontology Collections).

(3) Amphibians collected from a pocket within the Devensian sediments ("Pocket I" of HOLMAN, 1992a) collected by Martin R. Warren of the Cromer Museum, Norfolk. This material is in the Cromer Museum and the specimen numbers are prefixed by the abbreviation CMSH D (Cromer Museum Collections - Shropham - Devensian).

(4) Two snake vertebrae collected from a second pocket within the Devensian sediments ("Pocket 2" of HOLMAN, 1992a) collected by A. J. Stuart of the Castle Museum, Norwich, Norfolk. These un-numbered vertebrae are housed in the Shropham fossil collection at the Castle Museum

In the following annotated list of Shropham amphibians and reptiles, 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.

The Late Pleistocene Interglacial Age Herpetofauna at Shropham

Class Amphibia Linnaeus, 1758
Order Caudata Oppel, 1811
Family Salamandridae Gray, 1825
Genus *Triturus* Rafinesque, 1815
Triturus vulgaris (Linnaeus, 1758)
Smooth Newt

Material.-- A single trunk vertebra JCSHR (NP 89: 60).

Remarks.-- The trunk vertebrae of *Triturus vulgaris* have much higher neural spines than those of *T. cristatus* and *T. marmoratus*. The trunk vertebrae of *T. vulgaris* may be distinguished from those of *T. helveticus* in that the postzygapophyseal notch is narrower and more deeply indented in *T. vulgaris*. The smooth newt is said to be more terrestrial than many species in the genus and occurs in a wide variety of damp habitats in Britain and Europe today (ARNOLD and BURTON, 1978).

This species occurs in East Anglia today where it is widespread and either common or abundant (COOKE and SCORGIE, 1983).

Order Anura Rafinesque, 1815
Family Bufonidae Gray, 1825
Genus *Bufo* Laurenti, 1768
Bufo bufo (Linnaeus, 1758)
Common Toad

Material.-- A single left ilium MSUVP 1432 from Section U. A left and a right ilium JCSHR (NP 89: 61-62).

Remarks.-- The ilia of *Bufo bufo* have a low, non-triangular dorsal prominence and they lack the distinct ridge

("*calamita* ridge") on the anteroventral portion of the ilial shaft of *Bufo calamita*. The common toad has a wide range of habitats in Britain today, but it needs shallow, standing water to be able to breed. *Bufo bufo* is widespread and either common or abundant in East Anglia today, although it is said to be rather more local in east Norfolk (COOKE and SCORGIE, 1983).

Bufo calamita Laurenti, 1768
Natterjack Toad
Figure 2

Material.-- A single left ilium from a rather small individual MSUVP 1435 from Section H4.

Remarks.-- The ilia of *Bufo calamita* may be confidently distinguished from those of the other European species *Bufo bufo* and *B. viridis* (HOLMAN, 1989). The most important diagnostic characters of the ilia of *B. calamita* are (1) a high, triangular dorsal prominence above the acetabulum (see fig. 2), and (2) a ridge ("*calamita* ridge") on the anteroventral portion of the ilial shaft (see fig. 2).

I was able to study a large number of modern *B. calamita* ilia at the Museo National de Ciencias Naturales, Madrid, in 1992 where I found that the triangular dorsal prominence appeared to be the more reliable of the two characters. In the 39 available *B. calamita* skeletons the triangular ridge occurred in 38 (97.4%), whereas the "calamita ridge" occurred in 27 (69.2%). I have never seen the triangular prominence is the many modern *B. bufo* or several *B. viridis* ilia I have studied.

The Shropham natterjack toad (*Bufo calamita*) is of ecological and biogeographic importance. Today, the natterjack is mainly restricted to a few coastal dune populations in Britain. But the early Flandrian (Holocene) record (HOLMAN and STUART, 1991) indicates that the natterjack, an "r-selected" (pioneer) species, moved rapidly to colonize new areas in Britain after the retreating ice and was considerably more widespread than it is today. However, with the advent of scrub and forest vegetation, blocking out sunlight, and with human destruction of habitats in Britain, the natterjack became mainly restricted to its present coastal dune habitats.

Of interest in this light, is that in the southern part of its European range today (e.g. southern France and Iberia), the natterjack is found in a wide variety of habitats. Today, there are no modern records of *Bufo calamita* from the interior of East Anglia, although two pre-1960 records exist (FRAZER, 1983). Now two records or *B. calamita* are known from the interior of East Anglia, the Shropham record and one from the Middle Pleistocene interglacial East Barnham Farm site near Thetford in Suffolk (ASHTON *et al.*, 1994). These occurrences suggest to me that *Bufo calamita* may have been more widespread in Britain during the Pleistocene interglacial ages than it is today.

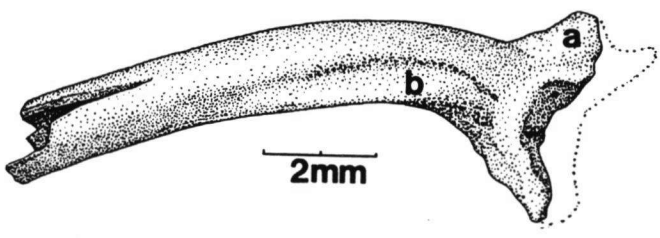

Fig. 2: Left ilium of natterjack toad (*Bufo calamita*) MSUVP 1435 from interglacial sediments of the Shropham Site, Norfolk. a. dorsal promonence; b, "*calamita* ridge".

Fig. 2: Linker ilium van de rugstreeppad (*Bufo calamita*) MSVUP 1435 uit interglaciale sedimenten van Shropham, Norfolk. a. dorsaal uitsteeksel; b. "*calamita* richel".

Family Ranidae Gray, 1825
Genus *Rana* Linnaeus,1758
Rana arvalis Nilsson, 1842
Moor Frog

Material.-- One left and three right ilia JCSHR (NP 89a: 29-32) [incorrectly reported as "39-32" by HOLMAN and CLAYDEN, 1990], and one left ilium JCSHR (NP 89b: 54).

Remarks.-- HOLMAN (1987) gave characters that distinguish the ilia of *R. arvalis* from other European *Rana*. This species does not occur naturally in Britain today, but is not uncommon in British interglacial sites (HOLMAN, 1993). Today the moor frog is found in damp fields and meadows, as well as fens and sphagnum bogs. It often occurs in the same area as *R. temporaria*, but prefers wetter habitats (ARNOLD and BURTON, 1978).

Rana temporaria Linnaeus, 1758
Common Frog

Material.-- A single right ilium MSUVP 1431 from Section U. A single right ilium JCSHR (NP 89: 27).

Remarks.-- The ilia of *Rana temporaria* may be distinguished from other European *Rana* on the basis of its poorly developed ilial blade or vexillum (HOLMAN, 1985). The common frog is largely terrestrial today except during the breeding season or during hibernation and occurs in a wide variety of damp places (ARNOLD and BURTON, 1978). Today the common frog is local and rather scarce in Norfolk (COOKE and SCORGIE, 1983).

Rana sp.
Water Frog

Material.-- One left and one right ilium JCSHR (NP 89: 33-34).

Remarks.-- These ilia have the steep slope of the tuber superior into the pars ascendens ilii as in "water frog" species such as *R. lessonae*, *R. ridibunda*, and the hybrid form *R. "esculenta"*, but I have not been able to assign these somewhat fragmentary ilia to any of these taxa with confidence. Water frogs do not occur natively in Britain today.

Rana sp. indet.
Indeterminate *Rana*

Material.-- Two right ilia and one sacral vertebra MSUVP 1434 from Section U. Two left and four right ilia JCSHR (NP 89a: 35-40), and four left and one right ilia JCSHR (NP 89b: 55-59).

Remarks.-- These elements are too fragmentary to identify other than as the genus *Rana*.

Class Reptilia Laurenti 1768
Order Testudines Batsch, 1788
Family Emydidae Lydekker, 1889
Genus *Emys* Dumeril 1806
Emys orbicularis (Linnaeus, 1758)
European Pond Tortoise
Figures 3 and 4

Material.--Two left and one right epiplastra, two left and one right hypoplastra, three left and three right xiphiplastra, two neurals, one pygal, 18 costals, 9 peripherals, one indeterminate plastral fragment, one left distal humerus, and one left proximal femur MSUVP 1437 from Section U. Two neurals JCSHR (NP 89: 9-10). Fifteen costals JCSHR (NP 88: 4,8; 89: 1-2; 89: 6; 89: 12-21). Five peripherals JCSHR (NP 88: 2,3,5; 89: 4-8). Two hyoplastra JCSHR (NP 89: 7; 89B: 9). Three shell fragments JCSHR (NP 88: 6-7; 89: 28).

Remarks.-- The European pond tortoise, *Emys orbicularis*, has been identified from Cromerian, Hoxnian, Ipswichian, and Flandrian temperate stages in Britain (STUART, 1979, 1982), but does occur in the native fauna of the British Isles today. Some shell characters that distinguish *Emys orbicularis* from its modern European emydid relative, *Mauremys caspica leprosa*, were given by HOLMAN (1995), and were useful in the identification of several of the Shropham bones.

Mean July temperatures greater than 18° C appear to be needed for the modern species to reproduce successfully; thus STUART (1979) suggested that temperatures in England were at least 2° C warmer than now when *E. orbicularis* inhabited England during the Pleistocene.

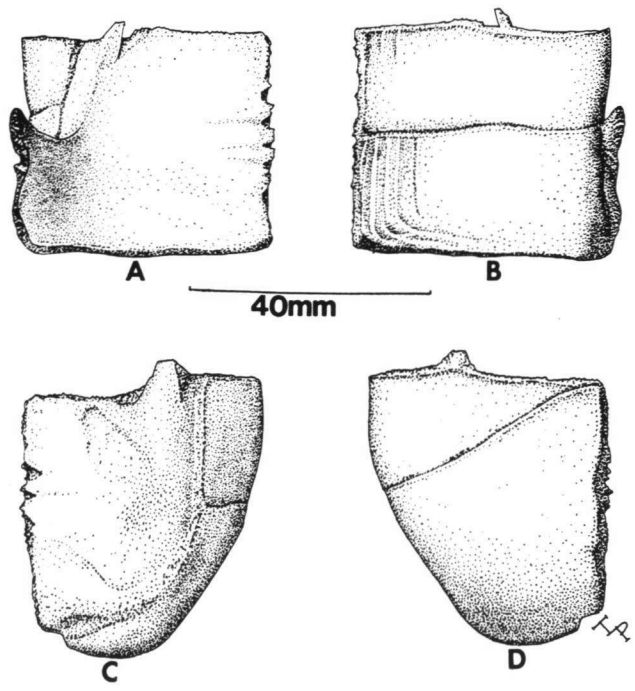

Fig. 3: Plastral bones of the European pond tortoise (*Emys orbicularis*) MSUVP 1437 from interglacial sediments of the Shropham Site, Norfolk. A. hypoplastron in dorsal view. B. same hypoplastron in ventral view showing growth rings. C. Xiphiplastron in dorsal view. D. same xiphiplastron in ventral view. The scale line applies to all figures.

Fig. 3: Botten van het plastron van de moerasschildpad (*Emys orbicularis*) MSUVP 1437 uit interglaciale sedimenten van Shropham, Norfolk. A. dorsaal aanzicht hypoplastron. B. ventraal aanzicht van hetzelfde hypoplastron met groeiringen. C. dorsaal aanzicht xiphoplastron. D. ventraal aanzicht van hetzelfde xiphoplastron. Alle figuren in dezelfde schaal.

Marks produced by growth rings (external annuli) in the epidermal scutes are evident in several of the Shropham *Emys orbicularis* bones, including hypoplastra and costals (see figs. 3 and 4). These rings in turtles are interpreted as being analagous to annual rings in trees (GIBBONS, 1976), and indicate alternate periods of dormancy and active growth in the turtles. The presence of these growth rings is here interpreted as indicating that during the time represented by the Shropham fauna periods of seasonal climatic change occurred that led to a cessesion of growth in *Emys orbicularis*.

Today, *Emys orbicularis* occurs in most parts of Europe except in the north and certain parts of the center and it also occurs in western Asia and northwestern Africa (ARNOLD and BURTON, 1978). This species is typically found in still or slow moving water with abundant aquatic vegetation.

Order Sauria McCartney, 1802
Family Lacertidae Bonaparte, 1831
Genus *Lacerta* Linnaeus, 1758
Lacerta cf. *vivipara* Linnaeus, 1758
Viviparous Lizard

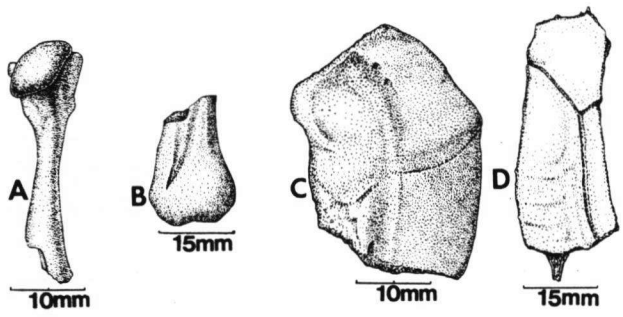

Fig. 4: Shell and limb bones of the European pond tortoise (*Emys orbicularis*) MSUVP 1437 from interglacial sediments of the Shropham Site, Norfolk. A. left femur missing the distal end. B. left distal humerus. C. right epiplastron in dorsal view. D. costal bone in dorsal view showing growth rings.

Fig. 4: Botten van het schild en de ledematen van de moerasschildpad (*Emys orbicularis*) MSUVP 1437 uit interglaciale sedimenten van Shropham, Norfolk. A. linker femur waarvan het distale gedeelte ontbreekt. B. distale gedeelte linker humerus. C. dorsaal aanzicht rechter epiplastron. D. dorsaal aanzicht rib met daarop groeiringen.

Material.-- A single vertebra MSUVP 1436. A single vertebra JCSHR (JC 89: 1), and five vertebrae JCSHR (NP 89: 22-26).

Remarks.-- These vertebrae are very morphologically distinct from those of *Anguis fragilis* and appear to be identical to those of adult *L. vivipara* in size and characters. Nevertheless, the fossils are tentatively assigned to *L. vivipara* because skeletons of *L. agilis* were not available for study.

The viviparous lizard is said to be widespread and fairly common in East Anglia today (COOKE and SCORGIE, 1983). In Norfolk it appears to be most common in heathlands (personal observations).

Order Serpentes Linnaeus, 1758
Family Colubridae Oppel, 1811
Genus *Natrix* Laurenti, 1768
Natrix natrix (Linnaeus, 1758)
Grass Snake
Fig. 5

Material.-- Two trunk vertebrae MSUVP 1430. A single vertebra JCSHR (NP 88: 1) and seven vertebrae JCSHR (JC 89: 2-8).

Remarks.-- These vertebrae have their hypapophyses obtuse or rounded distally (see fig. 5) and have robust parapophyseal processes as in *N. natrix* (SZYNDLAR, 1984). The species is widespread but not common in East Anglia today (COOKE and SCORGIE, 1983). It is rather locally common in parts of the Broads of Norfolk (personal observation). This species is said to be found in damp places over most of its range today (ARNOLD and BURTON, 1978).

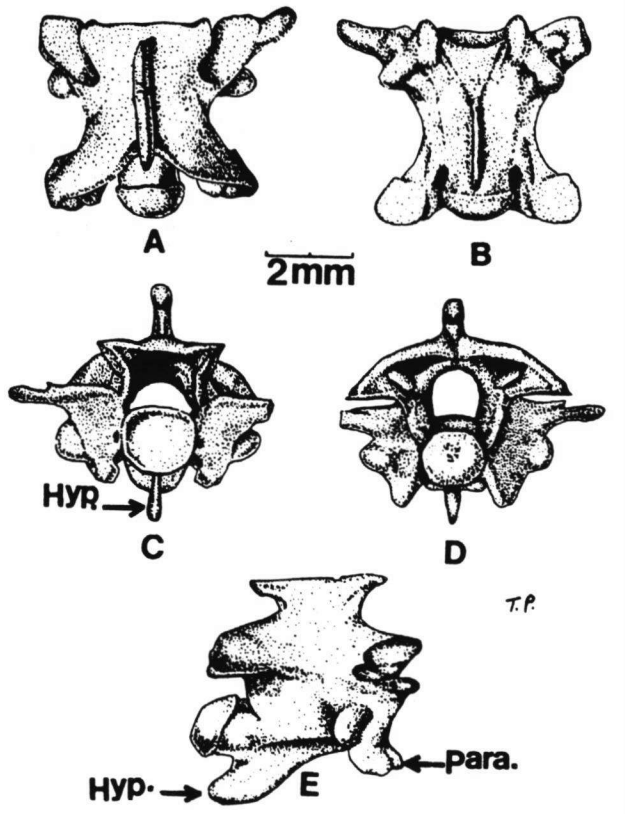

Fig. 5: Trunk vertebra of grass snake (*Natrix natrix*) JCSHR (NP 88: 1) from interglacial sediments of the Shropham Site, Norfolk. A. dorsal; B. ventral; C. anterior; D. posterior; E. lateral views. (Hyp) refers to the hypapophysis; (Para) refers to the parapophyseal process. The scale line applies to all of the figures. (From Holman and Clayden, 1990).

Fig. 5: Wervels van de ringslang (*Natrix natrix*) JCSHR (NP 88: 1) uit interglaciale sedimenten van Shropham, Norfolk. A. dorsaal aanzicht; B. ventraal aanzicht; C. voor aanzicht; D. achter aanzicht; E. zij aanzicht. (Hyp) staat voor hypapophysis; (Para) staat voor paraphophyseaal uitsteeksel. Alle figuren dezelfde schaal. (Uit Holman and Claydon, 1990).

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

Material.-- Seven vertebrae JCSHR (JC 89: 9-15).

Remarks.-- These vertebrae have their hypapophyses pointed distally and delicate, slender parapophyseal processes as described for *N. maura* and *N. tessellata* by SZYNDLAR (1984).

Both *N. maura* and *N. tesselata* are absent from the modern fauna of Britain today, but are found on the European Continent (Maps 115 and 116 in ARNOLD and BURTON, 1978).

Natrix sp. indet.

Material.-- Eight fragmentary vertebrae MSUVP 1433. Twelve vertebrae JCSHR (NP 89: 42-53) and 52 vertebrae JCSHR (JC 89: 16-67)

Remarks.-- I am unable to distinguish these fragmentary vertebrae to the specific level.

The Late Pleistocene Cold Stage (Devensian) Herpetofauna at Shropham

Rana *temporaria* Linnaeus, 1758
Common Frog

Material.-- One left and two right ilia CMSH D: 1-3.

Remarks.-- These ilia represent one large adult and two smaller adult common frogs.

Rana sp. indet.
Frog

Material.-- Four left and five right fragmentary ilia CMSH D: 4-12. Two fragmentary scapulae and a distal portion of a humerus CMSH D: 13-15. The ilia were identified using the characters for the identification of *Rana temporaria* previously discussed in this paper.

Remarks.-- The above fragmentary ila are identified as *Rana* in that they all have an ilial blade (vexillum). The fragmentary scapulae and the distal portion of the humerus are identified as *Rana* based on characters discussed in HALLOCK *et al.* (1990, see figs. 3 and 4). Several other fragmentary anuran bones from the Shropham Devensian are not assigned to genus. It seems probable that all of these anuran bones represent *R. temporaria*.

Natrix natrix (Linnaeus, 1758)
Grass Snake

Material.-- Two trunk vertebrae collected by A. J. Stuart of the Castle Museum, Norfolk, and housed in the Shropham fossil collection at the Castle Museum, Norfolk.

Remarks.-- These vertebrae were identified using the criteria previously discussed for the identification of *Natrix natrix* in this paper.

Discussion

In this section, comments on the interglacial herpetofauna will be made first, followed by comments on the cold-stage herpetofauna.

Paleogeographic Comments on the Interglacial Herpetofauna

The Shropham interglacial herpetofauna consists of at least 10 species, six amphibians and four reptiles. All of these species are living today and six of the ten species live in Britain. The four exotic species are moor frog (*Rana arvalis*), water frog species (*Rana* sp.), European pond tortoise (*Emys orbicularis*) and water snake (*Natrix maura* or *tessellata*).

The moor frog and water frogs occur nearest to Britain today across the English Channel in the low countries of Europe (ARNOLD and BURTON, 1978, maps 37 and 43). The European pond tortoise occurs nearest to Britain in the Rennes-Laval-Le Mans area in northwestern France today (ARNOLD and BURTON, 1987, map 48). At present, the water snakes are mainly restricted to the Mediterranean countries (ARNOLD and BURTON, 1978, maps 115 and 116).

The fact that 40% of the Shropham interglacial herpetofauna are exotic to Britain today is consistent with eight Ipswichian faunas discussed by HOLMAN (1993) which had a total of 11 herpetological species present, 45.5% of which were exotic. It is of interest that the only previously reported Ipswichian species absent from the Shropham interglacial herpetofauna was *Hyla meridionalis*, a form reported by HOLMAN (1992b) from the Itteringham fauna in Norfolk.

Occurrence of *Bufo calamita* in the Shropham Interglacial Herpetofauna

This is only the fourth report of the presently endangered natterjack toad (*Bufo calamita*) from pre-Flandrian Pleistocene deposits in Britain. The others are from the Ipswichian interglacial deposit at Selsey, West Sussex, and the Cromerian interglacial deposits at Boxgrove, West Sussex (HOLMAN, 1992c, 1993) and Barnham Farm, East, Suffolk (ASHTON *et al.*, 1994). The occurrences of the inland populations of the natterjack toad in the Norfolk and Suffolk are interpreted as possibly indicating a more widespread occurrence of this species in interglacial ages in Britain than today.

Ecological Setting of the Interglacial Herpetofauna at Shropham

The presence of *Emys orbicularis*, the water frogs, and the water snake in the Shropham interglacial herpetofauna indicate the presence of a quiet pool (fig. 6), one that probably had an ample growth of aquatic plants. All of the amphibian species could have utilized this habitat as a breeding site, and it would provide animals for *Natrix natrix* and the water snake to feed upon.

Fig. 6: Artist's concept of the quiet pool at Shropham during Ipswichian interglacial times. 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*) is on the log in the upper right. A hippopotamus is in the water in the upper left and a hyaena lurks on the shore in the upper right.

Fig. 6: Reconstructie van het meer bij Shropham tijdens het Eemien. Een ringslang (*Natrix natrix*) zit linksonder. Voor de ringslang zit een bruine kikker (*Rana temporaria*). Een moerasschildpad zont rechtsboven op de boomstam. Een nijlpaard is linksboven in het water en helemaal rechtsboven zoekt een hyena de oever af.

A moist grassy meadow that would support *Rana temporaria* and *Rana arvalis* was probably adjacent to the pool. A somewhat moist shrubby or wooded habitat adajacent to the meadow would support *Triturus vulgaris*, *Bufo bufo*, *Bufo calamita* and *Lacerta* cf. *vivipara*. A somewhat sandy component to the soil may be indicated by the presence of *Bufo calamita*.

Comment on the Devensian Cold-Stage Herpetofauna at Shropham

Only two species, *Rana temporaria* and *Natrix natrix*, were found in Devensian sediments at Shropham. The common frog is presently a cold-tolerant species that occurs well within the Arctic circle today (ARNOLD and BURTON, 1987, map 36). The grass snake just reaches the Arctic circle in Sweden today (ARNOLD and BURTON, 1978), but occurs well below the Arctic circle in the Rest of its European range (ARNOLD and BURTON, 1978; BANNIKOV *et al.*, 1977). This is the only record of a snake from any of the Pleistocene cold-stage faunas in Britain.

Acknowledgments

I gratefully acknowledge John D. Clayden for donating Shropham amphibian and reptile fossils collected by him to the Michigan State University Museum. I thank Martin R. Warren and Anthony J. Stuart for allowing me to study herpetological fossils collected by them at Shropham. My work at Shropham was supported by United States National Science Foundation Grant NSF BSR 851-5565. Teresa Petersen made the drawings for the figures for this paper.

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