AMPHIBIANS OF THE WHITEMOOR CHANNEL EARLY FLANDRIAN SITE NEAR BOSLEY, EAST CHESHIRE; WITH REMARKS ON THE FOSSIL DISTRIBUTION OF *BUFO CALAMITA* IN BRITAIN

J. Alan Holman* and Anthony J. Stuart†

*Michigan State University Museum East Lansing, Michigan, U.S.A. 48824-1045.
† Castle Museum, Norwich NR1 3LU.

ABSTRACT

A lacustrine *Chara* marl (ca. 10,000-8,800 radiocarbon years BP) at the Whitemoor Channel Site near Bosley, East Cheshire, yielded fossil amphibian remains, including palmate newt *Triturus helveticus*, smooth newt *Triturus vulgaris*, natterjack toad *Bufo calamita*, common toad *Bufo bufo*, common frog *Rana temporaria* and material belonging to these genera which probably represent the same five species. All of these species are extant and occur naturally in Britain today, although for the past two hundred years the natterjack toad *Bufo calamita* has occurred only locally in Britain, being essentially restricted to coastal dunes and inland heaths. The well-dated Flandrian (early Holocene) finds from Whitemoor Channel are an important addition to previous, poorly stratified, records from Cow Cave, Chudleigh, Devon, and Ightham Fissures, Sevenoaks, Kent. Taken together, these records demonstrate early colonisation of England by *B. calamita* after the last Cold Stage and suggest a wider geographical occurrence of the natterjack than in Britain today.

INTRODUCTION

In their account of the sediments infilling a former glacial meltwater channel cut into Upper Carboniferous sandstones and shales at Whitemoor near Bosley, Cheshire, (SJ917678) Johnson, Franks and Pollard (1970) described a fossiliferous shell marl or *Chara* marl ('white calcareous marl') containing amphibian remains. The occurrence of this highly calcareous sediment in an area of generally acidic bedrock reflects leaching of carbonate early in the Flandrian from freshly laid down glacial deposits. In an addendum to the above report, A. J. Stuart listed fishes: brown trout *Salmo trutta* and rudd *Scardinius erythropthalmus*; and amphibians: newt *Triturus* sp.; common frog *Rana temporaria*; and common toad *Bufo bufo*. We now present the results of a detailed study of the amphibian material.

Johnson *et al.* (1970) recorded the following section at the centre of the channel:

> Fen peat (flooring valley) 1.70m
>
> *Chara* marl 1.00m
>
> blue-grey calcareous mud 0.10m
>
> blue-grey silty clay (base not seen)

Toward the margin, the *Chara* marl was only 0.30m thick, and was absent altogether in borings only 20m from the centre of the depression. The marl comprised unconsolidated, fine, granular calcium carbonate of biogenic origin, principally the characteristic oogonia and ribbed stem components of stonewort *Chara*. Shells of freshwater Mollusca were abundant, comprising mainly *Lymnaea peregra, Planorbis albus,* and the rarer *Sphaerium corneum*. Ostracoda were also recorded.

The pollen diagram indicates open habitats with grasses and sedges during the deposition of the calcareous mud in pollen assemblage zone III at the end of the Devensian Lateglacial (Johnson *et al.*, 1970). Pollen assemblages from the overlying marl record the development of birch *Betula* woodland, with alder *Alnus*, hazel *Corylus* and willow *Salix*. Grasses, sedges and aquatic plants are also represented. These assemblages are characteristic of the very early part of the Flandrian or Holocene, representing pollen substages Fl Ia and Fl Ib of West (e.g. 1977), equivalent to zones IV and V of Godwin (e.g. 1975). Comparison with the radiocarbon-calibrated sequence at Red Moss, Lancashire, 53km to the northwest, (Hibbert, Switsur and West, 1971) suggests that the fossiliferous marl at Whitemoor spans the period from approximately 10,000 to 8,800 radiocarbon years before the present (BP). At the beginning of substage FlII (zone VI), marked by the expansion of pine *Pinus*, oak *Quercus* and elm *Ulmus*, deposition of peat began, indicating drying out of the lake and colonisation by fen vegetation.

The small auger used in the original survey by Johnson *et al.* (1970), while satisfactory for obtaining a series of pollen samples, produced only sparse vertebrate remains. Two larger samples of shell marl, totalling about 0.06 cubic metres, were recovered from beneath waterlogged fen peat by A. J. Stuart, using a purpose-built hand auger 20cm in diameter. Abundant amphibian remains and shells were readily obtained by washing the unconsolidated sediment through a millimetre sieve. The high concentration of bones probably reflects slow accumulation, averaging about 1mm of sediment per year.
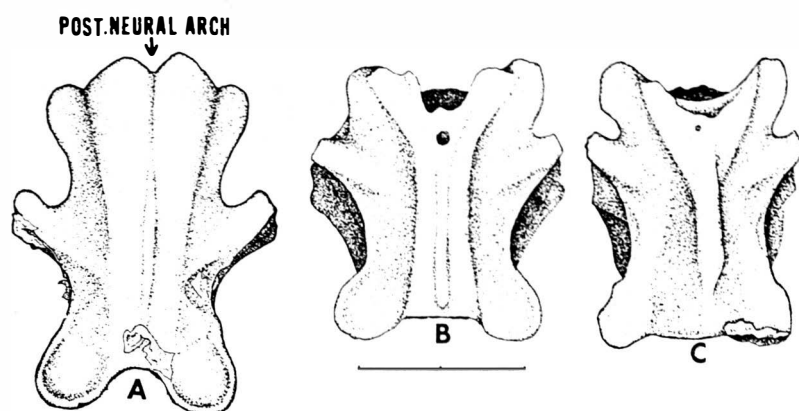
POST.NEURAL ARCH

Fig. 1 Trunk vertebrae of modern *Triturus*. A, *T. cristatus*; B, *T. vulgaris*; C, *T. helveticus*. The line equals 2mm and applies to all figures.

SYSTEMATIC PALAEONTOLOGY

The fossil material discussed herein is preserved in the collections of the Castle Museum, Norwich, under the accession number NCM 143.989. Numbers of individual specimens are shown in parentheses, e.g. NCM 143.989 (1).

Class Amphibia Linnaeus, 1758
Order Caudata Oppel, 1811
Family Salamandridae Gray, 1825
Genus *Triturus* Rafinesque, 1815

On the basis of the modern skeletons that were studied, the British species of *Triturus* may be distinguished from one another on the basis of several isolated postcranial elements, including vertebrate, humeri and femora. *Triturus cristatus* is much more osteologically distinct from *T. helveticus* and *T. vulgaris* than are the latter two species from each other. This corresponds with Arnold and Burton (1978) where *T. cristatus* is the nominate form of the *T. cristatus* group and *T. helveticus* and *T. vulgaris* are placed in the *T. vulgaris* group. Estes (1981) considers *T. cristatus* to be a primitive species of the genus *Triturus*. Arnold and Burton (1978) have shown that the fronto-squamosal arch is absent in *T. cristatus*, present but incomplete in *T. vulgaris* and complete in *T. helveticus*.

Trunk Vertebrae. — Based on modern skeletons examined: *T. cristatus* (2), *T. vulgaris* (6) and *T. helveticus* (1), the trunk vertebrae of all three species may be distinguished from each other (Fig. 1). The trunk vertebrae of *T. cristatus* are larger and have a lower neural spine than in *T. vulgaris* and *T. helveticus*. Moreover, in *T. cristatus* they have the posterior neural arch extending posterior to the postzygapophyses and a narrow, V-shaped notch; the posterior neural arch ends anterior to the postzygapophyses and has a U-shaped notch in *T. vulgaris* and *T. helveticus*.

The trunk vertebrae of *T. vulgaris* may be separated from those of *T. helveticus* on the basis of the narrowly U-shaped notch in the posterior neural arch of the former species and the broadly U-shaped notch in the latter species. None of the Whitemoor Channel vertebrae represents *T. cristatus*, but may vertebrae with the posterior neural arches complete could be assigned to either *T. vulgaris* or *T. helveticus*.

Humeri. — The humeri of *T. cristatus* have a more elongate crista ventralis (terminology of Duellman and

Trueb, 1987) and a thicker shaft than in *T. vulgaris* and *T. helveticus* (Fig. 2), but we have been unable to separate the humeri of the latter two species satisfactorily from one another. The single humerus from the Whitemoor Channel Site represents either *T. vulgaris* or *T. helveticus*.

Femora. — The femora of *T. cristatus* have the tibial end more widely flared, the medial part of the shaft wider, and the area between the trochanter and the femoral end more elongate than in *T. vulgaris* and *T. helveticus* (Fig. 3), but we cannot distinguish the femora of the latter two species. The three femora from the Whitemoor Channel Site represent either *T. vulgaris* or *T. helveticus* or both, but none represent *T. cristatus*.

Triturus vulgaris (Linnaeus, 1758) Smooth Newt

Material. — Ten vertebrae NCM 143.989 (1-10).

Remarks. — The smooth newt occurs in the area today (Yalden, 1986). This species is said to be more terrestrial than many species of the genus and occurs in a wide variety of damp habitats (Arnold and Burton, 1978).

Triturus helveticus (Razoumowsky, 1789) Palmate Newt

Material. — Twenty vertebrae NCM 143.989 (11-30).

Remarks. — The palmate newt occurs in the area today (Frazer, 1983). This species is said to be more aquatic than *T. vulgaris*. It breeds in a wide variety of aquatic habitats, sometimes lentic ones, and sometimes even in brackish water near the sea (Arnold and
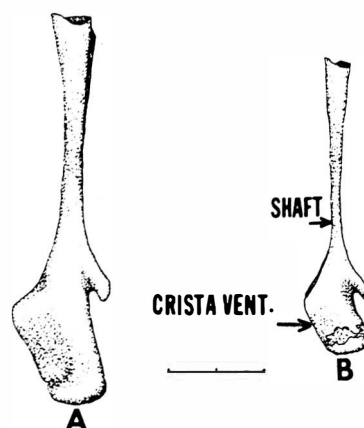

SHAFT
CRISTA VENT.

Fig. 2 Right humeri of modern *Triturus*. A, *T. cristatus*; B, *T. helveticus*. The line equals 2mm and applies to all figures.
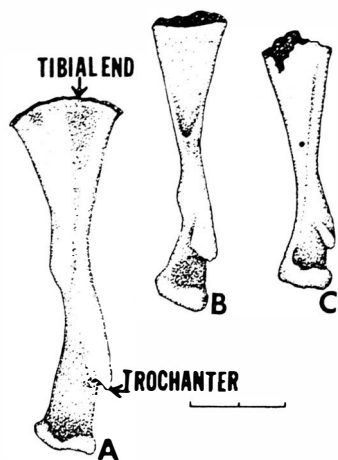
Fig. 3 Right femora of modern *Triturus*. A, *T. cristatus*; B, *T. vulgaris*; C, *T. helveticus*. The line equals 2mm and applies to both figures.
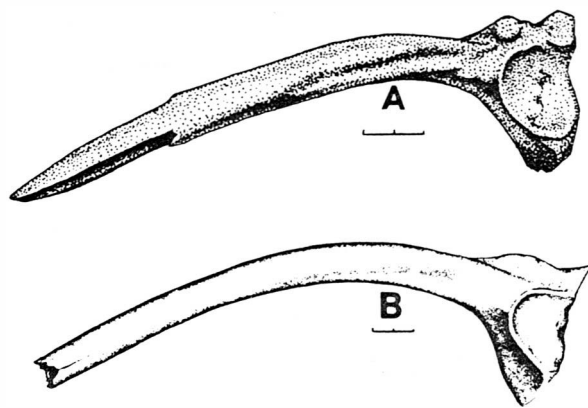

Fig. 4 Left ilia of fossil *Bufo* from the Whitemoor Channel site. A, *B. calamita* NCM 143.989 (97); B, *B. bufo* NCM 143.989 (104). Each line equals 2mm.

Burton, 1978), but tends to prefer more acidic waters than *T. vulgaris* (Yalden, 1986).

Triturus sp. indet.

Material. — Left dentary NCM 143.989 (31); nine atlantes NCM 143.989 (32-40); 51 vertebrae NCM 143.989 (41-91); right humerus NCM 143.989 (92); two right and one left femora NCM 143.989 (93-95).

Remarks. — We were unable to assign the non-vertebral elements to species, although we feel that *T. vulgaris* and *T. helveticus* are those represented. The above vertebrae were not assigned to species because diagnostic parts were missing.

Order Anura Rafinesque, 1815

Family Bufonidae Gray, 1825

Genus *Bufo* Laurenti, 1768

Holman (1989) discussed the identification of *Bufo bufo*, *Bufo calamita* and *Bufo viridis* on the basis of isolated ilia. Two ilial characters in combination enable one to identify fossil specimens as *B. bufo* or *B. calamita* with a high degree of confidence. (1) *B. bufo* has a low, roughened or rounded ilial prominence, whereas *B. calamita* has a relatively high and triangular one (Fig. 4a). An 'unusual' morph occasionally occurs in the ilium of *B. bufo*, however, where the ilial prominance arises from the shaft as a low, irregularly shaped crest (Holman, 1989a, p. 10, Fig. 1). (2) *B. bufo* lacks the elongate ventral ridge ('*calamita* ridge' of Holman, 1989b) that occurs on the posterior part of the ilial shaft and that is separated from the upper part of the shaft by an indented area in *B. calamita*. It appears likely that the differences in ilial structure between the two species reflect the differences in locomotion, as *B. calamita* makes 'mouse-like' dashes that *B. bufo* does not show. Böhme (1977) has provided a means for distinguishing the sphenethomoids and sacra of *B. bufo* and *B. calamita*, but these elements appear to be more variable than the ilia (Holman, 1989b).

Bufo calamita Laurenti, 1768 Natterjack Toad

Material. — Sacrum NCM 143.989 (96) and two left ilia NCM 143.989 (97-98) (Fig. 4a).

Remarks. — This record as well as other fossil records of *B. calamita* in England will be addressed in the discussion section of the present paper.

Bufo bufo (Linnaeus, 1758) Common Toad

Material. — Three left sphenethmoids (one with a supraoccipital attached) NCM 143.989 (99-101); two sacra (one partial) NCM 143.989 (102-103); and one left ilium NCM 143.989 (104) (Fig. 4b).

Remarks. — This toad occurs in the area today (Frazer, 1983). The common toad has a wide range of habitats, but it needs shallow, standing water to be able to reproduce.

Bufo sp. indet.

Material. — Four left exoccipitals NCM 143.989 (105-108); two parasphenoids NCM 143.989 (109-110); one left and one right dentaries NCM 143.989 (111-112); two left and two right angulosplenials NCM 143.989 (113-116); three atlantes NCM 143.989 (117-119); six left scapulae NCM 143.989 (120-125); four left and one right suprascapulae and two suprascapular fragments NCM 143.989 (126-132); two left humeri NCM 143.989 (133-134); one left and one right radioulnae NCM 143.989 (135-136).

Remarks. — These bones are easily distinguished from those of *Rana*, but we are unable to distinguish between *B. bufo* and *B. calamita* on the basis of these elements because of a lack of available comparative material of modern *B. calamita*.

Family Ranidae Gray, 1825

Genus *Rana* Linnaeus, 1758

Böhme (1977) has given characters that distinguish individual bones of certain species of *Rana* from each other. We have been able to identify *R. temporaria* on the basis of sphenethmoids, sacra and ilia using the characters pointed out by Böhme and by the examination of modern skeletal material.

Rana temporaria Linnaeus, 1758 Common Frog

Material. — Sacral vertebra NCM 143.989 (137); two right ilia NCM 143.989 (138-139); a partial associated skeleton NCM 143.989 (140).
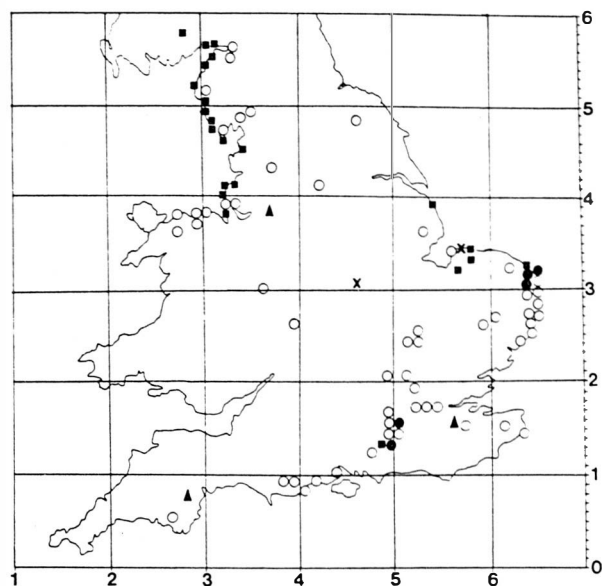
Fig. 5 Map of the distribution of fossil and modern *Bufo calamita* in England. Modified and redrawn from Frazer, 1983. Triangles indicate fossil records. Open circles indicate historic records up to and including 1959. Closed circles indicate records from 1960 through 1969. Squares indicate records from 1970 to 1983. X's indicate introduced individuals or populations.

Remarks. — The sacra of *R. temporaria* have their diapophyses more posteriorly directed than those of other British and European *Rana* and the ilial crest (vexillum of Böhme, 1977) of the ilium is quite reduced anteriorly compared with other British and European *Rana* (Böhme, 1977). The associated frog skeleton is identified as *R. temporaria* on the basis of the structure of the right sphenethmoid (Böhme, 1977, p. 291, Fig. 5). This fossil skeleton lacks both ilia as well as the sacrum.

The common frog is found in the area today (Frazer, 1983). This species may be found quite far from permanent water, but needs shallow, still water to be able to reproduce.

Rana sp. indet.

Material. — Right premaxilla NCM 143.989 (141); right maxilla NCM 143.989 (142); left angulosplenial NCM 143.989 (143); two atlantes NCM 143.989 (144-146); two left and two right humeri NCM 143.989 (146-149); four left radioulnae NCM 143.989 (150-153); one urostyle NCM 143.989 (154).

Remarks. — These skeletal elements are distinguishable from those of *Bufo bufo* and other European genera, but we are unable to determine what species of *Rana* they represent.

DISCUSSION

The Whitemoor Channel site, East Cheshire has yielded at least two species of newt and three species of anuran, all of which represent forms living in Britain today. Moreover, with the exception of a record of *Emys orbicularis* from the Flandrian of East Wretham near Thetford, Norfolk (A. Newton, 1862; Stuart, 1982)

assemblages from Flandrian sites in Britain have thus far yielded only extant British species (E. Newton, 1894; Holman, 1985, 1987a, 1988). This is in contrast to Cromerian, Hoxnian and Ispwichian interglacial herpetofaunas which have yielded exotic anurans and reptiles found on the European Continent today, but not occurring naturally in Britain (Holman, 1987b, 1987c; Holman, Clayden and Stuart, 1988; Holman, Stuart and Clayden, 1990, Stuart, 1982).

Beebee (1978) spurred an interesting exchange of ideas in the 1980's (Beebee, 1980, 1988/89; Walters, 1981; Wilkinson, 1988; Yalden, 1980a, 1980b, 1981) on the explanation for the restricted distribution of Britain's rare amphibians and reptiles (natterjack toad *B. calamita*, sand lizard *Lacerta agilis* and smooth snake *Coronella austriaca*).

In essence Beebee (1978) postulated that the present distribution of rare herpetological species resulted from human activities in the Neolithic which created heathland corridors in the dominant regional deciduous forst, connecting the West Midlands and northwest England with East Anglia. Yalden (1980a) drew attention to the climatic warming at the onset of the Flandrian (Holocene) from a little before 10,000 BP, which was so rapid that there was considerable delay before the arrival of forest trees, and suggested that the resulting open conditions would have allowed the rare species to colonise Britain extensively. The subsequent development of dense forest then restricted them to coastal dunes and heaths. Walters (1981) suggested that warmer climates in the past would have allowed the rare species to occupy a wider diversity of habitats in Britain as they do further south in mainland Europe, and agreed with Yalden that it was unnecessary to search for previous existing heaths and dunes when plotting dispersal routes. Wilkinson (1988) and Beebee (1988/89) further commented on *Bufo calamita* history in Britain, in short notes, based in part on poorly stratified (? Flandrian) records (Holman, 1985, 1988).

Since its first mention as a British species by Pennant in 1776 (Smith, 1973) *B. calamita* has occurred widely, but locally, in England and southwest Scotland, mostly confined to coastal dune and inland heath sites. It is also found in southwest Ireland. In recent decades it has become extinct at many localities where it was formerly present (Fig. 5) and its survival in Britain is now largely dependant on careful management of the remaining sites.

The natterjack is distributed from Iberia across to north-central Europe, reaching as far north as about 55° N in Britain and 58° N in south Sweden and Estonia (Arnold and Burton, 1978). The species exploits a wider range of habitats in southwest Europe, where it is also more abundant. Northward and eastward it becomes associated with sandy soils that provide warmer microclimates (Beebee, 1983). According to Beebee, all habitats outside the warm Iberian Peninsula share the same features; well-drained soils and low vegetation allowing high amounts of sunshine to reach ground level, so that summer temperatures can be much higher than typical for that latitude. Beebee regards *B. calamita* as primarily a species of southwest Europe, able to extend

its range elsewhere, including Britain, by exploiting locally warm habitats.

The fossil records of *B. calamita* are from: 1. ?Flandrian cave deposits from Cow Cave, Chudleigh, Devon (Holman, 1988); 2. ?Flandrian fissure deposits from Ightham Fissures, near Sevenoaks, Kent (Holman, 1985); and 3. early Flandrian (approximately 10,000 to 8,800 BP) from the present site at Whitemoor Channel, Cheshire.

The Cow Cave and Ightham sites lack precise stratigraphic information. They probably date from sometime within the Flandrian, within the time range of 10,000 BP to a few hundred years ago. The Ightham fissures also yielded *C. austriaca* (Holman, 1985). Today, *B. calamita* is apparently extinct in Devon, but there is a pre-1960 coastal record for the species (Frazer, 1983). The Chudleigh site is about 9km from the coast. In relation to the Ightham fossils, there are two pre-1960 records from Kent, one from the Dover-Deal area and the other from a more inland locality near Canterbury (Frazer, 1983).

The only well-dated fossils (those from the Whitemoor Channel) are of importance because they date from early in the Flandrian when most of the modern fauna and flora was immigrating from the Continent in response to climatic amelioration following the much more severe climates of the Last Cold Stage. Britain was then broadly connected to Continental Europe across the eastern Channel and the southern North Sea (e.g. Stuart, 1982). Substages Fl Ia and Fl Ib at Whitemoor (Johnson *et al.*, 1970), Red Moss (Hibbert *et al.*, 1971) and other sites in Cheshire and Lancashire cover the period of development of birch woodland in a landscape previously dominated by grasses and sedges. Since birch casts relatively light shade, it is probable that open, sunny environments would have been widespread throughout this period. The rapid temperature rise very early in the Flandrian is well shown in analyses of radiocarbon-dated beetle faunas from Britain by Atkinson *et al.* (1987). Their curve indicates that mean annual temperatures were already as high as today by about 9,500 BP. But values rather higher than those of today were not reached until much later in the Flandrian ('Climatic Optimum') about 5-7,000 BP.

In the early Flandrian, as today, Whitemoor was neither a coastal dune site nor heathland. There is no indication of heaths (Ericaceae) in the pollen diagram from the site (Johnson *et al.*, 1970). Given the nature of the bedrock and presence of glacial till ('boulder clay'), both sandy and clay soils would have been available locally. *Bufo calamita* in Britain and Ireland lives in coastal dunes or heathland. Reports from Cambridge-shire (Jenyns, 1830) and the Furness region (Frazer, 1983) actually reflect typical habitats (T. J. C. Beebee, personal communication to J.A.H.). Throughout its range today the natterjack breeds in shallow, often ephemeral, and preferably non-acid pools, unshaded by vegetation (Beebee, 1983). The Whitemoor pool, some 30 metres in diameter, shallow, highly calcareous and unshaded (there was no terrestrial plant material other than pollen in the sediment) would have met these criteria.

The natterjack occurs today in northern England only along coastal dunes, extending from Cheshire to Cumbria and the Scottish shore of the Solway Firth (Frazer, 1983; Beebee, 1983). There are a few pre-1960 records from inland sites in northern England (Fig. 5), although there are considered probably incorrect by Beebee (1983, Fig. 4).

The fossil evidence from the Whitemoor Channel therefore favours Yalden's view (1980a, 1980b, 1981) that the natterjack was spread more widely in Britain in the early Flandrian before the arrival of dense forest restricted it to local open sites. Coastal dune habitats were present throughout the Flandrian, and numerous pollen diagrams provide evidence of the Flandrian history of heathland in Britain. Pollen of Ericaceae, presumably mostly *Erica* and *Calluna*, pollen and plant macrofossils specially identified as heather *Calluna vulgaris*, and plant macrofossils only of crossed-leaved heath *Erica tetralix* occur throughout the Devensian Lateglacial and early Flandrian in moderate frequencies, becoming much more abundant from the beginning of substage Fl Id (zone VIIa, about 7,000 BP; Godwin, 1975). At first, heath communities probably existed locally on acid soils, and after about 7,000 BP greatly expanded with increased podsolisation (Godwin, 1975). From about 5,000 BP, with the arrival of Neolithic farmers, human activities — forest clearance, burning and grazing livestock — appear to have enhanced this natural succession. No doubt, as suggested by Beebee, the natterjack and other rare herpetological species would have expanded their ranges with the spread of heathland at this time.

The evidence from Whitemoor emphasises the potential for recovering fossil herpetological material from other well-stratified and dated late Quaternary sites, with the promise of telling us more about the origins of our present herpetofauna.

ACKNOWLEDGEMENTS

REFERENCES

Arnold, E. E. and Burton, J. A. (1978). *A Field Guide to the Reptiles and Amphibians of Britain and Europe*. London: Collins.

Atkinson, T. C., Briffa, K. R. and Coope, G. R. (1987). Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* 325 (6105), 587-592.

Beebee, T. J. C. (1978). An attempt to explain the distribution of rare herptiles *Bufo calamita*, *Lacerta agilis* and *Coronella austriaca* in Britain. *British Journal of Herpetology* 5, 763-770.

Beebee, T. J. C. (1980). Historical aspects of British herpetofauna distribution. *British Journal of Herpetology* **6**, 105.

Beebee, T. J. C. (1983). *The Natterjack Toad.* Oxford: University Press.

Beebee, T. J. C. (1988/89). Just a bit more about herp history in Britain. *British Herpetological Society Bulletin,* **26**, 28.

Böhme, G. (1977). Zur bestimmung quartärer Anuran Europas an Hand von Skelettelementen. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematik-Naturwissenschaft* **26**, 283-300.

Duellman, W. E. and Trueb, L. (1987). *Biology of Amphibians* New York: McGraw-Hill.

Estes, R. (1981). *Gymnophiona, Caudata: In, Handbuch der Paläoherpetologie.* Stuttgart and New York: Fischer Verlag.

Frazer, D. (1983). *Reptiles and Amphibians in Britain.* London: Collins.

Godwin, H. (1975). *The History of the British Flora (2nd Edition).* Cambridge: University Press.

Hibbert, F. A., Switsur, V. R. and West, R. G. (1971). Radiocarbon dating of Flandrian pollen zones at Red Moss, Lancashire. *Proceedings of the Royal Society of London B* **177**, 161-171.

Holman, J. A. (1985). Herpetofauna of the Pleistocene fissures near Ightham. Kent. *Herpetological Journal* **1**, 26-32.

Holman, J. A. (1987a). Additional records of British Pleistocene amphibians and reptiles. *British Herpetological Society Bulletin* **19**, 18-20.

Holman, J. A. (1987b). Herpetofauna of the Swanton Morley site (Pleistocene: Ipswichian). Norfolk. *Herpetological Journal* **1**, 199-201.

Holman, J. A. (1987c). Middle Pleistocene herpetological records from interglacial deposits at Sugworth, near Oxford. *British Herpetological Society Bulletin* **21**, 5-7.

Holman, J. A. (1988). Herpetofauna of the Late Devensian/Early Flandrian Cow Cave site, Chudleigh, Devon. *Herpetological Journal* **1**, 214-218.

Holman, J. A. (1989a). Additional herpetological records from the Middle Pleistocene (Cromerian Interglacial) freshwater bed, West Runton, Norfolk. *British Herpetological Society Bulletin* **27**, 9-12.

Holman, J. A. (1989b). Identification of *Bufo calamita* and *Bufo bufo* on the basis of skeletel elements. *British Herpetological Society Bulletin* **29**, 54-55.

Holman, J. A., Clayden, J. D. and Stuart, A. J. (1988). Herpetofauna of the West Runcton Freshwater Bed (Middle Pleistocene: Cromerian Interglacial), West Runcton, Norfolk. *Bulletin of the Geological Society of Norfolk* **38**, 121-136.

Holman, J. A., Stuart, A. J. and Clayden, J. D. (1990). A Middle Pleistocene herpetofauna from Cudmore Grove, Essex, England, and its paleogeographic and paleoclimatic implications. *Journal of Vertebrate Paleontology* **10**, 86-94

Jenyns, L. (1830). Some observations on the habits and character of the natterjack (*Bufo rubeta*). *Transactions of the Cambridge Philosophical Society* **3**, 373-377.

Johnson, R. H., Franks, J. W. and Pollard, J. E. (1970). Some Holocene faunal and floral remains in the Whitemoor meltwater channel at Bosley, East Cheshire. *North Staffordshire Journal of Field Studies* **10**, 65-74.

Newton, A. (1862). On the discovery of ancient remains of *Emys lutaria* in Norfolk. *Annual Magazine of Natural History* **3**, 224-228.

Newton, E. T. (1894). The vertebrate fauna collected by Mr. Lewis Abbott from the fissure near Ightham, Kent. *Quarterly Journal of the Geological Society of London* **50**, 183-204.

Sanchiz, F. B. (1977). La Familia Bufonidae (Amphibia, Anura) en el Tertiario Europea. *Trajabos sobre Neogene-Cuatanario* **8**, 75-111.

Smith, M. A. (1973). *British Amphibians and Reptiles (5th Edition)* London: Collins.

Stuart, A. J. (1982). *Pleistocene Vertebrates in the British Isles.* London and New York: Longman.

Walters, G. J. (1981). Historical aspects of the British herpetofauna distribution. *British Journal of Herpetology* **6**, 177.

West, R. G. (1977). *Pleistocene Geology and Biology: with Especial Reference to the British Isles.* London: Longman.

Wilkinson, D. M. (1988). The Flandrian history of rare herptiles in Britain: A consideration of the hypotheses of Beebee and Yalden. *Herpetological Society Bulletin* **25**, 39-41.

Yalden, D. W. (1980a). An alternative explanation of the distribution of the rare herptiles in Britain. *British Journal of Herpetology* **6**, 37-40.

Yalden, D. W. (1980b). Reply to T. J. C. Beebee. *British Journal of Herpetology* **6**, 105-106.

Yalden, D. W. (1981). Reply to G. J. Walters. *British Journal of Herpetology* **6**, 178.

Yalden, D. W. (1986). The distribution of newts, *Triturus* spp. in the Peak District, England. *Herpetological Journal* **1**, 97-101.