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 *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.

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 FI Ia and FI 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 FI I1 (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.

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 palmette 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.

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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.
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 Trirurus Rafinesque, 1815

On the basis of the modern skeletons that were studied, the British species of Trirurus may be distinguished from one another on the basis of several isolated postcranial elements, including vertebrae, humeri and femora. Trirurus 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 humerus 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 (Frazier, 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...
B. bufo
ilia NCM 143.989 (97-98) (Fig. 4a). Burton, 1978), but tends to prefer more acidic waters than T. vulgaris (Yalden, 1986).

**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 Raffineque, 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 prominence 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 sphenethmoid 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).

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.

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 sphenethroids (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 sphenethroids, 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).
Bufo circle s in dic ate records from 1960 thr ough 1969. Squares 
Rana in dividu als or populations. X’s ind icate in troduc ted 
indic ate hi storic records up to and including 1959. Closed 
Rana Emys orbicu/aris 
sacru m. This fossil ske leton lack s both ilia as well as the 
(vex illum ofBo hme, 
Frazer, 1983. Tria ngles indicate fossil records. Open circle s 
yield ed at le ast two specie s of newt and thr ee spe cies of

Remarks. — The sacra of R. temporaria have their diapophyses more posteriorly directed than those of 
other British and European Rana and the ilial crest 
(Böhme, 1977) of the ilium is quite reduced 
unne cessary to search for previ ous exi stin g 
habi tats in Britain as they do further south in mainl and 
allo wed the rare 

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 distin-

DISSCUSSION

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 

The natt erja ck is distribut ed from Ib eria 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 Bur ton, 1978). The specie s 
exploits a wider range of habitats in southwest Europe, 
where it is also more abundant. Northward and 
and extends 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

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, 
m 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

The natterjack is distributed from Iberia across to 
the explana tion for the rest ricted distribu ti on of 
Brita in’s rare amphibians and reptiles (natterjack toad 
B. calamita, sand lizard Lacerta agilis and smooth

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 
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 

palaeohertpetology in Britain
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 9 km from the coast. In relation to the Ightham fissiles, 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 F1a and F1b 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. Holman). 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 F1 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.

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