

REVIEW:

BRITISH QUATERNARY HERPETOFAUNAS: A HISTORY OF ADAPTATIONS TO
PLEISTOCENE DISRUPTIONS

J. ALAN HOLMAN

Michigan State University Museum, East Lansing, MI 48824, USA

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ABSTRACT

The British Quaternary herpetofauna and the modern one are the products of adaptations to several disruptive patterns. These include mass habitat loss due to glaciation, alternating cold and temperate climates, and the development of seaways isolating the British Islands. Fossil herpetofaunas are now known from all of the Middle and Upper Pleistocene stages (except the Beestonian) and from the Flandrian. The cold stages have yielded only *Rana temporaria*, *Lacerta vivipara* and *Natrix natrix*. The temperate stages have been enriched by exotic continental species including: *Pelobates fuscus*, *Pelodytes punctatus*, *Hyla* sp., *Rana arvalis*, *Rana esculenta* or *ridibunda*, *Rana lessonae*, *Emys orbicularis*, *Elaphe longissima*, and *Natrix maura* or *tessellata*. Middle Pleistocene Cromerian Interglacial faunas collectively have 38.5% exotic species and Middle Pleistocene Hoxnian Interglacial faunas have 46.5% exotic species. Late Pleistocene Ipswichian (Last Interglacial) faunas have 45.5% exotic species. The only exotic species recorded from the Flandrian (Holocene) is *Emys orbicularis*. The modern British amphibian fauna must have been in place early in the Flandrian (Holocene), as five of the six modern species occur at the Whitemoor Channel Site, East Cheshire, 10,000 to 8,500 BP; and there seems no reason to doubt that the modern reptile fauna was also then in place.

INTRODUCTION

The Pleistocene Epoch is characterised by climatic fluctuations and sea level changes brought on by advancing and retreating continental ice sheets over a period that began almost two million years before the present and that ended only about ten thousand years ago. The Pleistocene saw the rise and spread of *Homo sapiens* throughout the world and a great decrease in the mammalian megafauna by the end of the epoch. The Flandrian (Holocene) saw the eventual domination of the world by humans and their factories, crops and domesticated animals.

In Britain the evidence indicates that there were sharp contrasts in climate between glacial and interglacial stages wrought by shifting polar front positions in the North Atlantic (Stuart, 1982). These changes are reflected sharply by some elements of the mammalian fauna where arctic foxes, reindeer, and arctic voles occur during glacial periods; and African lions, African hippos and macaque monkeys occur in the interglacial ones.

For many years, the British Pleistocene herpetofauna has been neglected by vertebrate paleontologists. But in the last decade, interest has revived, and several articles (see references in this paper) have been written about the herpetofaunas of interglacial, and to a lesser extent, glacial sites. The purpose of this paper is to synthesize these works.

Significant Pleistocene faunas in Britain (Stuart, 1982) are mainly restricted to two interglacial stages (Cromerian and Hoxnian) in the Middle Pleistocene and one interglacial (Ipswichian) and one glacial stage (Devensian) in the Upper Pleistocene (Table 1). The Cromerian Middle Pleistocene Interglacial Stage is believed to have begun about 350,000 to 500,000 years before the present (BP) and the Hoxnian Middle Pleistocene Interglacial Stage is thought to have begun about 200,000 to about 250,000 BP.

The Ipswichian Late Pleistocene Interglacial Stage is thought to have begun about 120,000 BP and the Devensian Late Pleistocene Glacial Stage is believed to have begun about 110,000 BP. The Devensian is generally equated with the North American Wisconsinian and is thought to have ended about 10,000 BP.

The Flandrian (Holocene on a Worldwide basis) lasted from about 10,000 BP to the present, and is considered here not to have been part of the Pleistocene. The Flandrian also has significant British vertebrate fossil faunas.

Recently, it has been suggested that some sites yielding vertebrate fossils represent unnamed interglacial stages between the Cromerian and the Anglian and between the Hoxnian and the Ipswichian. Some of these faunas will be noted later.

PLEISTOCENE BARRIERS TO HERPETOLOGICAL
DISPERSAL

Disruptions of British herpetological communities in the Pleistocene include (1) massive glacial ice sheets that obliterated herpetological habitats, (2) alternating cold and temperate climates, and (3) the seaways that formed, isolating the British Islands.

ICE SHEETS

Ice sheets eliminated herpetological habitats in vast portions of Britain during Middle and Upper Pleistocene times. It is believed that the last glacial stage (Devensian) lasted about 100,000 years (110,000 - 10,000 BP), whereas the last interglacial (Ipswichian) lasted only about 10,000 years (120,000 - 110,000 BP) (Stuart, 1982). The chronology of the other glacial and interglacial stages (Table 1) are not well documented.

During the Anglian Glacial Stage, the ice advanced as far south as Finchley, North London, and across to the Severn Estuary leaving only the southern counties as possible



Fig. 1 Approximate distribution of the ice (areas enclosed by broken line) during the time of the Devensian glacial expansion about 18,000 BP. Britain and Ireland appear as they are today. (Modified from Sutcliffe, 1985).

herpetological habitats. During the succeeding Wolstonian glaciation possible herpetological habitats were again greatly restricted, but not to the extent as in the Anglian.

The last significant glaciation of the British Isles occurred in the later part of the Devensian when the ice advanced from about 18,000 to 15,000 BP (Fig. 1). This advance did not move as far south as the preceding ones, and left much of central and southern Britain as possible herpetological habitats.

LOW TEMPERATURES

As ice sheets obliterated herpetological habitats, one would expect that very cold temperatures existed south of the glacial boundaries, and that these low temperatures would have excluded all but the most cold-tolerant amphibians and reptiles.

The northern parts of the seas surrounding the British Isles were completely frozen over during the height of glacial times (Sutcliffe, 1985) and this would diminish the ameliorating climatic effects normally afforded by such large bodies of water.

Tundra vole (*Microtus gregalis*), woolly rhino (*Coelodonta antiquitatus*) and reindeer (*Rangifer tarandus*) occurred during Anglian glacial times and the latter two occurred in the Wolstonian glacial stage. Arctic lemming (*Dicrostonyx torquatus*), tundra vole (*Microtus gregalis*), arctic fox (*Alopex lagopus*), woolly rhino (*Coelodonta antiquitatus*), reindeer (*Rangifer tarandus*), and musk ox (*Ovibos moschatus*) occurred in the Devensian glacial stage (Stuart, 1982). These tundra and arctic mammals attest to the fact that temperatures must have been too low for all but the most cold-tolerant amphibians and reptiles.

SEAWAYS

During most of the Pleistocene the British Isles were connected to the European continent. Sea level changes in the British Late Pleistocene are a subject of some controversy (Stuart, 1982), but it is generally agreed that Britain first separated from Ireland and then from the continent early in the Flandrian (Holocene). The classic idea is that a very depauperate Devensian British herpetofauna became enriched from the continent during a warming trend that began about 10,000 years ago, and lasted until about 8,500 BP. Ireland has a smaller herpetofauna than Britain as a result of having been cut off earlier.

LAST 120,000 YEARS: YEARS BP AT START OF STAGE		STAGE
10,000		Flandrian Postglacial
20,000		Devensian Glacial
30,000		
40,000		
50,000		
60,000		
70,000		
80,000		
90,000		Ipswichian Interglacial
100,000		
110,000		
EARLIER STAGES: YEARS BP AT START OF STAGE		STAGE
?		Wolstonian Glacial
200-250,000		Hoxnian Interglacial
?		Anglian Glacial
350-500,000		Cromerian Interglacial

TABLE I. British Pleistocene Stages Referred to in Text

CHRONOLOGY OF BRITISH PLEISTOCENE HERPETOFAUNAS

The following chronological accounts are based mainly on interpretations made by Stuart (1982) and Kolfshoten, (1985, 1990). These reports indicate that the type section of the Cromerian (first glacial stage of the Middle Pleistocene) at West Runton, Norfolk, is older than the Little Oakley, Essex; Boxgrove, Sussex and Westbury, Somerset, sites and is roughly equivalent to the Sugworth, Berkshire, site. Moreover, it is possible that the Boxgrove and Westbury sites represent an unnamed stage between the "Cromerian" and the following Anglian glacial stage. Moreover, there is the strong possibility that the Stutton/Harkstead, Suffolk and Stoke Tunnel, Suffolk, Ipswichian sites may form a distinct stage from the later Itteringham, Norfolk; Swanton Morely, Norfolk and Shropham, Norfolk, sites.

Figure 2 indicates the most important British Pleistocene localities that have thus far yielded amphibian and/or reptile remains.

MIDDLE PLEISTOCENE SITES

Middle Pleistocene sites and their herpetofaunas are listed in Table 2. Exotic species are preceded by an asterisk (*) there and in the following discussion.

Cromerian Interglacial. Vertebrate faunas are well-known from the Cromerian temperate stage, especially the mammalian components (Stuart, 1982). The West Runton Site in Norfolk and the Westbury-sub-Mendip site in Somerset have especially large vertebrate assemblages (Stuart, 1982; Andrews, 1990).

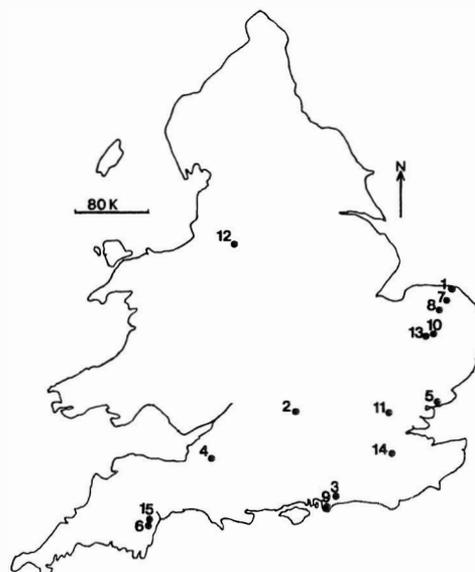


Fig. 2 Major British Pleistocene localities (closed circles) that have yielded fossil amphibians and/or reptiles. CROMERIAN INTERGLACIAL: (1) West Runton, Norfolk; (2) Sugworth, Berkshire; (3) Boxgrove, West Sussex; (4) Westbury-Sub-Mendip Cave, Somerset. HOXNIAN INTERGLACIAL: (5) Cudmore Grove, Essex. WOLSTONIAN GLACIAL: (6) Tornewton Cave, Devon. IPSWICHIAN GLACIAL: (7) Itteringham, Norfolk; (8) Swanton Morley, Norfolk; (9) Selsey, West Sussex; (10) Shropham (I), Norfolk. DEVENSIAN GLACIAL: (10) Shropham (D), Norfolk; (11) Nazeing, Essex. FLANDRIAN (HOLOCENE): (12) Whitmoor Channel, Cheshire; (13) East Wretham, Norfolk; (14) Ightham Fissures, Kent; (15) Cow Cave, Devon.

These faunas represent conditions somewhat warmer than occur in Britain today.

The combined herpetofaunas of the "earlier Cromerian" sites (West Runton and Sugworth) consist of *Triturus vulgaris*, *Bufo bufo*, **Rana esculenta* or *ridibunda*, **Rana arvalis*, *Rana temporaria*, *Anguis fragilis*, *Natrix natrix* and *Vipera berus*. Of the eight identified species, the two exotics form 25% of the combined faunas.

The combined herpetofaunas of the "later Cromerian" sites (Little Oakley, Boxgrove and Westbury) consist of *Triturus vulgaris*, **Pelobates fuscus*, **Pelodytes punctatus*, *Bufo bufo*, **Rana arvalis*, *Rana temporaria*, **Emys orbicularis*, *Anguis fragilis*, *Coronella austriaca* and *Vipera berus*. Of the 10 identified species, the four exotics form 40% of the combined faunas. It is interesting to note that the only British records for the exotic species **Pelobates fuscus* and **Pelodytes punctatus* are from these "later Cromerian" sites, as is the earliest British record of **Emys orbicularis*. Moreover, the earliest record of *Coronella austriaca*, a species occurring only in extreme southern England today, is from Westbury.

A technique used in North America to identify Pleistocene Paleoclimates looks at the closest area to the fossil sites where all of the extant fossil species could be found living together today. This "area of sympatry" concept was mainly developed by C. W. Hibbard in the 1950's. The closest area of sympatry of the Westbury fauna would be at about the Anger area of the Loire Valley in France. This simple method suggests that the Westbury herpetofauna lived in a somewhat warmer climate than did the West Runton one.

Middle Pleistocene	IPSWICHIAN (I) (11 herpetological species, 45.5% exotic)
CROMERIAN (I). (12 herpetological species, 41.7% exotic)	
<i>Triturus vulgaris</i> (1,4) * <i>Pelobates fuscus</i> (4) * <i>Pelodytes punctatus</i> (5) <i>Bufo bufo</i> (1,4) * <i>Rana arvalis</i> (1,2,3,4) * <i>Rana esculenta</i> or <i>ridibunda</i> (1) <i>Rana temporaria</i> (1,4,5) * <i>Emys orbicularis</i> (3,5) <i>Anguis fragilis</i> (1,4,5) <i>Coronella austriaca</i> (5) <i>Natrix natrix</i> (1,2,3,5) <i>Vipera berus</i> (1,5)	<i>Triturus vulgaris</i> (6) * <i>Hyla</i> sp. (3) <i>Bufo calamita</i> (5) <i>Bufo bufo</i> (3,5,6,8). * <i>Rana arvalis</i> (6,8) * <i>Rana esculenta</i> or <i>ridibunda</i> (3) <i>Rana temporaria</i> (3,6,8) <i>Lacerta</i> cf. <i>Lacerta vivipara</i> (6) * <i>Emys orbicularis</i> (1,2,3,4,5,6,7,8) * <i>Natrix maura</i> or <i>tessellata</i> (6) <i>Natrix natrix</i> (3,5,6,8)
Cromerian Herpetological Sites: 1, West Runton, Norfolk (Holman <i>et al.</i> , 1988; Holman, 1989). 2, Sugworth, Berkshire (Stuart, 1980; Holman, 1987c). 3, Little Oakley, Essex (Lister <i>et al.</i> , 1990). 4, Boxgrove, Sussex (Holman, 1992d). 5, Westbury-sub-Mendip, Somerset (Stuart, 1979; Holman, 1992e).	Ipswichian Herpetological Sites: 1, Bobbitshole, Suffolk (Stuart, 1979). 2, Harkstead, Suffolk (Stuart, 1979). 3, Itteringham, Norfolk (Hallock <i>et al.</i> , 1990). 4, Mudesley, Norfolk (Stuart, 1979). 5, Selsey, Sussex (Holman, 1992a). 6, Shropham (I), Norfolk (Holman & Clayden, 1990). 7, Stoke Tunnel, Suffolk (Stuart, 1979). 8, Swanton Morley, Norfolk (Stuart, 1979; Holman, 1987b).
ANGLIAN (G) (indefinite herpetological species, 0.0% exotic)	DEVENSIAN (G) (four herpetological species, 0.0% exotic)
<i>Bufo</i> sp. and/or <i>Rana</i> sp.	"amphibians" (5) <i>Bufo</i> sp. and/or <i>Rana</i> sp. (1) <i>Bufo</i> sp. (2) <i>Rana</i> sp. (2) <i>Rana temporaria</i> (3,4) <i>Lacerta vivipara</i> (2) <i>Natrix natrix</i> (3)
Anglian Herpetological Site: Halls Pit, Oxfordshire (Stuart, 1982).	Devensian Herpetological Sites: 1, Coston, Norfolk (Stuart, 1982). 2, Nazeing, Essex (Stuart, 1982). 3, Shropham (D), Norfolk (Holman, 1992c). 4, Upton Warren, Worcestershire (Stuart, 1982). 5, Wilments Pit, Middlesex (Stuart, 1982).
HOXNIAN (I) (15 herpetological species, 46.7% exotic)	FLANDRIAN (I) (10 herpetological species, 10.0% exotic)
<i>Triturus cristatus</i> (1) <i>Triturus vulgaris</i> (1) * <i>Hyla</i> sp. (1) <i>Bufo bufo</i> (1,2,3) * <i>Rana arvalis</i> (1,3) * <i>Rana esculenta</i> or <i>ridibunda</i> (1) * <i>Rana lessonae</i> (1) <i>Rana temporaria</i> (3) * <i>Emys orbicularis</i> (1,4) <i>Anguis fragilis</i> (1,3) <i>Lacerta</i> sp. (1) * <i>Elaphe longissima</i> (1) * <i>Natrix maura</i> or <i>tessellata</i> (1) <i>Natrix natrix</i> (1,3,4) <i>Vipera berus</i> (1)	<i>Triturus helveticus</i> (5,8) <i>Triturus vulgaris</i> (8) <i>Bufo Bufo</i> (1,2,3,5,6,8) <i>Bufo calamita</i> (2,5,8) <i>Rana temporaria</i> (1,2,3,5,6,7,8) <i>Emys orbicularis</i> (4) <i>Anguis fragilis</i> (2,3,5) <i>Coronella austriaca</i> (5) <i>Natrix natrix</i> (3,5,6) <i>Vipera berus</i> (2,5)
Hoxnian Herpetological Sites. 1, Cudmore Grove, Essex (Holman <i>et al.</i> , 1990). 2, Barnfield Pit, Swanscombe, Kent (Holman, 1987a). 3, Greenlands Pit, Essex (Holman & Clayden, 1988). 4, Ingress Vale, Swanscombe, Kent (Stuart, 1982; Holman, 1987a).	Flandrian Herpetological Sites: 1, Bathford, Somerset (Holman, 1987a). 2, Cow Cave, Devonshire (Holman, 1988). 3, Dog Holes, Lancashire (Holman, 1987a). 4, East Wretham, Norfolk (Stuart, 1979). 5, Ightham Fissures, Kent (Holman, 1985; 1987a). 6, Happaway Cave, Torquay, Devon (Holman, 1987a). 7, Netteswell, Essex (Holman, 1987a). 8, Whitmoor Channel, East Cheshire (Holman & Stuart, 1991).
Upper Pleistocene	
WOLSTONIAN (G) (one herpetological species, 0.0% exotic)	
<i>Bufo</i> sp. and/or <i>Rana</i> sp. (2) <i>Rana temporaria</i> (1)	
Wolstonian Herpetological Sites: 1, Tomewton Cave, Devonshire (Holman, 1990). 2, Waterhall Farm, Hertfordshire (Holman, 1990).	

TABLE 2. The British Pleistocene herpetofauna. * = exotic taxa; I = glacial stage; G = interglacial stage.

 THE NATIVE HERPETOFAUNA IN BRITAIN TODAY (Only *Lacerta agilis* is not known as a British Pleistocene Fossil)

Triturus cristatus
Triturus helveticus
Triturus vulgaris
Bufo bufo
Bufo calamita
Rana temporaria
Lacerta agilis
Lacerta vivipara
Anguis fragilis
Natrix natrix
Coronella austriaca
Vipera berus

TABLE 2. (Continued) The British Pleistocene herpetofauna.

Anglian Glacial. During the Anglian cold-stage, which possibly lasted about 100,000 years (Table 1), the ice advanced well into southern England leaving only a few southern counties as possible herpetological habitat. Vertebrate faunas are not nearly as abundant as in the Cromerian, and consist mainly of mammals, some of which are quite cold-adapted (eg. tundra vole, *Microtus gregalis* and reindeer, *Rangifer tarandus*). Anuran remains were found in association with several mammals (including tundra vole and reindeer) at Hall's Pit near Benson, Oxfordshire; but the amphibian remains were identified only as *Rana* sp. and/or *Bufo* sp. (Stuart, 1982). These are the only recorded herpetological remains from the Anglian as far as I am aware.

The meagre pollen data from Anglian sites indicate unwooded, cold conditions (Stuart, 1982). Therefore, the lack of reptilian remains from the Anglian is not surprising; and it would be expected that many of the herpetological species that occur in the succeeding Hoxnian Interglacial had to invade or re-invade formerly uninhabitable areas.

Hoxnian Interglacial. Fossil vertebrates of the Hoxnian temperate stage have been mainly recovered in the process of archaeological investigations. The Cudmore Grove fauna from Mersea island, Essex, however, is an exception. This fauna contains the only substantial herpetofauna from the Hoxnian and is the most important fossil herpetofauna known from Britain.

Pollen from this site indicates a later part of Stage II (Ho IIIb) which had a mixed oak forest with some late immigrating taxa such as *Carpinus betulus* and *Abies* (Holman, Stuart & Clayden, 1990).

Herpetological taxa identified from the Cudmore Grove site are *Triturus vulgaris*, *Triturus cristatus*, *Hyla* sp., *Bufo bufo*, *Rana arvalis*, *Rana esculenta* or *ridibunda*, *Rana lessonae*, *Emys orbicularis*, *Anguis fragilis*, *Lacerta* sp., *Elaphe longissima*, *Natrix maura* or *tessellata*, *Natrix natrix*, and *Vipera berus*. Of the 14 identified taxa; the seven exotic species form 50% of the fauna, the highest percentage of exotics from any single British Pleistocene herpetofauna known.

Oddly, the nearest area of sympatry for the Cudmore Grove herpetofauna would be in the Trieste area near the

Adriatic Sea. This is because of the combination of the mainly northern modern occurrence of *Rana arvalis* in western Europe with other largely southern species (see maps in Arnold & Burton, 1978).

The Greenlands Pit, Purfleet, Essex, site is the only other Hoxnian site in Britain with more than two herpetological species including *Bufo bufo*, *Rana arvalis*, *Rana temporaria*, *Rana* sp., *Anguis fragilis*, and *Natrix* cf. *natrix*. Allen (1977) pointed out the possibility that the deposit was laid down during another interglacial stage between the Hoxnian and the Ipswichian.

Of the five species identified, the one exotic species forms 20% of the fauna.

UPPER PLEISTOCENE SITES

Wolstonian Glacial. Vertebrate faunas are rather poorly known from the Wolstonian Cold Stage (Stuart, 1982). Evidence indicates that cold climates existed for much of this stage, and that the landscape was treeless and dominated by herbaceous vegetation. Reindeer, horses, mammoths and woolly rhinos have been recovered from Wolstonian sites (Stuart, 1988), but amphibian remains are scarce and no reptile remains have been reported from this stage.

Rana temporaria has been identified from Tornewton Cave, Devonshire, by Holman (1990) and *Bufo* sp. and/or *Rana* sp. have been identified from the Waterhall Farm Site, Hertfordshire (Stuart, 1982; Holman, 1990).

Ipswichian Interglacial. Vertebrate faunas from the Ipswichian/Last Interglacial may actually represent two temperate stages (e.g. Sutcliffe & Kowalski, 1976; contra Stuart, 1976, 1982). Herpetological evidence does little to reflect upon this as only two Ipswichian herpetofaunas are substantial, and both of these appear to represent the same temporal period within the Ipswichian (A. J. Stuart pers. comm.). All eight Ipswichian sites that contain herpetological remains contain the exotic European pond tortoise, *Emys orbicularis*. This species is important as it indicates a somewhat warmer summer climate than occurs in Britain today (Stuart, 1979, 1982).

The two substantial Ipswichian herpetofaunas are the Itteringham Site, Norfolk, and the Shropham Site, Norfolk. The combined herpetofaunas of these sites (considered to represent the same temporal stage of the Ipswichian, as presently conceived) include *Triturus vulgaris*, *Hyla* sp., *Bufo bufo*, *Rana arvalis*, *Rana esculenta* or *ridibunda*, *Rana temporaria*, *Emys orbicularis*, *Lacerta* cf. *L. vivipara*, *Natrix maura* or *tessellata* and *Natrix natrix*.

Of the 10 identified taxa, the five exotic species form 50% of the fauna, the same percentage as in the rich Hoxnian Cudmore Grove herpetofauna. But the closest area of modern sympatry would be in the eastern Baltic countries (see maps in Arnold & Burton, 1978).

Of additional Ipswichian interest is the natterjack toad, *Bufo calamita*, from the Selsey, Sussex Site (Holman, 1992a), as this is the earliest fossil record in Britain of this presently endangered species.

Devensian Glacial. The Devensian Cold Stage/Last Glacial is a critical unit of time to consider with respect to the depauperate nature of the modern British herpetofauna. The preceding Ipswichian Interglacial with its temperate herpetofauna consisting of about 46% exotic species (Table 2) lasted about 10,000 years. The Devensian that followed lasted about 100,000 years and had cold, sometimes savage, climates. Moreover, for most of the Devensian, a mixed savanna/tundra type flora occurred in the non-glaciated areas of Britain. There is no modern analog for this vegetation.

Vertebrate faunas are more abundant in the Devensian than in any other British Pleistocene cold stage and in general, mammalian faunas are well represented. But as might be expected, the few herpetological species recorded are cold-tolerant ones that today are able to adjust to conditions within or near the arctic circle (Holman, 1990).

The North American Wisconsinian glacial stage is temporally equivalent to the Devensian (Sutcliffe, 1985). During the Wisconsinian, especially during the last 25,000 years, disharmonious vertebrate communities with no modern analogs existed south of proglacial regions (Lundelius *et al.*, 1983). These communities consisted of mixtures of "northern" and "southern" species and they existed in the equable climates that occurred in these regions.

The model that was proposed to explain these mixed faunas was that many species forced southward by advancing glaciation were able to mix with the resident faunas because of the cool summer climates that occurred as part of the equable climates of the region. Thus, North America and Britain were very different in the problems confronting their respective vertebrate faunas. North America had a vast southern refugium where climates were equable and with summers that were cool enough to accommodate many species of northern immigrants and from which herpetological species could re-invade formerly glaciated area (Holman, 1992*b*). Britain's reinvasions however, came from a cool continental western Europe which was cut off from any large warm refugia by mountains.

Flandrian (Holocene on a Worldwide Basis). As the Flandrian climate warmed, the modern British herpetofauna plus *Emys orbicularis* reinvaded areas from which they were previously displaced by glaciers, cold climates and inhospitable ecological communities. The earlier separation of Ireland left it with a very depauperate herpetofauna. The later separation of Britain from the continent allowed it to accumulate a less depauperate herpetofauna of at least 13 species (counting the now absent *Emys orbicularis*).

Unfortunately there is poor stratigraphic control in most Flandrian herpetological sites because so many of them are from unstratified caves or fissures. The largest Flandrian herpetofauna comes from the Ightham Fissures Site near Sevenoaks, Kent and includes eight species: *Triturus helveticus*, *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Anguis fragilis*, *Coronella austriaca*, *Natrix natrix*, and *Vipera berus*. Holman (1985) postulated that this site might represent a time in the early Flandrian when the climate of Britain had become about as warm as it is today. But Stuart (in Holman & Stuart, 1991) cautions that the Ightham site could represent any time within the Flandrian from 10,000 years ago to a few hundred years ago.

Only two sites within the Flandrian have precise pollen dates. The first, the Whitmore Channel Early Flandrian site

near Bosley, East Cheshire, representing a period of 10,000 to 8,800 years BP (Holman & Stuart, 1991); contained five of the six native amphibian species *Triturus vulgaris*, *Triturus helveticus*, *Bufo calamita*, *Bufo bufo*, and *Rana temporaria*. This indicates that the modern amphibian fauna was in place in Britain early in the Flandrian, and there seems no reason to doubt that the modern reptile fauna was also then in place.

The second site, East Wretham, Norfolk, contains the only record of the European pond tortoise, *Emys orbicularis*, from the Flandrian of Britain. This site was pollen-dated to a warm period within the middle part of the Flandrian (Zone VIIa, F1 11d, Stuart, 1982).

SUMMARY

The modern British herpetofauna (Table 2) intimately reflects the Quarternary glaciology, climatology, ecology and geography of what is now the British Isles. The modern herpetofauna of Britain is clearly derived from adjacent areas in northwestern Europe. But during interglacial stages of the Pleistocene, several exotic continental species took advantage of somewhat warmer temperatures than occur in Britain today.

Until early in the Flandrian (Holocene) Britain and Ireland were connected to the European continent. From time to time in previous Pleistocene stages, ice sheets thrust southward over what are now these islands. The glaciers obliterated herpetological habitats. Moreover, cold climates and disturbed communities occurred in the proglacial areas. During these times only three species have been recorded in Britain, two of which (*Rana temporaria* and *Lacerta vivipara*) are probably the most cold-tolerant ones that exist in Europe today.

During the interglacial stages when the glaciers withdrew and climates became as warm or warmer than today, herpetological species reinvaded Britain and Ireland, presumably mainly from limited western European refugia north of the Pyrenees and Alps. Amongst these invaders were continental species that do not occur as natives in Britain today. These exotics (Table 2) are: *Pelobates fuscus*, *Pelodytes punctatus*, *Hyla* sp., *Rana arvalis*, *Rana esculenta* or *ridibunda*, *Rana lessonae*, *Emys orbicularis*, *Elaphe longissima*, and *Natrix maura* or *tessellata*. Of these forms, *Pelodytes punctatus*, *Elaphe longissima*, and *Natrix maura/tessellata* occur wholly south of the British Islands today; and with the exception of *Rana arvalis*, the others occur mainly south of Great Britain (Arnold & Burton, 1978).

The Cudmore Grove, Essex, fauna of the Hoxnian Interglacial Stage had the richest and most exotic Pleistocene herpetofauna in Great Britain with 14 species, half of which were exotic.

Ireland was cut off from the mainland first, and has a very depauperate modern herpetofauna of at most four species. Britain was cut off later, and its 12 modern species (Table 2) are several fewer than in adjacent continental areas.

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