

## HERPETOFAUNA OF THE LATE PLEISTOCENE FISSURES NEAR IGHTHAM, KENT

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### ABSTRACT

The late Pleistocene fissure deposits near Ightham, Kent, have yielded the remains of *Triturus* sp., *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Anguis fragilis*, *Natrix natrix*, *Coronella austriaca*, and *Vipera berus*. These are the first British fossil records of the British endangered species *Bufo calamita* and *Coronella austriaca*, and the first record of any kind of *Coronella austriaca* from Kent. *Rana temporaria* comprises 87 per cent of the minimum number of individuals of the fossil fauna. It is postulated that the fossil amphibians and reptiles accumulated during the early Flandrian Stage when the temperature first became as warm as it is in southern England today.

### INTRODUCTION

The fossiliferous fissures near Ightham, Sevenoaks Area, Kent, have yielded the largest Pleistocene herpetofauna thus far recorded from the British Isles. This paper details that fauna which provides the first British fossil records of *Bufo calamita* and *Coronella austriaca*.

E. T. Newton (1894) published on the vertebrate fauna collected by Lewis Abbott from the Ightham fissures. Among these vertebrate remains were quantities of anuran bones and some reptile elements. Newton (1894, pp. 189-190 and Plate 10) provided a short annotated list of the herpetological remains, and figured a few specimens. Abbott (1894) provided a detailed account of the fissures of SE England, a history of the Shode Valley where the Ightham fissures occur, and a specific geological description of the fissures that yielded the fossils. He also discussed the fossil plants and invertebrates found at the site. Stuart (1982) indicates concisely the status of the Ightham fissure deposits in his discussion of British cave and fissure Pleistocene vertebrate faunas as follows. "Few British examples have been described but the Ightham Fissures, near Sevenoaks, Kent, in Upper Greensand (Cretaceous), have yielded a rich late-Pleistocene fauna (Newton, 1894). It is now generally recognized that these deposits represent a considerable period of Devensian and Flandrian time". I shall comment on the possible age of the deposit based upon the herpetofauna in the discussion section of the present paper.

With the kind help of Dr. Angela Milner and Ms Sandra Graham of the Department of Palaeontology of the British Museum (Natural History), I was given the privilege of studying the Ightham Fissures herpetological fossils. These fossils came from three sources: (1) materials presented by Mr. Lewis Abbott, (2) materials from the Lewis Abbott collection presented by Sir H. H. Howorth in 1920, and (3)

collections acquired from Mr. F. Corner in 1916.

It became immediately clear that these collections were in need of re-study as certain species were unidentified and certain misidentifications had been made. Characters supplementing those given by E. T. Newton (1894) for the identification of British Pleistocene amphibians and reptiles are given in the present paper, and presence in the fauna of *Bufo calamita* and *Coronella austriaca*, previously unrecognized is documented.

### SYSTEMATIC PALAEOLOGY

In the following section, minimum numbers of individuals of each species are based either on the largest number of either non-paired elements or of right or left elements. For instance, if a species was represented by six skulls, and by four left and three right humeri, the minimum number of individuals would be six. If a species was represented by six skulls, and seven left and six right humeri, the minimum number of individuals would be seven. When fossils were in distinctly separate lots, as in *Triturus* below, each lot was counted as at least one individual.

Class Amphibia

Order Caudata

Family Salamandridae

*Triturus* sp.

*Identifiable material* — Lewis Abbott Collection: BM(NH) R-4735, a skull and an attached string of vertebrae; R-4736, 18 vertebrate and two fragmentary limbs. F. Corner Collection: BM(NH) R-10164, three vertebrae.

These three lots represent a minimum number of three individuals.

*Remarks* — This genus was reported by E. T. Newton (1894). The genus is osteologically different from other European caudates, but unfortunately there is not enough comparative material available at

the present time to determine what species is represented. Since specimen R-4735 has a nearly complete skull, it is possible that a specific determination may be made in the future. All three species of British newts, *Triturus cristatus*, *T. helveticus*, and *T. vulgaris* have been reported from the general area in modern times (Frazer, 1983, Figs. 27, 31, and 32).

#### Order Salientia

Since 1955 I have been impressed with the value of the ilium as the single best element upon which to base identifications when only disarticulated individual bones are available in the fossil record. The osteological structure of the ilium, and to a lesser extent the structure of the sacrum, reflects the mode of locomotion of the animals. Long-leaping anurans, hopping anurans, running or dashing anurans, walking anurans, climbing anurans, and burrowing ones all have different ilial structure, especially in the posterior part of the bone where the great ligaments attach. Convergence of these characters in different anuran families is not only of great interest, but might cause serious problems in the identification of early Tertiary anurans, but in late Pleistocene faunas, this has not been the case.

There are several thousand anuran bones from the Ightham Fissures, most of which are isolated postcranial elements. Among these postcranial

*Remarks* — The ilia of *Bufo bufo* and *Bufo calamita* are readily distinguishable (Fig. 1). As indicated by Frazer (1983) *Bufo bufo* is a hopping toad, whereas *Bufo calamita* is a running toad capable of making mouse-like dashes. This apparently is reflected in the ilia of the two species, especially in the posterior portion of the bone. *Bufo bufo* has a low, rounded ilial prominence that develops a roughened protuberance on it in older individuals (Fig. 1a, b). *Bufo calamita* on the other hand has a distinctive triangular ilial prominence that never develops a protuberance (Fig. 1c). *Bufo bufo* is a relatively common species in the general area today (Frazer, 1983, Fig. 18).

#### *Bufo calamita* Laurenti

*Identifiable material* — Lewis Abbott Collection: BM(NH) R-4730, one left ilium; R-10173, four left and six right ilia; R-10176, five left and six right ilia.

This is a minimum number of 12 *Bufo calamita* from the Ightham Fissures.

*Remarks* — Specimen R-4730 was figured and discussed by E. T. Newton (1894, Plate 10, Fig. 4) as *Bufo bufo*. The figure inadequately shows the triangular ilial prominence that distinguishes *B. calamita* readily from *Bufo bufo* which has a rounded, sometimes somewhat roughened ilial prominence as discussed in the previous section. The natterjack has not been recorded in Kent since 1960

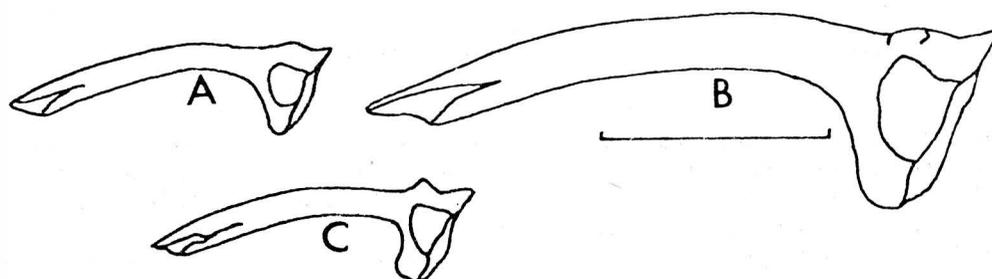


Fig. 1 Left ilia of A, young *Bufo bufo*, B, large adult *Bufo bufo*, C, adult *Bufo calamita* in lateral view. The line equals 20 mm.

elements are several hundred ilia that I believe may be identified to species with confidence in most cases. Other elements are so difficult to identify that they have been left in the category to which they were originally referred which was "*Rana-Bufo*".

#### Family Bufonidae

##### *Bufo bufo* Laurenti

*Identifiable material* — Lewis Abbott Collection: BM(NH) R-10170, one right ilium; R-10174, five left and four right ilia; R-10175, two left and four right ilia. F. Corner Collection: BM(NH) R-10171, four left and two right ilia.

This is a total minimum number of 12 individuals of *Bufo bufo* from the Ightham Fissures collections.

(Frazer, 1983, Fig. 22) and there are only two of these pre-1960 records.

#### Family Ranidae

##### *Rana temporaria* Linnaeus

*Identifiable material* — Lewis Abbott Collection: BM(NH) R-2920, three left and one right ilia; R-4731, one left ilium; R-10177, two left ilia; R-10178, 350 left and 383 right ilia. F. Corner Collection: BM(NH) R-10179, seven left and seven right ilia.

This is a minimum number of 391 individuals of *Rana temporaria* from the Ightham Fissures.

*Remarks* — Specimen R-4731, a left ilium, was correctly figured as *Rana temporaria* by E. T. Newton (1894, Plate 10, Fig. 1a, 2, and 3). The genus *Rana* may

be separated from the genus *Bufo* on the basis of the presence of an ilial blade (vexillum of Böhme, 1982) in *Rana* and its absence in *Bufo* (compare Figs. 1 and 2 of the present paper). The ilial blade in *Rana temporaria* appears to differ from European and American *Rana* in having an ilial blade that is depressed anteriorly

osteoderms, some with ribs attached; R-8931, an almost complete individual fine enough for a museum exhibit specimen; R-8932, four skull fragments, one left dentary, one pectoral girdle fragment, 38 vertebrae, a mass of osteoderms, and 27 single osteoderms, R-10163, 17 vertebrae and one rib, R-

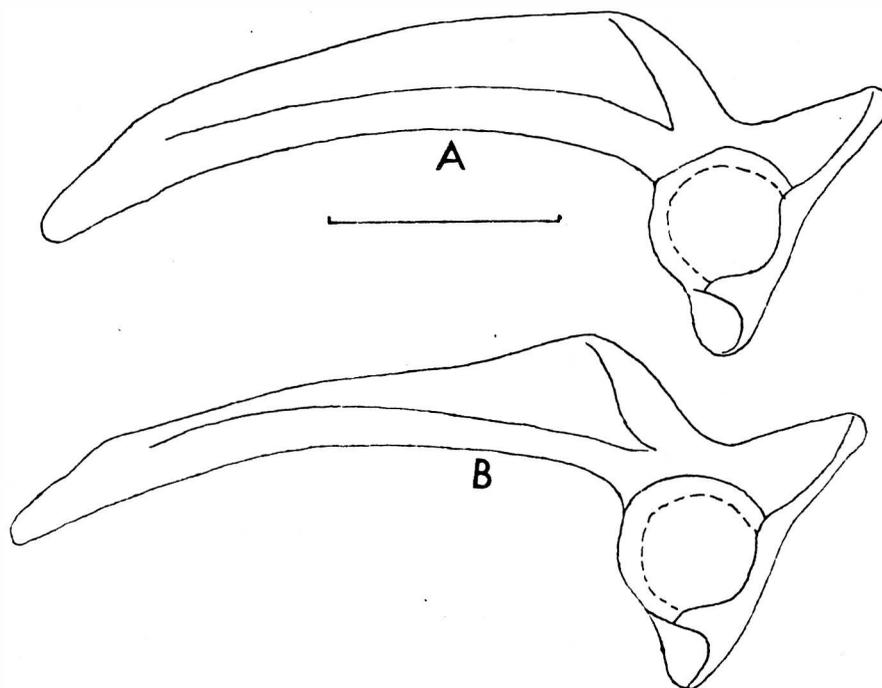


Fig. 2. Left ilia of A, *Rana esculenta*, B, *Rana temporaria* in lateral view. The line equals 10 mm.

(Fig. 2). Based on this character, all of the Ightham ilia appear to represent the common British frog *Rana temporaria*. *Rana temporaria* is quite easily distinguished from *Rana esculenta* which has a fully-developed ilial blade (Fig. 2). *Rana temporaria* occurs in the area today (Frazer, 1983, Fig. 12).

Class Reptilia

Order Squamata

Family Anguidae

*Anguis fragilis* Linnaeus

*Identifiable material* — Lewis Abbott Collection: BM(NH) R-10169, one left compound bone (posterior mandible), two left dentaries, eight vertebrae, five ribs, and a mass of osteoderms; R-4728, one body whorl of fused osteoderms and two single osteoderms; R-4734, two skull fragments, seven frontoparietals, 10 left and eight right compound bones, seven left and seven right dentaries, 429 vertebrae, 44 ribs, and five single osteoderms; R-10166, 2 caudal vertebrae; R-10167, six vertebrae and three ribs; R-10168, posterior section of skull. This is a minimum number of 11 slow worms in the L. Abbott Collection. F. Corner Collection: BM(NH) R-8929, fused mass of vertebrae, ribs, and osteoderms, R-8930, one posterior skull fragment, 59 vertebrae, and 10 masses of fused

10165, a mass of fused material consisting of at least three individuals based on three discernible left dentaries in the mass. This appears to be a minimum number of eight individuals in the F. Corner Collection.

A total minimum number of 19 slow worms is then represented in the Ightham Fissures material.

*Remarks* — *Anguis fragilis* skeletal elements, including skull bones, lower jaw bones, vertebrae, osteoderms, and even ribs are easily distinguishable from other British and European reptiles, mainly due to modifications for a limbless, fossorial condition. Smith (1973, Fig. 58) provides an illustration of an *Anguis fragilis* skull in three views, and another illustration (Fig. 57) of *Anguis fragilis* mid-caudal vertebrae compared to those of *Lacerta vivipara*.

Comparison of the Ightham fossils with four specimens from the Oxford University Museum and one from the Michigan State University Museum showed no trenchant differences. Nevertheless, one large lower jaw from BM(NH) R-4734 had a total length of 22.9 mm. This represents a much larger jaw than the largest Oxford specimen which had this measurement 17.0 mm, and came from an animal that was 290 mm in total length. Smith (1973) provides a measurement of a specimen of a slow worm from Kent which was the second largest he had seen in Britain,

and this specimen had a total length of 400 mm. Thus, by projection of relative proportions, the fossil probably was as large or larger than Smith's Kent animal.

Of possible taphonomic interest, I believe, is the fact that skeletal elements of *Coronella austriaca* were found associated with *Anguis fragilis* R-10166 and 10167 in the Abbott Collection and with R-8929 in the Corner Collection. Frazer (1983) states that *Coronella austriaca* feeds upon *A. fragilis* and provides an illustration of a smooth snake constricting a slow worm. Could the mass condition of much of the slow worm material at the Ightham Fissures be related to their having been stomach contents of smooth snakes?

#### Family Colubridae

##### *Coronella austriaca* Laurenti

*Identifiable material* — Lewis Abbott Collection: BM(NH) R-10159, one trunk vertebra; R-10160, 11 trunk vertebrae; R-10161, 11 trunk vertebrae; R-10162, two trunk vertebrae. F. Corner Collection: BM(NH) R-10158, right dentary; R-10156, one vertebra; R-10157, one vertebra. A minimum number of at least two individuals of smooth snake are represented at the Ightham Fissures.

*Remarks* — These vertebrae were found in boxes labelled *Anguis fragilis*, *Natrix natrix*, and *Vipera berus*. The trunk vertebrae of *Coronella austriaca* are quite

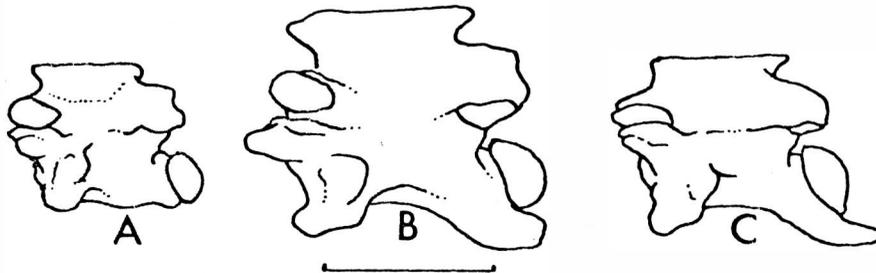


Fig. 3. Trunk vertebrae of A. *Coronella austriaca*, B. *Natrix natrix*, C. *Vipera berus* in lateral view. Modified from Szyndlar (1984). The line equals 4 mm.

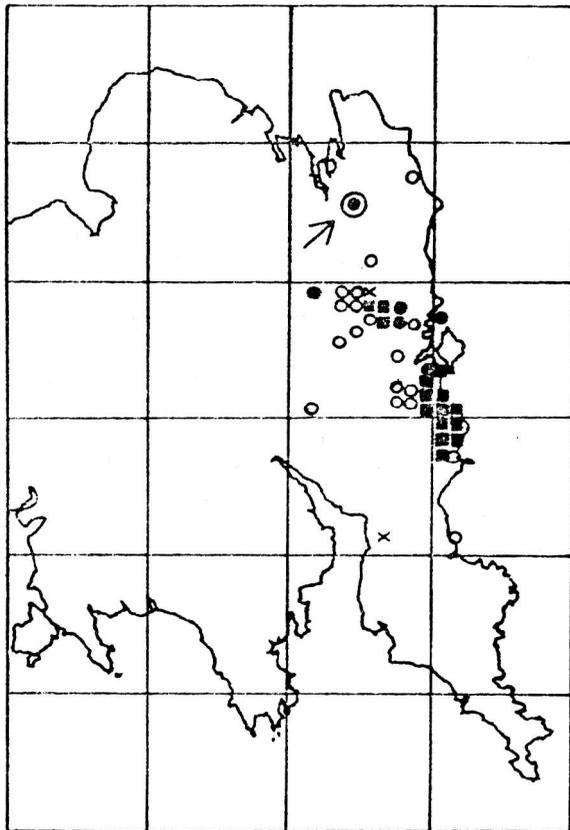


Fig. 4. Modern distribution of *Coronella austriaca* redrawn from Frazer (1983) and fossil distribution of this species from Ightham, Kent (dot surrounded by circle and indicated by arrow). Modern distribution symbols: open dot, up to and including 1959; closed dot, 1960-69 inclusive; closed squared, 1970 to present; X, introduction.

distinctive, especially from *Natrix natrix* and *Vipera berus* (Fig. 3) and also from snakes that occur on the European Continent today (Szyndlar, 1984). It is notable that *Coronella austriaca* trunk vertebrae have some characters in common with some New World colubrids of the Subfamily Xenodontinae, yet they are included in the colubrid family Colubrinae by Dowling and Duellman (1978). These possibly parallel vertebral characters include the broad haemal keel and depressed neural arch of *Coronella*. A combination of definitive characters for the trunk vertebrae of *Coronella* include (1) the lack of hypapophyses (immediately separating them from *Natrix natrix* and *Vipera berus*, Fig. 3), (2) a non-distinct, broad, haemal keel, (3) a low but not obsolete neural spine, and (4) a depressed neural arch.

The dentary of *C. austriaca* also appears to be distinctive, at least when compared with those of *Natrix natrix* and *Vipera berus* (figures of skulls of *Vipera berus* and *Coronella austriaca* are provided by Smith, 1973, Figs. 67 and 78). The Ightham fossil had a total of 27 tooth and alveolar spaces, with the posterior teeth being shorter and stouter than the anterior teeth. *Natrix natrix* appears to have fewer teeth and alveolar spaces (19 in an uncatalogued Oxford University Museum specimen), and all of the teeth almost equally long and slender.

The smooth snake, as far as I can determine, has never been recorded as a fossil in Britain, and has never been reported from Kent during prehistoric or historic times (Frazer, 1983, Fig. 44). If *Coronella austriaca* bones are present in other British Pleistocene fossil collections, it will be interesting to discover whether the species ever occurred outside of southern England, especially during interglacial stages.

The nearest modern records of *Coronella austriaca* to Ightham, Kent, are from Sussex and Surrey (Fig. 4). Data for this figure are from Frazer (1983).

*Natrix natrix* (Linnaeus)

*Identifiable material* — Lewis Abbott Collection: BM(NH) R-4732, posterior part of skull, one occipital complex, three fragmentary skull pieces, two pterygoids, six left and two right compound bones (posterior mandibles), one left and three right dentaries, 126 vertebrae, and one rib; R-2919, six vertebrae. F. Corner Collection: BM(NH) R-10153, 26 vertebrae; R-10155, one right dentary, and 145 vertebrae, two of which are pathologically fused.

There is a minimum number of two grass snakes from the Ightham Fissures.

*Remarks* — Most vertebrae of *Natrix natrix* may be distinguished from most vertebrae of *Vipera berus*. *Natrix natrix* has higher neural spines that are more concave anteriorly (in lateral view) than in *Vipera berus*; and *N. natrix* usually has a much less pointed hypapophysis than in *Vipera berus* (Fig. 3). *Natrix natrix* appears vertebrally separable from *Natrix tessellata* on the basis of the rounded rather than the truncated hypapophysis in *N. natrix* and on the much less gracile parapophyseal processes in *N. natrix* (Szyndlar, 1984). It has previously been pointed out that *Natrix natrix* trunk vertebrae may be separated from those of *Coronella austriaca* on the basis of the lack of hypapophyses in *C. austriaca*.

The compound bone (posterior mandible) of *Natrix natrix* appears to be readily distinguishable from that of *Vipera berus*. E. T. Newton (1894) gives these characters so clearly that I quote them here. "The hinder two-thirds of a mandibular ramus is referred to this species (*Vipera berus*), it agrees with the corresponding part of the viper in being anteriorly slender and rounded, deep in the coronoid region, and strongly curved from end to end. The common snake (*Natrix natrix*) has the ramus of the lower jaw less curved, stouter throughout, and not especially deep in the coronoid region".

*Natrix natrix* occurs in the general area today (Frazer, 1983, Fig. 43).

Family Viperidae

*Vipera berus* (Linnaeus)

*Identifiable material* — Lewis Abbott Collection: BM(NH) R-4729, left compound bone (posterior mandible) figured by E. T. Newton (1894, Plate 10, Fig. 18), R-4733, 53 vertebrae and one dentary bone. This is a minimum of two individuals based on the fact that the two above lots appear distinctive.

*Remarks* — Characters for distinguishing the vertebrae and compound bones of *Vipera berus* from other British snakes have been given in previous sections. Based on a single specimen of *Vipera ursini* (Michigan State University H432), it would appear that *V. berus* may have a somewhat higher neural spine. Szyndlar (1984) discusses further useful osteological characters of *Vipera berus*.

*Vipera berus* occurs in the general vicinity of the fossil site today (Frazer, 1983, Fig. 41).

DISCUSSION

The Ightham Fissures near Sevenoaks, Kent, have yielded the largest Pleistocene herpetofauna thus far reported from the British Isles. At least four species of amphibians and four species of reptiles are represented, and as Dr. A. S. Cooke has indicated (personal communication), it would be unusual to find as many forms in a single site anywhere in Britain today. Fig. 5 indicates the minimum number of individuals of each species represented. These numbers may be somewhat misleading as I believe that the absence of lacertids and the rarity of newts may be a reflection of the very small size of the individual bones of these forms. These tiny elements may have escaped detection by the early collectors, or they may have slipped through the collecting screens during the washing process. On the other hand, the large number of *Rana temporaria* bones compared with those of the two *Bufo* species, could be a reflection of their relative abundance at the time.

MINIMUM NUMBER OF INDIVIDUALS OF HERPETOLOGICAL SPECIES OF THE LATE PLEISTOCENE OF IGHTHAM, KENT

<u>Triturus</u> sp.	3
<u>Bufo bufo</u>	12
<u>Bufo calamita</u>	12
<u>Rana temporaria</u>	391
<u>Anguis fragilis</u>	19
<u>Natrix natrix</u>	8
<u>Coronella austriaca</u>	2
<u>Vipera berus</u>	2

Fig. 5. Minimum number of individuals of herpetological species from the late Pleistocene of Ightham Fissures, Kent.

The herpetofauna may bear importantly on the age of the deposit. As previously stated, the Ightham Fissures have been believed to represent a considerable amount of Devensian (last glacial stage) and Flandrian (10,000 year before present onward) time. Since the Ightham Fissures herpetofauna indicates as moderate a climate as would be expected in southeastern England today, one may rule out any full glacial time, at least during the slot represented by the herpetological fossils. However as pointed out by Stuart (1982), the Devensian was a long, complex, multicyclic stage, lasting from 50,000 to 10,000 years ago; hence just calling the Devensian a "cold stage" is probably an oversimplification. It is not beyond possibility that the herpetological fossils could represent some warming trend in the Devensian, but this would seem a less parsimonious choice than the following one.

It is believed that between about 10,600 and 10,100 years ago southern Britain had a Tundra vegetation, a periglacial climate, and an arctic fauna (Pennington, 1977; Coope, 1977). There appears to have been a warming trend after 10,100 years before present, so that by 9500 years ago southern England had a climate at least as warm as today (Coope, 1977; Osborne, 1974). During this warming trend the open Tundra vegetation was replaced by open birch scrub between about 9700 to 8700 years ago (Hibbert *et al.* 1971). After this came hazel scrub (8700-8100 years before present), then a hazel and pine mixture (8100-7100 years before present), and then deciduous forest (oak, elm, alder, hazel) from 7100-5000 years before present.

Based upon the preservation and apparent mineralization of the fossils, and on the basis of the occurrence of several extinct mammals from the same fissures at Ightham (E. T. Newton, 1894), I would venture a guess that the herpetofauna lived in early Flandrian times, probably around 9500 years ago when the temperature was as warm as it is in southern England today (Fig. 6).

BRITISH LATE PLEISTOCENE STAGES		POSTULATED CLIMATE	IGHTHAM, KENT, FISSURE SITE
FLANDRIAN		TEMPERATE	●
DEVENSIAN	LATE		
	MIDDLE	COLD	
	EARLY		
IPSWICHIAN		TEMPERATE	
WOLSTONIAN		COLD	

Fig. 6. Postulated time of occurrence (closed circle) of Ightham, Kent, Pleistocene herpetofauna.

It is certainly beyond the scope of this paper, which is mainly a preliminary faunal listing, to go into a detailed discussion of the palaeoecology of *Bufo calamita* and *Coronella austriaca*. Nevertheless, I have studied the herpetological collections at the British Museum (Natural History) from the temperate early middle Pleistocene Cromerian Stage from West Runton in Norfolk, and neither *Bufo calamita* nor

*Coronella austriaca* were present. *Bufo bufo*, *Rana temporaria*, *Natrix natrix*, and *Vipera berus*, however, were not uncommon. It may be that *Coronella austriaca* has never occurred outside of southern England, but that before the intensive alteration of natural habitats by humans it had a wider distribution in the southern part of the country.

What would the prehistoric habitat of *Bufo calamita* and *Coronella austriaca* have been like at Ightham, Kent? It is difficult to define the exact environment of the area during the time of the deposition of the bones, as the exact age of the site is hypothetical, and thus the composition of the surrounding vegetation can only be guessed. Nevertheless, it seems certain that the topography of the Kentish Rag of the Valley of the Shode where the fossils came from (E. T. Newton, 1894) was quite irregular and with numerous ledges and fissures.

One of the most interesting aspects of the late Pleistocene amphibian and reptile fauna in North America south of the glacial boundaries (Lundelius *et al.* 1983; Fay, 1984; Holman, 1985) is that although there was a widespread extinction of large mammalian species at the end of the Wisconsin Stage about 10,000 years ago; that taxonomically the herpetofauna essentially remained unchanged into the present. It is then noteworthy that in the first large late Pleistocene British herpetofauna documented, that this also appears to be the case. One may speculate then, that whatever biological attributes these poikilothermic animals had, that they allowed them to be more fit than the large mammals to withstand the marked changes (Stuart, 1982, p. 139) that characterized the Flandrian Stage.

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## SEASONAL CHANGES IN METABOLISM OF THE LIZARD *LACERTA VIVIPARA*

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### ABSTRACT

Acute oxygen consumption determinations for both adults and sub-adults of *L. vivipara* were made over the temperature range 5-30°C during summer and winter. During winter dormancy, both adults and sub-adults were found to have a metabolic rate lower than the metabolic rate of summer animals at each experimental temperature. This reduction of oxygen consumption in winter lizards can be interpreted as an "inverse compensation" (Precht's Type 5 pattern of response). It is concluded that this adjustment can reduce energy costs during the winter period and is a pre-requisite for survival during winter dormancy.

### INTRODUCTION

Some reptiles have evolved a number of ways by which they can tolerate low winter temperatures. For example, some species of reptiles which inhabit cool, temperate zones and high altitudes have low critical minimum temperatures, compared to their summer critical minimum temperature (Spellerberg, 1976). Instantaneous shifts in the metabolic rate-temperature curves (Aleksiuk, 1971; 1976a) of cool-temperature

species has been reported to be an adaptation to winter conditions. Many reptiles raise their metabolic rate after exposure to low temperature acclimation (Bennett and Dawson, 1976). In addition, a depression of body temperature below freezing point without internal ice formation, has been observed in few species (Lowe *et al*, 1971).

Winter dormancy in ectotherms has sometimes been called "brumation" to distinguish it from hibernation in endotherms, but it has not found universal