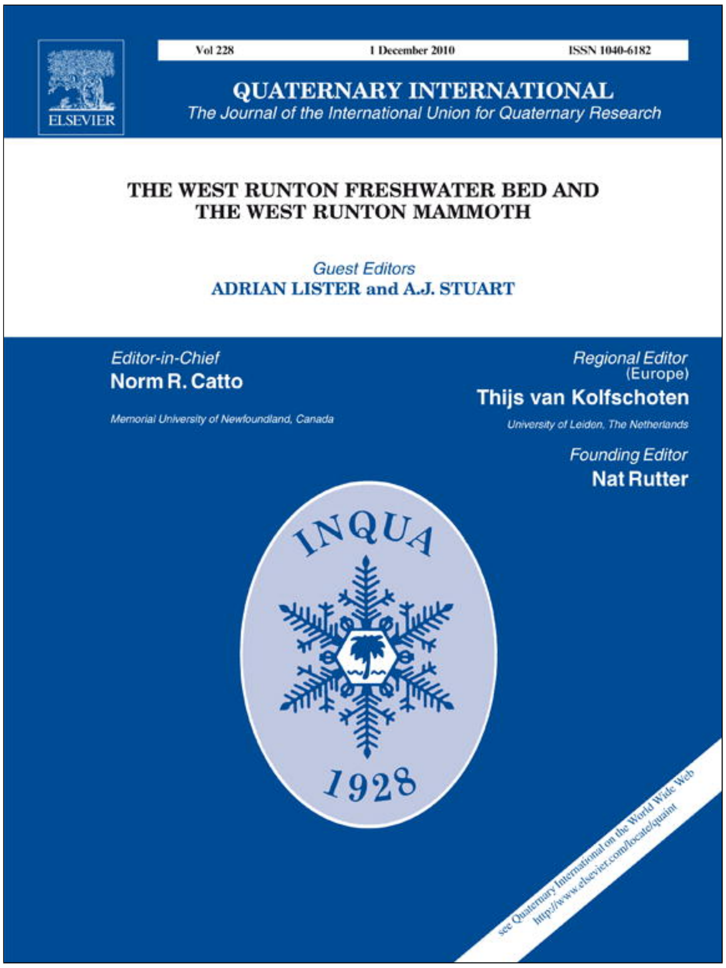
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Ectothermic vertebrates, climate and environment of the West Runton Freshwater Bed (early Middle Pleistocene, Cromerian)

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ABSTRACT

The ectothermic vertebrate fauna from the early Middle Pleistocene West Runton Freshwater Bed (WRFB; England, Norfolk) comprises 21 species (10 fishes, 8 amphibians and 3 reptiles). All recorded species are referred to recent forms, except a large newt (*Triturus* sp. nov.) probably belonging to the *Triturus cristatus* group, and an indeterminate colubroid snake showing viperid affinities. This indicates that the Cromerian herpetofauna of the British Isles is more diverse than previously thought and contains extinct species. Two fish species are new for the WRFB: the white bream (*Abramis bjoerkna*), and the ide (*Leuciscus* cf. *idus*). Based on the faunal composition the aquatic ecosystem can be reconstructed as a densely vegetated, large eutrophic freshwater body, representing a slow-flowing river or oxbow lake. The terrestrial ecosystem in the surrounding area represents moist woodland habitats. There are no indications of open landscapes in the immediate vicinity. The estimated palaeoclimatological parameters indicate similar summer temperatures to today (16–17 °C), probably cooler winters (−6 to −1.4 °C) and mean annual temperatures (6–8 °C), and significantly higher mean annual precipitation compared to present-day conditions.

1. Introduction

The Cromer Forest-bed Formation (CF-bF), comprising a complex and spatially varied sequence of freshwater and marine sediments, is exposed at intervals beneath Middle Pleistocene glaciogenic deposits (tills and outwash) in the cliffs and foreshore along the North Sea coast of northeast Norfolk and northeast Suffolk (West, 1980; Preece and Parfitt, 2000; Stuart and Lister, 2010a; Gibbard et al., 2010).

The CF-bF includes the West Runton Freshwater Bed (WRFB), the stratotype for the Cromerian interglacial stage, which is exposed at the base of the cliff at West Runton, near Cromer, Norfolk (52.941 N; 1.254 E). The WRFB, averaging ca. 1.6 m thick, and comprising organic rich silts, detritus muds, reworked silt clasts, scattered small pebbles and sand, is exposed over a length of about 250 m east of West Runton Gap (Woman Hithe). As described in other contributions to this issue, the WRFB is rich in a wide range of fossils, including beetles, pollen and plant macrofossils, non-marine molluscs, and vertebrates (West, 1980; Stuart, 1975; Stuart and Lister, 2010b).

The West Runton Freshwater Bed (WRFB) provides one of the richest and most diversified vertebrate fauna of early Middle Pleistocene age (Stuart, 1975; Stuart and Lister, 2010b). Within the excavated bone and tooth material, ectothermic vertebrates, especially fishes, are among the most numerous finds. Beside their huge quantity, fishes, amphibians, and reptiles are particularly important for the reconstruction of aquatic and terrestrial ecosystems, and represent ideal proxy organisms for estimating palaeoclimatic parameters such as temperature and precipitation (Böhme, 2003; Böhme et al., 2006).

Ectothermic vertebrates from the WRFB have been known since the classic works of Newton (1882a,b). He described eight species of fishes (Table 1), three species of amphibians, and two species of reptiles. Later, Stuart (1975) added two more fish taxa (Table 1), and Holman et al. (1988) and Holman (1989) increased the numbers of amphibian species to eight and of reptilian species to three. The last contribution to the WRFB herpetofauna came from Parfitt (1977) (unpublished manuscript, cited in Holman, 1998a,b) who made the first record of a tree frog.

2. Material and methods

Following the excavation of the West Runton mammoth in 1995 a large quantity of bones and teeth was recovered by screen

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Table 1
Ectothermic vertebrates from the West Runton Freshwater Bed, after Stuart, 1975, Holman, 1998a,b, and in the 1995 excavation, square 74 (this paper).

West Runton	WRE 95, BS sq. 74	Figure	Common name
Newton, 1882b			
Esox lucius	*Esox lucius*	Fig. 2, D	Pike
cf. *Gymnocephalus*	Percidae indet. (? *Gymnocephalus*)	Fig. 2, B	Ruff
Perca fluviatilis	*Perca fluviatilis*	Fig. 2, C	Perch
Tinca tinca	*Tinca tinca*	Fig. 2, F	Tench
Abramis brama	*Abramis bjoerkna*	Fig. 2, I	White bream
Scardinius erythrophtalmus	*Scardinius erythrophtalmus*	Fig. 2, G	Rudd
Rutilus rutilus	*Rutilus rutilus*	Fig. 2, J	Roach
cf. *Barbus*	–		
	Leuciscus cf. *idus*	Fig. 2, H	Ide
Stuart, 1975			
Anguilla anguilla	*Anguilla anguilla*	Fig. 2, A	Eel
Gasterosteus aculeatus	*Gasterosteus aculeatus*	Fig. 2, E	Three-spined stickleback
Holman, 1998a,b			
Triturus vulgaris	*Triturus vulgaris*	Fig. 3, A–E	Smooth newt
Triturus sp.	*Triturus* sp. nov. (aff. *T. cristatus*)	Fig. 2, K–O	New crested newt
Bufo bufo	*Bufo bufo*	Fig. 3, G	Common toad
Bufo sp.	–		
Hyla arborea	*Hyla arborea*	Fig. 3, F	Common tree frog
Rana arvalis	*Rana arvalis*	Fig. 3, J	Moor frog
Rana (*ridibunda*) sp.	*Rana* (*ridibunda*) sp.	Fig. 3, I	Water frogs
Rana temporaria	*Rana temporaria*	Fig. 3, H	Common frog
Rana sp.	*Rana*, cf. *R. dalmatina*	Fig. 3, K	Agile frog
Anguis fragilis	*Anguis fragilis*	Fig. 4, I, J	Slow worm
Natrix natrix	*Natrix natrix*	Fig. 4, A–D	Grass snake
Vipera berus	–		
	Colubroidea indet. (?Viperidae)	Fig. 4, E–H	Possible viper

washing of sediment from grid squares 73 and 74 (Fig. 1; Stuart and Lister, 2010a). This study analyzes in detail the ectotherm material coming from 21 samples of square 74 (Table 2; the materials from square 73 are studied only with regard to significant herpetological specimens). The samples represent stratified horizons of the sedimentary sequence of the excavation. All investigated material is stored in the collection of the Natural History Museum (London). The morphological comparison with recent species was made using

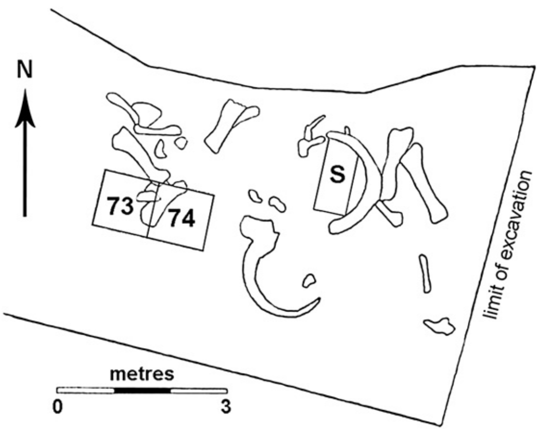

Fig. 1. West Runton Mammoth excavation 1995. Outline excavation plan, showing positions of sample columns 73 and 74 (small vertebrates) and 'S' (pollen, plant macrofossils, beetles). Columns 73 and 74, each 1 m square and 1.3 m thick (from 3.05 m to 4.35 m O.D) were sampled in twenty-seven 5 cm horizontal slices.

the osteological collection of the Bavarian State Museum for Palaeontology and Historical Geology in Munich ("Brunner collection") and the private collection of the author. For the methodology of estimating palaeoclimatic parameters, see Section 3.2.

3. Results

3.1. Taxonomic composition

The fish fauna of square 74 comprises ten species (Table 1). All taxa belong to extant species. The pike (*Esox lucius*) is represented by numerous cranial bones, vertebrae, teeth and scales. Perches (Percidae) are represented by two species: the perch (*Perca fluviatilis*), known from cranial bones, vertebrates and scales, and probably the ruff (*Gymnocephalus cernua*). The exact determination of the few cranial bones comparable to the latter species is not yet possible due to lack of recent comparative material. Also very frequent are remains of the eel (*Anguilla anguilla*; cranial bones, vertebrae) and the three-spined stickleback (*Gasterosteus aculeatus*; cranial bones, spines). The dominant fish family of the WRFB are the minnows (Cyprinidae), represented by five species. The morphology of pharyngeal teeth and bones was the basis for identification of the tench (*Tinca tinca*), the rudd (*Scardinius erythrophtalmus*), the roach (*Rutilus rutilus*), the white bream (*Abramis bjoerkna*), and the ide (*Leuciscus* cf. *idus*). The latter two species are new for the WRFB fauna. A possible barbel (cf. *Barbus*) and the bream (*Abramis brama*), mentioned by Newton (1882b), could not be identified in the samples. Instead of the bream, the white bream (*A. bjoerkna*) was present, distinguished from *A. brama* by pharyngeal teeth arranged in two rows instead of one (Fig. 2, I).

In contrast to the fishes, herpetofaunal remains are relatively rare in the WRFB (square 74). This is especially true for the newts and the reptiles. Only two vertebrae of the smooth newt (*Triturus vulgaris*) were found. A second newt species of larger dimensions was found in sample 107. It is not identical to any living species and is therefore described here in detail.

The single posterior thoracic vertebra has a size of >3.5 mm (Fig. 2, K to O); the posterior end of the neural arch is broken. The large dimensions (indicating an individual of 12–16 cm total length) and the deeply concave anterior border of the neural arch (between prezygapophyses) suggest a relationship to the *Triturus cristatus* group (including *T. cristatus*, *Triturus marmoratus* and *T. vittatus*). The neural spine is very low but distinct (Fig. 2, L, M), excluding *T. marmoratus* and *T. vittatus* which posses a high neural spine. In *T. cristatus cristatus*, the only one of the four sub-species available among comparative material, the neural spine is indistinct, especially in its anterior part. Unlike any of these three members of the *T. cristatus* group, the West Runton newt possesses a broad and very high neural arch, exceeding the height of the condyle by over 50% (Fig. 2, N, O), reminiscent of members of the small-sized *T. vulgaris* group. In all living *T. cristatus*-group species, the height of the neural arch is similar to that of the condyle. These characteristics indicate that the large newt from the WRFB could not be included in any living species and probably belong to a new fossil species. However, a single vertebra seems insufficient for a formal description and will be referred to as *Triturus* sp. nov (aff. *T. cristatus*).

Frogs are represented by six species: the common toad (*Bufo bufo*), the common tree frog (*Hyla arborea*), the moor frog (*Rana arvalis*), the water frog (*Rana* (*ridibunda*) sp.), the common frog (*Rana temporaria*) and possibly the agile frog (*Rana dalmatina*). Reptiles are documented by a single vertebra of the slow worm (*Anguis fragilis*) and five vertebrae of the grass snake (*Natrix natrix*). An additional snake vertebra shows undoubted viperid affinities

Table 2
Minimum numbers of individuals (MNI) for amphibians and reptiles in the 1995 West Runton excavation, square 74. Samples are in stratigraphical order (youngest at top). Note that the newt and reptile remains are based on one bone per sample. The bottom row shows the percentage composition of the amphibian assemblage.

Sample no.	Metres O.D.	*Triturus vulgaris*	*aff. Triturus cristatus*	*Bufo bufo*	*Hyla arborea*	*Rana arvalis*	*Rana* (*ridibunda*) sp.	*Rana temporaria*	*Rana*, cf. *R. dalmatina*	*Anguis fragilis*	*Natrix natrix*	Colubroidea indet.
29	4.10–4.05			1		?						
30	4.05–4.00					1						
31	4.00–3.95										1	
32	3.95–3.90									1		
33	3.90–3.85			1			1	1				
37	3.85–3.80	1		1		1	2	2				
38	3.80–3.75					2	3	1				
39	3.75–3.70					1	2	2				
40	3.70–3.65			1		1	3					
73	3.65–3.60						2					
74	3.60–3.55						1				1	
75	3.55–3.50							3	1		1	
76	3.50–3.45					3						
77	3.45–3.40	1				1	1				1	
78	3.40–3.35					3	2	1			1	
80	3.35–3.30			1	1		4					
102	3.30–3.25					1	3					
103	3.25–3.20						1					
104	3.20–3.15											
105	3.15–3.10			1		1	4	1				1
107	3.05–3.00		1					1				
%MNI		**3**	**1**	**9**	**1**	**24**	**43**	**18**	**1**			

(straight hypapophysis, short vertebral centrum, very low neural spine); however, the neural arch is uniformly vaulted and the zygosphene is relatively broad. Both features are unknown in recent and fossil European viperids. Ivanov (1996: Fig. 9 J) figured an early Biharian vertebra from Zabia Cave (Poland), referred by him to the *Vipera berus*, which shows a clearly vaulted neural arch. However, the vault is not so uniform as in the WRFB specimen (it seems rather uplifted above the zygantrum), and the zygosphene is much narrower, similar to the recent species. Since the WRFB vertebra shows no pathological features, its taxonomic affinities remain an open question. It will be named here as Colubroidae indet. (?Viperidae). Newton (1882a,b) mentions a *Vipera* sp. from West Runton, which Holman (1998a) refers to the adder *V. berus*. The old collections need to be checked to determine if this species is really present in the WRFB. The present investigation, however, did not find the adder in squares 73 and 74.

The distribution of the amphibian and reptile fossils through the profile of square 74 is shown in Table 2.

3.2. *Reconstruction of climatic parameters*

3.2.1. *Temperature*

Böhme (1996, 2000) distinguished six temperature-dependent herpetofaunal associations (Table 3) for the Pleistocene in Central Europe. The West Runton assemblage differs from faunas typical for interglacial warm optima in lacking *Emys orbicularis*, *Elaphe longissima*, *Bombina bombina*, and *Salamandra salamandra* (the latter possibly for ecological reasons other than temperature), and in the presence of *R. arvalis*. It has the most taxa in common (8 of 13) with associations typical for late interglacials and interstadials. Other taxa typical for this period but missing at West Runton, such as *Bufo viridis*, *Bufo calamita*, *Pelobates fuscus*, *Lacerta agilis*, and *Lacerta viridis*, are xeric elements and are probably absent because of the humid environment.

If the absence of the thermophiles *E. orbicularis* and *E. longissima* is interpreted in terms of temperature, then applying the classification of Böhme (1996, 2000) indicates maxima of 8.0 °C for mean annual temperature (MAT), −1.4 °C for mean January temperature (coldest month temperature, CMT), and 17.0 °C for mean July temperature (warmest month temperature, WMT). Conversely, the three typical late interglacial taxa *H. arborea*, *Rana* (*ridibunda*) sp., and *N. natrix* imply minima of 6 °C for MAT, −6 °C for CMT, and 16 °C for WMT.

3.2.2. *Humidity*

The reconstruction of mean annual precipitation (MAP) follows Böhme et al. (2006). This method is based on the relative abundance of six herpetological (excluding non-fossorial snakes) ecophysiological groups (aquatic, heliophobe, semi-aquatic + woodland, peri-aquatic, fossorial + arboreal, heliophile; for classification see Table 4) and represents a regression analysis with annual precipitation as the dependent variable and the relative frequencies of the groups as explanatory variables (for more details see Böhme et al., 2006). By constructing a normalized index using regression coefficients, the mean annual precipitation (MAP) is calculated by the equation

$$MAP = -35.646 + 2402.289 * Index$$

For the WRFB association the ecophysiological index is 0.38539, resulting in a MAP of 890 ± 255 mm (95% prediction interval), indicating humid climatic conditions.

4. Discussion

4.1. *Palaeobiogeography*

All the ten fish species recorded in the WRFB are currently known from the British Isles. The same is true for the smooth newt, the slow worm and the grass snake. In contrast, four of the six frog species are exotic continental taxa unknown from the British late Holocene (Holman, 1998a). These extralimital species are the common tree frog (*H. arborea*), the moor frog (*R. arvalis*), the water frog (*Rana* (*ridibunda*) sp. or *Rana ridibunda* complex), and the possible agile frog (*Rana* cf. *R. dalmatina*). If the taxonomic allocation of the latter is correct this will be the first record from Britain. The presence of *H. arborea* is, after East Farm, Barnham (Suffolk) (Holman, 1998a,b), the second record from the British Pleistocene, whereas *Rana* (*ridibunda*) sp. and *R. arvalis* are known, respectively, from two and four additional Pleistocene localities (Holman, 1998a,b). No palaeogeographical conclusions can be drawn from

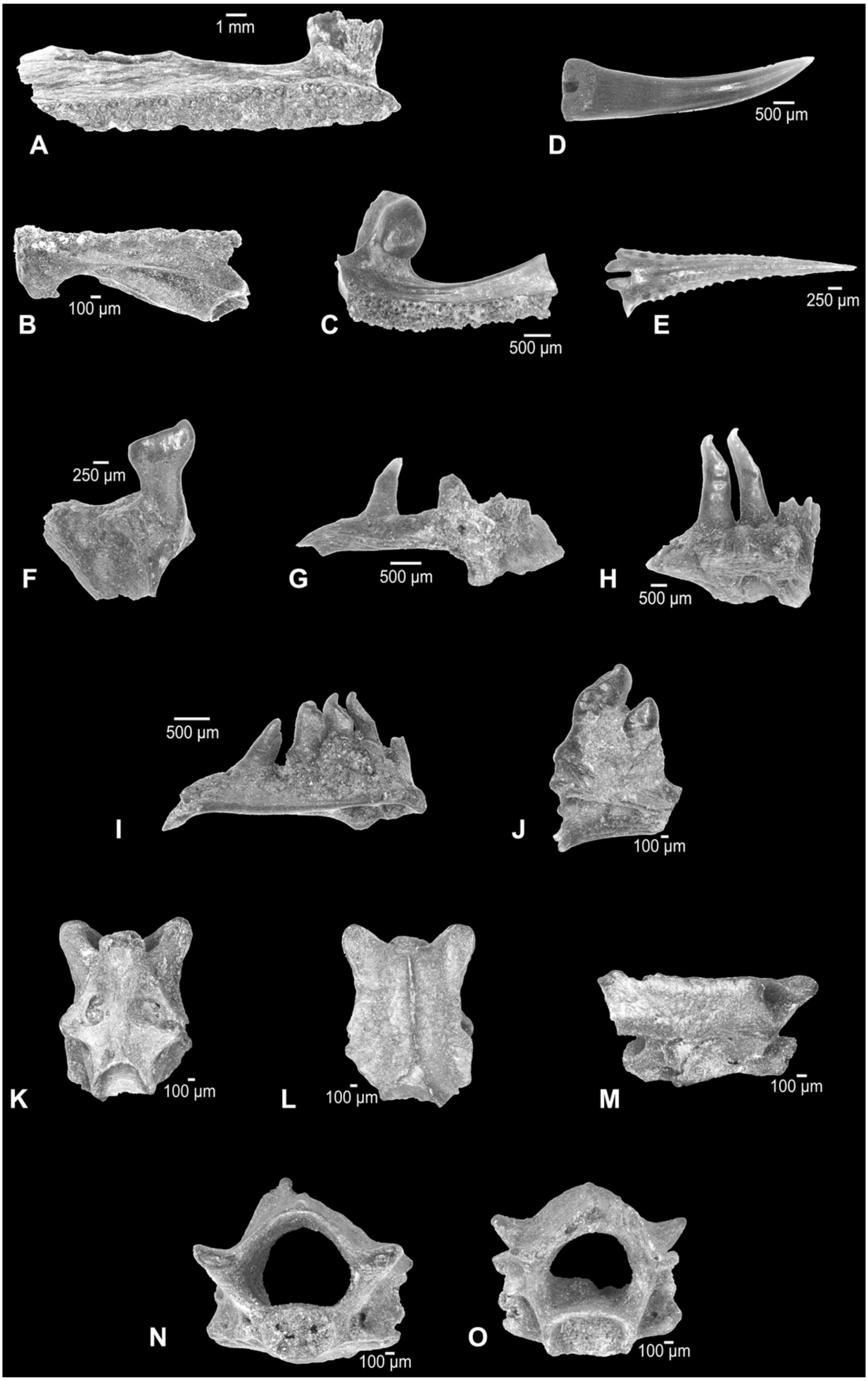

Fig. 2. A: *Anguilla anguilla*, left maxilla (square 74, sample 80). B: Percoidae indet. cf. *Gymnocephalus*, right dentary (square 74, sample 107). C: *Perca fluviatilis*, right premaxilla (square 74, sample 39). D: *Esox lucius*, tooth (square 74, sample 107). E: *Gasterosteus aculeatus*, dorsal spine (square 74, sample 107). F: *Tinca tinca*, pharyngeal bone fragment with tooth (square 74, sample 80). G: *Scardinius erythrophtalmus*, pharyngeal bone with tooth (square 74, sample 107). H: *Leuciscus* cf. *idus*, pharyngeal bone fragment with teeth (square 74, sample 32). I: *Abramis bjoerkna*, pharyngeal bone with teeth (square 74, sample 107). J: *Rutilus rutilus*, pharyngeal bone fragment with teeth (square 74, sample 80). K–O: *Triturus* nov. sp. (aff. *T. cristatus*), posterior thoracal vertebra (square 74, sample 107), K – ventral, L – dorsal, M – lateral, N – anterior, O – posterior.

Fig. 3. A–E: *Triturus vulgaris*, anterior thoracic vertebra (square 74, sample 77), A – ventral, B – dorsal, C – lateral, D – posterior, E – anterior. F: *Hyla arborea*, left ilium (square 74, sample 80). G: *Bufo bufo*, left ilium (square 74, sample 40). H: *Rana temporaria*, right ilium (square 74, sample 75). I: *Rana* (*Ridibunda*) sp., right ilium (square 74, sample 102). J: *Rana arvalis*, right ilium (square 74, sample 38). K: *Rana* cf. *R. dalmatina*, right ilium (square 74, sample 75).

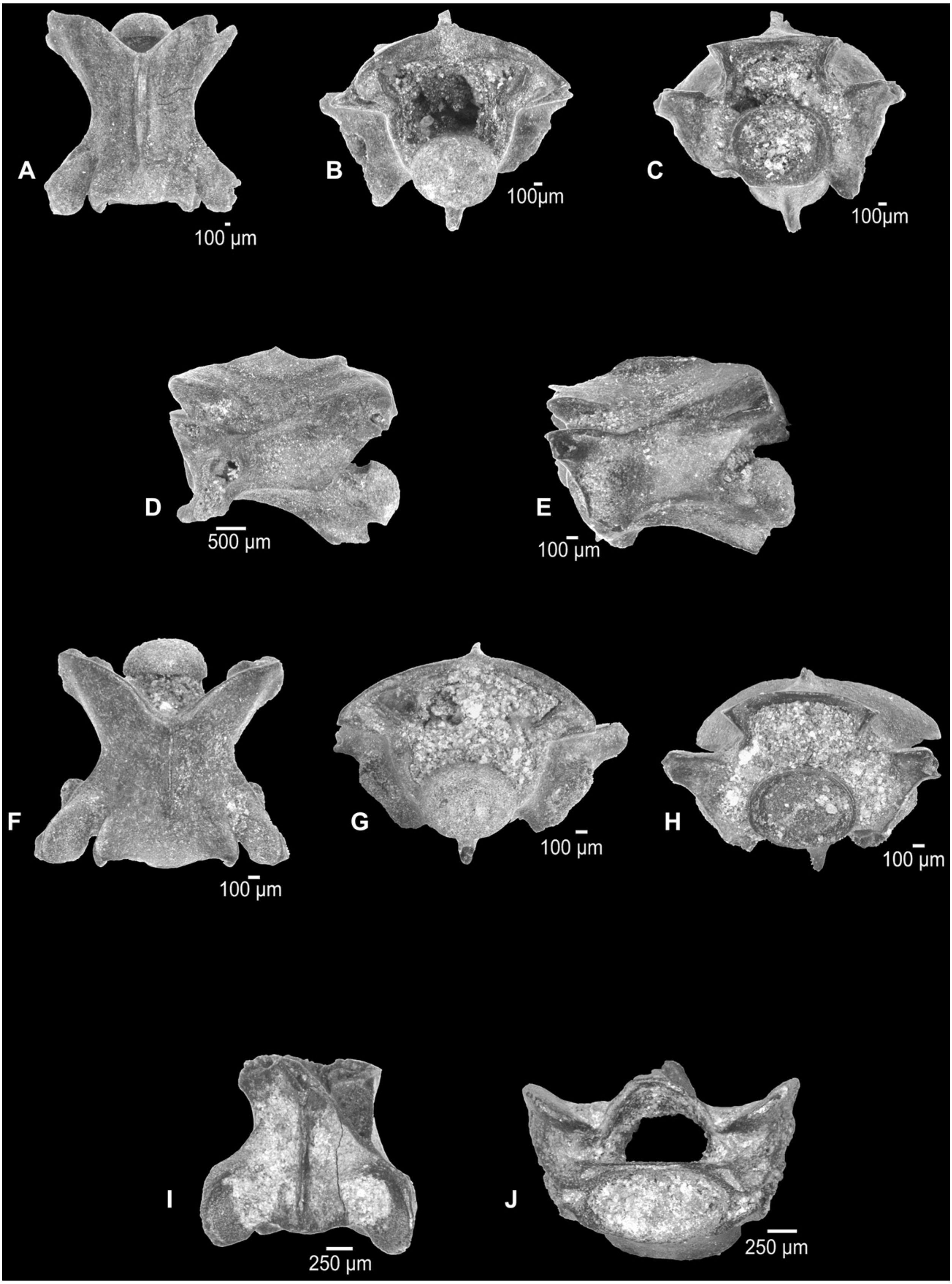

Fig. 4. A–D: *Natrix natrix*, thoracic vertebra (square 74, sample 74), A – dorsal, B – posterior, C – anterior, D – lateral. E–H: Colubroid indet. (?Viperidae), thoracic vertebra (square 74, sample 105), E – lateral, F – dorsal, G – posterior, H – anterior. I–J: *Anguis fragilis*, thoracic vertebra (square 74, sample 32), I – dorsal, J – posterior.

Table 3
Typical herpetological faunal associations for Pleistocene climatic cycles in Central Europe (modified after Böhme, 1996, 2000) in comparison with the assemblage from West Runton, square 74.

Species	WRE 95, sq. 74	Late glacial	Early interglacial	Interglacial climate optima	Late interglacial and interstadial	Latest interglacial to early glacial	Glacial
Salamandra salamandra				x			
Triturus cristatus	aff.		x	x			
Triturus vulgaris	x		x	x	x		
Bufo bufo	x	x	x	x	x		
Bufo calamita					x		
Bufo viridis					x	x	
Bombina bombina				x			
Hyla arborea	x			x	x		
Pelobates fuscus				x	x		
Rana dalmatina	cf.		x	x			
Rana temporaria	x		x	x	x	x	x
Rana arvalis	x	x	x		x		
Rana (*ridibunda*) sp.	x			x	x		
Emys orbicularis				x			
Anguis fragilis	x		x	x	x		
Lacerta agilis			x		x		
Lacerta viridis				x			
Lacerta vivipara			x			x	
Natrix natrix	x		x	x	x		
Vipera berus	?	x	x			x	
Coronella austriaca			x		x		
Elaphe longissima				x			

the two new species *Triturus* sp. nov (aff. *T. cristatus*) and Colubroidea indet. (?Viperidae). However, they indicate that the preglacial (Cromerian) herpetofauna from the British Isles is more diverse than previously thought and includes extinct species.

4.2. Reconstruction of the environment

The WRFB was deposited in a channel-like structure cutting into sediments of Beestonian age (Gibbard et al., 2010). The WRFB sediments consist of detritus-rich mud in a matrix of reworked marl, flint and quartz pebbles at the base, and clay, silt and sand, showing a fining-upward trend. Based on sedimentological criteria and freshwater as well as terrestrial mollusc data (Preece, 2010), these sediments are interpreted as having aggraded in an initially faster and later slow-flowing to still body of freshwater.

The record of aquatic ectotherms from the studied grid square 74 agrees well with this interpretation. Table 5 gives a summary of the spawning substrate, streaming preference and trophic type of the aquatic vertebrates. Besides taxa indifferent with regard to streaming conditions, only limnophilous species occur, preferring stagnant waters. This indicates that at the time of sedimentation the sampled profile represented a very slow-flowing body of water. The frequent presence of the catadromous eel (*A. anguilla*) in every sample may suggest persistent fluvial connection to the sea. However, recent eels are able to travel significant distances over moist land, thereby reaching endorheic or oxbow lakes. On this evidence, at least, it cannot be fully excluded that the habitat represents an oxbow lake disconnected from the main river.

Except for the grass snake (*N. natrix*) and the eel, all species probably spawned in the water itself. Seven of these 12 taxa are phytophilous, i.e. their preferred spawning habitats are aquatic macrophytes. The remaining taxa could have used both

Table 4
Summary of permanently or periodically terrestrial species, their habitat preferences, and their ecophysiologic groups (according to Böhme et al., 2006), and the resulting palaeo-precipitation estimates.

Species	Habitat	Ecophysiologic group	Index
Triturus vulgaris	Prefers moist habitat	Peri-aquatic	0.3918
Triturus nov. sp. (*T.* aff. *cristatus*)	Prefers moist woodland habitat	Peri-aquatic	0.3918
Bufo bufo	Prefers woodland habitat	Peri-aquatic	0.3918
Hyla arborea	Trees and shrubs near water	Peri-aquatic	0.3918
Rana temporaria	Indifferent	Peri-aquatic	0.3918
Rana cf. *R. dalmatina*	Indifferent	Peri-aquatic	0.3918
Rana arvalis	Near water bodies	Semi-aquatic	0.513
Rana ridibunda complex	Near water bodies	Semi-aquatic	0.513
Anguis fragilis	Subterraneous (soil, leaf litter)	Fossorial	0.0917
Natrix natrix	Prefers moist habitat	–	–
Colubroidea indet. (?Viperidae)	?	–	–
Ecophysiologic index			**0.38539**
Mean annual precipitation (in mm)			**890**
95% prediction interval (in mm)			**255**

Table 5
Summary of species that lived permanently or periodically in the West Runton water body and their spawning substrate, streaming preference and trophic (food) type.

Species	Spawning substrate	Streaming preference	Food type
Esox lucius	Phytophilous	Indifferent	Carnivorous
Gasterosteus aculeatus	Phytophilous	Limnophilous	Omnivorous
Anguilla anguilla		Indifferent	Omnivorous
Tinca tinca	Phytophilous	Limnophilous	Omnivorous
Abramis bjoerkna	Phytolithophilous	Indifferent	Omnivorous
Scardinius erythrophtalmus	Phytophilous	Limnophilous	Omnivorous
Rutilus rutilus	Phytolithophilous	Indifferent	Omnivorous
Leuciscus cf. *idus*	Phytolithophilous	Indifferent	Omnivorous
Percidae indet. (? *Gymnocephalus*)	Phytolithophilous	Indifferent	Omnivorous
Perca fluviatilis	Phytolithophilous	Indifferent	Omnivorous
Frog tadpoles		Limnophilous	Phytophagous
Triturus ssp. and their tadpoles	Phytophilous	Limnophilous	Carnivorous
Rana arvalis	Phytophilous	Limnophilous	Insectivorous
Rana ridibunda complex	Phytophilous	Limnophilous	Insectivorous
Natrix natrix		Limnophilous	Carnivorous

macrophytes and clastic sediment to spawn (phytolithophilous). This indicates a densely-vegetated substrate for the WRFB community. Anuran tadpoles are primary consumers, the moor and the water frog secondary consumers, and the newts, pike, and grass snake are predators, while the trophic position of the remaining aquatic vertebrates (9 of 15 species) is omnivorous, indicating a complex aquatic food web in a comparatively large, nutrient-rich environment.

In contrast to studies on ostracods (De Dekker, 1979), no indications of periodically increased salinity could be found, although oligohaline conditions cannot be excluded because all recorded freshwater fish taxa can tolerate up to at least 5‰ salt concentration.

In summary, the aquatic ecosystem is consistent with either a large and stagnant eutrophic freshwater lake, or a very slow-flowing river, with dense macrophyte vegetation and a complex food web.

For reconstruction of the landscape during the deposition of the WRFB, a summary of preferred land habitats for the 11 recorded herpetological species is given in Table 4. Because of the limited mobility of all taxa, statements are valid only for a restricted spatial scale of probably a few hundred metres surrounding the water body.

All recorded amphibian and reptile species prefer moist environments. Two thirds (67%) of the amphibian assemblage is represented by the two semi-aquatic frog species *R. arvalis* and *Rana* (*ridibunda*) sp. (Table 2). Species indicative of open landscapes, e.g. *Bufo viridis*, *Bufo calamita*, *Pelobates fuscus* or *Lacerta* ssp., are lacking. Since these taxa are recorded from other British sites of Middle Pleistocene age (Holman, 1998a,b), their absence at West Runton may indicate the absence of open habitats in the proximity. The common toad (*B. bufo*) is widely regarded as a woodland species, favouring areas with predictable climate (Kuzmin, 1995; Romero and Real, 1996). The same may be true for the large-sized newt *Triturus* aff. *cristatus*, since its nearest living relative, the crested newt (*T. cristatus*) prefers moist woodland habitats. All available indications suggest a moist woodland habitat surrounding the WRFB channel.

4.3. Climate

The WRFB herpetofauna shows most similarities to Central European late interglacial or interstadial assemblages. The estimated July temperatures are between 16 and 17 °C, which is similar to today in the same region (climate station Cromer: 16.5 °C). In contrast, the MAT was probably slightly cooler, between 6 and 8 °C (cf. 9.9 °C today), a result of cooler winter temperatures of −6 to −1.4 °C compared to 3.7 °C today. These values clearly indicate that the Cromerian interglacial (at least, pollen subzone IIa: Field and Peglar, 2010) is characterized by slightly cooler conditions compared to the interglacial climate optima of the Hoxnian/Holsteinian and Ipswichian/Eemian, when more temperate reptiles like *E. orbicularis* and *E. longissima* are present both in England and Central Europe (Böhme and Ilg, 2003).

The palaeo-precipitation estimate is based on nine taxa, providing a robust result according to the methodology of Böhme et al. (2006). This indicates that in contrast to the temperatures, the estimated precipitation value of 890 ± 255 mm is significantly higher than the present-day precipitation in the area. The estimate of palaeo-precipitation is not likely to be seriously biased by the wet local environment. For example, the recent herpetofauna of Norfolk produces an estimate of 629 ± 252 mm mean annual precipitation using the same methodology, which is very near the present-day value of 618 mm for the climate station of Cromer. Today, precipitation values similar to that estimated for the WRFB are characteristic of the western part of the British Isles, probably indicating a different mode of atmospheric circulation during the Cromerian interglacial.

5. Conclusions

The ectothermic vertebrate fauna from the WRFB is one of the richest in the British Pleistocene. In the screen-washed residue of square 74 from the 1995 West Runton Mammoth excavation, ten species of freshwater fishes, two species of newt, six frog species, and three reptile species (including two snakes) are identified. Most of the taxa corroborate the work of Newton (1882a,b), Stuart (1975), and Holman (1998a,b). New are the white bream (*A. bjoerkna*), the ide (*Leuciscus* cf. *idus*), an extinct relative of the crested newt (*Triturus* aff. *cristatus*), and probably the agile frog (*Rana* cf. *R. dalmatina*).

The reconstruction of the terrestrial ecosystem in the vicinity of the depositional site gives no evidence of open landscapes, but rather of moist woodland. The water body itself was densely vegetated and probably connected to the sea by a permanent outflow. The estimated climate parameters indicate slightly cooler but wetter condition compared to present-day values.

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