Reinterpretation of the Extinct Beaver Trogontherium (Mammalia, Rodentia)

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REINTERPRETATION OF THE EXTINCT BEAVER *TROGONTHERIUM* (MAMMALIA, RODENTIA)

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CONTENTS

A review of the literature reveals an unsatisfactory state of knowledge of the history of the extinct beaver *Trogontherium*. Investigation of European material in the light of recent stratigraphic interpretations is combined with an account of new anatomical evidence concerning the basicranium. Contrary to previous opinion it appears more probable that all material previously referred to this genus belongs to a single evolutionary lineage. Metrical and morphological differences between populations from different stratigraphical horizons are discussed in some detail with the conclusion that a considerable increase of size occurred in the genus during the Pliocene and

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Pleistocene, but also that the last representatives differed in morphology and may have been reduced in size. Knowledge of intrapopulation variation leads to the conclusion that a number of Pliocene specimens previously placed in several genera are referable instead to *Trogontherium*. This generic name is also applied to Late Miocene and Pliocene specimens of small size which appear to be directly ancestral to later larger populations. Anatomical, geological and palaeobotanical evidence bearing on the ecology of *Trogontherium* is reviewed. It is concluded that the habits of this animal resembled those of the living coypu (*Myocastor coypus*) and that the idea that it grazed with enlarged upper lips on floating vegetation arose from an anatomical misinterpretation. Proposed specific and subspecific taxonomy is followed by a review of information concerning absolute dating of localities under consideration.

1. INTRODUCTION

Beavers of the extinct genus *Trogontherium* existed alongside *Castor*, the living beaver, for most of the Pleistocene. Unlike *Castor*, *Trogontherium* was restricted to the Palaearctic region, where its distribution extended from eastern England to China. Later populations of *Trogontherium* were similar in body size to the recent European beaver, *Castor fiber* L. and the term 'giant beaver' is best used for the truly large extinct N. American *Castoroides*.

The purpose of this paper is to review European *Trogontherium* material in the light of recent advances in stratigraphy with particular regard to the British Pleistocene sequence. New evidence concerning the nature of the basicranium and variation in size and morphology is discussed and this leads to conclusions which differ substantially from those of previous work. In particular, it is evident that the remains of *Trogontherium* in Europe are derived from a single lineage which increased considerably in body size through the Pliocene and Pleistocene. Simplification of the currently confused taxonomy is suggested.

The genus *Trogontherium* was first described by Fischer de Waldheim (1809) on the basis of a skull from Pleistocene deposits on the shores of the sea of Azov. Although the stratigraphical context of this type specimen, now in Moscow, remains uncertain, remains of this large rodent have since been recovered from many Pleistocene deposits. In the last century specimens of *Trogontherium* were assigned to a number of taxa (e.g. *Conodontes boisvilletti* Laugel 1862) on the basis of considerable differences in the enamel pattern of the cheek tooth wear surfaces. However, Newton (1882, 1892) demonstrated that these differences were no greater than those due to different stages of wear in specimens from the English, Middle Pleistocene, Cromer Forest Bed Series. He suggested that all the material belonged to a single species, *T. cuvieri* Fischer. In addition he described a new species, *T. minus* Newton 1890, on the basis of a small maxilla from the Red Crag basement bed of Suffolk, England, a deposit currently placed at the base of the British Pleistocene sequence.

The other major contributor to our knowledge of *Trogontherium* was Schreuder who in 1929 reviewed available material from Tegelen, the Netherlands, and provided a detailed description of most skeletal elements. Apparent differences in the dentition and basicranium led her to suggest (Schreuder 1929, 1951) that the populations treated as a single species *T. cuvieri* by Newton (1892) belonged instead to two coeval taxa separated by the river Rhine. Specimens from England, France and Tegelen were treated by her as *Conodontes boisvilletti* in 1929, (*T. boisvilletti* in 1951); material from Mosbach and other German sites was placed with the Russian type as *T. cuvieri*. In a consideration of the ecology and habits of *Trogontherium*, Schreuder (1951) suggested that the animal was thoroughly aquatic, perhaps feeding largely on floating vegetation.

References to earlier work are given in extensive discussions by Newton (1882, 1892) and Schreuder (1929, 1951).

The idea of geographical separation proposed by Schreuder has since been confused by the description of specimens conforming to Schreuder's diagnosis of *T. boisvilletti* from Erpfingen to the east of the Rhine (Lehmann 1953); and specimens of *T. cuvieri* from Neede to the north of the Rhine (Hooijer 1959). Subsequent work on *Trogontherium* material (Guenther 1965; Dechaseaux 1967; Kretzoi 1969; Janossy 1969) has reflected this uncertainty and has emphasized the need for a reinvestigation of the evolutionary history of the genus.

2. British material and its stratigraphic context

British material was described by Owen (1846, 1869), Newton (1882, 1890, 1891, 1892, 1902, 1916) and Hinton (1914). Newer finds have been noted by Spencer (in West 1956) and Singer, Wymer, Gladfelter & Wolff (1973). The specimens are at present kept in the following collections; British Museum (Nat. Hist.) (B.M.N.H.); Norwich Castle Museum (N.C.M.); Ipswich Museum (I.M.); Institute of Geological Sciences (G.S.M.) and Colchester and Essex Museum (C.E.M.). Because the majority of the material was collected and described before the establishment of a Pleistocene stratigraphic sequence it is discussed here in terms of relative dating enabled by more recent work. This is summarized in the scheme proposed by Mitchell, Penny, Shotton & West (1973) which is used here as a stratigraphic framework (see table 1).

Table 1. British Pleistocene deposits, stages and continental equivalents (West 1972; Mitchell *et. al.* 1973; Stuart 1974.)

	stage	climate	principal strata
Upper	Flandrian (= Holocene)	t	glacial-interglacial succession
	Devensian (= Weichselian)	c, g, p	
	Ipswichian (= Eemian)	t	
	Wolstonian (= Saalian)	c, g, p	
Middle	Hoxnian (= Holsteinian)	t	
	Anglian (= Elsterian)	c, g, p	
	Cromerian	t	Cromer Forest-Bed Series and Weybourne Crag facies
	Beestonian	c, p	
	Pastonian	t	
Lower	Baventian	c, p	Norwich Crag and Red Crag
	Antian	t	
	Thurnian	c	
	Ludhamian	t	
	Waltonian (Pre Ludhamian)		
Pliocene			? Red Crag Nodule Bed Coralline Crag

t, temperate stage; c, cold stage; g, glacial deposits known; p. permafrost indications known.

(*a*) *Early Pleistocene or Pliocene*

A maxilla from the Red Crag basement bed (I.M. colln.) was described by Newton (1890) as *T. minus*. An upper incisor (B.M.N.H. colln M9595) also apparently from the basement bed at Felixstowe appears to be from a small (or young) specimen of *Trogontherium* and is here referred to *T. minus*. The Red Crag basement bed represents the winnowings of previous deposits by a transgressing sea and contains fossils derived from sediments of different ages. The basement bed is the lowest deposit in the British Pleistocene sequence as currently defined.

(*b*) *Early Pleistocene*

An upper incisor (I.M.) and part of a femur (G.S.M. 87971) have been recovered from crag deposits at Easton Bavents, Suffolk. The stratigraphy and dating of these deposits were discussed by Funnell & West (1962). Shelly crag correlated with zone Lu 3 (Antian) of the Ludham borehole underlies a blue sandy clay apparently deposited under cold conditions (Baventian). The deposits here may considerably pre-date those of the Cromer Forest-Bed series further north (West 1968; Zagwijn 1974).

A heavily mineralized distal half of a femur (B.M.N.H. M40979) from Norwich crag deposits at Thorpe, Norwich was referred by Owen (1846) to *Castor fiber*. It was correctly identified as *Trogontherium* by Newton (1891).

(*c*) *Middle Pleistocene*

(i) *Cromer Forest-Bed Series*

The majority of British *Trogontherium* specimens come from deposits outcropping around the East Anglian coast from Weybourne, Norfolk to Kessingland, Suffolk which date from a series of climatic oscillations preceding the major glaciation of Britain. As the period of accumulation is known to have covered at least two temperate stages (West & Wilson 1966), the dating of specimens from 'forest-bed' sites is no longer a straightforward proposition, particularly since each exposure may have included deposits from a number of stages.

Shelly sands outcropping on the foreshore at East Runton, Norfolk have yielded a few specimens of *Trogontherium* including the skull (B.M.N.H. M6127) described by Newton (1892). Differences between the deer fauna of East Runton and the Upper Freshwater Bed, West Runton were noted by Azzaroli (1953). Deposits dating from the Pastonian temperate phase are present at East Runton (West personal communication) and it seems likely that the fauna from the shelly sands dates from this period.

Abundant material of *Trogontherium* (B.M.N.H., N.C.M. colln) has been recovered from the marls and muds (Upper Freshwater Bed – U.F.B.) which outcrop beneath a cliff of Anglian glacial deposits at West Runton, Norfolk. These deposits date from the first two pollen zones of the Cromerian (sensu stricto) interglacial (West 1968) and the later part of the preceding cool phase (Beestonian). The fauna of these type Cromerian deposits has recently been revised by Stuart (1974, 1975). Many *Trogontherium* specimens from the U.F.B. were described and figured by Newton (1882) and today they form the largest sample of known stratigraphical context available from British deposits.

A lower incisor (G.S.M. colln) from crag deposits at Sizewell, Suffolk was referred by Newton (1890, 1891) to *T. minus*. The deposits at this site, which lies south of the area occupied by Cromer Forest-Bed series sediments, have been reinvestigated by West & Norton (1974). Palynological evidence related the upper crag deposits to a temperate stage of similar vegetational character to that forming the base of the Forest-Bed series further north. This stage is the Pastonian which West & Norton tentatively correlate with the 'Cromerian III' temperate phase of the Netherlands succession (Zagwijn, Montfrans & Zandstra 1971). Although the horizon of the Sizewell specimen is not recorded, stages earlier than Pastonian are represented at this site by deposits lying well below O.D. from which collection would have been impossible. The dimensions of this incisor tooth are small, but they are those of a young specimen of *T. cuvieri* (figure 5). The apparent Middle Pleistocene age of the Sizewell upper crag deposits suggests that it would be more reasonable to refer the tooth to *T. cuvieri* than to *T. minus*.

A reinvestigation of the Cromer Forest-Bed series is in progress (West personal communication) and the results of this study should help to clarify the stratigraphic context of *Trogontherium* specimens from other forest-bed localities (see Stuart 1974).

(ii) *Glacial–interglacial succession*

The Anglian stage during which the maximum glaciation occurred is represented by mainly unfossiliferous deposits and no *Trogontherium* remains of this age are known from Britain. Specimens dating from the succeeding Hoxnian interglacial have been recovered from four localities.

A right lower incisor from the *Neritina* (*Theodoxus*) bed, Dierden's Pit, Ingress Vale was described by Newton (1902) as *T. cuvieri*. Sutcliffe (1964) mentioned a fragment of castorid left tibia (B.M.N.H. M21981) from the same site and this specimen is here identified as *Trogontherium*. Faunal and geological evidence indicate that the high terrace deposits at Ingress Vale and Barnfield Pit, Swanscombe date from the Hoxnian and possibly early Wolstonian (Ovey 1964). Kerney (1971) suggested that the shelly sands at Dierden's Pit were formed in the late temperate substage HoIII.

A single upper premolar (B.M.N.H. M27985) from Copford, Essex was figured by Brown (1852) with no specific identification. The tooth was correctly determined as *Trogontherium* by Newton (1916) although by then it had already been given the name *Dipoides lydekkeri* by Schlosser (1902). Recent reinterpretation of the stratigraphy at Copford (Turner personal communication) suggests that the blue clay from which the tooth came probably dates from the first two zones of the Hoxnian interglacial.

The facial part of a skull of *Trogontherium* (C.E.M. colln) was recently recovered during excavations at Jaywick, Essex, about 2 km from the main Clacton channel site (Singer *et al.* 1973; Pike & Godwin 1953). The specimen was found in deposits which according to Wymer & Singer (1970) are unlikely to post-date zone HoIIb.

The stratigraphy and vegetational history of the deposits at Hoxne, Suffolk were investigated by West (1956). The *Trogontherium* remains (eight upper cheek teeth and a femur, I.M. colln) mentioned by Spencer (in West 1956) were recovered from layer E, a compact lake mud deposited in zones HoII and HoIII. Further specimens (incisor tooth fragments) recovered in recent excavations come from deposits which apparently post-date zone HoIII although derivation from earlier sediments is possible (Gladfelter personal communication). The name *T. lydekkeri* (Schlosser) used by Spencer (in West 1956) for the Hoxne remains is a junior synonym of *T. cuvieri* Fischer.

No remains of *Trogontherium* have been recovered from British deposits later than Hoxnian and the genus appears to have become extinct at the end of the Middle Pleistocene.

3. REINTERPRETATION OF THE BASICRANIUM

Schreuder (1929) drew attention to the unusual basicranial morphology shown by a skull fragment from the German Middle Pleistocene site Mosbach. On the basis of this and differences in the dentition she allocated specimens from Germany and Russia to *Trogontherium cuvieri* and specimens from England, France and Holland to *Conodontes* (later *Trogontherium*) *boisvilletti*. The distinction between these taxa was restated by Schreuder in 1951. Diagrammatic midline sections of the basicranium of *T. cuvieri* were given by her in 1929 (pl. III, fig. 2) and 1951 (fig. 5) and of *T. boisvilletti* in 1951 (fig. 3) and these are reproduced here as figure 2*a*, *b*. Despite the apparent difference in structure and proportions of the basicranial elements, no constant differences have been found between the postcranial bones of these taxa. Of recent authors only Guenther (1965) has doubted whether the taxa were as distinct as suggested by Schreuder. New specimens from Tegelen, Netherlands and preparation of the skulls from St Prest, France and East Runton, England provide new information indicating that the reconstruction of the basicranium of *T. boisvilletti* given by Schreuder (1951, fig. 3) requires revision.

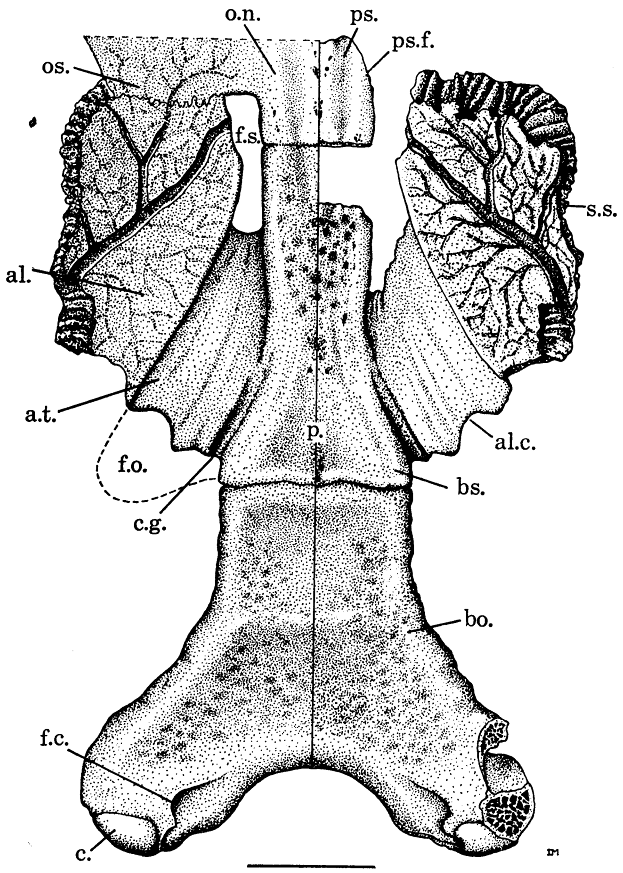

FIGURE 1. Dorsal view of basicranium of *Trogontherium* from Tegelen based on R.G.M. 28128 and 95405. Elements preserved are shown on the right while a reconstruction is given on the left of the drawing. The scale mark is 1 cm. al., alisphenoid; al. c., rear opening of alisphenoid canal; a.t., ala temporalis; bo., basioccipital; bs., basisphenoid; c., condyle; c.g., groove for internal carotid; f.c., condyloid foramen; f.o., foramen ovale and median lacerate foramen; f.s., sphenoidal fissure; o.n., path of optic nerve along dorsal surface of presphenoid; os., orbitosphenoid; p., position of pituitary; ps., presphenoid; ps.f., presphenoid foramen; s.s., squamosal suture of alisphenoid.

The new material from Tegelen includes R.G.M. 28128: fragmentary skull with part of presphenoid, part of basisphenoid and alisphenoids, and R.G.M. 95405: fragmentary skull with alisphenoids and fused basioccipital and basisphenoid. Figure 1 is a composite reconstruction based on these specimens. According to Schreuder (1929, p. 132) none of the three isolated basisphenoids available to her from Tegelen could have exceeded more than 22 mm in overall length, although the anterior portion was missing in all three cases. However, the length of basisphenoid R.G.M. 95405 (also lacking the anterior part) is 23.5 mm and it appears possible that the Tegelen basisphenoids could have been similar in length to that from Mosbach

(27 mm). The fusion of basisphenoid and basioccipital denied by Schreuder (1929; p. 131) but present in R.G.M. 95405, appears to be an age related feature as in *Castor*. The dimensions of the basisphenoid/basioccipital synostosis in R.G.M. 95405 are similar to those of the Mosbach specimen figured by Schreuder (1929, pl. III, fig. 1) (Tegelen: width 16.5 mm, height 8.6 mm; Mosbach: width 17.7, height 9.0). The rear sutural surface of the presphenoid R.G.M. 28128 is about 8 mm wide and 6 mm deep. The anterior articulation of the basisphenoid (missing in all specimens from Tegelen) must therefore have had these approximate dimensions and the anterior region of the basisphenoid must have been a box section of this size running forward from the front margin of the alae temporalis. The central part of the basisphenoid has an extremely open bone structure consisting of a series of sinuses assumed to be related to venous drainage of the pituitary region. The thickness of this region is variable ranging from 3.4 mm in M.B. Ma101 to 5.1 mm in R.G.M. 28128.

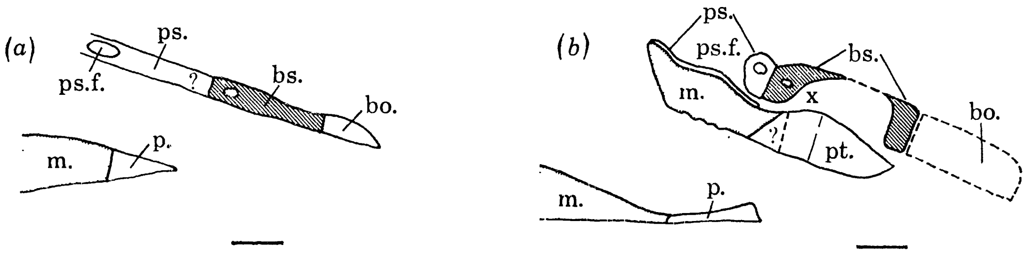

FIGURE 2. Midline sections of basicrania of *Trogontherium*, (*a*) from Tegelen and St Prest ('*T. boisvilletti*') and (*b*) from Mosbach ('*T. cuvieri*') redrawn from Schreuder (1951, figs 3 and 5). bo., basioccipital; bs., basisphenoid; m., maxilla; p., palatine; ps., presphenoid; ps.f., presphenoid foramen; pt., pterygoid; x, supposed 'ductus pneumaticus cranii'. Note the question mark in the presphenoid of (*a*) and between the maxilla and pterygoid of (*b*). The scale mark is 1 cm.

The presphenoid fragment R.G.M. 28128 is the only part of this bone available from Tegelen. It is small (8 mm wide, 6 mm long, 6 mm high) and represents the rear of the bone posterior to the large transverse presphenoid foramen. There are two grooves on the dorsal surface which in life would have underlain the optic nerves and this is similar to the situation in the living beaver *Castor fiber*. The ventral surface consists of smooth bone which roofed the nasopharyngeal passage.

The mid-line length of the basioccipital R.G.M. 95405 is about 19 mm and this specimen is approximately the same size as that figured by Schreuder (1929, p. II, fig. 10).

With this material we are in a position to reconstruct the proportions of the basicranial elements with some degree of accuracy since the size of the sphenoidal fissure may be assessed by the presence of finished or broken edges on the surrounding bones. The length of the presphenoid posterior to the transverse foramen was *ca.* 6 mm; the basisphenoid was at least 24 mm and probably not longer than 27 mm; the basioccipital was *ca.* 19 mm long.

The corresponding figures derived from Schreuder (1951, fig. 3) are presphenoid 19 mm; basisphenoid 22 mm; basioccipital 10 mm and these must be considered incorrect. Old and new reconstructions are compared in figures 2 and 3.

The morphology of the type skull of *Trogontherium boisvilletti* from St Prest, France, was described by Dechaseaux (1967). Sectioning of the skull has revealed a basicranial morphology identical to that reconstructed in figure 1 on the basis of new specimens from the Netherlands. It should be noted that the presence of prominent discontinuities in the St Prest basicranium as illustrated by Dechaseaux (1967, pl. I, fig. 2) was not confirmed by examination of the specimen. The proportions of the basicranial elements as determined by examination of the specimen (I.P. colln.) are: presphenoid rear of foramen *ca.* 5 mm; basisphenoid *ca.* 25 mm; basioccipital *ca.* 18 mm. The basisphenoid and basioccipital of the St Prest specimen are fused, while the presphenoid and basisphenoid are joined by a convoluted suture.

The details of the basicranium of the skull from East Runton, England (B.M.N.H. M6127) described by Newton (1892) were obscured by oxidized iron cemented deposits. Preparation of the specimen reveals a configuration similar the St Prest specimen with basioccipital and basisphenoid fused. The mid-line length of the basioccipital is *ca.* 18 mm.

The evidence from these skulls is in accordance with the proposed new reconstruction of the basicranium of specimens allocated by Schreuder to *Trogontherium boisvilletti*.

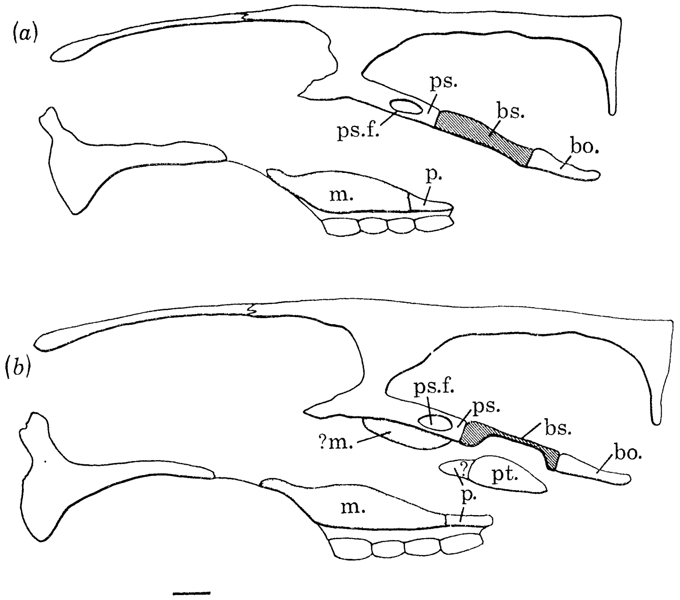

FIGURE 3. Midline reconstructions of the skull of *Trogontherium cuvieri*. (*a*) *T. c. boisvilletti* from Tegelen and St Prest. The correct proportions of the pre- and basisphenoid differ from Schreuder's reconstruction (fig. 2*a*). (*b*) *T. c. cuvieri* from Mosbach. In this alternative reconstruction of the specimen described by Schreuder (1929), and lost in the war, the upper nasal passage rejoins the lower beneath the presphenoid instead of passing into the presphenoid foramen (cf. figure 2*b*). It is uncertain whether the palatines met anterior to the pterygoids. The skull dimensions are based on specimens from East Runton and Taganrog (type of *T. cuvieri*). The scale mark is 1 cm; abbreviations are as in figure 2.

The partial skull from Mosbach, Germany described by Schreuder (1929) consisted of the maxillae and part of the basicranium. Six views of it are included in Schreuder's excellent illustrations (1929, pl. II, fig. 2; pl. III 1*a*–*c*; pl. IV 1*a*, *b*) together with the probable appearance in mid-line and transverse section (1929, pl. III, fig. 2; pl. IV, fig. 2). In ventral view the internal pterygoid plates met on the mid-line so that the internal narial opening was divided in a way similar to that found in the large extinct N. American *Castoroides* (Stirton 1965). The basisphenoid was hollowed out centrally, being paper thin on the mid-line, where some of the bone was broken away providing an opening from the pharynx to the cranial cavity which is most unlikely to have existed in life. Schreuder (1929, 1951) suggested that the cavity in the basisphenoid extended forward into the presphenoid foramen as a 'ductus pneumaticus cranii'. Such a connection between the orbits and the pharynx is again most unlikely, but reinvestigation of this interesting specimen is not possible as it was lost during the Allied bombing of Mainz (Schreuder 1951).

However, some information can be gained from Schreuder's figures, according to which the length of the presphenoid rear of the presphenoid foramen was *ca.* 6 mm and the length of the basisphenoid, which was preserved entire, was *ca.* 27 mm. The smooth rear margin of the basisphenoid indicated that it was not yet fused to the (missing) basioccipital, and the cheek tooth wear-stage suggests an age younger than the skull from East Runton in which these bones were fused. Schreuder's mid-line reconstruction of the Mosbach specimens is reproduced here as figure 2*b*. The photograph of the ventral view (Schreuder 1929, pl. II, fig. 2) indicates that the nasal passage was full of matrix at the time the plates were made, and this suggests the reason for the question mark in between the maxilla and pterygoids in her midline reconstruction. I propose that in view of this uncertainty, the specimen might be interpreted differently. Instead of passing through the presphenoid it is more likely that the upper pharyngeal passage reunited anteriorly with the lower nasal opening beneath the presphenoid (figure 3*b*). This interpretation retains the presphenoid as a roofing element of the nasal cavity in contrast to Schreuder's reconstruction where it is excluded by the maxilla.

The type skull of *T. cuvieri* (Moscow) was first described by Fischer de Waldheim (1809) and has since been refigured by Cuvier (1823), Rouillier (1847) and Gromova (1968). Although unable to see the original I have examined the cast (G.S.M. colln) used by Newton (1892) for his comparison of the skulls from East Runton, St Prest and Taganrog. The internal pterygoid laminae are well preserved but although they come close together on the mid-line it is impossible to judge whether they join. This specimen has a conspicuous hole *ca.* 9 mm wide and 6 mm deep in the basioccipital region, in a similar position to the large occipital fossa of *Castor*. In 1929, Schreuder agreed with Newton that this must have resulted from 'injudicious clearing away of matrix'. In 1951, after the loss of the Mosbach specimen, she suggested however that Newton had made an error and that the hole was an upper nasal passage similar to that of *Castoroides*. The concentric grooves visible on the cast of the Russian specimen lead me to agree with Newton (1892) that the hole has been excavated by rotation of a blunt instrument. The hole lies too far back to be considered an upper nasal passage and it must surely penetrate the basioccipital bone which is ridged in that region. At present it is not possible to estimate the lengths of the basicranial bones of the type specimen.

The reconstructions of the basicrania of *T. cuvieri* and *T. boisvilletti* given by Schreuder (figure 2) differed so greatly that it was not possible to derive one configuration from the other. Accordingly she supposed that the species represented separate lines of descent from *T. minus* which were coeval but separated in space by the river Rhine, and the stratigraphic evidence available at that time did not deny that possibility. The reinterpretation given here (figure 3) indicates that the proportions of the basicranial elements were the same in both taxa so that a direct phyletic connection is possible.

The probable stratigraphic relations of important *Trogontherium* localities in terms of the British sequence are summarized in table 2. The correlations are based largely on evidence from the mammalian fauna (see for example van der Meulen 1973; von Koenigswald 1973; Kretzoi 1965). Discussion of individual sites is given in Hooijer 1959 (Neede); Kretzoi & Vértes 1965 (Vértesszöllös); Brüning 1970 (Mosbach); Kretzoi 1965 (Voigtstedt); Zagwijn 1963 (Tegelen); Sulimski 1964 and de Bruijn 1974 (Weze) and Franzen & Storch 1975 (Dorn-Dürkheim). Specimens allocated on Schreuder's criteria of skull and tooth morphology to *Trogontherium cuvieri* (Neede, Vértesszöllös, Jockgrim, Mosbach, Mauer) postdate those which have been identified on Schreuder's criteria as *T. boisvilletti* (Voigtstedt, Süssenborn, St Prest, Tegelen, Cromer Forest-Bed series). Combining the results of reinvestigation of the basicranium and stratigraphy it is most economical to conclude that *T. cuvieri* postdated and was derived from *T. boisvilletti*.

In order to underline this relation and the similarity of the taxa they are treated here as temporal subspecies. *T. cuvieri boisvilletti* existed from the Early Pleistocene Tiglian through to the end of the Cromerian *sensu stricto* (Upper Freshwater Bed, West Runton) while the temporal range of *T. c. cuvieri* in Western Europe covered a period equivalent to the Anglian and Hoxnian stages of British stratigraphy (probable Elster/Holstein correlates).

TABLE 2. STRATIGRAPHIC ARRANGEMENT OF EUROPEAN *TROGONTHERIUM* LOCALITIES

Time axis not to scale. The crosses indicate probable gaps in the British sequence (see also Zagwijn 1975). The boundary between Villanyian/Biharian is placed in the Eburonian by van der Meulen & Zagwijn (1974).

	Britain		Continental Europe		*Trogontherium* taxa
	stages	localities	localities	stages	
Upper Pleist.	Flandrian	no record	no record	Flandrian	
	Devensian			Weichselian	
	Ipswichian			Eemian	
	Wolstonian			Saale	extinct
	Hoxnian	Hoxne	Neede clay	Holstein	—
		Ingress Vale			—
		Copford			—
		Clacton			—
	Anglian × × × × × × ×		Jockgrim	Elster	*T. cuvieri cuvieri*
			Vértesszöllös	400 ka	
Middle Pleist.			Mosbach		—
			Mauer		—
	Cromerian	U.F.B. West Runton	Voigtstedt		—
			Süssenborn		—
	Beestonian	C.F.B. Series			—
	× × × × × × × × × ×				—
	Pastonian	East Runton	St Prest		—
		Sizewell			—
	× × × × × × × × × ×				—
	Baventian	Easton Bavents		Eburonian	
				1.6 Ma	*T. cuvieri boisvilletti*
Lower Pleist.	Antian		Tegelen Clay	Tiglian C	—
	Thurnian				—
	Ludhamian				(*T. minus dacicum*)
	Pre Ludhamian				—
					—
	× × × × × × × × × ×		Hájnàčka	3–4 Ma	*T. minus minus*
		Red Crag			
Pliocene		Nodule Bed			

The changes through time in the basicranium appear to be related to a size increase in the genus which is discussed in subsequent sections. Mid-line apposition of the internal pterygoid plates of *T. cuvieri* was due to expansion of the insertion areas of the internal pterygoid muscles, while the excavation of the basisphenoid (of the order of 3 mm) may have acted to maintain the diameter of the upper nasal passage as the pterygoid plates grew together in ontogeny and phylogeny.

4. VARIATION WITHIN AND BETWEEN POPULATIONS

Although remains of *Trogontherium* are not especially common, a considerable amount of material has been recovered from Tegelen (Netherlands), Mosbach (West Germany) and the British Cromer Forest-Bed series. These three samples appear on faunal and vegetational evidence to date from separate periods in the Early and Middle Pleistocene and provide an opportunity to investigate changes in size and morphology through time in a limited geographical area. Material in the following collections was examined: B.M.N.H., G.S.M., N.C.M., I.M., R.G.M., T.M., S.M.F., H.L.D., N.H.M.M., G.U.H.

Intrapopulation variation may be considered to result from sexual dimorphism, ontogenetic changes and individual variability. Although sexual dimorphism is known to occur in rodents such as ground squirrels (Meyer 1953), recent beavers (*Castor fiber* L.) are not sexually dimorphic in skull measurements (Lavrov 1969). Measurements of *Trogontherium* remains from a single site do not yield bimodal histograms and the values of the coefficient of variation (V) do not suggest a greater variability than *Castor*. Accordingly it is assumed in the following account that there was no sexual dimorphism in the skeleton of *Trogontherium*.

Assessment of ontogenetic age relies on methods of absolute or relative age determination. While it is probable that the periosteal bone of *Trogontherium* contained periodic units such as those described in recent *Castor* by Klevezal & Kleinenberg (1969), these have not yet been examined in the fossil material. Periodic variations in cement optical density perhaps related to seasonal variations in physiology are visible in ground sections of *Trogontherium* cheek tooth roots but although further work may enable reliable absolute ageing it is more convenient at present to determine relative age by tooth wear and to compare this with wear rates in *Castor* for approximate absolute calibration.

TABLE 3. *TROGONTHERIUM* AGE CLASSES BASED ON LOWER PREMOLAR WEAR

age class	number of isolated loops on premolar	approx. crown height equivalent (mm)
1	0	5
2	0, 1†	5
3	2	5
4	3	5
5	4	5

† age classes 1 and 2 were distinguished by the wear pattern of the molar teeth.

The relative age classes adopted here are based in a study of changes in grinding surface enamel pattern of the lower cheek teeth in relation to tooth crown height in a large sample from Tegelen. The enamel flexids (Stirton 1935) became isolated with wear as islets on the grinding surface. The timing of changes in pattern in relation to crown height appears to have been relatively constant in the Tegelen population and the categories in table 3 were adopted.

The first age class also includes the time between birth and the eruption of the premolar (between six and ten months in *Castor*, Larson & van Nostrand 1968) and so probably corresponds to more than a fifth of the observed maximum life span, which was limited by the dentition. In the following account the effect of ontogeny has been minimized by excluding animals in the first two age groups from interpopulation statistical comparisons. This excludes at least the first two fifths of the maximum life span and covers the time of maximum growth.

(*a*) *Teeth*

(i) *Incisors*

The incisors of *Trogontherium* with characteristic finely rugose enamel form a considerable part of museum material of this genus. Metrical relations have not been investigated in detail although Hooijer (1959) noted some differences in the length/width index of lower incisors allocated to *T. cuvieri* and *T. boisvilletti* and Guenther (1965) demonstrated differences in the radius of curvature of upper and lower incisors in relation to the width. The present account uses scatter diagrams to compare the length and width of incisor cross section of material from European sites. The relation between these two measurements is a straight line for teeth from a single site over the size range investigated. As the backward extension of the line does not however intercept the axes at zero the length/width index used by Hooijer (1959) is size dependent and not a good measure of population differences. Although there is overlap in scatters from lower incisor samples from Tegelen (Early Pleistocene) and Mosbach (Middle Pleistocene) (figure 4) the scatters appear to be summarized best by separate trend lines. The reduced major axes shown here have the same slope but differ in location indicating that incisors from Tegelen are on average about one millimetre narrower than those from Mosbach. The maximum size is similar in both populations. The significance of the difference between the scatters was tested by covariance analysis (Kurten & Rausch 1959; Snedecor 1956) with the null hypotheses that both were derived from the same population. The variance ratio ($F = 16.9$, d.o.f. 1,54) corresponded to a low probability ($p = < 0.001$) and implies a highly significant difference between the samples.

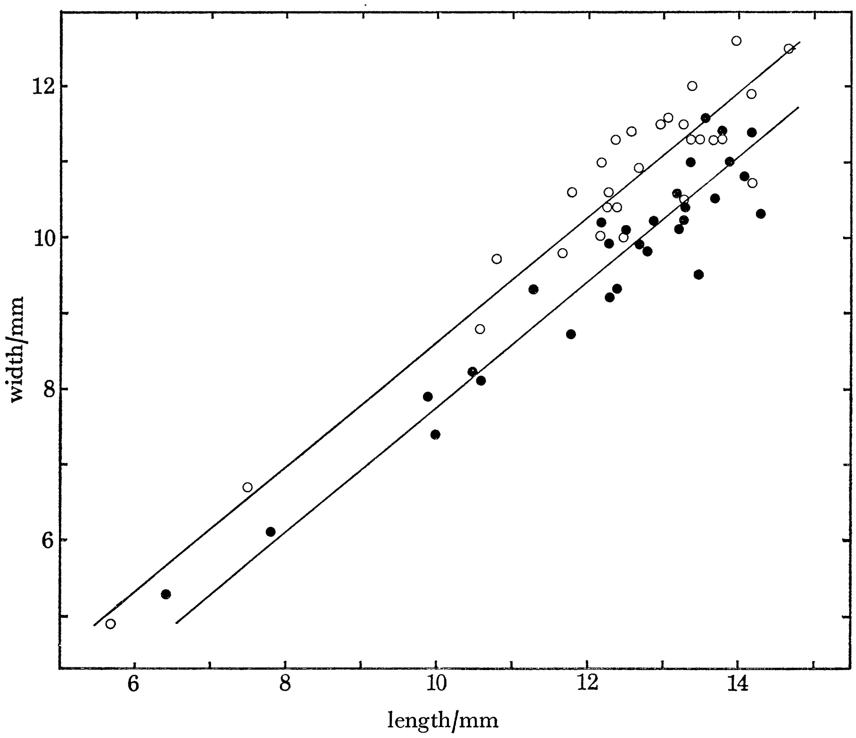

FIGURE 4. Scatter diagram of width against length of lower incisor cross-section in *Trogontherium* from Tegelen (●) and Mosbach (○). The trend lines are the reduced major axes indicating a significant difference in relative width between the samples (see text).

Measurements from specimens from other sites are compared with the reduced major axes of the Tegelen and Mosbach samples in figure 5. Measurements from Voigtstedt (Guenther 1965), Süssenborn (Kretzoi 1969), Episcopia (Schreuder 1935), Neede (Hooijer 1959) and Ingress Vale (Newton 1902) have been supplemented by values from teeth found at Mauer, Jockgrim and British Forest-Bed localities (G.U.H., H.L.D., B.M.N.H., G.S.M., N.C.M. collections). The sample from the Forest-Bed series dating from at least two climatic oscillations is intermediate in geological age between Tegelen and Mosbach samples but corresponds better to the trend line of the Tegelen sample. Remains from the Upper Freshwater Bed, West Runton (Cromerian) are the largest known of *Trogontherium*. The teeth from Voigstedt and Süssenborn, probably equivalent in age to the type Cromerian of West Runton (van der Meulen 1973), are of comparatively modest size and lie in a position intermediate between the Tegelen and Mosbach trend lines.

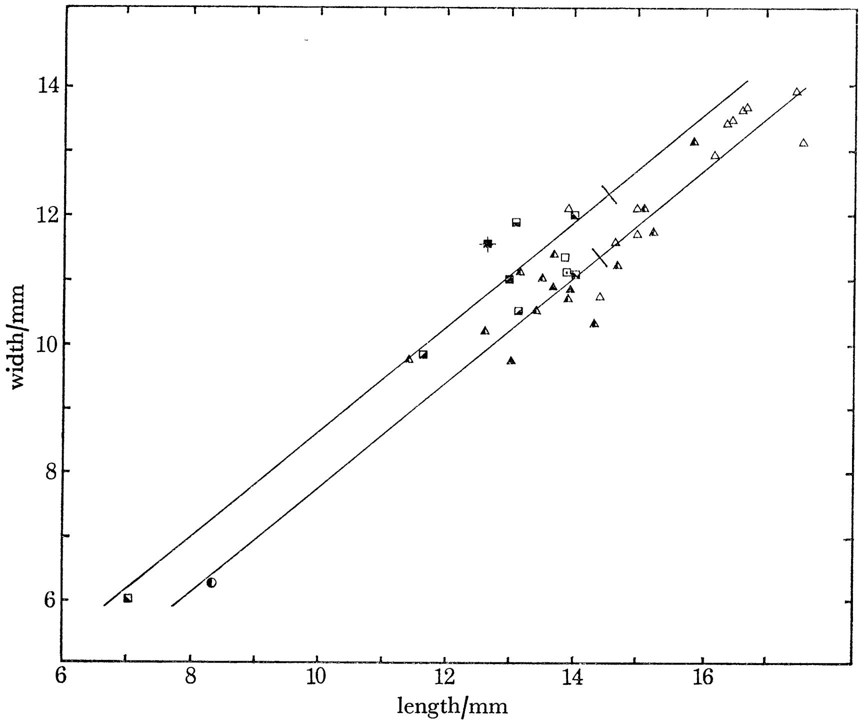

FIGURE 5. Scatter diagram of width against length of lower incisor cross-section in *Trogontherium* from Early and Middle Pleistocene sites. The trend lines are reduced major axes of the Mosbach and Tegelen samples (figure 4) with the upper limit of these scatters marked by transverse lines. Cromerian material from West Runton corresponds to the trend line of Tegelen but is of larger maximum size.

Key to figures 4, 5 and 6: △ U.F.B. West Runton, ▵ Undivided Cromer Forest-Bed series, ▲ East Runton, ◬ Easton Bavents, □ Suessenborn, ⧅ Voigtstedt, ◪ Jockgrim, ⊡ Mauer, ⬒ Episcopia, ■ Ingress Vale, ✱ Neede, ○ Mosbach, ● Tegelen, ◐ Sizewell.

Two teeth, from Neede and Ingress Vale, are derived from apparently Hoxnian deposits and it is notable that the Neede specimen falls to the left of the Mosbach trend line outside the scatter of material from this site

These scatter diagrams support the view that there was a significant progressive change in relative incisor dimensions through time and that the maximum size was attained in the Cromerian with a decrease in the subsequent (Mosbach) stage. Size differences between the three main samples are not due to ontogenetic effects since each sample consists mainly of old animals in which individual maximum size had been attained. In *Castor* the growth curve of incisor dimensions reaches a plateau at about five years of age (Mayhew 1975).

Rather fewer upper incisors are available for comparison since these appear to survive the processes of fossilization less well. British material from the Upper Freshwater Bed, West Runton is of very large size (see figure 6). A single young tooth from this site yields the two points connected by a line. Material from Voigtstedt lies on a similar trend to that from West Runton whereas Tegelen specimens appear to be relatively less wide. These conclusions are in accordance with those from lower incisor investigations.

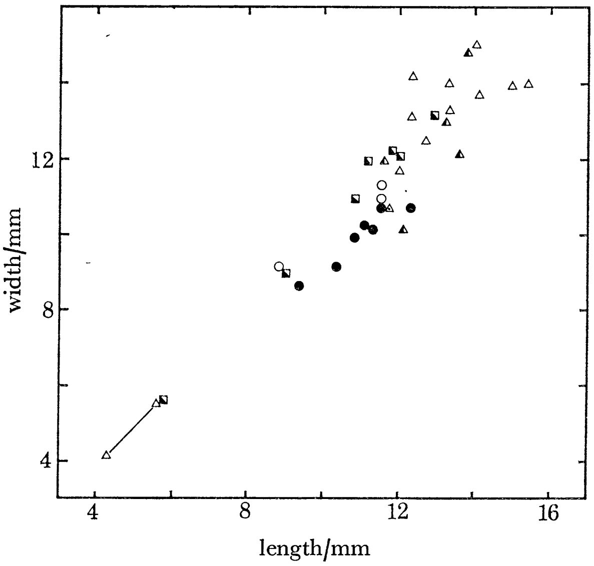

FIGURE 6. Scatter diagram of width against length of upper incisor cross section in *Trogontherium*. See figure 5 for key. Cromerian specimens (open triangles) are of extremely large maximum size and are similar in proportion to those from Voigtstedt (squares). Tegelen specimens (closed circles) are slightly narrower than teeth from later deposits.

(ii) *Cheek teeth*

The premolars of *Trogontherium* are massive teeth much larger and rather higher crowned than the molars. At least 6 mm of the crown of the lower premolar remains in aged specimens in which the crown of the third molar has been completely worn away. It seems possible that in some cases the lower third molar may have been lost before death. Dentitions sufficiently worn to have lost efficient grinding function occur in a number of specimens, leading to the conclusion that selection pressure for improvement of the dentition may have acted provided that these old animals were still of reproductive age. Functional improvement in the lower premolar of *Trogontherium* can be seen in a comparison of the wear surface enamel in different populations. In Early Pleistocene samples (Tegelen) the basic castorid pattern of four striids and flexids is supplemented in some teeth by an additional antero-internal striid which gives rise to a small indentation on the enamel of the wear surface. The antero-internal accessory striid does not extend below the base of the hypostriid and is thus not visible in old animals (age group 5) which inevitably bulk largely in the fossil sample. In teeth of younger age, 7 had a prominent fold, 16 had a small less obvious fold and 19 lacked it.

This indicates considerable variation in this character on which selection could have acted. Teeth from the Cromer Forest-Bed series are derived largely from old animals and as such are too worn to show the nature of the accessory fold. In those of younger age only a few specimens show additional enamel at the front of the crown. A small islet of enamel is isolated in the anterior dentine region of the wear surface of teeth illustrated by Newton (1882, pl. IX fig. 9). Such a condition has not been noted in specimens from Tegelen. An accessory fold starting below the wear surface and reaching below the base of the hypostriid is present in two associated lower premolars from Pakefield. As these are young teeth it is not possible to establish whether the accessory fold would have resulted in an additional islet of enamel on the wear surface.

All the lower premolars from Mosbach examined by Schreuder (1929) and myself (upwards of fifty specimens) show a long accessory flexid reaching from the top of the crown to below the end of the hypostriid. With wear, this flexid gave rise to a large isolated enamel islet lying anterior to the paraflexid.

The stratigraphic boundary between populations possessing a well developed antero-internal accessory fold and those in which it was poorly developed appears to lie between the Cromerian (zone II) and the 'Mosbach' stage (a non-glacial stage post-Cromerian and pre-Hoxnian in terms of the British sequence). The typical development of the fold is lacking in specimens from Tegelen, the Cromer Forest-Bed series, Erpfingen (Lehmann 1953, 1957) and Voigtstedt (Guenther 1965), but present in those from Neede (Hooijer 1959), Vértesszöllös (Kretzoi & Vértes 1965), Gombasek (Fejfar 1964), Mosbach and Jockgrim. Only a slight groove is present in specimens from Mauer.

The hypsodont cheek teeth of *Trogontherium* continued to be extruded after eruption although enamel formation at the base had already ceased. Deposition of dentine led to the formation of roots which were important in anchoring the remains of the crowns in old animals. The dentine of the roots was covered with a layer of cementum which occasionally extended up to cover the crown enamel (cf. Schreuder 1929) and has been observed as a thin layer lining the flexids but not occluding their cavity as in *Castor*. Measurement of hypsodont tooth crown dimensions is not easy as in young animals much of the crown is retained in the alveolus and in old animals most has been worn away. Apart from these practical considerations there are no grounds for supposing that comparisons based on size of hypsodont teeth should be any less pertinent than those from brachydont teeth providing that measurements can be accurately diagnosed and thus reproducible.

Schreuder (1929) pointed out that lower premolars from Mosbach were larger than those from Tegelen. Sizes of lower premolars from a number of sites are compared here in a scatter diagram of maximum antero-posterior length against width at the base of the hypostriid (figure 9). The Cromerian specimens from West Runton are larger than but similar in proportions to those from earlier deposits at East Runton and Tegelen. Mosbach specimens are relatively and occasionally absolutely longer than specimens from other sites and this difference in proportions is connected with the presence in premolars from Mosbach of the additional enamel fold discussed in detail above. Mandibular molar teeth from Mosbach do not possess any additional enamel folds and contribute relatively less to the total grinding surface than in animals from Tegelen. (Grinding areas (mm^2) recorded from associated teeth in the same stage of wear from Tegelen and Mosbach were: Tegelen; p4 69, m1 23. Mosbach; p4 95, m1 25).

Although the four cheek teeth together form a closely packed grinding unit, variation in dimensions along the crown heights causes overall measurements at the level of the alveolus to be subject to ontogenetic variation, being generally shorter in old and young specimens.

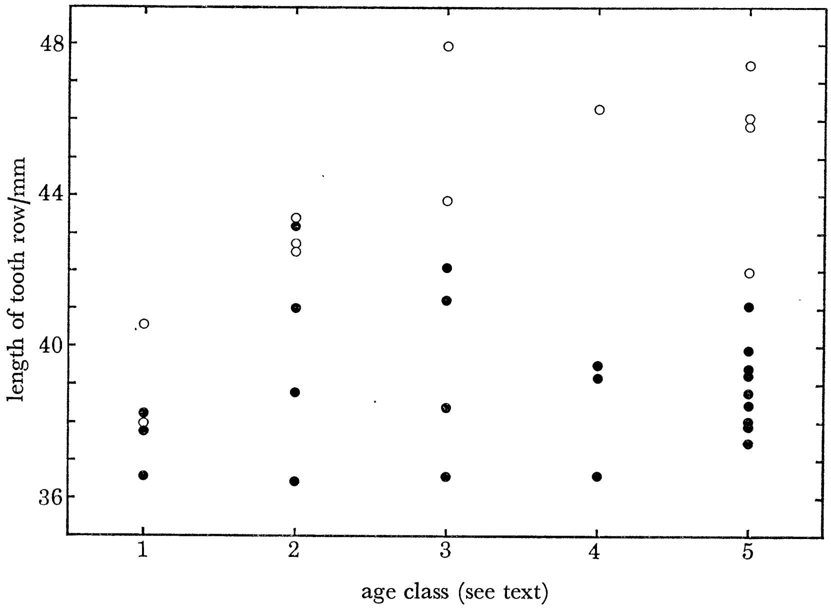

FIGURE 7. Regression of alveolar mandibular cheek tooth row length on age in samples of *Trogontherium* from Tegelen (●) and Mosbach (○). The pronounced age related change in the Mosbach sample is due to an additional enamel fold in the lower premolar.

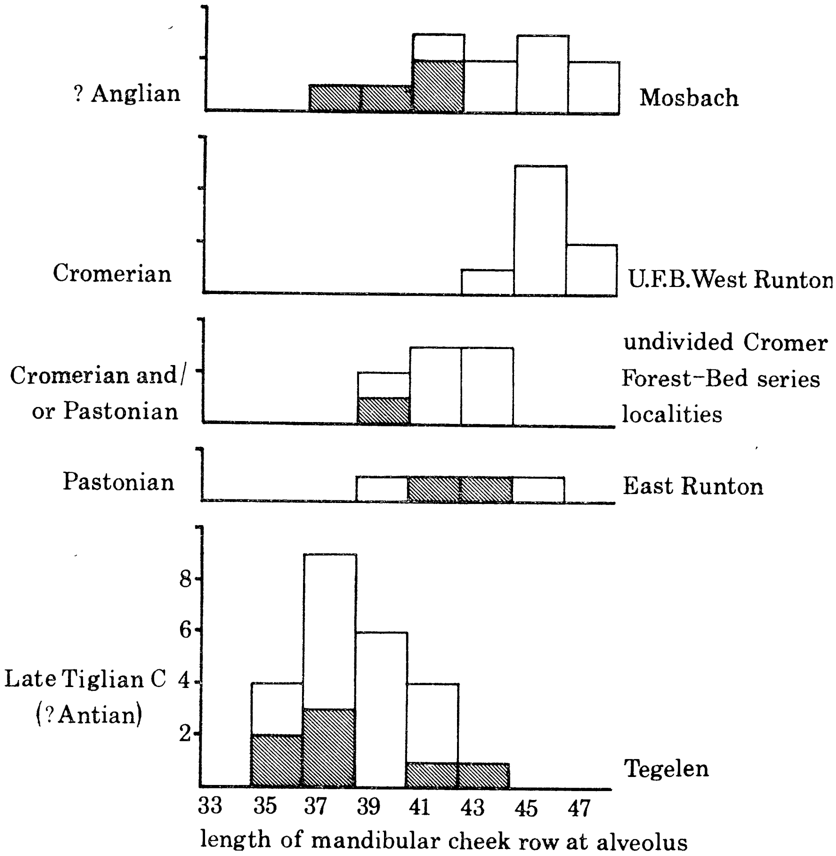

FIGURE 8. Histogram of alveolar mandibular cheek tooth row length of *Trogontherium* from Tegelen, the Cromer Forest-Bed series and Mosbach arranged in stratigraphic order. Young animals (age groups 1 and 2) shaded.

The regression of alveolar mandibular tooth row length on age in samples from Tegelen and Mosbach is given in figure 7 which illustrates overlap between the samples in the first two age groups. Values from these younger animals are stippled in the histogram (figure 8) comparing the same measurement in samples from Tegelen, Mosbach and the Cromer Forest-Bed series which indicates a substantial increase in size through the Middle Pleistocene.

Relatively few maxillae with cheek teeth are available for analysis of size variation within and between samples. The length over the upper cheek teeth at the level of the alveolus in some of the more important specimens is given in table 4.

TABLE 4. MAXILLARY TOOTH ROW LENGTH OF PLEISTOCENE *TROGONTHERIUM* MATERIAL

site	museum/spec. no.	length	age class†	source
Tegelen	R.G.M. 95405	36.1	1	D.F.M.
Tegelen	(n = 7)	37.5–39	?	Schreuder, 1929
East Runton	B.M.N.H. M6127	37.8	3	D.F.M.
St Prest	Inst. Pal. Paris	38.0	4	D.F.M.
Taganrog	Inst. Pal. Moscow	43.7	3	from cast, I.G.S. colln
Mosbach	specimens lost	40, 41	3	Schreuder 1929
Clacton	C.E.M. colln	*ca.*38	1 or 2	J. Heath personal communication

† Similar to that used for the lower dentition.

With the exception of the specimen from Taganrog (of unknown stratigraphic context) table 4 is in stratigraphic sequence with youngest material last.

The limited evidence supports the picture of a size increase in the Middle Pleistocene suggested by measurements of the lower dentition. Although associated and isolated upper teeth have been recovered from type Cromerian sediments at West Runton these remains are insufficient to allow even estimation of alveolar tooth row length. This is an unfortunate gap in the stratigraphic record since other skull remains from this site such as the premaxillae figured by Newton (1882, pl. XI, fig. 2, B.M.N.H. M6135) are the largest known of *Trogontherium*. The specimen (B.M.N.H. M6128) figured by Newton (1882) as a maxilla with premolar and first and second molars from West Runton in fact consists of the left premolar and first molar, with the damaged right premolar from the same aged individual inserted between them in a plaster matrix.

(*b*) *Skull*

Partial skulls from East Runton, Taganrog and St Prest were compared by Newton (1892) and these were considered together with Tegelen specimens by Schreuder (1929). Very few partial skulls and no complete ones have since been recovered. It appears that the skull dimensions reached a maximum in the Cromerian.

(*c*) *Postcranial skeleton*

Very few complete limb bones are available and it is difficult to assess intrapopulation variation of these elements. The following account compares some values from various sites by using an assumed value for the coefficient of variation (V) based on that for a subfossil sample of *Castor fiber* L., an animal of the same overall size as *Trogontherium*.

Measurements other than those taken by myself come from Schreuder (1929) and Guenther (1965).

(i) *Humerus*

Table 5. Humerus measurements with sites arranged in decreasing geological age

site	overall length	proximal width over head and greater tuberosity
Tegelen	85	24.8
Tegelen	—	22.3
West Runton U.F.B. B.M.N.H. M17823	—	29.3
West Runton U.F.B. B.M.N.H. M18080	—	27.3
Voigtstedt	94.0, 94.5, 95.3	—
Jockgrim	85	—
V (*Castor*)	2.7	3.2

The overall length and proximal width appear to be smaller in Tegelen specimens than in those from West Runton and Voigtstedt. Assuming that the value of the coefficient of variation (V), calculated from a sample of *Castor fiber*, is a reasonable estimate for that in *Trogontherium* the significance of the differences can be obtained by first calculating the standard deviation (s.d. $= VX/100$), and then using the fact that the distribution of differences between two values selected at random from a normal population is normal, with mean zero and standard deviation $=\sqrt{2}$ population s.d. The standardised normal deviates calculated from sample differences/$\sqrt{2}$ s.d. indicate that the humerus size increase from Tiglian to Cromerian and the subsequent decrease (Jockgrim) are significant ($p < \cdot 05$).

(ii) *Femur*

Table 6. Femur measurements with sites arranged in probable order of decreasing geological age

site	maximum length	width of distal epiphysis	length over first and second trochanters
Tegelen R.G.M.62883	113.0	33.8	50.5
Tegelen Schreuder 1929	103, 104.5, 104.5, 104.5, 104.5, 108, 108.5, 108.5		
Mundesley B.M.N.H. M40979	106.5	32.5	43.4
West Runton M18071	—	—	46.7
Voigtstedt	108	36	—
Voigtstedt	—	36.5	—
Jockgrim G.U.H. M.Y.H. 19	—	—	44.0
Mosbach N.H.M.M. 58 314	97.4	32.5	—
Mosbach N.H.M.M. 53 35	—	41.3	—
Mosbach N.H.M.M. 53 58	—	37.7	—
Mosbach	—	—	44.0
Hoxne I.M.	—	—	47.5

The femur lengths of Tegelen specimens yield the following statistics: mean 106.5, s.d. 3.18, range 103–113, $n = 9$ and $V = 3.0$. The coefficient of variation of the overall femur length in a sample of subfossil *Castor fiber* was 4.2 and this provides a check for the assumption of similar variability in both genera. Although there are many gaps in the table of measurements due to damaged material it is clear that no case for an increase in overall size through time can be made. Indeed it is notable that the femur from Mosbach is significantly smaller than the Tegelen mean ($t = 2.75$, $p < 0.02$)

(iii) *Tibia*

Table 7. Tibia measurements in order of decreasing geological age

site	maximum length	lateral width of distal articulation	antero-posterior width of distal articulation
Tegelen	153	30.0	16.0
Tegelen R.G.M.47409	—	29.2	15.7
East Runton B.M.N.H. M7020	—	—	17.4
East Runton B.M.N.H. M7022	—	—	15.1
Paston G.S.M.659	—	28.0	16.3
Mundesley B.M.N.H. M3573	—	—	17.5
Mundesley B.M.N.H. M7021	—	—	17.9
Mundesley G.S.M. 7345	—	34.3	20.9
West Runton U.F.B. N.C.M. 329.968	—	36.0	20.1
West Runton U.F.B. N.C.M. 3536	—	32.5	18.3
Jockgrim G.U.H.	—	27.6	15.5
Mosbach N.H.M.M. 1959/84	161	29.6	17.8

The tibia was fused to the fibula throughout life. Such fusion occurs in *Castor fiber* only in a few individuals of advanced age. The proximal part of the fibula and the proximal tibial epiphysis are almost invariably missing in fossil material and although the width of the distal part of the tibio-fibula provides a rough guide to size, the measurement includes the lateral and medial malleoli which were prominent and fragile structures in this genus. They are usually more or less abraded in fossil material but are well preserved in N.C.M. 329.968 (West Runton U.F.B.). The figures in the table provide some support for the suggestion of size fluctuations through the Middle Pleistocene. The difference in size between specimens from East Runton (Pastonian) and West Runton (Cromerian) is particularly striking and is significant at the 95% level if a value of $V = 5.0$ derived from the same measurement in *Castor* is assumed. However, with a value of V of 2.8 (as in *Castor*) for tibia overall length, the Mosbach specimen is not significantly larger than that from Tegelen.

In summary, although practically all elements of the skeleton of *Trogontherium* are known, only the teeth are sufficiently abundant to enable confident investigation of variation within and between populations. When ontogenetic differences are taken into account there is clear evidence of change in absolute size and relative proportion of the teeth through the Early and Middle Pleistocene in a small geographical area. The limited measurements from cranial and post-cranial bones in general support the sequence of size changes suggested by the dentition. It is possible that later populations may have differed from earlier ones in the proportions of the limb bones (for example, the femur may have become shorter and the tibia longer) but at present, discussion must be limited to statistical comparisons of isolated limb bones because hardly any articulated remains of *Trogontherium* have been recovered.

5. Evolutionary history of the genus *Trogontherium*

With the proposed reinterpretation of Pleistocene populations the history of the genus during this period can be viewed as an increase in size in a single lineage extending back into the Pliocene. Earlier representatives have been found at a number of localities dating back to Turolian and the purpose of this section is to review this material and to discuss changes particularly in comparison with those in the lineage leading to the extant beaver *Castor fiber*.

Stirton (1935) suggested that the genus *Trogontherium* originated from small 'Upper Miocene' forms placed by him in the genus *Monosaulax* and this view is reaffirmed here by the inclusion of these specimens in the genus *Trogontherium*, a step proposed independently by Franzen & Storch (1975). Since the review of Stirton (1935) the generic names *Steneofiber*, *Monosaulax* and *Palaeomys* have been applied indiscriminately in such a way as probably to confuse relationships and several new names have been introduced by Radulesco & Samson (1967, 1972) for material dating from 'Early Villafranchian' deposits in Roumania. The dental characters considered here to define the genus *Trogontherium* within the Castoridae are: more or less hypsodont cheek teeth with dentine roots and little or no crown cement; relatively large premolars; a long upper third molar with cone shaped wear surface and a number of extra enamel flexids; incisors with wrinkled enamel on the convex anterior face. Other skeletal characters are dealt with in detail in Schreuder (1929).

Teeth corresponding to this description but smaller than those of *T. cuvieri* have been recovered from Late Pliocene/Early Pleistocene deposits in England (Newton 1890), Czechoslovakia (Fejfar 1964) and Germany (Giebel 1860). These specimens are referred to the species *T. minus* Newton 1890, the nomenclature of which is discussed in a later section.

A mandible from Slatina, Roumania, of 'Upper Villafranchian' age described by Radulesco (in Conovici & Radulesco 1972) as *T. boisvilletti dacicum* n.ssp. has teeth intermediate in size between specimens of *T. minus* from Hájnàčka (Fejfar 1964) and material from Tegelen which is referred here to the subspecies *T. cuvieri boisvilletti*. This Roumanian material, which is valuable in providing a temporal and metric intermediate, will be arbitrarily treated here as a large subspecies of *T. minus* as I wish the specific boundaries of the generic lineage to be located near such biostratigraphically and absolutely well dated horizons as the Tegelen clay.

According to Radulesco & Samson (1967, 1972) at least five castorid taxa are represented by remains from Pliocene deposits (including 'Lower Villafranchian') in Roumania. A large species related to the living beaver *Castor* and referred by them to *Castor praefiber* Deperet 1890 was found at Malusteni, Beresti and Capeni. These localities have also yielded remains of smaller castorids all of which are referred here to the genus *Trogontherium*. Specimens allocated to *Zamolxifiber covurluiensis* by Radulesco & Samson (1967) included a mandible fragment with p4–m3, a lower premolar and a fragment of lower incisor. They noted that the internal pterygoid fossa of the mandible was divided into two; the anterior part being small, shallow and situated below the lower third molar. This is an accurate description of the insertion area of the superficial masseter muscle, pars reflexa, of *Trogontherium* which is also visible in the illustrations of Schreuder (1929, pl. V, fig. 10). The finely rugose enamel of the convex faced incisor, the roots of the cheek teeth, the absence (judging from their illustration) of crown cement and the nature of the striids all indicate that the material belongs instead to *Trogontherium*. The solitary lower premolar referred by Radulesco & Samson (1967) to *Romanocastor filipescui* was similar in size to teeth referred to *Zamolxifiber* but differed in striid lengths. The tooth differs significantly from *Trogontherium* only if one adopts a typological species concept based on inadequate knowledge of intrapopulation variation in crown morphology. The lower premolar type of *Romanocastor capeniensis* (see Radulesco & Samson 1972) is smaller than those discussed above but otherwise differs in no way from the morphology of *Trogontherium*. This Roumanian material is referred here to the species *T. minutum* (von Meyer 1838) which is considered to cover the initial time segment of a lineage leading to *T. minus* and finally *T. cuvieri*. *T. minus* is according to Radulesco & Samson (1972) known from Roumania only by an incisor, a fragmentary humerus and a metatarsal from Cernatu dating most probably from 'phase II of the lower villafranchian'.

The well preserved facial part of skull and partial lower jaw of a small castorid found at Weze, Poland, were referred by Sulimski (1964) to a new species *Steneofiber wenzensis*. The excellent figures given by this author indicate that despite the small size of this specimen it should be referred to *Trogontherium* on the basis of skull and tooth morphology. The elongate posterior palatal foramen, the depressions in the maxillae anterior to the premolar and the shape of the anterior masseteric muscle insertion areas are particularly characteristic. The lower premolar dimensions of the Weze specimen (figure 9) are similar to those of the specimen from Capeni identified by Radulesco & Samson (1972) as *Romanocastor capeniensis*. According to these authors however the Weze material is to be considered the type of a new genus, *Boreofiber*. Their generic description (Radulesco & Samson 1972) merely underlines the similarities between this material and that previously treated as *Trogontherium* and no characters separating the two genera are proposed. In the view of Radulesco & Samson the similarities between *Trogontherium*, '*Boreofiber*' and '*Steneofiber*' *minutus* are characters in common of no taxonomic relevance. In the view proposed here the similarities are taken as derived characters indicating that the three taxa should be included in a single genus *Trogontherium*.

The age of the material from Weze (a karst doline filling) is subject to discussion and can in any case be determined only biostratigraphically. According to Sulimski (1964) the remains of *Steneofiber wenzensis* were derived from older breccias of uncertain age whereas the main fauna from younger deposits appears to be Ruscinian on the basis of the rodent fauna (de Bruijn 1974).

New material from Dorn-Dürkheim, D.B.R., described by Franzen & Storch (1975) as *T. minutum rhenanum* n.ssp. represents an important sample of the early part of the lineage in which individual teeth are numerous enough to enable estimation of variation in size and morphology. The illustrations given by these authors leave no doubt that the material is correctly referred to *Trogontherium* despite its relatively small size. The Dorn-Dürkheim specimens are allocated by Franzen & Storch (1975) to the Turolian on biostratigraphic grounds and they suggest that Vallesian material from Spain is also referable to *Trogontherium minutum* (von Meyer). The type material of this species from Elgg, Switzerland, described by von Meyer (1838) as *Chalicomys minutus*, was redescribed by Stirton (1935) as '*Monosaulax*' *minutus*. This species was placed in a new genus *Euroxenomys* by Samson & Radulesco (1973) on the basis of differences between it and the North American genotype of *Monosaulax* Stirton 1935. In the usage of the present paper *Euroxenomys* is a synonym of *Trogontherium*.

A further specimen assignable to *T. minutum* was described from Pliocene deposits at Pont-de-Gail by Ginsburg (1975) as *Monosaulax sansaniensis*. A larger castorid identified as *Castor praefiber* was also present.

The size relationships of the material discussed above are summarised in figure 9 which compares maximum length and breadth of the lower premolar crown. All of the measurements are comparable, although those of the Dorn-Dürkheim (taken from Franzen & Storch 1975) and Weze (Sulimski 1964) material refer to similar dimensions at the wear surface. The proportions of the premolar in the three species of *Trogontherium* recognized here are similar whereas the absolute size differs markedly. In general the stratigraphic relations of the small specimens assigned to *T. minutum* agree with the assumption that this species pre-dated and gave rise to *T. minus*. An apparent exception to this is the lower premolar from Capeni which dates according to Radulesco & Samson (1972) from 'Villafranchien inferieur', phase I. These authors however use the term 'Villafranchien inferieur' in a sense wide enough to include the Weze castorid material which is of probable pre-Ruscinian age. The associated fauna from Capeni (Alimen, Radulesco & Samson 1968) consists only of larger mammals and might date from the later Pliocene or Early Pleistocene on the basis of the Proboscidea (see Tobien 1968). Recovery of micromammalia from the lignite at Capeni may be expected to enable a more precise dating of the deposit in relation to local European stratigraphic sequences and especially in relation to other castorid localities in the Balkan area. Until this is done it is not in my view necessary to regard the specimen from Capeni as invalidating the scheme of temporal succession of *Trogontherium* species proposed here.

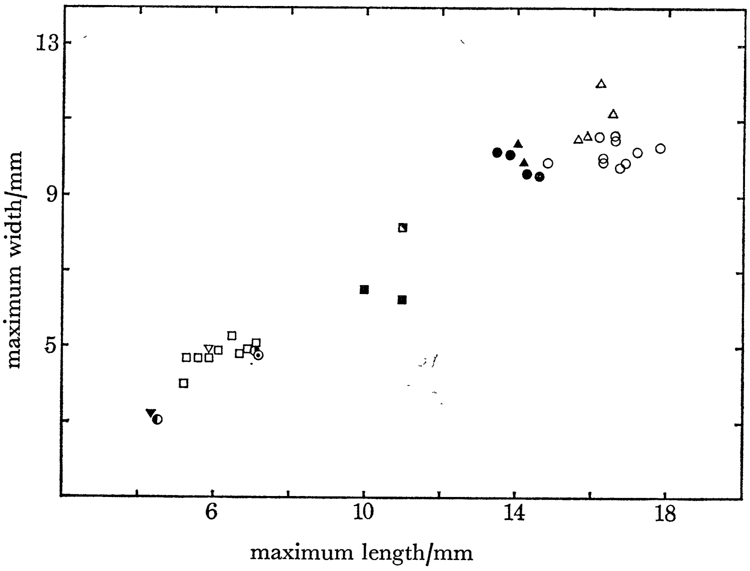

FIGURE 9. Scatter diagram of lower premolar dimensions of *Trogontherium* from Pleistocene and Pliocene localities demonstrating a size increase in this lineage over a time course of about six million years. The three groups correspond to the species. *T. minutum* (small), *T. minus* and *T. cuvieri* (large).

Key to figure 9; △ U.F.B. West Runton, ▲ East Runton, ○ Mosbach, ● Tegelen, ◪ Slatina, ■ Hájnáčka, □ Dorn-Duerkheim, ◑ Malusteni-Beresti ('Zamolxifiber'), ⊙ Malusteni-Beresti ('Romanocastor'), ▽ Pont-de-Gail, ▼ Weze, ◐ Capeni. References to these sites are given in the text.

The origin of the living genus *Castor* lies in the Vallesian and Turolian genus *Palaeomys* which had already acquired tooth crown cement and flattened faced incisors. In *Palaeomys* the cheek teeth possessed clear roots which appear to have consisted of dentine. In *Castor fiber* there are no dentine roots but the base of the tooth is covered by successive layers of cement which are layed down in annual units and partly compensate for wear at the top of the crown. The situation in later Pliocene beavers referred to *Castor praefiber* is uncertain but no dentine roots are present in British material from the Red Crag basement bed (L. Pliocene/E. Pleistocene) referred by Lankester (1864) and Hinton (1914) to *Castor veterior* Lankester. Some teeth from this source differ from later Pleistocene populations in the shorter length of the striae and striids (Stirton 1935) in respect of the total crown height (Mayhew 1975).

From the Turolian to the Middle Pleistocene the size of *Trogontherium* teeth more than doubled in linear dimensions whereas those of *Castor* did not increase in size to an extent greater than the fluctuations through the Pleistocene or current geographical size variation (Mayhew 1975). The change in relative size during this time may have had an effect on the ecological relations of the two species and in particular may have brought them into more direct competition since later populations of *Trogontherium* were similar in body size to *Castor*. Some modifications of the current views of the ecology of *Trogontherium* and their anatomical basis are discussed in the following section.

6. Ecological conclusions from anatomy, geology and palaeobotany

Present ideas on the ecology of *Trogontherium* are derived from the work of Schreuder (1929, 1951) who suggested that the animal was probably aquatic and had webbed hind feet. It was also suggested that the feeding habits included tree felling, using the large incisors, and browsing on floating vegetation with large, perhaps prehensile, lips. These views were based on the anatomical evidence then available and now require some revision. Other inferences of the ecology of *Trogontherium* particularly in relation to the extant beaver *Castor* may be drawn from geological and palaeobotanical investigations which will also be considered in an attempt to provide a more satisfactory synthesis.

The incisor teeth of *Trogontherium* had convex anterior enamel faces which determined that the cutting edges were rounded rather than straight as in *Castor*. The lower incisor was particularly sharp-pointed and its action during occlusion resulted in excavation of a large area to a thickness of only a few millimetres extending back as much as two centimetres from the rounded cutting edge of the upper incisor. Because the occlusal relation of the incisors did not have the cutting action necessary to slice woody tissue I regard it as unlikely that *Trogontherium* felled trees as Schreuder (1951) suggested. The upper incisor wear surface appears by its thinness to have been relatively weak although it may have functioned well for removal of bark. In a discussion of the habits of the extinct N. American beaver *Castoroides*, Stirton (1965) pointed to similar features of the incisors which suggested to him that this animal also did not systematically fell large trees. Remains of wood gnawed by beavers have occasionally been recovered from Pleistocene deposits and these, including specimens from the Cromer Forest-Bed series noted by McWilliams (1967), have tooth marks corresponding in shape to incisors of *Castor* rather than *Trogontherium*.

The muscle impressions and tubercles of the anterior parts of the premaxillae suggested to Schreuder (1929) that *Trogontherium* may have had powerful movable upper lips. This view was apparently reinforced by description of the large plate of bone on the maxilla anterior to the jugal buttress (Schreuder 1929, p. 125) as the attachment area of an ‘extraordinarily strong’ retrahens muscle of the upper lip. Schreuder (1929) noted that this strong plate of bone was represented in *Castor* by a ridge and that in *Castoroides* there appeared to be no indication of any equivalent ridge.

The plate of bone thought by Schreuder to have been primarily a site for lip retractor musculature attachment was rather the area of origin of the superficial masseter muscle which was relatively larger in *Trogontherium* than in *Castor*. Subsequent figures of the skull of *Castoroides* (Stirton 1965) show a large superficial masseter process and premaxillary tubercles similar to *Trogontherium*, yet the habit of browsing on floating vegetation has not apparently been attributed to this North American form.

The jaw muscles of *Trogontherium* which will be described in more detail elsewhere probably resembled those of *Castoroides*. As far as it is possible to judge from muscle scars, both genera appear to have differed from *Castor* in having relatively smaller temporal and relatively larger internal pterygoid and superficial masseter muscles. The origin and insertion of the superficial masseter in these three genera are compared in lateral and ventral view in figure 10. The base of the angular process in *Trogontherium*, which is preserved in only two specimens (R.G.M. colln), was remarkably expanded into a thin flat plate, in places less than 1 mm thick, which served as the insertion of the superficial masseter muscle. Judging by the cast available to me (U.M.Z.C. colln) a similar condition existed in *Castoroides*. Together with the lateral part of the angle beneath the condyle, this flat basal plate formed a medially opening pocket about

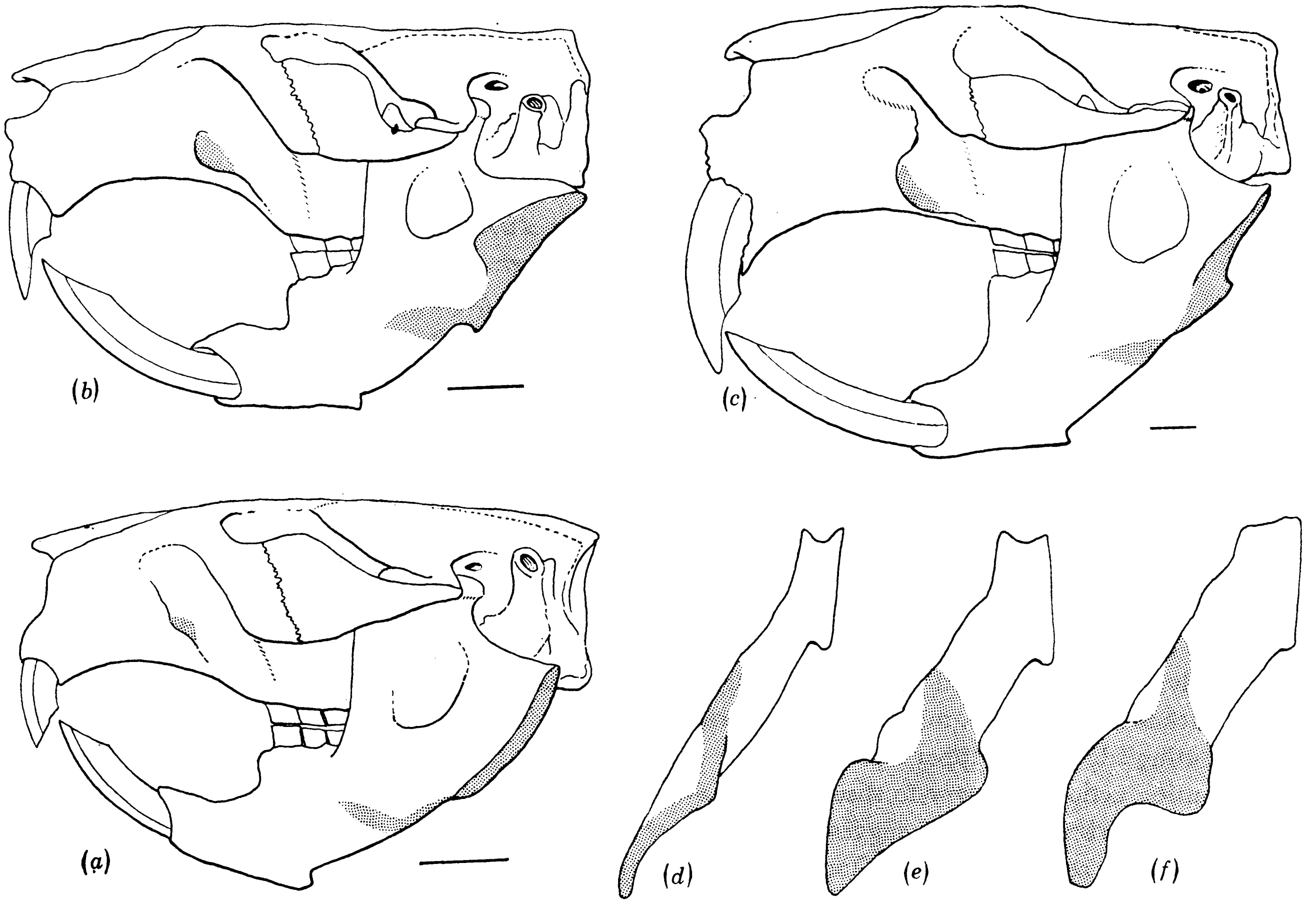

FIGURE 10. Superficial masseter muscle origin and insertion (stippled) of *Castor* (*a*, *d*), *Trogontherium* (*b*, *e*), and *Castoroides* (*c*, *f*). The larger areas of attachment in the two extinct forms indicate that the superficial masseter was more important than in *Castor*. The lateral views of the skull and mandible, and the ventral views of the mandible are reduced to the same size. The scale mark represents 2 cm. The sources used for the reconstruction of *Trogontherium* and *Castoroides* include Newton (1892), Schreuder (1929) and Stirton (1965) together with specimens and casts in U M.Z.C. and R.G.M. collections.

2 cm deep in *Trogontherium*, into which the internal pterygoid inserted. The close relation between the size of the internal pterygoid and superficial masseter muscles may thus be explained by their insertion onto opposite sides of the same expanded angular area of the mandible. Such functional relations between muscles may have limited the number of adaptive solutions to be expected in a group with similar qualitative anatomy such as the Castoridae. The mid-line apposition of the pterygoid plates and division of the nares in *Trogontherium* and *Castoroides* followed from size increases within these lineages and consequent disproportionate increases in the area of origin of the already large internal pterygoid muscles.

TABLE 8. RELATIVE PERCENTAGE OF *TROGONTHERIUM* AND *CASTOR* REMAINS FROM EUROPEAN LOCALITIES

locality	deposits	*Trogontherium* (%)	*Castor* (%)	reference
Tegelen	clay	v. common	v. rare	Schreuder, 1929
Voigtstedt	sand	94	6	Guenther, 1965
Mauer†	sand	79	21	personal observation
West Runton†	mud/sand	78	22	personal observation
Mosbach†	sand/gravel	*ca.* 50	*ca.* 50	personal observation
Kislang	sand	rarer	commoner	Kretzoi, 1969
Süssenborn	gravel	7	93	Kretzoi, 1969

† B.M.N.H., G.U.H., H.L.D., N.H.M.M. colln.

Remains of *Trogontherium* have in general been recovered from water lain deposits although a few also come from caves such as Erpfingen (Lehmann 1953) and human occupation sites at Vértesszöllös (Kretzoi & Vértes 1965) and Choukoutien (Young 1934). The abundance of *Trogontherium* remains compared with other taxa in water-lain sediments indicates strongly that it was associated with fluviatile and lacustrine environments and the interpretation that the large hind feet were webbed (Schreuder 1951) appears justified. The frequency of *Trogontherium* relative to *Castor* at a number of sites is given in table 8. As the skeletons of both animals potentially yielded a similar number of identifiable parts it may be concluded that in general they were not equally abundant in the same biotope. The apparent exception of Mosbach, which has yielded hundreds of specimens of both genera, may perhaps be due to the extensive reworking of the fossiliferous sands and gravels which has undoubtedly occurred at this site. The differences in representation of the two genera are related rather clearly to sediment type, with remains of *Trogontherium* predominating in fine grained sediments formed in slow-running or stagnant water conditions. Such a correlation suggests spatial separation between the genera with *Trogontherium* occupying the lakes and lower reaches of rivers. These observations do not support the view that the habits of *Trogontherium* resembled those of *Castor*, which on the evidence of gnawed wood have remained unchanged since at least the Middle Pleistocene. As *Castor* today occupies still-water environments it is possible that it may have been partly excluded from them while *Trogontherium* was extant and this interpretation implies some competition between the genera.

Palaeobotanical information is able to provide direct evidence of the presence of possible food plants of fossil mammals, and the sequence of vegetational changes enables statements about environmental variation through time. Some interpretations from palaeobotanical evidence will be made below concerning *Trogontherium* remains from Tegelen, West Runton, and Hoxne.

A pollen diagram through the Tegelen clay of the Russel-Tiglia-Egypt pit was given by

Zagwijn (1963). The Tegelen clay here was deposited in two cycles and divided on the basis of the pollen into a number of zones of the Tiglian C (TC2-6) and Eburonian (EbI and II). The climatic interpretation of the pollen suggested climatic optima in zones TC3 and TC5, becoming cooler especially at the beginning of the Eburonian. Remains of *Trogontherium* from Tegelen are, with few exceptions, of unknown horizon from a number of pits formerly dug at Tegelen. Sediment scrapings from R.G.M. ST95405, a partial skull from Kurstjens pit, yielded a pollen spectrum corresponding to the boundary between the Tiglian and Eburonian in the diagram from the Russel-Tiglia-Egypt pit *ca.* 1 km distant (P. L. Gibbard personal communication). This is in accordance with the view (Zagwijn personal communication) that the majority of *Trogontherium* specimens from the Tegelen clay were derived from the upper levels of this deposit, largely consisting of backswamp clay (Zagwijn 1963). Sections at the Russel-Tiglia-Egypt pit pass through a sandy channel deposit noted by Kortenbout van der Sluijs & Zagwijn (1962) dating from zone TC5. This sandy sediment has been screened in large quantities in order to recover the sparse small mammal remains (Freudenthal, Meijer & van der Meulen 1976) and a minimum of 100 m^3 has so far yielded a few bones and teeth of *Trogontherium*.

The vegetation during zone TC5 is known from the pollen and macroscopic plant remains considered by Zagwijn (1963) and the wood samples identified by van der Burgh (1974). Qualitative discussion of the vegetation is facilitated by these three lines of evidence since each is subject to different representational bias, but quantitative estimates of vegetational composition are on the other hand extremely difficult because of the influence of locally high production. The local vegetation at Tegelen during zone TC5 appears to have been a closed flood plain forest rich in woody species and thermophilous elements in which *Picea* and *Pterocarya* may have been particularly abundant.

The pollen from R.G.M. ST 95405 indicates a different vegetational environment with open ground at least locally, fewer thermophilous taxa and a relatively higher percentage of *Pinus* (P. L. Gibbard personal communication). The pollen spectrum obtained from this specimen is important in indicating that *Trogontherium* was not necessarily bound to warm interglacial closed forest vegetation. A similar result was obtained by Zagwijn (1963) in an analysis of clay adhering to a mastodont (*Anancus arvernensis*) molar recovered from a clay pit at Maalbeek. The profile at the pit belongs to a cool subarctic phase identified by Zagwijn (1963) as Eburonian Eb III, and the pollen from the tooth related it to the lower part of the deposits. The regional vegetation at that time contained few thermophilous taxa and there was considerable open ground. These results suggest that caution is necessary in drawing inferences of the climatic preferences of extinct mammalian lineages.

Pollen from interglacial deposits at Hoxne was described by West (1956). The *Trogontherium* remains mentioned by Spencer (in West 1956) came from the lake muds deposited in the early temperate zone HoII, during which the regional vegetation was mixed oak forest with local areas of open ground at the lake margin. Although the arboreal environment was very different, similar herbaceous taxa existed at Hoxne and Tegelen.

The vegetation from the Upper Freshwater Bed at West Runton was described by Duigan (1963) and West & Wilson (1966). The deposits from which *Trogontherium* remains have been recovered span the early part of the Cromerian interglacial (CrI, II) together with the last phase of the preceding Beestonian cool phase. The regional vegetation was dominated at first by birch and pine, with thermophilous elements moving in later. Non-arboreal pollen was high throughout the sequence so that open conditions existed at least locally. This is in keeping with the geological evidence which suggests a meandering river with ox-bow lakes in a shallow valley or flood plain. In such a situation, regeneration of trees may have been inhibited by high water table, changes of channel position and the feeding activity of large herbivorous mammals.

The common environmental elements in sites yielding *Trogontherium* appear to have been slow or still water with perhaps open ground along the banks. Botanical evidence suggests that these sites had more in common in respect of the herbaceous than the arboreal vegetation although it must be remembered that entomophilous taxa are underrepresented or lacking in the pollen record. It seems reasonable to regard *Trogontherium* as having lived in such riparian environments perhaps with the habits of the coypu (*Myocastor coypus*) which in my view provides in form and habits the closest recent analogue to this extinct form.

7. Taxonomy, nomenclature and dating

The evidence seen by the author compels the view that only a single species of *Trogontherium* existed at any time. The differences between various populations are interpreted as resulting from phyletic evolution in a single lineage, the division of which for taxonomic purposes is arbitrary. The taxonomy of such lineages has been discussed at length (Sylvester-Bradley 1956) with the reasonable conclusion that, where the two approaches yield contradictory results, division between taxa should be based on chronological rather than morphological criteria (Joysey 1972).

Three successive species of *Trogontherium* delimited by gaps in our stratigraphic knowledge are recognized within the time range Turolian to Middle Pleistocene covered by this paper. *T. minutum* existed through the Turolian giving rise to *T. minus* towards the end of the Ruscinian. The species *T. minus* is here considered to cover the next part of the lineage until the beginning of the Tiglian C of the Netherlands stratigraphic sequence (possible time equivalent of the Antian of the British sequence). *T. cuvieri* is first represented in the Early Pleistocene Tegelen clay (Tiglian C) and persisted until the end of the Middle Pleistocene making its last appearance in Britain at a number of Hoxnian localities.

These species may further be split subspecifically. Franzen & Storch (1975) have separated the Turolian population from Dorn-Dürkheim as *T. minutum rhenanum* on the basis of relatively larger size compared with the earlier type material of *T. minutum* (von Meyer 1838) from Elgg. The subspecific separation of remains from Slatina proposed by Conovici & Radulesco (1972) is followed although the material is referred here to *T. minus dacicum*. The smaller specimens from Hájnàčka and the Red Crag basement bed are treated as belonging to the subspecies *T. minus minus*. No evidence now exists that two taxa of *Trogontherium* were coeval in the Pleistocene and, in order to emphasize this, pre-Anglian and post-Cromerian populations are treated as temporal subspecies of *T. cuvieri*. *T.c. boisvilletti* lived from the Tiglian through the Cromerian whereas *T.c. cuvieri* existed during the Anglian and became extinct at the end of the Hoxnian.

The genus *Trogontherium* has been subject to several nomenclatural changes, not all of which have reflected advances in knowledge. The changes made in the present paper have not been made lightly and it is felt that they are largely necessitated by changes of taxonomic status revealed by new information. There are a number of potential difficulties in the nomenclature of species of *Trogontherium*, all of them concerned with the rule of priority and all resolvable in favour of the names used here if one considers stability to be more important than strict priority.

(*a*) The original description of *Trogontherium* (Fischer de Waldheim 1809) contains no specific name and the first binomial name used for the genotype skull is *Castor trogontherium* Cuvier 1812. The name *T. cuvieri* has however been generally attributed to Fischer de Waldheim (1809) since Cuvier's subsequent edition of 'Reserches sur les Ossemens fossiles' in 1823 in which the paragraph dealing with the genotype skull is headed 'Des Castors des terrains meubles et notamment de la grande espèce nommée *Trogontherium cuvieri* par M. de Fischer'. In view of this generally accepted usage which has been unquestioned for over a century and a half I see no merit in considering a change in nomenclature.

(*b*) Kretzoi (1965, 1969) and Janossy (1969) have resurrected on the grounds of priority the term ('*Diabroticus schmerlingii*') applied by Pomel (1848) to 'les mandibules attribuées par M. Owen au trogontherium ainsi que les dents déterminées comme d'Agouti par Schmerling'. In using '*Trogontherium schmerlingi* (Pomel 1848)' these authors are following a footnote by T. M. Stout, in Lehmann (1953), who recommended without any justification the replacement of *T. boisvilletti* by *T. cuvieri* and the replacement of *T. cuvieri* by *T. schmerlingi*.

First, the relevant part of the work of Pomel (1848) which is quoted above contains no indication in the form of bibliographic reference or description and the term '*Diabroticus schmerlingii*' is therefore a *nomen nudum*.

Secondly, the nomenclatural changes proposed by Stout (in Lehmann 1953) and amplified by Kretzoi (1969) have no logical basis and appear to arise from a misunderstanding of the literature.

Finally, all the specimens covered by the valid names mentioned by Kretzoi (1969) are included in the species *T. cuvieri* in the present paper. The relative stratigraphic positions of the subspecies *boisvilletti* (earlier) and *cuvieri* (later) as defined here are beyond question even though the stratigraphic context of the type skull of *T. cuvieri* remains uncertain.

(*c*) Giebel (1860) described a number of specimens including a figured maxilla from the brown coal of Rippersroda as *Hystriocomys* (sic) *thuringiacus*. The illustrated teeth appear to be referable to the genus *Trogontherium* and closely resemble the type of *T. minus* Newton 1890, suggesting that *H. thuringiacus* is a senior synonym for this taxon. However, as the location of Giebel's type material is unknown and because the name *T. minus* has been in exclusive use for this taxon since 1890 I agree with Radulesco & Samson (1972) that no nomenclatural change should be made on grounds of priority.

None of the sites discussed here have been dated by absolute methods but the following indirect evidence provides an approximate calibration. Normal magnetization in Hoxnian, Anglian, Cromerian, Pastonian and Baventian sediments from East Anglia recorded by van Montfrans (1971) suggests that these date from after the Brunhes-Matuyama boundary (0.7 Ma), although the Baventian and Pastonian might equally date from the Jaramillo normal event (0.86–0.92 Ma) or earlier. Normal polarity recorded in sediments of the Stradbroke borehole (van Montfrans 1971) dated as Ludhamian and pre-Ludhamian by Beck, Funnel & Lord (1972) implies an age at least equal to the Gilsa event (*ca.* 1.6 Ma) for this basal part of the English sequence.

In the Netherlands, superimposed sediments from boreholes record a number of Middle Pleistocene climatic oscillations ('Cromerian complex') which are not easily related to the British stratigraphic scheme (Zagwijn *et al.* 1971). These oscillations precede a major cool phase (Esterian = Anglian) which is dated on the presence of Eifel-derived augite to *ca.* 400 ka (Frechen & Lippolt 1965). Between the Elster and the Early Pleistocene Menapian cool phases at least three warm periods are now recognized, with the Brunhes–Matuyama boundary (0.7 Ma) located within this sequence between interglacials I and II (Zagwijn *et al.* 1971). According to these authors the Jaramillo normal event (0.86–0.92 Ma) may be located within the upper part of the Waalian C interglacial and the lower part of the succeeding Menapian cool phase. Normal magnetization recorded in Tegelen clay sediments (Tiglian C/Eburonian boundary) indicates that these are at least as old as the Gilsa normal event (1.6 Ma) (van Montfrans 1971). This date is in accordance with the presence of *Mimomys pliocaenicus* at Tegelen (TC 5) and St George-d'Aurac, France, which is radiometrically dated at 1.92 Ma (van der Meulen, Freudenthal *et al.* 1976).

The vertebrate localities at Hájnàčka which have yielded specimens of *T. minus* include in their sequence potentially datable tuffs for which an age 3–4 Ma would be expected by faunal correlation with other dated 'early villafranchian' localities (Berggren & van Couvering 1974). The Early Turolian fauna from Dorn-Dürkheim with *T. minutum* (Franzen & Storch 1975) can be dated at 8–10 Ma on similar grounds. Late Neogene dating and possible correlations of alternative stratigraphies are considered by Berggren & van Couvering (1974) in whose sense the terms Vallesian, Turolian and Ruscinian have been used here.

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List of museum abbreviations used in the text

B.M.N.H.	British Museum (Natural History) London
C.E.M.	Colchester and Essex Museum
G.S.M.	Institute of Geological Sciences London
G.U.H.	Geologisches Institut der Universitaet Heidelberg
H.L.D.	Hessisches Landesmuseum Darmstadt
I.M.	The Museum Ipswich
I.P.	Institut de Paléontologie Paris
M.B.	Museum fuer Naturkunde Berlin
N.C.M.	Norwich Castle Museum
N.H.M.M.	Naturhistorisches Museum Mainz
R.G.M.	Rijksgeologie Museum Leiden
S.M.F.	Forschungsinstitut und Museum Senckenberg Frankfurt
T.M.	Teyler Museum Haarlem
U.M.Z.C.	University Museum of Zoology, Cambridge

Unless otherwise indicated all measurements are in millimetres.

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