Early Cretaceous amphilestid ('triconodont') mammals from Mongolia

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Kielan-Jaworowska, Z. & Dashzeveg, D. 1998. Early Cretaceous amphilestid ('tricono-dont') mammals from Mongolia. — *Acta Palaeontologica Polonica*, **43**, 3, 413–438.

A small collection of ?Aptian or ?Albian amphilestid ('triconodont') mammals consisting of incomplete dentaries and maxillae with teeth, from the Khoboor locality, Guchin Us county in Mongolia, is described. *Guchinodon* Trofimov, 1978 is regarded a junior subjective synonym of *Gobiconodon* Trofimov, 1978. Heavier wear of the molariforms M3 and M4 than of the more anterior one – M2 in *Gobiconodon borissiaki* gives indirect evidence for molariform replacement in this taxon. The interlocking mechanism between lower molariforms in *Gobiconodon* is of the pattern seen in *Kuehneotherium* and *Tinodon*. The interlocking mechanism and the type of occlusion ally Amphilestidae with Kuehneotheriidae, from which they differ in having lower molariforms with main cusps aligned and the dentary-squamosal jaw joint (double jaw joint in Kuehneotheriidae). The main cusps in upper molariforms M3–M5 of *Gobiconodon*, however, show incipient triangular arrangement. The paper gives some support to Mills' idea on the therian affinities of the Amphilestidae, although it cannot be excluded that the characters that unite the two groups developed in parallel. Because of scanty material and ambiguity, we assign the Amphilestidae to order *incertae sedis*.

K e y   w o r d s : Mammalia, 'triconodonts', Amphilestidae, Kuehneotheriidae, Early Cretaceous, Mongolia.

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Introduction

Beliajeva *et al.* (1974) reported the discovery of Early Cretaceous mammals at the Khoboor locality (referred to also sometimes as Khovboor), in the Guchin Us Somon (County), Gobi Desert, Mongolia. The Khoboor beds have yielded the following mammals: Aegialodontia (Dashzeveg 1975; Dashzeveg & Kielan-Jaworowska 1984),

Triconodonta (Trofimov 1978), Eupantotheria (Dashzeveg 1979, 1994), Symmetrodonta (Trofimov 1980, 1997), Multituberculata (Trofimov 1980; Kielan-Jaworowska *et al.* 1987), Eutheria (Kielan-Jaworowska & Dashzeveg 1989, Sigogneau-Russell *et al.* 1992), and unidentified mammalian petrosal (Wible *et al.* 1995).

One of us (D.D.) assembled many years ago a modest collection of Khoboor mammals that is now housed at the Paleontological and Stratigraphic Section, Institute of Geology, Mongolian Academy of Sciences in Ulan Bator. The collection contains five triconodont fragmentary upper and lower jaws, and two isolated lower molariforms, and provides some information that is new on the morphology of taxa described by Trofimov (1978). The aim of the present paper is to describe this collection.

The age of the Khoboor beds is a matter of argument. As these beds yield *Gobiconodon borissiaki*, we tentatively accept that they are equivalent to the North American Cloverly Formation (?late Aptian or ?early Albian, see Ostrom 1970, and Cifelli *et al.* 1998) that has yielded a closely related species, *Gobiconodon ostromi*.

We follow the terminology of Jenkins & Schaff (1988) and the numbering of cusps and wear facets of Crompton & Jenkins (1968) and Crompton (1974).

Institutional abbreviations. — MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; PSS, Paleontological and Stratigraphic Section, Institute of Geology, Mongolian Academy of Sciences, Ulan Bator.

Review of the triconodont record and classification

Simpson (1928, 1929) revised the order Triconodonta Osborn, 1888 (known at that time only from the Middle and Late Jurassic of Europe and North America) and recognized within it one family Triconodontidae Marsh, 1887, with two subfamilies Triconodontinae Marsh, 1897 and Amphilestinae Osborn, 1888. Simpson (1945) followed his earlier classification, but extended the stratigraphic range of the Triconodonta to the ?Upper Triassic (*Eozostrodon* Parrington, 1941, based on isolated premolars, assigned to the Amphilestidae, being included). The discovery of *Morganucodon* dentary and teeth by Walter Kühne in the Liassic beds of England (Kühne 1949) led to the creation of a new triconodont family Morganucodontidae Kühne, 1958.

Jenkins & Crompton (1979) provided a more recent account of triconodont systematics. Given the many discoveries in the nearly 20 years since their paper, we briefly review the present knowledge on triconodonts.

The Morganucodontidae Kühne, 1958, known from the Rhaethian, Rhaeto-Liassic and Liassic of Europe, South Africa, China, and North America, are the oldest triconodonts (Butler 1939; Kühne 1949, 1958; Peyer 1956; Mills 1971; K. A. Kermack *et al.* 1973, 1981; Crompton 1974; Crompton & Jenkins 1968; Sigogneau-Russell 1978, 1983; Clemens 1980, 1986; Jenkins *et al.* 1983; Jenkins 1984; Gow 1986; Crompton & Luo 1993; Luo 1994; Luo & Wu 1994; Luo *et al.* 1995). The Morganucodontidae, especially *Morganucodon* (referred to sometimes also as *Eozostrodon*, but

see Clemens 1979) are among the best known Mesozoic mammals. They are represented by isolated teeth, jaw fragments, complete skulls and incomplete postcranial skeletons (Parrington 1947, 1971, 1978; Mills 1971; K. A. Kermack *et al.* 1973, 1981; Jenkins & Parrington 1976; Crompton & Luo 1993; Wible & Hopson 1993; Luo *et al.* 1995 and references therein).

In the Sinemurian to Pliensbachian Kayenta Formation of North America (Arizona), in addition to uncontested members of the Morganucodontidae (*Morganucodon*), there occurs *Dinnetherium* Jenkins *et al.*, 1983. It is known from an almost complete dentary and incomplete maxilla with three molars, assigned by Jenkins *et al.* (1983) to family *incertae sedis*, but placed by McKenna (in Stucky & McKenna 1993) in the Amphilestidae. However, as appears from data in Crompton & Luo (1993) and Luo & Wu (1995), there is very little difference in occlusal pattern between *Morganucodon* and *Dinnetherium*. McKenna & Bell (1997) did not include the Morganucodontidae within Mammalia.

Another group of the Rhaeto-Liassic triconodonts are the sinoconodonts known from almost complete skulls and dentaries (Patterson & Olson 1961; Zhang & Cui 1983; Crompton & Sun 1985; Crompton & Luo 1993; Luo 1994; Luo & Wu 1994). Mills (1971) proposed the triconodont family Sinoconodontidae. He also suggested that Amphilestinae should be removed from the Triconodonta and assigned to the Theria, an idea not accepted by subsequent authors except Freeman (1979, see also Jenkins & Crompton 1979; Stucky & McKenna 1993; McKenna & Bell 1997, and references therein).

K.A. Kermack *et al.* (1973) proposed two suborders within the order Triconodonta: Eutriconodonta K. A. Kermack *et al.*, 1973, with two families, Triconodontidae Marsh, 1887 and Amphilestidae Kühne, 1958; and Morganucodonta K. A. Kermack *et al.*, 1973, with the families Morganucodontidae Kühne, 1958, and Sinoconodontidae Mills, 1971. McKenna (1975) accepted K. A. Kermack *et al.*'s (1973) systematic proposal, while McKenna (in Stucky & McKenna 1993) assigned the rank of a subclass to the Triconodonta, the rank of an order to the Morganucodonta, and the rank of an order to the Eutriconodonta, with three families Sinoconodontidae, Amphilestidae and Triconodontidae. Finally, McKenna & Bell (1997) raised the Triconodonta Osborn, 1888 to the rank of an infraclass with four families: Austriconodontidae, Amphilestidae, Triconodontidae and Alticonodontidae.

Crompton & Sun (1985) argued that the Sinoconodontidae are a sister group of all other mammals. This idea has been supported by Crompton & Luo (1993), Wible & Hopson (1993) and Luo (1994, see also references therein). The placement of sinoconodontids as a sister group of all other mammals removes them from the triconodonts.

The last member of the Morganucodontidae (genus *Wareolestes* Freeman, 1979) is known from the Middle Jurassic Forest Marble Formation, Oxfordshire of England (Freeman 1979). The Morganucodontidae are absent from the Late Jurassic, where the Triconodontidae make their appearance, and the Amphilestidae are also present. Both these eutriconodont groups are known mostly from the Late Jurassic of Great Britain and North America (Simpson 1928, 1929; K. A. Kermack 1963, 1988; see also Clemens 1986, for review), and from Portugal (Krusat 1989).

Triconodontid (triconodontine) teeth and incomplete dentaries have also been found in the Aptian-Albian of Texas (Patterson 1956; Slaughter 1969; Turnbull 1995) and Montana (Cifelli *et al.* 1998), and at the Early–Late Cretaceous boundary of Utah (Cifelli & Madsen 1998). Sigogneau-Russell *et al.* (1990) discovered in the Early Cretaceous (?Berriasian) of Morocco a fragmentary edentulous dentary and several isolated teeth assigned to the Amphilestidae. Subsequently Sigogneau-Russell (1995) described from the same beds purported aquatic triconodont mammals.

Trofimov (1978) described from the Early Cretaceous (?Aptian or ?Albian) Khoboor beds of Mongolia two triconodont species, *Gobiconodon borissiaki* Trofimov, 1978 and *Guchinodon hoburensis* Trofimov, 1978, both belonging to monotypic genera, assigned to the Amphilestidae. The two Mongolian taxa are relatively well known, represented by fairly complete dentaries with molars and alveoli for other teeth, and fragmentary maxillae with molars from Mongolia. Maschenko & Lopatin (1998) reported the occurrence of *Gobiconodon borissiaki* in the Early Cretaceous of the Shestakovo locality in Siberia.

In the Middle or Late Jurassic of China an incomplete dentary with four molar teeth has been found, assigned by Chow & Rich (1984) to the monotypic genus *Klamelia* Chow & Rich, 1984. The authors erected within the Amphilestidae the subfamily Gobiconodontinae Chow & Rich, 1984, to which they assigned *Klamelia* and two Mongolian Early Cretaceous genera *Gobiconodon* and *Guchinodon*.

Jenkins & Schaff (1988) described from the Early Cretaceous Cloverly Formation in North America *Gobiconodon ostromi* Jenkins & Schaff, 1988, and erected the family Gobiconodontidae for it and for the tentatively assigned *Guchinodon*. They argued that several features set *Klamelia* apart from *Gobiconodon* and other amphilestids, and doubted that these forms are closely related. However, even if *Klamelia* is excluded from the Gobiconodontinae, the subfamily name Gobiconodontinae Chow & Rich, 1984 has priority over Gobiconodontidae Jenkins & Schaff, 1988, (see also McKenna & Bell 1997).

Cifelli *et al.* (1998) described a new triconodontid genus and species, *Corviconodon montanensis* from the Cloverly Formation based on a right dentary with incomplete molars; in addition they described a distal part of left lower molar, identified as gen. et sp. indet., and announced presence of one more triconodontid taxon in the Cloverly Formation.

The Late Cretaceous triconodontids are known only from North and South America. Triconodontine teeth in a fragment of a dentary (*Alticonodon* Fox, 1969) and isolated unidentified upper premolars have been discovered in Canada (Fox 1969, 1976). Isolated teeth of triconodonts, assigned to Austriconodontidae Bonaparte, 1992 (see Bonaparte 1986, 1992, 1994), have been reported from the Late Cretaceous (Los Alamitos Formation) of Argentina. *Alticonodon* Fox, 1969, from the Milk River Formation of Alberta, Canada, and *Austriconodon* Bonaparte, 1986, from the Los Alamitos Formation of Argentina, are the last known members of Triconodonta.

Kielan-Jaworowska (1997) argued that it appears from recent phylogenetic analyses (e.g., Crompton & Sun 1985; Rowe 1988; Wible & Hopson 1993, and Wible *et al.* 1995) and from the data discussed in her paper, that the order Triconodonta is polyphyletic. Similar conclusion was reached by Cifelli *et al.* (1998). We follow this attitude and we use the term 'triconodonts' in an informal meaning.

Systematic paleontology

Order *incertae sedis*
Family Amphilestidae Osborn, 1888
Subfamily Gobiconodontinae Chow & Rich, 1984

Remark. — Jenkins & Schaff (1984) erected a new family Gobiconodontidae (neglecting Gobico-nodontinae Chow & Rich, 1984), to include *Gobiconodon* Trofimov, 1978 and, tentatively, *Guchinodon* Trofimov, 1978 (regarded here a junior synonym of *Gobiconodon*). We restore the subfamily status of the Gobiconodontinae within Amphilestidae. The Gobiconodontinae share with known amphilestids the basic structure of the molars, differing from them in small details of molar structure and in enlargement of the most mesial lower tooth. We consider these characters sufficient to establish subfamilial but not familial distinction. *Klamelia* Chow & Rich, 1984, assigned by its authors to the Gobiconodontinae, probably does not belong to this subfamily (Jenkins & Schaff 1988).

Genus *Gobiconodon* Trofimov, 1978

Synonym *Guchinodon* Trofimov, 1978

Emended diagnosis. — Very small to medium-size (estimated skull length varies between 27 mm – *G. hoburensis* and 106 mm – *G. ostromi*) amphilestid 'triconodonts' with five rounded fossae on the palatal part of maxilla, situated close and slightly shifted posteriorly with respect to the corresponding upper molariform teeth. Five molariform teeth and five to six antemolariform teeth in the dentary. The i1 and c are semi-procumbent, p1–p3 with decreasing procumbency, p4 (disappearing in later ontogenetic stages in *G. ostromi*) vertical, with 3 cusps, molariform teeth with four or five cusps, m3 the largest. Main cusps in M3–M5 show incipient triangular pattern, with cusp A placed slightly more lingual than cusps B and C. Interlocking mechanism of lower molariforms of *Kuehneotherium* type, with cusp d of the anterior tooth fitting into embayment between small cusps e and f of the anterior cingulum of the succeeding molariform. Molariform teeth undergo replacement at least in *G. ostromi* and probably *G. borissiaki*. The main cusp a of lower molariforms occluded immediately in front of the distal margin of the corresponding upper molariform, between posterior cingulum, on which there is a small cusp D, and cusp C, rather than between cusps A and B, as in Morganucodontidae and Triconodontidae.

Species assigned. — *Gobiconodon borissiaki* Trofimov, 1978; *G. hoburensis* (Trofimov, 1978); *G. ostromi* Jenkins & Schaff, 1988.

Comments. — *Guchinodon hoburensis* Trofimov, 1978 differs from *Gobiconodon borissiaki* Trofimov, 1978 in being almost twice as small, in having a double-rooted p4, and in details of the position of the mental and infraorbital foramina. The dental formulae, arrangement of the teeth and molar structure are in both taxa similar, the small differences concern only the relative heights of cusps b and c, which results in a slightly different occlusal pattern; we assign to all these differences a specific, rather than generic value. On this basis we regard *Guchinodon* Trofimov, 1978 a junior subjective synonym of *Gobiconodon* Trofimov, 1978.

Gobiconodon borissiaki Trofimov, 1978
Figs 1–3, 9, 10A.

Gobiconodon borissiaki Trofimov; Trofimov 1978: pp. 214–215, fig. 1.
Gobiconodon borissiaki Trofimov; Maschenko & Lopatin 1998: pp. 234–236, figs 3, 4.

Material. – PSS 10–15b, damaged fragment of left maxilla with M2–M5; PSS 10–15a, partial left dentary with p2–m2, alveoli for p1 and broken alveoli for the canine and an incisor; PSS 10–15, crown of left m1; all from the Early Cretaceous (?late Aptian or ?early Albian) Khoboor Beds, Khoboor, Guchin Us somon, Gobi Desert, Mongolia.

Revised diagnosis. — Medium sized *Gobiconodon*, estimated length of the skull about 48–50 mm. Differs from *G. ostromi* and *G. hoburensis* in dimensions, being approximately intermediate in size

between these taxa. Differs from *G. hoburensis* and *G. ostromi* in having a single-rooted p4 (in *G. ostromi* it is incipiently double-rooted, either single-rooted or absorbed), which apparently does not disappear in adult ontogenetic stages, as characteristic of *G. ostromi* (but not of *G. hoburensis*). Differs from *G. ostromi* in having apparently more prominent cusps e and f on the anterior cingulum of m2–m5. Difference in size between i1 and c is smaller than in *G. ostromi*. Differs from *G. hoburensis* in having cusps b and c in lower molariform teeth much more pronounced, and cusp b in m1 placed lower. It shares these latter characters with *G. ostromi*.

Description. — *Maxilla and upper teeth.* The fragmentary maxilla PSS 10–15b is badly damaged (Fig. 1A–C). On the palatal process a shallow palatal fossa is preserved opposite M2, and hardly discernible opposite M3. The length of M2–M5 is 8.8 mm.

M2 in PSS 10–15b is slightly displaced lingually in relation to M3–M4. It is 2.6 mm long, 1.3 mm wide, roughly oval to rectangular in occlusal view, and only slightly worn. This is the highest tooth of the preserved series and narrower transversely than M3–M5. Cusp A is very high and trenchant, cusp B is low and set apart from A, and cusp C is higher than B and situated close to A. In contrast to succeeding molariforms the main cusps are aligned. There is also a minute cusp D, situated distal to C. The crescent-shaped mesiolingual cingulum bears a prominence, identified as cusp E. On the antero-buccal cingulum there is a minute cusp F, adhering buccally to cusp B. A cingulum extends along the buccal, distal and lingual margins, but is discontinuous mesially, as cusp B is situated on the mesial margin. The cingulum is especially prominent at the corners and nearly disappears opposite the middle of cusp A on both lingual and buccal sides. Minute, hardly discernible cuspules are present on the buccal cingulum opposite cusp B, on the distal part of cusp A, and at the distolateral corner. It seems possible that there were more cuspules, which were obliterated by wear.

M3 is very strongly worn. As preserved it is 2 mm long and 1.7 mm wide, but it was possibly wider, especially mesially, before wear. It differs from M2 in being wider and more rectangular (rather than oval) in occlusal view. The buccal margin is incurved in the middle; the lingual margin was possibly also incurved but this indentation has disappeared due to the almost complete wear of the distolingual corner. Of the three main cusps only cusp A has been preserved; it is strongly worn obliquely distolingually; due to wear it appears to be placed more mesially than it was in the unworn condition. Although cusps B and C are completely worn, the remaining traces show that cusp A was situated slightly more lingually than cusps B and C. In the place of the worn cusp C there is a wide, transverse groove. The strongly worn remnant of the cingulum is extensive at the mesiolingual corner, which indicates that cusp E might originally have been present, as in M2. Remnants of the cingulum have been preserved distally and buccally. On the distal cingulum remnant of minute cusp D has been preserved.

M4 is less worn than M3 and is wider in occlusal view. It is 2.3 mm long; its maximum width, across the mesial half, is 2 mm. Both buccal and lingual margins are incurved in the middle. A cingulum extended all around the tooth. Cusp A, due to the wear of its distal part, appears to be placed more medially than it originally was. The remnants of strongly worn cusps B and C show that cusp A was situated more lingually than cusps B and C, the three cusps forming an incipient triangle. Cusp B is almost completely obliterated; the preserved remnant shows that it is closely adjacent to cusp A. Cusp C became completely eroded by wear together with the distal cingulum (cusp D), leaving a deep transverse groove. The mesial part of the lingual cingulum is very prominent; although worn mesiolingually, the shape of the preserved part indicates the presence of worn cusp E. The distal part of the lingual cingulum and the distal cingulum are strongly worn. Along the middle part of the buccal cingulum traces of three cuspules can be recognized.

M5 (1.8 mm long, 1.8 mm wide mesially and 1.4 mm wide distally) is strongly asymmetrical; it is arranged obliquely with respect to other teeth, with the axis of the main cusps directed mesiobuccally-distolingually. It is only slightly worn, but cusp A has been broken. Cusp A is placed centrally and moved lingually with respect to cusps B and C, the three cusps forming an incipient obtuse triangle. Cusps B and C are of subequal size and are closely adjacent to cusp A. The difference between the sizes of cusps A, B and C is less dramatic than in M2. The tip of cusp B is worn obliquely mesiolingually. The buccal cingulum is strongly incurved medially; its mesial lobe is transversely wider and more
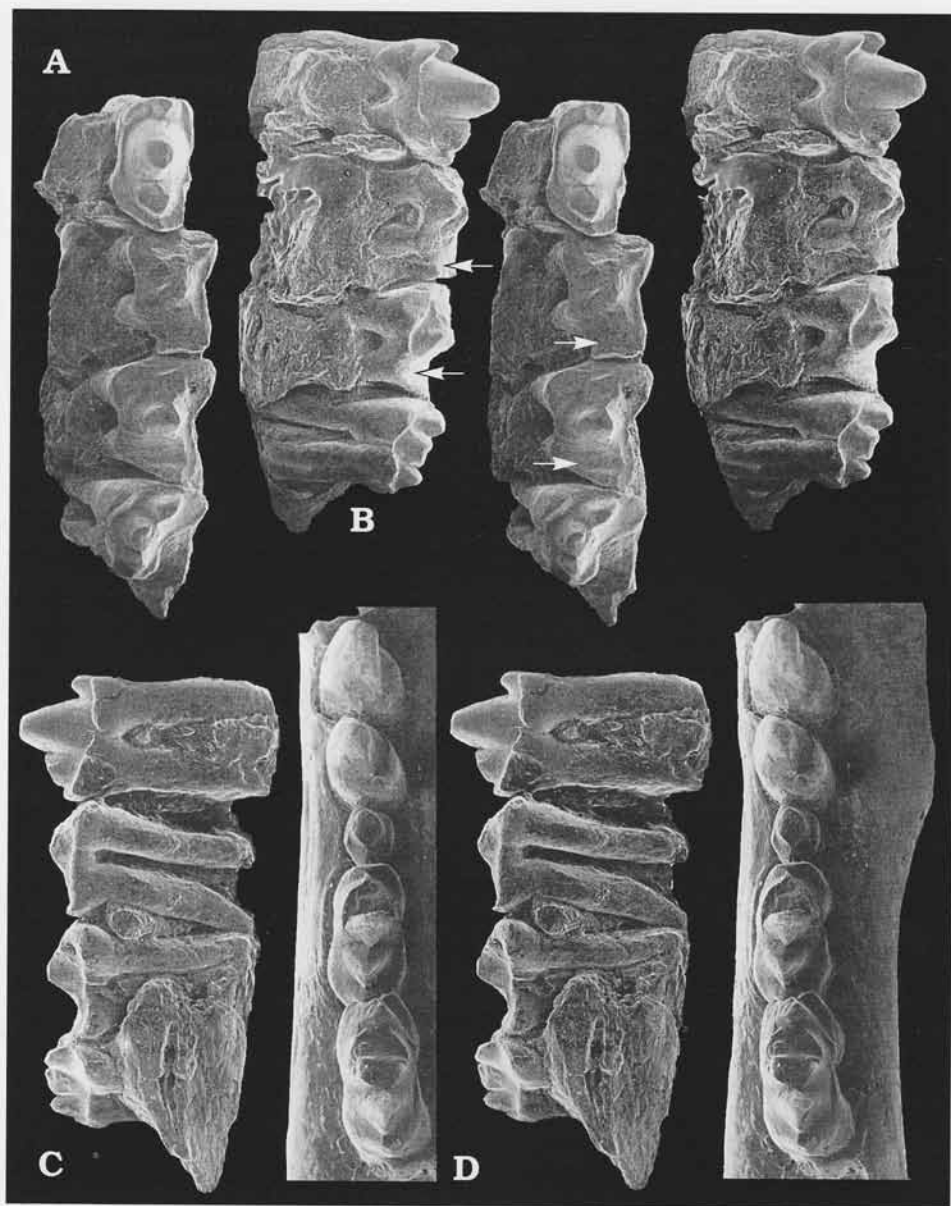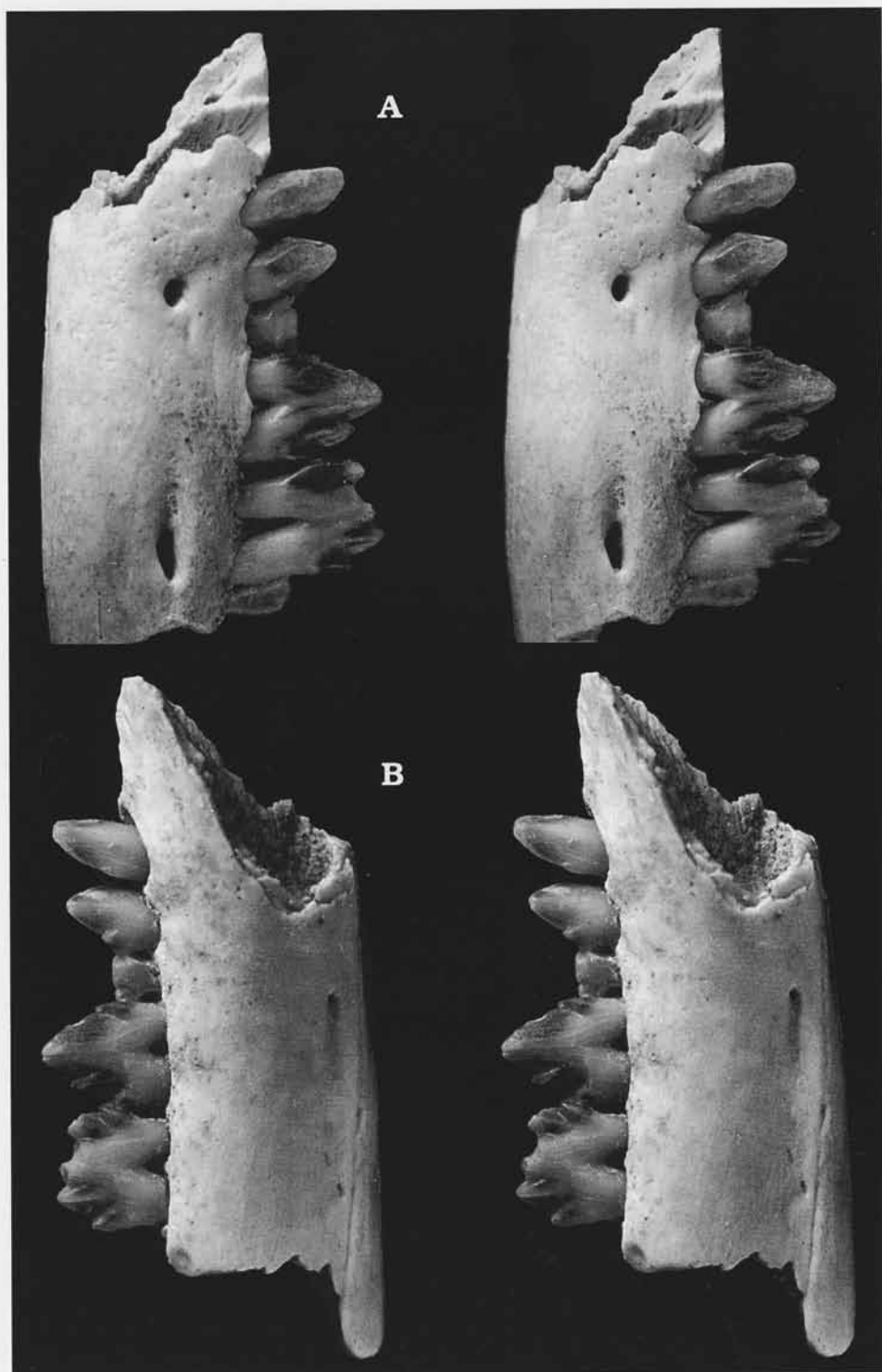
Fig. 1. *Gobiconodon borissiaki* Trofimov, 1978. Khoboor Beds, Khoboor, Gobi Desert, Mongolia. Damaged fragment of left maxilla with M2–M5 in occlusal (**A**), lingual (**B**), and buccal (**C**) views, PSS 10–15b. **D**. Incomplete left dentary with p2–m2, anterior part with alveoli for p1, canine and incisor not shown, occlusal view, PSS 10–15a, (see also Fig. 2). Arrows in **A** and **B** denote grooves in M3 and M4, into which occludes cusp a of corresponding lower molariform. Cusp terminology after Crompton & Jenkins (1968) is shown in Fig. 9. SEM stereomicrographs, × 8.

prominent than the distal lobe, on which a trace of a cuspule has been preserved. The lingual cingulum is also incurved in the middle, its mesial lobe being more prominent than the distal, but the distal
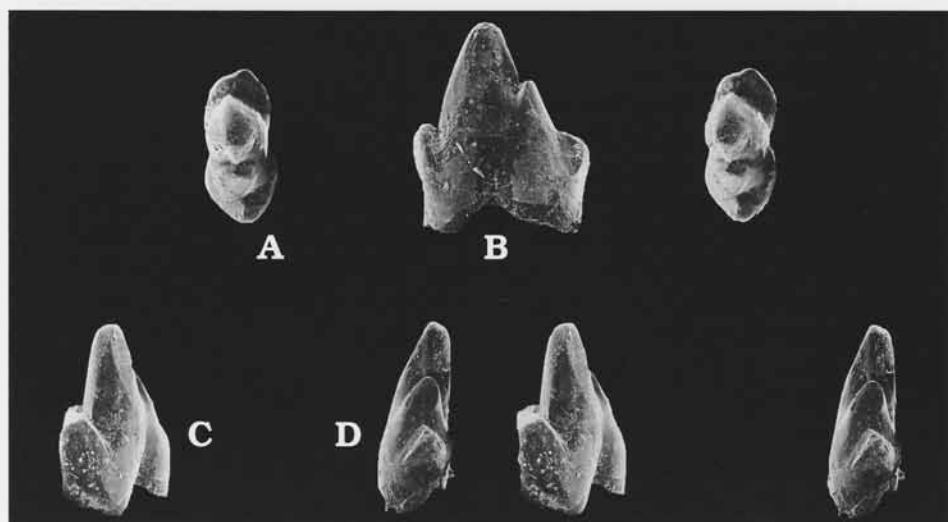
Fig. 3. *Gobiconodon borissiaki* Trofimov, 1978. Khoboor Beds, Khoboor, Gobi Desert, Mongolia. Crown of left m1, in occlusal (**A**), buccal (**B**), mesiobuccal (**C**), and distal (**D**) views, PSS 10–15. Cusp terminology after Crompton & Jenkins (1968) is shown in Fig. 9. All except **B**, SEM stereomicrographs, **B** – SEM micrograph, all × 8.

prominence is too small to be called cusp D, as in preceding teeth. The mesial cingulum disappears opposite cusp B, while the distal cingulum is prominent all along its length.

Dentary and lower teeth. The preserved part of the dentary (Figs 1D, 2) PSS 10–15a is robust, 4.6 mm deep below m2 in buccal view. Two mental foramina have been preserved; a rounded one 0.6 mm in diameter, placed below p3, and an oval one 1mm long, placed below m2. A small groove extends mesially from the oval mental foramen for a distance of 1.5 mm. On the lingual side a weak, thread-like groove (remnant of the Meckel's cartilage) extends mesioventrally along the lower margin, and disappears below p2. Above it there is a groove leading to a large nutrient foramen.

The alveolus for the incisor (Fig. 2A), which reaches back to below the p2–p3 embrasure, is incomplete but shows that the incisor was about 2.2 mm in diameter and semi-procumbent. The fragmentary alveolus for the canine also shows semi-procumbency. All premolariform teeth are single-rooted and p1–p3 show decreasing procumbency. The alveolus for p1 shows that p1 was slightly larger than p2. The p2 is peg-like, convex on the buccal side and concave on the lingual and mesial sides, with two minute, basal lingual cuspules. The p3 has a main cusp and a distolingual basal cusp, which is much bigger than the cuspules in p2. Both p2 and p3 are slightly bent mesiolingually.

The p4 is by far the smallest of all the teeth; it is vertical and has a main cusp, the lingual part of which is worn out horizontally, while the buccal part is worn out obliquely buccally. In buccal view it is roughly triangular in shape. In addition on the buccal side, below the main cusp there is an oval, longitudinally elongated wear facet. There are small mesial and distal basal cuspules.

The m1 preserved in the dentary (PSS 10–15a) is 2.6 mm long and 1.35 mm wide distally, the isolated m1 (PSS 10–15) is 2.4 mm long and 1.2 mm wide (Fig. 3). Cusp a is large and trenchant. Cusp b is situated very low (lower than in *G. hoburensis*); it is developed as a transverse cingulum which fits tightly to the base of cusp a, and is more prominent lingually than labially. Cusp c is

Fig. 2. *Gobiconodon borissiaki* Trofimov, 1978. Khoboor Beds, Khoboor, Gobi Desert, Mongolia. **A, B**. Incomplete left dentary with p2–m2, alveolus for p1 and broken alveoli for canine and incisor, in buccal and lingual views, PSS 10–15a, (see also Fig. 1D). Cusp terminology after Crompton & Jenkins (1968) is shown in Fig. 9. Stereophotographs, × 6.

larger than cusp b and placed higher. Cusp d is insignificantly higher than cusp b. Cusp d enters into embayment between cusps e and f of m2. A small lingual cingulum extends from the middle of cusp a towards cusp d. The isolated left m1 PSS 10–15 is slightly smaller than m1 in PSS 10–15a and less worn. On the upper margin of cusp b there are two minute cuspules.

The m2 is 2.8 mm long and 1.5 mm wide. It has 6 cusps. The central cusp a has been broken off. Cusp b and c are closely adjacent to cusp a, b being lower than c. There is a low, small lingual cusp e, not seen in buccal view and a tiny buccal cusp f. Cusp d of m1 does not fit completely into the embayment between cusps e and f, as m1 and m2 are too close to one another and m2 covers slightly dorsally m1. There is also distally placed cusp d, which worked in an interlocking mechanism with cusps e and f of the succeeding tooth (not preserved). A weak lingual cingulum extends from the middle of cusp a towards cusp d. On the mesial half of the lingual side of cusp a there is a minute basal cuspule.

Gobiconodon hoburensis (Trofimov, 1978)

Figs 4–8, 10B, 11.

Guchinodon hoburensis Trofimov; Trofimov 1978: p. 216, fig. 2.

Material. — PSS 10–37a, fragment of right maxilla with M1, alveoli for P3, P4, M2, M3; PSS 10–37b, fragment of left maxilla with M3–M5; PSS 10–37c, partial right dentary with m1–m5, distal margins of alveoli for canine and p1, complete alveoli for p2–p4; PSS 10–21 crown of isolated right m5; all from the Early Cretaceous (?late Aptian or ?early Albian) Khoboor Beds, Khoboor, Guchin Us somon, Gobi Desert, Mongolia.

Revised diagnosis. — Differs from *G. borissiaki* in being about 1.8 times smaller and in having a double-rooted p4; differs from *G. ostromi* in being almost 3 times smaller and in having p4 which apparently does not disappear during ontogeny. Differs from *G. borissiaki* and *G. ostromi* in having all the cusps (except cusp a) in lower molariform teeth less prominent, and cusp b in m1 situated relatively higher. The dentary is relatively wider mesially than in *G. borissiaki* and *G. ostromi*, which is related to a medial shift of i1 with respect to other teeth (it is more aligned in *G. borissiaki* and especially in *G. ostromi*). The three mental foramina are shifted slightly more anteriorly than in the two other species, especially *G. ostromi*. The palatal fossae are relatively deeper than in *G. borissiaki* (poorly known in *G. ostromi*). Differs from *G. borissiaki* in having the infraorbital foramen situated more anteriorly, above the P3–P4 embrasure, rather than above M1 (position not known in *G. ostromi*).

Description. — *Maxilla and upper teeth*. In two fragmentary maxillae PSS 10–37a and 10–37b, on the palatal part, there are deep, rounded palatal fossae situated almost opposite M1–M5, slightly shifted distally with respect to the middle of the respective upper molariforms. The mesial margin of the first fossa, which is distinctly smaller than the remaining ones (preserved in PSS 10–37a) is situated opposite the cusp A of M1. The last fossa, preserved in PSS 10–37b, is incomplete; only its anterior part, situated opposite the distal part of M5 has been preserved. The fossae received cusp a of the lower molariforms. The infraorbital foramen, of which the lower margin is preserved in PSS 10–37a, is situated above the P3–P4 embrasure.

P3, judging from the alveolus, preserved in PSS 10–37a, was possibly single-rooted. P4 was double rooted and short mesiodistally.

M1 is 1.6 mm long and 0.7 mm wide mesially. Cusps A, B and C are strongly eroded, but traces are preserved, showing that cusp C was larger than B, all three cusps being aligned. There is a worn buccal cingulum. The lingual cingulum is completely obliterated by wear distally, but a trace of it is still present mesially. Cusp B is worn obliquely mesiolingually, cusps A and C are worn obliquely distolingually.

M2 has not been preserved, but it seems possible that the most mesial tooth in PIN 3101-40, identified by Trofimov (1978) as P4, is in fact M2, the whole series preserved in PIN 3101-40 being M2–M5. If so, M2 in *G. hoburensis* would be of the same pattern as in *G. borissiaki*.
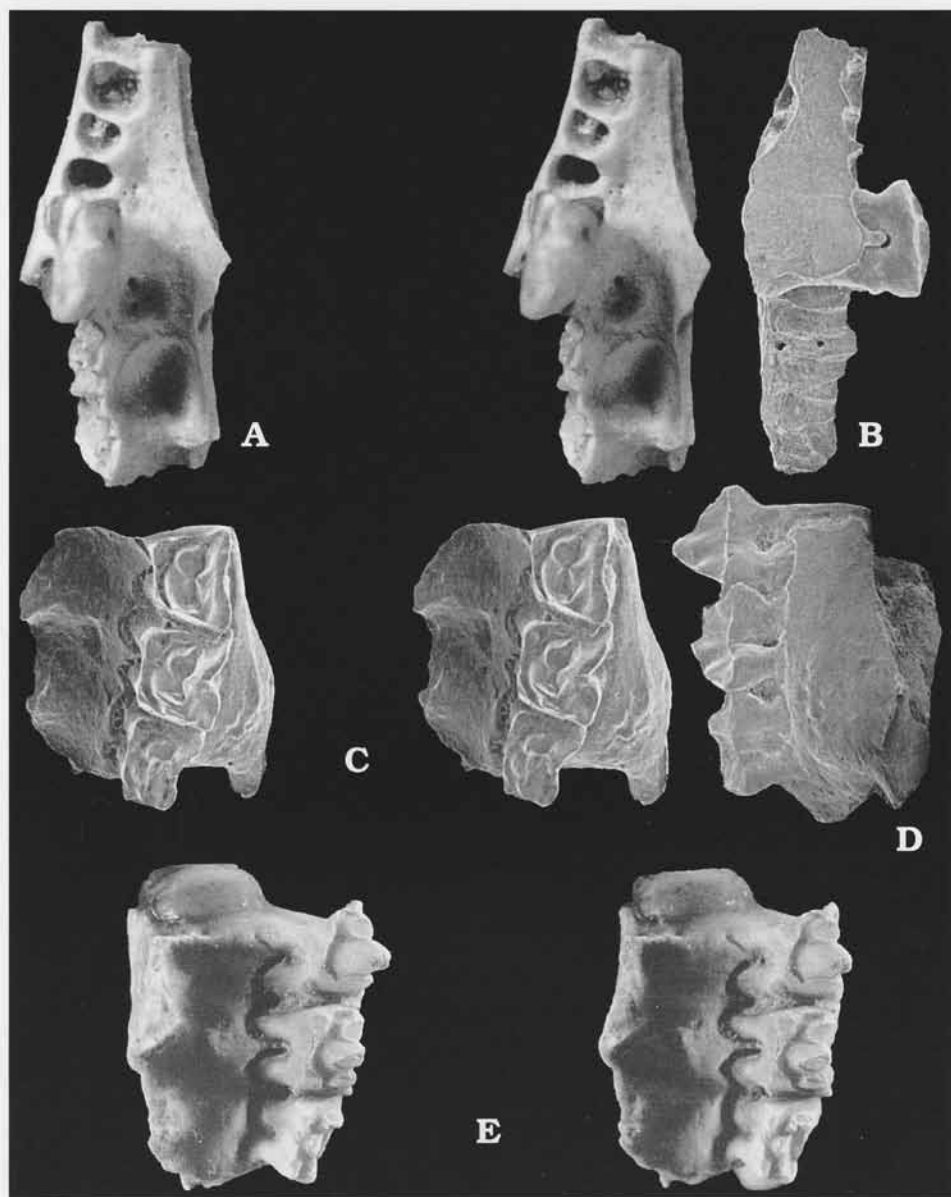
Fig. 4. *Gobiconodon hoburensis* (Trofimov, 1978). Khoboor Beds, Khoboor, Gobi Desert, Mongolia. **A**, **B**. Partial right maxilla, with alveoli for P2–P4, worn M1 and alveoli for M2 and M3, PSS 10–37a. **A**. SEM stereomicrograph in occlusal view. **B**. SEM micrograph in buccal view. **C–E**. Partial right maxilla with M3–M5, PSS 10–37b. **C**. SEM stereo-micrograph in occlusal view. **D**. SEM micrograph in buccal view. **E**. Stereo-photograph of the same showing lingual side of the teeth. Cusp terminology after Crompton & Jenkins (1968) is shown in Fig. 8. All × 10, **E** – coated with ammonium chloride.

M3 (PSS 10–37b) is 1.2 mm long and 1.0 mm wide mesially. It has a gently incurved ectoflexus and narrow buccal cingulum, with traces of worn cuspules. Of the three main cusps, cusp A is

Fig. 5. *Gobiconodon hoburensis* (Trofimov, 1978). Khoboor Beds, Khoboor, Gobi Desert, Mongolia. Montage-photograph of SEM micrographs PSS 10–37a (anterior photo) and 10–37b (posterior photo, reversed) in occlusal view, showing nearly complete maxilla. The most distal alveolus in PSS 10–37a, seen on the mounted photograph is for the anterior root of M3, (broken in PSS 10–37b), × 12.

moderately worn, cusp B is more strongly worn (in a mesiolingual direction) and cusp C is very strongly worn. The three cusps are arranged in an incipient triangle of about 158°. Distal to cusp C and adhering to it there is a distal cingulum that extends transversely across the tooth, developed as a narrow groove because of strong wear. The lingual cingulum almost disappears opposite cusp A, but is prominent mesially (with a cuspule) and distally, although distally it became almost completely eroded (in a distolingual direction). There is a distal cingulum, partly lost due to the wear. In M3 and in successive upper molars in front of cusp B there is a narrow mesial cingulum, but cusp E is not developed.

M4 is 1.3 mm long and 1.2 mm wide mesially. It differs from M3 in having the ectoflexus more strongly incurved medially. As a result the buccal cingulum is divided into two lobes (mesial and distal). There are worn but distinct cuspules on the cingulum. There are three main cusps, the central cusp A larger than cusps B and C, which are of approximately the same size. All are partly worn, B in a lingual direction, and A and C distolingually. The three main cusps form a slightly less obtuse angle (of 145°) than in M3. There is a very narrow distal cingulum, which in contrast to M3 is not worn. The lingual cingulum is distinct, partly worn, wider mesially and distally than medially.

M5 is 1.25 mm long and 0.9 mm wide mesially. As usual it is asymmetrical, being wider mesially than distally. The ectoflexus is smaller than in M4 and the buccal cingulum is not very prominent. Of the three main cusps only cusp B has been preserved; cusps A and C are broken off and the angle of a triangle formed by three main cusps is about 117°. The lingual cingulum is partly worn and is wider mesially than distally. The M5 is placed less obliquely with respect to M3 and M4 than in *G. borissiaki* (PSS 10–15b, see Fig. 1A).
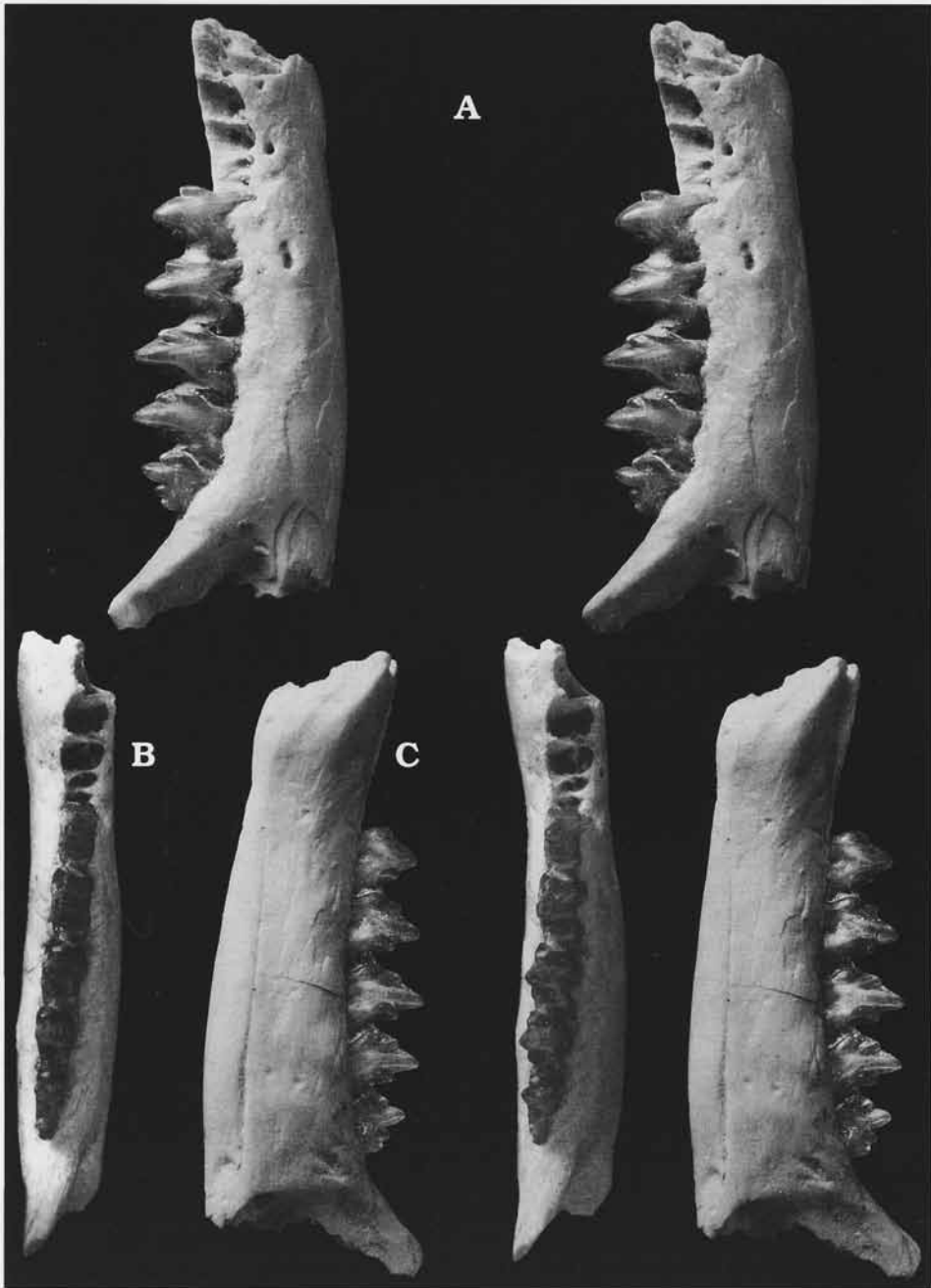
Fig. 6. *Gobiconodon hoburensis* (Trofimov, 1978). Khoboor Beds, Khoboor, Gobi Desert, Mongolia. Partial right dentary with m1–m5, alveoli for canine and for p1–p4, PSS 10–37c, in buccal (**A**), occlusal (**B**), and lingual (**C**) views. Cusp terminology after Crompton & Jenkins (1968) is shown in Fig. 8. All stereophotographs, × 6.
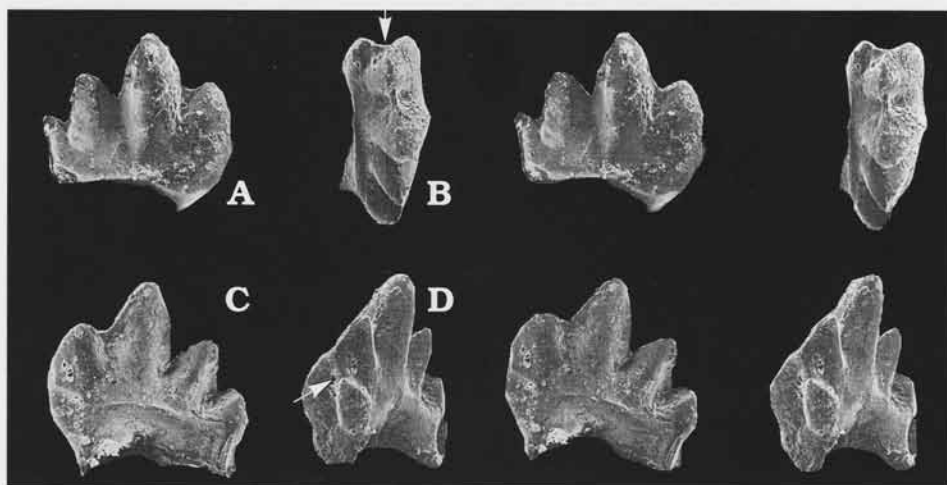
Fig. 7. *Gobiconodon hoburensis* (Trofimov, 1978). Khoboor Beds, Khoboor, Gobi Desert, Mongolia. Crown of right m5, in buccal (**A**), occlusal (**B**), lingual (**C**), and mesiolingual (**D**) views. PSS 10–21. Arrows in **B** and **D** denote embayment between cusps e and f, to receive cusp d of the preceding molariform. Cusp terminology after Crompton & Jenkins (1968) is shown in Fig. 8. All SEM stereomicrographs, × 16.

Dentary and lower teeth. PSS 10–37c (Fig. 6) is a right incomplete dentary with m1–m5 and alveoli (partly broken off) for the remaining teeth. The dentary is 2.5 mm deep below m1 (buccal view). The lower margin is slightly convex below p4–m5. An apparent convexity below p1–p3 on the lower margin, seen in Fig. 6A, C, is probably due to a crack. It is not seen on the drawings of the holotype PIN 3101/24 (Trofimov 1978, fig. 2). Three mental foramina are situated below the embrasures of p1–p2, p3–p4 and m1–m2, respectively. The coronoid process slopes at an angle of about 40° to the horizontal. The masseteric fossa does not reach anteriorly below m5. A fragment of the symphysis has been preserved. Behind the symphysis (lingual view) the dentary is slightly inflated. A hardly discernible remnant of the coronoid bone, united to the dentary, is seen in lingual aspect behind m5. Below the coronoid bone there is a rounded mandibular foramen. Extending anteriorly from below the mandibular foramen is a thread-like remnant of the Meckel's groove, very fine anteriorly, which reaches the mandibular symphysis.

The fragmentary alveoli for c-p4 (the alveolus for i1 is preserved in the holotype PIN 3101/24) indicate the presence of a semi-procumbent incisor and canine, p1–p3 with decreasing procumbency, and a very small, double-rooted p4. The lengths (maximum length seen in buccal view) and widths of m1–m5 are, respectively (in mm): m1 – 1.66 and 0.8; m2 – 1.86 and 0.9; m3 – 1.7 and 0.95, m4 – 1.77 and 0.8; m5 – 1.33 and 0.6.

On all the molars cusp a is very high and trenchant. The m1 is lower than m2–m4, the m3 being the tallest of all the teeth and m5 the lowest. On m1 cusp b is lower than cusp c (but still placed higher than in *G. borissiaki* and *G. ostromi*), on the succeeding teeth they are subequal in height. The m1–m3 appear four-cuspid in buccal aspect, cusp e, which originally might have been present, being completely obliterated by wear. Cups d is also worn, but its presence is more evident. In m4 and especially in m5, cusps e and d are less worn and better seen. In all the molars the lingual cingulum is present only mesially and lingually, disappearing entirely opposite cusp a. The mesial cingulum is prominent, developed as ridges from cusp b. In occlusal view cusp b is incurved, to receive the distal margin of p4. The buccal cingulum is not developed. In m3 and m4 the crown is shifted in relation to the roots, which are directed obliquely distoventrally. The m5 is situated relatively high on the coronoid process, its posterior root being completely embedded in the bone. In m5 cusps b and c are subequal in size and are placed more apart from cusp a than in preceding teeth.

Occlusion. — As the material of *Gobiconodon hoburensis* at our disposal is more complete than that of *Gobiconodon borissiaki*, we begin reconstruction of the occlusion in the two taxa with *G. hoburensis*.

In Fig. 8 we reconstruct the matching wear facets of molariform teeth in *G. hoburensis*, based on left M3–M4 (PSS 10–37b, the M5 preserved in this specimen is damaged and its wear facets have not been preserved) and right m1–m5 (PSS 10–37c). The upper molariform teeth used for reconstruction (PSS 10–37b) belonged to an older individual and show stronger wear than the lower teeth in the dentary (PSS 10–37c). Because of different individual age of the upper and lower teeth, when matching them together we reconstructed wear facet on cusp a of m2, not present in PSS 10–37c.

Of the upper molariform teeth the M3 is most worn and the degree of wear decreases posteriorly. On the lower molariform series there are small differences in the degree of wear, but generally the wear is smaller posteriorly, the m4 and m5 being slightly less worn than the others.
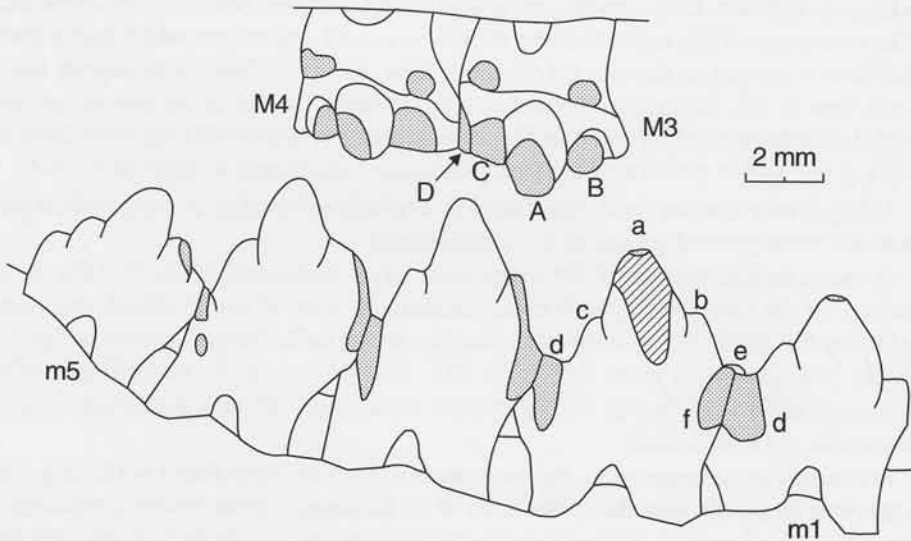

Fig. 8. *Gobiconodon hoburensis* (Trofimov, 1978). Diagram (camera lucida drawing) of wear facets resulting from occlusion, in buccal view. The facets on the lingual side of the upper teeth are likewise seen in buccal view as if the teeth were transparent. Lower teeth based on PSS 10–37c, upper teeth are based on PSS 10–37b, reversed. Dotted areas – preserved wear facets, hatched area – reconstructed wear facet.

The central cusp A of the upper molariforms occludes with cusp b of the preceding lower tooth and passes downwards to cusp f. On upper molariforms the facet is more evident on M4 than on M3 and is placed distolingually. On lower molariforms the largest joined facet on both cusps b and f is on m3, slightly smaller on m4, and on m5 the facet is only on cusp b. On m2 the facet has been produced only on cusp f (in lower part of the tooth) and cusp b has not been affected as yet. On m1 cusp f is not developed and cusp b has not been affected.

Cusp B of the upper molariforms (and corresponding anterior facet on the lingual cingulum) occludes with cusp c of the preceding lower tooth. On the upper molariforms the wear facet on cusp B is very distinct on both M3 and M4, and in M4 it is strongly concave. The corresponding facet on the lingual cingulum is well defined on all the molariforms, oval in shape (slightly elongated mesiodistally), smaller on M5 than on M3 and M4. On lower teeth the facet on cusp d is present on m1–m4, but is absent from m5. On m4 it is less extensive than on the preceding teeth, and consists of two separate facets, not joined as yet. In *G. ostromi* there is a distinct wear facet on cusp c (Jenkins & Schaff 1988: fig. 10a). In *G. hoburensis* cusp c is relatively less prominent than in *G. ostromi*; in PSS 10–37c (because of its young age), cusp c has not been affected as yet in any of the teeth, but there is instead an extensive facet on cusp d. In older lower molariforms the cusp c will be probably worn.

Cusp C and the distal cingulum (cusp D) occluded together with the central cusp a. In PSS 10–37b cusp C in M3 bears a strong facet, joined with a facet on the distal cingulum, both forming an almost transverse groove. On M4 the distal cingulum is not worn, but on both M3 and M4 there is a corresponding distinct wear facet, half-ellipsoidal in shape on the lingual cingulum. Cusp a on m1–m5 in PSS 10–37a does not bear a wear facet because of the young age of this individual. An exception are m1 and m2, on which an incipient wear facet is present on the very tip of cusp a, seen only in occlusal view, slightly larger on m1 than on m2. Because of the presence of this facet, the tips of m1 and m2 are less pointed than in succeeding teeth. In Fig. 8 we tentatively reconstruct the wear facet on cusp a in m1, which would develop on all the lower molariforms in older individuals.

In Fig. 9 we reconstruct the wear facets in available material of *G. borissiaki*, which are of the same general pattern as in *G. hoburensis*.

A characteristic feature of the upper teeth of *G. borissiaki* (PSS 10–15b) is the presence of the transverse groove in the location of cusps C and D (distal cingulum) caused by the work of cusp a of corresponding lower molariforms (arrows in Fig. 1A and B). This groove is more evident in PSS 10–15b than in the molariforms of *G. hoburensis* (PSS 10–37b, Fig. 4C, E) because of the more advanced individual age of the maxilla of *G. borissiaki*.

In contrast to the upper teeth, the lower teeth of *G. borissiaki* (PSS 10–15a, Figs 1D, 2) are even less worn than the lower teeth of *G. hoburensis* (PSS 10–37c). No wear is discernible on p2 and p3. The p4 (which was hitherto not known in *G. borissiaki*, and only alveoli are preserved in *G. ostromi*) shows distinct wear facets. Cusp a is completely worn horizontally on its lingual half, and obliquely ventrolaterally on the buccal half. Below this surface, on the buccal side, there is another vertically directed, oval wear facet.

On m1 the tips of cusp a, b and c are slightly worn horizontally, but there are no wear facets on the buccal side. On m2 the cusp a has been broken off and has been reconstructed in Fig. 9. Below the broken part on the buccal side there is a part of the wear facet, roughly triangular and pointed downwards. The presence of this facet indicates that the tip of cusp a was probably also worn. On cusp b there is a relatively large facet, pointed downwards, while in cusps b and f only tips of the cusps have been worn. Otherwise the pattern of occlusion is the same as in *G. hoburensis*.

Jenkins & Schaff (1988) reconstructed the medial translation and rotation of the dentary during closure in *G. ostromi*. The presence of palatal fossae on the maxilla in
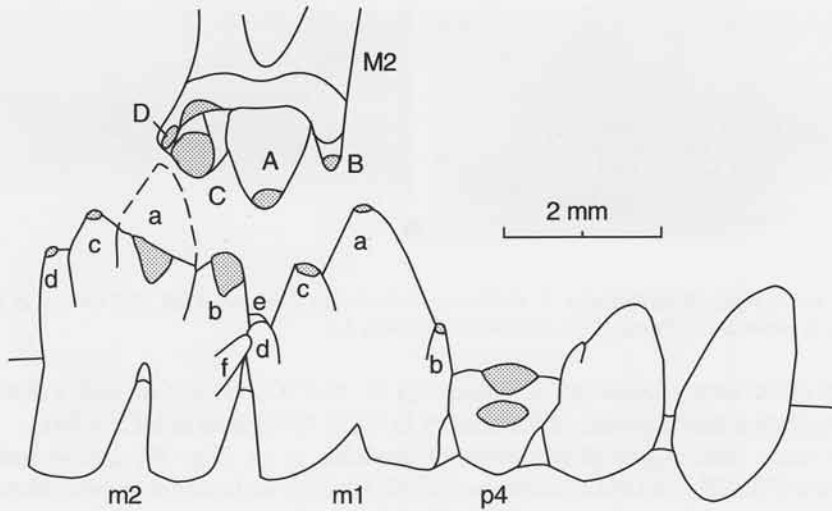
Fig. 9. *Gobiconodon borissiaki* Trofimov, 1978. Diagram (camera lucida drawing) of wear facets resulting from occlusion, in buccal view. The facets on the lingual side of the upper tooth are likewise seen in buccal view as if the tooth were transparent. Upper tooth based on PSS 10–15b, lower teeth on PSS 10–15a, reversed. Hatched areas – preserved wear facets.

G. borissiaki and *G. hoburensis*, which apparently received cusp a of the lower molariform teeth, gives support for the Jenkins & Schaff's supposition.

Comparisons. — The three species of *Gobiconodon* differ mostly in size. Other differences are probably related to increase of carnivorous habits in larger forms. This concerns increase of the size of the masseteric fossa, which in *G. hoburensis* is the shortest and does not extend below the distal part of m5; in *G. ostromi* it reaches below the m4–m5 embrasure and in *G. borissiaki* it is intermediate in its anterior extension between these two taxa. Another difference concerns the relative size and position of i1, which in *G. borissiaki* and *G. hoburensis* is relatively smaller and more shifted medially with respect to the row of other teeth than in *G. ostromi* (where it is relatively the largest and most aligned with other teeth). The p4, which is double-rooted in *G. hoburensis* and single-rooted in *G. borissiaki*, is on the way of disappearing in *G. ostromi*. This may be related to the shortening of the dentary.

G. *hoburensis* differs from *G. ostromi* and *G. borissiaki* also in having smaller cusp c in lower molariforms. This results in differences in occlusion: in *G. hoburensis* (at least in younger stages) the wear facet, produced by cusp B of upper molariforms, is on cusp d, rather than on cusp c as in the two other species.

Replacement of molariform teeth

Jenkins & Schaff (1980) described the replacement of molariform teeth in dentaries of *Gobiconodon ostromi* (MCZ 19965) as sequential, from front to back. In right and left dentaries of that specimen (figs 4A, B; 5A, B, 6A and 8 of their paper), there is a distance between the distal end of m5 and the base of the coronoid process. However, in another
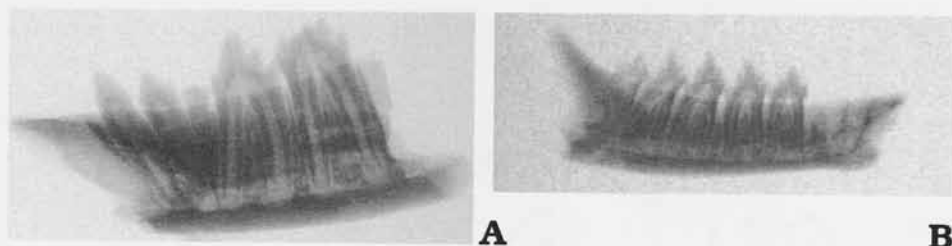
Fig. 10. Radiographs of the dentaries. **A**. *Gobiconodon borissiaki* Trofimov, 1978, PSS 10–15a. **B**. *Gobiconodon hoburensis* (Trofimov, 1978), PSS 10–37c. × about 3.6.

dentary of the same species (MCZ 19860, figs 4G and 5G), there is no such a distance. This suggests a longer growth of the dentary in MCZ 19965 than in MCZ 19860.

We made radiographs of the dentaries available to us (Fig. 10) and in both *G. borissiaki* (PSS 10–15a) and *G. hoburensis* (PSS 10–37c) we have not found evidence of tooth replacement. In the dentary of *G. borissiaki* the m2 erupted before m1, as it covers dorsally the m1 (Fig. 1D). The maxilla of *G. borissiaki* with M2–M5 (PSS 10–15b, Fig. 1A–C) shows notable differences in the degree of wear of teeth preserved, which indicates that they do not belong to the same generation. In teeth of the same generation, one should expect that M2 would be most strongly worn, and the degree of wear would decrease posteriorly. In our case, however, the most worn tooth of the preserved series is M3, then M4 and M5. The M2 is much less worn than M3 and M4, and the difference between M2 and M3 is so dramatic that we suggest that M2 belongs to the second (younger) generation than the remaining teeth. This, and the structure of the dentary (PSS 10–15a) gives indirect evidence for the replacement of molariform teeth in *G. borissiaki* (see also Jenkins & Schaff's 1988 similar observations on *G. borissiaki*).

The replacement of molariform teeth convincingly demonstrated for *G. ostromi* (Jenkins & Schaff 1988: fig. 8) is unique for 'triconodonts'. It would be difficult to presume that it was characteristic of only one species of *Gobiconodon* and not of all the species of this genus.

The lack of direct evidence of replacement of molariform teeth in *G. borissiaki* and *G. hoburensis* from the PSS collection (Fig. 10) may be also explained by the relatively young ontogenetic age of the individuals represented by the two specimens. Their teeth apparently represent the first generation, the teeth of the next generation not being formed as yet. In two relatively complete dentaries of *G. hoburensis* (Trofimov 1978, fig. 2, and Fig. 6 in this paper) the coronoid process starts below m5, which is situated at the base of the ascending ramus of the process. These dentaries, as well as that of *G. borissiaki* (Fig. 10A) probably are at the same level of ontogenetic development as the dentary of *G. ostromi* MCZ 19860 discussed above. This may explain the lack of evidence of tooth replacement in radiographed specimens.

Relationships of Amphilestidae

Occlusion. — Mills (1971: p. 53) stated: 'The English Amphilestinae would seem to belong to the Infra-Class Pantotheria, and their closest relations, as far as tooth morphology is concerned would be *Kuehneotherium* and the 'obtuse-angled' symmetrodonts

such as *Tinodon...*' It should be noted that the similarity of the amphilestid molariforms to those of symmetrodonts concerns the upper, but not the lower molariforms. This may be the reason that the taxonomic consequences of Mills statement have not been accepted by subsequent authors, although Freeman (1979) classified amphilestids as symmetrodonts. Crompton (1974) and Jenkins & Crompton (1979) pointed to a basically similar occlusal pattern in symmetrodonts (including *Kuehneotherium*) and amphilestids. Similarly, Fox (1985) discussed this problem, but did not include the amphilestids as symmetrodonts, pending description of new amphilestids fossils under study at that time at Harvard University (announced by Jenkins & Crompton 1979).

Jenkins & Schaff (1988) and we (this paper) confirmed the observations of Mills (1971), Crompton (1974), and Jenkins & Crompton (1979), on the similarity of the occlusal pattern between the amphilestid Gobiconodontinae and early symmetrodonts. In *Gobiconodon* the main cusp a of lower molariform occluded immediately in front to the distal margin of the corresponding upper molariform between cusp C and D (distal cingulum), as in *Kuehneotherium*, rather than between cusps A and B as in Morganucodontidae and Triconodontinae.

Interlocking mechanism. — The interlocking mechanism of the lower molariforms in *Gobiconodon* resembles that in *Kuehneotherium* (Crompton 1974; Luo 1994) and *Tinodon* (Crompton & Jenkins 1967; Jenkins & Crompton 1979; Prothero 1981). In the dentary of *G. borissiaki* (PSS 10–15a, Fig. 1D), on the mesial margin of m2 there are two cingulum cusps e and f, with an embayment between them, to receive the cingulum cusp d of m1. However, in this individual, because of the young age, the perfect interlocking has not been achieved as yet, as the mesial cingulum of m2 partly covers dorsally the distal cingulum of m1. One can visualize that, with the further growth of the dentary, the distance between m1 and m2 will increase, and the discussed cusps would interlock. In the dentary of *G. hoburensis* (PSS 10–37c) in spite of wear of cusp f (buccal cusp on the mesial cingulum), the interlocking mechanism is very well seen in occlusal and lingual views, especially between m2 and m3 (Figs 6B, C and 8). The isolated m5 of *G. hoburensis* shows very clearly the mesial cusps e and f, with an embayment between them (Fig. 7B, D), which demonstrates the interlocking mechanism as in *G. borissiaki*. Jenkins & Schaff (1988) did not describe the interlocking mechanism in *G. ostromi*, but careful examination of the stereo-photographs of this taxon in occlusal view, especially figs 6D and 7E in their paper, allows us to conclude that the interlocking mechanism was apparently of the same type as in the two other species of *Gobiconodon*.

The interlocking mechanism in other taxa of the Amphilestidae, to our knowledge, has not been described. It is clear, however, that in Kuehneotheriidae, *Tinodon* and Gobiconodontinae cusp d of the anterior molariform (forming a structure referred to by Crompton 1974 as the talonid) fits into the embayment between cusps e and f of the succeeding molariform. This mechanism differs in details from the system that occurs in Morganucodontidae. The posterior margin of molariforms in *Morganucodon* (Crompton 1974) and *Dinnetherium* (Jenkins *et al.* 1983) is broad and fits into a shallow embayment between cusps b and e on the succeeding molar. Triconodontidae, *Amphitherium* and Docodonta display the interlocking mechanism of *Morganucodon*

pattern, different from that in *Kuehneotherium, Tinodon* and Gobiconodontidae (Kron 1979; Prothero 1981; Luo 1994; Cifelli *et al.* 1998).

Cusp arrangement. — 'Triconodonts' differ from symmetrodonts, among others, in the arrangement of main cusps on molariforms, which in the triconodonts are arranged mesiodistally, while in symmetrodonts they form a triangle. In all three species of *Gobiconodon*, the cusps of lower molariforms are arranged mesiodistally, but the upper molariforms show incipient triangular arrangement. In both Mongolian species of *Gobiconodon* the degree of triangular arrangement increases posteriorly. In *G. boris-siaki* (Fig 1A) the cusps on M2 are arranged mesiodistally, the only M3 available to us is very strongly worn out, but apparently also cusp A was placed more lingually than cusps B and C. On M4 cusp A is placed distinctly more lingually than cusps B and C, and on M5, this is still more strongly expressed. Because of strong wear we were able to measure the angle between the main cusps only in M5 (117°). In *G. hoburensis* M1 shows mesiodistal arrangement of cusps, M2 has not been preserved, and M3–M5 show incipient triangular arrangement, the angle between the cusps increasing poste-riorly. The tentatively estimated cusp angles are M3 – 158°, M4 – 145° and M5 – 117° (Fig. 11). In *G. ostromi* (see Jenkins & Schaff 1988, figs 7F and 10B) only M3 and M5 of upper molariforms are known, and both, but especially M5, show deviation from mesiodistal arrangement of the main cusps. The angle between the cusps of upper molariforms in *Gobiconodon* species is extremely obtuse. As other amphilestid taxa are known from dentaries with teeth or isolated teeth (Simpson 1925, 1928, 1929; Jenkins & Crompton 1979; Sigogneau-Russell *et al.* 1990), it is impossible to judge whether the incipient triangular arrangement of the cusps of upper molariforms is characteristic only for the Gobiconodontinae, or for all the Amphilestidae.

Only isolated upper and lower molariforms are known in *Kuehneotherium*, al-though Mills (1984) reconstructed its upper and lower molariform series. As (except for two teeth) he did not illustrate these molariforms in occlusal view, it is difficult to compare upper molariform series of *Gobiconodon* and *Kuehneotherium*. *Tinodon* is known only from the lower teeth.
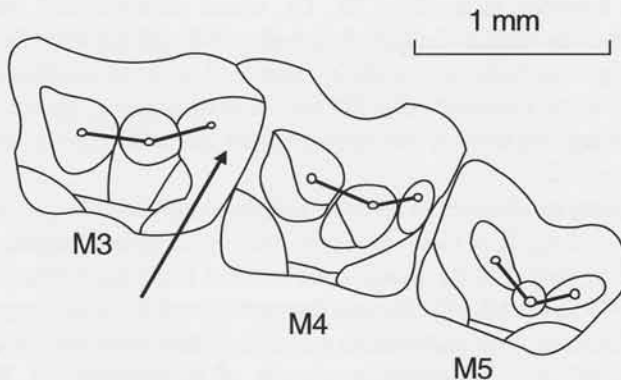

Fig. 11. *Gobiconodon hoburensis* (Trofimov, 1978). Diagram (camera lucida drawing of PSS 10–37b), showing incipient triangular pattern of cusps A, B and C in M3–M5. The arrow in M3 denotes groove made by cusp a of the corresponding lower molariform.

Premolar resorption. — Gill (1974) described resorption of premolars in *Kuehneotherium*, basing on four incomplete, mature dentaries, in which the roots have been resorbed and replaced by spongy bone. Jenkins & Schaff (1988) described resorption of p4 in *Gobiconodon ostromi*. Gill (1974) argued that resorption was probably common to all very early mammals, and if so, its presence in *Kuehneotherium* and *Gobiconodon* does not indicate relationship.

Angular process of the dentary. — Among early mammals, the angular process occurs in the Morganucodontidae, including *Dinnetherium*, and in Docodonta (*Haldanodon*), but is absent in the Kuehneotheriidae, and in all the later symmetrodonts, the Triconodontidae, Amphilestidae and in Multituberculata. It occurs in eupantotheres and all the later Theria, except some highly specialized forms. It is absent in extant monotremes, but occurs in their fossil representatives (Archer *et al.* 1992). Dr Zhexi Luo drew our attention to the fact that, although the angle of the dentary is obtuse in *Kuehneotherium*, it still retained the contact with the reflected lamina of the angular, characteristic of *Morganucodon* (Crompton & Luo 1993: fig. 4.7). Thus the angular process of the dentary of *Kuehneotherium* shows an intermediate condition between the more prominent and primitive angle of *Morganucodon*, and the lack of a distinct angle in *Gobiconodon* and *Triconodon*. Therefore the structure of the angular process does not indicate a relationship between the Amphilestidae with Kuehneotheriidae.

Postcranial skeleton. — The postcranial skeleton is not known in Kuehneotheriidae. Among the Amphilestidae, large fragments of the postcranial skeleton have been found for *Gobiconodon ostromi* (Jenkins & Schaff 1988). Of interest is the scapula attributed by Jenkins & Schaff (1988) to *G. ostromi*, which has both infraspinous and supraspinous fossae. Similar scapulae have been found in an Early Cretaceous triconodontid from the Cloverly Formation (Jenkins & Crompton 1979) and in a triconodontid mammal from the Late Jurassic of China (personal communication from Zhexi Luo, May 1998). As infraspinous and supraspinous fossae occur also in multituberculate scapulae (Kielan-Jaworowska & Gambaryan 1994), this structure evidently developed in parallel in mammalian evolution, and the presence in *Gobiconodon* of a scapula similar to that of therians does not indicate its therian affinities.

Conclusions

Two characters (occlusal pattern and interlocking mechanism) ally the Gobiconodontinae (and possibly all the Amphilestidae) with the Kuehneotheriidae, and if so, with Theria. The scapula of *Gobiconodon* is therian-like, but the significance of this is unclear because similar scapulae evidently appeared elsewhere, independently in other lineages. The same concerns the incipient triangular arrangement of the cusps of upper molariforms, a character that does not occur in lower molariforms.

Luo (1994) argued that *Haldanodon*, *Megazostrodon*, morganucodontids, triconodontids, and other mammals form a monophyletic group. He regarded (after Crompton 1974), among others, the following dental characters as apomorphic for the group: a one-to-one occlusal relationship between the opposing upper and lower molars, interlocking of adjacent molars; development of constant wear facets, and diphyodont

dental replacement. Luo (1994) did not discuss the amphilestids, which share the characters of the above-cited mammals, except the dental replacement.

As far as dental replacement is concerned, in *Sinoconodon,* which is a sister taxon of all other mammals, the three posterior molars were replaced once (Zhang *et al.* in press). In *Megazostrodon* the second molariform may be replaced (Gow 1986). Zhang *et al.* (in press) pointed that it is not clear whether the molar replacement occurred in *Morganucodon,* while Parrington (1971) believed that molars were not replaced in this taxon. As discussed in the foregoing section, Amphilestidae (or at least Gobiconodontinae – Jenkins & Schaff 1988, and this paper) are rare among mammals in replacing their molariforms. The problem arises to whether the Kuehneotheriidae indeed had mammalian tooth replacement (Mills 1971; Parrington 1978), or rather shared the replacement of molariforms with *Sinoconodon, Megazostrodon* and Gobiconodontinae. The only dentary of *Kuehneotherium* with teeth is a fragment dissected and figured by Parrington (1978: fig. 4d), showing m4 with roots, and roots of m3 and m5. Otherwise *Kuehneotherium* is known from isolated teeth and isolated dentaries and maxillae, the latter not figured (D. M. Kermack *et al.* 1968; Mills 1971, 1984; Parrington 1971, 1978; Gill 1974). It is not possible to demonstrate the replacement of molariforms on such incomplete material.

The data presented in this paper give some support to Mills' idea on the therian affinities of the Amphilestidae although it cannot be excluded that the characters that unite the two groups may have developed in parallel. Amphilestidae are characterized by replacement of molariforms, which is a plesiomorphic character, characteristic only of few very primitive mammals. On the other hand, they have a typical mammalian single jaw joint between the dentary and the squamosal. Kuehneotheriidae apparently had a double jaw joint, possibly with a full complement of the reptilian bones in the lower jaw. It is not known whether they replaced their molariforms or not. The triangular cusp arrangement of the molariform teeth of Kuehneotheriidae is more advanced than that in the Amphilestidae. As long as Early Jurassic or Late Triassic ancestors of the Amphilestidae are not known it is impossible to suggest e.g., sister group relationships between the discussed groups.

In view of these scanty and ambiguous data, the systematic position of the Amphilestidae must remain open and we classify them in the order *incertae sedis.*

Acknowledgements

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Wczesnokredowe „trykonodonty" z rodziny Amphilestidae z Mongolii

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Streszczenie

W pracy opisano niewielką kolekcję niekompletnych żuchw i szczęk z zębami ssaków z rodziny Amphilestidae (zaliczanej do parafiletycznej grupy „trykonodontów"). Kolekcja ta pochodzi ze stanowiska Hobur w regionie Guczin Us w południowej Mongolii. Wiek osadów z Hoburu został określony jako apt lub alb. Z osadów tych Trofimov (1978) opisał dwa rodzaje: *Gobiconodon* (z gatunkiem typowym *G. borissiaki*) i *Guchinodon* (z gatunkiem typowym *G. hoburensis*). Porównanie nowych okazów obu tych gatunków wykazało, że różnice między nimi dotyczą wymiarów oraz proporcji między wielkością guzków na zębach i mają charakter różnic gatunkowych, a nie rodzajowych. Na tej podstawie zaproponowano uznanie nazwy *Guchinodon* Trofimov, 1978 za młodszy synonim rodzaju *Gobiconodon* Trofimov, 1978.

Wykazano, że u *Gobiconodon borissiaki* górne trzonowce M3 i M4 wykazują większe starcie niż trzonowiec M2, co uznano za pośredni dowód przemawiający za wymianą zębów trzonowych u tego gatunku. Wymiana trzonowców była wcześniej stwierdzona u amerykańskiego gatunku *Gobiconodon ostromi*. Zbadano też nie opisywany wcześniej mechanizm blokujący (*interlocking mechanism*) występujący między dolnymi trzonowcami obu badanych gatunków i stwierdzono, że mechanizm ten jest tego samego typu co u symetrodontów *Kuehneotherium* i *Tinodon*, a odmienny od typu występującego u „trykonodontów" z rodziny Triconodontidae. Również i typ okluzji występujący u badanych „trykonodontów" jest zbliżony do typu charakterystycznego dla symetrodontów, co zgadza się z wcześniejszą sugestią Millsa (1971) dotyczącą okluzji u innych amfilestydów. Tak więc mechanizm blokujący i typ okluzji sugerują pokrewieństwo Amphilestidae z Kuehneotheriidae. Amphilestidae różnią się jednak od Kuehneotheriidae obecnością pojedynczego stawu żuchwowego (u Kuehneotheriidae staw żuchwowy jest złożony, przejściowy między stawem typu gadziego i ssaczego) oraz układem guzków na zębach. U Amphilestidae guzki na dolnych trzonowcach ułożone są w prostej linii, gdy u Kuehnoetheriidae tworzą one zaczątkowy trójkąt. Jednakże na tylnych górnych trzonowcach u obu badanych gatunków gobikonodonta występuje zaczątkowe trójkątne ułożenie guzków.

Praca dostarcza pewnego poparcia dla poglądu Millsa (1971) o pokrewieństwach amfilestydów ze ssakami właściwymi (Theria *sensu lato*), do których należą między innymi wymarłe Kuehneotheriidae, oraz współczesne torbacze i łożyskowce. Nie jest jednak wykluczone, że cechy zbliżające Amphilestidae i Kuehneotheriidae mogły powstać w obu grupach niezależnie. W związku z niekompletnym poznaniem Amphilestidae, rodzinę tę zaliczono do rzędu *incertae sedis*.