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Gobiconodonts from the Early Cretaceous of Oshih (Ashile), Mongolia

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ABSTRACT

We describe here the first discovered mammalian remains from the Mongolian Early Cretaceous locality Oshih (Ashile). Four fragmentary, tooth-bearing specimens, probably corresponding to three individuals, have been recovered. All the fossils can be assigned to the family Gobiconodontidae (Chow and Rich, 1984). The specimens include three lower jaw fragments and one upper jaw fragment, and represent at least two different taxa.

Gobiconodon hopsoni, n. sp., is described and diagnosed here. This new species is larger than *G. ostromi* (Early Cretaceous Cloverly Formation, USA); thus, it is the largest triconodont and one of the largest Mesozoic mammals known. *Gobiconodon* sp., found also at Oshih, is slightly larger than *G. borissiaki,* from the Early Cretaceous of Khoobur, Mongolia, but smaller than *G. ostromi.* The specimens of this second species are poorly preserved and provide insufficient data for a diagnosis.

The status of the different species of *Gobiconodon* and the new gobiconodontid *Hangjinia* is reviewed. In gobiconodontids and Triconodontidae, the maxillae appear to make a significant contribution to the orbital rim, a condition unusual among basal mammals, in which the lacrimal and jugal are the main components. Other triconodonts such as *Jeholodens,* likely an ''amphilestid'', appear to show the primitive mammalian condition for this feature. We present a brief consideration of triconodont relationships and discuss alternative placements of *Gobiconodon* among Mammaliaformes.

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INTRODUCTION

Early Cretaceous mammals are rare; only about two dozen fossil-bearing localities are known worldwide. Nevertheless, these few localities have produced specimens crucial to our understanding of early mammalian evolution (Patterson, 1956; Kermack et al., 1968; Hu et al., 1997, 1998; Ji et al., 1999) and have spawned a prolific literature. Early Cretaceous localities yielding mammals have been discovered in Central Asia (Dashzeveg, 1975, 1994; Trofimov, 1975, 1980; Nessov, 1985; Kielan-Jaworowska et al., 1987; Kielan-Jaworowska and Dashzeveg, 1989, 1998; Sigogneau-Russell et al., 1992; Nessov and Kielan-Jaworowska, 1991; Nessov et al., 1994; Maschenko and Lopatin, 1998), Japan (Rougier et al., 1999), China (Yabe and Shikama, 1938; Shikama, 1947; Hu et al., 1997, 1998; Ji et al., 1999), Europe (Owen, 1871; Simpson, 1928; Clemens, 1963; Kielan-Jaworowska and Ensom, 1991, 1994; Sigogneau-Russell and Ensom, 1994; Cuencas-Bescós et al., 1995, 1996; Canudo and Cuencas-Bescós, 1996, Ensom and Sigogneau-Russell, 1998), North America (Patterson, 1956; Slaughter, 1969; Turnbull, 1971; Fox, 1975; Butler, 1978; Cifelli and Eaton, 1987; Jenkins and Schaff, 1988; Eaton and Nelson, 1991; Cifelli et al., 1998; Cifelli and Madsen, 1998; Cifelli, 1999), Australia (Archer et al., 1985; Rich et al., 1989, 1997, 1998, 1999; Flannery et al., 1995), Africa (Jacobs et al., 1988; Brunett et al., 1990; Sigogneau-Russell, 1991a, 1991b, 1992, 1995a, 1995b), and South America (Bonaparte, 1986; Bonaparte and Rougier, 1987; Rougier et al., 1992).

These localities have frequently provided a unique mixture of late representatives primarily of Jurassic mammalian lineages, such as triconodonts, symmetrodonts and multituberculates, and basal members of groups that later dominated the Cretaceous and Tertiary, such as basal tribosphenic mammals and early therians. During the Early Cretaceous, the relatively diverse mammalian fauna of the subsequent Late Cretaceous was taking shape (Turnbull, 1971; Butler, 1978; Lillegraven et al., 1979; Kielan-Jaworowska, 1992; Cifelli, 1993b). The recent finding of a tribosphenic mammal in the Middle Jurassic of Madagascar (Flynn et al., 1999) confirms early suggestions that Tribosphenida is a relatively ancient group (Patterson, 1956; Simpson, 1961). Although Early Cretaceous specimens of metatherians and eutherians are rare (Kielan-Jaworowska and Dashzeveg, 1989; Cifelli and Eaton, 1987; Sigogneau-Russell et al., 1992; Cifelli, 1993a, 1993b, 1999), these tantalizing animals suggest that a basal diversification of tribosphenic mammals took place during the Early Cretaceous, as suggested earlier by Fox (1975) and Butler (1978, 1992). The interplay of these basal tribosphenic mammals with the more archaic non-tribosphenic fauna has not yet been fully explored. Therefore, new Early Cretaceous localities providing evidence of any of these groups are welcomed.

The relatively generalized tribosphenic molars of the Early Cretaceous produced in the Mesozoic a variety of tooth morphologies representing a fair diversity of feeding strategies, with the only notable exception being a highly specialized herbivorous role, which was monopolized by multituberculates during most of the Mesozoic and at least the early part of the Tertiary (Krause, 1986). Triconodonts (sensu lato; Rougier et al., 1996a) were mostly carnivorous-insectivorous forms that reached the Late Cretaceous (Fox, 1969; Bonaparte, 1986, 1992), but that were more diverse and abundant during the Jurassic (Owen, 1871; Simpson, 1928, 1929; Kermack, 1963; Rasmussen and Callison, 1981; Krusat, 1989; Chow et al., 1991; Engelmann and Callison, 1998; Heinrich, 1998) and Early Cretaceous (Patterson, 1956; Slaughter, 1969; Sigogneau-Russell, 1995a; Cifelli et al., 1998; Cifelli and Madsen, 1998). Triconodonts are not known, however, in the rich Late Cretaceous localities of Central Asia (Bonaparte and Kielan-Jaworowska, 1987; Jerzykiewicz and Russell, 1991; Dashzeveg et al., 1995).

We report here on a new Early Cretaceous mammalian locality providing evidence of gobiconodontid triconodonts (Trofimov, 1978; Jenkins and Schaff, 1988; Maschenko and Lopatin, 1998; Kielan-Jaworowska and Dashzeveg, 1998). Although the mammalian fossils we describe are not spectacular, the locality is potentially important because of

its extensive and excellent exposures. The specimens described here permit the description of a new species of *Gobiconodon.*

MATERIALS, METHODS, AND GEOLOGICAL SETTING

During 1997 and 1999 the field expeditions of the American Museum of Natural History and Mongolian Academy of Sciences revisited the Early Cretaceous outcrops at Oshih, in the northern expanses of the Gobi Desert, Mongolia. The site was discovered by the Third Central Asiatic Expedition in 1922 (Osborn, 1923, 1924a, 1924b; Berkey and Morris, 1927; Andrews, 1932). The dinosaurs described from Oshih include the relatively abundant ornithischian *Psittacosaurus mongoliensis* (Osborn, 1923, 1924a), the sauropod *Asiatosaurus mongoliensis,* and the theropod *Prodeinodon mongoliensis* (Osborn, 1924b). Oshih is the type locality for all of these dinosaurs (Osborn, 1923, 1924b). In addition to new specimens of these taxa, our recent work in this locality has uncovered several small dinosaurs, including primitive dromaeosaurs, a variety of small, as yet unidentified, theropods (M. Norell, personal commun.), as well as the first mammals, as described herein, from this site.

Oshih, also known classically as Ashile and Oshih Nur (Berkey and Morris, 1927), on the northern slopes of the Arts Bogd, is a depression formed by erosion along a mostly east-west axis, exposing a thick column of claystone, sandstone, intraformational conglomerates, and basalts (Berkey and Morris, 1927). Oshih is known by today's inhabitants simply as Osh (D. Dashzeveg, personal commun.). The original name of the Oshih Formation (Berkey and Morris, 1927) is considered in the Russian literature (Shuvalov, 1975) as part of the Tevsh (Undurukhin) Svita. This unit is considered to have correlative exposures in the Altai area, in addition to Oshih. The age of the Tevsh Svita rests on these reported correlations and extrapolation to the dated sequences in the eastern Gobi (Jerzykiewicz and Russell, 1991). The Tevsh Svita is considered to be of ''Tsagantsavian'' age based on its molluscan taxa (Shuvalov, 1975). A radioisotopic age of 130 m.y. has been obtained for the Tsagantsavian basalts (Samiolov et al., 1988), supporting a Valanginian–Neocomian age for the unit. If these region-wide correlations hold, Oshih would be older than Khoobur, the other Mongolian Early Cretaceous locality yielding mammals. Khoobur, thought to be of Aptian–Albian age (Dashzeveg, 1975; Jerzykiewicz and Russell, 1991; Kielan-Jaworowska and Dashzeveg, 1989, 1998) is approximately 90 km NNW of Oshih and is the type locality of *Gobiconodon borissiaki* (Trofimov, 1978), the type species of *Gobiconodon.* Kielan-Jaworowska and Dashzeveg (1998) have reviewed the triconodont fauna from Khoobur. They subsumed *Guchinodon hoburensis* (Trofimov, 1978) under *Gobiconodon hoburensis* and argued in favor of amphilestid affinities for gobiconodontids. The recent AMNH–Mongolian Academy of Sciences Expeditions have also collected a few specimens of both *Gobiconodon* species at Khoobur.

In 1997, we recovered four fragmentary mammalian specimens, referable to gobiconodontid triconodonts, in the middle section of the gray-whitish Cannonball Member at the Oshih Depression (Berkey and Morris, 1927). The first two specimens were found by Bolortsetseg Minjin, one of our Mongolian colleagues, approximately 50 yards apart in the same stratigraphic position. The first sublocality, a small mound of friable, clean, grayish sandstone, produced three lower jaw fragments; the two additional specimens were found by some of the authors (MCM and GR). The second sublocality, of similar lithology, yielded the maxillary fragment described here.

In addition to Khoobur and Oshih, a third Asiatic locality, this one in western Siberia (Maschenko and Lopatin, 1998), yielded a gobiconodontid jaw. The specimen (PIN N 3101/09), collected in the Ilek Svita and dated as Neocomian (Osyko, 1958), or Aptian–Albian (Rozhdestvensky, 1960), is rather poor, but it has been identified as *Gobiconodon borissiaki.* Recently, Godefroit and Guo (1999) reported on a new gobiconodontid, *Hangjinia chowi,* from the Early Cretaceous Ordos Basin of northern China. Therefore, gobiconodontids are now recorded at four Early Cretaceous sites in Asia: two in Mongolia, one in Siberia, and one in northern China.

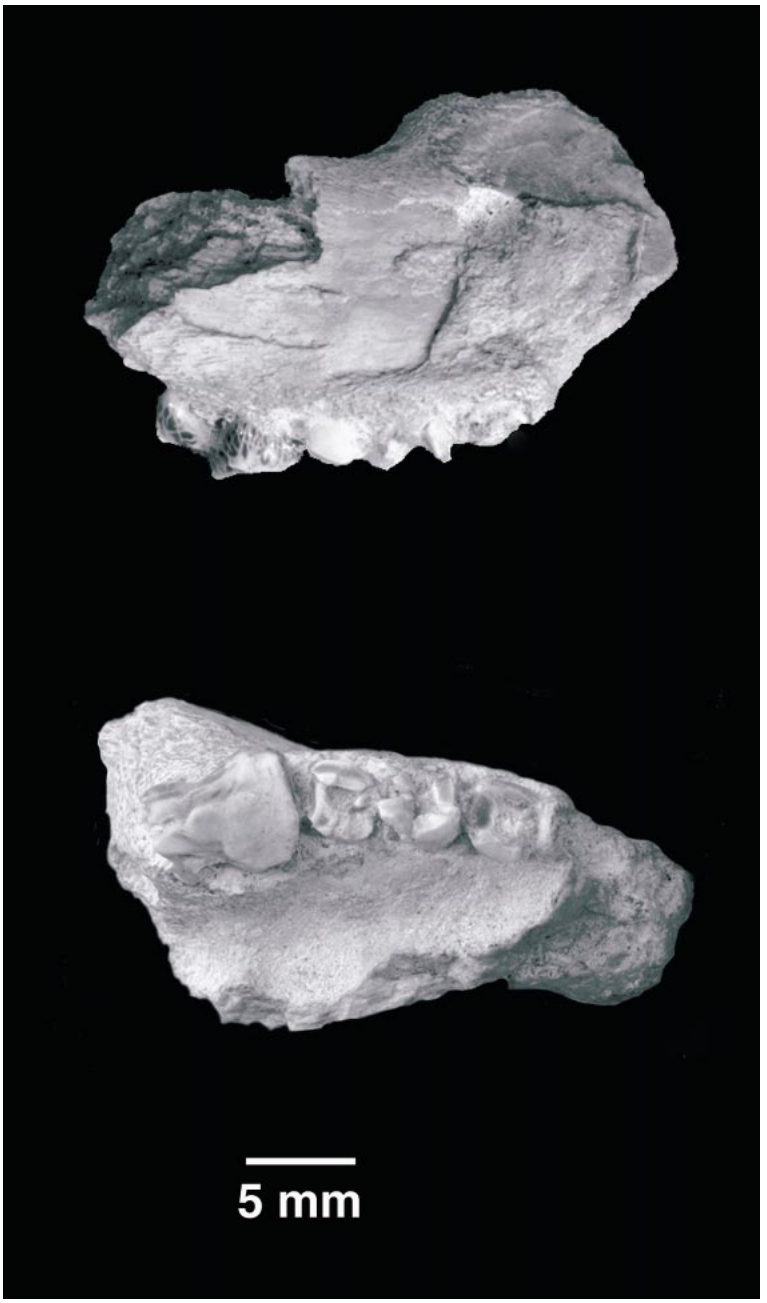

Fig. 1. PSS-MAE 140, Holotype of *Gobiconodon hopsoni,* sp. nov. Fragmentary right maxilla in **(top)** labial and **(bottom)** occlusal views. Abbreviations: Ant. Inf., anterior infraorbital foramen; Art., artifact; Buc. Cr., buccinator crest. M3, M4, roots or alveoli for the third and fourth molariform; Orb, orbital margin; Post. Inf., posterior infraorbital foramen.

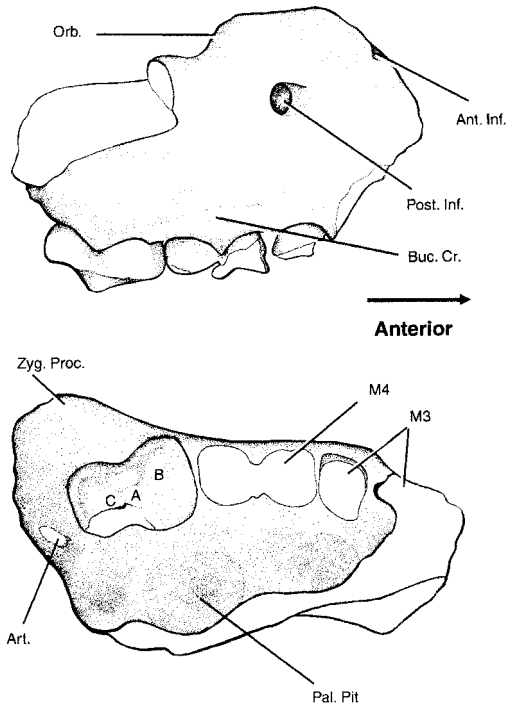

Fig. 1. Continued

Fairly complete gobiconodontid skeletons have been collected from the Early Cretaceous Cloverly Formation (Ostrom, 1970; Jenkins and Schaff, 1988) in Montana and Wyoming, USA. The Cloverly Formation can be correlated to the Aptian–Albian Trinity Group of Texas (Jacobs et al., 1991). A putative Late Jurassic gobiconodontid was described by Chow and Rich (1984) from the Shishugou Formation, China, but the gobiconodontid affinities of this specimen have been questioned (see comments of a reviewer in the original paper; in Jenkins and Schaff, 1988; and below).

We use the terms premolariform and molariform here instead of premolar and molar because it has been shown that the ''molars'' undergo replacement in at least one species of *Gobiconodon* (Jenkins and Schaff, 1988). The definition of molars and premolars is based on the absence or presence, respectively, of deciduous elements rather than on morphology (Clemens and Lillegraven, 1986). Therefore, lacking the proper ontogenetic stages, it is difficult to ascertain the nature of the dental elements being described. Five molariforms are believed to have been present in the lower jaws of gobiconodontids, and the same number is supposed to have been present in the maxilla (Trofimov, 1978; Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998). The features preserved in the specimens described below support affinities with gobiconodontid triconodonts. Therefore, for descriptive purposes we will assume that five molariforms were also present in the gobiconodontids from Oshih, and our nomenclature reflects this assumption. Remember, however, that the dental formula in general, and the number of postcanines in particular, is not known with certainty for any of these taxa. The homology of the anterior dental elements is particularly problematic.

Throughout the paper we use Mammalia to refer to the crown group and its fossil relatives (Rowe, 1987, 1988). The term triconodont is used informally to refer to mammaliaforms with three major cusps arranged approximately in a line or with a small angle between them. They correspond to taxa traditionally included in the order Triconodonta, the most generalized Mammaliaformes (Crompton and Jenkins, 1979), now regarded as a paraphyletic taxon (Rougier et al., 1996a, 1999; Ji et al., 1999). The term triconodontids refers to members of the monophyletic group Triconodontidae (Crompton and Jenkins, 1968; Hopson and Crompton, 1969; Jenkins and Crompton, 1979; Rougier et al., 1996a, 1996b; Cifelli et al., 1998, Ji et al., 1999). The term amphilestids, a paraphyletic taxon, is used to collectively refer to the taxa traditionally included in Amphilestidae (Simpson, 1928; Mills, 1971; Jenkins and Crompton, 1979). The dental terminology employed here follows that of Crompton and Jenkins (1968) as applied to gobiconodontids by Jenkins and Shaff (1988) in particular, and to triconodonts in general.

A general cladistic analysis of these triconodonts is not attempted here, owing to the incompleteness of the specimens. Instead, the general framework of triconodont phylogeny provided by the results of Ji et al. (1999) and our own analysis Rougier et al. (1999, in prep.) is used to discuss the interrelationship of the known gobiconodontids, to revise their

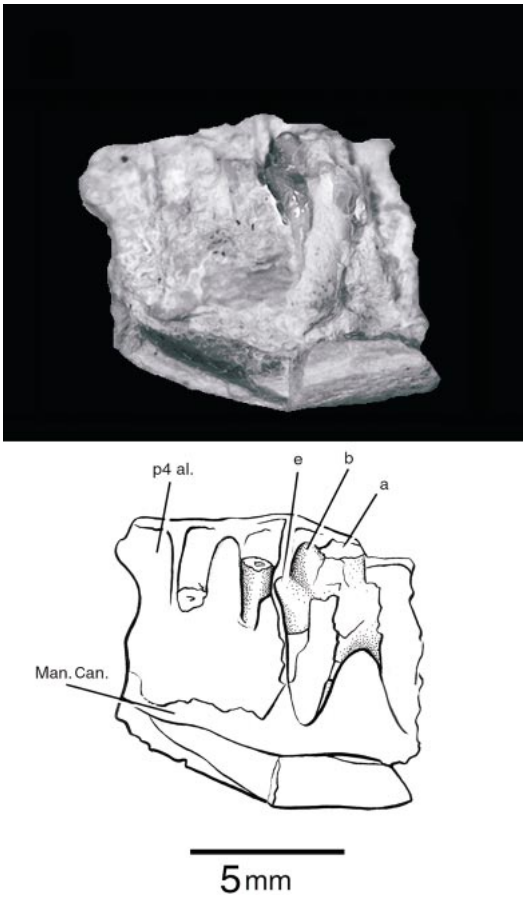

Fig. 2. PSS-MAE 139, *Gobiconodon hopsoni*, sp. nov., fragment of a right dentary in lingual aspect. Abbreviations (for cusp nomenclature see Introduction): p4 al, alveolus for the p4; Man. Can., mandibular canal (endocast).

diagnosis, and to address their position among basal mammals.

Institutional Abbreviations

AMNH American Museum of Natural History, Department of Vertebrate Paleontology, New York, USA

BMNH The Natural History Museum, London, United Kingdom

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, USA

PIN Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia

PSS-MAE Paleontological and Stratigraphic Section (**PSS**) of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia, and collections of the joint Mongolian Academy of Sciences–American Museum of Natural History Expeditions (**MAE**)

USNM United States National Museum of Natural History, Washington, D.C., USA

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA

ORDER INCERTAE SEDIS

FAMILY GOBICONODONTIDAE CHOW AND RICH, 1984
(= Gobiconodontinae Chow and Rich, 1984; Gobiconodontidae Jenkins and Schaff, 1988)

Gobiconodon Trofimov, 1978

Type Species: *Gobiconodon borissiaki* Trofimov, 1978.

Emended Generic Diagnosis: Small to medium-sized triconodonts, with large procumbent i1 and correspondingly enlarged I1; reduction of number of incisors to 1 or 2; conic and pointed posterior incisors, canines, and anterior premolariforms. Anterior premolariforms (p1-p3) with tall central cusp and crown height greater than mesiodistal measurement. Accessory cusp on these premolariforms very small to absent. Procumbent i-p1. Rounded muscular depression on medial aspect of lower jaw, anteroventral to mandibular foramen (fig. 4; Kielan-Jaworowska and Dashzeveg, 1998: fig. 6c). Separate infraorbital canals connecting orbit with rostrum (see below). Anterior molariform teeth undergo replacement (documented in *Gobiconodon ostromi*, and probable in the remaining *Gobiconodon* species); this feature, however, may be plesiomorphic and not diagnostic. Rounded fossa in the base of the lesser trochanter of the femur and heavier appendicular skeleton (larger cross-section diameter) than other Mesozoic and basal tribosphenic mammals.

Gobiconodon hopsoni, new species
Figures 1, 2

Etymology: After Dr. James A. Hopson, one of a selected few who can comfortably straddle the blurry non-mammalian cynodont/mammalian boundary, with impressive contributions to both segments of therapsid history.

HOLOTYPE: Partial right maxilla (PSS-MAE 140) preserving the last molariforms and fragments of the two preceding molariforms.

REFERRED SPECIMEN: PSS-MAE 139, a fragment of right lower jaw with a broken, unerupted molariform and alveoli for two more anterior teeth.

TYPE LOCALITY: Oshih, Cannonball Member of Oshih Formation of Berkey and Morris (1927), possibly equivalent of Tevsh Formation (Undurukhin), Valanginian-Neocomian (Samiolov et al., 1988). The lower jaw specimens were collected at 44°54′02″N; 102°53′11″E.

REPOSITORY: Paleontological and Stratigraphic Section (PSS) of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia. The specimens are temporarily stored at the Department of Vertebrate Paleontology, AMNH.

DIAGNOSIS: Large gobiconodontid with deep ectoflexus in a lingually positioned M5. Upper dental arcade forms a closer dental arch than in other species of *Gobiconodon,* with the last molariforms projecting medially more pronouncedly than in other species of *Gogiconodon.* Labial cingulum on the M5 broader than that of *G. ostromi.* Zygoma is deeper in *G. hopsoni* than in *G. ostromi,* and projects more posteriorly, closer to the alveolar margin. *G. hopsoni* is the largest species of *Gobiconodon* described so far (appendix 1).

DESCRIPTION

MAXILLA (fig.1)

The maxilla is fragmentary, preserving only the root of the zygomatic process, the floor of the orbit, part of the palate, the alveolar margin, and portions of the infraorbital canal.

The lateral aspect of the maxilla is moderately convex without defining a large cheek lateral to the teeth. A small to medium-sized foramen opens laterally at the level of the posterior root of the M3 (fig. 1: Post. Inf.). The foramen leads posteromedially into a canal that opens in the orbit above the orbital platform. We interpret this to be an infraorbital canal, because in mammals the only canal of this size connecting the orbit with the lateral aspect of the rostrum is the infraorbital canal (Sisson and Grossman, 1955; Evans and Christensen, 1979). A portion of another larger canal (fig. 1: Ant. Inf.) can be seen at the broken anterior edge of the maxilla. This canal opens in the floor of the orbital platform as a small infraorbital foramen, lying medial to the infraorbital canal. Judged from the size and orientation of the preserved canal, the more anterior infraorbital foramen was much larger than the more posterior one, and it opened to the rostrum at the level of the M2 or M2-M1. Multiple rostral exits of the infraorbital canal are frequent among Mesozoic mammaliaforms (Kermack et al., 1981; Hahn 1985, Kielan-Jaworowska et al., 1987; Lillegraven and Krusat, 1991; Rougier, 1993; Engelmann and Callison, 1998), but we are unaware of other Mesozoic mammaliaforms showing separate infraorbital foramina in the orbit for what are essentially separate infraorbital canals.

The relative size of the infraorbital foramina in this specimen conforms to those of other Mesozoic mammaliaforms, such as morganucodontids (Kermack et al., 1981), basal multituberculates (Hahn, 1985), *Vincelestes* (Rougier, 1993), and a Jurassic paurodontid (Hopson et al., 1999), in which the posterior branches of the infraorbital canal are smaller and more ventral than the larger anterior opening.

A faint crest runs along the alveolar edge of the maxilla proximally from the base of the zygomatic process to the broken anterior margin. This crest corresponds to the site of attachment of the buccinator muscle in living mammals (Turnbull, 1970; Evans and Christensen, 1979).

The zygomatic process originates directly lateral to the last molariform. A sizable portion of the process is broken, in particular, the section that would have formed the lower border of the orbit. There is no recognizable facet for the jugal in the preserved portion of the maxilla. A rugose area near the base of the zygomatic process marks the insertion of a strong masseter muscle. The alveolar and zygomatic processes are connected by a gently sloping curve, contrasting with the sharp posterior margin of this area in *Gobiconodon ostromi* (cf. Jenkins and Schaff, 1988: figs. 4, 5, 7; and fig. 1 here). The pre-

served morphology of this fragment suggests that the jugal made little contribution to the anterior contour of the orbit and was probably restricted to its posteroventral margin. A substantial part of the anteroventral margin of the orbit was formed by the maxilla, as indicated by the finely rugose, free edge of the maxilla in our specimen. The same condition is present in *G. ostromi.*

In ventral view, the palatal process of the maxilla exhibits deep palatal fossae for the lower molariforms. As noted also by Kielan–Jaworowska and Dashzeveg (1998), the pattern of the fossae clearly suggests that the occlusion between upper and lower elements alternated; that is, a lower molariform occluded between two upper molariforms. The pattern of the fossae also indicates that a lower molariform occluded behind the last preserved upper molariform. Given that mammalian lower teeth occlude in front of the corresponding upper teeth when the occlusion is alternated, the lower dentition either had one more molariform than the upper dentition, or the small hole observed in the maxilla (labelled as artifact in fig. 1B) represents an alveolus for a more posterior tooth than the one preserved. The latter possibility, however, is unlikely (see comments below).

Upper Dentition (fig. 1)

The M5 is the only dental element that is almost completely preserved. A small portion of the distolingual corner of the crown has been chipped away. The specimen is an old individual, and there is heavy wear on the crown. The M5 has two anteroposteriorly compressed roots set widely apart. The crown is subrectangular in occlusal view and was covered by a thick layer of enamel that has been worn down on the lingual aspect of the tooth. Cusp **A** (fig. 1) is the tallest cusp and is in a central position. Remnants of cusps **B** and **C** are anteroposteriorly aligned with **A** and can be recognized on the crown, but their relative development is uncertain. Cusp **C** seems to have been slightly more labial in position than either **A** or **B.** A moderate, almost unworn labial cingulum extends the length of the labial edge of the crown. The cingulum is quite conspicuous posteriorly, but disappears mesially at about the level of the worn cusp **B,** where it merges into the wear facet. The labial margin of the tooth presents a relatively shallow ectoflexus that divides the margin into two subequal lobes. The lingual side of the crown is either broken or too worn to preserve any evidence of a lingual cingulum. The wear facet, however, slopes mesiolingually from **A.** The mesial and distal margins of this molariform are slightly concave to flat. The M5 is more lingual than the M4, a condition accentuated in the more distal portion than in the more mesial portion of the M5, resulting in a lingually curving tooth row. The roots of the M4 and M3 in conjunction with the M5 form a broad, lingually concave arch, suggesting a rapid narrowing of the rostrum in front of the M3-M4 and possibly of the palate behind M5.

The crown of the M4 is missing, but the roots are well preserved. Their transverse section is more circular than the roots of the M5. However, both roots retain a somewhat angular outline. Both M4 and M3 have conspicuous thickenings around the mesial, distal, and lingual aspects of the roots at the alveolar level, which cannot be seen in figure 1. Similar projections of the roots are known in other triconodont lower dentitions, including some amphilestids such as *Phascolodon* (USNM 2703), *Aploconodon* (USNM 2791), and *Gobiconodon borissiaki* (PSS-MAE collection and Maschenko and Lopatin, 1998: fig. 4c). The M3 is represented only by its distal root and the alveolus of the mesial root.

The slightly triangular outline of the upper molariform crown in gobiconodontids and ''amphilestids'' (Mills, 1971; Kielan-Jaworowska and Dashzeveg, 1998) was produced by extensive wear along the lingual slopes of cusps **A, B,** and **C.** The postnatal ''matching'' of upper and lower wear facets by extensive remodeling of the crown through wear is a primitive feature of mammaliaforms (Crompton and Jenkins, 1968) retained by *Gobiconodon.* The extensive wear on the M5 of *G. hopsoni,* especially of the smaller cusps **B** and **C,** imparts to this molariform a somewhat triangular crown pattern.

In ventral view, distomedially from the M5, there is a small circular opening into the substance of the maxilla (Art. in fig. 1). This

hole shows no alveolar walls or remnants of teeth. It is also separated from the M5 by a substantial bar of bone, which makes it unlikely that the opening is an alveolus of a more posterior molariform. In addition, the distal aspect of the crown of the M5 has no facet for contact with a tooth occupying a more distal position on the tooth row. It is theoretically possible that the aperture in the maxilla represents a crypt for an unerupted molariform. This interpretation is also unlikely, because of the advanced age of the specimen as shown by the strong wear of the M5. Although late eruption of the last molariforms (Thomas, 1887; Simpson, 1928, 1929; Cifelli et al., 1998) is well documented in triconodonts, the age suggested by the wear in the last preserved molariform seems to be too great to expect subsequent eruption at a new position. Although the opening is in line with the remaining dental elements, we consider it an artifact, and we believe the last preserved molariform to be the last of the series.

DENTARY (fig. 2)

PSS-MAE 139 is a poorly preserved fragment of a right lower jaw found by screen washing. The specimen is also referred to *Gobiconodon hopsoni*; the attribution is based on the fact that this specimen is dentally also a triconodont and that it matches in size the maxillary specimen described above. The jaw represents a segment between the anterior and the posterior molariforms, with one partially preserved unerupted tooth. This element is likely the m2 and will be so referenced subsequently. In front of the m2 is the partial root of another double-rooted element, and further anteriorly, a larger alveolus for a large single-rooted tooth. The latter alveolus corresponds to the p4 of gobiconodontids, which is variably reduced in *G. ostromi* (Jenkins and Schaff, 1988) and the gobiconodontids from Khoobur (Kielan-Jaworowska and Dashzeveg, 1998; personal obs.). In *G. borissiaki,* this tooth position has only one root, but in *G. hoburensis* the p4 has two roots (Kielan-Jaworowska and Dashzeveg, 1998). On the other hand, *G. ostromi* (Jenkins and Schaff, 1988) seems to be polymorphic regarding the presence or absence of a p4 because it is present in the specimen MCZ 19860, but absent in MCZ 19965. The p4 in MCZ 19860 also has contralateral differences; its root is single on one side and ''incipiently double'' on the other (Jenkins and Schaff, 1988). The differential presence of a p4 in *G. ostromi* probably cannot be explained by resorption and plugging of the alveolus by bone as occurs in early mammaliaforms such as *Sinoconodon* (Crompton and Luo, 1993), *Kuehneotherium* (Gill, 1974), and basal mammals such as *Phascolotherium* (BMNH 112). The specimen of *G. ostromi* preserving the alveoli for the p4 (MCZ 19860) appears to be older than the other specimen, which has no evidence of the alveolus (MCZ 19965). In *G. hopsoni,* the alveolus for the p4 is immediately mesial to that of the m1 and it is not separated from it as in *G. ostromi.*

The only tooth preserved in PSS-MAE 139, the presumed m2, was erupting. In life, the cusp **a,** the tallest in the crown, would already have cut through the gum. Unfortunately, most of cusp **a** and the posterior part of the crown are missing. The anterior cingular cusp, **e,** and cusp **b** are complete. They are sharp and conical. The lingual aspect of **e** and most of the anterior slope of **b** are grooved for the reception of the cuspule **d** on the distal margin of the preceding molariform. This groove almost reaches the apex of the cusp **b,** as in *Gobiconodon borissiaki* but not in *G. ostromi.* Cusp **e** is also far more mesial to **b** than in *G. ostromi,* but is similar to *G. borissiaki* in this respect. A cusp **f** is missing or minimally developed in *G. hopsoni.* The impression of the distal root shows that it slants posteriorly, as do the distal roots of the posterior molariforms in the Mongolian species of *Gobiconodon,* particularly in *G. hoburensis. G. ostromi,* with the exception of the m5, has roots directed more or less vertically. The broken dentary exposes part of the mandibular canal (fig. 2: Man. Can.).

There is a small mental foramen on the labial surface of the dentary at the level between the p4 and m1. The incomplete edge of a second foramen and the small canal leading to it are exposed on the broken anterior margin of the dentary. There are fo-

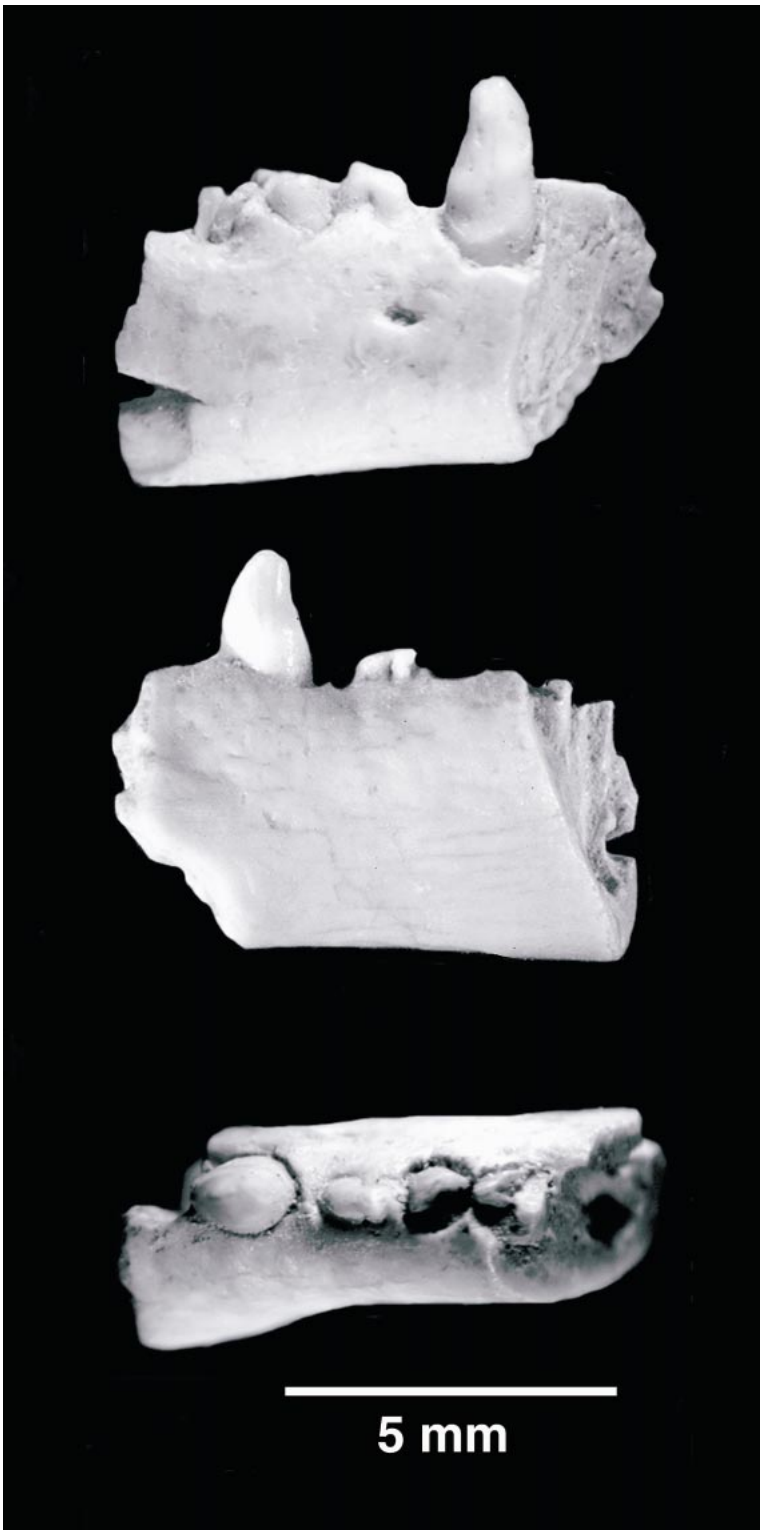

Fig. 3. PSS-MAE 137, anterior fragment of a right dentary of *Gobiconodon* sp. indet. in **(top)** lingual, **(middle)** labial, and **(bottom)** occlusal views. Abbreviations (for tooth nomenclature see introduction): Men. For., mental foramen; Sym., symphysis.

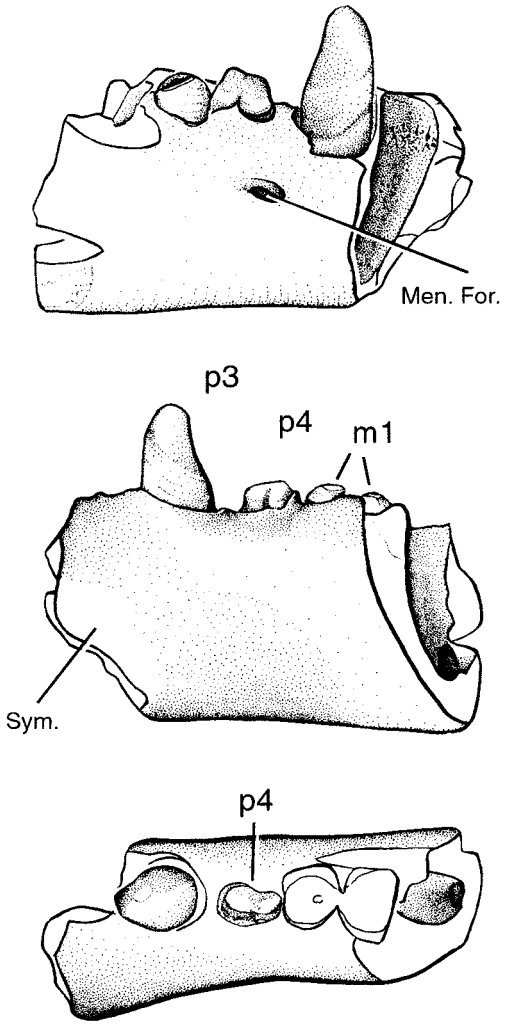

Fig. 3. Continued

ramina in equivalent positions in both *Gobiconodon ostromi* and *G. borissiaki.*

Also along the labial surface of the jaw there are rounded depressions between the successive lower teeth. These depressions accommodated the upper molariforms, underlying the alternate mode of occlusion of gobiconodontids where each upper tooth occludes between two lower ones.

It is difficult to be certain about the tooth replacement pattern because the specimens are incomplete, but the erupting tooth suggests it was replacing a functional tooth because it is coming up in an alveolus that already shows root impressions. If our identification of the p4 alveolus is correct, then *Gobiconodon hopsoni* probably had the same pattern of tooth replacement as did *G. ostromi,* in which the anterior molariforms are replaced. So far, there is no direct evidence supporting a similar pattern in the other known Mongolian species of *Gobiconodon* (Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998) for which several specimens are known, including the modest recent collection by the Mongolian Academy of Sciences and the AMNH. Kielan-Jaworowska and Dashzeveg (1998), however, indicated indirect evidence in favor of molariform replacement among the gobiconodontids from Khoobur.

Gobiconodon sp.

Figures 3, 4

Two specimens, PSS-MAE 137 (fig. 3) and PSS-MAE 138 (fig. 4), represent a second gobiconodontid taxon at Oshih. Both were found at the same locality where the lower jaw fragment of *Gobiconodon hopsoni* was discovered. These two specimens, the proximal and distal portions of a right lower jaw, were found a few inches away from each other and may belong to the same individual. One of the reviewers of an earlier version of this paper was concerned with the difference in size of the two fragments, which at first might mitigate against interpreting the fragments as one individual. However, the anterior portion of the jaw is much more slender than the posterior portion in some gobiconodontids, especially in *G. ostromi* (Jenkins and Schaff, 1988; fig. 5). We have matched both fragments of *Gobiconodon* sp. on the outline of *G. ostromi* (fig. 5). This illustration shows that the anterior fragment (PSS-MAE 137) is about 10% smaller than expected if the proportions of *G. ostromi* are followed. The difference in size does not seem to preclude these two fragments being attributed to one specimen. If both fragments belong indeed to one individual, then the middle portion of the jaw bearing m2 and the mesial half of m3 has been lost (fig. 5). These fragments are slightly larger than corresponding portions of *G. borissiaki,* but smaller than those of *G. ostromi.*

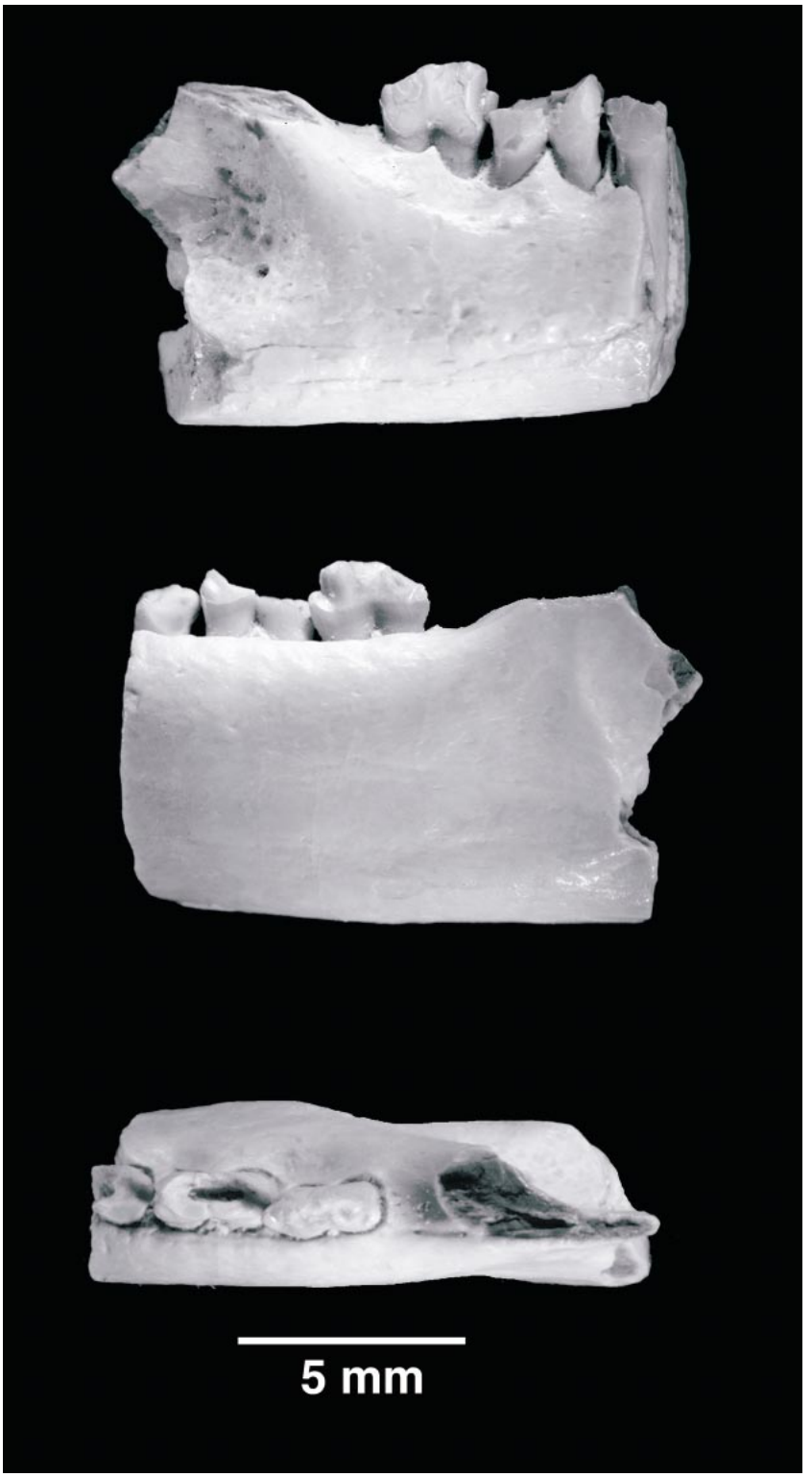

Fig. 4. PSS-MAE 138, posterior fragment of a right dentary of *Gobiconodon* sp. indet. in **(top)** lingual, **(middle)** occlusal, and **(bottom)** labial views. Abbreviations: Mas. for., masseteric foramen; Mas. fos., masseteric fossa; M. gr., Meckel's groove; M. pit, mandibular pits; M. sc., muscular scar.

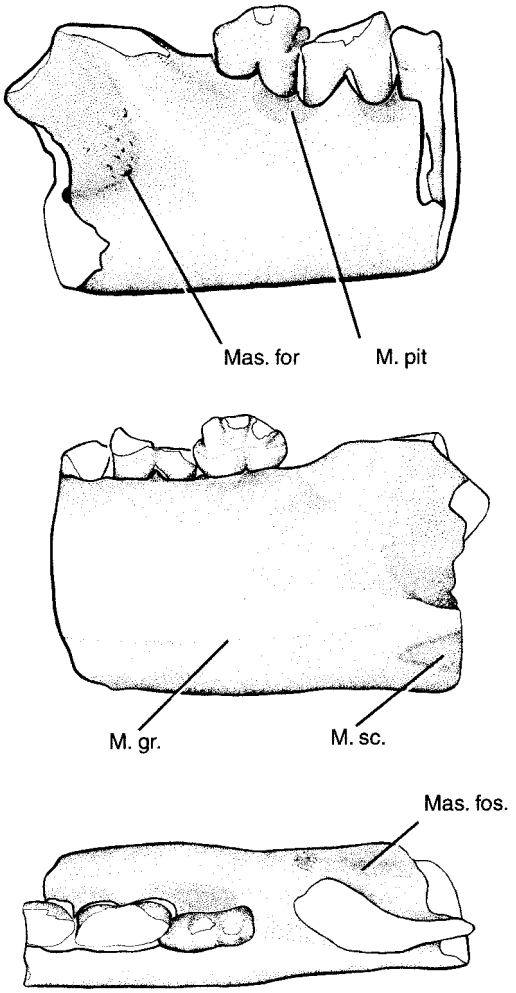

Fig. 4. Continued

The proximal fragment (PSS-MAE 137) includes part of the symphysis, an incomplete alveolus similar to that of the caniniform p3, a complete caniniform p3, a small, double-rooted premolariform, and the roots of a large, double-rooted, probably molariform tooth.

According to the tooth identifications by Trofimov (1978), Jenkins and Schaff (1988), and Kielan-Jaworowska and Dashzeveg (1998), the first preserved alveolus corresponds to the p2. The alveolus suggests that the p2 was subequal in size to the following tooth, p3, but was placed more lingually in the jaw. Gobiconodontids show a great difference in height between the labial and lingual margins of the anterior alveoli, particularly i1-p2. Our specimen agrees well with the condition of other gobiconodontids. On the lingual aspect, the distalmost extent of the symphysial expansion is preserved, and no remnant of a Meckelian groove is discernible. The symphysis extends back to the level of the caniniform p3. The strong medial bulging of the symphysial area is also present in the other species of *Gobiconodon* and suggests that, as in other gobiconodontids, the symphysis was rather vertically oriented. Unfortunately, preservation is not sufficient to be certain about this feature. On the labial side, a small mental foramen is located at mid-mandibular height between the p3 and p4.

The p3 is a stout, erect caniniform tooth with a slightly flattened anterior surface and distinct wear facets on its labial surface. The apex is blunt, and two wear facets run posteroventrally on the labial surface of the tooth; a low ridge separates these facets. On the labial aspect of the tooth, a distinct ridge runs along the base of the crown and could be considered as a labial cingulum. However, when the alveolus was complete, this line was probably inside the alveolus and is more likely to correspond to the thickening of the roots at the alveolar level that we have observed in other gobiconodontids (see below) than to a true cingulum. Unlike *Gobiconodon borissiaki,* in *Gobiconodon* sp. the p3 lacks accessory cusps; only the central cusp, likely serially homologous to **a,** is present on the crown. As with p2, the lingual wall of the alveolus for the p3 is much taller than the labial wall.

The p4 is very small and separated from the p3 by a short diastema. Both p3 and the restored m1 tower over the minute premolariform. The p4 has two subequal roots that are fused, or nearly fused, to the alveolus. If there was any periodontal ligament, it was negligible. Heavy wear, oriented mesiolabially, obscures crown features of this small tooth. Nevertheless, what remains suggests that a main central cusp was present, possibly accompanied by small mesial and distal accessory cuspules. Only the roots of the m1 are present. They are subequal in size, but differ in cross section; the mesial root is subcircular, while the distal root is more angular.

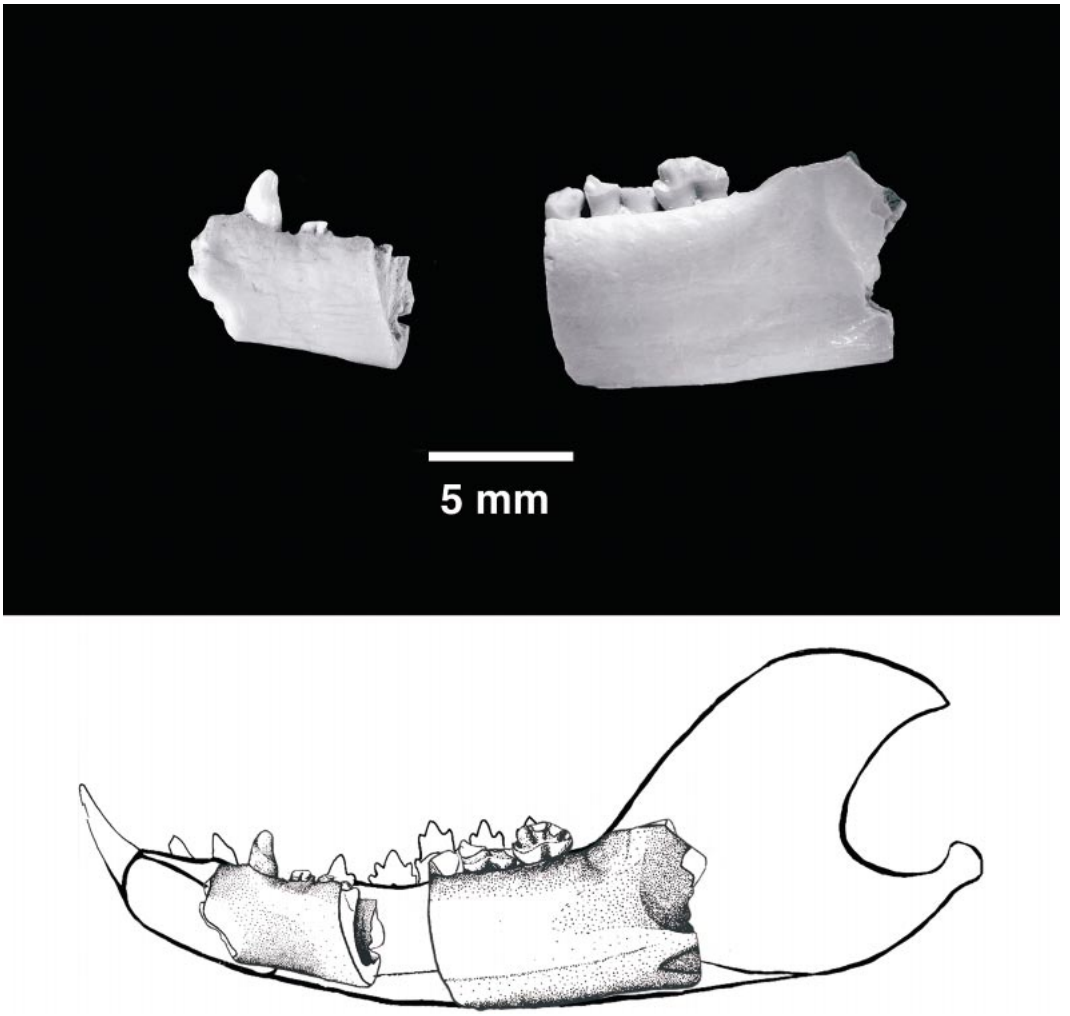

Fig. 5. Specimens PSS-MAE 137 and 138, *Gobiconodon* sp. indet. **(top)** at the same scale. **(Bottom)** the specimens fitted to the outline of the lower jaw of *G. ostromi* showing general agreement of morphology, with the exception of the proportionally larger teeth in the Mongolian species of *Gobiconodon* and the more slender anterior portion of the lower jaw.

The alveolus for the anterior root of the m2 is preserved in PSS-MAE 137. The alveolus suggests that the m2 was subequal to m1 or perhaps marginally larger. The anterior root would slant posteriorly a little.

The second fragment, PSS-MAE 138, includes the posterior root of the m3, m4-m5, and the anterior portion of the masseteric fossa (fig. 4). On the posterior root of the m3, only the sharp distal edge of cusp **d** is preserved. This cusp fits snugly in the notched mesial aspect of the m4. The notch on the m4 is formed by a low, but distinct, cusp **e** and the anterior surface of **b.** Kielan-Jaworowska and Dashzeveg (1998) reported that in *Gobiconodon hoburensis* the contact between succeeding teeth is formed by cusp **d** fitting between a mesiolingual cusp **e** and a mesiolabial cusp **f.** A cusp **f**, however, seems to be very small and rapidly eroded or missing altogether. Cusp **d** is supported labially by the anterior slope of **b.** The remaining cusps of the crown are missing.

The m5 is the best preserved molariform of this jaw fragment. The contact between m4 and m5 is different from that between m3

and m4. The distal cusp **d** of the m4 does not fit in an embrasure between cusp **e** and the anterior slope of **b,** or possibly cusp **f.** A mesiobuccal cusp or extension of the crown is absent, and cusp **d** abuts directly labial to cusp **e.** Cusp **b** is away from the front of the tooth and a cusp **f** is absent; cusp **e,** however, is prominent. In short, m4 does not interlock with m5, but is arranged en echelon. In all other species of *Gobiconodon*, cusp **d** of the m4 interlocks with cusp **e** and either the slope of **b** or cusp **f** (Kielan-Jaworowska and Dashzeveg, 1998: fig. 7). All the remaining major cusps of the m5 are damaged and worn, but enough remains to show that they were essentially aligned anteroposteriorly. On the lingual side of the m5, a moderate cingulum runs from cusp **e** to cusp **d.** The roots of the molariforms do not show the thickening at the level of the alveolus present in *G. borissiaki* and the fragmentary lower jaw referred to *G. hopsoni*. The roots of the m5 are directed less distally than those of the m5 of the Asiatic species of *Gobiconodon* (Kielan-Jaworowska and Dashzeveg, 1998; personal obs.) and are more similar to those of *G. ostromi* (Jenkins and Schaff, 1988).

The dentary is robust, with thick cortical bony walls that are thicker than those of *Gobiconodon borissiaki.* The masseteric fossa is the most conspicuous feature on the labial surface of the dentary; it is moderately deep and limited ventrally by a thick and blunt masseteric ridge. This fossa extends anteriorly, but stays behind the level of the m5. The anterior limit of the fossa was formed by a mostly missing coronoid ridge. In the anterior part of the masseteric fossa, a small foramen opens into the substance of the dentary. This foramen occupies a position similar to the masseteric foramen, or labial mandibular foramen, of other Mesozoic mammals (Dashzeveg and Kielan-Jaworowska, 1984; Rougier, 1993; Cifelli et al., 1998).

On the labial aspect of the body of the jaw, between the lower molariforms, conspicuous depressions corresponding to the position of the upper molariforms can be identified. Similar depressions are present in *Gobiconodon ostromi,* but not in the remaining Asiatic species, and these may simply be related to the larger size of *G. ostromi* and *G. hopsoni.*

On the lingual aspect of the dentary, a very subtle sulcus runs mesiodistally along the ventral third of the dentary toward the broken edge of the mandibular foramen. This sulcus is the impression of the remnant of Meckel's cartilage. It is less pronounced than in other species of *Gobiconodon.* The mandibular foramen is very posteriorly placed and marks the anterior edge of the pterygoid fossa. The mesialmost edge of this fossa extends mesiodorsally from the foramen in the broken base of the coronoid process. An incomplete oval depression lies ventral to the mandibular foramen, a muscle scar likely produced by the medial pterygoid (fig. 4). This depression is known in all species of *Gobiconodon,* but not in other Mesozoic mammals, and is a good diagnostic feature for this group.

The last molariform in *Gobiconodon* sp. is located well in front of the anterior edge of the masseteric fossa, and the molariform alveolus is directly at the base of the coronoid process. The m5 is also close to the base of the coronoid process in *G. hoburensis*, but not in described specimens of *G. borissiaki* or *G. ostromi.* In the latter two taxa, there is a space between the last molariform and the origin of the coronoid process (Trofimov, 1978: fig. 1; Jenkins and Schaff, 1988: figs. 4, 6). The masseteric fossa in *G. ostromi* and *G. borissiaki* extends anteriorly to at least the level of m5 (Kielan-Jaworowska and Dashzeveg, 1998). However, a specimen of *G. borissiaki* (PSS-MAE 143) collected recently in Khoobur by the AMNH–Mongolian Academy of Sciences Expeditions shows an empty alveolus for a double-rooted tooth at the base of the coronoid process. Consequently, in this specimen there is no space between the back edge of the alveolus and the anterior aspect of the masseteric ridge. It is possible that the differences in this character between specimens of *G. borissiaki* may be explained by differences in ages of the specimens, as also suggested by Kielan-Jaworowska and Dashzeveg (1998). Juvenile or young individuals have a shorter jaw than do adults, but tooth crowns do not grow after eruption. Therefore, the teeth are closer to the coronoid process or even medial to it in young specimens of other mammals. The jaw PSS-MAE 143 shows little or no wear on cusp **a** or the distal half of the freshly erupted m4,

suggesting that the specimen is a young adult and supporting the idea of ontogenetic change in relative position of the molariforms and coronoid process. The similarities in the position of the last molariform and coronoid process in the fragment of *Gobiconodon* sp. (PSS-MAE 138) and *G. hoburensis* are probably of little consequence.

If the two fragments of *Gobiconodon* sp. described above (PSS-MAE 137 and 138) do belong to the same individual, the jaw should rapidly decrease in height anteriorly, as is suggested by the match of the fragments of *Gobiconodon* sp. on the outline of *G. ostromi* (fig. 5). The other species of *Gobiconodon* do not show the same anterior tapering of the dentary.

DISCUSSION

Gobiconodontid Diversity

Gobiconodontids have been reported from the Jurassic and Early Cretaceous sediments of Mongolia (Trofimov, 1978; Kielan-Jaworowska and Dashzeveg, 1998), China (Chow and Rich, 1984), the United States (Jenkins and Schaff, 1988), and Russia (Maschenko and Lopatin, 1998).

The only purported Jurassic gobiconodontid is *Klamelia zhaopengi* (Chow and Rich, 1984) from the lower Shishugou Formation, Xinxiang, China. The specimen consists of a poorly preserved anterior fragment of a left lower jaw. Chow and Rich interpreted the lower jaw as preserving the last premolar (premolariform of this report) and evidence of at least six molars (molariforms of this report). In the original description, they also noted the criticism of an anonymous reviewer. The reviewer suggested that the anteriormost element could be interpreted as a double-rooted canine and the following elements as premolars (premolariforms). We believe the interpretation of the reviewer to be correct. Chow and Rich (1984: 230) disregarded the reviewer's interpretation because: 1) Mongolian gobiconodontids are known to have ''a similar pattern of relatively numerous molars and a reduction in the number of antemolariforms, and a shortening of the jaw'', and 2) the anteriormost tooth cannot be a canine because it has two roots and a small posterior accessory cusp. Argument 1 is circular, because the comparison is *limited* to gobiconodontids, assuming that the form in question is a gobiconodontid. If the spectrum of comparisons is restricted in this way, it is no surprise *Klamelia* will share similarities with gobiconodontids. The so-called pattern is vague because the presence of five molariforms in gobiconodontids is probably a primitive feature for mammaliaforms in general, present in most non-tribosphenic groups. If the interpretation of four premolariforms in gobiconodontids is correct, the number of premolariforms does not seem to be reduced because the presence of four elements is also probably the primitive condition for mammaliaforms. Another fact mitigating against gobiconodontid affinities for *Klamelia* is that, if the original interpretation is accepted, the conspicuous single-rooted anterior premolariforms present in all the species of *Gobiconodon* are missing in *Klamelia.* This feature of the premolariforms is in fact one of a few diagnostic features of gobiconodontids. Argument 2 is weakened by the presence of ''two-rooted'' canines with accessory cusps in a variety of Mesozoic taxa such as docodonts (Krusat, 1980; Lillegraven and Krusat, 1991), symmetrodonts, and dryolestoids (Martin, 1997, 1999).

Although we are convinced that *Klamelia* is not closely related to *Gobiconodon,* we are uncertain about the affinities of *Klamelia* with other groups of mammaliaforms. The peculiar double-rooted premolariforms and the presence of conspicuous internal and external cingula suggest it is a basal mammaliaform, but its morphology does not resemble that of any other group. We agree with the doubts raised by Jenkins and Schaff (1988) concerning the affinities of *Klamelia.* In our opinion, no diagnostic gobiconodontid traits are preserved in *Klamelia*; consequently, it should not be grouped with other gobiconodontids. *Klamelia* is considered here as Mammaliaformes *incertae sedis.*

Gobiconodon sp. from Oshih is similar in size to *G. borissiaki,* the former being only slightly larger. In addition, *Gobiconodon* sp. lacks a posterior accessory cusp on p3 and cusp **f** is absent or indistinct, while *G. borissiaki* has an accessory cusp on p3 and possibly a cusp **f.** *Gobiconodon* sp. also has a small diastemata between p3 and p4, absent

in the other Asiatic species (unknown in *G. hopsoni*). These differences may justify the erection of a new species, but until better material is recovered we refrain.

Four (five if *Gobiconodon* sp. is a distinct taxon) species are now included under the genus *Gobiconodon*: two from Khoobur, Mongolia (Trofimov, 1978; Kielan-Jaworowska and Dashzeveg, 1998), one of which is also known from Siberia, Russia (Maschenko and Lopatin, 1998); one from the Cloverly Formation, USA (Jenkins and Schaff, 1988); and a fourth one described here. Differences in morphology among the four species of *Gobiconodon* are substantial, including differences in size, root number of some postcanines, details of cusp morphology, and development of diastemata among the elements of the anterior dentition. These differences are at least as significant as those used to establish generic differences among other triconodont groups such as Triconodontidae. For instance, *Priacodon, Triconodon,* and *Trioracodon* differ from each other in details similar to those among the species of *Gobiconodon*. Kielan-Jaworowska and Dashzeveg (1998) have recently subsumed the genus *Guchinodon* (Trofimov, 1978) under *Gobiconodon* (Trofimov, 1978). As shown by our treatment here of the species of *Gobiconodon,* we provisionally accept their proposal, and, given the fragmentary nature of the specimens described, we also allocate the new species from Oshih to *Gobiconodon.* It should be noted, however, that the attribution of all these specimens to *Gobiconodon* is accepted here only to avoid changing once more the status of *Guchinodon* and to avoid unnecessary proliferation of new taxa based on incomplete specimens.

A new gobiconodontid genus, *Hangjinia,* was described recently by Godefroit and Guo (1999) on the basis of an isolated left lower jaw preserving, as interpreted originally by the authors, i3, p1, and an unerupted m2. This animal was diagnosed by a marked reduction in the number of postcanines and a more primitive precanine dentition than in *Gobiconodon,* with three incisors. The first four alveoli are large and subcircular. These alveoli also have a labial margin much lower than the lingual margin, agreeing in this feature with other gobiconodontids (see Trofimov, 1978: fig. 1). The first alveolus is larger than the second, but is proportionately not so large as in *Gobiconodon.* Only the third tooth is preserved. It is tall and conical, like that of *Gobiconodon.* The specimen can be reinterpreted following the homologies traditionally accepted for gobiconodontids. These dental elements would be i1-p2 using Jenkins and Schaff's (1988) nomenclature. We are not necessarily suggesting here that the homologies implied by Godefroit and Guo (1999) in their tooth identification of *Hangjinia* are wrong; they may well be correct. We think, however, that there is no reason to interpret the anterior dentition of *Hangjinia* any differently than that of *Gobiconodon.* It seems to us that both *Gobiconodon* and *Hangjinia* have either a relatively normal number of incisors and a very reduced count of premolariforms, or a reduced count of incisors and a relatively generalized number of premolariforms. At present, either argument is defensible, and essentially can be condensed to the arguments in favor of the traditional interpretation as discussed by Jenkins and Schaff (1988: 4). Godefroit and Guo (1999) did not discuss their reasons for identifying the canine as the fourth dental element in the jaw. Until compelling reasons are provided to change Jenkins and Schaff's (1988) interpretation of the tooth homologies in gobiconodontids, we prefer to follow their interpretation of the anterior dentition of *Gobiconodon* and apply the same rationale to *Hangjinia.*

The posterior dentition of *Hangjinia* is separated from the dental elements discussed above by a small diastema. Four molariforms are present behind this diastema; these were originally interpreted as p1, p2, m1, and m2 (Godefroit and Guo, 1999). The first molariform is incompletely preserved, but, as the authors indicated, it is asymmetrical, with a tall cusp **a** and small secondary cusps. The morphology of this element is similar to that of the asymmetric m1 of *G. borissiaki* (cf. Kielan-Jaworowska and Dashzeveg, 1998: figs. 2, 9). The remaining elements are either not preserved or not erupted, so little morphological detail can be appreciated.

It is also possible that the only known specimen of *Hangjinia chowi* is, in fact, a juvenile individual as suggested by the ex-

tension of the roots almost to the ventral edge of the jaw (cf. Godefroit and Guo, 1999: pl. 1d, and Kielan-Jaworowska and Dashzeveg, 1998: fig. 10). This could explain the presence of only four molariforms, rather than five, which is the primitive condition for amphilestids and gobiconodontids. As already mentioned, late eruption of the last molariform is common among triconodonts (Thomas, 1887; Simpson, 1928, 1929; Cifelli et al., 1998).

In summary, we believe that at present it is best to interpret the dentition of *Hangjinia* as following a pattern similar to that of other gobiconodontids. Therefore, we favor the following mandibular dental formula for *Hangjinia*: i1, c1, p2, m4. This reinterpretation of the Chinese specimen permits viewing *Hangjinia* as a derived gobiconodontid, rather than an aberrant one as originally proposed. *Hangjinia* would have lost the tooth positions homologous to the p3, p4, and m5 of *Gobiconodon*; however, some of these putative losses might only be apparent and due to the juvenile stage of the *Hangjinia* type specimen.

Zygomatic Arch in Mesozoic Mammaliaforms

The zygomatic arch in mammals usually involves three elements: maxilla, jugal, and squamosal. In a few groups of living mammals (e.g., tenrecids, soricids, and pholidotans), the zygomatic arch is incomplete or absent (McDowell, 1958; Novacek, 1986, 1993). In these instances, the jugal is frequently absent, while the maxilla and squamosal may be variously developed (Novacek, 1993).

It has long been known that the jugal is also absent or very reduced in monotremes (Gaupp, 1908; Gregory, 1910; Zeller, 1989, 1993). The absence or reduction of the jugal, and the concomitant enlargement of the maxilla in addition to a reduced alisphenoid (Kermack and Kielan-Jaworowska, 1971; Kielan-Jaworowska, 1971), have been used as features relating monotremes to multituberculates, once thought to have lost their jugals (Kielan-Jaworowska, 1971, 1974). More recently, purported jugals have been reported in several multituberculates (Hahn, 1987; Hopson et al., 1989; Wible and Rougier, 2000), but these are small laminar elements. All known examples of the jugal in multituberculates are placed medially along the zygomatic arch, overlapping the maxilla and squamosal, which form the bulk of the zygomatic arch.

Recently, Engelmann and Callison (1998) described in detail a specimen of the triconodontid *Priacodon* from the Late Jurassic Morrison Formation. In their descriptions these authors pointed out that the maxilla had a very extensive zygomatic process. The same is probably true for other Triconodontidae described by Simpson (1925a, 1925b, 1928, 1929). A maxillo-jugal suture was recognized by Simpson in these forms, but it is likely an artifact (Engelmann and Callison, 1998; personal obs.).

The maxillary described here demonstrates that this bone reaches the orbital margin, an unusual feature among mammals with well developed jugals and lacrimals in which the anterior and ventral orbital margin is normally formed by the jugal and lacrimal. Other Mesozoic mammaliaforms with a triconodont dentition for which the skulls are known show a primitive pattern with a relatively well-developed jugal. This includes *Morganucodon* (Kermack et al., 1981), *Megazostrodon* (Gow, 1986), and *Sinoconodon* (Crompton and Sun, 1985; Crompton and Luo, 1993). A complete triconodont skeleton named the type of *Jeholodens jenkinsi* (Ji et al., 1999) preserves a complete skull, although it is substantially flattened. The skull is not described in detail, but in the illustrations of the specimen a bilateral jugal can be identified. A lacrimal bone is also indicated. Although the details of the constitution of the zygomatic arch in *Jeholodens* are uncertain, both the jugal and lacrimal were apparently of generalized mammalian proportions. *Jeholodens* was originally interpreted as the sister group of Triconodontidae (Ji et al., 1999).

Members of Triconodontidae have their posterior upper molariforms on the root of the zygomatic arch (Simpson, 1925a, 1925b, 1929; Engelmann and Callison, 1998), which explains in part the extensive maxillary contribution to the zygomatic arch. On the other hand, gobiconodontids and *Jeholodens* do not

show a continuation of the molariforms onto the zygomatic arch (Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998; this report) and exhibit a more generalized morphology. However, the arrangement of the tooth row with regard to the zygomatic arch is not the only factor controlling the contribution of the maxilla to the zygomatic arch. Multituberculates and monotremes show a zygomatic arch formed mainly by the maxilla and squamosal, and they either have molars that do not extend onto the zygoma (multituberculates) or have a reduced or absent dentition (monotremes).

Phylogenetic position of Gobiconodontids Among Triconodontids

Gobiconodontids have an unusual anterior dentition with highly modified premolariforms, canines, and incisors. Modifications of the mesial teeth are so extreme as to cast doubt on the nature and basic homologies of the elements, including identification of incisors, canine, and premolariforms (Jenkins and Schaff, 1988). The combination of a highly modified antemolariform dentition and relatively generalized molariform morphology makes gobiconodontids a challenging group to work with because of the combination of plesiomorphic and autapomorphic traits. The systematic position of gobiconodontids has been specifically discussed in a handful of papers (Trofimov, 1978; Chow and Rich, 1984; Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998). These authors, however, limited their discussion to comparison with amphilestids (Mills, 1971; Crompton, 1974) or amphilestid-like animals. Close similarities of the gobiconodontid postcanines with those of amphilestids have been emphasized repeatedly (Trofimov, 1978; Chow and Rich, 1984; Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998). The molariform morphology of amphilestids, e.g., a dominant cusp **a** and subequal cusps **b** and **c,** is plesiomorphic and cannot be used to argue for close affinities between gobiconodontids and amphilestids (Rougier et al., 1999; in prep.). In fact, the basic traits of the amphilestid dentition are already present in the Early Jurassic *Dinnetherium* (Jenkins et al., 1983; Jenkins and Schaff, 1988).

Ji et al. (1999) provided the only previously published study that simultaneously addresses the relationships of *Gobiconodon* among other triconodonts and the relationships of triconodonts in general among Mesozoic mammaliaforms. To compare the results of Ji et al. (1999), we present here a character list (appendix 2), data matrix (appendix 3), and the cladogram (fig. 6) resulting from our ongoing studies of triconodont relationships (Rougier et al., 1999; in prep.). The results of Ji et al. (1999) and our study do not differ dramatically in their positioning of *Gobiconodon* among triconodonts. *Gobiconodon* is regarded as the sister group of some amphilestids plus Triconodontidae in Ji et al. (1999), and it is placed as the sister group of the triconodontid lineage (fig. 6, node 9) by Rougier et al. (1999; in prep.). The placement of *Gobiconodon* with triconodontids is weakly supported by the reduction in the number of lower incisors. The anterior reduction of the jugal and the consequent maxillary contribution to the orbital rim is also a derived feature shared by gobiconodontids and Triconodontidae that potentially could be used to link these groups. The significance of this character, however, is unclear because the maxilla also borders the orbital rim in multituberculates and monotremes, which in addition to reduced jugals also have reduced lacrimals. Unfortunately, we have very limited cranial information for many of the taxa relevant for an assessment of gobiconodontid affinities.

Ji et al. (1999) agreed with Hu et al. (1997, 1998) in placing *Gobiconodon* outside Mammalia, i.e., outside the group formed by the common ancestor of monotremes and therians plus all its descendants. This view offers a radically different alternative from that supported previously (Rougier, 1993; Rowe, 1993; Rougier et al., 1996a, 1996b; McKenna and Bell, 1997) which considered gobiconodontids and triconodontids as members of Mammalia.

In fact, the analysis of Ji et al. (1999: fig. 5) presented *Gobiconodon* and *Jeholodens* as successive outgroups of Mammalia. Although the support for each of these nodes is relatively high (12 transformations for the

node grouping *Jeholodens, Gobiconodon,* and Mammalia, and 5 transformations for *Gobiconodon* plus Mammalia), the internal consistency of the matrix is rather poor. Several characters contradict the most parsimonious arrangement presented by Ji et al. (1999), supporting a placement among Mammalia for *Jeholodens* and *Gobiconodon*. Even accepting all the characters and scorings in the matrix by Ji et al. (1999), the inclusion of *Jeholodens* and *Gobiconodon* in Mammalia is only 2 steps longer than their shortest trees of 210 steps. Curiously enough, reanalysis of the Ji et al. (1999) matrix using Pee Wee (version 2.7) (Goloboff, 1993a, 1993b) yields the traditional tree topology with both *Jeholodens* and *Gobiconodon* included in Mammalia. Pee Wee uses Goloboff's (1993a) function of homoplasy to produce a weighting strategy for the characters. This function has the shape of a concave curve, whose concavity can be altered by changes in a constant K. The matrix was run with the default constant, K = 3, which only moderately penalizes homoplastic characters. Obviously, more concave functions also recover triconodontids as mammals. We acknowledge that the use of a concave function of homoplasy may be controversial, but it serves here to illustrate that the characters supporting the exclusion of triconodontids and *Gobiconodon* from Mammalia are more homoplastic overall than those supporting the alternative inclusion of these forms in Mammalia. Even without any challenge of the factual basis of the matrix presented by Ji et al. (1999), their conclusions are very sensitive to small changes in the weighting strategy chosen (they used the default weighting for PAUP).

One of us (GWR) has restudied *Jeholodens.* Our interpretation of the specimen differs in specific points from that published by Ji et al. (1999). For example, *Jeholodens* possesses a well-developed cusp **e** clearly visible on the m2, which was omitted in the

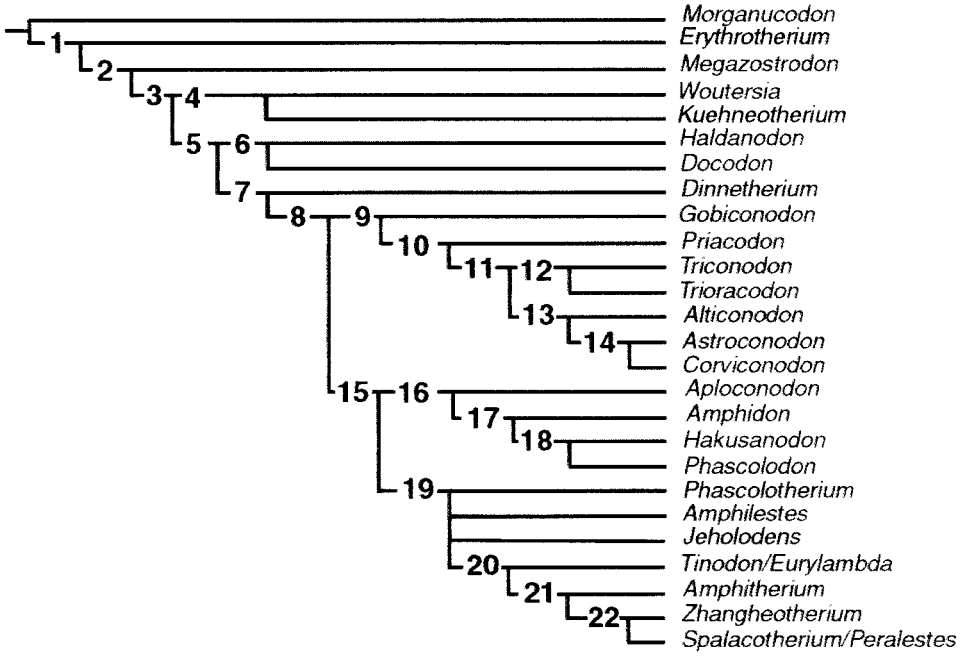

Fig. 6. Strict consensus resulting from three most parsimonious trees found by NONA version 2.0 (Goloboff, 1993b). Analysis of matrix in appendix 3 resulted in three trees of 138 steps in length that were found to be the most parsimonious solutions after 500 heuristic searches. Gobiconodontid affiliation with Triconodontidae is only weakly supported by the reduction in number of the lower incisors and could also be ambiguously supported by the shallow grooving of the mesial root in molariforms to receive the preceding molariform.

illustration of the specimen (Ji et al., 1999, fig. 2) and reported as absent. The occlusal outline of the upper molars is markedly triangular, indicating an alternating occlusion instead of the tooth-on-tooth occlusion suggested in the original description. The characters of the labial aspect of the dentition are not accessible, and thus the scoring of these features by Ji et al. (1999) is problematic. Altering the matrix presented by Ji et al. (1999) to reflect our interpretation of the specimen places both *Gobiconodon* and *Jeholodens* inside Mammalia. Likewise, our study of triconodont relationships results in trees with a length of 138 that also support *Gobiconodon* and *Jeholodens* as mammals. The strict concensus tree presented in figure 6 is the result of three independent trees. Those trees differ in alternative resolutions of the relationships of *Amphilestes, Phascolotherium,* and *Jeholodens. Jeholodens* clusters among the paraphyletic amphilestids. Our results suggest that several traditional groups of Mesozoic mammaliaforms such as Triconodonta, Symmetrodonta, and Amphilestidae are not monophyletic. Smaller subgroups of these higher level taxa including Triconodontidae and Spalacotheriidae, however, are supported.

CONCLUSIONS

Gobiconodontids are a conspicuous group of triconodont mammals with a derived antemolar dentition and a generalized molariform series. The recently described *Hangjinia* can be reinterpreted in agreement with this pattern. Species of *Gobiconodon* have a large maxillary contribution to the orbital rim and more than one maxillary foramen for separate infraorbital canals. Gobiconodontids include some of the largest Mesozoic mammals; *G. hopsoni* (based on teeth size) is approximately the size of a *Didelphis virginiana* (skull length of about 12 cm). The postcranial skeleton of *G. ostromi* is, however, more robust than that of modern mammals of similar size, such as didelphids; thus skull size may not be an accurate descriptor of body size if modern analogs are followed. The replacement of the anterior molariforms seen in *G. ostromi* is yet to be directly documented in the species from Khoobur, *G. borissiaki* and *G. hoburensis,* and it is uncertain if this is a retained primitive feature or an autapomorphic trait. Gobiconodontids are mammals (i.e., members of the crown group Mammalia), but alternative hypotheses of their relationships within Mammalia are only weakly supported.

The derived maxillary and antemolariform morphology of *Gobiconodon* has no parallel in amphilestids, including *Jeholodens.* Reported similarities between Amphilestidae and gobiconodontids are limited to plesiomorphic features of the molariform dentition in both groups. Most traditional groups of Mesozoic mammaliaforms, such as Triconodonta, Amphilestidae, and Symmetrodonta, seem to be paraphyletic.

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APPENDIX 1: Measurements

Gobiconodon hopsoni (type), PSS-MAE 140
M5 length: 6 mm (estimated)
M5 width: 4.1 mm
M4 length: 5.2 mm
Gobiconodon hopsoni, PSS-MAE 139
Too incomplete to provide meaningful measurements
Gobiconodon sp., PSS-MAE 137
p3 length: 1.25 mm
p3 height: 2.54 mm
Mandibular height under p3: 3 mm (estimated)
p4 length: 1 mm (estimated)
p4 height: 0.6 mm
Mandibular height under p4: 3.9 mm
m1 length: 1.83 mm
Mandibular height under m1; 4mm (estimated)
Gobiconodon sp., PSS-MAE 138
m5 length: 2.28 mm
Mandibular height under m5: approximately 5mm under anterior root, approximately 6 mm under posterior root
m4 length: 6.57 mm
Mandibular height under m4: approximately 5 mm

APPENDIX 2: Character List

Lower dentition

1) *Number of lower incisors*—four or more (0), three (1), or less than three (2). Ordered.
2) *Large mesial incisor*—absent (0) or present (1).
3) *Canine shape*—caniniform (0), premolariform (1), or incisiviform (2).
4) *Number of lower canine roots*—one (0) or two (1).
5) *Number of lower premolariforms*—four or more (0) or three or less (1).
6) *Tall, peglike, uniradiculated anterior lower premolariforms*—absent (0) or present (1).
7) *Symmetrical premolariforms*—absent (0) or present (1).
8) *Last lower premolariform*—taller than the first molariform (0) or shorter or subequal (1).
9) *Cusp* **c** *in the last premolariform*—present on crown (0) or connected to the cingulum or absent (1).
10) *Number of lower molariforms*—less than five (0), five (1), or more than five (2).
11) *Occlusion of molariforms*—**A** cusp occludes between **a** and **c** cusps (0) or **A** occludes either posterior to **c** and/or in the anterior face of **b** (1).
12) *Crown cusps on the first lower molariform*—arranged in line (0), forming an open triangle (1), or forming a more acute triangle (2). Ordered.
13) *Height of the crown with regard to the length in lower molariforms (m2 consider when available)*—taller than long (0) or shorter than long (1).
14) *Locking mechanism between lower molariforms*—attained by interlocking cusps or notched cingula (0), attained by cusps and a shallowly excavated anterior root (1), or locking involves a deeply excavated anterior root (2).
15) *Lingual lower molariform cingulum*—straight with cuspules (0), smooth and undulant (1), or absent (2).
16) *Ratio between crown height to jaw height under the tallest molariform*—less than twice (0) or twice or more (1).
17) *Recumbent molariform crown cusps*—absent (0) or present (1).
18) *Cusp* ***a*** *position*—mesially on crown (0) or centrally placed on molariform crown (1).
19) *Bulging of the labial slope of cusp* **a**—absent (0), moderate (1), forming a rounded eminence at the base of the crown (2), or forming the apex of an acute triangle (3).
20) *Cusp* **a** *height*—tallest (0) or subequal to **b** or **c** (1).
21) *Relative height of cusps* **b** *and* **c**—**b** $<$ **c** (0), **b** $\cong$ **c** (1), or **b** $>$ **c** (2).
22) *Cusp* **b**—connected to the cingulum (0) or on crown, independent from cingulum (1).
23) *Cusp* **b** *position*—aligned with **a** along the mandibular axis (0), lingual to **a** in posterior molariforms forming an angle of less than 20° with the mandibular axis (1), or lingual to **a** forming an angle more than 20° (2). Ordered.
24) *Cusp* **c** *position*—aligned with **a** in the mandibular axis (0), lingual to **a** in posterior molariforms forming an angle of 25° or less with the mandibular axis (1), or lingual to **a** forming an angle more than 25° (2). Ordered.
25) *Cusp* **c**—present (0) or absent (1).
26) *Conspicuous shelf formed by cusp* **d** *on back of molariform*—absent (0) or present (1).
27) *Cusp* **d**—Small cingular cusp (0) or tall, incorporated into the crown (1).

28) *Accessory cusp* **f**—absent (0) or present (1).
29) *Cusp* **e**—present (0) or absent (1).
30) *Kühnecone (cusp* **g**)—present (0), connected to cusp **a** by crest (1) or absent (2).
31) *Size of the last lower molariform*—strongly reduced, about 50% or less of preceding tooth (0) or subequal to larger than the preceding tooth (1).
32) *Last lower molariform*—crown and accessory cusps present (0) or cingulum and cingular cusps very reduced to absent (1).
33) *Number of roots on the last molariform*—two (0) or one (1).
34) *Mesio distal change of molariform size*—subequal (0), increases posteriorly (1), or decreases posteriorly (2).
35) *Section of the molariform roots*—oval or circular (0) or anteroposteriorly compressed (1).
36) *Alignment of the last molar with regard to the coronoid process*—medial (0) or in line (1).
37) *Wear facets*—developed by extensive wear of the cusps, which changes the shape of the crown (0) or crown shape present upon eruption of the teeth, with only limited remodeling by wear facets (1).

Lower jaw

38) *Number of large mental foramina*—less than three (0) or three or more (1).
39) *Height of the lower jaw ramus between the canine and the last molariform*—subuniform (0) or becomes higher posteriorly (1).
40) *Shape of the ventral edge of the lower jaw*—convex ventrally (0) or nearly straight (1).
41) *Coronoid process*—mesiodistally narrow (0) or broad (1).
42) *Coronoid process*—rear slope straight and directed posteriorly (0) or approaching the vertical or concave (1).
43) *Masseteric ridge*—small to absent (0) or forming a prominent shelf (1).
44) *Medial flange*—present (0) or absent (1).
45) *Pseudangular process*—present (0) or absent (1).
46) *Dentary expanded posteriorly supporting the condyle ventrally*—absent (0) or present (1).
47) *Remnant of the dental lamina*—present (0) or absent (1).
48) *Meckelian groove*—confluent with the ventral edge of the jaw approximately at the level of the first molariform (0), without reaching the lower margin (1), or lacking (2).
49) *Pterygoid fossa*—absent (0) or present (1).
50) *Broad groove for the attachment of postdentary elements*—present (0) or absent (1).
51) *Dentary–squamosal articulation*—supplemented by a mechanically strong malleus (articular)–incus (quadrate) articulation (0) or only load bearing articulation between skull and lower jaw (1).
52) *Pterygoid crest*—absent (0), strong straight crest connecting the ventral edge of the jaw with the condyle (1), curved around the ventral edge of the jaw (2), or ending at the angular process (3).
53) *Shelflike lateral ridge of the dentary*—present (0) or absent (1).
54) *Angular process*—absent (0) or present (1).
55) *Coronoid bone*—present (0) or absent (1).

Upper dentition

56) *Flat occlusal surface on upper molariforms*—absent (0) or present (1).
57) *Labial margin of posterior upper molariforms*—straight or slightly concave/convex (0) or bilobated (1).
58) *Number of principal cusps on the last upper molariform*—three (0) or two (1).
59) *Outline of the last upper molariform in occlusal view*—oval (0) or triangular (1).

APPENDIX 3: Data Matrix

Taxon	Character state											
		10		20		30		40		50		
Morganucodon	00000	00000	00000	00000	00000	00000	01000	00000	00000	00000	00000	0000
Erytrotherium	A0000	00100	00000	00000	00000	00000	???00	00000	00000	00000	00000	0000
Megazostrodon	00000	00101	10000	00000	01000	10000	11000	00000	00000	11000	00?00	0100
Kuehneotherium	00000	00??2	1A000	00110	B1110	00102	1?0?0	00000	00000	01000	00000	01??
Woutersia	?????	?????	1?000	?0110	B1010	00100	????0	?0???	?????	?????	?????	0A??
Dinnetherium	00000	00101	00001	00100	11000	00100	11000	00100	11000	11000	00110	0100
Haldanodon	A0011	00101	?1100	10110	?10?1	10001	11000	00000	11000	01100	00000	0000
Docodon	A0010	00102	?1100	10110	?10?1	10001	11000	00000	11000	01110	00000	0000
Jeholodens	A10?1	0011?	10001	00110	11000	00?02	???00	?0?00	11?11	11?11	12100	00??
Priacodon	20001	00000	00101	00100	11000	00012	11010	10000	11111	11111	11101	1111
Triconodon	B0000	00000	00101	10101	11000	00012	11010	10011	11111	11111	11101	1001
Triorachodon	B0000	00000	00101	10101	11000	00012	11010	10011	11111	11111	11101	1011
Astroconodon	??000	00001	00121	11101	11000	01012	11010	00?1?	?????	?1?1?	1??01	10??
Alticonodon	?????	?????	??121	?0101	11000	01012	11010	?0???	?????	?1?1?	1????	1???
Corviconodon	??000	00?01	00121	11101	11000	01012	00010	00?10	1?111	?1211	1B??1	????
Aploconodon	?????	?????	??0?2	00110	11000	0?002	00100	10???	???11	?1?11	????0	????
Phascolotherium	00011	01111	10001	00110	11000	00102	11?00	10100	11011	11011	12100	????
Amphilestes	00010	01011	10001	00110	11000	00102	11000	10100	11011	11011	12100	????
Amphiodon	????1	0??00	10001	00110	11000	00102	00120	10?00	1?011	11011	121?0	????
Hakusanodon	??011	00101	10001	00120	21000	00102	00120	10100	??011	?1011	12???	????
Phascolodon	?????	?????	1?001	00120	21000	00102	00120	?0???	?????	?1?11	???0?	????
Gobiconodon	21201	101?1	10011	A0100	11000	00102	11020	10110	11011	11011	12100	0100
Tinodon/Eurylambda	A0111	01110	11001	00130	11110	00102	11000	10000	11011	11011	12100	01??
Zhangheotheriids	11101	00112	12001	00130	11220	00002	01101	00100	01011	11?11	12100	0001
Spalacotheriids	A0011	00102	12001	00130	11220	00002	11001	01100	11011	11011	12100	0100
Amphitherium	00010	00112	12102	00130	11220	00102	10000	01100	11011	11011	13110	0??1

Polymorphic conditions: A = 0,1; B = 1,2.

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