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Two new species of *Gobiconodon* (Mammalia, Eutriconodonta, Gobiconodontidae) from the Lower Cretaceous Shahai and Fuxin formations, northeastern China

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Two new gobiconodontid mammals, *Gobiconodon tomidai* **sp. nov.** and *Gobiconodon haizhouensis* **sp. nov.**, from the Lower Cretaceous (Aptian to Albian) Shahai and Fuxin Formations, respectively, in Liaoning Province, northeastern China, are described. *Gobiconodon tomidai* **sp. nov.** is a small-sized species of the genus characterised by the lower dental formula 2.1.2.5, a double-rooted p2, the molariform crown being mesiodistally longer than tall, and a distinct and almost continuous lingual cingulid on m2–m4. *Gobiconodon haizhouensis* **sp. nov.** is of similar size to *Gobiconodon tomidai* **sp. nov.** and is characterised by the lower dental formula 2.1.3.5, the molariform crown being slightly taller than the mesiodistal length, and a well-developed and almost continuous lingual cingulid on m1–m3. The new materials indicate that the upper molariform count of most species of *Gobiconodon* is likely to be four, one less than the lower molariform count. *Gobiconodon* is the second mammalian genus common to the Jehol and Fuxin mammalian faunas.

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Keywords: China; Early Cretaceous; *Gobiconodon haizhouensis*; *Gobiconodon tomidai*; Gobiconodontidae; Mammalia

Introduction

The Gobiconodontidae are a family of eutriconodontans that were widely distributed in the Northern Hemisphere during the Early Cretaceous. The family is known to have occurred in Asia including Siberia (Trofimov 1978; Kielan-Jaworowska and Dashzeveg 1998; Maschenko and Lopatin 1998; Godefroit and Guo 1999; Rougier et al. 2001; Tang et al. 2001; Li et al. 2003; Minjin et al. 2003; Meng et al. 2005; Lopatin and Averianov 2006; Yuan et al. 2009; Lopatin 2013), North America (Jenkins and Schaff 1988), Europe (Cuenca-Bescós and Canudo 2003; Sweetman 2006) and Morocco (Sigogneau-Russell 2003), the only Gondwanan record to date. Because of their wide distribution, gobiconodontids are important members of Early Cretaceous Northern Hemisphere mammalian faunas.

Gobiconodontids are characterised mainly by a reduction in the number of antemolariform teeth and an enlarged first lower incisor. Here, we regard the Gobiconodontidae as including three genera: *Gobiconodon* Trofimov, 1978, *Hangjinia* Godefroit and Guo, 1999, and *Meemannodon* Meng, Hu, Wang and Li, 2005. Another genus, *Repenomamus* Li, Wang, Wang and Li, 2000 is also considered by some authors to be a member of the family (e.g. Kielan-Jaworowska et al. 2004), and we agree that there is a close relationship between *Repenomamus* and gobiconodontids. One notable shared characteristic, the replacement pattern of molariform teeth in *Repenomamus* and *Gobiconodon* (Jenkins and Schaff 1988; Meng et al. 2003), strongly supports this view. *Repenomamus* is, however, considered herein to belong in another family, the Repenomamidae, to which it was originally ascribed (Li et al. 2000). The first lower incisor is indeed enlarged in *Repenomamus*, but the second incisor as well as the canine and premolariforms are also enlarged, nearly sub-equal in size to the first incisor (Li et al. 2000; Hu, Meng, et al. 2005); the first lower incisor in gobiconodontids is, on the contrary, obviously the largest tooth in the lower dentition, much larger than the second incisor, canine and premolariforms. *Liaoconodon* Meng, Wang and Li, 2011 has sub-equal-sized lower incisors, canine and first premolariform, and *Repenomamus* is more similar to *Liaoconodon* than to gobiconodontids in this respect. *Repenomamus* shares incipient triangulation of the primary cusps on upper molariforms with gobiconodontids (Wang, Hu, Meng, et al. 2001, supplementary figure 1), but this characteristic is also seen in 'amphilestid' taxa, as discussed by Gao et al. (2009), and is not an autapomorphy of the Gobiconodontidae. *Klamelia* Chow and Rich, 1984 was originally assigned to the Gobiconodontidae [more precisely, to the Gobiconodontinae, which was subsequently raised to a family by Jenkins and Schaff (1988)], but is now generally excluded from the family (e.g. Jenkins and Schaff 1988; Kielan-Jaworowska et al. 2004; Martin and Averianov 2007). The

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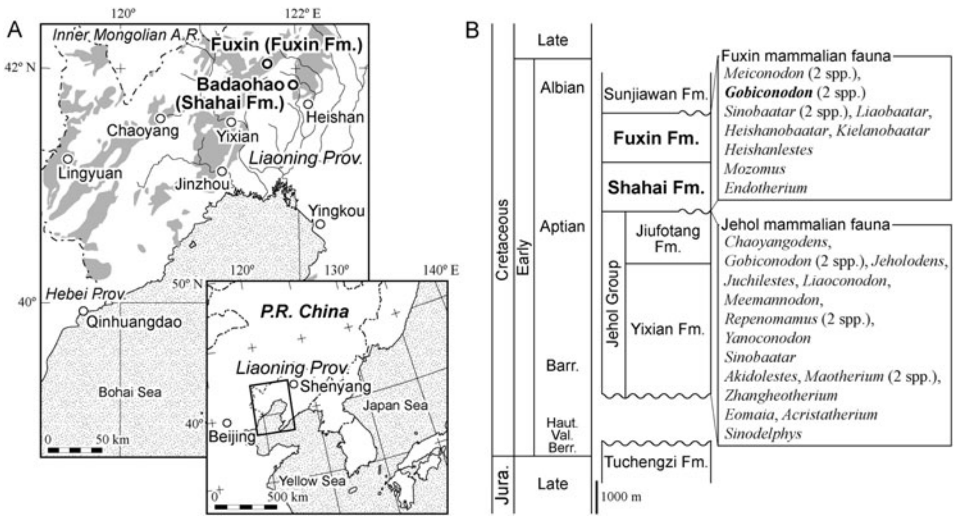

Figure 1. (A) The locations of Badaohao and Fuxin City, Liaoning Province, northeastern China. The grey areas in the enlarged map show the distribution of late Mesozoic strata in Liaoning Province (modified after Editorial Board of Chinese Geologic Maps 2002). (B) Schematic stratigraphic table of the major late Mesozoic strata distributed in western Liaoning Province, northeastern China, and mammalian fossil records for the Jehol and Fuxin mammalian faunas.

Early Jurassic *Huasteconodon* Montellano, Hopson and Clark, 2008 is also assigned by them to the Gobiconodontidae primarily on the basis of incipient triangulation of the primary cusps on the upper molariforms, which, as discussed earlier, is not unique to gobiconodontids. Attribution of *Huasteconodon* to the Gobiconodontidae is controversial due to lack of data, and in view of this and the large temporal gap between the occurrence of *Huasteconodon* and other gobiconodontids of uncontroversial affinities, we tentatively exclude the genus from the Gobiconodontidae.

Here are described two new species of *Gobiconodon* based on two new specimens from the Lower Cretaceous of China, although the gobiconodontid affinities of one (IVPP V14510) has previously been reported (Kusuhashi et al. 2008, 2010; Kusuhashi, Hu, Wang, Hirasawa, et al. 2009). The specimens were recovered from carbonaceous rocks of the Shahai and Fuxin Formations (Aptian to Albian) at small coal mines in the Badaohao (Heishan County) and Fuxin City areas, respectively, in Liaoning Province, northeastern China (Figure 1). The Shahai and Fuxin Formations have yielded a number of other mammals (Shikama 1947; Wang et al. 1995, 2006; Wang, Hu, Li, et al. 2001; Hu, Fox, et al. 2005; Hu, Wang, et al. 2005; Li et al. 2005; Kusuhashi, Hu, Wang, Hirasawa, et al. 2009; Kusuhashi, Hu, Wang, Setoguchi, et al. 2009, 2010), such as eutriconodontans including triconodontid *Meiconodon* Kusuhashi, Hu, Wang, Hirasawa and Matsuoka, 2009; multituberculates including *Sinobaatar* Hu and Wang, 2002, *Liaobaatar* Kusuhashi, Hu, Wang, Setoguchi and Matsuoka, 2009, *Heishanobaatar* Kusuhashi, Hu, Wang, Setoguchi and Matsuoka, 2010, and *Kielanobaatar* Kusuhashi, Hu, Wang, Setoguchi and Matsuoka, 2010; spalacotheriids including *Heishanlestes* Hu, Fox, Wang and Li, 2005; the stem zatherian including *Mozomus* Li, Setoguchi, Wang, Hu and Chang, 2005; and eutherians including *Endotherium* Shikama, 1947. The Shahai Formation conformably (or partly unconformably) overlies the Jiufotang Formation, the upper part of the Jehol Group that is famous for the Jehol Biota, and the Fuxin Formation conformably overlies the Shahai Formation (e.g. Wang et al. 1989; Yang and Li 1997; see Kusuhashi, Hu, Wang, Hirasawa, et al. 2009; Kusuhashi, Hu, Wang, Setoguchi, et al. 2009, for more details of the geological setting). Therefore, the mammalian fauna from the Shahai and Fuxin Formations (herein called the Fuxin mammalian fauna) is slightly younger than that from the Jehol Group (herein called the Jehol mammalian fauna).

Currently, two different definitions of the Eutriconodonta are used in general. Kielan-Jaworowska et al. (2004) applied the Eutriconodonta (originally defined as a suborder of the order 'Triconodonta' by Kermack et al. 1973) as an order that is an obviously separated group from morganucodontids and other stem mammaliaforms; the order is composed of triconodontids and closely related taxa including gobiconodontids and 'amphilestids'. Although this systematics is still accepted by various authors, monophyly of this group has been questioned (e.g. Rougier et al. 2007), and Gaetano and Rougier (2011) proposed a revised definition of the Eutriconodonta as a clade composed of gobiconodontids and triconodontids. In either case, gobiconodontids belong to the Eutriconodonta. We here simply adopt the order without discussing its definition, and where necessary, we add *sensu lato* for the definition of Kielan-Jaworowska et al. (2004).

The terms premolariform and molariform are used here, following the concept of Rougier et al. (2001, 2007). Lower incisors, premolariforms and molariforms are abbreviated as lowercase i, p and m, respectively, followed by numbers indicating the order of teeth in each tooth class counting from the mesial to the distal end of each. The upper dentition is distinguished from the lower by using upper-case I, P and M. In this paper, numbers do not necessarily indicate the homology of teeth, but only denote their positions. Cusp terminology follows that of Crompton and Jenkins (1968) (Figure 2), which is not coincident with that of Slaughter (1969) and Trofimov (1978). The term 'molariform' within single quotation marks is used as an adjective simply meaning that a tooth is morphologically similar to molariforms.

Trofimov (1978) described the lower dental formula of *Gobiconodon* as 3.1.4.5 and this was followed by others who considered the antemolariforms of the genus to comprise an enlarged incisor, a canine and three to four premolariforms (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Maschenko and Lopatin 1998; Li et al. 2003; Kielan-Jaworowska et al. 2004). Meng et al. (2005) challenged this and concluded that the lower dental formula of gobiconodontids is 2.1.2–3.5, a view later accepted by Yuan et al. (2009). Rougier et al. (2007) proposed another interpretation, 3.1.2.5, but here we follow Meng et al. (2005).

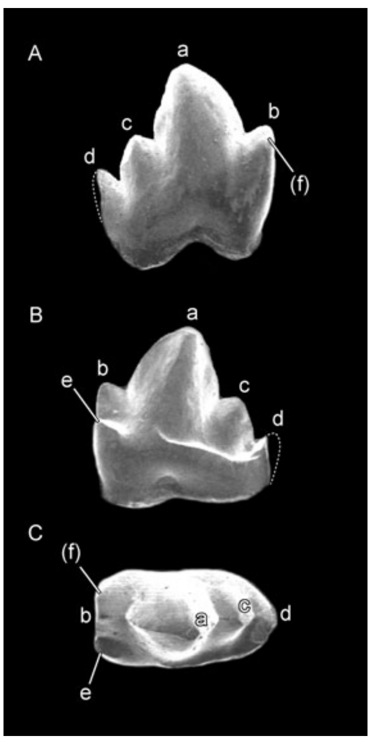

Figure 2. Cusp terminology used in the text showed on the right m1 of *Gobiconodon haizhouensis* **sp. nov.**: (A) labial view; (B) lingual view and (C) occlusal view, left to mesial. Note that cusp f of the tooth is not distinct but there is a minute swelling at the mesiolabial face of cusp b.

Institutional abbreviations

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PSS, Paleontological and Stratigraphic Section, Institute of Geology, Mongolian Academy of Sciences, Ulan Bator, Mongolia.

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758

Order **Eutriconodonta** Kermack, Mussett and Rigney, 1973

Family **Gobiconodontidae** Chow and Rich, 1984

Genus ***Gobiconodon*** Trofimov, 1978

Type species

Gobiconodon borissiaki Trofimov, 1978.

Included species

Type species, *Gobiconodon hoburensis* (Trofimov, 1978), *Gobiconodon hopsoni* Rougier, Novacek, McKenna and Wible, 2001, *Gobiconodon luoianus* Yuan, Xu, Zhang, Xi, Wu and Ji, 2009, *Gobiconodon ostromi* Jenkins and Schaff, 1988, *Gobiconodon palaios* Sigogneau-Russell, 2003, *Gobiconodon zofiae* Li, Wang, Hu and Meng, 2003, *Gobiconodon tomidai* **sp. nov.** and *Gobiconodon haizhouensis* **sp. nov.**

***Gobiconodon tomidai* sp. nov.**

(Figures 3 and 4, Table 1)

Type and only known specimen

A partial right lower jaw with i1–i2, broken canine, alveoli for p1–p2 and m1, and variably preserved m2–m5 (IVPP V14510).

Type locality and horizon

Badaohao, Heishan, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Shahai Formation.

Etymology

'Tomida', in honour of Dr Yukimitsu Tomida, who is one of the leading Japanese vertebrate palaeontologists working intensely on Asian small mammals and who is a good friend of the authors.

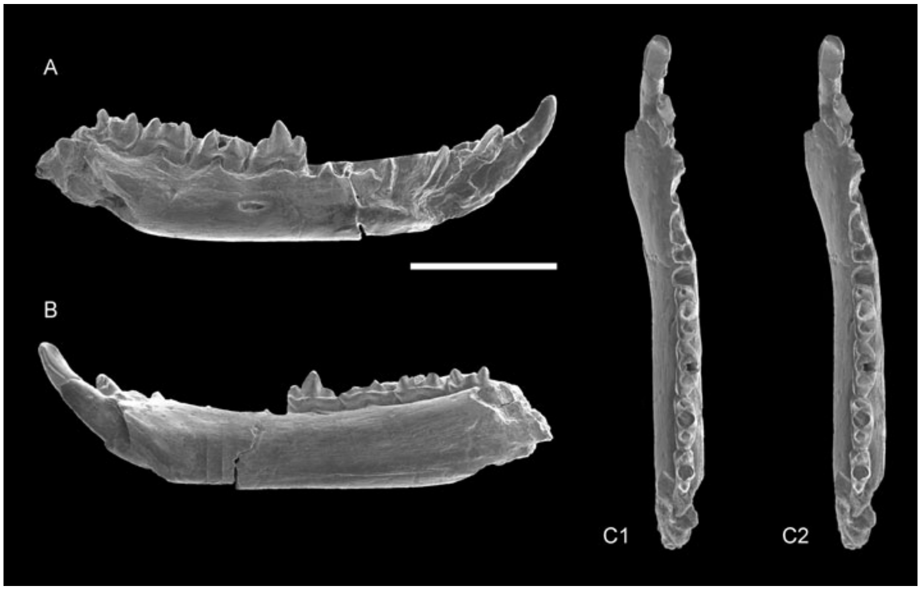

Figure 3. Scanning electron micrographs of the holotype (IVPP V14510) of *Gobiconodon tomidai* **sp. nov.** A partial right lower jaw with i1–i2, broken canine, alveoli for p1–p2 and m1, and variably preserved m2–m5; Lower Cretaceous Shahai Formation, Badaohao, Heishan, Liaoning, northeastern China. (A) Labial view; (B) lingual view and (C) occlusal view, stereopair. Scale bar = 5 mm.

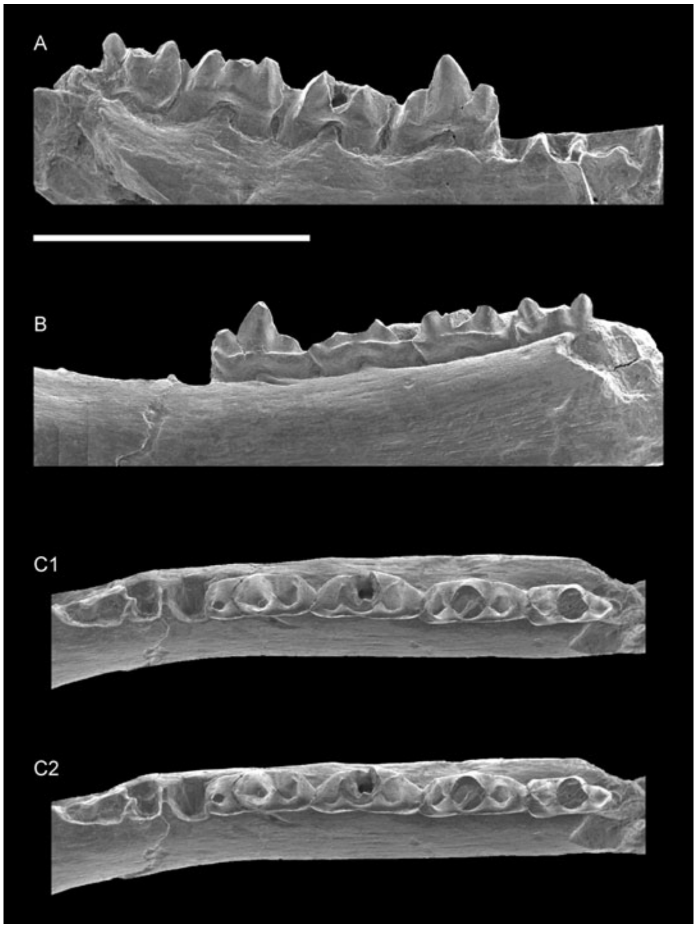

Figure 4. Scanning electron micrographs of the postcanine teeth of *Gobiconodon tomidai* **sp. nov.** Holotype (IVPP V14510): (A) labial view; (B) lingual view and (C) occlusal view, stereopair. Scale bar = 5 mm.

Table 1. Measurements (mm) of lower postcanine teeth in *Gobiconodon haizhouensis* **sp. nov.** and *Gobiconodon tomidai* **sp. nov.**

Premolariforms

	p1			p2			p3		
	L	*W*	*H*	*L*	*W*	*H*	*L*	*W*	*H*
Gobiconodon haizhouensis (IVPP V14509)	1.35	0.83	1.17	1.37	0.92	1.18	1.27	0.79	0.98

Molariforms

	m1			m2			m3			m4			m5		
	L	*W*	*H*	*L*	*W*	*H*	*L*	*W*	*H*	*L*	*W*	*H*	*L*	*W*	*H*
Gobiconodon tomidai (IVPP V14510)	–	–	–	1.99	0.78	1.44	2.07	0.86	–	2.00	0.79	–	–	0.72	–
Gobiconodon haizhouensis (IVPP V14509)	1.72	0.94	1.85	1.81	0.97	1.85	1.66	0.94	1.88	1.50	0.88	1.50	1.22	0.75	1.22

Notes: *H*, height; *L*, mesiodistal length; *W*, labiolingual width.

Diagnosis

A small species of *Gobiconodon* bearing the following unique combination of characters: lower dental formula 2.1.2.5; an enlarged i1, more than twice as tall as i2; a double-rooted p2; m2–m4 with a distinct and almost continuous lingual cingulid; and crowns of m2–m5 that are mesiodistally longer than tall.

Differential diagnosis

Differs from other eutriconodontans *sensu lato* except for gobiconodontids in having an enlarged i1 that is much larger than i2 and reduced number of incisors and premolariforms. Differs from other gobiconodontids in having a double-rooted p2. Differs from most gobiconodontids but resembles *Gobiconodon haizhouensis* **sp. nov.**, *Gobiconodon hoburensis* and *Gobiconodon palaios* in its smaller size. Differs from *Gobiconodon borissiaki*, *Gobiconodon haizhouensis* **sp. nov.**, *Gobiconodon hoburensis*, *Gobiconodon luoianus* and *Gobiconodon zofiae* but resembles *Gobiconodon ostromi*, *Hangjinia chowi* and *Meemannodon lujiatunensis* in having only two premolariforms. Differs from *Meemannodon lujiatunensis* in having a proportionally larger i2, a developed cusp b on m1, and molariform cusps b and c less distant from cusp a. Differs from *Gobiconodon hopsoni*, *Gobiconodon ostromi*, *Gobiconodon zofiae* and *Meemannodon lujiatunensis* but resembles *Gobiconodon borissiaki*, *Gobiconodon haizhouensis* **sp. nov.**, *Gobiconodon hoburensis* and *Gobiconodon luoianus* in having closely packed p2–m1 without a diastema between adjacent teeth. Differs from *Gobiconodon borissiaki*, *Gobiconodon hoburensis*, *Meemannodon lujiatunensis* and *Gobiconodon zofiae* in having a distinct and almost continuous lingual cingulid on m2–m4. Differs from *Hangjinia chowi* and *Gobiconodon luoianus* in having an ultimate premolariform strongly reduced in size. Differs from *Gobiconodon borissiaki*, *Gobiconodon haizhouensis* **sp. nov.** and *Gobiconodon hoburensis* in having molariforms (m2–m5) that are mesiodistally longer than tall with cusps b and c projecting from lower positions. Differs from *Gobiconodon ostromi* in lack of an obvious diastema between p2 and m1. Although the new species cannot be adequately compared with *Gobiconodon palaios*, which is known only from several isolated upper teeth, the geographical and temporal distances between the new species and *Gobiconodon palaios* suggest that it is highly likely to represent different species from *Gobiconodon palaios*.

Description

Only the horizontal ramus of the right dentary is preserved, and its anterolabial part is broken. It is slender, with a maximum preserved height of 2.3 mm below m4. The posterior part of the bone is slightly but not distinctly higher dorsoventrally than the anterior part, and the anterior portion of the dentary is slightly medially inflected. The symphysis extends posteroventrally terminating below the canine. There is at least one mental foramen, which is situated 0.8 mm below the distal root of m2. A Meckelian groove is present on the posterolingual side. This extends parallel to the ventral margin of the bone and approximately 0.5 mm above it. The groove extends anteriorly to at least below m3, but its anterior extent cannot be determined due to damage. The posterior part of the groove is slightly widened dorsoventrally. The mandibular foramen is not present on the preserved part of the dentary.

The right i1, i2 and a broken canine are preserved. The i1 is a large procumbent, recurved tooth and is the tallest of those preserved. It is slightly acuminate apically and the apicodistal part of it is somewhat spatulate with a flattened face. The i2 is also procumbent and lies immediately distolabial to i1. The crown of i2 is damaged but was probably conical. The i2 is much smaller than i1, the latter being more than twice as tall as the former. Judging from the alveolus exposed as a result of damage to the dentary, i2 has a relatively long root extending below the canine. There is a short diastema between i2 and the canine. The canine is badly damaged, and its crown shape is unknown. It is procumbent but less than the incisors. Its preserved portion and the exposed part of the alveolus indicate that it was probably as large as or slightly smaller than i2.

Although premolariforms are missing, the alveoli for two premolariforms (p1 and p2) are preserved. There are short diastemata between the canine and p1 and between p1 and p2. Judging from the preserved alveoli, p1 was a single-rooted tooth and probably as large as the canine, whereas p2 was a double-rooted tooth and was much smaller than p1 and m1. A similar size difference between the last premolariform and the first molariform is observed in other species of *Gobiconodon* (Kielan-Jaworowska and Dashzeveg 1998; Li et al. 2003). There is no evidence for the former presence of another premolariform, such as a plugged alveolus or diastema between the posteriormost premolariform and the first molariform, as reported for *Gobiconodon ostromi* by Jenkins and Schaff (1988).

All of the preserved molariforms, m2–m5, are damaged. The mesial three are sub-equal in length and width, whereas m5 is slightly smaller than the others (Table 1). All are estimated to be mesiodistally longer than high. Mesial to m2, there are alveoli for the double-rooted m1. Based on the alveoli, m1 appears to be smaller than m2, and of similar size to m5. The three primary cusps and cusp d are mesiodistally aligned in occlusal view in m2–m5. On m2–m4, a lingual cingulid is well developed, whereas it is absent from m5. A labial cingulid is absent from all preserved molariforms. All are double rooted and basally both roots, for each tooth, are of similar diameter. All are slightly recurved. All of the molariforms are worn; the degree of wear is greatest on m3, greater on m4 than on m2, and least on m5.

The m2 is the best preserved of the molariforms. Cusp a is the largest and is slightly recumbent in lateral view. Cusps b and c are well developed from the position about half the height of cusp a. Cusp c is strongly worn but based on dimensions of its base it appears to have been as large as cusp b. Cusp b is not recumbent but the inclination of cusp c cannot be determined. At the mesiolingual base of cusp b, there is a tiny cusp e. A distinct cusp f is not present on the mesiolabial face of the tooth, but there is a ridge that extends apicobasally. The mesial margin of m2 is indented between cusp e and mesiolabial ridge for the reception of cusp d of m1. Basally on the crown and distal to cusp c, a well-developed but strongly worn cusp d is present fitting into the mesial indent of m3, which is similar to that of m2. Cusp d of m2 is slightly smaller than those of m3 and m4. A blunt ridge connects cusps a and b. There may have been a ridge connecting cusps a and c, but this cannot be determined with certainty due to damage and wear. The tips of cusps a and b, the mesiolabial face of cusp b and the labial face of the notch between cusps a and b are slightly worn. A more strongly developed wear facet is present on the labial surface of the notch between cusps a and c. Of the cusps, cusp d is the most worn being almost entirely worn away, and a large wear facet affects the distolabial face of cusp c and cusp d of m2 and the mesiolabial face of cusp b of m3, which was probably formed by occlusion with cusp A of upper molariform.

On both m3 and m4, cusp a is broken away at the base, but it was undoubtedly the largest of three primary cusps. Cusps b and c are almost worn away and because of this, it is difficult to compare their sizes on m3. However, the wear is less accentuated on m4, and cusp b of this tooth appears to be slightly larger than cusp c. On both molariforms (m3–m4), cusp e is present at the mesiolingual base of cusp b, and a wear facet affects cusps b and e. Because of the severe wear, it is impossible to ascertain whether or not the teeth possessed cusp f but on m4 there is a possible remnant of the ridge similar to that on m2. A well-developed m3 cusp d fits closely into the mesial indent of m4 and the same applies to the relationship between m4 and m5. In m3, cusp d is greatly worn in the same manner as seen in m2, whereas it is worn but still present in m4.

Cusp a of m5 is also broken at the base, but the other two primary cusps are preserved. Cusp a is estimated to be the largest of the cusps, and cusp b is slightly larger than cusp c. Blunt ridges are preserved on the distal margin of cusp b and the mesial margin of cusp c, and the three primary cusps are probably connected by a ridge. Cusp e is present. Cusp f is absent, and the ridge observed in m2 is not apparent because of the wear. The distobasal part of the crown is damaged, and cusp d is missing. Moderate wear facets are present on the mesiolabial and the distolabial faces of cusp b, and the distal half of the tooth is unworn.

Remarks

The mesialmost of the preserved molariforms is identified as m2 based on the presence of a mesial indent for interlock with cusp d of the preceding tooth. Interlock between molariforms of *Gobiconodon* is widespread but probably not so much between the last premolariform and the first molariform, as seen in *Gobiconodon haizhouensis* **sp. nov.** described later, and the m1 of *Gobiconodon borissiaki* and *Gobiconodon ostromi*, which lacks a mesial indent (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998, figure 3), although *Gobiconodon hoburensis* seems to have interlock between p3 and m1 (Kielan-Jaworowska and Dashzeveg 1998). Based on the alveoli, m1 is estimated to have been smaller than m2 (Figure 4) as is the case for other gobiconodontids. Conversely, m2 is generally sub-equal in size to m3 in gobiconodontids, and this also suggests that the tooth identified as m2 of the described specimen is not the first molariform. The ultimate premolariform is also usually substantially smaller than the first molariform in other species of *Gobiconodon* (the exception being *Gobiconodon luoianus*; Yuan et al. 2009), and the size difference between the two is usually much greater than that between m1 and m2 (Trofimov 1978; Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Li et al. 2003). The estimated size difference between m2 and the preceding tooth in the described specimen does not support identification of the mesialmost preserved molariform as m1, and the alveoli for the tooth mesial to those for what is assumed to be m1 are much smaller (Figure 4), strongly suggesting that they are those for the ultimate premolariform. The labiolingual width of the crown of m5 is less than that of the other molariforms, lending support to the conclusion that this tooth is the last molariform in the series, a conclusion supported by the condition observed in other species of *Gobiconodon* (Trofimov 1978; Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Li et al. 2003). An alternate possibility that m1 in our interpretation is actually p3 cannot be completely eliminated. If so, *Gobiconodon tomidai* **sp. nov.** resembles most other species of *Gobiconodon* in having three premolariforms, but *Gobiconodon tomidai* **sp. nov.** is still clearly distinguished from the others in having a double-rooted p2 and p3, and in p3 much larger than p2 (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Rougier et al. 2001; Li et al. 2003; Yuan et al. 2009).

The degree of wear on m3 and m4 is noticeably greater than that on m2 suggesting m2 erupted later than m3 and m4; this is, however, uncertain because cusp d of m2 is apparently worn continuously with cusp b of m3. If m2 erupted later than m3, the wear could have commenced on m3 and extended to m2 as it erupted. The distal half of m5 is unworn, implying that there was no upper molariform that occluded with this part (see the 'Discussion' section).

Gobiconodon haizhouensis sp. nov.

(Figures 5 and 6, Table 1)

Type and only known specimen

An almost complete right dentary with i1–i2, an alveolus for a canine, p1–p3 and m1–m5 (IVPP V14509). Only the canine is missing.

Type locality and horizon

Fuxin, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Fuxin Formation.

Etymology

'Haizhou' is an ancient name for Fuxin, the type locality of the species.

Diagnosis

A small species of *Gobiconodon* bearing the following unique combination of characters: lower dental formula 2.1.3.5; an enlarged i1 about two times taller than the i2; p2 as tall as but mesiodistally longer than p1 at the base of the crown; a small, double-rooted and 'molariform' p3; m1–m3 with a well-developed and almost continuous lingual cingulid; and molariform crowns that are slightly taller than the mesiodistal length.

Differential diagnosis

Differs from other eutriconodontans *sensu lato* except for gobiconodontids in having an enlarged i1 that is much larger than i2 and a reduced number of antemolariforms. Differs from most gobiconodontids but resembles *Gobiconodon hoburensis*, *Gobiconodon palaios* and *Gobiconodon tomidai* **sp. nov.** in its small size. Differs from *Gobiconodon ostromi*, *Gobiconodon tomidai* **sp. nov.**, *Hangjinia chowi* and *Meemannodon lujiatunensis* but resembles *Gobiconodon borissiaki*, *Gobiconodon hoburensis*, *Gobiconodon luoianus* and *Gobiconodon zofiae* in having three lower premolariforms. Differs from *Meemannodon lujiatunensis* in having a proportionally larger i2, a developed cusp b on m1, and molariform cusps b and c less distant from cusp a. Differs from *Hangjinia chowi* in having a double-rooted premolariform and an ultimate premolariform strongly reduced in size. Differs from *Gobiconodon hopsoni*, *Gobiconodon ostromi*, *Gobiconodon zofiae* and *Meemannodon lujiatunensis* but resembles *Gobiconodon borissiaki*, *Gobiconodon hoburensis*, *Gobiconodon luoianus* and *Gobiconodon tomidai* **sp. nov.** in having closely packed p2–m1 without a diastema between adjacent teeth. Differs from *Gobiconodon tomidai* **sp. nov.** and *Meemannodon lujiatunensis* in having a taller molariform crown relative to the mesiodistal length. Differs from *Gobiconodon borissiaki*, *Gobiconodon hopsoni* and *Gobiconodon luoianus* but resembles *Gobiconodon hoburensis* and *Gobiconodon zofiae* in having a double-rooted p3 that is markedly smaller than the other premolariforms. Differs from *Gobiconodon luoianus* and *Gobiconodon zofiae* in having a procumbent p1 (Yuan et al. 2009, noted that p1 of *Gobiconodon zofiae* is procumbent, but actually it is almost erect). Differs from *Gobiconodon*

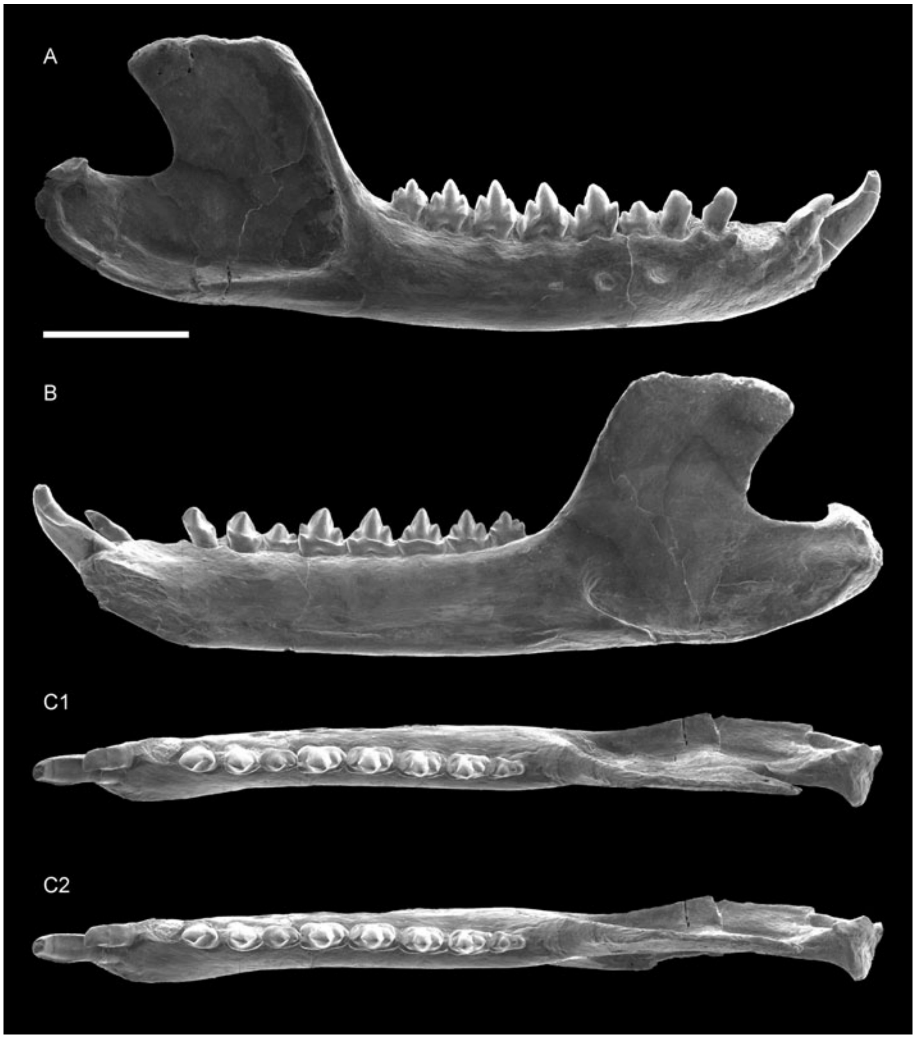

Figure 5. Scanning electron micrographs of the holotype (IVPP V14509) of *Gobiconodon haizhouensis* **sp. nov.** An almost complete right dentary with i1–i2, p1–p3, and m1–m5; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. (A) Labial view; (B) lingual view and (C) occlusal view, stereopair. Scale bar = 5 mm.

borissiaki, *Gobiconodon hoburensis*, *Gobiconodon zofiae* and *Meemannodon lujiatunensis* in having a well-developed and almost continuous lingual cingulid on m1–m3. Differs from *Gobiconodon ostromi* in the absence of a lingual cingulid on m5. Differs from *Gobiconodon tomidai* **sp. nov.** in having a single-rooted p2. Differs from *Gobiconodon hoburensis* in having molariform cusps b and c more distant from cusp a. The new species cannot be adequately compared with *Gobiconodon palaios*, as is the case for *Gobiconodon tomidai* **sp. nov.**, but it is highly likely to represent different species from *Gobiconodon palaios*.

Description

The dentary is well preserved; only a small part of the coronoid process is broken and missing. The posterior part of the horizontal ramus is not distinctly dorsoventrally higher than the anterior part; it is approximately 3.0 mm high below p1 and 3.3 mm high below m5. The ventral margin of the dentary is slightly convex. The symphysis extends posteroventrally terminating below p1. There is no angular process as seen in most other eutriconodontans *sensu lato* (e.g. Kielan-Jaworowska et al. 2004; Gaetano and Rougier 2011). The dentary condyle projects posteriorly and is positioned at almost the same level as the alveolar margin of the horizontal ramus. The coronoid process extends posterodorsally and the angle between the horizontal ramus and the coronoid process is about 120°. At least three mental foramina are present below the postcanines: the anterior one is situated about 1.0 mm below the point between the root of p2 and the mesial root of p3; the middle one is about 1.1 mm below the mesial root of m1; and the posterior one is 1.1 mm below the

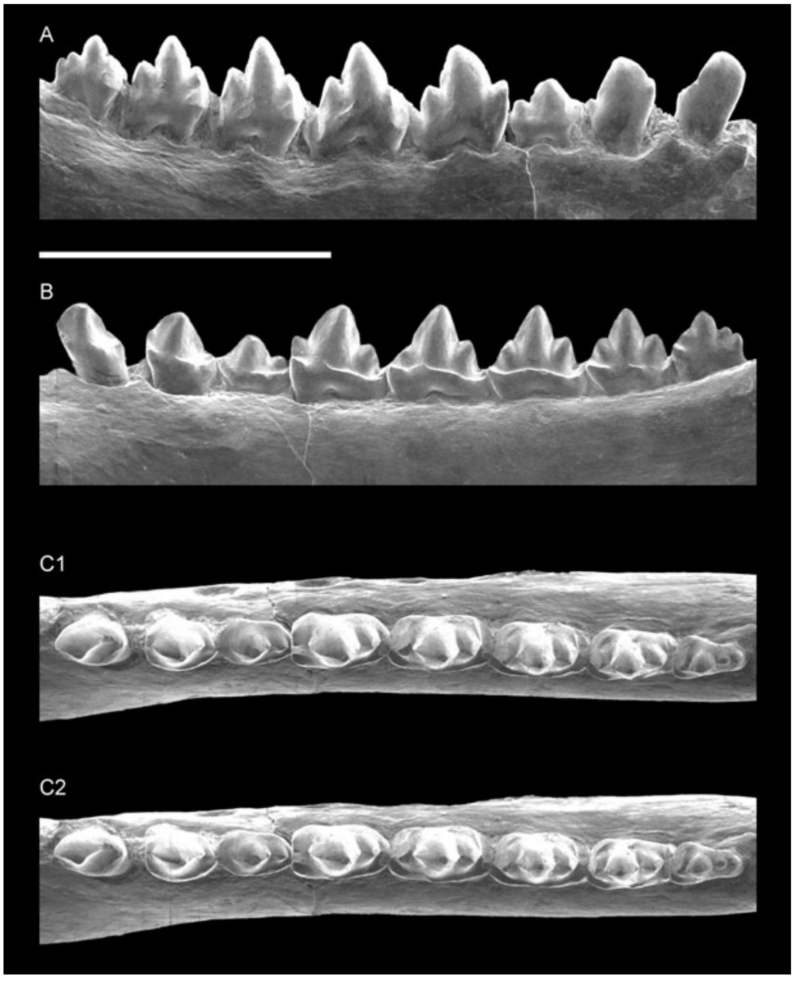

Figure 6. Scanning electron micrographs of the postcanine teeth of *Gobiconodon haizhouensis* **sp. nov.** Holotype (IVPP V14509). (A) Labial view; (B) lingual view and (C) occlusal view, stereopair. Scale bar = 5 mm.

mesial root of m2. The posterior foramen is smaller than the other two more anterior foramina. Two small foramina might have been present below p1 and the canine, but this is unclear because of damage to this part of the bone. The masseteric fossa terminates below the anterior base of the coronoid process. There is no masseteric foramen. The pterygoid fossa extends to lie below and slightly posterior to the anterior base of the coronoid process, and a mandibular foramen is present at the anteriormost extent of the fossa. There is no facet for a coronoid bone, the presence of which was suggested for *Gobiconodon ostromi* by Jenkins and Schaff (1988). A shallow, discontinuous and indistinct Meckelian groove extends anteriorly from a point below the anterior end of the coronoid process to below m4; it is subparallel to and approximately 0.5 mm above the ventral margin of the bone.

The i1 is a large, procumbent and recurved tooth. The apical part of the crown thins mesiodistally with a relatively flattened apicodistal face. On the labial and lingual sides of i1, there are distinct ridges along the crown. The labial ridge extends from the apex to near the base of the tooth, whereas the lingual one extends from the apex to the mid height of the crown. The i1 is the tallest of the preserved lower teeth. The i2 is also procumbent and lies immediately distolabial to i1. The apical part of the crown of the i2 is also thinned mesiodistally. It is smaller than the i1; the latter is about twice as tall as the former. The canine is missing, and the alveolus for a single-rooted canine is damaged. In view of this, it is difficult to estimate the size of the canine. However, based on the gap between i2 and p1, the canine was relatively small and probably similar size to the i2.

All of the postcanine teeth are preserved. The p1 is a single-rooted tooth with a spatulate crown. It is slightly procumbent, but the procumbency is much less than that of i1 and i2. There is no cuspule on p1. The p2 is a single-rooted tooth with a much more robust coronal base of the root than that of p1. A coronoapically oriented shallow sulcus is present on both the labial and lingual surfaces of the root of p2. The p2 has a dominant cusp a, and a tiny cusp c is present distally to cusp a. A cuspule possibly representing cusp b is present mesially and slightly labial to cusp a, and is positioned much higher than cusp c. A blunt lingual cingulid is present. The p2 is erect, and there is a short diastema between p1 and p2. The p3 is a double-rooted tooth, and the crown morphology of p3 is similar to those of molariforms with three mesiodistally aligned primary cusps; cusp a is much larger than the other two cusps and the sizes of cusps b and c are difficult to compare because cusp b is worn. The p3 has a slightly crenulated lingual cingulid, which is especially well developed at the distolingual margin of the tooth. It is slightly elongated distally extending to the distolingual base of cusp c, but there is no cusp d. Cusp e is also absent. A wear facet is present on the labial face of the notch between cusps a and b, and cusp b is almost worn away. Because of this wear, it is unclear whether or not cusp f was present. The tip of cusp a of p3 is missing, but p3 is undoubtedly the smallest of the preserved lower teeth. There is no diastema between p2 and p3.

All molariforms are double rooted; the distal root is slightly more robust than the mesial one. The mesial three molariforms are sub-equal in size; m2 is slightly larger than the others (Table 1). The m4 is smaller than the mesial three molariforms and m5 is the smallest of the molariforms. Both m4 and m5 decrease in labiolingual width distally. The m5 is erupted from a slightly higher position (the anteriormost part of the anterior slope of the coronoid process) than the other molariforms.

The three primary cusps and cusp d are mesiodistally aligned in occlusal view. The apices of the primary cusps are joined by ridges on m1 and m5; the ridge on cusp b is not preserved due to wear on m2–m4. The cusp d of m5 is also connected with cusp c by a ridge, whereas it is not connected with cusp c on m1. Because of wear, it is uncertain whether or not cusp d is joined with cusp c by a ridge on m2–m4. Cusp a is much larger than the others and is slightly recumbent in lateral view. Cusp a of m1 is mesiodistally broader than those in the other molariforms. Cusps b and c are sub-equal in size on m1–m4, whereas cusp b is larger than cusp c on m5. Cusps b and c project from almost the same height on m1 and m4; cusp c projects from a slightly higher position than cusp b in m2 and m3; cusp b projects from a position higher than that of cusp c on m5. Cusp d is distinct on all molariforms and fits into the mesial indent of the subsequent molariform on m1–m4. The mesial indent on m2–m5 is limited by cusp e lingually. Its labial limitation is unknown due to wear, but the position and size of the indent show that it was formed in a similar manner to those in *Gobiconodon tomidai* **sp. nov.** There is no mesial indent on m1, but m1 is positioned immediately distal to p3 without a diastema. Cusp e is present at the mesiolingual base of the crown on m1 and m5; it is present but more like a cingulid on m2 and m4; it becomes the mesial part of the lingual cingulid on m3. A distinct cusp f is absent from m1, but there is a minute swelling at the mesiolabial face of cusp b; the presence of cusp f on m2–m5 is uncertain because of the severe wear. The lingual cingulid is well developed on m1–m3; it extends continuously from the mesiolingual end to the distolingual end of the crown on m3, whereas it is discontinuous at the mesiolingual base of cusp a on m1 and m2. The lingual cingulid is less distinct on m4, but there are discontinuous cingulids at the distolingual part and the position below the distal end of cusp a. The lingual cingulid is absent from m5. There is no labial cingulid on all molariforms. The mesiolabial face of cusp b is greatly worn on m2–m5, and a large wear facet affects the mesiolabial face of cusp b of the tooth and the labial face of cusp d and the distolabial face of cusp c of the preceding tooth, whereas there is no facet developed on cusp b of m1. There is a small facet on the labial base of the crown below the notch between cusps a and c on m2 and m3. The distal half of m5 is unworn. The degree of wear is greater in m2 and m3, and m1 is least worn.

Remarks

The crown of the ultimate lower premolariform of the described specimen is similar to those of molariforms with accessory cusps b and c (‘molariform’; Figure 6), but the tooth is identified as a premolariform because it lacks cusp d and there is no interlock between this tooth and the tooth identified as m1. Furthermore, this is the smallest tooth among the postcanines; p3 is also the smallest postcanine tooth in other gobiconodontids, e.g. *Gobiconodon borissiaki*, *Gobiconodon hoburensis* and *Gobiconodon zofiae* (Kielan-Jaworowska and Dashzeveg 1998; Li et al. 2003). A small ultimate premolariform is also known for *Gobiconodon* sp. described by Rougier et al. (2001). A double-rooted ‘molariform’ ultimate premolariform is also found in *Gobiconodon zofiae*, although the tooth in *Gobiconodon zofiae* lacks a distally elongated lingual cingulid (Li et al. 2003).

The degree of wear decreases distally from m2 to m5, and m1 is less worn than the other molariforms. This is probably because this tooth erupted later than the other four. This is supported by the facts that the wear facet present on the distolabial part of m1 is very small compared with the large facet on the mesiolabial part of m2 and that the morphology of cusp a of m1 is mesiodistally broader than and slightly different morphologically from those of the other molariforms.

Discussion

Although the two new species are known only from lower jaws, these, and especially that of *Gobiconodon haizhouensis* **sp. nov.**, provide information about their upper dentition. The m5s of both specimens have wear facets mesially but not distally. An m5 in the same condition is seen in a specimen of *Gobiconodon hoburensis* (PSS 10-37c; Kielan-Jaworowska and Dashzeveg 1998) and the type specimen of *Gobiconodon zofiae* (IVPP V12585; but this state of wear was not described by Li et al. 2003). *Gobiconodon* is known to have embrasure occlusion (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; see also Kielan-Jaworowska et al. 2004), and the mode of wear on the m5 suggests that the mesial part of the tooth occludes with the distal part of the ultimate upper molariform. No obvious wear facet is developed on the mesial part of the m1 of *Gobiconodon haizhouensis* **sp. nov.** This is probably because the upper tooth that occludes with the mesial part of m1 is small and does not occlude efficiently with the mesial part of m1. *Gobiconodon zofiae* has a very small P3 (Li et al. 2003), and *Gobiconodon haizhouensis* **sp. nov.** is similar to *Gobiconodon zofiae* in having a small and 'molariform' ultimate lower premolar. We, therefore, assume that the ultimate upper premolariform of *Gobiconodon haizhouensis* **sp. nov.** is similar to that of *Gobiconodon zofiae* in view of the absence of an obvious wear facet on the mesial part of m1 of the new species. Cusp b of the p3 of *Gobiconodon haizhouensis* **sp. nov.** is almost worn away suggesting the presence of a relatively large P2. The P2 of *Gobiconodon haizhouensis* **sp. nov.** is therefore also assumed to be similar to the large and trenchant P2 of *Gobiconodon zofiae* (Li et al. 2003), although the wear facet on p3 of *Gobiconodon zofiae* is not obvious.

These observations lead to the conclusion that there were only four upper molariforms in *Gobiconodon haizhouensis* **sp. nov.** If this is the case, the condition in the new species matches that determined for *Gobiconodon zofiae* (Li et al. 2003). Interestingly, the mesial part of the m1 of a specimen (PSS 10-37c) of *Gobiconodon hoburensis* is also unworn, although it has a broad wear facet on the distal part (Kielan-Jaworowska and Dashzeveg 1998). In common with *Gobiconodon haizhouensis* **sp. nov.** and *Gobiconodon zofiae*, *Gobiconodon hoburensis* also has a small double-rooted p3. We agree with the view of Li et al. (2003) and consider that the upper molariform count of *Gobiconodon hoburensis* is four and not five, as previously determined based on fragmentary specimens (e.g. Kielan-Jaworowska and Dashzeveg 1998). Jenkins and Schaff (1988) reconstructed the occlusal relationships between the upper and lower molariforms and concluded that cusp a of a lower molariform occludes with the distal part of the corresponding upper molariform, and this was followed by Kielan-Jaworowska and Dashzeveg (1998). This is, however, unlikely because a lower tooth is generally positioned slightly mesially to the corresponding upper tooth in eutriconodontans *sensu lato* (Kielan-Jaworowska et al. 2004, p. 227), although the dental homology has not clearly been established for gobiconodontids. We agree with the alternate reconstruction, i.e. that cusp A of an upper molariform occludes with the embrasure between the corresponding and the succeeding lower molariform (Kielan-Jaworowska et al. 2004, p. 228, but not p. 242). In any case, five upper molariforms would form a wear facet on either the mesial part of m1 or the distal part of m5, and this is not congruent with the condition observed in the specimens of *Gobiconodon haizhouensis* **sp. nov.**, *Gobiconodon hoburensis* and *Gobiconodon tomidai* **sp. nov.**

Gobiconodon luoianus was reported as having five upper and lower molariforms, although the lower molariform count is quite uncertain because the distal lower molariforms are not visible in the type specimen (Yuan et al. 2009). Yuan et al. (2009) interpreted a right upper tooth positioned slightly mesial to m1 as 'M1'. If the *in situ* occlusal relationship between the right upper and lower jaws is preserved in the specimen, this interpretation appears to be inappropriate because M1 is probably positioned slightly distal to m1, as mentioned earlier. It is possible that the right 'M1' of Yuan et al. (2009) is actually P3. The crown of the tooth is not fully 'molariform' with a weak cusp c and an absence of cusp b (Yuan et al. 2009), and this fact supports our view. This tooth is not much smaller than the molariforms, differing in this respect to P3 of *Gobiconodon zofiae*, but it is similar to p3, which is also not very much smaller than m1 (Yuan et al. 2009). The right 'M3' of Yuan et al. (2009) can therefore be reinterpreted as M2. Only four left upper molariforms are preserved in the type specimen of *Gobiconodon luoianus*; the second was considered to correspond with the right 'M3' based on its shape, size and position (Yuan et al. 2009). On the basis of our reinterpretation of the right molariforms, this tooth can be identified as M2. The four left molariforms are, thus, reinterpreted as M1–M4.

The upper molariform count in all species of *Gobiconodon* is therefore likely to be one less than the lower, and that of at least most species of *Gobiconodon* is four rather than five, as noted by Li et al. (2003). An upper molariform count representing a similar condition is seen in *Repenomamus*, which has four upper and five lower premolariforms (Hu, Meng, et al. 2005). There is also a possibility that the present occlusal relationship between the right upper and lower jaws of the holotype specimen of *Gobiconodon luoianus* does not represent *in situ* condition because of postmortem deformation, and that the upper molariforms now occlude with the lowers at a position more mesial than in life. If this is true and the molariform attribution of Yuan et al. (2009) is correct, *Gobiconodon luoianus* may have six lower molariforms.

The two new *Gobiconodon* species demonstrate a partial similarity between the Jehol mammalian fauna and the Fuxin mammalian fauna; both are known from western Liaoning, China, and the latter is slightly younger than the former. Despite genera common to both, these two mammalian faunas are very different in detail (Kusuhashi et al. 2010). Eutherians and multituberculates dominate the Fuxin mammalian fauna, each group making up about one-third of the mammalian fossil assemblage in terms of the number of specimens, whereas these groups are minor elements in the Jehol mammalian fauna, and only two eutherian (*Eomaia* Ji, Luo, Yuan, Wible, Zhang and Georgi, 2002 and *Acristatherium* Hu, Meng, Li and Wang, 2009) and one multituberculate (*Sinobaatar*) species are known among 18 mammalian species in 15 genera (Hu et al. 1997, 2009; Ji et al. 1999, 2002, 2009; Li et al. 2000, 2003; Hu and Wang 2002; Luo et al. 2003, 2007; Rougier et al. 2003; Hu, Meng, et al. 2005; Meng et al. 2005, 2011; Li and Luo 2006; Gao et al. 2009; Yuan et al. 2009; Hou and Meng 2014). In contrast, about half (10 species in 8 genera) of the described species of the Jehol mammalian fauna are eutriconodontans *sensu lato* (Figure 1). Eutriconodontans appear to have remained relatively diverse in the Fuxin mammalian fauna, with at least four species in two genera (*Gobiconodon* reported here and *Meiconodon*; Kusuhashi, Hu, Wang, Hirasawa, et al. 2009); however, *Meiconodon* belongs to the family Triconodontidae, which is not known in the Jehol mammalian fauna. Previously only one multituberculate genus, *Sinobaatar*, was known to be common to both mammalian faunas, and the new discovery of *Gobiconodon* in the Fuxin mammalian fauna adds another common genus to the faunas (Figure 1). Further studies on the Fuxin mammalian fauna are now in progress and will reveal the mammalian faunal transition in Asia during the middle to late Early Cretaceous.

Conclusions

Two new Early Cretaceous species of *Gobiconodon*, *Gobiconodon tomidai* **sp. nov.** and *Gobiconodon haizhouensis* **sp. nov.** were discovered in the Shahai and Fuxin Formations, respectively, in Liaoning, northeastern China. On the basis of the new material and previously reported specimens, the upper molariform count of most species of *Gobiconodon* is thought to be four, one less than the lower. *Gobiconodon* is the second mammalian genus common to the Jehol and Fuxin mammalian faunas.

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