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New gobiconodontid (Eutriconodonta, Mammalia) from the Lower Cretaceous Shahai and Fuxin formations, Liaoning, China

KUSUHASHI Nao[1] WANG Yuan-Qing[2,3,4*] LI Chuan-Kui[2] JIN Xun[2]

(1 *Department of Earth's Evolution and Environment*, *Graduate School of Science and Engineering*, *Ehime University* Matsuyama, Ehime 790-8577, Japan nkusu@sci.ehime-u.ac.jp)
(2 *Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences*, *Institute of Vertebrate Paleontology and Paleoanthropology*, *Chinese Academy of Sciences* Beijing 100044, China
* Corresponding author: wangyuanqing@ivpp.ac.cn)
(3 *CAS Center for Excellence in Life and Paleoenvironment* Beijing 100044, China)
(4 *College of Earth and Planetary Sciences*, *University of Chinese Academy of Sciences* Beijing 100049, China)

Abstract Eutriconodontans are one of the key members of mammals to our understanding of the evolution and transition of mammalian fauna in Asia during the Cretaceous. Two gobiconodontid and two triconodontid species have previously been reported from the upper Lower Cretaceous Shahai and Fuxin formations. Here we describe two additional eutriconodontans from the formations, *Fuxinoconodon changi* gen. et sp. nov. and ?Gobiconodontidae gen. et sp. indet. This new species is attributed to the Gobiconodontidae, characterized by having an enlarged first lower incisor, reduction in the number of incisors and premolariforms, proportionally large cusps b and c being well distant from cusp a on the molariforms, presence of a labial cingulid, and a unique mixed combination of molariform characters seen on either the first or the second, but not both, generations of molariforms in *Gobiconodon*. Together with the four known species, eutriconodontans remained diverse to some extent in the late Early Cretaceous in Asia, although their family-level and generic level diversity appears to have been already reduced at that time.

Key words Liaoning, Northeast China; Early Cretaceous; Mammalia, Eutriconodonta, Gobiconodontidae

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1 Introduction

The Eutriconodonta (*sensu* Kielan-Jaworowska et al., 2004; not Gaetano and Rougier, 2011) were a group of mammals globally distributed during the Jurassic to the Early Cretaceous (e.g., Kielan-Jaworowska et al., 2004; Rougier et al., 2007a; Gaetano and Rougier, 2011, 2012), but to date their Late Cretaceous descendants are known only from North

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America (e.g., Kielan-Jaworowska et al., 2004). Although *Austrotriconodon* Bonaparte, 1986 from the Upper Cretaceous of Argentina was originally ascribed to 'triconodont' mammals (Bonaparte, 1986, 1992) and later attributed to ?Eutriconodonta (Kielan-Jaworowska et al., 2004), they are now considered as trechnotherian mammals (Gaetano et al., 2013). In Asia, eutriconodontans have not yet been known from the Upper Cretaceous, in contrast with the relatively diverse Early Cretaceous records (e.g., Kielan-Jaworowska et al., 2004; Meng, 2014; Meng et al., 2015; Lopatin and Averianov, 2015; Kusuhashi et al., 2016). Such a difference in eutriconodontan diversity may indicate a faunal transition in Asia during the Cretaceous.

Diverse eutriconodontans of several families are known from Asia until the early Aptian, showing that they were major members of the mammalian faunas in the late Early Cretaceous in Asia. Within the 20 currently known mammalian species from the Barremian to lower Aptian Jehol Group (here consisting of the Yixian and Jiufotang formations in ascending order) of northeastern China (Meng, 2014 and references therein; Han and Meng, 2016; Bi et al., 2018), there are ten eutriconodontan species of eight genera, including *Jeholodens jenkinsi* Ji et al., 1999, *Repenomamus robustus* Li et al., 2000, *R. giganticus* Hu et al., 2005b, *Gobiconodon zofiae* Li et al., 2003, *G. luoianus* Yuan et al., 2009, *Meemannodon lujiatunensis* Meng et al., 2005, *Yanoconodon allini* Luo et al., 2007, *Juchilestes liaoningensis* Gao et al., 2009, *Liaoconodon hui* Meng et al., 2011, and *Chaoyangodens lii* Hou & Meng, 2014, although *G. luoianus* was suggested to be a junior subjective synonym of *G. zofiae* by Lopatin and Averianov (2015). *Gobiconodon* and *Meemannodon* belong to Gobiconodontidae. *Repenomamus* is originally ascribed to Repenomamidae, but sometimes treated as a member of Gobiconodontidae (e.g., Kielan-Jaworowska et al., 2004; Lopatin and Averianov, 2015). *Jeholodens* and *Yanoconodon* belong to the Jeholodentidae (Luo et al., 2007), which might be either monophyletic (e.g., Gao et al., 2009) or paraphyletic (Meng et al., 2011). *Juchilestes* were referred to the paraphyletic family 'Amphilestidae' (Gao et al., 2009) or the Amphidontidae (Lopatin et al., 2010). The family-level attribution of the other two species, *L. hui* and *C. lii*, is currently unknown. Eutriconodontans that are almost contemporaneous with Jehol mammals are also known from Russia and Japan. *Gobiconodon*, 'amphilestid' *Kemchugia* and amphidontid *Acinacodus* were reported from the Ilek Formation (Barremian–Aptian; Kurochkin et al., 2011; O'Connor et al., 2014) of Siberia, Russia (Maschenko and Lopatin, 1998; Averianov et al., 2005; Lopatin et al., 2010). *Hakusanodon*, which is probably closely related with *Juchilestes*, is known from the Kuwajima Formation (?uppermost Hauterivian–lower Aptian; Matsumoto et al., 2006; Sakai et al., 2019) of Japan (Rougier et al., 2007b). *Gobiconodon* is also reported from a possibly slightly earlier age in Mongolia (Rougier et al., 2001; Minjin et al., 2003).

Eutriconodontans seem to be still relatively diverse during the late Early Cretaceous in Asia. Four eutriconodontans are now known from the Aptian–Albian Shahai and Fuxin formations overlying the Jehol Group in almost the same geographic area, although the mammalian faunal composition is obviously different (Kusuhashi et al., 2010).

Eutriconodontans from the Shahai and Fuxin formations include *Gobiconodon haizhouensis* Kusuhashi et al., 2016, *G. tomidai* Kusuhashi et al., 2016, *Meiconodon lii* Kusuhashi et al., 2009a, and *M. setoguchii* Kusuhashi et al., 2009a. Lopatin (2017) noted that *G. haizhouensis* is possibly a junior subjected synonym of *G. hoburensis* (Trofimov, 1978), known from the Lower Cretaceous of Mongolia. This possibility should be examined further, but in either case there are two species of *Gobiconodon* known from the formations. *Meiconodon* belongs to the Triconodontidae (Kusuhashi et al., 2009a), which has not yet been known from the Jehol Group. All known eutriconodontan specimens from the Aptian–Albian Höovör and neighboring localities in Mongolia have been referred to *Gobiconodon* (e.g., Trofimov, 1978; Kielan-Jaworowska and Dashzeveg, 1998; Kielan-Jaworowska et al., 2004; Lopatin, 2013, 2017; Lopatin and Badamgarav, 2013; Lopatin and Averianov, 2015), and a possible triconodontid specimen was reported from the ?Aptian Kitadani Formation in Fukui Prefecture, Japan (Miyata et al., 2016). Gobiconodontid *Hangjinia* Godefroit & Guo, 1999, was reported from Nei Mongol, China (Aptian–Albian, Sereno, 2010; or ?Barremian, Kielan-Jaworowska et al., 2004), which was later referred to *Gobiconodon* by Lopatin and Averianov (2015). Gobiconodontids are also known from the Lower Cretaceous (?Barremian–Albian) of Gansu, China (Tang et al., 2001).

Here we describe a new genus and species of the Gobiconodontidae from the Fuxin Formation, and an isolated lower molariform of ?gobiconodontid from the Shahai Formation. These materials further support the view that eutriconodontans remained diverse to some extent in the late Early Cretaceous in Asia.

Institutional abbreviations IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; MCZ, Museum of Comparative Zoology, Harvard University, USA; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

2 Geological background and methods

The specimens described in this paper were collected from carbonaceous rocks of the Shahai and Fuxin formations at small coalmines in Badaohao (Heishan County) and Fuxin, respectively, in Liaoning Province, northeastern China (Fig. 1A). The Shahai Formation conformably (or partly unconformably) overlies the Jiufotang Formation, which composes the upper part of the Jehol Group, and the Fuxin Formation conformably overlies the Shahai Formation (Fig. 1B; e.g., Wang et al., 1989; Yang and Li, 1997; Li and Matsuoka, 2015; see Kusuhashi et al., 2009a, b, for more details of the geological setting). The depositional ages of the Shahai and Fuxin formations remain uncertain. Referring the radiometric ages of the underlying Yixian and Jiufotang formations (Swisher et al., 1999, 2002; He et al., 2004, 2006; see also Pan et al., 2013), we tentatively consider them to be Aptian to Albian in age.

The Shahai and Fuxin formations have yielded various mammals, such as

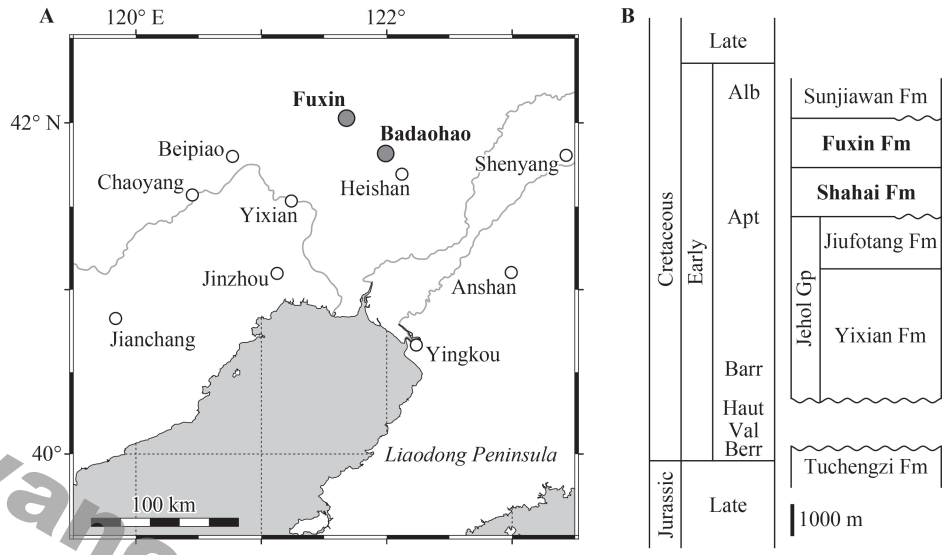

Fig. 1 Map showing the locations of Badaohao and Fuxin where the fossils were collected (A) and schematic stratigraphic table of the major late Mesozoic strata in western Liaoning Province (B)
Adopted from Wang et al. (1989), Yang and Li (1997), and Li and Matsuoka (2015) among others
Abbreviations: Alb. Albian; Apt. Aptian; Barr. Barremian; Berr. Berriasian; Fm. Formation; Gp. Group; Haut. Hauterivian; Val. Valanginian

eutridoconodontans, multituberculates, spalacotheriids, stem zatherian, and eutherians (Shikama, 1947; Wang et al., 1995, 2018; Hu et al., 2005a, c; Li et al., 2005; Kusuhashi et al., 2009a, b, 2010, 2016). Among more than one hundred mammalian specimens recovered from the formations, eutriconodontans account for only about 10% of the fossil specimens, whereas eutherians and multituberculates reach about 45% and 40%, respectively, showing an obvious composition change from the Jehol Group (Kusuhashi et al., 2010).

The terms premolariform and molariform are used here instead of premolar and molar, following the concept of Rougier et al. (2001, 2007b). Lower incisors, canine, deciduous canine, premolariforms, and molariforms are abbreviated as lowercase i, c, dc, p, and m, respectively. Numbers following abbreviations indicate the order of teeth in each tooth class counting from mesial to distal. They only denote the position and do not necessarily indicate the tooth homology. Although the replacement of molariforms in gobiconodontids and some other taxa was reported (e.g., Jenkins and Schaff, 1988; Wang et al., 2001; Kielan-Jaworowska et al., 2004; Hu et al., 2005b; Lopatin et al., 2010; Lopatin and Averianov, 2015), a sufficient amount of specimens to identify generations of molariforms have yet to be discovered, so we do not distinguish molariform generations for the materials described below. Cusp terminology in the present paper follows that of Crompton and Jenkins (1968), which was also adopted by Jenkins and Crompton (1979), Kielan-Jaworowska et al. (2004) and others but not coincident with those of Slaughter (1969) or Trofimov (1978). The dental formula of antemolariforms is not clearly known for gobiconodontids (see Meng et al., 2005; Rougier et al., 2007b; Lopatin and Averianov, 2015). We adopt herein the hypothetical basic lower dental formula of Meng et

al. (2005), 2.1.3.5. This formula is different from those adopted by various authors in previous studies (Trofimov, 1978; Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998; Maschenko and Lopatin, 1998; Li et al., 2003; Kielan-Jaworowska et al., 2004; Rougier et al., 2007b; Lopatin and Averianov, 2015).

We here regard the family Gobiconodontidae as including *Gobiconodon*, *Hangjinia*, *Meemannodon*, *Repenomamus*, and *Spinolestes*. As mentioned earlier, *Repenomamus* is originally attributed to the Repenomamidae, which is followed by some authors (e.g., Meng et al., 2015; Kusuhashi et al., 2016). If so, *Spinolestes* may also be excluded from the Gobiconodontidae, because *Spinolestes* seems to be a sister taxon of the clade that consists of *Gobiconodon* and *Repenomamus* (Martin et al., 2015). Although Lopatin and Averianov (2015) considered that *Hangjinia* is referable to *Gobiconodon*, we tentatively retain the genus because this synonymy did not rely on sufficient comparison or discussion. Averianov et al. (2005) suggested that *Repenomamus* may be a junior subjective synonym of *Hangjinia*, but this is neither adopted here, because it is still difficult to discuss this based on the fragmentary specimen of *Hangjinia*. *Huasteconodon* Montellano et al., 2008, is originally attributed to the family, but this attribution needs further investigation because the incipient triangulation of the primary cusps on the upper molariforms is no longer a diagnostic character of the Gobiconodontidae (Gao et al., 2009; Lopatin and Averianov, 2015; Kusuhashi et al., 2016). We here tentatively exclude this poorly known genus from the Gobiconodontidae, following Lopatin and Averianov (2015) and Kusuhashi et al. (2016).

Hangjinia, *Meemannodon*, and *Spinolestes* are monotypic genera, whereas ten species have been recognized for *Gobiconodon*: *G. bathoniensis* Butler & Sigogneau-Russell, 2016, *G. borissiaki* Trofimov, 1978 (type species), *G. haizhouensis*, *G. hoburensis*, *G. hopsoni* Rougier et al., 2001, *G. luoianus*, *G. ostromi* Jenkins & Schaff, 1988, *G. palaios* Sigogneau-Russell, 2003, *G. tomidai*, and *G. zofiae*. Both *G. bathoniensis* and *G. palaios* are known only from isolated upper teeth, molariforms of which have the incipient triangulation of the primary cusps (Sigogneau-Russell, 2003; Butler and Sigogneau-Russell, 2016), and the attribution of these species to *Gobiconodon* should, again, be examined further (Lopatin and Averianov, 2015). As mentioned earlier, *G. haizhouensis* and *G. luoianus* are suggested to be synonyms of *G. hoburensis* and *G. zofiae*, respectively (Lopatin and Averianov, 2015; Lopatin, 2017). Although we admit to these possibilities, a more precise comparison based on the specimens should be carried out, and here we conservatively retain all ten species for comparison. There also are several specimens attributed to *Gobiconodon* sp. (Rougier et al., 2001), *Gobiconodon* sp. A and B (Averianov et al., 2005), and ?*Gobiconodon* (Sweetman, 2006). The last one is only known from an isolated premolariform tooth from the Britain, and its attribution to the genus is questionable (Lopatin and Averianov, 2015). We exclude this one from the comparison below, because premolariforms have yet to be known from our materials described below. Two species of *Repenomamus* are currently known: *R. robustus* (type species) and *R. giganticus*, neither have had their taxonomic position doubted.

Specimens were scanned by 225kV X-ray micro-computed tomography (micro-CT; developed by the Institute of High Energy Physics, Chinese Academy of Sciences) at the Key Laboratory of Vertebrate Evolution and Human Origins, IVPP, Chinese Academy of Sciences, Beijing. The specimens were scanned with beam energy of 120 kV (IVPP V 14511) or 110 kV (V 22643) and a flux of 100 μA at a detector resolution of 18.82 μm (V 14511) or 4.70 μm (V 22643) per pixel using a 360° rotation with a step size of 0.5° and an unfiltered aluminum reflection target. A total of 720 transmission images were reconstructed in a 2048 × 2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics, Chinese Academy of Sciences. Multiplanar reconstructions and surface renderings were performed using AMIRA 5.3.2 software at the Museum of Nature and Human Activities, Hyogo, Japan.

3 Systematic paleontology

Mammalia Linnaeus, 1758

Eutriconodonta Kermack et al., 1973

Gobiconodontidae Chow & Rich, 1984

***Fuxinoconodon* gen. nov.**

Type and only known species *Fuxinoconodon changi* gen. et sp. nov.

Etymology The generic name is after Fuxin City where the holotype of the type and only known species was collected; conodon, Latin (conus) and Greek (odon), means 'conetooth'.

Diagnosis As for the type and only known species.

***Fuxinoconodon changi* sp. nov.**

(Figs. 2–4)

Holotype and only known specimen Fragment of right lower jaw with variably preserved dc, c, and m1–m4, and alveoli for i1–i2 and p1–p3 (IVPP V 14511; Figs. 2–4).

Type locality and horizon Nanhuang Coal Mine No. 3, Fuxin, Liaoning, northeastern China; Fuxin Formation, Early Cretaceous (Aptian–Albian).

Etymology In honor of late geologist Mr. Chang Zheng-Lu who has kindly and thoroughly supported our paleontological study of Mesozoic mammals in Fuxin and neighboring areas.

Diagnosis A medium sized gobiconodontid characterized by the following combination of characters: the lower dental formula 2.1.3.?5; incisors procumbent; i1 enlarged, larger than i2; the canine conical, procumbent, reduced in size, smaller than the i1; p1–p2 single rooted, semiprocumbent; p3 double rooted, erected, much smaller than molariforms; molariform cusps lanceolate in lateral view at least on m4; cusp a distinct, erected or very slightly curved distally; cusps b and c well developed, well distant from cusp a, splayed, project from lower positions; cusp d developed; cusp e developed on molariforms except for m1; cusp f absent;

lingual cingulid developed at least on m1–m3; labial cingulid present at least on m1–m4; the mesial embayment for interlock present except for m1; interlocking between molariforms developed.

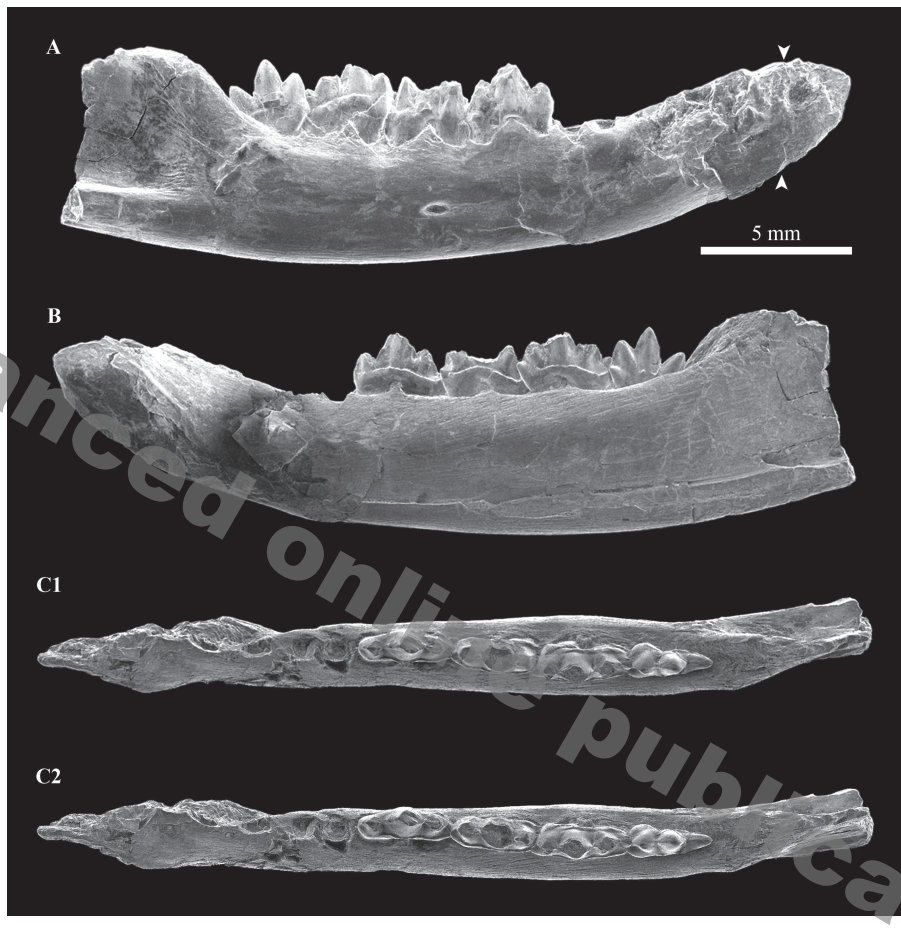

Fig. 2 Scanning electron micrographs of the holotype (IVPP V 14511) of *Fuxinoconodon changi* gen. et sp. nov., a partial right dentary with broken dc, c, m1–m4, alveoli for i1–i2 and p1–p3, from Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China
A. labial view; B. lingual view; C. occlusal view, stereopair, left to anterior
Small arrows in A indicate the position of the transverse section in Fig. 4B

Differential diagnosis Resembles gobiconodontids, jeholodentids, and triconodontids but differs from the other eutriconodontans in having a molariform interlock between the mesial embayment and the cusp d of a preceding molariform (but not as developed as in triconodontids) and in the absence of the distinct molariform cusp f. Resembles gobiconodontids and jeholodentids but differs from the other eutriconodontans in the reduction in the number of incisors and premolariforms and in having the enlarged i1. Differs from triconodontids and maybe jeholodentids but resembles gobiconodontids and other eutriconodontans in having the distinct cusp e on molariforms. Differs from jeholodentids

in the convex ventral margin of the dentary. Differs from *Gobiconodon*, *Hangjinia*, *Meemannodon*, *Repenomamus*, and *Spinolestes* in having molariforms with the following combination of characters: crown low relative to length; the cusp a less curved distally and erect on the m4; cusps b and c proportionally larger, well distant from the cusp a, lanceolate, splayed, project from lower positions; the lingual cingulid well developed; the labial cingulid present; interlocking developed from m1. Differs from *Repenomamus* in having i1 being much larger than i2; from *Spinolestes* in the lack of the wide Meckelian groove on the dentary, the less developed molariform cusp e, and primary molariform cusps aligned along the mesiodistal line; and from *Meemannodon* in the distinct cusp b on m1.

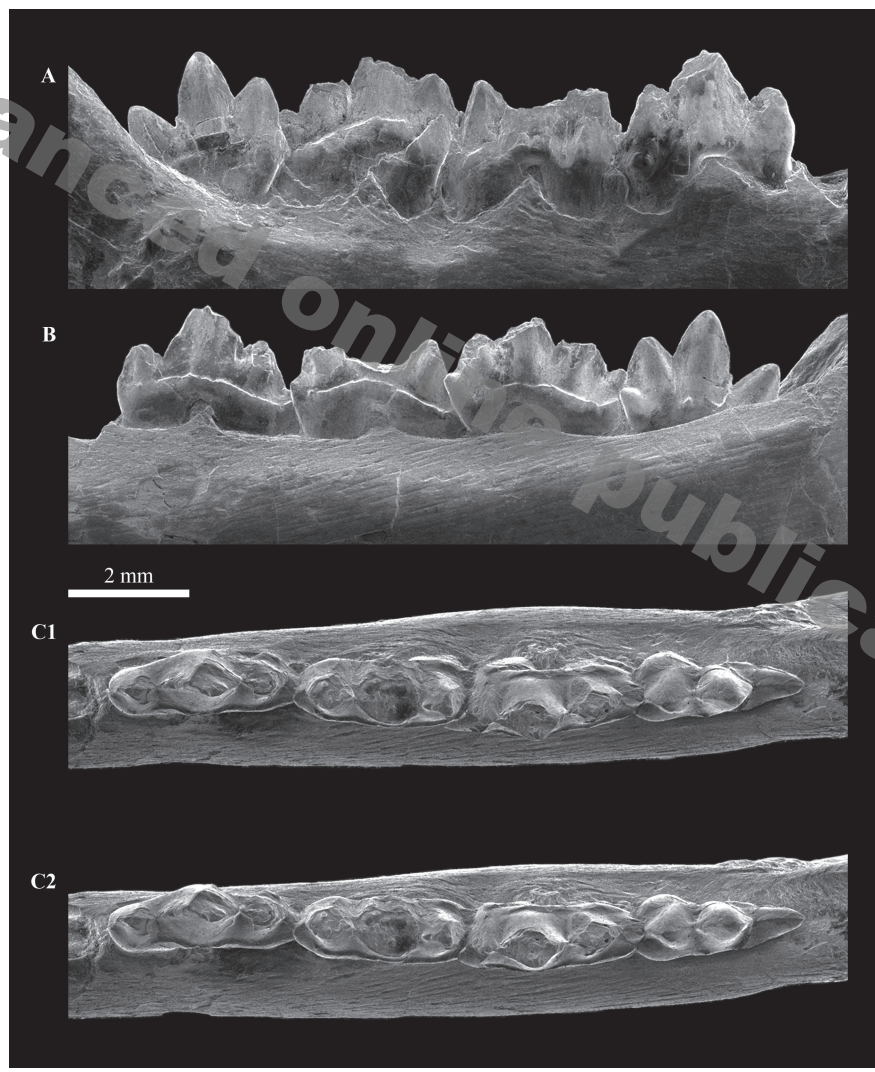

Fig. 3 Scanning electron micrographs of the m1–m4 of the holotype (IVPP V 14511) of *Fuxinoconodon changi* gen. et sp. nov. from Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China
A. labial view; B. lingual view; C. occlusal view, stereopair, left to anterior

Description The posterior part of the dentary of V 14511 is broken, and the mandibular corpus and the anterior portion of the coronoid process are preserved (Fig. 2). The mandibular corpus is approximately 4.3 mm deep below m1, and is almost constant in depth below molariforms, whereas it deepens posteriorly at the more anterior part. The ventral margin of the dentary is convex in lateral view. The symphysis extends posteroventrally to the point below the p1. Judging from the symphysis, the anteriormost part of the dentary is almost fully preserved although it is crushed. At least three mental foramina are present; the anteriormost one is situated at about 2.0 mm below the canine, the second one is at about 1.8 mm below the mesial root of the p3, and the third one is at 2.3 mm below the position between the mesial and distal roots of the m2. The anterior part of the masseteric fossa reaches the level of anterior base of the coronoid process. There is no masseteric foramen. The anterior part of the shallow pterygoid fossa reaches the level of the anterior base of the coronoid process in the posterolingual preserved part of the dentary. The fossa is ventrally bordered by the medial pterygoid ridge (of which only the anterior end is preserved). Immediately anterodorsal to the anterior end of the ridge, there is a mandibular foramen that opens posteriorly. From this point (about 2.4 mm anterior to the posterior margin of the preserved part of the dentary), the Meckelian groove extends anteriorly, and is subparallel to and approximately 1.4 mm above the ventral margin of the dentary. The anterior end of the groove is unclear because the dentary is slightly collapsed at and parallel to the groove and the medial pterigoid ridge. Because of this damage, the original depth of the groove is unknown, but it is estimated to be shallow, most probably much shallower and less obvious than those in *Liaoconodon*, *Repenomamus*, and some species of *Gobiconodon*, which are known to have an ossified Meckelian cartilage (Wang et al., 2001; Meng et al., 2003, 2011).

Antemolariforms are poorly preserved on the dentary of V 14511. A broken tooth and a vertical section of a broken erupting tooth are barely observable (Fig. 4A). The latter is situated immediately distal to the former, and they are interpreted as the deciduous and successive canines, respectively. The successive canine is possibly conical and relatively small but slightly larger than the deciduous one. Both of them are procumbent. Mesial to and slightly below the deciduous canine, there is a mediolaterally crushed and broken alveolus (Fig. 4A), and this is interpreted as an alveolus for the i2, which is estimated to be as large as the canine. The alveolus for the i1 is also crushed but present mesiolingually to the alveolus for the i2 (Fig. 4A). Based on the alveolus, the i1 is estimated to be much larger than the i2 and the canine. The i1 and i2 were procumbent. The mediolaterally compressed alveoli for i1 and i2 can be observed on the reconstructed section from the micro-CT images (Fig. 4B). Distal to the canine, there are alveoli for the single-rooted p1–p2 and the double rooted p3 (Fig. 4A). Judging from the alveoli, the p1 and p2 are sub-equal in size and procumbent to semiprocumbent, and the p3 is smaller than the molariforms. There are short diastemata between the canine and the p1, the p1 and the p2, and the p2 and the p3, but not between the p3 and the m1.

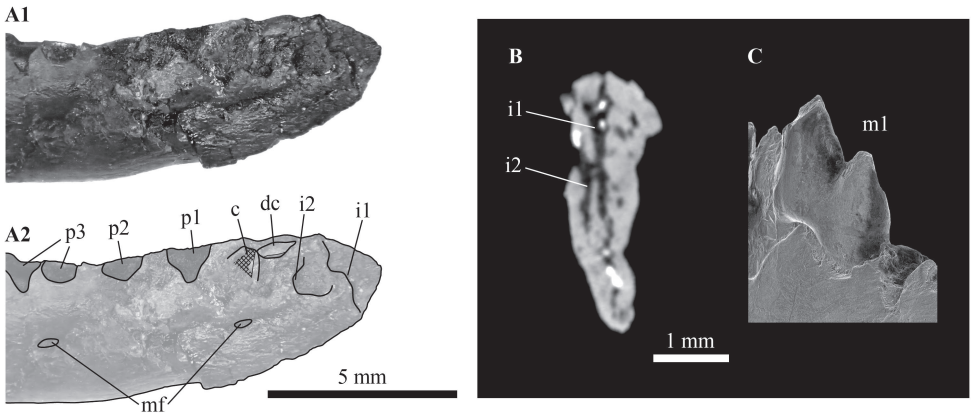

Fig. 4 Holotype (IVPP V 14511) of *Fuxinoconodon changi* gen. et sp. nov. from Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China

A. a photograph (A1) and an interpretive sketch (A2) of the anterior part of the dentary, the hatched area on the canine is broken; B. reconstructed micro-computed tomography images showing the laterally compressed alveoli for i1 and i2 in a transverse section at the position indicated in Fig. 2A, left to labial; C. a scanning electron micrograph of the m1 in mesiolabial view. Abbreviations: c. canine; dc. deciduous canine; i. incisor; m. molariform; mf. mental foramen; p. premolariform

Four lower molariforms (m1–m4) are preserved on the dentary, of which the m4 is not completely erupted (Figs. 2–3). All preserved molariforms are double-rooted. The preserved molariforms are sub-equal in size, with m3 being slightly larger than the others (Table 1). Each tooth has three primary cusps and a distal cusp d; cusps b and c are well developed, and distantly separated from cusp a. The three primary cusps and cusp d are aligned mesiodistally in occlusal view. Cusp d on m1 and m2 fits closely into the mesial embayment of the m2 and m3, respectively, whereas on m3 it does not yet completely fit into the mesial embayment of the erupting m4. Cusp a is much larger and taller (where known) than the others on each of the molariforms, and it is slightly curved distally in lateral view on m1, whereas it is straightly erected on m4. The cusp a of the m3 is probably also erected. There is a distinct cusp e at the mesiolingual base of the cusp b on m2–m4. It is absent on m1, but there is a minute swelling at the same location. Cusp f is highly probably absent or at least not developed on all the preserved molariforms, although the mesiolabial part of the crown on each m2 and m3 is worn. On m1–m3, the lingual cingulid is well developed and slightly undulant. The lingual cingulid of m4 is not fully observable, but it is much weaker than those on m1–m3. The labial cingulid is present on m2–m4 at the base of cusps a and c, but it is partly worn and broken in m2 and m4. A shorter and blunter one is present on m1 at the distolabial base of cusp c, but it is highly probably not extended mesially.

The tip of cusp a is broken in the m1 of V 14511. Cusp c projects from a slightly higher position than cusp b. At the mesial base of the crown, there is no apparent embayment for an interlocking mechanism (Fig. 4C). The apices of the primary cusps and probably cusp d are joined by ridges, and a short ridge extends from the tip of cusp b on its mesial face. The

m1 is less worn than the m2. No obvious wear facet is present on the mesiolabial face of cusp b and the labial face of the notch between cusps a and b. The labial surface of the notch between cusps a and c is damaged, but a large facet as seen on m2 is not present. The only obvious wear facet on the tooth is found at the distolabial face of cusp c with cusp d, but it is not as developed as the corresponding one on the m2. This part of the tooth was worn with the mesiolabial face of cusp b of the m2.

Cusp a of m2 is broken away at its base. Cusp b of m2, whose tip is broken and missing, is estimated to be as large as cusp c, and unlike m1, cusp b rises at the position as high as cusp c. Cusp d is barely visible, because it fits very closely into the mesial embayment of the m3, and also because it is strongly worn. Ridges probably join cusp apices, but are now only preserved on the distal surface of cusp b and the mesial surface of cusp c. The m2 is strongly worn at the labial faces of the notches between cusps a and b, and cusps a and c, and at the distolabial face of cusp c with cusp d and the mesiolabial face of cusp b of the m3.

The apical half of cusp a and the tip of cusp c are broken away on m3. Cusp b is estimated to be as large as cusp c, but it projects from the position higher than cusp c. Cusp e is larger and more distinct than that of m2. The apices of the primary cusps and cusp d are joined by ridges. The mesial face of cusp b is strongly worn and the presence of the ridge is uncertain. Except for this part, this tooth is less worn than the m2. Only a small facet is observed on the distolabial face of the preserved part of cusp c. Other wear facets are unclear because of the damage to cusps a and c, but there are, at least, no facets as large as those on the m2. Cusp d is apparently unworn.

The m4 has not completely erupted and thus the posterior part of the tooth, including cusp d, is not observable. Three trenchant primary cusps are well preserved and lanceolate in lateral view, cusp b rising at higher position than cusp c. Cusps b and c are splayed, projecting away from each other at a relatively large angle. Cusp e is as distinct as that of the m3. Cusp f is absent, but the mesiolabial base of the crown is somewhat swelling. The apices of all the primary cusps and probably cusp d are joined by ridges, and a ridge extends from the tip of cusp b to its mesial base. This tooth is unworn.

Tooth measurements Presented in Table 1.

Remarks We identified the mesialmost preserved molariform of V 14511 as m1 because the embayment for the interlock with the preceding tooth is absent on its mesial base of the crown (Fig. 4C). As was noted by Kusuhashi et al. (2016), the interlock between the ultimate premolariform and the first molariform is usually not developed among gobiconodontids, although the interlock is not developed even between mesial molariforms of the first generation at least in a species of *Gobiconodon* (Lopatin and Averianov, 2015). The mesial part of the mesialmost preserved molariform of V 14511 is not worn, whereas it has a wear facet on the distal part; a similar wear pattern is observed on m1 of some species of *Gobiconodon* (Kusuhashi et al., 2016). The great size difference between the mesialmost preserved molariform and the preceding tooth estimated from alveoli, which is also commonly seen in *Gobiconodon*, further supports this identification.

Table 1 Measurements of lower molariforms in the holotype (IVPP V 14511) of *Fuxinoconodon changi* gen. et sp. nov. and ?Gobiconodontidae gen. et sp. indet. (V 22643) with those of type specimens of other gobiconodontids (mm)

	m1			m2			m3			m4			m5		
	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H
Fuxinoconodon changi															
IVPP V 14511	3.23*	1.13	2.00	2.99*	1.14	–	3.40	1.15	–	2.87*	1.08	2.16	–	–	–
Gobiconodontidae gen. et sp. indet.							2.55	0.80	2.04						
IVPP V 22643*															
Gobiconodon haizhouensis															
IVPP V 14509	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
Gobiconodon tomidai															
IVPP V 14510	–	–	–	1.99	0.78	1.44	2.07	0.86	–	2.00	0.79	–	–	0.72	–
Gobiconodon borissiaki															
PIN 3101/9	2.8	1.3	–	–	1.3	–	2.75	1.5	–	2.7	1.5	–	2.5	1.15	–
Gobiconodon hoburensis															
PIN 3101/24	1.5	0.9	–	1.6	0.9	–	1.6	0.95	–	1.45	0.85	–	1.4	0.65	–
Gobiconodon luoianus (41H III-0320)															
right	3.0	3.5	–												
left	3.0	2.8	–	3.0	3.2	–									
Gobiconodon ostromi (MCZ 19965)															
right	4.75	2.10	–	–	–	–	4.90	2.25	–	4.60	2.40	4.60	4.05	2.30	3.70
left	4.50	2.20	4.55	4.80	–	–	4.85	2.75	–	–	2.55	–	–	2.30	–
Gobiconodon zofiae															
IVPP V 12585	2.30	0.90	–	2.30	0.95	–	2.50	1.05	–	2.55	1.00	–	1.95	0.75	–
Meemannodon lujiatunensis															
IVPP V 13102	5.33	2.90	4.78	6.95	3.30	6.08	7.62	3.56	6.98	7.43	3.69	7.28	–	–	–
Repenomamus giganticus															
IVPP V 14155	7.5	4.7	–	8.3	5.0	–	8.0	–	–	7.5	4.8	–	6.1	4.2	–
Spinolestes xenarthrosus															
MCCMLH30000							2.06	1.14	–	1.77	1.04	–			

Note: Measurement values of *G. borissiaki* and *G. hoburensis* are from Lopatin and Averianov (2015) and those of the other type specimens of previously known species except for *G. zofiae* are from their original descriptions cited in the text. Tooth generations are not considered here. * Estimated to be slightly larger than these values, because the cusp d of these tooth are not fully visible. H. height; L. mesiodistal length; W. labiolingual width

The m1 of V 14511 is less worn than the m2. This possibly implies a molariform replacement as seen in *Gobiconodon* and some other eutriconodontan taxa (e.g., Jenkins and Schaff, 1988; Wang et al., 2001; Kielan-Jaworowska et al., 2004; Hu et al., 2005b; Lopatin et al., 2010; Lopatin and Averianov, 2015). However, it is premature to discuss molariform replacement for the species due to the lack of strong evidence.

Tooth designation of the antemolariforms is somewhat ambiguous. There are six alveoli and two broken teeth preserved on the dentary of V 14511 (Fig. 4A). The distalmost two alveoli are obviously for a double-rooted tooth, and the others are for single-rooted teeth. Therefore, there were seven antemolariform teeth on the dentary. The distal one of the two broken teeth is still erupting and in contact with the mesial broken tooth. They are likely to be of the same tooth locus, and thus we consider that there are six antemolariform loci. The number of tooth loci is then within the range of the general number in gobiconodontids, and we simply adopt the lower dental formula of gobiconodontids (two incisors, canine, and three premolariforms; Meng et al., 2005) to the antemolariforms of V 14511.

?Gobiconodontidae Chow & Rich, 1984

Gen. et sp. indet.

(Fig. 5)

Referred specimen An isolated left lower molariform (IVPP V 22643; Fig. 5).

Locality and horizon Badaohao, Heishan, Liaoning, northeastern China; Early Cretaceous (Aptian–Albian); Shahai Formation.

Measurements See Table 1.

Description V 22643 is a damaged left lower molariform tooth. The tooth is double-rooted, and the distal root is slightly stronger than the mesial. The distolabial part of cusp a is broken, and cusp d is broken away from its base. The tip and the lingual face of cusp b are slightly damaged. Three primary cusps and cusp d are aligned mesiodistally in occlusal view, but cusp d is very slightly shifted lingually. Cusp a is prominent and slightly curved distally in lateral view. Cusps b and c are well developed. They are almost the same in height, and project from almost the same level, but cusp b is mesiodistally longer than cusp c. They are well distant from cusp a, and thus the tooth crown is mesiodistally longer than height. Cusp e is present at the lingual base of cusp b. The distinct cusp f is absent but the mesiolabial base of the crown has an indistinct swelling. The mesiobasal part of the crown is indented for the reception of cusp d of the preceding tooth (Fig. 5D). This embayment extends to the coronal part of the mesial face of the mesial root as a groove (Fig. 5D). The lingual cingulid is present only at the base of cusp c; it extends mesially to the distal base of cusp a. The labial cingulid is absent. The apices of the primary cusps and probably cusp d are joined by ridges, and a ridge extends from the tip of cusp b to its mesiolabial base. There is a wear facet at the distolabial face of cusp c, which extends to the labial face of the crown below the notch between cusps c and d. No other wear facet is observed on the preserved part of the crown.

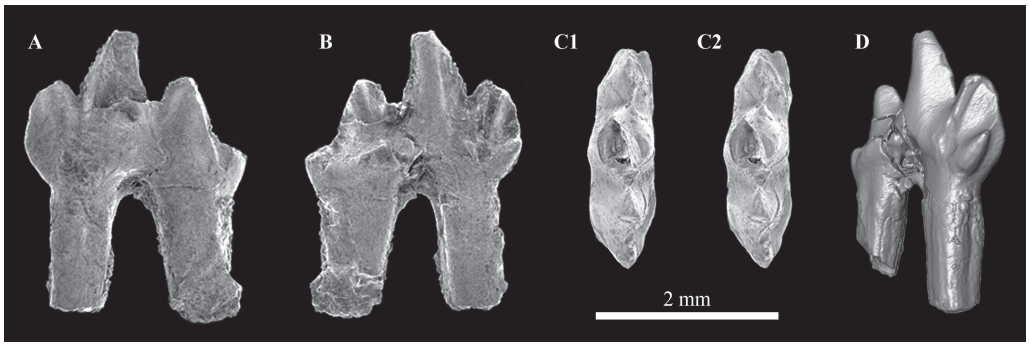

Fig. 5 The molariform of ?Gobiconodontidae gen. et sp. indet. (IVPP V 22643) from Lower Cretaceous Shahai Formation, Badaohao, Heishan, Liaoning, northeastern China
A–C. Scanning electron micrographs: A. labial view, B. lingual view, C. occlusal view, stereopair, top to anterior; D. V 22643 reconstructed from micro-computed tomography images of V 14511 using AMIRA 5.3.2 software in mesiolingual view

4 Comparison and concluding remarks

IVPP V 14511 has only six tooth loci mesial to the first molariform, which here is interpreted to be two incisors, one canine and three premolariforms. The presence of an enlarged i1 and the reduction in the number of incisors and premolariforms are unique for gobiconodontids among eutriconodontans (Ji et al., 1999; Kielan-Jaworowska et al., 2004; Luo et al., 2007; Lopatin and Averianov, 2015; Martin et al., 2015). At the mesial base of the crown of each m2–m4, there is an embayment for receiving cusp d of the preceding tooth in V 14511. Among eutriconodontans, similar interlocking patterns are known only for gobiconodontids, jeholodentids, and triconodontids, although the interlocking in triconodontids is a more derived vertical tongue-in-groove pattern (e.g., Ji et al., 1999; Kielan-Jaworowska et al., 2004; Luo et al., 2007; Lopatin and Averianov, 2015). V 14511 is distinguished from triconodontids in having distinct cusp e on m2–m4. In the original description of jeholodentids, the molariform cusp e is reported to be absent (Ji et al., 1999; Luo et al., 2007) but was coded as present by Luo et al. (2007; p. 17 of the supplementary information). If it is absent, the presence of molariform cusp e in V 14511 also distinguishes it from jeholodentids because this is one of the diagnostic features of the family (Luo et al., 2007). Rougier et al. (2001), however, asserted that there is a well-developed cusp e on m2 of *Jeholodens*. The ventral margin of the dentary in V 14511 is rounded and convex in lateral view. A flat to slightly concave ventral margin of the dentary is another diagnostic feature of the Jeholodentidae, and the specimen is different from them in this point. Therefore, V 14511 morphologically complies well with and only with the Gobiconodontidae, and we attribute the specimen to that family.

Molariforms of *Gobiconodon* were intensively studied and described by Lopatin and Averianov (2015) based on specimens of *G. borissiaki* and *G. hoburensis* from Mongolia, and they recognized the lower molariforms of at least three and two generations in their specimens of *G. borissiaki* and *G. hoburensis*, respectively. V 14511 is different from *Gobiconodon* in the

lower molariform morphology, showing a mixture of features characterizing the molariforms of the first or the later generations in *Gobiconodon*. Lopatin and Averianov (2015) noted that there are obvious morphological differences between the first and second (and probably later) generations in *G. borissiaki* and *G. hoburensis*. According to their study, lower molariforms of the first generation are characterized by a lower crown, a less distally curved cusp a (but it is clearly curved distally at least on m3–m4), proportionally larger cusps b and c that are more distant from the cusp a, faint lingual cingulid, and weak interlocking between mesial molariforms (at least in *G. hoburensis*). Although the authors did not clearly state it, it is likely also a feature of first generation molariforms that cusps b and c project from lower positions. The molariforms of the second generation have taller crown, a more strongly distally curved cusp a, relatively small cusps b and c that are not very distant from the cusp a, well developed lingual cingulid, and well developed interlocking among all molariforms (Lopatin and Averianov, 2015). Cusps b and c generally project from higher positions. Lower molariforms in V 14511 have some features seen in those of the first generation in *Gobiconodon*: molariform crowns are relatively low compared with the second generation of *Gobiconodon*; the cusp a is slightly curved distally in m1 (but the erect cusp a in m4 is not seen in distal molariforms of any generation in *Gobiconodon*); and proportionally larger cusp b and c are well distant from the cusp a, and project from lower positions. At the same time, however, they also show features of the second generation in *Gobiconodon*: the lingual cingulid is well developed, and the m1 and the m2 are tightly interlocked with the following teeth. The combination of these characters is not seen in any species of *Gobiconodon* of which the lower molariforms are described (Trofimov, 1978; Jenkins and Schaff, 1988; Kielan-Jaworowska and Dashzeveg, 1998; Maschenko and Lopatin, 1998; Li et al., 2003; Minjin et al., 2003; Lopatin and Averianov, 2015; Kusuhashi et al., 2016; Lopatin, 2017). On m1 and probably m2 of *G luoianus*, cusp b is weak and cusp c is undeveloped, which is apparently different from the condition seen in V 14511 with developed cusps b and c on molariforms. V 14511 is also different from *Gobiconodon* in having labial cingulid on molariforms. On at least m4 of V 14511, primary cusps are lanceolate, and cusps b and c are splayed much wider than those on any molariforms in *Gobiconodon* including *Gobiconodon* sp. A of Averianov et al. (2005). These obvious differences suggest that V 14511 does not belong to a species of *Gobiconodon*, considering the generally similar morphology between different species of *Gobiconodon*.

Morphological variations of the molariforms between generations are unknown for V 14511 and the other gobiconodontids, namely, *Hangjinia*, *Meemannodon*, *Repenomamus*, and *Spinolestes*. Therefore, we simply compare molariform morphology of V 14511 to theirs regardless of their generations. V 14511 is different, at least from *Meemannodon* and *Repenomamus*, in having distinct labial and lingual cingulids on the molariforms (Wang et al., 2001; Meng et al., 2005). *Spinolestes* also seems to lack labial cingulid (or at least developed labial cingulid) on the lower molariforms. Known molariforms of *Hangjinia*, *Meemannodon*, and *Repenomamus* are different from those of V 14511 but similar to those of the second

generation of *Gobiconodon* in having a distally curved cusp a (at least in *Meemannodon* and *Repenomamus*), and cusps b and c, which are relatively small, not well distant from the cusp a, not splayed widely, and projected from a relatively high position (Godefroit and Guo, 1999; Wang et al., 2001; Meng et al., 2005). In *Meemannodon*, m1 lacks cusp b, whereas it is present on m1 of V 14511. Among gobiconodontids, the molariforms of V 14511 are in general most similar to those of *Spinolestes*. Cusp a on the lower molariform in the type specimen of *Spinolestes xenarthrosus* Martin et al., 2015, was identified as the replaced m3 (Martin et al., 2015); this tooth is erect and lanceolate in lateral view, cusps b and c on which are well distant from cusp a. There are, however, some apparent differences between the lower molariforms of V 14511 and *Spinolestes*. The cusp b is slightly shifted lingually in *Spinolestes*, showing a week angulation of the primary cusps in occlusal view, whereas the primary cusps are aligned along the mesiodistal line in V 14511. Cusp d is much less developed in *Spinolestes*, being smaller than the cusp e, but it is distinct and much larger than cusp e in V 14511.

In addition to these molariform morphologies, V 14511 shows further differences from other gobiconodontids. *Repenomamus* is known to have robust dentary and proportionally smaller teeth (Li et al., 2000; Hu et al., 2005b). Even ontogenetic variations are taken into account, V 14511 is substantially different from the lower jaws of *Repenomamus*. The i1 of *Repenomamus* is enlarged and i2 as well as the canine are relatively not small either, being nearly sub-equal in size to the i1 (Li et al., 2000; Hu et al., 2005b); the genus is more similar to *Liaoconodon* in this character than it is to other gobiconodontids (Meng et al., 2011). The i1 of V 14511 is estimated to be proportionally much larger than the i2 and the canine. On the dentary of the type specimen of *S. xenarthrosus*, there is a wide Meckelian groove (Martin et al., 2015). Although V 14511 is not thought to be of a much later ontogenetic stage than the type specimen of *S. xenarthrosus*, the Meckelian groove is not very distinct. V 14511 is, therefore, not likely to belong to any known genera of gobiconodontids, and thus we propose to establish a new genus and species of the Gobiconodontidae, *Fuxinoconodon changi*.

The isolated lower molariform (V 22643) has a mesial embayment that extends to the coronomesial surface of the mesial root as a groove, which indicates, as mentioned earlier, an interlocking pattern similar to those in gobiconodontids, jeholodentids, and triconodontids. The absence of a distinct cusp f also supports this view (e.g., Kielan-Jaworowska et al., 2004). The presence of cusp e distinguishes this specimen from triconodontids and maybe jeholodentids as seen above. The great size difference between cusp a and cusps b and c provides additional evidence to distinguish this specimen from triconodontids (e.g., Kielan-Jaworowska et al., 2004). We, therefore, consider that V 22643 can probably be attributed to the Gobiconodontidae, but this attribution is less confident because it currently cannot be sufficiently compared with molariforms of jeholodentids, which have been neither described in detail nor figured clearly.

Compared with gobiconodontids, V 22643 is roughly in the size range of the lower molariforms of *Gobiconodon borissiaki*; it is thus clearly larger than those of *G. haizhouensis*, *G. hoburensis*, *G. tomidai*, and *Spinolestes xenarthrosus*, and smaller than those of

Fuxinoconodon changi, *G. luoianus*, *G. ostromi*, *G. zofiae*, *Meemannodon lujiatunensis*, *Repenomamus giganticus*, and *R. robustus* (Jenkins and Schaff, 1988; Wang et al., 2001; Meng et al., 2005; Lopatin and Averianov, 2015; Martin et al., 2015; Kusuhashi et al., 2016). It shares many characters with the molariforms of the first generation of *Gobiconodon*: the crown is longer than high; cusp a is slightly curved distally; cusps b and c are quite distant from cusp a and project from relatively low positions; the lingual cingulid is not very developed. Therefore, V 22643 might be referable to a species of *Gobiconodon*, which is different from species already known from the Shahai and Fuxin formations, but here we conservatively assign it to ?Gobiconodontidae gen. et sp. indet., because sufficient material for comparison to determine its affiliation is not available at the present time.

Fossil mammals from the Shahai and Fuxin formations now include five, or more probably six, different eutriconodontan species, suggesting that eutriconodontans were still relatively diverse in the late Early Cretaceous in Asia. Compared with the fossil records of eutriconodontans from earlier ages, especially those from the Jehol Group, it is clear that the family-level diversity had been reduced. As mentioned earlier, eutriconodontans of three or probably even more families have been known from the Jehol Group (Meng, 2014; Meng et al., 2015), whereas those of only two families have been recognized from the Shahai and Fuxin formations to date (Kusuhashi et al., 2009a, 2016). Moreover, one of these two families, the Triconodontidae, is currently unknown from the Jehol Group, and thus the Gobiconodontidae is the only known family that survived from the age of the Jehol Group into that of the Shahai and Fuxin formations. This family-level shrinkage is also the case for eutriconodontans from other almost contemporaneous Asian localities; most of them belong to the Gobiconodontidae (Trofimov, 1978; Kielan-Jaworowska and Dashzeveg, 1998; Godefroit and Guo, 1999; Lopatin, 2013, 2017; Lopatin and Badamgarav, 2013; Lopatin and Averianov, 2015), except for one possible triconodontid specimen (Miyata et al., 2016). Furthermore, most of these gobiconodontids are attributed to a single genus *Gobiconodon*, implying that their generic level diversity was also lower than those of the earlier age. This shows that eutriconodontans had already started declining during this time period. As mentioned earlier, eutherians and multituberculates are dominant in the mammalian fossil assemblage from the Shahai and Fuxin formations. Eutriconodontans seems to have lost their position in mammalian fauna through the competition with other mammals.

Gobiconodontids are also known in older fossil records including those from the Jehol Group (Maschenko and Lopatin, 1998; Rougier et al., 2001; Li et al., 2003; Minjin et al., 2003; Averianov et al., 2005; Hu et al., 2005b; Meng et al., 2005; Yuan et al., 2009), but interestingly larger species seems to have disappeared in the late Early Cretaceous. Gobiconodontids are known to include large to very large species, compared with other Mesozoic mammals (e.g., Jenkins and Schaff, 1988; Li et al., 2000; Kielan-Jaworowska et al., 2004; Hu et al., 2005). *Fuxinoconodon changi* is currently the largest known gobicondontid of the late Early Cretaceous, but it is much smaller than some older species from Asia, such as *Gobiconodon*

hopsoni, *Meemannodon lujiatunensis*, *Repenomamus giganticus*, and *R. robustus*, and highly probably smaller than *G. luoianus* and *G. zofiae*. The cause of this reduction of body size is currently unknown, but it might be, at least partly, related with the decline of eutriconodontans.

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辽宁下白垩统沙海组和阜新组真三尖齿兽类戈壁尖齿兽科新材料

楠桥直[1]　　王元青[2,3,4]　　李传夔[2]　　金　迅[2]

(1 日本爱媛大学大学院理工学研究科 爱媛 790-8577)

(2 中国科学院古脊椎动物与古人类研究所，中国科学院脊椎动物演化与人类起源重点实验室 北京 100044)

(3 中国科学院生物演化与环境卓越创新中心 北京 100044)

(4 中国科学院大学地球与行星科学学院 北京 100049)

摘要：真三尖齿兽类是了解亚洲白垩纪哺乳动物群演化和转变的重要成员之一。到目前为止沙海组和阜新组(下白垩统上部)已经发现了两种戈壁尖齿兽科以及两种三尖齿兽科的真三尖齿兽类。描述了这些地层产出的真三尖齿兽类的其他材料，包括一新属新种——常氏阜新尖齿兽(*Fuxinoconodon changi* gen. et sp. nov.)和一枚左下臼齿(鉴定为 ?Gobiconodontidae gen. et sp. indet.)。这种新的真三尖齿兽类被归入戈壁尖齿兽科(Gobiconodontidae), 其特征为：第一下门齿大、门齿和前臼齿的数目变少、臼齿b尖和c尖较大而独立，以及臼齿具有分别属于*Gobiconodon*第一代或第二代臼齿上独有特征的组合。新材料与同一地区相同层位已经报道的4种真三尖齿兽类表明，虽然科级和属级的多样性似乎已经减少，但亚洲早白垩世晚期仍存在比较多样的真三尖齿兽类。

关键词：辽宁，早白垩世，阜新组，沙海组，哺乳动物，真三尖齿兽类，戈壁尖齿兽科

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