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Isolated dinosaur teeth from the Lower Cretaceous Shahai and Fuxin formations of northeastern China

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ABSTRACT

Isolated dinosaur teeth recovered from seven localities near Fuxin (western Liaoning Province, northeastern China) are described. They come from sediments belonging to the Shahai and Fuxin formations, considered to be Aptian to Albian in age. Seven taxa have been recognized. They include the oviraptorosaur *Incisivosaurus*, dromaeosaurid theropods, *Euhelopus*-like sauropods, as well as indeterminate nodosaurid, ankylosaurid, iguanodontoid and basal neoceratopsian ornithischians. The Shahai and Fuxin dinosaur faunas show the persistence of some Jehol biota taxa such as the highly specialised *Incisivosaurus*, basal titanosauriform sauropods, basal neoceratopsians and some dromaeosaurids, and the addition of more derived iguanodontoids and ankylosaurians. The persistence of some dinosaurs of the Jehol Biota into the Shahai and Fuxin formations suggests a long term stability of Liaoning terrestrial environments during the Early Cretaceous. Despite sampling bias and the rather small sample that must be taken into account, teeth abundances show a significant compositional difference between the localities of the Shahai and Fuxin formations, neoceratopsian teeth representing one third of dinosaur tooth remains in the Shahai Formation whereas they are totally absent in the Fuxin Formation. Ankylosaur teeth, in contrast, represent 3% of total remains in the Shahai Formation, whereas they seem to be the only herbivorous dinosaurs in the Fuxin Formation with 40% of the total number of teeth (the rest being theropod dinosaur teeth). Although a difference in micro-environmental conditions between Shahai and Fuxin localities may at least partly explain such pattern, the unusual and unbalanced faunal composition of Fuxin localities remains enigmatic and will need further field collecting in order to be clarified.

1. Introduction

Since the late 1990s, extensive field collections focused on finding Mesozoic mammals were carried out in small coal mines in Badaohao (Heishan County) and the Fuxin City area in western Liaoning Province, northeastern China, by joint Chinese–Japanese research teams (Fig. 1a). During these excavations, many isolated dinosaur remains were recovered from seven mines, but little attention has been paid to them (Wang et al., 1995; Xu et al., 1998; Zhao and Zhao, 1999), most of the effort being devoted to articulated dinosaur fossils coming from the underlying Jehol Group. Here we provide a detailed description of 37 well preserved isolated dinosaur teeth from six localities of the Shahai and Fuxin formations, and discuss their possible environmental and ecological implications.

1.1. Geological setting

Dinosaur teeth were collected from the Shahai Formation at a small coal mine in Badaohao (Heishan County) and from the Fuxin Formation at small coal mines (Dongfang #1, Hanjiadian #6, Nanhuang #2, Nanhuang #3 and Mingda coal mines) in Fuxin City area (Fig. 1a). Late Mesozoic non-marine sediments distributed in western Liaoning Province mainly consists of the Tuchengzi Formation, the Yixian and Jiufotang formations of the Jehol Group, and the Shahai, Fuxin and Sunjiawan formations, in stratigraphic ascending order (e.g., Wang et al., 1989; Jin, 1996; Yang et al., 1997; Fig. 1b). The Tuchengzi Formation is correlated to the ?Upper Jurassic–Lower Cretaceous, and the other five formations are Early Cretaceous in age (Wang et al., 1989; Jin, 1996; Yang et al., 1997; Swisher et al., 2002). The Shahai Formation is widely distributed, but not well exposed, in the Fuxin-Yixian-Jinzhou Basin. It conformably (e.g., Wang et al., 1989; Jin, 1996) or unconformably (e.g., Chen, 1988) overlies the Jiufotang Formation (belonging to the Jehol Group) and is conformably overlain by the Fuxin Formation (Wang et al.,

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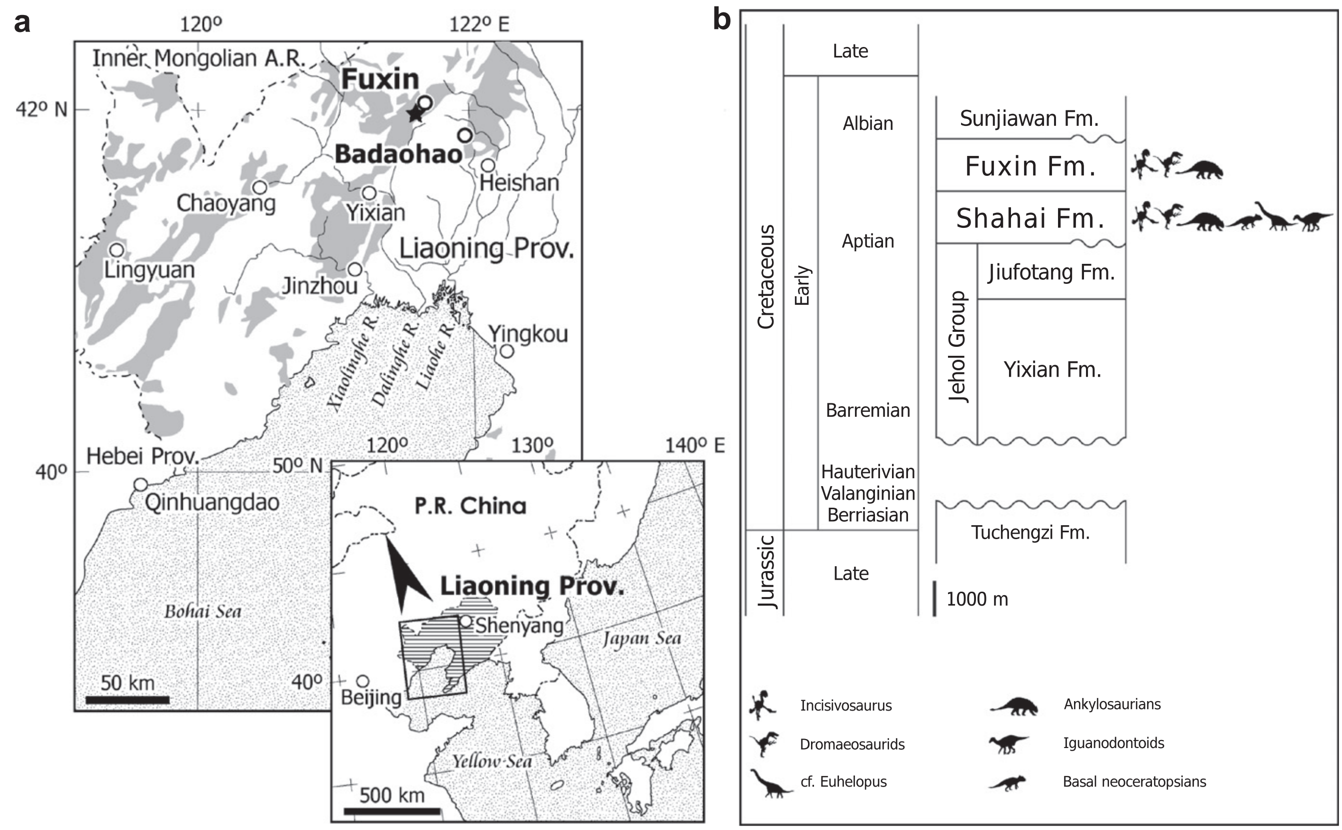

Fig. 1. (a) Distribution of the late Mesozoic strata in the Liaoning Province (gray areas in the enlarged map; modified after the Editorial Board of Chinese Geologic Maps, 2002) and the locations of Badaohao (Shahai Formation) and small coal mines around Fuxin City (Fuxin Formation). Nanhuang #2, Nanhuang #3, Dongfang #1, Hanjiadian #6 and Mingda localities belonging to the Fuxin Formation are situated within the black star. (b) Schematic stratigraphic table shows the late Mesozoic formations exposed in western Liaoning Province, northeastern China. Identified dinosaur taxa are plotted in front of their corresponding formations.

1989; Jin, 1996). Numerous fossils have been collected from the middle part of the formation, which mainly consists of sandstones and mudstones with intercalated coal measures. Vertebrate remains from the formation contain fishes, turtles, lizards, dinosaurs (e.g., Wang et al., 1995; Jin, 1996) and various mammals including "symmetrodontans" (Hu et al., 2005), "eupantotherians" (Li et al., 2005) and multituberculates (Kusuhashi et al., 2009b). The Fuxin Formation is mainly exposed in the Fuxin-Yixian-Jinzhou Basin. The formation conformably overlies the Shahai Formation and is conformably (Jin, 1996) or unconformably (Yang et al., 1997) overlain by the Sunjiawan Formation. Jiang and Sha (2006) divided the Sunjiawan Formation into two formations and indicated that the lower one disconformably overlies the Fuxin Formation. The Haizhou Formation, referred to by several authors (e.g., Wu et al., 1992; Zhu and Zhang, 1992), is considered to be synonymous with the Fuxin Formation (Yang et al., 1997). The Fuxin Formation is mainly composed of mudstones, sandstones and conglomerates, numerous intercalated coal measures (e.g., Wang et al., 1989; Wu et al., 1992), and abundant vertebrate fossils have been collected from several coal horizons. These fossils include remains of fishes, turtles, lizards, dinosaurs (e.g., Shikama, 1947; Young, 1960; Wang et al., 1995) and mammals including eutherians (Shikama, 1947), multituberculates (e. g., (Kusuhashi et al., 2009b) and "triconodonts" (e. g., Kusuhashi et al., 2009a). The depositional ages of the Shahai and Fuxin formations remain ambiguous. Neither reliable radiometric ages nor available index fossils have been reported from these formations, and thus their ages are necessarily based on the ages of underlying formations. From the Jehol Group, radiometric ages of −130 to −120 Ma have been reported by several authors (e.g., Smith et al., 1995; Swisher et al., 1999; He et al., 2004, 2006; Chang et al., 2009), and the group is now generally thought to be Barremian to Aptian in age. On the basis of this correlation of the underlying Jehol Group, the Shahai and Fuxin formations are interpreted as Aptian or younger in age. Although there is no secure evidence to constrain an upper limit for the depositional age of the Shahai and Fuxin formations, considering the age uncertainty of the overlying Sunjiawan Formation (considered either as late Early Cretaceous (e.g., Sha, 2007) or early Late Cretaceous (e.g., You et al., 2003a)), they were tentatively attributed to the Aptian–Albian time span (Kusuhashi et al., 2009a,b).

2. Teeth description

2.1. Theropods

Theropod dinosaurs are represented by isolated tooth crowns of two size ranges, large (from about 3.5 to 4 cm long apico-basally) and small (from 0.5 to 2 cm long apico-basally). As large teeth are too broken to be described properly, only small teeth are considered.

SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
MANIRAPTORA Gauthier, 1986
OVIRAPTOROSAURIA Barsbold, 1976
INCISIVOSAURUS Xu et al., 2002a
Cf. *Incisivosaurus*.

2.1.1. Description

Specimens consist of two right (V16742.1; Badaohao locality, Shahai Formation, and V16742.2; Nanhuang #3 locality, Fuxin

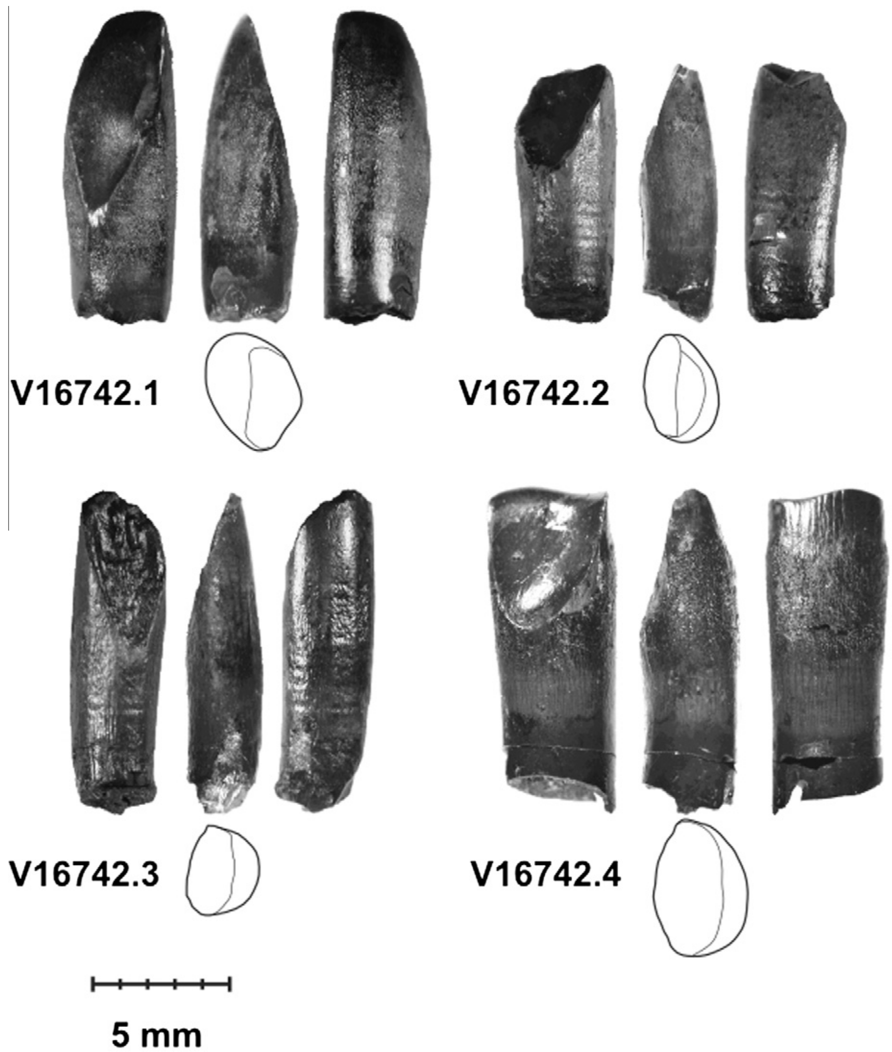

Fig. 2. Cf. *Incisivosaurus* teeth. V16742.1: first right premaxillary tooth (Badaohao, Shahai Fm.). V16742.2: first right premaxillary tooth (Nanhuang #3 locality, Fuxin Fm.). V16742.3: first left premaxillary tooth (Nanhuang #3 locality, Fuxin Fm.). V16742.4: first premaxillary tooth of indeterminate position (Dongfang #1 locality, Fuxin Fm.).

Fm.), one left (V16742.3; Nanhuang #3 locality, Fuxin Formation) first premaxillary teeth and one of indeterminate position (V16742.4; Dongfang #1 locality, Fuxin Formation) (Fig. 2). These teeth have a general peg-like morphology with a bevelled tip due to the large, high-angled and slightly concave wear facet on the lingual surface. Crowns are slightly compressed labio-lingually, giving an ovoid cross section. Tooth crowns tend to become longer mesiodistally from the base to half of the wear facet, and then shorter up to the tip. Most of the enamel surface is wrinkled, and the labial face bears several blurred apico-basal ridges, giving the surface a fluted appearance. On the lingual face, the wear facet has an asymmetrical ellipsoid outline with the more convex part marking the distal border of the tooth. The wear facet terminates basally with a V-shaped outline marked by an apico-basal ridge that extends toward the base of the crown.

2.1.2. Discussion

Comparison with the type specimen of *Incisivosaurus gauthieri* (IVPP V13326; Xu et al., 2002a) allows direct match of most of the teeth. At first glance, *Incisivosaurus* premaxillary teeth resemble those of some titanosaurid, diplodocid or nemegtosaurid sauropods. The peg-like morphology, wrinkled enamel and bevelled wear facet can be observed on the teeth of some forms belonging to these three lineages. However, the very small size (less than 10 mm long), the marked lateral asymmetry of the crown due to its position (left or right premaxillary), the slight mesiodistal enlargement at mid-height of the wear facet level and the apicobasal ridges on the labial face allow to distinguish *Incisivosaurus* premaxillary teeth from sauropod teeth. It is noteworthy that *Incisivosaurus gauthieri* is only known from one almost complete skull and cervical vertebrae recovered from from the lower part of the Yixian Formation at the Lujiatun locality in Liaoning province (Xu et al., 2002a). The discovery of teeth in three different localities of both the Shahai and Fuxin formations suggests that *Incisivosaurus* was not a rare element of Early Cretaceous faunas of northeastern China.

DROMAEOSAURIDAE Matthew and Brown, 1922

Dromaeosauridae indet.

2.1.3. Description

Specimens consist of eleven maxillary or dentary tooth crowns coming from the Badaohao locality of the Shahai Formation (V16743.1, V16743.2, V16743.3) and from the four localities Dongfang #1 (V16743.4), Hanjiadian #6 (V16743.5), Nanhuang #2 (V16743.6, V16743.7) and Nanhuang #3 (V16743.8, V16743.9, V16743.10, V16743.11) belonging to the Fuxin Formation, as well as one premaxillary or anterior dentary tooth from the Nanhuang #3 locality (V16743.12; Fig. 3). Maxillary or dentary tooth crowns have apico-basal lengths ranging from about 5 mm to 20 mm (Table 1), are laterally compressed with LCI (Lateral Compression Index (Grigorescu, 1984)) of 0.4–0.5 and strongly curved distally so that the tip extends behind the level of the crown base. Moreover, the bases of some crowns have a central depression on both lingual and labial faces corresponding to the end of the central longitudinal depression of the root. Both carinae are serrated with continuous posterior and anterior serrations starting at about one third of crown height, where curvature becomes steeper. DSDI (Denticle Size Difference Index (Rauhut and Werner, 1995) values vary from 1.0 to 1.5 (Table 1), with posterior denticles being generally larger than anterior ones. Denticles are almost as high as they are long and have a rather rounded tip. Posterior denticles of V16743.6, V16743.4, V16743.8 and V16743.11 tend to point slightly toward the tip of the crown. V16743.12 is comparatively less compressed laterally with a LCI of 0.7, and the anterior carina is displaced from the midline. Both carinae bear nine denticles per mm. V16743.2 differs from the other teeth in having crown surfaces ornamented with "hairline" apico-basal striations. The tooth crown is compressed labio-lingually (LCI of 0.4) with a central depression on both sides that extends toward the tip. The tooth is strongly curved distally so that the apex extends behind the level of the crown base. Only the distal carina bears serration with a DDC (Distal Denticle Count) of 9 denticles per mm.

2.1.4. Discussion

These teeth may be attributed to the family Dromaeosauridae on the basis of general shape, DSDI and denticle morphology as recognized by Currie et al. (1990), Rauhut and Werner (1995) and Baszio (1997). However, caution must be exercised when attributing taxonomic significance to isolated theropod teeth, as functional convergences may be involved and characteristics usually used for

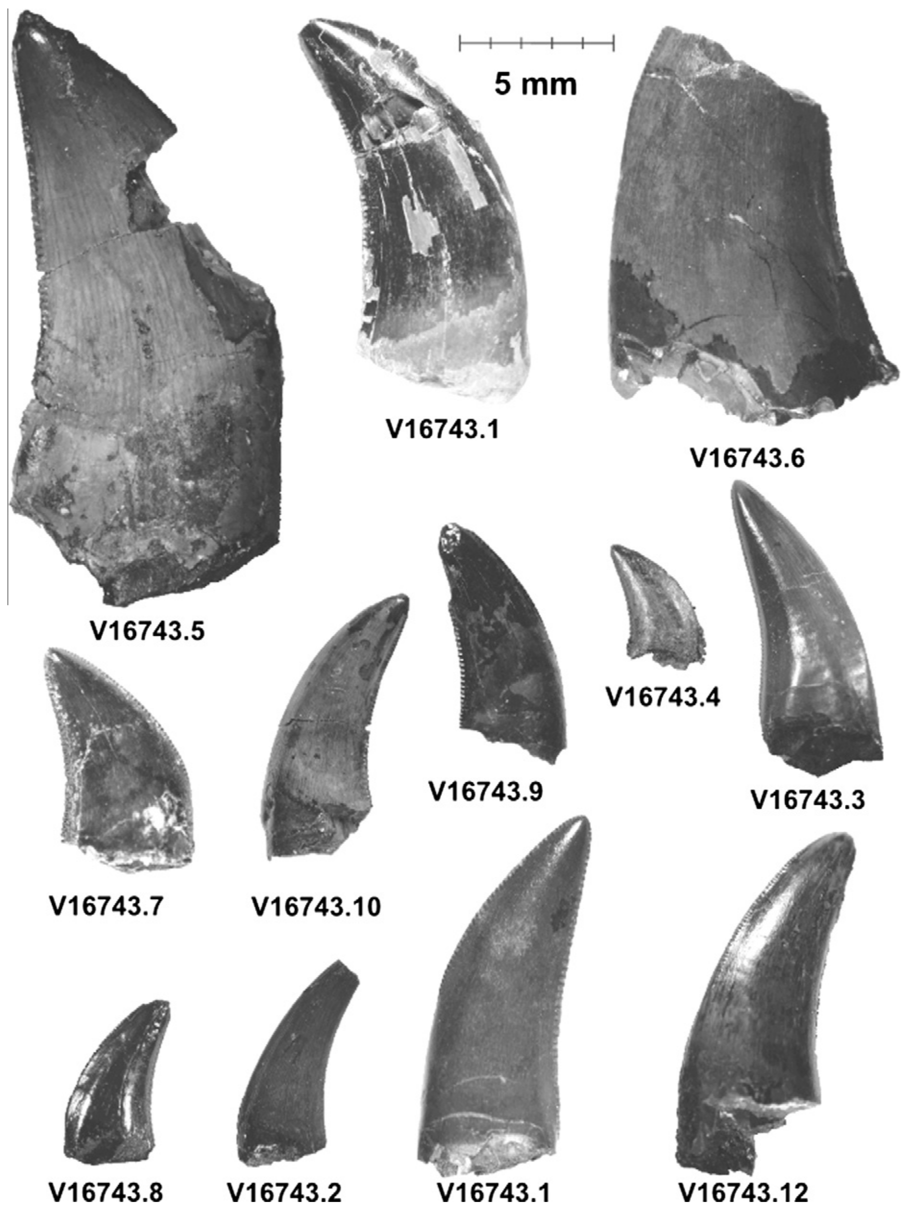

Fig. 3. Dromaeosaurid teeth. V16743.1, V16743.2 and V16743.3: maxillary or dentary tooth crowns (Badaohao, Shahai Fm.). V16743.4: maxillary or dentary tooth crown (Dongfang #1, Fuxin Fm.). V16743.5: maxillary or dentary tooth crown (Hanjiadian #6, Fuxin Fm.). V16743.6 and V16743.7: maxillary or dentary tooth crowns (Nanhuang #2, Fuxin Fm.). V16743.8, V16743.9, V16743.10 and V16743.11: maxillary or dentary tooth crowns (Nanhuang #3, Fuxin Fm.). V16743.12: premaxillary or anterior dentary tooth (Nanhuang #3, Fuxin Fm.).

Table 1
FABL (Fore-Aft Basal Length), BW (Basal Width), LCI (Lateral Compression Index), MDC (Mesial Denticle Count), DDC (Distal Denticle Count) and DSDI (Denticle Size Difference Index) values or range of values for Shahai and Fuxin dromaeosaurid teeth used in this study.

IVPP number	FABL (CBL)	BW (CBW)	LCI	MDC/mm	DDC/mm	DSDI
V16742.1	5.7	3.1	0.54	7–8	7–8	1
V16742.2	3.0	1.2	0.40	–	9	–
V16742.3	4.0	1.8	0.45	8	8	1
V16742.4	2.4	1.0	0.42	10–11	7–8	1.4
V16742.5	8.9	4.4	0.49	6	5–6	1
V16742.6	9.2	4.2	0.46	8	6	1.3
V16742.7	4.4	2.0	0.45	7–8	7	1
V16742.8	3.1	1.2	0.39	10–11	7–8	1.4
V16742.9	3.5	1.9	0.54	7	7–8	1
V16742.10	3.5	1.8	0.51	11	7–10	1.1–1.5
V16742.11	4.7	2.4	0.51	7	6	1.2
V16742.12	4.7	3.4	0.72	9–10	9	1

tooth descriptions can be correlated to each other (Farlow et al., 1991). The proposed quantitative methodology to identify isolated theropod teeth proposed by Smith et al. (2005) was not used in this study as the Early Cretaceous record of well known dromaeosaurids is very scarce and such method would lack a regional comparison database, hence the attribution to indeterminate dromaeosaurids. Six dromaeosaurid species from the Early Cretaceous of East Asia have been erected so far: *Sinornithosaurus millenii* (Xu et al., 1999) and *Graciliraptor lujiatunensis* (Xu and Wang, 2004) from the Yixian Formation of Liaoning (China), *Microraptor zhaoianus* (Xu et al., 2000b), *Cryptovolans pauli* (Czerkas et al., 2002) and *Microraptor gui* (Xu et al., 2003) from the Jiufotang Formation of Liaoning, and *Shanag ashile* (Turner et al., 2007) from Öösh (Mongolia). Posterior teeth of *S. ashile* and *M. zhaoianus* and *M. gui* differ from those from the Shahai and Fuxin formations in bearing denticles on the distal carinae only and their premaxillary teeth lack serrations (Xu et al., 2000b, 2003; Xu and Wu, 2001; Hwang et al., 2002). *G. lujiatunensis* and *S. millenii*, to the contrary, have tooth morphologies and serration patterns that match those of the Shahai and Fuxin teeth. Thus, they might belong to one of these two genera with the exception of V16743.1, V16743.6 and V16743.5 which are larger than those of *G. lujiatunensis* and *S. millenii*. Isolated dromaeosaurid teeth have been reported in other Early Cretaceous formations, viz. the Okurodani (or Okura) (Evans et al., 1998) and Kitadani (Azuma and Tomida, 1995) formations of the Tetori Group of central Japan, the Lower Xinmingbao Group of Mazongshan area, Gansu Province (Dong, 1997), the Murtoi Formation at the Mogoito locality in Buryatia, western Transbaikalia, Russia (Averianov et al., 2003) and the Ilek Formation in Western Siberia (Averianov et al., 2003). Dromaeosaurids were thus quite abundant and diverse in Asia during the Early Cretaceous. The peculiar striations observed on the enamel surfaces of V16743.2 enamel surfaces remains enigmatic as the only mention of such a pattern is from some isolated teeth recovered from the lowermost Cretaceous Rabekke Formation of Bornholm, Denmark and tentatively attributed to either a dromaeosaurid theropod or a bird (Lindgren et al., 2008).

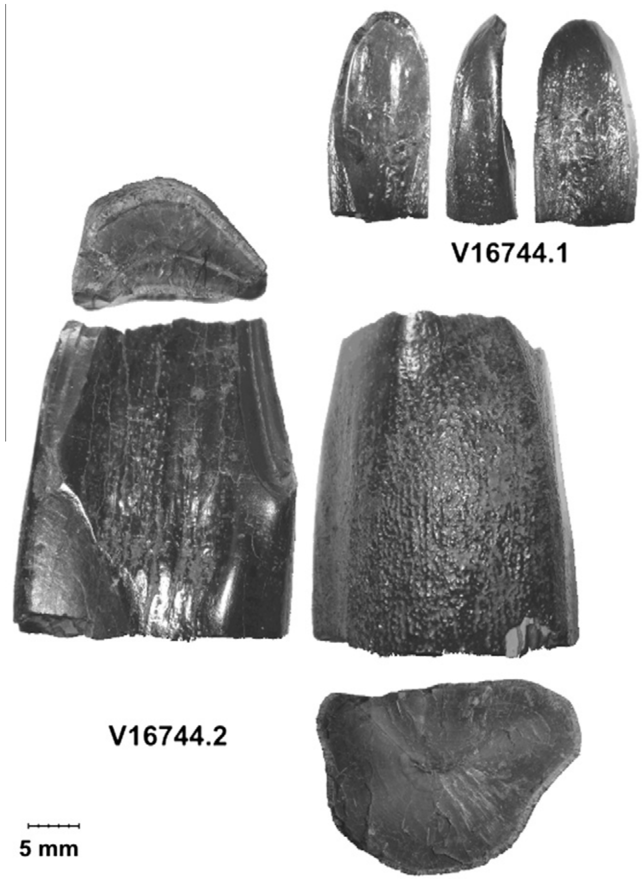

Fig. 4. Cf. *Euhelopus* teeth. V16744.1 and V16744.2: tooth crowns (Badaohao, Shahai Fm.).

2.2. Sauropods

SAURISCHIA Seeley, 1887
SAUROPODA Marsh, 1878
EUSAUROPODA Upchurch, 1995
TITANOSAURIFORMES Salgado et al., 1997
EUHELOPUS Romer, 1956
Cf. Euhelopus.

2.2.1. Description

Two partial tooth crowns have been recovered from the locality of Badaohao (V16744.1 and V16744.2) (Fig. 4). In V16744.1 the apicalmost part of the crown is present, but V16744.2 lacks the tip. These robust teeth have a mesiodistally concave lingual side and a strongly convex labial side with two apico-basal grooves situated mesially and distally, respectively. This results in an asymmetrical D-shaped cross section with the apex of the 'D' situated closer to the mesial crown margin than to the distal one. The unbroken apex of V16744.1 is slightly recurved lingually, and constitutes the starting point of a lingual, apico-basal ridge slightly displaced toward the distal side of the tooth. This ridge and the raised edges of the crown delimit two oval depressions extending to most of the lingual side of the crown. Such pattern on the lingual side of the tooth seems also present on V16744.2, but strongly attenuated by wear. A smooth bulge is present on the distal part of the lingual surface, under the distal oval depression on both teeth, but is less pronounced in V16744.2 than V16744.1 due to wear. Most of the crown surfaces are covered with wrinkled enamel becoming smooth and unwrinkled toward the apex. Large wear facets are present on the mesial and distal parts of the lingual side of V16744.2, whereas only the most apical part of V16744.1 is worn lingually, exposing the underlying dentine. Another large wear facet is present on the mesiobasal part of the lingual side of V16744.2, indicating the presence of an overlapping tooth in the jaw, thus an imbricated arrangement of the teeth.

2.2.2. Discussion

These two teeth having similar morphologies can both be referred to Eusauropoda based on the following features: wrinkled tooth enamel; lingual concavity; D-shaped cross section as well as mesial and distal grooves on the labial crown surface (Upchurch, 1998; Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004; Wilson and Upchurch, 2009). They are in many respects similar to the teeth recovered from the Lujiatun locality (Yixian Formation) and to those from 'La Cantalera' (Barremian of Spain), both referred to the Chinese genus *Euhelopus* (Canudo et al., 2002; Barrett and Wang, 2007,). The type species of *Euhelopus*, *Euhelopus zdanskyi*, is a basal titanosauriform sauropod described from a partial skeleton (including teeth) recovered from the Lower Cretaceous Mengyin Formation of Shandong Province (China). *Euhelopus* teeth possess on their lingual surface, close to the distal border, a sub-circular boss. Although this feature has morphological variability and is not present on all teeth of *E. zdanskyi*, its absence in other sauropods allowed the referral of the Lujiatun and 'La Cantalera' teeth to this genus (Barrett and Wang, 2007; Canudo et al., 2002). Such bosses are also present on V16744.2 and V16744.1, but are less prominent and rounded than those present on *E. zdanskyi* or on the Lujiatun and Spain specimens. On the basis of these features, the sauropod teeth from Badaohao can be referred to a *Euhelopus*–like titanosauriform.

2.3. Thyreophora

ORNITHISCHIA Seeley, 1887
THYREOPHORA Nopcsa, 1915
ANKYLOSAURIA Osborn, 1923
ANKYLOSAURIDAE Brown, 1908
?Ankylosauridae indet.

2.3.1. Description

Three tooth crowns have been recovered from the Fuxin Formation at the Nanhuang #3 locality (V16745.1, V16745.2 and V16745.3; Fig. 5). They are compressed labio-lingually, have general leaf-shaped morphology and are about 5 mm wide. Crown carinae bear large denticles (at least more than seven; ten for V16745.3 which is unworn). On V16745.1, the occlusal face is truncated by a very well developed wear facet reaching the base of the crown. Crown bases are greatly swollen but do not form a cingulum or at most a weekly developed one (V16745.3). Crown surfaces are rugose and bear some weakly developed apico-basal ridges, some of them originating from the denticles.

2.3.2. Discussion

See below (discussed with nodosaurids).
NODOSAURIDAE Marsh, 1890
?Nodosauridae indet.

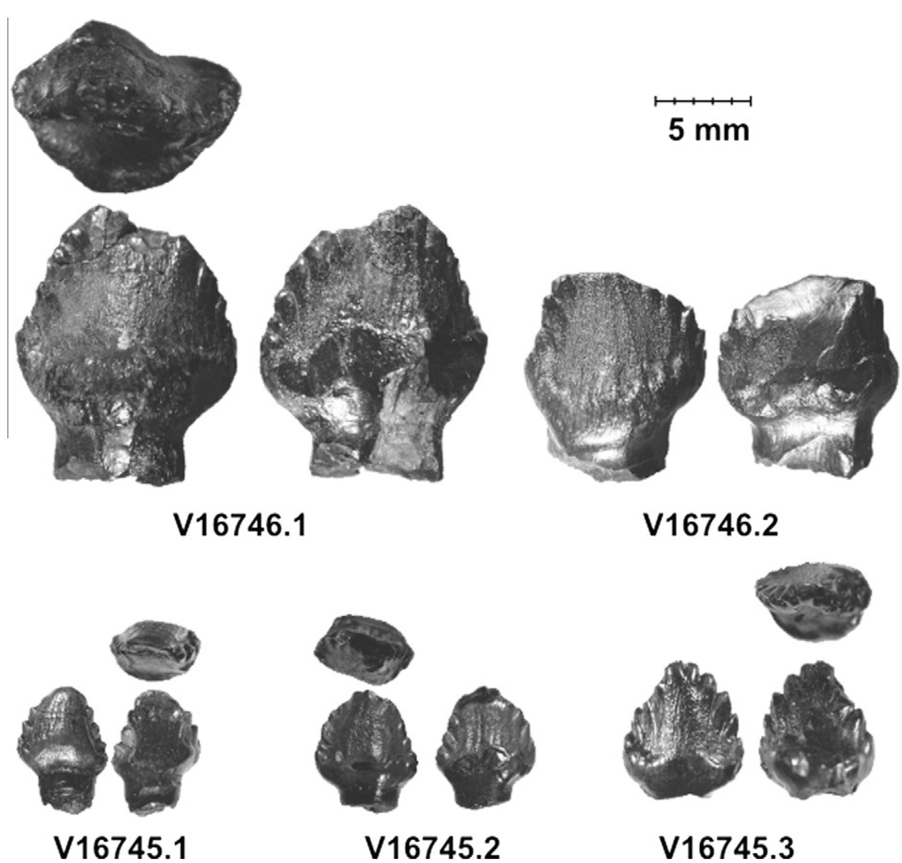

Fig. 5. Nodosaurid and ankylosaurid teeth. V16745.1, V16745.2 and V16745.3: Ankylosaurid tooth crowns (Nanhuang #3, Fuxin Fm.). V16746.1: Nodosaurid tooth crown (Nanhuang #3, Fuxin Fm.). V16746.2: Nodosaurid tooth crown (Mingda, Fuxin Fm.).

2.3.3. Description

One tooth crown has been recovered from the Nanhuang #3 locality (V16746.1) and one from the Mingda locality (V16746.2), both belonging to the Fuxin Formation (Fig. 5). They are compressed labio-lingually, have a general leaf-like shape and are about 10 mm wide. Crown carinae bear denticles (at least more than nine). On V16746.2, the occlusal face is marked by a well developed wear facet truncating the apicalmost part of the crown. The base of the crown is swollen and forms a marked cingulum. This cingulum is higher on the occlusal face than on the non-occlusal one where it is apically arched. Crown surfaces are wrinkled and bear several weakly developed apico-basal ridges. On V16746.2, the cingulum bears about six not clearly formed denticles from which apico-basal ridges start. The preserved root portions show a constriction below the crown-root junction.

2.3.4. Discussion

The teeth described above can be attributed to ankylosaurs on the basis of their leaf-like shape, their labio-lingually compression and the presence of an apical cusp with a series of secondary cusps along the edge of the crowns (Coombs, 1990). They are tentatively referred to two families. The two large teeth V16746.2 and V16746.1 may belong to nodosaurid ankylosaurs on the basis of the following features: the presence of a well developed cingulum at the base of the crown (Coombs, 1990) and the root constriction under the root-crown contact (Carpenter et al., 1995). In contrast, V16745.1, V16745.2 and V16745.3 have more ankylosaurid traits: small teeth with a swollen crown base that does not form a marked cingulum (Coombs, 1990) and a developed wear facet on the crown face rather than apical (Carpenter, 2004). Because ankylosaur teeth have a very conservative morphology and a limited use in taxonomy (Coombs, 1990), restricted at best to identification at the family level (Coombs and Maryanska, 1990), only speculations can only be made about the taxonomic attribution of the teeth from the Fuxin Formation. From a temporal point of view, possibly contemporaneous ankylosaurs from eastern Asia include the ankylosaurid *Gobisaurus domoculus* from the Ulansuhai Formation of Inner Mongolia, China (Vickaryous et al., 2001), the nodosaurid *Zhongyuansaurus luoyangensis* from the Early Cretaceous of Henan Province, China (Xu et al., 2007) and the ankylosaurid *Shamosaurus scutatus* from the Dzunbain Formation of Mongolia (Tumanova, 1983). Although that the material of these three ankylosaurs includes a few teeth, these have not been figured and only a very brief description of *Gobisaurus* has been published. *G. domoculus* teeth are of large size (up to 9.5 mm width) and possess an incipient cingulum along the lingual surface (Vickaryous et al., 2001), a combination of characters absent on the teeth from Fuxin. From a geographical point of view, two ankylosaur species recovered from Liaoning province have been described so far: the nodosaurid *Liaoningosaurus paradoxus* from the Lower Cretaceous Yixian Formation (Xu et al., 2001) and the ankylosaur of uncertain family *Crichtonsaurus bohlini* (Dong, 2002) from the lower Upper Cretaceous or upper Lower Cretaceous (Sha, 2007) Sunjiawan Formation. The general morphology of *Liaoningosaurus* teeth is very different from that of the teeth from the Fuxin Formation, but a possible reason might be that the type species of *L. paradoxus* is a juvenile individual (Xu et al., 2001), and its teeth may be different from those of an adult. On the other hand, the teeth of *C. bohlini* (IVPP V12745) look very similar to V16745.1, V16745.2 and V16745.3, especially because of their matching size and morphology of the swollen crown bases.

2.4. Ornithopoda

ORNITHISCHIA Seeley, 1887
ORNITHOPODA Marsh, 1881
IGUANODONTIA Sereno, 1986
IGUANODONTOIDEA Sereno, 1986
Iguanodontoidea indet.

2.4.1. Description

Three tooth fragments have been recovered from the Badaohao locality. They consist of left (V16747.1) and right (V16747.2) maxillary teeth as well as a right dentary tooth (V16747.3) (Fig. 6).

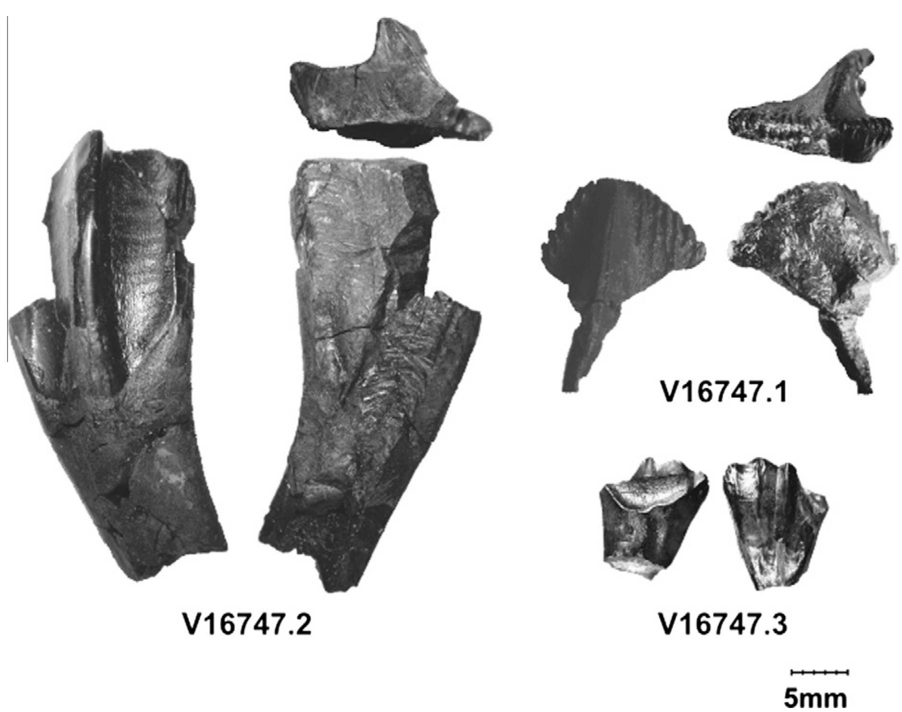

Fig. 6. Iguanodontoid teeth. V16747.1: left maxillary tooth (Badaohao, Shahai Fm.). V16747.2: right maxillary tooth (Badaohao, Shahai Fm.). V16747.3: right dentary tooth (Badaohao, Shahai Fm.).

Maxillary teeth. Crown and root of V16747.2 are partially preserved. The crown lacks the most apical part and a portion of its anterior half, and the root lacks its most basal part. The tooth is mesially concave and the crown coated with enamel only on the labial surface. A strong primary ridge very slightly offset distally from the midline bisects vertically the labial surface. The mesial and distal borders are thickened by a marginal shoulder that extends from the base of the crown to the most apical part of the fragment. The surfaces of the mesial and distal edges are indented by a vertical channel which marks the position of adjacent replacement crowns. Unlike V16747.2, V16747.1 has only the most apical part of the crown preserved. The mesial and distal borders bear denticles close to the apex. The denticles are well developed, formed from curved ledges extending from the lingual to the labial surface of the edges and having additional mammillations on the apicalmost part of the ledges. On the mesiolabial surface, four small weak ridges, 3–4 mm long, extend vertically from the denticles. No other secondary ridges can be observed on both the mesial and distal preserved surfaces.

Dentary tooth. V16747.3 is the crown of a right dentary tooth close to the limit between crown and root. The developed wear facet on the labial face and the fact that only half of the crown remains indicate that V16747.3 was a functional tooth. The lingual surface is covered with enamel. It bears a primary ridge dividing the surface into unequal halves. The mesial half is bisected by a lower secondary ridge parallel to the primary ridge. Between the two major ridges, two narrow wrinkles follow the major ones but merge into a single one in the middle of the basal half of the crown. The three first basal denticles are preserved on the mesial edge of the crown. They have a crenulated ledge shape that wraps around the edge of the crown.

2.4.2. Discussion

These teeth can be referred to derived iguanodontians according to the following features (Norman, 2004): crowns are buccolingually compressed and mesiodistally expanded, presenting a flattened, shield-shaped face subdivided by a submedian, prominent primary ridge buccally (maxillary teeth) or a much less prominent primary ridge and a secondary ridge situated mesial to the primary one (dentary teeth); maxillary and dentary crowns only enameled buccally and lingually, respectively; crowns bear mammillated denticles. Several Asian species of Early Cretaceous iguanodontians have been described. They include the Chinese species *Jinzhousaurus yangi* from the Yixian Formation of Liaoning (Wang and Xu, 2001), *Nanyangosaurus zhugeii* from the Sangping Formation of Henan (Xu et al., 2000a), *Probactrosaurus mazongshanensis* (Lü, 1997) and *Equijubus normani* (You et al., 2003b) from the Xinminbao Group of Gansu, *Lanzhousaurus magnidens* from the Lanzhou Basin of Gansu (You et al., 2005a), *Penelopognathus weishampeli* from the Bayan Gobi Formation of Inner Mongolia (Godefroit et al., 2005), as well as *Probactrosaurus gobiensis* and *Probactrosaurus alashanicus* from the Dashuigou Formation of Inner Mongolia (Rozhdestvensky, 1966). It is noteworthy that, according to Norman (Norman, 2002), *P. alashanicus* is a junior synonym of *P. gobiensis*, and that *P. mazongshanensis* might not belong to *Probactrosaurus* based upon tooth morphology. Other Asian species are *Altirhinus kurzanovi* from Mongolia (Norman, 1998) and *Fukuisaurus tetoriensis* from the Kitadani Formation of Japan (Kobayashi and Azuma, 2003). Other iguanodontian remains that share dental similarities with *Probactrosaurus* have been recovered from the Khok Kruat Formation of Thailand (Buffetaut et al., 2005, 2006). As *N. zhugeii* is only known from post-cranial elements, direct comparison with our material is not possible. The Badaohao maxillary teeth V16747.2 and V16747.1 share similarities with those of *Probactrosaurus* and the Thai iguanodontian in having only one prominent and sub-central ridge (no secondary ridge), and differ from *Jinzhousaurus*, *Equijubus* and *Lanzhousaurus* teeth that possess two or more subsidiary ridges, a more primitive condition (You et al., 2003b, 2005a; Barrett et al., 2009). The comparison with *A. kurzanovi* and *F. tetoriensis* is complicated by the presence in these two species of maxillary teeth lacking secondary ridges and others having one on the mesial half of the lingual surface (Norman, 1998; Kobayashi and Azuma, 2003). The dentary tooth V16747.3 seems to possess one primary ridge and one secondary ridge, but as part of the distal portion of the crown is broken, the absence of a distal subsidiary ridge is not certain. V16747.3 can thus match the morphology of *P. gobiensis* in having only two ridges on the lingual surface (Norman, 2002), but also those of *A. kurzanovi*, *P. mazongshanensis*, *P. weishampeli* and *F. tetoriensis* which also possess a distal ridge on some teeth (Godefroit et al., 2005; Kobayashi and Azuma, 2003; Lü, 1997; Norman, 1998).

2.5. Ceratopsia

ORNITHISCHIA Seeley, 1888
CERATOPSIA Marsh, 1890
NEOCERATOPSIA Sereno, 1986
Neoceratopsia indet.

2.5.1. Description

One second (V16748.1) and one third (V16748.2) dentary teeth, one premaxillary tooth (V16748.3), and eight maxillary or dentary teeth (V16748.4, V16748.5, V16748.6, V16748.7, V16748.8, V16748.9, V16748.10 and V16748.11) have been recovered from the Shahai Formation at the Badaohao locality (Fig. 7). The crowns of maxillary or dentary teeth are compressed labio-lingually, seem to bear enamel on both faces and have five to eleven marginal denticles. The root is straight, compressed antero-posteriorly, and bears a lateral groove on one or both sides. On one side, the crown surface is convex and bisected by a strong primary ridge displaced from the mid line and that extends vertically from the base of the crown to the tip. On both sides of this ridge, secondary ridges extend either parallel to the primary ridge or at an angle to it. The mesial and distal borders of V16748.8 are swollen and join the basal end of the primary ridge with a trident-like shape, a feature that is not very marked on the other teeth. On the other side of the crown, the teeth have a well developed wear facet that forms a cutting edge on the apicalmost part. The crown of the premaxillary tooth V16748.3 is only slightly compressed labio-lingually and pointed, and bears rostral and caudal carinae, whereas the root is circular in cross section and the crown-root contact is constricted. V16748.1 is strongly compressed labio-lingually, the crown has a lanceolate shape with carinae bearing small denticles. Both labial and lingual sides of the crown bear a central swollen ridge that extends obliquely from the base to the tip of the crown. V16748.2 has a swollen crown with a fluted surface bearing on its labial face vertical and parallel ridges originating from the marginal denticles and ending at the base of the crown. The lingual surface bears a larger central ridge and secondary ridges extending from the base or from the primary ridge to the tip of the crown where they form denticles.

2.5.2. Discussion

The maxillary or posterior dentary teeth bear a characteristic synapomorphy of neoceratopsians which is the offset of the primary ridge (You and Dodson, 2003; Butler et al., 2008). It is noteworthy that these teeth also share morphological similarities with the two basal cerapodans of uncertain phylogenetic position *Changchunsaurus parvus* (Zan et al., 2005) and *Albalophosaurus yamaguchiorum* (Ohashi and Barrett, 2009) from the Quantou Formation of China and Kuwajima Formation of Japan, respec-

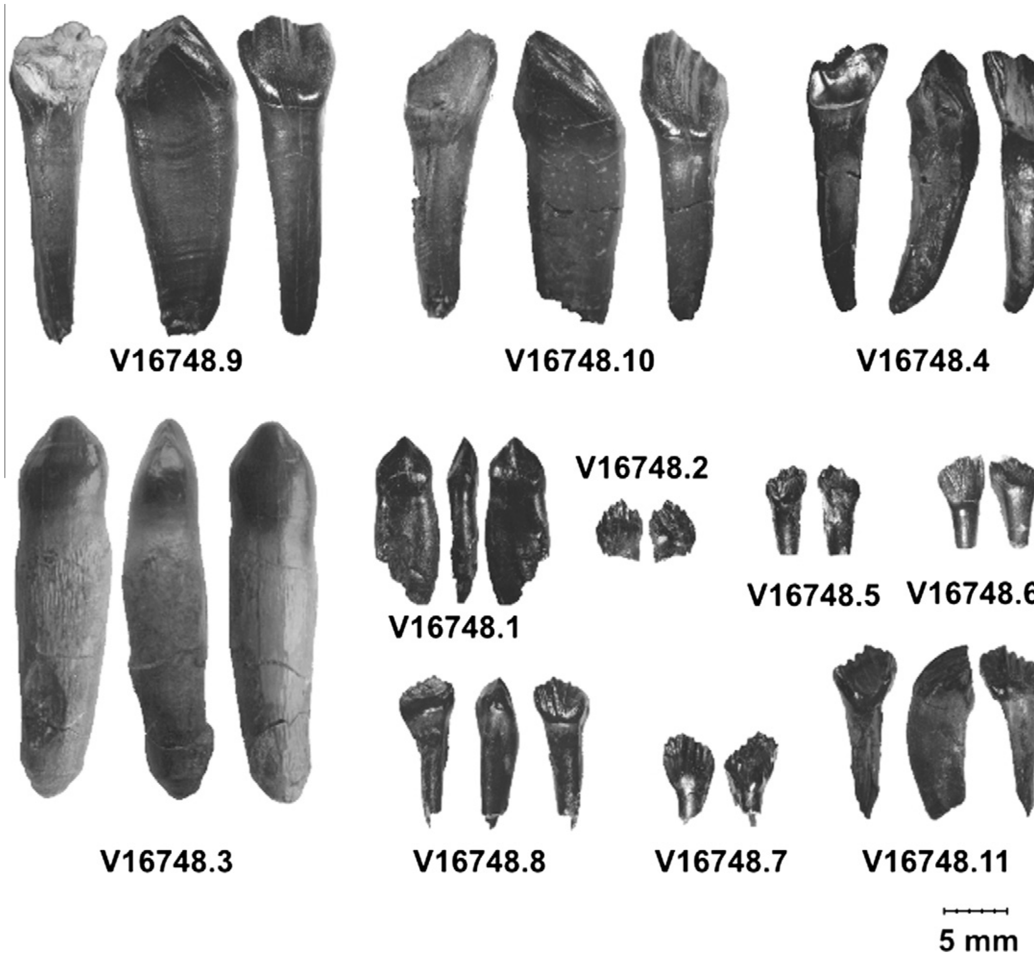

Fig. 7. Neoceratopsian teeth. V16748.1: second dentary tooth (Badaohao, Shahai Fm.). V16748.2: third dentary tooth (Badaohao, Shahai Fm.). V16748.3: premaxillary tooth (Badaohao, Shahai Fm.). V16748.4, V16748.5, V16748.6, V16748.7, V16748.8, V16748.9, V16748.10 and V16748.11: eight maxillary or dentary teeth (Badaohao, Shahai Fm.).

tively. However, in *C. parvus* and *A. yamaguchiorum*, the primary and secondary ridges are less prominent and less developed than those of the studied teeth which more closely resemble those of basal neoceratopsians in this respect. The presence of enamel on both faces of dentary or maxillary teeth indicates that the Badaohao ceratopsian differs from coronosaurian and leptoceratopsid neoceratopsians (Jin et al., 2009) and from *Yamaceratops dorngobiensis* from the Lower Cretaceous Khugenetslavkant Sandstone of the Gobi Desert in Mongolia (Makovicky and Norell, 2006). Comparison with the type specimens of *Archaeoceratops oshimai* (IVPP V11114) and *Liaoceratops yanzigouensis* (IVPP V11115) allows a direct match of some teeth from Badaohao: V16748.1 corresponds to a second left dentary tooth and V16748.2 to a third left dentary tooth of *A. oshimai*. V16748.3 is similar to premaxillary teeth of both *A. oshimai* and *L. yanzigouensis*. *A. oshimai* and *L. yanzigouensis* are two primitive neoceratopsians recovered from the Lower Cretaceous Xinminbao Group near Mazongshan in Gansu Province, China (Dong and Azuma, 1997) and from the Yixian Formation of Liaoning (Xu et al., 2002b), respectively. Other basal neoceratopsians from the Early Cretaceous of northeastern China include *Auroraceratops rugosus* from the Xinminpu Group of Gansu Province (You et al., 2005b) and *Helioceratops brachygnathus* from the Quantou Formation of Jilin Province (Jin et al., 2009). The premaxillary tooth from Badaohao differs from those of *A. rugosus* ones in lacking striations on the crown surface. Therefore, the Badaohao teeth may be referred to either *L. yanzigouensis*, *A. oshimai* or *H. brachygnathus*.

3. General discussion and conclusion

Despite the fragmentary nature of the Shahai and Fuxin dinosaur remains and the relatively poor diagnostic characteristics of isolated dinosaur teeth, significant taxonomic, biostratigraphic and paleoecological information can be inferred from the collected specimens. First, the Shahai and Fuxin dinosaur faunas show a transitional state between the vertebrate communities of the Jehol Biota and Late Cretaceous dinosaur faunas. Some taxa such as the oviraptorosaur *Incisivosaurus*, basal neoceratopsians, basal titanosauriform sauropods and small dromaeosaurid theropods seem to have persisted from the Yixian Formation to the Shahai Formation, and for some of them to the Fuxin Formation and the Late Cretaceous, whereas some more derived taxa, iguanodontoid ornithopods and ankylosaurs that are more derived than those of the Jehol Biota appeared after the deposition of the Jiufotang Formation. From a biostratigraphic point of view, the Fuxin and Shahai dinosaur faunas share common elements with other Early Cretaceous Asian dinosaur faunas such as iguanodontians, basal titanosauriforms and basal neoceratopsians with the Aptian–Albian Xinmingbao Formation of Gansu Province (Tang et al., 2001), basal titanosauriforms and iguanodontians with the Aptian–Albian Khok Kruat Formation of northeastern Thailand (Buffetaut et al., 2005), or iguanodontians and basal titanosauriforms with the Early Cretaceous Kuwajima Formation of Japan (Hirayama et al., 2003). Moreover, the presence of the genus *Incisivosaurus* in both the Yixian and in the Shahai and Fuxin formations suggests a short age differ-

Table 2
Number of teeth and percentage of represented taxa in Shahai and Fuxin formations.

Formation	Fuxin		Shahai	
Taxon	*N*	%	*N*	%
Ankylosauria	17	40	1	3
Theropoda	25	60	11	35
Sauropods	0	0	4	13
Ceratopsians	0	0	11	35
Iguanodontoid	0	0	4	13
Total	42		31	

ence between these formations, assuming a limited longevity of dinosaur genera (about 7 ± 3 millions of years according to Dodson, 1990). Because the age of the Sunjjiawan Formation (uncomformably overlying the Fuxin Formation) remains ambiguous, sometime considered as late Early Cretaceous (e.g., Sha, 2007), sometime as early Late Cretaceous (e.g., You et al., 2003a), these new data further support a late Early Cretaceous age for the Shahai and Fuxin faunas, most probably within the Aptian to Albian interval. The persistence of *Incisivosaurus*, an oviraptorosaur with an extremely high degree of heterodonty (Xu et al., 2002a) which may be an indication of feeding specialisation, suggests a relatively long term stability of Early Cretaceous terrestrial environments in northeastern China, at least during the deposition of the Yixian, Jiufotang, Shahai and Fuxin formations. Indeed, diverse and abundant fossil plant assemblages characterize the Early Cretaceous deposits in western Liaoning, mainly in the Yixian, Shahai and Fuxin formations, and a subtropical to temperate upland forest vegetation type persisted all along this timespan in western Liaoning (e.g., Saiki and Wang, 2003).

Based on a total of 73 identifiable teeth recovered from both the Shahai and Fuxin formations, including those described here (Table 2), differences in the abundances of the various taxa between the Shahai and Fuxin formations can be observed (Fig. 8). Sauropods and iguanodontoids have only been recovered from deposits of the Shahai Formation at Badaohao locality, and seem to be absent from the Fuxin Formation. However, due to the extreme scarcity of their fossil remains in the Shahai Formation, as well as in the Jehol Group (Barrett and Wang, 2007), their absence in the Fuxin Formation can be either a collecting bias or a real absence. Basal neoceratopsian teeth, which are abundant in the Shahai Formation, are absent in the Fuxin Formation, whereas ankylosaurs are rare in the Shahai Formation but are abundant and are the only herbivorous dinosaurs in the studied localities of the Fuxin Formation. As studied ankylosaur and neoceratopsian teeth are close in size, and considering the non selective collecting method used during field excavations, a sampling bias alone is hardly plausible to explain such a trend. The apparent replacement of autochthonous neoceratopsians by ankylosaurs between the Shahai and Fuxin formations may be a result of competition for food resources or a difference of local environmental conditions during the deposition of the Fuxin Formation. A possible difference of local environment between the Badaohao site and those of the Fuxin Formation, which are a few kilometres distant from each other and in which sediments are slightly different is the most likely explanation, as these two dinosaur groups may have been restricted to different micro-habitats suitable for foraging specific plants. Ankylosaurs, for instance, are usually considered to be denizens of wet and well vegetated environments (Vickaryous et al., 2004) whereas basal neoceratopsians can be found in a wider range of sedimentary environments (You and Dodson, 2004). It is noteworthy that the dinosaur faunal composition found in Fuxin localities, only composed by theropods and ankylosaurs is clearly unusual and unbalanced. At this point, no explanation can be proposed and additional sampling in the Fuxin and Shahai formations is needed to better constrain the relative abundances of the different taxa in order to confirm the observed patterns.

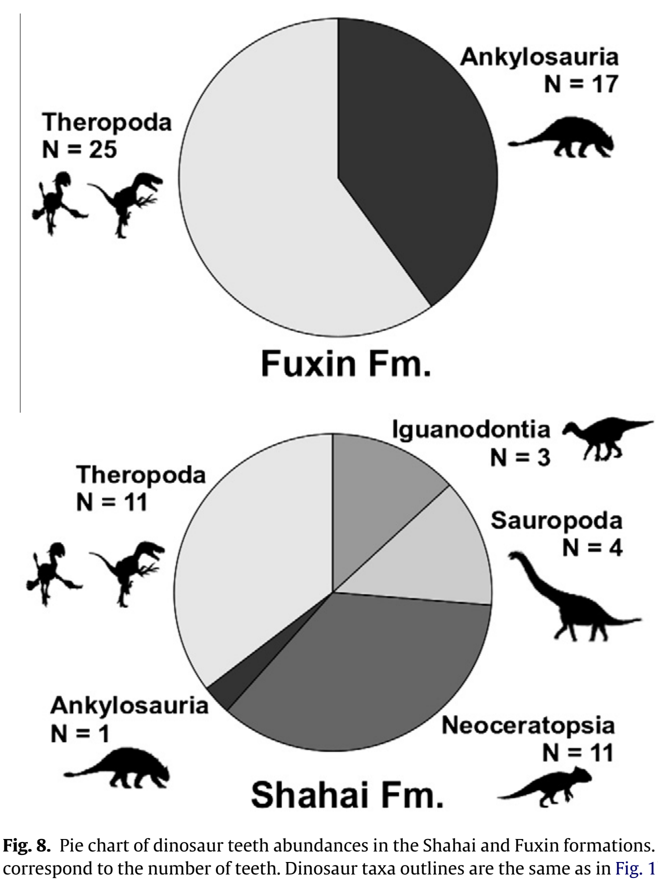

Fig. 8. Pie chart of dinosaur teeth abundances in the Shahai and Fuxin formations. *N* correspond to the number of teeth. Dinosaur taxa outlines are the same as in Fig. 1b.

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