A NEW THERIZINOSAUR FROM THE LOWER JURASSIC LOWER LUFENG FORMATION OF YUNNAN, CHINA

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ABSTRACT—A specimen collected from the Lower Jurassic Lower Lufeng Formation of Yunnan, China, represents a new genus and species of therizinosauroid theropod. It comprises an incomplete left mandibular ramus and is here named *Eshanosaurus deguchiianus.* Distinctive characteristics of the new species include the presence of a round fenestra in the posterior portion of the dentary, small size of tooth denticles, and denticles almost perpendicular to the anterior and posterior edges of tooth crowns. The discovery of *Eshanosaurus deguchiianus* extends the record of therizinosauroids from the Early Cretaceous back to the Early Jurassic. Recent phylogenetic hypotheses placing therizinosauroids within Coelurosauria imply this is the oldest known coelurosaur, and that diversification of the group began much earlier than was previously indicated by the fossil record.

INTRODUCTION

Therizinosauroidea (''segnosaurs'') are a poorly known group of dinosaurs with an unusual combination of features. When the Segnosauria were first described they were interpreted as theropods (Perle, 1979, 1981; Barsbold and Perle, 1980; Barsbold, 1983), but this interpretation was later questioned, and subsequently suggested segnosaurian affinities include Ornithischia (Paul, 1984), Sauropodomorpha (Gauthier, 1986; Sereno, 1989), and Saurischia sedis mutabilis (Barsbold and Maryańska, 1990). Substantial evidence for theropod affinities was provided by the discovery of *Alxasaurus elesitaiensis* (Russell and Dong, 1994), which possesses numerous theropod synapomorphies, especially in its forelimb. Specimens of the latter also revealed similarities with the poorly known *Therizinosaurus cheloniformis,* and hence the Segnosauridae was synonymized with the Therizinosauridae and the Therizinosauroidea was erected to include this family and *Alxasaurus* (Russell and Dong, 1994). A redescription of the only segnosaur skull known, that of *Erlikosaurus andrewsi* (Clark et al., 1994) presented further evidence for theropod affinities, especially with Coelurosauria. Recent phylogenetic studies further support the coelurosaurian affinities of Therizinosauroidea (Sues, 1997; Makovicky and Sues, 1998; Sereno, 1999). The discovery of *Beipiaosaurus* indicates that, ancestrally, therizinosaurs possessed the functionally tridactyl hindfoot typical of theropods rather than the sauropodomorph-like tetradactyl hindfoot and thus provides new evidence for the theropod affinities of therizinosaurs (Xu et al., 1999).

Most fossils definitively referable to this group are recorded from Late Cretaceous deposits (Barsbold and Maryanska, 1990). The earliest record is from the lower part of the Yixian Formation (Xu et al., 1999), the age of which is controversial (Xu and Wang, 1998) and probably Early Cretaceous according to the latest radiometric date (Swisher et al., 1998). In 1971, Zhao Xijin collected the specimen described here, a dentary and part of the splenial, from the Lower Jurassic Lower Lufeng Formation. Though the fossil material is limited, it shows enough apomorphies to indicate its reference to Therizinosauroidea, and thus represents the oldest known member of this group, more than doubling its known stratigraphic range. This has very important implications for the hypothesized relationship of birds to non-avian theropod dinosaurs in that it effectively counters the arguments that all derived non-avian theropods are geologically too recent to have been ancestral to birds (Zhao and Xu, 1998). Due to the importance of this material and a few unusual features, which are important for character distributions among basal therizinosauroids, we here present a detailed description and propose a new Linnean binomen for this material.

The specimen was collected from marlite beds of Lower Lufeng Formation in the Dianzhong Basin, Eshan County, Yunnan, southeastern China. The Dianzhong Basin is filled with more than 2,000 m of Middle Mesozoic red sediments. The sequence comprises the Proterozoic Kunyang Group dolomitic limestone, the Upper Triassic Yipinglang Group sandstones and mudstones, the Lower Jurassic Lower Lufeng Formation redbeds and the Middle Jurassic Upper Lufeng Formation redbeds. The marlite beds containing the therizinosaur material are at the base of the Lower Lufeng Formation. Numerous prosauropod specimens (probably *Lufengosaurus*) were collected from the Dull Purplish Beds of the Lower Lufeng Formation at this site, about 200 m above the therizinosaur-bearing bed.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881
THERIZINOSAUROIDEA Maleev, 1954
ESHANOSAURUS DEGUCHIIANUS, gen. et sp. nov. (Figs. 1, 2)

Holotype—IVPP V11579 (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; Figs. 1, 2), incomplete left mandible with dentition.

Horizon and Locality—Lower part of Lower Lufeng Formation, Eshan County, Yunnan, southeastern China; age: Early Jurassic, Hettangian stage (Sun and Cui, 1986; Luo and Wu, 1994).

Etymology—Generic name refers to the geographic region that includes the type locality, and specific name is in honor of Hikaru Deguchiianus, who gave encouragement and support to the first author in studying dinosaurs.

Diagnosis—A small therizinosauroid distinguishable from other therizinosauroids by the presence of a round fenestra in the posterior portion of the dentary (but see discussion); tooth denticles smaller relative to those in other therizinosauroids; tooth denticles almost perpendicular to the anterior and posterior margins of the crown.
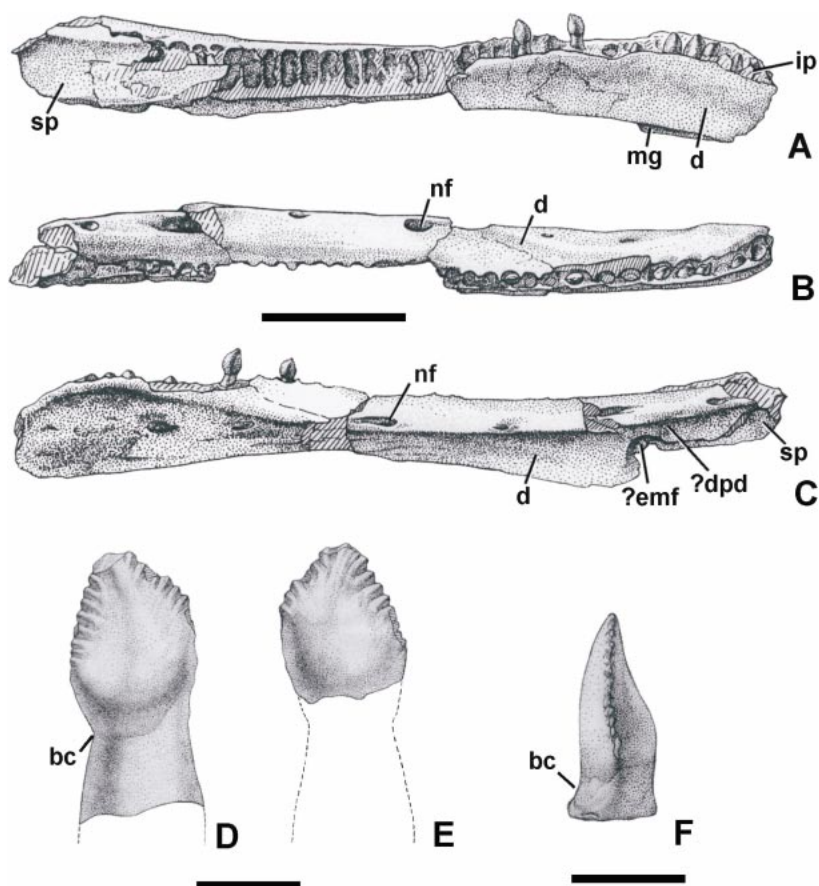
FIGURE 1.   Holotype of *Eshanosaurus deguchiianus,* gen. et sp. nov. (IVPP V11579); left mandible in medial (**A**), dorsal (**B**) and lateral (**C**) views. Scale bar equals 2 cm. Fifteenth dentary tooth in medial (**D**) and lateral (**E**) views. The lower portion of the fiftheeth dentary tooth is obscured by the dentary bone. Scale bar equals 2 mm. Twelfth dentary tooth in posterior view (**F**). Scale bar equals 2 mm. **Abbreviations**: **bc**, basal constriction; **d**, dentary; **?dpd**, ?dorsoposterior process of dentary; **?emf**, ?external mandibular fenstra; **ip**, interdental plate; **mg**, Meckelian groove; **nf**, nutrient foramina; **sp**, splenial.

DESCRIPTION

Only the broken left mandibular ramus is preserved, consisting of most of the left dentary and part of the splenial, both incomplete ventrally (Figs. 1A–C, 2A–C). In lateral view, the dorsal edge of the dentary is straight throughout most of its length but curves downward rostrally, and posteriorly it rises upward to form the beginning of a low coronoid process. The preserved ventral margin describes a gently concave arc due to the downturned rostral end and the descent of the ventral margin posteriorly. The dentary is bifurcated posteriorly around a small, round fenestra, the anterior margin of which lies anterior to the posterior end of the dentary tooth row. In dorsal view, the anterior end of the dentary curves slightly laterally while the posterior end curves slightly medially, giving it a slightly sigmoid shape. Teeth are present at the anterior end of the dentary, but because the dentary is incomplete anteriorly it is unclear whether its rostral end is edentulous, as in other therizinosauroids except *Alxasaurus.* The tooth row is strongly inset for most of its length due to the presence of a broad, flat shelf lateral to the dentition posterior to the sixth preserved tooth. The shelf broadens gradually to face first somewhat dorsolaterally and then dorsally, and is convex dorsally at its posterior end. Along the length of the shelf, four relatively large foramina lie near the lateral edge, the third one being the largest. Similarly spaced foramina lie on the lateral surface of the dentary anterior to the shelf. A strongly developed lateral ridge extends along the lateral edge of the shelf, and below this ridge the lateral surface of the dentary is gently concave. In medial view, dorsally pointed, triangular interdental plates are present, as in most theropods and prosauropods (Galton, 1990). Those of the symphyseal region are more broadly exposed due to the lower medial surface of the dentary here. The dorsal part of the Meckelian groove is deeply incised into the medial surface of the dentary. Anteriorly, it becomes shallower until it terminates below the third preserved tooth. It broadens posteriorly, connecting with the possible external mandibular fenestra. In medial view, the dorsal margin of the Meckelian groove is straight posteriorly and curves downward anteriorly.

Alveoli for 34 closely spaced teeth are preserved and several more could be present in the now missing portion of the symphysial region. Most of the teeth are missing but five anterior teeth (third, fifth to seventh and ninth), two in the middle of the row (twelfth and fifteenth), and one posterior tooth (thirty second) are present. Among the preserved teeth, the crowns of the anterior teeth are larger than those in the middle of the tooth row. The crowns are lanceolate, transversely compressed, and completely enameled, with convex lingual and labial surfaces. The anterior edge is convex and bears fewer marginal denticles than the concave distal edge. A constriction is evident between the base of the crown and the root. Most teeth show no wear, but the tip of the fifteenth dentary tooth shows some evidence of wear (Fig. 1D, E). The roots of the teeth are nearly circular
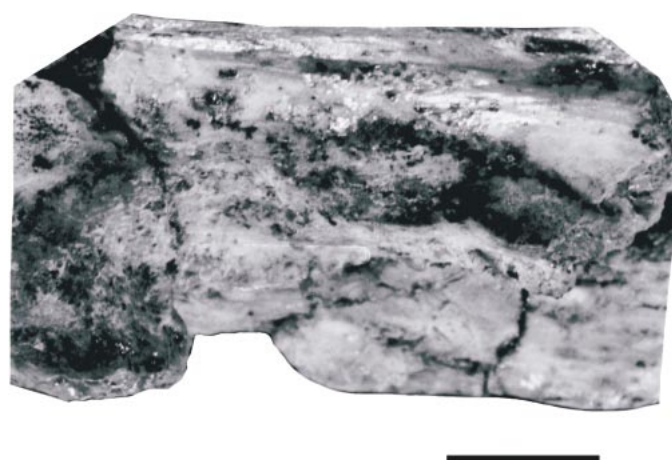
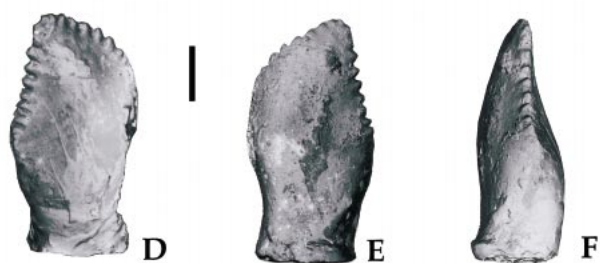FIGURE 3. External mandibular fenestra (?) of holotype of *Eshanosaurus deguchiianus.* Scale bar equals 0.5 cm.

FIGURE 2. Holotype of *Eshanosaurus deguchiianus*; left mandible in medial (**A**), dorsal (**B**) and lateral (**C**) views. Twelfth dentary tooth was removed when these photos were taken. Scale bar equals 3 cm. Twelfth dentary tooth in medial (**D**), lateral (**E**), and posterior (**F**) views. Scale bar equals 1 mm.

in cross-section but compressed slightly mediolaterally. The third, sixth, seventh, ninth and thirty second alveoli show tooth replacement, in the following relative degrees of eruption: 6 = 7>3>9>32.

The teeth are serrated anteriorly and posteriorly. The anterior edge of a middle tooth has 3.5 denticles per mm, the posterior edge 4.4 denticles per mm. For teeth of this size (Fig. 2D, E), these denticles are smaller than in other therizinosauroids (Clark et al., 1994; Russell and Dong, 1994) and troodontids (Farlow et al., 1991).

DISCUSSION

The Lufeng specimen (IVPP V11579) previously was identified as the earliest therizinosauroid but not given a Linnean binomen (Zhao and Xu, 1998). Further study suggests that, though the material is limited, it shows sufficient features to distinguish it from all known therizinosauroids. We will discuss below the phylogenetic position of *Eshanosaurus.*

Therizinosauroid Affinity of *Eshanosaurus*—The identification of *Eshanosaurus* as a therizinosauroid was based on comparisons with other theropods as well as basal sauropodomorphs and ornithischians, however, less emphasis was placed on comparisons with the latter two groups considering their distant relationships to theropods (Zhao and Xu, 1998). However, the theropod affinities of *Eshanosaurus* were recently questioned (Mr. Lamanna, pers. comm.) and we will therefore compare *Eshanosaurus* with basal sauropodomorphs and ornithischians to support its therizinosauroid affinities.

1. Anterior teeth larger than middle and posterior teeth (Figs.

1A, 2A). Although most of the dentary teeth of *Eshanosaurus* are missing, it is obvious from the alveoli that the anterior teeth are larger than middle ones. In *Eshanosaurus,* the crowns of the three preserved anterior teeth are more than 1.5 times larger than those of the two teeth in the middle of the jaw. A distal decrease in tooth size is uniquely shared by *Eshanosaurus* and other therizinosauroids among theropods (Clark et al., 1994). Among dinosaurs, only some derived sauropods, i.e., *Omeisaurus* (He et al., 1984), share this feature, yet they are apparently different from *Eshanosaurus* in other features. In some prosauropods, the anterior teeth are also large, but they are at most subequal in size to the middle teeth (Galton, 1990:fig. 15.3). In ornithischians, the anterior teeth are much smaller than the middle teeth in size and the middle teeth attain the maximum tooth size along the tooth rows (Sereno, 1986).

2. Small size and large number of the teeth (Figs. 1A, 2A). This feature is shared by therizinosauroids, troodontids and ornithomimosaurs among theropods (Clark et al., 1994; Perez-Moreno et al., 1994). The total number of teeth of *Eshanosaurus* is at least 34, which is more than in Therizinosauridae (including *Erlikosaurus* and *Segnosaurus*) and similar in number to the two relatively primitive therizinosauroids *Alxasaurus* (Russell and Dong, 1994) and *Beipiaosaurus* (Xu et al., 1999). Some prosauropods have a large number of dentary teeth but never more than 30 (Galton, 1990). The comparative size of dentary teeth to mandible of all known prosauropods is larger than that of *Eshanosaurus.* In known Early Jurassic ornithischians, the dentary tooth number is much less than 34.

3. Recurvature of dentary teeth (Figs. 1D, E, 2D, E). Most theropods have recurved tooth crowns. Among therizinosauroids, *Eshanosaurus, Beipiaosaurus* (Xu et al., 1999), and *Segnosaurus* (Barsbold, 1983) have slightly recurved tooth crowns whereas *Alxasaurus* and *Erlikosaurus* have nearly symmetrical tooth crowns in labial view. Recurvature is absent in maxillary and dentary teeth of ornithischians (Sereno, 1986). Prosauropods have weakly recurved teeth (Galton, 1990).

4. Denticles almost perpendicular to the anterior and posterior edges of tooth crowns (Figs. 1D, E, 2D, E). In herbivorous dinosaurs, including ornithischians and sauropodomorphs, the denticles of tooth crowns tend to be apically directed (Fig. 4A, C). While in carnivorous dinosaurs, the denticles are perpendicular to the cutting edges of tooth crowns (Gal-
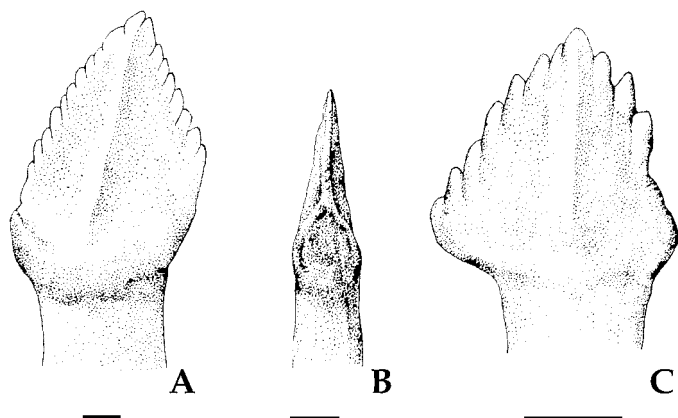
FIGURE 4.   A prosauropod tooth (*Azendohsaurus*) in lateral (**A**) and anterior (**B**) views. Scale bar equals 1 mm and 2 mm respectively. An ornithischian tooth (*Lesothosaurus*) in medial view (**C**). Scale bar equals 1 mm. Modified from figure 16.3, K and 16.4, A and K in Galton (1986).

FIGURE 5.   Dentary tooth of *Beipiaosaurus* in lateral (**A**) and anterior (**B**) views. Scale bar equals 1 mm.

ton, 1986). *Eshanosaurus* shares this feature with most carnivorous dinosaurs and thus differs from prosauropods in which the denticles of tooth crowns are set at an angle of about 45 degrees to the cutting edges (Galton, 1990), and ornithischians in which the denticles are almost paralleled to the anterior and posterior margins (Fig. 4C). Derived therizinosauroids other than *Eshanosaurus* are similar to prosauropods and ornithischians in having apically directed denticles (Fig. 5A)

5. Tooth crowns asymmetrical in anterior view (Figs. 1F, 2F). As in *Beipiaosaurus* (Fig. 5B) and *Segnosaurus,* the crowns of dentary teeth of *Eshanosaurus* are asymmetrical in anterior view, whereas in all prosauropods except *Yunnanosaurus* the crowns are symmetrical in anterior view (Fig. 4B; Galton, 1986, 1990). The teeth of *Yunnanosaurus* are, however, apparently different from those of *Eshanosaurus* in other features (Galton, 1986:figs. 16.3, 16.4).

6. The presence of a constriction between tooth crown and tooth root (Figs. 1D–F, 2D–F). Similar to other therizinosauroids, there is a distinct constriction between crown and root in *Eshanosaurus*. This feature is shared by therizinosauroids, troodontids, *Pelecanimimus* (Perez-Moreno, 1994) and basal birds among theropods (Clark et al., 1994). In prosauropods and ornithischians, a basal constriction is also present between the crown and root, however, it is in a different position than in theropods. In prosauropods and ornithischians, the tooth crown forms a basal constriction whereas in theropods, including basal birds, both the tooth crown and the root contribute to the formation of the basal constriction.

7. Tooth root slightly wider than the crown mesiodistally (Fig. 1D, E). In most theropods, the tooth root is subequal or wider than the crown mesiodistally. Similar to other therizinosauroids (Fig. 5) and most theropods, the tooth root is slightly wider than the crown in lateral view in *Eshanosaurus*. In all known ornithischians and prosauropods, the tooth crown is distinctly wider than the root in lateral view (Fig. 4A, C).

8. Root with a subcircular cross section. In *Eshanosaurus,* the tooth root is subcircular in cross section and lacks the mediolateral compression typical of theropod teeth. This feature is shared by other therizinosauroids among theropods (Clark et al., 1994), prosauropods and ornithischians.

9. Presence of interdental plates (Figs. 1A, 2A). Interdental plates are present in theropods and some prosauropods (Galton, 1990) among dinosaurs. No ornithischian was reported to have interdental plates developed in the jaws. However, *Eshanosaurus* clearly has interdental plates on the dentary, and differs from all known ornithischians in this feature.

10. Presence of a flat and broad shelf lateral to the tooth row (Figs. 1B, 2B). One of the most striking therizinosauroid features of *Eshanosaurus* is the presence of a shelf lateral to the tooth row and a few large nutrient foramina below it. This has been interpreted previously as evidence for cheeks (Paul, 1984). This shelf is found in therizinosauroids, some ornithischians and incipiently in some prosauropods among dinosaurs, but in therizinosauroids the shelf is distinctly broader and flatter. The mandibular shelf of *Eshanosaurus* is very flat and about 8 mm in transverse width along most of its length, which is very broad compared to the mandible size (Figs. 1B, 2B), and thus similar to the therizinosauroid condition. The structure of the shelf of *Eshanosaurus* is also the same as in *Alxasaurus* (Russell and Dong, 1994) and *Erlikosaurus* (Clark et al., 1994) in that the shelf is forming a right angle with the lateral surface of the mandible.

11. Downturned anterior end of the dentary (Figs. 1A, B, 2A, B). This feature is shared by therizinosauroids, ornithomimosaurs (Clark et al., 1994) and, to a lesser degree, *Caudipteryx* (Ji et al., 1998) among theropods. Some prosauropods and ornithischians also share this feature.

In summary, *Eshanosaurus* is distinguishable from prosauropods on the presence of the following characters: anterior teeth larger than middle and posterior teeth, small size and large number of the teeth (more than 34), denticles almost perpendicular to the anterior and posterior edges of tooth crowns, tooth crowns asymmetrical in anterior view, the presence of a basal constriction between crown and root of theropod type, tooth root slightly wider than the crown mesiodistally, and presence of a flat and broad shelf lateral to the tooth row. It differs from ornithischians on the presence of the following characters: anterior teeth larger than middle and posterior teeth, small size and large number of the teeth (more than 34), recurvature of dentary teeth, denticles almost perpendicular to the anterior and
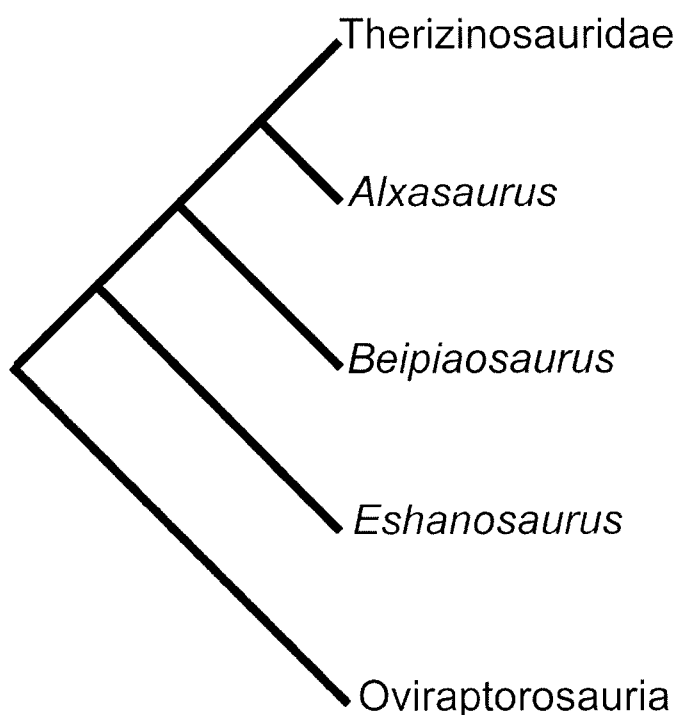
FIGURE 6. Cladogram showing a speculative set of relationships between *Eshanosaurus* and other therizinosauroids. Modified from Xu et al. (1999:fig. 4).

posterior edges of tooth crowns, the presence of a basal constriction between crown and root of theropod type, tooth root slightly wider than the crown mesiodistally, presence of interdental plates, and presence of a flat and broad shelf lateral to the tooth row. Other therizinosauroids share all above characters but character 4 (denticles almost perpendicular to the anterior and posterior edges of tooth crowns).

Based on above comparisons, we believe that *Eshanosaurus* is most parsimoniously explained as a member of Therizinosauridea and our former identification is correct (Zhao and Xu, 1998).

Autopomorphies of *Eshanosaurus*—*Eshanosaurus deguchiianus* differs from other therizinosauroids in having following autopomorphies:

12. The presence of a round fenestra in the posterior portion of the dentary (Figs. 1C, 2C, 3). In *Eshanosaurus,* a small, round fenestra located in the posterior portion of the dentary. It is about 7 mm in diameter, and connected with the Meckelian canal medially. A fenestra in this position has not been reported previously in dinosaurs and thus represents a distinct autapomorphy of *Eshanosaurus*. It could be homologous to the external mandibular fenestra, but the latter occurs posterior to the dentary rather than within it. If the fenestra in *Eshanosaurus* is the external mandibular fenstra, then *Eshanosaurus* has following three autopomorphies related to the external mandibular fenestra: (1) The shape of the external mandibular fenestra of *Eshanosaurus* is very unusual for a theropod. In most known theropods, the external fenestra is oval, bordered anteriorly and ventrally by the dentary, dorsally and posteriorly by the surangular and posteroventrally by the angular. In *Eshanosaurus,* though not completely preserved, the external fenestra is clearly rounded in outline and very small (Figs. 1C, 2C, 3). The dentary also participates in the posterior border of the mandibular fenestra (possibly correlated to the small size of the external mandibular fenestra). which is distinct from the condition in all other known theropods. The shape of the tentatively identified mandibular fenestra is considered to be autapomorphic of *Eshanosaurus*. (2) Anterior position of the tentatively identified external mandibular fenestra (Figs. 1C, 2C). What appears to be the external mandibular fenestra is located anterior to the posterior end of the dentary tooth row. This has not been reported in other theropods. In some basal sauropodomorphas and primitive theropods such as *Herrerasaurus* (Sereno and Novas, 1992) and prosauropods such as *Plateosaurus* (Galton, 1984), the external mandibular fenestra is relatively anteriorly positioned but does not reach to the posterior end of the dentary tooth row. The only other known dinosaur possibly sharing this feature is the basal ornithischian *Lesothosaurus* (Weishampel and Witmer, 1990:fig. 19.1a; but see Sereno, 1991:fig. 13F), where the anterior margin of the external mandibular fenestra is anterior to the posterior end of the dentary tooth row. (3) The presence of a long posterodorsal process of the dentary (Figs. 1C, 2C). A posterodorsal process of the dentary is absent in other therizinosauroids except *Eshanosaurus*.

13. Small size of tooth denticles (Figs. 1D, E, 2D, E). The denticles of the teeth in *Eshanosaurus* are comparatively smaller than in other therizinosauroids (Clark et al., 1994; Russell and Dong, 1994; Xu et al., 1999), but similar in size to those of all other theropods except troodontids (Farlow et al., 1991). This feature also differs from prosauropods and ornithischians, in which the denticles are coarser (Galton, 1986).

Based on characters 12, 13, and 4 (denticles almost perpendicular to the anterior and posterior edges of tooth crowns), *Eshanosaurus* was erected as a new genus and species among therizinosauroids.

Systematic Position of *Eshanosaurus*—The limited material makes it difficult to analyze the phylogenetic position of *Eshanosaurus*. A few features may be, however, helpful to deducing its systematic position.

The tooth number of *Eshanosaurus* is similar to that of the two relatively primitive therizinosauroids *Alxasaurus* (Russell and Dong, 1994) and *Beipiaosaurus* (Xu et al., 1999). Recurvature of tooth crowns may represent another plesiomorphic condition. Among therizinosauroids, *Eshanosaurus, Beipiaosaurus* (Xu et al., 1999), and *Segnosaurus* (Barsbold, 1983) have slightly recurved tooth crowns, which is more similar to most other theropods. *Alxasaurus* and *Erlikosaurus* have nearly symmetrical tooth crowns in labial view, which may represent further adaptation to herbivorous diet. Besides these two presumably plesiomorphic characters, there are additional features suggesting *Eshanosaurus* is more primitive than other therizinosauroids.

If the round fenestra on the posterior dentary is the external mandibular fenestra, the posterior dentary of *Eshanosaurus* is bifurcated as in oviraptorosaurians. The presence of the posteriorly bifurcated dentary is presumably synapomorphic for therizinosauroid-oviraptorosaurian clade, and the lack of this feature in other therizinosauroids except *Eshanosaurus* is most parsimoniously explained as a synapomorphy of other therizinosauroids rather than the plesiomorphic condition. The size of the denticles is similar to that of most other theropods but smaller than that of other therizinosauroids. The small size of the denticles is presumably plesiomorphic for the Therizinosauroidea. The perpendicular denticles to the tooth edge are typical of theropod teeth. Most therizinosauroids have apically oriented denticles, which may represent an adaptation to herbivorous
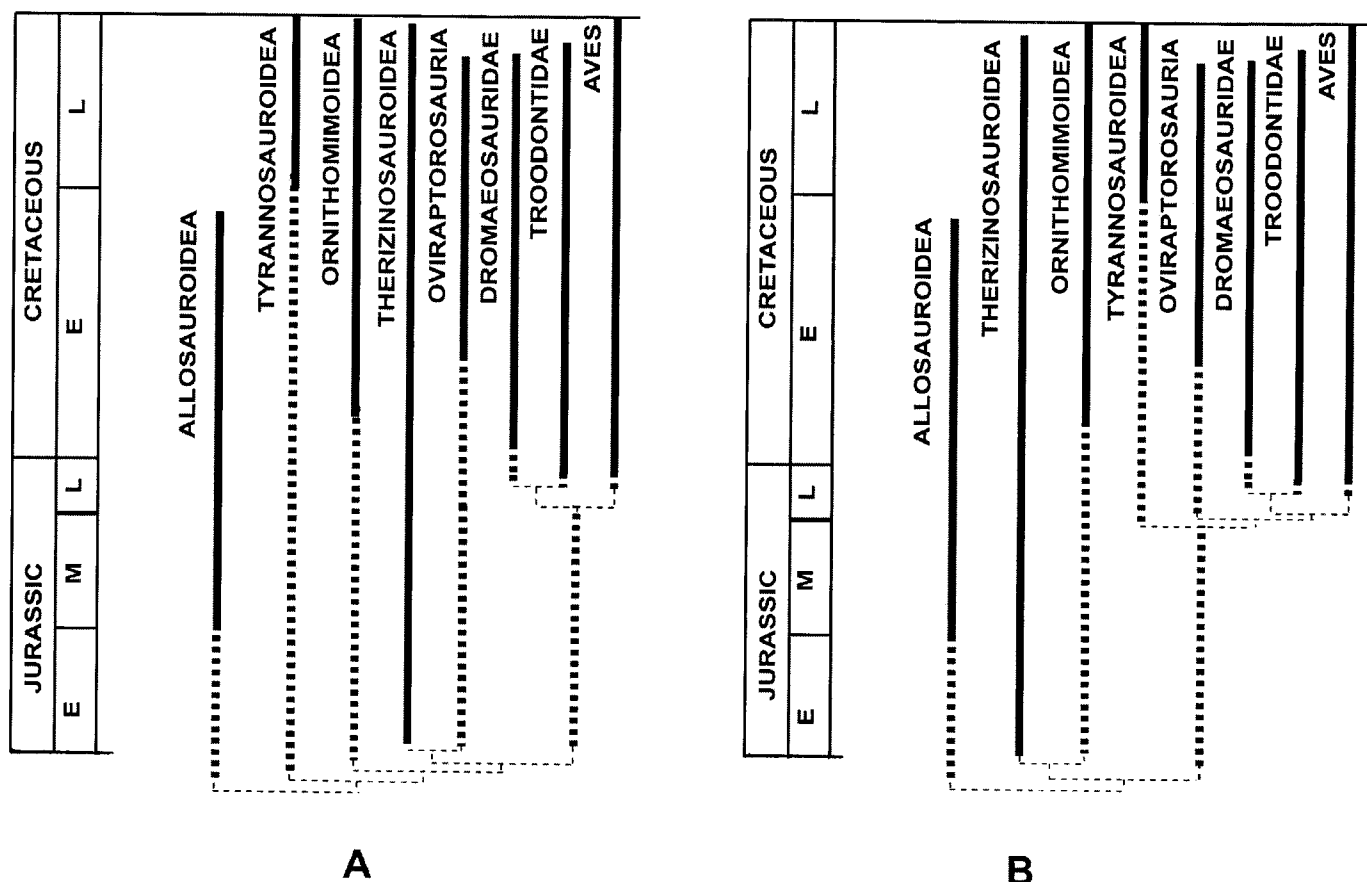
FIGURE 7.   The timing of divergence of major coelurosaurian dinosaur groups based on a phylogeny proposed by Makovicky and Sues (1998) (**A**) and by Sereno (1999) (**B**), respectively. Dashed bars represent the ghost lineages.

diet. *Eshanosaurus* may be more primitive by retaining the typical theropod condition.

The above analysis suggests that *Eshanosaurus* may represent a basal therizinosauroid (Fig. 6), yet a numerical cladistic analysis is difficult due to the limited material of *Eshanosaurus* (Zhao and Xu, 1998).

Implications of *Eshanosaurus*—The discovery of *Eshanosaurus* is important for the understanding the timing of divergence of coelurosaurian dinosaur groups. The position of Therizinosauroidea within Coelurosauria is supported by numerous characters (Clark et al., 1994; Sereno, 1999; Makovicky and Sues, 1998; Xu et al., 1999) but their precise relationships are debated. Thus far the strongest evidence is for a close relationship with Oviraptorosauria (Makovicky and Sues, 1998; Xu et al., 1999), but affinities with Ornithomimosauria have also been hypothesized (Sereno, 1999). The presence of a derived clade of coelurosaurians in the Early Jurassic indicates that basal divergence within Coelurosauria dates back at least to this time. Thus, there are significant gaps in the fossil record of this group, mainly through the poorly known Middle Jurassic. If a Therizinosauroidea–Oviraptorosauria relationship (Makovicky and Sues, 1998; Xu et al., 1999) is correct, it suggests that most coelurosaurian groups originated no later than the Early Jurassic. This implies many ghost lineages, which is unexpected but possible (Fig. 7A). A Therizinosauroidea–Ornithomimosauria relationship (Sereno, 1999) might be more concordant with the current fossil records as it has fewer ghost lineages than the former hypothesis (Fig. 7B).

The occurrence of *Eshanosaurus* also suggests that therizinosauroids and other major groups of coelurosaurians differ-entiated prior to the breakup of Pangea. Therizinosauroids represent the group of coelurosaurs with the longest (though not continuous) fossil record. Their fossil record extends from Early Jurassic (Hettangian) through Late Cretaceous (Maastrichtian), about 136 million years. From the Middle Jurassic through Early Cretaceous Chinese dinosaur assemblages were dominated by endemic taxa, but in the Early Jurassic and from the Early Cretaceous Aptian–Albian through the end of the Cretaceous they share faunal similarities with other continents, particularly with North America (Luo and Wu, 1994; Russell, 1994). The tetrapod assemblages of the Lower Lufeng Formation show close similarity to those of other continents (Luo and Wu, 1994). Until recently the therizinosauroid fossil record was restricted to Asia (Barsbold and Maryanska, 1990; Russell and Dong, 1994) from Early Jurassic through end of Cretaceous, though a questionable record was reported from North America (Currie, 1987; but see Barsbold and Maryanska, 1990).

ACKNOWLEDGMENTS

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