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A New Species of *Chungchienia* (Tillodontia, Mammalia) from the Eocene of Lushi, China

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ABSTRACT

A new species of *Chungchienia* from the Eocene of Lushi, Henan, is described. Based on dental features such as a distinctive hypoconulid lobe on m3, the new material decisively reallocates *Chungchienia*, previously believed to be either an edentate, a tillodont, or a taeniodont, to the order Tillodontia. The new species shows that *Chungchienia* is a highly specialized tillodont, having rootless hypsodont cheek teeth with only the labial

surface covered with enamel. Shared similarities such as a long diastema before p3 suggest that *Chungchienia* is more closely related to the trogosine genus *Tillodon* from North America than to other tillodonts. Phylogenetic relationships of tillodonts indicate possible multiple dispersal events in a two-way exchange of tillodonts between North America and Asia during the Eocene.

INTRODUCTION

Tillodontia is an extinct group of early Tertiary mammals known in North America, Europe and Asia. Five tillodont genera have been reported from North America: *Esthonyx* Cope, 1874; *Trogosus* Leidy, 1871; *Tillodon* Gazin, 1953; *Megalestonyx* Rose,

1972; and *Azygonyx* Gingerich, 1989. Two genera were reported from Europe: *Plesiesthonyx* Lemoine, 1891, and *Franchaius* Baudry, 1992. Several taxa from Asia have also been included in Tillodontia, including *Adapidium* Young, 1937; *Basalina* Dehm and

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Oettingen-Spielberg, 1958; *Kuanchuanus* Chow, 1963a; *Lofochaius* Chow et al., 1973; *Meiostylodon* Wang, 1975; and *Dysnoetodon* Zhang, 1980. More recently, Ting and Zheng (1989) restudied *Interogale* and *Anchilestes*, which were previously assigned to Anagalida (Huang and Zheng, 1983; Qiu and Li, 1977), and found them to be primitive tillodonts.

Conventionally, tillodonts have been related one way or another to arctocyoniid condylarths (Gregory, 1910; Gazin, 1953; Van Valen, 1963; Rose, 1972; Szalay, 1977), although McKenna (1975) placed the Tillodontia in the Mirorder Eparctocyonia that accommodates Arctocyonia, Tubulidentata, Dinocerata, Embrithopoda, and Artiodactyla. With discoveries of early pantodont and tillodont material from China, the hypothesis that tillodonts are akin to pantodonts was proposed and became more popular (Chow and Wang, 1979; Gingerich and Gunnell, 1979; Lucas and Schoch, 1981; Stucky and Krishtalka, 1983; Lucas, 1993). Although Lucas believed that the similarities between tillodonts and pantodonts are mostly among derived forms of these two groups, a tillodont-pantodont relationship may still be suggested by the possible sister taxon of tillodonts, i.e., *Deltatherium* (Chow and Wang, 1979; Lucas, 1993), because McKenna (1975) considered *Deltatherium* to be a pantodont (but see Lucas, 1993). However, while Lucas considered *Deltatherium* the sister group to Tillodontia instead of being included in the order, McKenna (personal commun.) now prefers to put the genus in the order on the basis of a premolar loss, although Lucas thought that the lack of P1/p1 was a converged feature in *Deltatherium* and Esthonychidae.

Based on their new analysis of *Interogale* and *Anchilestes*, Ting and Zheng (1989) concluded that tillodonts probably have affinities with anagalids, an alternative hypothesis that calls for future testing to determine whether or not these two genera are actually tillodonts (Lucas, 1993). Regardless of their relationships with pantodonts or anagalids, the fossil record points to an Asian origin of tillodonts and their dispersal from Asia to North America across Beringia during the late Paleocene and early Eocene (Krause and Maas, 1990).

While previous studies focused on Asian

taxa that may represent roots and stems of tillodonts that are still obscured in phylogenetic bushes of early mammals, we report here a new species of *Chungchienia* that certainly qualifies as a new twig in the tillodont clade, based on material collected by J. Wang and Y. Tong from the Lushi Basin, Henan. *Chungchienia* was proposed by Chow (1963b) and has long been considered either an edentate or a taeniodont, but was recently placed in Tillodontia (Schoch, 1986). Because of the new light shed on these relationships by the Lushi material described here, the tillodont affinity of *Chungchienia* is confirmed. This genus is believed to be the most specialized tillodont known. *Chungchienia* further diversifies Asian tillodonts and indicates the possibility of two-way interchange of this order between Asia and North America during the Eocene, given the derived similarities shared by this genus and the North American *Tillodon*.

ORDER TILLODONTIA MARSH, 1875

FAMILY ESTHONYCHIDAE COPE, 1883

SUBFAMILY TROGOSINAE GAZIN, 1953

Chungchienia Chow, 1963

INCLUDED SPECIES: *C. sichuanica* and *C. lushia*, new species.

REVISED DIAGNOSIS: Large tillodont; all known teeth (i2, p3 and/or p4, m1–3) rootless; i2 extremely large, gliriform, and with enamel covering the entire anterior surface; a long diastema before p3; all cheek teeth hypsodont (both root and crown hypsodonty), with enamel restricted to the entire labial surface of the tooth body that extends deeply into the mandible; flat grinding surfaces of teeth, owing to early wear of cusps; p3 and/or p4 columnar, showing no division of trigonid and talonid; trigonid and talonid of m1–2 forming two lobes (tooth double-columnar) with the trigonid lobe slightly narrower than the talonid lobe; crown of m3 trilobed (tooth tri-columnar) owing to a large hypoconulid.

Chungchienia lushia, new species

HOLOTYPE: A left i2, a right p3 (or p4), a left m1, a right m2 and m3 (V10805; Institute

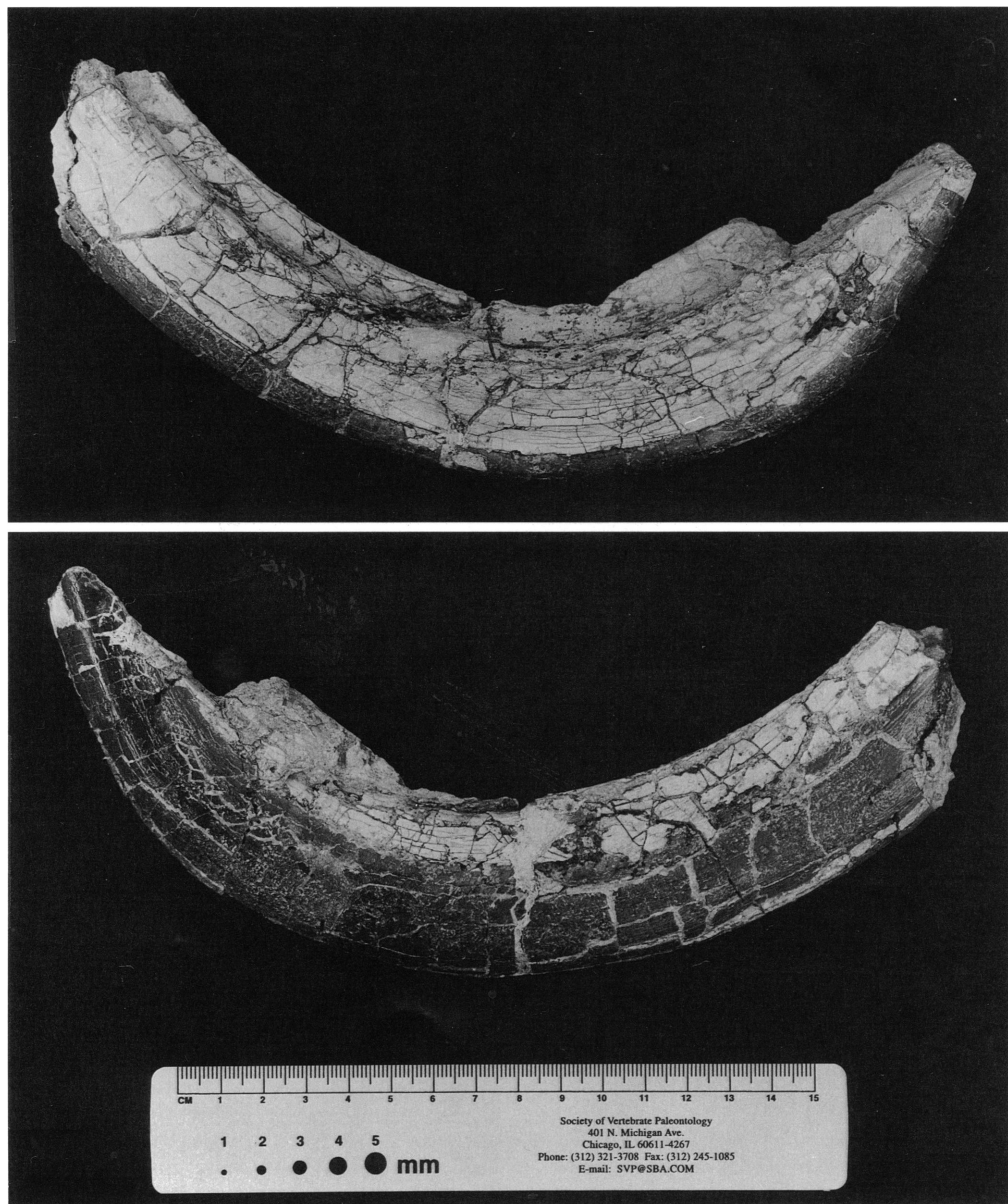


Fig. 1. Lingual (upper) and labial (lower) views of the second left lower incisor (V10805).

of Vertebrate Paleontology and Paleoanthropology, Beijing, P.R.C.) (fig. 1, 2).

LOCALITY AND AGE: Specimens were collected from a pit in a small valley about 300 m southwest of Xiaowan village, Lushi County, Henan province. The locality is between the Xiejiagou and Mengjiapo sites reported by Chow et al. (1973). Age determi-

nation of the Xiaowan site is difficult based on scattered fossils. However, given its occurrence between Mengjiapo and Xiejiagou in which middle Eocene taxa such as *Hyrachyus* and *Uintatherium* were found (Tong and Wang, 1980, 1981), beds yielding *C. lushia* are probably within sediments of age equivalent to the Irдин Manha Fm. (middle

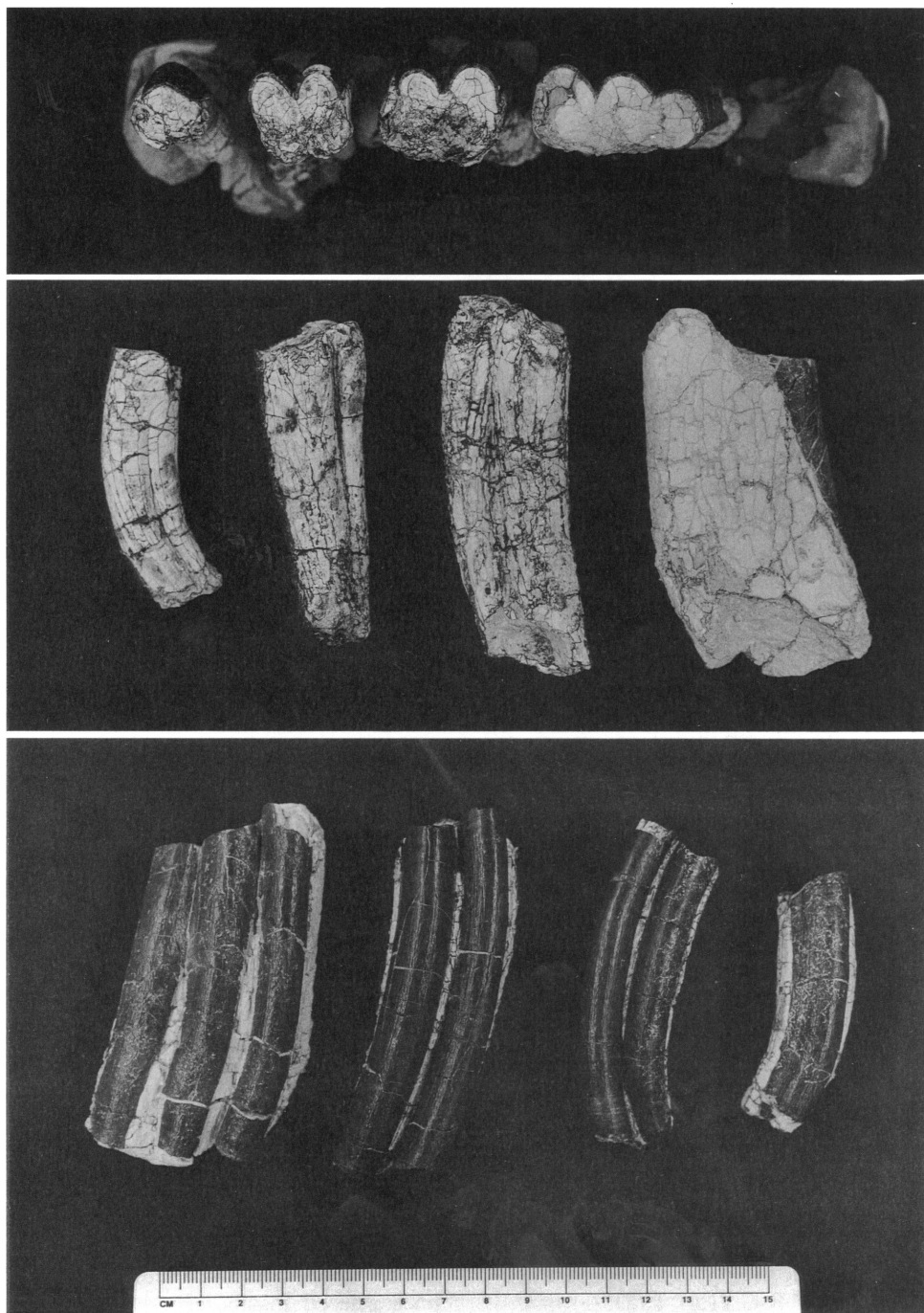


Fig. 2. Top to bottom: crown, lingual, and labial views of a right p3 (or p4), a left m1, a right m2 and m3 (V10805).

Eocene) of Inner Mongolia or slightly younger.

ETYMOLOGY: Species name adopted from the county Lushi.

DIAGNOSIS: Differs from *C. sichuanica* in being larger and p3 (p4) less transversely compressed; enamel band on p3 (p4) about 70% broader than that of *C. sichuanica* and its posterior border with the dentine not marked by groove; dentine consisting of a homogeneous labial and rugose lingual portions, contrasting with the two-layered dentine in *C. sichuanica* (see Chow, 1963b: fig. 1).

DESCRIPTION: The left i2 is complete. It is a long, gliriform, and robust tooth, with the enamel wrapping around the anterior and most of the labial surfaces throughout the entire tooth body. The enamel layer becomes thinner from ventral to labial side. The tip of the tooth is chisel-shaped, convex anteriorly, and flat posteriorly. The labial surface of the tooth is uneven in that the lateral side is a longitudinal ridge about 10 mm higher than the lingual side. From the tip to the proximal end, the incisor is 260 mm long.

The p3 (p4) is columnar and rootless, arching anterolaterally. The anterolabial surface is covered with a longitudinal enamel band, measuring 15 mm wide near the crown and 13 mm near the base, throughout the entire tooth body. Most of the tooth surface is exposed dentine. The enamel layer is decorated with transverse as well as longitudinal fine lines. The enamel is brown in color, in contrast with the white dentine, and its anterior and posterior boundaries with the dentine are sharply defined. The dentine is dense and is filled with minute cracks, which may be post-mortem fractures. There is a groove on the lingual side of the tooth, indicating an originally double-rooted tooth. The crown outline is roughly square, bearing a wear surface that slopes posteriorly.

The m1 is both root and crown hypsodont, therefore rootless, and bowed laterally and leaning forward. It tapers gradually from the crown to the root end. The trigonid and talonid form the anterior and posterior lobes, with the posterior one being slightly wider and longer than the anterior one. The enamel is present only on the labial surface, whereas the lingual side of the tooth is bare dentine

with a rough surface. The trigonid and talonid portions of the tooth are separated by a deep longitudinal groove on both the lingual and labial sides; therefore, the tooth is double-columned. Along the bottom of the labial groove, a narrow band of white dentine is exposed, so the enamel is discontinuous therein. The trigonid and talonid bear no remaining cusps but form grinding surfaces, with the trigonid being slightly higher than the talonid. The dentine consists of two areas: labially it is dense and uniform, whereas lingually it is rugose and filled with minute cracks. Loss of enamel may be responsible for this morphology, but it seems unlikely that this is a preservational artifact. There is no distinct boundary between these two portions of dentine. The wear surface of the labial side of the crown is smooth and lower, in contrast to the rough and higher wear surface of the lingual portion. This suggests that the labial dentine, although it appears to be denser, is not any harder than the lingual dentine.

The m2 is similar to m1 in general morphology but is larger in all dimensions. The dentine of the two molars is stained with light purple color. The m3 differs considerably from m1–2 in having a large hypoconulid lobe; therefore, the m3 is triple-columnar with the crown outline being much longer but narrower than that of m1 and m2. The trigonid is higher than the talonid, although the boundary between them is not distinct. The dentine is totally white, indicating that the condition of the m3 is slightly different from that of the other color-stained cheek teeth; it is probably from a different individual as well. The enamel surrounding the hypoconulid column extends to the lingual side of the tooth, and the lingual surface is bare dentine otherwise. Unlike the other cheek teeth that taper from the crown toward the root, m3 flares slightly in the opposite direction. The dentine on the lingual portion of the tooth is rougher in texture, but not so much as that in m1 and m2. The labial enamel is continuous near the crown from the trigonid column to hypoconulid column, and is increasingly separated by broader dentine bands toward the base. In all cheek teeth, the enamel layer from crown end to root end shows no significant change in thickness.

Measurements of V10805 (mm):

	Length	Width
I2	43	28
p3 (p4)	19	17
m1	24	24
m2	28	26
m3	43	22

DISCUSSION

The link between *C. sichuanica* and *C. lushia* is p3 (or p4), which is the only tooth that permits comparison. They are considered to be the same tooth, either a p3 or a p4. They are similar in general morphology, including the distribution of enamel, curvature of the tooth, and wear pattern of the crown. On the other hand, they have several differences, as listed in the diagnosis. Judged from its position relative to the diastema, the only preserved tooth in the Sichuan specimen should be a premolar rather than m1, as previously identified by Chow (1963b). Chow also observed a longitudinal trough along the ventral side of the mandible and suspected that it was for housing a large chisel-like incisor. Such an incisor is confirmed by the Lushi specimens.

Considering the single tooth to be a rootless, cylindrical m1, Chow (1963b) placed *Chungchienia* into Edentata when he first proposed this taxon based on the specimen collected from Sichuan, Henan (=Honan). Romer (1968: 219) was surprised by the abrupt appearance of an Asian edentate, supposedly a ground sloth, and commented: "Both in time and space we are far, far removed from any situation in which we would expect a ground sloth." Then he suggested that *Chungchienia* is a taeniodont. Although Chow et al. (1973) still regarded *Chungchienia* an edentate, an alternative and more recent concept endorses Romer's view that *Chungchienia* is a taeniodont (Ding, 1979; Hoffstetter, 1982; Russell and Zhai, 1987; Rose and Emry, 1993). A substantial phylogenetic analysis of *Chungchienia* since its publication was given by Ding (1987), who discussed the phylogenetic position of *Ernanodon*, a possible edentate from South China. Because the enamel band, narrow but distinctive, does not fit the overall edentate

dental evolution characterized by enamel degeneration, and because a long diastema and other features in the lower dentition do not compare with those of any taeniodont, Ding concluded that it is equally difficult to place *Chungchienia* into either Edentata or Taeniodontia on the basis of available material. Schoch (1986), however, explicitly assigned *Chungchienia* to Tillodontia, which is supported by the Lushi specimens.

The tillodont identification of the Lushi specimens was suggested by M. C. McKenna (personal commun.) in a brief examination of the specimens and has proven to be correct. The decisive reallocation of *Chungchienia* into Tillodontia on the basis of the new material resolves the uncertainties that remained from its affiliation with either edentates or taeniodonts. Quite convincingly, as shown in the Lushi specimens, the cheek teeth of *Chungchienia* are not those of an edentate. The enlarged second lower incisor, the double-columned and triple-columned lower molars consequent to prominent trigonid and talonid lobes, and the unilateral distribution of enamel on the labial surface of cheek teeth, are typical of neither edentates nor taeniodonts. In this regard, edentates and taeniodonts are more similar to each other in having columnar cheek teeth in which the trigonid and talonid are no longer recognizable.

The lower molars of tillodonts have a U-shaped trigonid with a metastylid and a somewhat rounded talonid basin; the cheek teeth are unilaterally high crowned even in primitive forms. The talonid basin of m3 is elongate because of the enlarged hypoconulid, and a third lobe is universally present in tillodonts. As a highly derived form, *Chungchienia* possesses derived features that are not present in other tillodonts. However, most of these can be interpreted as advanced in a morphological spectrum ranging from primitive to derived features. For instance, the hypsodont teeth and the unilateral distribution of the enamel on cheek teeth are already initiated in more primitive forms such as *Tillodon* and *Trogosus*. As stated by Gazin (1953: 33): "The external hypsodonty of the lower teeth as compared with the more brachyodont appearance of the lingual wall is characteristic of all the tillodonts, but be-

comes increasingly distinctive in the later forms." It must be pointed out that in all tillodonts except *Chungchienia*, the hypsodonty applies to tooth crown only. In those forms, cheek teeth are primitively rooted and the enamel does not extend into the jaw bones. Nonetheless, the outline of the tooth crowns of *Chungchienia*, particularly that of m3, remains little changed, which reveals its relationships. The trilobed crown shape of m3 in *Chungchienia* is most comparable to that of large tillodonts: *Tillodon* and *Trogosus*. The wear pattern of the cheek teeth is such that the labial side of dentine is more worn than the lingual side, which also resembles that of other tillodonts.

In conventional classification, Tillodontia consists of a single family, Esthonychidae Cope, 1883, which was divided into two subfamilies (Gazin, 1953): Esthonychinae and Trogosinae. This classification was supported by Rose (1972) who pointed out that Esthonychinae is characterized by large but rooted second incisors and that Trogosinae possesses large gliriform second incisors that grow from persistent pulp. However, a large and rooted second incisor appears to be primitive for tillodonts; therefore it is inadequate for diagnosing a taxon within the group. Recent phylogenetic analyses confirmed the monophyly of Trogosinae and showed the paraphyly of Esthonychinae (Baudry, 1992; Lucas, 1993; fig. 3). Lucas redefined Trogosinae by including *Megalesthyx* and *Adapidium* in the subfamily, based not on gliriform second incisors as advocated by Rose but on a set of characters that allows a broader conception of Trogosinae including *Megalesthyx* and *Adapidium*. Inclusion of primitive Asian forms, such as *Lofochaius* and *Meiostylodon* in Esthonychidae and *Interogale* and *Anchilestes* in the Tillodontia, was considered to be questionable (Gingerich, 1989; Lucas, 1993). Although phylogenetic relationships of tillodonts have been explored (Baudry, 1992; Lucas, 1993), there is no comprehensive taxonomy encompassing all these taxa. In addition, problems exist concerning the taxonomic status of some tillodont taxa such as *Kuanchuanus* and *Plesiasthyx* (e.g., Baudry, 1992; Lucas, 1993).

Chungchienia is readily assignable to the

subfamily Trogosinae in any case, because it possesses large, gliriform second incisors and reduced talonids on p3–p4 (Gazin, 1953; Rose, 1972; Lucas, 1993). *Chungchienia* is similar to *Tillodon* and *Trogosus* in having greatly enlarged body size, deepened mandibular symphysis, and in the position of the mental foramen. *Chungchienia* is furthermore similar to *Tillodon* in several aspects: a greatly elongate rostrum suggested by the large second incisor, a narrow M3 reflected by the narrow m3 (Lucas, 1993), and a distinct diastema before p3. As Gazin (1953: 49) noted: "Lower canine and p2 are spaced and well separated from p3" in *Tillodon*. The longer diastema in *Chungchienia*, as shown in the Sichuan specimen, may have resulted from loss of p2 and/or p3. In *Tillodon*, p3 is small relative to p4. This tooth may be lost in *Chungchienia*, which is why we consider the tooth of *C. sichuanica* to be either a p3 or a p4. The canine and p2 are small and the canine is somewhat vertical in *Tillodon*, differing from the condition in *C. sichuanica*, in which a large alveolus in the mandible suggests a sizable and procumbent canine (Chow, 1963b).

Among Asian forms, *Kuanchuanus* is believed to be a member of the subfamily Trogosinae (Rose, 1972; Baudry, 1992), although Lucas (1993) further regarded it as a junior synonym of *Trogosus*. In spite of its taxonomic position, *Kuanchuanus*, like *Trogosus*, appears more primitive than *Tillodon* in being smaller and having a narrow gap between p2 and p3. Another possible tillodont of China is represented by an enlarged incisor (i2) from the middle Eocene Guangzhuang Formation of Shandong. This specimen was called "Unbestimmbare Ungulatenzähne" by Zdansky (1930) and is believed to be *Chungchienia* (Lucas, personal commun.), which, if confirmed, broadens the distribution of the genus.

Given the derived similarities of *Chungchienia* and North American *Tillodon*, it is possible that *Chungchienia* is a derivative of North American forms rather than of Asian tillodonts, although it can be argued that those similarities are a result of parallel evolution. The relationship shown in figure 3 suggests that migration of tillodonts between Asia and

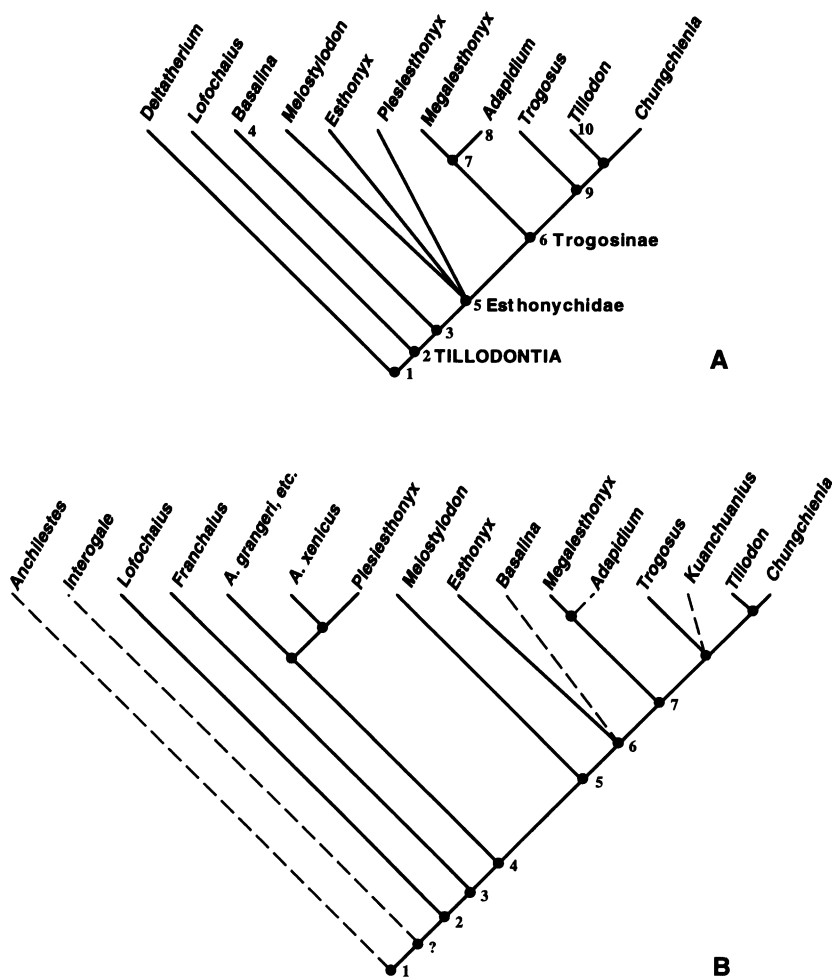


Fig. 3. Two recent phylogenetic hypotheses of tillodonts: **A**, modified from Lucas, 1993; and **B**, from Baudry, 1992, with *Chungchienia* inserted in both. Lucas' hypothesis employs *Deltatherium* as the sister taxon of Tillodontia, whereas Baudry's includes all tillodont genera known, without providing an out-group. Features diagnosing various nodes were provided by Lucas (1993: table 14.2) and Baudry (1992: fig. 12).

North America may have occurred more than once and that a dispersal from North America to Asia during the middle or late Eocene is possible.

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