A REASSESSMENT OF *DIANCHUNGOSAURUS LUFENGENSIS* , AN ENIGMATIC REPTILE FROM THE LOWER LUFENG FORMATION (LOWER JURASSIC) OF YUNNAN PROVINCE, PEOPLE'S REPUBLIC OF CHINA

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Source: Journal of Paleontology, 79(5):981-986.
Published By: The Paleontological Society
DOI: http://dx.doi.org/10.1666/0022-3360(2005)079[0981:ARODLY]2.0.CO;2
URL: http://www.bioone.org/doi/full/10.1666/0022-3360%282005%29079%5B0981%3AARODLY%5D2.0.CO%3B2

J. Paleont., 79(5), 2005, pp. 981–986

0022-3360/05/0079-981$03.00

A REASSESSMENT OF *DIANCHUNGOSAURUS LUFENGENSIS* YANG, 1982a, AN ENIGMATIC REPTILE FROM THE LOWER LUFENG FORMATION (LOWER JURASSIC) OF YUNNAN PROVINCE, PEOPLE'S REPUBLIC OF CHINA

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ABSTRACT—*Dianchungosaurus lufengensis* was erected on the basis of fragmentary isolated jaw elements (a left premaxilla and left and right partial lower jaws) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan Province, China. Yang referred *Dianchungosaurus* to the Heterodontosauridae (Ornithischia, Ornithopoda), as several features appeared to indicate affinity with the southern African genus *Heterodontosaurus*. However, reexamination of the type material demonstrates that the holotype specimen of *Dianchungosaurus* represents a chimaera of prosauropod dinosaur and mesoeucrocodylian remains: the mesoeucrocodylian premaxilla is distinctive and allows the genus to be diagnosed on the basis of several autapomorphic features. Revision of this genus thereby invalidates the only reported occurrence of a heterodontosaurid dinosaur from Asia.

INTRODUCTION

THE LOWER Lufeng Formation of Yunnan Province, People's Republic of China, has yielded abundant material of terrestrial vertebrates, including tritylodontid synapsids, mammals, protosuchian crocodylomorphs, and a diverse dinosaur fauna (Young, 1951; Dong, 1992; Luo and Wu, 1994, 1995; Lucas, 2001). This thick sequence of mudstones and siltstones was deposited in a variety of fluvial and lacustrine environments and is currently considered to be of Early Jurassic (Hettangian–Sinemurian) age (Luo and Wu, 1994).

Remains of ornithischian dinosaurs are rare in the assemblage, but four taxa have been named on the basis of unique, fragmentary specimens: *Tatisaurus oehleri* Simmons, 1965, *Dianchungosaurus lufengensis* Yang, 1982a, *Tawasaurus minor* Yang, 1982b, and *Bienosaurus lufengensis* Dong, 2001. Because Early Jurassic ornithischians are poorly known globally (Sereno, 1991), this material is potentially interesting both paleobiogeographically and phylogenetically. However, the poor quality of these specimens severely limits their utility. *Tatisaurus* Simmons, 1965, originally referred to the Ankylosauria, was later transferred to the Stegosauria (Dong, 1990), and is now considered to represent an indeterminate basal thyreophoran (Coombs et al., 1990). Lucas (1996a) synonymized *Tatisaurus* with the English Lower Jurassic basal thyreophoran *Scelidosaurus* Owen, 1861 [as *S. oehleri* (Simmons, 1965)], but this suggestion has yet to be confirmed. Most recently, a new ankylosaur (*Bienosaurus* Dong, 2001) was named on the basis of an incomplete mandible and fragmentary cranial material, but the ankylosaurian affinities and validity of this taxon are doubtful (J. C. Parish, personal commun., 2003). Finally, it has been demonstrated that *Tawasaurus* Yang, 1982b is not an ornithischian at all, but a juvenile prosauropod (Sereno, 1991).

Dianchungosaurus Yang, 1982a was erected on the basis of fragmentary jaw material from the Dark Red Beds (Sinemurian: Luo and Wu, 1994, 1995) of the Lower Lufeng Formation in the vicinity of Chang village, Lufeng County, Yunnan. It was referred to the Heterodontosauridae, because several features appeared to indicate affinity with the southern African genus *Heterodontosaurus* Crompton and Charig, 1962 (Yang, 1982a). If correctly characterized, *Dianchungosaurus* would thus represent the only reported occurrence of Heterodontosauridae in Asia (Weishampel and Witmer, 1990). However, this material has not been examined in detail since its initial description. Some authors have provisionally retained *Dianchungosaurus* as a valid heterodontosaurid (Sun et al., 1992; Lucas, 1996b, 2001), whereas others have suggested that it is a nomen dubium, though still potentially referable to this clade (Weishampel and Witmer, 1990). Here we present a redescription of *Dianchungosaurus* and a reappraisal of its taxonomic and systematic position.

ABBREVIATIONS

BMNH, The Natural History Museum, London, United Kingdom; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; SAM, South African Museum, Cape Town, South Africa.

DESCRIPTION

The hypodigm of *Dianchungosaurus lufengensis* consists of a left premaxilla (holotype, IVPP V4735a: Figs. 1, 2) and conjoined partial right and left lower jaws (paratype, IVPP V4735b: Fig. 3).

In lateral view (Figs. 1.1, 2.1), the anterior margin of the premaxilla (IVPP V4735a) slopes strongly dorsally and is oriented at approximately 60° to the almost horizontally oriented ventral margin. The dorsal margin slopes gently posteroventrally from its highest point at the anterior margin. Although the maxillary process is broken dorsally, the base of the process is relatively long anteroposteriorly. The lateral surface of the premaxilla is smoothly convex dorsoventrally and anteroposteriorly and does not bear any nutritive foramina, or any rugosity suggestive of a rhamphotheca. Anteriorly, a dorsoventrally thin, anteriorly directed process appears to have been ''pinched out'' from the main body of the bone. Yang (1982a) suggested that a chevron-shaped feature close to the posterior margin of the premaxilla represented the maxillary suture, with the portion of bone posterior to this representing the anteriormost part of the maxilla. However, the ''suture'' cannot be traced dorsally, ventrally, or posteriorly, and it seems most likely that it is simply a crack on the lateral margin of the premaxilla (contra Yang, 1982a).

The premaxilla is damaged medially, and no clear articular surface for the right premaxilla can be determined (Fig. 1.2). In ventral view, the bone is bluntly rounded anteriorly and is transversely broad (Figs. 1.3, 2.2). A complete premaxillary secondary palate would have been present. The area between the tooth row and the medial edge of the premaxilla forms a shallow, longitudinal depression that extends along the ventral surface of the

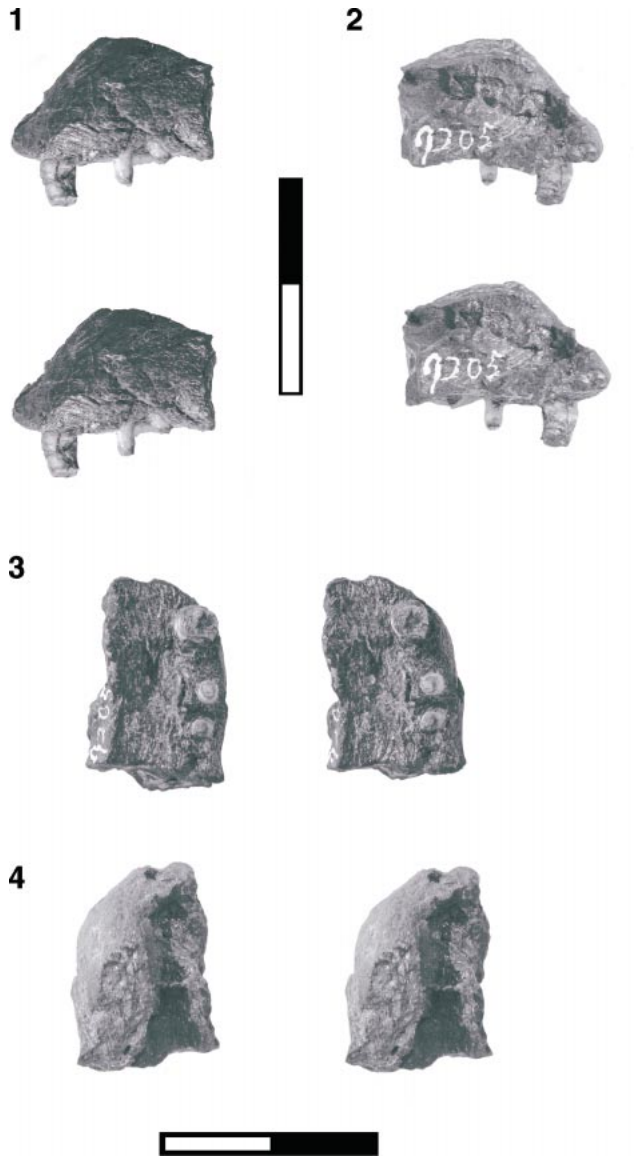

FIGURE *1*—Stereophotographs of the holotype specimen of *Dianchungosaurus lufengensis* Yang, 1982a (IVPP V4735a) in *1,* lateral, *2,* medial, *3,* ventral, and *4,* dorsal views. Scale bars equal 2 cm.

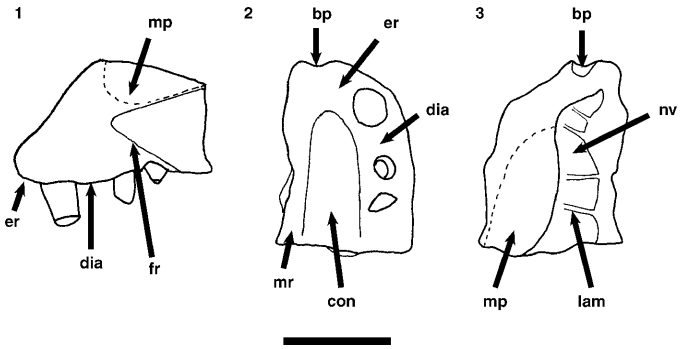

FIGURE *2*—Line drawings of the holotype specimen of *Dianchungosaurus lufengensis* (IVPP V4735a) in *1,* lateral, *2,* ventral, and *3,* dorsal views. Abbreviations: bp, blind-ending pit; con, shallow concavity; dia, diastema; er, edentulous region; fr, fracture; lam, bony lamina traversing nasal vestibule; mp, base of broken maxillary process; mr, midline ridge; nv, nasal vestibule. Scale bar equals 1 cm.

bone, with a low ridge bounding the depression medially. Hence, in the complete skull, it is likely that the entire premaxillary palate would have been vaulted, with two parallel depressions separated by a narrow, midline elevation. A large gap, wide enough to accommodate two teeth, but lacking alveoli, separates the first premaxillary tooth from the medial margin of the bone. As a result, a broad edentulous region would have been present between the two first premaxillary teeth in the articulated snout. In anterior view, a large, apparently blind-ended pit is situated in the body of the bone just dorsal to this edentulous region; it is possible that this pit communicated with the nasal vestibule, but the specimen is too poorly preserved to confirm this.

As preserved, the medial surface of the premaxilla is deeply excavated, forming a large nasal vestibule that is subdivided by very thin, bony laminae (Figs. 1.2, 2.3). The vestibule is a broad channel, bounded laterally by the main body of the premaxilla and medially by a thin ridge of bone. In medial view, a distinct rim of bone extends dorsally from just above the anteromedial corner of the bone at its midline suture toward the base of the maxillary process, and represents the lateral margin of the external naris. The nasal process is either broken or may have been completely absent. The proximity of the narial opening to the medial margin of the bone indicates that the external nares were positioned very close to the midline and thus to each other (Figs. 1.4, 2.3); if the internarial bar was genuinely absent, the external nares may have been confluent, though the presence of a very slender median premaxillary process cannot be discounted.

There are three premaxillary teeth (Figs. 1.1, 1.4, 2.1). The first (mesialmost) tooth has the longest crown and the widest crown base (both mesiodistally and labiolingually). The remaining teeth decrease in size posteriorly, and are reduced in apicobasal length, mesiodistal width, and labiolingual width. Teeth 1 and 3 are subconical, are not mesiodistally expanded relative to the roots, and lack bulbous bases. In contrast, tooth crown 2 is slightly expanded mesiodistally and has a slightly bulbous base. None of the teeth are labiolingually compressed, all are gently recurved, and all lack denticles, carinae, and ornamented enamel. In apical view, tooth 1 has a D-shaped cross section, with curved margin of the ''D'' facing mesially, and a broad groove extending over the distal surface of the crown. Teeth 1 and 2 are separated by a broad gap; a much narrower gap separates teeth 2 and 3. The teeth are not medially inset, but are situated at the lateral margin of the premaxilla. Sun et al. (1992) suggested that a fourth tooth was present, but although a slight depression is situated distal to the third premaxillary tooth, this depression is definitely not an alveolus.

The paratype consists of two partial mandibles that are held together by matrix (IVPP V4735b: Fig. 3). The jaws are generally shallowest anteriorly. The left mandibular fragment contains the roots of five erupted teeth, one erupted tooth crown, and one unerupted tooth. An additional erupted tooth is lodged in-between the two jaw rami, embedded in the matrix (Fig. 3.1). The shorter, right jaw fragment contains five erupted teeth: the posteriormost three teeth are complete, whereas the anterior two teeth are damaged apically (Fig. 3.2). The teeth are not deeply inset with respect to the lateral margin of the jaw, though there is a slight indication of a low, rounded ridge on the labial surface of the dentary.

Three large nutrient foramina are present on the lateral surface of the right dentary (the posteriormost foramen is broken posteriorly); one or possibly two foramina are present on the anterior part of the left dentary's lateral surface. Both dentaries have a subelliptical cross section, being slightly dorsoventrally convex laterally and planar medially. They are anteriorly shallow, and

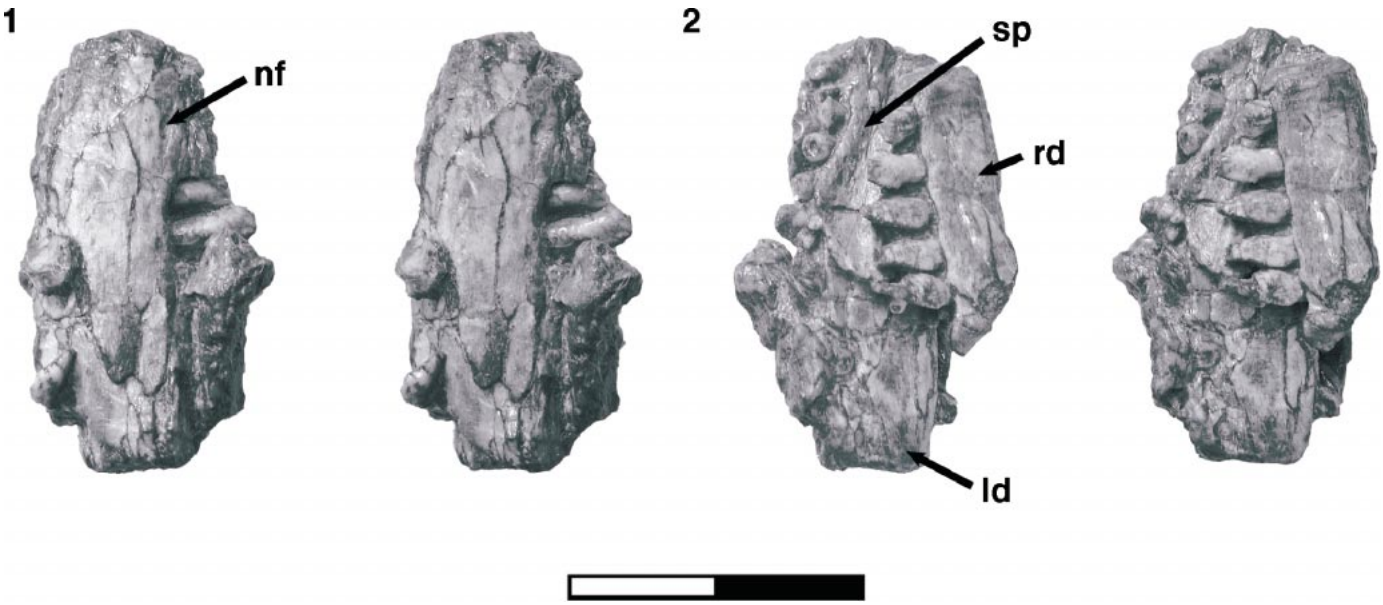

FIGURE 3—Stereophotographs of the paratype specimen of *Dianchungosaurus lufengensis* (IVPP V4735b) in *1*, left lateral and *2*, right lateral views. Abbreviations: ld, left dentary; nf, nutrient foramen; rd, right dentary; sp, splenial. Scale bar equals 2 cm.

increase slightly in dorsoventral height posteriorly. The open Meckelian canal of the left dentary is visible ventrally due to the displacement of the splenial. Sandwiched between the two jaw rami is the left splenial, which has become detached and has been displaced slightly dorsally. The splenial is a transversely thin, flat sheet of bone, whose ventral margin is curved slightly laterally.

In labial view, the teeth are elongated apicobasally, forming long isosceles triangles that are much taller than they are broad. The crown is mesiodistally expanded relative to the tooth root; the two sides converge apically. The teeth are transversely compressed and a cingulum is absent. All of the teeth are slightly asymmetrical in labial view, as the tip is oriented distally. Both mesial and distal edges of the crowns are coarsely denticulate, with the denticles oriented at an angle of approximately 45° with respect to the long axis of the crown. In mesial or distal views, the teeth are symmetrical about their long axes. The lingual surface of the teeth bears a slight concavity towards the distal margin.

COMPARISONS

Yang (1982a) referred *Dianchungosaurus* to the Heterodontosauridae on the basis of comparisons with *Heterodontosaurus*. In particular, he suggested that these genera shared the following character states: presence of a caniniform premaxillary tooth; presence of three premaxillary teeth; the trilobate structure of the dentary teeth; premaxilla that is straight and flat dorsally and narrow posteriorly; and similar size. However, none of these characters can be regarded as reliable. First, in *Heterodontosaurus* the third premaxillary tooth is the largest (SAM–PK–K337, SAM–PK–K1332; Charig and Crompton, 1974), whereas in *Dianchungosaurus* the largest premaxillary tooth is mesialmost (see also Yang, 1982a), so these structures cannot be compared directly. Among other heterodontosaurids, *Abrictosaurus* Hopson, 1975 displays a similar condition to *Heterodontosaurus* (BMNH RU B.54, BMNH RU A.100; Thulborn, 1970; reports of only two premaxillary teeth in the holotype of *Abrictosaurus* [BMNH RU B.54] are in error, contra Thulborn [1974]). Second, although three premaxillary teeth are present in *Dianchungosaurus*, this character is not confined to heterodontosaurids, but occurs in a variety of Mesozoic tetrapods, including tritylodontids and other dinosaur clades. Third, the dentary teeth are completely different in structure from those of heterodontosaurids. Heterodontosaurid teeth have denticles confined to the apicalmost third of the crown and the crowns are tall, almost parallel-sided, frequently display large, obliquely inclined wear facets, and possess a strong centrally positioned ridge or eminence and prominent secondary ridges at the mesial and distal crown margins (e.g., BMNH RU B.54, BMNH RU A.100, SAM-PK-K337, SAM-PK-K1332; Thulborn, 1970, 1974; Charig and Crompton, 1974; Gow, 1975, 1990; Hopson, 1975; Weishampel and Witmer, 1990). None of these features characterize any of the dentary teeth of *Dianchungosaurus*. Referral to the Heterodontosauridae (and to most other basal ornithischian and saurischian clades) is also precluded by the broad, rounded shape of the premaxilla: the rostral margins of premaxilla converge at a much narrower, more acute angle in heterodontosaurids (SAM–PK–K1332: and in most other basal ornithischians and saurischians). Furthermore, the medial positioning and probable confluence of the external nares not only exclude *Dianchungosaurus* from the Heterodontosauridae, but also indicate that the premaxilla is not referable to any dinosaur clade. Other suggested shared character states mentioned by Yang (1982a) (e.g., similar size, outline of premaxilla) are either too vague for accurate comparison or are found in taxa other than heterodontosaurids.

Although the premaxilla of *Dianchungosaurus* cannot be referred to the Dinosauria, the paratype specimen exhibits several character states that indicate that the lower jaws pertain to a small (juvenile) prosauropod dinosaur. The morphology and distribution of the denticles, the lanceolate shape of the tooth crowns in labial view, and the labiolingual compression and symmetry of the crowns in mesial view are all features characteristic of prosauropod teeth (Galton, 1985, 1986). Other features of the paratype (presence of nutrient foramina in the dentary, lack of marked emargination of the anterior portion of the tooth row) are also consistent with this interpretation. Prosauropods are the most abundant vertebrates in the Lower Lufeng fauna (Young, 1941a, 1941b, 1942, 1947a, 1947b, 1951), but the fragmentary nature of the paratype specimen means that it cannot be referred with confidence to any of the prosauropod genera known from this horizon. However, because the paratype of *Dianchungosaurus* lacks

the unique subconical, edenticulate teeth that characterize *Yunnanosaurus* Young, 1942, referral to the latter genus is precluded. The paratype specimen should henceforth be regarded as Prosauropoda indeterminate.

As dinosaur affinities have been rejected for the *Dianchungosaurus* premaxilla, the combined presence of thecodont teeth and of a well-developed secondary palate indicates that the holotype is referable to either a cynodont or a crocodylomorph. Only two clades of nonmammalian cynodont are known from the Lower Jurassic: tritylodontids and tritheledontids. Tritylodontid synapsids are abundant in the Lower Lufeng fauna and a variety of genera have been described (e.g., Young, 1947c; Cui, 1976, 1981; Sun, 1984; Luo and Wu, 1994). However, several lines of evidence indicate that referral to the latter clade is unlikely. Tritylodontids primitively possess three teeth in each premaxilla (usually termed incisors), with the second tooth exhibiting considerable expansion and forming a prominent tusk (e.g., Clark and Hopson, 1985). This contrasts strongly with the situation in *Dianchungosaurus*, where the first premaxillary tooth is the most prominent; consequently, *Dianchungosaurus* lacks this unambiguous tritylodontid synapomorphy. In addition, several other features separate *Dianchungosaurus* from described Lower Lufeng taxa. For example, a medially situated incisive foramen is present in the premaxillary palate of *Bienotherium* Young, 1940 (see also Young, 1947c) and *Bienotheroides* Yang, 1982c (see Sun, 1984), but is absent in *Dianchungosaurus*. Lower Lufeng tritylodontids that lacked an incisive foramen (*Dianzhongia* Cui, 1981, *Yunnanodon* Cui, 1986) differ from *Dianchungosaurus* in having only two, rather than a minimum of three, premaxillary teeth (Cui, 1976, 1981), though it should be noted that in both of these taxa the rostrum is damaged and a very small first incisor may have been present. Referral to the Tritheledontidae (a clade currently unknown from the Lower Lufeng Formation) is precluded by the presence of three premaxillary teeth in *Dianchungosaurus*: all tritheledontids possess only two pairs of premaxillary teeth (Shubin et al., 1991).

Several crocodylomorphs have been described from the Lower Lufeng Formation, but many taxa are based on fragmentary material or have damaged skull rostra (e.g., Young, 1951; Simmons, 1965; Luo and Wu, 1994; Harris et al., 2000), thus limiting comparisons with *Dianchungosaurus*. The sphenosuchian *Dibothrosuchus* Simmons, 1965 can clearly be distinguished from *Dianchungosaurus* by the presence of five premaxillary teeth, the lack of a well-developed secondary palate, the presence of an incisive foramen, and the marked separation of the external nares in the former (Wu, 1986; Wu and Chatterjee, 1993). Comparisons with the protosuchian *Platyognathus* Young, 1944 are hampered by the poor preservation of the snout in the latter, but the dentitions of the two taxa are distinct: in *Platyognathus*, the teeth increase in size from anterior to posterior (Wu and Sues, 1996), whereas the converse is true in *Dianchungosaurus*. The presence of a premaxillary secondary palate and the possible confluence of the external nares suggest that if the holotype of *Dianchungosaurus* is referable to the Crocodylomorpha it represents an early representative of the Mesoeucrocodylia (cf. Tykoski et al., 2002), though it is too fragmentary to allow determination of its position within this clade. The holotype of *Dianchungosaurus* represents a rare early record of Mesoeucrocodylia, whose other Lower Jurassic members include *Calsoyasuchus* Tykoski, Rowe, Ketcham, and Colbert, 2002 and thalattosuchians (Tykoski et al., 2002).

The foregoing discussion demonstrates that the hypodigm of *Dianchungosaurus* is a chimaera, composed of crocodyliform and prosauropod material. Although fragmentary, the holotype specimen clearly differs from other Lower Lufeng crocodylomorphs for which appropriate comparative material is available. Indeed, the premaxillary dentition of *Dianchungosaurus* is highly distinctive, with the first tooth significantly larger than the second or third tooth and inset from the medial margin of the premaxilla, and the presence of a diastema between the first and second tooth (IVPP V4735a; Yang, 1982a). This is in marked contrast to the situation in *Dibothrosuchus* and *Platyognathus*, where the teeth extend to the midline, increase in size posteriorly, and lack significant diastemas between them (Wu, 1986; Wu and Chatterjee, 1993; Wu and Sues, 1996). These features, in combination with the relatively derived systematic position and early occurrence of *Dianchungosaurus*, suggest that it should be retained as a provisionally valid taxon of mesoeucrocodylian, despite the poor quality of the holotype specimen, until such time as additional material is discovered that will allow a more thorough appraisal of its status. In order to stabilize the nomenclature of *Dianchungosaurus*, the undiagnostic and unrelated paratype specimen (IVPP V4735b) should no longer be included in discussions of the characteristic features of this genus; because paratypes lack a name-bearing function, this is permitted by the articles of the ICZN (see International Committee on Zoological Nomenclature, 1999: Article 72.1.3).

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Hay, 1930 sensu Walker, 1970
CROCODYLIFORMES Benton and Clark, 1988
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
Genus DIANCHUNGOSAURUS Yang, 1982a
Figures 1.1–1.4, 2.1–2.3

Dianchungosaurus lufengensis YANG, 1982a (partim), p. 38, figs. 1, 2.
Dianchungosaurus lufengensis YANG, 1982a (partim). WEISHAMPEL AND WITMER, 1990, p. 487.
Dianchungosaurus lufengensis YANG, 1982a (partim). SUN, LI, YE, DONG, AND HOU, 1992, p. 151.
Dianchungosaurus lufengensis YANG, 1982a (partim). LUO AND WU, 1994, p. 255.
Dianchungosaurus lufengensis YANG, 1982a (partim). LUCAS, 1996b, p. 24.
Dianchungosaurus lufengensis YANG, 1982a (partim). LUCAS, 2001, p. 133.

Type species.—*Dianchungosaurus lufengensis* Yang, 1982a, by monotypy.

Revised diagnosis.—A mesoeucrocodylian with the following autapomorphies: distinct diastema separating the mesial margin of the first premaxillary tooth alveolus and the medial margin of the premaxilla; a second diastema separating the first and second premaxillary teeth; and caniniform first premaxillary tooth, significantly larger than the second and third premaxillary teeth.

Type.—Holotype, IVPP V4735a (field number 7205), an isolated left premaxilla.

Occurrence.—Dark Red Beds, Lower Lufeng Formation. Lower Jurassic (Sinemurian: see Luo and Wu, 1994). Chang village, Lufeng County, Yunnan Province, People's Republic of China.

Discussion.—Sun et al. (1992) incorrectly listed the holotype as IVPP V7205. 7205 is the field collection number noted by Yang (1982a), not the formal accession number of the specimen. Yang (1982a) listed a number of character states in the diagnosis based on the paratype specimen: as the hypodigm of *Dianchungosaurus* is a chimaera, these character states should now be disregarded. Many of Yang's (1982a) proposed diagnostic character states are inadequate to distinguish *Dianchungosaurus* from other taxa (e.g., thick, strong premaxilla; nostril wide and low; ventral border of premaxilla on the same level as that of the maxilla; premaxillary teeth conical); valid autapomorphies are included in the revised diagnosis (see above).

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
SAUROPODOMORPHA Huene, 1932
PROSAUROPODA Huene, 1920
Genus and species INDETERMINATE
Figure 3.1, 3.2

Dianchungosaurus lufengensis YANG, 1982a (partim), p. 38, figs. 1, 2.
Dianchungosaurus lufengensis YANG, 1982a (partim). WEISHAMPEL AND WITMER, 1990, p. 487.
Dianchungosaurus lufengensis YANG, 1982a (partim). SUN, LI, YE, DONG, AND HOU, 1992, p. 151.
Dianchungosaurus lufengensis YANG, 1982a (partim). LUO AND WU, 1994, p. 255.
Dianchungosaurus lufengensis YANG, 1982a (partim). LUCAS, 1996b, p. 24.
Dianchungosaurus lufengensis YANG, 1982a (partim). LUCAS, 2001, p. 133.

Material examined.—IVPP V4735b (field number 7211), cojoined partial left and right dentaries with teeth and left splenial.
Occurrence.—As above.

CONCLUSIONS

Reexamination of the type material demonstrates that the hypodigm of *Dianchungosaurus lufengensis* is a chimera, with the holotype representing a mesoeucrocodylian and the paratype an indeterminate prosauropod dinosaur. Use of the name *Dianchungosaurus* should henceforth be restricted to the holotype specimen (IVPP V4735a) in order to stabilize the use of this taxon name, until such time that further material comes to light. Revision of this genus invalidates the only reported occurrence of a heterodontosaurid dinosaur from Asia and highlights further the paucispecific nature of the Lower Lufeng Formation ornithischian fauna. The only definite ornithischian materials known from this unit are the fragmentary holotype specimens of *Tatisaurus* (Simmons, 1965) and *Bienosaurus* (Dong, 2001) and some indeterminate postcranial material (Irmis, 2002). This is somewhat surprising because, although ornithischians are not diverse in the Lower Jurassic, they are more conspicuous members of penecontemporaneous faunas in southern Africa (*Lesothosaurus* Galton, 1978, heterodontosaurids), Europe (*Scelidosaurus*), and North America (basal thyreophorans) (Weishampel, 1990). The reasons for the extreme rarity of ornithischians in the Lower Jurassic of China are unclear at present. The presence of a mesoeucrocodylian in the Lower Lufeng Formation provides further evidence for the early radiation of this clade in the Lower Jurassic and also increases the geographical range of this clade to incorporate eastern Asia at this time.

ACKNOWLEDGMENTS

PMB thanks the collections staff of IVPP for access to material in their care, Z. Zhou and X.-L. Wang for their hospitality, and P. Upchurch for help in data collection while in China. J. A. Hopson, J. M. Clark, and Wu Xiao-Chun provided useful discussion on Lower Jurassic crocodylomorphs and cynodonts, and S. Modesto, D. Dilkes, and M. Carrano provided helpful reviews of an earlier draft. W. Gao and J.-L. Huang took the photographs for Figures 1 and 3. D. B. Norman (University of Cambridge) provided access to cranial material of *Heterodontosaurus*, which was on loan to him from the SAM. Thanks to S. Kaal, D. Ohland, and R. Smith for permission to work with the SAM material. PMB was funded by a travel grant from The Royal Society of London and XX was supported by grants from the National Natural Science Foundation of China (40125006).

REFERENCES

BENTON, M. J., AND J. M. CLARK. 1988. Archosaur phylogeny and the relationships of the Crocodylia, p. 295–338. *In* M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods. Volume 1. Oxford University Press, Oxford.
CHARIG, A. J., AND A. W. CROMPTON. 1974. The alleged synonymy of *Lycorhinus* and *Heterodontosaurus*. Annals of the South African Museum, 64:167–189.
CLARK, J. M., AND J. A. HOPSON. 1985. Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. Nature, 315:398–400.
COOMBS, W. P. JR., D. B. WEISHAMPEL, AND L. M. WITMER. 1990. Basal Thyreophora, p. 427–434. *In* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria (first edition). University of California Press, Berkeley.
CROMPTON, A. W., AND A. J. CHARIG. 1962. A new ornithischian from the Upper Triassic of South Africa. Nature, 196:1074–1077.
CUI, G.-H. 1976. *Yunnania*, a new tritylodont genus from Lufeng, Yunnan. Vertebrata PalAsiatica, 14:85–90. (In Chinese with English summary)
CUI, G.-H. 1981. A new genus of Tritylodontoidea. Vertebrata PalAsiatica, 19:5–10, 1 pl. (In Chinese with English summary)
CUI, G.-H. 1986. *Yunnanodon*, new name (mammal-like reptiles: Tritylodontidae) for *Yunnania* Cui, 1976. Vertebrata PalAsiatica, 24:79. (In Chinese and English)
DONG, Z.-M. 1990. Stegosaurs of Asia, p. 255–268. *In* K. Carpenter and P. J. Currie (eds.), Dinosaur Systematics: Approaches and perspectives. Cambridge University Press, Cambridge.
DONG, Z.-M. 1992. The Dinosaurian Faunas of China. Springer-Verlag, Berlin, 188 p.
DONG, Z.-M. 2001. Primitive armored dinosaur from the Lufeng Basin, Yunnan, p. 237–242. *In* D. H. Tanke and K. Carpenter (eds.), Mesozoic Vertebrate Life. Indiana University Press, Bloomington.
GALTON, P. M. 1978. Fabrosauridae, the basal family of ornithischian dinosaurs (Reptilia: Ornithopoda). Paläontologische Zeitschrift, 52: 138–159.
GALTON, P. M. 1985. Diet of prosauropods from the Late Triassic and Early Jurassic. Lethaia, 18:105–123.
GALTON, P. M. 1986. Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs, p. 203–221. *In* K. Padian (ed.), The Beginning of the Age of the Dinosaurs. Cambridge University Press, Cambridge.
GOW, C. E. 1975. A new heterodontosaurid from the Red Beds of South Africa showing clear evidence of tooth replacement. Zoological Journal of the Linnean Society of London, 57:335–339.
GOW, C. E. 1990. A tooth-bearing maxilla referable to *Lycorhinus angustidens* Haughton, 1924 (Dinosauria: Ornithischia). Annals of the South African Museum, 99:367–380.
HARRIS, J. D., S. G. LUCAS, J. W. ESTEP, AND J.-J. LI. 2000. A new and unusual sphenosuchian (Archosauria: Crocodylomorpha) from the Lower Jurassic Lufeng Formation, People's Republic of China. Neues Jahrbuch für Geologie und Paläontology, Abhandlungen, 215:47–68.
HAY, O. P. 1930. Second Bibliography and Catalogue of the Fossil Vertebrata of North America. Volume 2. Carnegie Institution of Washington Publication, 390. Carnegie Institution of Washington, Washington, DC, 1,074 p.
HOPSON, J. A. 1975. On the generic separation of the ornithischian dinosaurs *Lycorhinus* and *Heterodontosaurus* from the Stormberg Series (Upper Triassic) of South Africa. South African Journal of Science, 71: 302–305.
HUENE, F. 1920. Bemerkungen zur systematic und stammesgeschichte einiger reptilien. Zeitschrift für Inducktive Abstammungs- und Vererbungslehre, 24:162–166.
HUENE, F. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Monographien Geologie und Paläontologie, series 1, 4:1–361.
INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1999. International Code of Zoological Nomenclature (fourth edition). International Trust for Zoological Nomenclature, London, 306 p.
IRMIS, R. 2002. [Abstract]. The first reported ornithischian dinosaur postcrania from the Early Jurassic Lufeng Formation, China. Journal of Vertebrate Paleontology, 22(3-Suppl.):70A.
LUCAS, S. G. 1996a. The thyreophoran dinosaur *Scelidosaurus* from the Lower Jurassic Lufeng Formation, Yunnan, China. Museum of Northern Arizona Bulletin, 60:81–85.
LUCAS, S. G. 1996b. Vertebrate biochronology of the Jurassic of China. Museum of Northern Arizona Bulletin, 60:23–33.

LUCAS, S. G. 2001. Chinese Fossil Vertebrates. Columbia University Press, New York, 375 p.

LUO, Z.-X., AND X.-C. WU. 1994. The small tetrapods of the Lower Lufeng Formation, Yunnan, China, p. 251–270. *In* N. C. Fraser and H.-D. Sues (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge.

LUO, Z.-X., AND X.-C. WU. 1995. Correlation of vertebrate assemblage of the Lower Lufeng Formation, Yunnan, China, p. 83–88. *In* A.-L. Sun and Y. Wang (eds.), 6th Symposium on Mesozoic Terrestrial Ecosystems and Biotas, Short Papers. China Ocean Press, Beijing.

OWEN, R. 1842. Report on British Fossil Reptiles, Pt. II. Reports of the British Association for the Advancement of Science, 11:60–204.

OWEN, R. 1861. A monograph of the fossil Reptilia of the Liassic formations. I. *Scelidosaurus harrisonii*. Monographs of the Palaeontographical Society, 13:1–14.

SEELEY, H. G. 1887. On the classification of the fossil animals commonly called Dinosauria. Proceedings of the Royal Society of London, 43: 165–171.

SERENO, P. C. 1991. *Lesothosaurus*, ''fabrosaurids,'' and the early evolution of Ornithischia. Journal of Vertebrate Paleontology, 11:168–197.

SHUBIN, N. H., A. W. CROMPTON, H.-D. SUES, AND P. E. OLSEN. 1991. New fossil evidence on the sister-group of mammals and early Mesozoic faunal distributions. Science, 251:1063–1065.

SIMMONS, D. J. 1965. The non-therapsid reptiles of the Lufeng Basin, Yunnan, China. Fieldiana, Geology, 15:1–93.

SUN, A.-L. 1984. Skull morphology of the tritylodont genus *Bienotheroides* of Sichuan. Scientia Sinica (series B), 27:970–984.

SUN, A.-L., J.-L. LI, X.-K. YE, Z.-M. DONG, AND L.-H. HOU. 1992. The Chinese Fossil Reptiles and their Kins. Science Press, Beijing, 260 p.

THULBORN, R. A. 1970. The systematic position of the Triassic ornithischian dinosaur *Lycorhinus angustidens*. Zoological Journal of the Linnean Society of London, 49:235–245.

THULBORN, R. A. 1974. A new heterodontosaurid dinosaur (Reptilia: Ornithischia) from the Upper Triassic Red Beds of Lesotho. Zoological Journal of the Linnean Society of London, 55:151–175.

TYKOSKI, R. S., T. B. ROWE, R. A. KETCHAM, AND M. W. COLBERT. 2002. *Calsoyasuchus valliceps*, a new crocodyliform from the Early Jurassic Kayenta Formation of Arizona. Journal of Vertebrate Paleontology, 22:593–611.

WALKER, A. D. 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. Philosophical Transactions of the Royal Society of London, series B, 257:323–372.

WEISHAMPEL, D. B. 1990. Dinosaurian distribution, p. 63–139. *In* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria (first edition). University of California Press, Berkeley.

WEISHAMPEL, D. B., AND L. M. WITMER. 1990. Heterodontosauridae, p. 486–497. *In* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria (first edition). University of California Press, Berkeley.

WHETSTONE, K. N., AND P. J. WHYBROW. 1983. A ''cursorial'' crocodilian from the Triassic of Lesotho (Basutoland), southern Africa. Occasional Papers of the Museum of Natural History, University of Kansas, 106:1–37.

WU, X.-C. 1986. A new species of *Dibothrosuchus* from Lufeng Basin. Vertebrata PalAsiatica, 24:42–62, pls. 5, 6. (In Chinese with English summary)

WU, X.-C., AND S. CHATTERJEE. 1993. *Dibothrosuchus elaphros*, a crocodylomorph from the Early Jurassic of China and the phylogeny of the Sphenosuchia. Journal of Vertebrate Paleontology, 13:58–89.

WU, X.-C., AND H.-D. SUES. 1996. Reassessment of *Platyognathus hsui* Young, 1944 (Archosauria: Crocodyliformes) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China. Journal of Vertebrate Paleontology, 16:42–48.

YANG, Z.-J. 1982a. [A new genus of dinosaur from Lufeng County, Yunnan Province], p. 38–42. *In* M.-Z. Zhou (ed.), [Collected works of Yang Zhongjian]. Academia Sinica, Beijing. (In Chinese)

YANG, Z.-J. 1982b. [A new ornithopod from Lufeng, Yunnan], p. 29–35. *In* M.-Z. Zhou (ed.), [Collected works of Yang Zhongjian]. Academia Sinica, Beijing. (In Chinese)

YANG, Z.-J. 1982c. [*Bienotheroides*], p. 10–13. *In* M.-Z. Zhou (ed.), [Collected works of Yang Zhongjian]. Academia Sinica, Beijing. (In Chinese)

YOUNG, C. C. 1940. Preliminary note on the Mesozoic mammals of Lufeng, Yunnan, China. Bulletin of the Geological Society of China, 20: 93–111.

YOUNG, C. C. 1941a. A complete osteology of *Lufengosaurus huenei* Young (gen. et sp. nov.) from Lufeng, Yunnan, China. Palaeontologica Sinica (series C), 7:1–53.

YOUNG, C. C. 1941b. *Gyposaurus sinensis*, Young (sp. nov.) a new Prosauropoda from the Upper Triassic Beds at Lufeng, Yunnan. Bulletin of the Geological Society of China, 21:207–253.

YOUNG, C. C. 1942. *Yunnanosaurus huangi* Young (gen. et sp. nov.), a new Prosauropoda from the Red Beds at Lufeng, Yunnan. Bulletin of the Geological Society of China, 22:63–104.

YOUNG, C. C. 1944. On a supposed new pseudosuchian from Upper Triassic saurischian-bearing Red Beds of Lufeng, Yunnan, China. American Museum Novitates, 1264:1–4.

YOUNG, C. C. 1947a. On *Lufengosaurus magnus* Young (sp. nov.) and additional finds of *Lufengosaurus huenei* Young. Palaeontologica Sinica (series C), 12:1–53, pl. 1.

YOUNG, C. C. 1947b. Further notes on *Gyposaurus sinensis* Young. Bulletin of the Geological Society of China, 28:91–103, pls. 1–5.

YOUNG, C. C. 1947c. Mammal-like reptiles from Lufeng, Yunnan, China. Proceedings of the Zoological Society of London, 117:537–597.

YOUNG, C. C. 1951. The Lufeng saurischian fauna. Palaeontologica Sinica (series C), 13:1–96.

ACCEPTED 25 AUGUST 2004