

First report of *Megapnosaurus* (Theropoda: Coelophysoidea) from China

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The biota of the Lower Jurassic Lufeng Formation (Yunnan Province, China) is critical to understanding Early Jurassic tetrapod evolution and biogeography. Theropod dinosaur material from the Lufeng Formation remains enigmatic and poorly known. For this reason, any theropod material that can be unequivocally identified as a particular taxon is valuable in understanding the theropod fauna of the Lufeng Formation. Here, two specimens are reported as being the first record of the dinosaur *Megapnosaurus* from the Lufeng Formation, and the whole of Asia. The presence of *Megapnosaurus* is consistent with previous work suggesting an Early Jurassic age for the Lufeng Formation. It also greatly extends the geographic range of the genus, and confirms the pangeographic distribution of Early Jurassic terrestrial tetrapods.

INTRODUCTION

The Lufeng Formation is a series of Lower Jurassic non-marine redbed sediments from Yunnan Province, China (Fang et al. 2000). The formation is well known for its diverse assemblages of terrestrial vertebrates, especially prosauropod dinosaurs, therapsids, and mammals (Young 1951, Sun et al. 1985). Collections have been made from the strata for over 50 years; much of the early work on the saurischian dinosaur fauna was published by Young (e.g., 1941, 1947, 1948, 1951). The fauna of the Lufeng Formation is important to our understanding of Early Jurassic tetrapod evolution and biogeography, because it is one of the only diverse assemblages of its age in Asia.

Whereas prosauropods and synapsids are relatively common in the Lufeng Formation, theropod dinosaurs remain relatively rare and enigmatic. *Sinosaurus triassicus* Young 1948 and *Lukousaurus yini* Young 1948 were the first putative theropods named from the formation. Hu (1993) briefly described “*Dilophosaurus*” *sinensis* from the Lufeng, and a therizinosaurid was recently described from the strata and named *Eshanosaurus deguchiianus* Xu, Zhao, and Clark 2001 (Zhao and Xu 1998). Unfortunately, these taxa remain poorly understood, and some may not even be theropods (see Discussion below).

Thus, unequivocal, identifiable theropod fossils from the Lufeng Formation are important, because most material previously labeled as such is ambiguous at best. Simmons (1965) figured and briefly described theropod material from the Catholic University of Peking collection held at the Field Museum of Natural History, Chicago, but subsequent studies of Early Jurassic theropod taxa have overlooked this material. Furthermore, Simmons’s description misidentified elements and lacked good Early Jurassic theropod material for comparison. Here, material first published by Simmons (1965) is redescribed and refigured, and its implications are discussed.

Abbreviations—**FMNH CUP**, Field Museum of Natural History (Catholic University of Peking collection), Chicago, Illinois; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MNA**, Museum of

Northern Arizona, Flagstaff, Arizona; **QG**, Queen Victoria Museum, Salisbury, Zimbabwe.

GEOLOGIC SETTING

The Lower Jurassic Lufeng Formation is a sequence of terrestrial strata that crops out in Yunnan Province, southern China (Fang et al. 2000). It is composed of interbedded sandstones, siltstones, and mudstones that were initially regarded as Late Triassic in age (Bien 1941), but are now widely recognized as being of Early Jurassic age based on the fossil biota (Sun et al. 1985, Luo and Wu 1994).

The most recent stratigraphic nomenclature of Fang et al. (2000) is used in this paper, although it is useful to note previous names for the lithostratigraphic units in question. The Lufeng Formation has previously been referred to as the Lower Lufeng Series and the Lower Lufeng Formation (Bien 1941, Sheng et al. 1962, Sun et al. 1985). It was informally divided into two subunits, the lower “Dark Purple Beds” and upper “Deep Red Beds” (Bien 1941). Fang et al. (2000) formalized these units into the Shawan Member and Zhangjiawa Member, respectively. The specimens discussed here originate from the more fossiliferous Zhangjiawa Member, which is composed of interbedded red mudstones and siltstones (Fang et al. 2000).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen 1842

THEROPODA Marsh 1881

COELOPHYSOIDEA Holtz 1994

Megapnosaurus Ivie, Slipinski and Wegrzynowicz 2001

cf. *Megapnosaurus* sp.

(Figs. 1, 2)

PODOKESAURIDAE Simmons 1965:figs. 7e, 10b, p. 55–59.

Material—FMNH CUP 2089, distal humerus, proximal radius and ulna, fragments of metacarpals and phalanges; FMNH CUP 2090, right distal tarsals II and III and proximal metatarsals II and III.

Locality—Zhangjiawa Member of the Lufeng Formation, Ta Ti, Yunnan Province, China.

Syntarsus Raath 1969 is a junior homonym of the zoopherid beetle *Syntarsus* Fairmaire 1869, so Ivie et al. (2001) provided the replacement name *Megapnosaurus* for the theropod dinosaur. Regardless of the controversy surrounding this replacement name (Holden 2002), it is valid, and must be used according to the rules of nomenclature.

DESCRIPTION

Simmons (1965) noted that both specimens (FMNH CUP 2089 and 2090) were found in association with the holotype of the crocodylomorph *Dibothrosuchus elaphros* Simmons 1965 (FMNH CUP 2081). FMNH CUP 2089 and 2090 are much too large to pertain to *Dibothrosuchus*, differ greatly from the morphology described for *Dibothrosuchus* (Simmons 1965, Wu and Chatterjee 1993), and would also duplicate elements found in FMNH CUP 2081. No other dinosaur remains were found with the holotype of *Dibothrosuchus*, so it is plausible to assume that both specimens belong to the same individual. Furthermore, the proportions of each specimen suggest that they both belonged to an animal of the same size. It should be noted that the specimens are generally poorly preserved, and they were further damaged by preparation, presumably in the 1950s or 1960s.

FMNH CUP 2089

This specimen consists of a semi-articulated left distal humerus, proximal ulna, and proximal radius (Fig. 1). Diagenetically attached to the ulna is a bone that is tentatively identified as a vertebra. Also found with this specimen are uninformative, badly preserved fragments of metacarpals and phalanges. This specimen was identified erroneously by Simmons (1965) as a distal femur, proximal tibia, and proximal fibula. What was previously labeled a distal femur much more closely matches the morphology of a distal humerus, and lacks well developed condyles and a crista tibiofibularis, which would be expected for a distal femur. The “tibia” is actually an ulna, because it plainly has an olecranon process and sigmoid notch. Simmons’s “fibula” does not match the morphology of any archosaur fibula, and is instead a proximal radius, similar to other coelophysoid radii (Welles 1984, Raath 1969).

The distal humerus (Fig. 1A, B, C) has a preserved length of 55 mm, and the shaft is convexly bowed posteriorly (Fig. 1A, B). The proximal broken end has a maximum diameter of 9 mm, and shows that the bone is thin-walled and hollow in transverse section. The shaft broadens to a distal end with a maximum width of 21 mm. In *Megapnosaurus rhodesiensis* (Raath 1969), the distal condyles are only weakly developed (Fig. 1C), and have a maximum width of 17 mm (Raath 1969). There is a pronounced rim around the distal condyles, and this feature was described by Raath (1990) for some specimens of *Megapnosaurus rhodesiensis*. However, homology of this feature with *M. rhodesiensis* is not certain due to

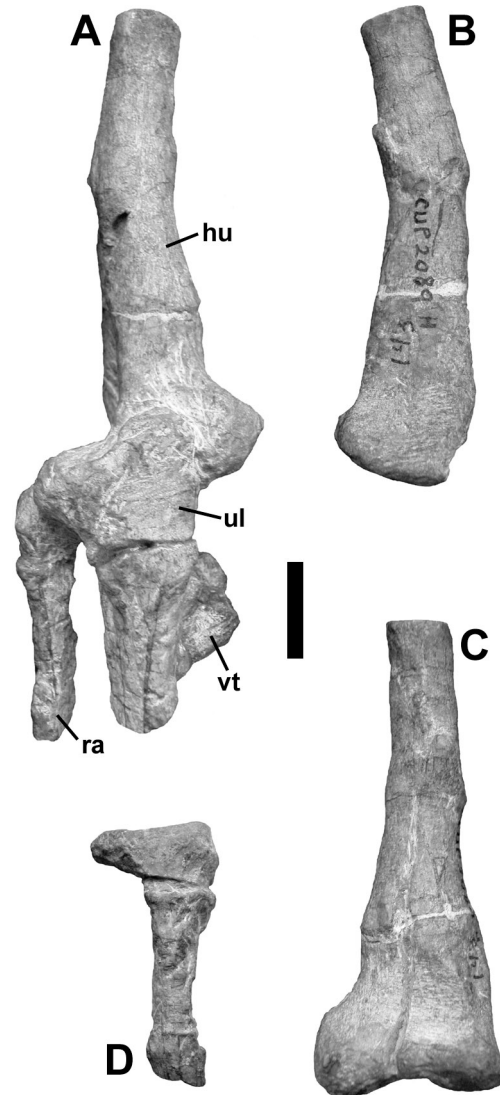


Fig. 1. cf. *Megapnosaurus* sp. (FMNH CUP 2089) from the Lufeng Formation, China. **A.** medial view of left humerus, lateral view of left ulna, anterior view of left radius; **B.** lateral view of left humerus; **C.** anterior view of left humerus; **D.** medial view of left radius. **Abbreviations:** hu, humerus; ra, radius; ul, ulna; vt, vertebra. Scale bar equals 1 cm.

poor preservation and preparation damage.

The proximal ulna has a preserved length of 35 mm, and is medio-laterally compressed. The proximal end is 19 mm wide and has a well-developed olecranon process that projects dorsally and a sigmoid notch that opens anteriorly (Fig. 1A). The olecranon process is not as large relative to the rest of the ulna as in the holotype of *Megapnosaurus rhodesiensis* (Raath 1969); however, Raath (1990) notes that this can vary among individuals. The shaft narrows distally down to a broken end with a maximum diameter of 8.5 mm.

The proximal radius has a preserved length of 31 mm. The proximal margin is widely expanded to 15 mm with a slightly concave surface and well-developed posterior process (Fig.

ID). This process is unusually well accentuated, although it is emphasized by bone loss from poor preservation and preparation. Such a posterior process is seen in *Megapnosaurus* (Raath 1969: plate II), *Dilophosaurus* Welles 1970 (Welles 1984), and to a lesser extent in *Coelophysis* Cope 1889 (Colbert 1989: fig. 72), and may be a synapomorphy of Coelophysoidea. The shaft constricts distally and terminates in a broken end 6 mm in diameter.

FMNH CUP 2090

This specimen consists of distal tarsals and proximal metatarsals II and III from the right pes (Fig. 2). Based on comparison with the holotype (QG/1) pes of *Megapnosaurus rhodesiensis* figured by Raath (1969: pl. V), approximately two-thirds of each metatarsal is preserved. Distal tarsals II and III are fused to the proximal end of each metatarsal (Fig. 2B, C). The metatarsals themselves are fused to each other for the proximal half of their preserved length. Although this can occur through diagenesis, no visible break or suture between the bones is seen where they are fused, and the morphology matches exactly that described by others for *Megapnosaurus* (Raath 1969, Rowe 1989, Tykoski 1998).

Distal tarsal II and metatarsal II have a combined preserved length of 40 mm (Fig. 2B). The proximal articular surface is ovate in proximal view, with a maximum diameter of 11 mm, and it protrudes posteriorly (Fig. 2A). The shaft of metatarsal II gradually narrows distally to a 5 mm diameter at the broken end.

Distal tarsal III and metatarsal III have a combined preserved length of 42 mm (Fig. 2C). In proximal view, the articular surface is trapezoidal in profile (Fig. 2A), with a maximum width of 10 mm. The articular surface has a slightly convex posterior margin, and the anterior margin is slightly concave (Fig. 2A), although this may be a result of damage from preparation. The proximal end is also expanded medially. Distal tarsal III of FMNH CUP 2090 resembles the holotype pes of *Megapnosaurus kayentakatae* (Rowe 1989) (MNA V2623), as it is thickest along its posterior edge, and it seems to partially overlap distal tarsal II (Tykoski 1998).

DISCUSSION

FMNH CUP 2090 can be referred without question to the Ceratosauria (as defined by Holtz 2000). A synapomorphy of this clade is the fusion of distal tarsals II and III to their respective metatarsals (Rowe 1989, Rowe and Gauthier 1990, Tykoski 1998, Holtz 2000). This specimen does not represent a more advanced theropod (tetanuran) because the proximal end of metatarsal III is not hourglass shaped (Carrano et al. 2002). Within this group, FMNH CUP 2090 can be referred to the genus *Megapnosaurus*, based on the fused metatarsals II and III, which is an unambiguous synapomorphy of the genus (Raath 1969, Rowe 1989, Rowe and Gauthier 1990, Tykoski 1998). However, because of the poor preservation and preparation of the specimen, one cannot be 100% certain that diagenesis did not create

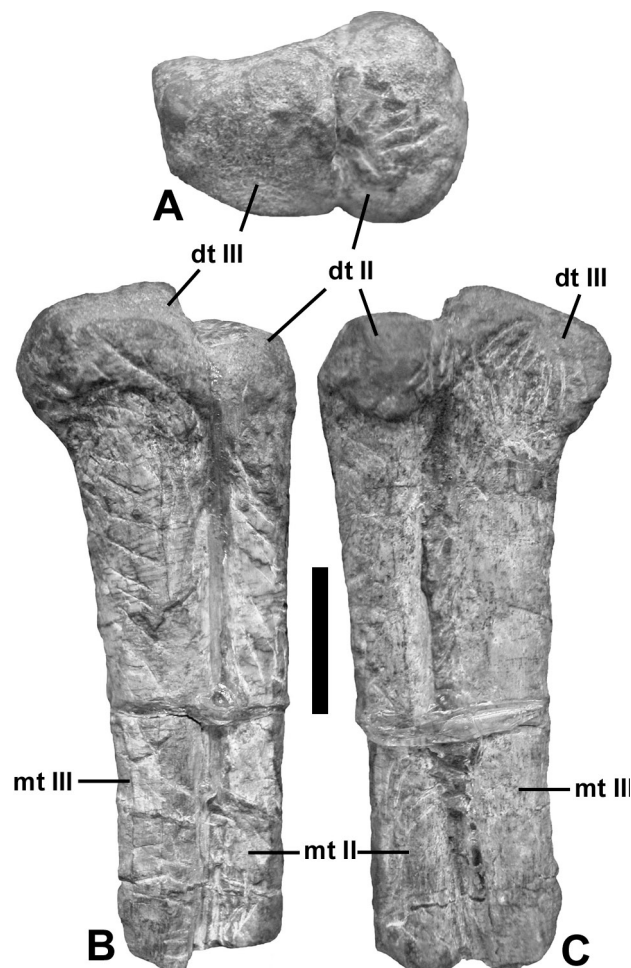


Fig. 2. cf. *Megapnosaurus* sp. (FMNH CUP 2090) from the Lufeng Formation, China. A. proximal view of right distal tarsal II and III; B. anterior view of distal tarsals and metatarsals II and III; C. posterior view of distal tarsals and metatarsals II and III. Abbreviations: mt II, metatarsal II; mt III, metatarsal III; dt II, distal tarsal II; dt III, distal tarsal III. Scale bar equals 1 cm.

the fusion of the two metatarsals. Therefore, the specimen is referred to cf. *Megapnosaurus* sp. No characters have been observed that allow the specimen to be referred to either an existing or a new species of *Megapnosaurus*.

Alone, FMNH CUP 2089 cannot be referred to the genus *Megapnosaurus*. Nevertheless, its association with FMNH CUP 2090 strongly suggests that both specimens came from the same individual. Furthermore, the curved shaft of the humerus is consistent with a sigmoid profile, a synapomorphy of Coelophysoidea (Holtz 2000). Additionally, FMNH CUP 2089 does not have flattened distal humeral condyles, the condition seen in the more advanced clade Tetanurae (Carrano et al. 2002). Although FMNH CUP 2089 can only be constrained to Coelophysoidea, it is highly unlikely that two coelophysoid specimens with non-duplicating elements that are found together would represent two different individuals or taxa.

Megapnosaurus has long been hypothesized to share a close affinity with the Late Triassic genus *Coelophysis* (Raath 1969, Colbert 1989, Rowe 1989, Tykoski 1998). Both of these genera are grouped within the clade Coelophysoidea, a plesiomorphic lineage of the theropod clade Ceratosauria (Rowe 1989, Rowe and Gauthier 1990, Tykoski 1998, Holtz 2000, Carrano et al. 2002). Recent analyses, though, suggest that Ceratosauria as it is traditionally defined is paraphyletic (Carrano et al. 2002, Rauhut 2003). However, clades within this paraphyletic group, such as Coelophysoidea (excluding *Dilophosaurus*) or Neoceratosauria, have retained their monophyly, and can still be recognized by a suite of synapomorphies (Carrano et al. 2002).

Other purported theropod taxa from the Lufeng Formation include *Sinosaurus triassicus* Young 1948, *Lukousaurus yini* Young 1948, "*Dilophosaurus*" *sinensis* Hu 1993, and *Eshanosaurus deguchiiianus* Xu, Zhao, and Clark 2001. The holotype of *Sinosaurus*, IVPP V 34 (Young 1948, Sun et al. 1992), consists of a maxilla fragment that contains little phylogenetic information, and so the name is here restricted to the holotype and considered a *nomen dubium*. Other material referred to this taxon consists of indeterminate theropod teeth and prosauropod elements (Sun et al. 1992). The holotype of *Lukousaurus*, the anterior portion of a skull (IVPP V 23), most likely represents a crocodylomorph instead of a theropod, as does the material referred to this taxon by Simmons (1965) (Irmis, pers. obs.). Welles and Long (1974) described an unusually large "ceratosauroid" astragalocalcaenum from the Lufeng Formation. This specimen is very similar to matching coelophysoid elements, unfortunately, it was not associated with other material.

"*Dilophosaurus*" *sinensis* was briefly named and described in a preliminary note (Hu 1993). Its referral to the genus *Dilophosaurus* was based solely on the presence of a paired nasolacrimal crest on the skull. However, this character is not limited to *Dilophosaurus* (Rowe 1989), and the material described by Hu (1993) possesses several unusual characters that suggest it does not belong to the genus *Dilophosaurus*, and may not even belong to the Ceratosauria (Lamanna et al. 1998; Tykoski 1998). For example, the description of "*D.*" *sinensis* mentions the presence of five premaxillary teeth, multiple maxillary fenestrae, and opisthocelous cervical vertebrae; all these characters are unambiguous synapomorphies of the more advanced clade Tetanurae or groups within it, not of the Ceratosauria (Holtz 2000). Further investigations of the phylogenetic position of "*Dilophosaurus*" *sinensis* await a detailed description of the animal.

Eshanosaurus deguchiiianus consists of a single dentary, which was recently described by Zhao and Xu (1998) and Xu et al. (2001) as the earliest known therizinosaur. If correct, this would extend the fossil record of therizosaurs 80 million years earlier than previously thought, and has major implications for the divergence times of theropod dinosaurs. Although such a temporal gap does not automatically render this phylogenetic hypothesis invalid, it does promote skepti-

cism. Prosauropods have dentaries that are convergent with those of therizosaurs and are common in the Lufeng Formation. Of the eleven characters cited by Xu et al. (2001) as evidence of a therizinosaur affinity for *Eshanosaurus*, they admit that ten are found in some form in other dinosaurs, such as ornithischians and prosauropods (Xu et al. 2001). Further work and additional material is needed to elucidate the phylogenetic position of *Eshanosaurus*, but it must be seriously considered that *Eshanosaurus* is in fact an aberrant prosauropod instead of a therizinosaur. Thus, the material described in this study represents one of the few well-understood theropod specimens from the Lufeng Formation.

BIOCHRONOLOGIC SIGNIFICANCE

The Lufeng Formation has long been known to contain a distinct, biostratigraphically useful fauna referred to as the "Lufeng Saurischian Fauna" (e.g., Young 1951). This fauna is characterized by an abundance of the prosauropod dinosaurs *Lufengosaurus* Young 1941 and *Yunnanosaurus* Young 1942, and the synapsid *Bienotherium* Young 1940 (Sun et al. 1985). For unknown reasons, Lucas (1996a, 2001) renamed this the "Dawan land-vertebrate faunachron." Because these two biochronological units are synonymous, Fang et al. (2000) suggested that the older "Lufeng Saurischian Fauna" be retained, and this is followed here. This fauna, recognizable in Early Jurassic continental strata throughout China, is a useful regional biostratigraphic tool (Lucas 2001). The presence of *Megapnosaurus* in the Lufeng Formation adds an additional index taxon to the Lufeng Saurischian Fauna.

Megapnosaurus is known from the Early Jurassic Period of both North America and Africa, and now Asia (Raath 1969, Rowe 1989). Its presence in the Lufeng Formation confirms the conclusions of earlier workers that the strata are Early Jurassic in age (Sun et al. 1985, Luo and Wu 1994). The presence of *Megapnosaurus* in three continents during the Early Jurassic suggests its potential to be a global Early Jurassic index taxon for terrestrial sediments.

Although biostratigraphic methodology is beyond the scope of this paper, it is worth noting that only low-level monophyletic taxa are useful as biostratigraphic markers (Angielczyk and Kurkin 2003). If it is found that the genus *Megapnosaurus*, as now defined, is paraphyletic or polyphyletic, then it is useless for biostratigraphy. Furthermore, the use of genera for correlation on a global scale only provides coarse resolution, and should be used with caution. I feel that it is inappropriate to use genera, such as *Megapnosaurus*, to correlate globally at a finer scale than epoch (e.g., Early Jurassic).

Rauhut and Hungerbühler (2000) described a theropod pelvis from the Late Triassic fissure fills of Wales. Interestingly, they refer it to *Megapnosaurus*, which would not only be the first occurrence of the genus in Europe, but also the first report of the genus in the Triassic Period. If this specimen is actually *Megapnosaurus*, it negates the biostratigraphic potential of *Megapnosaurus* discussed above. However, the

authors never described any discrete synapomorphies that link the Welsh pelvis firmly with *Megapnosaurus*, to the exclusion of other ceratosaurs. They did mention the presence of a pubic fenestra adjacent to the obturator foramen, a character seen in *Megapnosaurus*; however, this character is also present in the ceratosaurs *Coelophysis*, *Segisaurus*, and *Ceratosaurs* (Tykoski 1998). At present, it is best to regard the Welsh pelvis as an indeterminate coelophysoid. Nevertheless, it is possible that future work on the specimen could show it is indeed *Megapnosaurus*.

Raath (1972) and Gow and Latimer (1999) referred Late Triassic theropod footprints to *Megapnosaurus*. However, it is unlikely that ichnofossils can be assigned with confidence to specific body fossil taxa (Baird 1980, Carrano and Wilson 2001). Thus, these footprints cannot be reliably referred to *Megapnosaurus* unless a *Megapnosaurus* skeleton is preserved at the end of the trackway.

BIOGEOGRAPHIC SIGNIFICANCE

The presence of *Megapnosaurus* in Asia, specifically China, represents a large geographic range extension for the taxon. This is not completely unexpected, as *Megapnosaurus* was already known from various sites within North America and Africa. The type species, *M. rhodesiensis*, was originally described by Raath (1969, 1977) from the Lower Jurassic Forest Sandstone of Zimbabwe. It has since been found in a variety of other Early Jurassic localities in South Africa (Raath 1980, Munyikwa and Raath 1999). Rowe (1989) named *M. kayentakatae* from the Lower Jurassic Kayenta

Formation of Arizona, U.S.A. This species is now known from several individuals from various localities throughout the Kayenta Formation (Tykoski 1998). Lucas and Heckert (2001) referred material from the ?Lower Jurassic Moenave Formation of Arizona to *Megapnosaurus* sp., but they did not cite any synapomorphies that are exclusive to *Megapnosaurus*. Further study and description of the material is needed before its phylogenetic placement can be reliably determined. Munter (1999) also reported the occurrence of *Megapnosaurus* from the ?Early Jurassic locality of Huizachal Canyon in Tamaulipas, Mexico; this material has yet to be described. *Megapnosaurus* has also been reported from the Late Triassic of Wales (Rauhut and Hungerbühler, 2000), although this occurrence is doubtful (see Biochronologic Significance section). *Megapnosaurus* is the only Early Jurassic theropod presently known with such a wide geographic distribution. This global range provides evidence that the coelophysoid radiation that began during the Late Triassic continued into the Early Jurassic.

A wide range of other tetrapod taxa occur on more than one continent during the Early Jurassic Period (Fig. 3). *Clevosaurus* Swinton 1939, a terrestrial sphenodontid, is known from China, North America, and South Africa during the Early Jurassic (Wu 1994, Sues and Reisz 1995, Sues et al. 1994). The crocodylomorph *Protosuchus* Brown 1934 is known from both eastern and western North America, and South Africa (Colbert and Mook 1951, Sues et al. 1996, Gow, 2000). The prosauropod dinosaur *Massospondylus* Owen 1854 is known from North America, South Africa (Attridge et

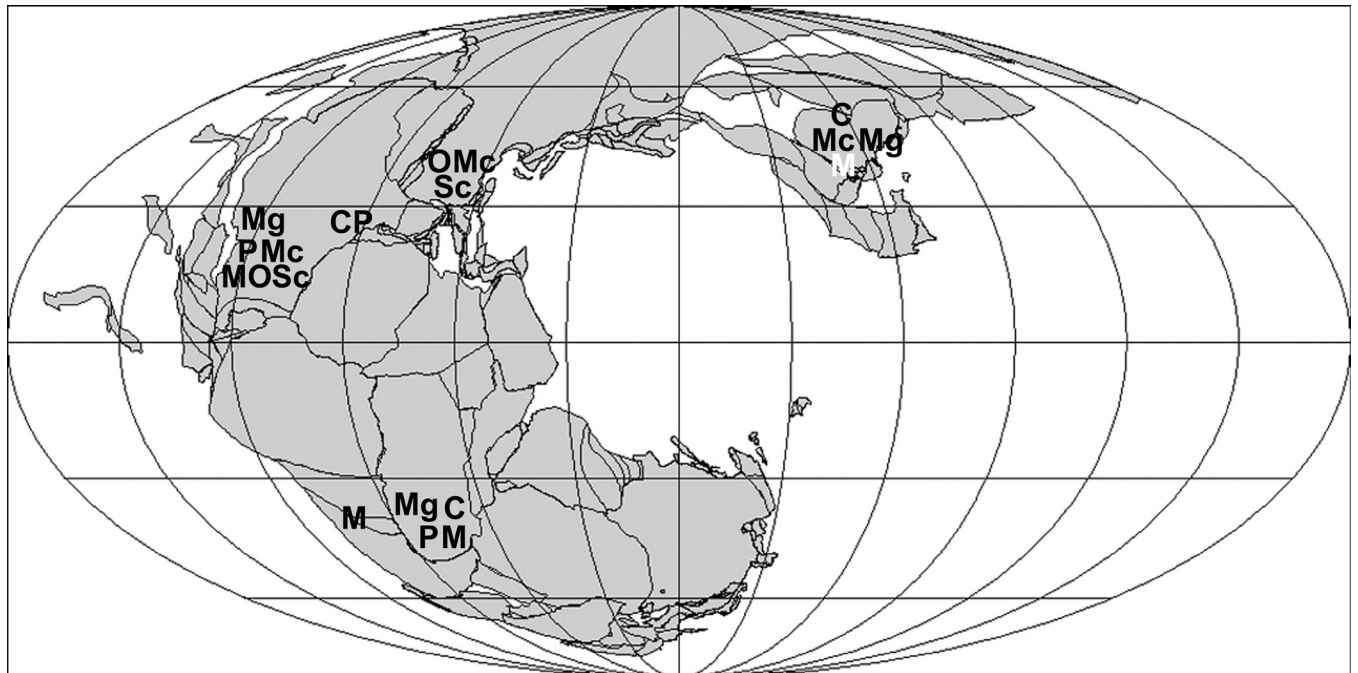


Fig. 3. Map of the continents during the Early Jurassic Period, showing distribution of selected pancontinental tetrapod genera. Map created using software from Schettino and Scotese (2001). **Abbreviations:** C, *Clevosaurus*; M, *Massospondylus* (M in white represents sister taxon *Lufengosaurus*); Mc, *Morganucodon*; Mg, *Megapnosaurus*; O, *Oligokyphus*; P, *Protosuchus*; Sc, *Scelidosaurus*.

al. 1985), and Argentina (Martinez 1999), and is the sister taxon to *Lufengosaurus* Young 1941 from China (Hinic 2002, Yates and Kitching 2003). Ornithischians from China are poorly represented, although they seem to be related to taxa elsewhere in the world (Lucas 1996b, Irmis 2002). The thyreophoran dinosaur *Scelidosaurus* Owen 1861 is known from both Britain and North America (Padian 1990), and Lucas (1996b) referred *Tatisaurus oehleri* Simmons 1965 from the Lufeng Formation to this genus. However, Lucas did not cite any discrete synapomorphies that link *Tatisaurus* with *Scelidosaurus*, although it is clear that *Tatisaurus* is a thyreophoran. Many synapsids also were pancontinental, with the tritylodont *Oligokyphus* Hennig 1922 known from both North America and Europe (Attridge et al. 1985, Sues 1986). In addition, *Kayentatherium* Kermack 1982, from the southwestern U.S.A., is most closely related to *Bienotherium* of China (Sues 1986). The mammaliaform *Morganucodon* Kühne 1949, like *Megapnosaurus*, is known from three continents: North America, Europe, and Asia (Attridge et al. 1985). It thus seems that the Early Jurassic Period is similar to the Late Triassic Period in that both have a global distribution of congeneric taxa (Lucas 1998).

CONCLUSIONS

FMNH CUP 2089 and 2090 represent the first record of *Megapnosaurus* from China, and the whole of Asia. Besides being some of the only well-understood theropod material from the Lufeng Formation, these specimens also increase the known diversity of the Lufeng fauna. Now that *Megapnosaurus* is known from three continents during the Early Jurassic Period, its wide geographic range makes it a possible index taxon for Early Jurassic biochronology, and strengthens the evidence for an Early Jurassic age for the Lufeng Formation. Finally, the fact that *Megapnosaurus* and other terrestrial tetrapods were pancontinental during the Early Jurassic suggests that the breakup of Pangaea did not present serious barriers to dispersal of terrestrial vertebrates.

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