N. Jb. Geol. Paläont. Abh. **215** (1) 47–68 Stuttgart, Januar 2000

A new and unusual sphenosuchian (Archosauria: Crocodylomorpha) from the Lower Jurassic Lufeng Formation, People's Republic of China

Jerald D. Harris, Spencer G. Lucas, John W. Estep, Albuquerque
and **Jianjun Li,** Beijing

With 6 figures

HARRIS, J. D., LUCAS, S. G., ESTEP, J. W. & LI, J. (2000): A new and unusual sphenosuchian (Archosauria: Crocodylomorpha) from the Lower Jurassic Lufeng Formation, People's Republic of China. – N. Jb. Geol. Paläont. Abh., **215**: 47–68; Stuttgart.

Abstract: We name and describe a new sphenosuchian, *Phyllodontosuchus lufengensis*, from the Lower Jurassic dark red beds of the Lufeng Formation near Dawa, Yunnan Province. The taxon differs from other sphenosuchians in possessing a markedly heterodont dentition, with six recurved, pointed teeth at the rostral end and at least 12 small, isoform, leaf-shaped (phylloform) teeth with crenelated caudal margins. The discovery of *Phyllodontosuchus* demonstrates both that heterodonty within the Crocodylomorpha is not restricted to the Notosuchidae and that crocodylomorphs may have deviated from strict carnivory at least twice.

Introduction

Early ancestors of extant crocodilians, as exemplified by the Triassic forms *Sphenosuchus* and *Pedeticosaurus* (HOEPEN 1915), have long been recognized in the fossil record (HUENE 1925; BROOM 1927). WALKER (1970) recognized that these primitive forms (including *Sphenosuchus* and several others), as well as derived forms and all forms occurring temporally between, form a monophyletic taxon, the Crocodylomorpha. The earliest and most primitive of these taxa were originally grouped in the Pedeticosauridae (HOEPEN 1915). BONAPARTE (1971, 1972) diagnosed and defined a

0077-7749/00/0215-0047 $ 5.50

larger, more inclusive group, the Sphenosuchia. The nature of the Sphenosuchia has undergone numerous analyses with differing results: CLARK (1986), BENTON & CLARK (1988), and PARRISH (1991) found the Sphenosuchia to be paraphyletic, but more recent analyses (SERENO & WILD 1992, WU & CHATTERJEE 1993) support monophyly of the group.

Unambiguous members of the Sphenosuchia include *Sphenosuchus acutus* (HAUGHTON 1915, HUENE 1921, BROOM 1927, WALKER 1990, PARRISH 1991) and *Pedeticosaurus leviseuri* (BONAPARTE 1972, GOW & KITCHING 1984) from South Africa, *Saltoposuchus connectens* (HUENE 1921, SERENO & WILD 1992) and *Dyoplax arenaceus* (LUCAS et al. 1998) from Germany, *Hesperosuchus agilis* (COLBERT 1952, PARRISH 1991) from Arizona and *Parrishia mccreai* (LONG & MURRY 1995) from New Mexico, USA, *Pseudhesperosuchus jachaleri* (BONAPARTE 1971) from Argentina, *Terrestrischus gracilis* (CRUSH 1984) from England, and *Dibothrosuchus elaphros* (SIMMONS 1965, WU 1986, WU & CHATTERJEE 1993) from China. Less certain members are *Trialestes romeri* (in part; REIG 1963; BONAPARTE 1971) from Argentina and *Hallopus victor* (MARSH 1877, 1890, HUENE & LULL 1908, WALKER 1970) from Colorado, USA. *Dyoplax, Pseudhesperosuchus, Saltoposuchus, Terrestrisuchus, Parrishia*, and *Hesperosuchus* (PARRISH 1991, LONG & MURRY 1995) are from Upper Triassic sediments; the remaining taxa have all been recovered from Lower Jurassic rocks, except *Hallopus*, which is from Upper Jurassic strata (AGUE et al. 1995).

A small (71.4 mm), badly crushed skull was collected in a nodule from the dark red beds of the Lufeng Formation near Dawa, Yunnan Province, People's Republic of China. A skull of the early mammal *Morganucodon* was recovered from the same locality (LUO et al. 1995). The specimen is housed at the Beijing Museum of Natural History and numbered BVP 568-L 12. Because of the imperfect state of preservation, the phylogenetic placement of the skull was initially unclear, and it was originally considered a possible primitive ornithischian dinosaur. The specimen clearly displays a large antorbital fenestra, indicating that it is a member of the Archosauria (Archosauriformes sensu GAUTHIER et al. 1988). Further examination has revealed that the specimen displays several autapomorphies of the Sphenosuchia, including a sagittal crest and a lateral rim on the quadrate. We here designate and describe the skull as the holotype of a new sphenosuchian, *Phyllodontosuchus lufengensis*.

Systematic Paleontology

Archosauria COPE, 1869
Crurotarsi SERENO et ARCUCCI, 1990
Suchia KREBS, 1974
Crocodylomorpha WALKER, 1970
Sphenosuchia Bonaparte, 1971
Phyllodontosuchus n. g.

Etymology: Greek phyllon, "leaf," odontos, "tooth," and souchos, "crocodile." The name refers to the leaf-shape of the mid- and caudal maxillary teeth.
Type Species: *Phyllodontosuchus lufengensis* n. sp.
Type Locality: Laozufen site, Dawa locality, Lufeng basin, near Dawa Village (approximately 2 km north-northeast of the Lufeng County seat), Yunnan Province, People's Republic of China.
Stratigraphic Position: Dark red beds of the Lufeng Formation (per Luo & Wu 1994).
Age: Lower Jurassic (Sinemurian, 201-195 Ma per Gradstein et al., 1995) (Lucas 1996).
Diagnosis: Differs from other sphenosuchians in possessing markedly heterodont dentition, with at least six small, recurved, teeth rostrally and the remaining (12?) teeth small, leaf-shaped (phylloform), and crenelated on the caudal carina.

Phyllodontosuchus lufengensis n. sp.

Etymology: The species name *lufengensis* refers to the Lufeng Formation, from which the holotype was recovered.
Holotype: BVP568-L12 (a cast is reposited at the New Mexico Museum of Natural History and cataloged as NMMNH C-3088).
Diagnosis: As for genus.
Type Locality: As for genus.

Description: Unfortunately, much of the detail in the only known skull of *Phyllodontosuchus* is not discernible due to nuances of preservation, including crushing and similarity of the bone to the surrounding matrix. Nevertheless, enough detail is preserved to permit diagnosis.

Because the external nares are not preserved, it is likely that most, if not all, of the visible dentigenous skull bone belongs to the maxilla and not the premaxilla. The maxilla (Figs. 1, 2, 5A-B) is 26.2 mm long, 3.7 mm tall at the rostral end, and 9 mm tall just rostral to the antorbital fossa. It bounds the antorbital fossa (including the antorbital fenestra) ventrally and rostrally. The jugal process is rostrocaudally elongate and of short, uniform dorsoventral height. It appears to extend caudally to a point beneath the rostral margin of the orbit. The dorsal edge of the maxilla on the right side, bounding the ventral margin of the antorbital fossa, bears a thin, laterally-projecting ridge. Dorsal to this, a thin sheet of bone projects dorsally. This condition of the ventral margin of the antorbital fossa is similar to that illustrated and described as "trough-shaped" for *Saltoposuchus* by Sereno & Wild (1992).

The lacrimal, best viewed on the left side (Figs. 1, 5A), is 10.2 mm tall and bounds the antorbital fossa cranially and the rostral margin of the orbit caudally. The element is roughly hourglass-shaped in lateral view. There is a pronounced ridge that runs rostrodorsally from the caudoventral corner, creating a depression on the lateral surface that forms the caudoventral corner of the external antorbital fossa.

Fig. 1. Stereophotographs of the skull of *Phyllodontosuchus lufengensis*, BVP568-L12 in right lateral view. Scale = 2 cm.

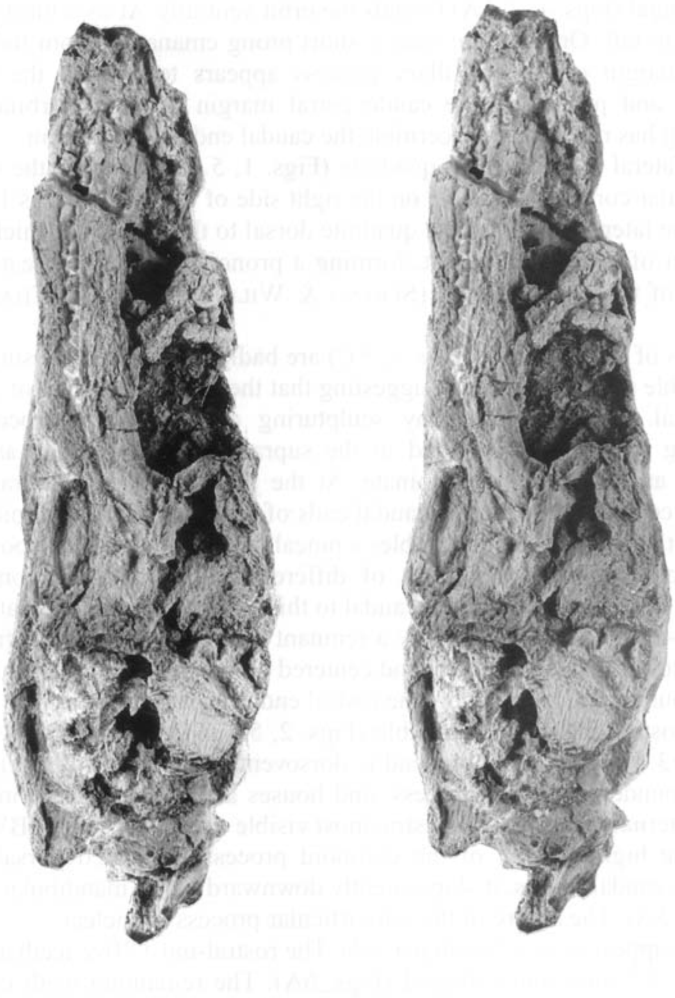

Fig. 2. Stereophotographs of the skull of *Phyllodontosuchus lufengensis*, BVP 568-L12 in left lateral view. Scale = 2 cm.

The jugal (Figs. 1, 2, 5A) bounds the orbit ventrally. At its widest point, it is 5.1 mm tall. On the right side, a short prong emanating from the rostrodorsal margin of the maxillary process appears to overlap the maxilla dorsally and just reach the caudoventral margin of the antorbital fossa. Crushing has rendered indiscernible the caudal end of the element.

The lateral margin of the quadrate (Figs. 1, 5 A), including the external mandibular condyle, is visible on the right side of the skull, and is 11.5 mm long. The lateral margin of the quadrate dorsal to the condyle is thicker than the sheet of bone medial to it, forming a pronounced ridge, a feature diagnostic of the Sphenosuchia (SERENO & WILD 1992, WU & CHATTERJEE 1993).

Bones of the skull roof (Figs. 3, 5 C) are badly fragmented; no sutures are discernible on any fragment, suggesting that the specimen is that of an adult individual. None displays any sculpturing as in modern crocodilians. Crushing has apparently filled in the supratemporal fenestrae, and their outlines are likewise indeterminate. At the juncture of several fragments, roughly centered between the caudal ends of the orbits, is a small pit which, upon initial examination, resembles a pineal foramen, but which upon closer inspection is simply the result of differential diagenetic motion at the juncture of several cracks. Just caudal to this is a small fragment that bears a small, 6-mm-long crest, possibly a remnant of the frontal crest. A fragment located towards the caudal end and centered on the midline of the skull bears a low, rounded ridge, probably the rostral end of a parietal crest.

The rostral end of the mandible (Figs. 2, 5 A, 5 B, 5 D) is dorsoventrally narrow (3.8 mm). The caudal end is dorsoventrally wider (8.2 mm), with a broad, rounded coronoid process, and houses a very large (8.5 mm long), ovate external mandibular fenestra, most visible on the left side of BVP 568-L12. The highest point of the coronoid process is located dorsal to the fenestra; caudal to this, it slopes gently downward to the mandibular cotyles (Figs. 1, 5A). The nature of the retroarticular process is unclear.

There appear to be 17 teeth per side. The rostral-most ?five teeth are short (roughly 2.7 mm) and recurved (Figs. 6A). The remaining teeth could be described as leaf-shaped (as in the leaves of the aspen tree, *Populus* spp.) or spade-shaped: their bases are rostrocaudally broad and taper to a point distally (Fig. 6 B). All of the phylloform teeth are approximately identical in size (1.7 mm wide and 2.0 mm long). Although not denticulate, the phylloform teeth possess extremely fine crenelations on their caudal margins (none is apparent on the cranial margin in any preserved phylloform tooth) (Figure 6 B).

Is BVP 568-L12 a dinosaur?: Within the Dinosauria, some members of both the Ornithischia and the Prosauropoda possess leaf-shaped teeth.

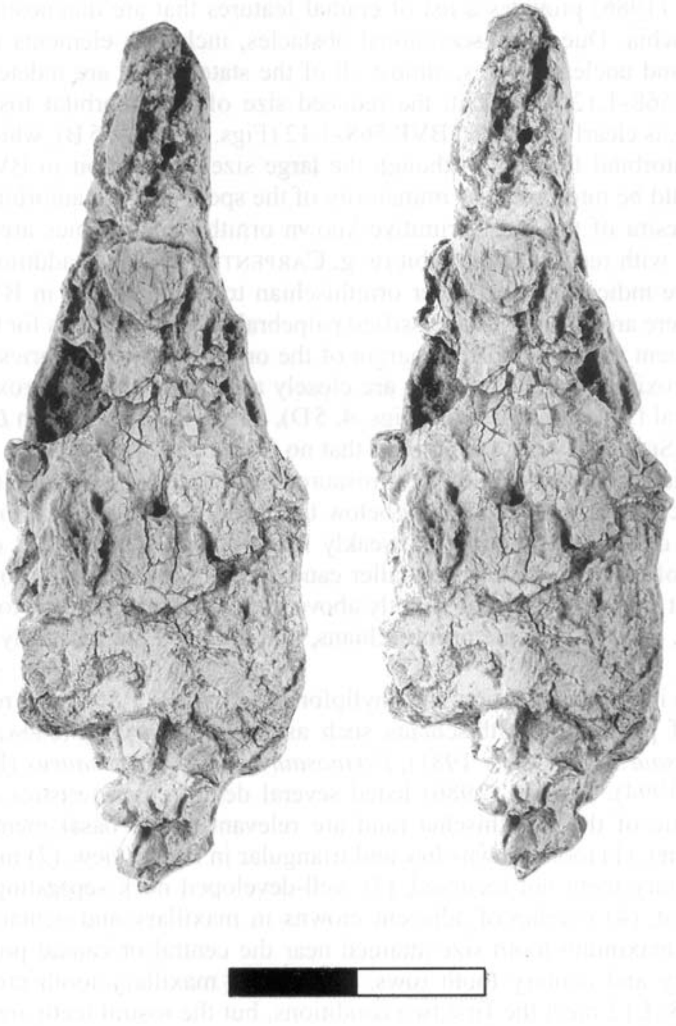

Fig. 3. Stereophotographs of the skull of *Phyllodontosuchus lufengensis*, BVP 568-L12 in dorsal view. Scale = 2 cm.

SERENO (1986) provides a list of cranial features that are diagnostic of the Ornithischia. Due to preservational obstacles, including elements not preserved and unclear sutures, almost all of the states listed are indeterminate in BVP 568-L12. One trait, the reduced size of the antorbital fossae and fenestra, is clearly absent in BVP 568-L12 (Figs. 1, 2, 5A, 5B), which has a large antorbital fenestra. Although the large size of the orbit in BVP 568-L12 could be interpreted as immaturity of the specimen, the antorbital fossa and fenestra of the most primitive known ornithischian babies are greatly reduced with respect to the orbit (e. g. CARPENTER 1994). In addition, there are some indications that other ornithischian traits are absent in BVP 568-L12. There are no signs of an ossified palpebral, including facets for them on the element along the rostral margin of the orbit. The two dentaries are not fused proximally, although they are closely appressed along approximately the rostral fifth of their length (Figs. 4, 5D), unlike the condition in *Lesothosaurus* (SERENO 1991); this implies that no predentary was present.

Cranial characteristics of the Prosauropoda (GALTON 1990) include: (1) jaw articulation situated slightly below the level of the maxillary tooth row and (2) dentition homodont or weakly heterodont. BVP 568-L12 displays neither of these characters: the taller caudal end of the mandible forces the jaw joint to be located at or slightly above the level of the dentary tooth row (Figs. 1, 5A), as in some ornithischians, and the teeth are markedly heterodont.

Upon initial examination, the phylloform teeth of BVP 568-L12 resemble those of primitive ornithischians such as *Lesothosaurus* (SERENO 1991), *Scutellosaurus* (COLBERT 1981), *Pekinosaurus*, and *Tecovasaurus* (HUNT & LUCAS 1994). SERENO (1986) listed several dental characteristics that are diagnostic of the Ornithischia (and are relevant to the basal members in particular): (1) tooth crowns low and triangular in lateral view, (2) maxillary and dentary teeth not recurved, (3) well-developed neck separating crown from root, (4) overlap of adjacent crowns in maxillary and dentary teeth, and (5) maximum tooth size attained near the central or caudal portion of maxillary and dentary tooth rows. The caudal maxillary tooth crowns of BVP 568-L12 meet the first two conditions, but the rostral teeth are indeed recurved. The third and fourth conditions cannot be assessed, and the fifth is not met because the phylloform teeth appear to be of similar size throughout the row. In addition, the rostral-most teeth of BVP 568-L12 appear to be recurved, unlike those of any known ornithischians except *Lesothosaurus* and the Heterodontosauridae. In *Heterodontosaurus* and *Abrictosaurus*, there are only three elongate, non-phylloform teeth that vary in size (WEISHAMPEL & WITMER 1990); in contrast, BVP 568-L12 has at least five rostrally-located, recurved teeth that appear to be of similar size. *Lesothosaurus* possesses six, similarly-sized premaxillary teeth, but which possess a

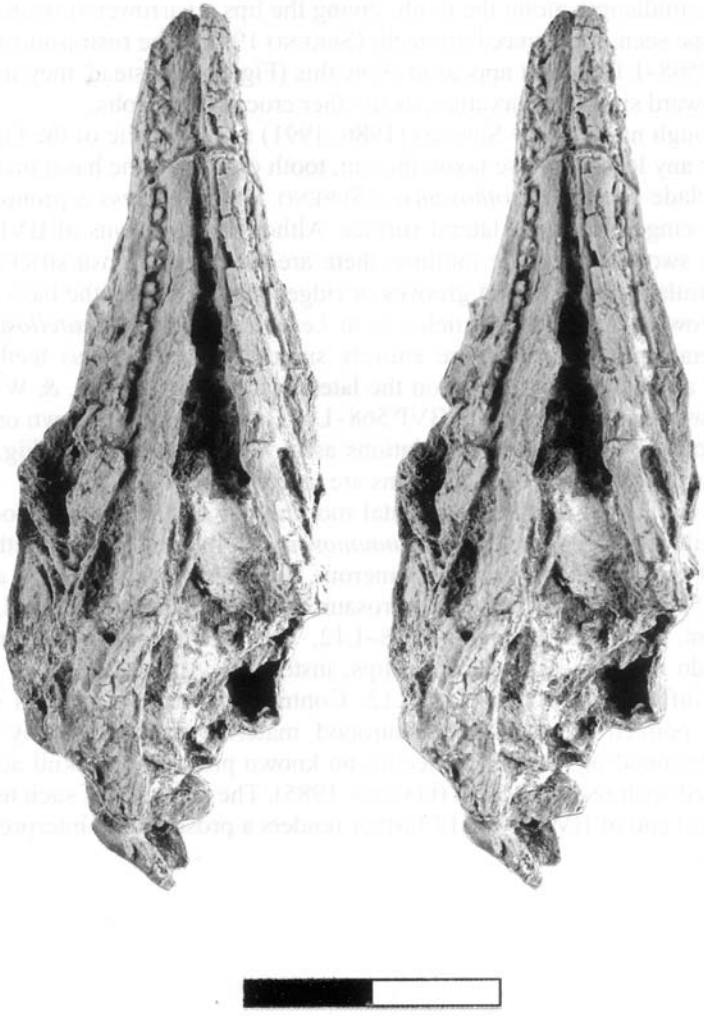

Fig. 4. Stereophotographs of the skull of *Phyllodontosuchus lufengensis*, BVP568-L12 in ventral view. Scale = 2 cm.

swelling midlength along the tooth, giving the tips a narrower version of the leaf shape seen in the maxillary teeth (SERENO 1991). The rostral-most teeth of BVP568-L12 do not appear to show this (Fig. 6A); instead, they imply a trend toward simple recurvature, as in other crocodylomorphs.

Although not cited by SERENO (1986, 1991) as diagnostic of the Ornithischia or any less-inclusive taxon therein, tooth crowns of the basal members of the clade (except *Lesothosaurus* [SERENO 1991]) possess a pronounced midline cingulum on the lateral surface. Although the crowns of BVP 568-L12 are swollen along the midline, there are no cingula sensu stricto (Fig. 6B). Similarly, there are no grooves or ridges that lead from the base of the tooth crown to marginal denticles as in *Lesothosaurus* and *Scutellosaurus*: the lateral crown surfaces are entirely smooth. *Lesothosaurus* teeth also possess a transverse cingulum on the lateral face (WEISHAMPEL & WITMER 1990), which is also absent in BVP 568-L12. In addition, no known ornithischian possesses marginal crenelations as in *Phyllodontosuchus* (Fig. 6B). Lastly, all known early ornithischians are larger than BVP 568-L12.

GALTON (1985) detailed the dental morphology of the Prosauropoda. In almost all prosauropods (except *Yunnanosaurus*), the phylloform teeth, like those of ornithischians, possess numerous large denticles, which are absent in BVP568-L12. Similarly, many prosauropod teeth possess a vertical, axial cingulum, also lacking in BVP568-L12. The peculiar teeth of *Yunnanosaurus* do not possess phylloform tips; instead they taper to a blunt point, clearly different from BVP568-L12. Contrary to frequent reports of recurved, pointed teeth with prosauropod material (taphonomically associated theropod or rauisuchian teeth), no known prosauropod skull actually possessed such recurved teeth (GALTON 1985). The presence of such teeth at the rostral end of BVP568-L12 further renders a prosauropod interpretation dubious.

Fig. 5. Skull of *Phyllodontosuchus lufengensis*, BVP568-L12. (A) Right lateral view. Arrow indicates position of teeth shown in Figure 6A. (B) Left lateral view. Arrow indicated position of tooth shown in Figure 6B. (C) Dorsal view. (D) Ventral view. Scale bar = 2 cm.

Abbreviations: **aof** = antorbital fossa and fenestra, **emf** = external mandibular fenestra, **lac** = lacrimal, **ltf** = lateral temporal fenestra, **mxjg sut** = maxilla/jugal suture, **orb** = orbit, **qdr** = quadrate, **sgcr** = sagittal crest.

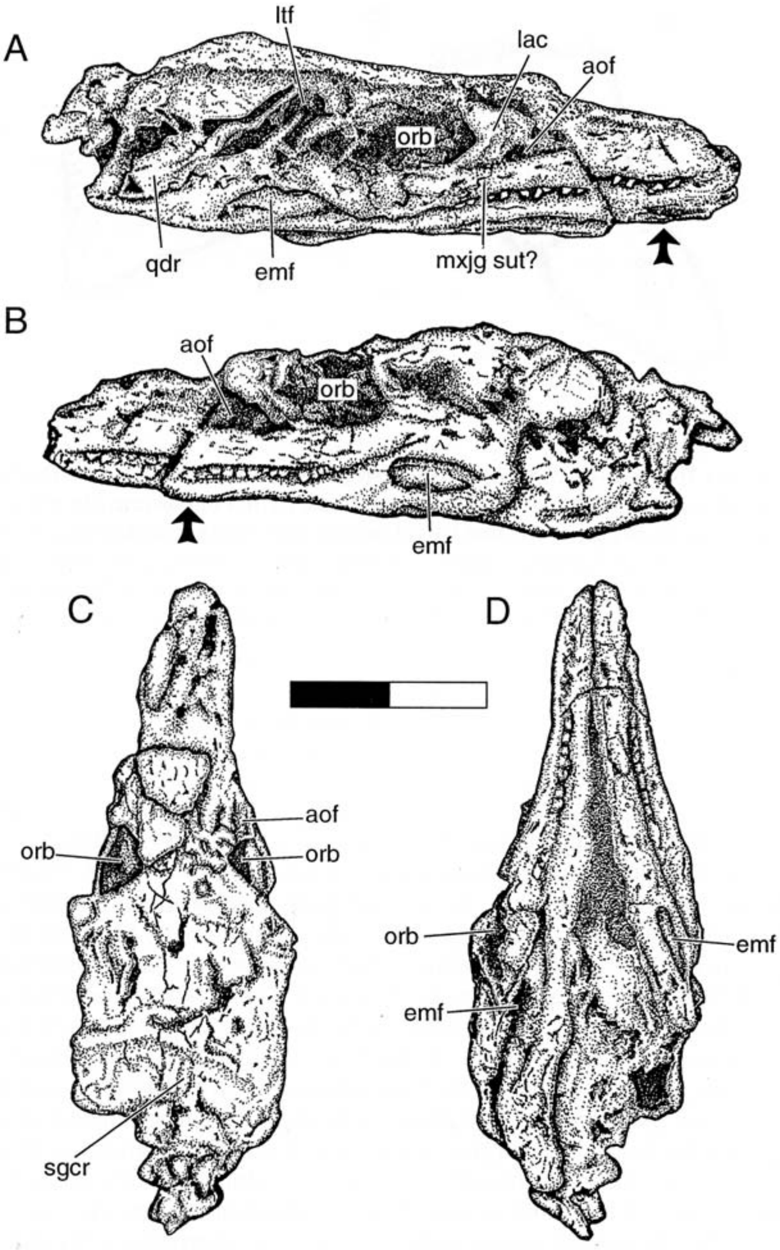

Fig. 5 (Legend see p. 56)

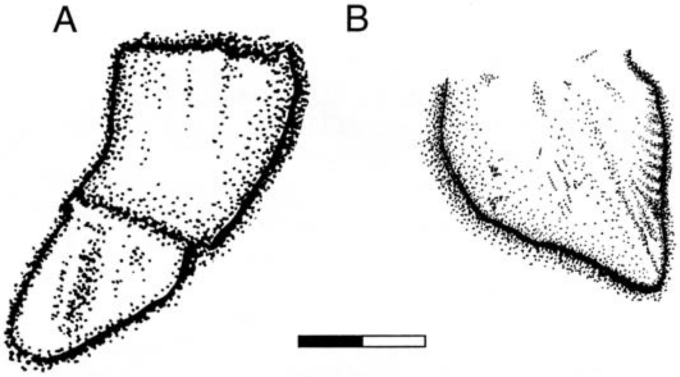

Fig. 6. (**A**) Example of conical, recurved, rostral maxillary teeth of *Phyllodontosuchus lufengensis*, BVP568-L12. Cranial is to the right. For position of teeth in the specimen, see Figure 5A. Note that lateral surface of tooth tip is broken and missing. (**B**) Example of phylloform, caudal maxillary tooth of *Phyllodontosuchus lufengensis*, BVP568-L12. Cranial is to the left. For position of tooth in the specimen, see Figure 5B. Note fine crenelations on the caudal margin of the tooth. Scale = 1 mm.

Is BVP568-L12 a crocodylomorph?: Clark (1986) and Benton & Clark (1988) analyzed the relationships of the members of the Crocodylomorpha, within which they found differing phylogenetic positions of "sphenosuchian" taxa, consisting of *Pseudhesperosuchus* + (*Saltoposuchus* + *Terrestrisuchus* + (*Dibothrosuchus* + *Sphenosuchus* + ("Kayentasuchus" + Crocodyliformes [= Auritosuchia per Clark 1986]))). They thus concluded that the Sphenosuchia is paraphyletic, and could therefore be diagnosed only by possessing synapomorphies of the Crocodylomorpha as a whole but lacking the autapomorphies of the Crocodyliformes (the first monophyletic clade within the Crocodylomorpha). Skull characteristics considered diagnostic of the Crocodylomorpha ennumerated by Benton & Clark (1988) include: (C1) squamosal broadly overhangs quadrate laterally, (C2) postfrontal absent, (C3) post-temporal fenestra small or absent, (C4) prootic does not broadly contact rostral surface of paroccipital process, (C5) primary contact of quadrate with prootic, (C6) pneumatic space in body of basisphenoid, (C7) mastoid antrum enters into prootic, (C8) jugal does not participate in antorbital fossa, and (C9) quadrate foramen wholly within quadrate. Of these, SERENO & WILD (1992) found only 1, 2, and 8 to be diagnostic of the Crocodylomorpha. They added to these two traits: (C10) nasal excluded from margin of antorbital fossa (thus, in the Crocodylomorpha, the antorbital fossa is bounded solely by the lacrimal and the maxilla), and (C11) squamosal and paroccipital process for tongue-in-groove articulation.

The preservation of BVP568-L12 renders the assessment of many of these traits difficult or impossible. There does not appear to be a postfrontal, although the element could have been lost or fused. The jugal does not appear to participate significantly in the antorbital fossa, although no sutures are clearly defined in this area. The tooth row persists caudally to a point beneath the orbit, well behind the antorbital fossa, indicating that a portion of the maxilla persists well beyond the caudal limit of the antorbital fossa. On the right lateral side, a possible suture between the maxilla and the jugal may indicate an overlap of the maxillary prong of the jugal dorsal to the caudal process of the jugal (Fig. 5A). If this is accurate, it would limit the exposure of the jugal to a miniscule portion of the caudoventral corner if it is exposed there at all.

The analysis of PARRISH (1991), like that of CLARK (1986) and BENTON & CLARK (1988), found the Sphenosuchia to be paraphyletic with the internal structure *Saltoposuchus* + *(Pseudhesperosuchus* + (*Sphenosuchus* + *(Dibothrosuchus* + Crocodyliformes))). PARRISH agreed with CLARK (1986) and BENTON & CLARK (1988) that only character (C3) is diagnostic for the Crocodylomorpha (and thus, of the basal Sphenosuchia + Crocodyliformes), noting that the remaining characters are either plesiomorphic for the Crocodylomorpha or are indeterminate in numerous sphenosuchian taxa. In addition to that, he considered numerous other skull characteristics as diagnostic of the Crocodylomorpha (reformatted by SERENO & WILD [1992]), including: (P1) lateral articulation between premaxilla and maxilla fused, (P2) sagittal crest present, (P3) quadrate shifted rostrally, (P4) lower jaw swollen rostrally, (P5) teeth with swollen crowns, and (P6) parietals fused. The lower jaw of BVP568-L12 is not noticeably swollen rostrally. The fragment on the skull roof of BVP568-L12 which possesses the rostral end of a sagittal crest indicates that the parietals are fused. The dorsal end of the quadrate is located further rostrally than the distal end (although this may be a result of crushing). Both of these features imply sphenosuchian affinities for BVP568-L12.

Unlike the previous analyses, that of SERENO & WILD (1992) found the Sphenosuchia to be monophyletic as initially suggested by WALKER (1970) and CRUSH (1984), diagnosed by autapomorphies independent of other crocodylomorphs. They listed four diagnostic skull characteristics of a monophyletic Sphenosuchia: (S 1) prefrontal with posterior process deflected under frontal, (S 2) squamosal arcuate in dorsal view, (S 3) squamosal margin of supratemporal fossa bounded in part by a rim, and (S4) caudal process of squamosal forked. Additional possible characteristics (with equivocal distributions in their analysis) include: (S5) ventral margin of the antorbital fossa trough-shaped, and, in agreement with PARRISH (1991; character P2 herein), the presence of a sagittal crest the length of the parietals. Equivocal cranial characteristics that they considered possibly diagnostic of a more exclusive clade containing *Saltoposuchus* + *Pedeticosaurus* + *Terrestrisuchus* include: (S6) postorbital bar slender and (S7) lateral rim on quadrate. Of SERENO & WILD's characteristics, both the wall-and-trough on the maxilla along the ventral margin of the antorbital fenestra and the lateral rim on the quadrate can be discerned on BVP568-L12, supporting its placement in the Sphenosuchia.

Like SERENO & WILD (1992), the analysis of WU & CHATTERJEE (1993) supported a monophyletic Sphenosuchia; unlike the former, however, their analysis found a series of nested clades within the Sphenosuchia (*Saltoposuchus* + *Pseudhesperosuchus* + (*Hesperosuchus* + (*Sphenosuchus* + *Dibothrosuchus*)))). They concur with SERENO & WILD (1992) by finding character (S7) diagnostic of the Sphenosuchia and added (W1) maxilla terminates rostral to the orbit, (W2) dorsoventrally expanded lateral end of the paroccipital process reaching to the outermost edge of the occiput and interlocking with the squamosal, and (W3) retroarticular process transversely broad with a pronounced dorsomedial projection at the mediocaudal edge. The maxilla of BVP568-L12 clearly does not terminate rostral to the orbit, as the tooth row reaches about one-third of the way under the orbit, though it is unclear how much of this is due to diagenetic shifting of the dorsal portion of the skull with respect to the ventral. However, the distal end of the lower jaw in BVP568-L12 does not appear to be significantly expanded beyond the rest of the mandibular body. The other characters cited by WU & CHATTERJEE for the Sphenosuchia cannot be discerned.

Within the Sphenosuchia, WU & CHATTERJEE found a monophyletic Sphenosuchidae (*Pseudhesperosuchus* + (*Hesperosuchus* + (*Sphenosuchus* + *Dibothrosuchus*))), diagnosed by the presence of a sagittal crest (character P2 herein) plus (W4) T-shaped crest on the surface of the parietal and squamosal, and (W5) pentagonal supraoccipital with a ventral process. The presence of the sagittal crest on BVP568-L12 indicates that it is a member of the Sphenosuchidae. The clade *Hesperosuchus* + (*Sphenosuchus* + *Dibothrosuchus*) is diagnosed by (W6) preantorbital portion of maxilla longer than postantorbital portion, (W7) maxillary portion of the secondary palate enlarged, (W8) longitudinal frontal crest(s), and character (P5). Only the status of the maxilla can be determined in BVP568-L12, where the preantorbital portion is far longer than the postantorbital portion. The only cranial characteristic uniting WU & CHATTERJEE's clade *Sphenosuchus* + *Dibothrosuchus* is identical to character (P6), which is indeterminate in BVP568-L12.

CLARK (1986) and BENTON & CLARK (1988) listed numerous cranial autapomorphies of the Crocodyliformes (all crocodylomorphs exclusive of the Sphenosuchia), including (a) otoccipital contacts ventromedial part of quadrate to enclose carotid artery and cranial nerves IX-XI, (b) basisphenoid rostrum (= cultriform process) dorsoventrally expanded, (c) basipterygoid processes reduced and basipterygoid joint closed suturally, (d) pterygoid extends dorsally to form ventrolateral edge of trigeminal foramen, (e) otoccipitals broadly meet dorsal to foramen magnum, (f) eustachian tubes enclosed between basioccipital and basisphenoid, (g) antorbital fenestra much smaller than orbit, (h) premaxilla and maxilla sutured together caudally, (i) parietal lacking broad occipital portion, (j) quadrate hollow with several fenestrae on dorsal surface, (k) mastoid antrum extends into supraoccipital, (1) two palpebrals present, (m) "skull table" in temporal region with nearly flat dorsal surface, (n) postorbital lies medial to jugal on postorbital bar, (o) quadratojugal broad, and (p) maxilla shorter than jugal. WU & CHATTERJEE (1993) found characters (C3), (P1), (P5), and (P6), as well as (k) above, plus (q) ascending process of maxilla vertical, (r) maxillary component of secondary palate enlarged, (s) lateral edge of squamosal grooved, (t) dorsomedial process of quadrate, (u) copious rostral extent of rostrodorsal process of quadrate, and (v) supraoccipital does not contribute to foramen magnum, to be diagnostic of Crocodyliformes. (J. CLARK, pers. communication, 1998) notes that a strong rostrodorsal inclination of the quadrate (character (P3) herein) is also seen in some crocodyliforms, and that a new specimen of the sphenosuchian *Hesperosuchus* (CLARK & SUES, in preparation) possesses palpebrals (character 1 herein). As before, only a few of these traits can be assessed in BVP568-L12. However, BVP568-L12 has a very large antorbital fenestra compared to the orbit, lacks evidence of palpebrals, does not appear to have a vertical ascending process of the maxilla, and appears to have a longer maxilla than jugal. The absence of crocodyliform autapomorphies indicates that BVP568-L12 is not a crocodyliform despite having crocodylomorph (and sphenosuchian) autapomorphies.

Other Considerations: The presence of an antorbital fenestra in BVP568-L12 clearly indicates that it is an archosauromorph, but in the early Mesozoic, there are a number of aberrant archosauromorphs which have thus far defied classification into better-known taxa. The Megalancosauridae, as exemplified by *Megalancosaurus* from the Upper Triassic of Italy, have peculiar bird-like skulls (RENESTO 1994). Although currently known only from Upper Triassic sediments, it is conceivable that members of the group could extend into the Lower Jurassic, and thus comparison to BVP568-L12 is appropriate. Cranial characteristics considered diagnostic of the Megalancosauridae include (1) triangular skull with long, pointed premaxillae which surround large nares caudally, (2) frontals narrow and form dorsal margin of large, round orbits, (3) jugal triradiate, (4) upper temporal fenestra larger than lower one, (5) teeth small, pointed, and isodont (larger in premaxilla) (RENESTO 1994).

BVP568-L12 possesses heterodont teeth. Although no sutures are clearly visible, the premaxillae of BVP568-L12 appear to be much shorter than the maxilla, and are not long and pointed as in *Megalancosaurus*. Thus, it appears that BVP568-L12 is not a megalancosaurid.

Late Triassic and Jurassic members of the Choristodera have been identified. Examples include *Pachystropheus* from the Upper Triassic of England (STORRS et al. 1996) and *Cteniogenys* from the Middle Jurassic of England (EVANS 1990). This temporal range indicates that BVP568-L12 could represent an early choristodere. Most of the cranial characteristics of the Choristodera outlined by EVANS (1990) are impossible to assess in BVP568-L12, but two, (1) preorbital skull length elongate (> 50 % total skull length), and (2) dentary symphysis very elongate, are not present. It thus appears that BVP568-L12 is not a choristodere.

The recent discovery of a purported therizinosauroid theropod dinosaur from the Lufeng Formation (ZHAO & XU 1998), based on a dentary with two teeth in situ, bears mentioning to ensure that BVP568-L12 is not the skull of the same taxon. The teeth in the dentary of the unnamed therizinosauroid possess numerous denticles as well as a well-defined, central cingulum. Although it is conceivable that the as-yet unknown dentary teeth of *Phyllodontosuchus* may match this morphology, such a vast differentiation of the post-caniniform maxillary and dentary teeth would be unprecedented, even within the heterodont Crocodylomorpha. It seems unlikely that the jaw described by ZHAO & XU belongs to *Phyllodontosuchus*.

In summary, the cranial morphology of BVP568-L12 shows more similarities with the basal Crocodylomorpha (Sphenosuchia) than any other. It displays the following sphenosuchian cranial synapomorphies: (1) postfrontal absent, (2) jugal minimally participant in or absent from antorbital fossa, (3) sagittal crest present, (4) fused parietals, (5) dorsal end of quadrate shifted rostrally (also seen in some crocodyliforms), (6) ventral margin of antorbital fossa trough shaped, and (7) lateral rim on quadrate. A further characteristic, (8) preantorbital portion of maxilla longer than postantorbital portion, seems to indicate that BVP568-L12 belongs to a clade nested deeper within the Sphenosuchia (per WU & CHATTERJEE 1993). The possession of phylloform teeth, however, is autapomorphic within the Sphenosuchia, and indicates that BVP568-L12 represents a hitherto unknown taxon.

Discussion

Relationships within the Sphenosuchia: Because of the lack of detail preserved in the only known skull of *Phyllodontosuchus*, no rigorous analysis of its relationships within the Sphenosuchia could be performed; until new and better-preserved specimens are discovered, the taxon is not phylogenetically informative. However, we maintain that a comparison based on the autapomorphic dentition of *Phyllodontosuchus* is useful. Most sphenosuchians possess isodont, recurved teeth indicative of a carnivorous habit.

Among the Sphenosuchia, heterodonty has been described for *Dibothrosuchus* (WU & CHATTERJEE 1993), *Hesperosuchus* (COLBERT 1952, PARRISH 1991, LONG & MURRY 1995), *Pedeticosaurus* (GOW & KITCHING 1984), and *Sphenosuchus* (WALKER 1990), though in the last it is restricted to the dentary. In these forms, the premaxillary and rostral-most maxillary and dentary teeth are recurved, but the caudal maxillary and dentary teeth are lanceolate in shape (COLBERT 1952, WALKER 1990, PARRISH 1991) in reference to their mediolaterally compressed, rostrocaudally expanded tips which are separated from their cylindrical shafts by a constriction. The morphology of the tips of these lanceolate forms is similar to the teeth of *Phyllodontosuchus*, and it is conceivable that its autapomorphic phylloform morphology may have evolved from the lanceolate form via reduction and, ultimately, elimination of the cylindrical shaft. Although crenelations similar to those of *Phyllodontosuchus* (Fig. 6 B) have not been described in other sphenosuchian taxa, COLBERT (1952) and PARRISH (1991; also LONG & MURRY 1995) note that the lanceolate teeth of *Hesperosuchus* are serrated. The crenulations of *Phyllodontosuchus* may be a novel development or derived from serrations in an ancestral taxon.

LANGSTON (1965: 13) emphasized the fact that "crocodilian teeth are usually inadequate for systematic purposes;" this implies that erecting a new crocodylomorph taxon based solely on tooth characteristics is a dubious procedure. However, LANGSTON, was referring to the broadly generalized conical and recurved teeth that are widespread throughout the Crocodylomorpha. In light of subsequent discoveries of specialized tooth morphologies in various crocodylomorph taxa, a situation analogous to some herbivorous dinosaurs as well as mammals (which use classifications based on tooth morphology), the use of tooth morphology as a diagnostic characteristic of specialized members of the Crocodylomorpha is justified.

Habit of *Phyllodontosuchus* and the History of Heterodonty in the Crocodylomorpha: Heterodonty is not without precedent within the Crocodylomorpha. Edentosuchids, including *Edentosuchus*, from the Lower Cretaceous of China (LI 1985) and a probable related form from the Lower Jurassic of Arizona (CLARK 1986), have been confirmed as crocodyliforms by CLARK (1986) and are possibly mesosuchians (LI 1985). Both the Chinese and Arizona specimens possess differentiated incisiform, caniniform, and post-caniniform teeth. In the Chinese form, the incisiform and enlarged caniniform teeth are pointed and recurved, but the post-caniniform teeth are cylindrical and possess marked, flat occlusal surfaces, indicating mastication. The Arizona specimen is similar except that the premaxillary teeth are conical and not recurved and the post-caniniform teeth are broad mediolaterally and possess two cusps. These cusps also demonstrate wear, again indicative of mastication. Although none of the edentosuchid teeth are described as possessing serrations or crenulations, the enamel on the surface of at least some of the teeth possess vertically-oriented enamel wrinkles (Li 1985, Clark 1986). The broad post-caniniform teeth of edentosuchids is unlike the leaf-shaped teeth of *Phyllodontosuchus*. The possession of cusps and marked wear facets indicate more advanced masticatory ability than is currently known for *Phyllodontosuchus*.

Members of the mesoeucrocodylian family Notosuchidae include *Candidodon* from the Early Cretaceous of Brazil (Carvalho 1994), *Malawisuchus* from the Early Cretaceous of Malawi (Gomani 1997), and *Chimerasuchus* from the Early Cretaceous of China (Wu & Sues 1996), which are all similar to *Phyllodontosuchus* in possessing conical, recurved rostral teeth and non-conical teeth caudally. The notosuchian taxa differ from *Phyllodontosuchus* because the caudal teeth of the former are cuspidate, and not leaf-shaped. Similarly, *Phyllodontosuchus* appears to lack a rostrocaudally elongate articular cotyle, which implies that the taxon lacked the proal (rostral-caudal) jaw movement present in *Malawisuchus* and *Chimerasuchus* (Wu & Sues 1996, Gomani 1997). However, the notosuchian taxa are all Early Cretaceous in age, and their close relationships to each other imply a radiation of small, heterodont crocodylomorphs at that time. *Phyllodontosuchus* predates all the notosuchian taxa and shows that heterodonty, and possibly a deviation from strict carnivory, occurred multiple times within the Crocodylomorpha.

Phyllodontosuchus is also similar to the heterodont edentosuchid and notosuchian taxa in being small in size: skulls of *Edentosuchus* and the Arizona form are between 60-70 mm (Clark 1986); skulls of *Malawisuchus* (based on measurements provided by Gomani [1997]) average 60.3 mm in length, and the estimated length of the single known skull of *Chimerasuchus* is 135 mm (Wu & Sues 1996), all comparable to the skull of *Phyllodontosuchus*. The consistent pairing of small size and heterodonty of these crocodylomorphs implies an ecological coupling and an expansion of the niches crocodylomorphs occupied in the past, beyond the strict carnivory/piscivory seen in extant forms. The small size, multicusped teeth, and capacity for proal jaw movement in *Malawisuchus* have been implicated as adaptations for insectivory as well as carnivory of snails and small tetrapods (Clark et al. 1989, Gomani 1997). The multicusped teeth plus proal jaw movement of *Chimerasuchus* have been interpreted as adaptations for at least facultative herbivory (Wu et al. 1995, Wu & Sues 1996). No potential dietary preferences have been suggested for edentosuchids, but the implicative presence of marked wear on the teeth suggests a diet not limited to meat.

The lack of cusps and proal jaw movement in *Phyllodontosuchus* implies that the sphenosuchian did not grind its food; however, neither did primitive, putatively herbivorous ornithischians with leaf-shaped teeth such as *Lesotho-*

saurus, which instead masticated via simple shearing (Weishampel 1984). However, isognathy (simple bilateral occlusion, per Ryan & Vicakryous (1997), indicating that some processing of the bolus was accomplished by the teeth) was present in *Lesothosaurus*, but because neither the lingual surfaces of the maxillary teeth nor the labial sides of the dentary teeth of BVP568-L12 can be examined for wear facets, the degree to which *Phyllodontosuchus* could orally process food remains indeterminate.

Acknowledgements

Conversations with Drs. Chris Gow (University of Witwatersrand) and Chris Brochu (Field Museum of Natural History) were very helpful; Dr. Gow provided details of *Pedeticosaurus* for comparison. Review comments by Dr. Gow and Dr. James Clark (George Washington University) were extremely helpful and greatly appreciated. Peter Reser (New Mexico Museum of Natural History) expertly prepared and molded and cast the specimen.

References

Ague, J. J., Carpenter, K. & Ostrom, J. H. (1995): Solution to the *Hallopus* enigma. – Amer. J. Sci., **295**: 1-17.

Benton, M. J. & Clark, J. M. (1988): Archosaur phylogeny and the relationships of the Crocodylia. – In: Benton, M. J. (Ed.): The Phylogeny and Classification of the Tetrapods, **1**: Amphibians, Reptiles, Birds: 295-338; Clarendon Press.

Bonaparte, J. F. (1971): Los tetrapodos del sector superior de la formación Los Colorado, La Rioja, Argentina. – Opera Lilloana, **22**: 1-183.

– (1972): *Pedeticosaurus leviseuri* van Hoepen, a probable protosuchian. – Nas. Mus., Navorsinge - Researches, Bloemfontein, **2**: 301-305.

Broom, R. (1927): On *Sphenosuchus* and the origin of the crocodiles. – Proc. Zool. Soc. London, **1927**: 359-370.

Carpenter, K. (1994): Baby *Dryosaurus* from the Upper Jurassic Morrison Formation of Dinosaur National Monument. – In: Carpenter, K., Hirsch, K. F. & Horner, J. R. (Eds.): Dinosaur Eggs and Babies: 288-297; Cambridge University Press, 372 pp.

Carvalho, I. S. (1994): *Candidodon*: um crocodilo com heterodontia (Notosuchia, Cretáceo Inferior - Brasil). – An. Acad. Brasil. Ci., **66**: 331-345.

Clark, J. M. (1986): Phylogenetic relationships of the crocodylomorph archosaurs, volumes 1 and 2. Ph.D. dissertation, Univ. of Chicago, 556 pp.

Clark, J. M., Jacobs, L. L. & Downs, W. R. (1989): Mammal-like dentition in a Mesozoic crocodylian. – Science, **244**: 1064-1066.

Colbert, E. H. (1952): A pseudosuchian reptile from Arizona. – Bull. Amer. Mus. Natur. Hist., **99**: 565-592.

– (1981): A primitive ornithischian dinosaur from the Kayenta Formation of Arizona. – Mus. Northern Arizona Press Bull. Ser., **53**: 1-61.

CRUSH, P. J. (1984): A late Upper Triassic sphenosuchid crocodilian from Wales. – Palaeontology, **27**: 131-157.

EVANS, S. E. (1990): The skull of *Cteniogenys*, a choristodere (Reptilia: Archosauromorpha) from the Middle Jurassic of Oxfordshire. – Zool. J. Linnean Soc., **99**: 205-237.

GALTON, P. M. (1985): Diet of prosauropod dinosaur from the late Triassic and early Jurassic. – Lethaia, **18**: 105-123.

– (1990): Basal Sauropodomorpha - Prosauropoda. – In: WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (Eds.): The Dinosauria: 320-344; University of California Press, 733 pp.

GAUTHIER, J., KLUGE, A. G. & ROWE, T. (1988): Amniote phylogeny and the importance of fossils. – Cladistics, **4**: 105-209.

GOMANI, E. M. (1997): A crocodyliform from the Early Cretaceous Dinosaur Beds, northern Malawi. – J. Vertebrate Paleont., **17**: 280-294.

GOW, C. E. & KITCHING, J. W. (1988): Early Jurassic crocodilomorphs from the Stormberg of South Africa. – N. Jb. Geol. Paläont., Mh., **1988**: 517-536.

GRADSTEIN, F. M. AGTERBERG, F. P., OGG, J. G., HARDENBOL, J., VAN, VEEN, P., THIERRY, J. & HUANG, Z. (1995): A Triassic, Jurassic and Cretaceous time scale. – In: BERGGREN, W. A., KENT, D. V. & AUBRY, M. P. (Eds.): Geochronology, Time Scales and Global Stratigraphic Correlation, SEPM Spec. Publ., **54**, 95-126, SEPM.

HAUGHTON, S. H. (1915): A new thecodont from the Stormberg beds. – Ann. South Afr. Mus. **12**: 98-105.

HOEPEN, E. C. N., VAN. (1915): A new pseudosuchian from the Orange Free State. – Ann. Transvaal Mus., **5**: 83-87.

HUENE, F. VON (1921): Neue Pseudosuchier und Coelurosaurier aus dem Württembergischen Keuper. – Acta Zoologica, **2**: 329-403.

– (1925): Die Bedeutung der *Sphenosuchus*-Gruppe für den Ursprung der Krokodile. – Z. induktive Abstammlungs - und Vererbungslehre, **38**: 302-322.

HUENE, F. VON & LULL, R. S. (1908): On the Triassic reptile, *Hallopus victor* Marsh. – Amer. J. Sci. (4th ser.), **25**: 113-118.

HUNT, A. P. & LUCAS, S. G. (1994): Ornithischian dinosaurs from the Upper Triassic of the United States. – In: FRASER, N. C. & SUES, H.-D. (Eds.): In the Shadow of the Dinosaurs, 227-241; Cambridge University Press, 435 pp.

LANGSTON, W., Jr. (1965): Fossil crocodilians from Columbia and the Cenozoic history of the Crocodilia in South America. – Univ. California Publ. Geol. Sci., **52**: 1-169.

LI, J. (1985): Revision of *Edentosuchus tienshanensis* Young, – Vertebrata PalAsiatica, **23**: 196-206.

LONG, R. A. and MURRY, P. A. (1995): Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. – New Mexico Mus. Natur. Hist. Sci. Bull., **4**: 1-254.

LUCAS, S. G. (1996): Vertebrate biochronology of the Jurassic of China. In: MORALES, M. (Ed.): The Continental Jurassic. – Mus. Northern Arizona Bull., **60**, 23-33, Museum of Northern Arizona, 588 pp.

LUCAS, S. G., HUNT, A. P. & WILD, R. (1998): *Dyoplax* O. FRAAS, a Triassic sphenosuchian from Germany. – Stuttgart. Beitr. Naturkde., (B. Geol. Paläont.), **263**: 1-13.

LUO, Z. & WU, X.-C. (1994): The small tetrapods of the Lower Lufeng Formation, Yunnan, China. In: FRASER, N. C. and SUES, H.-D. (Eds.): In the Shadow of the Dinosaurs, 251-270, Cambridge University Press, 435 pp.

LUO, Z., LUCAS, S. G., LI, J. & ZHEN, S. (1995): A new specimen of *Morganucodon oehleri* (Mammalia, Triconodonta) from the Liassic Lower Lufeng Formation of Yunnan, China. – N. Jb. Geol. Paläont., Mh., **1995**: 671-680.

MARSH, O. C. (1877): Notice of some new vertebrate fossils. – Amer. J. Sci., (3), **14**: 249-256.

– (1890): Distinctive characters of the Order Hallopoda. – Amer. J. Sci., (3), **39**: 415-417.

PARRISH, J. M. (1991): A new specimen of an early crocodylomorph (cf. *Sphenosuchus* sp.) from the Upper Triassic Chinle Formation of Petrified Forest National Park, Arizona. – J. Vertebrate Paleont., **11**: 198-212.

REIG, O. A. (1963): La presencia de dinosaurios saurisquios en los 'Estratos de Ischigualasto (Mesotriàsico superior) del los Provincias de San Juan y La Rioja (Republica Argentina). – Ameghiniana, **3**: 3-20.

RENESTO, S. (1994): *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. – J. Vertebrate Paleont., **14**: 38-52.

RYAN, M. J. & YICKARYOUS, M. K. (1997): Diet. – In: CURRIE, P. J. and PADIAN, K. (Eds.): Encyclopedia of Dinosaurs, 169-174, Academic Press, 869 pp.

SERENO, P. C. (1986): Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). – Nat. Geogr. Res., **2**: 234-256.

– (1991): *Lesothosaurus*, "fabrosaurids," and the early evolution of Ornithischia. – J. Vertebrate Paleont., **11**: 168-197.

SERENO, P. C. & WILD, R. T. (1992): *Procompsognathus*: theropod, "thecodont" or both? – J. Vertebrate Paleont., **12**: 435-458.

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

STORRS, G. W., GOWER, D. J. & LARGE, N. F. (1996): The diapsid reptile, *Pachystropheus rhaeticus*, a probable choristodere from the Rhaetian of Europe. – Palaeontology, **39**: 323-349.

WALKER, A. D. (1970): A revision of the Jurassic reptile *Hallopus victor* (MARSH), with remarks on the classification of crocodiles. – Philos. Trans. Roy. Soc. London, B, **257**: 323-371.

– (1990): A revision of *Sphenosuchus acutus* HAUGHTON, a crocodylomorph reptile from the Elliot Formation (late Triassic or early Jurassic) of South Africa. – Philos. Trans. Roy. Soc. London, B, **330**: 1-120.

WEISHAMPEL, D. B. (1984): Evolution of Jaw Mechanisms in Ornithopod Dinosaurs. – VIII + 110 S., 20 Abb.; Berlin (Springer-Verlag).

WEISHAMPEL, D. B. & WITMER, L. M. (1990): *Lesothosaurus, Pisanosaurus*, and Technosaurus. – In: WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (Eds.): The Dinosauria: 416-425, University of California Press, 733 pp.

Wu, X. (1986): A new species of *Dibothrosuchus* from Lufeng Basin. – Vertebrata PalAsiatica, **24**: 43-62.
Wu, X. & Chatterjee, S. (1993): *Dibothrosuchus elaphros*, a crocodylomorph from the Lower Jurassic of China and the phylogeny of the Sphenosuchia. – J. Vertebrate Paleont., **13**: 58-89.
Wu, X. & Sues, H.-D. (1996): Anatomy and phylogenetic relationships of *Chimerasuchus paradoxus*, an unusual crocodyliform reptile from the Lower Cretaceous of Hubei, China. – J. Vertebrate Paleont., **16**: 688-702.
Wu, X., Sues, H.-D. & Sun, A. (1995): A plant-eating crocodyliform reptile from the Cretaceous of China. – Nature, **376**: 678-680.
Zhao, X. & Xu, X. (1998): The oldest coelurosaurian. – Nature, **394**: 234-235.

Manuscript received December 8, 1998.
Revised version accepted by the Tübingen editors February 10, 1999.

Addresses of the authors:

Jerald D. Harris, Spencer G. Lucas, John W. Estep, New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104, USA.
Jianjun Li, Beijing Museum of Natural History, 126 Tian Qiao South St., Beijing, People's Republic of China.