

A new choristodere (Reptilia: Diapsida) from the Lower Cretaceous of western Liaoning Province, China, and phylogenetic relationships of Monjurosuchidae

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The publication of the scientific name *Monjurosuchus splendens* in 1940 documented the first tetrapod fossil of the later world-renowned Jehol Biota. For more than half a century since this discovery, however, *Monjurosuchus* has remained as a monotypic genus of the family Monjurosuchidae, and the relationships of the family with choristoderes have not been correctly recognized until quite recently. In this paper, a new monjurosuchid is named and described based on a nearly complete skull and postcranial skeleton from the Early Cretaceous Chiufotang Formation exposed near Chaoyang, western Liaoning Province, China. This new material documents the first occurrence of monjurosuchid choristoderes outside the type Lingyuan area, and extends the geological range of the family from the Yixian Formation to the younger Chiufotang Formation. Cladistic analyses were conducted with inclusion of monjurosuchids, and the results support the placement of the family Monjurosuchidae as a primitive clade outside the Neochoristodera. A new classification scheme is proposed for choristoderes on the basis of the recovered phylogenetic framework of the group. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 145, 427–444.

ADDITIONAL KEYWORDS: Chiufotang Formation – Choristodera – choristoderan phylogeny – Early Cretaceous – Jehol Biota – osteology.

INTRODUCTION

The Early Cretaceous deposits in western Liaoning Province of China are world renowned for the superb preservation of fossils of the Jehol Biota. Among early discoveries made during the 1930s to 1940s, *Monjurosuchus splendens* (Endo, 1940; Endo & Shikama, 1942) was the first fossil tetrapod known from the Biota, and it initiated a series of important discoveries from the area, including, most recently, feathered dinosaurs (e.g. Ji *et al.*, 2001; Xu *et al.*, 2003) and early mammals (e.g. Hu *et al.*, 1997; Luo *et al.*, 2003). The holotype and the paratype of *Monjurosuchus splendens* were collected in 1934 from the 'Lycoptera beds' at Tanankou (Chinese Pinyin as Danangou), approximately 10.5 km south-west of the city of Lingyuan (Fig. 1) in western Liaoning Province (then Jehol Province). Later discoveries were made at nearby

sites, including Niuyingzi (27 km south of Lingyuan) and Dawangzhangzi (some 20 km south-west of Lingyuan). Some 180–200 km east of the Lingyuan sites, undescribed *Monjurosuchus*-like fossils are also known from at least two localities near Yixian: several undescribed specimens from the classic locality Tsaozushan (Chinese Pinyin as Zaocishan: 21 km south-west of Yixian), and from Toutai (18 km north of Yixian). More recently, new material has been found at Shangheshou near the city of Chaoyang (Fig. 1), some 110 km north-east of Lingyuan; this material is described in the present paper.

The 'Lycoptera beds' exposed near Lingyuan were first viewed as belonging to the Chiufotang (also spelled as Jiufotang by some authors) Formation of purported Triassic-Jurassic age (Endo, 1940), and the fossil beds at Tsaozushan were considered to be the Tsaozushan Formation of the Middle or Upper Jurassic (Endo & Shikama, 1942). However, these same beds were regarded by most Oriental geologists as belonging to the Lower Cretaceous in accordance with

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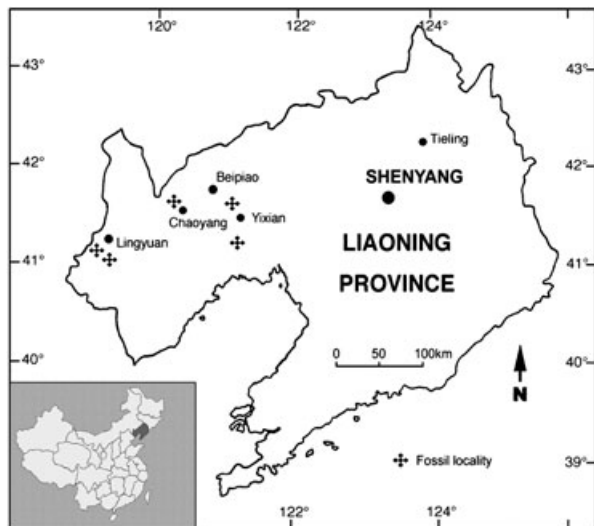


Figure 1. Map showing geographical location of monjurosuchid fossil sites in China: Shangheshou near Chaoyang, Jingangshan (Zaocishan) near Yixian, Doutai near Yixian, and Niuyingzi and Dawangzhangzi near Lingyuan.

A. W. Grabau's theory' (Endo & Shikama, 1942: 15). Recent studies of fossils and regional stratigraphy have shown that the '*Lycoptera* beds' near Lingyuan are actually part of the Early Cretaceous Yixian Formation with a radiometric date of 123–126 Myr (Smith *et al.*, 1995; Ji *et al.*, 2004), and the fossil beds at the Tsaotzushan locality are stratigraphically slightly higher than the Lingyuan beds, but are still part of the Yixian Formation, with a radiometric date of 122 Myr (Smith *et al.*, 1995; Ji *et al.*, 2004). The new material described in this paper was collected from the Shangheshou site, where the fossil beds are regarded as the Early Cretaceous Chiufotang Formation (Wang & Zhou, 2003). If correctly correlated, this material documents a new occurrence of monjurosuchid fossils from a geologically younger horizon than the Yixian Formation, although no radiometric dates are available from the Chiufotang Formation.

More than 60 years have elapsed since Endo's (1940) description of the holotype and paratype, yet *Monjurosuchus splendens* has remained a taxonomic enigma. This animal was classified in the Thecodontia (Endo, 1940) and the Rhynchocephalia (von Huene, 1942; Kuhn, 1969; Sun *et al.*, 1992), but with little character support in either case. These taxonomic uncertainties were worsened by the loss of the holotype and paratype specimens during World War II. It was not until 2000 that the relationship of the genus with choristoderes was recognized, based on studies of new specimens from the type area and horizon (Gao *et al.*, 2000). *Monjurosuchus* is placed in the family Monjurosuchidae, and has remained the monotypic

genus of the family since Endo's (1940) original publication. However, the new discovery from Shangheshou provides the basis for recognition of a new taxon of the family Monjurosuchidae, from outside the type Lingyuan area. This paper presents a detailed description of the osteological morphology of this new reptile, and examines the relationships of the family Monjurosuchidae with other choristoderes.

ANATOMICAL ABBREVIATIONS USED IN FIGURES

Ang, angular; c, coronoid; cla, clavicle; cor, coracoid; den, dentary; ectf, ectepicondylar foramen; entf, entepicondylar foramen; eptg, ectopterygoid; fem, femur; fi, fibula; fr, frontal; hb, hyoid bone; hu, humerus; il, ilium; intcl, interclavicle; isc, ischium; ju, jugal; lac, lacrimal; m, maxilla; na, nasal; neo, neomorph; pa, parietal; pal, palatine; palf, palatal foramen; pm, premaxilla; po, postorbital; pof, postfrontal; pra, prearticular; prf, prefrontal; ptg, pterygoid; pub, pubis; qj, quadratojugal; qu, quadrate; rad, radius; sa, surangular; sc, scapula; sv, sacral vertebra; spl, splenial; sq, squamosal; ti, tibia; ul, ulna; vom, vomer.

SYSTEMATIC PALAEOONTOLOGY

SUBCLASS DIAPSIDA OSBORN, 1903

ORDER CHORISTODERA COPE, 1876

FAMILY MONJUROSUCHIDAE ENDO, 1940

GENUS *PHILYDOSAUROS* GEN. NOV.

Type species: Philydosaurus proseilus sp. nov.

Diagnosis: As for the type and only known species.

Range: Early Cretaceous, western Liaoning, China.

PHILYDOSAUROS PROSEILUS SP. NOV.

(FIGS 2–5)

Etymology: *Philydros* + *sauros* (Gr.), water-loving lizard, referring to the presumed aquatic life style of the animal; *proseilos* (Gr.), meaning toward the sun, similar in meaning to the place name Chaoyang.

Holotype: PKUP V2001, nearly complete skull and lower jaws in association with partial postcranial skeleton.

Type locality and horizon: China, western Liaoning Province, Shangheshou near the city of Chaoyang; Early Cretaceous Chiufotang Formation.

Known distribution: China, western Liaoning Province, Early Cretaceous Chiufotang Formation.

Diagnosis: A medium-sized monjurosuchid choristodere sharing with *Monjurosuchus* the following

derived character states: frontal markedly narrow and hourglass-shaped; anterior extension of lacrimal close to nasal/prefrontal suture; supratemporal fenestra small; infratemporal fenestra closed by expansion of surrounding elements, including postorbital, quadra-tojugal and squamosal.

Differing from *Monjurosuchus* in having a more elongate skull; elongate narial openings and orbits; presence of a 'supratemporal trough' formed by the postorbital and postfrontal and containing the supratemporal fenestra; a distinct antorbital ridge on dorsal surface of prefrontal; postfrontal ridge forming medial border of 'supratemporal trough'; hypertro-

phied postorbital and squamosal carrying a dorsal ridge to form lateral border of the 'supratemporal trough'; temporal process of parietal short, roughly 1/3 of parietal length; a deep U-shaped post-temporal incision at the midline of the occiput; low-crowned dentition; strongly elongated iliac blade with parallel dorsal and ventral borders; presence of a distinct spike-like posterior process of ischium.

Anatomical description

The holotype (PKUP V2001) includes a nearly complete skull, mandibles and postcranial skeleton missing minor parts of the limbs (Fig. 2). The entire

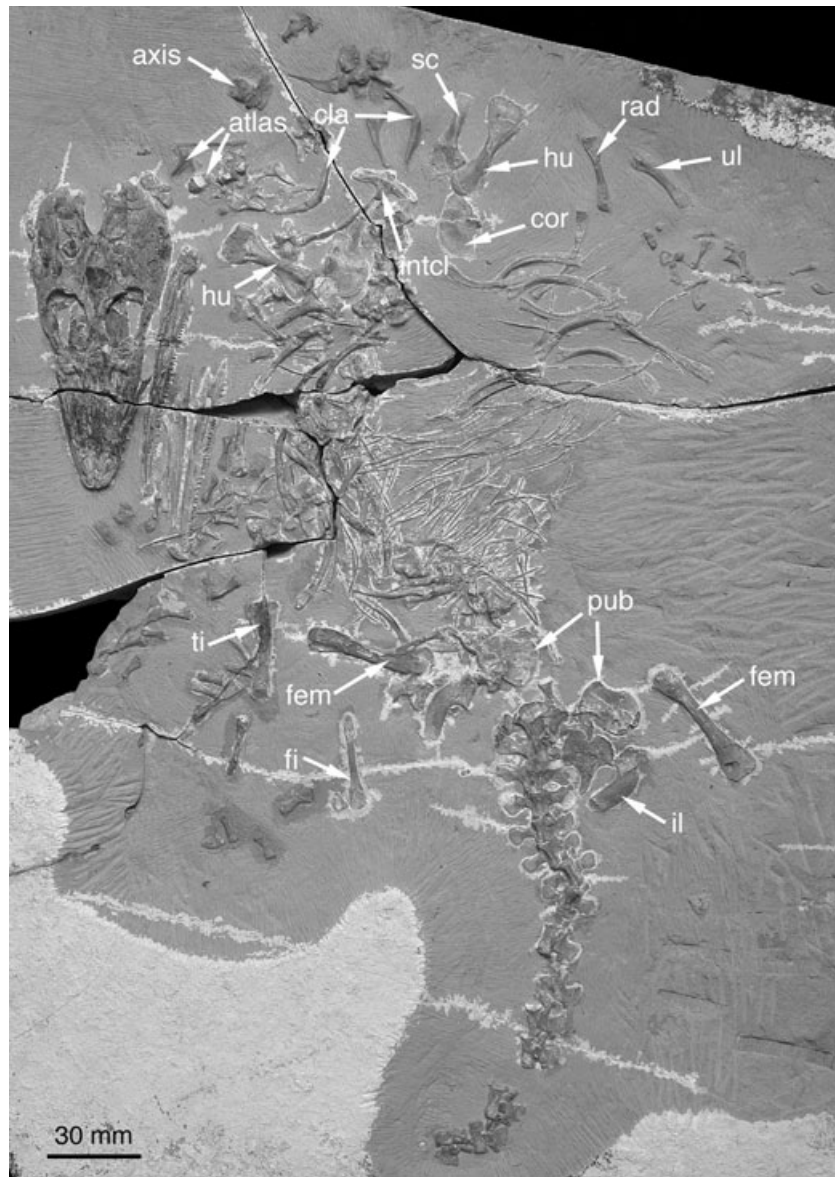


Figure 2. *Philydrosaurus proseilus* gen. et sp. nov., holotype (PKUP V2001) from Shangheshou near Chaoyang, western Liaoning Province; Early Cretaceous Chiufotang Formation.

skeleton is preserved in a volcanic shale slab, and was exposed in dorsal view after preparation of the specimen.

Skull roof. The cranial skeleton is nearly completely preserved, and is dorsoventrally compressed as in other choristoderes (Fig. 3). The general configuration of the skull in dorsal view, however, is sharply different from the type genus *Monjurosuchus*, as the skull of the new form is substantially more elongated, with the antorbital portion slightly longer than the postorbital portion. The total length of the skull is approximately 103 mm, with the antorbital portion 40 mm, the orbit 25 mm, and the postorbital portion 38 mm long. The

external narial openings are paired, elongated and are nearly terminal in position. With a strong interorbital constriction, the orbit is large but more dorsally than laterally orientated. The orbit is longer than wide, differing from that in *Monjurosuchus* (Gao *et al.*, 2000). The supratemporal fenestra of *Philydrosaurus proseilus* is unique: it is small and connects with an anterior trough formed by the postorbital and postfrontal (Fig. 3). The infratemporal fenestra is completely closed by expansion of the surrounding bones, including the postorbital, quadratojugal and squamosal. The closing of the infratemporal fenestra is apparently a synapomorphic feature of the Monjurosuchidae, as it also occurs in the type genus *Monjurosuchus* (Gao

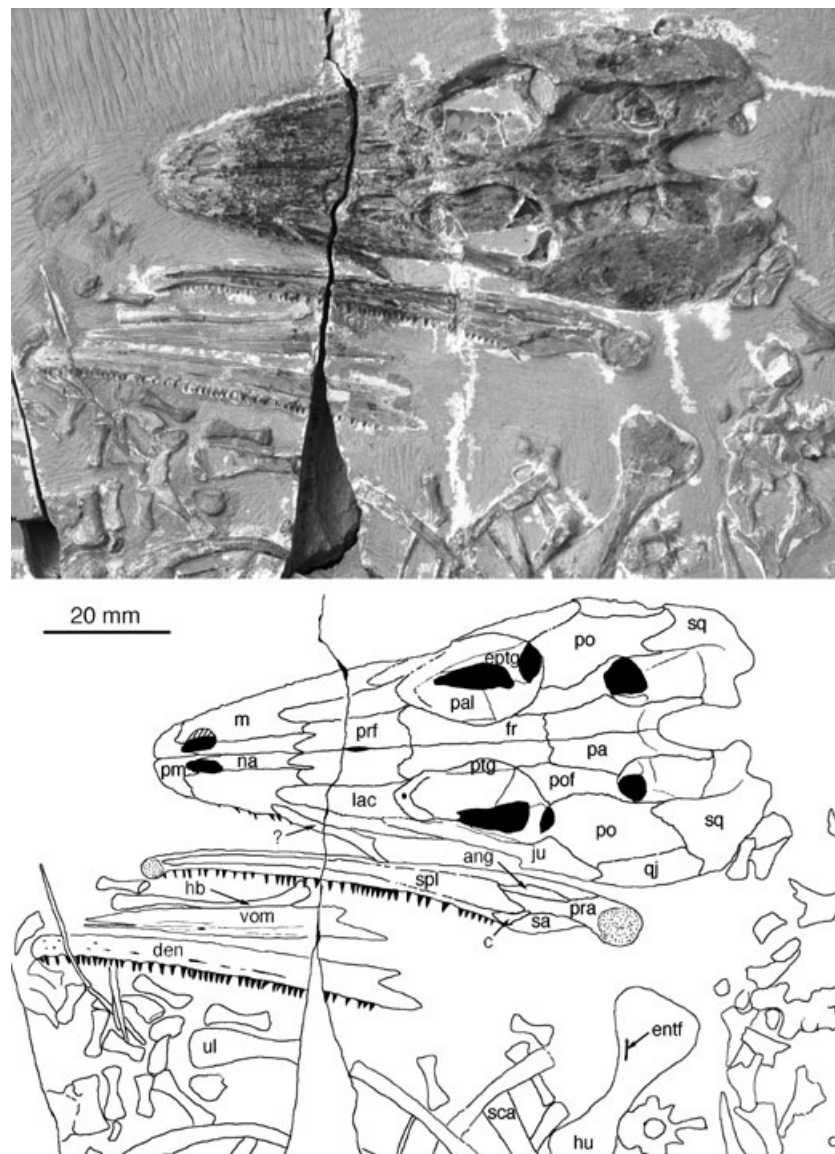


Figure 3. *Philydrosaurus proseilus* gen. et sp. nov., photograph and line drawing of the holotype skull and mandibles (PKUP V2001).

et al., 2000). No post-temporal fenestra is developed: the extremely short temporal process of the parietal is in full contact with the squamosal and the quadrate (see below).

The premaxillae are small, paired elements that meet along a midline suture. The body of the premaxilla is penetrated by several foramina for nerves and vessels, and these are associated with small bumps developed as surface ornamentation. Each premaxilla has a slender but well-defined dorsal process that forms 1/3–1/2 of the medial border of the external nares (the dorsal process of the left premaxilla extends to the level of the posterior border of the narial openings). The posterior end of the dorsal process narrows between the slender anterior processes of the nasals that form the posterior part of the medial border of the external nares. The posterior margin of the premaxillary body is notched for the anterior border of the narial opening, and lateral to the opening is the irregular suture that marks the articulation between the premaxilla and maxilla. Posteroventrally, the premaxilla has a well-developed tooth-bearing process extending to the midlevel of the narial opening.

The nasals are paired, very narrow, elongated (20 mm long) and extend posteriorly to contact the prefrontal at the midlevel of the snout. Anteriorly, the nasal forms the posterior, but not part of the lateral, border of the narial opening. A slender anterior process of the bone contacts the dorsal process of the premaxilla to form a large part of the internarial septum. Laterally, the nasal has a long, straight suture with the maxilla, and posteriorly it is developed as a slender process that pinches between the anterior process of the prefrontal and the dorsal rim of the maxilla.

The prefrontals are paired and elongated, being the same length (20 mm) as the nasals. A midline sutural contact between the prefrontals is clearly visible as in other choristoderes generally; however, a narrow opening is evident within the midline suture; such a prefrontal fontanel has never previously been recorded in other choristoderes, including a small subadult skull of *Champsosaurus* (RTMP 94.163.1, see Gao & Fox, 1998) from the Upper Cretaceous Dinosaur Park Formation of western Canada. The dorsal surface of the prefrontal of this new animal is unique in having a sharp elongate ridge running anteriorly from the orbital rim to the level of nasal/prefrontal articulation. The prefrontal contacts the nasal anteriorly, the frontal posteriorly, and the lacrimal and maxilla laterally.

The frontals are paired, elongated and hourglass-shaped, with a strong interorbital constriction. Having a greatest length of 26 mm, the frontal is longer than the prefrontal, and equal in length to the parietal (26 mm). The anterior part of the frontal is broken bilaterally, but it seems to lack an anteromedial

process. The anterolateral processes are in articulation with the prefrontal but barely contact the lacrimal. The anterior and posterior width of the paired frontals is 11 mm, and the interorbital width, 5 mm. The frontal contacts the postfrontal posterolaterally along a short straight suture, and meets the parietal posteriorly at a contact that is roughly transverse to the long axes of these bones. The latter suture is at about the same level as the anterior border of the 'supratemporal trough' or the posterior border of the orbits.

The parietals are paired, having a total length of 26 mm, including the short temporal process. The dorsal surface of the parietal table is smooth, but a prominent longitudinal ridge is developed that flanks the lateral border of the table. This lateral ridge also forms the medial border of the small supratemporal fenestra, and is continuous anteriorly with the ridge of the postfrontal that extends to the posteromedial border of the orbit. There is no parietal foramen. The temporal process of the parietal is extremely short (9 mm long), roughly 1/3 of the total length of the bone (26 mm). The two temporal processes form a deep U-shaped post-temporal incision medially on the occiput (Fig. 3).

The maxillae are well preserved on both sides. As in other choristoderes, the maxilla lacks a well-defined dorsal process, but inrolls medially to contact the elongated nasal bone. The maxilla has a short anterior process that is in articulation with the premaxilla and forms the lateral border of the narial opening. Medially, the maxilla has a long suture with the nasal and posteriorly contacts the lacrimal: the lateral wall of the maxilla sharply descends to meet the lacrimal and jugal. The slender posterior process of the maxilla is largely obscured on the right side, but the better-exposed left side seems to show it terminates at a level close to the posterior border of the orbit. This interpretation is supported by the fact that the lower dentition also terminates at this level, as shown by the disarticulated left mandible (Fig. 3).

Anterior to the orbit, the lacrimal is located in a longitudinal depression that is deep and wide in its posterior part but gradually becomes narrow and shallow anteriorly, terminating not far behind the narial opening. The lacrimal is quite narrow and elongated (25 mm long), with its anterior extremity reaching beyond the level of the nasal/prefrontal suture. Medially, it meets the prefrontal, and laterally the maxilla and anterior process of the jugal. The medial edge of the lacrimal contacts the prefrontal in the longitudinal depression developed dorsally on the snout (Fig. 3). The posterior border of the lacrimal is deeply notched for the anterior border of the orbit, and the dorsal rim of the orbit is ornamented with prominent tuberosities. The lacrimal foramen is identifiable on

both sides, despite the dorsoventral compression of the skull. This foramen penetrates the lacrimal, the primitive condition differing from the derived pattern in which the foramen is bordered by the lacrimal, prefrontal and palatine as in neochoristoderes (see Gao & Fox, 1998).

The postorbital and postfrontal are separate, and both enter the posterior border of the orbit (Fig. 3). This morphology is primitive in diapsids and differs from the fused condition in some but not all derived choristoderes (Gao & Fox, 1998; Evans & Manabe, 1999; Ksepka, Gao & Norell, 2005). In dorsal view, the postfrontal is substantially smaller than the postorbital, but overlaps the latter element in the 'supratemporal trough.' Dorsally, the postfrontal displays a short but prominent ridge that runs from the posterior border of the orbit to meet the lateral ridge of the parietal. Medial to this ridge, the postfrontal contacts both the frontal and the parietal along a short, straight suture; the posterior extension of this suture enters obliquely into the 'supratemporal trough' that separates the postfrontal from a small lateral projection of the parietal. Also within the trough, the postfrontal overlaps the postorbital to form much of the anterior border of the supratemporal fenestra. Lateral to the postfrontal, the postorbital is greatly hypertrophied as the main element that closes the infratemporal fenestra. Dorsally, the postfrontal displays a strongly developed ridge that joins with the ridge from the squamosal to form the lateral border of the 'supratemporal trough'. Lateral to the dorsal ridge, the postorbital has an extensive sutural contact posteriorly with the squamosal and ventrally with the quadratojugal. As a diagnostic feature of the family Monjurosuchidae, these three elements together have entirely closed the infratemporal fenestra, leaving no trace of the opening.

The jugal and the quadratojugal are preserved on both sides in the holotype. The anterior process of the jugal forms the lower border of the orbit and extends anteriorly to the lateral surface of the posterior process of the maxilla. The anterior tip of the process is damaged on both sides, but it probably terminated at a level slightly anterior to the orbit, as interpreted from the articular surface of the jugal on the maxilla. The postorbital, or dorsal, process of the jugal is low but well defined, forming a small part of the posteroventral border of the orbit. From the postorbital process, the dorsal margin of the jugal descends posteriorly to meet the quadratojugal. The short posterior process of the jugal fits into a small notch on the quadratojugal slightly anterior to the craniomandibular joint. The quadratojugal is a much smaller bone in comparison to the jugal and squamosal. It is located between the jugal and the squamosal, and dorsally contacts the enlarged postorbital.

The squamosal is greatly expanded as a major element that closes the infratemporal fenestra. The dorsolateral exposure of the squamosal is roughly a triangular plate, with a flattened surface rugosely ornamented. In dorsal view, the medial extension of the squamosal forms part of the floor of the 'supratemporal trough', and meets the temporal process of the parietal. The anterior border of this medial extension is thin, slightly concave and overlaps the quadrate. Posteriorly, this extension has two prominent processes separated from one another by a small notch (Fig. 3). The medial process forms a small part of the lateral border of the narrow U-shaped post-temporal incision, and the lateral process forms the posterior extremity of the temporal region.

Braincase and palate: Only a small part of the lateral wall of the braincase is exposed in the supratemporal fenestra within the 'supratemporal trough', and the lateral wall is badly crushed on both sides. However, it is clear that a downgrowth of the parietal forms a small part of the braincase wall, and it has a dorsally concave border for articulation with a small bone, presumably the neomorph as in other known choristoderes (Fox, 1968). A neomorph occurs in neochoristoderes and possibly in *Cteniogenys* (Evans, 1990), but this element cannot be identified positively for this new form because of breakage and distortion of the braincase. By the same token, a pterygoquadrate foramen is not identifiable on the new specimen, and the ventral parts of the braincase cannot be exposed without damaging the specimen; therefore, knowledge of the morphology of this part of the skull must await discovery of better preserved material.

Within the orbit, the pterygoid and ectopterygoid are partly exposed in dorsal view. The short medial process of the ectopterygoid forms the posterior border of the suborbital fenestra and overlaps the short lateral process of the pterygoid. A slender anterior process of the ectopterygoid extends along the medial side of the anterior process of the jugal, terminating slightly anterior to the midlevel of the suborbital fenestra; therefore, the short anterior extension of the process allows a small part of the jugal to enter the lateral border of the suborbital fenestra (Fig. 3). The anterior extension of the pterygoid is greatly widened as a plate that forms the entire medial border of the suborbital fenestra. The midline suture of the pterygoids is obscured by the frontal, and thus, the taxonomically significant feature of the interpterygoid foramen cannot be observed in this specimen. The anterior end of the pterygoid is badly damaged on both sides, and the pattern of the pterygoid/palatine articulation cannot be determined. Posterior to the suborbital fenestra, only a small part of the subtemporal fenestra is exposed behind the medial process of the

ectopterygoid; therefore, the actual size of the fenestra is unknown in the holotype of the new taxon.

Disarticulated from the palate, the left palatine is exposed in close association with the skull (partly obscured by the left maxilla). Most of the palatine is a thin plate, but it is slightly thickened posteriorly at the notch for the suborbital fenestra. Along the dorso-medial border of the palatine, the articular surface for the greatly elongated vomer can be seen. This surface is about half the width of the palatine, indicating an extensive articulation between the two bones. Although exposed in dorsal view, the exposed lateral edge seems to show that the palatine has a toothed ventral surface, but the distribution pattern of the palatal teeth cannot be ascertained in the absence of a ventral view.

Also disarticulated from the skull, the right vomer is nearly completely preserved in close association with a hyoid bone. Exposed in dorsal view, the vomer is greatly elongated, with a total length of 50 mm. The anterior extremity of the vomer is narrowly pointed but deeply bifurcated by a fissure 10 mm in length. About 19 mm from the anterior tip, a small vomerine foramen opens close to the medial border of the bone. Along this border, a well-defined ridge runs from the vomerine foramen to the posterior end of the anterior fissure. The vomer posteriorly has a notch for articulation with the pterygoid and posterolaterally an articular surface for the palatine. Lying to the side of the vomer is a slender bone 32 mm in length. This is probably one of the hyoid elements that are also known for some champsosaurs (Gao & Fox, 1998: fig. 5).

Mandibles: Before burial, both mandibles of the holotype (PKUP V2001) were disarticulated from the skull (Fig. 3). The left mandible is nearly completely preserved and is exposed in medial view; the dentary of the right mandible is exposed in lateral view but the postdentary parts are missing. The total length of the mandible is 83 mm as measured from the nearly complete left element. With a total length of 63 mm, the dentary is the longest mandibular bone and covers a large part of the lateral side of the lower jaw. As shown in the right mandible, the strongly convex lateral surface of the dentary is penetrated by rows of small foramina. The foramina on the anterior part of the jaw are closely spaced, while those on the posterior part are increasingly widely spaced; they are accompanied by narrow and posteriorly extending grooves that housed lateral cutaneous branches of the mandibular ramus of the trigeminal nerve and accompanying blood vessels. The posterior end of the dentary is bifurcated for articulation with the surangular bone (missing on the right mandible along with the other postdentary elements). Medially, the dentary carries a well-developed subdental shelf, the depth of which is

roughly equal to the tooth height. Below the shelf is the Meckelian canal that opens medially as a narrow groove for the anterior one-third of the dentary length, but is closed by the splenial for the posterior two-thirds. Anteriorly, the mandibular symphysis is extremely short and lacks a posterior extension as seen in advanced neochoristoderes. The splenial has been crushed into the Meckelian canal, but it shows that its posterior extremity terminates as a short tongue slightly beyond the posterior end of the tooth row. This tongue is wedged between the coronoid and the anterior extension of the prearticular, but may have a short ventral sutural articulation with the angular bone. The coronoid is a small triangular bone without a prominent dorsal process. It sends a short posteroventral process to articulate with the splenial and the prearticular, thereby contributing to a small part of the lower border of the mandibular fossa. Behind the fossa is the articular surface for the craniomandibular joint. From the length of the mandible, this joint is interpreted as being located roughly at the same level as the occipital condyle. The articular surface is at the posterior extremity of the jaw, and thus a retroarticular process is undeveloped in this animal.

Dentition: On the holotype specimen, marginal teeth are observed on both upper and lower jaws. Anteriorly, the upper dentition is exposed on both sides, but its more posterior parts are imbedded in matrix making the total number of the maxillary teeth indeterminate.

As a result of the disarticulation of the lower jaws from the skull, the lower dentition on the left is exposed in medial view and that on the right in lateral view (Fig. 3). The left dentary has as many as 41 teeth preserved, with tooth spaces for 18–19 others. The right dentary carries 46 teeth and tooth spaces for 11 others. The teeth are generally low crowned but sharply pointed, although the anterior teeth are more slender and slightly taller than the posterior ones. The tooth crowns are weakly striated on their medial sides, but are smooth, without striations, laterally.

As best shown on the left mandible, the mode of tooth attachment is subthecondont (referred to as protothecondont by some authors): the teeth are set in a shallow dental groove containing shallow sockets for the tooth bases as in other choristoderes, including *Cteniogenys* (Evans, 1990; Gao & Fox, 1998). No enlarged caniniform teeth are developed anteriorly on the marginal tooth row, unlike some other primitive diapsids (see Evans, 1988; de Braga & Rieppel, 1997). None of the upper or lower dentition shows any indication of basal infolding of the tooth enamel. Such basal infolding occurs in Champsosauridae and Simodosauridae, but is absent in *Cteniogenys* (Evans, 1990; Gao & Fox, 1998). Therefore, this character

alone places the new choristodere and the *Monjurosuchidae* outside the *Neochoristodera*.

Vertebral column and ribs: There are 38 vertebrae preserved in the holotype, including 24 presacrals, three sacrals and 13 anterior caudals (Fig. 2). Most of the presacrals are disarticulated, with ribs, the pectoral girdle and limb elements scattered nearby, while the sacrals and caudals are basically in articulation. All of the vertebrae have a centrum of amphiplatyan type, with essentially flat articular surfaces both anteriorly and posteriorly. The centra of the cervical vertebrae are slightly shorter than those of the dorsal vertebrae, and the caudal centra are generally more elongated than the dorsal centra (see below). In contrast to the condition in *neochoristoderes*, the neurocentral sutures of this new form are fully closed, and none of the vertebrae show disarticulation of the neural arch from the centrum.

Among the cervical series, the atlas is incompletely preserved, with a disarticulated centrum and pleurocentrum located posterolateral to the skull. The centrum is short with a slightly convex ventral surface, and the pleurocentrum in lateral view is an inverted L-shaped structure as in other *choristoderes* (Evans, 1990). The axis is nearly complete with a low crown-shaped neural spine extending posteriorly far beyond the centrum. The articular surface of the anterior zygapophysis is oval and faces dorsolaterally at roughly a 45° angle in relation to the sagittal plane. The articular surface of the posterior zygapophysis, also oval in shape, faces ventrolaterally with a similar angle as the anterior zygapophysis. The short centrum (6.5 mm long) of the axis is about half the length of the crown-shaped neural spine, with an articular surface anteriorly indicating that the unpreserved odontoid process was free from the centrum as in other *choristoderes*, but the process itself is not preserved in PKUP V2001. Six rib-bearing vertebrae are also identified as cervicals, as these show a short centrum (6.5–7 mm long) with a well-developed ventral crest, and separated capitulum and tuberculum for articulation with double-headed ribs. Several cervical ribs are scattered nearby the cervicals. These ribs are short and straight, having a spiky distal end but a bifurcated proximal end (capitulum and tuberculum) for articulation with the diapophysis and the parapophysis of the vertebrae.

The remaining 16 presacrals are identified as dorsal vertebrae, because they show the unification of the diapophysis with the parapophysis and thus articulated with single-headed (holocephalous) ribs. In addition, the centrum of all of these is more elongated (8–9.5 mm long) than that of the cervicals, and has a flat ventral surface lacking a ventral crest. The small spinous process below the postzygapophyses that is

present in *simoedosaurids* (Sigogneau-Russell, 1981) is absent in the presacrals of the new taxon. More than 20 ribs are preserved in association with the dorsal vertebrae. All of these are uncapitate and are pachyostotic, with a thickened distal end. The anterior surface of the dorsal ribs is convex in cross section, but the posterior surface has a well-developed groove running longitudinally along the ribs.

Three sacrals are identified clearly in the holotype. The second and third are preserved in articulation, but the first has broken away and is preserved in close association with the left pubis. Each sacral has robust transverse processes, and each carries sacral ribs that are not fused to the vertebra. The distal end of these ribs is strongly widened and is in contact with its neighbouring sacral rib to enclose a fenestra. The centrum of the sacrals is 8 mm long, similar to that of the posterior presacrals; however, the ventral surface is narrowed with strong lateral concavities. This morphology of the sacral centra shows the transition from the dorsal to the caudal series.

Of the caudal series, the first six vertebrae are preserved in ventral view in full articulation, while the remaining seven are preserved in lateral view and are disarticulated. The caudal centra vary in length from 8 to 9.5 mm as in the dorsal series, but are more slenderly built and are strongly compressed bilaterally. The ventral surface of the centrum has a groove that is flanked by well-developed ridges. None of the preserved caudals show any sign of neurocentral sutures, indicating the closure of the suture between the neural arch and centrum in the caudal series. The zygapophyses are essentially vertical as in other *choristoderes*. Each of the six anterior caudals bears ribs. The ribs are expanded in a horizontal plane, and are tightly articulated with the vertebrae, although a suture is visible. The first pair of ribs is the most robustly built in the caudal series, but the remainder progressively diminish posteriorly in length and thickness.

Gastralia: As in *Monjurosuchus*, a mass of gastralia is developed on the ventral aspect of the trunk region (Fig. 2). The gastralia (or the so-called ventral ribs) are slender and rod-like structures scattered in the abdominal region. The individual elements are cylindrical and more or less spindle-like with pointed ends, but their original pattern cannot be determined because of their postmortem disarticulation.

Pectoral girdle and forelimb: The interclavicle is a T-shaped structure, with the crossbar slightly shorter than the stem (23 mm vs. ?25 mm). Anteriorly, the crossbar has a well-developed shelf that reinforces the articulation with the clavicles. Beneath the shelf is a groove for the interlocking articulation of the interclavicle with the lower half of the clavicle. Because the

interclavicle is exposed in ventral view, the entire groove can be observed in this specimen. The stem is a narrow, lanceolate structure. The posterior end of the stem is concealed by the left coracoid plate. Judging from the exposed part, the stem is at least the same length (23 mm) as the crossbar, and may well be slightly longer than the latter. Both clavicles are well preserved, and slightly disarticulated from the other girdle elements (Fig. 4). The clavicle is a boomerang-shaped structure, with a thick, curved middle part and thinner and straight lateral ends. Both clavicles are exposed in anterior view, and thus the posterior edges that interlock in the groove of the interclavicle cannot be observed.

The scapula and the coracoid plate, although disarticulated, are well preserved on both sides of this specimen. The scapula is shorter than the humerus (27 mm vs. 34 mm), as measured from the left elements. The scapular blade is narrow and tall, with the dorsal end only 5.5 mm wide; the ventral end of the scapula is much broader, about 12 mm wide at the level of the glenoid. Posteriorly at the same level, a small triangular supraglenoid buttress borders the dorsal rim of the glenoid cavity. The buttress displays a small depression, but a supraglenoid foramen is not evident in the depression. Slightly above the buttress a small but prominent tubercle is developed for attachment of pectoral muscles. To our knowledge, such a structure is not previously known in choristoderes, and its function and distribution among choristoderes requires further investigation. The anterior border of the scapular blade is straight dorsally but curves more ventrally, where it matches the curvature of the clavicle. At the base of the scapular blade is a smooth bulge that may represent the remnant acro-

mion process (see de Braga & Rieppel, 1997 for evaluation of this structure).

The coracoid is a single element, taking the form of a suboval plate with a rounded lower border. A second coracoid ossification is present in primitive reptiles (Captorhinidae and *Palaeothyris*) including early diapsids (Araeoscelidia), and the loss of this ossification has been interpreted as a derived condition for neodiapsids (Gauthier, Kluge & Rowe, 1988; Sauria; Evans, 1988; but see also Rieppel, 1993; de Braga & Rieppel, 1997). The middle part of the dorsal border is significantly thickened for the glenoid cavity, which is short and less screw-shaped than in other choristoderes. A small coracoid (supracoracoid) foramen opens anteroventral to the glenoid cavity; this penetrates the coracoid plate and serves for the passage of the supracoracoid nerve and its associated vessels (Romer, 1956).

The bones of the forelimbs are disarticulated but are in close association with the remainder of the specimen (Fig. 2). The left humerus is exposed in lateral view, while the right is exposed ventrally. The humerus is shorter but more massively built than the femur, and is longer than the scapula (34 vs. 27 mm). The shaft of the humerus is short but is strongly constricted (4 mm at its narrowest). The proximal end of the bone is expanded (11 mm), while the distal end is even wider (14 mm). The two ends are twisted relative to each other at a small angle of less than 45°, as observed on both sides of the specimen.

In dorsal view, the proximal articular surface of the humerus is well ossified, indicating that this individual was mature at death. The anterior border of the bone is straighter than the posterior border, with the greatest curvature at the anterior border of the shaft. The proximal dorsal surface of the bone is generally

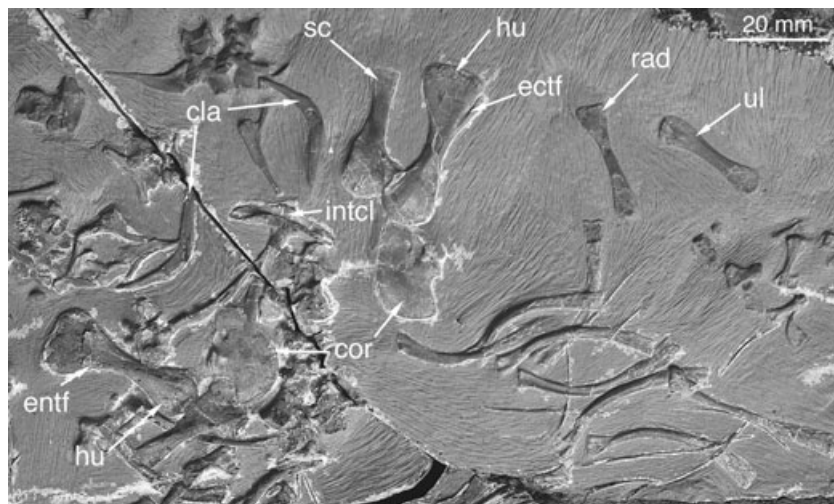


Figure 4. *Philydrosaurus proseilus* gen. et sp. nov., pectoral girdle and fore limb of the holotype (PKUP V2001). Note arrows pointing to ect- and entepicondylar foramina.

convex, but is anterodorsally concave at the deltoid crest. The delto-pectoral crest is well developed, curving from the anterior border of the articular surface and then extending towards the shaft. Distally, the dorsal surface is slightly concave, in contrast to the proximal dorsal surface. Anterodistally, the ectepicondyle is a poorly defined structure with a low, smooth ridge running towards the shaft. Anterior to the low ridge is a deep and narrow fissure representing the ectepicondylar foramen (Fig. 4). The supinator process (supracondylar process) is also a weakly developed structure that is set off from the ectepicondyle by the ectepicondylar groove. The posterodistal region of the humerus is expanded to a much greater degree than the anterodistal region, although the entepicondyle itself is weakly developed. Proximal to the condyle and distal to the shaft, another narrow fissure is present on the posterior border of the humerus. This fissure is the posterodorsal opening of the entepicondylar foramen (see below), representing the primitive morphology within choristoderes.

In ventral view, the proximal ventral surface is deeply concave with a triangular depression tapering towards the shaft. Anterior to the depression is a well-defined crest that supports a tubercle (slightly damaged on the right humerus of the holotype) for the attachment of the supracoracoideus muscle (Romer, 1956). A large part of the distal ventral surface is damaged on the right humerus; consequently, the structure of epicondyles, trochlea (ulnar condyle) and the capitellum (radial condyle) cannot be observed. However, a narrow fissure-like structure is clearly identifiable as the entepicondylar foramen. This foramen

occurs in primitive diapsids (Reisz, 1981), but is lost in many advanced diapsid groups including most neochoristoderes. In this new choristodere, the fissure opens on the anterodorsal border of the humerus at the base of the shaft and at a level slightly higher than the ectepicondylar foramen (Figs 3, 4).

The disarticulated epipodial elements of the forelimb are completely preserved on the left side, but partly missing on the right. The epipodial is roughly two-thirds the length of the humerus; the ulna (24 mm) is slightly shorter and thicker than the radius (25 mm). Evans (1988) regarded a radius longer than the ulna as diagnostic of the Younginiformes, while Rieppel (1994) and de Braga & Rieppel (1997) later showed that this feature had evolved independently within Eosauropterygia, Prolacertiformes and Younginiformes. As in other choristoderes, there is no development of either an olecranon process or a sigmoid notch on the proximal end of the ulna in this new form. Loss of the process and notch has been recognized as a neodiapsid condition (see Evans, 1988; see also de Braga & Rieppel, 1997).

All of the elements of the manus, including carpals, are scattered on the shale slab, and thus the relative length of the digits and the phalangeal formula of the manus are indeterminable on the holotype. Six carpal elements can be identified on the associated part of the left manus.

Pelvic girdle and hind limb: All three ossifications of the pelvis (ilium, pubis and ischium) are preserved on both sides in close association, although disarticulated (Fig. 5). Both ilia are exposed in lateral view. The dor-

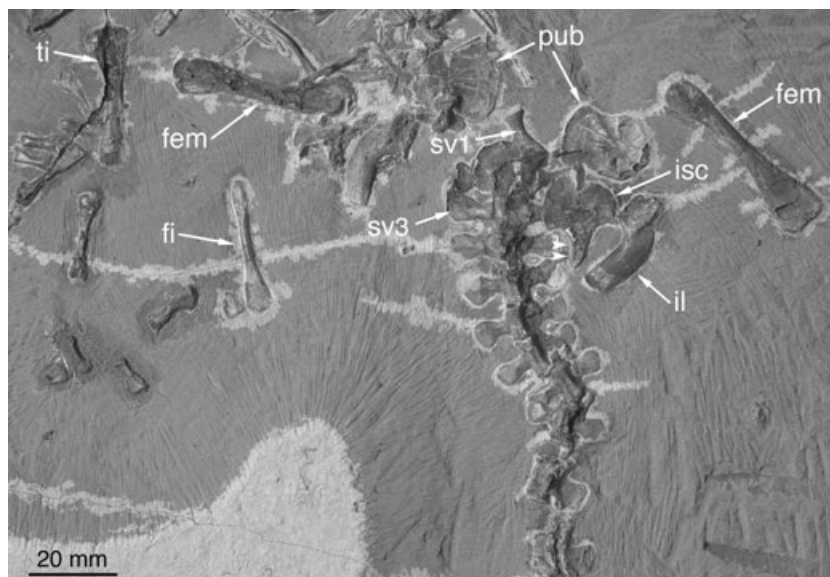


Figure 5. *Philydrosaurus proseilus* gen. et sp. nov., pelvic girdle, hind limbs and anterior caudal vertebrae of the holotype (PKUP V2001). Double arrows pointing to the ischium spike.

sal iliac blade of this new form differs from that of *Monjurosuchus* in having a greater elongation posteriorly, parallel dorsal and ventral borders, and in lacking a constricted neck between the blade and the acetabulum. However, the blade retains a primitive morphology, including its lack of an anterior extension and the steep angle it makes with the horizontal plane (see character coding below). The lateral surface of the blade is convex and mostly smooth, but the dorsal border and the posterodorsal part are rugous for attachment of axial muscles (Romer, 1956). The triangular base of the ilium is occupied by the acetabulum, with a well-developed supra-acetabular buttress forming the dorsal border.

The puboischiadic plate consists of a well-ossified pubis and ischium. The pubis is a broad plate with rounded dorsal and ventral rims. The straight posterior border is tightly articulated with the ischium and lacks a thyroid fenestra (see Carroll & Currie, 1991; de Braga & Rieppel, 1997; for evaluation). The lower part of the anterior border is weakly notched, but a pectineal tubercle (term of Romer, 1956) is absent. Posterodorsally, the pubis has a small obturator foramen (Romer, 1956: for the nerve of the same name) opening anteroventral to the acetabulum. Above the foramen, the dorsal rim of the pubis is slightly thickened for articulation with the ilium and contributes little to the acetabulum.

The ischium of this animal is unique among choristoderes in having a well-developed spike (a horn-like process) projecting posteriorly from the middle part of the posterior border of the ischiadic plate (Fig. 5). Such a strong process may have provided attachment for ligaments or tendons of a powerful tail in this animal. Anterior to the spike, the ischiadic plate is dorsally narrow and ventrally expanded in lateral view. The dorsal rim of the plate is thickened, forming a small part of the acetabulum.

The femur (44 mm long) is more slender than the humerus and is roughly 130% the length of the latter element. The bone is weakly sigmoid (best shown on the right femur) as in adult specimens of *Monjurosuchus* (see Gao *et al.*, 2000). The proximal end of the femur has a greatest width of 10 mm, and the distal end, 10.5 mm; the diameter of the shaft is 4 mm at its narrowest. The right femur is partly damaged, but shows a shallow proximal depression representing the reduced intertrochanteric fossa. Anterior to the fossa is a longitudinal ridge (damaged), the proximal end of which is the broken base of the internal trochanter. As in *Champsosaurus* (Romer, 1956), this trochanter is set off slightly from the femoral head and is in a ventral position. There is no indication of a fourth trochanter, although the proximal base of the femoral shaft is damaged. The distal end of the femur lacks a clearly defined median notch, and thus

the two distal condyles are poorly separated from one another.

The tibia and fibula are only preserved for the right hind limb, whereas those on the left are missing, together with the left pes. As in the forelimb, the epipodial segment of the hind limb is significantly shorter than the propodial (femur). The tibia is slightly longer than the fibula (33 mm vs. 31 mm), and is more robustly built than the latter. The proximal end of the tibia has a greatest width of 11 mm, while the distal end narrows to 6.5 mm. The condition of the cnemial crest cannot be interpreted, as the anterior surface of the tibia is badly damaged. The fibula is straight and is much more slender than the tibia; its widened distal end is about 6 mm, while the narrowed proximal end is only 4 mm wide. The right pes is incompletely preserved, with digital elements scattered but in association with the epipodial. Only two tarsals can be found on the specimen; others are not preserved. Four metatarsals can be identified, among which is metatarsal V. This has an expanded proximal end, but the short shaft is straight with no plantar tubercles. Like the manus, the relative length and phalangeal formula of the pes are indeterminable because of poor preservation.

PHYLOGENETIC RELATIONSHIPS AND CLASSIFICATION

A recent study of *Monjurosuchus* based on the specimens from the Lingyuan area clarified several anatomical ambiguities of the genus, and demonstrated the relationship of the Monjurosuchidae with choristoderes (Gao *et al.*, 2000). However, the detailed relationships of the Monjurosuchidae within the Choristodera remain to be scrutinized. To resolve this problem, a parsimony analysis was performed using PAUP v.3.1 (Swofford, 1993). The data matrix for this analysis contains 13 basic taxa, including 11 ingroup and two outgroup taxa coded with 75 characters. The matrix was expanded and modified from Gao & Fox (1998), Evans & Manabe (1999), and Ksepka *et al.* (2005). Modifications of character description and coding from previous data sets are explained below (see Appendix 1). Besides *Monjurosuchus* and the new form described in this paper, the taxon *Hyphalosaurus* is included in the analysis because it represents another choristodere from the Liaoning fossil beds (Gao *et al.*, 2000). The Late Triassic taxon *Pachystropheus* from England is a possible choristodere (Storrs, Gower & Large, 1996) known only from incomplete and disarticulated postcranial material. Previous analyses (Evans & Manabe, 1999; Evans & Klembara, 2005; Ksepka *et al.*, 2005) have consistently shown that inclusion of this taxon in a phylogenetic analysis only generates multiple trees with poor resolution

because of the lack of knowledge concerning phylogenetically significant cranial characters. Therefore, this problematic taxon is excluded from the parsimony analysis in this paper.

Using the Branch-and-Bound search option, parsimony analysis was conducted utilizing a Macintosh G5 desktop computer. All characters were unordered and equally weighted, and ACCTRAN tree optimization was used to minimize possibilities of parallelisms. Tracing character evolution was performed with MACCLADE v.3.01 (Maddison & Maddison, 1992). Trees were rooted using the primitive diapsids Araeoscelidia and *Youngina* (Younginiformes) as successive outgroups. Two MPTs (most parsimonious trees) were found (Fig. 6), with a tree length of 123 steps, consistency index of 0.85, and a retention index of 0.87. Comparison of the two MPTs and character support for choristoderan clades are discussed below.

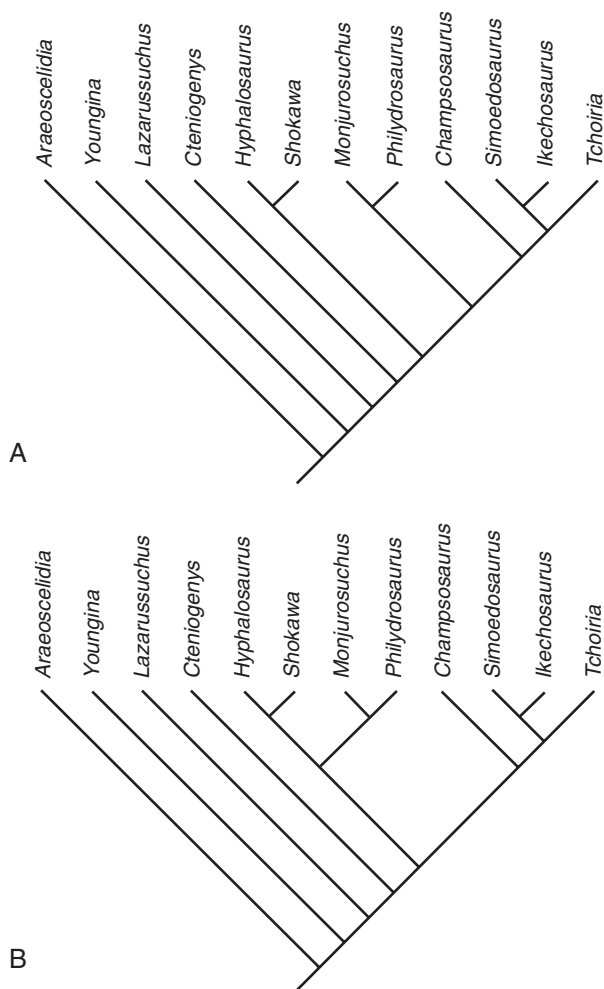


Figure 6. Comparison of the two equally parsimonious trees (TL = 123 steps; CI = 0.85; RI = 0.87) derived from analysis of data presented in Appendices 1 and 2.

MONJUROSUCHIDAE AS A MONOPHYLETIC FAMILY

Two genera and species are currently classified in the family Monjurosuchidae: the type species *Monjurosuchus splendens* from the Yixian Formation exposed near Lingyuan, and *Philydrosaurus proseilus* gen. et sp. nov. described here from the Chiufotang Formation exposed near Chaoyang. With inclusion of these two taxa in a revised data set (Appendix 2), a parsimony analysis revealed that the monophyly of the family is supported by the following synapomorphies: dorsal process of squamosal absent (13-2; unknown for *Hyphalosaur* and *Shokawa*); supratemporal fenestra smaller than orbit (14-0; character reversal); infratemporal fenestra closed (15-1; homoplastic in *Lazarussuchus*, see Evans & Klembara, 2005); post-temporal fenestra absent (47-1; also in *Simoedosauridae*); posterior process of ischium strongly developed (75-1; uniquely diagnostic for the family Monjurosuchidae).

A POSSIBLE MONJUROSUCHIDAE– HYPHALOSAURIDAE CLADE

Hyphalosaur and *Shokawa* are two morphologically peculiar, long-necked choristoderes known from the Lower Cretaceous of China and Japan (Evans & Manabe, 1999; Gao, Tang & Wang, 1999). Both MPTs (Fig. 6) recognize a *Hyphalosaur*–*Shokawa* clade, for which the name Hyphalosauridae (fam. nov.) is proposed here. The grouping of the two forms in the family Hyphalosauridae is unambiguously supported by two uniquely derived character states of the two genera of the family: cervical vertebral count more than 16 (67-1); and caudal neural spines tall and narrow (72-1). Because the skull morphology is either poorly known or entirely unknown for the two forms, the diagnosis of the family would be enhanced by further study of the known material and discovery of new material.

Within the phylogenetic framework of the Choristodera, both Monjurosuchidae and Hyphalosauridae are recognized as robust familial groups outside the neochoristoderan clade; however, the two MPTs differ from one another in placing the two families as either successive sister groups with the Neochoristodera (Fig. 6A), or grouped together as the sister group with the Neochoristodera (Fig. 6B). The grouping of Monjurosuchidae with Hyphalosauridae as sister groups is weakly supported by the following two character states: lateral borders of frontals strongly constricted (3-1; unknown for *Shokawa*); and orbit large and dorsally orientated (11-1; unknown for *Shokawa*). Because the current data matrix contains a large amount of missing data for the basic taxa of the two families, the robustness of the possible Monjuro-

suchidae–Hyphalosauridae clade must be tested further when new data become available.

TAXONOMIC DIVERSITY AND HIGHER-LEVEL
CLASSIFICATION OF CHORISTODERES

Order Choristodera

For more than a century since Cope's (1876) naming of the group, the order Choristodera has been known mostly from the Champsoosauridae and Simoedosauridae. The contents of the Choristodera, however, have been significantly expanded recently by recognition of the membership of *Cteniogenys* and *Monjurosuchus* in this group (Evans, 1989, 1990; Gao *et al.*, 2000), and by the discovery of new morphotypes including the long-necked *Hyphalosaurus* from China (Gao *et al.*, 1999) and *Shokawa* from Japan (Evans & Manabe, 1999). By current understanding, the order Choristodera includes five families: Cteniogenidae, Monjurosuchidae, Hyphalosauridae, Simoedosauridae and Champsoosauridae. The relationships of these families are depicted in cladograms resulting from this study (Fig. 6).

The taxonomically problematic taxon *Lazarussuchus* is excluded from the order Choristodera in this paper (see Gao & Fox, 1998, for discussion). Independent phylogenetic analyses consistently place *Lazarussuchus* outside the choristoderan clade (Gao & Fox, 1998; Evans & Manabe, 1999; Ksepka *et al.*, 2005; this paper; but see also Evans & Klembara, 2005, for different interpretations). *Lazarussuchus* shares with choristoderes several character states including: parietal foramen absent (4-1; also absent in many other aquatic reptiles); caudal zygapophyses lie nearly or completely vertical (58-1); and fibula narrow at proximal end and flared at distal end (70-1). None of these are individually diagnosable for the Choristodera, and possible homologies of these characters in *Lazarussuchus* with choristoderes need to be further investigated. According to Hecht's (1992) description, *Lazarussuchus* displays several features that are not otherwise known in choristoderes: paired narial openings located far back from the tip of the snout; prefrontals entering narial opening; vertebral centrum amphicoelous and notochordal; and presence of four sacral vertebrae with fused ribs. In addition, uniquely diagnostic character states, such as presence/absence of a neomorph bone in the braincase and presence/absence of a pterygoquadrate foramen, are unknown for *Lazarussuchus*. Until these anatomical ambiguities can be clarified, *Lazarussuchus* is best treated as a taxon outside the Choristodera.

With the exclusion of *Lazarussuchus*, the order Choristodera can be unambiguously diagnosed by the following derived character states: prefrontals having median sutural contact for their entire length (2-2);

parietal foramen absent (4-1; possibly homoplastic in *Lazarussuchus* and in many other aquatic reptiles); choana retracted close to midpoint of marginal tooth row (20-1); pterygoid flange consisting of pterygoid and ectopterygoid with a horizontal overlap (23-1); basipterygoid/pterygoid joint a sutural contact (24-1); parasphenoid and pterygoid having a clear sutural contact (25-1); postorbital process of jugal much shorter than anteroventral process (28-1); interpterygoid vacuity enclosed anteriorly by pterygoids and posteriorly by parasphenoid (33-1; further modification in Champsoosauridae); neomorph in braincase present as part of external wall of braincase and medial wall of temporal fossa (40-1; unknown for *Lazarussuchus*); free odontoid process unfused to axis (50-1); vertebral centra amphiplatyan with notochordal canal closed (52-1); sacral vertebrae three in number (56-1); sacral and caudal ribs remain free from vertebrae (57-1).

Suborder Neochoristodera

Consisting of the traditional familial groups, Champsoosauridae and Simoedosauridae (Fig. 6), the taxon Neochoristodera as named by Evans & Hecht (1993) designates the same clade as the name Champsoosauriformes Hay, 1929. However, the name Neochoristodera has been widely accepted, while the name Champsoosauriformes has not been mentioned in the literature for more than 50 years; thus, the latter name is here treated as a nomen oblitum (a forgotten name).

The suborder Neochoristodera is a robust clade that can be unambiguously diagnosed by the following synapomorphies: external nares terminal and confluent (1-2; possibly also in *Cteniogenys*); dorsal flange of maxilla low and strongly inrolled (6-2); nasals elongate and fused (9-2); nasals intervene between premaxillae (10-1); orbit small and dorsally directed (11-2); dorsal process of squamosal slender and elongate to middle level of infratemporal fenestra (13-1); supratemporal fenestra posteriorly flared and substantially larger than orbit (14-2); vomer/maxilla contact present (19-1); palatal foramen opens between pterygoid and palatine without contribution from the vomer (21-2); quadratojugal bears a cotyle meeting a rounded quadrate articulation (26-1); pterygoid process of quadrate low, slender and horizontal with a reduced pterygoid facet (27-1); nasopalatal trough present (29-1); pterygoids meeting in a long midline suture (31-1); interpterygoid vacuity small and near posterior border of suborbital fenestra (32-1); basal infolding of tooth enamel present (37-1); pterygoquadrate foramen present and enclosed between neomorph and quadrate (41-1); neurocentral sutures remain open in adult (51-1); presacral vertebral centra short and spool-like (53-1); number of ossified carpal elements seven or fewer (60-1); bone structure pachyos-

otic in adult (62-2); iliac blade dorsal margin essentially horizontal, blade expanded (63-1); clavicular facet on interclavicle continuous across midline in smooth curve (66-1); constriction of ilium between iliac blade and acetabulum as a well-defined neck (74-1; reversal in *Ikechosaurus*).

CONCLUSIONS

The study of new fossil material from Liaoning and the re-examination of the phylogeny of choristoderes leads to the following conclusions:

1. The new specimen PKUP V2001 represents a new monjurosuchid choristodere from outside the type Lingyuan area. The new discovery extends the geological range of the family from the Early Cretaceous Yixian Formation to the geologically younger Chiufotang Formation.
2. Study of the new specimen stimulates a phylogenetic analysis to resolve the relationships of Monjurosuchidae within the Choristodera, and the phylogenetic results place the family outside the Neochoristodera, but in a more derived position than the Cteniogenidae.
3. Two long-necked forms, *Hyphalosaurus* and *Shokawa*, are grouped in the same clade based on unique characters, and a new family name, Hyphalosauridae, is proposed for the clade.
4. A possible Monjurosuchidae–Hyphalosauridae clade is weakly supported, but the robustness of this grouping needs to be critically tested by further study based on more and better-preserved material than available at present.
5. The order Choristodera contains five well-established familial groups, including the Cteniogenidae, Monjurosuchidae, Hyphalosauridae, Champsosauridae and Simoedosauridae.

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APPENDIX 1

CHARACTERS AND CHARACTER STATES USED IN PHYLOGENETIC ANALYSIS

Characters are from previous data sets in Gao & Fox (1998), Evans & Manabe (1999), and Ksepka *et al.* (2005). Changes of character coding and description are explained below, and new characters added to previous data sets are denoted with an asterisk. All characters are unordered.

1. External nares: paired, oval nearly terminal (0); paired, elongate, dorsally placed (1); terminal and confluent (2).
2. Prefrontals: anterolateral and separated by frontals (0); median contact limited to posterior two-thirds of length (1); having median contact entire length of element (2).
- *3. Lateral borders of frontals: more or less parallel (0); strongly constricted (1). The derived state is known for *Monjurosuchus*, the new genus and species described in this paper, and the long-necked *Hyphalosaurus*.
4. Parietal foramina: present (0); absent (1).
5. Preorbital skull proportions: moderately short lack of elongation (0); elongate but less than 50% of skull length (1); more than 50% of skull length (2).
6. Dorsal flange of maxilla: low and vertical (0); prominent process confined to anterior part of maxilla and weakly inrolled (1); low flange elongated and strongly inrolled (2).
7. Lacrimal extension: lacrimal enters external narial opening (0); lacrimal retracted posteriorly from the opening, but remains elongate (1); lacrimal reduced to small triangular bone dorsally in front of orbit (2). Because the lacrimal of *Youngina* has retracted from the narial opening but remains relatively long and exposed laterally, the outgroup Younginiformes is coded as (1), contra previous coding in Evans & Manabe (1999).
8. Lacrimal perforation: perforated by one or two foramina (0); lacrimal foramen between lacrimal, prefrontal, and palatine (1).
9. Nasals: short and paired (0); elongate and paired (1); elongate and fused (2).
10. Nasal/premaxilla contact: nasals contact but do not intervene between premaxillae (0); nasals intervene between premaxillae (1); nasals do not contact premaxillae (2).
11. Orbit size and orientation: large and laterally directed (0); large and dorsally directed (1); small and dorsally directed (2). The derived state (1) is added to distinguish the condition in monjurosuchids and possibly in *Hyphalosaurus*.
12. Postfrontal/postorbital fusion: postfrontal and postorbital discrete and both enter the orbital margin (0); postfrontal and postorbital discrete, postorbital excluded from orbital margin (1); postfrontal and

- postorbital fused (2). N.B. Evans & Manabe (1999) report evidence of a suture between the bones in one specimen of *Tchoiria*, so the state is given as variable (1/2) pending more information.
13. Dorsal process of squamosal: broad and short (0); slender and elongate to middle level of inferior temporal opening (1); dorsal process absent (2). The derived state (2) is added to differentiate the monjurosuchid condition.
 14. Supratemporal fenestra: smaller than orbit (0); about same size as orbit (1); posteriorly flared and substantially larger than orbit (2).
 - *15. Infratemporal fenestra: present (0); closed by expansion of surrounding elements (1). Pending the condition in *Hyphalosaurus* and *Shokawa*, the derived state is currently diagnostic for the Monjurosuchidae.
 16. Parietal: having a broad contact with the postorbital/postfrontal complex (0); reduced contact (1).
 17. Location of squamosal/parietal suture in occiput: near posterior end of supratemporal fenestra (0); half way along fenestra (1).
 18. Nasal/prefrontal contact: straight-line contact dorsolateral on snout (0); short, broad V-shaped contact at dorsal midline (1); long, narrow pinched wedge (2).
 19. Vomer/maxilla contact: absent (0), present (1). Besides the two outgroups, coding of *Cteniogenys* with the primitive state follows Evans & Manabe (1999).
 20. Location of choana: anteriorly close to premaxilla (0); retracted close to midpoint of marginal tooth row (1); choana displaced far back (2).
 21. Palatal foramen: absent with vomer, palatine, and pterygoid meeting at closed three point suture (0); opening at juncture between three palatal bones (1); between pterygoid and palatine, without contribution from the vomer (2).
 22. Internarial: absent (0); present (1).
 23. Pterygoid flange: consisting of pterygoid only, ventrally directed (0); consisting of pterygoid and ectopterygoid, having a horizontal overlap (1).
 24. Basipterygoid/pterygoid joint: process-cotyle contact as part of a metakinetic joint (0); process and cotyle are reduced and two bones are sutured (1); two bones are fused (2).
 25. Parasphenoid/pterygoid contact: no contact (0); clear suture contact (1); tight contact or fusion (2).
 26. Quadratojugal/quadrangle articulation: having a simple overlapping facet for the quadrangle (0); quadratojugal bears a cotyle meeting a rounded quadrangle process (1).
 27. Pterygoid process of quadrangle: broad, vertically orientated with a large pterygoid facet (0); low, slender, and horizontal with a reduced pterygoid facet (1).
 28. Postorbital (dorsal) process of jugal: as prominent as anteroventral process (0); prominent but much shorter than anteroventral process (1); little or no process (2).
 29. Nasopalatal trough: absent (0); present (1).
 30. Palatal teeth: palate covered by shagreen of small teeth (0); paired pterygoid tooth batteries separated by nasopalatal trough (1); narrow rows of pterygoid teeth separated by nasopalatal trough (2).
 31. Midline contact of pterygoids: separate or just touching in the midline anteriorly (0); long midline suture (1).
 32. Size and location of interpterygoid vacuity: large and extends anterior to suborbital fenestra (0); small and near posterior border of fenestra (1).
 33. Enclosure of interpterygoid vacuity: enclosed anteriorly by pterygoids but open posteriorly (0); enclosed anteriorly by pterygoids and posteriorly by parasphenoid (1); enclosed both anteriorly and posteriorly by pterygoids (2). Evans & Manabe (1999) code *Tchoiria* (1/2) without comment. *Tchoiria* is coded (1) as in Gao & Fox (1998) based on photos of PIN3386/1.
 34. Shape of parasphenoid: isocetes triangle with long rostrum (0); broad anteriorly with short rostrum and moderate posterolateral expansion (1); slender anteriorly with long rostrum and strong posterolateral wing-like expansion (2). *Tchoiria* is coded (1) as in Gao & Fox (1998) based on PIN3386/1.
 35. Basal tuberculae of braincase: weakly developed (0); moderately expanded laterally (1); strongly expanded posterolaterally and wing-like (2).
 36. Marginal tooth sockets: circular (0); transverse expansion occurs in anterior part of tooth row (1).
 37. Basal infolding of tooth enamel: absent (0); present (1). The derived state occurs in Champsosauridae and Simoedosauridae.
 38. Location of craniomandibular joint: about the same level as mandibular condyle (0); anterior to condyle (1); posterior to condyle (2).
 39. Shape of suborbital fenestra: narrow, elongate (0); subtriangular with straight medial edge (1); short, kidney-shaped (2).
 40. Neomorph in braincase: absent (0); present as part of external wall of braincase and medial wall of temporal fossa (1).
 41. Pterygoquadrate foramen: absent (0); present and enclosed between neomorph and quadrate (1).
 42. Paroccipital process/quadrangle contact: only tip of process meets quadrate (0); elongate process lies in trough of quadrate and neomorph (1); elongate process lies in trough of quadrate lined with thin sheet of neomorph (2).
 43. Mandibular symphysis: small and terminal (0); slightly extended but confined anteriorly without inclusion of the splenial (1); strongly elongate with longer inclusion of the splenial (2).
 44. Lateral exposure of splenial: splenial confined to medial side of mandible (0); exposed on ventrolateral surface of mandible (1).
 45. Orientation of paroccipital processes: horizontal (0); slightly depressed (1); strongly deflected ventrally (2).

46. Supraoccipital/parietal contact: supraoccipital free from parietal (0); supraoccipital lightly arched, suture surfaces for parietal placed anteriorly (1); supraoccipital keeled, parietal facets extend to posterior margin (2).
47. Posttemporal fenestra: present (0); absent by loss (1). The derived state occurs in both Simoedosauridae and Monjurosuchidae, but the nature of the absent condition in these two groups requires further investigation.
48. Pila antotica: remains unossified (0); ossified as part of the sphenoid (1).
49. Posterior opening of the interior carotid artery: opens ventrolaterally without penetrating parasphenoid (0); opens ventrally, penetrates parasphenoid (1).
50. Atlas-axis complex: little or no development of anterior odontoid prominence of axis (0); free odontoid process unfused to axis (1).
51. Neurocentral sutures: closed in adult (0); remain open in adult (1). Evans (1990) coded *Cteniogenys* with the derived state, but described a large specimen (BMNH R11771) as having the sutures closed. Because of this uncertainty, this character is coded as unknown for *Cteniogenys*. In previous literature, coding of *Shokawa* as having the derived state here is in conflict with the coding of the cervicals of the same taxon as having the sutures closed in adult (Evans & Manabe, 1999: character 62). Because of this ambiguity, *Shokawa* is coded as unknown, and the conflicting character 62 in Evans & Manabe (1999) is excluded from this analysis (see below).
52. Vertebral centra: amphicoelous and notochordal (0); amphiplatyan with notochordal canal closed (1).
53. Presacral vertebral centra: elongate (0); short and spool-like (1).
54. Ventromedial crest of dorsal vertebrae: anterior dorsal vertebrae are strongly keeled like the cervical vertebrae (0); low or no keels (1).
55. Small spinous processes below presacral zygapophyses: absent (0); present (1).
56. Number of sacral vertebrae: two sacrals (0); three sacrals (1); four sacrals (2). Coding of *Lazarussuchus* follows the description by Hecht (1992).
57. Sacral and caudal ribs: fused to vertebrae in adults (0); remain free (1).
58. Caudal zygapophyses: lie at small angle to the horizontal (0); nearly or completely vertical (1).
59. Centra of caudal vertebrae: bear shallow ventral groove for caudal blood vessels (0); groove is flanked by deep ventral flanges (1).
60. Number of ossified carpal elements: nine or more (0); seven or fewer (1). Coding of *Monjurosuchus* based on the neotype GMV 2167, which shows 10 carpal elements (Gao *et al.*, 2000).
61. Flexor tubercle or process on ventral surface of ungual: distinct and well developed (0); low and reduced (1).
62. Bone structure: cancellous (0); having reduced medullary cavity (1); pachyostotic in adult (2).
63. Iliac blade dorsal margin: essentially vertical or at a steep angle to the horizontal in adults (0); dorsal margin essentially horizontal, blade expanded (1).
64. Interclavicle shape: rhomboid (0); T-shaped (1). The primitive diapsid *Petrolacosaurus* has the interclavicle with a diamond-shaped head (Reisz, 1981); thus, the outgroup is coded with the primitive state. Coding of *Shokawa* follows Evans & Manabe (1999).
65. Interclavicle stem: long, slender, and essentially parallel-sided (0); flask-shaped, broad in anterior and central portions, tapering distally (1); stem shorter than lateral processes (2). Coding of the outgroup based on Reisz (1981), contra Evans & Manabe (1999), who coded the derived state (1) for the outgroup.
66. Clavicular facets on interclavicle: meet at angle at midline (0); continuous across midline in smooth curve (1).
67. Cervical vertebral count: 6–9 (0); ≥ 16 (1). Primitive diapsid *Petrolacosaurus* has 6 cervicals (Reisz, 1981), while the most common number for reptiles is 8–9 (Romer, 1956); the derived state is known for *Shokawa* and *Hyphalosaurus* from Asia.
68. Cervical vertebral centra length: longer than high (0); shorter than high (1).
69. Dorsal vertebral centrum shape: subcylindrical (0); cylindrical (1).
70. Fibula shape: (0) proximal and distal ends of similar width (1) proximal end narrow, distal end flared. The coding for *Shokawa* follows Evans & Manabe (1999).
71. Gastralia thickness: thin, lightly built (0); robust, almost as thick as axial ribs, and pachyostotic (1).
72. Caudal neural spines: (0) low (1) tall and narrow.
- *73. Entepicondylar foramen of humerus: present (0); absent (1).
- *74. Constriction of ilium between iliac blade and acetabulum: absent or poorly defined (0); well-defined neck present (1). Primitive diapsid *Araeoscelis* lacks such a neck, while a well-defined neck is known for *Champsosaurus* + *Simoedosaurus* + *Tchoiria*.
- *75. Posterior process of ischium: absent (0); strongly developed (1).

APPENDIX 2

MATRIX OF CHARACTER CODINGS USED IN THE PHYLOGENETIC ANALYSIS OF CHORISTODERES

										10										20
<i>Araeoscelidia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Youngina</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tchoiria</i>	2	2	0	1	1/2	2	1	1	2	?	2	1/2	1	2	0	1	0	2	1	1
<i>Ikechosaurus</i>	2	2	0	1	1	2	1	?	2	1	2	2	1	2	0	1	1	1	?	1
<i>Simoedosaurus</i>	2	2	0	1	1	2	1	1	2	1	2	2	1	2	0	1	1	1	1	1
<i>Champsosaurus</i>	2	2	0	1	2	2	2	1	2	1	2	1	1	2	0	0	0	2	1	2
<i>Shokawa</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pachystropheus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cteniogenys</i>	2	2	?	1	1	1	1	0	0/1	2	0	0	?	1	?	0	0	?	0	1
<i>Lazarussuchus</i>	1	1	?	1	1	1	2	0	1	0	0	2	?	1	1	0	0	2	?	0
<i>Monjurosuchus</i>	0	2	1	1	0	?	1	0	?	0	1	0	2	0	1	0	?	0	?	?
<i>Philydrosaurus</i>	1	?	1	1	1	?	1	?	1	0	1	0	2	0	1	0	?	0	?	?
<i>Hyphalosaurus</i>	?	?	1	1	0	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?
																				30
<i>Araeoscelidia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Youngina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tchoiria</i>	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1
<i>Ikechosaurus</i>	2	0	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1
<i>Simoedosaurus</i>	2	0	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1
<i>Champsosaurus</i>	2	1	1	2	2	1	1	1	1	2	1	1	2	2	2	0	1	1	2	1
<i>Shokawa</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
<i>Pachystropheus</i>	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cteniogenys</i>	1	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	?	0	1
<i>Lazarussuchus</i>	?	0	?	?	?	?	?	?	?	?	0	?	?	?	0	0	0	0	0	?
<i>Monjurosuchus</i>	?	0	?	?	?	?	?	?	1	?	?	?	?	?	?	0	0	0	?	?
<i>Philydrosaurus</i>	?	0	?	?	?	?	?	?	1	?	?	?	?	?	?	0	0	0	1	?
<i>Hyphalosaurus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	?
																				50
<i>Araeoscelidia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Youngina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tchoiria</i>	1	?	2	0	1	1	1	?	1	1	1	1	1	1	1	?	1	1	?	?
<i>Ikechosaurus</i>	1	?	2	0	1	2	1	1	1	?	1	1	1	1	1	1	1	?	0	?
<i>Simoedosaurus</i>	1	1	1	0	1	2	1	1	1	1	1	1	1	1	1	1	1	1	0	1
<i>Champsosaurus</i>	1	2	2	1	2	1	0	0	0	1	1	1	1	1	0	1	1	1	0	1
<i>Shokawa</i>	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pachystropheus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cteniogenys</i>	?	?	1	0	0	?	?	0	0	1	1	1	0	0	0	?	1	1	1	?
<i>Lazarussuchus</i>	?	?	1	0	?	?	?	?	?	?	0	0	0	0	0	2	0	1	0	0
<i>Monjurosuchus</i>	?	?	0	0	?	?	1	?	?	?	0	1	?	?	0	1	1	1	?	0
<i>Philydrosaurus</i>	?	?	0	0	?	?	1	?	?	?	0	1	?	1	0	1	1	1	1	?
<i>Hyphalosaurus</i>	?	?	0	?	?	?	?	?	?	?	0	1	?	?	?	1	1	?	?	0
																				70
<i>Araeoscelidia</i>	0	0	0	0	0	0	?	0	0	0	?	?	0	0	0					
<i>Youngina</i>	0	0	0	1	0	0	0	0	0	0	0	0	?	0	0					
<i>Tchoiria</i>	?	1/2	1	1	1	1	0	0	1	1	?	0	0/1	1	0					
<i>Ikechosaurus</i>	1	?	1	1	0	?	0	0	0/1	1	1	0	?	0	0					
<i>Simoedosaurus</i>	?	2	1	1	1	1	0	1	1	1	1	0	?	1	0					
<i>Champsosaurus</i>	1	2	1	1	1	1	0	0/1	1	1	1	0	1	1	0					
<i>Shokawa</i>	?	1/2	0	0	0	0	1	0	1	0	1	1	?	?	?					
<i>Pachystropheus</i>	?	1	0	0	2	0	?	0	0	?	?	1	?	0	?					
<i>Cteniogenys</i>	1	1	0	?	?	?	?	0	0	?	0	0	?	?	?					
<i>Lazarussuchus</i>	0	0	0	?	?	?	0	0	0	1	0	0	?	?	0					
<i>Monjurosuchus</i>	?	?	0	?	?	?	0	?	?	1	0	0	0	0	1					
<i>Philydrosaurus</i>	?	?	0	1	?	?	0	?	?	1	0	0	0	0	1					
<i>Hyphalosaurus</i>	?	?	0	?	?	?	1	?	?	1	1	1	?	0	0					