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Source: American Museum Novitates, 2005(3468) : 1-22

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2005)468<0001:ANCFTC>2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3468, 22 pp., 11 figures March 24, 2005

A New Choristodere from the Cretaceous of Mongolia

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ABSTRACT

The remains of a choristodere recently discovered at Two Volcanoes, a new locality in the Gobi Desert of Mongolia, are described in this paper. Consisting of a fairly complete skull and partial postcranial skeleton, this specimen represents a new species of the genus *Tchoiria*. The new species differs from *Tchoiria namsarai* in having a much smaller number of teeth. Several elements preserved in this specimen are unknown in *T. namsarai* and thus provide new information about the genus. Phylogenetic analysis with the addition of data from the new specimen confirms the basal position of *Tchoiria* in Simoedosauridae.

INTRODUCTION

The Choristodera are a clade of aquatic and semi-terrestrial fossil diapsids. Twelve previously described genera have been assigned to the Choristodera, but one, *Lazarussuchus*, lacks the derived character states that diagnose the group (Gao and Fox, 1998) and must be placed outside of the group, probably as a sister taxon. Of the remaining genera *Champsosaurus*, *Simoedosaurus*, *Ikechosaurus*, and *Tchoiria* form a well-supported clade of large Cretaceous and early Tertiary forms, named Neochoristodera by Evans and Hecht (1993).

?*Khurendukhosaurus* and ?*Irenosaurus* are poorly known genera that appear to belong to the Neochoristodera or a more inclusive clade within the Choristodera. ?*Khurendukhosaurus* is known from postcranial material representing a small and apparently plesiomorphic choristodere. ?*Irenosaurus* is known only from fragmentary postcranial material including a humerus and vertebrae

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ISSN 0003-0082

(PIN 3368/2), and may be synonymous with another genus (Efimov and Storrs, 2000). Based on the highly incomplete nature of the known material it is best not to speculate on the relationships of these taxa until more is known of their morphology.

The remaining taxa include several small forms, all seemingly plesiomorphic to the Neochoristodera. *Cteniogenys* is quite small (about 150 mm in length, excluding the tail) and primitive in a number of characteristics relative to the Neochoristodera (Evans, 1990). Another primitive genus, *Monjurosuchus*, reaches moderate size (~300 mm) and is unique in the secondary closure of the infratemporal fenestrae (Gao et al., 2000). The recently discovered *Shokawa* represents a new morphotype within the Choristodera characterized by an extremely long neck relative to body size (Evans and Manabe, 1999). *Hyphalosaurus* was originally classified as a diapsid of uncertain affinity (Gao et al., 1999), but is now considered to be a choristodere closely related to *Shokawa* (Gao et al., in prep.).

Pachystropheus has been reinterpreted as a primitive choristodere (Storrs and Gower, 1993). Although cladistic analysis indicates that *Pachystropheus* may share a sister group relationship with the two long-necked genera, near complete lack of cranial material makes this relationship tentative at best (Evans and Manabe, 1999), and new material is needed to resolve the basal taxonomy of the Choristodera.

The first specimen of *Tchoiria* was discovered in 1971 at Hüren Dukh, Mongolia, by the Soviet–Mongolian paleontological expedition (Efimov, 1975). A partial skull and partial postcranial skeleton (PIN 3386/1) were recovered from the Aptian Hühteeg horizon. The remains were assigned to the type species, *Tchoiria namsarai*. The specimen described in this paper shares features diagnostic of *Tchoiria*, but differs from *T. namsarai* in certain features and is thus considered a separate species of the genus.

Two additional species of *Tchoiria* have been described, but both have subsequently been reassigned to other genera. Efimov (1979) named and described the species *Tchoiria magnus* on the basis of a partial mandible and portions of postcranial material of a very large choristodere (PIN 559/501) from the Lower Cretaceous of Khamaryn Khural, Mongolia. Efimov (1983) later redescribed the material, and reassigned the species to the genus *Ikechosaurus* on the basis of the rectangular tooth bases. The incomplete nature of the known material for this specimen makes it difficult to diagnose, and it may be better left *incertae sedis* until more material is discovered. Efimov (1983) named the species *Tchoiria egloni* on the basis of some vertebrae and limb bones (PIN 3386/2) from the same locality as the holotype of *T. namsarai*. Efimov (1988) later reassigned this material, erecting the questionable genus *Irenosaurus*. The holotype material of *Irenosaurus elongi* is differentiated from *Tchoiria* primarily by the lack of a prominent entepicondylar groove and more elongate dorsal vertebrae (Efimov, 1988). The differences in the humerus may be related to ontogeny (Efimov and Storrs, 2000). The neural spines of the dorsal vertebrae have a primitive shape, with a concavity above the prezygapophyses in lateral view, and are distinct from dorsals preserved in *Tchoiria*. New material is needed to confirm the validity of the genus ?*Irenosaurus*.

INSTITUTIONAL ABBREVIATIONS: **AMNH,** American Museum of Natural History; **GIN,** Geological Institute of the Mongolian Academy of Sciences; **PIN,** Paleontological Institute, Russian Academy of Sciences.

MATERIALS AND METHODS

The specimen was collected during the 1998 field expedition of the Mongolian Academy of Sciences–American Museum of Natural History Paleontological Project. The specimen was collected in a large indurated boulder at Two Volcanoes, a new locality in southern Mongolia (fig. 1). Vertebrate fossils at this locality are uncommon, but some dinosaur bones, a few turtles, and abundant invertebrates have been found. Spatulate sauropod teeth (fig. 2) collected at this site resemble teeth from the Early Cretaceous Öösh Formation described by Osborn (1924) as *Asiatosaurus mongoliensis*.

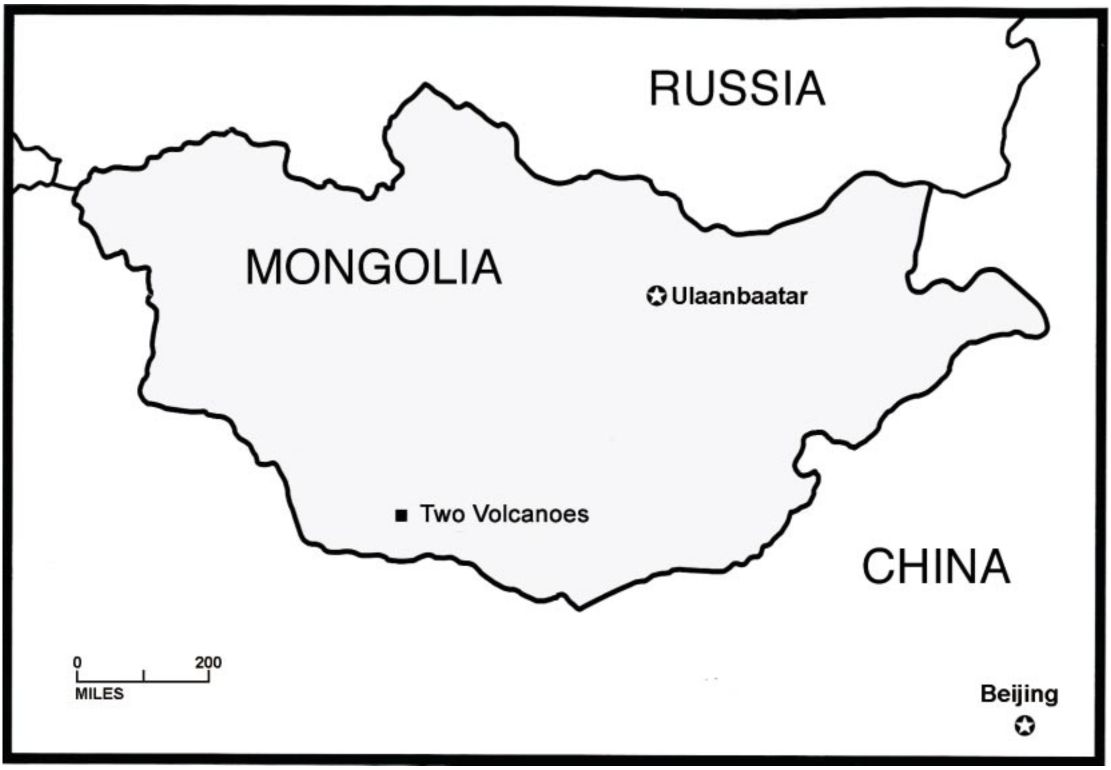

Fig. 1. Map of Mongolia showing the collection locality.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA OSBORN, 1903

CHORISTODERA COPE, 1876

NEOCHORISTODERA EVANS AND HECHT, 1993

SIMOEDOSAURIDAE LEMOINE, 1884

TCHOIRIA EFIMOV, 1975

Tchoiria klauseni, new species

HOLOTYPE: The holotype (IGM 1/8) consists of an incomplete skull and partial disarticulated postcranial skeleton. The following elements are preserved: a skull nearly complete on the right side and fragmentary on the left, missing the tip of the snout and distorted in the braincase region; partial right dentary and splenial in articulation; five cervical, six dorsal, three sacral, and four caudal vertebrae or vertebral elements; several ribs and gastralia; right coracoid, fragment of scapular blade; right radius, right ulna; right ilium, partial right ischium, partial right pubis; right femur.

ETYMOLOGY: Named in honor of James Klausen, the preparator of the holotype, in recognition of years of dedicated volunteer service to the American Museum of Natural History.

TYPE LOCALITY AND HORIZON: The type locality is Two Volcanoes (43°49.503′N, 99°19.546′E; fig. 3). The fossil beds at Two Volcanoes are composed of light-colored fine sands interbedded with coarser sands. The age of this locality has not been firmly established; however, the freshwater invertebrate fauna and the presence of spatulate sauropod teeth suggest an Early Cretaceous Aptian age roughly equivalent to beds of the ‘‘Hütheg Svita’’ (Shuvalov, 2000). A more well-constrained age for Two Volcanoes awaits further work.

DIAGNOSIS: *Tchoiria klauseni* can be differentiated from the type species *T. namsarai* by the smaller number of teeth in the maxilla and the symphyseal portion of the dentary. There are slightly more than 34 teeth in the

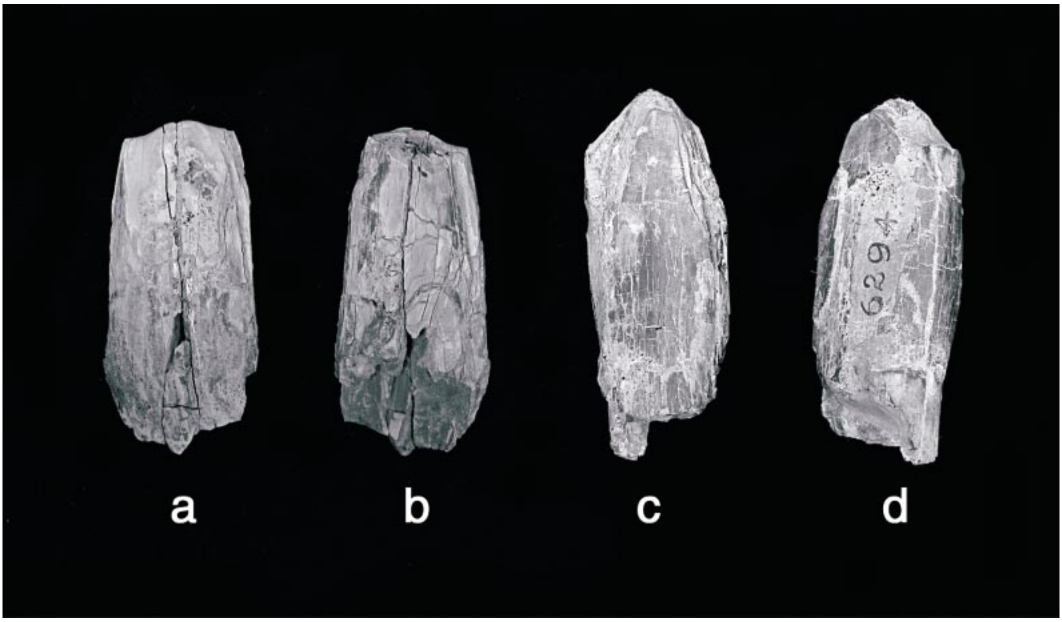

Fig. 2. Sauropod tooth from Two Volcanoes in (**a**) labial and (**b**) lingual view and AMNH 6294, a tooth assigned to *Asiatosaurus mongoliensis* in (**c**) labial and (**d**) lingual view.

maxilla of *T. klauseni* while there are more than 60 in the maxilla of *T. namsarai*. There are 12 teeth in the symphyseal portion of the dentary in *T. klauseni* and 17 teeth in the symphyseal portion of the dentary in *T. namsarai*.

DESCRIPTION

SKULL

The skull resembles other neochoristoderes in general appearance in that the postorbital region is flared, the snout is elongated and narrow, and the orbits are small and dorsally directed (fig. 4). The skull is quite flat dorsoventrally. Although the skull is flattened in all neochoristoderes, it is evident from the orientation of the temporal bars that the degree of flatness in this specimen has been somewhat exaggerated by postmortem crushing. In dorsal view the skull is nearly complete on the right side, except for the tip of the snout, and fragmentary on the left side. The palatal region is fairly complete but the posterior region has suffered a good deal of distortion. Although many of the posterior cranial bones are present, most have been displaced from their original position.

The holotype skull of *T. klauseni* is larger and more robust than that of *T. namsarai* (PIN 3386/1), though in the absence of data on the age or sex of these specimens it remains uncertain whether this difference is appropriate in diagnosing the species. The snout is relatively wide immediately in front of the orbits, but narrows anteriorly. The anterior tip of the snout was lost to erosion, so the exact proportions of the skull and nature of the external narial opening are uncertain. Examination of the nasal cavity where the snout is broken reveals that it is a laterally expanded oval in cross section at this point. The nasals are fused into a single element. The nasals intervene between the maxillae, but it is uncertain how far posteriorly they extend, and whether they thin to a narrow splint or a broad triangular point.

The premaxillae are not preserved. The right maxilla is missing only the anterior tip and the left is less complete. A row of foramina lines the lateral border of the maxilla slightly above the tooth level. The posterior foramina are contiguous with posteriorly running grooves. There are 34 alveoli observable in the right maxilla, though it is likely

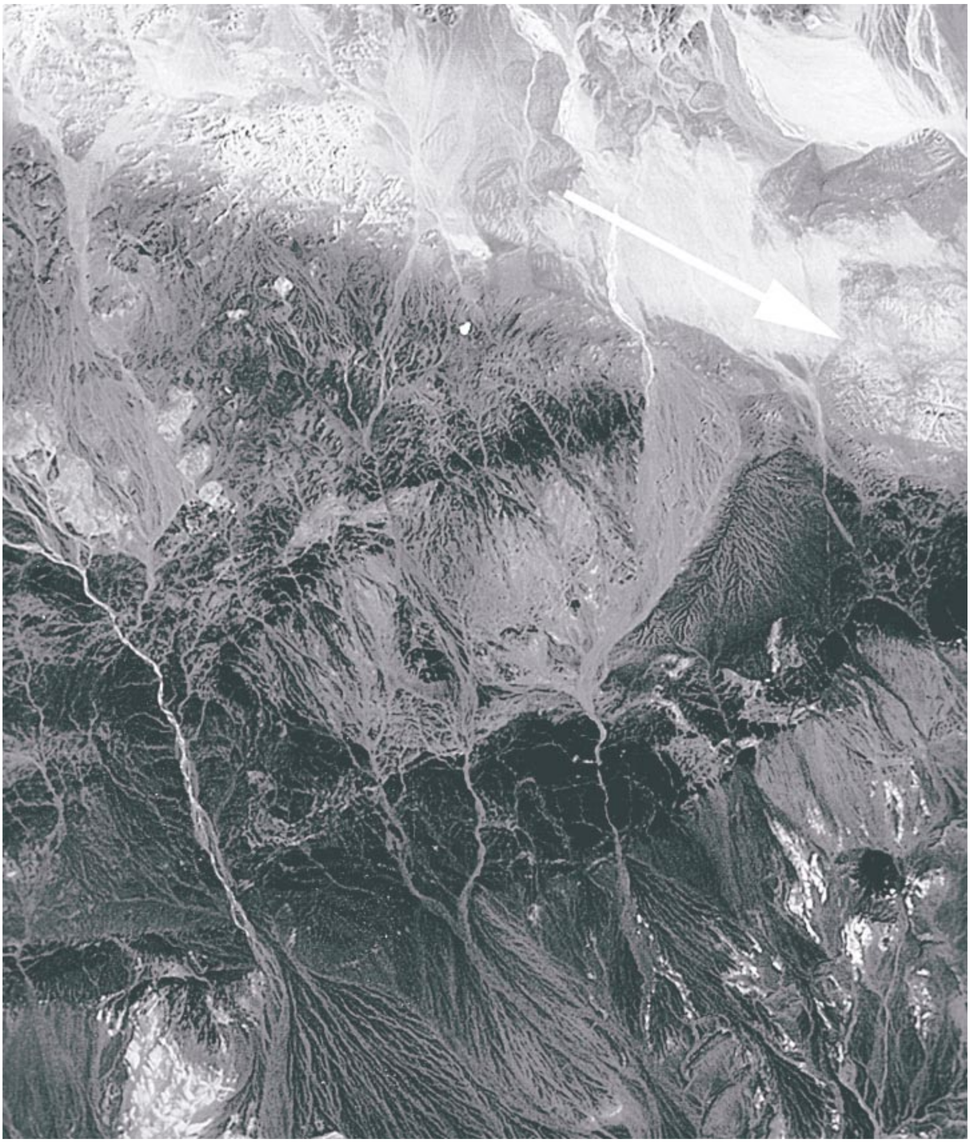

Fig. 3. Satellite photo of Two Volcanoes Locality, white arrow pointing to location where the specimen was collected.

several are missing from the anterior end. In the holotype of *T. namsarai* (PIN 3386/1), the number is much greater, with over 60 in each maxilla. The alveoli are subcircular to ovate and fairly shallow. The marginal alveoli of *Champsosaurus* are circular, while those of simoedosaurids are transversely expanded in the anterior part of the tooth row. The expansion is noticeably weaker in *Tchoiria* than in *Simoedosaurus* and *Ikechosaurus* (Gao and Fox, 1998). The marginal teeth are conical and longitudinal striations are visible on several teeth. The anterior teeth are largest, and the teeth become progressively smaller posteriorly. There is a more pronounced size decrease in the posterior maxillary teeth in *T. namsarai*, allowing for a greater number of teeth to be accommodated in nearly the same amount of space. Complete teeth exhibit a slight medial curve.

Fig. 4. The holotype skull of *Tchoiria klauseni* (IGM 1/8) in dorsal and ventral views. Light gray represents preserved areas of the palatal dental batteries, dark gray represents matrix. Abbreviations are listed in appendix 4.

Several broken teeth show that the enamel is infolded at the base. Grooves cut into the medial bases of some teeth were apparently caused by erupting teeth, though none are preserved in situ. These grooves may exaggerate the degree of expansion in some alveoli.

The orbits are suboval, longer than wide, and much wider at the posterior margins than the anterior margins. They are surrounded by a raised rim, which is very rugose except for the lacrimal portion of the orbital border, which is smoother and less elevated.

The prefrontals and frontals form the in-

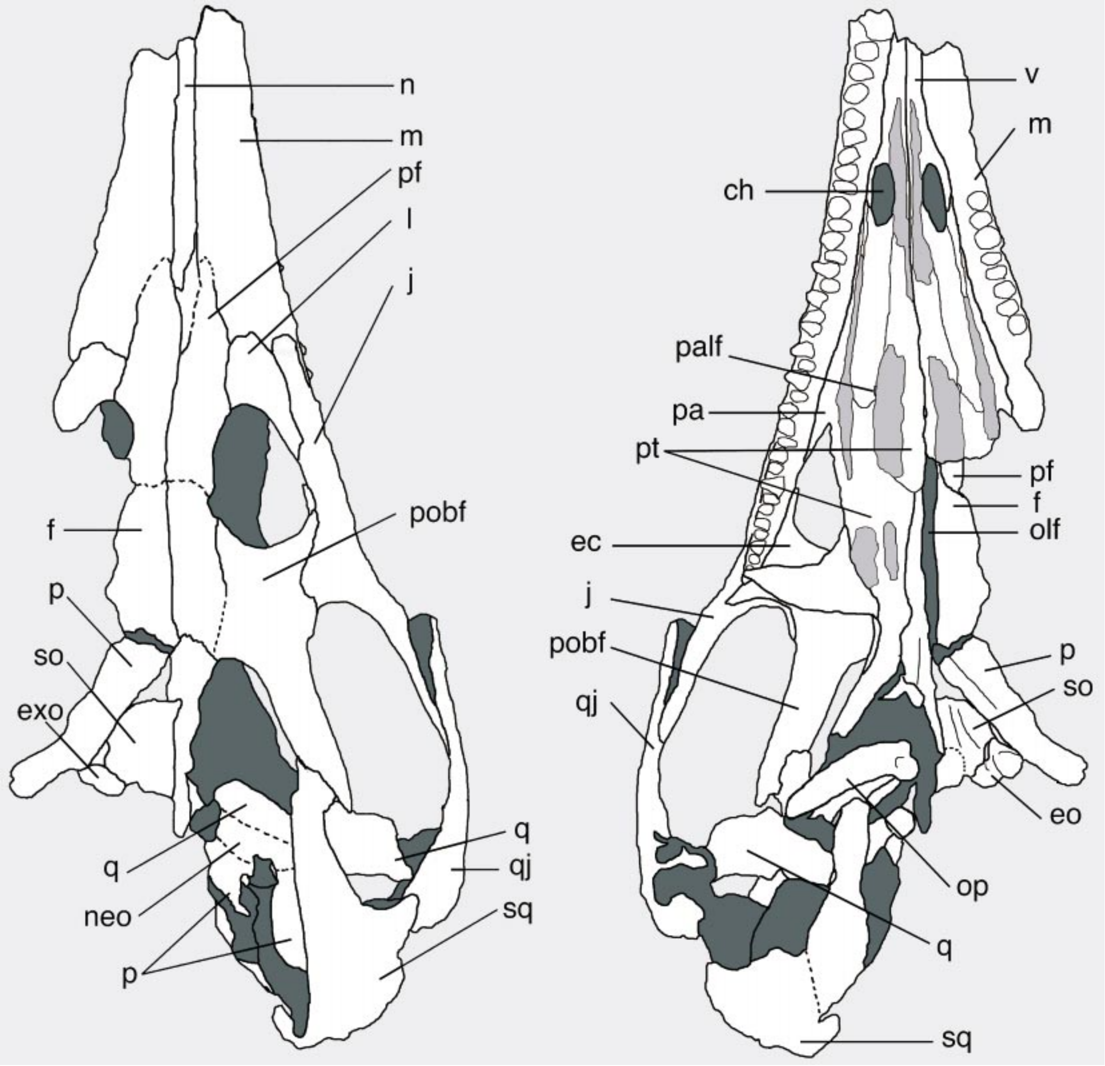

Fig. 4. Continued.

terorbital bar, and the bar is about the width of the orbit halfway between the anterior and posterior orbital margins. It is arched, elevating the medial orbital border. Ventrally, the olfactory canal runs along the interorbital bar at midline. The frontals project between the prefrontals to form the dorsal border of the olfactory canal for most of its path along the interorbital bar. The olfactory canal continues anteriorly between the ventral flanges of the prefrontals into the snout region, where the pterygoids form a ventral border enclosing it. Computed tomography scanning of *Ikechosaurus* has revealed that the olfactory canal extends from this point into a large Cavi Nasi Proprium, divided into an upper olfactory region and lower respiratory region (Lu et al., 1999).

The lacrimal forms the anterior border and part of the lateral border of the orbit. It is moderately sized and subtriangular in dorsal view, with a rounded anterior point. The lacrimal extends to overlap the jugal along the anterior half of the lateral border of the orbit. The lacrimal foramen opens between the lacrimal, palatine, and prefrontal on the anterior

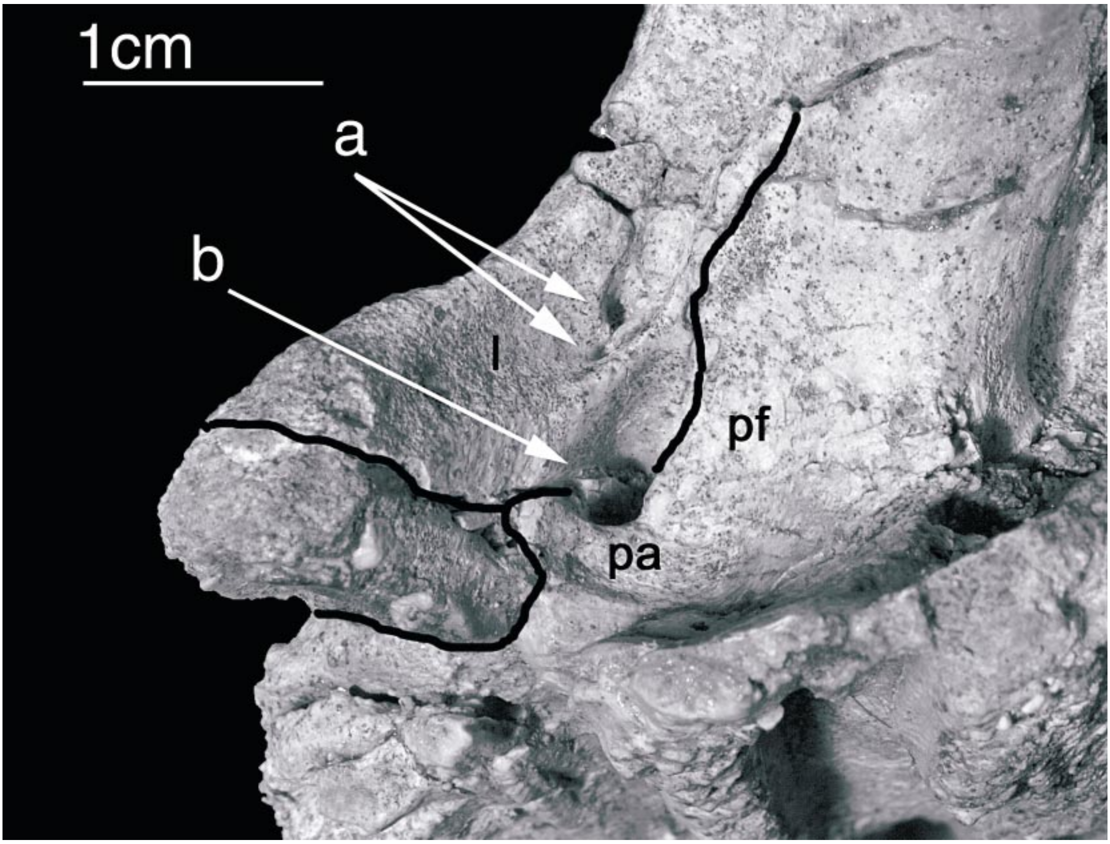

Fig. 5. Posterior view of the anterior wall of left orbit. **a**, Two small foramina perforating lacrimal. **b**, lacrimal duct opening between lacrimal, palatine, and prefrontal. Abbreviations are listed in appendix 4.

wall of the orbit (fig. 5). A crest superior to the lacrimal foramen separates it from two smaller foramina that perforate the posterior surface of the lacrimal.

The jugal forms the majority of the lateral border of the orbit. The anterior process extends to sit in a notch on the dorsal surface of the maxilla and is bordered medially by the lacrimal. The anterior process extends as far as the anterior border of the lacrimal, as in *Champsosaurus* and *Ikechosaurus*. The posterior process of the jugal joins the quadratojugal to form the inferior temporal bar. The dorsal process is fairly prominent, unlike that of *Simoedosaurus* and *Ikechosaurus*, but similar to the condition in *Champsosaurus* and *Cteniogenys*. It contacts the postorbitofrontal at a suture running from near the medial border of the inferior temporal fenestra to near the lateral border of the orbit, and so makes up the anterior border of the inferior temporal fenestra.

The postorbitofrontal, an element derived from the fusion of the postorbital and postfrontal (Russell-Sigogneau and Russell, 1978), forms the posterior border of the orbit. It meets the dorsal process of the jugal laterally and the frontal medially. Ventrally, at the anterolateral corner, the postorbitofrontal overlaps the jugal, as in *Simoedosaurus* (Erickson, 1987). The postorbitofrontal has a small contact surface with the parietal posteromedially. The posterior process of the postorbitofrontal articulates with the squamosal to form the anterior portion of the superior temporal bar.

The quadratojugal forms the posterior portion of the inferior temporal bar. The slender anterior process articulates with the posterior process of the jugal in an oblique suture with the quadratojugal on the lateral side. The quadratojugal widens posteriorly where it meets the squamosal. The nature of this suture is obscured by breakage in the area. Ventrally, the quadratojugal is encrusted in matrix, but it is possible to observe the condyle for articulation with the quadrate. As a matter of preservation the quadrate has been detached from the quadratojugal and displaced from its original orientation. The rounded quadrate process is visible, as is the condyle for the articular.

The squamosal forms the posterolateral corner of the skull. To prevent thin and fragile bone from crumbling, a block of matrix was retained in this region as the specimen was being prepared. The slender anterior process of the squamosal forms the posterior portion of the superior temporal bar, articulating with the posterior process of the postorbitofrontal. A raised crest begins at the level of the posterior margin of the inferior temporal fenestra and runs along the medial margin of the squamosal on the dorsal surface. The ventral surface of the squamosal is smooth. The contacts between the squamosal and the parietal, quadrate, neomorph, and quadratojugal are obscured by breakage and the supportive matrix. A matrix-filled gap may represent the suture between the squamosal and parietal, in which case this suture is located near the posterior margin of the superior temporal fenestra. However, the possibility that the gap is a crack and the suture lies farther forward cannot be ruled out.

The parietals form the posterior portion of the skull roof along with the supraoccipital. The parietals meet the frontals at a point slightly anterior to the superior temporal fenestra. The posterior processes of the parietals extend less than half of the length of the superior temporal fenestra before curving laterally. The contacts with the squamosal, prootic, and neomorph are indeterminate due to breakage.

The palate is covered in very small teeth. These palatal teeth are arranged in several paired complexes (fig. 4). A single row of teeth runs along a ventral ridge on each palatine beginning slightly posterior to the choanae. Near the anterior border of the suborbital fenestra, the ridge widens and the tooth row widens to three or four teeth across. Due to wear, it is uncertain whether the row continues onto the pterygoid uninterrupted or a toothless gap exists at the posterior end of the palatine. Such a gap is present in *T. namsarai* (Efimov, 1975: fig. 1). A battery several teeth wide is present on the pterygoid in alignment with the palatine tooth row, and ends at the same level as the marginal tooth row. A row of palatal teeth is present on each vomer, beginning posterior to an area of smooth bone at the anterior part of the vomer. These rows widen to several teeth wide in front of the choanae, thin to a single tooth row between the choanae, and then widen to a width of several tooth positions again posterior to the choanae. Wear makes it uncertain if these rows are continuous with batteries on the pterygoids, but it seems likely there was a toothless gap between them. The pterygoid batteries are quite extensive, reaching a width of seven teeth. The choanal grooves separate the palatine and pterygoid rows, and the vomeral rows are separated from each other by a trough between the vomers. The degree to which the medial complexes are separated on the pterygoids is obscured by wear and breakage.

The pterygoid flange overlaps the inferior process of the ectopterygoid, which borders the posterior and posteromedial edges of the maxilla. Though there are no teeth visible on the transverse process of the pterygoid, it is worn, and teeth may have been eroded away. The quadrate process of the right pterygoid is preserved. Strong ridges run along the exposed ventral side, presumably for attachment of the pterygoideus muscle. There is no evidence of an internarial, but nothing is preserved anterior to the vomers, so its presence cannot be decidedly ruled out.

The choanae are subovular and posteriorly displaced from the external nares. They are bordered anteriorly and medially by the vomers and laterally by the palatines. The superior borders of the choanae are ridged and grooved. The anterior boarder of the right choana is at the level between the 27th and 28th marginal tooth positions, counting from the posterior-most tooth. The pterygoids are elongate and contact the vomers near the posterior border of the choanae, though the suture is not identifiable due to wear. Posteriorly, each choana is contiguous with a groove that runs to the posterior border of the pterygoid tooth battery. The palatal foramen opens between the pterygoid and palatine as in other neochoristoderes.

The suborbital fenestra is relatively long and appears subtriangular, with a straight lateral edge and a partly round medial edge. The medial edge appears to constrict the palate between the suborbital fossae as in *Champsosaurus*. However, along the medial edge thin portions of pterygoid have broken off, causing the foramen to appear larger and likely more rounded. The maxilla participates in the border of the suborbital fenestra as in *Ikechosaurus* (Brinkman and Dong, 1993) and *Champsosaurus*. The maxilla is excluded from the suborbital border by the palatine and ectopterygoid in *Simoedosaurus* (Russell-Sigogneau and Russell, 1978).

The shape of the interpterygoid vacuity is unclear due to distortion of the region, but the medial surface of the right pterygoid indicates it was elongate. The vacuity appears to have extended anteriorly to a point somewhere within the middle third of the suborbital fenestra. The pterygoids form the anterior border, but the posterior border is not observable. In *T. namsarai* the interpterygoid vacuity is very large and is enclosed posteriorly by the broadly bifurcated anterior process of the parasphenoid.

Although the occipital condyle has been displaced from its original position, the craniomandibular joint was located posterior to the occipital condyle as indicated by the position of other elements. The right condyle for the articulation with the mandible has been displaced forward and rotated, but its true position is discernable and confirmed by the quadratojugal. The occipital condyle has been disarticulated from the rest of the skull along with the parasphenoid and basisphenoid. However the position of the exoccipitals, supraoccipital, and parietals, in articulation but slightly displaced, indicates the location of the foramen magnum and thus the occipital condyle. In *T. namsarai* the craniomandibular joint is located on the level of or slightly posterior to the occipital condyle.

The braincase region is distorted and broken, but some observations can be made. The supraoccipital is a triangular bone that forms the dorsal border of the foramen magnum, contacting the exoccipitals ventrally at its posterolateral angles. A high midline crest at the anterior apex grades into the flat dorsal surface posteriorly. There is a notch at midline on the posterior border. The supraoccipital remains attached to the right parietal but has separated from the left parietal leaving the sutural contact surface exposed. The parietals partially overlap the supraoccipital at its anterior end. The posterior portion of the supraoccipital is exposed dorsally, as in *Champsosaurus*, rather than being completely covered by the parietals, as in *Simoedosaurus* and *Ikechosaurus* (Brinkman and Dong, 1993). Dorsal exposure of the supraoccipital also occurs in *T. namsarai* (Efimov, 1975). The left exoccipital is preserved attached to the supraoccipital and the right is missing. The exoccipital is an hourglass-shaped bone forming the lateral wall of the foramen magnum.

The bones that enclose the posterior cavity of the braincase (sensu Fox, 1968) and form the medial wall of the temporal fenestrae are partially preserved and visible in dorsal view, though they have been rotated from their original position. The overlapping contact between the neomorph and quadrate can be traced, but these bones are broken near the anterior portion of the contact so the location of the pterygoquadrate foramen is uncertain. The prootic and the contact between the neomorph and parietal are not identifiable.

The second region of the braincase, the anterior trough (sensu Fox, 1968), and the underlying basioccipital, basisphenoid, and parasphenoid are heavily obscured by matrix. To better examine this region, a fragment of skull comprising the posterior end of the left pterygoid attached to the above-mentioned complex was left free during preparation. The parasphenoid has been worn away in most areas, but a concretion cast preserves a portion of its outline. The degree of posterolateral expansion is unclear. The rostrum of the parasphenoid is also obscured as it is overlapped by the left pterygoid. However, the lateral edge is visible on the right side. Though the anterior end is incomplete, it is clear that the rostrum is quite long and that it widens anteriorly. The basisphenoid especially is encrusted in hard matrix and is thus

Fig. 6. Rostral portion of the mandible in dorsal and medial views.

visible only as a rough outline on the dorsal side. The occipital condyle is fairly well exposed and takes the shape of an oval knob, wider than high. There is a shallow longitudinal groove on the posterior face of the condyle.

The basal tuberculae of the basioccipital are missing. The right opisthotic is preserved with attached cranial bone, presumably the neomorph and possibly some of the parietal. This fragment is attached to a block of supportive matrix. Due to displacement the orientation of the paroccipital process is uncertain.

MANDIBLE

The right half of the mandible is preserved from the anterior tip to tooth position 34, including the entire length of the symphysis (fig. 6). The splenial and dentary are identifiable. The Meckelian canal is exposed medially at the symphysis.

The splenial lines the dentary along most of the preserved medial side of the mandible, decreasing in height near the symphysis where the dentary overrides it. The splenial plays a minor role in the formation of the symphysis, and is not visible on the lateral side of the mandible anywhere along the preserved area. The symphysis is relatively short compared to *Champsosaurus* but more extensive than in *Simoedosaurus*. Several foramina are present on the lateral and ventral surfaces of the symphysis. Foramina posterior to the symphysis are contiguous with posteriorly running grooves, and are aligned in two horizontal rows on the lateral side of the mandible.

The right half of the symphysis contains 12 alveoli. The completely preserved mandible of *T. namsarai* contains 17 alveoli in each half of the symphysis. The preserved anterior symphysial teeth are slightly larger than the posterior ones. The tooth row is bordered medially by a raised edge of bone, formed by the dentary at and directly behind the symphysis, and by the splenial and dentary posteriorly. The teeth are moderately posteromedially recurved and come to sharp conical points.

AXIAL SKELETON

Preservation varies along the vertebral column, which is disarticulated except for two sacral vertebrae. All of the vertebrae have an amphiplatyan centrum, with the notochordal canal closed. The neural arch remains unfused to the centrum except in the mid and posterior caudal vertebrae. No comparison can be made with *T. namsarai*, the holotype of which includes only seven cervical and dorsal centra.

Three elements of the atlas–axis complex are preserved: the left atlantal neurocentrum and the axial centrum and neural arch. There are two articular faces on the anterior surface of the axial centrum, indicating the existence of a free odontoid process and axial intercentrum. There is a slight roughened keel on

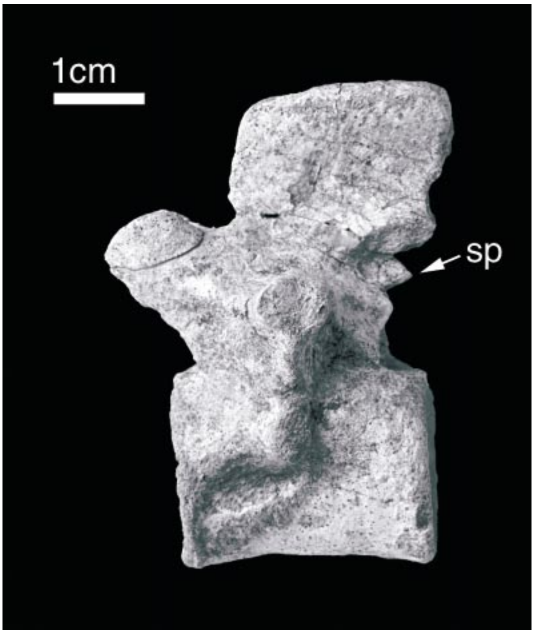

Fig. 7. Dorsal vertebra, anterior = left. Abbreviations are listed in appendix 4.

the ventral surface of the axial centrum, and the neural spine is low.

The total number of presacral vertebrae is uncertain. In addition to the elements of the atlas–axis complex, at least three cervicals of varying completeness are preserved. The preserved cervical vertebral centra are longer than high and higher than wide. They have strong ventromedial keels. The cervicals bear parapophyses that are separate from the diapophyses for support of bicapitate ribs.

Six dorsals of varying completeness are preserved. The dorsal vertebrae centra have smooth round ventral surfaces. The centra are longer relative to width than in *Simoedosaurus* and *Ikechosaurus*, with length/width ratios falling between 1.2:1 and 1.4:1. However, the dorsals are similar to those of *Simoedosaurus* and *Ikechosaurus* in possessing small spinous processes below the postzygapophyses (fig. 7). The spinous processes do not bear the accessory facets previously noted as present in *Simoedosaurus* but absent in *Ikechosaurus* (Evans and Manabe, 1999). The parapophyses and diapophyses of the dorsals are contiguous and bear single headed ribs.

Three sacral vertebrae are preserved, all of which are complete except for the first sacral, which is missing the neural arch. The articular surfaces for the rib on the first sacral centrum are bordered on all sides by cortical bone. All three right sacral ribs are complete. The sacral ribs remain unfused to the sacral vertebrae, and are marked by a slightly raised ridge running anterodorsally about one-third of the way between the articular facets for the sacral vertebral centrum and the ilium, similar to the condition in *Simoedosaurus* (Sigogneau-Russell, 1981) The second sacral rib has the greatest distal expansion and the largest articular surface for the ilium; the first sacral rib has the smallest. There are anterior and posterior articular surfaces at the distal expansion of the second sacral rib for contact with the first and third sacral. There is no articular surface on the posterior edge of the third sacral rib indicating contact with the first caudal rib.

Two mid caudals and two posterior caudals are preserved. The caudal centra are longer relative to width and height than the presacral vertebrae. Unlike those of the presacral vertebrae, the neural arches of the mid and posterior caudals are fused to the centra. The ribs of the mid caudals are fused to the centra, while posterior caudals lack ribs. The only intact mid caudal rib is short, anteroposteriorly wide, and dorsoventrally flattened. The mid and posterior caudal centra are widest at the articular facets for the adjacent centra, and narrow midway between. Each of the caudal centra has a deep groove bordered by a pair of ventral flanges, a feature seen in *Cteniogenys* and *Shokawa* as well as the poorly known *Pachystropheus*, but previously unrecorded in neochoristoderes. Posteroventral facets on the centra of the mid and posterior caudals indicate these vertebrae bore unfused hemal arches, several of which are preserved disarticulated from the centra.

Several ribs are preserved. The ribs are much thicker than the preserved gastralia. Two broken ribs appear to be pachyostotic. Only two gastralia elements are preserved, presumably lateral elements. They are similar to those of other neochoristoderes.

APPENDICULAR SKELETON

A complete right coracoid and a fragment of scapular blade are preserved. The coracoid

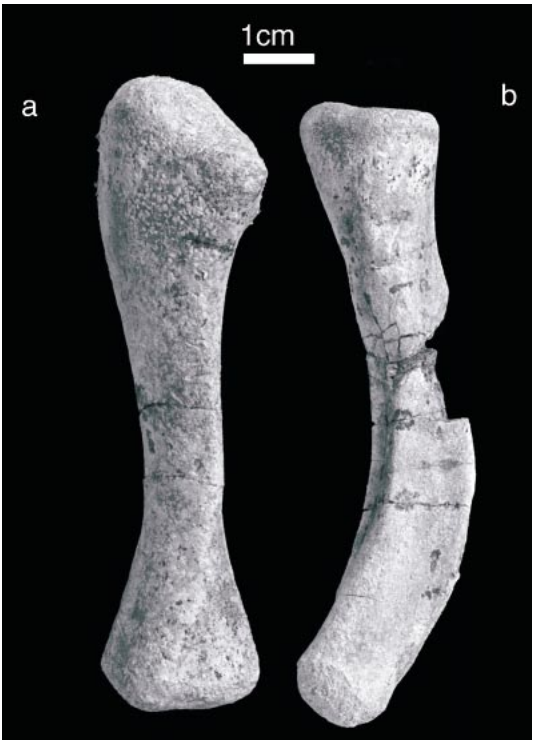

Fig. 8. Right ulna (**a**) and radius (**b**) in postaxial view.

is a suboval plate perforated by a coracoid foramen anterior to the glenoid fossa. A large tubercle sits posterior and dorsal to the glenoid fossa. Based on the blade fragment, the scapular blade appears to have been relatively long and narrow.

The right ulna is complete and the right radius is slightly damaged (fig. 8). All other pectoral limb elements are missing. The radius has a concave medial edge and narrows into sharp ridges at its medial, lateral, and ventral edges, creating a subtriangular cross section at midshaft. The ulna is expanded at its distal and proximal ends. There is a short, blunt olecranon process at the proximal expansion.

The right ilium is complete and the right ischium and pubis are fragmentary (fig. 9). The iliac blade has a slightly projecting anterior process, more prominent than in most *Champsosaurus* and *Simoedosaurus*, but less developed than in *Ikechosaurus* (Brinkman and Dong, 1993). The blade is quite low and the posterior process is very long. There is little constriction of the neck between the blade and acetabular region. The shape of the ilium is known to vary ontogenetically (Erickson, 1972); thus the proportional differences with other taxa may be phylogenetically insignificant. If changes with age match those estimated for *Champsosaurus* (Erickson, 1972: fig. 54), IGM 1/8 could represent a young adult individual.

The ischium is very thick at the acetabular region, where the rough articular surfaces for the pubis and ilium and a smoother acetabular face are complete. Although most of the anterior and medial borders of the blade are missing, the posterior border is complete. The edge is smooth and lacks the prominent tubercle present in *Champsosaurus* and *Simoedosaurus*. This tubercle marks the attachment site for a large tail ligament and tendon (Erickson, 1972). Its absence in *T. klauseni* may be indicative of a more terrestrial ecology requiring less use of the tail for locomotion. The pubis is complete at the acetabular region and the blade is fragmentary but preserves the pubic foreman.

The right femur is completely preserved (fig. 10). The internal trochanter is pronounced and is separated from the articular surface at the proximal end. A ridge extending from the internal trochanter runs distally along the posterior side of the femur, disappearing slightly before reaching the condyles. No other hindlimb elements are preserved in IGM 1/8.

COMMENTS ON SEVERAL ANATOMICAL FEATURES OF *TCHOIRIA*

Previous phylogenetic analyses (Gao and Fox, 1998; Evans and Manabe, 1999) have placed *Tchoiria* as a basal member of the family Simoedosauridae, and the discovery of IGM 1/8 provides new fossil material to better understand the morphology of this important taxon. In this context, the following anatomical structures are worth noting:

The postorbitofrontal is a single element in IGM 1/8. The state is unknown in the holotype of *T. namsarai*; however, Evans and Manabe (1999) noted what appeared to be sutures between the postorbital and postfrontal in GIN 39-54-01, a specimen assigned to

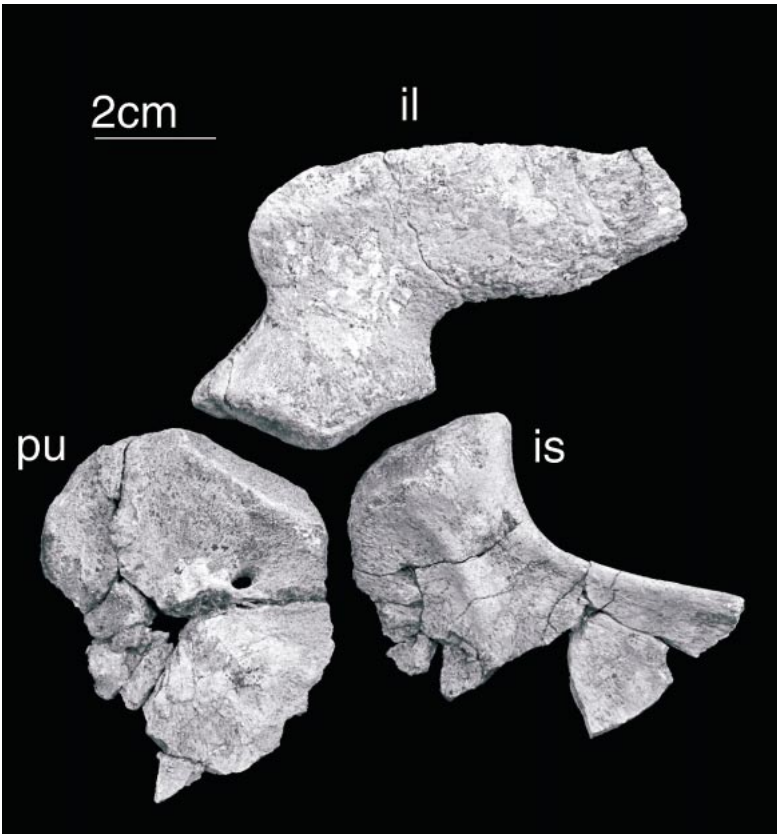

Fig. 9. Right pelvic girdle, lateral view, anterior = left. Abbreviations are listed in appendix 4.

Tchoiria. The postorbital and postfrontal are fused in other genera of the Simoedosauridae and remain separate in *Champsosaurus*, though the bones are fused in one specimen of *Champsosaurus lindoei* (Gao and Fox, 1998). Further study is necessary to determine whether the fusion of these elements is due to intraspecific or interspecific variation in *Tchoiria*.

Evans and Manabe (1999) coded *Simoedosaurus* and *Champsosaurus* as having a lacrimal foramen opening between the lacrimal, prefrontal, and palatine, while coding *Tchoiria* as having a lacrimal perforated by one or more foramina. However, a lacrimal foramen between the lacrimal, prefrontal, and palatine is present in *T. klauseni*. Efimov (1975) noted two small foramina piercing the lacrimal and separated from each other by a short crest in *T. namsarai*, but did not mention a lacrimal foramen between the lacrimal, prefrontal, and palatine. As two small foramina piercing the lacrimal as well as a larger lacrimal foramen between these three bones are present in *T. klauseni*, it seems likely that the lacrimal duct opens between the lacrimal, palatine, and prefrontal in all neochoristoderes. The presence of small foramina piercing the lacrimal as seen in both species of *Tchoiria* appears to be variable. Russell-Sigogneau and Russell (1978) noted a small foramen perforating the lacrimal in *Simoedosaurus*, but Erickson (1987) found no evidence of this feature in the holotype of *Simoedosaurus dakotensis*. This feature appears to be absent in *Champsosaurus* and is uncertain in *Ikechosaurus*.

In the original description of *T. namsarai*, Efimov (1975) identified a supratemporal bone contacting the parietal and prootic anteriorly, the quadrate and neomorph laterally, and the squamosal posteriorly. There is no

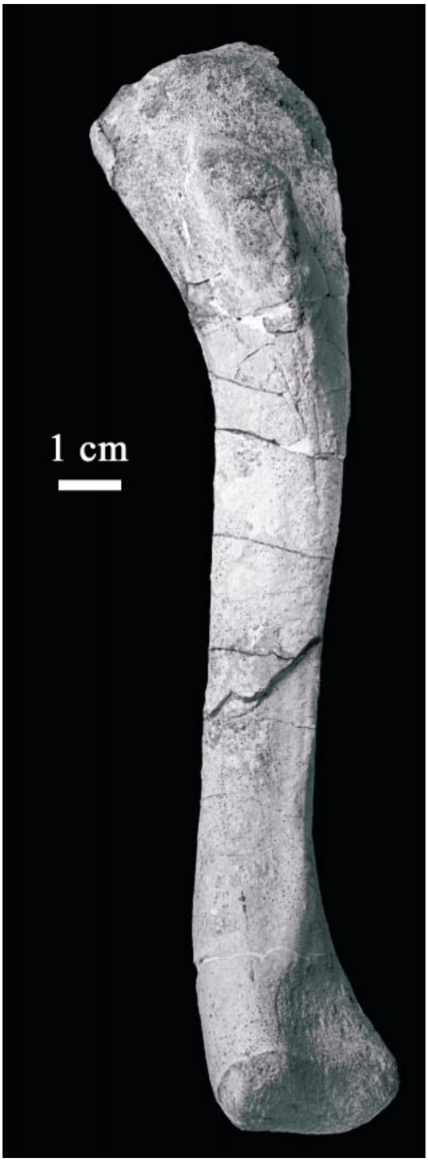

Fig. 10. Right femur, anteroventral view.

evidence of a supratemporal in IGM 1/8 or any other choristodere, and it appears the region identified as the supratemporal in Efimov's (1975) figure 1 is actually part of the parietal and possibly also part of the neomorph. Although only part of the neomorph is distinguishable in IGM1/8, it is clear the bone is significantly larger than the region identified as the neomorph in the cited figure. The neomorph was, until recently, believed to be a very small bone in *Champsosaurus*, but Gao and Fox (1998) illustrated that it is elongate in this genus, as in *Simoedosaurus* and *Ikechosaurus*. It is likely that the neomorph is of comparable size in both species of *Tchoiria* as well.

Several elements missing from the holotype of *T. klauseni* are present in the holotype of *T. namsarai* and worth referring to. Efimov (1975) noted the presence of a slight coronoid process and a poorly developed retroarticular process on the complete mandible, which contains as many as 150 teeth, as well as a greatly elongated entepicondylar groove on the humerus. The morphologies of the well-preserved scapula, clavicle, and interclavicle are typical of neochoristoderes.

PHYLOGENETIC DISCUSSION

Efimov (1975) considered *Tchoiria* to be a more generalized choristodere relative to *Champsosaurus* and *Simoedosaurus*, while not hypothesizing which genus it was more closely related to. He considered the shorter snout, more anterior choana, large interpterygoid vacuity, shorter mandibular symphysis, and posterior location of the craniomandibular joint as evidence that *Tchoiria* may have been less specialized for aquatic predation than *Champsosaurus*.

The information obtained from this study allows the coding of some previously missing data for the genus *Tchoiria*. A phylogenetic analysis incorporating these additional codings was conducted using the exhaustive search option in PAUP* 4.0b10 (Swofford, 2002). A matrix of 69 characters from a recent analysis by Evans and Manabe (1999) was used with modifications (described in appendix 2). Six choristodere genera and *Lazarussuchus* were included, and *Youngina* was used as an outgroup. The poorly known choristodere *Pachystropheus* was excluded from the analysis because of the extremely high percentage of missing data for this taxon. A single most parsimonious tree of 106 steps was recovered (fig. 11). Bootstrap support values from 1000 replicates computed in PAUP* and Bremer support values calculated manually in PAUP* are shown in figure 11. Our analysis produced results similar to previous analyses (Gao and Fox, 1998;

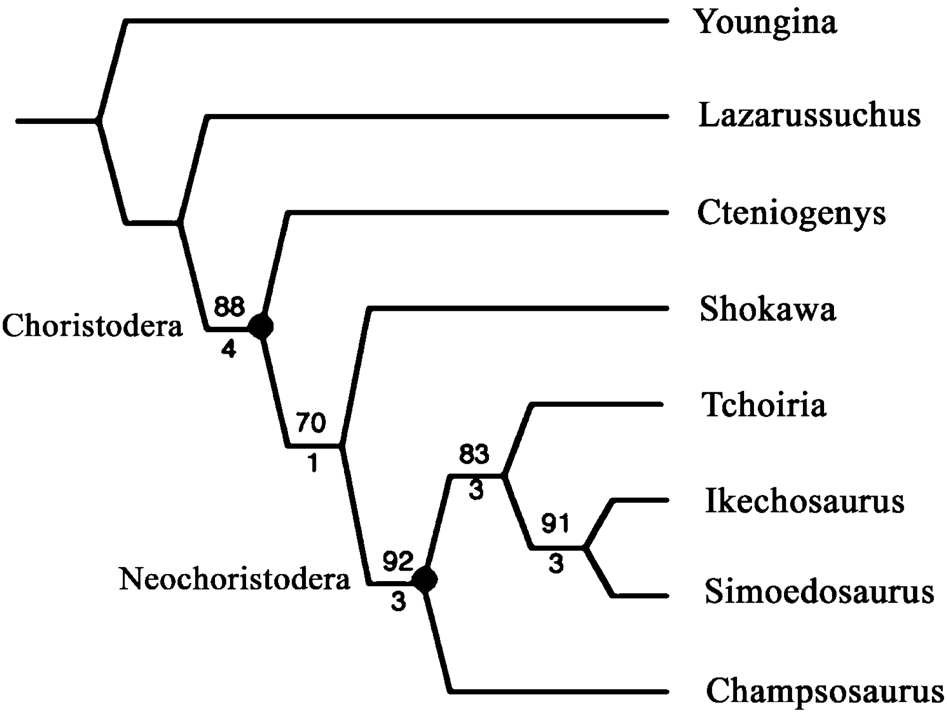

Fig. 11. Most parsimonious tree from phylogenetic analysis using characters listed in appendix 2. Tree length = 106 steps, CI = 0.925, RI = 0.889, RC = 0.822. Bootstrap values are shown above the node to which they refer; Bremer support values are shown below the node to which they refer.

Evans and Manabe, 1999), placing *Tchoiria* as the basal genus of the clade Simoedosauridae as sister taxon to a *Simoedosaurus–Ikechosaurus* clade.

The new species *T. klauseni* can be identified as a member of the clade Simoedosauridae by a suite of derived character states including reduced contact between the parietal and postorbitofrontal, craniomandibular joint located posterior to occipital condyle, paired palatal tooth batteries, and small spinous processes below the dorsal postzygapophyses. *T. klauseni* and *T. namsarai* share these synapomorphies of the Simoedosauridae, but also retain primitive features such as a prominent dorsal process of the jugal and a lightly arched supraoccipital with the sutural surfaces for the parietals placed anteriorly. These two features are shared with *Champsosaurus*. *Tchoiria* exhibits an intermediate condition between primitive choristoderes and more advanced members of the Simoedosauridae in several traits, suggesting directional trends in the shortening of the vertebral centra and the expansion of the marginal alveoli over the evolutionary history of the Simoedosauridae.

With the addition of the new species, *Tchoiria* can be diagnosed as a genus of the family Simoedosauridae possessing the autapomorphies of the family listed by Gao and Fox (1998) while also lacking the following synapomorphies of *Simoedosaurus* and *Ikechosaurus*: postorbital process of jugal low or lost and supraoccipital keeled with parietal facets extending to the dorsal margin. Several additional characters may be diagnostic of *Tchoiria,* but remain unknown in one of the species. Gao and Fox (1998) list two autapomorphies for *Tchoiria*: interpterygoid foramen posteriorly closed by notched anterior process of parasphenoid and anterior process of parasphenoid strongly widened and bifurcated at its tip. The states of these characters are not discernable in *T. klauseni* because the interpterygoid region is poorly preserved in the holotype. The parasphenoid does widen at the anterior process, but whether or not it bifurcates is unknown. The squamosal/parietal suture in the occiput is located halfway along the superior temporal fenestra in *Simoedosaurus* and *Iketchosaurus*. Evans and Manabe (1999) code this suture as near the posterior end of the fenestra for *Tchoiria*, but the state remains uncertain in *T. klauseni*. The absence of the posterior ischial tubercle is potentially diagnostic of *Tchoiria*, pending information on the state in *T. namsarai*.

The new species *T. klauseni* represents a typical neochoristodere. These large choristoderes were presumably aquatic to semiaquatic piscivores, roughly similar to modern gavials and crocodiles. The clade existed from at least the Early Cretaceous until the early Eocene. They are unique in having survived the K/T extinction only to go extinct shortly afterwards. Although competition with crocodylians has been suggested as a factor in the decline of neochoristoderes, no rigorous evaluation has been conducted of this hypothesis, and the cause remains unknown.

ACKNOWLEDGMENTS

We thank members of 1998 Mongolian Academy of Sciences–American Museum of Natural History field team for excavation of the specimen. We thank D. Dashzeveg for help in Mongolia. The specimen was skillfully prepared by Jim Klausen and photographed by Mick Ellison. We thank Erin Lamm for translating passages from French references. We thank Makoto Manabe and Susan Evans for reviews and Susan Evans for helpful discussions. Ke-qin Gao's research is supported by a grant from the National Natural Science Foundation of China (NSFC 40272006).

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APPENDIX 1

MEASUREMENTS (IN MILLIMETERS)

	Centra length	Centra width (posterior end)	Centra height (posterior end)	Max. height (including neural spine)
VERTEBRAE				
Cervicals				
axis	24.0	19.3	21.8	x
indet.	23.8	21.0	22.1	x
indet.	23.4	21.7	22.3	59.5
indet.	24.5	21.0	22.1	x
Dorsals				
indet.	27.2	22.4	21.8	53.1
indet.	27.7	22.0	21.2	51.2
indet.	26.9	21.5	21.3	52.6
indet.	27.8	21.5	20.5	x
indet.	27.9	20.1	19.3	x
indet	27.8	19.6	19.3	x
Sacrals				
first	28.5	x	x	x
second	26.0	x	17.5	45.4
third	26.5	18.6	18.0	47.7
Caudals				
indet. mid	26.1	15.7	17.0	46.0
indet. mid	27.2	16.2	16.4	x
indet post.	26.0	12.4	14.4	31.8
indet post.	25.3	10.8	11.4	x

FORELIMB	Proximodistal length
Ulna	88.1
Radius	87.3

HINDLIMB	Proximodistal length
Femur	181.1

APPENDIX 2

CHARACTERS AND CHARACTER STATES USED IN PHYLOGENETIC ANALYSIS

Characters are from previous analyses by Gao and Fox (1998), which were modified from Evans (1990) and Hecht (1992), and Evans and Manabe (1999). Characters 66 and 71 of the matrix of Evans and Manabe were excluded, as character 66 represents only an autapomorphy of *Shokawa* and character 71 is phylogenetically uninformative with the exclusion of *Pachystropheus*. Where codings differed between the two previous matrixes, other than the coding of previously missing data, an explanation of the selected coding is given. All characters are unordered.

1. **External nares:** (0) paired, oval, nearly terminal, (1) paired, elongate, dorsally placed, (2) terminal and confluent.
2. **Prefrontals:** (0) anterolateral and separated by frontals, (1) median contact limited to posterior half of length, (2) having median contact entire length of element.
3. **Parietal foramen:** (0) present, (1) absent.
4. **Preorbital skull proportions:** (0) moderately short and rounded, (1) elongate but less than 50% of skull length, (2) more than 50% of skull length.
5. **Dorsal flange of maxilla:** (0) low and vertical, (1) prominent process confined to anterior part of maxilla and weakly inrolled, (2) low flange elongated and strongly inrolled.
6. **Lacrimal extension:** (0) lacrimal enters external narial opening, (1) lacrimal retracted posteriorly from the opening, but remains elongate, (2) lacrimal reduced to small triangular bone.
7. **Lacrimal perforation:** (0) lacrimal foramen pierces lacrimal only, (1) lacrimal foramen between lacrimal, prefrontal, and palatine. (*Tchoiria* is coded (1) based on the presence of a foramen between the lacrimal, prefrontal, and palatine in *T. klauseni*.)
8. **Nasals:** (0) short and paired, (1) elongate and paired, (2) elongate and fused.
9. **Nasal/premaxilla contact:** (0) nasals contact but do not intervene between premaxillae, (1) nasals intervene between premaxillae, (2) nasals do not contact premaxillae.
10. **Orbit size and orientation:** (0) large and laterally directed, (1) small and dorsally directed.
11. **Postfrontal/postorbital fusion:** (0) postfrontal and postorbital discrete and both enter the orbital margin, (1) postfrontal and postorbital discrete, postorbital excluded from orbital margin, (2) postfrontal and postorbital fused. (Evans and 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.)
12. **Dorsal process of squamosal:** (0) broad and short, (1) elongate and slender to middle level of inferior temporal opening.
13. **Upper temporal fenestra:** (0) smaller than orbit, (1) about same size as orbit, (2) posteriorly flared and substantially larger than orbit.
14. **Parietal:** (0) having a broad contact with the postorbital/postfrontal complex, (1) reduced contact.
15. **Location of squamosal/parietal suture in occiput:** (0) near posterior end of superior temporal fenestra, (1) half way along fenestra.
16. **Nasal/prefrontal contact:** (0) straightline contact dorsolateral on snout, (1) short, broad V-shaped contact at dorsal midline, (2) nasals form long, narrow pinched wedge.
17. **Vomer/maxilla contact:** absent (0), present (1). (This character follows the definition of Evans and Manabe, 1999, pertaining to the contribution of these bones contacting to an extended primary palate).
18. **Location of choana:** (0) anteriorly close to premaxilla, (1) retracted close to midpoint of marginal tooth row, (2) choana displaced far back. (State 1 is assigned to *Tchoiria*, *Ikechosaurus*, and *Simoedosaurus* following Gao and Fox, 1998, as the choana of these species appear from illustrations to be situated near the midpoint of the marginal tooth row rather than displaced as far back as in *Champsosaurus*.)
19. **Palatal foramen:** (0) absent with vomer, palatine, and pterygoid meeting at closed three point suture, (1) opening at juncture between three palatal bones, (2) between pterygoid and palatine, without contribution from the vomer.
20. **Internarial:** (0) absent, (1) present.
21. **Pterygoid flange:** (0) consisting of pterygoid only, ventrally directed, (1) consisting of pterygoid and ectopterygoid, having a horizontal overlap.
22. **Basipterygoid/pterygoid joint:** (0) process–cotyle contact as part of a metakinetic joint, (1) process and cotyle are reduced and two bones are sutured, (2) two bones are fused.
23. **Parasphenoid/pterygoid contact:** (0) no contact, (1) clear sutural contact, (2) tight contact or fusion.
24. **Quadratojugal/quadrate articulation:** (0) having a simple overlapping facet for the quadrate, (1) quadratojugal bears a cotyle meeting a rounded quadrate process.

APPENDIX 2
(Continued)

25. **Pterygoid process of quadrate:** (0) broad, vertically oriented with a large pterygoid facet, (1) low, slender, and horizontal with a reduced pterygoid facet.
26. **Postorbital (dorsal) process of jugal:** (0) as prominent as anteroventral process, (1) prominent but much shorter than anteroventral process, (2) little or no process.
27. **Nasopalatal trough:** (0) absent, (1) present.
28. **Palatal teeth:** (0) palate covered by shagreen of small teeth, (1) paired pterygoid tooth batteries separated by nasopalatal trough, (2) narrow rows of pterygoid teeth separated by nasopalatal trough.
29. **Midline contact of pterygoids:** (0) separate or just touching in the midline anteriorly, (1) long midline suture.
30. **Size and location of interpterygoid vacuity:** (0) large and extends anterior to suborbital fenestra, (1) small and near posterior border of fenestra.
31. **Enclosure of interpterygoid vacuity:** (0) enclosed anteriorly by pterygoids but open posteriorly, (1) enclosed anteriorly by pterygoids and posteriorly by parasphenoid, (2) enclosed both anteriorly and posteriorly by pterygoids. (Evans and Manabe, 1999, code *Tchoiria* [1/2] without comment. *Tchoiria* is coded [2] in agreement with Gao and Fox, 1998, based on photos of PIN 3386/1.)
32. **Shape of parasphenoid:** (0) isoceles triangle with long rostrum, (1) broad anteriorly with short rostrum and strong posterolateral expansion, (2) slender anteriorly with long rostrum and strong posterolateral winglike expansion. (Evans and Manabe, 1999, code *Tchoiria* [1/2] without comment. *Tchoiria* is coded [2] in agreement with Gao and Fox, 1998, based on PIN 3386/1.)
33. **Basal tuberculae of braincase:** (0) weakly developed, (1) moderately expanded laterally, (2) strongly expanded posterolaterally and winglike.
34. **Marginal tooth sockets:** (0) circular, (1) transverse expansion occurs in anterior part of tooth row.
35. **Basal infolding of tooth enamel:** (0) absent, (1) present.
36. **Location of craniomandibular joint:** (0) about the same level as occipital condyle, (1) anterior to condyle, (2) posterior to condyle.
37. **Shape of suborbital fenestra:** (0) narrow, elongate, (1) subtriangular with straight medial edge, (2) short, kidney shaped.
38. **Neomorph in braincase:** (0) absent, (1) present as part of external wall of braincase and medial wall of temporal fossa.
39. **Pterygoquadrate foramen:** (0) absent, (1) present and enclosed between neomorph and quadrate.
40. **Paroccipital process/quadrate contact:** (0) only tip of process meets quadrate, (1) elongate process lies in trough of quadrate and neomorph, (2) elongate process lies in trough of quadrate lined with thin sheet of neomorph.
41. **Mandibular symphysis:** (0) small and terminal, (1) slightly extended but confined anteriorly without inclusion of the splenial, (2) strongly elongate with longer inclusion of the splenial. (Codings follow Gao and Fox, 1998, defining state 1 to exclude the splenial.)
42. **Lateral exposure of splenial:** (0) splenial confined to medial side of mandible, (1) exposed on ventrolateral surface of mandible.
43. **Orientation of paroccipital processes:** (0) horizontal, (1) slightly depressed, (2) strongly deflected ventrally.
44. **Supraoccipital/parietal contact:** (0) supraoccipital free from parietal, (1) supraoccipital lightly arched, sutural surfaces for parietal placed anteriorly, (2) supraoccipital keeled, parietal facets extend to posterior margin.
45. **Posttemporal fenestra:** (0) present, (1) absent by loss.
46. **Pila antotica:** (0) remains unossified, (1) ossified as part of the sphenoid.
47. **Posterior opening of the interior carotid artery:** (0) opens ventrolaterally without penetrating parasphenoid, (1) opens ventrally, penetrates parasphenoid.
48. **Atlas–axis complex:** (0) little or no development of anterior odontoid prominence of axis, (1) free odontoid process unfused to axis.
49. **Neurocentral sutures:** (0) closed in adult, (1) remain open in adult.
50. **Vertebral centra:** (0) amphicoelous and notochordal, (1) amphiplatyan with notochordal canal closed.
51. **Presacral vertebral centra:** (0) elongate, (1) short and spoollike. (*Champsosaurus* and *Tchoiria* are coded [1] following Gao and Fox, 1998, who interpret this character according to its original evaluation [Evans, 1990]. To avoid confusion, state [0] has been changed from longer than wide to elongate. Although the vertebral centra of *Champsosaurus* are longer than wide, the difference is slight compared to the elongation in *Cteniogenys* and *Lazarussuchus*.)
52. **Ventromedial crest of dorsal vertebrae:** (0) anterior dorsal vertebrae are strongly keeled like the cervical vertebrae, (1) low or no keels.

APPENDIX 2
(Continued)

53. **Small spinous processes below presacral zygapophyses:** (0) absent, (1) present, (2) present with accessory facets. (Gao and Fox, 1998, code *Ikechosaurus* as present with accessory facets. Based on the description by Brinkman and Dong, 1993, *Ikechosaurus* is coded as present, without facets for this character.)
54. **Number of sacral vertebrae:** (0) two sacrals, (1) three sacrals, (2) four sacrals.
55. **Sacral and caudal ribs:** (0) fused to vertebrae in adults, (1) sacral ribs free, caudal ribs fused, (2) sacral and caudal ribs free.
56. **Caudal zygapophyses:** (0) lie at small angle to the horizontal, (1) nearly or completely vertical. (All choristoderes and *Lazarussuchus* were scored 1 for this character as in Gao and Fox, 1998, as the caudal zygapophyses in all examined specimens and illustrations were nearly vertical.)
57. **Centra of caudal vertebrae:** (0) bear shallow ventral groove for caudal blood vessels, (1) groove is flanked by deep ventral flanges.
58. **Number of ossified carpal elements:** (0) nine or more, (1) seven or less.
59. **Flexor tubercle or process on ventral surface of ungual:** (0) distinct and well developed, (1) low and reduced.
60. **Bone structure:** (0) cancellous, (1) having reduced medulary cavity, (2) pachyostotic in adult.
61. **Iliac blade dorsal margin:** (0) essentially vertical or at a steep angle to the horizontal in adults, (1) dorsal margin essentially horizontal, blade expanded.
62. **Cervical neurocentral suture:** (0) closed, (1) open.
63. **Interclavicle shape:** (0) rhomboid, (1) T shaped.
64. **Interclavicle stem:** (0) long, slender, and essentially parallel sided, (1) flask shaped, broad in anterior and central portions, tapering distally, (2) stem shorter than lateral processes.
65. **Clavicular facets on interclavicle:** (0) meet at angle at midline, (1) continuous across midline in smooth curve.
66. **Cervical vertebral centra length:** (0) longer than high, (1) shorter than high.
67. **Dorsal vertebral centrum shape:** (0) subcylindrical, (1) cylindrical.
68. **Fibula shape:** (0) proximal and distal ends of similar width, (1) proximal end narrow, distal end flared.
69. **Gastralia thickness:** (0) thin, lightly built, (1) robust, almost as thick as axial ribs, and pachyostotic.

APPENDIX 3

Data Matrix Used to Produce the Tree in Figure 11

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Youngina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lazarussuschus	1	1	1	1	1	?	0	1	0	0	?	?	1	?	0	1	?	0	?	0	?	?	?
Cteniogenys	2	2	1	1	1	1	0	0/1	2	0	0	?	1	0	0	?	0	1	1	0	1	1	1
Shokawa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tchoiria	2	2	1	1/2	2	1	1	2	?	1	1/2	1	2	1	0	2	1	1	2	0	1	1	1
Ikechosaurus	2	2	1	1	2	1	?	2	1	1	2	1	2	1	1	1	?	1	2	0	1	1	1
Simoedosaurus	2	2	1	1	2	1	1	2	1	1	2	1	2	1	1	1	1	1	2	0	1	1	1
Champsosaurus	2	2	1	2	2	2	1	2	1	1	1	1	2	0	0	2	1	2	2	1	1	2	2

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Youngina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lazarussuschus	?	?	?	?	0	0	?	?	0	0	0	?	0	0	?	?	?	1	0	?	?	?	?
Cteniogenys	0	0	1	0	0	0	0	1	0	0	0	0	?	0	1	?	?	1	0	0	?	?	0
Shokawa	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	0	0	?	?	?	?
Tchoiria	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	?	2	0	1	1	1	?
Ikechosaurus	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1	1	?	2	0	1	2	1	1
Simoedosaurus	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	0	1	2	1	1
Champsosaurus	1	1	1	1	2	1	1	2	2	2	0	1	1	2	1	1	2	2	1	2	1	0	0

	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
Youngina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lazarussuschus	?	?	0	0	0	0	0	2	0	1	0	0	0	0	0	0	?	?	?	0	0	1	0
Cteniogenys	0	1	1	1	0	0	0	1	2	1	1	?	1	1	0	0	?	?	?	0	0	?	0
Shokawa	?	?	1	1	0	?	0	1	1	?	1	?	?	1/2	0	0	0	0	0	0	1	0	1
Tchoiria	1	1	1	1	1	1	1	1	2	1	1	?	?	1/2	1	1	1	1	1	0	1	1	?
Ikechosaurus	1	?	1	1	1	1	1	1	2	?	0	?	1	?	1	1	1	0	?	0	0/1	1	1
Simoedosaurus	1	1	1	1	1	1	2	1	2	1	0	1	?	2	1	1	1	1	1	1	1	1	1
Champsosaurus	0	1	1	1	1	1	0	1	2	1	0	1	1	2	1	1	1	1	1	0/1	1	1	1

APPENDIX 4

Anatomical Abbreviations Used in Figures

ch	choana	q	quadrate
ec	ectopterygoid	qj	quadratojugal
exo	exoccipital	pa	palatine
f	frontal	p	parietal
il	ilium	palf	palatal foramen
is	ischium	pf	prefrontal
j	jugal	pobf	postorbitofrontal
l	lacrimal	pt	pterygoid
m	maxilla	pu	pubis
n	nasal	so	supraoccipital
neo	neomorph	sp	spinous process
olf	olfactory canal	sq	squamosal
op	opisthotic	v	vomer

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