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PACHYCHEILOSUCHUS TRINQUEI, A NEW PROCOELOUS CROCODYLIFORM FROM THE LOWER CRETACEOUS (ALBIAN) GLEN ROSE FORMATION OF TEXAS

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ABSTRACT—A new mesoeucrocodylian, *Pachycheilosuchus trinquei*, from the Lower Cretaceous (Albian) Glen Rose Formation, exhibits progressive caudal-to-cranial vertebral procoely. This modification is characterized by an intermediate semi-procoelous condition in which the posterior condyle is dimpled by a concavity. *Pachycheilosuchus* differs from all known crocodyliforms in having an expanded maxillary margin that displaces the tooth row medially, and in possessing a cervical shield formed by the complete fusion of six osteoderms. Phylogenetic analysis indicates a sister taxon relationship with the weakly defined Atoposauridae. The presence of variable procoely in both *Pachycheilosuchus* and the closely related atoposaurid *Theriosuchus* indicates convergent evolution of the character with Eusuchia. Sediments at the locality were deposited in near-shore, marine-to-brackish waters, suggesting that *Pachycheilosuchus* inhabited euryhaline marine environments.

INTRODUCTION

A fossil locality (SMU loc. 331) in southeastern Erath County, north central Texas (Fig. 1a), yields a varied vertebrate fauna, including a new taxon of atoposaurid mesoeucrocodylian. This study describes this new crocodyliform, provides a phylogenetic context that establishes a sister group relationship with the Atoposauride while examining the validity of that clade, and provides partial resolution and clarification of the crocodyliform informally referred to as the ''Glen Rose Form.''

The Glen Rose Formation is famous for its dinosaur trackways (Farlow, 1981, 1987; Kuban, 1989), and also contains locally abundant vertebrate fossils. These are primarily sharks and bony fishes (Thurman, 1971, 1974; Huggins, 1990; Barck, 1992), but include turtles, crocodyliforms, theropods (Winkler et al., 1990), and a pterosaur (Murry et al., 1991).

Isolated crocodyliform elements previously recovered from the Glen Rose and other formations within the Trinity Group were considered to represent a single taxon informally referred to as the ''Glen Rose Form'' (Langston, 1974; Benton and Clark, 1988; Brochu, 1999). SMU 331 is the only Trinity Group locality that has produced representative elements of an entire crocodyliform skeleton. These elements now allow description of a new taxon from the mixture of elements collectively referred to as the ''Glen Rose Form,'' and provide documentation of vertebral procoely in a non-eusuchian lineage.

Geologic Setting—The Glen Rose Formation comprises a wedge of predominately marine carbonate sediments that was deposited across the central Texas platform during the first major transgression of the Trinity Group at the base of the Comanchean Series (Hayward and Brown, 1967). In north central Texas, the Trinity Group is composed of the Twin Mountains, Glen Rose and Paluxy formations. The Glen Rose is underlain by the terrigenous clastics of the Twin Mountains, with which it has a gradational relationship, and is overlain by the Paluxy Formation, a package of loosely consolidated sediments that ranges from continental clastics to deltaic and beach deposits (Hayward and Brown, 1967). To the north and west the three formations are laterally equivalent to the Antlers Formation. In north central Texas, the limit of Glen Rose transgression may be observed in the varied lithology of silt and sandstones, shales, and often arenaceous limestones indicative of near-shore, marginal marine waters (Rodgers, 1967).

The onset of Glen Rose transgression was Late Aptian (approximately 112 Ma, Jacobs and Winkler, 1998). The *Kazanskyella spathi* ammonite zone of Late Aptian age occurs at the base of the Glen Rose, whereas the Early Albian *Hypacanthoplites comalensis* zone occurs 20–30 m above the *Corbula* interval that is basal within the Thorp Spring Member of the Glen Rose (Jacobs and Winkler, 1998). The outcrop at SMU locality 331 occurs just below the contact with the overlying Paluxy Formation and thus is of early Albian age.

Sedimentology and Depositional Environment of SMU Locality 331—The outcrop consists of a <1 m thick section exposed at a low-water crossing of an unpaved farm road (Fig. 1b). The section consists of a basal mudstone unit underlying ledge-forming, bedded limestones. Bedding is sub-parallel and hummocky, and often delineated by thin (1–5 mm) layers of silt and clay. In the bone-bearing horizon, silt and carbonate mud lenses predominate.

Bones are oriented parallel to bedding planes. Crocodyliform elements make up 90% of the vertebrate elements. All bones are completely disarticulated with only rare occurrence of anatomically associated groupings. Most bones are well preserved and exhibit little evidence of transport abrasion. A small percentage (<1%) of the elements are rounded and polished by apparent hydraulic action. A relatively complete crocodiloid egg was recovered in association with the bones (Rogers, 2000), and small crocodiloid eggshell fragments are common in the silt and mud lenses.

Current flow structures, e.g., cross-bedding and ripple marks, are absent from the mudstone and silt lenses, and the bedded limestones. Hummocky bedding is typically restricted to shallow-marine sediments, and is generally attributed to periodic storm wave action (Boggs, 2001). Storm surge at SMU loc. 331 likely induced sediment reworking that mixed unabraded and polished fossil bones.

Ostracodes are present throughout the section, represented primarily by *Asciocythere rotunda*, which is interpreted as a brackish water inhabitant (Davis, 1974). The common occurrence of ostracodes, combined with a complete absence of foraminiferans, is a strong indicator of brackish waters, ostracodes being more tolerant than forams of varying salinity (Brasier, 1980). Other marine invertebrates such as echinoids and corals that are common in Glen Rose open water marine depositional facies are rare, with only a few echinoid spine fragments present.

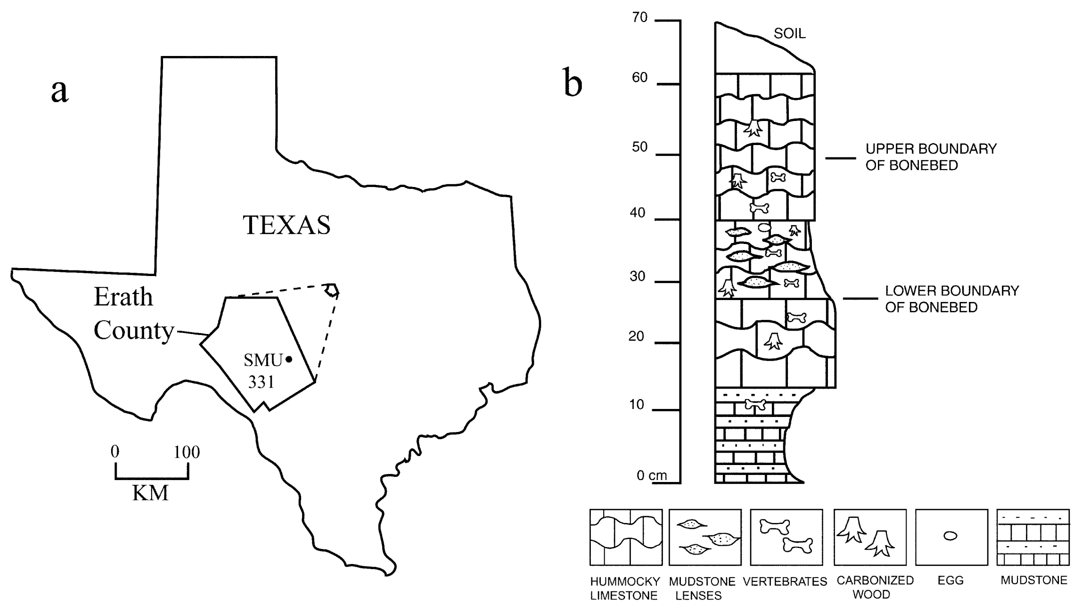

FIGURE 1. SMU locality 331, Erath County, Texas; stratigraphic column of SMU loc. 331.

The vertebrate fossils also suggest a brackish-water environment. A variety of fishes was recovered, including amiiforms, albulids, pycnodonts, and rays, all taxa recorded from sediments deposited by euryhaline waters (Thurman, 1974; Huggins, 1990; Williamson et al., 1993; Grande and Bemis, 1998).

Sediments of SMU loc. 331 indicate deposition during regression in shallow, near-shore, protected, brackish waters. Brackish water and terrestrial fossils, and the rarity of open water marine invertebrate and vertebrate fossils at the site support this interpretation. Oyster beds at the overlying contact with the Paluxy Formation indicate shallow marine water, while the excellent preservation of the crocodiloid egg suggests minimal transport and proximity to the shore.

Institutional Abbreviations—**BMNH**, The Natural History Museum, London; **IPFUB**, Institut für Paläontologie der Freien Universität Berlin; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **SMU**, Shuler Museum of Paleontology, Southern Methodist University, Dallas; **TMM**, Texas Memorial Museum, Austin; **USNM**, United States National Museum, Washington.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Benton and Clark, 1988
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
PACHYCHEILOSUCHUS, gen. nov.

Type Species—*Pachycheilosuchus trinquei*, gen. et sp. nov.

Etymology—From the Greek *pachy*, thick; *cheil*, lip; and *souchus*, crocodile. Refers to the expanded maxillary margin.

Diagnosis—As for the type and only known species.

PACHYCHEILOSUCHUS TRINQUEI, sp. nov.
(Fig. 3)

Holotype—SMU 75278, a right maxilla.

Referred Material—Elements representing a minimum of 13 individuals, including: maxillae, SMU 75009, SMU 75277–75278, SMU 75289–75291; dentaries, SMU 75278–75279; teeth, SMU 75092, SMU 75103; associated left and right dentaries and surangulars, SMU 75299; surangulars, SMU 75290, SMU 75313–75315; jugals, SMU 75302, SMU 75304–75307; frontals, SMU 75308–75309, SMU 75311–75312, squamosal, SMU 75303; postorbital, SMU 75310; parietal, SMU 75090; quadrates, SMU 75281–75286; basioccipital, SMU 75287; cervical vertebrae, SMU 75103–75111; dorsal vertebrae, SMU 75153–75168; sacral vertebrae, SMU 75112–75115; caudal vertebrae, SMU 75116–75150; ribs, SMU 75169–75201; scapulae, SMU 75068–75076; coracoids, SMU 75063–75067; humeri, SMU 75028–75033; radii, SMU 75262–75268, SMU 75295; ulnae, SMU 75050–75052; radiale, SMU 75272; phalanges, SMU 75274, SMU 75294; ungual, SMU 75273; ilia, SMU 75055–75059; ischia, SMU 75060–75063; pubis, SMU 75296; femora, SMU 75010–75026; tibiae, SMU 75034–75047; fibulae, SMU 75048–75049; metatarsals, SMU 75269–75271; SMU 75293, SMU 75316; calcaneum, SMU 75276; and osteoderms, SMU 75202–75260.

Locality and Horizon—SMU locality 331, Erath County, Texas, Lower Cretaceous (Albian) Glen Rose Formation. Exact locality data is on file at the Shuler Museum of Paleontology, Southern Methodist University, Dallas.

Etymology—In honor of Lance Trinque, a dedicated field assistant who helped in discovery and excavation of SMU locality 331.

Diagnosis—The following derived characters diagnose this taxon: (1) the dorsoventrally compressed maxilla has minimal sculpturing and an expanded lateral margin, with a dorsal ridge that is bordered by an elongate furrow defining the medial boundary of the margin; (2) ventrally, the expanded margin of the maxilla displaces the tooth row medially by a distance exceeding the diameter of the largest alveoli; (3) the posteromedial edge of the maxilla enters the margin of an antorbital fenestra; (4) a broad shelf separates the ectopterygoid from the tooth row; (5) the tooth row ends well anterior to the posterior tip of the maxilla.

DESCRIPTION

More than 250 relatively complete elements of *Pachycheilosuchus* were recovered, with an approximately equal number of fragments. A series of left femora provides a minimum number of individuals (MNI) of 13. From these iso-

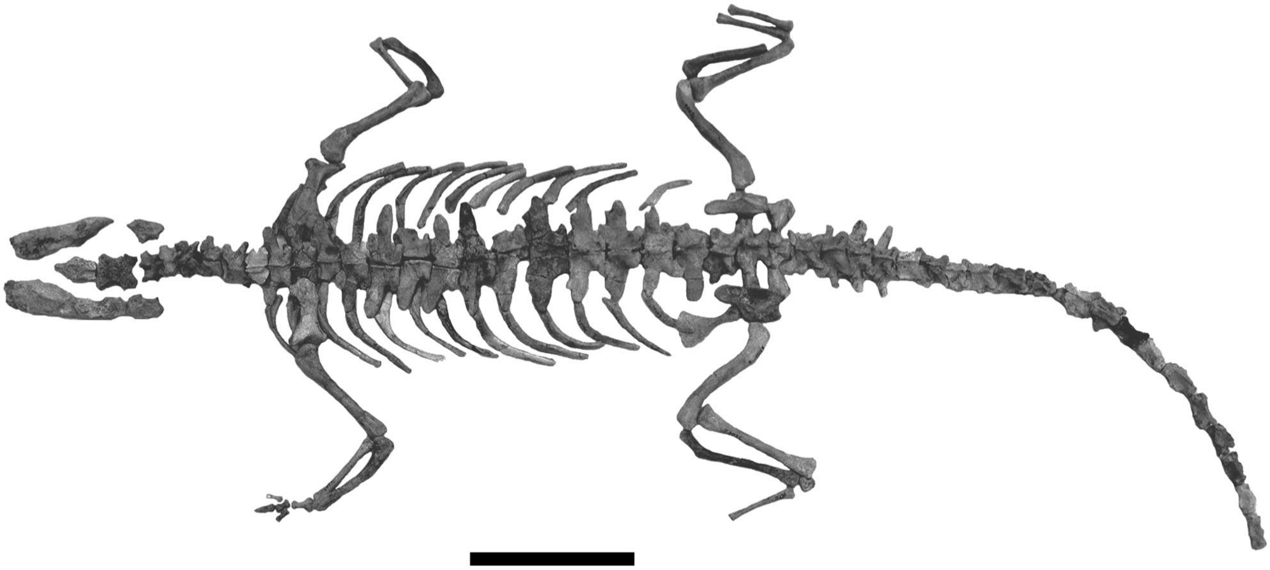

FIGURE 2. Composite skeleton of *Pachycheilosuchus trinquei*. Scale bar equals 10 cm.

lated elements a relatively complete composite skeleton was reconstructed (Fig. 2). Measurements of individual elements are provided in Table 1.

Cranium

Cranial bones representing significant portions of the snout, skull table, lower temporal bar, and mandible, were recovered. Relatively complete elements include maxillae, jugals, quadrates, dentaries, surangulars, a parietal, a basioccipital; less complete elements include squamosals, frontals, and a postorbital. The palate is incomplete, and thus position of the internal choanae is uncertain.

The maxilla (Fig. 3) is dorsoventrally compressed, with minimal dermal sculpture. The entire lateral margin is expanded to form a marginal ''lip'' that overhangs the tooth row. Dorsally, the medial margin of the lip is defined by a distinct ridge (SMU 75278, Fig. 3a). The ridge is bordered medially by a long, shallow depression that parallels the lip for the anterior 80% of the maxilla. A series of nutrient foramina and nerve passages of varying size mark the dorsolateral edge of the lip.

The dorsal surface of the maxilla is mildly convex. Anteriorly, the dorsal surface is inclined at an angle of 15° from the snout centerline to the lateral margin. Posteriorly the maxilla is taller, with a medial inclination angle of ~45°. The posteromedial edge of the maxilla enters the margin of the antorbital fenestra immediately anterior to the jugal-maxillary suture, approximately even with the penultimate tooth position.

The lateral margin of the maxilla is almost straight, with two lateral expansions separated by a shallow emargination. There is no notching for accommodation of dentary teeth and the labial edge of the maxilla is not festooned. The ventral surface of the maxilla also exhibits the expanded margin, which separates the tooth row from the edge of the maxilla (SMU 75278, Fig. 3b). This is unlike all recent crocodylians, which have teeth set in alveoli along the lateral margin of the maxilla. Among fossil eusuchians, *Stangerochampsa* possesses a tooth row set partially medial to the maxillary margin, but without expansion of the labial margin (Wu et al., 1996). The distance between the lateral edge of the maxilla and the labial edge of the tooth row is greater than the alveolar diameter (1.7–1.9 mm). Posteriorly, the margin is 3.5 mm wide; at midpoint it expands to 4.5 mm, and anteriorly constricts to 2.5 mm. The are 12 alveoli preserved in the maxilla. More alveoli were likely present, although damage to the anterior margins of all specimens leaves the exact number in question. The tooth row roughly mirrors the lateral margin of the maxilla, and thus is almost linear. A row of nutrient foramina borders the tooth row medially. No alveoli are enlarged, none are confluent, and there is no alveolar groove. The tooth row is distinguished by a lack of variation, having evenly spaced alveoli of similar diameter set into a flat, smooth palatal surface.

The ectopterygoid sutural facet is preserved along the posteromedial margin. The anterior edge of this suture is marked by a medial concavity within the maxilla and by the sharp edge of the palatal fenestra. The ectopterygoid-maxillary suture within the fenestra is posterior to the tooth row. A broad shelf of the maxilla separates the tooth row from the ectopterygoid.

Among the four relatively complete maxillae, one displays an oval 5 mm × 6.5 mm puncture mark (SMU 75278, Fig. 3a). Rims of fractured bone along the margin are collapsed into the puncture cavity. This puncture is probably a bite mark of a larger predator.

The frontal plate is eroded but appears solid, thick, and well sculptured (SMU 75311, Fig. 4a). Lateral notches form the anterolateral margins of the orbit. The orbital rims are not elevated. The frontal does not enter the supratremporal fenestrae. A deep olfactory groove is present on the ventral side of the frontal plate.

The dorsal surface of the parietal is well sculptured and constricted anteriorly by the edges of the supratemporal fenestrae (SMU 75909, Fig. 4b). The parietals form the complete medial margins of the fenestrae, with deep descending lateral crests that form the medial fenestral walls. The parietal plate is dorsally flat, with a notched posterior margin. It shows no evidence of a sagittal crest. The posterior ventral surface is rough, indicating a tight suture with the supraoccipital. The parietal-squamosal suture is long and rugose, while the suture with the postorbital is narrow. The parietal lacks external foramina.

A partial squamosal (SMU 75303) resembles the parietal in sculpture and thickness. The rim bordering the supratemporal fenestra is slightly elevated.

TABLE 1. Table of measurements (in mm) for selected elements of *Pachycheilosuchus trinquei*.

Element	Measurement	Nos. of element	Range	Mean
Frontal	W—posterior to orbit margins	2	3.6–14.4	14.0
Parietal	L—AP(anterior-posterior) width anterior to temporal fenestra	1	N/A	23.6
Jugal	H—DV(dorsal–ventral) posterior to postorbital bar	1	N/A	21.7
Quadrate, r.	L—AP	3	9.2–25.9	22.4
Quadrate, l.	L—AP	3	8.4–26.0	22.3
Basioccipital	W—outside tubera	1	N/A	12.0
Dentary, r.	L—AP	2	62.0–87.3	74.7
Dentary, l.	L—AP	1	N/A	60.3
Surangular, r.	L—AP	1	N/A	38.4
Surangular, l.	L—AP	1	N/A	41.0
Cervical vertebrae	L—centrum AP	9	10.7–13.4	11.7
	W—centrum lateral posterior	9	8.1–9.4	8.3
	H—ventral base to spine tip	9	21.6–28.3	23.9
	W—postzygapophyses tip	9	17.7–27.0	21.3
Dorsal vertebrae	L—centrum AP	16	13.3–21.9	17.6
	W—centrum lateral posterior	16	7.8–10.8	9.3
	W—transverse process tip	10	46.6–68.7	57.7
Sacral vertebrae	L—AP centrum	5	14.8–16.8	16.1
	W—centrum lateral posterior	5	9.9–11.7	10.8
	W—transverse process tip	5	55.1–64.9	61.8
First caudal vertebrae	L—AP centrum	1	N/A	17.5
	W—centrum lateral posterior	1	N/A	12.4
Caudal vertebrae	L—AP centrum	34	14.0–26.6	20.1
	W—centrum lateral posterior	34	5.7–11.2	7.6
Dorsal ribs	L	18	36.2–64.8	52.3
Scapula, r.	L—proximal head to blade margin	3	36.8–42.6	39.7
	W—blade AP	3	15.2–17.6	16.0
	Blade thickness at distal margin	3	1.3–1.6	1.4
Scapula, l.	L—proximal head to blade margin	4	31.7–49.0	41.9
	W—blade AP	2	26.7–29.6	28.2
	Blade thickness at distal margin	4	0.9–1.5	1.3
Coracoid, r.	L—proximal head to blade margin	2	35.3–38.0	36.7
	W—blade AP	2	13.0–13.8	13.4
	Blade thickness at distal margin	2	1.7–2.5	2.1
Coracoid, l.	L—proximal head to blade margin	1	N/A	36.5
	W—blade AP	1	N/A	>9.0
	Blade thickness at distal margin	1	N/A	2.4
Humerus, r.	L	5	68.5–95.0	81.8
	W—mediolateral (ML) midshaft	5	5.8–8.8	7.3
Humerus, l.	L	1	N/A	68.5
	W—ML midshaft	1	N/A	5.8
Radius, r.	L	2	43.7–51.5	47.6
	W—DV midshaft	2	3.7–3.8	3.8
Radius, l.	L	4	37.0–45.5	41.8
	W—DV midshaft	4	3.0–3.8	3.4
Ulna, r.	L	1	N/A	49.3
	W—DV midshaft	1	N/A	4.3
Radiale	L	1	N/A	11.1
Ungual, indt. pos.	L	1	N/A	11.6
Illium, r.	L—AP	3	38.0–43.8	40.9
Illium, l.	L—AP	1	N/A	40.9
Ischium, r.	L—iliac facet to blade margin	3	32.7–39.1	35.6
	W—AP blade	3	18.7–19.9	19.3
	W—blade distal margin	3	0.9–1.3	1.2
Pubis, l.	L—articular facet to blade margin	1	N/A	38.5
	W—AP blade	1	N/A	22.4
	W—blade distal margin	1	N/A	0.8
Femur, r.	L	6	66.0–88.9	75.1
	W—ML midshaft	6	5.5–8.0	6.5
Femur, l.	L	9	38.1–91.2	75.3
	W—ML midshaft	9	2.4–7.5	5.8
Tibia, r.	L	7	47.7–87.4	74.0
	W—ML midshaft	7	4.9–5.5	5.3
Tibia, l.	L	5	59.8–73.8	68.5
	W—ML midshaft	5	4.2–6.4	5.5
Fibula, l.	L	1	N/A	72.3
	W—AP midshaft	1	N/A	3.6
Metatarsal, indt. pos.	L	1	N/A	43.2
Metatarsal, r1	L	1	N/A	41.5
Metatarsal, r2	L	1	N/A	45.6
Metatarsal, l3	L	1	N/A	40.1
Phalanx, indt.	L	1	N/A	12.7
Cervical shield	DV thickness	1	N/A	10.5
	L—AP	1	N/A	30.4
	W	1	N/A	12.7

TABLE 1. Continued.

Element	Measurement	Nos. of element	Range	Mean
Osteoderm, r. dorsal	DV thickness	8	3.2–5.2	4.2
	L—AP	8	15.1–21.0	18.8
	W	8	17.2–26.3	22.1
Osterderm, l. dorsal	DV thickness	10	2.9–5.2	4.3
	L—AP	10	17.3–23.4	19.8
	W	10	18.2–31.3	23.8
Osterderm, lateral	L—AP	20	12.5–21.1	16.1
	W	20	13.4–27.7	16.2
	DV thickness	20	2.9–5.8	4.7
Osteoderm, caudal	L—AP	13	10.0–19.8	15.3
	W	13	3.7–7.8	6.2
	DV thickness	13	3.2–7.7	5.5

A fragmentary left postorbital (SMU 75310) represents the anterolateral corner of the skull table. The postorbital bar appears to be displaced medially from the skull roof. The sculptured dorsal surface enters the anterolateral margin of the supratemporal fenestrae, with a recessed, unsculptured wall descending into the opening.

The jugal is plate-like and well sculptured (SMU 75304, Fig. 4c). The ascending process of the postorbital bar is inclined posteriorly. Anterior to the bar, a curved notch forms the inferior margin of the orbit. Posterior to the bar, the dorsal margin of the jugal rises as a thin upwardly convex wall that forms the inferior margin of the infratemporal fenestra. Paired foramina pierce the medial surface of the jugal immediately posterior to the ascending process of the postorbital bar. A thick shelf-like process that projects from the medial wall provides a sturdy buttress for the suture with the ectopterygoid (SMU 75304, Fig. 4d). The posterior process of the jugal is damaged on all specimens. A sulcus borders the ventral jugal margin.

FIGURE 3. *Pachycheilosuchus trinquei* right maxilla (SMU 75278), dorsal view, note expanded lateral margin; ventral view, note displacement of alveoli from lateral margin. Scale bars equal 1 cm.

The robust quadrate is typically crocodyliform, with a deeply notched mandibular fossa and a deep fissure for the cranioquadrate passage (SMU 75284, Fig. 4e). Rugose suture facets reflect firm contact with the braincase and dermal bones. A foramen aereum is not present.

The basioccipital comprises the complete occipital condyle (SMU 75287, Fig. 4f). It bears a dorsal sagittal trough that represents the floor of the foramen magnum. A medial eustachian notch divides the ventral surface into paired basal tubera.

Mandible

The dentary of *Pachycheilosuchus* is dorsoventrally compressed (SMU 75279, Fig. 4g). The mandibular symphysis is short, extending to the anterior margin of the fourth alveolus (SMU 75279, Fig. 4h). The symphyseal angle is about 30°. Sutural surfaces show that the splenial was not involved in the symphysis.

There are 15 evenly spaced alveoli of approximately equal diameter. Those posterior to the symphysis are set in an alveolar groove. There is no lateral expansion of the labial margin of the dentary, and the tooth row is set along the lateral edge. Anteriorly, the alveoli are set along the extreme margin of the dentary at a mildly procumbent angle. This suggests that the anterior teeth protruded outside the edge of the dentary margin. Partial crocodyliform dentaries from the Lower Cretaceous of New South Wales, Australia exhibit similar procumbent anterior tooth placement (Molnar and Willis, 2001).

There is no festooning of the labial margin, which curves towards the symphysis. The anterior tip of the dentary terminates in a sharp point. Rough pitting and grooves sculpture the ventral surface and a row of nutrient foramina parallels the labial margin. The splenial surface of the dentary spans the medial margin of that bone posterior to the symphysis (SMU 75279, Fig. 4i). The large posterior opening of the Meckelian fossa is prominent within the splenial groove at a point one-third of the total dentary length from the tip of the posterior process. A medial mandibular foramen connects the fossa with the lateral surface of the dentary. The posterior process of the dentary is unforked, ending in a single sharp point. There is no evidence of a mandibular fenestra. On the dorsal margin the articular facet for the surangular is a slightly roughened, longitudinal concave shelf. A narrower facet is present for the angular ventromedially.

Half of the total length of the ventral surface of the surangular (SMU 75299) is involved in the suture with the dentary. The anterodorsal surface of the surangular has a cupped concavity for insertion of mandibular adductor muscles. Posterior to this concavity, a suture facet for the articular occupies the remaining dorsal margin. Three foramina are located on the medial margin superior to the suture with the dentary.

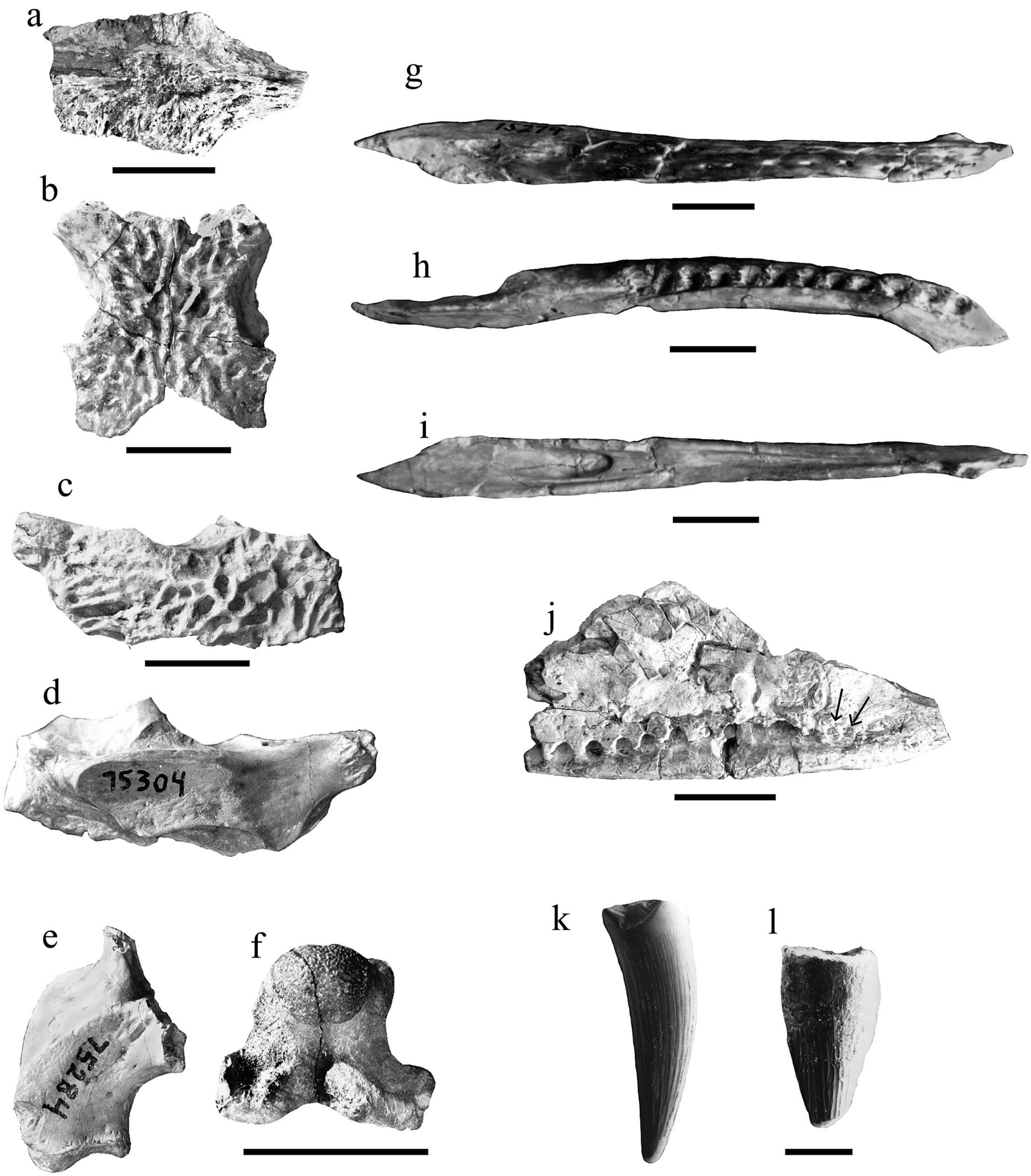

FIGURE 4. *Pachycheilosuchus trinquei* cranial elements, (**a**) frontal (SMU 75311), dorsal view, (**b**) parietal (SMU 75909), dorsal view, (**c**) left jugal (SMU 75304), lateral view, (**d**) left jugal, medial view, note buttressed shelf, (**e**) right quadrate (SMU 75284), ventral view, (**f**) basioccipital (SMU 75287), posterior view, (**g**) left dentary (SMU 75279), lateral view, (**h**) left dentary, dorsal view, (**i**) left dentary, medial view, (**j**) right maxilla (SMU 75009), ventral view, posterior to right, arrows point to broken tooth bases, (**k**) anterior tooth (SMU 75336), (**l**) posterior tooth (SMU 75337). Scale bars for a–j equal 1 cm, for k–l equal 2 mm.

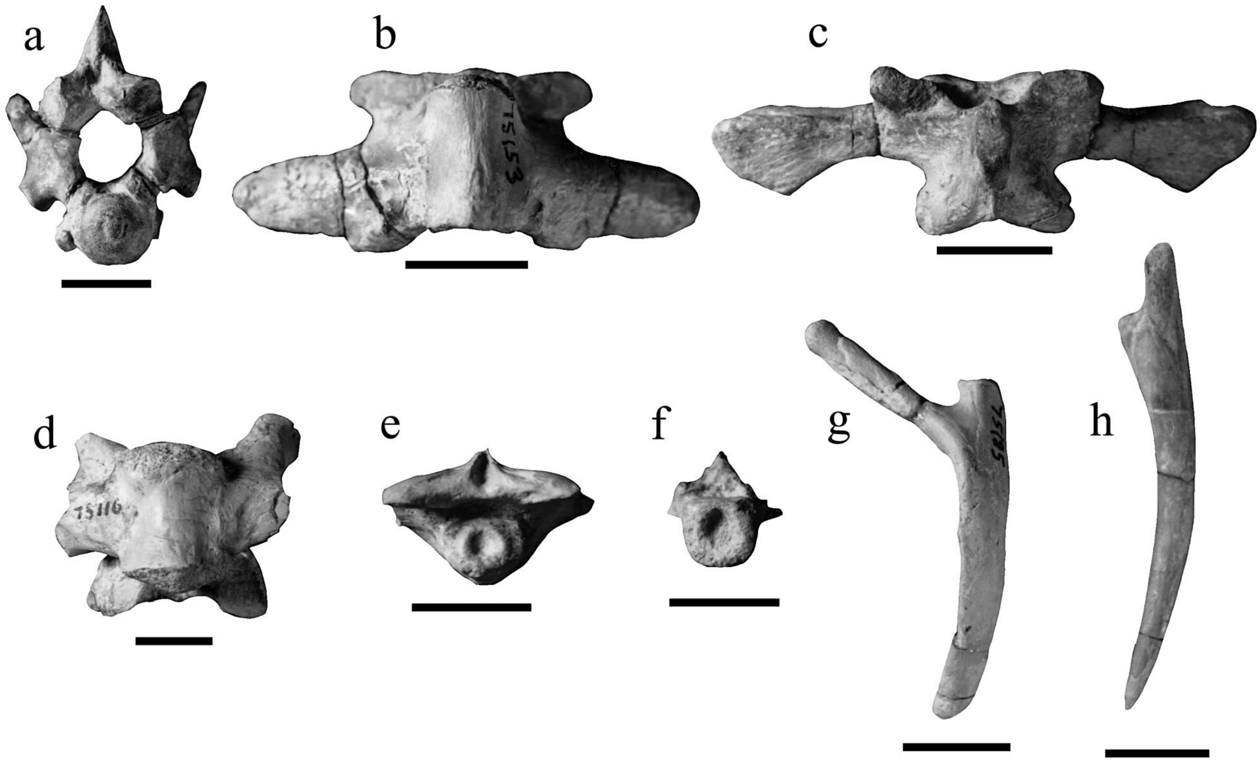

FIGURE 5. *Pachycheilosuchus trinquei* vertebrae and ribs, (**a**) anterior cervical vertebra (SMU 75107), caudal view, (**b**) anterior dorsal vertebra (SMU 7513), ventral view, (**c**) first sacral vertebra (SMU 75114), dorsal view, (**d**) biconvex first caudal vertebra (SMU 75116), ventral view, (**e**) anterior caudal vertebra (SMU 75131), posterior view, (**f**) posterior caudal vertebra (SMU 75150), posterior view, (**g**) anterior left dorsal rib (SMU 75185), anterolateral view, (**h**) posterior left dorsal rib (SMU 75196), medioventral view. Scale bars equal 1 cm.

Dentition

A right maxilla (SMU 75009) retains three broken teeth in posterior alveoli (Fig. 4j). Tooth base diameters range from 1.4–1.5 mm.

Sixty-nine isolated teeth were recovered. The teeth are referred to *Pachycheilosuchus* based upon their basal diameter, which is consistent with the diameters of the alveoli in tooth bearing elements of *Pachycheilosuchus*, their close association with other elements of *Pachycheilosuchus*, and their uniform morphology.

The teeth are conical, with little to no lateral compression. They vary slightly in height and degree of curvature. Most are 4.5–5.5 mm tall, gently curved, and longitudinally striated (SMU 75336, Fig. 4k). A few teeth are shorter, straighter, more conical, and exhibit more lateral compression (SMU 75337, Fig. 4l). They are likely from positions more posterior in the series than the slender teeth. Occlusal wear is limited to apical facets, with no variation in wear between the two dental morphologies.

Vertebral Column

A representative vertebral column was reconstructed from 63 relatively complete vertebrae. The number of vertebrae is unknown; however, the column was assembled with a standard crocodyliform number of 24 pre-sacral vertebrae, beginning with the third cervical vertebra (the atlas and axis were not recovered), and using seven cervicals, 15 dorsals (2 ribless posteriormost dorsals provide a short lumbar region), 2 sacrals, and 18 caudals. The representative column was assembled by identifying individual vertebrae with characters diagnostic of anterior, intermediate, and posterior positions of each region of the vertebral column.

The cervicals are the most strongly procoelous of the vertebrae. The posterior condyles exhibit a distinct concave dimple centered on the condyle, which is partially filled by a secondary ossified plug (SMU 75107, Fig. 5a). This character is repeated and modified throughout the vertebral column. The neural spines of the cervicals are anteriorly positioned atop the neural arch, with the anterior edge slightly posterior to the anterior margin of the centrum. On putative posterior cervicals the spines are posteriorly inclined. Anterior and dorsal margins are blade-like. Midway in the reconstructed cervical series, the posterior margin of the spine develops a central fissure that in life was filled by elastic ligament. The pre- and postzygapophyses are dorsal to the neural canal with medially inclined articular facets. The angle of inclination is 20°–29°. These facets become subhorizontal posteriorly. The parapophyses and diapophyses are pronounced, with distinct anteroposteriorly elongate rib facets. Progressing posteriorly from vertebrae assigned to positions C3 through C9, the parapophyses migrate from a ventrally directed orientation positioned anteriorly on the centrum to a laterally directed orientation just beneath the neurocentral suture. The diapophyses remain uniformly centered laterally upon the neural arch throughout the cervical series, with modification posteriorly in the series limited to a change in facet orientation from a ventrally to laterally directed, almost horizontal position. An hypopophysis is absent from the anterior cervicals, but appears as a knob-like process midway through the series.

Of the 18 dorsal vertebrae, one mid-series dorsal retains a complete spine. Throughout the dorsal series the spines span the neural arch anteroposteriorly. The preserved spine is blade-like, has a transversely expanded dorsal margin, and narrows posteriorly. Two vertebrae interpreted as D1 and D2 have small knob-like hypapohyses. Zygapophyseal facet inclination in the anterior dorsals is subhorizontal. At position D3 the zygapophyses are horizontal and the hypapophysis is absent. The parapophyses on the more anterior dorsals are located immediately above the neurocentral suture; posteriorly they progressively migrate laterally onto the transverse processes. At D4 the parapophysis arises fully from the neural arch. The parapophyses of D9 are at the mid-point of the wing-like transverse processes. In the most posterior dorsal that still retains rib facets (~D13), the parapohyses lie immediately anteromedial to the terminal diapophyseal facet. The facets do not merge into a terminal synpophysis.

The most posterior dorsal vertebrae lack diapophyses and parapophyses. Throughout the dorsal series a posteriorly-progressing modification of the transverse processes occurs as they elongate and widen into horizontal wing-like blades (SMU 75153, Fig. 5b). The processes are normal to the sagittal plane. The transverse processes of the posterior ribless dorsals (lumbars) are short and narrow. The centra in these vertebrae are laterally expanded. All dorsal centra are procoelous, and retain the posterior condylar dimple observed in the cervicals. The central plug, however, is absent. The dimple expands in the posterior dorsals, developing into a distinct posterior concavity, but it disappears in the most posterior dorsal.

Centra of the sacral vertebrae are laterally expanded, forming an elongate oval in cross section. The ventral surface is shallowly saddle-shaped. The first sacral is marginally procoelous, with a slightly concave cotyle, and a barely convex posterior condyle. The second sacral is amphicoelous, with both anterior and posterior cotyles slightly concave. Zygapophyseal facets are horizontal and smaller than those of the dorsals. The neural spine of the first sacral is robust, inclined anteriorly, tapers posteriorly, and has a laterally expanded apex (SMU 75114, Fig. 5c). Fused ribs create robust transverse processes that expand distally and end in slightly concave iliac articular facets.

The first caudal vertebra is biconvex (SMU 75116, Fig. 5d), with a concave dimple somewhat above the center of the posterior condyle. The transverse processes are broken, but appear to slant posteriorly. The centrum is laterally expanded, similar to the sacrals. A short neural spine spans the full length of the neural arch anteroposteriorly. The spines of the anterior caudals are slightly taller than the spine of the first sacral. The transverse processes are short, narrow, and are directed posteriorly. In anterior caudals the pre- and postzygapophyses are horizontal, transversely ovate, and normal to the sagittal plane. In posterior caudals the zygapophyses are oriented longitudinally (parasagittaly). The posterior caudals have small zygapophyseal facets, reduced neural spines, transversely cylindrical centra, paired ventrolateral keels, and progressively larger condylar dimples. The dimple is gradually modified as the central dimple expands, leaving a large concavity with a thickened rim. The modification continues until the rim disappears and the vertebrae become amphicoelous (SMU 75131, Fig. 5e; SMU 75150, Fig. 5f).

Only fragments of cervical ribs were recovered. Thirteen pairs of typically crocodyliform dorsal ribs were matched to vertebrae (SMU 75185, Fig. 5g, h). Gastralia and haemal arches were not recovered.

Pectoral Girdle and Forelimbs

Left and right scapulae, coracoids, humeri, radii, ulnae, and elements of the carpus and manus were recovered. The blade of the scapula has a strongly concave anterior margin and a semi-convex posterior margin (SMU 75073, Fig. 6a). A convex bend is present midway down the posterior edge, beyond which the margin is approximately straight. The dorsal edge of the blade is convex. The posterior edge of the scapular blade is thickened and rounded. The dorsal edge of the blade is slightly wider than the articular border for the coracoid, and thus is the widest part of the scapula.

The blade of the coracoid is less than half the width of its articular border with the scapula (SMU 75063, Fig. 6b). Like the scapula, its posterior edge is thicker than its anterior edge. The scapular border extends farther anteriorly than posteriorly. The coracoid foramen is moderately offset from the center of the proximal head and lies near the center of the coracoid shaft.

Articulated, the scapula and coracoid align to produce a smoothly curved arc. The articular surfaces of the glenoid fossa are smooth and of equal length. Both elements contribute equally to the glenoid fossa.

The humerus exhibits typical crocodyloid morphology (SMU 75028, Fig. 6c). The proximal head of the humerus is moderately offset from the slightly curved shaft. It is convex dorsally, strongly inturned medially, and expanded transversely. The deltopectoral crest is well developed, expanding from a sharp proximal crest into a distinct tuberosity that tapers distally and disappears along the shaft. A small corresponding tuberosity is located on the shaft dorsal to the deltopectoral crest. The distal humerus is downturned in line with the shaft curvature. Twin distal condyles are separated by a strong trochlear groove. Muscle attachment ridges mark the shaft near both the proximal end and the distal condyles.

The ulna exhibits a pronounced curvature. The proximal end is strongly inturned and expanded into a triangular head (SMU 75292, Fig. 6d). The shaft is markedly curved and compressed anteroposteriorly. The distal end of the ulna is flattened with a moderately convex distal face.

The radius is less robust than the ulna, with a slender, straight shaft (SMU 75263, Fig. 6e). The proximal end is expanded and has distinct articular facets, whereas the distal end is less expanded and is triangular in plan view.

Of the carpus, only a left radiale (SMU 75272) was recovered. It is a short, stout bone, two thirds as wide as long (8.3 mm $\times$ 12.2 mm). The proximal end is expanded with a broad radial articular facet. The shaft terminates in a minor distal expansion and a shallow facet. Elements of the manus recovered include phalanges of indeterminate position and an isolated ungual.

Pelvic Girdle and Hindlimbs

Pelvic girdle elements include complete left and right ilia, left ischium and a left pubis. The ilium is robust, has a large, well-defined acetabulum, a prominent postacetabular process that makes up one-third of the total element length of the ilium, and a small, pointed, preacetabular process (SMU 75057, Fig. 6f). The acetabulum is open ventrally between pubic and iliac articular peduncles. A strong dorsal supraacetabular crest is present. The facets for sacral rib articulation are rugose. Superior to the facets, a pronounced sulcus spans the width of the ilium, crossing the pre- and postacetabular processes. The dorsal margin of the ilium is slightly sinusoidal.

The ischium has an expanded posterior process and a small, elongate anterior process (SMU 75060, Fig. 6g). These processes articulate with the ilium, thus completing the acetabular perforation. The ischial blade is wider than the articular processes. It thins ventromedially to a sharp edge ($<$0.5 mm thick).

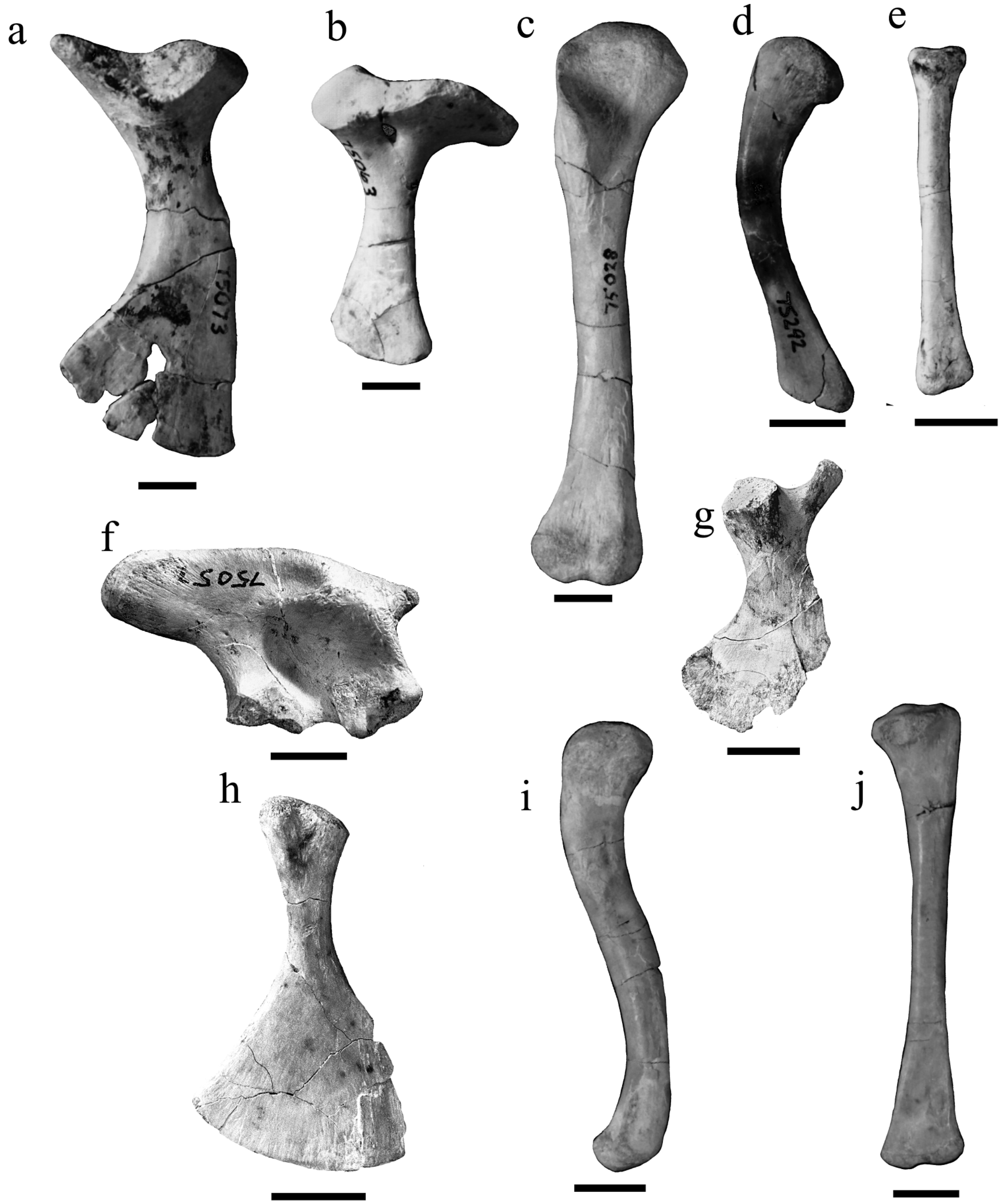

FIGURE 6. *Pachycheilosuchus trinquei* girdle and limb bones, (**a**) left scapula (SMU 75073), medial view, (**b**) left coracoid (SMU 75063), ventral view, (**c**) right humerus (SMU 75028), ventral view, (**d**) left ulna (SMU 75292), medial view, (**e**) left radius (SMU 75263), dorsal view, (**f**) left ilium (SMU 75057), medial view, (**g**) left ischium (SMU 75060), medial view, (**h**) left pubis (SMU 75296), dorsomedial view, (**i**) left femur (SMU 75015), lateral view, (**j**) right tibia (SMU 75037), medial view. Scale bars equal 1 cm.

Articulation with the pubis appears limited to a minor facet on the anterior process of the ischium.

The pubis has a broadly expanded transverse blade that arises from the lateromedially compressed shaft (SMU 75296, Fig. 6h). The anterior margin of the blade is convex and the posterior margin is concave. The distal margin is arcuate. The pubic blade tapers distally to end in a thin edge (0.5 mm).

Hind limb bones include five or more specimens of both left and right femora and tibiae, and single left and right fibulae. Tarsal bones recovered include a partial left calcaneum, right metatarsals I and II, and left metatarsal III.

The femur is sigmoidally curved, with the proximal and distal ends positioned in different planes due to twisting of the shaft (SMU 75015, Fig. 6i). The proximal end is compressed dorsoventrally. A well-developed fourth trochanter is present about a quarter of the length below the proximal end. The shaft between is noticeably constricted between the proximal end and the fourth trochanter.

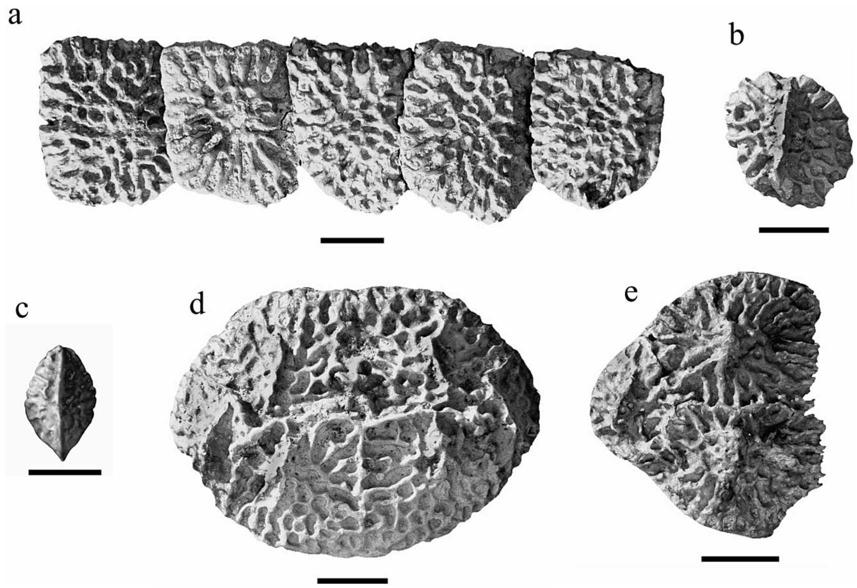

FIGURE 7. *Pachycheilosuchus trinquei* osteoderms, (**a**) right lateral series of unassociated dorsal osteoderms in imbricated position (SMU 75235–75239), midline at top, anterior to right; note medial suture facets, (**b**) lateral osteoderm (SMU 75222), (**c**) caudal osteoderm (SMU 75254, (**d**) cervical shield (SMU 75202), (**e**) incomplete cervical shield (SMU 75205), note visible sutures. Scale bars equal 1 cm.

The tibia is robust with a straight, smooth shaft (SMU 75037, Fig. 6j). The triangular proximal end contains a shallow articular facet. Viewed ventrally, the distal end is expanded into a U-shaped condyle that produces a large facet for articulation with the astragulus.

The fibula has a flattened, inturned head. A medial longitudinal ridge on the shaft is expanded into a tubercle just below the head of the tibia. The ridge grades into the shaft distally. A partial calcaneum has the calcaneal tuber broken away. The metatarsals are slender and straight, with flattened proximal ends. Paired distal condyles are present for articulation with the proximal phalanges.

Osteoderms

The osteoderms are heavily sculptured with deep pits that generally lengthen into sinuous grooves along the margins. A variety of morphologies reflect varying body positions. Palpebrae were not recovered.

The dorsal osteoderms are sub-rectangular in outline, with an anteroposterior length about two-thirds the mediolateral width (SMU 75235–75239, Fig. 7a). The dorsal osteoderms have a smooth, well-defined anterior shelf for imbrication with the tapered margin of the preceding osteoderm. There are no anteriorly directed lateral articular processes like those seen in the Goniopholidae and some other mesosuchian crocodilians. Dorsal osteoderms are bordered by a suture only on their medial margin, which indicates that no more than two rows of dorsal armor were present. Lateral margins of the dorsal osteoderms have a rounded, tapered edge. Keels are largely absent from the dorsal osteoderms, occurring as slight ridges in only 2 of the 24 specimens recovered. Other keeled osteoderms with rounded outlines and tapered edges may represent isolated lateral scutes (SMU 75222, Fig. 7b).

Caudal osteoderms are small, elongate, and keeled, with an oval, ventrally excavated base (SMU 75254, Fig. 7c). The keels taper to a sharp edge that is obliquely angled and projects posteriorly beyond the edge of the osteoderm. The keels are generally taller than those of the lateral osteoderms.

An autapomorphy for *Pachycheilosuchus* is a massive cervical shield, composed of six osteoderms fused into a single robust plate (SMU 75202, Fig. 7d). When fully fused, the shield shows no evidence of sutures, and has anteroposteriorly oriented dorsal ridges. Origin of the shield from six separate osteoderms is demonstrated by less completely fused specimens, which retain distinct sutures. Figure 7e (SMU 75205) illustrates an incomplete shield of three partially fused osteoderms. Several extant crocodylians have nuchal osteoderms clustered in a similar arrangement (Brazaitis, 1973; Ross and Mayer, 1983), however, none possesses a cervical shield composed of fused osteoderms, nor is the character reported in other fossil crocodyliforms.

DISCUSSION

The ''Glen Rose Form''

Fossils of the ''Glen Rose Form'' currently under study at the University of Texas by Dr. Wann Langston and examined for this study include an almost complete skull (USNM 22039), two partially articulated skeletons (TMM 42995-2, TMM 40644-1), and disarticulated, fragmentary elements including vertebrae with dimples on the posterior condyles. Comparison of this material with *Pachycheilosuchus* reveals that the specimens contain elements of at least two taxa. *Pachycheilosuchus* differs from the USNM skull in having deeper dermal sculpting, a more dorsoventrally compressed maxilla with an expanded lateral margin that is not festooned, a straighter, more gracile dentary, and less heterodonty. The partial skeletons, though incompletely prepared, appear more gracile than *Pachycheilosuchus* and show no evidence of procoelous vertebrae.

The isolated vertebrae and associated disarticulated elements (TMM 40595, TMM 41306, TMM 41307) are identical to *Pachycheilosuchus*. Brochu (1996) figured one of these *Pachycheilosuchus* vertebrae (TM 40595) in his examination of ontogenetic neurocentral suture closure. Two other Glen Rose fossil localities (SMU 327 and 335) in north central Texas have produced isolated crocodyliform elements attributable to *Pachycheilosuchus*.

The skull (USNM 22039) and the partial skeletons at the University of Texas represent a second taxon, which for convenience will continue to be referred to herein as the ''Glen Rose Form.'' The partial resolution of this material into at least two taxa will require revised scoring of ''Glen Rose Form'' characters in phylogenetic analyses, and these new data must be considered when reviewing previous analyses that include the ''Glen Rose Form'' (Benton and Clark, 1988; Brochu, 1997a, b, 1999, 2000; Buscalioni et al., 2001).

Vertebral Centrum Modification

The presence of a concave dimple centered on the posterior vertebral condyle is rare in crocodyliform vertebrae. Known occurrence of dimpled posterior condyles in mesoeucrocodylian vertebrae appears limited to *Pachycheilosuchus* and *Theriosuchus*. Joffe (1967) described an anterior caudal vertebra of *Theriosuchus pusillus* (BMNH 48216) as being procoelous with a central depression, and mentions the occurrence of this character in a small crocodilian from Texas. Buffetaut (1982) noted that these specimens were intermediate in morphology between mesosuchians (which are now regarded by some as primitive members of Mesoeucrocodylia) and eusuchians, and suggested the possibility that they might represent convergent lineages. Brinkmann (1992) described an isolated procoelous vertebra (IPFUB 102/59.1) with a central depression that was recovered in association with *Theriosuchus* and *Bernissartia* from the Upper Barremian of Spain. He referred the vertebra to *Bernissartia*. However, this would be the first report of this character in *Bernissartia* and it seems more likely that the vertebra is from *Theriosuchus*, with which it accords morphologically.

The representative composite vertebral column of *Pachycheilosuchus* allows discussion of the morphological variation along the column. The posterior caudal vertebrae of *Pachycheilosuchus* are amphicoelous, with approximately equal anterior and posterior cotyles (SMU 75131, Fig. 8a, b). Anteriorly, the caudals develop a thickened rim around the posterior cotyle, which indicates incipient development of a posterior condyle, (SMU 75150, Fig. 8c). Except in the first caudal, which is biconvex, the trend toward more progressive procoely progresses cranially within the column. The rim margins continue to expand centripetally, gradually reducing the posterior concavity to a minor dimple. The buttressed, inflexible sacral region precludes development of the posterior condyle on the anterior sacral. All other dorsal vertebrae show the central dimple, and the anteriorly progressive development of a hemispheric condyle is evident (SMU 75164, 75153, Fig. 8d, e). The trend culminates within the cervical series, where the closure of the residual dimple is accomplished by development of a distinct central plug (SMU 75107, Fig. 8f). The anterior cervicals have a complete posterior condyle, but often display traces of the condylar dimple.

The mechanical advantage of the stronger, more flexible procoelous vertebra is well understood (Troxell, 1925), and procoelous vertebrae have long been recognized as a derived crocodyliform character that has served as one diagnostic character of Eusuchia (Benton and Clark, 1988). Although Buffetaut (1982) presented a schematic figure illustrating a *Theriosuchus* vertebra as an intermediate condition between amphicoelous and procoelous, the mechanism for the development of procoely from the primitive amphicoelous morphology is unclear. *Pachycheilosuchus trinquei* demonstrates one method of accomplishing the transition to procoely.

Ontogeny

Although size is considered characteristic of certain crocodyliform taxa, it is difficult to determine maturity of an individual or define a species based upon size. Owing to indeterminate growth and varying growth rates, size is usually regarded as an unreliable measure of age and maturity. In a study of extant crocodilians, Mook (1921) described numerous characters that can be used to determine levels of maturity including skull proportions; size, shape and placement of supratemporal fenestrae; morphology of the skull table; and degree of ossification and sculpture of dermal bone. Other authors have examined patterns of ossification in order to determine degree of osteological development (Rieppel, 1993; Brochu, 1996). Hutton (1986) described a reliable method for determining the age of living specimens of *Crocodylus niloticus*, based upon deposition of cortical laminae in limb bones and osteoderms. Similar methods have since been used to estimate the individual age of fossil crocodylians (de Buffrenil and Buffetaut, 1981; Erickson and Brochu, 1999).

Two methods were used to estimate the total length of *Pachycheilosuchus*. The first method employed a regression formula based upon the ratio of head length to total body length for *Crocodylus porosus* developed by Jackson and Campbell (1974). Because a complete skull was not available, a proxy length was derived from total dentary length. Three measured dentaries of *Alligator mississippiensis* equal approximately 91 percent of total skull length. If a similar ratio held in *Pachycheilosuchus*, use of the dentary length as a proxy for skull length should yield a conservative estimate of total body length. Thus, using the formula, $y = -4.39 + 7.49x$, where y is total length and x is head length, and a head length proxy from an average dentary length of 85.4 mm, a total body length of 63.5 cm was calculated. A second length estimation of 80 cm was provided by measurement of the composite skeleton reconstructed from *Pachycheilosuchus* elements mentioned herein.

An ontogenetic age of selected *Pachycheilosuchus* elements was estimated by examining cortical bone growth, using methods from Hutton (1986). Representative specimens of a humerus (SMU 75300) and femur (SMU 75301) were examined for evidence of cortical laminae characteristic of annual growth cycles. Both elements had eight preserved cumulative laminae (SMU 75300, Fig. 9). Although expansion of the medullary cavity can obliterate innermost laminae, a minimum age of eight years is indicated. Many other limb bones from the site are of approximately equal diameter, which suggests relatively equivalent age and development (SMU 75300 is 8.3 mm in diameter, measured just distal to the deltopectoral crest; five other right humeri range from 8.0–9.7 mm in diameter). Comparisons with recent crocodylians such as *Caiman crocodilus crocodilus*, which is known to be sexually mature at four years, and *Crocodylus palustris*, which is sexually mature at 6.6 years (Ferguson, 1985), suggest that some recovered *Pachycheilosuchus* elements represent sexually mature individuals.

Closure of vertebrae neurocentral sutures is another indicator of relative maturity in crocodilians (Brochu, 1996). These sutures close in a caudal to cranial sequence during ontogeny (Rieppel, 1993; Brochu, 1996). Dorsal vertebrae of *Pachycheilosuchus* show full closure in all but one specimen. Most cervical vertebrae are fractured, somewhat obscuring the sutures, but all appear to have complete closure.

The calculated body length of 63.5 cm allows comparison with egg and body sizes of sexually mature extant crocodylians. The complete crocodiloid egg recovered in association with *Pachycheilosuchus* elements is 49 mm long (Rogers, 2000). Measurements of average body length at sexual maturity and egg length for nine extant crocodylian taxa were taken from Fer-

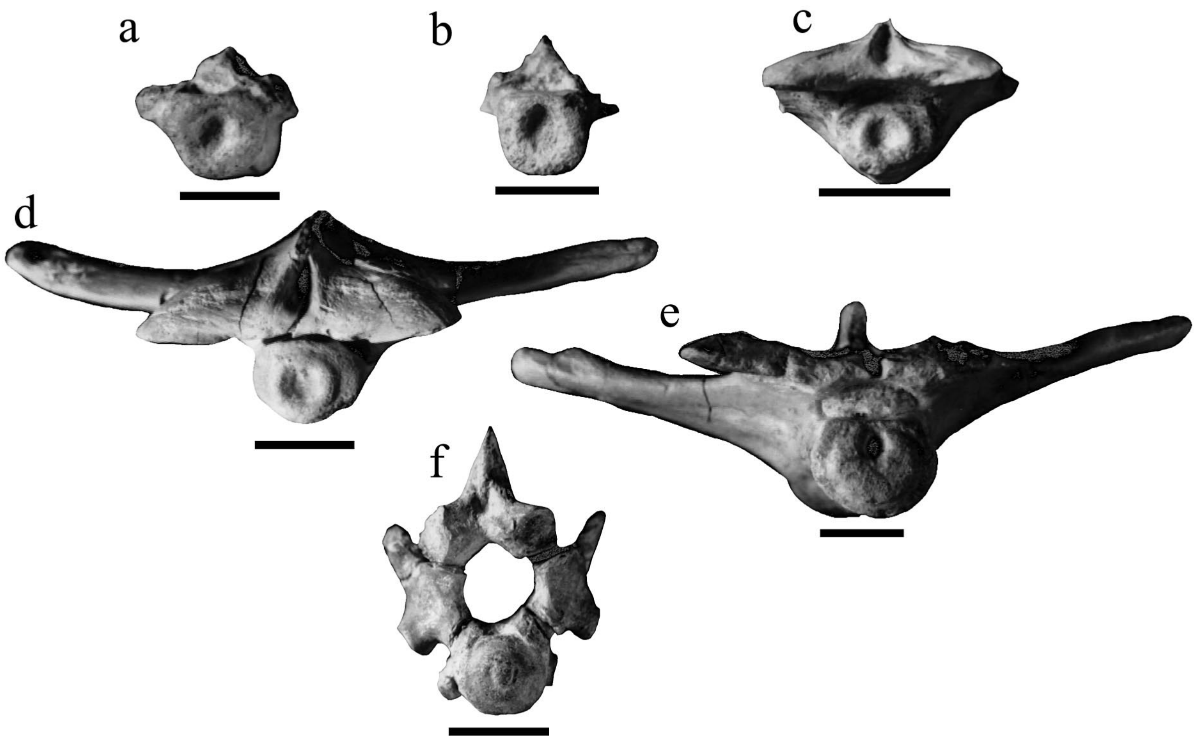

FIGURE 8. *Pachycheilosuchus trinquei* vertebrae, (**a**) posterior caudal vertebra (SMU 75131), anterior view, (**b**) posterior view, (**c**) anterior caudal vertebra (SMU 75150), posterior view, (**d**) posterior dorsal vertebrae (SMU 75164), posterior view, (**e**) anterior dorsal vertebrae (SMU 75153), posterior view, (**f**) mid-series cervical vertebra (SMU 75107). Scale bars equal 1 cm.

guson (1985), and egg length was plotted as a function of body length (Fig. 10). Utilizing the resultant regression, y = 16.6x + 47.08 (standard error = 6.48) with the calculated *Pachycheilosuchus* body length of 63.5 cm, an egg length of 56 mm was obtained. The length of the egg (49 mm) falls within the lower end of the range of standard error, demonstrating that *Pachycheilosuchus* was of sufficient size to have produced the egg.

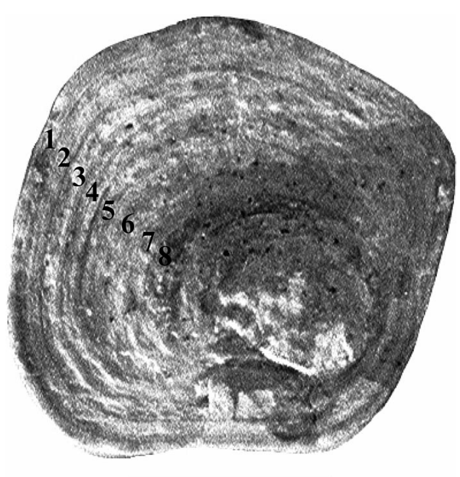

FIGURE 9. *Pachycheilosuchus trinquei* humerus cross section at mid-shaft, illustrating annual growth lines. Eight annual growth cycles are numbered. Scale bar equals 5 mm.

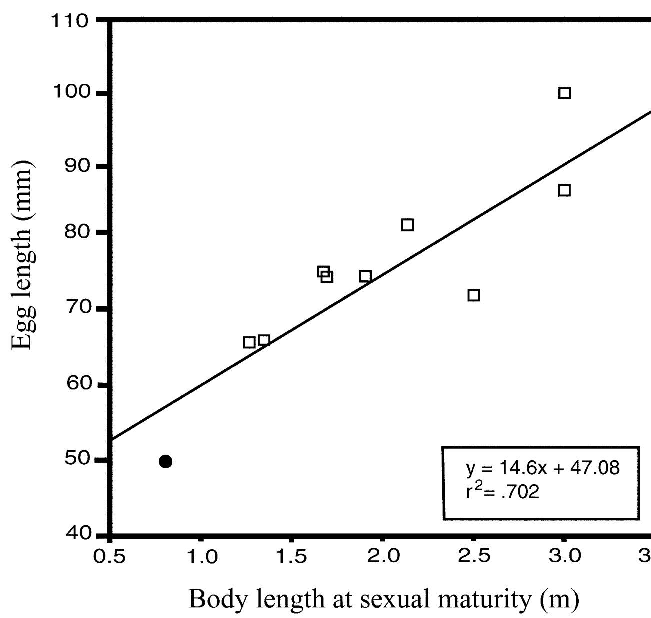

FIGURE 10. Comparison of body length to egg length in extant crocodylians (data from Ferguson, 1985) and *Pachycheilosuchus trinquei*. Open squares indicate extant crocodylians, solid circle indicates *Pachycheilosuchus* (length determined using skull/body length regression from Jackson and Campbell, 1974).

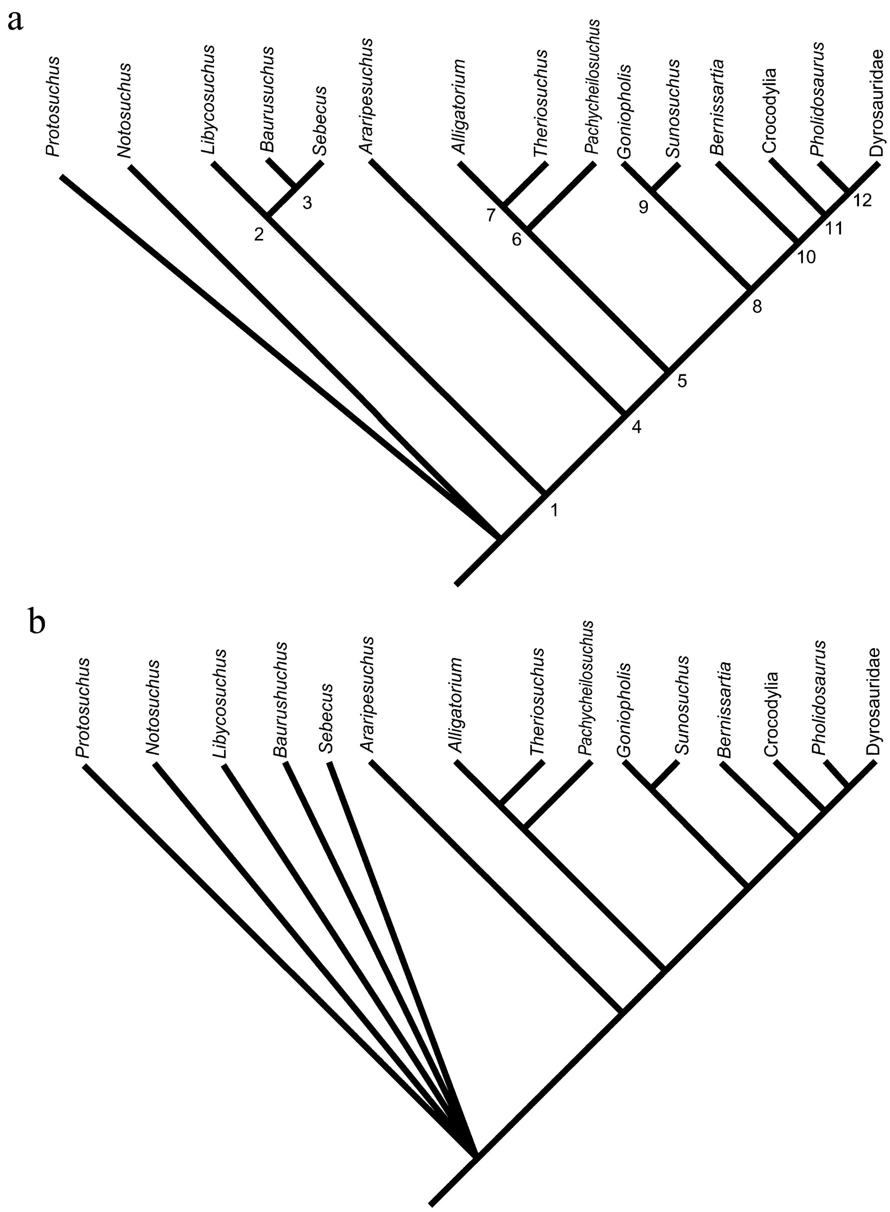

FIGURE 11. (**a**) cladogram of tree 1, arbitrarily chosen from 6 most parsimonious trees. Tree length 164 steps, C.I. 0.660, R.I. 0.590. Characters for each node and terminal taxa are listed in Appendix 3, (**b**) strict consensus of six most parsimonious trees.

Phylogenetic Relationships

One hundred and twelve characters (Appendix 1) were used to assess phylogenetic relationships of *Pachycheilosuchus*, employing PAUP, version 3.1.1 (Swofford, 1993). Characters 1–101 are taken from Clark (1994), with modifications of 92–94 reflecting the incipient procoelous condition; characters 102–110 are from Buckley and Brochu (1999). Characters 111 and 112 are new for this study. Fifteen representative mesoeucrodylian taxa, exclusive of thalattosuchians, were included in the analysis, with *Protosuchus* used as an outgroup (Appendix 2). Character scoring for taxa other than *Pachycheilosuchus* and *Sunosuchus* is from Buckley and Brochu (1999), and scoring for *Sunosuchus* is from Wu et al. (1997). A heuristic search employing 1,000 iterations of random stepwise addition was used to yield six most parsimonious trees, each with a length of 164 steps, a consistency index (C.I.) of 0.660, and a retention index (R.I.) of 0.590. Figure 11a illustrates one arbitrarily chosen tree (Appendix 3 lists unambiguous apomorphies defining each node and terminal taxa) and a strict consensus tree is shown in Figure 11b.

The results of the analysis show a general congruence with Buckley and Brochu (1999) and Clark (1994). Basal taxa are not resolved; however, these relationships are peripheral to this study, and do not affect determination of relationships between *Pachycheilosuchus* and more derived taxa. Bereft of previously attributed ''Glen Rose Form'' characters, *Pachycheilosuchus* is found to be a sister taxon to Atoposauridae, represented by *Theriosuchus* and *Alligatorium*, in all six trees.

A number of small, brevirostrine mesoeucrocodylians have been included in Atoposauridae, and several authors have identified characters diagnostic of the clade (Kuhn, 1968; Steel, 1973; Buscalioni and Sanz, 1988). Characters common to these

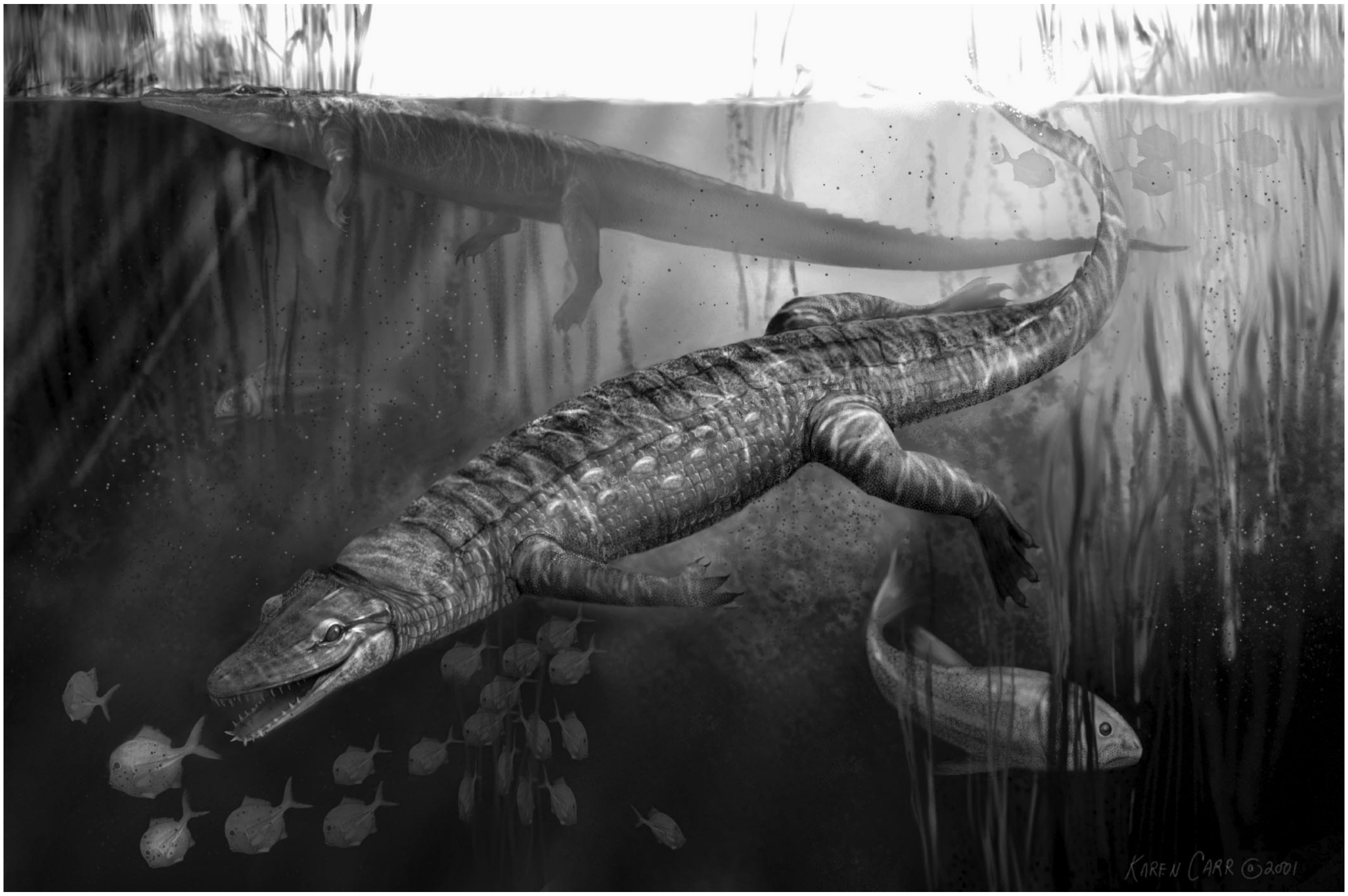

FIGURE 12. Life reconstruction of *Pachycheilosuchus*. Original art by Karen Carr.

studies include: small overall size; brevirostry; large orbits; divided external nares; small supratemporal fenestrae; and reduced armor. All of these characters are shared by *Pachycheilosuchus*, *Alligatorium*, and *Theriosuchus*, but are also found in other crocodyliform clades. A life reconstruction of *Pachycheilosuchus* is shown in Figure 12.

These studies and other recent analyses by Clark (1994) and Wu et al. (1996) indicate that Atoposauridae is a monophyletic clade that is united by a similarity in size and general morphology, rather than by diagnostic synapomorphies. This is supported by this analysis, where *Alligatorium* and *Theriosuchus* are placed in a monophyletic clade that is supported by two unambiguous diagnostic characters, nos. 31 and 83. Bootstrap analysis provides support for the clade, which occurs in 88% of the replicates. Morphological characteristics shared by *Alligatorium*, *Theriosuchus*, and *Pachycheilosuchus* include: a broad, wide, rostrum; laterally compressed posterior teeth; fused frontals; absence of a mandibular fenestra; an unsculptured, columnar, temporal bar; an anterior scalpular margin that is more concave than the posterior margin; an anterior iliac process that is much shorter than the posterior process; and a jugal in which the anterior process is as broad as the posterior. Characters diagnostic of the unnamed clade that unites these three taxa in this analysis include similar jugal and vertebral morphologies (characters shared among the three taxa include nos. 17, 92, and 93). However, the group is not supported by 50% of bootstrap replicates.

Atoposauridae is the only non-eusuchian clade reported to exhibit some form of procoely, as seen in *Theriosuchus* and in *Brillanceausuchus barbouriensis*, another small procoelous atoposaurid from the Early Cretaceous of Africa (Michard et al., 1990). Procoelous vertebrae, previously considered diagnostic of a close relationship with Eusuchia, could suggest a eusuchian relationhip for *Pachycheilosuchus*. Position of the choanae would seem to be an important character in assessing this, but unfortunately is unknown in *Pachycheilosuchus*. An alternate phylogeny of sister taxa relationship between *Pachycheilosuchus* and Eusuchia was tested using MacClade v. 3.08 (Maddison and Maddison, 1992). Forcing *Pachycheilosuchus* into a sister taxon relationship with Crocodylia produced an alternate tree with 169 steps, requiring *Pachycheilosuchus* to possess six more eusuchian synapomorphies in order to make this relationship more parsimonious than that illustrated in Figure 11. Based upon the results of this analysis, the possibility that procoelous vertebrae may have evolved in parallel in more than one mesoeucrocodylian lineage appears reasonable.

ACKNOWLEDGMENTS

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LITERATURE CITED

Barck, A. 1992. Paleontology of the Glen Rose Formation (Lower Cretaceous), Hood County, Texas. Texas Journal of Science 44:3–23.

Boggs, S., Jr. 2001. Principles of Sedimentology and Stratigraphy. Prentice Hall, Englewood Cliffs, 726 pp.

Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia; pp. 295–338 *in* M. J. Benton (ed.), The Phylogeny and Classification of the Terapods, Vol. 1. Clarendon Press, Oxford.

Brasier, M. D. 1980. Microfossils. George Allen & UNWIN LTD, London, 193 pp.

Brazaitis, P. 1973. The identification of living crocodilians. Zoologica 58:59–101.

Brinkmann, W. 1992. Die Krokodilier-Fauna aus der Unter-Kreide (Ober-Barremium) von Uña (Provinz Cuenca, Spanien). Berliner Geowissenschaftliche Abhandlungen E 5:1–143.

Brochu, C. A. 1996. Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. Journal of Vertebrate Paleontology 16:49–62.

——— 1997a. Fossils, morphology, divergence timing, and the phylogenetic relationships of *Gavialis*. Systematic Biology 46:479–522.

——— 1997b. A review of ''*Leidyosuchus*'' (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. Journal of Vertebrate Paleontology 17:679–697.

——— 1999. Phylogeny, systematics and historical biogeography of Alligatoroidea. Society of Vertebrate Paleontology Memoir 6:9–100.

——— 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. Copeia 2000: 657–673.

Buckley, G. A., and C. A. Brochu. 1999. An enigmatic new crocodile from the Upper Cretaceous of Madagascar. Special Papers in Palaeontology 60:149–175.

Buffetaut, E. 1982. Radiation évolutive, paléoécologie et biogéographie des Crocodiliens mésosuchiens. Memoires de la Société Géologique de France, No. 142, 86 pp.

Buscalioni, A. D., and J. L. Sanz. 1988. Phylogenetic relationships of the Atoposauridae (Archosauria, Crocodylomorpha). Historical Biology 1:233–250.

———, F. Ortega, D. B. Weishampel, and C. M. Jianu. 2001. A revision of the crocodyliform *Allodaposuchus precedens* from the Upper Cretaceous of the Hateg Basin, Romania. Its relevance in the phylogeny of Eusuchia. Journal of Vertebrate Paleontology 21:74–86.

Clark, J. M. 1994. Patterns of evolution in Mesozoic crocodyliformes; pp. 84–97 *in* N. C. Frazier and H. D. Sues (eds.), In the Shadow of the Dinosaurs. Cambridge University Press, New York.

Davis, K. W. 1973. Stratigraphy and depositional environments of the Glen Rose Formation, north–central Texas. Baylor Geological Studies, Bulletin 26, 43 pp.

de Buffrenil, V., and E. Buffetaut. 1981. Skeletal growth lines in an Eocene crocodilian skull from Wyoming as an indicator of ontogenic age and paleoclimatic conditions. Journal of Vertebrate Paleontology 1:57–66.

Erickson, G. M., and C. A. Brochu. 1999. How the 'terror crocodile' grew so big. Nature 398:205–206.

Farlow, J. O. 1981. Estimates of dinosaur speeds from a new trackway site in Texas. Nature 294:747–748.

——— 1987. A guide to Lower Cretaceous dinosaur footprints and tracksites from the Paluxy River Valley, Somervell County, Texas. Field Trip Guidebook, South–Central Section, Geological Society of America, Baylor University, Waco, Texas, 50 pp.

Ferguson, M. W. J. 1985. Reproductive biology and embryology of the crocodilians; pp. 330–491 *in* C. Gans (ed.), Biology of the Reptilia, Vol. 14. John Wiley and Sons, New York.

Grande, L., and W. E. Bemis. 1998. A comprehensive study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Journal of Vertebrate Paleonotology Memoir 4.

Hayward, O. T., and L. F. Brown Jr. 1967. Comanchean (Cretaceous) rocks of central Texas; pp. 31–48 *in* L. Hendricks (ed.), Comanchean (Lower Cretaceous) Stratigraphy and Paleontology of Texas. Society of Economic Paleontologists and Mineralologists Publication No. 67-8.

Huggins, H. H. 1990. Phyllodont (Paralbulinae) fish toothplates from the Lower Cretaceous Glen Rose Formation of central Texas. Texas Journal of Science 42:77–81.

Hutton, J. M. 1986. Age determination of living Nile crocodiles from the cortical stratification of bone. Copeia 1986:332–341.

Jackson, J. F., and H. W. Campbell. 1974. On the maximum total length of the salt-water crocodile (*Crocodylus porosus*). Journal of Herpetology 8:381–384.

Jacobs, L. L., and D. A. Winkler. 1998. Mammals, archosaurs, and the Early to Late Cretaceous transition in north-central Texas; pp. 253–280 *in* Y. Tomida, L. J. Flynn, and L. L. Jacobs (eds.), Advances in Vertebrate Paleontology and Geochronology. National Science Museum Monographs, no. 14, Tokyo.

Joffe, J. 1967. The 'dwarf' crocodiles of the Purbeck Formation, Dorset: a reappraisal. Palaeontology 10:629–639.

Kuban, G. 1989. Color distinctions and other curious features of dinosaur tracks near Glen Rose, Texas; pp. 427–440 *in* D. D. Gillette and M. G. Lockley (eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge.

Kuhn, O. 1968. Die Vorzeitlichen Krokodile. Verlag Ogben, Munich, 124 pp.

Langston, W. 1974. Nonmammalian Comanchean tetrapods. Geoscience and Man 8:77–102.

Maddison, W. P., and D. R. Maddison. 1992. MacClade: Analysis of Phylogeny and Character Evolution, Version 3.08. Sinauer Associates, Inc. Sunderland, Massachusetts, 398 pp.

Michard, J., F. de Broin, and M. B. et Joseph Hell. 1990. Le plus ancien crocodilien néosuchien spécialisé à caractères ''eusuchiens'' du continent Africain (Crétacé inférieur, Cameroun). C.R. Acad. Sci. Paris, t. 311(II):365–371.

Molnar, R. E., and P. M. A. Willis. 2001. New crocodyliform material from the Early Cretaceous Griman Creek Formation, at Lighthouse Ridge, New South Wales; pp. 75–82 *in* G. C. Grigg, R. Seebacher, and C. E. Franklin (eds.), Crocodilian Biology and Evolution. Surrey Beatty & Sons, Chipping Norton.

Mook, C. M. 1921. Notes on the postcranial skeleton in the crocodilian. Bulletin of the American Museum of Natural History 44:67–100.

Murry, P. A., D. A. Winkler, and L. L. Jacobs. 1991. An azhdarchid pterosaur humerus from the Lower Cretaceous Glen Rose Formation of Texas. Journal of Paleontology 65:167–170.

Rieppel, O. 1993. Studies on skeleton formation in reptiles. V. patterns of ossification in the skeleton of *Alligator mississippiensis* Daudin (Reptilia, Crocodylia). Zoological Journal of the Linnean Society 109:301–325.

Rodgers, R. W. 1967. Stratigraphy of Glen Rose limestone, central Texas; pp. 119–130 *in* L. Hendricks (ed.), Comanchean (Lower Cretaceous) Stratigraphy and Paleontology of Texas. Society of Economic Paleontologists and Mineralologists Publication No. 67-8.

Rogers, J. V. 2000. A complete crocodiloid egg from the Lower Cretaceous (Albian) Glen Rose Formation, central Texas. Journal of Vertebrate Paleontology 20:780–783.

Ross, F. D., and G. C. Mayer. 1983. On the dorsal armor of the Crocodilia; pp. 305–331 *in* A. G. Rhodin and K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology. Harvard University Press, Cambridge.

Steel, R. 1973. Handbuch der Paleoherpetologie, Vol. 16. Crocodylia. Fischer Verlag, Stuttgart, 116 pp.

Swofford, D. L., and D. P. Begle. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Thurman, J. 1971. Cartilaginous fishes of the Trinity Group and related rocks (Lower Cretaceous) of north central Texas. Southeastern Geology 13:207–227.

——— 1974. Lower vertebrate faunas of the Trinity Division in north–central Texas. Geoscience and Man 8:103–129.

Troxell, E. L. 1925. Mechanics of crocodile vertebrae. Bulletin of the Geological Society of America 36:605–614.

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

Wellnhofer, P. 1971. Die Atoposauridae (Crocodylia, Mesosuchia) der Oberjura-Plattenkalke Bayerns. Palaeontographica 138A:133–165.

Whetstone, K. N., and P. S. Whybrow. 1983. A ''cursorial'' crocodilian from the Triassic of Lesotho (Basutoland), Southern Africa. Occasional Papers of the Museum of Natural History, University of Kansas 106:1–37.

Williamson, T. E., J. I. Kirkland, and S. G. Lucas. 1993. Selachians from the Greenhorn Cyclothem (''Middle'' Cretaceous: Cenomanian-Turonian), Black Mesa, Arizona, and the paleogeographic distribution of Late Cretaceous selachians. Journal of Paleontology 67:447–474.

Winkler, D. A., P. A. Murry, and L. L. Jacobs. 1990. Early Cretaceous (Comanchean) vertebrates of central Texas. Journal of Vertebrate Paleontology 10:95–116.

Wu, X., D. R. Brinkman, and A. P. Russel. 1996. A new alligator from the Upper Cretaceous of Canada and the relationships of early eusuchians. Palaeontology 39:351–375.

———, H. D. Sues, and Z. Dong. 1997. *Sichuanosuchus shuhanensis*, a new? Early Cretaceous protosuchian (Archosauria: Crocodyliformes) from Sichuan (China), and the monophyly of Protosuchia. Journal of Vertebrate Paleontology 17:89–103.

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APPENDIX 1

List of characters used in the phylogenetic analysis. Characters 1 to 101 are taken from Clark (1994), with modification of 92–94 to reflect a semi-procoelous vertebral morphology. Characters 102–110 are from Buckley and Brochu (1999), whose matrix also utilized characters 1–101 from Clark (1994). Characters 111 and 112 are new for this study. Following Clark (1994), characters 15, 37, 49, 67 and 77 are treated as ordered.

1. External surfaces of cranial and mandibular bones smooth (0) or heavily ornamented, with deep grooves and pits (1)
2. Rostrum narrow anterior to orbits, broadening abruptly at orbits (0) or broad throughout (1)
3. Rostrum higher than wide (0) or nearly tubular (1) or wider than high (2) (unordered)
4. Premaxilla forms at least ventral half of internarial bar (0) or forms little, if any, of internarial bar (1)
5. Premaxilla narrow anterior to nares (0) or broad, similar in breadth to the part lateral to nares (1)
6. Dorsal part of premaxilla vertical, nares laterally oriented (0), or dorsal part of premaxilla nearly horizontal, nares dorsolaterally or dorsally oriented (1)
7. Palatal parts of premaxillae do not meet posterior to incisive foramen (0) or meet posteriorly along contact with maxillae (1)
8. Premaxilla loosely overlies maxilla on face (0), or premaxilla and maxilla sutured together along butt joint (1)
9. Premaxilla and maxilla with broad contact on face, rostrum does not narrow at contact (0), or broad, laterally open notch between maxilla and premaxilla (1), or rostrum constricted at contact with premaxilla and maxilla, forming narrow slit (2), or rostrum constricted at contact with premaxilla and maxilla, forming broad, laterally directed concavity (3) (unordered)
10. Posterior ends of maxillae do not meet on palate anterior to palatines (0), or ends do meet (1)
11. Nasal contact lacrimal (0) or do not (1)
12. Lacrimal contacts nasal along medial edge only (0) or on medial and anterior edges (1)
13. Nasal takes part in narial border (0) or does not (1)
14. Nasal contacts premaxilla (0) or does not (1)
15. Descending process of prefrontal does not contact palate (0), or contacts palate (1), or contacts palate in robust suture (2) (ordered)
16. Postorbital anterior to jugal on postorbital bar (0), postorbital medial to jugal (1), or postorbital lateral to jugal (2) (unordered)
17. Anterior part of jugal as broad as posterior part (0) or about twice as broad as posterior part (1)
18. Jugal transversely flattened beneath lateral temporal fenestra (0) or rod-shaped beneath fenestra (1)
19. Quadratojugal narrows dorsally, contacting only a small part of postorbital (0), or quadratojugal extends dorsally as a broad sheet contacting most of postorbital portion of postorbital bar (1)
20. Frontals narrow between orbits (similar in breadth to nasals) (0) or are broad, about twice nasal breadth (1)
21. Frontals paired (0) or fused (1)
22. Dorsal surface of frontal and parietal flat (0) or with narrow midline ridge (1)
23. Frontal extends well into supratemporal fossa (0) or extends only slightly or not at all (1)
24. Supratemporal roof with complex dorsal surface (0), or dorsally flat ''skull table'' developed, with squamosal and postorbital with flat shelves extending laterally beyond quadrate contacts (1)
25. Postorbital bar weak, lateral surface sculpted (if skull sculpted) (0), or postorbital bar robust, unsculpted (1)
26. Postorbital bar transversely flattened, unsupported by ectopterygoid (0), or postorbital bar columnar, supported by ectopterygoid (1)
27. Vascular opening on lateral edge of dorsal part of postorbital bar absent (0) or present (1)
28. Postorbital without anterolateral process (0) or with anterolateral process (1)
29. Dorsal part of postorbital with anterior and lateral edges only (0) or with anterolaterally facing edge (1)
30. Dorsal end of postorbital bar broadens dorsally, continuous with dorsal part of postorbital (0), or dorsal part of postorbital bar constricted, distinct from dorsal part of postorbital (1)
31. Bar between orbit and supratemporal fossa broad and solid, with broadly sculpted dorsal surface (0), or bar narrow, with sculpturing on anterior part only (1)
32. Parietal without broad occipital portion (0) or with broad occipital portion (1)
33. Parietal with broad, sculpted region separating fossae (0) or with sagittal crest between supratemporal fossae (1)
34. Postparietal (dermosupraoccipital) a distinct element (0) or not distinct (fused with parietal?) (1)
35. Posterodorsal corner of squamosal squared off, lacking extra ''lobe'' (0) or with unsculpted ''lobe'' (1)
36. Posterior edge of squamosal nearly flat (0), or posterolateral edge of squamosal extends posteriorly as a long process (1)
37. Palatines do not meet on palate below narial passage (0), or form palatal shelves that do not meet (1), or meet ventral to narial passage, forming part of secondary palate (2) (ordered)
38. Pterygoid restricted to palate and suspensorium, joint with quadrate and basisphenoid overlapping (0), or pterygoid extends dorsally to contact laterosphenoid and form ventrolateral edge of trigeminal foramen, strongly sutured to quadrate and laterosphenoid (1)
39. Choana opens ventrally from palate (0) or opens posteriorly into midline depression (1)
40. Palatal surface of pterygoid smooth (0) or sculpted (1)
41. Pterygoids separate posterior to choanae (0) or are fused (1)
42. Choana moderate in size, less than one-fourth of skull breadth (0), or choana extremely large, nearly half of skull breadth (1)
43. Pterygoids do not enclose choanae (0) or enclose choanae (1)
44. Choanae situated near anterior edge of pterygoids (or anteriorly) (0) or in middle of pterygoids (1)
45. Quadrate without fenestrae (0), or with single fenestra (1), or with three or more fenestrae on dorsal and posteromedial surfaces (2) (unordered)
46. Posterior edge of quadrate broad medial to tympanum, gently concave (0), or posterior edge narrow dorsal to otoccipital contact, strongly concave (1)
47. Dorsal, primary head of quadrate articulates with squamosal, otoccipital, and prootic (0) or with prootic and laterosphenoid (1)
48. Ventrolateral contact of otoccipital with quadrate very narrow (0) or broad (1)
49. Quadrate, squamosal, and otoccipital do not meet to enclose cran-

ioquadrate passage (0), enclose passage near lateral edge of skull (1), or meet broadly lateral to passage (2) (ordered)

50. Pterygoid ramus of quadrate with flat ventral edge (0) or with deep groove along ventral edge (1)
51. Ventromedial part of quadrate does not contact otoccipital (0) or contacts otoccipital to enclose carotid artery and form passage for cranial nerves IX–XI (1)
52. Eustachian tubes not enclosed between basioccipital and basisphenoid (0) or entirely enclosed (1)
53. Basisphenoid rostrum (cultriform process) slender (0) or dorsoventrally expanded (1)
54. Basipterygoid process prominent, forming movable joint with pterygoid (0), or basipterygoid process small or absent, with basipterygoid joint closed suturally (1)
55. Basisphenoid similar in length to basioccipital, with flat or concave ventral surface (0), or basisphenoid shorter than basioccipital (1)
56. Basisphenoid exposed on ventral surface of braincase (0) or virtually excluded from ventral surface by pterygoid and basioccipital (1)
57. Basioccipital without well-developed bilateral tuberosities (0) or with large, pendulous tubera (1)
58. Otoccipital without laterally concave descending flange ventral to subscapsular process (0) or with flange (1)
59. Cranial nerves IX–XI pass through common large foramen vagi in otoccipital (0), or cranial nerve IX passes medial to nerves X and XI in separate passage (1)
60. Otoccipital without large ventrolateral part ventral to paroccipital process (0) or with large ventrolateral part (1)
61. Crista interfenestralis between fenestrae pseudorotunda and ovalis nearly vertical (0) or horizontal (1)
62. Supraoccipital forms dorsal edge of foramen magnum (0), or otoccipitals broadly meet dorsal to the foramen magnum separating supraoccipital from foramen (1)
63. Mastoid antrum does not extend into supraoccipital (0) or extends through transverse canal in supraoccipital to connect middle ear regions (1)
64. Posterior surface of supraoccipital nearly flat (0) or with bilateral posterior prominences (1)
65. One small palpebral present in orbit (0), or two large palpebrals present (1), or one large palpebral present (2) (unordered)
66. External nares divided (0) or confluent (1)
67. Antorbital fenestra as large as orbit (0), or about half the diameter of the orbit (1), or much smaller than orbit (2), or absent (3) (ordered)
68. Supratemporal fenestrae much longer than orbits (0) or equal in length to or shorter than orbits (1)
69. Choanae confluent (0) or divided by septum (1)
70. Dentary extends posteriorly beneath mandibular fenestra (0) or does not extend beneath fenestra (1)
71. Retroarticular process very short and robust (0), or absent (1), or short, robust, and ventrally situated (2), or posterodorsally curving and elongate (3), or posteroventrally projecting and paddle-shaped (4), or posteriorly projecting from ventral part of mandible and attenuating (5) (unordered)
72. Prearticular present (0) or absent (1)
73. Articular without medial process articulating with otoccipital and basisphenoid (0) or with process (1)
74. Dorsal edge of surangular flat (0) or arched dorsally (1)
75. Mandibular fenestra present (0) or absent (1)
76. Insertion area for M. pterygoidus posterior does not extend onto lateral surface of angular (0) or extends onto lateral surface of angular (1)
77. Splenial not involved in symphysis (0), or involved slightly in symphysis (1), or involved extensively in symphysis (2) (ordered)
78. Posterior two premaxillary teeth similar in size to anterior teeth (0) or much longer (1)
79. Maxillary teeth homodont, with lateral edge of maxilla straight (0), or teeth enlarged in the middle of tooth row, with edge of maxilla extending outward at these loci (1), or teeth enlarged and edge of maxilla curved in two waves (‘‘festooned’’) (2) (unordered)
80. Anterior dentary teeth opposite premaxilla-maxilla contact no more than twice the length of other dentary teeth (0) or more than twice the length (1)
81. Dentary teeth posterior to tooth opposite premaxilla–maxilla contact homodont (0) or enlarged opposite smaller teeth in maxillary tooth row (1)
82. Anterior and posterior scapular edges symmetrical in lateral view (0), or anterior edge more strongly concave than posterior edge (1)
83. Coracoid no more than half the length of scapula (0) or about equal in length to scapula (1)
84. Anterior process of ilium similar in length to posterior process (0) or one-quarter or less the length of posterior process (1)
85. Pubis rodlike, without expanded distal end (0) or with expanded distal end (1)
86. Pubis forms anterior half of ventral edge of acetabulum (0), or pubis at least partially excluded from the acetabulum by an anterior process of the ischium (1)
87. Distal end of femur with large lateral facet for fibula (0) or with very small facet (1)
88. Fifth pedal digit with (0) or without (1) phalanges
89. Atlas intercentrum broader than long (0) or as long as broad (1)
90. Neural spines on posterior cervical vertebrae as broad as those on anterior cervical vertebrae (0) or anteroposteriorly narrow, rodlike (1)
91. Cervical vertebrae without well-developed hypapophyses (0) or with well-developed hypapophyses (1)
92. Cervical vertebrae amphicoelous or amphiplatyan (0) or semi-procoelous (1) or procoelous (2)
93. Trunk vertebrae amphicoelous or amphiplatyan (0) or semi-procoelous (1) or procoelous (2)
94. All caudal vertebrae amphicoelous or amphiplatyan (0), or first caudal vertebra biconvex, with other caudal vertebrae procoelous (1), or first caudal vertebrae biconvex, with other caudal vertebrae semi-procoelous, amphicoelous or amphiplatyan (2) or all caudal vertebrae procoelous (3) (unordered)
95. Dorsal osteoderms rounded, ovate (0), or rectangular, broader than long (1), or square (2) (unordered)
96. Dorsal osteoderms with straight anterior edge (0) or with anterior process laterally on anterior edge (1)
97. Dorsal osteoderms in two parallel, longitudinal rows (0) or in more than two longitudinal rows (1)
98. Some or all osteoderms imbricated (0), or osteoderms sutured to one another (1)
99. Tail with dorsal osteoderms only (0) or completely surrounded by osteoderms (1)
100. Osteoderms absent from ventral part of trunk (0) or present (1)
101. Osteoderms with longitudinal keels on dorsal surfaces (0) or without keels (1)
102. Surangular forms only the lateral wall of glenoid fossa (0) or surangular forms approximately one-third of glenoid fossa (1)
103. Anterior margin of femur linear (0) or anterior margin of femur bears flange for coccygeofemoralis musculature (1)
104. Teeth without carinae, or with smooth carinae (0) or teeth serrated (1)
105. Dentary smooth lateral to seventh alveolus (0) or dentary with large occlusion pit lateral to seventh alveolus (1)
106. Scapular blade no more than twice the length of the scapulocoracoid articulation (0) or scapular blade very broad and greater than twice the length of the scapulocoracoid articulation (1)
107. Dorsal edge of dentary straight (0) or dorsal edge of dentary sinusoidal, with two concave waves (1)
108. Compressed dentary (0) or transversely expanded dentary, almost as wide as high (1)
109. Lateral surface of dentary continuous, without longitudinal groove (0) or lateral surface of dentary with longitudinal groove (1)
110. Splenial thin posterior to symphysis (0) or splenial robust dorsally posterior to symphysis (1)
111. Cervical osteoderms not fused into cervical shield (0) or multiple cervical osteoderms fused into shield (1)
112. Maxillary alveoli set along lateral margin of maxilla (0) or maxillary alveoli displaced medially by expansion of maxillary lateral margin (1)

APPENDIX 2. Matrix of character states for 15 taxa used in phylogenetic analysis. Characters are listed in Appendix 1.

Taxa	Character											
	10	20	30	40	50	60	70	80	90	100	110	
Protosuchus	000?000010	0000?00011	00?0000001	0111?00000	0000000?00	00000000?0	?0?0?001?0	10000?0000	000??00100	000???????	?00000000?	00
Notosuchus	?12?001101	0100111010	11?110?011	0000002??0	?000201120	11?1000?10	?110??10??	5?010?110?	0??1?????0	0?0???????	?0??0?0000	?0
Libycosuchus	?10?001101	??00?11010	10?110?011	000?002???	??00?11120	11?1010??0	???0?0?0??	5?0001?000	0????????0	0?0???????	???1??00??	?0
Barusuchus	0000001111	??00?11010	1??110?011	0?????2?10	11??111120	11?1000??0	?11??03?01	5?01011101	0?????????	0?????????	?0?1??0011	??
Sebecus	1000?01101	0000?11000	11?111?0?1	0001012110	1100?11120	1111000??0	?1??103000	5100011000	0????????0	?00???????	?0010?001?	??
Araripesuchus	1121011121	0100211010	1011110011	0001?02110	100011112?	11?1000??0	?11?101000	5?00011010	11111111?0	10002?0???	?010011100	00
Alligatorium	112101?03?	0000?10000	101111?00?	100?10???0	??00??11??	1??1000???	????10?0??	4?00101?10	1101111100	????1?0010	0000001100	??
Theriosuchus	112101?131	0100110000	1101111001	1001102110	10001?11?0	1111000???	??1?10200?	4?001?1010	11?1??1??0	?00?1100?1	1000001100	00
Pachycheilosuchus	112???????	??????00??	101111???1	0001??????	????0101??	??????????	??????2???	???01?0?0?	0111111??0	01121000??	0000000100	11
Goniopholis	112?11?131	?010?11000	101111?001	0001002?10	1000?11120	11?1010?10	?1?011301?	4?001?1010	11?1??1??0	?00?1100?1	1000001100	?0
Sunosuchus	0?2?011131	1?10?11000	1001111000	0001002110	1?00111120	11110100?0	?01021301?	4100011020	1??1111?0?	00001100?1	1?????????	??
Bernissartia	112?111131	??00?11000	10?111?001	000?002???	??0001112?	11?10100?0	?1???130??	4?0010?010	11?1?11??0	0001101011	0000001100	00
Crocodylia	1120111131	0000211000	1001111001	0001002110	1011011120	1111010010	1110013100	3100011010	1111111101	1221101011	1000001100	00
Pholidosaurus	101??11101	??11?11101	100111?001	000100211?	1000011120	11?101??10	?100?1300?	300???2?0?	??11?1???0	??0??1?0??	?0000?0100	?0
Dyrosauridae	011??1?101	?010?11?00	100011?101	0011012?10	1010011120	11?1011?10	?10101311?	3?00??2?00	0????????0	100??????1	?100000100	?0

APPENDIX 3

List of unambiguous apomorphies for each node and every terminal taxa listed in Figure 14a. Numbers in parentheses indicate state for the character at that node.

Node 1: 46
Node 2: 104
Node 3: 2
Node 4: 6, 26, 79, 81, 107(1)
Node 5: 19, 27, 29, 71
Node 6: 17, 92, 93
Node 7: 31, 83
Node 8: 56, 66
Node 9: 13, 69
Node 10: 45, 94, 97
Node 11: 71, 91
Node 12: 3, 13, 63, 79, 107(2)
Notosuchus: 22, 34, 74, 78
Libycosuchus: 56
Baurusuchus: 9, 74, 78, 80
Sebecus: 19, 26
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