

A NEW CROCODYLIFORM FROM THE MIDDLE CRETACEOUS GALULA FORMATION, SOUTHWESTERN TANZANIA

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ABSTRACT—A new taxon of peirosaurid crocodyliform, *Rukwasuchus yajabalijekundu*, gen. et sp. nov., is described on the basis of a well-preserved partial skull from the middle Cretaceous Galula Formation exposed in southwestern Tanzania. The skull is distinguished from those of other crocodyliforms by the presence of a mediolaterally narrow, elongate, and septate internal narial fenestra (choana) located anteriorly on the pterygoid; a markedly depressed posterior border of the parietal, excluding the supraoccipital from the dorsal cranial table; and a ventrally directed descending process of the postorbital with a well-developed posteroventral process. The lateral surface of the braincase is exquisitely preserved and includes a well-developed laterosphenoid bridge dividing the foramina for the three primary branches of the trigeminal nerve. In overall morphology, the holotype skull and isolated teeth compare closely with *Hamadasuchus rebouli* from the middle Cretaceous Kem Kem Beds of Morocco. Reevaluation of the problematic putative African peirosaurid taxa *Stolokrosuchus lapparenti* and *Trematochampsia taqueti* reveal a number of derived cranial characters shared with Peirosauridae and *Araripesuchus*. A close relationship between *Rukwasuchus* and other African members of Peirosauridae is supported by a parsimony analysis of Crocodyliformes. As the only known sub-Saharan peirosaurid from Africa, *Rukwasuchus* represents the only link between middle Cretaceous southern vertebrate faunas and much more abundant, taxonomically diverse, and potentially penecontemporaneous faunas from northern Africa.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The non-marine Cretaceous vertebrate record from Africa has received considerable attention over the past quarter-century, resulting in a surge of new discoveries that have enhanced our understanding of the evolutionary and biogeographic history of this largely undersampled continent (Jacobs et al., 1990, 1992, 1993; Sereno et al., 1994, 1996, 1998, 1999, 2004; Gomani, 1997, 1999, 2005; Smith et al., 2001, 2010; O'Leary et al., 2004; Sereno and Larsson, 2009; Le Loeuff et al., 2010). However, much of this research has focused on the relatively well-exposed and expansive circum-Saharan deposits known historically for their Cretaceous terrestrial vertebrate faunas, including those from Algeria (Lapparent, 1960; Bassoulet and Iliou, 1967), Cameroon (Flynn et al., 1987; Jacobs et al., 1988, 1989, 1996; Brunet et al., 1990), Egypt (Stromer, 1936; Rauhut and Werner, 1997; Smith et al., 2001), Ethiopia (Goodwin et al., 1999), Libya (Nessov et al., 1998; Rage and Cappetta, 2002; Le Loeuff et al., 2010; Smith et al., 2010), Mali (O'Leary et al., 2004), Morocco (Lavocat, 1954; Sigogneau-Russell et al., 1998; Cavin et al., 2010), Niger (Lapparent, 1960; Taquet, 1976, 1982; Sereno et al., 1994, 1996, 1998, 1999, 2004; Sereno and Brusatte, 2008), Sudan (Buffetaut et al., 1990; Rauhut and Werner, 1995), and Tunisia (Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988; Benton et al., 2000). By comparison, Cretaceous localities that preserve terrestrial vertebrate remains from sub-Saharan regions of Africa are notoriously scarce, with comparatively less diverse faunas known from South Africa (Broom,

1904; Galton and Coombs, 1981; Rich et al., 1983; Ross et al., 1999; de Klerk et al., 2000; Forster et al., 2009), Malawi (Colin and Jacobs, 1990; Jacobs, 1990; Jacobs et al., 1990, 1992, 1993; Gomani, 1997, 1999, 2005), Tanzania (Krause et al., 2003; O'Connor et al., 2006, 2010; Gottfried et al., 2009), and Angola (Jacobs et al., 2006; Mateus et al., 2011).

Perhaps for no other vertebrate clade is this sampling disparity more obvious than in the African crocodyliform record. The known diversity of Cretaceous African non-marine crocodyliforms has expanded rapidly in the past decade, with 16 circum-Saharan crocodyliform taxa currently recognized (Table 1). By contrast, only two Cretaceous crocodyliform taxa are currently known from sub-Saharan localities, the small, mammal-like notosuchians *Malawisuchus mwakasyungutiensis* and *Pakasuchus kapilimai* (Clark et al., 1989; Gomani, 1997; O'Connor et al., 2010). Despite being of similar age, these two southern forms do not appear to share close phylogenetic affinities with any of their northern counterparts. Indeed, the preponderance of crocodyliforms from northern Africa and lack of sub-Saharan forms precludes meaningful investigations into the intracontinental biogeographic history of the group.

The diverse non-marine vertebrate fauna recovered from the middle Cretaceous Galula Formation exposed in southwestern Tanzania (Fig. 1) includes fishes, turtles, mammals, and both sauropodomorph and theropod dinosaurs (Krause et al., 2003; O'Connor et al., 2006; Gottfried et al., 2009). Crocodyliform remains thus far recovered include exquisitely preserved specimens of the small, mammal-like notosuchian *Pakasuchus kapilimai* (O'Connor et al., 2010) and the new medium- to large-bodied peirosaurid crocodyliform taxon described herein.

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TABLE 1. African crocodyliforms from Cretaceous non-marine sediments.

Taxon	Continental region	Country	Geologic unit	Age	Reference
<i>Aegisuchus wimeri</i>	Northern Africa	Morocco	Kem Kem beds	Cenomanian	Holliday and Gardner, 2012
<i>Aegyptosuchus peyeri</i>	Northern Africa	Egypt	Bahariya Formation	Cenomanian	Stromer, 1933
<i>Anatosuchus minor</i>	Northern Africa	Niger	Elrhaz Formation	Aptian–Albian	Sereno et al., 2003; Sereno and Larsson, 2009
<i>Araripesuchus wegeneri</i>	Northern Africa	Niger	Elrhaz Formation	Aptian–Albian	Buffetaut and Taquet, 1979; Buffetaut, 1981; Sereno and Larsson, 2009
<i>Brillanceausuchus babouriensis</i>	Northern Africa	Cameroon	Babouri-Figuil beds	Barremian	Michard et al., 1990
<i>Elosuchus cherifiensis</i>	Northern Africa	Algeria, Morocco	'Continental intercalaire,' Kem Kem beds	Albian–Cenomanian	Lavocat, 1955; Lapparent de Broin, 2002
<i>Elosuchus felixi</i>	Northern Africa	Niger	'Continental intercalaire'	Albian–Cenomanian	Lapparent de Broin, 2002
<i>Hamadasuchus rebouli</i>	Northern Africa	Morocco	Kem Kem beds	Aptian–Cenomanian	Buffetaut, 1994; Larsson and Sues, 2007
<i>Kaprosuchus saharicus</i>	Northern Africa	Niger	Echkar Formation	Cenomanian	Sereno and Larsson, 2009
<i>Laganosuchus maghrebenensis</i>	Northern Africa	Morocco	Kem Kem beds	Cenomanian	Sereno and Larsson, 2009
<i>Laganosuchus thaumastos</i>	Northern Africa	Niger	Echkar Formation	Cenomanian	Sereno and Larsson, 2009
<i>Libycosuchus brevisrostris</i>	Northern Africa	Egypt	Bahariya Formation	Cenomanian	Stromer, 1914
<i>Sarcosuchus imperator</i>	Northern Africa	Niger	Elrhaz Formation	Aptian–Albian	Broin and Taquet, 1966; Sereno et al., 2001
<i>Stolokrosuchus lapperenti</i>	Northern Africa	Niger	Elrhaz Formation	Aptian–Albian	Larsson and Gado, 2000
<i>Stomatosuchus platyrostris</i>	Northern Africa	Egypt	Bahariya Formation	Cenomanian	Stromer, 1925
<i>Trematochampsia taqueti</i>	Northern Africa	Niger	'Senonian' beds	Turnonian-Coniacian	Buffetaut, 1974, 1976
<i>Malawisuchus mwakasyungutiensis</i>	Southern Africa	Malawi	'Dinosaur' beds	Aptian	Clark et al., 1989; Gomani, 1997
<i>Pakasuchus kapilimae</i>	Southern Africa	Tanzania	Galula Formation	Aptian–Cenomanian	O'Connor et al., 2010
<i>Rukwasuchus yajabaliyekundu</i>	Southern Africa	Tanzania	Galula Formation	Aptian–Cenomanian	This paper

Peirosaurid crocodyliforms represent a diverse group of terrestrial and semiaquatic taxa known exclusively from Cretaceous Gondwanan localities. Although most peirosaurids are currently known from South America (e.g., Price, 1955; Gasparini et al., 1991; Carvalho et al., 2004, 2007; Leardi and Pol, 2009; Campos et al., 2011), purported African peirosaurid taxa have also been described from localities in Morocco (Buffetaut, 1994; Larsson

and Sues, 2007) and Niger (Buffetaut, 1974, 1976; Larsson and Gado, 2000). The presence of a peirosaurid crocodyliform in the middle Cretaceous of Tanzania expands the geographic distribution of the group within Africa during this period and provides one of the first clear faunal links between circum-Saharan and sub-Saharan localities. Additionally, the well-preserved skull of the new peirosaurid provides an opportunity to reevaluate

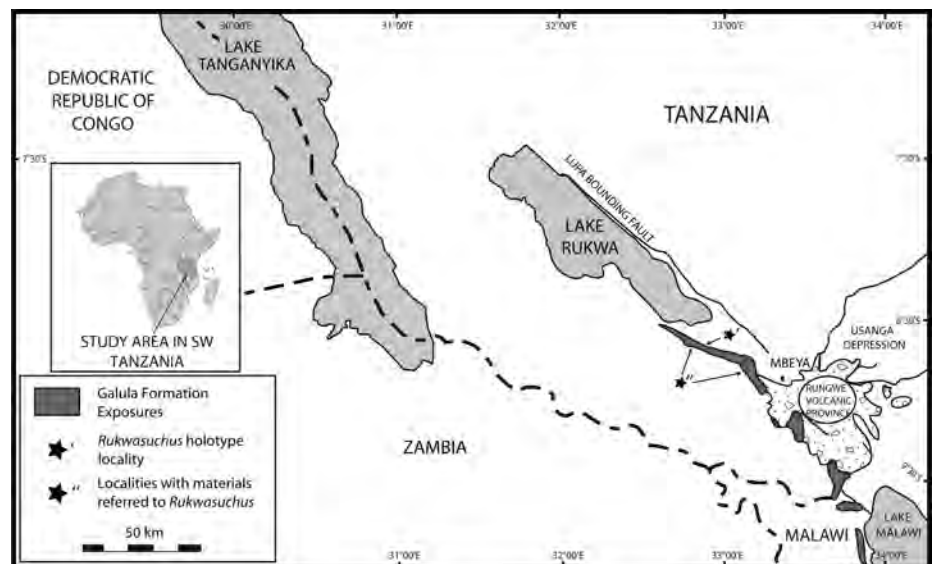


FIGURE 1. Map of the Rukwa Rift Basin (RRB) depicting outcrop areas of the middle Cretaceous Galula Formation and the localities from which *Rukwasuchus yajabaliyekundu* materials have been recovered. Inset illustrates the approximate location of the RRB in southwestern Tanzania.

the morphology and phylogenetic affinities of other purported African peirosaurid taxa.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, U.S.A.; **FMNH**, The Field Museum, Chicago, U.S.A.; **MNN**, Musée National du Niger, Niamey, Republic of Niger; **MPMA**, Museu de Paleontologia de Monte Alto, Monte Alto, Brazil; **MZSP-PV**, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; **ROM**, Royal Ontario Museum, Toronto, Canada; **RRBP**, Rukwa Rift Basin Project, Tanzanian Antiquities Unit, Dar es Salaam, Tanzania.

Computed Tomography

The holotype skull (RRBP 08630) of *Rukwasuchus yajabaliyekundu* was scanned on a Philips Brilliance computed tomography 64-channel scanner using the following protocol: 120 kVp, 200 mA, and a slice thickness of 0.67 mm. Computer visualization and postscan processing of DICOM files were completed in Avizo 6.3 (Visualization Sciences Group/FEI, Burlington, Massachusetts, U.S.A.).

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970

CROCODYLIFORMES Hay, 1930 (sensu Clark in Benton and Clark, 1988)

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

PEIROSOSAURIDAE Gasparini, 1982

RUKWASUCHUS YAJABALIJEKUNDU, gen. et sp. nov. (Figs. 2–4)

Etymology—*Rukwasuchus*, from ‘Rukwa,’ referring to Lake Rukwa of southwestern Tanzania and the structural rift basin of the same name in which the specimens described herein were preserved, and ‘Souchos’ (Greek), in reference to the crocodile-headed god of ancient Egypt; *yajabaliyekundu*, from Kiswahili meaning ‘of/from the red outcrop,’ in reference to the Red Sandstone Group deposits exposed in the Rukwa Rift Basin.

Holotype—RRBP 08630, partial skull including the cranial table, braincase, and interorbital region but lacking the rostrum, anterior palate, lacrimals, jugals, quadratojugals, and mandible (Figs. 2–4). Discovered by E. K. Lund on July 25, 2008.

Type Locality—Locality ‘Namba 2’ (RRBP 2007-02), approximately 25 km south of Lake Rukwa in the Galula Study Area, Namba Member, Galula Formation, Rukwa Rift Basin, southwestern Tanzania (locality coordinates on file at Ohio University and with the Tanzania Antiquities Unit).

Age and Distribution—The holotype skull was recovered from the Namba Member of the Galula Formation of the Red Sandstone Group. Based on several lines of geologic and faunal data, the age of the Galula Formation has been constrained to the middle Cretaceous (Aptian–Cenomanian) (O’Connor et al., 2006; Roberts et al., 2010).

Localities and Tentatively Referred Specimens—Isolated tooth (RRBP 07351), isolated tooth (RRBP 07369), and isolated tooth (RRBP 09362)—locality RRBP 2007-01; isolated tooth (RRBP 09367)—locality RRBP 2009-01. All isolated teeth referred to *Rukwasuchus* are morphologically similar, size consistent with the skull, and cannot be referred to the only other known crocodyliform from the Galula Formation, *Pakasuchus kapilimai*.

Diagnosis—Peirosaurid crocodyliform that differs from other crocodyliforms in the following features and combination of features: mediolaterally restricted and anteriorly positioned internal narial fenestra (choana); dorsally upturned tip of the posterior process of the squamosal; otic aperture separated from the posterior margin of the skull by an anteroposteriorly elongate posterior descending lamina of the squamosal; depressed posterior

margin of the parietal; ventrally, rather than anteroventrally, directed descending process of the postorbital; and well-developed laterosphenoid bridge and accessory bridge separating the three main foramina associated with primary divisions of the trigeminal nerve (CN V).

DESCRIPTION

Cranial Morphology

The holotype (RRBP 08630) of *Rukwasuchus yajabaliyekundu* is represented by a partial skull that includes most of the skull table, braincase, and orbital region. The rostrum, anterior regions of the palate, and lateral dermatocranial elements (lacrimal, jugal, quadratojugal) are not preserved. Additionally, several portions of the skull, including the pterygoids and portions of the right cranial table, quadrate, and occiput, are incomplete due to pre- or syndepositional processes. Nevertheless, represented portions of the skull are extremely well preserved and undistorted, capturing exquisite detail of the lateral surface of the braincase wall not typically observable in fossil crocodyliforms.

Frontal—The frontal is fully fused, consisting of a broad, horizontally oriented dorsal lamina with two (left and right) thin, ventrally directed descending laminae (Figs. 2A, C, 3A, C). As in other peirosaurids, the orbital margins of the dorsal lamina are moderately elevated, producing a smoothly concave dorsal surface between the orbits. The elevated orbital margin is continuous with the similarly elevated orbital rims of the postorbital posteriorly and the prefrontal anteriorly. The external surface of the dorsal lamina is moderately sculpted with rounded, irregular grooves, crenulations, and pits. As in other peirosaurids, the frontal contributes to the formation of the supratemporal fossae. Posterolaterally, the anteromedial margin of each supratemporal fossa is present as a weakly raised ridge, separating the smooth surface of the floor of the fossa from the external sculpturing present anteriorly.

The dorsal lamina of the frontal meets that of the parietal posteriorly in a transverse suture. Laterally, the suture between the frontal and the postorbital is elevated above the contact with the parietal. The frontal narrows anteriorly between the prefrontals, contacting the nasal in a transverse suture. In dorsal view, the contact between the anterior process of the frontal and the prefrontals forms an anterolaterally concave suture (Fig. 2A, C).

The descending lamina projects ventrally from the lateral (orbital) margin of the frontal, terminating as the crista cranii frontalis. Posteriorly, it meets the orbital lamina of the postorbital in a ventromedially directed suture. At the ventral termination of this suture, it meets the anterolateral lamina of the laterosphenoid in a broad, anteroposteriorly directed suture (Fig. 4B). Anteriorly, the descending process passes medial to the orbital lamina of the prefrontal, tapering into the ventral surface of the anterior process of the frontal. Thus, the ventrolaterally concave lateral surface of the descending process, together with the orbital laminae of the prefrontal and postorbital, forms the rounded dorsomedial portion of the orbit.

Prefrontals—The prefrontals are anteroposteriorly elongate, each consisting of a sculpted dorsal lamina and a smooth, ventrally directed orbital lamina. A prominent descending process projects ventromedially from the orbital lamina to contact the dorsal surface of the anterior process of the pterygoid.

The external surface of the dorsal lamina of the prefrontal, like that of the frontal, is ornamented with rounded crenulations and pits. It is distinctly elongate and oriented along an anteroposterior axis. Its posterior border arises from the midpoint of the orbit, arching anteromedially in sutural contact with the dorsal lamina of the frontal. Medially, the dorsal lamina of the prefrontal borders the anterior process of the frontal in a subparallel, anteriorly directed suture. The anterior-most extent of the prefrontals

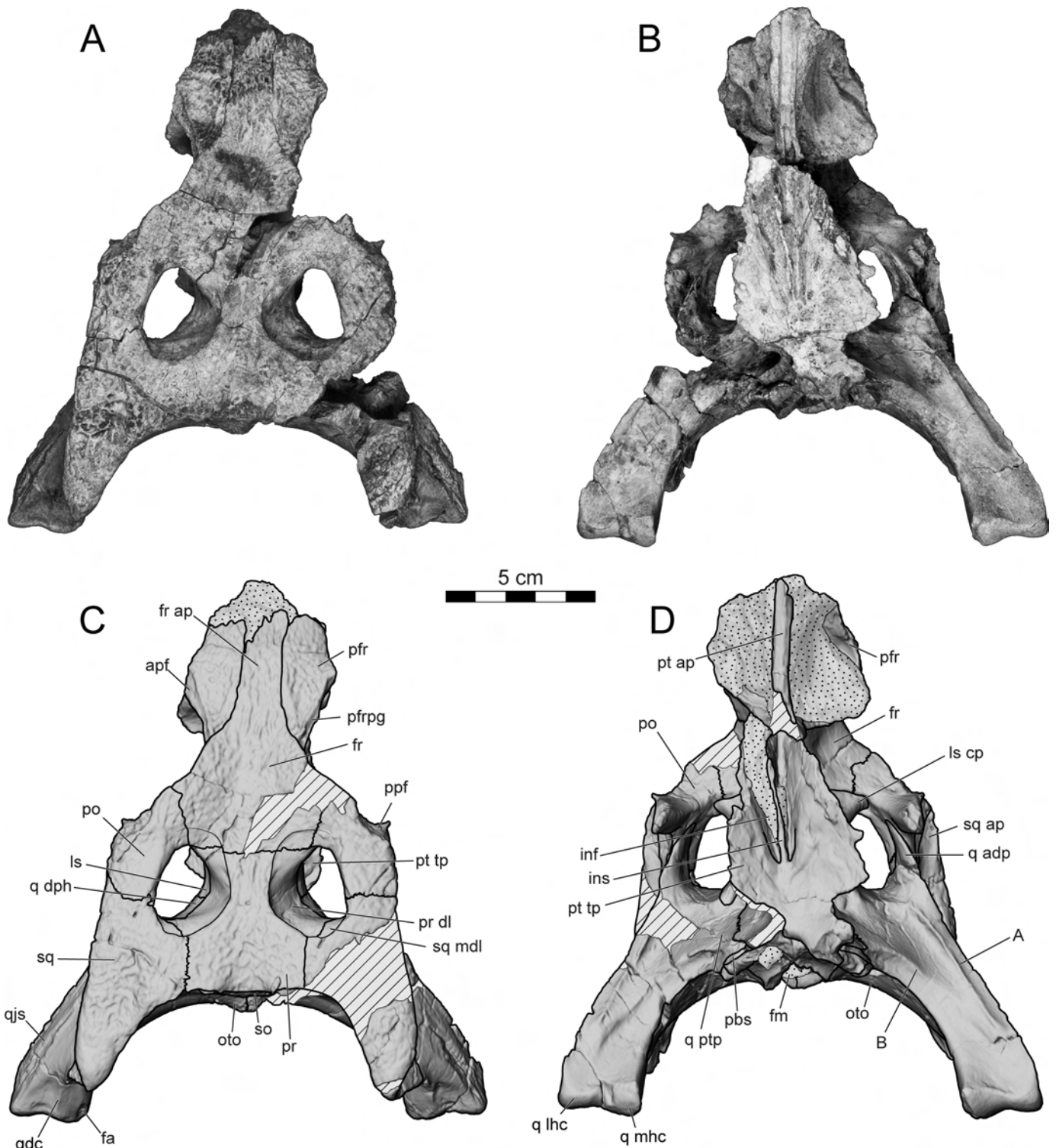


FIGURE 2. Skull of *Rukwasuchus yajabaliyekundu* (RRBP 08630) in **A**, dorsal and **B**, ventral views with labeled illustrations in **C**, dorsal and **D**, ventral views. Cross-hatching indicates broken surfaces, stippling indicates remaining sandstone matrix. **Abbreviations:** **A**, adductor 'crest A'; **apf**, anterior palpebral facet; **B**, adductor 'crest B'; **fa**, foramen aereum; **fm**, foramen magnum; **fr**, frontal; **fr ap**, frontal anterior process; **inf**, internal narial fenestra; **ins**, internal narial septum; **ls**, laterosphenoid; **ls cp**, laterosphenoid capitate process; **oto**, otoccipital; **pbs**, parabasisphenoid; **pfr**, prefrontal; **pfrpg**, prefrontal palpebral groove; **po**, postorbital; **ppf**, posterior palpebral facet; **pr**, parietal; **pr dl**, parietal descending lamina; **pt ap**, pterygoid anterior process; **pt tp**, pterygoid transverse process; **q adp**, quadrate anterodorsal process; **q dph**, quadrate dorsal primary head; **q lhc**, quadrate lateral hemicondyle; **q mhc**, quadrate medial hemicondyle; **q ptp**, quadrate pterygoid process; **qdc**, quadrate body dorsal crest; **qjs**, quadratojugal suture; **so**, supraoccipital; **sq**, squamosal; **sq ap**, squamosal anterior process; **sq mdl**, squamosal medial descending lamina.

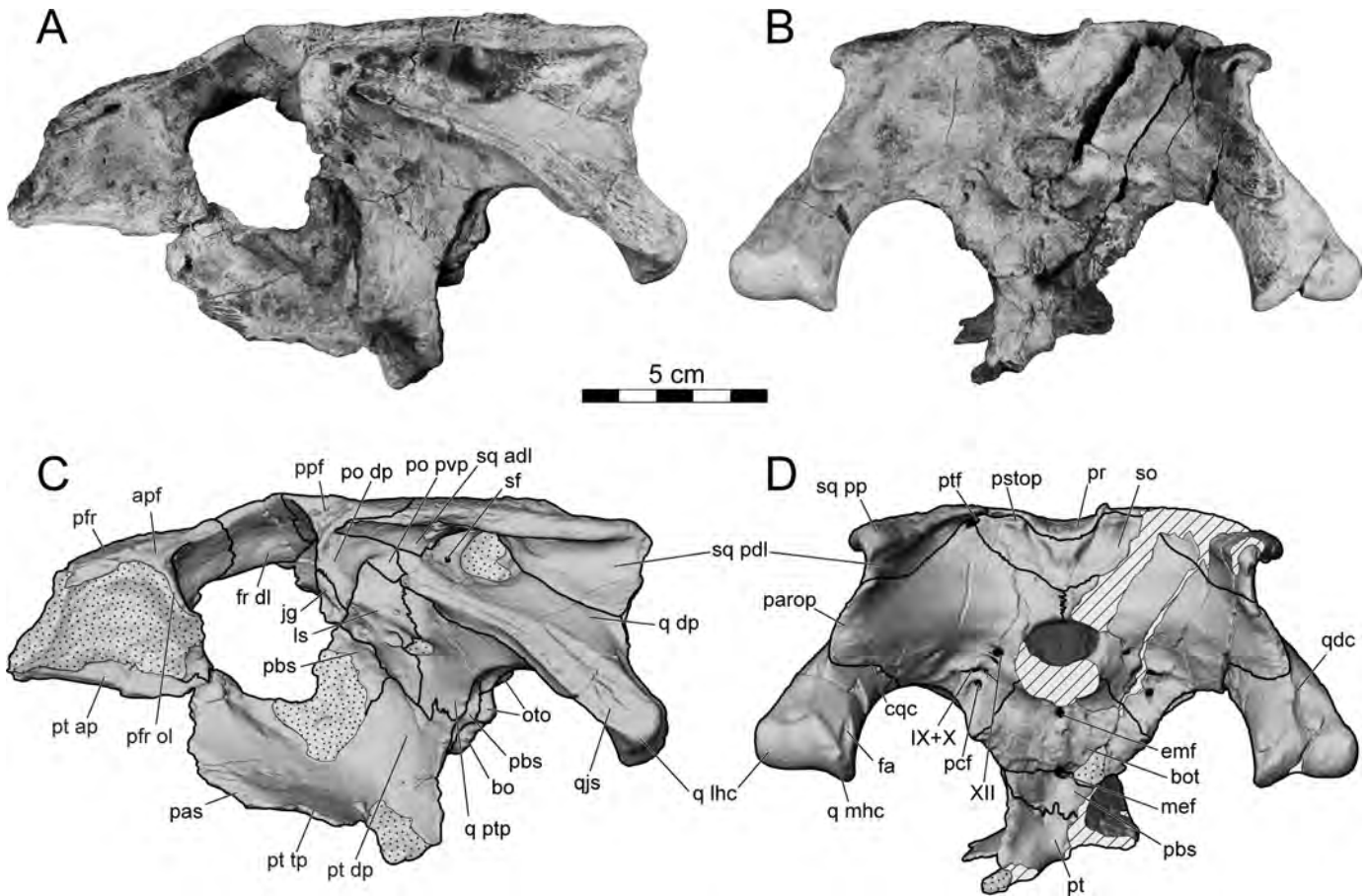


FIGURE 3. Skull of *Rukwasuchus yajabaliyekundu* (RRBP 08630) in **A**, lateral and **B**, posterior views with labeled illustrations in **C**, lateral and **D**, posterior views. Cross-hatching indicates broken surfaces, stippling indicates remaining sandstone matrix. **Abbreviations:** apf, anterior palpebral facet; bo, basioccipital; bot, basioccipital tuber; cqc, cranioquadrate canal; emf, emissary foramen; fa, foramen aereum; fr dl, frontal descending lamina; jg, jugal; ls, laterosphenoid; mef, median Eustachian foramen; oto, otoccipital; parop, paroccipital process; pas, palatine suture; pbs, parabasisphenoid; pcfc, posterior carotid foramen; pfr, prefrontal; pfr ol, prefrontal orbital lamina; po dp, postorbital descending process; po pvp, postorbital posteroventral process; ppf, posterior palpebral facet; pr, parietal; pstop, postoccipital process; pt, pterygoid; pt ap, pterygoid anterior process; pt dp, pterygoid dorsal process; pt tp, pterygoid transverse process; ptf, posttemporal fenestra; q dp, quadrate dorsal process; q lhc, quadrate lateral hemicondyle; q mhc, quadrate medial hemicondyle; q ptp, quadrate pterygoid process; qdc, quadrate body dorsal crest; qjs, quadratojugal suture; sf, siphoneal foramen; so, supraoccipital; sq adl, squamosal anterior descending lamina; sq pdl, squamosal posterior descending lamina; sq pp, squamosal posterior process; IX+X, foramen for glossopharyngeal and vagus nerves; XII, hypoglossal foramen.

is not preserved, precluding an assessment of their relationship with the nasals. Beginning posteriorly at the contact with the orbital margin of the frontal, the orbital margin of the dorsal lamina is elevated relative to the anterior border of the orbit. This gives the impression of a strongly anteroventrally directed prefrontal when viewed laterally (Fig. 3A, C). The orbital margin of the prefrontal is grooved for articulation with the anterior palpebral. This groove extends anteriorly onto the dorsal lamina at its confluence with the orbital lamina to form a distinct dorsolaterally directed shelf that would presumably continue onto the external surface of the lacrimal as an articular facet for the anterior margin of the anterior palpebral (Figs. 2A, C, 3A, C).

The orbital lamina descends from the posterior half of the prefrontal, contributing to the anterior and medial portions of the orbital wall. Posteriorly, the orbital lamina meets and overlies the anterior half of the descending process of the frontal. The orbital lamina abruptly curves laterally at the front of the orbit toward a broad suture with the orbital lamina of the lacrimal. Extending ventromedially from the orbital lamina is the descending process of the prefrontal (prefrontal pillar) (Fig. 2A, C). A laminar

medial projection extends from the midpoint of each descending process, the two (left and right) meeting at the midline in a complex suture to form a distinct, dorsally directed prong that projects into the space between the orbital laminae of the prefrontals. Ventral to the contact between the two medial laminae, the descending processes converge near the midline to contact the dorsal surface of the anterior process of the pterygoid.

Postorbital—The postorbital consists of distinct anteromedial, posterior, and descending processes that trifurcate from a central body. The dorsal surfaces of the anteromedial and posterior processes combine to form a continuous dorsal lamina positioned at the anterolateral corner of the cranial table. This dorsal lamina is ornamented externally by moderate pitting and crenulations.

The dorsal lamina of the anteromedial process separates the orbit from the supratemporal fenestra, contributing to the borders of both. The dorsal lamina of the anteromedial process contacts the posterolateral corner of the dorsal lamina of the frontal in an anterolaterally directed suture. The posteromedial corner of the anteromedial process of the postorbital is moderately depressed, contributing to the anterolateral wall of the

supratemporal fossa and forming the anterolateral border of the supratemporal fenestra. Within the supratemporal fossa, the anteromedial process has minimal contact with the descending lamina of the parietal.

The dorsal lamina of the posterior process forms most of the lateral border of the supratemporal fenestra and terminates posteriorly at a sutural contact with the anterior process of the squamosal. In dorsal view, this suture crosses the cranial table transversely from the medial margin of the supratemporal fenestra before sharply transitioning to an oblique orientation, extending anterolaterally to the lateral margin of the cranial table (Fig. 2A, C). Laterally, the extension of the squamosal extends anteriorly along the ventral aspect of the dorsal lamina of the posterior process (Fig. 3A, C).

A prominent, anterodorsally directed depression is present on the anterolateral corner of the postorbital at the confluence of the three major processes. The depression is subtriangular in overall morphology, with the apex of the triangle directed ventrolaterally toward the base of the descending process, and served as the articular facet for the posterior palpebral (Figs. 2A, C, 3A, C).

The descending process is bifurcate, projecting ventrally from the dorsal lamina and the base of the posterior palpebral facet to form the dorsal portion of the postorbital bar. A well-developed posteroventral process extends from the posterior surface of the descending process at the apex of the infratemporal fenestra. The anterolateral edge of the descending process forms a sharp crest delimiting the posterior margin of the orbit. The ventral end of the descending process forms an oblique sutural surface for contact with the ascending process of the jugal, with the former extending posteromedially to the latter (Fig. 3C). The posteroventral projection of the descending process arises at an angle of approximately 60° from the base of the descending process and delimits the apical margin of the infratemporal fenestra. This posteroventral projection consists of a thin plate overlying the anterodorsal process of the quadrate and likely terminated in a contact with the quadratojugal (the latter is not preserved on this specimen).

The orbital lamina of the postorbital receives contributions from portions of the anteromedial and descending processes. It consists of a smooth sheet of bone forming the posterodorsal portion of the orbital wall and contacts the descending lamina of the frontal anteromedially. Posterior to the orbital lamina, the postorbital is contacted by the capitate process of the laterosphenoid in a small notch at the base of the anteromedial and descending processes of the postorbital.

Parietals—The parietals are fused to form a single structure consisting of a horizontally oriented dorsal lamina from which two descending processes (left and right) extend ventrolaterally. The dorsal lamina of the parietal forms the central and posterior portions of the cranial table. As in the other elements of the cranial table, the external surface of the dorsal lamina is ornamented with an irregular pattern of rounded crenulations and pits.

The dorsal lamina is relatively wide posteriorly, narrowing anteriorly between the supratemporal fossae. Anteriorly, it widens to meet the dorsal lamina of the frontal in a broad, transversely oriented suture. In dorsal view, the posterior margin of the dorsal lamina is straight, overlapping the supraoccipital entirely. The posterior margin is notably depressed in posterior view between the posttemporal fenestrae (Fig. 3B, D). Posterolaterally, the dorsal lamina of the parietal meets the medial process of the squamosal in an anteroposteriorly directed suture. The free lateral margins of the dorsal lamina of the parietal forms the posteromedial and medial margins of the supratemporal fenestrae.

The descending processes of the parietal (*crista cranii parietalis*) project ventrolaterally from the lateral margins of the dorsal lamina as dorsolaterally concave laminae. They form the entire medial wall, along with portions of the anterior and posterior walls, of the two supratemporal fossae (Fig. 2A, C). Anteriorly,

each descending process flares laterally to contact the lateral third of the dorsal lamina of the frontal and a small portion of the anteromedial processes of the postorbital. The ventral margins of the descending processes of the parietal are in sutural contact anteriorly with the posterolateral lamina of the laterosphenoid and posteriorly with the dorsal primary head of the quadrate. Posterolaterally, each descending process of the parietal contacts the medial process of the ipsilateral squamosal.

Squamosals—The squamosals are triradiate in general form, consisting of distinct anterior, medial, and posterior processes, each of which gives rise to descending laminae that project ventrally. The dorsal surfaces of all three processes form a continuous dorsal lamina of the posterolateral cranial table and bound the posterior and lateral margins of the supratemporal fenestrae. The external surface of the dorsal lamina of the squamosal is ornamented with irregular crenulations and pits.

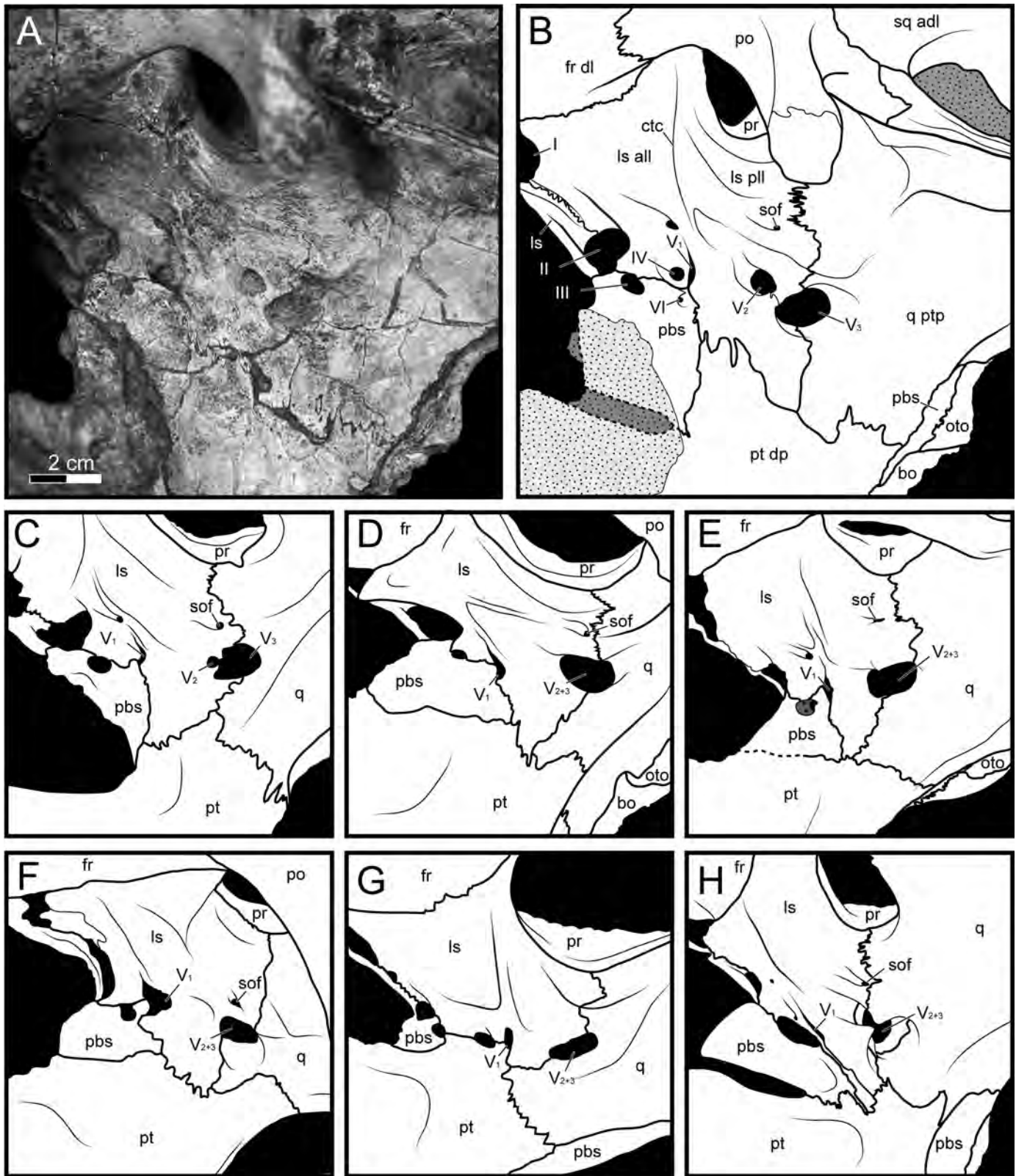
The anterior process of the squamosal contacts the posterior process of the postorbital in a broad suture. In dorsal view, this suture extends transversely from the lateral margin of the supratemporal fenestra before arching anterolaterally to the border of the cranial table (Fig. 2A, C). The anterior process of the squamosal continues anteriorly along the lateral surface of the postorbital as a subtriangular projection, extending to the base of the posterior palpebral facet of the postorbital (Fig. 3A, C). Projecting ventrally from the anterior process of the squamosal is a robust anterior descending lamina, visible laterally within the external otic recess (Fig. 3A, C). Beginning dorsal to the otic aperture, this descending lamina flares anteriorly in contact with the anterodorsal process of the quadrate and the posteroventral projection of the descending process of the postorbital.

The medial process of the squamosal is short, extending to contact the lateral projection of the dorsal lamina of the parietal along a moderately elevated suture. A small, anteromedially directed, dorsally concave medial lamina projects ventrally from the junction of the medial and anterior processes to form the posterolateral wall of the supratemporal fossa.

The posterior process of the squamosal is subtriangular in dorsal view, projecting posteriorly beyond the occipital surface at the level of the cranial table. The posterior termination of the process is rounded in dorsal view (Fig. 2A, C) and slightly upturned in lateral view (Fig. 3A, C). External ornamentation extends the length of the process, although it becomes less prominent near the posterior terminus. A well-developed posterior descending lamina projects ventrally from the medial and posterior processes of the squamosal. Beginning at the contact with the parietal medially, the posterior descending lamina flares ventrolaterally in posterior view (Fig. 3B, D), where it broadly underlaps the paroccipital process of the otoccipital. In lateral view, the posterior descending process can be seen to originate dorsal to the otic aperture, flaring posteriorly in broad sutural contact with the dorsal process of the quadrate. The posterior free margin of the posterior descending lamina is oriented weakly anteroventrally from the tip of the posterior process.

The lateral margin of the dorsal lamina of the squamosal overhangs the otic aperture to form a deep external otic recess, as in other crocodyliforms. This recess is expanded dorsally above the otic aperture as a shallow concavity. Posteriorly, the external otic recess is open ventral to the dorsal lamina of the posterior process and lateral to the posterior descending lamina of the squamosal. This is in contrast to the posteriorly closed external otic recesses of many derived neosuchians and crocodylians.

Quadrate—As in other crocodyliforms generally, each quadrate is oriented posteroventrally and consists of a main body with dorsal and pterygoid processes and an anterodorsal region consisting of a dorsal primary head and an anterodorsal process. Extending from the level of the otic aperture, the anterodorsal region of the quadrate projects anteriorly, dorsally, and medially below the cranial table, where it forms the dorsal



primary head. The dorsal primary head is inclined medially, contacting the posterolateral lamina of the laterosphenoid in a broad vertical suture anteriorly and the descending process of the parietal dorsally. The medial surface of the dorsal primary head is smoothly continuous with the anterodorsal process along the posterior wall of the adductor chamber. Laterally, the anterodorsal process of the quadrate continues around the wall of the adductor chamber as a thin triangular lamina, terminating medial to the descending process of the postorbital. In lateral view, the anterodorsal process meets the anterior descending lamina of the squamosal anterior to the otic recess and the posteroventral process of the postorbital (Fig. 3A, C). Along its posterior margin, the anterodorsal process forms the anterior boundary of the otic aperture.

The otic aperture is irregular in shape, with rounded anterior and dorsal margins and a distinct posteroventral extension. A semilunar concavity surrounds the otic aperture anteroventrally on the surface of the quadrate, meeting the descending process of the squamosal anteriorly to form an ovoid otic depression within the external otic recess. A single, small siphoneal foramen pierces the anterodorsal process within the otic depression, just anterior to the otic aperture (Fig. 3A, C).

The body of the quadrate is robust and elongate, inclined posteroventrally as in many other crocodyliforms. The lateral surface is rugose over a wide area, covered with a number of longitudinally oriented striations representing the broad sutural surface for the quadratojugal (Fig. 3A, C). Posteroventrally, the quadratojugal suture extends onto the lateral surface of the lateral hemicondyle of the quadrate, indicating that the quadratojugal contributed, in part, to the formation of the lateral articular surface of the lateral hemicondyle. Anterodorsally, the suture becomes narrower, extending to the posteroventral projection of the postorbital and indicating contact between the quadratojugal and postorbital. A short dorsal process extends from the anterodorsal half of the quadrate body to contact the posterior descending process of the squamosal along an oblique suture and the paroccipital process of the otoccipital posteromedially. The dorsal process of the quadrate is anteroposteriorly long, resulting in broad separation of the otic aperture from the posterior margin of the skull. The dorsal surface of the body of the quadrate posterior to the dorsal process is divided by a prominent but low crest extending between the dorsal process and the medial hemicondyle. This crest effectively divides the posterodorsal surface of the quadrate body in posterior view into a posterodorsal surface and a smoothly convex posteromedial surface. The center of the posteromedial surface is pierced by the foramen areum near the medial hemicondyle. Ventral to the paroccipital process of the otoccipital, the posteromedial surface of the quadrate contributes to the formation of the cranioquadrate passage (Fig. 3B, D).

The distal portion of the body of the quadrate is subrectangular in coronal section and well developed, projecting ventrolaterally from the occiput (Fig. 3B, D). The two hemicondyles of the

articular surface are separated by a pronounced oblique sulcus (oriented along a posterolateral to anteromedial axis). The medial hemicondyle is larger than the lateral hemicondyle, its long axis oriented strongly dorsolaterally from its sharply pointed ventromedial margin. The lateral hemicondyle is more rounded, its axis oriented roughly dorsoventrally.

The pterygoid process of the quadrate projects anteromedially from the body. At its ventral termination, it meets the dorsal process of the pterygoid in a wide interdigitating suture. Anteriorly, it meets the lateral bridge of the laterosphenoid in a dorsoventrally oriented suture that terminates at the posterior opening of the trigeminal foramen. Here, the pterygoid process contributes to the posterior margin of the foramen for the passage of the mandibular branch of the trigeminal nerve (CN V₃) (Fig. 4A, B).

The ventral surface of the quadrate is marked by two distinct and elongate crests corresponding to the areas of attachment of portions of the adductor musculature. Extending parallel to the lateral margin of the quadrate from the ventral margin of the adductor chamber to the approximate midpoint of the body of the quadrate is a prominent ridge corresponding to 'crest A' of Iordansky (1964). Medially, the posterior free edge of the dorsal process of the pterygoid is continuous with a distinct ridge extending along the pterygoid process of the quadrate onto the ventral surface of the body of the quadrate. This ridge corresponds to 'crest B' of Iordansky (1964). This pattern of crests, including the extreme development of 'crest A' and the continuity of 'crest B' with the pterygoid margin, is also observed in other peirosaurids, including *Hamadasuchus*, *Stolokrosuchus*, and *Montealtosuchus*, as well as in *Araripesuchus wegneri*.

Pterygoid—The pterygoid is unpaired, consisting of four primary processes: a tall dorsal process, a pair of broad, plate-like transverse processes, and an elongate anterior process. The four processes converge posteroventrally on a broad pterygoid plate exposed posterior to the internal narial fenestrae. Much of the anterior process and lateral portions of the transverse processes are incomplete in RRBP 08630.

The dorsal process of the pterygoid ascends nearly vertically and laterally overlies the main body of the parabasisphenoid, broadly contacting on each side the pterygoid process of the quadrate, the lateral bridge of the laterosphenoid, and the base of the parabasisphenoid rostrum (Figs. 3A, C, 4A, B). Posteriorly, the dorsal process of the pterygoid is overlain by a thin sheet of the parabasisphenoid. In cross-section, the dorsal process is triradiate, consisting of two smooth anterolaterally facing surfaces converging anteriorly at the midline and a deeply concave posterior surface. The two posterolaterally free edges of the dorsal process of the pterygoid form thin, sharp crests, each of which is continuous dorsally with a similar crest on the pterygoid process of the ipsilateral quadrate to form 'crest B' on the ventral surface of the body of the quadrate (Figs. 2B, D, 3A, C); this condition is also present in other peirosaurids, *Araripesuchus*, and mahajan-gasuchids.

← FIGURE 4. Comparison of the lateral braincase wall (laterosphenoids) of selected meoseucrocodylian taxa in ventrolateral view illustrating variation in the shape of the laterosphenoid bridge and its relationship with foramina of the trigeminal system. **A**, photograph and **B**, interpretive line drawing of the left laterosphenoid of *Rukwasuchus yajabaliyekundu*, RRBP 08630 (character state 302.2). Interpretive line drawings of the laterosphenoids of **C**, *Hamadasuchus rebouli*, ROM 52620 (character state 302.2); **D**, *Stolokrosuchus lapparenti*, MNN GDF 600 (character state 302.2); **E**, *Montealtosuchus amarali*, MPMA 16-0007-04 (character state 302.2); **F**, *Araripesuchus wegneri*, MNN GAD 19 (reversed) (character state 302.2); **G**, *Mariliasuchus amarali*, MZSP-PV 50 (character state 302.1); and **H**, *Crocodylus acutus*, AMNH R-66635 (character state 302.3). Illustrations **C–F** are left lateral views, **G–H** are reversed right lateral views. Stippling indicates remaining sandstone matrix. **Abbreviations:** **bo**, basioccipital; **ctc**, cotylar crest; **fr**, frontal; **fr dl**, frontal descending lamina; **ls**, laterosphenoid; **ls all**, laterosphenoid anterolateral lamina; **ls pll**, laterosphenoid posterolateral lamina; **oto**, otoccipital; **pbs**, parabasisphenoid; **po**, postorbital; **pr**, parietal; **pt**, pterygoid; **pt dp**, pterygoid dorsal process; **q**, quadrate; **q ptp**, quadrate pterygoid process; **sof**, suborbital nerve foramen; **sq adl**, squamosal anterior descending lamina; **I**, olfactory foramen; **II**, optic foramen; **III**, oculomotor foramen; **IV**, trochlear foramen; **V₁**, ophthalmic nerve foramen; **V₂**, maxillary nerve foramen; **V₂₊₃**, combined maxillary and mandibular nerve foramen; **V₃**, mandibular nerve foramen; **VI**, abducens foramen.

The base of the transverse process of the pterygoid is laminar, projecting ventrolaterally from the pterygoid plate and the lateral margins of the internal narial fenestrae. The dorsal surfaces of the transverse processes are smoothly continuous with the anterolateral surfaces of the dorsal process and the dorsolateral surfaces of the anterior process of the pterygoid. The ventral surfaces of the transverse processes are smooth, converging on the broad and weakly concave, ventrally facing pterygoid plate. The posterior margin of the pterygoid plate is rounded and strongly concave along the midline. Anteriorly, the contact with the ipsilateral palatine is preserved on the dorsolateral surface of the left transverse process, indicating a broad scarf joint between the two elements. Although the distal halves of both transverse processes are incomplete in RRBP 08630, they can reasonably be assumed to have been broad, laminar, and plate-like, as in *Hamadasuchus*.

The anterior process of the pterygoid forms the dorsolateral roof of the internal nares, extending anteriorly to contribute to the roof of the nasopharyngeal canals. A thin vertical lamina of the anterior process forms a median septum between the internal nares. Anteriorly, much of the anterior process is missing in RRBP 08630, with only a thin, rod-like extension present ventral to the frontals. The descending processes of the prefrontals (prefrontal pillars) contact the dorsal surface of the anterior process close to the midline.

Laterosphenoids—The laterosphenoids are exquisitely preserved, consisting of broad laminar elements forming the anterolateral braincase wall (Figs. 3A, C, 4A, B). In general form, each laterosphenoid consists of an anterolateral and posterolateral lamina, divided by a sharp cotylar crest.

The anterolateral lamina of the laterosphenoid contacts the descending lamina of the frontal dorsally in a broad suture extending posterolaterally to the rounded subtriangular capitate process medial to the descending process of the postorbital. Medially, the anterolateral laminae of the left and right laterosphenoids meet in a broad suture enclosing the olfactory fissure dorsally and forming a broad sulcus from the optic foramen ventrally (Fig. 4B). Ventrally, the anterolateral lamina contacts the parabasisphenoid to enclose the exit for the oculomotor nerve (CN III) and is pierced by a foramen for the passage of the trochlear nerve (CN IV).

Beginning at the capitate process, the posterolateral lamina of the laterosphenoid sweeps posteriorly to form the anteromedial wall of the adductor chamber, meeting the descending process of the parietal dorsally. Posteriorly, the laterosphenoid contacts the dorsal primary head of the quadrate in a broad, dorsoventrally oriented, interdigitating suture.

Ventral to the posterolateral lamina, the laterosphenoid forms a broad, plate-like bridge over the trigeminal fossa that would have divided the branches of the trigeminal nerve (CN V). Along its anterior edge, the laterosphenoid bridge is continuous with the cotylar crest dorsally (Fig. 4B). Here, an opening medial to the anterior margin corresponds to the exit of the ophthalmic division of the trigeminal nerve (CN V₁). Ventrally, the laterosphenoid bridge contacts the parabasisphenoid and pterygoid to exclude them from the trigeminal fossa. The posterior contact between the laterosphenoid bridge and the pterygoid process of the quadrate extends dorsally to the trigeminal foramen. Here, the exits for the maxillary and mandibular branches of the trigeminal nerve (CN V_{2,3}) are further divided by a small accessory bridge, from which a faint sulcus for the mandibular nerve courses anteriorly (Fig. 4B). A small foramen for the passage of the suborbital nerve is present on the posterolateral lamina dorsal to the trigeminal foramen.

Parabasisphenoid—As in other crocodyliforms, the basisphenoid is coossified with the parasphenoid in *Rukwasuchus*. Much of the contribution of the parabasisphenoid to the floor of the braincase is hidden in ventral view by the dorsal process of the

pterygoid. The parabasisphenoid is exposed anteriorly on the braincase, where it forms the plate-like parabasisphenoid rostrum, and posteriorly, where it is present as a thin sheet that extends between the basioccipital and pterygoid, and the otoccipital and pterygoid process of the quadrate (Figs. 3A, C, 4A, B).

Anteriorly, the parabasisphenoid emerges from the medial surface of the dorsal process of the pterygoid to form the transversely compressed, plate-like parabasisphenoid rostrum (cultriform process). The parabasisphenoid rostrum is subrectangular in lateral view, extending parallel to the dorsal surface of the anterior process of the pterygoid, but separated from it by an elongate gap. The parabasisphenoid rostrum widens dorsally, contacting both laterosphenoid bridges along its posterodorsal border and the anterolateral laminae of the laterosphenoids dorsally. A semicircular depression with a small foramen is present immediately anterior to the dorsal-most contact between the parabasisphenoid and the lateral bridge of the laterosphenoid. This foramen likely represents the exit of the abducens nerve (CN VI). Anterior to this foramen, the parabasisphenoid forms a dorsoventrally short laminar pedicle contacting the anterolateral lamina of the laterosphenoid dorsally and forming the lateral wall of the hypophyseal fossa. Anterior to this pedicle is the ovoid opening for the oculomotor nerve (CN III). The anterior-most portion of the parabasisphenoid forms the ventral rim of the optic foramen.

In posterior and lateral views, the parabasisphenoid is visible as a modest sheet of bone between the basioccipital and the dorsal process of the pterygoid (Fig. 3). Along the midline, the parabasisphenoid forms a deep recess around the median Eustachian foramen, descending ventrally on the posterior surface of the pterygoid as a thin subtriangular lamina. Dorsally, the parabasisphenoid disappears between the pterygoid process of the quadrate and the ventral margin of the otoccipital (Figs. 3A, C, 4A, B).

Supraoccipital—The supraoccipital is a ‘U’-shaped element underlying the parietal and exposed only on the occipital surface of the skull (Fig. 3B, D). The dorsal margin of the supraoccipital is ventrally deflected at the midline and capped dorsally by a corresponding ventral deflection in the posterior margin of the dorsal lamina of the parietal. Immediately lateral to this depression are two well-developed, dorsolaterally directed postoccipital processes (Fig. 3B, D). A raised, rounded ridge on the occipital surface underlies the postoccipital processes. Dorsolateral to each postoccipital process near the parietosquamosal suture, the supraoccipital forms the ventral margins of the posttemporal fenestrae. A distinct bulge on the midline of the occipital surface is flanked on each side by semicircular concavities. Ventrally, the supraoccipital is excluded from the margin of the foramen magnum by the otoccipitals along a rounded, ventrally convex suture.

Otoccipitals—The otoccipitals, each derived from the fusion of the ipsilateral exoccipitals and opisthotics as in other crocodyliforms, together constitute most of the occipital surface of the skull (Fig. 4B, D). With the exception of the ventral margin, the otoccipitals form the rim of the foramen magnum and join one another on the midline in a broad, dorsoventrally directed suture. The descending pillars of the otoccipitals form the lateral margins of the foramen magnum, presumably terminating on the dorsolateral margin of the occipital condyle as in other crocodyliforms (this region is incomplete in RRBP 08630). Dorsally, the otoccipitals meet the supraoccipital in a broad, ‘U’-shaped suture terminating dorsolaterally at the posttemporal fenestrae. Dorsolaterally, the otoccipitals are in sutural contact with the posterior descending laminae of the squamosals, overlying them in a broad scarf joint. Here, the lateral regions of the otoccipitals form broad, subrectangular paroccipital processes overlying the posterior descending laminae of the squamosals as described above and the dorsal processes of the ipsilateral quadrates to which the otoccipitals are firmly and broadly sutured. Numerous

striations radiate laterally over the posterior surface of the paroccipital process along its lateral margin (Fig. 3B). Ventral and medial to the suture between the paroccipital process of the otoccipital and the dorsal process of the quadrate is the opening of the cranioquadrate canal (Fig. 3B, D), which travels anterodorsally between the two elements.

The ventral portion of the otoccipital thins medial and ventral to the cranioquadrate canal, becoming tightly sutured to the medial surface of the quadrate and to the dorsolateral margin of the parabasisphenoid and basioccipital. The free ventral margin of the otoccipital follows the contour of the quadrate, arching medially and ventrally to meet the basioccipital along a dorsomedially oriented suture extending to the occipital condyle. Ventrally, the otoccipital contributes to the lateral portion of the rugose basal tuber (Fig. 3B, D).

The posterior surface of the otoccipital is divided by a broad, rounded convexity that extends laterally from the descending pillars to the distal terminus of the paroccipital process. Dorsal to this convexity the otoccipital surface is smooth and unbroken. Ventral to the convexity and lateral to the occipital condyle, the otoccipital surface is pierced by five foramina on the left side and four on the right side (Fig. 3B, D). The medial-most foramina of the left otoccipital are closely paired and likely represent a variant in the pattern of the exit of nerves, with this pair represented by a single opening on the right otoccipital. Ventrolateral to this (these) foramen (foramina), and lateral to the occipital condyle, a third small foramen pierces the otoccipital. These groups of foramina, three on the left and two on the right, served as exits for the anterior and posterior roots of the hypoglossal nerve (CN XII). Immediately lateral to the ventral hypoglossal foramen is a fourth (on the right side), larger, ventrally directed foramen overhung by a sharp mediolaterally oriented crest. This large foramen served as the exit for the vagus and glossopharyngeal nerves (CN X and CN IX) and the sympathetic contributions to CN VII and CN IX (Iordansky, 1973). Immediately ventral to the vagal foramen is the ventrolaterally directed posterior carotid foramen for passage of the internal carotid artery.

Basioccipital—The basioccipital is subtriangular in posterior view, contributing to the occipital condyle dorsally and the broad, posteriorly directed basioccipital plate and basal tubera ventrally (Fig. 4B, D). The basioccipital is incomplete in RRBP 08630, missing most of its condylar contribution. The entire basioccipital plate forms a planar surface directed posteroventrally at an angle of approximately 30° relative to the face of the supraoccipital.

Dorsally, the basioccipital contacts the descending pillars of the otoccipitals ventrolateral to the foramen magnum. From the occipital condyle, the sutures between the basioccipital and the otoccipitals extend ventrolaterally to the lateral rugosities of the basal tubera (Fig. 3B, D). Ventrally and ventrolaterally, the basioccipital underlies the parabasisphenoid, enclosing the ventral portion of the Eustachian system. The large circular median Eustachian foramen is centered at the base of the basioccipital in a deep recess between the basioccipital and parabasisphenoid. The lateral Eustachian foramina are smaller and slit-like, situated between the basisphenoid and parabasisphenoid ventral to the basal tubera of the basioccipital. Posteriorly, the surface of the basioccipital plate is divided by a rugose median crest running dorsally to a foramen situated at the base of the occipital condyle. This small foramen may represent the remnant of the craniopharyngeal duct or, more likely, the exit of an emissary vein associated with the ventral longitudinal dural venous sinus (Kley et al., 2010). Lateral to the median crest, the surface of the basioccipital plate is smooth and moderately concave. The ventral and ventrolateral margins of the basioccipital are markedly rugose, overhanging the parabasisphenoid as short, mediolaterally wide basal tubera (Fig. 3B, D).

Dentition—A total of four isolated teeth from the Galula Formation are typically peirosaurid and are tentatively referred

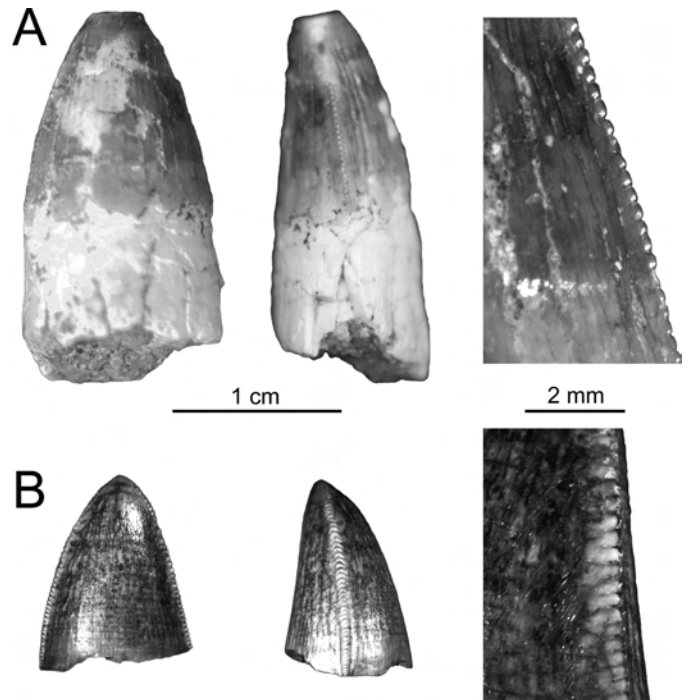


FIGURE 5. Isolated crocodyliform teeth from the Galula Formation tentatively referred to *Rukwasuchus yajabaliyekundu*. **A**, RRBP 09362, isolated tooth in lingual and mesial/distal views with close-up of denticle morphology. **B**, RRBP 09367, isolated tooth in labial and mesial/distal views with close-up of denticle morphology.

to *Rukwasuchus* on the basis of size and similarity with other peirosaurid taxa (Fig. 5). The only other currently recognized crocodyliform from the Galula Formation, *Pakasuchus kapilimai*, is much smaller and exhibits a suite of highly specialized mammal-like cuspidate teeth and small peg-like teeth that are easily distinguishable from the isolated teeth described here. In overall form, these teeth are subconical and moderately laterally compressed, with distinct denticulations on the mesial and distal carinae. The enamel of the crown is covered in weak longitudinal striations and crenulations. The junction between the base of the crown and the root in RRBP 09362 (Fig. 5A) appears weakly constricted as in other peirosaurid taxa.

Cranial Endocast

Computed tomography of the braincase of the holotype (RRBP 08630) of *Rukwasuchus yajabaliyekundu* provides a basis for characterizing the cranial endocast, including selected components of cranial nerve and endocranial vascular systems. Due to the exquisite nature of the lateral braincase wall, it is also possible to infer aspects of the distal morphology (e.g., position, orientation) of cranial nerve trunks. By contrast, exceptionally dense matrix located immediately superficial to the endocranial surface of the opisthotics precludes an assessment of inner ear (e.g., generalized labyrinthine organization, size/orientation/shape of the semicircular canals, etc.) structure. Relatively superficial structures within the cranial cavity, such as components of dural venous sinus system, are better able to be characterized due to their association close to or within external layers of the meninges, the outer layer of which is in tight association with the endocranial surface (for a discussion of this topic, see Jerison, 1973; Hopson, 1979; Witmer et al., 2008). Whereas in some cases (e.g., adjacent to the cerebral hemispheres) it is indeed possible to profile gross

organization of actual neural tissues because there is a relatively direct relationship between these and the inner bony surface of the cranial cavity, in other cases (e.g., in the region of the hind-brain) the underlying brain or brainstem anatomy is completely obscured by overlying meningeal-vascular structures.

Herein we describe the endocast of *Rukwasuchus* and profile other structures by linking foramina or canals on the external surface of the braincase with the endocranial cavity. Similar to our previous work on endocranial organization in mesoeucrocodylians (see Kley et al., 2010), our intent here is to (1) characterize gross endocranial morphology in *Rukwasuchus*, (2) conduct broad comparisons with representative extant Crocodylia in order to constrain soft-tissue inferences in this

taxon, and (3) provide a novel neuromorphological datapoint among the extremely diverse mesoeucrocodylians.

The scan data set of RRBP 08630 reveals important details regarding the cranial endocast morphology. However, certain regions of this specimen are either not preserved (e.g., anteroventral wall of the cranial cavity) or are infiltrated with dense matrix (e.g., the inner ears), thereby preventing an assessment of the respective morphologies. The overall shape of the cranial endocast (Fig. 6) is generally consistent with that observed in the extant crocodylians *Gavialis gangeticus* (Wharton, 2000) and *Crocodylus johnstoni* (Witmer et al., 2008). This includes broad cerebral hemispheres that taper anteriorly and posteriorly and a long, narrow olfactory tract terminating in a moderately broad

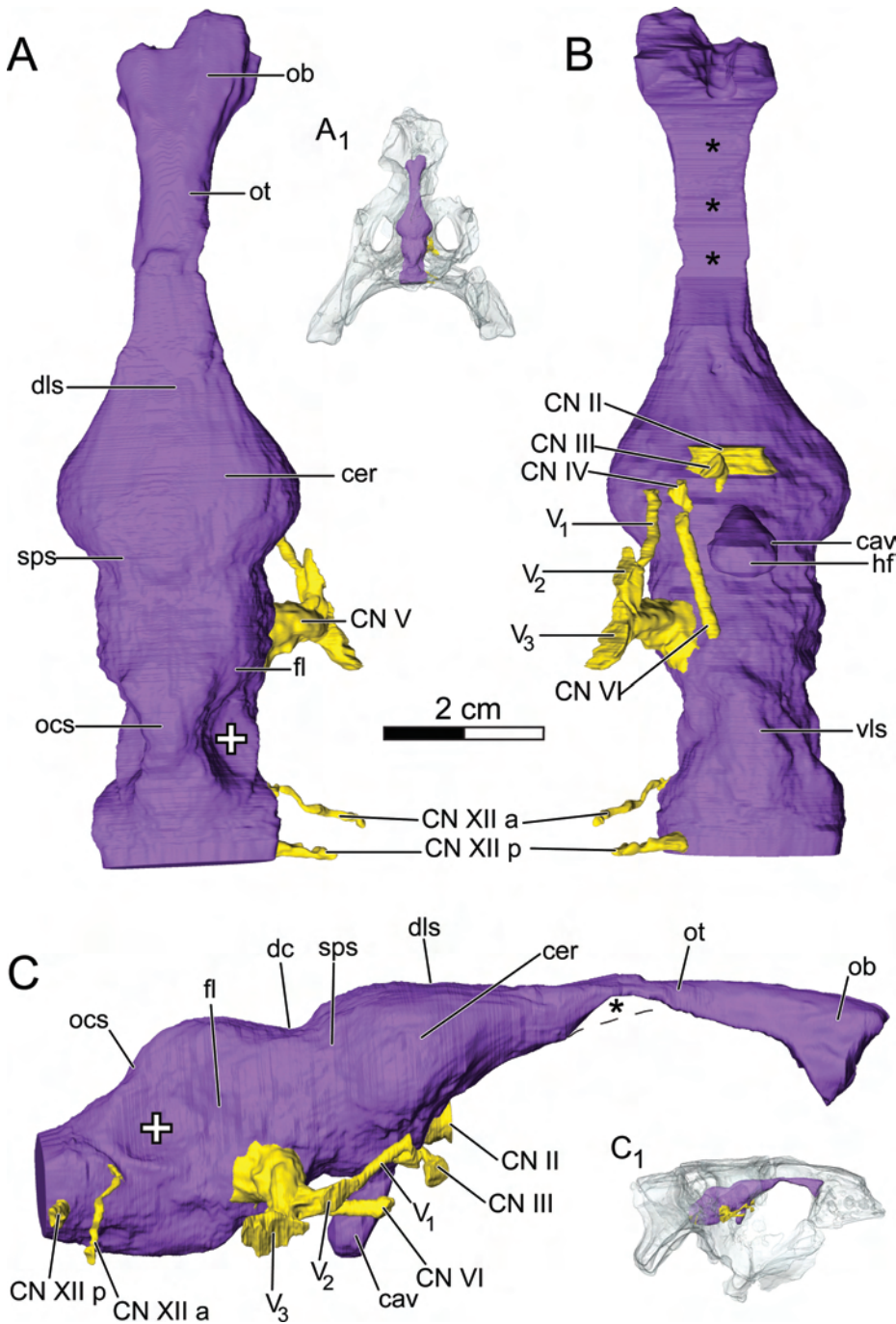


FIGURE 6. Volume rendering of the endocranial cavity based on CT (computed tomography) scan of RRBP 08630. Digital endocast (purple) in dorsal (A), ventral (B), and right lateral (C) views, with selected cranial nerve trunks (yellow) depicted. A₁ and C₁ illustrate the reconstructed endocranial volume set within projections of the reconstructed and semitransparent skull. Asterisks in B and C and the dashed line in C serve to illustrate those parts of the olfactory tract for which the contour is estimated based on the absence of the anteroventral-most floor of the cranial cavity. Abbreviations: **cav**, endocast of cavernous sinus; **cer**, endocast of cerebrum; **CN II**, endocast of optic nerve; **CN III**, endocast of oculomotor nerve; **CN V**, endocast of trigeminal nerve; **CN VI**, endocast of abducens nerve; **CN XII a**, endocast of anterior rootlets of hypoglossal nerve; **CN XII p**, endocast of posterior rootlets of hypoglossal nerve; **dc**, dorsal contour; **dls**, endocast of dorsal longitudinal dural venous sinus; **fl**, endocast of flocculus (cerebellar auricle); **hf**, endocast of hypophyseal (pituitary) fossa; **ob**, endocast of olfactory bulb; **ocs**, endocast of occipital dural venous sinus; **ot**, endocast of olfactory tract; **sps**, sphenoparietal dural venous sinus; **vls**, endocast of ventral longitudinal dural venous sinus.

olfactory bulb. Regarding the latter, the olfactory bulbs appear very well developed and ventrally deflected in *Rukwasuchus* when compared with the condition in extant crocodylians and fossil crocodyliforms in which the situation is known. Another distinctive feature of *Rukwasuchus* relates to the dorsal contour of the endocast. Whereas the dorsal contour along the olfactory apparatus, the forebrain (i.e., the cerebral hemispheres), and the hindbrain appears unremarkable and generally curvilinear as noted in other crocodylians, there is a significant postcerebral concavity along the dorsal aspect of the endocast (Fig. 6C). This appears unique among the crocodyliforms (fossil and Recent) thus far surveyed (e.g., Witmer et al., 2008; Sereno and Larsson, 2009; Kley et al., 2010). Forebrain organization is generally similar to other mesoeucrocodylians (e.g., *Anatosuchus minor*, *Araripesuchus wegneri*; Sereno and Larsson, 2009) in having a modestly high, spade-shaped cerebrum that tapers anteriorly and posteriorly. This is in stark contrast to the dorsoventrally expanded cerebrum exhibited by the notosuchian *Simosuchus clarki* (see Kley et al., 2010).

The endocranial reconstruction also highlights the main dorsal midline components of the dural venous sinus system (Fig. 6A), including the dorsal longitudinal sinus overlying the cerebrum and olfactory apparatus and the occipital dural venous sinus overlying the tectum, cerebellum, and medulla (note that these regions of the central nervous system are not specifically considered as part of the endocast; see Sedlmayr, 2002; Sampson and Witmer, 2007). The ventral midline of the endocast (Fig. 6B) is notable for the large hypophysal fossa and the paired cavernous dural venous sinuses located posteroventral to the cerebral hemispheres, the postpituitary notch, and a representation of ventral longitudinal dural venous sinus positioned ventral to the hindbrain. The sphenoparietal dural venous sinus passes transversely just posterior to the cerebral hemispheres, connecting the dorsal longitudinal sinus to the cavernous sinus (see Witmer et al., 2008). The transverse dural venous sinus occupying the tectal-otic sulcus is not visible on the endocast, but can be semiconstrained as passing along the anterior edge of the flocculus. The position of the flocculus can be inferred based on its common placement just anterior to where the opisthotics project medially into the cranial cavity (i.e., that point where the hindbrain region of the endocast is transversely pinched; Fig. 6A, B). As noted above, due to mineral/sediment infiltration within the interior of elements making up the lateral braincase wall, we are unable to characterize components of the endosseous labyrinth.

COMPARISONS

The circum-Saharan African crocodyliform record includes several putative peirosaurid taxa known from a number of middle Cretaceous localities, including *Hamadasuchus rebouli* from the Aptian–Cenomanian of Morocco (Buffetaut, 1994; Larsson and Sues, 2007), *Trematochampsia taqueti* from the Turonian–Coniacian (early Senonian) of Niger (Buffetaut, 1974, 1976), and *Stolokrosuchus lapparenti* from the Aptian of Niger (Larsson and Gado, 2000). Additional remains from Morocco (Rauhut and López-Arbarello, 2006; Cavin et al., 2010) and the Cretaceous of Mali (Hill et al., 2010) may also be referable to Peirosauridae. Among other African crocodyliforms with potentially close links with peirosaurids, the recent phylogenetic analysis of Turner and Sertich (2010) supported Sereno and Larsson's (2009) placement of *Kaprosuchus saharicus* from the Aptian–Cenomanian of Morocco and *Mahajangasuchus insignis* from the Maastrichtian of Madagascar in the Mahajangasuchidae, the sister taxon of Peirosauridae. A number of features distinguish *Rukwasuchus* from other peirosaurids and related mesoeucrocodylian taxa.

In addition to its diagnostic features, *Rukwasuchus* can be easily distinguished from *Stolokrosuchus* on the basis of its taller, narrower skull and ellipsoidal, rather than subcircular, supratem-

poral fenestrae. The flat and heavily sculpted squamosal, posteriorly overhanging parietal, and elongate, dorsoventrally compressed quadrate body of *Trematochampsia* are significantly different from those of *Rukwasuchus*. In overall form, the skull of *Rukwasuchus* compares most closely with *Hamadasuchus*. However, the internal narial fenestrae (choanae) of *Hamadasuchus* are transversely broad and located posteriorly, near the posterior margin of the pterygoid plate, whereas in *Rukwasuchus* the narrow internal narial fenestrae are widely separated from the posterior margin of the broad pterygoid plate. Additionally, the contact between the frontal and postorbital forms an elevated dorsal peak in *Rukwasuchus*, a feature absent in *Hamadasuchus*. Moreover, the otic aperture is separated from the posterior margin of the skull by a relatively wide dorsal process of the quadrate and the descending process of the postorbital is more ventrally directed. Finally, the paroccipital process is more rectangular in *Rukwasuchus*.

Nevertheless, there are many similarities shared between *Rukwasuchus* and other African peirosaurid taxa. *Rukwasuchus*, *Hamadasuchus*, and *Stolokrosuchus* all share a depressed posterior parietal border. These three taxa and *Trematochampsia* also all share an anteriorly projected anterior process of the squamosal that nearly reaches the orbital margin below the dorsal lamina of the postorbital. The morphology of the laterosphenoid and laterosphenoid bridge are also remarkably similar among these taxa (Fig. 4). Teeth tentatively referred to *Rukwasuchus* are generally similar in size and morphology to those of *Hamadasuchus* (Larsson and Sues, 2007), and both exhibit distinctly denticulate carinae. In particular, the low, laterally compressed morphology of RRBP 09362 (Fig. 5A) strongly resembles the posterior maxillary teeth of *Hamadasuchus*.

PHYLOGENETIC RELATIONSHIPS

Taxon Sampling and Data Set

The phylogenetic position of *Rukwasuchus yajabaliyekundu*, together with that of other purported African peirosaurids, was tested using an extension of the data set of Turner and Sertich (2010). The data set was altered by the inclusion of additional characters and the modification of some character definitions and scorings (Appendices 1, 2; Supplementary Data). Although several taxa were added to this analysis, including *Pakasuchus kapilimai*, the only other crocodyliform thus far recovered from the Galula Formation of Tanzania, an overall reduction of derived taxa was undertaken. The original analysis by Turner and Sertich (2010) resulted in a significant loss of resolution among neosuchian taxa relative to previous versions of the same data set (e.g., Turner and Buckley, 2008). This loss of consensus was likely the result of increased character and taxon sampling aimed at addressing basal mesoeucrocodylian interrelationships at the expense of more derived neosuchian crocodyliforms. In an attempt to improve resolution among derived mesoeucrocodylians, a number of neosuchian taxa included in the original data set were not included in this analysis. Taxa excluded include those with proportionally high amounts of missing data (e.g., *Alligatorium*, *Hylaeochampsia*) and those from otherwise well-represented clades (e.g., goniopholidids, thalattosuchians). Thus, the total data set in this analysis is based on 71 taxa and 308 morphological characters (Appendix 2).

Trematochampsia taqueti is an enigmatic taxon based on a large collection of isolated cranial and postcranial elements from a single locality near In Beceten, Niger. Larsson and Sues (2007) recently cast doubt on the validity of *Trematochampsia*, specifically questioning the association of the many cranial and postcranial elements with a single taxon. The ambiguous placement of *Trematochampsia* in analyses in which it is included (Larsson and Sues, 2007; Turner and Buckley, 2008) has been interpreted as an indication of character conflict, likely the result of its potentially

composite nature. In order to address these problems, specimens referred to *Trematochamps* were reexamined and the data set revisited. Detailed reinvestigation (by J.J.W.S.) of the In Beceten collection and the cranial specimens referred to *Trematochamps taqueti* by Buffetaut (1976) validated their original referral of the materials to a single species. Consistency in patterns of complementary element suturing, ornamentation, size, and abundance supported this interpretation. However, the presence of more than one crocodyliform taxon in the overall collection and the generally conservative morphology of the crocodyliform postcranial skeleton prevented confident association of postcranial material with *Trematochamps taqueti*. As such, only cranial characters were considered in the data set utilized herein with scorings based on elements figured by Buffetaut (1976).

Similarly, the problematic putative peirosaurid taxon *Stolokrosuchus lapparenti* was reinvestigated as part of this analysis. Originally described as a longirostrine peirosaurid from the Aptian of Niger by Larsson and Gado (2000), *Stolokrosuchus* has been recovered outside Peirosauridae by several independent analyses of mesoeucrocodylian interrelationships (e.g., Carvalho et al., 2004; Jouve et al., 2006; Turner and Buckley, 2008; Jouve, 2009; Andrade et al., 2011), as well as by the previous version of this data set (Turner and Sertich, 2010). Alternative placement of *Stolokrosuchus* is potentially a result of its longirostrine morphology and the absence of a posterior palate in the only known specimen. Critical reexamination of the holotype was undertaken as part of this investigation.

Results

The data set was analyzed using equally weighted parsimony in TNT version 1.1 (Goloboff et al., 2008a, 2008b). A heuristic tree search strategy of 1000 replicates of Wagner trees (random addition sequences) was conducted followed by tree bisection and reconnection (TBR) branch swapping (holding 10 trees per replicate). Best trees obtained were subjected to an additional round of TBR branch swapping. The analysis resulted in 112 most parsimonious trees of 1346 steps (consistency index = 0.285, retention index = 0.669), found in 626 of the 1000 replicates (Fig. 7).

Character support of nodes present in most parsimonious reconstructions was calculated using jackknife resampling (Farris et al., 1996) and Bremer support (Bremer, 1988, 1994). Jackknife support was calculated using TNT using 1000 replicates for which the probability of independent character removal was set to 0.20. Jackknife replicates were analyzed using 10 replicates of RAS followed by TBR branch swapping (holding 10 trees per replicate) and are summarized using GC frequencies (Goloboff et al., 2008a, 2008b). Bremer support was calculated using negative constraints employed by the BREMER.RUN script supplied with TNT.

All of the most parsimonious hypotheses that emerged from this analysis place *Rukwasuchus* in a close relationship with either *Stolokrosuchus* or *Hamadasuchus*, resulting in an unresolved trichotomy in the strict consensus (Fig. 7). These three taxa are found to be closely related to *Trematochamps*, forming a monophyletic clade of African taxa within Peirosauridae. A close sister-group relationship between Peirosauridae and Mahajangasuchidae is supported, as in the previous version of this analysis (Turner and Sertich, 2010). Moreover, a close sister-group relationship between this clade and *Araripesuchus* is recovered, as hypothesized in previous analyses (e.g., Buckley and Brochu, 1999; Buckley et al., 2000; Turner, 2004, 2006). Overall, peirosaurids are found to be more closely related to ziphosuchians within a monophyletic Notosuchia, than to neosuchians, a relationship also conserved from the earlier analysis (Turner and Sertich, 2010).

The unresolved trichotomy that includes *Rukwasuchus*, *Hamadasuchus*, and *Stolokrosuchus* is supported by two synapomorphies: the presence of a depressed posterior parietal border (character 306.1) and external contact between the lacrimal and

nasal (character 11.0). In the absence of rostral morphology, only the parietal depression (Fig. 8) is known for *Rukwasuchus*.

Notably, a clade consisting of all four purported African peirosaurids is supported by the presence of two synapomorphies: the presence of an anteriorly projecting anterior process of the squamosal to near the level of the orbit (character 288.1) and the exclusion of the parabasisphenoid from the ventral braincase by the pterygoid and quadrate (character 56.1; Fig. 4). The recovery of both *Stolokrosuchus* and *Trematochamps* as derived peirosaurids is novel relative to previous versions of this data set (Turner and Buckley, 2008; Turner and Sertich, 2010), thus reconciling the placement of *Stolokrosuchus* with the topologies of Larsson and Sues (2007) and Sereno and Larsson (2009). As discussed above, ambiguity over the associations of specimens referred to the fragmentary taxon *Trematochamps taqueti* have led to its exclusion from many recent analyses. Reconciliation of character conflict (i.e., exclusion of potentially problematic cranial and postcranial associations) in this analysis likely contributed to its well-supported placement among peirosaurids.

Five character states unambiguously diagnose Peirosauridae: the presence of a large fenestra on the ventral surface of the premaxilla-maxilla contact (character 9.2); the absence of supraoccipital exposure on the dorsal cranial table (171.0); the presence of a wedge-like anterior process of the maxilla on the lateral premaxilla-maxilla suture (213.1); a perinarial fossa occupying much of the surface of the premaxilla ventral to the external naris (226.3); and a prominent depression on the maxillary palate at the level of the sixth or seventh alveolus (290.1). Of these, only one—absence of dorsal supraoccipital exposure—is known for *Rukwasuchus*. The monophyly of Peirosauridae is well supported by earlier versions of this data set (e.g., Turner and Buckley, 2008; Turner and Sertich, 2010) with similar character support. In contrast, the analysis of Sereno and Larsson (2009) recovered a close relationship between members of Peirosauridae and *Sebecus*.

The close relationship between Peirosauridae and Mahajangasuchidae is well supported, with nine characters uniting the two clades. These include a short, broad, and robust retroarticular process (character 71.1); an enlarged dentary tooth opposite the premaxilla-maxilla contact (80.1); a shallow, anteriorly tapering mandibular symphysis in lateral view (103.1); the absence of aligned neurovascular foramina on the lateral surface of the maxilla (138.0); a posteroventrally directed quadrate body (149.0); the absence of an unsculptured region on the lateral surface of the dentary (155.0); a dorsally robust splenial posterior to the mandibular symphysis (161.1); a long paroccipital process lateral to the cranioquadrate opening (268.1); and a complex interdigitating surangular-dentary suture (289.1).

Araripesuchus is recovered as the sister taxon to Peirosauridae + Mahajangasuchidae. This topology is supported by nine synapomorphies, including a flattened posterior process of the jugal (character 18.0); a cylindrical postorbital bar (26.1); a quadrate body divided into two surfaces by a distinct crest (150.2); a straight dorsal dentary margin with an abrupt dorsal expansion (159.1); a surangular that does not reach the posterior tip of the retroarticular process (301.1); a laterosphenoid bridge contacting the parabasisphenoid (302.1; Fig. 4); an anteriorly placed incisive foramen contacted posteriorly by an anterior extension of the palatal processes of the maxillae (303.1); a well-developed posteroventral process of the postorbital (305.1; Fig. 9); and a 'crest B' on the ventral surface of the quadrate continuous with the free edge of the dorsal process of the pterygoid (308.1; Fig. 10).

DISCUSSION AND BIOGEOGRAPHIC IMPLICATIONS

The recovery of *Rukwasuchus yajabaliyekundu* as a peirosaurid is well supported in this analysis, extending the middle

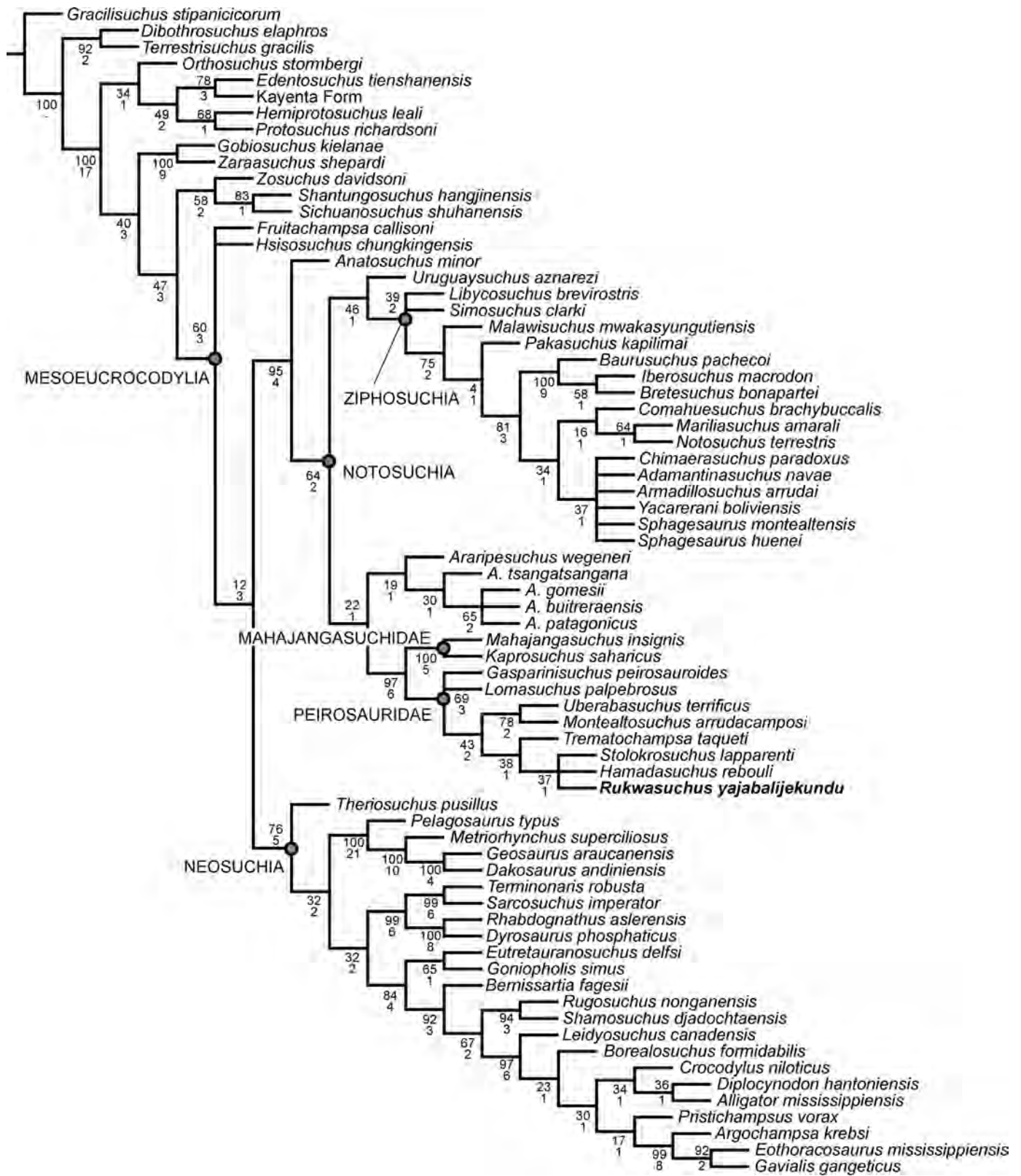


FIGURE 7. Phylogenetic placement of *Rukwasuchus yajabaliyekundu* (in bold) shown in a strict consensus of 112 most parsimonious reconstructions of 1339 steps in an analysis of 308 characters and 71 crocodylomorph taxa with *Gracilisuchus* as the outgroup. The consistency index is 0.285 and the retention index is 0.669. A pair of numbers representing GC values (top number) and Bremer support values (bottom number) is given at each node.

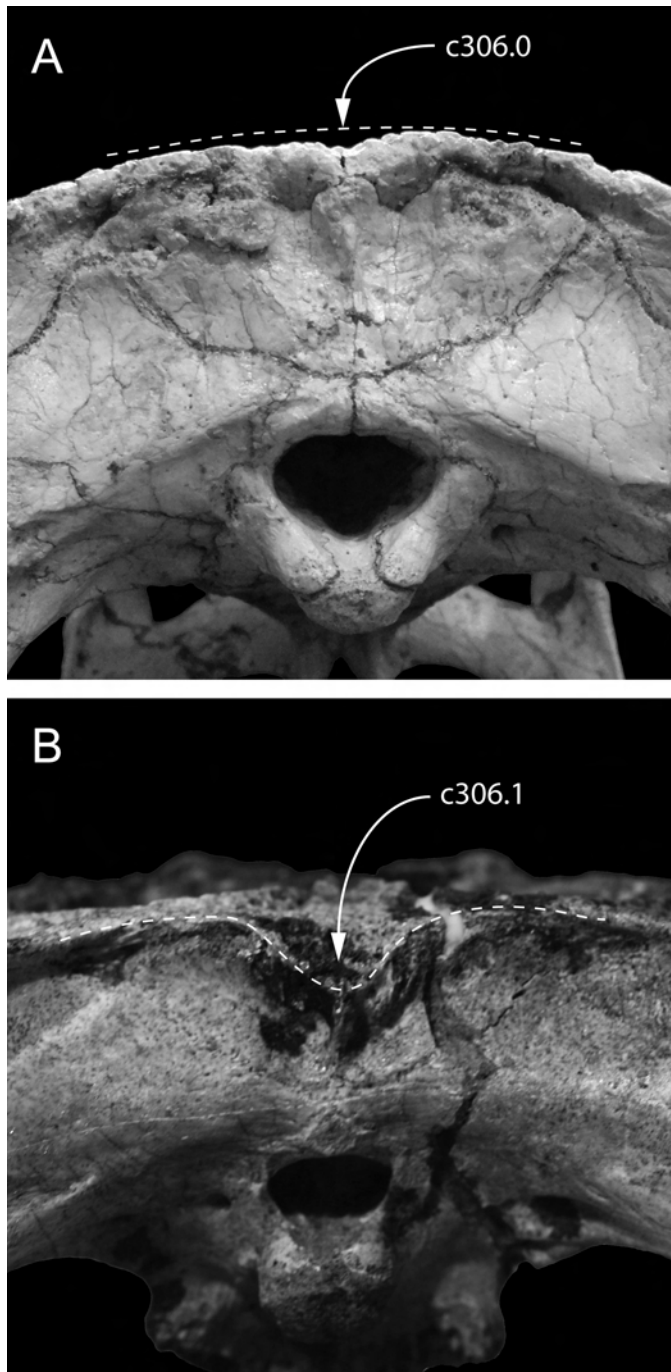


FIGURE 8. Systematic variation in the conformation of the posterior border of the parietal among peirosaurid crocodyliforms. **A**, *Montealtosuchus arrudacamposi*, MPMA 16-0007-04, posterior view of the parietal showing the plesiomorphic condition of a dorsally flat or gently convex posterior parietal margin (character state 306.0). **B**, *Stelokrosuchus laparenti*, MNN GDF 600, posterior view of the parietal showing the derived condition of a ventrally depressed posterior parietal margin (character state 306.1).

Cretaceous range of the group into sub-Saharan Africa. Peirosaurid taxa are known from the middle and Late Cretaceous of South America (Price, 1955; Gasparini et al., 1991; Carvalho et al., 2004, 2007; Leardi and Pol, 2009; Campos et al., 2011) and the middle Cretaceous of Africa (Buffetaut, 1974, 1976,

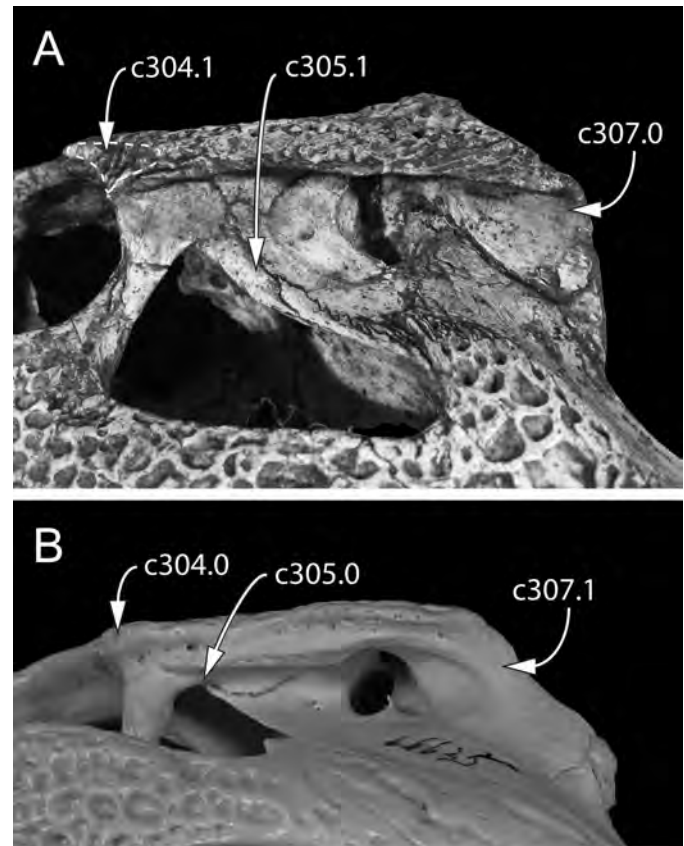


FIGURE 9. Systematic variation in the postorbital and external otic recess of crocodyliforms. **A**, *Hamadasuchus rebouli*, ROM 52620, in left lateral view showing the presence of a triangular depression on the postorbital (character state 304.1), a well-developed posteroventral postorbital process (character state 305.1), and a posteriorly open external otic recess (character state 307.0). **B**, *Crocodylus acutus*, AMNH R-66635, in left lateral view showing the absence of a postorbital depression (character state 304.0), the absence of a posteroventral postorbital process (character state 305.0), and an external otic recess closed posteriorly by the posterior descending lamina of the squamosal (character state 307.1).

1994; Larsson and Gado, 2000; Larsson and Sues, 2007). Connections between the western Gondwanan landmasses of Africa and South America persisted until approximately the end of the Early Cretaceous (Lawver et al., 1992; Müller et al., 1993; Pletsch et al., 2001). It is perhaps not surprising then that middle Cretaceous faunal links between the two landmasses have been well established for many vertebrate clades (for a recent review, see Gheerbrant and Rage, 2006), including the crocodyliform taxa *Araripesuchus* and *Sarcosuchus* (Buffetaut and Taquet, 1977, 1979). The support, though weak, in this analysis for a monophyletic African peirosaurid clade is therefore interesting in this context but must be tested further through improved taxon sampling before any major paleobiogeographic conclusions can be drawn. This includes potentially coeval South American peirosaurid taxa (e.g., *Caririsuchus* [Kellner, 1987; Buffetaut, 1991], *Barcinosuchus* [Leardi and Pol, 2009]). Nevertheless, the presence of a peirosaurid taxon in Tanzania increases the Cretaceous diversity and geographic range of the group in Africa.

Potential middle Cretaceous links between sub-Saharan localities and well-known circum-Saharan faunas have been proposed previously on the basis of fragmentary specimens. This includes the pleurodiran turtle *Platycheloides nyasae*, named on the

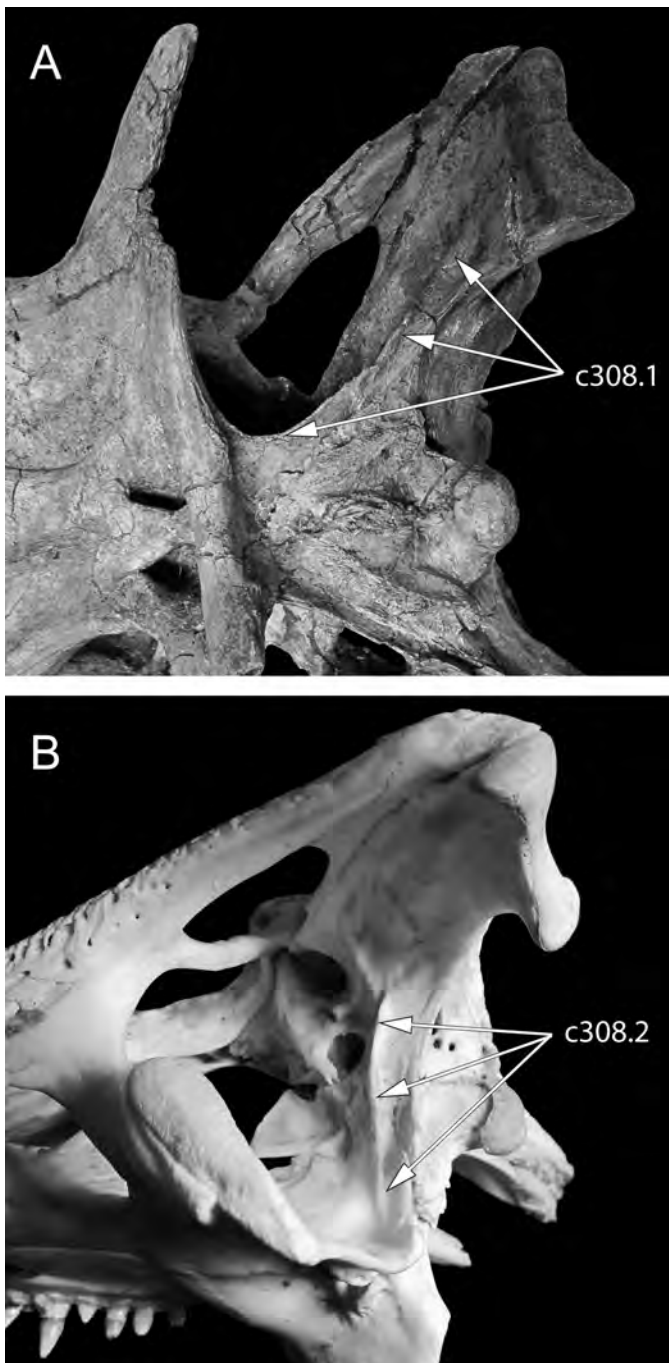


FIGURE 10. Systematic variation in the conformation of 'crest B' on the ventral surface of the quadrate body. **A**, *Mahajangasuchus insignis*, FMNH PR 2448, in ventral view showing 'crest B' continuous with the free posterior edge of the dorsal process of the pterygoid (character state 308.1). **B**, *Caiman yacare*, AMNH R-97296, in ventrolateral view showing 'crest B' on the lateral surface of the dorsal process of the pterygoid and ventral quadrate (character state 308.2).

basis of fragmentary remains from the Dinosaur Beds of Malawi (Haughton, 1928) and a complete shell from Gadoufaoua, Niger (Broin, 1980). Unfortunately the specimen from Malawi is likely too fragmentary to be of taxonomic value (Gaffney et al., 2006). Isolated crocodyliform and theropod dinosaur teeth from the Dinosaur Beds of Malawi resemble those of northern taxa, but are

non-diagnostic to lower-level clades (Jacobs et al., 1990). Conversely, diagnostic titanosaurian sauropod material from Malawi (Jacobs et al., 1993; Gomani, 1999, 2005) or Tanzania (O'Connor et al., 2006; Gorscak et al., 2011) does not compare closely with any sauropodomorph material yet reported from circum-Saharan localities. The small, mammal-like notosuchian crocodyliforms *Malawisuchus mwakasyungutiensis* from Malawi and *Pakasuchus kapilimai* from Tanzania appear to share more similarities with each other and South American taxa than with notosuchian crocodyliforms from circum-Saharan Africa (O'Connor et al., 2010). Thus, the close relationship between *Rukwasuchus* and the northern taxa *Hamadasuchus rebouli* and *Stolokrosuchus lapparenti* provides the first strong faunal link between the two African regions. Discovery of more complete specimens of *Rukwasuchus* would provide the opportunity to refine its phylogenetic affinities and the paleobiogeographic history of African peirosaurids during the Cretaceous.

ACKNOWLEDGMENTS

We thank D. Kamamba, F. Ndunguru, J. Temba (Tanzania Antiquities Unit), P. Msemwa (Tanzania Museum and House of Culture), I. Marobhe, and N. Boniface (University of Dar es Salaam), and the Tanzania Commission for Science and Technology for logistical support. Thanks are also due to N. Stevens, E. Roberts, Z. Jinnah, and S. Ngasala for various forms of support on this project. We are immensely grateful to J. Groenke, S. Egberts, and W. Holloway for their skillful mechanical and digital preparation of the holotype and referred specimens, and to J. Sands, C. Pugh, and B. Keener (Holzer Clinic, Athens, Ohio) for assistance with computed tomography scanning. For assistance in the field, we thank S. Burch, J. P. Cavigelli, M. Getty, E. Lund, E. Simons, V. Simons, T. Hieronymus, G. Masai, and A. Mussa. Thanks also to D. Krause, P. Sereno, K. Seymour, D. Evans, I. Carvalho, A. Campos, S. Tavares, L. Ribeiro, and R. Allain for access to specimens. A. Turner, D. Krause, and N. Kley provided feedback on an earlier version of the manuscript. This research was supported by the National Science Foundation (DEB-1011302, EAR-0617561, EAR-0854218), the National Geographic Society (CRE), and Ohio University Heritage College of Osteopathic Medicine and Office of Research and Sponsored Programs.

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Submitted October 29, 2012; revisions received June 17, 2013; accepted June 23, 2013.

Handling editor: Emily Rayfield.

APPENDIX 1. Additional character descriptions and modifications to the data matrix of Turner and Sertich (2010).

Character 150 (modified from Pol, 1999:character 167): Quadrate body in posterior view: with only one plane facing posterodorsally (0); with two distinct faces, a posterodorsal one and a posteromedial one bearing the foramen aereum (1); with two distinct faces divided by a distinct dorsal crest, a posterodorsal one and a posteromedial one bearing the foramen aereum (2).

The original character of Pol (1999) considered only the first two character states. An additional state was added to the modified version above to distinguish taxa in which the quadrate body is divided by a crest. In contrast to the dorsoventrally compressed quadrate body of many

neosuchians, the quadrate body of many basal mesoeucrocodylians is divided into a posteriorly or posterodorsally directed surface and a posteromedially directed surface bearing the foramen aereum. In some basal mesoeucrocodylian taxa, the boundary between these two surfaces is divided by a sharp crest running between the medial hemicondyle and the base of the dorsal process of the quadrate at its juncture with the paroccipital process of the otoccipital.

Character 302 (modified from Sereno and Larsson [2009:character 165] and Brochu [1997:character 115]): Laterosphenoid bridge dividing branches of the trigeminal nerve (CN V): absent (0); present, contacting pterygoid and quadrate ventrally (1); present, contacting parabasisphenoid, pterygoid, and quadrate ventrally (2); present, broadly contacting pterygoid and quadrate ventrally but separated from the parabasisphenoid by an extension of the laterosphenoid (3).

The original character of Brochu (1997:character 115) considered the presence or absence of a pterygoid contribution to the base of the laterosphenoid bridge. Sereno and Larsson (2009:character 165) considered the presence or absence of the laterosphenoid bridge. The new character proposed here combines both of these characters to encompass the presence/absence of the structure in crocodylomorphs and its morphological variation. In some crocodyliforms, the laterosphenoid bridge consists of a simple, small, pillar-like structure contacting the pterygoid and quadrate ventrally to divide the trigeminal foramen (Fig. 4G). In these taxa, the laterosphenoid bridge does not approach the anterior exposure of the parabasisphenoid, thus allowing the pterygoid to form a portion of the trigeminal foramen. In *Araripesuchus* and peirosaurids, the laterosphenoid bridge contacts the parabasisphenoid in a broad suture, separating the pterygoid from the trigeminal foramen (Fig. 4B–F). In crocodylians and derived neosuchians, an extension of the laterosphenoid contacts the parabasisphenoid anteriorly, separating it from the laterosphenoid bridge, but also excluding the pterygoid from the trigeminal foramen (Fig. 4H).

Character 303 (new): When enclosed by a secondary palate, incisive foramen located: posteriorly, at the junction of the premaxillary and maxillary palatal processes (0); anteriorly, contacted by anterior extension of palatal processes of maxillae (1); anteriorly, enclosed by palatal processes of premaxillae (2).

The location of the incisive foramen relative to the tooth row in crocodylians was considered by Brochu (1997, 1999) and is included in modified form in this data set (character 270). However, the position of the incisive foramen within the palate and its relationship with the palatal processes of the premaxilla and maxilla vary among mesoeucrocodylians. Plesiomorphically, the incisive foramen is located at the junction of the premaxilla and maxilla on the palate. This condition is also present in many ziphosuchian crocodyliforms, including *Baurusuchus*, *Sphagesaurus*, and *Mariliasuchus*, among others. In *Araripesuchus* and peirosaurids, the incisive foramen is located anteriorly between the premaxillae but is contacted posteriorly by an anterior extension of the palatal processes of the maxilla. In many neosuchians, the palatal processes of the premaxilla meet posterior to the incisive foramen, separating it from the maxilla.

Character 304 (modified from Sereno and Larsson, 2009:character 72): Triangular depression on anterodorsal surface of postorbital for palpebral element: absent (0); present (1).

A well-developed posterior palpebral facet is present in many notosuchian taxa. In many of these taxa, the facet

is subtriangular in dorsal view, with the apex forming an anterolaterally directed point on the corner of the cranial table. This facet also contributes to the formation of a sharp crest on the dorsal postorbital bar delimiting the posterodorsal margin of the orbit.

Character 305 (modified from Sereno and Larsson, 2009:character 67): Postorbital posteroventral process: absent or poorly developed (0); present as an elongate process (1).

Both Sereno and Larsson (2009:character 67) and Brochu (1997:character 76) include versions of this character in their data sets. However, in both cases, the morphology characterized includes the pattern in which other elements are contacted by the posteroventral process of the postorbital. The character included here only encompasses the presence and degree of formation of the posteroventral process. Some ziphosuchians, *Araripesuchus*, and peirosaurids share a well-developed posteroventral process of the postorbital. A similarly well-developed process is also present in some eusuchians (e.g., *Paleosuchus*).

Character 306 (new): Posterior border of the dorsal lamina of the parietal: dorsally convex or flat (0); or depressed, with distinct convexity on the margin (1).

The dorsal lamina of the parietal of most crocodylomorphs is moderately convex to flat. In some mesoeucrocodylian taxa, the dorsal lamina of the parietal is dorsally concave. This is further accentuated in some peirosaurid taxa (i.e., *Hamadasuchus*, *Stolokrosuchus*, *Rukwasuchus*), in which the posterior border of the parietal is significantly depressed, creating a 'U'-shaped supraoccipital in posterior view (Fig. 8B).

Character 307 (modified from Sereno and Larsson, 2009:character 57): Posterior region of external otic recess: open posteriorly (0); bounded posteriorly by posteroventrolateral extension of posterior descending lamina of squamosal (1).

In crocodyliforms, the dorsal laminae of the squamosal and postorbital extend laterally to overhang the otic aperture, forming the external otic recess. In many basal mesoeucrocodylian and basal neosuchian taxa, the external otic recess is open posteriorly below the posterior process of the squamosal. In derived neosuchians and eusuchians, the external otic recess is closed posteriorly by a ventrolateral extension of the posterior descending lamina of the squamosal.

Character 308 (new): Adductor 'crest B' (Iordansky, 1964) on ventral surface of quadrate: absent (0); present as continuation of posterior free edge of pterygoid onto ventral surface of quadrate (1); present, arising from lateral surface of pterygoid and continuing onto ventral surface of quadrate (2).

The pattern of adductor crest expression and development is highly variable among Crocodylia, often in correlation with ontogenetic stage and size (Iordansky, 1964, 1973). Nevertheless, the pattern of their expression can be of phylogenetic utility where consistent generalized patterns can be observed more broadly among crocodyliforms. The pattern of adductor 'crest B' expression in crocodyliforms can be generalized to conform to one of two states in addition to the plesiomorphic absence of 'crest B.' In some crocodyliforms, including *Araripesuchus*, peirosaurids, and some basal neosuchians, the free, posterior edge of the dorsal pterygoid process does not meet the basioccipital, instead forming a crest continuous with 'crest B' (Fig. 10A). In derived neosuchians and crocodylians, the free edge of the dorsal pterygoid process tapers at its contact with the basioccipital, with 'crest B' originating on the lateral surface of the pterygoid and continuing onto the quadrate (Fig. 10B).

APPENDIX 2. Character scorings for taxa added to the expanded data set of Turner and Sertich (2010).

Pakasuchus kapilimai

101??0?1?21?0?111100101111?01100010221101000?11?2011?100
0?10?1?03?31102?01011?0101?111??01?0?11?0?122?13?01
?0??01100?1001?000?011021011100001010010100011011010
011?00000000010000121010110100100001110000000000000000
0??000?00100?0??0?00?000001000000?0?00?10?11?0??000100
0011-0010-0000101?0?11??1000

Rukwasuchus yajabaliyekundu

20????????????11????101110011000102?110100?111120111101
10100110[23]??12??
?01?????????????????0?????????0??0002??????????????0
0?1?00?1?????0?01?????????00?1?1001??01??0?0?1?0?00??
??0??0?????1??0?????0?00000?0?0?0??0?1011?0?0??0?
??0??-??1?0?????1?????11101

Stolokrosuchus lapparenti

202000012200001110001011110011100101211010[01]?111120111
1010010?1?0?021?0[123]??0121000?????????????????10?1
100??01?????011011110110110000000120011101002??00?0001
1000021001100?0?0?010100?000?00?010?100001?1000011?000
00?????0?3000000?1?000000010?000000100?00????1011011?1??
?0000?00??100?1?0??00001?01?2111101

Trematochampsia taqueti

201?00?1[12]?1????110?010[01]11110100001022???????11112?
11?1010010?110[23]?21??[23]?01?121[12]11?????????000???
????030?[12]00??01?????1101?????0?0000?00120[01]?1100
?02??[01]011130?1000011?001??0?00??00?000?00??10?10
0?????0001?00?00?0??0??0?00??0?0000?0?000001?0?0
0????[01]0?1[01]01?????000?00??011????00001?0?1??110
0?