A NEW EUTHEROCEPHALIAN (THERAPSIDA, THEROCEPHALIA) FROM THE UPPER PERMIAN MADUMABISA MUDSTONE FORMATION (LUANGWA BASIN) OF ZAMBIA

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ABSTRACT—A new therocephalian therapsid, Ichibengops munyamadziensis, gen. et sp. nov., is described on the basis of two partial skulls from the upper Permian (Wuchiapingian) upper Madumabisa Mudstone Formation of the Luangwa Basin, Zambia. The specimens offer insights into the diversity of therocephalians in a poorly sampled region, preserving unique maxillary structures, dental morphology that is intermediate between basal therocephalians and eutherocephalians, and a maxillovomerine bridge forming an incipient secondary palate. A phylogenetic analysis of 135 craniodental and postcranial characters from 56 therapsid taxa (including 49 therocephalians) recovered by the Society of Vertebrate Paleontology, a furrowed or ridged surface texture on the palatal surface of the palatine, and a possible maxillovomerine bridge forming an incipient secondary palate. Ichibengops shares with Chthonosaurus several features, including a ventral maxillary flange in which the upper postcanines are situated (also in Lycosuchus), anteroposteriorly short suborbital vacuities with strongly scalloped anterior borders, a furrowed or ridged surface texture on the palatal surface of the palatine, and a possible maxillovomerine bridge (although this latter structure is incompletely preserved in Chthonosaurus). The new taxon, along with its proposed relationship to Chthonosaurus, adds to a list of sister-group pairs of Wuchiapingian tetrapods in southern Gondwana and Laurussia, indicating that effective, though largely unknown, dispersal routes persisted in Pangea at least through early late Permian times.

http://zoobank.org/urn:lsid:zoobank.org:pub:3C00620E-64B4-4CF0-BFAD-0336AE7C8196

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

INTRODUCTION

Therocephalians were one of the main groups of non-mammalian therapsids and an important component of middle to late Permian terrestrial ecosystems. The earliest therocephalians, which were relatively large-bodied carnivores, are best known from the middle Permian Tapinocephalus and Pristerognathus assemblage zones of South Africa’s Karoo Basin (van den Heever, 1994; Abdala et al., 2008; Smith et al., 2012). By late Permian times, the group had already achieved a broad geographic distribution and diversified into a range of presumed ecologies and both large and small body sizes (Abdala et al., 2008; Huttenlocker, 2013, 2014). In addition to occurring in the late Permian Tropidostoma through Dicynodon assemblage zones in the Karoo Basin, Permian therocephalians also have been recovered from Cistecephalus zone–equivalent beds in Tanzania (von Huene, 1950; Kemp, 1972a, 1972b; Sidor et al., 2010) and Zambia (Drysdall and Kitching, 1963; Kitching, 1963; Kemp, 1975). In the Northern Hemisphere, Permian therocephalians are abundant and well known from Russia (Ivakhnenko, 2011), although the relationship of some of these forms to the better-known taxa from the Karoo remains incompletely understood (Huttenlocker, 2009, 2013). Therocephalians survived the end-Permian mass extinction mostly as small-bodied generalists and persisted until the Middle Triassic in both the Northern and Southern Hemispheres (Keyser, 1973; Sun, 1991; Battail and Surkov, 2000; Lucas, 2001; Botha-Brink and Modesto, 2011; Huttenlocker et al., 2011; Ivakhnenko, 2011; Huttenlocker and Sidor, 2012; Huttenlocker, 2013).

To date, the therocephalian fossil record of Zambia has lacked meaningful descriptive work. Instead, reference to tentative field identifications or the inclusion of names in faunal lists has predominated. For example, Drysdall and Kitching (1963:17) state, “A single Therocephalian resembling Pristerognathus” was collected from their locality 20. Similarly, Kemp (1975:415) noted the collection of two “whaitsiid-like therocephalians” from the mid-Luangwa Valley. Sidor et al. (2013) included the occurrence of Therapsidae microps, also known from South Africa and Tanzania, in their faunal list for the Luangwa Basin, but did not cite a voucher specimen.

Here we report on a new basal eutherocephalian from the Madumabisa Mudstone Formation of the Luangwa Basin, Zambia. The new taxon is established on the basis of two specimens showing unique maxillary structures, a dentition that is intermediate between basal therocephalians and more derived eutherocephalians, and interesting evidence of an incipient secondary palate that is superficially similar to that of whaitsiids. The new taxon, previously reported by Sidor et al. (2013) by its two specimen numbers, has important evolutionary implications for palatal architecture in therocephalians. In addition, as an endemic Zambian taxon, it sheds light on Gondwanan therocephalians outside South Africa and expands our knowledge about the group’s morphological evolution and biogeographic radiation.

Institutional Abbreviations—NHCC, National Heritage Conservation Commission, Lusaka, Zambia; SAM, Iziko South African Museum, Cape Town, South Africa.

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GEOLOGIC CONTEXT

The geology of the Luangwa Basin has been reported by several authors, although most work has taken place in the northern part of the basin (Dixey, 1937; Drysdall and Kitching, 1962, 1963; Utting, 1978; Banks et al., 1995). The preserved sequence parallels much of what is seen in nearby basins in Tanzania, Malawi, and Mozambique, as well as in the Mid-Zambezi Basin of southern Zambia and northern Zimbabwe (Bond, 1935; Nyame and Utting, 1997; Catuneanu et al., 2005). Confusingly, the name Madumabisa Mudstone Formation is used in both the Luangwa and Mid-Zambezi basins.

In the Luangwa Basin, the Madumabisa Mudstone Formation was formally divided into upper and lower members by Drysdall and Kitching (1963), who related them to Dixey’s (1937) K3 and K5 units. Based on the lithology and fossil content of the Munyamadzi area, we consider the fossils described herein to have come from the upper member, although discontinuous and patchy outcrops make a precise stratigraphic level difficult to determine (see Angielczyk et al., 2014, for detailed discussion of the Munyamadzi dicynodont fauna). Based on the occurrence of biostratigraphically useful dicynodonts, Angielczyk et al. (2014) considered the upper Madumabisa to correlate with the *Cistecephalus* Assemblage Zone of South Africa, as well as the Usili Formation of Tanzania, and the Chiweta beds of Malawi (Sidor et al., 2010, 2013). This scheme contrasts with previous correlations, which either suggested multiple faunas with the upper formations (referred to as *Tapinocephalus* Biozone and *Chthonosaurus* Biozone sensu Kemp, 1975). A revised stratigraphic correlation of the rocks of the Luangwa Basin is provided in Figure 1.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA Osborn, 1903
THERAPSIDA Broom, 1905
EUTHERIODONTIA Hopson and Barghusen, 1986
THEROCEPHALIA Broom, 1903
EUTHEROCEPHALIA Hopson and Barghusen, 1986

**ICHIBENGOPS MUNYAMADZIENSIS**, gen. et sp. nov. (Figs. 2–5)

**Etymology**—The generic name refers to the prominent groove present on the maxilla, by combining the local Bemba word for scar (ichibenga) with the common Greek suffix for face or look (ops). The species name recognizes the Munyamadzi River and surrounding Munyamadzi Game Management Area, where the fossils were collected.

**Holotype**—NHCC LB36, a partial skull missing the anterior snout and preserving the left side of its dorsal surface and a complete anterior palate (Figs. 2, 3, 5).

**Referred Material**—NHCC LB38, which preserves the middle one-third of the skull, from the mid-snout to mid-orbital regions (Figs. 4, 5).

**Locality and Horizon**—Both specimens were collected from rocks of the Madumabisa Mudstone Formation (Luangwa Basin) exposed in the Munyamadzi Game Management Area, Northern Province, Zambia. Based on faunal comparisons, these beds are considered equivalent to the *Cistecephalus* Assemblage Zone of South Africa and thus late Permian (Wuchiapingian) in age (Rubidge et al., 2013; Angielczyk et al., 2014). Detailed locality information is available to qualified researchers at the NHCC or by contacting the authors.

**Diagnosis**—Autapomorphic in its possession of postcanine dentition situated on conspicuous ventral maxillary flange (also in *Chthonosaurus* and *Lycosuchus*) medial to a distinctive longitudinal groove with anterior pocket on the lateral surface of the maxilla. Shares with *Chthonosaurus velocidens* a wavy or poorly ossified anterior border of the suborbital vacuity; furrowed or ridged surface texture on the palatal surface of the palate; and possibly a maxillolamincal bridge (although this region is damaged in *Chthonosaurus*). Differs from *Chthonosaurus* in absence of median frontonasal crest; slightly shorter postcanine tooth crown apices; frontal suture with nasal relatively straight (forms an anterior process extending between nasals in *Chthonosaurus*); and midline vomerine keel extends onto interchoanal body of vomer (keel is restricted more posteriorly in *Chthonosaurus*).

**Description**

The two specimens described here, NHCC LB36 and LB38, were surface collected from the Madumabisa Mudstone Formation of Tanzania, and the Chiweta beds of Malawi (Sidor et al., 2010, 2013). Recent work has shown the fauna of the upper Madumabisa Mudstone Formation to be equivalent to the *Cistecephalus* Assemblage Zone of South Africa (Sidor et al., 2010; Angielczyk et al., 2014). Skull silhouette indicates stratigraphic position of the therapsid fossils. **Abbreviations**: Cap, Capitanian; Chx, Changxingian; Fm., Formation; Wor, Wordian; Wuc, Wuchiapingian.
FIGURE 2. Holotype skull of Ichibengops munyamadziensis, gen. et sp. nov., (NHCC LB36) in dorsal (A) and ventral (B) views. Abbreviations: cr ch, crista choanalis; ect, ectopterygoid; ept, epipterygoid; f, frontal; f m-p, maxillopalatine foramen; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; p q pt, quadrate process of pterygoid; pal, palatine; pf, prefrontal; po, postorbital; pro, prootic; pt, pterygoid; so, supraoccipital; sq pro pr, processus prootica of squamosal; v, vomer; v ipt, interpterygoid vacuity; v sorb, suborbital vacuity.
Formation as isolated nodules in 2009. In both cases, the nodules consisted of light brown, silty mudrock partially weathered on the dorsal surface such that much of the skull roof is poorly preserved and certain sutural details are difficult to reconstruct. The anterior and posterior portions of the skulls, including tip of the snout and occiput, also have been largely weathered away, leaving behind mostly the mid-portion of each skull. The estimated maximum skull length of NHCC LB36, the more complete of the two specimens, is approximately 87 mm, whereas the referred specimen is slightly larger. Mechanical preparation of each specimen’s ventral surface revealed that the palatal surfaces were largely intact.

Skull Roof

The maxilla is the anterior-most element preserved on the skull roof in each specimen, the premaxilla and septomaxilla being completely weathered away. The maxilla is a large bone with a tall dorsal lamina and a long, posteriorly tapering process supporting the jugal underneath the orbit. Dorsally, the maxilla contacts the nasal and prefrontal, restricting the lacrimal from contact with the nasal (Figs. 2–4). Ventrally, the postcanine series preserves as many as six teeth situated on a distinct ventral maxillary flange that is superficially similar to that in lycosuchids (van den Heever, 1994). However, this flange is accentuated by the lateral emargination of the maxilla formed by a deeply hollowed, longitudinal pocket located just lateral to and running parallel with the postcanine series (Figs. 3–5). The topography of this pocket is complex, with a long posterior furrow that opens into one or two anterior lobes (Fig. 5B, C). This extensive structure differs from the shallow and anteriorly restricted suborbital groove found behind the tooth row in lycosuchids and Chthonosaurus. In the latter cases, the appearance of a shallow groove is likely a by-product of the maxillary flange. Deep, longitudinal furrows follow from the posterior portion of the groove onto the palatal surface of the maxilla and the postero-lateral surface of the palatine. In the holotypic specimen (NHCC LB36), much of the outer portion of the maxilla has been abraded on the right side of the skull, exposing a large, open cavity housed within the maxilla. This cavity likely corresponds to the anterior maxillary sinus of Sigurdsen (2006), which was homologized with the maxillary sinus of anomodonts and cynodonts and suggested to have contained the maxillary branches of the trigeminal and facial nerves. A small foramen (maxillopalatine foramen) with an external groove is located on the maxilla-palatine suture at about the level of the fourth or fifth postcanine counted moving anteriorly from the rear of the tooth row. Just anterior and medial to this region, the medial border of the maxilla shares a short portion of the crista choanalis and expands into a sharp median process that contacts the vomer. This junction forms a sharp, flattened maxillovomerine bridge that superficially resembles that of waiatuiids (Mendrez, 1975:fig. 5), although it is more vaulted.

The lacrimal is a thin element located along the anterior border of the orbit (Figs. 3, 4). It is relatively short anteroposteriorly but tall, with much of its body forming the anterior wall and floor of the orbit. The surface preservation in both specimens is poor, but a sutural contact with the nasal could not be identified (an interpretation consistent with the overall brevity of its facial exposure). This differs from the condition of lycideopid baurioids in which there is nasal-lacrimal contact, but is similar to most other theroccephalians. The location of the lacrimal foramen inside the orbital wall could not be identified in the specimens. Chthonosaurus, however, bears a pit on the external surface of the lacrimal, where the lacrimal foramen is usually located in hofmeyriids.

Only the posterior portions of the nasals are preserved in either specimen, and the dorsal surface is substantially weathered. The nasals appear to have been long and narrow, and they had an irregular transverse suture with the frontals positioned just anterior to the orbits (Figs. 2, 4). In the holotype, the left nasal is weathered such that an impression of its internal surface is preserved, demonstrating longitudinal ridges within the nasal.
FIGURE 4. Referred specimen of Ichibengops munyamadziensis (NHCC LB38). Skull in dorsal (A) and ventral (B) views. Abbreviations: co, coronoid; cr ch, crista choanalis; f, frontal; f m-p, maxillopalatine foramen; l, lacrimal; m, maxilla; m groove, maxillary groove; n, nasal; pal, palatine; part, prearticular; pf, prefrontal; pt, pterygoid; r lam, reflected lamina of angular; v, vomer.
cavity (Fig. 2A). Such ridges have been described in other therocephalians and likely correspond to attachment sites of cartilages supporting olfactory epithelia (e.g., Sigurdsen, 2006; Huttenlocker et al., 2011; Sigurdsen et al., 2012).

The prefrontal is long both anteriorly and posteriorly, bearing a long sutural contact with the nasal and frontal. The posterior process does not contact the postorbital, however, allowing the frontal to contribute to the dorsal border of the orbit, as in most other therocephalians.

The frontal is thin and narrow, being about as wide as the nasal. It is just longer than the anteroposterior length of the orbit, reaching anteriorly in front of the orbit and posteriorly to the rear portion of the postorbital bar where it meets the parietal. A narrow lappet separates the prefrontal and postorbital along the roof of the orbit.

The postorbital, preserved on the left side of the holotypic skull, forms the posterior bar of the orbit and is fairly robust (Figs. 2, 3). Its ventral process is long and likely shared a broad sutural overlap with the jugal in life, although this area of the jugal is not preserved in either specimen. The jugal makes up almost the entire suborbital bar and extends anteriorly to about the level of the anterior border of the orbit, just below the lacrimal.

Little of the squamosal is present, but portions are preserved surrounding the braincase in the holotype. The posterior region near the prootic shows a finger-like projection (processus prootica) that is inflected medially and contacts a lateral process of the prootic (Fig. 3). This entire structure bounds the pterygoparoccipital foramen as in other scylacosaurian therocephalians.

FIGURE 5. The maxilla and postcanine dentition of Ichibengops munya madziensis. A, high-magnification image of the postcanine dentition of NHCC LB38 showing buccolingual compression and faint mesial and distal carinae. Hatched lines indicate broken surfaces; B, stereopair of NHCC LB36 postcanine teeth and maxillary groove in left ventrolateral view; C, stereopair of NHCC LB38 postcanine teeth and maxillary groove in right lateral view. Scale bars equal 2 cm.
Braincase and Occiput

The parietal forms the broad lateral walls of the braincase and the medial border of the temporal fenestra. Given the abbreviated anteroposterior length of the parietal, the length of the temporal fenestra was likely also very short, perhaps only slightly longer than the diameter of the orbit. Weathering has exposed a fairly large pineal enclosure at about the midpoint of the parietal in the holotype, but the full extent of the parietal crest and dorsal exposure of the pineal canal is uncertain due to damage in this region. Some therocephalians may show a bulbous pineal enclosure internally but lack a dorsal foramen (e.g., Chthonosaurus, Theriognathus).

The interparietal (postparietal) is not preserved. Instead, it is shaved away such that the anterior vault of the tectum synoticum is exposed on the occipital surface and the supraoccipital can therefore be seen wedging between the parietals at the rear of the braincase (Fig. 2A). Although little of the neurocranium is preserved, this and the otic capsules are preserved largely on the left side of the skull in the holotypic specimen, where the intact left prootic is seen in articulation with the processus prooticus of the squamosal (Fig. 2A). A delicate anterior process is also preserved on the left prootic.

The exoccipitals and basioccipital are not preserved.

Palate and Splanchnocranium

The vomer presents the typical therocephalian shape, broadening anteriorly between the choanae toward its presumed articulation with the premaxilla, although this is not preserved. A strong midline keel is present posteriorly in the holotype and spans most of the length of the vomer, including a portion of the anterior (interchoanal) process. A short midline suture may be present posteriorly as well in the specimens, but sutures are difficult to delineate in NHCC LB36 and this region is damaged in NHCC LB38. Anteriorly in the holotype, however, the vomer is strongly fused into a single element. Anterolaterally, the vomer of NHCC LB36 bears paired transverse processes that drop down to contact the maxilla, forming the maxillovomerine bridge as in whaitsiids (Mendrez, 1975:fig. 5) and Lycideops (Mendrez, 1975:fig. 11). However, the processes are sharp and flange-like, oriented more ventrolaterally and meeting the maxilla below the level of the main body of the vomer and giving its anterior portion a somewhat vaulted appearance. This morphology is unlike that of the whaitsiid Theriognathus, where the contact is smooth and relatively horizontal (Kemp, 1972b:fig. 20). Although the anterior portion of the vomer is not preserved in Chthonosaurus, Ivakhnenko (2011) recognized a dorsoventrally flattened median projection of the maxilla near the canine buttress resembling the maxillary contribution to the bridge in whaitsiids, suggesting a possible bridge in Chthonosaurus as is present in *I. mnyamadziensis*.

The palatine is a very broad element and forms the majority of the length of the crista choanalis medially. The paired palatines are separated on the midline by the vomer anteriorly and pterygoids posteriorly, as in other therocephalians and most other therapsids except gorgonopsians. The crista choanalis is sharp, well developed, and extends posteriorly behind the postcanine tooth row to about the level of the transverse suture shared by the vomer and pterygoids. As such, the crista choanalis ends well anterior to the suborbital vacuity. The palatal surface of the palatine is very rugose posteriorly, bearing numerous longitudinal furrows that continue from the maxilla. The posterior margin is wavy and strongly scalloped where it forms the anterior border of the suborbital fenestra. This scalloped texture along the anterior margin of the suborbital vacuity is also present in *Chthonosaurus* (Vjuschkov, 1955; Tatarinov, 1974; Ivakhnenko, 2011) and Karenites (Tatarinov, 1995) and likely indicates the thin and poorly ossified nature of this border. Aside from this anterior scalloping, which likely stems from the ossification of the membrane bone, the suborbital vacuities are relatively short anteroposteriorly and somewhat rounded in ventral view. This contrasts with the long and suboval or subtriangular vacuities found in some other therocephalians such as Ictidosuchoides, Regisaurus, or Tetracyodon (Mendrez, 1975; Huttenlocker, 2013).

The ectopterygoid, well preserved on the left side of the holotype, is a thin element bracing the palatine to the pterygoid transverse process. It forms the lateral wall of the suborbital vacuity and bears a tiny foramen on its ventral surface (Fig. 2B).

The pterygoid is a paired, multipartite element bearing an anterior process, transverse process or ‘flange,’ quadrate process, and a posterior process that joins to the para-basiphenoid complex. It wedges between the palatines anteriorly and forms the medial border of the suborbital vacuity. The holotype preserves a median suture dividing the left and right pterygoids on the midline and a narrow ventral median crest bearing the bases of at least two or three weathered denticles (Fig. 2B). The medial border of each suborbital vacuity is formed by the ventral intermediate crest of the pterygoid. Further posterolaterally, the pterygoid transverse flange is very broad, nearly reaching the level of the suborbital bar and zygoma with a strong ventral and posterior orientation, as is characteristic of most other therocephalians. The ventral edges of the pterygoid flanges sweep sharply posteriorly and mediadly around the interpterigoid vacuity and brace against the rostrum of the parabasal. The interpterigoid vacuity is moderately large, unlike that of *Lycideops* and whaitsiids where it is mostly closed off or fissure-like, but it is not as large as in Chthonosaurus or as wide and heart-shaped as in many baurioids (Huttenlocker, 2013). The quadrate process is long and thin, extending obliquely toward the vicinity of the unpreserved quadrate-quadrateotjugal. Notably, a thin, bony webbing stretches between the quadrate process and transverse flange on the dorsolateral surface of the pterygoid. This webbing is occasionally present in therocephalians, but is fairly conspicuous in NHCC LB36 (Fig. 2B) and shows a scalloped appearance.

The epipterygoid is a tall, strut-like element forming the lateral wall of the braincase in NHCC LB36 (Fig. 3). It is situated between the pterygoid quadrate process (below) and parietal (above). It is well ossified, more anteroposteriorly expanded than in lycosuchids and scylacosaurids, and forms small projections along its posterior edge. A small notch on the posterior edge is roofed by a tall posterior apophysis at the midpoint of the element where there is also some modest waisting. Dorsal to this region, the epipterygoid continues to expand again toward its contact with the supraoccipital and parietal.

Mandible

Very little of the mandible is preserved in either specimen, although portions of the postdentary bones have come to rest on the underside of the skull of NHCC LB38 (Fig. 4B). Preserved elements include the reflected lamina of the angular, a splint-like element interpreted as the rear portion of the prearticular, and a broad, flat coronoid. These elements are not complete enough to glean functional or phylogenetically informative characters. The reflected lamina, however, is fairly large and preserves the series of shallow, radiating fossae typical of other therocephalians (e.g., Huttenlocker, 2009:fig. 1).

Dentition

The upper dentition is incompletely preserved, with the premaxillary dentition and canines having been weathered away. However, four maxillary postcanine teeth are preserved in the
Phylogenetic Position

which may preserve a posterior (distal) carina on some Ichibengops 100 generations. Figure 6 summarizes these results, and the sup-
generations), and the posterior distribution was sampled every  
with variable character rates. The analysis was run until the stan-
parsimony analysis using a heuristic search and the tree-bisec-
multistate taxa were treated as ‘polymorphisms’ in the parsi-
4.0b10 (Swofford, 1999) and a Bayesian analysis in MrBayes v.  
2008; Huttenlocker et al., 2011; Huttenlocker, 2013). The excellent  
dentition have become increasingly important for understanding  
tures in early therocephalians, detailed studies of the palate and  
of morphological conservatism of cranial shape and skull roof fea-
ded as missing (i.e., Alopecodon, Darsuchus, Scylacosaurus, Perplexisa-
1975; Hopson and Barghusen, 1986; Kemp, 1986; Abdala et al.,  
with supporting morphological character list and updated scorings for  
Ichibengops and Chthonosaurus (PIN 521/1) are provided in  
Results of parsimony and Bayesian analyses support a sister-
were used. However, additional runs excluding taxa in which 60% or more  
their presence. Therefore, resolution of chthonosaurids as the sis-
taxa such as the enigmatic Perplexisaurus and Ichibengops and is  
therefore dependent upon the accuracy and completeness of character codings in these taxa. More complete specimens of  
Wuchiapingian-aged theroccephalians will help to clarify prob-
lematic relationships in this part of the tree, including whether chthonosaurusids are basal eutheroccephalians or are closer to  
Future discovery of specimens preserving more of the dentition and lower jaw elements will help to clarify this issue,  
because many shared characteristics of hofmeyriids and what-

DISCUSSION

Phylogenetic Position

The phylogenetic position of Ichibengops was preliminarily assessed by Huttenlocker (2013, 2014), but the taxon was identi-
fied solely by the two specimen numbers in those studies (NHCC LB36, LB38). To examine character evolution in early euther-
ccephalians and the biogeographic affinities of Ichibengops to  
other theroccephalians, we present a new analysis using the origi-

Evolution of the Palate and Dentition in Early Eutheroccephalians

Dental Arcade and Tooth Surface Texture—Given the degree of morphological conservatism of cranial shape and skull roof fea-
tures in early theroccephalians, detailed studies of the palate and  
dentition have become increasingly important for understanding theroccephalian diversity and morphological evolution (Mendrez,  
2008; Abdala et al., 2008; Huttenlocker et al., 2011; Huttenlocker, 2013). The excellent preservation and surface texture of the upper postcanine dentition in Ichibengops and its intermediate phylogenetic position between middle Permian scylacosaurians and more morphologically derived  
eutheroccephalians present an opportunity to discuss evolutionary patterns in theroccephalian dental morphology. The extent of the  
aleovalar pattern in Ichibengops, from the maxillolumbarine bridge to the back of the tooth row, permitted space for approximately  
seven conical upper postcanine teeth. Six to seven upper postca-

holotype; in the referred specimen, five worn roots are present  
on the left side of the skull and six well-preserved tooth crowns  
are present on the right side. There may have been space for as  
many as seven postcanine teeth based on the relative positions of  
the maxillolumbarine bridge and maxillopalatine foramen, which  
typically delimit the anterior extent of the maxillary postcanines.  
The postcanine tooth row extends posteriorly to about the level  
of the anterior margin of the lacrimal when viewed laterally, and  
with the posterior rim of the choana and the vomer-pteryg-
goid suture when viewed ventrally.  

The individual postcanine teeth are nicely preserved in NHCC  
LB38, showing a smooth texture lacking the longitudinal fluting  
seen in some early akidognathids and icthyosuchid baurioids ( 
Huttenlocker et al., 2011; Huttenlocker, 2013). They are slightly  
bucolingually compressed and thus oval in cross-section. The  
better-preserved postcanines also reveal a weak longitudinal  
carina on both their mesial and distal surfaces (Fig. 5A),  
although these carinae are smooth and unserrated. This condi-
tion differs from the smoothly rounded cross-section of the post-
canines in many other eutheroccephalians, including hofmeyriids  
and baurioids (Huttenlocker, 2013). Possible exceptions include  
akkidognathids such as Promoschorhynchus (A.K.H., personal  
observation of SAM-PK-K10014) and Cerdosuchoides, both of  
which may preserve a posterior (distal) carina on some  
postcanines.

Evolution of the Palate and Dentition in Early Eutheroccephalians

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eutheroccephalians present an opportunity to discuss evolutionary patterns in theroccephalian dental morphology. The extent of the 
aleovalar pattern in Ichibengops, from the maxillolumbarine bridge to the back of the tooth row, permitted space for approximately seven conical upper postcanine teeth. Six to seven upper postcanines is a reasonable estimate for a basal eutheroccephalian, given that many early scylacosaurian and eutheroccephalian taxa exhibited approximately this number (e.g., some scylacosaurids, Chthonosaurus, Annatherapsidus, Akidognathus, Promoschorhynchus, hofmeyriids). Moreover, the postcanine crowns are not as laterally compressed as in lycosuchids and scylacosaurids, and they lack serrations. Instead, they are suboval in cross-section and bear smooth (non-serrated) mesial and distal carinae. Similar carinae have been described in the poorly known Russian taxon Kotelcephalon, a dubious taxon based on isolated fragments (Ivakhnenko, 2011), and they are also present in at least some akidognathids (e.g., Promoschorhynchus, Cerdosuchoides). Later eutheroccephalians (e.g., hofmeyriids, baurioids) appear to have lacked carinae altogether and generally exhibited more peg-like dentition with a smoothly rounded cross-section, although later baurioids from the late Early and Middle Triassic (e.g., ordosiids, baurioids) exhibited more bucolingually expanded postcanines with complex crowns and precise occlusion (Fig. 6).
Maxillary Grooves—One of the most unusual and apomorphic features of the new taxon is the deeply incised maxillary groove oriented parallel to the postcanine row. The significance of this structure in a therocephalian is unclear, because it might pertain to muscle attachments, sensory functions, or accommodation of soft-tissue structures (i.e., glands), among other explanations. Maxillary grooves adjacent to the tooth row are rare but have been discussed in some tetrapods in the context of purported venom delivery adaptations, a hypothesis consistent with the location of the structure.
relation to the postcanine dentition and the serous-secretory parotid gland (e.g., Fox and Scott, 2005; Gong et al., 2010). Similar interpretations in other fossil taxa have been problematic (Folinsbee et al., 2007; Gianechini et al., 2011). For example, the ‘subnarial fossa’ in the dromeosaurid dinosaur Sinornithosaurus was suggested to have housed a venom gland (Gong et al., 2010), but its structure was not distinctly different from that of other dromeosaurids that lacked independent indicators of a venom delivery system and may alternatively represent pneumatized craniofacial sinuses (Gianechini et al., 2011). Among theropods, however, the akidnognathid Euchambersia provides some of the best evidence of a venom delivery system in an extinct non-riptop tetrapod (Hotton, 1991; Sues, 1996; Folinsbee et al., 2007). In this taxon, a large-maxillary fossa is located behind the upper canine, and the canine bears a broad groove that communicates with this fossa. Interestingly, the postcanine dentition was completely lost. Whether a similar configuration of the canine was present in Ichibengops will remain uncertain until the discovery of more complete material that preserves the anterior portions of the snout.

**Secondary Palate**—The secondary palate of some therapsids, as in Ichibengops, contributes a bony partition that separates the anterior portion of the nasal cavity from the oral cavity, and opens more directly into the pharynx. Past authors have ascribed numerous functions to the secondary palate in fossil therapsids, including the simultaneous permission of breathing and mastication (McNab, 1978; Hillenius, 1994), increasing mechanical integrity to the snout (Thomason and Russell, 1986), and/or sucking in juveniles (Maier et al., 1996; Maier, 1999). Notably, the structural origin of this feature in theroccephalians predates that of complex postcanines with precise tooth-to-tooth occlusion, suggesting that this configuration of the palate could have facilitated mastication only later in theroccephalians (as in cynodonts), but mastication did not drive its early evolution. This contrasts with cynodonts, which evolved complex dentition before forming a completely enclosed secondary palate (e.g., Procyonosuchus, galesaurids). A bony or incipient secondary palate is found in at least three of the major therapsid subclades during the Permian: dicyonodonts, cynodonts, and theroccephalians (Mendrez, 1975; Hopson and Barghusen, 1986; Maier, 1999; Angielczyk and Walsh, 2008; Angielczyk, 2009; Huttenlocker, 2009, 2013). However, its structural arrangement and contributing elements varied among and even within these groups. For example, in early cynodonts, an incipient secondary palate was largely formed by paired or adjoining processes of the palatines (e.g., Thrinaxodon; Abdala and Allinson, 2005), whereas the structure was formed mostly by the maxilla and vomer in theroccephalians and was positioned more anteriorly. Within theroccephalians, at least two groups were previously known to have a secondary palate: (1) whaitsiids, where it was formed by the maxilla and distinctive laterally oriented processes of the vomer, and (2) baurioids, where it was either formed by the suturing of the maxilla and vomer or by the ventral closure of the maxilla on the midline in more derived forms (Mendrez, 1975). The anatomy and phylogenetic position of Ichibengops introduces an even more complex evolutionary scenario, suggesting the possibility that a bony secondary palate evolved as many as four or five times in therapsids, and did so relatively early on during the early late Permian. The latter scenario is dependent upon whether Ichibengops and cithonosaurs are interpreted as close relatives of the whaitsiids (which share the derived character state of a maxillovomerine bridge) rather than basal eutheroccephalians.

**Biogeographic Implications**

Malawi, Mozambique, Tanzania, and Zambia all have tetrapod assemblages considered to be roughly equivalent in age to the Cistecephalus Assemblage Zone of the South African Karoo Basin. Surprisingly, the tetrapod fauna of the upper Madumabisa Mudstone Formation of the Luangwa Basin was found to be most similar to that of the Karoo Basin by Sidor et al. (2013; also see Angielczyk et al., 2014), despite being in closer proximity to the Usili Formation of the Ruhuhu Basin (Tanzania). Nevertheless, all of the assemblages included a high number of shared taxa with fewer endemics than Middle Triassic faunas found in the same basins, suggestive of a broad Permian Gondwanan faunal province (Abdala and Allinson, 2005). The record of Ichibengops contributes new information to this picture. Ichibengops is an endemic taxon known only from the upper Madumabisa Mudstone assemblage of the Luangwa Basin, but its phylogenetic position, particularly its sister-group relationship to the Russian eutheroccephalian Cithonosaurus, suggests a shared early divergence with extra-African taxa during or prior to the early late Permian (Wuchapingian). Interestingly, Ichibengops and Cithonosaurus are not the only pair of late Permian theroccephalian sister taxa to show a split between Gondwana and Laurasia, other noteworthy examples including Moschowhaisia (Russia) and Theriochambersia (South Africa, Tanzania, Zambia), and Karenites (Russia) and an undescribed karenitid from the same formation as I. munyamadziensis (Huttenlocker, 2013; Sidor et al., 2013).

A similar pattern of low-level sister groups found in Laurasia and Gondwana can be found in other taxa that are more or less contemporary with Ichibengops. The pattern is perhaps most apparent among dicynodonts, where recent phylogenies (Kammerer et al., 2013; Castaninina et al., 2013) suggest at least six instances: (1) Dajuigingshanodon (China) and ‘higher cryptodonts’ (the clade including Oudenodon and Geikia; primarily Gondwana); (2) Tropidostoma (South Africa) and Australobarbarus (Russia); (3) Dnotocyclis (South Africa, Zambia) and Idalesaurus (Russia); (4) Geikia locusticeps (Tanzania) and Geikia elginensis (Scotland); (5) Katumbia (Zambia, Tanzania), and Elph (Russia); and (6) Daptocephalus (South Africa) and Peramodon (Russia). Dicctodon feliceps also is noteworthy in this context for being the only Permian dicynodont species currently documented to occur in both Gondwana (South Africa, Zambia) and Laurasia (China) (Angielczyk and Sullivan, 2008). Using a phylogeny with less extensive taxon sampling, Angielczyk and Kurkin (2003) argued that the Russian cryptodonts in their analysis (Australobarbarus and Idalesaurus) likely represented dispersal events into Laurasia from Gondwana, but noted that the situation for dicynodonts was uncertain and depended strongly on the phylogenetic placement of Interpessaurus and Elph. Kurkin (2011) proposed a somewhat different scenario, with the origin of cryptodonts and dicynodontoids (oudenodontids and dicynodontids in that study) in the Northern Hemisphere and subsequent dispersal into Gondwana. The deep nesting of Australobarbarus, Idalesaurus, and G. elginensis within the primarily Gondwanan cryptodonts in phylogenetic analyses with broader taxon sampling provides renewed support for interpreting the Laurasian occurrences of Australobarbarus, Idalesaurus, and G. elginensis as cases of dispersal into Laurasia from Gondwana (Kammerer et al., 2011, 2013; Castaninina et al., 2013). Under a simple parsimony optimization of distribution, Dajuigingshanodon also is repossessed as a dispersal event from Gondwana in these trees. The situation for Dicynodontoidae is more complex. The basal position of Gordonia and the subclade including Elph, Interpessaurus, and Katumbia make a Laurasian origin of Dicynodontoidae equally parsimonious as a Gondwanan origin. Likewise, the basal dicynodontoids (primarily species formerly included in Dicyonodon; see Kammerer et al., 2011) do not seem to form geographically defined subclades, suggesting that members of this assemblage were able to disperse relatively freely between Gondwana and Laurasia. Regardless of these details, it does not appear that dicynodont dispersal was
occurring preferentially between Laurasia and any of the main African basins. South Africa (Tropidostoma/Australobarbus; Odontocycloides/Idelesaurus; Daptocephalus/Peramodon), Tanzania (G. locusticeps/G. elginensis; Katumbia/Elph), and Zambia (Odontocycloides/Idelesaurus; Katumbia/Elph) all have similar numbers of taxa with sister groups located in Laurasia.

Other late Permian examples of low-level sister taxa that are split between Gondwana and Laurasia include the protorosaurian archosauromorphs *Aenigmatrophaeus* (Tanzania) and *Protorosaurus* (Germany, England) (Ezcurra et al., 2014), the pareiasaurs *Pareaisachus* (South Africa, Zambia) and *Shihitlenfellea* (China) (Tsuiji et al., 2013), the biarmosuchians *Paraburmeita* (South Africa) and *Proburneit (= Protosaurus)* (Russia) (Smith et al., 2006), the gogonopsians *Sauroctonus progressus* (Russia) and *Sauroctonus parringtoni* (Tanzania) (Gebauer, 2007, 2014), as well as specimens attributed to the genus *Procynosuchus* (South Africa, Tanzania, Zambia, and Germany) (Sues and Boy, 1988; Kammerer and Abdala, 2009). Taken together, these sister-group pairs show that biogeographic connections existed between high-latitude faunas in Laurasia and Gondwana, implying the existence of effective, if currently largely unknown, dispersal routes (e.g., Sidor et al., 2005; Kemp, 2006). However, these sister pairs are relatively rare in the clades to which they belong, suggesting that diversification within particular faunal provinces predominated over dispersal between provinces. The rich tetrapod assemblages of South Africa, Tanzania, and Zambia are particularly valuable in this regard because they provide insight into how diversification and extinction drove patterns of endemism and cosmopolitanism within a single province. Future collecting will continue to shed light on the biogeographic history and connectivity of contemporaneous therapsid faunas during the Permian-Triassic transition.

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