Taxonomic Revision of Therocephalians (Therapsida: Theriodontia) from the Lower Triassic of Antarctica

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Taxonomic revision of therocephalians (Therapsida: Theriodontia) from the Lower Triassic of Antarctica

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ABSTRACT

We reevaluate the taxonomic status of therocephalian fossils recovered from the lower Fremouw Formation (Lower Triassic) of the central Transantarctic Mountains, Antarctica. The material, which includes mostly fragmentary juvenile specimens, is reidentified using an apomorphy-based approach. We recognize the presence of three higher-level taxa: Eutherocephalia, Akidnognathidae, and Baurioidea. The only genus-level identification is for a partial lower jaw and pterygoid tentatively attributed to the baurioid, *Ericiolacerta parva*. An indeterminate theriodont partial skull is reassigned to the therocephalian family Akidnognathidae. The holotypes of *Pedaeosaurus parvus* and *Rhigosaurus glacialis* are represented by indeterminate juvenile baurioids and, in the absence of clear autapomorphies, are considered nomina dubia. The results of the taxonomic revision indicate that the therocephalian fauna of Antarctica lacks endemic genera and thus corresponds to that of the Triassic *Lystrosaurus* Assemblage Zone fauna of South Africa's Karoo Basin. More generally, we consider the southern Gondwanan basins of South Africa and Antarctica to sample a broadly distributed Lower Triassic tetrapod fauna, although the latter basin documents the first occurrence of several taxa (e.g., *Kombuisia*, *Palacrodon*). More precise (i.e., species-level) identifications are needed to better constrain the biogeographic signal for therocephalians, but the presence of juveniles strongly suggests that this group of therapsids, like dicynodonts, were year-round high-latitude inhabitants during Early Triassic times.

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INTRODUCTION

Over 40 years of collecting in the Triassic Fremouw Formation of Antarctica has produced a diverse terrestrial vertebrate fauna (Colbert, 1982; Hammer, 1990). Taxa currently recognized include the temnospondyl amphibians *Kryostega* and *Parotosuchus* (Sidor et al., 2008a, 2008b), the reptiles *Palacrodon*, *Procolophon*, and *Prolacerta* (Colbert and Kitching, 1975; Colbert 1987; Gow, 1992, 1999), the dicynodont therapsids *Kombuisia*, *Lystrosaurus*, and *Myosaurus* (Hammer and Cosgriff, 1981; Fröbisch et al., 2010), the therocephalians *Ericiolacerta*, *Pedaeosaurus*, and *Rhigosaurus* (Colbert and Kitching, 1981), and the cynodont *Thrinaxodon* (Colbert and Kitching, 1977). Several widely distributed genera (e.g., *Lystrosaurus*, *Myosaurus*, *Procolophon*, *Prolacerta*, and *Thrinaxodon*) form the biostratigraphic basis for correlating the rocks of upper Balfour and Katberg formations of South Africa with the lower Fremouw strata of Antarctica (Lucas, 1998; Rubidge, 2005). However, as noted by Sidor et al. (2008a), the South African assemblage is substantially more diverse, likely as a result of much more intensive collecting.

Recent fieldwork efforts (Sidor et al., 2007, 2008a, 2008b) and renewed interest in the Permo-Triassic mass extinction (Ward et al., 2005; Collinson et al., 2006; Retallack et al., 2007) have prompted a reevaluation of the Early Triassic vertebrate fauna of Antarctica, and especially reported differences between it and the better-known Karoo record. For example, Colbert and Kitching's (1981) description of five noncynodont theriodont specimens from near Shackleton Glacier, including two specimens assigned to the therocephalian *Ericiolacerta parva*, was the first to extend the geographic range of *Ericiolacerta* and Gondwanan "scaloposaurids" outside South Africa (although other "scaloposaurid" records were known in Russia, e.g., Tatarinov, 1974). However, the material also included cranial remains of a small theriodont of unknown affinities, and two new genera that the authors also assigned to the therocephalian family Scaloposauridae: *Pedaeosaurus parvus* and *Rhigosaurus glacialis*. Thus, the Triassic theriodont fauna of Antarctica was considered to include rare elements not represented elsewhere in Gondwana, a pattern mirrored by the endemic Antarctic temnospondyl amphibian record (Cosgriff, 1984; but see Sidor et al., 2008a). Here we reassess the Antarctic therocephalian record to better understand its relationship to other coeval Gondwanan faunas.

ABBREVIATIONS

Institutional: **AMNH**, American Museum of Natural History, New York; **CAMZM**, Museum of Zoology, Cambridge University, Cambridge; **NHMUK**, Natural History Museum, London.

GEOLOGICAL SETTING

Over 600 meters in thickness, the Fremouw Formation is a laterally extensive sequence of siliciclastic and volcaniclastic sediments that rests conformably on top of the Buckley Formation, and ranges laterally from approximately 83° to 86° S latitude near the Shackleton and Beardmore glacier regions of the central Transantarctic Mountains (Barrett et al., 1986).

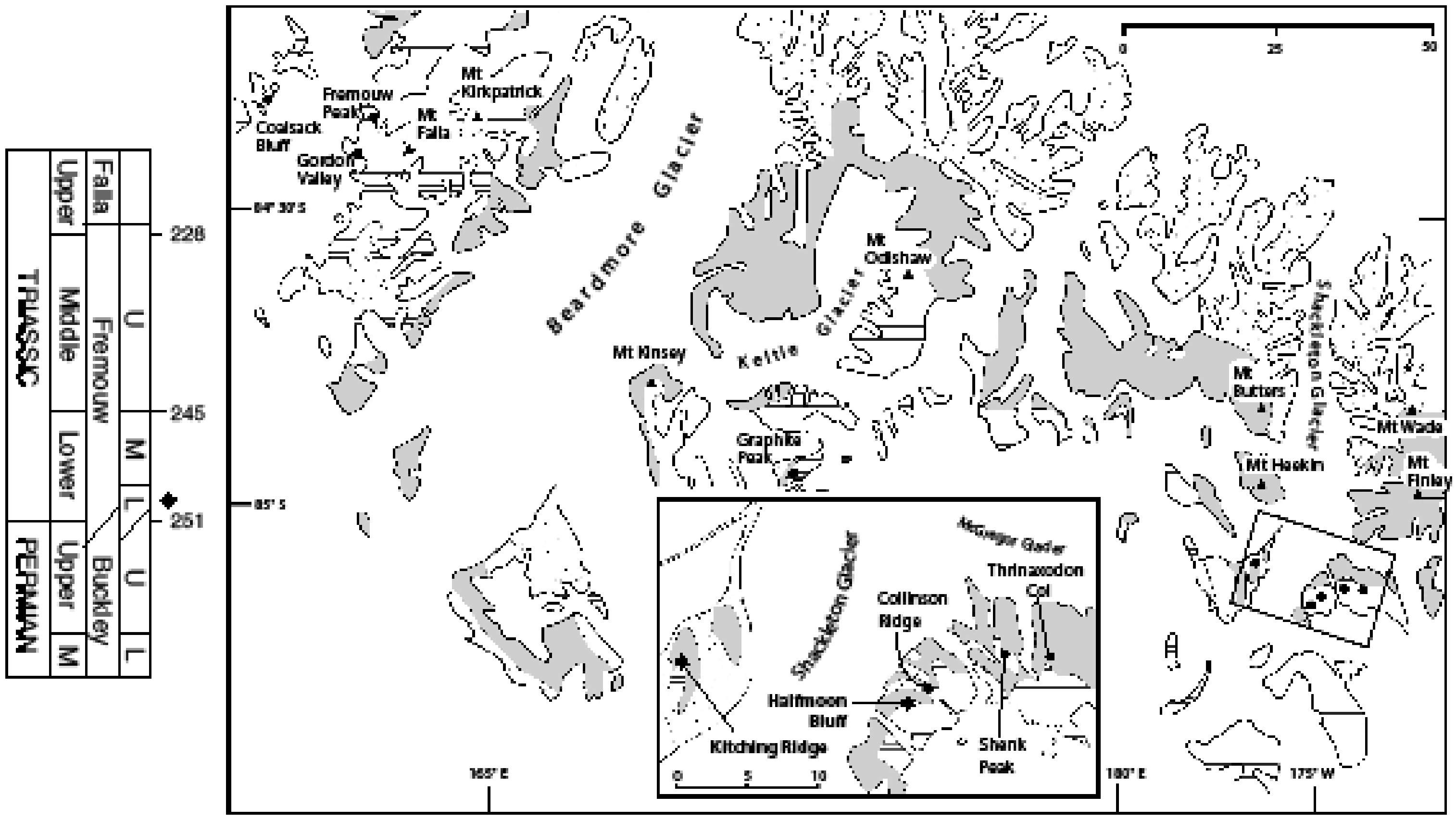

FIG. 1. Geology and geography of the Permo-Triassic vertebrate-bearing localities in the vicinity of the Beardmore and Shackleton glaciers, central Transantarctic Mountains. Star indicates position of therocephalian localities (Kitching Ridge, Halfmoon Bluff, *Thrinaxodon* Col) in the lower Fremouw Formation of Cumulus Hills, Shackleton Glacier region (inset). Gray areas represent exposures of the Buckley Formation; striped areas represent exposures of the Fremouw Formation; hatched areas represent igneous intrusions or metamorphic pre-Devonian basement; dotted areas represent surficial cover. Scale bars are in kilometers. (Map modified from Axsmith et al., 2000 and Collinson et al., 2006.)

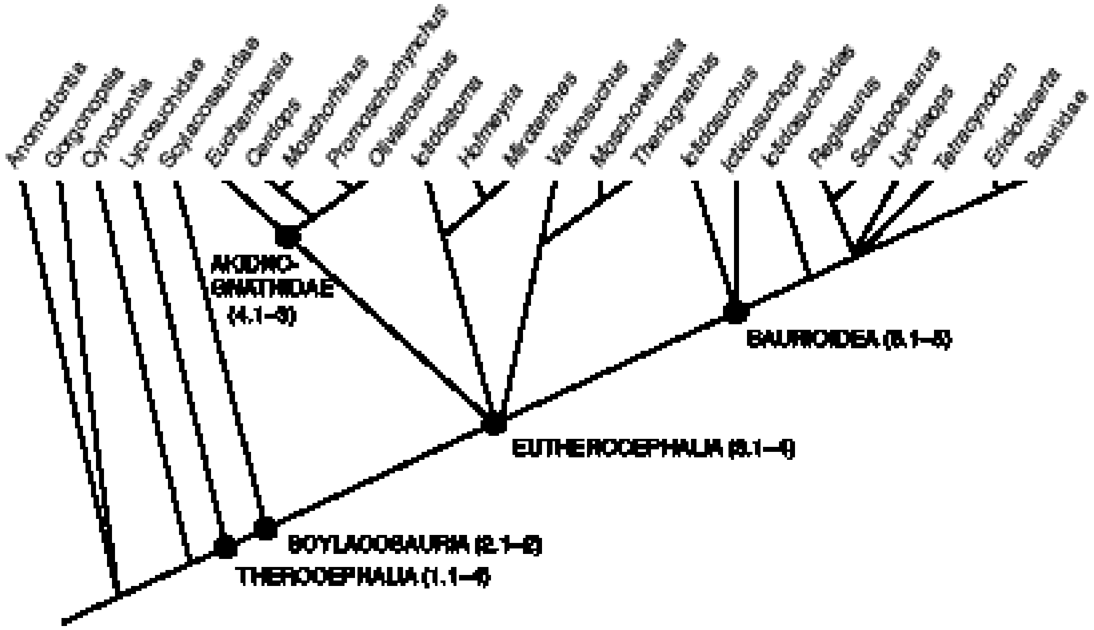

FIG. 2. Consensus cladogram summarizing the results of several recent analyses of therocephalian relationships (Hopson and Barghusen, 1986; van den Heever, 1994; Botha et al., 2007; Abdala, 2007; Huttenlocker, 2009; Huttenlocker et al., 2011). Numbers in parentheses indicate apomorphies observable in the studied specimens and listed in table 1.

Although most of the Fremouw Formation is considered Triassic in age and most of the Buckley is Permian, their contact is diachronous across the basin (McManus et al., 2002; Collinson et al., 2006). As a result, at some localities rocks below the first prominent sandstone (i.e., below the defined base of the Fremouw) can be Triassic.

Fremouw sediments were deposited in an alluvial setting dominated by coarse channel sands with subangular quartzose clasts indicative of a low-sinuosity (i.e., braided) system (Barrett et al., 1986; Isbell and MacDonald, 1991). The formation is informally subdivided into three members: lower, middle, and upper (Collinson and Elliot, 1984; Barrett et al., 1986). The lower member, ranging from 75 to 125 m in thickness, is well-exposed in the Shackleton Glacier region where it is characterized by the cyclic deposition of green mudstones, siltstones, and large channel sands (Collinson and Elliot, 1984). Vertebrate skeletons are often localized within ferruginous, olive-green siltstones exhibiting root traces and other evidences of soil formation (i.e., Dolores pedotype of Retallack et al., 1998, 2007; Retallack and Krull, 1999). Bone-bearing horizons, however, can be found both within the olive-green rooted siltstones (where articulated specimens are common) and as disarticulated, possibly transported, aggregations in the conglomeratic sandstone bodies (Barrett et al., 1968; Elliot et al., 1970; Kitching et al., 1972).

The therocephalian-bearing localities at Kitching Ridge, Halfmoon Bluff (Sentinel Hill), and *Thrinaxodon* Col (Cumulus Hills) are situated within the lower Fremouw Formation in the

Shackleton Glacier region of the Transantarctic Mountains (fig. 1). The vertebrate material frequently occurs in the finer-grained siltstone units of the lower member, preserved as semiarticulated specimens. The association of the therocephalian fossils with those of *Thrinaxodon* and *Lystrosaurus* strongly supports an earliest Triassic age for the lower member, equivalent to the *Lystrosaurus* Assemblage Zone (LAZ) of the Karoo Basin, South Africa (Kitching et al., 1972; Groenewald and Kitching, 1995; Lucas, 1998; Rubidge, 2005). Interestingly, therocephalian fossils have not been recovered from equivalent outcrops of the Fremouw Formation at Graphite Peak or at Beardmore Glacier localities, despite the occurrence of *Thrinaxodon* and *Lystrosaurus*.

SYSTEMATIC FRAMEWORK

Colbert and Kitching's (1981) recognition of two endemic therocephalian genera from the lower Fremouw Formation of Antarctica was a significant contribution to the knowledge of therocephalian biogeography and diversity at high paleolatitudes. Nevertheless, their account was hindered by a combination of the imperfect state of preservation of the referred material and by a limited understanding of therocephalian systematics and character polarity in the group. In particular, the therocephalian family "Scaloposauridae" is diagnosed largely by juvenile characters and has been argued to represent a wastebasket taxon likely containing juvenile therocephalians belonging to other known families (Kemp, 1982, 1986; Hopson and Barghusen, 1986; Huttenlocker, 2009). As such, we will use the term in quotes throughout this paper

To reassess Colbert and Kitching's (1981) findings, we follow an apomorphy-based approach that is built on recent analyses of therocephalian morphology and systematics. We identified characteristics of systematic value on all the relevant Antarctic material and assessed their level of phylogenetic generality (table 1; see Nesbitt and Stocker, 2008). The cladogram in figure 2 represents a consensus topology derived from the work of Hopson and Barghusen (1986), van den Heever (1994), Botha et al. (2007), Abdala (2007), Huttenlocker (2009), and Huttenlocker et al. (2011), although Therocephalia is considered monophyletic, as traditionally held (contra Botha et al., 2007, and Abdala, 2007). The apomorphies identified on the Antarctic material (figs. 3–7) are characters stemming from the analyses of Botha et al. (2007), Huttenlocker (2009), and Huttenlocker et al. (2011), although some are new.

SYSTEMATIC PALEONTOLOGY

Therapsida Broom, 1905
Eutheriodontia Hopson and Barghusen, 1986
Therocephalia Broom, 1903
Eutherocephalia Hopson and Barghusen, 1986

Definition: All scylacosaurian therocephalians (sensu van den Heever, 1994) sharing a more recent common ancestry with *Theriognathus microps* and *Akidnognathus parvus* than with *Scylacosaurus sclateri*.

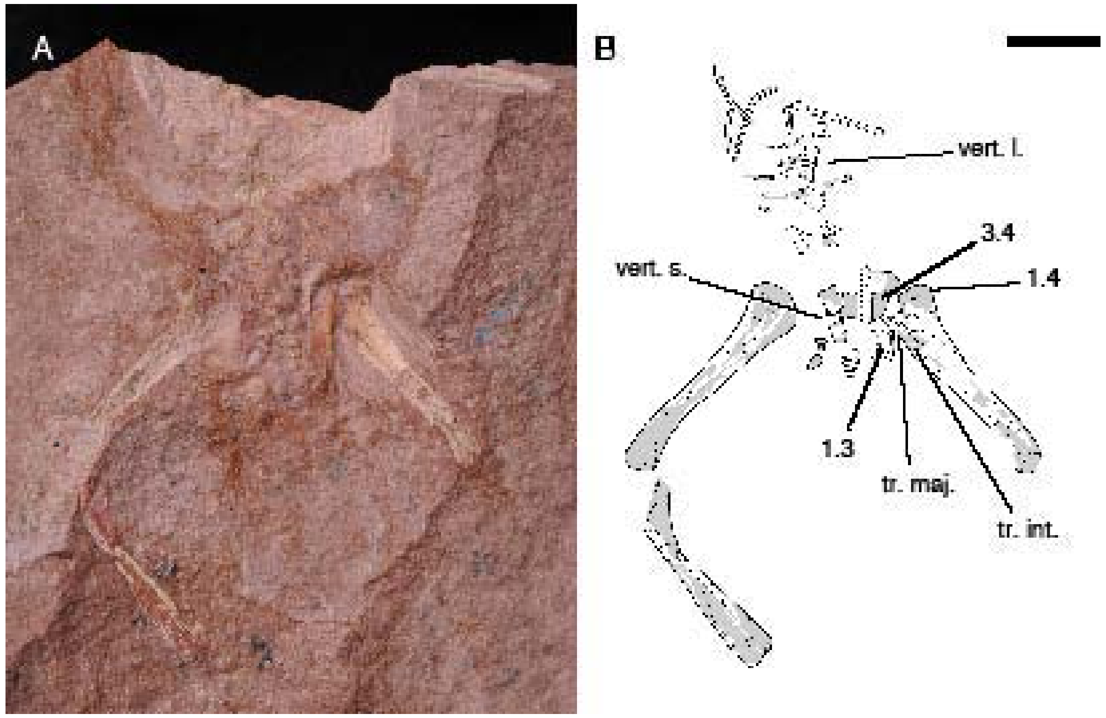

FIG. 3. AMNH FARB 9550, Eutherocephalia indet., partially articulated posterior skeleton in ventral view. Numbers refer to apomorphies listed in table 1. Gray areas indicate impression. Abbreviations: tr. int.: internal trochanter; tr. maj.: trochanter major; vert. l.: lumbar vertebrae; vert. s.: sacral vertebrae. Scale bar = 10 mm.

Diagnosis: Postfrontal absent (but polymorphic in *Hofmeyria*); dorsal surface of the paroccipital process deeply hollowed in the floor of the posttemporal fenestra; dentary broadly overlaps surangular; lateral mandibular fenestra present between dentary and anterodorsal portion of angular; anterior dentition bears smooth cutting edges that lack serrations; incisors, precanines, and canines commonly possess longitudinal facets or grooves; well-developed obturator foramen bordered by pubis and ischium (rather than a small foramen confined to the pubis); femur with long, slender diaphysis that is round in cross section (rather than oval).

Referred Specimen: AMNH FARB 9550 (fig. 3), articulated posterior skeleton, including lumbar vertebrae with ribs, partial pelvis (pubis and ischium), left and right hind limbs with semiarticulated pedes.

Locality and Horizon: Kitching Ridge, near the junction of the Shackleton and McGregor glaciers, central Transantarctic Mountains; lower Fremouw Formation, Victoria Group, Beacon Supergroup.

Remarks: AMNH FARB 9550 was originally assigned to *Ericiolacerta parva* by Colbert and Kitching (1981) due to the size of the specimen and its collection near AMNH FARB 9542 (see below). The material consists of a posterior skeleton with ribs, vertebrae, and an articulated pelvic girdle and hind limbs (fig. 3). There are apparently five thoracic ribs preserved in slight disarticulation, followed by as many as five (revised from three) lumbar vertebrae bearing laterally the impressions of their associated, fused lumbar ribs, then as many as three or four broken sacral vertebrae. There are no centra associated with the last two lumbar vertebrae, indicating that they were not fused to the neural arches (a likely indicator of the specimen's immaturity). The number of caudal vertebrae cannot be determined. The sacral count was limited to three by Colbert and Kitching (1981) based on the apparent presence of three sacral vertebrae in *Ericiolacerta*, and in other therapsids in general. However, the number of sacral vertebrae varies from three to four in therocephalians (Fourie and Rubidge, 2007, 2009). AMNH FARB 9550 exhibits a few apomorphies that are consistent with an assignment to Eutherocephalia. The most notable apomorphies are the broad, flat puboischiatic plate (table 1: 1.3) bearing an enlarged obturator foramen between the pubis and ischium (table 1: 3.4), the generally gracile hind limbs with distinctively long diaphyses, and the presence of a well-developed trochanter minor near the femoral head (table 1: 1.4), and characteristically long, thin internal trochanter visible on the left femur in anteroventral view.

Few characters are available in the postcrania of AMNH FARB 9550 to merit a more specific taxonomic assignment than Eutherocephalia. For example, Colbert and Kitching (1981: figs. 6, 7) correctly noted the absence of a tuber calcis on the posterior side of the calcaneum. The tuber calcis was originally regarded by the authors as an autapomorphy of *Ericiolacerta* (based on the holotype; Watson, 1931), which incidentally confounded the assignment of AMNH FARB 9550, as it lacks this feature. However, the tuber calcis is present in other baurioids as well, including regisaurids (Kemp, 1978, 1986) and bauriids (Schaeffer, 1941; King, 1996), but is apparently absent in nonbaurioids where this region is preserved (e.g., *Mirotenthes*, lycosuchids, scylacosaurids; Fourie and Rubidge, 2009). The combination of a broader phylogenetic distribution than previously supposed (i.e., across Baurioidea), coupled with its absence in AMNH FARB 9550, weakens the utility of this character in assigning this specimen to *Ericiolacerta* or to any other baurioid genus.

Akidnognathidae Nopsca, 1928

Definition: All eutherocephalians sharing a more recent common ancestry with *Akidnognathus parvus* than with either *Bauria cynops* or *Theriognathus microps*.

Diagnosis: Enlarged, anteriorly oriented external nares; pronounced facial exposure of the septomaxilla, broadly overlapping the premaxilla; short but deep maxilla; median frontonasal ridge (as in whaitsiids); anterior portion of vomer expanded, underlapping the ventral surface of the premaxilla; alveolar margin of maxillary slightly convex laterally in palatal view, rather than straight or concave; fossa for lower canine partially roofed by premaxilla and maxilla; spatulate incisors with mesiolingual and distolingual crests and concave lingual surface; pterygoid teeth absent.

Referred Specimen: AMNH FARB 9527 (fig. 4), left maxilla with dentition, jugal, and dentary.

Locality and Horizon: Halfmoon Bluff, Sentinel Hill, near confluence of Shackleton and McGregor glaciers, central Transantarctic Mountains; lower Fremouw Formation, Victoria Group, Beacon Supergroup.

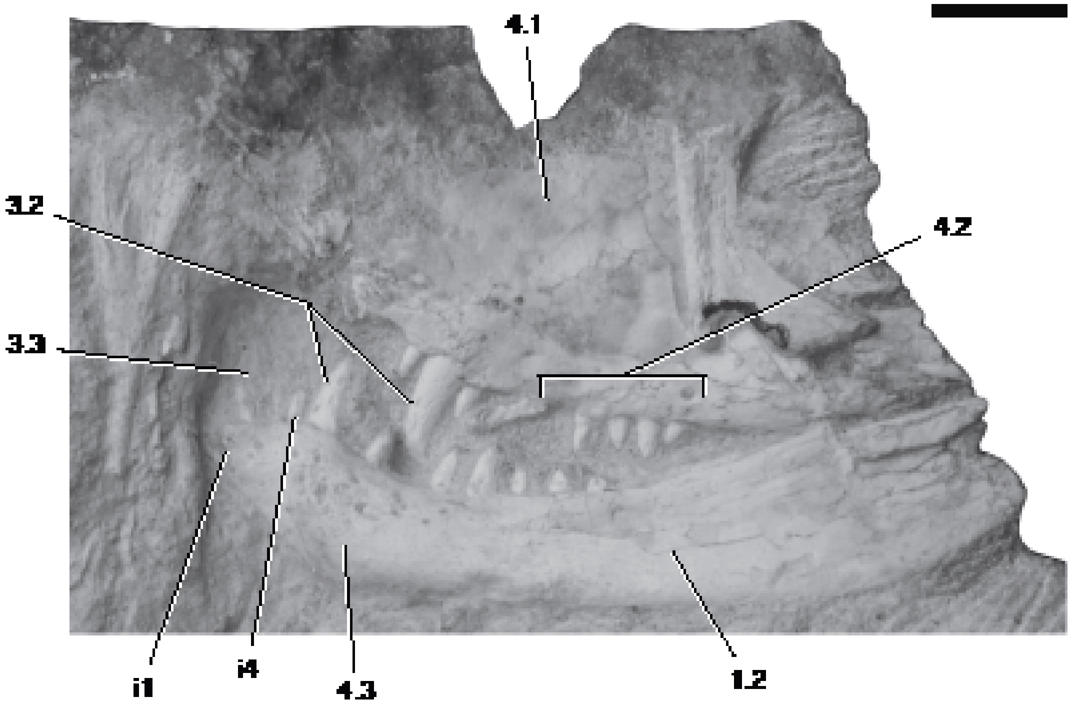

FIG. 4. AMNH FARB 9527, Akidnognathidae indet., partial skull and lower jaw. Numbers refer to apomorphies listed in table 1. Abbreviations: i1, exposed root of first lower incisor; i4, fourth lower incisor. Scale bar = 5 mm.

Remarks: The tooth formula of AMNH FARB 9527 as preserved was correctly described by Colbert and Kitching (1981), although they suggested the possibility of additional marginal teeth not preserved in the specimen. We recognize at most six upper postcanines present in the specimen. An additional unprepared jaw, which was not discussed by Colbert and Kitching (1981), remains in the matrix and also preserves dentition. A shallow lateral dentary groove is present in the left lower jaw (fig. 4; table 1: 1.2), consistent with its identification as a therocephalian. Other features visible in the specimen are consistent with an assignment to the Eutherocephalia, in particular space for four lower incisors (as opposed to three in more basal therocephalians) and teeth lacking serrations.

Among eutherocephalians, the specimen may be most precisely referred to Akidnognathidae. Unlike hofmeyriids, whaitsiids, and baurioids, the specimen exhibits a robust dentary with a relatively enlarged lower canine for its small size and a distinct mental protuberance (table 1: 4.3) as in akidnognathids (but also present in Middle Permian lycosuchids and scylacosaurids). The maxilla further resembles that of akidnognathids with its deep facial exposure (table 1: 4.1) and slightly convex alveolar margin when viewed ventrolaterally (table 1: 4.2). At least one upper precanine maxillary tooth is preserved within the precanine diastema, anterior to the enlarged canine. The postcanines are few in number when compared to "scaloposaurids"

TABLE 1. Selected apomorphies represented in the studied material (figs. 2–7), based on recent cladistic studies. Abbreviations: BAS, Botha, Abdala, and Smith (2007); H, Huttenlocker (2009).

1. THEROCEPHALIA
    1.1. Greatest width of zygomatic arch at back of the arch (H: 103)
    1.2. Lateral dentary groove present (BAS: 41; H: 110)
    1.3. Broad, horizontally oriented puboischiatic plate (H: 85)
    1.4. Distinct trochanter minor present on femur (H: 87)
2. SCYLACOSAURIA
    2.1. Thin, ventromedian crest on pterygoid present (not in form of tubercle) (H: 41)
    2.2. Paired parasagittal ridges extending from transverse flange of pterygoid to contact with parabasisphenoid (H: 106)
3. EUTHEROCEPHALIA
    3.1. Postfrontal absent (BAS: 15; H: 22)
    3.2. Smooth incisor and canine cutting margins (lacking serrations) (BAS: 50; H: 101)
    3.3. Four lower incisors (BAS: 49; H: 104)
    3.4. Moderately enlarged obturator foramen present between pubis and ischium (H: 86)
4. AKIDNOGNATHIDAE
    4.1. Short, high maxilla
    4.2. Alveolar margin slightly convex laterally in ventral view.
    4.3. Enlarged lower canine producing strong mental protuberance (also in scylacosaurids).
5. BAURIOIDEA
    5.1. Anterior border of orbit on transverse midline of skull (H: 16)
    5.2. Palatal processes of maxillae and palatines broad, contacting or nearly contacting the vomer anteroventrally (H: 37)
    5.3. Enlarged interpterygoid vacuity (H: 49)
    5.4. Dentary long, slender with smooth ventral edge and tapering anteriorly (H: 61, 62)
    5.5. Postcanines numerous (more than seven)

of similar size (only six upper postcanines and six lower postcanines are present), and the upper postcanine row does not extend posterior to the anterior border of the orbit. In these respects, the specimen closely resembles the akidnognathid *Promoschorhynchus*, which demonstrates an identical tooth count (I5-pC(1-2)-C1-PC(5-6)/i4-c1-pc6). However, the incisors, precanine and canine of *Promoschorhynchus* bear distinctive flat, longitudinal facets (Huttenlocker et al., 2011). By contrast, the anterior dentition of AMNH FARB 9527 is smooth, as in *Moschorhinus* and *Cerdops*, as well as some specimens of *Olivierosuchus*. It is unclear, however, how the morphology and formula of the dentition change during ontogeny. The inferred stratigraphic position of AMNH FARB 9527 is also consistent with an assignment to the akidnognathids *Promoschorhynchus*, *Moschorhinus*, or *Olivierosuchus*, all of which have been recovered from coeval LAZ rocks in South Africa (Huttenlocker et al., 2011). Thus, we conservatively refer AMNH FARB 9527 to Akidnognathidae.

Baurioidea Broom, 1911

DEFINITION: All eutherocephalians sharing a more recent common ancestry with *Bauria cynops* than with either *Akidnognathus parvus* or *Theriognathus microps*.

DIAGNOSIS: Long, low maxilla with height less than 40% its length; rostrum appears low relative to raised orbits and antorbital buttress; anterior border of orbit located on or behind anteroposterior midpoint of skull (as in scylacosaurids and some akidnognathids); squamosal and paroccipital process of opisthotic form a distinct, posteriorly projecting “mastoid process” (as in some akidnognathids); palatal process of maxilla bears well-developed crista choanalis, contacting or nearly contacting the vomer medially, and extending posteriorly onto the palatine; interpterygoid vacuity of adults large and somewhat heart shaped; dentary is long, slender, and relatively straight with smooth ventral edge; upper incisors numerous, greater than five (except in *Bauria*).

Referred Specimens: AMNH FARB 9548 (fig. 5A), crushed skull with lower jaw preserved in occlusion and associated right and left femora and tibiae; AMNH FARB 9525 (fig. 5B), partial skull with anterior portion of dentary.

Locality and Horizon: AMNH FARB 9548 is from Kitching Ridge, near the junction of the Shackleton and McGregor glaciers, central Transantarctic Mountains; lower Fremouw Formation, Victoria Group, Beacon Supergroup; AMNH FARB 9525 is from *Thrinaxodon* Col at Mt. Kenyon, 7 km south of McGregor Glacier, central Transantarctic Mountains; lower Fremouw Formation, Victoria Group, Beacon Supergroup.

Remarks: Colbert and Kitching (1981) erected *Pedaeosaurus parvus* on the basis of a unique combination of plesiomorphic and derived characters in AMNH FARB 9548, which they designated as the holotype. Specifically, the plesiomorphic retention of a pineal foramen was considered diagnostic for the new genus, as a pineal foramen is apparently absent in *Ericiolacerta* and was interpreted as absent in *Scaloposaurus* by the authors. However, study of the holotype of *Scaloposaurus constrictus* (NHMUK R1723) and additional specimens reveals that *Scaloposaurus* also exhibits a pineal foramen, as do more basal baurioids (e.g., *Ictidosuchoides*, *Ictidosuchops*). Assignment of AMNH FARB 9548 to "Scaloposauridae" was based on its relatively small size (skull length approximately 28 mm), slender dentary with a low coronoid process, and a wide intertemporal region (Colbert and Kitching, 1981). However, these features are broadly distributed in most juvenile eutheriodonts regardless of their taxonomic affinities (Hopson and Barghusen, 1986; Kemp, 1986).

AMNH FARB 9548 (fig. 5A) is dorsoventrally flattened such that the lower jaw is displaced onto the palate. In ventral view, a broad palatal process of the right maxilla is preserved overlapping the anteriorly displaced right palatine (both were interpreted as "palatal plates of the maxillae or ... premaxillae" by Colbert and Kitching, 1981: 15). A sharp crista choanalis preserved on the palatine would have continued anteriorly onto the ventrally broad maxilla, resembling the condition in some baurioids (table 1: 5.2). The specific arrangement of these elements around the vomer, however, cannot be determined. The dorsal aspect demonstrates the absence of a postfrontal, as in baurioids and all other eutherocephalians (table 1: 3.1; Colbert and Kitching, 1981: fig. 10). The long, straight dentary, having a loosely articulated symphysis, is also typical of baurioids (fig. 5A; table 1: 5.4). Although the morphology of the crowns is not preserved, the alveoli and partially preserved roots of at least nine maxillary teeth (the canines modest and nondistinct) and at least six postcanine dentary teeth are present in the specimen (fig. 5A). The high tooth count further supports an assignment to Baurioidea (table 1: 5.5). Although a single lower canine is observable, the anterior lower incisors could not be distinguished in the specimen. Moreover, no autapomorphic features could be distinguished in the associated postcrania.

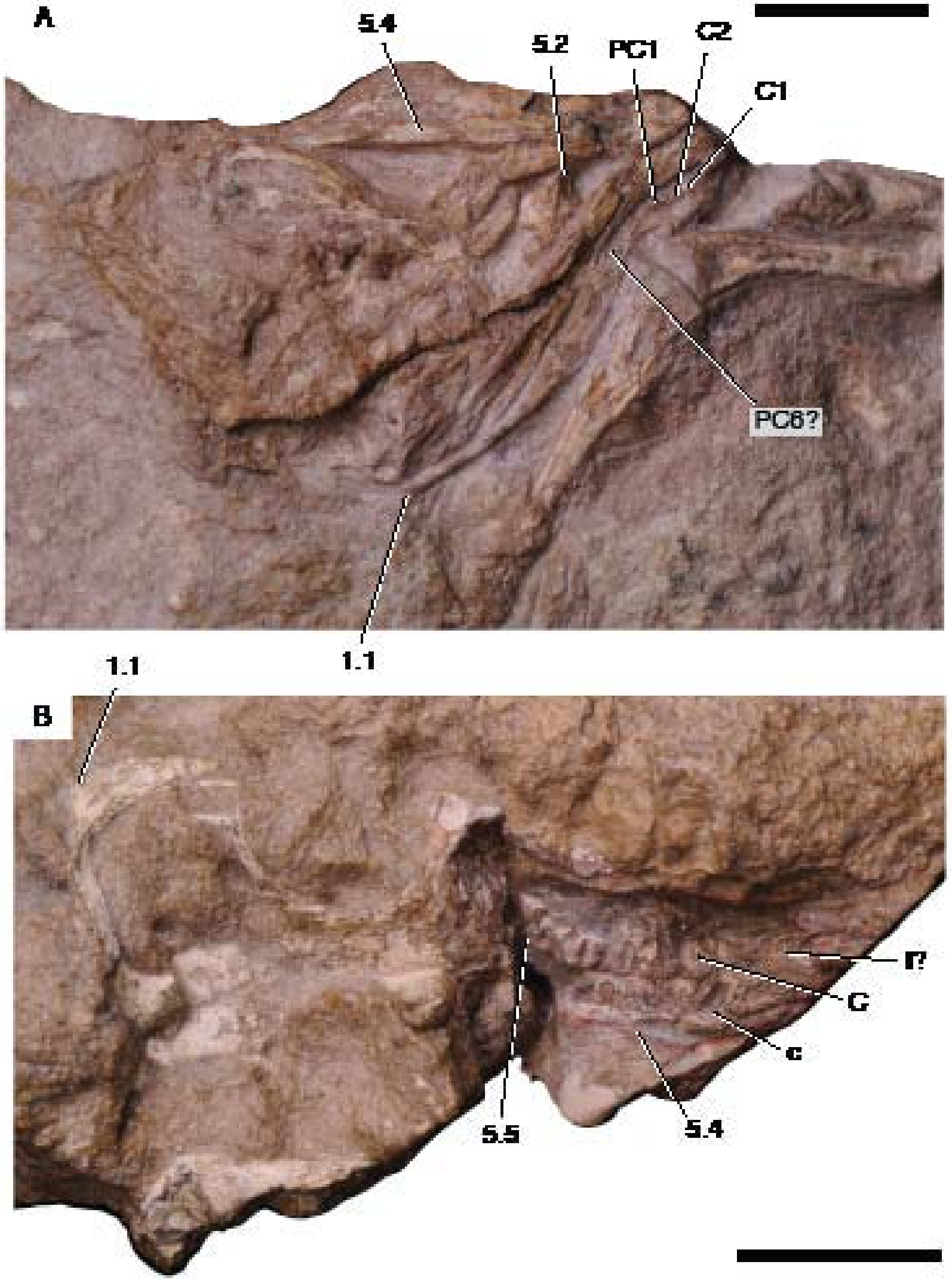

FIG. 5. (**A**) AMNH FARB 9548, Baurioidea indet., crushed skull and lower jaw in ventral view, with associated postcrania. Abbreviations: C1, first upper canine; C2, second upper canine; PC1, root of first upper postcanine tooth; PC6?, root of possible sixth upper postcanine tooth. (**B**) AMNH FARB 9525, Baurioidea indet., partial skull and lower jaw in right lateral view. Abbreviations: c, impression of lower canine; C, root of upper canine; I?, root of possible upper incisor. Numbers refer to apomorphies listed in table 1. Scale bars = 10 mm.

AMNH FARB 9525 (fig. 5B), which Colbert and Kitching (1981) designated as the holotype of *Rhigosaurus glacialis*, preserves a partial skull roof, missing basicranial and palatal elements, with a twisted rostrum and anterior portion of the left dentary. The snout is torqued and the right side of the rostrum missing, so that the left maxilla and associated dentary are visible in medial view. Although Colbert and Kitching (1981) attempted a detailed description of the skull, many of the diagnostic areas were either damaged or missing. For example, the authors wrote, in error, that the "flat parietals, lacking a pineal opening" revealed affinities to the Scaloposauridae (Colbert and Kitching, 1981: 16). Notwithstanding the contradictory presence of a pineal foramen in *Scaloposaurus* noted above, this region in the specimen displays a cranial fontanelle between the parietals (probably owing to its juvenile status) and is damaged in the area where the pineal foramen would normally be located. The anterior portion of the dentary is long and straight (table 1: 5.4) with a large canine alveolus and as many as seven poorly preserved lower postcanine alveoli. Colbert and Kitching (1981) also reported the presence of several lower incisors, yet none is preserved in the specimen or figured in their publication. In general, the teeth and the deformed anterior snout are poorly preserved, showing only a few alveoli and making impossible the determination of a complete tooth count. An enlarged upper canine is present, with as many as four teeth preserved anterior to it (although it is impossible to distinguish whether they reside in the maxilla or premaxilla). There are at least seven upper postcanines (table 1: 5.5), as noted by Colbert and Kitching (1981). In summary, the lack of autapomorphies suggests that AMNH FARB 9525 is best regarded as an indeterminate baurioid therocephalian.

Ericiolacerta parva Watson, 1931

Holotype: CAMZM T 369, skull, lower jaw and nearly complete skeleton; Harrismith, Free State, South Africa, *Lystrosaurus* Assemblage Zone (Lower Triassic), Balfour Formation, Beaufort Group.

Revised Diagnosis: Small baurioid with well-developed secondary palate, in which palatal processes of the maxillae meet at the midline, ventral to the anterior portion of the vomer; two highly procumbent lower incisors present the dentary; upper and lower caniniform teeth reduced or absent.

Referred Specimen: AMNH FARB 9542 (figs. 6, 7), disarticulated cranial material including pterygoid and associated left dentary with imperfectly preserved dentition.

Locality and Horizon: AMNH FARB 9542 is from Kitching Ridge, near the junction of the Shackleton and McGregor glaciers, central Transantarctic Mountains; lower Fremouw Formation, Victoria Group, Beacon Supergroup.

Remarks: As Colbert and Kitching (1981) described AMNH FARB 9542 in detail, we will highlight only its most pertinent features. The pterygoids are paired, tetraradiate in structure (with anterior, transverse, quadrate, and parabasisphenoid processes), and preserved in ventral view (fig. 6). The left transverse flange is damaged and missing in the specimen. Anteriorly, both the intermediate and median ventral crests (diagnostic for scylacosaurian therocepha-

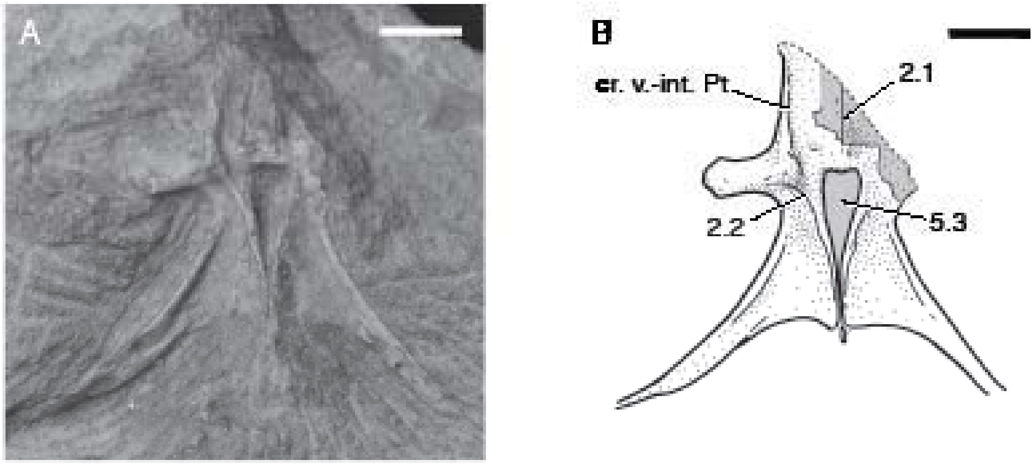

FIG. 6. AMNH FARB 9542, cf. *Ericiolacerta parva*, isolated pterygoid in ventral view. Numbers refer to apomorphies listed in table 1. Abbreviation: cr. v.-int. Pt, intermediate ventral crest of pterygoid. Scale bar = 5 mm.

lians) are visible in the specimen (fig. 6; table 1: 2.1). The intermediate ventral crest is edentulous (as in most eutherocephalians) and converges with a paired, posteriorly sweeping ventral rim of the parabasisphenoid process as in scylacosaurids and eutherocephalians (table 1: 2.2). These paired processes border an enlarged, heart-shaped interpterygoid vacuity typical of most baurioids and juvenile eutherocephalians in general. The stout transverse flange, preserved only on the right side, borders a very large suborbital vacuity approximating the condition in the types of *Ericiolacerta* and *Scaloposaurus* (Mendrez, 1975; Mendrez-Carroll, 1979). Colbert and Kitching (1981) noted the lateral extent of the transverse flange is unexpectedly short in AMNH FARB 9542, as it does not reach beyond that of the quadrate ramus. However, the lateral extent of the quadrate ramus is not easily distinguishable in the type of *Ericiolacerta*. In *Scaloposaurus*, the transverse flange only extends laterally to the lateral limits of the quadrate ramus.

The dentary (fig. 7) is a slender element with a smooth, but slightly rounded ventral margin (lacking a sharp angular process). Along with the dentition, this element provides the most compelling evidence, albeit modest, for an assignment to *Ericiolacerta parva* (Colbert and Kitching, 1981). Although the crown of the first incisor is missing, its root is preserved in its alveolus (fig. 7) and demonstrates that it was large and procumbent, as in the type (Watson, 1931: figs. 4–6). There is likewise no indication of an enlarged lower canine. Rather, the anterior incisor is immediately followed by a smaller alveolus for another small, somewhat procumbent tooth, then a series of at least six irregularly spaced teeth. The dental patterns, including irregular spacing of the individual teeth, as well as an anterior accessory cusp and strong wear facet on the distal edge of the last dentary tooth (pc 6?), are consistent with what was described in *Ericiolacerta* by Crompton (1962), who reconstructed the tooth-wear and replacement patterns. Colbert and Kitching (1981) interpreted space for additional teeth between these, accommodating nine small dentary teeth behind the anterior incisiforms, with the posteriormost dentition bearing wear facets and accessory cusps, as in the type (Watson, 1931; Crompton, 1962).

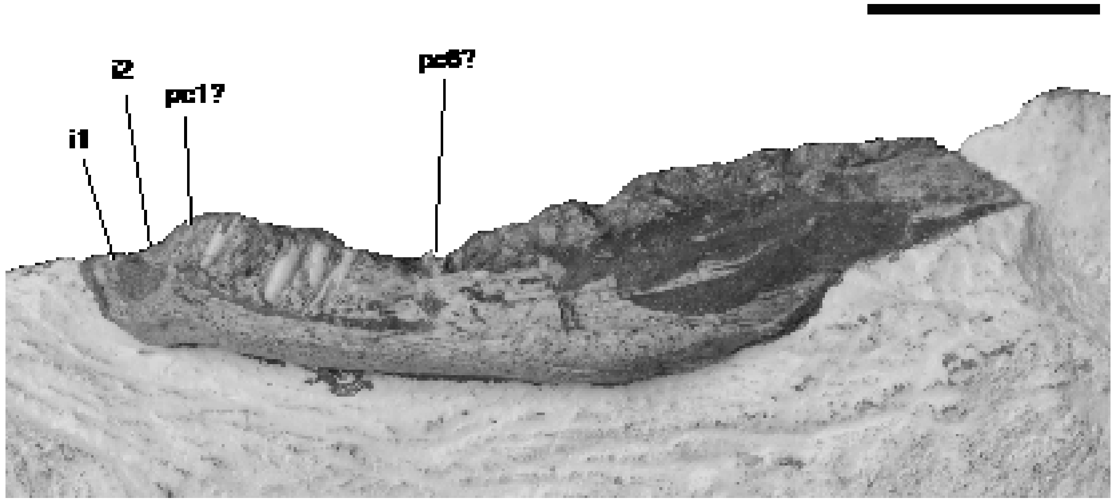

FIG. 7. AMNH FARB 9542, cf. *Ericiolacerta parva*, isolated left dentary in lateral view. Numbers refer to apomorphies listed in table 1. Abbreviations: i1, root of first lower incisor; i2, root of second lower incisor; pc1?, possible first lower postcanine tooth; pc6?, possible sixth lower postcanine tooth. Scale bar = 5 mm.

However, additional alveoli are not clearly distinguishable in AMNH FARB 9542. The crowns of the anterior dentary teeth are broken, making impossible the determination of whether they had accessory cusps.

DISCUSSION

Taxonomic status of *Pedaeosaurus* and *Rhigosaurus*

Reexamination of the holotypes of the Antarctic therocephalians *Pedaeosaurus parvus* (AMNH FARB 9548) and *Rhigosaurus glacialis* (AMNH FARB 9525) leads us to conclude that the species were established on nondiagnostic material referable only to Baurioidea (table 2). Usage of the names *Pedaeosaurus* and *Rhigosaurus* should therefore be discontinued and the genera regarded as nomina dubia.

Colbert and Kitching (1981: 12) diagnosed *Pedaeosaurus parvus* as a small “scaloposaurid” in which the “characters of the skull and dentition are in general those seen in *Ericiolacerta*,” yet differs from *Ericiolacerta* on the basis of a “well-defined pineal foramen.” It is unclear why the presence of a pineal foramen influenced their establishment of the new taxon, as this feature (and thereby the diagnosis) is consistent with a possible affinity to *Scaloposaurus*. Nevertheless, such synonymy cannot be confirmed given the poor state of preservation anteriorly in the palate, a region that is most useful in diagnosing *Ericiolacerta* and *Scaloposaurus* (based on whether the maxillae share a suture at the midline in the former, or suture to the vomer in the latter).

Likewise, diagnosis of *Rhigosaurus glacialis* by Colbert and Kitching (1981: 16) was: “large orbits and a broad temporal region; frontals between the orbits are broad, parietals broad and flat; no pineal foramen; temporal fenestra broad and postorbital bar probably incomplete; jugal-

TABLE 2. Summary of taxonomic conclusions.

Specimen	Colbert and Kitching (1981)	This Study
AMNH FARB 9525	*Rhigosaurus glacialis*	Baurioidea indet.
AMNH FARB 9527	Theriodontia indet.	Akidnognathidae indet.
AMNH FARB 9542	*Ericiolacerta parva*	cf. *Ericiolacerta parva*
AMNH FARB 9548	*Pedaeosaurus parvus*	Baurioidea indet.
AMNH FARB 9550	*Ericiolacerta parva*	Eutherocephalia indet.

squamosal bar deep beneath the temporal opening ... at least four upper incisors followed by an enlarged canine ... 7+ simple, pointed postcanine teeth are approximately equal to each other in size and regularly spaced ... dentary is straight and seemingly rather heavy—not slender; several lower incisors; postcanine teeth similar to those in the maxilla.” Many of these characters represent juvenile features (e.g., large orbits; broad intertemporal region with broad, flat parietals), plesiomorphies shared with other baurioid therocephalians (e.g., at least seven simple, pointed postcanine teeth, approximately equal to each other in size), or misinterpretations of poorly preserved material (e.g., no pineal foramen; seemingly heavy dentary; several lower incisors).

Our taxonomic conclusions are summarized in table 2. This revision has reduced the nominal species diversity of lower Fremouw Formation therocephalians from three species (*Ericiolacerta parva*, *Pedaeosaurus parvus*, *and Rhigosaurus glacialis*) plus one indeterminate higher taxon (Theriodontia) to one species (*Ericiolacerta parva*) and three higher therocephalian taxa not diagnosable to species (Akidnognathidae, Baurioidea, and Eutherocephalia). However, despite lower taxonomic resolution, our apomorphy-based reexamination of the Antarctic therocephalian material arguably permits a more accurate assessment of the taxonomic composition of the lower Fremouw fauna.

Lower Triassic Faunas of Antarctica

Lacking definitive endemic therocephalians, the lower Fremouw Formation appears to host a fauna not substantially different from its Karoo Basin counterpart (Sidor et al., 2008a). Indeed, we suggest that therocephalians had a wide biogeographic distribution across high-latitude basins during Early Triassic times. However, the collection of more complete material is required to better resolve the taxonomic identities of the akidnognathid and baurioid therocephalians recognized from the lower Fremouw Formation. Given the small sample size available, future collecting has the potential to reveal rare endemic elements among the lower Fremouw fauna, if present. Additional therocephalian material (preferably of adult specimens) is needed to better resolve the taxonomic identities of the Antarctic therocephalians, and further constrain their biogeographic distributions and biostratigraphic correlations with the LAZ of South Africa.

Collinson and Hammer (2007) suggested that climatic amelioration allowed some earliest Triassic tetrapods to disperse into higher paleolatitudes (~41°–65° S latitude) along a continuous foreland basin that stretched between the African and Antarctic components of southern Pangaea. Our recognition of an akidnognathid suggests that the lower Fremouw fauna of the Shackleton Glacier region may represent the earliest portion of the Triassic, as akidnognathids are not represented in the postextinction recovery fauna recorded in the Katberg Formation of the Karoo Basin (Smith and Botha, 2005; Botha and Smith, 2006). Alternatively, it is possible that the lower Fremouw fauna represents a later part of the LAZ and that akidnognathids persisted in Antarctica longer than at lower latitudes. Unfortunately, the fossil assemblage at Sentinel Hill, where AMNH FARB 9257 was collected, includes records with only limited biostratigraphic utility (*Lystrosaurus curvatus*, *Prolacerta broomi*, and one indeterminate temnospondyl fossil).

Fröbisch et al. (2010) argued that the small adult body size of the dicynodont *Kombuisia antarctica* suggested that the species was likely a year-round inhabitant, and not a seasonal migrant to the Antarctic portions of Pangaea. The overall smaller size of the therocephalians described here, and especially the recognition of their juvenile status, corroborates Fröbisch et al.'s (2010) suggestion.

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