NEW MIDDLE TRIASSIC TETRAPODS FROM THE UPPER FREMOUW FORMATION OF ANTARCTICA AND THEIR DEPOSITIONAL SETTING

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ABSTRACT—Renewed field work in the Beardmore Glacier region of Antarctica has led to a new collection of tetrapod fossils from the upper member of the Fremouw Formation near Fremouw Peak. This locality records a sedimentary environment remarkably similar to that preserved at Gordon Valley, the only other locality known to preserve Cynognathus Assemblage Zone-equivalent taxa from Antarctica. Fossil bones are generally disarticulated and mixed with logs and reworked mudrock clasts, forming an intraformational channel-lag conglomerate. To date, very few bones of small-bodied taxa have been recovered from the upper Fremouw conglomerates, suggesting that they did not survive the reworking process. We use an apomorphy-based approach to record three previously unrecognized taxa from the upper Fremouw Formation: the dicynodont Angonisaurus, an indeterminate therocephalian therapsid, and an indeterminate crown-group archosaur. Combined with previous data, our work demonstrates that 10 distinct taxa can be recognized from the upper Fremouw, including two endemic temnospondyl species. Our recognition of Angonisaurus in the upper Fremouw Formation provides a new piece of evidence in favor of a correlation with the Cynognathus C subzone (uppermost Burgersdorp Formation) of South Africa and the Lifua Member of the Manda beds of Tanzania.

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

INTRODUCTION

Middle Triassic tetrapod fossils from Antarctica were first reported by Hammer et al. (1986) after their discovery near the base of the upper Fremouw Formation at Gordon Valley in the Beardmore Glacier region. Subsequent publications have documented a temnospondyl assemblage with strong similarity to that of the Cynognathus Assemblage Zone (AZ) of the Karoo Basin of South Africa (Hammer et al., 1987, 1990; Hammer, 1988, 1990, 1995), although at least two endemic forms have also been noted (Sidor et al., 2008a, 2014). Importantly, Gordon Valley provided the only evidence regarding the tetrapod community inhabiting the Antarctic portion of southern Pangea during the Middle Triassic until Sidor et al. (2007) described a temnospondyl snout fragment from comparable beds near Fremouw Peak.

In late 2010 and early 2011, our team returned to Fremouw Peak and made a collection of fossils with detailed stratigraphic and sedimentological data (Fig. 1). The bulk of the fossils recovered were temnospondyl remains, most of which are still being prepared. However, also included were several amniote fossils that represent important new occurrence records. This contribution therefore has two aims: first, we describe the depositional setting of the fossils at Fremouw Peak and compare it with that at Gordon Valley; second, we describe the vertebrate fossils and assess their implications for the taxonomic diversity and biostratigraphic correlation of the upper Fremouw Formation. In addition to the illustrations included here, photographs of the specimens are available in Supplementary Data.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, U.S.A.; NHMUK, Natural History Museum, London, U.K.; SAM, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UWBM, University of Washington Burke Museum, Seattle, U.S.A.

GEOLOGIC CONTEXT

Stratigraphy and Sedimentology

The Beacon Supergroup of Antarctica is a thick Cape/Karoo-aged continental succession that accumulated in one of several retroarc foreland basins that formed along the landward side of the Gondwanide orogenic belt from Devonian to Jurassic times (Collinson et al., 1994). Shallow subduction along the southern margin of the Gondwanan plate induced at least five episodes of thrusting and uplift (De Wit and Ransome, 1992), each leading to excessive loading and downward flexure of the crust and periods of sediment accumulation in the foreland (Catuneanu et al., 1998). The Fremouw Formation is a 600–700-m-thick fluvial succession in the middle of the Beacon Supergroup and is an upward-coarsening, tectonically controlled megasequence that prograded into the Beacon Basin during Early–Middle Triassic times. It has been informally subdivided by Collinson and Elliot (1984) into a lower siltstone-dominated unit representing lacustrine/floodplain environments (Hammer et al., 1990; Collinson et al., 1994), a middle alternating sandstone/siltstone unit with more stable low-sinuosity meanderbelts and thick crevasse splay sequences filling the vegetated interchannel lowlands (Barrett et al., 1986), followed by a switch to unstable braidplains in the upper volcanioclastic pebbly sandstone-dominated unit. The latter unit has been interpreted as a response to active volcanism linked with increasing gradients in the basin (Isbell and Macdonald, 1991).
The tetrapod fossils from Fremouw Peak described here come from two separate 1-m-thick conglomeratic sandstone beds in the lowermost strata of the upper member of the Fremouw Formation. Both conglomerates form the coarsest unit of ~10-m-thick upward-fining channel-floodplain sequences (Figs. 1, S1). The disarticulated bones are mixed up in a chaotic mélange of reworked boulders of locally derived rooted siltstone and cross-bedded sandstone, carbonized logs, and woody plant debris, as well as some extrabasinal clasts of micaceous schist and small, rounded quartz pebbles all floating in a coarse arkosic-wacke matrix. Both intraformational conglomerate beds overlie a gently undulating scoured surface and grade upwards into a typical low-sinuosity channel-fill sequence of trough cross-beded coarse-grained sandstone, and medium- to fine-grained ripple cross-laminated sandstone that is distinctively convoluted in places. This grades upwards into horizontally laminated fine sandstone with comminuted plant fragments, capped by olive-gray siltstone with columnar polygonal ped structures and abundant white root molds. The convex upper surfaces of the columnar peds are commonly iron-stained and in places intensively bioturbated with vertical Skolithos-type burrows. These surfaces are interpreted as the result of shrink-swell movements of a clay-rich soil in response to highly seasonal rainfall regime, similar to the gilgai structures of modern vertisols.

Similar tetrapod fossils have been recovered from upper Fremouw exposures at Gordon Valley approximately 9 km from the Fremouw Peak locality (Fig. 1; Hammer et al., 1990). Our recent investigations at this site confirm Isbell and Macdonald’s (1991) interpretation that the disarticulated bones are associated with an intraformational channel-lag conglomerate. We have located multiple bones in the basal conglomerates of two successive channel-fill sequences (see Fig. S1), and we are confident that they occur at the same stratigraphic level as those at Fremouw Peak. We cannot prove that the same two channel fills are present at both localities, but their near-identical lithological and sedimentological character suggests that this is indeed the case. Krissek et al. (1991) concluded that the upper bone-bearing conglomerate at Gordon Valley was more widespread than would normally be associated with a within-channel lag and proposed that it represents a single large, unchannelized, low-density debris flow from the main channel onto the adjacent floodplain.

Vertebrate Taphonomy

Vertebrate fossils occur within two successive low-sinuosity channel-lag deposits at the onset of the higher-energy volcanioclastic sandstone-dominated upper Fremouw sedimentation. They occur as isolated complete and broken elements interspersed within the other clasts and are often preserved at a high angle, suggesting a short-lived erosion and resedimentation episode. The complete elements tend to be denser bones such as the dicynodont squamosal, temnospondyl mandibles, and vertebral. The increased concentration of fossil bones at these levels, as well as their intimate association with reworked pedogenically modified floodplain alluvium, suggests that many of the bones have been reworked from the immature vertisols into which these wide, shallow channels had incised. This architecture would explain their high disarticulation ratio as well as a preponderance of preburial breakage. A large temnospondyl skull from the Gordon Valley locality figured by Hammer (1990; see also Sidor et al., 2014) is nearly complete and its presence in the conglomerate suggests that it was picked up from the floodplain surface. To date, very few bones of small-bodied taxa have been recovered from the upper Fremouw conglomerates, and it is possible that they did not survive the reworking process.

SYSTEMATIC PALEONTOLOGY

AMNIOTA Haecikel, 1866
Referred Material—UWBM 95538, partial left squamosal.

Horizon and Locality—Collected from Fremouw Peak locality UWBM C1593 at 84°16.766′S, 164°17.629′E, central Transantarctic Mountains, Antarctica.

Taxonomic Note—The shape of the quadrate and zygomatic portions of the squamosal are intact and permit direct comparison with the holotype of Angonisaurus from Tanzania, although this anatomical region is not well preserved in recently described South African specimens (Hancox et al., 2013:fig. 2). Based on the revised diagnosis of Angonisaurus provided by Hancox et al. (2013), the current specimen is referable by virtue of its squamosal margin being robust and thickened and the near-vertical orientation of the quadrate ramus of the squamosal. In addition, the quadrate and zygomatic rami meet at an angle of slightly over 90° in posterior view, and the latter ramus is vertically oriented. We tentatively recognize the thickened squamosal margin to be an autapomorphy of Angonisaurus, but agree with Hancox et al. (2013) that additional material will be needed in order to parse the observed morphological variation into genus- and species-level synapomorphies.

Description—UWBM 95538 consists of the complete quadrate ramus, posterior part of the zygomatic ramus, and broken medial attachment area of the left squamosal of a large dicynodont. The quadrate ramus is relatively thin, except near its lateral margin where the bone is remarkably robust and thick (approximately 26 mm). Breakage and gaps along the posterior margin of the squamosal show the bone to have thick cortices, with a dense medullary region sandwiched in between. In areas not affected by breakage, the bone surface is well preserved, but often riddled with small cracks and fractures. The bone is black in color, except where it was exposed at the surface, where it has weathered to a light gray.

In anterior view (Fig. 2B), a well-defined fossa for the quadrate-quadratoidugal complex trends ventrolaterally from the broken base of the zygomatic ramus. The medial margin of the fossa is formed by a near-vertical ridge. Medial to this ridge, the contact between the paroccipital process of the opisthotic and squamosal is present medially as a shallow fossa. The bulk of the anterior surface of the squamosal is a large fossa representing the origination site for the M. adductor mandibulae externalis lateralis in life (Crompton and Hotton, 1967).

In general, the posterior surface of the squamosal is the best preserved (Fig. 2C). Its central area is a relatively shallow fossa, bounded by complete lateral and ventral margins. Dorsally, the thickened rim of the squamosal is broken to expose the triple-junction between the quadrate, zygomatic, and temporal rami in cross-section. Compared with many other dicynodonts, the angle between the quadrate and zygomatic rami is quite large and slightly exceeds 90°. This is in contrast to most Permian dicynodonts in which the quadrate and zygomatic rami form an acute angle (King, 1988). In addition, the dorsal portion of the quadrate ramus is remarkably wide in Angonisaurus, giving the skull a distinctive shape in dorsal view (Cox and Li, 1983:fig. 1). The medial margin of the squamosal shows a complex set of articular contacts for the paroccipital process of the opisthotic as well as the supraoccipital. A near-vertical ridge is slightly eroded, but corresponds to the support for what Cox (1959) termed the tympanic process of the paroccipital. A smooth surface on the medial margin of the squamosal represents the floor of the posttemporal fenestra (Fig. 2C). In lateral view (Fig. 2A), the shape and thickness of the quadrate ramus is extremely similar to that of the holotype of Angonisaurus cruickshanki from Tanzania (NHMUK R9732; see Hancox et al., 2013:fig. 5).

FIGURE 2. Isolated left squamosal attributed to Angonisaurus sp. (UWBM 95538) from the upper Fremouw Formation of Antarctica. A, left lateral view; B, anterior view; C, posterior view. Inset skull shows preserved portion of squamosal in gray (modified from Cox and Li, 1983). Areas lacking stippled represent broken surface. Abbreviations: popf, fossa for paroccipital process; ptf, location for posttemporal fenestra; qf, fossa for quadrate; qr, quadrate ramus of squamosal; zr, zygomatic ramus of squamosal.
Referred Material—UWBM 96187, incomplete left ilium.

Horizon and Locality—Collected from Fremouw Peak locality UWBM C1594 at 84°16.737′S, 164°17.171′E, central Transantarctic Mountains, Antarctica.

Taxonomic Note—Although incomplete, the ilium preserves two therapsid autapomorphies: a sharp anterior process located along the anterior edge of the dorsal iliac blade and a shallow anterior fossa located immediately behind the anterior process on the lateral surface, corresponding to the origin of the M. puboischiofemoralis internus (Kemp, 1978, 1986; Sues, 1986). These features are present to varying degrees of development in all therapsids preserving the pelvis, although the lack of pelvic material in some of the least-derived therapsids (e.g., sphenacodontids and Lycosuchus) makes the phylogenetic placement of these features equivocal.

Description—The acetabular portion of the ilium is well preserved, although much of the dorsal- and posterior-most extent of the iliac blade is broken away. However, an impression of the medial surface of the iliac blade is preserved and shows its dorsal margin to have sloped slightly posterovertrally. The specimen has a preserved length of 39.1 mm between the pubic and ischial rami and a maximum preserved height of 46.9 mm from the ventrall-most point of the acetabulum to the top of the iliac impression.

The anterodorsal region preserves the anterior process of the iliac blade, a narrow projection that forms an acute angle (∼60°) with the pubic ramus when viewed in lateral aspect (Fig. 3). The anterior process is well developed and bears a broadly concave anterodorsal margin (‘notch’) characteristic of the group (Kemp, 1986; Huttenlocker, 2009). Immediately behind this process on the lateral surface is a broad, shallow depression (M. puboischiofemoralis internus fossa) that is immediately followed by a rounded ridge extending to the dorsal-most point of the ilium. In other therapsids, this ridge is followed posteriorly by a second shallow fossa corresponding to the origin of the M. iliofemoralis (Kemp, 1978), but damage to the specimen limits useful description of this area. Even though much of the posterior process is missing, the posteroventral contour is preserved, demonstrating an acute angle (∼50°) formed between the ventral margin of the posterior process and the ischial ramus. As a result, the ventral margins of the anterior and posterior processes together form a strongly horizontal orientation. The acetabulum is deeply concave and roofed by a well-developed supraacetabular buttress. Inside the acetabulum, a small, vertically oriented ridge is preserved just posterior to the midline of the acetabulum, representing a possible ligamentous attachment site seen in some other therapsids (A.K.H., pers. observ.).

AMNIOTA Haecelk, 1866
REPTILIA Linnaeus, 1758
ARCHOSAURIA Cope, 1869
Gen. et sp. indet. (Figs. 3, S3)

Referred Material—UWBM 95548, proximal right femur.

Horizon and Locality—Collected from Fremouw Peak locality UWBM C1601 at 84°16.750′S, 164°17.032′E, central Transantarctic Mountains, Antarctica.

Taxonomic Note—UWBM 95548 shares features with crown-group archosaurs and their outgroups (e.g., Euparkeria capensis), including a distinct femoral head with a smooth transition to a straight, non-expanding shaft and a large medullary cavity surrounded by a cortical bone wall that constitutes under one-third of the total diameter of the shaft (0.32). There are three proximal tubera (a single lateral; two medial) on the proximal surfaces. The possession of a proximal anteromedial tuber was found to be an unambiguous synapomorphy of Archosauria by Nesbitt (2011) and therefore leads us to place UWBM 95548 within crown-group Archosauria.

Description—UWBM 95548 is the proximal half of a right femur. The midshaft break begins on the anteromedial surface and trends distally to the posterolateral surface over the course of approximately 5 cm of shaft length. The distal half of the femur was lost due to erosion prior to the specimen’s discovery. UWBM 95548 exhibits decent preservation of the bone surface and is relatively complete. The only sign of distortion is a large depression occupying the proximal half of the posteromedial surface, which partially crushes the posteromedial tuber. Abrasion is apparent on all proximal surfaces, the posterior face of the greater trochanter, and the fourth trochanter, though not enough to destroy key anatomical features.

UWBM 95548 is 163 mm long and 103 mm in circumference at approximately midshaft (i.e., below the fourth trochanter and above the break). The proximal surface is 52 mm wide and between 11 and 18 mm across. In general, the femoral cross-section is flattened in the anterolateral-posteromedial dimension. This shape appears to be natural and not due to deformation.

UWBM 95548 has a distinct femoral head that smoothly and quickly tapers into a straight, non-expanded femoral shaft, as in Euparkeria and pseudosuchian archosaurs (Nesbitt, 2011).
FIGURE 4. Proximal right archosaur femur (UWBM 95548) from the upper Fremouw Formation of Antarctica. A, anterolateral view; B, posteromedial view; C, proximal view (with anterior towards the top of the page). Areas lacking stipples represent broken surfaces. Abbreviations: amt, anteromedial tuber; ft, fourth trochanter; gr, groove; gt, greater trochanter; if, M. iliofemoralis insertion site; lia, linea intermuscularis cranialis; lip, linea intermuscularis caudalis; lt, anterolateral tuber; pmt, posteromedial tuber.

dinosauriform *Marasuchus* shares this morphology, whereas the femoral heads of silesaurids and dinosaurs are separated from the shaft by a notch or emargination (Sereno and Arcucci, 1994; Novas, 1996). The expansion of the head is within the flattened plane that characterizes the entire bone. The proximal end of the femur has three proximal tubera (Fig. 4C), which are present in all members of crown Archosauria: one anterolateral tuber and an anteromedial and a posteromedial tuber (Nesbitt, 2011). The anterolateral tuber is mound-like, as in most pseudosuchians (Nesbitt, 2011), and the largest of the proximal tubera. The anteromedial tuber is part of the articular surface of the femur and the posteromedial tuber is located in the middle of the posteromedial surface. The two medial tubera are approximately equal in size, as in ‘rauisuchian’ and crocodylomorph pseudosuchians and several dinosauriforms (Nesbitt, 2011). The region of the greater trochanter is distinct, but worn, exposing cancellous bone. A deep groove dominates the proximal surface and is flanked on either side by delicate ridges of bone. Several disparate pseudosuchian and avemetatarsalian archosaur taxa possess a similar groove, as well as the non-archosaurian archosauromorphs *Erythrosuchus* and *Chanaresuchus* (Ezcurra, 2006; Nesbitt, 2011). The anterolateral tuber reinforces the ridge on the anterolateral side of the groove.

The anterolateral surface of the shaft also features a low trochanter. This trochanter is slightly smaller than the anterolateral tuber, though of a similar proximodistally elongated, mound-like morphology, and located at about the level that the femoral head merges with the shaft. There is no trochanteric shelf, which leads us to hypothesize that the trochanter served as the insertion point for an undifferentiated M. iliofemoralis in life (Hutchinson, 2001). A robust linea intermuscularis cranialis occupies the lateral edge of the femur, running from the distal edge of the M. iliofemoralis insertion to the break.

The posteromedial surface of the shaft is dominated by the low fourth trochanter, insertion site of the M. caudifemoralis longus in life (Hutchinson, 2001). The fourth trochanter is also mound-like and rises symmetrically from the shaft, as in *Euparkeria* and pseudosuchian archosaurs (Langer and Benton, 2006; Nesbitt, 2011), including ‘rauisuchians’ (Sill, 1974). The linea intermuscularis caudalis runs through the fourth trochanter and is visible distally.

The broken distal end allows for an assessment of bone wall thickness, which we calculated as a proportion of the maximum and minimum diameters of the shaft. In both cases, the bone wall makes up roughly 33% of the diameter of the shaft, which is consistent with non-archosaurian archosauromorphs and most pseudosuchian archosaurs, but not avemetatarsalians (Hutchinson, 2001; Nesbitt, 2011).

**DISCUSSION**

**Tetrapod Diversity of the Fremouw Formation**

Sidor et al. (2008a) reviewed the tetrapod assemblages of the Fremouw Formation. They noted that the lower and upper members of the formation host assemblages that are similar to those known from the *Lystrosaurus* and *Cynognathus* AZs of the Karoo Basin of South Africa (Rubidge, 2005). Vertebrate fossils from the lower Fremouw are known from a variety of localities spanning the Beardmore and Shackleton glacier regions, and historically this member has been subjected to the bulk of vertebrate paleontological research effort. Sidor et al. (2008a) noted
TABLE 1. Vertebrate taxa recognized from the upper Fremouw Formation of Antarctica.

| Taxonomic group | Voucher specimen | Literature reference |
|-----------------|------------------|----------------------|
| Temnospondyli   |                  |                      |
| *Antacotosuchus polyodon* | AMNH 24421 Sidor et al. (2014) | |
| Benthosuchidae indet. | AMNH 24415 Hammer (1990) | |
| *Kryostega collisoni* | AMNH 24419 Sidor et al. (2008a) | |
| Parotosuchus sp. | UWBM 88571 Sidor et al. (2007) | |
| Therapsida      |                  |                      |
| *Angonisaurus* sp. | UWBM 95538 This paper | |
| Cynognathus sp. | AMNH 24422 Hammer (1995) | |
| Diademodontidae indet. | AMNH 24421 Hammer (1995) | |
| Kannemeyeriidae indet.* | AMNH 24403 Hammer (1995) | |
| Therocephalia indet. | UWBM 96187 This paper | |
| Reptilia        |                  |                      |
| *Archosaurus* indet. | UWBM 95548 This paper | |

*A fragmentary dicynodont maxilla with tusk was discussed by Hammer (1995; see also Hammer et al., 1990). This material is diagnostic as a kannemeyeriiform dicynodont, but a more precise identification is difficult to establish.

The occurrence of 14 species, but taxonomic revisions of therocephalians by Huttenlocker and Sidor (2012) and the recognition of a distinct Antarctic species of Kombuisia by Fröbisch et al. (2010) revise this number to 12. The bulk of these species are also known from the Karoo, but the corresponding South African record has higher taxonomic richness (27 species; Smith et al., 2012). Notably, lower Fremouw fossils include therapsids and temnospondyls of small body size as well as juvenile or subadult individuals.

Within the upper Fremouw Formation, our current work indicates that 10 distinct taxa can be recognized (Table 1), compared with 36 species from the Cynognathus AZ of the Karoo (Sidor et al., 2013). Estimates of abundance are more difficult to make, but Smith et al. (2012) noted 767 specimens from the Cynognathus AZ of the Karoo, whereas Hammer (1990) noted that approximately 50 upper Fremouw specimens were collected at Gordon Valley. The UWBM collection made in 2010–2011 adds a total of 27 specimens from Gordon Valley and Fremouw Peak. Clearly a variety of factors (e.g., outcrop availability, worker effort) have contributed to the Antarctic fossil record being a fraction of that from the corresponding South African beds. Yet despite its depauperate nature, the upper Fremouw Formation has yielded two endemic species (viz., *Kryostega collisoni* and *Antarctosuchus polyodon*; Table 1) and one taxonomic record not recognized in South Africa (viz., a crown-group archosaur).

It is possible that the variance in taxonomic diversity between the lower and upper Fremouw fossil assemblages is primarily attributable to differences in their depositional sedimentary environment. Whereas the lower Fremouw preserves facies similar to those seen in the equivalent Karoo beds, the upper Fremouw fossils found to date have all come from low-sinuosity channel-lag conglomerates. The pervasive bone fragmentation and the chaotic texture of these matrix-supported conglomerates support the conclusion that the paucity of small bones and articulated skeletons is mainly due to a taphonomic bias in favor of denser elements, such as lower jaws, that are better able to survive high-energy transportation. Almost the opposite is true for the bone-bearing interval in the lower Fremouw strata just above the Permo-Triassic boundary at Graphite Peak. Here the succession is dominated by mudrocks (mainly siltstone) deposited on seasonally flooded, sparsely vegetated floodplains, an environment that is much more conducive to rapid burial and preservation of small- and medium-sized skeletons. The lower Fremouw taphonomic signature is characterized by fully articulated, partially articulated and disarticulated but still associated skeletons, some of which may have been confined by underground burrows (Sidor et al., 2008b). Thus, compared with the upper Fremouw channel-hosted fossil assemblages, the lower Fremouw floodplain-hosted assemblages sample a wider range of environments, with much less transportation and reworking, which probably accounts for their greater taxonomic richness.

**New Taxonomic Records**

The presence of dicynodonts in the upper Fremouw Formation has been noted previously (e.g., Hammer, 1988, 1990, 1995), with the single figured specimen, AMNH 24403, representing a partial maxilla preserving the base of a large tusk. Because the morphology preserved is not particularly diagnostic, previous workers have referred the specimen to an indeterminate kannemeyeriid or kannemeyeriiform. The recognition of *Angonisaurus* in the upper Fremouw is the first genus-level dicynodont identification possible and furthermore indicates that at least two dicynodont taxa co-occurred, a tusked and tuskless form. In the Manda beds of Tanzania, a tusked dicynodont attributed to the genus *Rech- nisaurus* is known to co-occur with *Angonisaurus* (Cox, 1991).

Therocephalian fossils have not been reported from the upper Fremouw Formation, although they occur in the underlying Lower Triassic lower Fremouw Formation (Colbert and Kitching, 1981; Huttenlocker and Sidor, 2012). The ilium described here is quite large, suggesting a body size somewhat greater than that of the Gondwanan baurioids of the *Cynognathus* AZ of South Africa (e.g., *Microgompophodon*, maximum skull length = 87 mm; *Bauria*, maximum skull length = 130 mm), but likely smaller than the large, carnivorous therotheriophalians of the Permian, such as *Moschorinus* (maximum skull length = 260 mm: Huttenlocker and Botha-Brink, 2013). Figure 4 compares the ilium morphology and sizes of UWBM 96187 and a Triassic specimen of *Moschorinus*, the currently largest known therotheriophalidian predator of the Triassic. UWBM 96187 is only slightly smaller than the latter specimen (acetabulum length = 32 mm), but is larger than contemporaneous baurioids from South Africa in which the hip structure is known (e.g., *NMOR 3189*, acetabulum length = 10 mm). If our identification of UWBM 96187 is correct, then it would represent a rare instance of Antarctic tetrapods with larger body size than their South African contemporaries. Such large size is unexpected for a Gondwanan therotheriophilian of the *Cynognathus* AZ, but similarly large forms are known from Triassic rocks in China based mainly on cranial material (Lucas, 2001). For example, the ordochelosauriform *Hachena* has an approximate skull length of 157 mm (Sun and Hou, 1981) and *Traversodontoides* likely had a skull length of ~180 mm, although the skull is incompletely preserved (length estimated from Sun, 1981). Although somewhat smaller-bodied, the ilium of *Orodosiodon* from the Triassic Ordos Basin of northwest China has been described, and bears an acetabulum length of approximately 25 mm (length estimated from Hou, 1979), slightly less than that of the Antarctic specimen. Perhaps the unusual size of UWBM 96187 reflects the general rarity and poor sampling of therotheriophalians from Middle Triassic rocks (i.e., their abundance and taxonomic richness being relatively low in the *Cynognathus* AZ, in spite of having a global distribution up until the time of their extinction). As an alternative hypothesis, the large size of the Fremouw Peak specimen could represent an instance of Bergmann’s rule (Meiri and Dayan, 2003), which suggests that high-latitude taxa tend to have larger body size than their lower latitude relatives (although this does not explain the large size of some Chinese taxa). Little attention has been drawn to instances of Bergmann’s rule for the Triassic tetrapods of Antarctica (but see Smith et al., 2011, for an archosauriform example) and more research will be needed to understand the extent to which it is expressed in high-latitude faunas during the Triassic (Colbert and Kitching, 1975, 1977; Colbert, 1987).
Archosauromorphs were previously recorded from the lower Fremouw Formation by Cosgriff (1983) and Smith et al. (2011), but the overlying Middle Triassic rocks have not yielded a comparable specimen until now. UWBM 95548 is assigned to crown-group Archosaurus based on the presence of the anteromedial tuber. Nesbitt (2011:193) emphasized the possession of an anteromedial tuber on the proximal femur as an unambiguous synapomorphy of Archosaurus. Within archosaurs, we hypothesize that UWBM 95548 pertains to a member of the Pseudosuchia, and not Avemetatarsalia, on the basis of (1) a femoral head that smoothly transitions into the femoral shaft without interruption; (2) the mound-like and symmetrical morphology of important muscle attachment sites such as the anterolateral tuber, M. iliofemoralis insertion, and fourth trochanter; (3) cortical bone thickness greater than measured avemetatarsalians; and, more subjectively, (4) the greater prevalence of pseudosuchian rather than avemetatarsial archosaurs in lower Middle Triassic formations worldwide (Nesbitt et al., 2010, 2011).

Crown-group archosaurs, in the form of an erpetosuchid, several paracrocodylomorph taxa (sensu Nesbitt, 2011), and three worldwide (Nesbitt et al., 2010, 2011). The greater prevalence of pseudosuchian rather than avemetatarsalians, but within the range of most pseudosuchians; and, more subjectively, (4) the greater prevalence of pseudosuchian rather than avemetatarsial archosaurs in lower Middle Triassic formations worldwide (Nesbitt et al., 2010, 2011).

Crown-group archosaurs, in the form of an erpetosuchid, several paracrocodylomorph taxa (sensu Nesbitt, 2011), and three dinosauromorphs are known from Cynognathus AZ-equivalent strata worldwide (Huene, 1938, 1939; Charig, 1956; Krebs, 1969; Zhang, 1975; Galton and Walker, 1996; Benton and Gower, 1997; Gower and Semnikov, 2000; Nesbitt, 2005; Sen, 2005; Butler et al., 2009, 2011; Nesbitt et al., 2010, 2011, 2013; Schoch et al., 2010; Benton, 2011; Nesbitt and Butler, 2013; Peecook et al., 2013). If our referral of UWBM 95548 to a crown-group archosaur is correct, then it represents the first record from Antarctica and helps confirm the broad geographic distribution of taxa within the Cynognathus AZ times (Nesbitt et al., 2010; Butler et al., 2011). The Cynognathus AZ of South Africa records at least three non-archosaurian archosauriforms: Erythrosuchus africanus, Euparkeria capensis, and a Garjainia-like erythrosuchid (Broom, 1905b, 1913; Rubidge, 2005). The absence of crown-group archosaurs from the Burgersdorp Formation of the Karoo Basin is therefore curious given the amount of worker effort expended over the last century, although it is important to note that Cynognathus AZ outcrop, especially for subzone C, is relatively limited (Fröbisch, 2013:fig. 2). Our knowledge of Triassic archosauromorphs has grown rapidly within the last two decades through the revision of existing records and new sampling, both taxonomic and geographic, which leaves open the possibility that the Cynognathus AZ of the Karoo Basin will produce crown-group archosaurs.

We infer that UWBM 95548 would be approximately 300 mm in length when complete. This value is based on comparisons with the Triassic archosauriforms Batrachotomus kuperzellenis (SMNS 52970; Gower and Schoch, 2009), Euparkeria capensis (SAM-PK-K10548; Botha-Brink and Smith, 2011), and Proterosuchus fergusi. SAM-PK-K10548 measures 68 mm in total length and is fully adult, based on comparison with the largest known specimen of the species. UWBM 95548 is therefore much larger than adult Euparkeria or Proterosuchus (Iemora ~150 mm; Cruickshank, 1972), but smaller than Erythrosuchus, which had a humeral length of over 400 mm and an estimated body length of 4.5 m (Gower, 2003). Combined with the large non-archosaurian archosauriform humerus described from the lower Fremouw Formation by Smith et al. (2011; AMNH 24262), this suggests that archosauriforms with body sizes of over 3 m were present in Antarctica during the Early and Middle Triassic.

Biostratigraphic Implications

Biostratigraphic correlations of the upper Fremouw fauna have uniformly suggested a close correspondence to the Cynognathus AZ of South Africa (Hammer, 1990, 1995; Lucas, 1998, 2010; Hancox, 2000; Abdala et al., 2005; Sidor et al., 2007, 2008a; Fröbisch, 2009). However, when the tripartite subdivision of the Cynognathus AZ is considered (Hancox et al., 1995), the various authors listed above have disagreed on which subzone provides the most appropriate correlation. For example, Sidor et al. (2007) suggested correlation with the A subzone, Abdala et al. (2005) with the B subzone, and Fröbisch (2009) with the B and C subzones. Sidor et al. (2013) have suggested that the increasingly fragmented faunas inferred for the Middle Triassic would make long-distance biostratigraphic correlations more difficult, which appears to be the case for Antarctica. Nonetheless, we believe that our recognition of Angonisaurus from the upper Fremouw Formation provides a new piece of evidence in favor of a correlation with the Cynognathus C subzone, as does, albeit to a lesser degree, the recognition of Antarctosuchus polyodon as the sister taxon to Paracyclotosaurus (Sidor et al., 2014).

Hancox et al. (2013) mentioned the presence of Angonisaurus in the upper Fremouw Formation, but hesitated to draw a definitive biostratigraphic correlation to the Cynognathus C subzone. They noted that first-appearance data do not always match perfectly for the Karoo and Antarctic records (e.g., Fröbisch et al., 2010) and that the sample sizes involved are extremely limited. However, Angonisaurus is seemingly rare in all basins in which it has been recovered and the disregard of a biostratigraphic datum seems unparsimonious. Interestingly, the remains of at least two dicynodonts are known from the upper Fremouw. In addition to Angonisaurus, an indeterminate tusked kannemeyeriid was reported from Gordon Valley (Hammer et al., 1990; Hammer, 1995). Although Hammer's usage of ‘kannemeyeriid’ was essentially a placeholder for any large Triassic dicynodont, the specimen is distinguishable from Angonisaurus by virtue of its possession of a maxillary tooth. Kannemeyeri and Angonisaurus are not known to co-occur in Cynognathus C subzone and previous reports of their co-occurrence in the Ntwere Formation of Zambia (e.g., Hancox and Rubidge, 1996) are in error (Hancox et al., 2013; Angielczyk et al., 2014). At present, we consider the evidence to best support a correlation of the upper Fremouw Formation with the Cynognathus C subzone (uppermost Burgersdorp Formation) as well as the Lifuw Member of the Manda beds (e.g., Abdala et al., 2005).

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LITERATURE CITED

Abdala, F., P. J. Hancox, and J. Neveling. 2005. Cynodonts from the uppermost Burgersdorp Formation, South Africa, and their bearing on the biostratigraphy and correlation of the Triassic Cynognathus Assemblage Zone. Journal of Vertebrate Paleontology 25:192–199.
Angielczyk, K. D., J. S. Steyer, C. A. Sidor, R. M. H. Smith, R. L. Whitley, and S. Tolan. 2014. Permian and Triassic dicynodont (Therapsida: Anomodontia) faunas of the Luangwa Basin, Zambia: taxonomic update and implications for dicynodont biogeography and biostratigraphy; pp. 93–138 in C. F. Kammerer, K. D. Angielczyk, and J. Fröbisch, (eds.), The Early Evolutionary History of Synapsida. Springer, Dordrecht.
Barrett, P. J., D. H. Elliot, and J. F. Lindsay. 1986. The Beacon Supergroup (Devonian–Triassic) and Ferrar Group (Jurassic) in the Beardmore Glacier area, Antarctica; pp. 339–428 in M. D. Turner and J. F. Splettstoesser (eds.), Geology of the Central Transantarctic Mountains. American Geophysical Union, Antarctic Research Series 36.

Benton, M. J. 2011. Archosaur remains from the Otter Sandstone Formation (Middle Triassic, late Anisian) of Devon, southern UK. Proceedings of the Geologists’ Association 122:25–33.

Benton, M. J., and D. J. Gower. 1997. ‘Richard Owen’s giant Triassic frogs’—a new look at the remains from the Otter Sandstone Formation, UK. Palaeontology 40:737–750.

Benton, M. J. 2011. Archosaur remains from the Otter Sandstone Formation, Devon, UK. Palaeontology 54:715–724.

Benton, M. J. 2000. The evolution of the tetrapods. Academic Press, London.

Benton, M. J. 2011. The Triassic archosauriform reptile Euparkeria capensis, from South Africa. Journal of Vertebrate Palaeontology 31:1289–1292.

Bent, P. H. 1983. A new genus of Triassic dicynodont from East Africa. Palaeontology 26:483–488.

Bent, P. H. 1983. A new dicynodont reptile from the Middle Triassic of East Africa. Palaeontology 26:489–492.

Bent, P. H. 1983. A new dicynodont reptile from the Middle Triassic of East Africa. Palaeontology 26:493–494.

Butler, R. J., D. J. Gower, and A. G. Sennikov. 2000. Early archosaurs from Russia; pp. 140–159 in M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, UK.

Haeckel, E. 1866. Generelle Morphologie Der Organismen. Reimer, Berlin, 1036 pp.

Hammer, W. R. 1988. The Cynognathus zone (late Early Triassic) vertebrate fauna from Antarctica. Antarctic Journal of the United States 23(5):10–11.

Hammer, W. R. 1990. Triassic terrestrial vertebrate faunas of Antarctica; pp. 42–50 in T. N. Taylor and E. L. Taylor (eds.), Antarctic Paleobiology: Its Role in the Reconstruction of Gondwana. Springer Verlag, New York.

Hammer, W. R. 1995. New therapsids from the upper Fremouw Formation (Triassic) of Antarctica. Journal of Vertebrate Paleontology 15:105–112.

Hammer, W. R., J. W. Collinson, and W. J. I. Ryan. 1990. A new Triassic vertebrate fauna from Antarctica and its depositional setting. Antarctic Science 2:163–167.

Hammer, W. R., J. W. Ryan, and S. L. DeFauw. 1987. Comments on the vertebrate fauna from the Fremouw Formation (Triassic), Beardmore Glacier region, Antarctica. Antarctic Journal of the United States 22(5):32–35.

Hammer, W. R., J. W. Ryan, J. W. Taplin, and S. L. DeFauw. 1986. New vertebrates from the Fremouw Formation (Triassic) Beardmore Glacier region, Antarctica. Antarctic Journal of the United States 21(5):24–26.

Hancox, P. J. 2000. The continental Triassic of South Africa. Zentralblatt für Geologie und Paläontologie 1998:1285–1324.

Hancox, P. J., and B. S. Rubidge. 1996. The first specimen of the Mid-Triassic dicynodont Angonisaurus from the Karoo of South Africa: implications for dating and biogeography of the Cynognathus Assemblage Zone, Upper Beaufort Group. South African Journal of Science 92:391–392.

Hancox, P. J., K. D. Angelieczky, and B. S. Rubidge. 2013. Angonisaurus and Shansiodon, dicynodonts (Therapsida, Anomodontia) from subzone C of the Cynognathus Assemblage Zone (Middle Triassic) of South Africa. Journal of Vertebrate Paleontology 33:655–676.

Hancox, P. J., M. A. Shishkin, B. S. Rubidge, and J. W. Kitching. 1995. A threefold subdivision of the Cynognathus Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical implications. South African Journal of Science 91:143–144.

Hou, L. 1979. On a new theriodont from Inner Mongolia. Vertebrata PalAsiatica 17:121–130.
