

## A BURROW CAST WITH *LYSTROSAURUS* SKELETAL REMAINS FROM THE LOWER TRIASSIC OF SOUTH AFRICA

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### ABSTRACT

We report on a large burrow cast with skeletal contents from Lower Triassic strata of the Palingkloof Member of the Balfour Formation, which forms the lowermost portion of the *Lystrosaurus* Assemblage Zone (LAZ) of South Africa. The burrow cast is similar to large burrow casts previously described from the LAZ that were identified as large-scale *Scoyenia* domichnia. It is the first large burrow cast from the LAZ found to contain diagnostic fossil bone. The burrow cast is a relatively straight, subhorizontal (inclined ~12°), dorsoventrally compressed tube consisting of an entry ramp and living chamber; the entrance to the burrow is not preserved and there is no evidence that the ramp formed a spiral section. The skeletal material comprises a single, partial, disarticulated skeleton of a juvenile animal that can be assigned with confidence to the dicynodont genus *Lystrosaurus*. Whereas similar large-diameter burrow casts from strata slightly higher in the LAZ have been attributed to *Lystrosaurus*, we present an alternative hypothesis that a carnivorous tetrapod constructed the burrow. Our preferred hypothesis is supported by the observation that the interred *Lystrosaurus* skeleton is too small to be the maker of this particular burrow, by the general observation that carnivorous tetrapods construct relatively straight burrows, and by the partial, disarticulated state of the skeleton, which we interpret as the remains of larded prey. We suggest that akidnognathid theriodonts of the genera *Moschorhinus* or *Olivierosuchus*, the most conspicuous large predators of the LAZ, were the constructors of large-diameter, subhorizontal burrows.

### INTRODUCTION

Lower Triassic rocks of South Africa record a diverse ichnofauna of vertebrate and invertebrate burrows and the possible remains of other forms of shelter burrows (Groenewald, 1991; Damiani et al., 2003; Abdala et al., 2006; Gastaldo and Rolerson, 2008). Some of the largest burrow casts have been attributed to species of the dicynodont synapsid genus *Lystrosaurus*, the most numerous, large vertebrate taxon present in the Induan–Olenekian *Lystrosaurus* Assemblage Zone (LAZ). Groenewald (1991) described large, single burrows (20–45 cm in diameter and up to 100 cm long; burrow type “1b” according to his table 2) that he regarded as assignable to the ichnogenus *Scoyenia*. Two of the alleged *Lystrosaurus* burrow casts documented by Groenewald (1991) contained bone fragments, but these were either undiagnosable or (at the time) awaiting formal taxonomic identification. The burrow casts mentioned by Retallack et al. (2003) were large structures attributed to the ichnogenus *Histioderma* and contained remains that they referred to *Lystrosaurus*. Retallack et al. (2003), however, provided neither illustrations nor descriptions of the body fossils.

Identifications of dicynodonts of the genus *Lystrosaurus* as the tracemakers (or occupants) of large burrow casts in the rocks of the LAZ, such as those by Groenewald (1991) and Retallack et al. (2003),

are based on circumstantial evidence: fossils of *Lystrosaurus* are the most commonly encountered vertebrates in the LAZ, and most *Lystrosaurus* skeletons are of the appropriate size to have occupied large burrows. The lack of documentation that would confirm individuals of *Lystrosaurus* as the tracemakers of the large burrow casts is regrettable because it precludes independent assessment of the taxonomic affinities of the associated skeletons. This oversight is important because the LAZ includes other large tetrapods—the archosauriform reptile *Proterosuchus fergusi* and the theriodont synapsids *Moschorhinus kitchingi* and *Olivierosuchus parringtoni*—that, despite being less common members of the LAZ, are potential alternative candidates for burrow constructors.

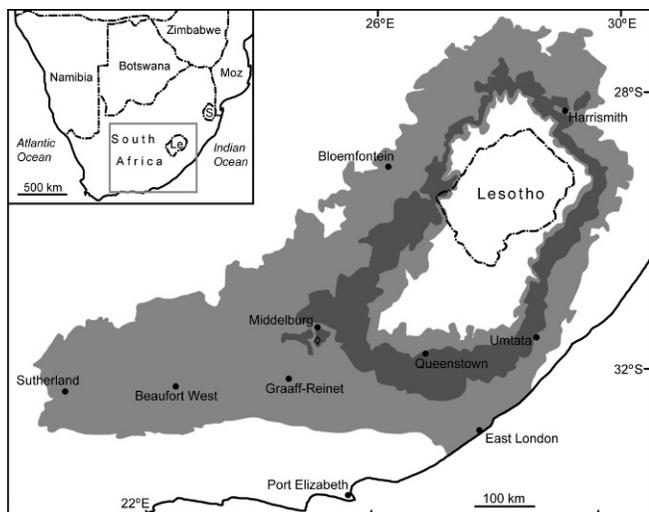
Recent prospecting of LAZ rocks in the vicinity of Middelburg, Eastern Cape Province, South Africa (Fig. 1), resulted in the discovery of a large burrow cast that entombs skeletal remains. This burrow cast resembles structures from the Katberg Formation that were described by Groenewald (1991, p. 21) and classified by him as large-scale *Scoyenia* domichnia (dwelling burrows). As those burrow casts lack surficial ornamentation consisting of longitudinal striations, one of the diagnostic characters of the ichnogenus *Scoyenia* (Frey et al., 1984), we henceforth refer to these large-diameter, subhorizontal burrows as type 1b burrow casts, following Groenewald’s (1991, table 2) informal designation. The new burrow cast was found on the Middelburg district farm Barendskraal, which preserves a relatively rich LAZ fauna that includes *Lystrosaurus* spp., *M. kitchingi*, *P. fergusi*, and several smaller synapsid and reptilian taxa (Damiani et al., 2004). Thus, all large LAZ faunal elements that are potential makers of large burrows are present at Barendskraal. We prepared the living chamber of the burrow cast to exhume the skeletal remains and to examine the evidence for the hypothesis that large burrow casts from the *Lystrosaurus* AZ are attributable to dicynodonts of the genus *Lystrosaurus*.

### MATERIAL AND METHODS

The burrow cast described here has been accessioned into the collections of the National Museum, Bloemfontein as NMQR 3606. The burrow terminus—interpreted as the living chamber—and adjoining section of the ramp were collected by us in 2007 from ~30 m from the base of Maanhaar hill on the farm Barendskraal (Fig. 2). The burrow cast is positioned stratigraphically 2 m below the lowermost sandstone assigned to the Katberg Formation on Barendskraal, and, thus, NMQR 3606 comes from the uppermost strata of the argillaceous Palingkloof Member of the Balfour Formation (Fig. 3).

Skeletal remains collected from Maanhaar have been assigned to *Lystrosaurus* sp., the procolophonoids *Owenetta kitchingorum*, *Saurodektes rogersorum*, Procolophonoidea indet., and small baurioid therocephalians (Damiani et al., 2004), whereas those referred to *Moschorhinus kitchingi* and *Proterosuchus fergusi* were collected from exposures elsewhere on the farm (Agterkamp) in 2001 and 2002

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**FIGURE 1**—Geographic location of the Middelburg district farm Barendskraal (open diamond) in southeastern South Africa. Light gray shading indicates Beaufort Group exposures exclusive of *Lystrosaurus* Assemblage Zone rocks (dark gray shading). Main map redrawn from Groenewald and Kitching (1995); inset map redrawn from Groenewald (1991). Abbreviations (inset map): Le = Lesotho, Moz = Mozambique, S = Swaziland.

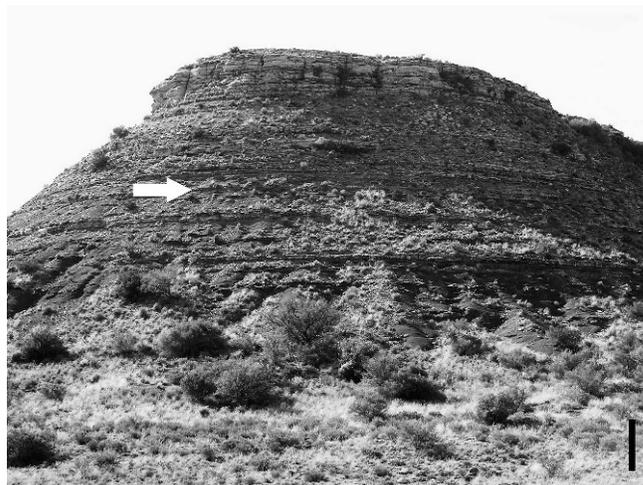
(Damiani et al., 2004). To this faunal list we are able to add the theriodont *Olivierosuchus parringtoni*, following our collection in 2007 of a partial theriodont skeleton that we refer to this species (Botha-Brink and Modesto, unpublished data, 2010).

The collected portions of the burrow cast were prepared mechanically, with a pneumatic aircsibe, from the upper surface downwards in the expectation of revealing an articulated skeleton in dorsal aspect. The upper surfaces—although not necessarily the anatomical dorsal surfaces—of the skeletal contents were exposed after the approximate upper 75%–80% of the burrow cast was removed. The skeletal elements were then photographed, and the diagnostic elements were illustrated as specimen drawings.

## DESCRIPTION

The burrow fill consists of the same gray mudstone that surrounds the burrow cast (Fig. 4). The burrow ramp descends at an angle of  $\sim 12^\circ$  with respect to the surrounding strata and then levels out for the final  $\sim 25$  cm forming the living chamber. The burrow cast is flattened slightly by lithostatic compression, and a layer of sandy mudstone truncates the top of the ramp portion of the burrow cast. No obvious scratch marks were in evidence (Fig. 5). The cross section through the living chamber was (prior to preparation)  $\sim 12$  cm tall and 34 cm wide. The collected portions of the burrow cast have been reduced to 2–3 cm thick in the course of preparation undertaken to expose the skeletal contents.

Body fossils consist of disarticulated cranial and postcranial elements (Fig. 6). The bones are well preserved and exhibit no weathering or signs of scavenging, although there is peculiar damage to a single element (a scapula). The recognizable cranial elements consist of a premaxilla and a maxilla. The former element, preserved ventral side up at the end of the living chamber, is characterized by a tall, slightly convex anterior surface that meets both lateral surfaces along rounded, anterodorsally aligned corners, terminating ventrally with a U-shaped palatal rim (Figs. 7A–B). Parallel, paired anterior palatal ridges and a single, median posterior palatal ridge are well exposed on the palatal portion of the bone. The strongly developed, ventrally extended premaxilla is diagnostic of the genus *Lystrosaurus*. It has an extensive facial portion, which distinguishes it from other dicynodonts (Cluver,



**FIGURE 2**—Photograph of Maanhaar hill on the Middelburg farm Barendskraal, showing outcrop of the Lower Triassic *Lystrosaurus* Assemblage Zone, with position of burrow (NMQR 3606) indicated by arrow. Scale bar 10 m.

1971). The maxilla (Figs. 7C–D) is a left element preserved at the bottom of the entry ramp ( $\sim 35$  cm from the premaxilla). It is complementary to the premaxilla in size. Exposed in lateral aspect, it is a quadrangular element in outline, with a distinct palatal rim, a weakly sigmoidal anterodorsal margin for contact with the premaxilla and shallow embayment for the external naris, a weakly concave dorsal margin for contact with the nasal and the lacrimal, posterior process for underlying the jugal, and slightly sigmoidal posteroventral margin forming the anterior part of the ventral margin of the skull roof. The posteroventral region is moderately swollen for the tusk, which is preserved as a stump.

There are  $\sim 32$  postcranial bones and 8 unidentifiable bone fragments strewn across the floor of the living chamber and the base of the ramp. Two of these elements, a left scapula and a right ilium, allow confident assignment to *Lystrosaurus*. None of the remaining postcranial bones exhibit diagnostic features that would contradict the taxonomic assignment to the genus *Lystrosaurus*. Remarkably, only three vertebral elements are exposed. These consist of three centra; the lack of neural arches fused to these centra indicates an ontogenetically young age. Ten appendicular elements are present, among which the most informative are the scapula and the ilium. The extensive anteroposterior expansion—described as widely flaring by Ray (2006, table 1)—of the scapular blade (Figs. 7E–F) is a diagnostic feature of the genus *Lystrosaurus*. Ray (2006, table 1) also describes the scapula of *Lystrosaurus* as being distinguished by a thickened caudal margin, but this is not evident in our specimen. The absence of such thickening may be attributed to the immaturity (small size) of the skeleton: the scapula of NMQR 3606 is 33% the height of a scapula from a presumed adult *Lystrosaurus* that was described and illustrated by Ray (2006, fig. 2a). The scapula (Figs. 7E–F) is interesting from a taphonomic perspective in exhibiting a conspicuous emargination that is  $\sim 15$  mm deep (anteroposteriorly) and 17 mm wide (dorsoventrally).

Two deep, rounded notches in the posterodorsal margin of the iliac blade are the most distinctive features of the ilium (Figs. 7G–H). Among therapsids, iliac notches have been documented only in the genus *Lystrosaurus* (Watson, 1912; Ray, 2006). The ilium is exposed in medial aspect, revealing an extensively roughened surface for the attachment of the sacral ribs. The remaining appendicular elements comprise limb bones, including both clavicles, a coracoid, a humerus, a femur, and several epipodial elements. The ends of pro- and epipodials are not finished in periosteal bone, which is additional evidence of the ontogenetically young age of the skeleton. Like the cranial elements, the ilium and the other large appendicular bones are positioned  $\leq 10$  cm



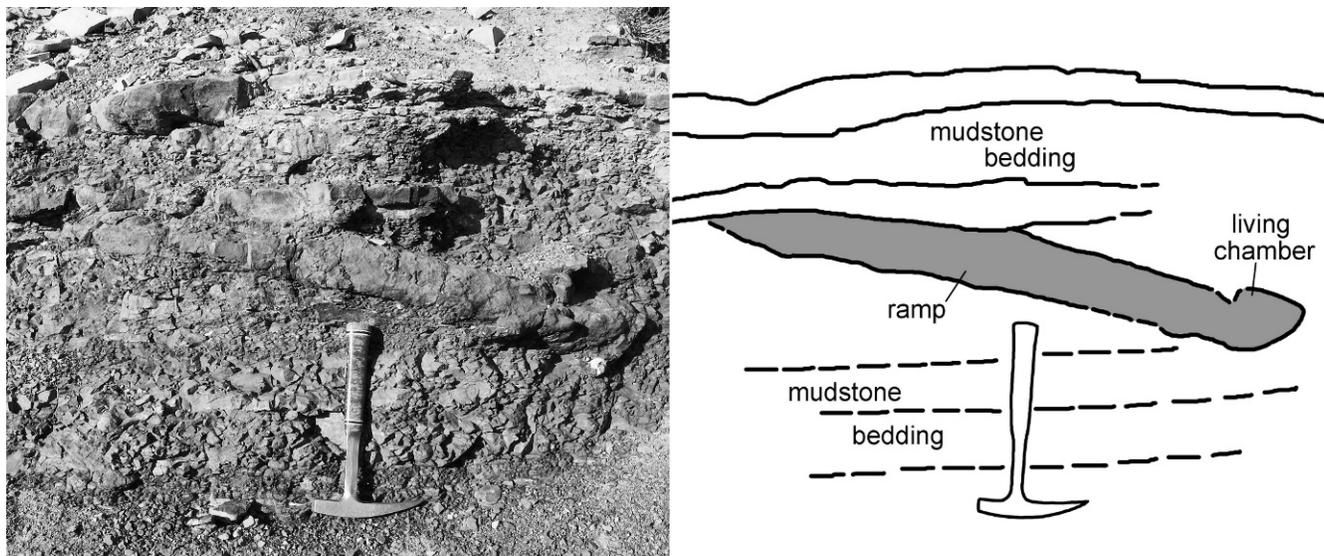


FIGURE 4—Photograph and interpretive sketch of burrow cast as found on the hillside of Maanhaar on Barendskraal. Burrow cast in gray in sketch. Rock hammer 31 cm long.

water-mediated (fluvial) distribution of vertebrate bones (e.g., Weigelt, 1989), although it is possible that rapid flooding of the burrow may have disarticulated and rearranged the bones. Such a scenario, however, does not account for the absence of most of the skull and over half of the postcranial skeleton. Alternatively, the preserved distribution of the disarticulated elements is suggestive of animal-mediated repositioning: a relatively large animal may have occupied the burrow after the

*Lystrosaurus* carcass had become skeletonized. This occupant could have pushed the largest *Lystrosaurus* elements to the periphery of the living chamber, and concomitantly pressed the ribs, relatively flat bones, and small elements (e.g., vertebral centra) into the floor of the burrow. The latter possibility would have been facilitated if some sediment had accumulated after the *Lystrosaurus* individual had been skeletonized but prior to re-occupation. The putative subsequent occupant, or perhaps it was the original burrow constructor, may have also removed some or all of the elements that are missing from NMQR 3606. Secondary occupation of burrows is not uncommon among recent fauna (Kinlaw, 1999). For example, extant reptiles and other tetrapods readily move into burrows made by other species (Hoogland, 1995; Kerr and Bull, 2004; White and Cameron, 2009), sometimes even when the original trace-maker is still present (Taber, 1945; Witz et al., 1991).

As this is the first large burrow cast discovered to contain skeletal contents, it represents an apt test of Groenewald's (1991) hypothesis that *Lystrosaurus* constructed these types of burrows. The appendicular morphology of the genus *Lystrosaurus* is well known, and those who have considered the functional significance of the limbs (e.g., King and Cluver, 1991; Ray, 2006) consider that members of *Lystrosaurus* were well adapted for a burrowing lifestyle. Further support for the hypothesis of burrowing for *Lystrosaurus* comes from the observation that these types of burrow casts are not uncommon ichnological structures of vertebrate origin in the LAZ (at least three localities: Groenewald, 1991; this study). It seems reasonable, therefore, to attribute large burrow casts to *Lystrosaurus* because this genus is the most common faunal element of LAZ, comprising up to 95% of the fossils (Groenewald and Kitching, 1995).

Evidence that fails to support the hypothesis that NMQR 3606 was constructed by an individual of *Lystrosaurus* is that the burrow is of a size greater than expected to have been constructed by an individual of the size of the interred juvenile *Lystrosaurus*. The size of the preserved cranial elements suggests a skull that was  $\leq 10$  cm broad, which would seem too small for the entry tunnel, which we estimate to have been  $\geq 30$  cm. It is generally held that most burrowing tetrapods construct the tunnel portions of their burrows to be only as large as needed to fit their bodies (Voorhies, 1975; White, 2005; Gobetz, 2006). Thus, NMQR 3606 appears to be too large for the interred *Lystrosaurus*. A minority interpretation was offered by Groenewald et al. (2001), who proposed that the relatively wide and longitudinally ridged-bottomed burrow tunnels of the Middle Triassic cynodont genus *Trirachodon* were attributable to two-way traffic, an idea that is plausible given the

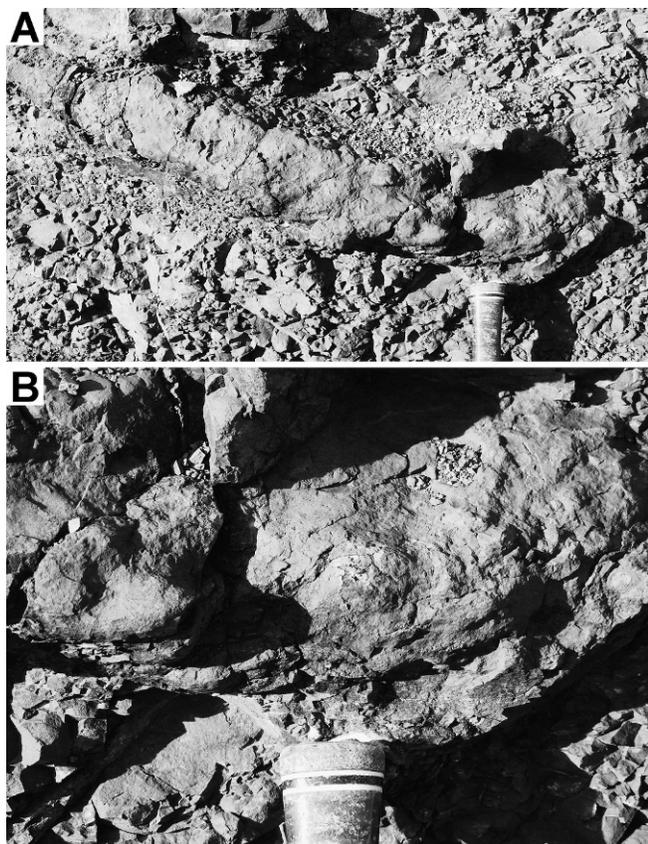
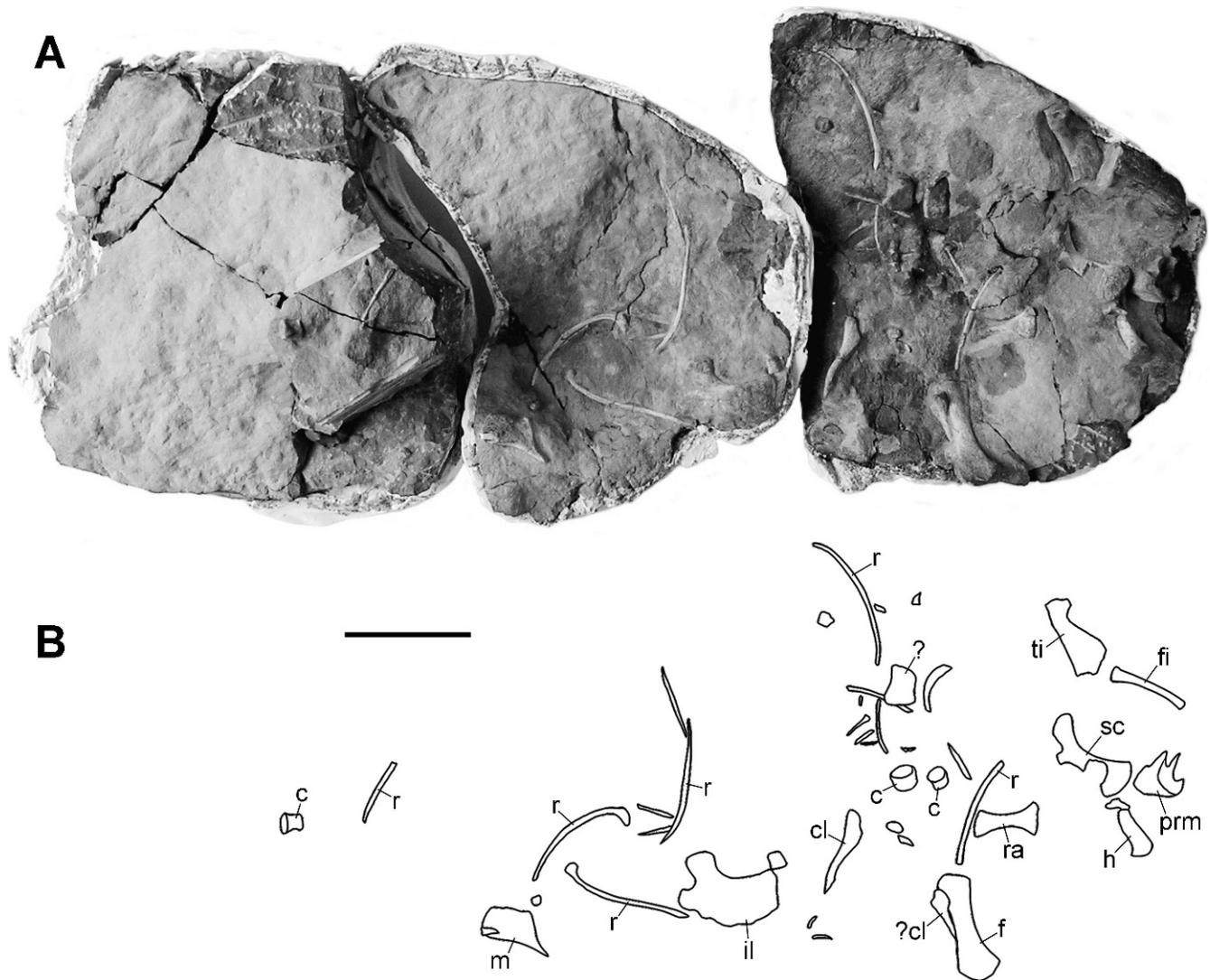


FIGURE 5—Photographs of *in situ* burrow cast showing surface details of (A) ramp and terminal chamber and (B) close up of terminal chamber. Hammer handle 51 mm wide.

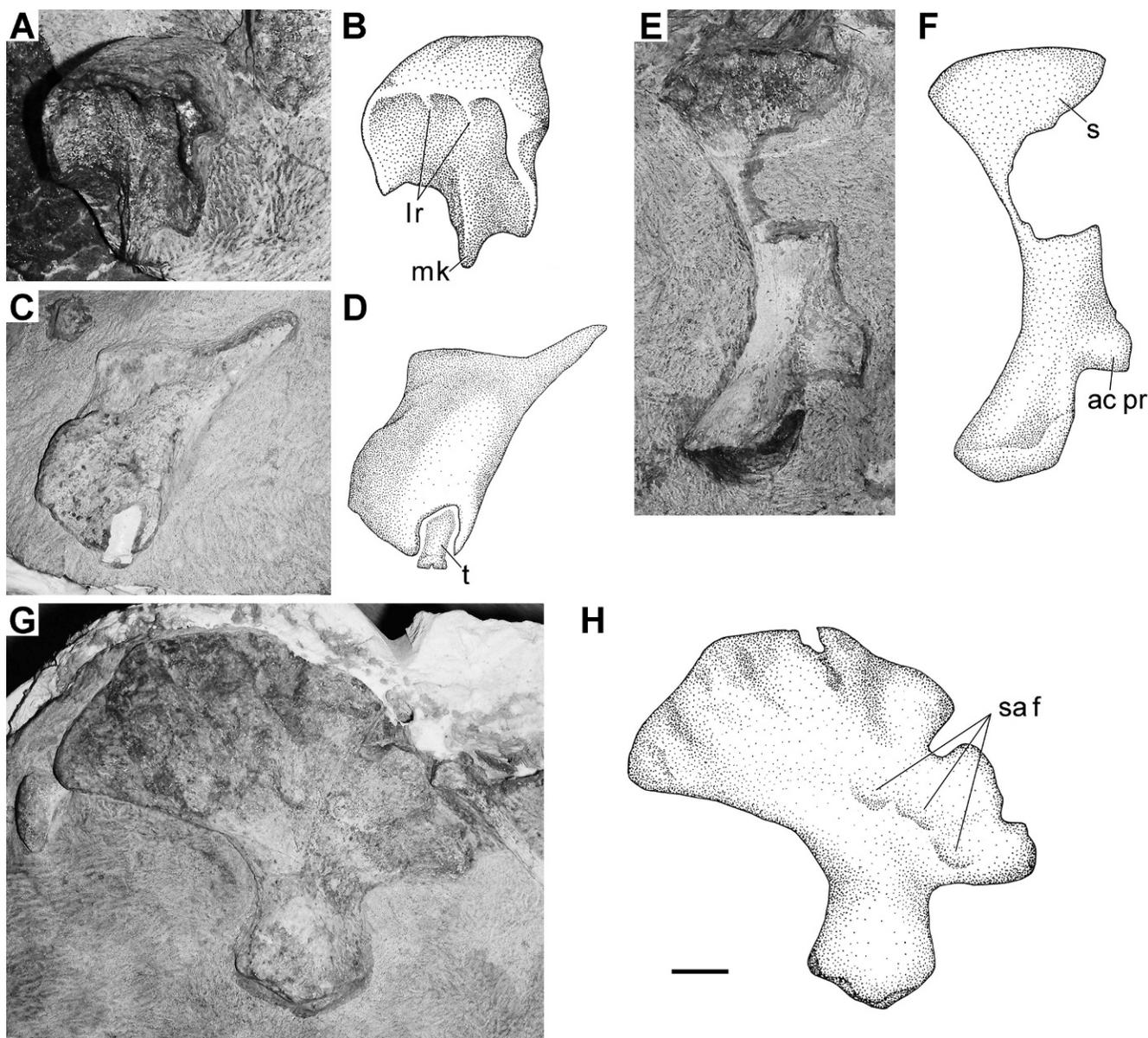


**FIGURE 6**—Top view of the prepared living chamber and lowermost section of the ramp of burrow cast NMQR 3606 (A) and bone outlines (B). Burrow entrance is to the left. Abbreviations: c = centrum, cl = clavicle, f = femur, fi = fibula, h = humerus, il = ilium, m = maxilla; prm = premaxilla, r = rib, ra = radius, sc = scapula, ti = tibia. Scale bar 10 cm.

apparent colonial nature of the tracemakers; Hasiotis et al. (2004), however, have documented in extant and fossil burrows that the central furrow in burrows is produced by one individual large enough to straddle the ridge as it excavated and traveled through the burrow. The observation that NMQR 3606 is the only burrow known from Barendskraal, however, argues against the tracemaker as a member of a colonial or gregarious species, and we conclude that it is unlikely that our burrow cast was constructed and occupied by more than a single individual. The lack of identifiable scratch marks could mean that the burrow was relatively old by the time the remains were deposited in the terminal chamber (and the infilling of the burrow): the tracemaker of this burrow could have erased surficial markings with general use. This interpretation is compatible with the idea that burrowers generally do not dig tunnels with diameters much greater than will admit their own bodies. Accordingly, the lack of scratch marks does not support the hypothesis that a tetrapod the size of the entombed *Lystrosaurus* juvenile constructed NMQR 3606.

Thus, the alternative hypothesis that NMQR 3606 was made by a species of another tetrapod genus needs to be considered. The attribution-by-greater-numbers hypothesis, based on the observation that *Lystrosaurus* is the numerically dominant genus of the LAZ, is not

an infallible line of reasoning: the most common body fossils are not necessarily correctly attributable to associated trace fossils. For example, amniote eggs collected from the Mongolian Cretaceous by the American Museum of Natural History Asiatic Expeditions were originally attributed to protoceratopsian ornithischians, the most commonly encountered body fossils in the same rocks, but it was realized recently that the eggs are of theropod parentage (Norell et al., 1994). The only other burrow cast from the LAZ that is confidently associated with a body fossil is attributed to the cynodont genus *Thrinaxodon* (Damiani et al., 2003). The *Thrinaxodon* burrow cast described by those authors, which consists of living chamber and the adjoining tunnel, includes the skeleton of a well-ossified, presumably adult *Thrinaxodon*. This burrow cast is about one-third the diameter of a large burrow cast similar to the one described in this paper. This size difference indicates that it is highly unlikely that the primary occupant of NMQR 3606 was a *Thrinaxodon*. Other cynodonts are known from the LAZ, but they are approximately the same size as *Thrinaxodon*, and much less common. The only other dicynodont genus known from the LAZ is *Myosaurus*, for which burrow casts are not known. *Myosaurus* is a close relative of the Permian cistecephalid genera *Cistecephalus* and *Kawingasaurus* (Angielczyk, 2007; Fröbisch, 2007), which are regarded



**FIGURE 7**—Photograph of premaxilla in ventral view (A) and interpretive drawing of same in anteroventral view (B). Photograph of left maxilla in lateral view (C) and interpretive drawing of same (D). Photograph of left scapula in medial view (E) and interpretive drawing of same (F). Photograph of right ilium in medial view (G) and interpretive drawing of same (H). Abbreviations: ac pr, acromion process, lr = lateral ridges, mk = median keel, s = scapular blade, sa f = sacral rib facets, t = tusk. Scale bar 1 cm.

as the dicynodont taxa most highly adapted to a fossorial mode of life (Cox, 1972; Cluver, 1978). The phylogenetic propinquity of *Myosaurus* to these cistecephalids suggests that it, too, was a digger. The 11 known specimens of *Myosaurus*, all of which are skulls (Hammer and Cosgriff, 1981), however, indicate a tetrapod that is smaller than *Thrinaxodon*. The only other genus of LAZ dicynodont is, therefore, clearly not the constructor of these large burrows. NMQR 3606 is much too large to have been constructed by any of the small diapsids or relatively numerous procolophonoid reptiles, none of which were larger than *Thrinaxodon*. The only remaining possible alternatives in the LAZ fauna are the archosauriform genus *Proterosuchus* and akidnognathid theriodonts of the genera *Moschorhinus* and *Olivierosuchus*. The burrowing abilities of these carnivorous taxa have yet to be assessed, however, and specimens of *Proterosuchus* are more rare than those of the theriodonts. *Moschorhinus* is by far the most common large carnivorous tetrapod of the LAZ but, surprisingly, its postcrania have yet to be described, and we can only assess its potential as a burrower

by proxy. Our own work on *Olivierosuchus* reveals that this theriodont is now known from four specimens (Botha-Brink and Modesto, unpublished data, 2010), including the one from Barendskraal, which is also the largest (skull length of ~11 cm). Interestingly, the known pectoral appendicular morphology of *Olivierosuchus* is consistent with a burrowing habit (Brink, 1965; Botha-Brink and Modesto, unpublished data, 2010): the manual unguals are spadelike and 50%–60% longer than the penultimate phalanges. The *Olivierosuchus* individual from Barendskraal appears to be too small for NMQR 3606, but we envision that individuals of this genus could have constructed those on the smaller end (~20 cm diameter) of the spectrum of type 1b burrows described by Groenewald (1991). If the manual morphology of *Moschorhinus* was similar to that of *Olivierosuchus*, large individuals of the former genus could have been responsible for the largest (up to 45 cm diameter) burrow casts documented by Groenewald (1991).

Accordingly, large-diameter, subhorizontal burrows may be the products of akidnognathids, which were the largest theriodonts of the

LAZ. This attribution accords well with the simple, straight structure of large-diameter burrows noted by Groenewald (1991) and evident in NMQR 3606, and the general view that carnivores construct relatively straight burrows (Voorhies, 1975; Gobetz, 2006; Hembree and Hasiotis, 2008). The simple architecture of large-diameter burrows contrasts with that of the longer, coiled, large-scale *Daimonelix*-like burrow casts from other LAZ localities, which were attributed to *Lystrosaurus* by Groenewald (1991), and with the coiled *Daimonelix*-like burrows constructed by the Permian dicynodont *Diictodon* (Smith, 1987).

Further evidence that our burrow cast was not constructed by *Lystrosaurus* is the observation that the juvenile skeleton interred in NMQR 3606 is not preserved in the articulated, curled-up attitude of documented therapsid occupants of Permian and Triassic burrows (e.g., Smith 1987; Damiani et al., 2003). The juvenile *Lystrosaurus* skeleton of NMQR 3606 is disarticulated and incomplete and, thus, it is possible that the skeleton represents the remains of a carcass that was dragged into the burrow by a carnivorous tetrapod. The relatively pristine state of all elements but one, however, might argue against the interpretation that the juvenile dicynodont was a prey item or a scavenged carcass. Skeletons that have been interpreted as having been preyed upon, or scavenged by, carnivorous tetrapods exhibit clear and unmistakable tooth marks (Fiorillo, 1991; Erickson and Olson, 1996; Reisz and Tsuji, 2006). Multiple tooth marks may be present on a single bone (Fowler and Sullivan, 2006) or individual tooth marks are present on several elements (Reisz and Tsuji, 2006). The single, possible exception in NMQR 3606 is the damaged scapula. The roughly polygonal outline of the emargination in the scapula, however, does not seem to be consistent with a tooth puncture or a bite mark from a jaw with several teeth. Such akidnognathids as *Moschorhinus* and *Olivierosuchus* possessed conspicuous canines and incisors (Brink, 1965), which one might expect to have left a mark on at least one of the preserved elements if the *Lystrosaurus* skeleton represents the remains of a meal. *Moschorhinus* and *Olivierosuchus*, however, are characterized also by a reduced number of postcanine teeth (3–4 postcanines; Brink, 1965; Durand, 1991), and this suggests that the postcanine teeth of these akidnognathids played a minor role in food processing. If so, akidnognathids might not be expected to leave tooth marks on the bones of their prey, particularly if their feeding strategy was to use their larger and anteriorly placed teeth, the canines and the incisors, to nip off limbs and chunks from the torso of their prey into pieces that were small enough to swallow whole, which could have included whole bones.

We feel that the available evidence favors the hypothesis that the juvenile dicynodont was a larded prey item, and that the burrow maker was a carnivorous member of the LAZ fauna. Both the partial skeleton and the burrow might have been abandoned, perhaps temporarily, by the tracemaker, with the skeleton disturbed subsequently, possibly when the original occupant returned to its burrow, or perhaps in an exploratory investigation by another tetrapod. Pursuant to this hypothesis, the numerical dominance of *Lystrosaurus* individuals in the LAZ fauna accords well with the idea that species of this genus would be the most common prey in that fauna. Thus, the discovery of *Lystrosaurus* skeletal remains should be anticipated in at least some burrow casts attributable to coeval carnivores.

## CONCLUSIONS

A burrow cast containing skeletal contents is described from the lowermost Triassic strata of the Palingkloof Member, Balfour Formation in the Karoo Basin, South Africa, strata that are regarded as forming the base of the *Lystrosaurus* Assemblage Zone. The skeletal contents comprise the partial, disarticulated skeleton of a single tetrapod that can be assigned with confidence to the dicynodont therapsid genus *Lystrosaurus*. The burrow cast is most similar to those described from higher sections in the LAZ comprising Groenewald's

(1991) type 1b burrow casts. Thus, the specimen described here represents the oldest large-diameter burrow cast in the LAZ. The *Lystrosaurus* skeleton is the first such remains to be described in detail from a large burrow cast collected from the LAZ, and at first glance lends some support to previous work that tentatively attributed large-diameter burrow casts to *Lystrosaurus*. The partial *Lystrosaurus* skeleton does not exhibit obvious signs of scavenging, apart from inexplicable damage to a single appendicular element, and disarticulation and the incomplete nature of the *Lystrosaurus* skeleton is suggestive of post-mortem disturbance. Furthermore, the burrow appears to be too large to have been constructed by the interred *Lystrosaurus* individual. Accordingly, we favor the alternative interpretation that a carnivorous member of the LAZ constructed the burrow, and that the *Lystrosaurus* skeleton represents a larded prey item. Suitable candidates for the burrow maker can be found among akidnognathid theriodonts, of which numerous specimens exist in museum collections and exhibit a range in size that is compatible with the tracemakers of large-diameter, subhorizontal burrows of the LAZ. Support for our preferred hypothesis is the relatively simple design of the burrow cast, which is superficially similar in construction, but not in size, to burrow casts constructed by the cynodont genus *Thrinaxodon*, and our own observations on the appendicular morphology of the akidnognathid *Olivierosuchus*, which we believe is consonant with burrowing abilities, and is a suitable proxy for its larger relative *Moschorhinus*. Ongoing fieldwork in the LAZ has yielded further large burrow casts (Smith and Botha-Brink, 2009). We expect that any skeletal remains found within these structures will be invaluable towards testing the hypothesis that large-diameter, subhorizontal burrow casts of the LAZ are attributable to predators for whom members of the genus *Lystrosaurus* were principal prey.

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