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A taxonomic revision of the genus Procolophon and the phylogenetic relationships of Procolophonoid reptiles

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2008-03-18T08:54:02Z
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PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2006, v. 21, p. 507–512
Research Note
DOI: 10.2110/palo.2005.P06-001R

FAUNAL AGGREGATION IN THE EARLY TRIASSIC KAROO BASIN: EARLIEST EVIDENCE OF SHELTER-SHARING BEHAVIOR AMONG TETRAPODS?

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ABSTRACT

The first report of a multitaxon aggregation from the Early Triassic *Lystrosaurus* Assemblage Zone is presented here. The aggregation includes two vertebrates—the suricate-sized cynodont *Galesaurus planiceps* and a gecko-like procolophonoid *Owenetta kitchingorum*—and a diplopod millipede. The high degree of articulation of the skeletal remains and the preservation of delicate bones *in situ* suggest that the animals were either rapidly buried or died in a place protected from weathering and agents of dispersal. Two hypotheses are possible to explain this multitaxon aggregation: trapping in a floodplain gully followed by immediate burial or shelter-sharing. The latter hypothesis is favored after the analysis of the fossil evidence recorded in the South African Karoo Basin.

INTRODUCTION

An unusual aggregation of two amniotes—the suricate-sized cynodont *Galesaurus planiceps* and the gecko-like procolophonoid *Owenetta kitchingorum*—as well as a diplopod millipede (probably juliform), from the Lower Triassic, Katberg Formation of the Karoo Basin in South Africa, is presented here. Different interpretations are discussed to explain this particular aggregation of taxa, and a behavior-driven assemblage is favored as the more likely cause. This represents the first multispecific behavioral aggregation reported from this basin or any of the equivalent-age basins from the other Gondwanan continents.

The South African Karoo Basin is an important source of data for understanding the evolution of vertebrate communities during the late Paleozoic and early Mesozoic. Fossils from the Karoo, besides providing information about Permian to Jurassic faunas, give the most detailed record on changes of terrestrial vertebrate communities during the Permo-Triassic extinction (Rubidge et al., 1995; Smith, 1995). The superb preservation of many of the fossils and associated traces in the Karoo has also provided, in several instances, additional information about animal behavior in ancient times (Ellenberger, 1974; Smith, 1995; Smith and Evans, 1995, 1996; Groenewald, 1991; Groenewald et al., 2001; Damiani et al., 2003). A number of monospecific tetrapod aggregations have been reported in the Karoo. Some of these involve physical accumulations of disarticulated skeletal elements from several individuals of the same taxon into a bonebed (e.g., Smith and Botha, 2005) and as such are not considered to be evidence of cohabitation. There are, however, several instances of aggregations of two or more behaviorally aligned or intertwined fully articulated skeletons in contact with each other, such as the Late Permian diapsid *Youngina* (Smith and Evans, 1995, 1996) and the milleretid *Milleropsis* (Watson, 1957; Gow, 1972), as well as for the Early Triassic procolophonoids *Procolophon* (deBraga, 2003) and *Owenetta kitchingorum* (Reisz and Laurin, 1991; Reisz and Scott, 2002) and the archosaur *Euparkeria* (Ewer, 1965). Monospecific aggregations are also fairly common in the Early Triassic cynodont *Thrinaxodon* (Brink, 1965; Damiani et al., 2003; Smith and Botha, 2005), and the authors found a previously unreported occurrence involving two individuals of the dicynodont *Lystrosaurus* in the collection of the Bernard Price Institute (BP/1/4276). A spectacular example, dubbed the Nine-Dragon Panel, involves nine fully articulated behaviorally aligned specimens of the Middle Triassic dicynodont *Parakannemeyeria*. This was excavated from the middle Triassic Kelemayi Formation of Xinjiang Province of China (Sun, 1989).

MATERIAL AND ASSOCIATED FAUNA

The material described (RC 845) is housed in the Rubidge Collection, Wellwood farm, Graaff Reinet, Eastern Cape Province, and was collected by B.J. Kitching on the farm Fairydale, Bethulie District, Free State Province (Fig. 1A). The material was originally in a dorsoventrally flattened, carbonate-rich concretion broken into three parts. The only portion of the skeleton visible when the fossil was studied in the collection was the partially prepared galesaurid skull and some postcranial elements exposed on the sides of the concretion. The procolophonoid remains were found only when preparation of the galesaurid skeleton was near completion.

Sediment surrounding the skeletons is a carbonate-rich, reddish-brown siltstone. Unfortunately, there is no information regarding the exact site and geological context of the find. The farm Fairydale, however, is a well known and productive fossil locality first discovered by James Kitching (see Kitching, 1977). At the time the fossil was collected, the farm Fairydale comprised two properties, Fairydale 193 and the adjoining property Donald 207. The fossiliferous exposures are in fact located on the farm Donald 207 (Fig. 1B); however, the fossils were accessioned under the farm name Fairydale, because this was where the main residence was situated. Many fossils from Fairydale are housed in the collection of the Bernard Price Institute, including an articulated skeleton of the cynodont *Thrinaxodon liorhinus*, many specimens of the dicynodont *Lystrosaurus*, the procolophonoids *Owenetta kitchingorum* and *Procolophon trigoniceps*, and therocephalians (Kitching, 1977; F. Abdala, personal observation, 2005). In addition, there are many unprepared fossil-bearing concretions. Similar fossil collections from Donald 207 are also housed in the National Museum, Bloemfontein, and the Iziko South African Museum, Cape Town.

SEDIMENTARY ENVIRONMENT

On the farm Donald 207 a total of 200 m of strata in the lower and middle part of the Early Triassic Katberg Formation are exposed and lie between 40 and 240 m above the Permian–Triassic boundary. The most extensive exposures of nodule-bearing red mudrock on Donald 207 are on the lower slopes of Swartberg Mountain (Fig. 1B) and constitute a roughly 60-m-thick succession of dark reddish brown (2.5 YR 3/6) and olive (5Y5/6) siltstone with numerous thin (<1.5 m) pale olive (5YR 6/3) tabular sandstone bodies (see Fig. 2).

The 6.5-m-thick tabular body of fine- to medium-grained sandstone that forms the base of the succession exposed on the farm has a distinctively irregular basal contact caused by numerous eroded runnels filled with lenses of reworked pedogenic carbonate peloids and mudrock clasts.

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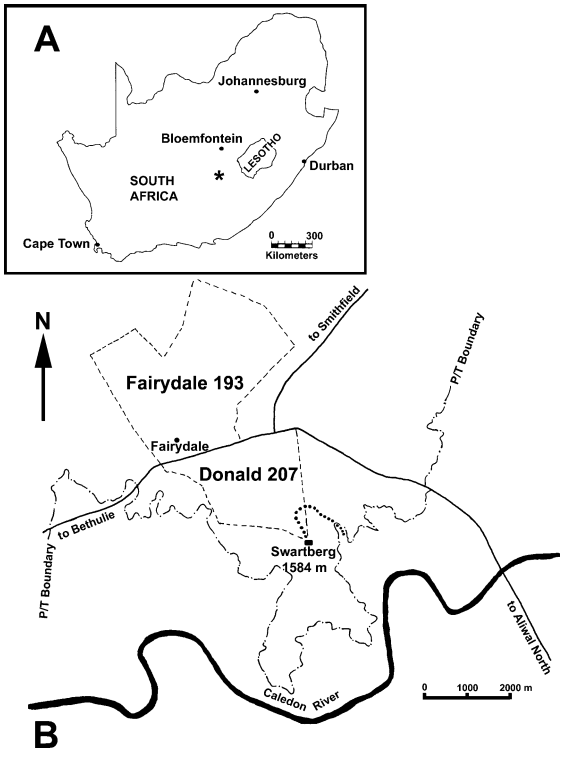


FIGURE 1—Locality map. (A) Asterisk indicates the Bethulie District in the Free State Province, where the farms Fairydale 193 and Donald 207 are found. (B) Boundaries of the two portions that make up the farm Fairydale. Dashed line is the outcrop of the Permian-Triassic boundary event bed. Dotted line is the path of the measured section in Figure 2.

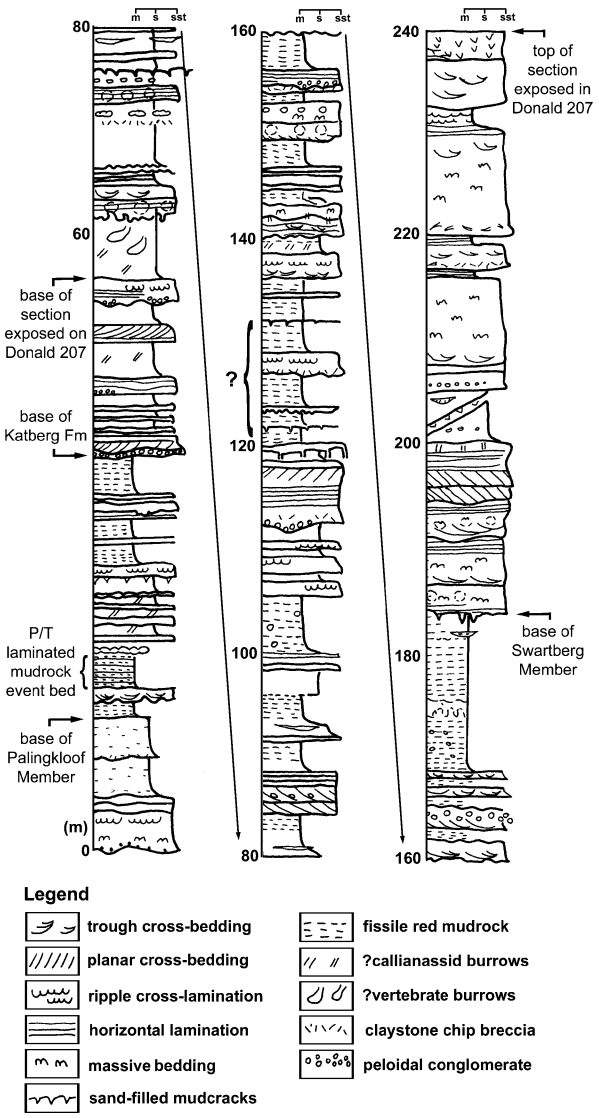


FIGURE 2—Sedimentological log of a section measured up from the Permian-Triassic boundary (Palingkloof Member) on the adjoining farm, through the entire exposure of Lower Triassic lower Katberg strata on the farm Donald 207, where the study specimen is most likely to have been found. The section ends in the middle Katberg (Swartberg member) on top of Swartberg Mountain (see Figure 1B). ? is used for levels where the fossil assemblage was most likely found.

The conglomerates grade upward into horizontally laminated, medium-scale trough cross-bedded and ripple cross-stratified sandstone. Distinctive horizons of spherical to oblate, dark brown calcareous concretions first appear in these sandstones. These are a well-documented early diagenetic feature of the Katberg Formation sandstones (Johnson, 1976). Recent studies interpret the depositional environment of the lower and middle Katberg Formation in a braided fluvial fan system prograding from the southern Gondwanide Mountains into a vast semiarid foreland basin (Smith, 1995; Ward et al., 2000). The uppermost ripple cross-laminated sandstone stringers form an undulating surface of sandstone ridges and siltstone-filled swales. These swale-fill siltstones are host to numerous medium to large *Lystrosaurus* skeletons found within brown weathering smooth-surfaced calcareous nodules. The fossil assemblage comprises articulated specimens, partially articulated and associated remains, as well as bonebeds of several disarticulated but otherwise undamaged *Lystrosaurus* remains displayed in a chaotic melange. These have been interpreted as drought accumulations in an arid floodplain setting (Smith and Botha, 2005).

The lowermost sandstone is interpreted as a low-sinuosity channel subject to highly fluctuating discharge and, at times, emergent midchannel bars. The ancient channel has eroded into a semiconsolidated floodplain soil, reworking the paleocaliche and clay-rich peds into a lag conglomerate. The margins of this channel appear to have been a preferential site for the preservation of *Lystrosaurus* skeletons. The succeeding sequence has fewer large channels and is dominated by sand-rich crevasse-splay sequences and silt-dominated, unconfined flood deposits. This is the sequence in which most of the pedogenically modified red mudrocks are found, and it is believed that the fossil material described herein (RC 845) was collected from this silt-dominated semiarid floodplain alluvium.

DESCRIPTION

The specimens under study are exceptionally well preserved and without any trace of preburial weathering. Two animals in the assemblage, *Galesaurus planiceps* and one of the *Owenetta kitchingorum* individuals, present the skull articulated to the complete vertebral column. These individuals possess many ribs articulated to the vertebrae and girdles with partial limbs located in normal anatomical position (Fig. 3). The skeletons are aligned side by side with their dorsal surfaces facing away from each other. The procolophonoid skeleton from the tip of the snout to the last sacral vertebra is 116 mm long and extends from the pelvic region to the midtrunk region of the galesaurid (Fig. 3A). A fragment of the posterior roof of the skull of a second specimen of *Owenetta kitchingorum* is also present. Parts of the limbs of the articulated animals and the complete body of the third specimen were originally outside the concretion in which the skeletons were preserved. Therefore, it is more likely that this nodule had already weathered out of the rock and was loose and broken when it was collected.

The *Galesaurus* skeleton is approximately 308 mm long from the tip of the snout to the fifth caudal vertebra. The skull and lower jaw are articulated, with such delicate and easily dislodged bones as the quadrates, stapes, and hyoids still *in situ* (Fig 3A). The vertebral column

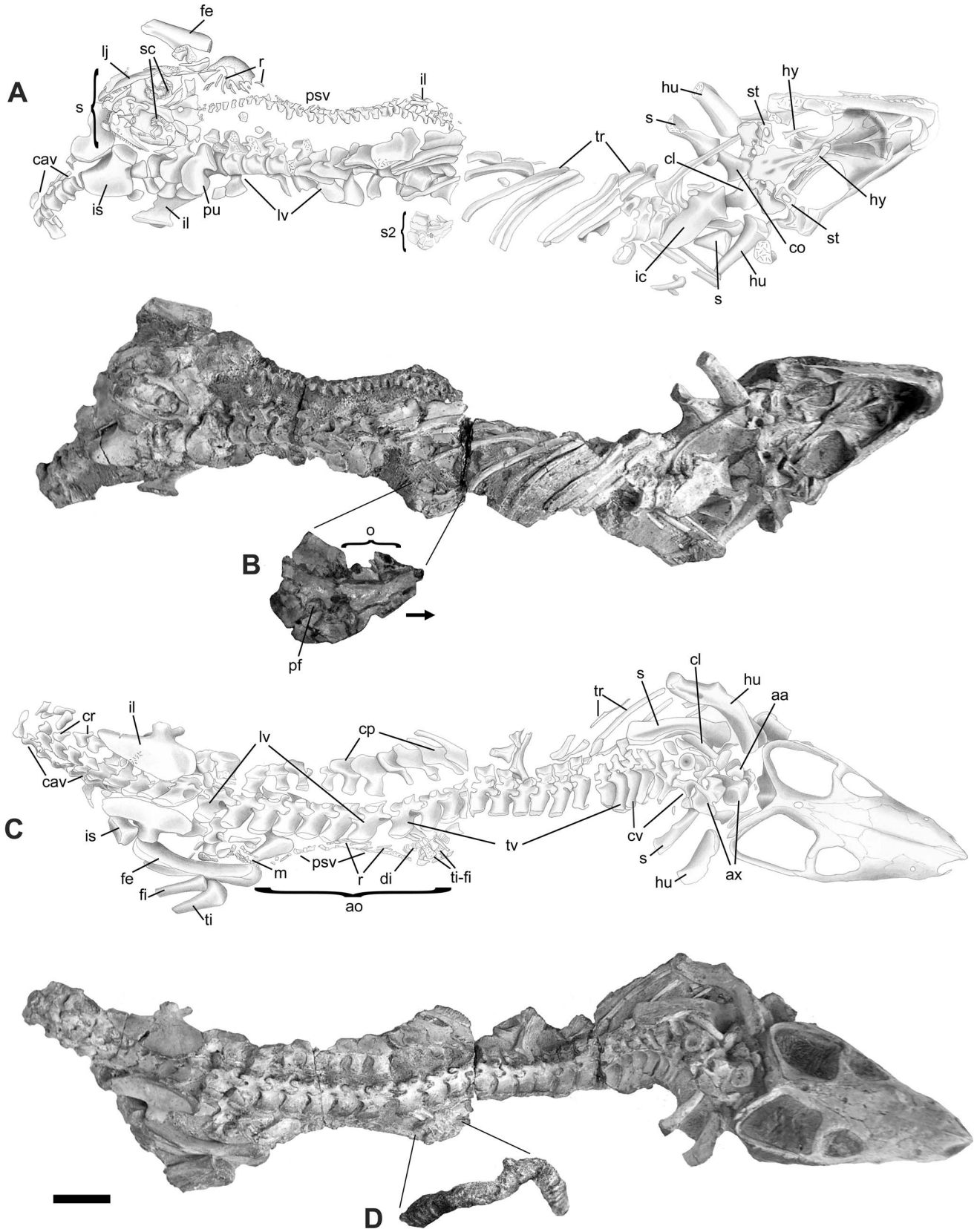


FIGURE 3—Photograph and interpretive drawing of RC 845, including a skeleton of the cynodont *Galesaurus planiceps*, two individuals of the procolophonoid *Owenetta kitchingorum*, and a diplopod millipede. (A) *G. planiceps* in ventral view and both *O. kitchingorum* individuals in dorsal view. (B) Close-up of the juvenile *O. kitchingorum* cranium. (C) *G. planiceps* in dorsal view, and portion of the adult *O. kitchingorum* in ventral view. (D) Close-up of the diplopod millipede that lies on the tibia and fibula of the adult *O. kitchingorum*. Abbreviations: aa, neural arch of the atlas; ao, adult *O. kitchingorum* remains; ax, axis; c, cranium of the adult *O. kitchingorum;* c2, cranium of the juvenile *O. kitchingorum* (arrow indicates anterior direction); cav, caudal vertebrae; cl, clavicle; co, coracoid; cp, costal plates; cr, caudal ribs; cv, cervical vertebrae; fe, femur; fi, fibula; hu, humerus; hy, hyoid; ic, interclavicle; il, ilium; is, ischium; lv, lumbar vertebrae; lj, lower jaw; m, procolophonoid manus; o, orbit; pf, pineal foramen; psv, presacral vertebrae; pu, pubis; r, ribs; s, scapula; sc, sclerotic bones; st, stapes; ti, tibia; tr, thoracic ribs; tv, thoracic vertebrae. Scale bar for (A) and (C) represents 20 mm.

comprises 26 elements, including cervical, dorsal, sacral, and five proximal caudal vertebrae, with many articulated ribs (including those from the caudal vertebrae; Fig. 3C). The left scapular girdle and interclavicle are complete, and the clavicle is in contact with the acromion. The left humerus is almost complete, whereas the right scapula and humerus are partially preserved. The right coracoid is also present. Both pelvic girdles are preserved, and the ilia and the right ischium are in place, while the left ischium and pubes are displaced slightly anteriorly with one pubis covering the other (Fig. 3A).

In the procolophonoid, the skull and lower jaws are also articulated, but the right postorbital, supratemporal, and jugal are slightly displaced dorsally with respect to the remaining skull roof, and the facial bones are partially disarticulated (Fig. 3A). Fragile and rarely preserved sclerotic bones are present in both orbits. The vertebral column is represented by 28 elements with several articulated ribs. The left clavicle, scapula, and anterior coracoid and the left portion of the interclavicle are visible. Most of the left forelimb is preserved, including the minute bones of the right manus. The right ilium is the only element preserved from the pelvic girdle, and the femur, tibia, and fibula appear to be articulated. A cylindrical, segmented trunk of a diplopod, with no preserved appendages, is preserved over the hind limb (Figs. 3C and 3D).

The second procolophonoid specimen is represented by the posterior portion of the skull roof, including frontals, parietals, and supratemporals as visible elements (Fig. 3B). The margin of the pineal foramen on the left parietal is also evident. This specimen is markedly smaller than the articulated procolophonoid and represents a juvenile.

DISCUSSION

The high degree of articulation of the bones (taphonomic class B of Smith, R.M.H., 1993) of *Galesaurus planiceps* and *Owenetta kitchingorum* and the preservation of delicate skeletal elements in articulation suggest that the animals died in a place protected from both biological (e.g., scavengers, trampling) and physical (e.g., flooding, wind, rainsplash) agents of bone dispersal. They were also permanently buried soon after death (Behrensmeyer, 1991; Smith, R.M.H., 1993; Lyman, 1994).

The fossils described here can be interpreted as drowned carcasses of the animals that were washed into a narrow erosion gully or a shrinkage crack in the floodplain alluvium during an overbank flood and presumably buried in the same event. Thus the bodies avoided weathering and disarticulation by other bone-modifying agents. Unfortunately, the sedimentological context that would provide key evidence to solve the circumstance of the burial (Voorhies, 1975) is not known.

Alternative interpretations to explain the taphonomic style and biological association of the fossils here presented imply behavior-driven activity, such as an accumulation of procolophonoid remains through predation by the galesaurid. Galesaurid cynodonts are interpreted as insectivorous (Kemp, 2005) or insectivorous and carnivorous (Hopson, 1969; Kemp, 1982). The postcanines of this cynodont are tiny bladelike teeth with the main cusp strongly curved backward and a posterior accessory cusp (Kemp, 2005). The lack of occlusion between postcanines in this cynodont (Crompton, 1972) implies that they did not extensively process the food in the oral cavity (Crompton, 1985). Therefore, they probably caught, cut, and swallowed the entire prey (i.e., insects or tiny vertebrates) in a way similar to that of most of the extant carnivorous lizards (Smith, K.K., 1993). The backward-curved main cusp of the postcanines is most likely for preventing the escape of small prey from the oral cavity. This is the role of the strongly recurved teeth of snakes (Edmund, 1969) and of the postcanines with backward-curved cusps present in several pinniped carnivores, one of the few groups of living mammals with this kind of cusp orientation (Hilson, 1990; see also Ji et al., 2006). The body length of larger specimens of *Owenetta kitchingorum* is about one half to two-thirds (considering the missing tail) the body length of *Galesaurus planiceps*, which is regarded as being excessively large for a prey that would have to be caught and swallowed entirely by the galesaurid. In addition to the relative sizes of predator and prey, the fully articulated skeleton, especially the vertebral column and ribs, and the absence of any kind of cutting or puncture marks on the procolophonoid, also contribute to exclude the possibility of predator lair as an explanation for this rare association. We should mention, however, that predation by *Galesaurus* on tiny young *Owenetta* represents a highly plausible potential interaction. The partial skull of the smaller procolophonoid individual preserved in the assemblage might conceivably represent an indication of predatory activity by the cynodont. Behavior of this kind has been described for the tuatara, which shares burrows with the fairy prions and preys on the chicks and eggs of this bird (Walls, 1978; Markwell, 1998).

Another behavior-driven explanation for this association is that these animals shared the same shelter in life. There is growing evidence of underground burrowing behavior in several tetrapods at various time intervals in the Karoo succession. These include the Late Permian dicynodont *Diictodon* (Smith, 1987) and the cynodonts *Thrinaxodon* (Damiani et al., 2003) and *Trirachodon* (Groenewald et al., 2001) from the Early Triassic, whose complete skeletons were found within burrow casts. Fossilized remains of *Lystrosaurus* and *Procolophon* were also found in at least four different burrow types from the *Lystrosaurus* Assemblage Zone (Groenewald, 1991). Anatomical studies also show skeletal adaptations for burrowing in the diminutive dicynodont *Cistecephalus* (Cluver, 1978) and in *Procolophon* (deBraga, 2003). In addition, monospecific aggregations of juvenile tetrapods with intertwined and side-by-side disposition of the individuals have also been interpreted as evidence of ''confined cavities beneath fallen logs or underground burrow'' environments (Smith and Evans, 1996, p. 301). Thus, tetrapod burrowing was widespread in the Late Permian to Early Triassic semiarid environments of the Karoo Basin, involving several groups of amniotes of varying body mass responsible for a variety of burrow geometries.

Fossorial and semifossorial behavior is common in modern tetrapods living in semiarid ecosystems, and burrowing is generally accepted as a primary adaptation to withstand extreme meteorological and climatic conditions (Kinlaw, 1999). Avoidance of predation of infant broods, hibernation, and food storage are also interpreted as selective advantages of burrowing beyond the simple need to survive extremes of temperature and humidity (Boucot, 1990). A number of living vertebrate species in semiarid environments are known to share shelters with other species. Several species of reptiles and amphibians hibernate together (Gregory, 1982). The kangaroo rat, the gopher tortoise, and the aardvark (antbear) share their burrows with several reptiles, amphibians, and mammals and with numerous invertebrates (Kinlaw, 1999). The host in these examples does not necessarily benefit from the guests, but the relationship is not harmful, representing commensalism within burrows or mutual tolerance between the involved species (Vaughan, 1961; Kinlaw, 1999). In other cases, the guest may have a predatory relationship with the host; as noted above, the tuatara preys on the eggs and chickens of the fairy prion (Walls, 1978; Markwell, 1998), and gopher snakes are known to prey on the pocket gophers whose burrows they share (Vaughan, 1961). Other possible interactions in burrows are known. Ground squirrels compete for possession of the burrow system with the pocket gophers who construct the burrows (Vaughan, 1961), and the tuatara interferes in the nesting chambers of fairy prions, excluding breeding prions or causing nest desertion (Walls, 1978).

Noteworthy examples of fossil vertebrate burrows containing skeletons of more than one taxon are known from the Early Miocene of Nebraska, United States, where a curled skeleton of the carnivore *Zodiolestes* was found inside a daimonelix burrow constructed by the beaver *Palaeocastor* (Martin and Bennett, 1977; Meyer, 1999). Burrows containing articulated skeletons of at least four species of extinct carnivores, plus a few herbivorous bone fragments, are also known from this North American region (Hunt et al., 1983).

A specimen of *Thrinaxodon liorhinus*, a contemporaneous basal cynodont with skeletal morphology and size similar to those of *Galesaurus planiceps*, has been described from inside an interpreted burrow cast in

the underlying Palingkloof Member on the farm Elim 623, some 15 km northeast of Donald 207 (Damiani et al., 2003). In addition, two skeletons of *Owenetta kitchingorum* were found in a head-to-tail position at Donovan's Kop some 20 km west-southwest of Fairydale from the same stratigraphic interval as the study specimen (Reisz and Laurin, 1991; Reisz and Scott, 2002). This head-to-tail arrangement is common aestivation behavior in modern lizards (deBraga, 2003).

Living diplopods avoid light and usually live beneath fallen leaves, stones, bark, and logs, and many are cave dwellers (Ruppert et al., 2004). Scavenging habits were previously suggested for similar diplopods found in the *Owenetta kitchingorum* aggregation from Donovan's Kop (Reisz and Laurin, 1991). These millipedes, however, are notorious for being predominantly detritivorous and occasionally herbivorous (Labandeira, 1999; Ruppert et al., 2004).

CONCLUSIONS

A shelter-sharing interpretation for the multitaxa aggregation of cynodont, procolophonoid, and diplopod in the Early Triassic Katberg Formation is favored, and it is proposed that the individuals were most likely preserved in a confined cavity or in a burrow. This interpretation is based on the high degree of articulation, outstanding state of preservation of delicate skeletal elements, and side-by-side position of the vertebrate skeletons. The presence of a light-avoiding arthropod in the fossil association also supports the underground-shelter hypothesis. In addition, the fact that representatives from both cynodonts and procolophonoids are linked with burrowing behavior reinforces the contention that this is a behavior-driven association. The favored interpretation of this rare fossil assemblage indicates that this represents the earliest recorded example in the fossil record of a behavior-driven association involving two different groups of terrestrial tetrapods.

ACKNOWLEDGMENTS

The University of the Witwatersrand, National Research Foundation (NRF), and the Palaeontological Scientific Trust (PAST) provided financial support for this research. We thank M. Raath, S. Kaal, and R. Rubidge for access to material, and the latter also for graciously allowing further preparation of RC 845, skilfully conducted by C. Dube at the Bernard Price Institute, University of the Witwatersrand. H. M. Wilson provided information about diplopods. L. Backwell, J. Neveling, M. Raath, and R. Rogers made comments and suggestions on early versions of the manuscript. Two anonymous reviewers and S. Hasiotis provided comments and suggestions that improved the final version of this paper.

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ACCEPTED MAY 11, 2006

