Migration of Triassic tetrapods to Antarctica

J. W. Collinson[1] and W. R. Hammer[2]

[1]Byrd Polar Research Center and School of Earth Sciences, Ohio State University, Columbus, OH. 43210 USA (**jwcollinson@comcast.net**)
[2]Augustana College, Rock Island, IL. 61201 (glhammer@augustana.edu)

Summary The earliest known tetrapods in Antarctica occur in fluvial deposits just above the Permian-Triassic boundary in the central Transantarctic Mountains. These fossils belong to the *Lystrosaurus* Zone fauna that is best known from the Karoo basin in South Africa. The Antarctic fauna is less diverse because of fewer collecting opportunities and a higher paleolatitude (65° vs. 41°). Many species are in common. *Lystrosaurus maccaigi*, which is found near the base of the Triassic in Antarctica, has been reported only from the Upper Permian in the Karoo. Two other species of *Lystrosaurus* in Antarctica are also likely to have originated in the Permian. We hypothesize that tetrapods expanded their range into higher latitudes during global warming at the Permian-Triassic boundary. The migration route of tetrapods into Antarctica was most likely along the foreland basin that stretched from South Africa to the central Transantarctic Mountains along the Panthalassan margin of Gondwana.

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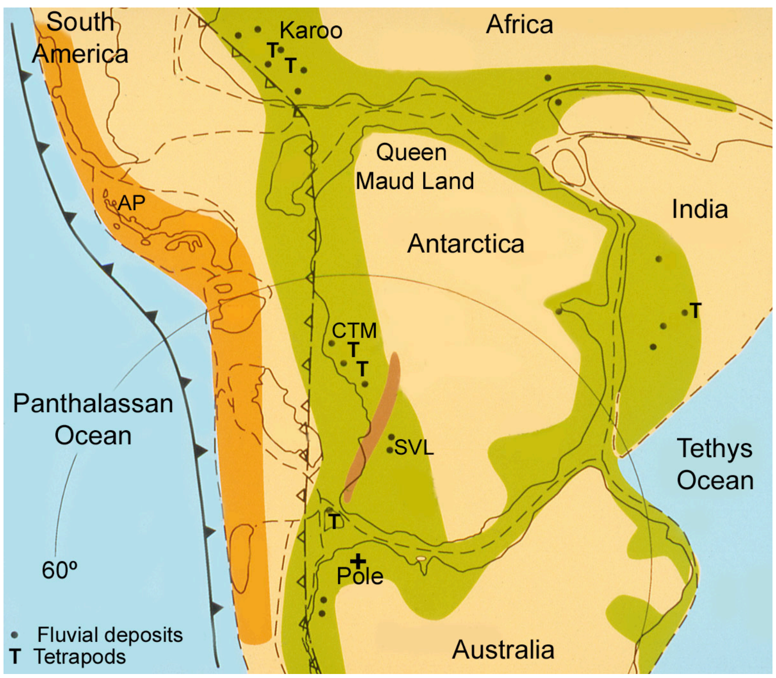

Figure 1. Early Triassic map of southern Gondwana. The green areas represent possible basin areas. The central Transantarctic (CTM) and the Karoo occupied a foreland basin behind a fold-thrust belt and volcanic arc along the Panthalassan Ocean margin.

Introduction

Fossil evidence suggests that tetrapods inhabited Antarctica during much of the Mesozoic and the early part of the Cenozoic eras. Tetrapod fossils are known from the Lower Triassic (Colbert, 1982), Middle Triassic (Hammer et al., 1990), and Lower Jurassic of the central Transantarctic Mountains (Hammer and Hickerson., 1994), from the Upper Triassic of southern Victoria Land (Hammer et al., 2004), and from the Cretaceous (Olivero et al., 1991), and Neogene of the Antarctic Peninsula region (Marenssi et al., 1994) (Fig 1). Plate tectonic reconstructions place Antarctica at high latitudes since the Early Permian (Grunow, 1999). From the perspective of today, it is difficult to imagine how tetrapods, most of them ectotherms, could have survived a polar climate. They did not survive the onset of colder conditions and the glaciation of Antarctica 35 million years ago. However, there is still the question as to when they first migrated into Antarctica.

In Late Permian, long after Early Permian Gondwanan glaciation, tetrapod faunas occupied the Karoo basin in South Africa (Rubidge, 2005). Greenhouse warming in the Late Permian resulted in extensive *Glossopteris* forests in Antarctica (Taylor et al., 2000). It is possible that tetrapods may have migrated into Antarctica at the same time that they occupied southern Africa, but no identifiable Permian tetrapods have been found. Larsson (1995) reported bone fragments in sandstone of possible Permian age in Queen Maud Land. This part of Antarctic would have been close to southern Africa in Gondwana reconstructions (Fig.1). If tetrapods found their way into Antarctica in the Late Permian, widespread coal measure swamp environments would not have been conducive to bone preservation. In the Lower Triassic of Antarctica fossils are abundant in some stratigraphic sections, but absent in others, although the facies appear to be the same. It is possible that Permian tetrapods will eventually be found in Antarctica, but until then the most likely hypothesis is that sudden warming near the Permian-Triassic boundary resulted in the expansion of tetrapod habitats poleward (Collinson et al., 2006).

Antarctic and Karoo tetrapods

With the discovery of reptile skeletons in the Shackleton Glacier area in 1970, it became apparent that Antarctic tetrapods were closely related to those of South Africa (Kitching et al., 1972). The Karoo and Antarctic faunas share several species in common. Many more taxa are represented in South Africa, but the Antarctic faunal list is probably longer than has been described, because not all the collected material has been prepared. Also, collecting efforts have been much more extensive in the Karoo. But, the South African fauna may have been more diverse, because the Karoo basin had a more temperate climate at a lower paleolatitude of about 41º (Ward et al., 2005, supplement). The central Transantarctic Mountains were located at a polar paleolatitude of about 65º (Grunow, 1999).

Using carbon isotopes and magnetostratigraphy for physical correlation, Ward et al. (2005) constructed a detailed biostratigraphic record of tetrapod occurrences from a few well-exposed stratigraphic sections across the Karoo basin. They demonstrated that the range of *Lystrosaurus*, a genus associated with the Early Triassic *Lystrosaurus* Zone, extended down into the latest Permian *Dicynodon* Zone. Several genera crossed the Permian-Triassic boundary. New genera typical of the *Lystrosaurus* Zone mostly first occur 10 m to 30 m above the boundary. Based on statistical analyses, Ward et al. (2005) extended the range of some of these genera to the boundary or into the Permian. Marshall (2005) reanalyzed their statistics and came up with slightly different ranges, but both studies agreed that most of the common Triassic tetrapods, except for a couple of species of *Lystrosaurus*, first occur 10 m to 30 m above the Permian-Triassic boundary.

Physical means of detailed correlation are not yet possible in the Antarctic sequence. Magnetostratigraphy has not proved to be useful because heat from Jurassic diabase intrusions has completely destroyed the original magnetic signatures. A carbon isotope profile has been established in the Graphite Peak section (Krull and Retallack, 2000), but has not yet been applied to other sections. By their very nature, fluvial sequences are difficult to correlate because of frequent hiatuses that result from stream migration. However, a possible datum horizon is the extinction level of the *Glossopteris* flora noted by Retallack et al. (1996). This may be at or just below the Permian-Triassic boundary. At some localities this is the contact where the Buckley coal measures are overlain by the sandstone and green-gray mudstone of the Fremouw Formation. In the Shackleton Glacier area this horizon lies within the lower part of the Fremouw Formation (Collinson et al., 2006). Most of the identifiable tetrapod fossils have been found in the stratigraphic sections shown in figure 2. Assuming that this datum horizon is approximately a time line, all the first occurrences of common Antarctic tetrapods first occur 7 m to 15 m above this datum. The large tetrapod, *L. maccaigi*, which occurs near the base of the Shenk Peak section, has been found only in the latest Permian in South Africa. It is possible that the other two Antarctic *Lystrosaurus* genera, *L. murrayi* and *L. curvatus*, may also have originated in the latest Permian.

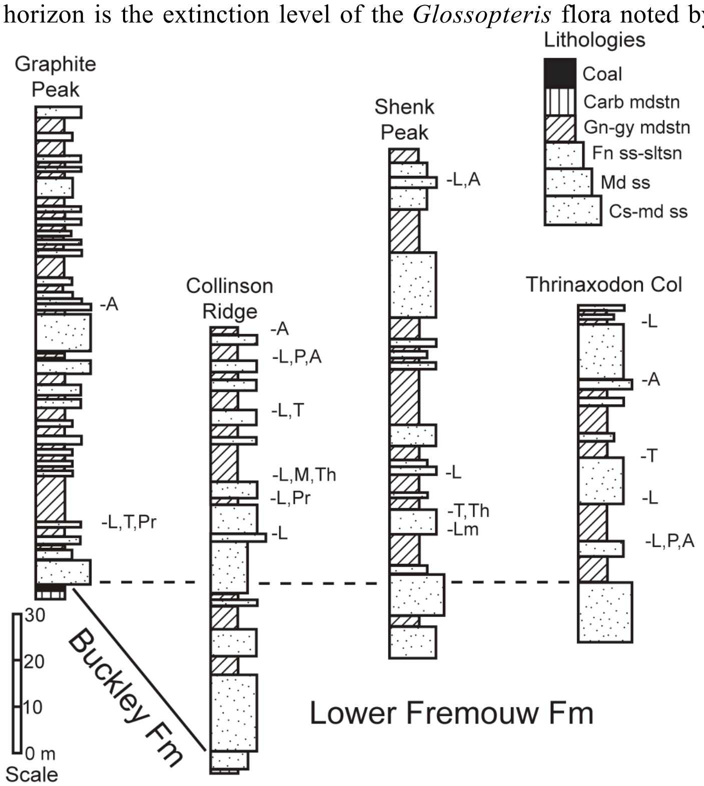

Figure 2. Stratigraphic sections with abundant tetrapod fossils. Graphite Peak is near the head of the Beardmore glacier and the other sections are in the Cumulus Hill near the Shackleton Glacier. Dashed line represents datum horizon at last occurrence of coal, fossil wood, or carbonaceous rock. A=amphibian, L=*Lystrosaurus* sp., Lm=*Lystrosaurus maccaigi*, M=*Myosaurus*, T=*Thrinaxodon*, Th=thecodont, P=*Procolophon*, Pr=*Prolacerta*.

Migration

In spite of the differences in latitude, the Lower Triassic sequences in the Karoo and central Transantarctic Mountains are quite similar. Both sequences are composed of low sinuosity fluvial sandstones interbedded with greenish-gray or reddish-brown floodplain deposits. This is not the case below the Permian-Triassic boundary; although both sequences are carbonaceous, fluvial styles are different. The entire Upper Permian in Antarctica consists of coal measures. The environment for coal deposition had apparently shifted poleward as the southern Africa part of Gondwana moved into drier mid-latitudes. In the Karoo basin, meandering stream deposition was replaced at the Permian-Triassic boundary by low-sinuosity braided stream deposition. In Antarctica low-sinuosity braided stream deposition continued across the boundary, but coal deposition ceased.

Lystrosaurus, an herbivore, may have survived the Permian-Triassic boundary extinctions because it may have subsisted on a type of vegetation that did not become extinct with *Glossopteris*. Herbivores that depended on *Glossopteris* plants would not have fared so well. If the vegetation across the boundary in the Karoo was similar to that of the Early Triassic of Antarctica, the *Lystrosaurus* Zone fauna would have been able to migrate to high latitudes as global warming shifted the temperate belt poleward.

The migration route of tetrapods into Antarctica was most likely along the foreland basin that stretched from South Africa to the central Transantarctic Mountains along the Panthalassan margin of Gondwana (Veevers et al., 1994) (Fig. 1). Paleoclimate models suggest that Late Permian climate was comparatively mild in land areas bordering the Gondwanan continental margin, even at high latitudes, owing to warm ocean temperatures (Kiehl and Shields, 2005).

Conclusions

Global warming, one of the causes of the mass extinctions at the Permian-Triassic boundary, shifted warm temperate climatic belts poleward, permitting the expansion of mid-latitude Karoo tetrapod faunas into the polar region of Antarctica. This could have happened in the latest Permian, but tetrapod fossils have been found in Antarctica only above the Permian-Triassic boundary. Although a similar fauna managed to live across a broad latitudinal belt, Karoo faunas would be expected to have been more diverse. This is suggested by fewer taxa in Antarctica, but data are inadequate to substantiate this. This poleward expansion of tetrapods managed to exist throughout the Mesozoic and into the early Cenozoic until the climate cooled and ice conditions prevailed in Antarctica.

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