



Nycteroleter affinities of a Permian parareptile from the South African Karoo Basin

JUAN CARLOS CISNEROS and LINDA AKIKO TSUJI

The Middle Permian *Tapinocephalus* Assemblage Zone in South Africa has produced a rich record of tetrapods dominated by dinocephalian therapsids and pareiasaurid parareptiles. In this study we reassess the affinities of a specimen from this horizon previously identified as a procolophonoid and provide evidence that it is instead referable to a nycteroleter parareptile, an identification that is more compatible with the age of this fossil. Accordingly, this specimen represents the first record of a nycteroleter in Gondwana.

Introduction

Nycteroleters (sensu Müller and Tsuji 2007) are small-to medium sized parareptiles, being notable for displaying a suite of characters that combine procolophonoid and pareiasaurid features. They are recorded primarily in the upper Kazanian and early Tatarian (Permian: Guadalupian) of the Russian Cis-Urals (Ivakhnenko et al. 1997). A nycteroleter from the Chickasha Formation in Oklahoma, USA referred to the genus *Macroleter* (Tsuji 2006), the nycteroleters are poorly known and although a recent analysis confirms their monophyly (Müller and Tsuji 2007), little detailed morphological information has been published.

Institutional abbreviations.—NM, National Museum, Bloemfontein, South Africa; PIN, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Other abbreviations.—AZ, Assemblage Zone; FAD, First Appearance Datum.

Material and geologic setting

A postcranium embedded in a green sandstone NM QR3061 (Fig. 1), comprising an articulated, partial vertebral column with nine presacrals, thirteen proximal caudals; and other poorly preserved elements including partial ribs, a probable pubis, a partial femur, two (?) partial tibiae and a fibula. Collected by Patrick Bender at Farm Blaaukrantz (Bloukrantz) in Leeu Gamka, Prince Albert District, Western Cape Province (32°58'30''S; 22°02'10''E) from low to middle *Tapinocephalus* AZ, Guadalupian (Gow and Rubidge 1997; Kitching 1977). Material studied for comparative purposes includes *Macroleter poezicus*

(PIN 4543/3) from the Mezen River Basin, Russia (late Kazanian to early Tatarian), and *Rhipaeosaurus tricuspis* (PIN 164/2), from near Belebey, Bashkortostan, Russia (latest Kazanian) (Golubev 2005).

Comparisons and discussion

The description of NM QR3061 provided by Gow and Rubidge (1997) is accurate and needs no additions or amendments. Our comparisons are focused on the dorsal vertebrae, which are the best preserved and most diagnostic elements of this specimen. We consider certain features of NM QR3061 to be incompatible with its current identification as a procolophonoid; the referral of the specimen to Parareptilia, however, is indeed correct. The presacral vertebrae evince swollen neural arches, a condition that is characteristic of most members of this group. Other Palaeozoic tetrapods such as seymouriamorphs, diadectids and captorhinids also possess swollen neural arches; however, the presacral vertebrae of these groups are anteroposteriorly compressed in comparison with those of parareptiles. In addition, the pleurocentra of captorhinids are not constricted ventrally to accommodate large intercentra, a condition that differs from NM QR3061 (Gow and Rubidge 1997).

Despite a positive identification as a parareptile, the specimen under study cannot be referred to a pareiasaurid, a millerettid or to *Eunotosaurus*; the parareptiles present in the *Tapinocephalus* AZ (Gow and Rubidge 1997). Millerettids are much smaller than NM QR3061, and feature anteroposteriorly elongated vertebrae with short zygapophyses. The enigmatic *Eunotosaurus* is comparable in size with NM QR3061; however, the vertebrae of this taxon are even more anteroposteriorly elongated than in the Millerettidae. In addition, the ribs of NM QR3061 are slender (Gow and Rubidge 1997) in contrast to the plate-like ribs of *Eunotosaurus*. The well-ossified condition of the specimen indicates a mature developmental stage that precludes its referral to the much larger pareiasaurids. The only pareiasaurid that is compatible in size to NM QR3061 is *Pumiliopareia pricei*. This taxon, however, occurs in the Upper Permian *Cistecephalus* AZ of South Africa, thus being separated from NM QR3061 by a considerable time interval. Pareiasaurid vertebrae are more anteroposteriorly compressed and feature the presence of laterally excavated pleurocentra (Boonstra 1934; Jalil and Janvier 2005), in contrast with NM QR3061. Furthermore, NM QR3061 features notochordal pleurocentra, a feature not present in pareiasaurids (Gow and Rubidge 1997).

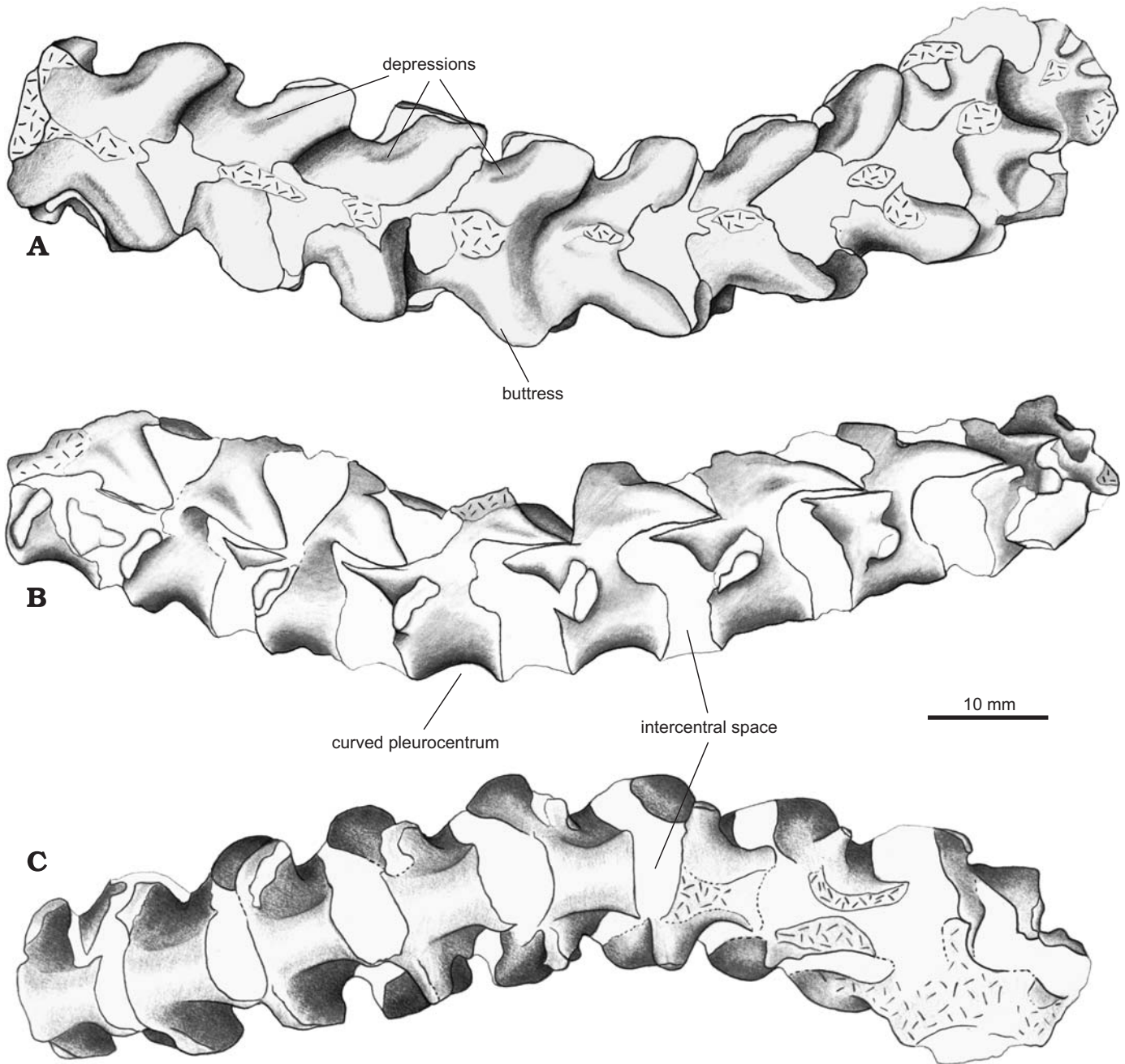


Fig. 1. Parareptilian specimen (NM QR3061) from the *Tapinocephalus* AZ (Permian, Guadalupian) of the South African Karoo. Presacral vertebrae in dorsal (A), lateral (B) and ventral (C) views.

The only other parareptilian group recorded in the Karoo Basin is the Procolophonoidea, making it a natural candidate for comparisons with NM QR3061. Permian procolophonoids (e.g., the owenettids *Owenetta rubidgei*, *Barasaurus besairiei*), however, are quite small and gracile forms. NM QR3061 is comparable in size with large specimens of the Early Triassic *Procolophon trigoniceps*, but the two are separated by an extremely long time interval. NM QR3061 can be distinguished from the procolophonoids due to the presence, in the latter, of laterally pinched pleurocentra that possess a ventral ridge extending longitudinally (personal observation by JCC). The owenettid procolophonoids

also exhibit much shorter zygapophyses than those of the specimen under study, resulting in the silhouette of their vertebrae appearing much more rectangular in dorsal view (Reisz and Scott 2002: fig. 1). NM QR3061 shares with these taxa the presence of a butress along the dorsal surface of the postzygapophyses. In the specimen under study, however, this structure is more developed and a prominent anterior depression is evident (Fig. 1A). This depression is not visible in the Permian procolophonoids. On this basis, we discard procolophonoid affinities for NM QR3061.

As the specimen must be a parareptile, and cannot be referred to any of those taxa discussed above, very few options for

assignment remain, none of which are Gondwanan. No comparisons are possible with the enigmatic lanthanosuchoids from the Lower–Middle Permian of USA and Russia (sensu deBraga and Reisz 1996) because the postcranium of these forms is not known. The parareptile *Nyctiphruretus acudens* from the Middle Permian of Russia features vertebrae similar to those of procolophonoids in having laterally pinched pleurocentra, and this taxon is considerably smaller than NM QR3061. The bolosaurids, a group present in the Lower and Middle Permian of North America, Europe and China (Li and Cheng 1995; Reisz et al. 2007), are also much smaller and possess considerably shorter zygapophyses than NM QR3061 (Berman et al. 2000), and so can also be excluded.

The only parareptiles that are comparable to the Karoo specimen are the poorly known nycteroleters from the Russian Cis-Urals. The clade includes six genera, and with the exception of the small *Nycteroleter*, all are compatible in size with NM QR3061. The group is mainly known from cranial remains, but postcranium has been found for *Rhipaeosaurus tricuspidens* (Efremov 1940; Chudinov 1957), *Bashkyroleter bashkyricus* (Efremov 1940; Chudinov 1957), *Emeroleter levis* (currently undescribed) and *Macroleter poezicus* (Fig. 2). The vertebrae of NM QR3061 are almost identical in appearance to those of these taxa, sharing a number of characters. The vertebrae of *Rhipaeosaurus* and *Macroleter* are anteroposteriorly elongated to an extent equivalent to those of NM QR3061 (i.e., more than in pareiasaurids but less than in millerettids). The pleurocentra of these genera are “beveled” in lateral view, due to the presence of large intercentra (Fig. 1B, C), a character displayed by NM

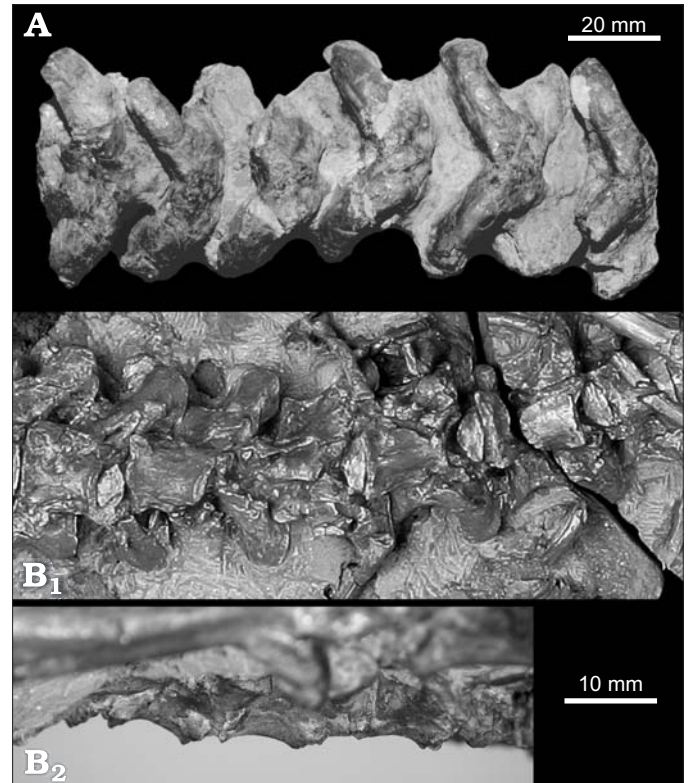


Fig. 2. Nycteroleter parareptile vertebrae. A. *Rhipaeosaurus tricuspidens* Efremov, 1940; PIN 164/2, presacral vertebrae in dorsal view. B. *Macroleter poezicus* Tverdokhlebova and Ivakhnenko, 1984; PIN 4543/3, presacral vertebrae in ventral (B₁) and ventrolateral (B₂) views.

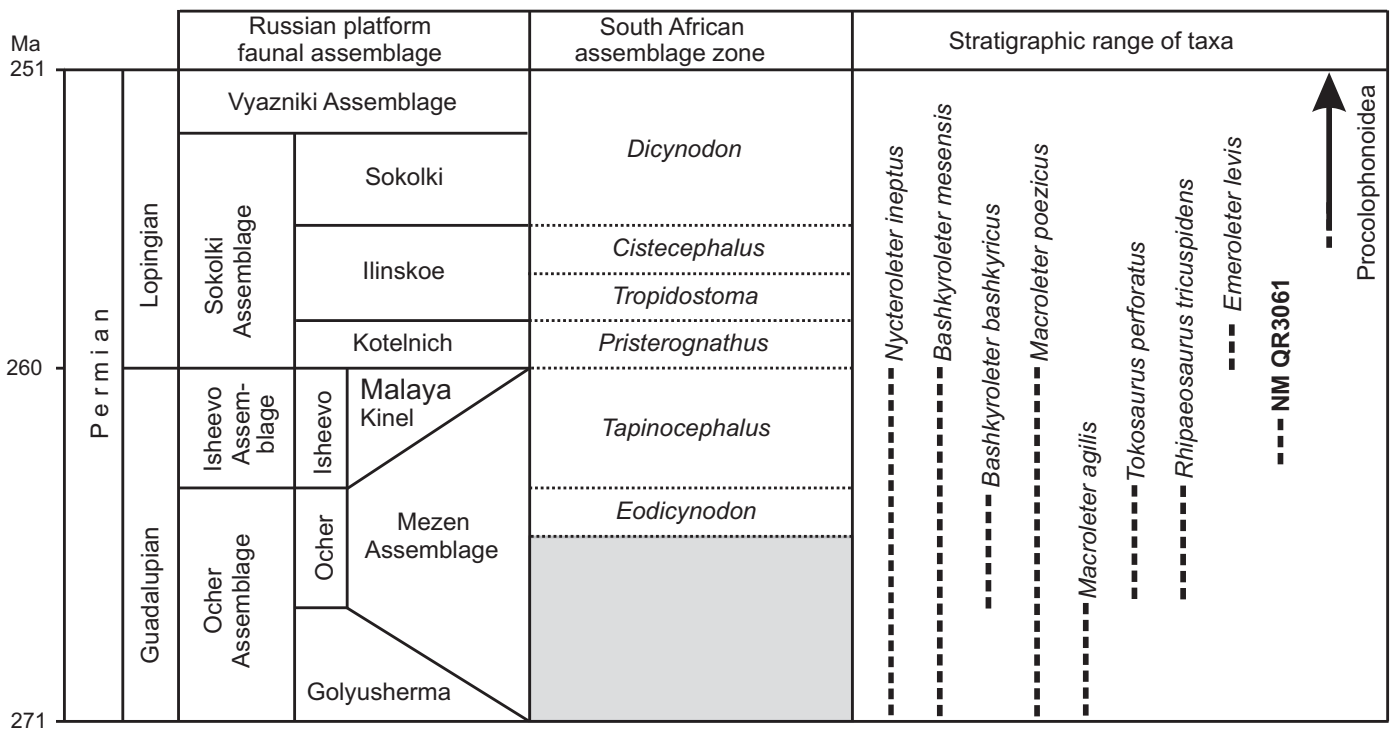


Fig. 3. Correlation table for the Russian Platform and the South African Karoo Basin showing the maximum stratigraphic ranges of nycteroleters and the Permian record of Procolophonoidea. Compiled from Ivakhnenko et al. (1997), Reisz and Laurin (2002), Smith and Keyser (1995b), Golubev (2005) and Lucas (2005). Dates after Gradstein et al. (2005).

QR3061 (Gow and Rubidge 1997). The ventral margin of the pleurocentra in *Rhipaeosaurus*, *Macroleter* and NM QR3061 are smoothly curved (Fig. 1B), lacking the distinct ventral ridge present in procolophonoids and pareiasaurids (Figs. 1, 2). A high postzygapophyseal buttress (Figs. 1, 2) is present in these taxa and also in NM QR3061. In nycteroleters the buttress is bordered anteriorly by a prominent depression or sulcus (Reisz and Laurin 2001), a character displayed by NM QR3061 (Fig. 1, also portrayed by Gow and Rubidge 1997: fig. 1B). The postzygapophyses of nycteroleters project far laterally from the vertebral body, bearing the dorsal buttress for their entire length. Among Permian parareptiles, long postzygapophyses that bear a buttress limited by a prominent anterior sulcus are only known in the nycteroleters. Thus, we consider NM QR3061 to represent a nycteroleter, which constitutes the first member of this group found in Gondwana. We cannot, however, provide a generic identification on the basis of the present specimen, and considering its provenance, the possibility that NM QR3061 could represent a new taxon should not be rejected.

The affiliation of NM QR3061 with the nycteroleters is stratigraphically more consistent than the procolophonoid identification proposed by Gow and Rubidge (1997). The FAD of *Owenetta rubidgei*, considered the oldest procolophonoid prior to the description of NM QR3061, is in the upper part of the *Cistecephalus* AZ of the Karoo Basin (Smith and Keyser 1995b). This horizon is well above the base of the *Tapinocephalus* AZ, where NM QR3061 was found (Fig. 3). Consequently, the referral of NM QR3061 to a procolophonoid parareptile by Gow and Rubidge (1997) would imply a considerable extension of the stratigraphic range of Procolophonoidea. The Russian nycteroleters are found in the Mezen, Ochersky, and Sokolki subassemblages (Ivakhnenko et al. 1997; Golubev 2000: fig. 3). The nycteroleter *Macroleter* from Mezen is also found in the Chickasha Formation of USA (Reisz and Laurin 2001) and it was employed to propose a correlation of continental strata of North America and Russia (for a debate regarding this correlation see Lucas 2002; Reisz and Laurin 2002). The maximum time range of all nycteroleters, considered together, spans the Guadalupian and the earliest Lopingian (Fig. 3). The *Tapinocephalus* AZ is considered to be late Guadalupian (Rubidge 2005), and therefore falls well within the stratigraphic range of the nycteroleters.

The presence of a member of the nycteroleter clade in South Africa expands substantially the geographic range of this poorly known group, a fact not surprising when considering that the closely related procolophonoids and pareiasaurids also possess trans-Pangaean distributions. Recent phylogenetic analysis suggest that nycteroleters, until now restricted to Laurasia, represent the sister group to the pareiasaurids (Tsuji 2006). The oldest pareiasaurids are Gondwanan: *Embrithosaurus*, *Bradysaurus*, and *Nochelesaurus* from the *Tapinocephalus* AZ, and *Provelosaurus* from the Rio do Rasto Formation of Brazil (Rubidge 2005; Cisneros et al. 2005). Therefore, the identification of a nycteroleter in Gondwana has important implications for pareiasaurid and nycteroleter biogeography, but more descriptive and phylogenetic work is required in order to clarify the origin of these groups.

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Juan Carlos Cisneros [cisneros.jc@gmail.com], Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. Present address: Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul (CNPq), Porto Alegre, CP 15001, 91501-970, Brazil;

Linda Akiko Tsuji [linda.tsuji@mfn-berlin.de], Museum für Naturkunde Berlin, Invalidenstrasse 43, D-10115, Berlin, Germany.