The first complete vertebral column of a basal tapinocephalid dinocephalian (Synapsida: Therapsida)

Romala Govender*1, Bruce S. Rubidge* and Alain J. Renaut

Non-mammalian therapsids (‘mammal-like reptiles’) were the most common continental vertebrates during Permian-Triassic times. A rich fossil record from several continents documents the acquisition of mammalian characteristics among advanced therapsids. In contrast, the record of the early and most basal therapsids is poorly known and restricted to only a few countries. Dinocephalians are a major subgroup of basal therapsids and are impressive because of their large size. They were the first terrestrial tetrapods to attain body lengths in excess of three metres. Members of this group are known predominantly from South Africa, South Africa, Zimbabwe and recently China and Brazil. Although dinocephalians are relatively abundant, most genera are represented by very fragmentary cranial and postcranial material. This paper reports on the first completely articulated dinocephalian vertebral column with associated limbs, a find that has significance for the understanding of the morphology and palaeobiology of this important group of extinct tetrapods.

Dinocephalians comprise four families, of which the most abundant are the carnivorous Anteosauridae and the herbivorous Tapinocephalidae. Anteosaurids are represented by genera from Russia,7 Brazil,5 China, and South Africa, whereas the Tapinocephalidae are represented by genera from South Africa and Russia.7 Anteosauridae is considered to be the most basal dinocephalian family, whereas Tapinocephalidae is the most derived.5-7 In 1984, John Nyaphuli discovered the skulls and associated skeletons of two dinocephalians (Fig. 1) in a fluvially deposited sandstone body of the Eodicynodon Assemblage zone on the farm Modderdrift, Prince Albert.5 Five skulls were described by Rubidge,* who recognized a new genus and species, Tapinocaninus pamelae (NMQR 2987), which has been identified as the most basal tapinocephalid dinocephalian.5–7

Over the past 17 years, the postcranial of the holotype* has been prepared systematically to reveal a specimen of scientific importance. All the vertebrae (from the first cervical to the last caudal) are preserved in articulation, enabling us confidently to determine that Tapinocaninus has 36 vertebrae. These comprise 8 cervicals, 16 dorsals, 5 lumbars, 2 sacrals and 7 caudals. The only other tapinocephalid with a relatively complete postcranial skeleton is a mounted specimen of Moschops (AMNH 5552), in the American Museum of Natural History in New York. That specimen has been reconstructed as having a vertebral column consisting of 6 or 7 cervical vertebrae, 21 or 22 dorsal and lumbar vertebrae, 3 sacral vertebrae, and of the 29 caudal vertebrae only five are genuine. It is uncertain that all the bones attributed to this specimen actually belong to it, as it was found in association with seven other conspecific individuals.12

The cervical vertebrae of Tapinocaninus have caudally curved neural spines (Fig. 2), and are taller and anteroposteriorly narrower than those of the other vertebrae. The prezygapophyses are positioned in front of the cranial margin of the neural spine (except the axis) and are directed dorsally (except those of the axis, which are directed laterally). All the postzygapophyses project beyond the caudal margin of the neural spine and are directed ventrally. Cervical transverse processes are directed ventrally and the distal ends point cranially. In the dorsal region the prezygapophyses face dorsally, whereas the ventrally facing postzygapophyses do not extend beyond the caudal margin of the neural spine. The laterally directed transverse processes of the dorsal vertebrae are shorter and stouter than those of the cervical region. The prezygapophyseal articular surfaces of the lumbar vertebrae are directed anterodorsally, whereas those of the postzygapophyses point posteroventrally. The short transverse processes are ankylosed to the short lumbar ribs.

The caudal series is the least well preserved, but it is evident when compared to the rest of the neural vertebrae that the neural spine is elongated and the dorsomedially directed prezygapophyses are situated well in front of the neural spine. Caudal postzygapophyses project beyond the caudal margin of the neural spine and are directed ventrolaterally. Only seven

---

*Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa.

1Author for correspondence. E-mail: romala@worldonline.co.za
vertebrae are preserved, with the last being very small and is thus probably the terminal member of the series. This caudal count is much less than the 29 reconstructed caudal vertebrae in the Moschops specimen (AMNH 5552), and the approximately 60 caudals of the Russian anteosaurid Titanophoneus. Watson considered Tapinocephalus to have had a short tail, and the five preserved caudals in the American Museum of Natural History specimen corresponds closely with that of Tapinocaninus, suggesting that tapinocephalids probably had short tails.

A distinguishing feature of the vertebrae of Tapinocaninus is the presence of a laterally facing fovea situated at the base of the neural spine of the cervical vertebrae (Fig. 2). Such a feature is unknown in any South African dinocephalian and is not present in the Moschops specimens in the American Museum of Natural History. This feature is present in a number of ‘pelycosaurs’, especially the sphenacodontids, and is considered characteristic of Dimetrodon. It is also present in all the vertebral column. The significance of this may become apparent by more extensive morphological and phylogenetic research currently under way.

We are indebted to John Nyaphuli, who discovered and helped collect the specimen, as well as to the numerous preparators who have worked on the specimen over the past 17 years. They are Petrus Chalatsi, Chartlon, Caiphus Hatswayo, Joel Moloi, John Mothama, Jimmy Ndimane, Christian Nyaphuli, Joseph Sithole, Sam Tshabalala, and Amos and Enoch Zondi. Johann Welman and Chris Engelbach of the National Museum, Bloemfontein, are thanked for permission to work on the specimen over an extended period. B.S.R. is grateful to Mark Norell, Chris Collins and Judy Galkin for their kind hospitality and assistance while on a research visit to study the Moschops specimens in the American Museum of Natural History. The National Research Foundation and the University of the Witwatersrand are acknowledged for financial support. We greatly appreciate the time and effort of Sean Modesto and an anonymous referee for their constructive comments.

Received 18 October 2001. Accepted 10 July 2002.


Fig. 1. Skull and complete skeleton of the holotype of Tapinocaninus pamelae (NMQR 2967) as seen in oblique dorsal view, with their discoverer, John Nyaphuli.

Fig. 2. Lateral view of cervical vertebrae of Tapinocaninus (NMQR 2967) showing the fovea situated at the base of the neural spine (C3 = cervical 3). Scale bar = 10 cm.

Fig. 3. Ventral view of cervical vertebrae of Tapinocaninus (NMQR 2967) showing the intercentra (C6 = cervical 6). Scale bar = 10 cm.