

Taxonomic re-evaluation of tapinocephalid dinocephalians

Saniye Atayman, Bruce S. Rubidge & Fernando Abdala

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, Private Bag 3, WITS, 2050 South Africa
E-mail: saniye.atayman@students.wits.ac.za / bruce.rubidge@wits.ac.za / nestor.abdala@wits.ac.za

Tapinocephalid dinocephalians are morphologically the most diverse Middle Permian herbivorous tetrapod group from South Africa. Although they were the first large and the most successful therapsid group to have existed at that time on land, they all became extinct by the Middle to Late Permian (Boonstra 1971). They are well represented in South Africa (Boonstra 1963; Boonstra 1969; Rubidge 1991) and are less diverse in Russia (Tchudinov 1983; Ivachnenko 2003), Zimbabwe (Boonstra 1946; Lepper *et al.* 2000; Munyikwa 2001) and possibly Brazil (Langer 2000). They are most abundant in the *Eodicynodon* and *Tapinocephalus* assemblage zones of the Beaufort Group of South Africa (Haughton & Brink 1954; Boonstra 1963, 1969; Rubidge 1991, 1995), which are considered to be the equivalents of Russian Zone I and Zone II (Efremov 1938, 1952) and the *Titanophoneus* Superzone (Ivachnenko *et al.* 1997). Boonstra (1969) used the following characters to define South African tapinocephalid dinocephalian: (1) absence of canine, (2) intermeshing upper and lower incisors, (3) crushing heel and talon on all teeth and (4) moderately to greatly developed pachyostosis. By contrast the most recently described tapinocephalid, *Tapinocaninus pamela*, has a canine tooth in both upper and lower jaws (Rubidge 1991). This character is also present in the Russian tapinocephalid *Ulemosaurus svijagensis* (Riabinin 1938; Efremov 1940).

Taxonomically, tapinocephalid dinocephalians were first considered to be a new family of the Dinosauria (Owen 1876). After Seeley (1894) used the term 'Dinocephalia' for *Delphinognathus* (Seeley 1892) and *Tapinocephalus* (Owen 1876), they were placed in the order Anomodontia. Broom (1905a,b) upgraded the taxon to the order Dinocephalia and described a tapinocephalid *Pelosuchus*. In following years Broom (1911, 1912, 1914) added three more genera, *Moschops*, *Taurops* and *Moschognathus* to the group. Watson (1914) revised the Dinocephalia and recognized the following genera: *Psigalion*, *Mormosaurus*, *Lamiosaurus*. Later, Haughton (1915a,b) added the genera *Struthiocephalus* and *Moschosaurus* to the Dinocephalia. Broom (1923) recognized the suborders Titanosuchia and Tapinocephalia. Gregory (1926) proposed three subfamilies for the South African tapinocephalid dinocephalians, namely Moschosaurinae (including *Moschosaurus*), Moschopinae (including *Delphinognathus*, *Moschops*, *Moschognathus*, *Taurops*, *Psigalion* and *Lamiosaurus*) and Tapinocephalinae (*Tapinocephalus*, *Mormosaurus* and *Struthiocephalus*). Later, three new genera, *Taurocephalus* (Broom 1928), *Criocephalus* (Broom 1928) and *Keratocephalus* (von Huene 1931), were assigned to the taxon. Boonstra (1936) reconsidered the taxonomy of South African tapinocephalids and elevated Gregory's (1926)

subfamilies to family level and also added one more subfamily as follows: Moschosauridae (including *Moschosaurus*), Moschopidae (including *Delphinognathus*, *Moschops*, *Moschognathus*, *Psigalion* and *Lamiosaurus*), Tapinocephalidae (*Tapinocephalus*, *Taurops* and *Keratocephalus*) and Mormosauridae (*Mormosaurus*, *Taurocephalus* and *Struthiocephalus*).

After a detailed revision of dinocephalian taxonomy, Boonstra (1969) further synonymised the following genera: *Taurops* and *Moschognathus* with *Tapinocephalus* and *Moschops*; *Psigalion* with *Moschops*; *Moschosaurus* with *Struthiocephalus*; *Pelosuchus* with *Keratocephalus*, and included *Lamiosaurus* in titanosuchids. This new taxonomy included the latest founded new genera *Avenantia* (Boonstra 1952a), *Riebeeckosaurus* (Boonstra 1952c), *Struthiocephaloides* (Boonstra 1952d) and a new subfamily to Gregory (1926), while discarding its taxon Moschosauridae after synonymizing *Moschosaurus* with *Struthiocephalus*. Boonstra (1969) grouped South African tapinocephalids in four subfamilies; Struthiocephalinae (including *Struthiocephalus*, *Struthiocephalellus*, *Struthionops* and *Taurocephalus*), Moschopinae (including *Moschops*, *Delphinognathus*, *Avenantia*), Tapinocephalinae (including *Tapinocephalus*, *Mormosaurus*, *Phocosaurus* and *Keratocephalus*) and Riebeeckosaurinae (*Riebeeckosaurus*), on the basis of the degree of pachyostosis and the length of the snout. Subfamilies Struthiocephalinae and Riebeeckosaurinae included taxa having long snouts. However, Riebeeckosaurinae is represented only by *Riebeeckosaurus* (Boonstra 1952b), which does not have preserved snout. Genera comprising the subfamilies Moschopinae and Tapinocephalinae are all considered to have short snouts. However the moschopin *Avenantia* has no preserved snout. The original descriptions of the tapinocephalin *Tapinocephalus* (Owen 1876) and *Phocosaurus* (Seeley 1888) are based mainly on postcranial material Boonstra (1955a, 1956). The associated cranial material of *Phocosaurus* was known only much later (Boonstra 1956). The holotype material of *Phocosaurus* (Seeley 1888) was first described as *Pareiasaurus* by Owen (1876a), and was later referred to *Tapinocephalus* by Lydekker (1890). Watson (1914) referred it again to *Phocosaurus*.

King (1988, p. 10) included genera in the subfamilies Tapinocephalinae and Moschopinae into the tribe Tapinocephalini, considering that 'pachyostosis as a character is variable within the subfamily and not a fool-proof guide to relationship'. She considered tapinocephalid dinocephalians in three tribes without any synonymization as follows: Struthiocephalini, Tapinocephalini, Riebeeckocepalini. Because she considered *Struthionops* to be short-snouted, King (1988) assigned it to the tribe Tapinocephalini rather than Struthiocephalini. This taxonomy also includes the only Russian tapinocephalid, *Ulemosaurus*, also in the tribe Tapinocephalini.

Tchudinov (1983) considered two groups of Dinocephalia, Titanosuchia and Tapinocephalia, the last including Tapinocephalidae as the only family. In this taxonomy *Ulemosaurus* (Riabinin 1938) was assigned to genus *Moschops* (Tatarinov 1965; Tchudinov 1983), which was previously considered to be closely related to *Moschops*

Table 1. Currently recognized tapinocephalid dinocephalian genera listed according to date of description.

Genus	Species	Synonym	Institution* housing holotype	Institution* housing referred specimens
<i>Tapinocephalus</i>	<i>Tapinocephalus atherstonei</i> Owen, 1876	<i>Taurops macrodon</i> Broom, 1912	AMNH	SAM, TM, BPI
<i>Delphinognathus</i>	<i>Delphinognathus conocephalus</i> Seeley, 1892		SAM	AMNH
<i>Phocosaurus</i>	<i>Phocosaurus megischion</i> Seeley, 1888		BMNH	SAM
<i>Moschops</i>	<i>Moschops capensis</i> Broom, 1911	<i>Moschognathus whaitsi</i> Broom, 1914	AMNH, SAM	SAM, BPI
	<i>Moschops koupensis</i> Boonstra, 1957	<i>Pinigalion oweni</i> Watson, 1914		
	<i>Moschops whaitsi</i> (Broom, 1914) Boonstra 1969	<i>Moschoides romeri</i> Bryne, 1937		
	<i>Moschops oweni</i> (Watson, 1914) Boonstra 1969	<i>Agnosaurus pianaari</i> Boonstra, 1952b		
<i>Mormosaurus</i>	<i>Mormosaurus seeleyi</i> Watson, 1914		BMNH	SAM
<i>Struthiocephalus</i>	<i>Struthiocephalus whaitsi</i> Houghton, 1915a	<i>Struthiocephalellus</i> Boonstra, 1955b	SAM, FMNH	SAM, BPI
		<i>Moschosaurus longicesps</i> Houghton, 1915b		
		<i>Struthiocephalus kitchingi</i> Brink, 1957		
		<i>Struthiocephalus milleri</i> Olson & Broom, 1937		
		<i>Struthiocephalus rheederi</i> Broom, 1937		
		<i>Struthiocephalus akraalensis</i> Boonstra, 1952e		
<i>Taurocephalus</i>	<i>Taurocephalus lerouxi</i> Broom, 1928		AMNH	
<i>Criocephalus</i>	<i>Criocephalus</i> Broom, 1928		KM	SAM
<i>Keratocephalus</i>	<i>Keratocephalus moloch</i> von Huene, 1931	<i>Pelosuchus priscus</i> Broom, 1905b	UT	SAM
<i>Ulemosaurus</i>	<i>Ulemosaurus svijagensis</i> Riabinin, 1938		PIN	
<i>Struthiocephaloides</i>	<i>Struthiocephaloides cavifrons</i> Boonstra, 1952f		SAM	
<i>Struthionops</i>	<i>Struthionops intermedius</i> Boonstra, 1952g		SAM	
<i>Avenantia</i>	<i>Avenantia kruisvleiensis</i> Boonstra, 1952		SAM	SAM
<i>Riebeeckosaurus</i>	<i>Riebeeckosaurus longirostris</i> Boonstra, 1952		SAM	
<i>Tapinocaninus</i>	<i>Tapinocaninus pamela</i> Rubidge, 1991		NMQR	ROZ K

*Institutional abbreviations: AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; BPI, Bernard Price Institute for Palaeontology, Johannesburg; FMNH, Field Museum of Natural History, Chicago; KM, McGregor Museum, Kimberley; PIN, The Museum of the Paleontological Institute of the Russian Academy of Sciences, Moscow; SAM, Iziko South African Museum; NM, National History Museum, Bloemfontein; UT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; ROZ K, Roy Oosthuizen; TM, Transvaal Museum, Pretoria.

(Riabinin 1938; Efremov 1940). Ivakhnenko (1994, 2003) later placed *Ulemosaurus* in a new family, Ulemosauridae, together with the South African genus *Tapinocaninus* (Rubidge 1991). The latter genus, based on five skulls, is considered the most basal tapinocephalid (Rubidge 1991).

Recent studies on the stratigraphic ranges of tetrapod taxa in the Beaufort Group have revealed a large number of genera of tapinocephalid dinocephalians (all considered to be herbivores) in the *Tapinocephalus* Assemblage Zone relative to the number of herbivorous genera from any other assemblage zones of the Beaufort Group (Nicolas 2007; Rubidge 1995). This, together with the fact that most of the tapinocephalid genera are based on very fragmentary material and have not been researched for more than 30 years, is a clear indication of the necessity for a taxonomic revision of this group. Our preliminary assessment suggests that some of the holotypes are juvenile specimens, and that there is thus further synonymization in this chequered group are expected.

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