

TAXONOMIC REVISION OF THE SHORT-SNOUTED  
TAPINOCEPHALID DINOCEPHALIA  
(AMNIOTA-THERAPSIDA) - THE KEY TO  
UNDERSTANDING MIDDLE PERMIAN TETRAPOD  
BIODIVERSITY

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I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



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4 day of February 2020 in Johannesburg, South Africa

## ABSTRACT

The middle Permian period marks the origin and rapid diversification of therapsid synapsids such that all the main therapsid families (with exception of the Cynodontia) were already present at that time. Dinocephalia, apart from being the earliest large therapsids, comprised a major component of the middle Permian terrestrial ecosystems and despite their taxonomic diversity and apparent ecological success they went extinct at the end of the Capitanian stage of the Middle Permian, thus having the dubious distinction of being the first therapsid lineage to face extinction. The most diverse dinocephalian family, in terms of both species and numbers of individuals, are the Tapinocephalidae. This herbivorous group of derived dinocephalians (comprising both short- and long-snouted forms) are known from Russia, Zimbabwe, Tanzania and are most abundantly represented by discoveries from the South African Karoo Supergroup. Taxonomic revision of the short-snouted tapinocephalids, for the first time accompanied by detailed anatomical descriptions and illustrations of representative cranial material, enabled recognition of eight monospecific genera out of 23 described holotypes. These are *Tapinocaninus pamela*, *Ulemosaurus svijagensis*, *Riebeeckosaurus longirostris*, *Moschognathus whaitsi*, *Agnosaurus pienaari*, *Moschops capensis*, *Criocephalosaurus vanderbyli*, *Tapinocephalus atherstonei*. *Mormosaurus* and *Keratocephalus* are now considered to be long-snouted, and *Keratocephalus* is synonymised with *Struthiocephalus whaitsi*.

Because of the relatively large number of specimens, cranial characters which modify during ontogenetic development were recognized for *Moschops*, and for the first time an ontogenetic growth series is presented for this species. The first extensive phylogenetic analysis of the Tapinocephalidae shows that the South Africa Karoo Supergroup hosts both the most basal and most derived tapinocephalid dinocephalians, and future studies will determine their use as biostratigraphic indicator taxa.

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*to Julie, Pelin, Mete and Alper*



*“Dünyada her şey için, medeniyet için, hayat için muvaffakiyet için en hakiki mürşit ilimdir, fendir. İlim ve fennin haricinde mürşit aramak gaflettir, cehalettir, dalalettir.”*

*“For everything in the world, for civilisation, for life, for success the most genuine guide is science. To seek a guide outside science is aberration, ignorance, perversion.”*

Mustafa Kemal Atatürk.  
22 September 1924  
Samsun, Turkey

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## **INSTITUTIONAL ABBREVIATIONS**

**AMNH**, American Museum of Natural History, New York, USA; **NHMUK**, The Natural History Museum United Kingdom, London, United Kingdom; **BPI**, Evolutionary Studies Institute (former Bernard Price Institute) University of the Witwatersrand, Johannesburg, South Africa; **CGP**, Council for Geosciences, Pretoria, South Africa; **FMNH**, Field Museum of Natural History, Chicago, USA; **UT (GPIT)**, Institute und Museum für Geologie und Paläontologie der Eberhard-Karls-Universität Tübingen, Germany; **KMG**, McGregor Museum, Kimberley, South Africa; **NHMB**, Natural History Museum of Bulawayo, Zimbabwe; **NMQR**, National Museum, Bloemfontein, South Africa; **PIN**, Museum of the Paleontological Institute of the Russian Academy of Sciences, Moscow; **SAM**, Iziko, South African Museum, Cape Town, South Africa; **TKNP**, Tankwa Karoo National Park; **TM**, Ditsong Museum, Pretoria, South Africa.

## ANATOMICAL ABBREVIATIONS

**al-** alveolus, **an-** angular; **ar-** articular; **ara-** articular apex; **arf-** articular fossa; **art,** articular; **af-** articular fossa; **bo-** basioccipital; **bok-** basioccipital keel; **bs-** basisphenoid; **bsk-** basisphenoidal keel; **c-** canine; **co-** choana, **d-** dentary; **dentary alveolar border;** **dpq-** Dorsal process of the quadrate; **ds-** dentary symphysis; **dsl-** dentary sulcus; **ect-** ectopterygoid; **ef-** ectopterygoid foramina; exoccipital; **f-** frontal; **hf-** hypoglossal foramen; **i-** incisor; **inp-** internarial process of septomaxilla; **ic-** foramen for internal carotid; **ipv-** interpterygoid vacuity; **ir-** incisor roots; **j-** jugal; **jf-** jugular foramen; **l-** lacrimal; **lfp-** lateral flange of the pterygoid; **mx-** maxilla; **mr-** midline ridge; **mf-** meckelian fossa; **ms-** muscle scar; **no-** narial opening; **ng-** nasal groove; **oc-** occipital condyle; **or-** orbit; **p-** parietal; **pc-** postcanine; **pca-** postcanine alveoli, **pce-** postcranial element; **pe-** posterior extension of septomaxilla; **pb-** palatine boss; **pbp-** palatine boss of the pterygoid; **pfa-** anterior palatine foramen; **pfp-** posterior palatine foramen; **pl-** palatine; **ppk-** posparietal keel; **pra-** prearticular; **pbp-** palatine boss of the pterygoid; **pmx-** Premaxilla; **po-** Postorbital; **poc-** Paraoccipital process of the opisthotic; **pof;** Postfrontal; **pp-** Postparietal; **ppmk-** posparietal midline keel; **pr-** pineal opening rim; **prf-** prefrontal; **psr-** parasphenoidal rostrum; **ptf-** post-temporal fenestra; **q-** quadrate; **qdp-** quadrate dorsal process; **qf-** foramen quadratum; **qj-** quadratojugal; **qpt-** quadrate ramus of pterygoid; **rap-** retroarticular process; **rc-**

replacement canine; **ri**- replacement incisor; **rl**- Reflected lamina; **rpc**- replacement postcanine;

**sa**- surangular; **sf**- squamosal facet; **smx**- septomaxilla; **sp**- splenial; **spf**- splenial fossa, **sps**- splenial symphysis; **sq**- squamosal; **sqs**- squamosal sulcus; **st**- stapes; **stb**- base of stapes; **sth**- head of stapes; **stf**- stapedia foramen; **v**-vomer; **vch**- vomerine channel; **vcr**- vomer lateral crista on its dorsal surface; **vd**- vomerine dorsal process; **vd**- vomer dorsal keel, **vlr**- vomer lateral ridge on its ventral surface; **vmr**-vomer midline ridge; **vp**-vomer posterolateral process; **vmt**- vomer midline trough.