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2020

https://hdl.handle.net/10539/31602

Neumann, Saniye. (2019). Taxonomic revision of the short-snouted tapinocephalid dinocephalia (amniota-therapsida) :the key to understanding middle Permian Tetrapod biodiversity, University of the Witwatersrand, https://hdl.handle.net/10539/31602

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

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A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

Johannesburg, 2020



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.



Saniye Neumann

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 pamelae, 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.

ACKNOWLEDGEMENTS

I am indebted to my supervisors, Prof. Dr. Bruce S. Rubidge and Dr. Fernando Abdala for their unceasing support and guidance throughout this project. The African Origins Platform of the National Research Foundation (NRF), DST (Department of Science and Technology) /NRF Centre of Excellence in Palaeosciences, and the Palaeontological Scientific Trust (PAST) are acknowledged for financial support, without which this research would not have been possible.

For access to the material I studied I would like to thank the following past and present museum curators and staff members for guiding me through the museum collections and enabling me to examine dinocephalian specimens: Dr. Roger Smith, Dr. Claire Browning, Ms. Sheena Kaal and Zaituna Skosan (Iziko Museum in Cape Town, South Africa), Dr. Jennifer Botha and Ms. Elize Butler (National Museum in Bloemfontein, South Africa), Dr. Heidi Fourie (Ditsong [Transvaal] Museum in Pretoria, South Africa), Dr. Johann Neveling and Ms. Nonhlanha Mchunu (Council for Geosciences in Pretoria, South Africa), Dr A. Kurkin (Paleontological Museum of the Russian Academy of Sciences in Moscow, Russia), Ms Sandra Chapman, Dr. Michael Day (Natural History Museum in London), Mr Carl Mehling (American Museum of Natural History in New York), Dr Juliane Hinz (Institut für Geologie und Paläontologie der Eberhard-Karls-Universität Tübingen), Dr. Bernard Zipfel and Mr. Sifelani Jirah (Evolutionary Studies Institute in Johannesburg). I thank Dr. Christian Kammerer, Dr. Jun Liu and Dr. Kenneth Angielczyk for sharing part of their photographic collection of

dinocephalian and other therapsid specimen. Special acknowledgments to Mr. Pepson Mukanela and the other members of the fossil preparation laboratory of Evolutionary Studies Institute for their help in the preperation of the tapinocephalid specimen. I also would like acknowledge Dr. Christian Kammerer, Dr. Michael Day, Dr. J. Benoit, Mr. Sifelani Jirah and Mr. Luke Norton for sharing their knowledge about dinocephalians and other palaeontological matters.

I am indebted to the following for their help in translating some of the non-English literature to English: Prof. Dr. Boris Natalin (Russian), Dr. Marina Yudovskaya (Russian), Dr. Tea Jashashvili (Russian), Prof. Dr. A.M. Celâl Şengör (German, French), Dr. Frank H. Neumann (German, Afrikaans), Dr. Bernard Zipfel (Afrikaans).

I would like to deliver my special thanks to my life-time mentors and friends Prof. Dr. A.M. Celâl Şengör and Dr. Frank H. Neumann for their continuous support and many good discussions. I am also greateful to Prof A. M. C. Şengör for providing me with some of the rare literature during this study. A special thank also to my dear friends Dr. Tea Jashashvili and Dr. Aurore Val for the test CT scans of some of the dinocephalian specimens and Dr. Sena Akçer, Dr. Asım Şengör, Ms. Doa Güney and Ms. Özlem Gelincik for the encouragement received during this study.

Last but not least, I am grateful for the enduring support and patience of my family in Istanbul and Mersin, Turkey. I particularly would like to salute my

mother Ms. Rûkiye Güven for her respect and love for science and my daughter Julie Isabella Ilkay for her never-ending curiosity.

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**; c-** choana, **d-** dentary; da- **dentary alevolar border; dpq-** Dorsal process of the quadrate; **ds-** dentary symphisis; **dsl-** dentary sulcus; **ect-** ectopterygoid; **ef-** ectopterygoidal foramina; exoccipital; **f-** frontal; **hf-** hypoglossal foramen; **i-** incisor; **inp-** internarial process of septomaxilla; **ic-** foramen for internal carotid; **ipv-** interpterygoidal vacuity; ir- incisor roots; **j-** lugal; **jf-** jugular foramen; **l-** lacrimal; **lfp-** lateral flange of the pterygoid; **mx-** maxilla; **mr-** midlne ridge; **mf-** meckelian fossa; **ms-** muscle scar; **no-** narial opening; **ng-** nasal groove; **oc-** occipital condyle; **or-** orbit; **p-** parietal; **pc-** postcanine**; pca-** postcanine alveaoli**, pce-** postcranial element; **pe-** posterior extention 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 pterigoid; **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-** stapedial foramen; **v-**vomer; **vch**-vomerine channel; **vcr-** vomer lateral crista on its dorsal surface; **vdp**- vomerine dorsal processl; **vdk-** vomer dorsal keel, **vlr-** vomer lateral ridge on its ventral surface; **vmr**-vomer midline ridge; **vp-**vomer posterolateral process; **vmt-** vomer midline trough.