# The small dicynodont *Katumbia parringtoni* (VON HUENE, 1942) (Therapsida: Dicynodontia) from the Upper Permian Kawinga Formation of Tanzania as gorgonopsian prey

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## Abstract

A dicynodont mandibular symphysis found as fossil stomach content of the type specimen of the gorgonopsid *"Aelurognathus" parringtoni* (VON HUENE, 1950) is redescribed from the Kawinga Formation (Tatarian) of Usili, Ruhuhu Basin, southwestern Tanzania. It is shown to belong to the rare, small taxon *Katumbia parringtoni* (VON HUENE, 1942), as it shows a morphology practically identical to recently described specimens of this taxon but widely different from all other dicynodonts of the Kawinga Formation. This provides the first direct evidence of predation of a carnivorous therapsid on a particular dicynodont taxon.

K e y w o r d s : Gorgonopsia, Dicynodontia, predation, Katumbia, Ruhuhu Basin, Kawinga Formation.

# Zusammenfassung

Die Unterkiefersymphyse eines Dicynodonten, die als fossiler Mageninhalt des Gorgonopsiers "Aelurognathus" parringtoni (VON HUENE, 1950) in der tatarischen Kawinga-Formation von Usili im Ruhuhu-Becken Südwest-Tansanias gefunden wurde, wird neu beschrieben. Es wird gezeigt, dass sie dem seltenen, kleinwüchsigen Taxon Katumbia parringtoni (VON HUENE, 1942) zugewiesen werden kann, da ihre Morphologie mit jüngst beschriebenem, neuem Material dieser Art sehr gut übereinstimmt, sich aber stark von allen anderen Dicynodonten der Kawinga-Formation unterscheidet. Es handelt sich hierbei um den ersten direkten Nachweis von Prädation eines karnivoren Therapsiden im Bezug auf ein spezifisches Dicynodonten-Taxon.

#### 1. Introduction

In 1950 FRIEDRICH VON HUENE published his extensive monograph on the theriodonts of the Ruhuhu Basin in southwestern Tanzania, collected by ERNST and MARIA NOWACK for the Palaeontological Museum of Tübingen University. He described, among many other important specimens, a skeleton of a new gorgonopsian species, Aelurognathus parringtoni, from Mount Usili (the species probably does not represent Aelurognathus, see GEBAUER 2007, and is therefore referred to as "Aelurognathus" parringtoni below). This unique specimen, the single representative of its species (Fig. 1), probably still represents the most complete and best preserved gorgonopsian skeleton worldwide. VON HUENE noted the presence of the symphysis of a small anomodont in the rib cage of this skeleton, and indicated that it represented part of the gorgonopsian's fossil stomach content, a conclusion that seems viable, although original field records for the specimen are not available, because the symphysis was apparently discovered during preparation of the skeleton. Preparation was carried out by the skilled preparator WETZEL under VON HUENE's direction and was already completed before World War II. The war and its aftermath hampered publication of the material until 1950. Although the possibility of a circumstantial co-occurrence of the gorgnopsidan skeleton and anomodont mandible can not be ruled out with absolute certainty, it appears exceedingly unlikely, as no other tetrapod fossils were found in the close vicinity of the specimen, and the mandibular fragment was discovered from within the rib cage of the predator.

Although VON HUENE (1950) refers the dicynodont symphysis to *Dicynodon*, this should not be seen as being intended as a proper taxonomic assignment, the name being used in a more general sense (i. e., that of the catch-all genus that *Dicynodon* was in 1950 and, basically, still is).

For more than half a century, this dicynodont specimen remained indeterminable, due to our lack of information on the morphology of many East African taxa. This situation has improved considerably in recent years, due to a renewed interest in the fauna of the Kawinga Formation. Recently, ANGIELCZYK (2007) redescribed the species Cryptocynodon parringtoni, previously only known from a badly eroded single skull (VON HUENE 1942; KEYSER 1993; MAISCH 1995) attributed to a variety of genera, including Pristerodon and Diictodon, by previous authors. He demonstrated that the taxon represented a hitherto unrecognised genus of small upper Permian dicynodont instead, which was named Katumbia. This genus is only known from the Ruhuhu Basin and further strengthens the case for considerable endemism of its fauna (see, e.g., MAISCH 2002, 2005). ANGIELCZYK (2007) also described mandibular material of *Katumbia parringtoni* for the first time, and this prompted me to do a re-investigation of the small dicynodont jaw symphysis preserved as stomach content of *"Aelurognathus" parringtoni*, which turned out to be identifiable as a member of this species.

This is to my knowledge the first reported case, where a predator-prey relationship of two Permian therapsid taxa can be unequivocally demonstrated on the basis of direct fossil evidence. Hitherto, only predation of unknown archosaurs on Triassic dicynodonts was recorded in a few cases (CRUICKSHANK 1986; VEGA-DIAS & SCHULTZ 2007).

#### Institutional abbreviations

GPIT Institut für Geowissenschaften, Universität Tübingen, Germany

UMZC University Museum of Zoology, Cambridge, UK

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#### 2. Material and methods

GPIT RE/7113, holotype skeleton of "Aelurognathus" parringtoni (VON HUENE, 1950) from the Kawinga Formation of Usili, Ruhuhu Basin, southwestern Tanzania (Fig. 1), including a small smyphysis of Katumbia parringtoni (VON HUENE, 1942) as stomach content. The latter specimen is here labelled as GPIT RE/7113 A (Fig. 2A–B).

#### 3. Description

The specimen consists of the larger part of both dentaries, including the entire dentary portion of the mandibular symphysis (Fig. 2A-B). Much of the anterior and posterolateral dorsal margins of the fused dentaries are missing. The fact that they are completely fused clearly indicates that the specimen does not represent a juvenile. The posteriormost portions of both dentaries are missing, the left one being slightly more complete (Fig. 2B). The other mandibular bones, even the splenials, have detached from the conjoined dentaries. It is visible, though, that the splenials took part in the formation of the mandibular symphysis but did not have a pronounced anterodorsal process intruding between the dentaries on the anterior symphyseal surface, as it is found in many other dicynodonts. The absence of the splenials is very unusual in dicynodont fossils, as these elements are usually strongly coossified with the dentaries. It can be seen as evidence that the specimen really represents part of an at least partially digested individual. Bite marks are not evident, and the bone surface has largely suffered too much from mechanical preparation as to be sure about etching marks. The disconnection of the mandibular elements is therefore the best indication for the specimen really representing part of the stomach content of the gorgonopsian.

The dentary symphysis is rather massive. Its anterior surface is smooth and convex both transversely and dorsoventrally. It is therefore not as pronouncedly squared off as illustrated for Katumbia (ANGIELCZYK 2007, compare Fig. 2C). There is no medial ridge on the anterior symphyseal surface. The dorsal margin of the symphysis, although incomplete, was clearly strongly extended and somewhat upturned in a beak-like fashion (Fig. 2B). Behind the upturned anterior margin, the dorsal surface of the dentary forms a deeply concave trough that narrows somewhat posteriorly (Fig. 2A). The anterior and lateral dentary surfaces meet in pronounced ridges. If there were dentary tables at all, they must have been exceedingly short and situated close to the anterior edge of the symphysis, a position in which they are indeed found in Katumbia (ANGIEL-CZYK 2007). An indistinct dorsal dentary sulcus can be followed for some distance on the left dentary (Fig. 2A). The lateral dentary surface is first flattened, then forms a sharpened ventrally concave lateral dentary shelf that is quite pronounced (Fig. 2B). The dentary surface below this ridge is smooth and slopes strongly medially and must have formed the dorsal border and dorsomedial wall of the mandibular fenestra, the shape of which can not be ascertained due to the lack of the postdentary bones.

## 4. Comparison

As evident from the above description, the specimen agrees very closely with Katumbia parringtoni, as described by ANGIELCZYK (2007, see Fig. 2). The only significant difference is the slightly less squared-off shape of the dentary symphysis in dorsal view, which may be easily attributed to the incomplete preservation of the present specimen as well as individual variation. It should also be borne in mind that the specimen is somewhat smaller than the mandible decribed by ANGIELCZYK (2007), so ontogenetic variation can not be ruled out as well. The other smaller dicynodonts from the Kawinga Formation are completely different in mandibular morphology. Kawingasaurus fossilis has a low, elongated, shovel-like dentary symphysis (Cox 1972). Kingoria nowacki (Cox 1958; KING 1988) lacks a dorsal dentary sulcus, has an elongated and blunt tip of the dentaries, and possesses a very pronounced dorsally concave lateral dentary shelf. It is also unlikely that we deal with a juvenile of one of the larger forms, not only for the fusion of the dentaries, but also for morphological reasons. The dorsal dentary tables of Dicynodon and *Pelanomodon* are pronounced and large structures,



Fig. 1. The type skeleton of "Aelurognathus" parringtoni (VON HUENE, 1950), GPIT RE/7133, as mounted at the Palaeontological Museum of Tübingen University. – Total length is about 170 cm.



**Fig. 2.** Lower jaws of *Katumbia parringtoni* (VON HUENE, 1942) from the Kawinga Formation (Tatarian) in comparison. – **A–B**. GPIT/ RE/7113 A from Usili, Ruhuhu Basin, southwestern Tanzania. This specimen was found as stomach content of the gorgonopsid "*Ae-lurognathus*" parringtoni (VON HUENE, 1950). **A**. Dorsal view. **B**. Left lateral view (inverted to allow for better comparison). **C–D**. Specimen UMZC T791 from Katumbi Viwili, Ruhuhu Basin, southwestern Tanzania. **C**. Symphyseal region in dorsal view, **D**. Right lateral view (C and D modified from ANGIELCZYK 2007). – Abbreviations: d.d.s. = dorsal dentary sulcus, l.d.s. = lateral dentary shelf.

situated far posterior to the anterior mandibular margin. The latter is also the case in the giant *Rhachiocephalus*. *Pachytegos* is an endothiodontid that retains postcanine dentition. Identification is therefore not possible with any of these genera. The specimen is consequently identified as *Katumbia parringtoni* (VON HUENE, 1942).

### 5. Conclusions

Prior to the description of the lower jaw of Katumbia parringtoni, it remained impossible to identify the specimen found as stomach content of "Aelurognathus" parringtoni further than "unidentifed dicynodont" or "anomodont". With the new information now at hand due to the description of additional material of the long-misunderstood and enigmatic "Crvptocvnodon" parringtoni by AN-GIELCZYK (2007) it was easy to identify the historical specimen with this small and rare component of the dicynodont fauna of the Kawinga Formation. There are few clear instances where active predation or scavenging in Permian terrestrial ecosystems could be documented, only one of which includes non-mammalian synapsids (EATON 1964; MUNK & SUES 1993; REISZ & TSUJI 2006). Here now is clear evidence not only that gorgonopsians indeed ate dicynodonts, something assumed for quite a long time, but also that a particular taxon of dicynodont, Katumbia parringtoni, was among the prey of a particular taxon of gorgonopsian, "Aelurognathus" parringtoni. It can not be decided, however, whether the Katumbia specimen fell victim to active predation or was scavenged upon, both possibilities are plausible with the data at hand.

It is only through such exceedingly rare findings, that we can get a picture of predator-prey relations in ancient ecosystems that come anywhere close to the truth. Future findings from East Africa and elsewhere will hopefully help to improve our understanding of these relations among the therapsid-dominated terrestrial ecosystems of the late Permian of Gondwana, something that is highly important also for any meaningful discussion of the effects of the P/Tr-event on these terrestrial ecosystems.

#### 6. References

ANGIELCZYK, K. D. (2007): New specimens of the Tanzanian dicynodont "Cryptocynodon" parringtoni VON HUENE, 1942 (Therapsida, Anomodontia), with an expanded analysis of Permian dicynodont phylogeny. – Journal of Vertebrate Paleontology, **27**: 116–131.

- Cox, C.B. (1958): On the anatomy of a new dicynodont genus with evidence of the position of the typanum. – Proceedings of the Zoological Society of London, 132: 321– 367.
- Cox, C. B. (1972): A new digging dicynodont from the Upper Permian of Tanzania. – In: Joysey, K. A. & KEMP, T. S. (eds.): Studies in Vertebrate Evolution: 173–189; Edinburgh (Oliver & Boyd).
- CRUICKSHANK, A. R. I. (1986): Archosaur predation on a Middle Triassic dicynodont. – Palaeontology, 29: 415–422.
- EATON, T. H. (1964): A captorhinomorph predator and its prey (Cotylosauria). American Museum Novitates, **2169**: 1–3.
- GEBAUER, E. V. I. (2007): Phylogeny and evolution of the Gorgonopsia with a special reference to the skull and skeleton of GPIT/RE/7113 (*Aelurognathus*?' *parringtoni*). IV + 316 pp.; Dissertation Universität Tübingen (unpublished).
- HUENE, F. VON (1942): Die Anomodontier des Ruhuhu-Gebietes in der Tübinger Sammlung. – Palaeontographica, Abteilung A, 44: 154–184.
- HUENE, F. VON (1950): Die Theriodontier des ostafrikanischen Ruhuhu-Gebietes in der Tübinger Sammlung. – Neues Jahrbuch für Geologie und Paläontologie Beilage-Band, 92: 47–136.
- KEYSER, A. W. (1993): A re-evaluation of the smaller Endothiodontidae. – Memoirs of the Geological Survey of South Africa, 82: 1–53.
- KING, G. M. (1988): Handbuch der Paläoherpetologie. Teil 17 C: Anomodontia. 174 pp.; Stuttgart, New York (G. Fischer).
- MAISCH, M. W. (1995): Taxonomic revision of *Cryptocynodon* parringtoni v. HUENE, 1942 (Therapsida, Dicynodontia) from the Late Permian of Tanzania. – Neues Jahrbuch für Geologie und Paläontologie Monatshefte, **1995**: 594–604.
- MAISCH, M. W. (2002): Observations on Karroo and Gondwana vertebrates. Part 3. Notes on the gorgonopsians from the Upper Permian of Tanzania. – Neues Jahrbuch für Geologie und Paläontologie Monatshefte, **2002**: 237–251.
- MAISCH, M. W. (2005): Observations on Karroo and Gondwana vertebrates. Part 6. A new rhachiocephalid dicynodont (Therapsida) from the Upper Permian of the Ruhuhu Basin (Tanzania). – Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 237: 313–355.
- MUNK, W. & SUES, H.-D. (1993): Gut contents of *Parasaurus* (Pareiasauria) and *Protorosaurus* (Archosauromorpha) from the Kupferschiefer (Upper Permian) of Hessen, Germany. Paläontologische Zeitschrift, **67**: 169–176.
- REISZ, R. R. & TSUJI, L. A. (2006): An articulated skeleton of Varanops with bite marks: the oldest known evidence of scavenging among terrestrial vertebrates. – Journal of Vertebrate Paleontology, 26: 1021–1023.
- VEGA-DIAS, C. & SCHULTZ, C. (2007): Evidence of archosauriform feeding on dicynodonts in the Late Triassic of Brazil. – PaleoBios, 27: 62–67.

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