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# Re-assessment of *Silphoictidoides ruhuhuensis* VON HUENE, 1950 (Therapsida, Therocephalia) from the Late Permian of Tanzania: one of the most basal baurioids known

MICHAEL W. MAISCH

## Abstract

The known material of the small therocephalian *Silphoictidoides ruhuhuensis* VON HUENE, 1950, is re-investigated. Additional description of the cranial osteology and a new diagnosis of the taxon are provided. It is demonstrated that contrary to recent claims *Silphoictidoides* represents a valid genus that is so far endemic to the Ruhuhu Basin and distinct from any described forms from the South African Karoo Basin. Phylogenetic analysis indicates that the genus is one of the most basal known representatives of the important therocephalian clade Baurioidea.

**Key words:** Therocephalia, *Silphoictidoides*, Ruhuhu Basin, Usili Formation, morphology, taxonomy, phylogeny.

## 1. Introduction

When describing the theriodonts of the Permo-Triassic strata of the Ruhuhu Basin in the Tübingen collection in 1950, the famous German palaeoherpetologist FRIEDRICH FREIHERR VON HUENE introduced a new taxon of “ictidosuchid” therocephalian from the Upper Permian Usili (Kawinga) Formation of Mt. Kingori. Despite being based on two almost complete and well preserved skulls, skillfully prepared by VON HUENE’S preparator W. WETZEL, the taxon has escaped the attention of almost all later workers on the group. It was briefly discussed by MENDREZ (1972), who underlined its status as a valid genus separate from the South African forms known at that time, but was not considered in the recent, detailed studies on therocephalian phylogeny by HUTTENLOCKER (2009, 2014) and SIGURDSEN et al. (2012). Most recently it was claimed (HUTTENLOCKER & SIDOR 2016) that *Silphoictidoides* is most probably a synonym of the South African genus *Ictidosuchoidea*, but no detailed analysis of the type material was provided to substantiate that claim.

The purpose of this paper is threefold. First it supplements the only existing description of this taxon by VON HUENE (1950). Second it supports the validity of *Silphoictidoides*, which is demonstrably different from any known Upper Permian “scaloposaur” from South Africa – note that the term “scaloposaur” is used here in a colloquial sense to refer to small-sized, sometimes juvenile therocephalians, in fact representing an array of different forms

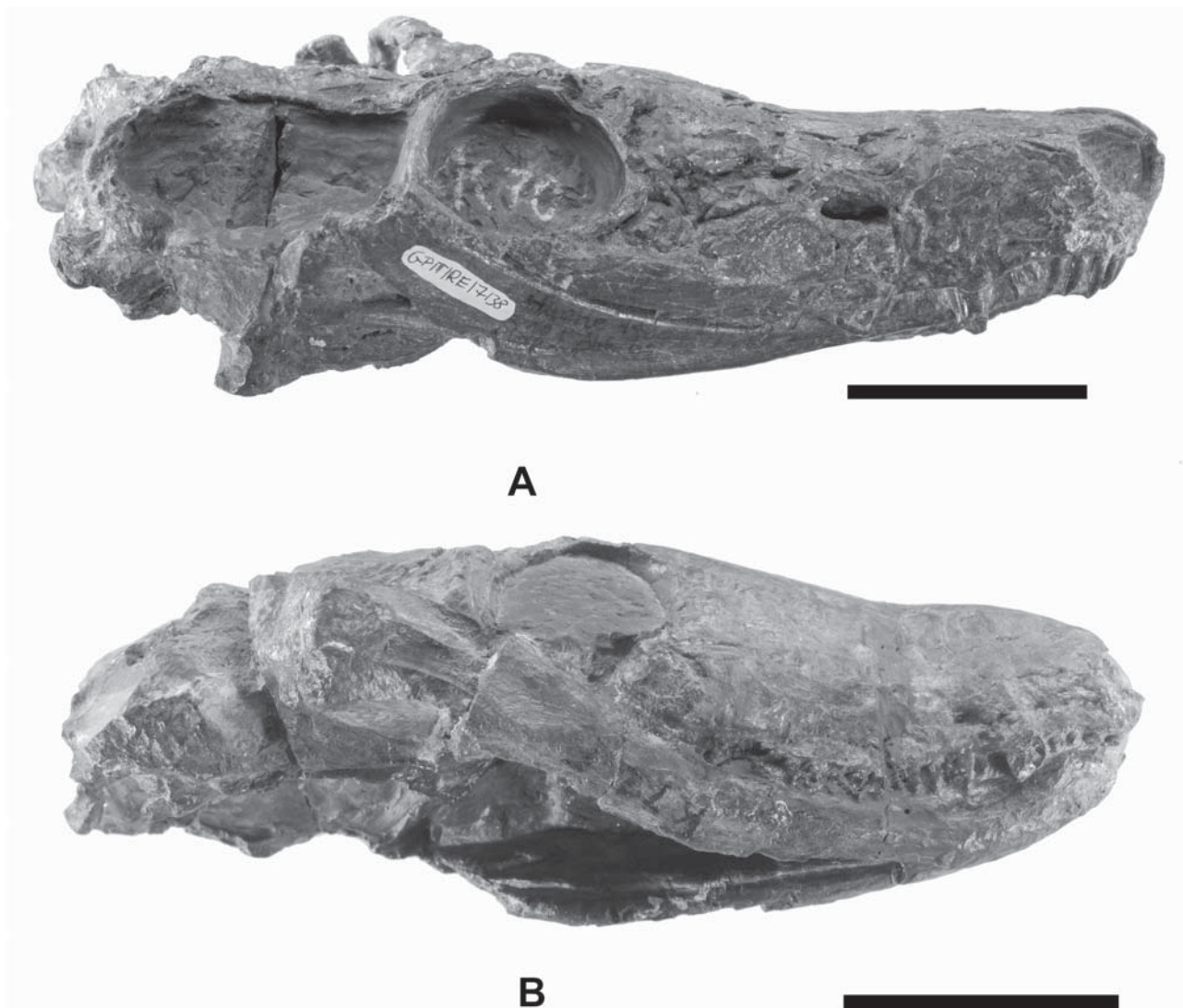
that have been traditionally grouped together. Third, the phylogenetic position of *Silphoictidoides* is investigated for the first time by rigorous parsimony analysis, and it is demonstrated to represent a baurioid, being one of the most basal taxa of this important and diverse therocephalian clade.

**Institutional abbreviations:** GPIT – Institut für Geowissenschaften, Tübingen.

**Abbreviations used in figures:** an = angular, boc = basioccipital, bs = basisphenoid, d = dentary, e.n. = external naris, ex = exoccipital, f = frontal, f.ipt. = fenestra interpterygoidea, f.l. = foramen lacrimale, f.m. = foramen magnum, f.mx. = foramen maxillare, f.p. = foramen parietale, f.pt. = fenestra posttemporalis, f.smx. = foramen septomaxillare, f. sob. = fenestra suborbitalis, f.temp. = fenestra temporalis, ip = interparietal, j = jugal, l = lacrimal, l.r.a. = lamina reflecta angularis, mx = maxilla, n = nasal, o = orbit, op = opisthotic, pa = parietal, pal = palatine, pmx = premaxilla, por = postorbital, prf = prefrontal, pt = pterygoid, soc = supraoccipital, sq = squamosal, t = tabular

## Acknowledgements

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**Fig. 1.** *Silphoictidoides ruhuhuensis* VON HUENE, 1950 from the Usili Formation (Upper Permian) of Kingori, Ruhuhu Basin, Tanzania. **A:** holotype, GPIT/RE/7138 **B:** referred specimen GPIT/RE/7139. In right lateral view. Scale bar equals 40 mm.

## 2. Systematic palaeontology

Therapsida BROOM, 1905

Theriodontia OWEN, 1876

Terocephalia BROOM, 1905

Baurioidea BROOM, 1911

Genus *Silphoictidoides* VON HUENE, 1950

Type species: *Silphoictidoides ruhuhuensis* VON HUENE, 1950

**Holotype:** GPIT/RE/7138 (formerly GPIT K 70), an almost complete skull and mandible (Figs. 1A, 2A, 3A, 4A, 5, 7).

**Referred material:** GPIT/RE/7139 (formerly GPIT K 125), an incomplete skull and mandible (Figs. 1B, 2B, 3B, 4B, 8) and associated right humerus.

**Type locality:** Kingori, Ruhuhu Valley, Tanzania.

**Type horizon:** Usili (Kawinga) Formation; Late Permian (Lopingian), coeval to the ?*Cistecephalus* to *Daptocephalus* assemblage zones of the South African Karoo (SIDOR et al. 2010; ANGIELCZYK et al. 2014a, b).

**Diagnosis:** Small therocephalian (skull length less than 200 mm); rostrum moderately long, narrow and low; lacrimal and nasal not in contact; lacrimal subequal in size to prefrontal, maxilla-prefrontal contact thus very short (though basically



**Fig. 2.** *Silphoictidoides ruhuhuensis* VON HUENE, 1950 from the Usili Formation (Upper Permian) of Kingori, Ruhuhu Basin, Tanzania. **A:** Holotype, GPIT/RE/7138. **B:** Referred specimen GPIT/RE/7139. In left lateral view. Scale bar equals 40 mm.

a homoplastic reversal, this can be – within the context of basal baurioids – regarded as a potentially autapomorphic feature distinguishing the taxon from *Ictidosuchops* and *Ictidosuchooides*; postorbital bar completely ossified; no skull roof or mandibular bosses present; foramen parietale well-developed and enclosed by anterior extension of parietal crest; parietal intertemporal exposure narrow; posterodorsal inclination of temporal skull roof absent; occipital condyle somewhat tripartite and formed by basioccipital and exoccipitals; two functional upper precanines and one upper canine of moderate size present; no longitudinal grooves on upper incisors; up to eleven monocuspid upper postcanines; no teeth on pterygoid boss; interpterygoid vacuity well developed.

### 3. Description

VON HUENE (1950) already provided a rather extensive and largely accurate description accompanied by several line drawings. Some additional observations were later made by MENDREZ (1972). Thus, description here focuses on points of phylogenetic interest or those overlooked by previous studies. The description is mainly based on the better preserved holotype skull, GPIT/RE/7138, with reference to the referred material indicated as such. The specimens are generally well preserved. The holotype skull has suffered damage from superficial erosion, though, particularly in the skull roof and occiput, so that sutures



**Fig. 3.** *Silphoictidoides ruhuhuensis* VON HUENE, 1950 from the Usili Formation (Upper Permian) of Kingori, Ruhuhu Basin, Tanzania. **A:** Holotype, GPIT/RE/7138. **B:** Referred specimen GPIT/RE/7139. In dorsal view. Scale bar equals 40 mm.

are often very difficult to detect. The cranial sutures are clearer in the referred specimen, GPIT/RE/7139, at least in the dermal roofing elements. The latter has suffered more from lateral compression and also lacks the tip of the snout and a large portion of the occiput and posterior temporal arcade.

**General skull shape** (Figs. 1–5, 7–8): The rostrum is moderately long and narrow, as well as quite low. The dorsal outline of the preorbital region is not only straight but even slightly concave in both specimens, much more so in the holotype. The apparent differences (see

also measurements given in Table 1) seem to result from a combination of the smaller size of the referred specimen, as well as a slight lateral compression of it. The holotype, on the other hand, seems to have been slightly compressed dorsoventrally, if at all. The nares are moderately large and anterolaterally directed in the holotype. The incompleteness of the referred specimen makes assessment of this character more difficult, but it appears to have displayed a similar morphology.

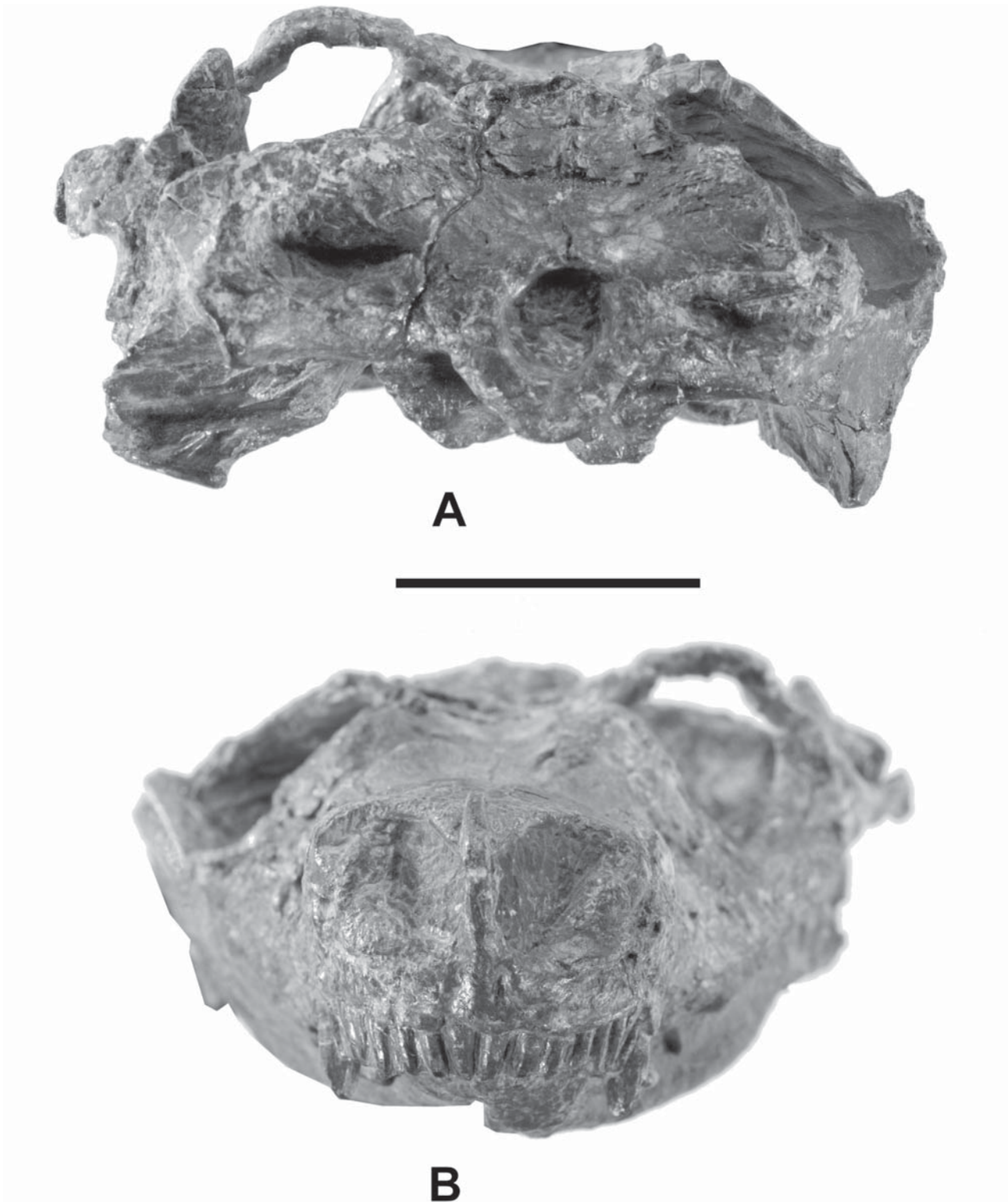
There is a distinct postcaniniform constriction in both specimens. Only a slight indication of a preorbital



**Fig. 4.** *Silphoictidoides ruhuhuensis* VON HUENE, 1950 from the Usili Formation (Upper Permian) of Kingori, Ruhuhu Basin, Tanzania **A:** Holotype, GPIT/RE/7138. **B:** Referred specimen GPIT/RE/7139. In ventral view. Scale bar equals 40 mm.

depression is present in both specimens, not comparable to that in basal therocephalians. The anterior orbital border is situated at almost mid-length of the skull. The interorbital region is narrow (less than 20% skull length). The suborbital bar is very shallow posteriorly and only moderately deep anteriorly. The suborbital bar is not lat-

erally expanded. The postorbital bar is completely ossified but extremely slender, as best seen in the holotype. Both specimens show a distinctly concave ventral border of the zygomatic arch much better preserved in GPIT/RE/7138. The zygomatic arch is very slender. It reaches its greatest width towards the back of the arch. As in most



**Fig. 5.** *Silphoictidoides ruhuhuensis* VON HUENE, 1950 from the Usili Formation (Upper Permian) of Kingori, Ruhuhu Basin, Tanzania. **A, B:** Holotype, GPIT/RE/7138 in anterior and posterior view. Scale bar equals 20 mm.

therocephalians, the temporal fenestra is distinctly larger than the orbit. The temporal fenestra is anteroposteriorly enlarged, as in all therocephalians.

A posterodorsal inclination of the temporal region, reaching its maximum height where the parietal crest meets the lambdoidal (= occipital) crest, is absent. The intertemporal region is narrow in both specimens, as in all therocephalians. Suborbital vacuities, bordered by palatine, pterygoid and ectopterygoid are prominent in both specimens.

**Skull roof** (Figs. 1–3, 5A, 7A, B, 8A, B): A rostral process of the premaxilla is clearly seen in the holotype which also shows a moderate upturning of the premaxillary alveolar margin.

The septomaxilla is of considerable size in both specimens but does not strongly overlap the premaxilla anterovertrally. A distinct septomaxillary foramen is present between septomaxilla and maxilla.

The facial plate of the maxilla is rather low. There is a row of distinct maxillary foramina some distance above the alveolar border. The entire maxilla is pierced by numerous additional small foramina and markedly sculptured in the holotype. The distinct maxillary groove seen in *Ichibengops* (HUTTENLOCKER et al. 2015) is absent. There is a distinct concavity of the ventral maxillary margin anterior to the canine in both specimens. A broad excavation or pit in the maxilla immediately posterior to the dominant canine, which is autapomorphic for *Euchambersia*, is absent. The posterior region of the maxillary facial plate is not distinctly folded inward onto the palatal region. A maxillary process bearing a crista choanalis closely approaching the vomer is seen in both specimens. The palatal exposure of the maxilla is extensive. This is a homoplasy between baurioids, whaitsiids and cynodonts. Whether a paracanine fossa for the reception of the lower canines was present remains unclear as both specimens are preserved with articulated mandibles.

The posterior border of the nasals is rather straight, more so in the referred specimen GPIT/RE/7139 (Fig. 8). There is no fronto-nasal crest in the two specimens. The anterior portion of the nasals shows a distinct sculpture of irregular grooves and pits in the holotype. A nasal-lacrimal contact is absent (Figs. 7, 8). The prefrontal and lacrimal extend almost equally far forward on the lateral surface of the skull. The jugal does extend only slightly beyond the anterior orbital margin in both specimens. A small postorbital jugal process is clearly present in the holotype (Fig. 7).

A prefrontal-postorbital contact is absent, as best seen in the referred specimen (Fig. 8). There is no indication of a postfrontal.

The parietals participate in the posterodorsal border of the temporal fenestra in the holotype, as in all adequately known therocephalians. There is a well-developed foramen

parietale in both specimens. A parietal expansion posteriorly on the midline behind the region of the parietal foramen is present. The parietal crest is about as long as half of the temporal fenestra in the holotype. The parietal crest extends anteriorly in both specimens to enclose the foramen parietale (Figs. 7, 8).

A posteroventral process of the squamosal is present. A medially directed process of the squamosal contacting the prootic is distinct in the holotype, but the condition remains unclear in the referred specimen.

**Palate, occiput and braincase** (Figs. 4, 5B, 7C, D, 8C): An anterior expansion of the vomer is present in both specimens. The vomers are certainly fused anteriorly in the holotype, possibly showing an indistinct suture posteriorly. A ventromedian crest between the palatines on the posterior portion of vomer is present. There is no strong anterior vaulting of the vomer in the holotype, as in all adequately known scylacosaurid therocephalians (HUTTENLOCKER 2009).

Palatine teeth are absent in both specimens as in all adequately known therocephalians.

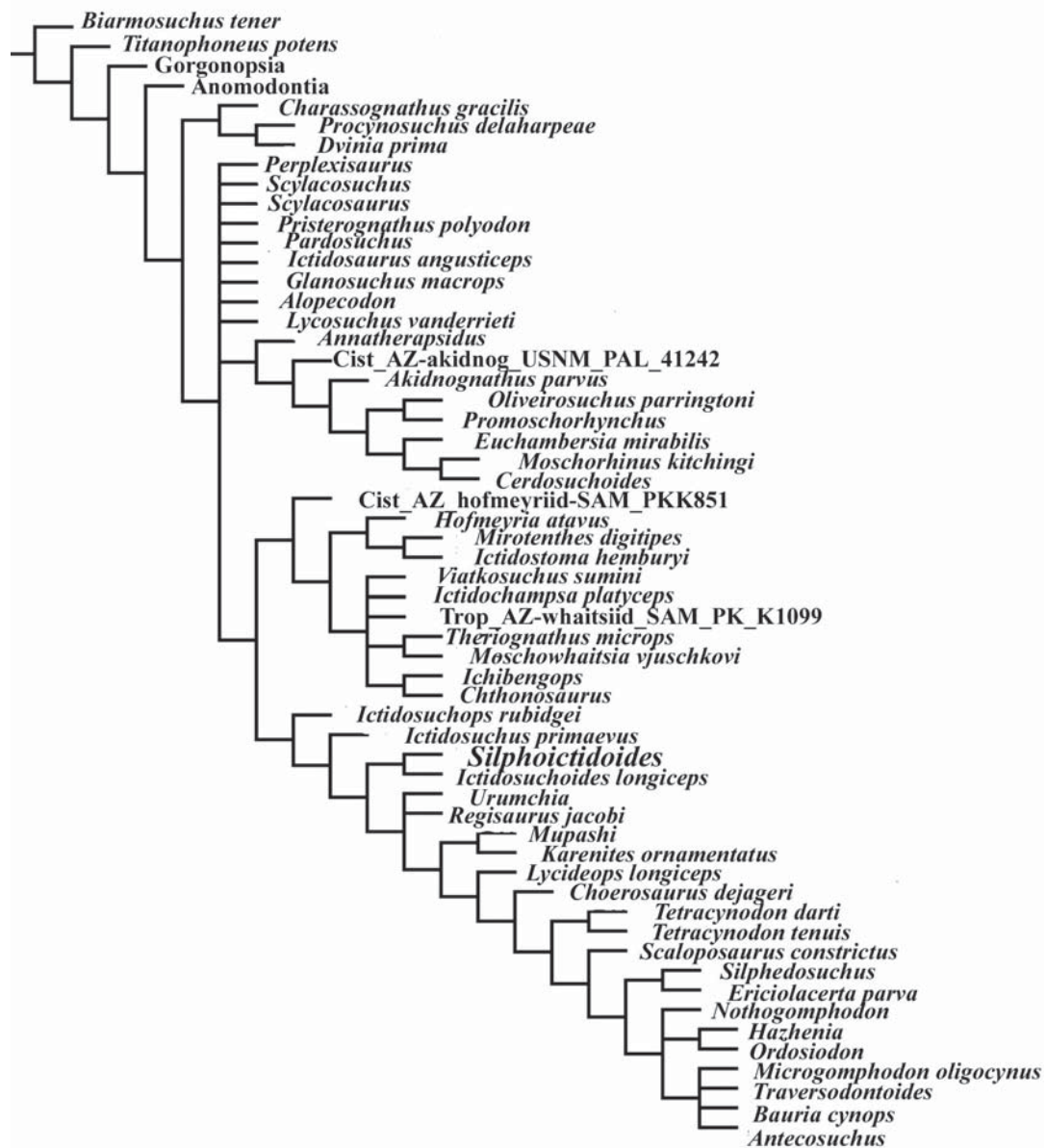
There is a clear median tubercle of the pterygoids anterior to the fenestra interpterygoidea in both specimens (Figs. 7, 8). Pterygoid teeth are absent in both specimens, including those on the transverse processes. Although pterygoid teeth are retained by a variety of therocephalians, those on the transverse process are generally absent except in the basal taxon *Lycosuchus* (VAN DEN HEEVER 1994). The pterygoid flanges display the usual derived therocephalian condition, being sharp and projected posteriorly, which is modified only in the aberrant *Euchambersia mirabilis*. The pterygoid transverse flanges are positioned at about the same level as the posterior orbital margin. The interpterygoid vacuity is enlarged and approximately teardrop-shaped, with the anterior end positioned between transverse flanges of pterygoids. Distinct parasagittal ridges run from the medial posterior flare of the transverse flanges towards the basioccipital.

The epipterygoid is only well visible in the holotype. It just contacts the parietal, as in all adequately known therocephalians, but fails to contact the frontal. The ascending process of the epipterygoid is somewhat expanded. No posterior epipterygoid apophysis is seen. The trigeminal nerve must have had its exit between prootic incisure and epipterygoid; a distinct closed foramen is absent. There is no indication of an epipterygoid/prootic overlap in the holotype.

The tubera basisphenoidalia are large in both specimens, as usual for therocephalians, but not as much as in *Lycosuchus*.

The dorsal surface of the processus paroccipitalis is distinctly concave and completely transversely oriented in the holotype. An opisthotic dorsolateral process is present. It excludes the supraoccipital from the





**Fig. 6.** Strict consensus of 100 most parsimonious trees, TL 390 steps, CI = 0,428 and RI = 0, 785 obtained by including *Silphoictidoidea ruhuhuensis* in the data matrix of HUTTENLOCKER & SIDOR (2016) with the codings listed in Appendix 1.

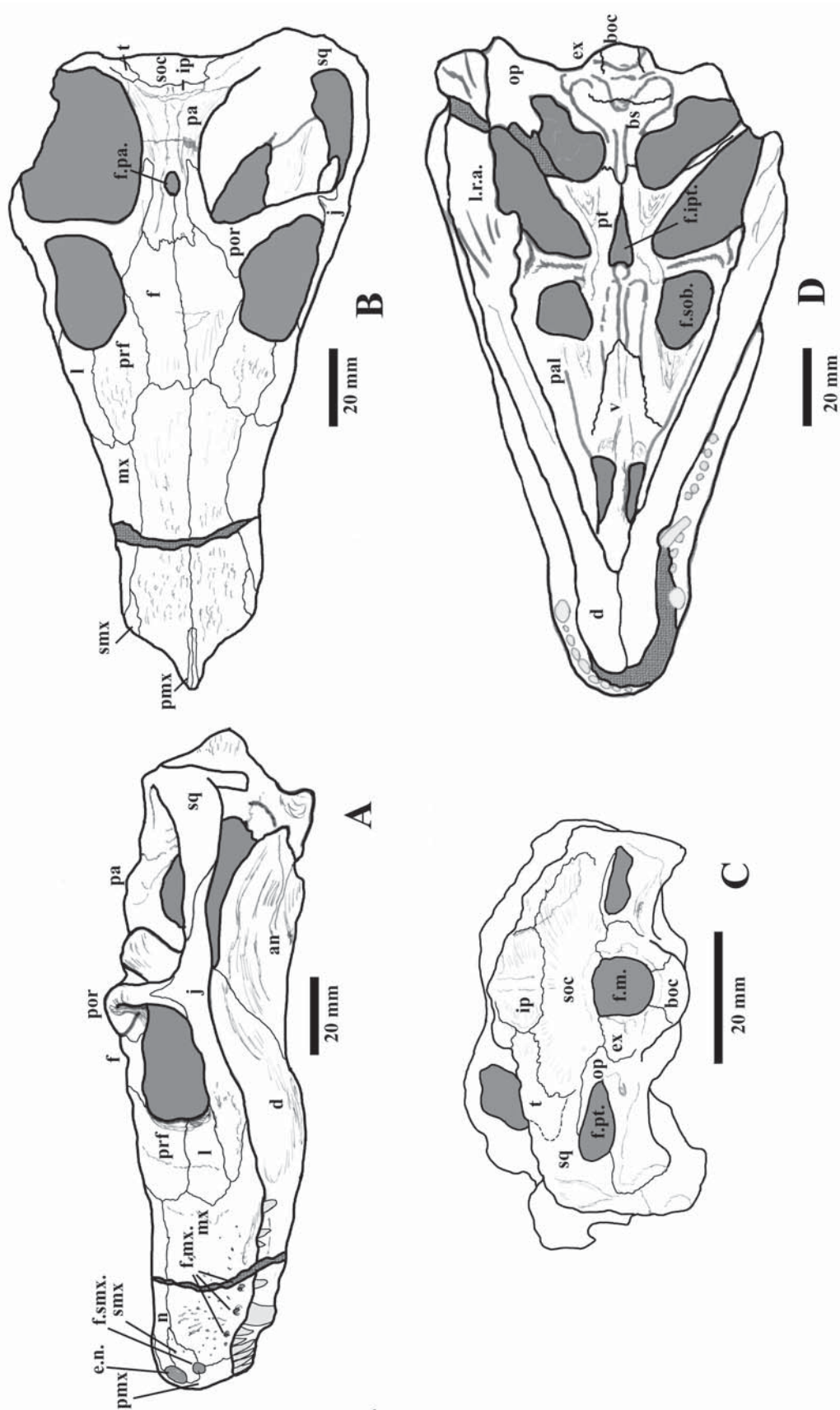
posttemporal fenestra. A distinct mastoid process sensu CROMPTON (1955), who introduced this character, is found in the holotype, as in other adequately preserved baurioids and akidnognathids such as *Promoschorhynchus* and *Oliveirosuchus*.

Due to insufficient preservation it remains unclear whether the tabular contacts the opisthotic, but it seems unlikely (dashed suture in Fig. 7C). It is of rather small size (if one compares, e.g. *Regisaurus* as described by MENDREZ 1972), being a high and narrow, dorsomedially inclined element. It nearly contacts the dorsal margin of

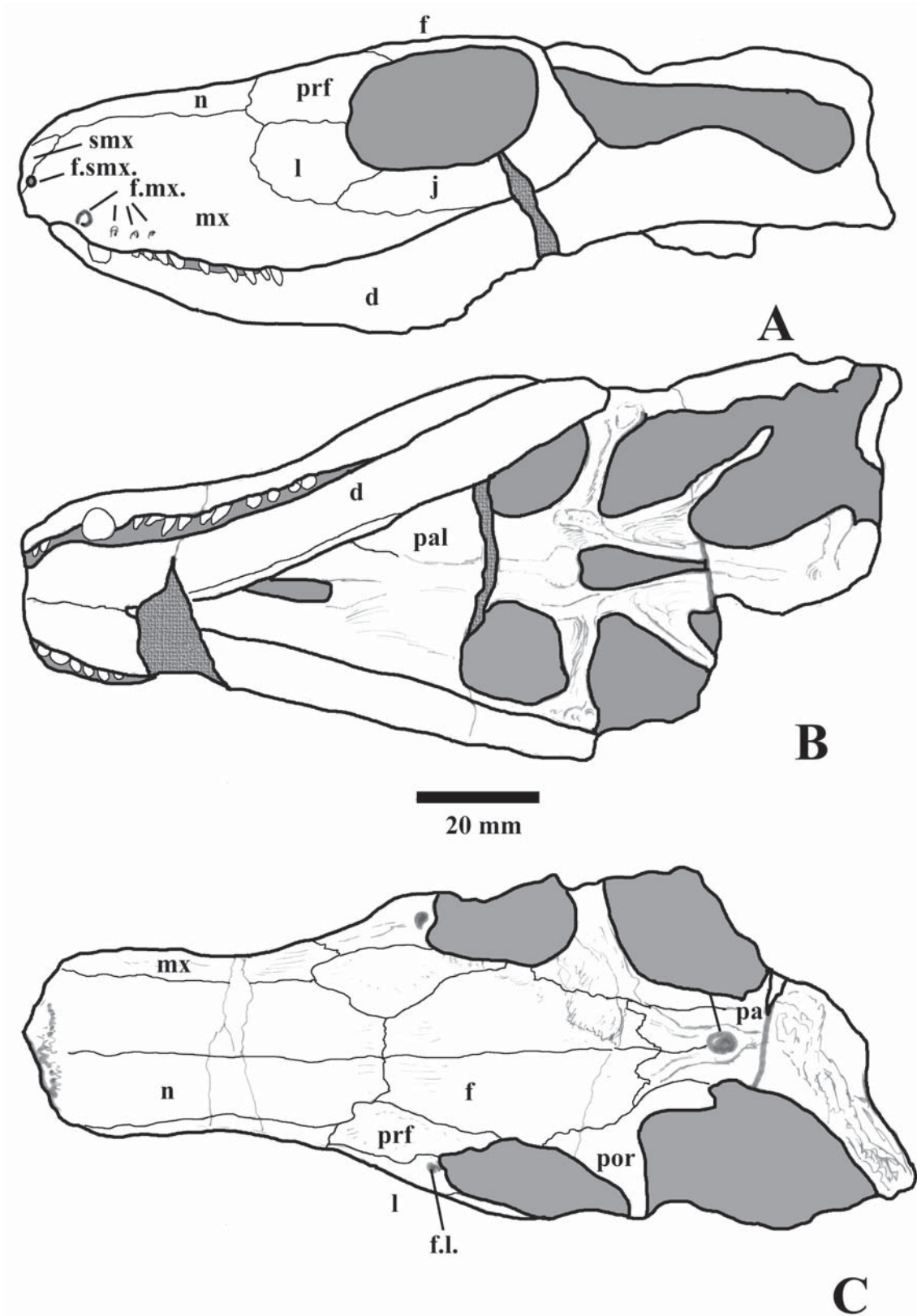
the interparietal and contributes significantly to the formation of the lambdoidal crest.

There is a single, but clearly tripartite, occipital condyle in the holotype. As sutures are not very clear in the much weathered occiputs of both specimens, the contribution made by the exoccipital may be debatable, but seems to have been most likely as figured in Fig. 7C and D. The rather tripartite shape suggests that the exoccipitals participated in the formation of the condyle.

The quadrate-quadratejugal complex is clearly reduced in height in the holotype, as in all adequately known



**Fig. 7.** Interpretative line drawings of the holotype of *Silphoictidoides ruhuhuensis* von HUENE, 1950, GPIT/RE/7138 in **A:** lateral, **B:** dorsal, **C:** occipital and **D:** ventral view. Scale bars equals 20 mm.



**Fig. 8.** Interpretative line drawings of the referred skull of *Silphoictidoides ruhuhuensis* VON HUENE, 1950 GPIT/RE/7139 in **A:** lateral, **B:** dorsal and **C:** ventral view. Scale bar equals 20 mm.

therocephalians. It is situated in a distinct depression on the anterior face of the squamosal (quadrate recess). The presence of a posteroventral process on the quadrate that fits into a posterior notch of the squamosal is seen on the left side of the holotype specimen. The stapedes are absent in both specimens.

**Lower jaw** (Figs. 1, 2, 4, 7A, D, 8A, C): The dentary is long and slender, but with a distinct dorsoventral curvature in both specimens. The dentary continuously tapers anteriorly in both specimens, as in many derived therocephalians, including adequately known baurioids such as *Ictidosuchus*. In ventral view, the area between left and right dentaries widens greatly posteriorly. There is no specialized boss on the posteroventral face of the dentary. There is only a slight thickening of the symphyseal region. The postcanine constriction is only slightly developed. A shallow lateral dentary sulcus is present in both specimens. There is no pronounced dentary angle. The dentary does not show a fossa masseterica. Dentary height increases posteriorly, the postdentary bones are reduced so that a free standing coronoid process is formed. The coronoid process extends up to the dorsal orbital half. The posterodorsal coronoid margin is rather rounded.

The postdentary bones are slightly lower than the dentary and the angular is clearly positioned dorsal to the dentary in both specimens. The splenial is entirely covered by the dentary, as in all therocephalians. There is a distinct small mandibular fenestra in the holotype (see Fig. 1A; it is obscured by compression on the left side of the specimen). This is a potential eutheriocephalian autapomorphy (HUTTENLOCKER 2009). The reflected lamina is only partially preserved in the holotype (best seen in right lateral view, Fig. 1A), but it appears to be moderately large, although not extending below the dentary. As far as preservation allows to assess, the lamina reflecta was of normal size and not reduced in the holotype. Nothing definite can be made out about potential ornamentation of the reflected lamina.

**Dentition** (Figs. 1, 2, 5B, 7A, D, 8A, C): There are six upper incisors in the holotype, as in most baurioids except bauriamorphs like *Bauria* and *Microgomphodon* where there are only four (BRINK 1963; ABDALA et al. 2014). The marked lateral overlap of the maxilla on the premaxilla, seen in many small therocephalians, makes it appear as if there were three precanines in lateral view of the skull (see Fig. 7A), which is definitely not the case. There is no indication of longitudinal grooves in the upper incisors. None of the specimens shows interlocking incisors, as, with exception of some akidnognathids (e.g., *Promoschorhynchus*), do all adequately known therocephalians. The incisors are rather straight and conical. The cusps of the upper incisors are smoothly ridged in both specimens. At least two upper precanines are present. The upper canine is of moderate size. There are no

ridges alongside the anterior upper canine surface as in *Euchambersia mirabilis* (BÉNOIT et al. 2017). There are numerous upper postcanines (most probably 11) in both specimens. There are no distinct cusps in the rather slender and tall upper postcanines. The relative length of the maxillary tooth row exceeds 50% of the total maxillary length. The lower dentition remains unknown, due to the occluded mandible present in the specimens.

#### 4. *Silphoictidoides* – a valid genus so far endemic to East Africa

Very few modern studies of therocephalians are available, particularly with regard to the small forms (“scaloposaurs”), some of which may actually represent juvenile specimens of other taxa (MENDREZ-CARROLL 1979; HUTTENLOCKER 2009; SIGURDSEN et al. 2012). A large-scale revision of these forms is long overdue. The cladistic approach by HUTTENLOCKER (2009, 2014) and the recent re-description of *Tetracynodon darti* by SIGURDSEN et al. (2012) have, however, much improved the general understanding of these forms and their interrelationships. It is only within the context these authors have recently provided that a meaningful re-evaluation of *Silphoictidoides* has become possible.

Of the valid genera of therocephalians, *Silphoictidoides* is here compared mainly to *Scaloposaurus*, *Regisaurus*, *Urumchia*, *Tetracynodon*, *Choerosaurus*, *Lycideops*, *Karenites*, *Mupashi*, *Ictidosuchops*, *Ictidosuchus* and *Ictidosuchoides* as all other smaller-sized therocephalians known are too far removed from it morphologically and – as demonstrated below – phylogenetically to make close comparison necessary. *Lycideops*, *Choerosaurus* and *Tetracynodon* differ by the contact of lacrimal and nasal in the skull roof, which is not present in *Silphoictidoides*. These three taxa can also be distinguished from *Silphoictidoides* by the absence of the foramen parietale, considerably more elongate snouts and rather straight zygomatic arches (see SIGURDSEN et al. 2012). *Regisaurus* differs by the complete reduction of the foramen parietale, the lack of precanines and the occipital condyle being exclusively formed by the basioccipital (MENDREZ 1972). Whereas the postorbital bar is complete in *Silphoictidoides*, it is incomplete in *Tetracynodon* and *Choerosaurus*, and lacking in *Scaloposaurus*. In contrast to *Silphoictidoides*, both *Tetracynodon* and *Scaloposaurus* display rather wide and flat parietals (MENDREZ-CARROLL 1979; SIGURDSEN et al. 2012). *Choerosaurus* further differs by the presence of unusual skull bosses (HAUGHTON 1929; BÉNOIT et al. 2016).

The genus *Urumchia* from China very closely resembles *Regisaurus* in palatal structure, but it is somewhat larger, with a rather short and massive skull and few postcanines (SUN 1991). The genus *Karenites* from Russia

has no parietal foramen, a very low coronoid process and multicuspid postcanines, as well as an unusually sculptured skull roof (TATARINOV 1995; IVAKHNENKO 2011). The recently described karenitid *Mupashi* from the Upper Permian of Zambia (HUTTENLOCKER & SIDOR 2016) is also distinct in many features. It has, e.g., only a slit-like parietal foramen, a distinctive boss at the dentary angle, as does *Karenites* (TATARINOV 1995; IVAKHNENKO 2011) and at least 15 upper postcanines, as well as a highly reduced interpterygoid vacuity.

Most difficult to compare is the South African genus *Ictidosuchus*, as modern descriptions of this form are scarce. *Ictidosuchus* was originally based on an incompletely preserved skull and mandible and some associated postcrania (BROOM 1900, 1901; BOONSTRA 1935). It clearly differs from *Silphoictidoides* in several features. Its rostrum is shorter and broader, it retains a posterodorsal inclination of the temporal skull roof coming to a point where it meets the lambdoidal crest, it lacks a forward extension of the parietal crest that includes the parietal foramen, and it possesses longitudinal grooves on the incisors and has a considerably larger upper canine. None of these features may be seen as autapomorphic on their own, but in combination they indicate generic difference between the two taxa.

*Ictidosuchops* and *Ictidosuchooides* were based on better material (articulated skulls), which was well described by BRINK (1961). MENDREZ (1972), who did not discuss *Ictidosuchus*, already pointed out some differences between these genera and *Silphoictidoides*. *Ictidosuchops* is distinguished by a wider intertemporal region, incomplete postorbital bar, missing anterior extension of the parietal

crest, reduced lacrimal, three precanines, and the presence of pterygoid boss teeth. *Ictidosuchops* further differs by a shorter rostrum and a larger upper canine (coming closer to *Ictidosuchus* in this respect), as well as the presence of only five upper incisors. In combination these features, again, can be used to uphold a generic distinction.

*Ictidosuchooides* was distinguished from *Silphoictidoides* by MENDREZ (1972) by a smaller parietal foramen, a wider interparietal and the presence of two functional canines (which may just be a transitional stage in tooth replacement; C. KAMMERER, pers. comm.). It also retains a posterodorsal temporal inclination, just as *Ictidosuchus*, and lacks the anterior extension of the parietal crest (as *Ictidosuchops* and *Ictidosuchus*). As seen in the detailed description of BRINK (1961), there are also considerable differences in the configuration of the skull roof bones. The maxilla is much longer in *I. longiceps*, whereas the lacrimal reaches much less forwards than in *S. ruhuhensis* on the lateral side of the skull. The contact between maxilla and prefrontal thus is much more extensive in *I. longiceps* (compare Fig. 7A and BRINK 1961: fig. 42). The configuration in *S. ruhuhensis* is more reminiscent in this respect of forms such as *Regisaurus* (MENDREZ 1972) than it is of *Ictidosuchooides*. This can be seen as at least a potential autapomorphic feature of the genus *Silphoictidoides* (although it is a homoplastic reversion).

Although there remains no doubt that *Ictidosuchooides* and *Silphoictidoides* are very closely related, they are sufficiently different to indicate taxonomic separation. Ontogenetic differences can be safely excluded, as the material of both species is very comparable in size. The basal skull length is (131) to 150 mm in BRINK's (1961)

**Table 1.** Measurements [in millimetres]. Some measurements of the referred specimen remain uncertain due to incomplete preservation. The somewhat smaller referred specimen differs mainly due to a somewhat shorter and laterally compressed snout. The shorter snout appears to be ontogenetically caused, as the specimen is somewhat smaller and snout length tends to increase ontogenetically in most eutheriodonts. The higher snout can be attributed to distortion.

	GPIT/RE/7138/B	GPIT/RE/7139
Basal skull length (tip of snout to tip of condyle)	142.5	ca. 120
Largest skull length /to posterior margin of skull)	148	ca. 124
Minimal intertemporal width	11.5	ca. 12
Minimal interorbital width	22	23
Length of orbit (left side)	31.5	23
Length of temporal fenestra lateral (left side)	32	31
Length of temporal fenestra medial (left side)	28	25
Maximum length of temporal fenestra (measured obliquely)	42	40
Minimal width of snout	33	25
Height of snout behind canines	21.5	22
Preorbital length	70,5	ca. 57
Occipital width of skull	45	ca. 36
Length of lower jaw	123	-
Pretemporal length of skull	98	ca. 86

material (three specimens) of *Ictidosuchoides longiceps* versus (120) to 142 mm in *Silphoictidoides* (see Table 1).

KAMMERER (2008) suggested that Triassic specimens referred to *Ictidosuchoides* and *Ictidosuchops* were “indefinite juvenile baurioids”. This suggestion seems plausible and illustrates the dire necessity of a thorough revision of these taxa. At any rate, *Silphoictidoides* is unlikely to be a juvenile of another taxon. The two skulls discovered agree very well in size and show no distinctive juvenile features. The only other therocephalians so far known from the Usili Formation are whatsiids (attributed to several South African taxa by VON HUENE 1950, to *Theriongnathus* by MAISCH 1999, followed by HUTTENLOCKER & ABDALA 2015).

Furthermore, the demonstrable differences between *Ictidosuchoides* and *Silphoictidoides* also refute the recent claim by HUTTENLOCKER & SIDOR (2016) that the two genera should be synonymized, although they certainly were right in recognizing their very close relationship. One may argue that the features distinguishing *Silphoictidoides* from its South African relatives are rather insignificant. But as very comparable features are currently used to keep the South African genera apart, and as *Silphoictidoides* differs more widely from any of these than they differ from each other it is certainly not advisable to synonymize the genus with any of the known South African forms. It is therefore a valid genus of therocephalian characterised by a unique set of features (see diagnosis) that so far seems to be endemic to the Ruhuhu Basin of Tanzania, just as quite a number of dicynodont and gorgonopsian species (although some recent studies, including KAMMERER’S (2016) thorough revision of the rubidgeine gorgonopsians, have eliminated a few taxa), as far as is currently known. Lacking clear-cut autapomorphies, it must, nonetheless, be considered to be almost a “metataxon” at the moment, but with more data on the South African forms becoming available, as expected considering the remarkably intense ongoing therocephalian research, this must not be the final word on that matter.

Although the fauna of the Usili Formation shows clear similarities to that of the latest Permian *Cistecephalus* to *Daptocephalus* assemblage zones of South Africa (SIDOR et al. 2010; ANGIELCZYK et al. 2014a, b) (including the common occurrence of the whatsiid therocephalian *Theriongnathus microps* (MAISCH 1999; HUTTENLOCKER & ABDALA 2015), it is still distinguished by its own “flavour” (see SIDOR et al. 2010). The more we learn about the fauna, the more it seems to become “similar but distinct”. *Silphoictidoides* just adds to this view. Even if the South African “ictidosuchids” should be generically synonymized in a future study, there remains enough reason to keep *S. ruhuhuensis* at least as a distinct species, as it is more different to any of them than they are among each other.

## 5. Phylogenetic analysis of *Silphoictidoides* – a basal baurioid

*Silphoictidoides ruhuhuensis* was coded for the most recent and extensive data matrix published by HUTTENLOCKER & SIDOR (2016) which expands on earlier matrices by HUTTENLOCKER (2009), SIGURDSEN et al. (2012), HUTTENLOCKER (2014), and HUTTENLOCKER et al. (2015).

The data were analyzed with TNT (GOLOBOFF et al. 2008). Trees were rooted on the outgroup, *Biarmosuchus tener*. Characters were treated as unweighted and unordered. A traditional search was done, as in the original analysis, using 100 replicates, tree bisection and reconnection branch swapping and a random addition sequence in effect.

100 most parsimonious trees were retained with a length of 390 steps (9 steps longer than the original analysis), a consistency index of 0.428 and a retention index of 0.785. This comes close to the original values of the analysis by HUTTENLOCKER & SIDOR (2016). Resolution is limited in the strict consensus tree in the basal therocephalians, as it is in the original analysis. The monophyla of the higher therocephalians, discussed at length by HUTTENLOCKER & SIDOR (2016) are, however, well reproduced. *Silphoictidoides* is found to be the sister taxon of *Ictidosuchoides longiceps*, being comfortably placed within basal Bauriamorpha. The results are shown in Fig. 6.

Closer comparison to the results of HUTTENLOCKER & SIDOR (2016) shows major agreement. The basal polytomy is, however, more extensive, including *Scylacosuchus*, *Glanosuchus* and *Priosterognathus*. The Akidnognathidae and Moschorhininae of HUTTENLOCKER & SIDOR (2016) is found with the exact same topology. *Ichibengops* and *Chthonosaurus*, united in the Chthonosauridae by HUTTENLOCKER & SIDOR (2016) also form a monophylum in the present analysis. However, they are found in a much more derived position within the Whatsiioidea, which is somewhat surprising. The Whatsiioidea otherwise shows the same topology as in the original analysis.

The polytomy of the basal baurioids *Ictidosuchops*, *Ictidosuchus* and *Ictidosuchoides* found in the original analysis is resolved due to the inclusion of *Silphoictidoides*. *Ictidosuchops* is found to be the most basal baurioid, followed by *Ictidosuchus*, whereas *Ictidosuchoides* and *Silphoictidoides* are sister-taxa. *Urumchia* and *Regisaurus*, forming a monophylum in HUTTENLOCKER & SIDOR’S (2016) analysis instead form a polytomy with the higher baurioids. *Mupashi* and *Karenites* are sister-taxa, as in the original analysis. *Lycideops*, *Choerosaurus* and *Tetracynodon* are, however, not found to be monophyletic but form successive sister groups to the Bauriamorpha. The Bauriamorpha is found to be monophyletic, as is the Bauriidae, but with considerably less resolution than in the original analysis.

## 6. Conclusions

The limited resolution, which is actually found in all current analyses of therocephalian interrelationships is certainly due to several reasons. First of all many taxa lack adequate modern descriptions. Second a lot of taxa have been prone to the traditional “headhunting” practices of many former palaeontologists working in the Karoo, so that very limited data on the potentially very significant postcranial skeleton are available. Thirdly the taxonomy of many therocephalian groups is still in need of much revision, the “scaloposaurs” forming no exception. The analyses of previous authors, on which the present one is almost exclusively based, have therefore be seen as work in progress. With more descriptions and revisions of therocephalians becoming available, our understanding of phylogeny will surely improve.

At any rate, as far as current knowledge allows to assess, *Silphoictidoidea* can be relatively safely placed within the Baurioidea as a rather basal member of the group, close to such South African genera *Ictidosuchops*, *Ictidosuchus* and particularly *Ictidosuchoidea*. When VON HUENE (1950) laconically stated “die beiden kleinen Therocephalenschädel gehören offensichtlich in die Familie der Ictidosuchiden” [the two small therocephalian skulls obviously belong to the family Ictidosuchidae] (VON HUENE 1950: 101) he was perfectly right, except that the Ictidosuchidae is today regarded as a paraphyletic assemblage of basal baurioids. With our fluctuating state of knowledge on therocephalian phylogeny even this may change in the future.

## 7. References

- ABDALA, F., JASHASHVILI, T., RUBIDGE, B. S. & VAN DEN HEEVER, J. A. (2014): New material of *Microgomphodon oligocynus* (Eutherapsida, Therocephalia) and the taxonomy of southern African Bauriidae. In: KAMMERER, C. F., ANGIELCZYK, K. D. & FRÖBISCH, J. (Eds.): Early Evolutionary History of the Synapsida, p. 209–231; Dordrecht (Springer).
- ANGIELCZYK, K. D., HUERTAS, S., SMITH, R. M. H., TABOR, N. J., SIDOR, C. A., STEYER, J. S., TSUIJI, L. A. & GOSTLING, N. J. (2014a): New dicynodonts (Therapsida, Anomodontia) an updated tetrapod stratigraphy of the Permian Ruhuhu Formation (Songea Group, Ruhuhu Basin) of southern Tanzania. – *Journal of Vertebrate Paleontology*, **34**: 1408–1426.
- ANGIELCZYK, K. D., STEYER, J. S., SIDOR, C. A., SMITH, R. M. H., WHATLEY, R. L. & TOLAN, S. (2014b): Permian and Triassic dicynodont (Therapsida, Anomodontia) faunas of the Luangwa Basin, Zambia: taxonomic update and implications for dicynodont biogeography and biostratigraphy. In: KAMMERER, C. F., ANGIELCZYK, K. D. & FRÖBISCH, J. (Eds.): Early Evolutionary History of the Synapsida, p. 93–138; Dordrecht (Springer).
- ARCHIBALD, J. D. (1994): Metataxon concepts and assessing possible ancestry using Phylogenetic Systematics. – *Systematic Biology*, **43**: 27–40.
- BÉNOIT, J., MANGER P. R., FERNANDEZ, V. & RUBIDGE, B. S. (2016): Cranial Bosses of *Choerosaurus dejageri* (Therapsida, Therocephalia): Earliest Evidence of Cranial Display Structures in Eutheriodonts. – *PLoS ONE*, **11** (8): e0161457. doi:10.1371/journal.pone.0161457
- BÉNOIT, J., NORTON L. A., MANGER P. R. & RUBIDGE B. S. (2017): Reappraisal of the envenoming capacity of *Euchambersia mirabilis* (Therapsida, Therocephalia) using  $\mu$ CT-scanning techniques. – *PLoS ONE*, **12** (2): e0172047.
- BOONSTRA, L. D. (1935): On some South African reptiles of the suborder Therocephalia preserved in the American Museum of Natural History. – *American Museum Novitates*, **771**: 1–12.
- BROOM, R. (1900): On a new theriodont reptile (*Ictidosuchus primaevus*) from the Karroo Beds, South Africa. – *Annals and Magazine of Natural History*, **6**: 314–316.
- BROOM, R. (1901): On *Ictidosuchus primaevus*. – *Transactions of the South African Philosophical Society*, **11**: 177–184.
- BRINK, A. S. (1961): On some small therocephalians. – *Palaeontologia Africana*, **7**: 155–182.
- BRINK, A. S. (1963): On *Bauria cynops* BROOM. – *Palaeontologia Africana*, **8**: 39–56.
- CROMPTON, A. W. (1955): A revision of the Scaloposauridae with special reference to kinetism in this family. – *Navorsing van die Nasionale Museum, Bloemfontein*, **1**: 149–183.
- GOLOBOFF, P. A., FARRIS, J. S. & NIXON, K. C. (2008). TNT, a free program for phylogenetic analysis. – *Cladistics* **24**: 774–786.
- HUENE, F. VON (1950): Die Theriodontier des ostafrikanischen Ruhuhu-Gebiets in der Tübinger Sammlung. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **92**: 47–136.
- HUTTENLOCKER, A. (2009): An investigation into the cladistic relationships and monophyly of therocephalian synapsids (Amniota: Synapsida). – *Zoological Journal of the Linnean Society*, **157**: 865–891.
- HUTTENLOCKER, A. K. (2014): Body size reductions in nonmammalian eutheriodont therapsids (Synapsida) during the end-Permian mass extinction. – *PLOS One*, **9** (2): e87553.
- HUTTENLOCKER, A. K. & ABDALA, F. (2015): Revision of the first therocephalian (Therapsida), *Therionathus microps* OWEN, and implications for cranial ontogeny and allometry in non-mammalian eutheriodonts. – *Journal of Paleontology*, **89**: 645–664.
- HUTTENLOCKER, A. K. & SIDOR, C. A. (2016): The first kareнитid (Therapsida, Therocephalia) from the Upper Permian of Gondwana and the biogeography of Permo-Triassic therocephalians. – *Journal of Vertebrate Paleontology*, **36**: c111897.
- HUTTENLOCKER, A. K., SIDOR, C. A. & ANGIELCZYK, K. D. (2015): A new eutheroccephalian (Therapsida: Therocephalia) from the upper Madumabisa Mudstone Formation (Luangwa Basin) of Zambia. – *Journal of Vertebrate Paleontology*, **35**: e969400.
- HAUGHTON, S. H. (1929): On some new therapsid genera. – *Transactions of the Royal Society of South Africa*, **28**: 55–78.
- IVAKHNENKO, M. F. (2011): Permian and Triassic therocephals (Eutherapsida) of Eastern Europe. – *Palaeontological Journal*, **45**: 981–1144.
- KAMMERER, C. F. (2008): A new therocephalian from the *Cistecephalus* Assemblage Zone of South Africa and new information on therocephalian systematics. – *Journal of Vertebrate Paleontology*, **28** (Supplement 3): 98A–99A.
- KAMMERER, C. F. (2016): Systematics of the Rubidgeinae (Therapsida: Gorgonopsia). – *PeerJ*, **4**: e1608; DOI 10.7717/peerj.1608

- MAISCH, M. W. (1999): The tetrapods from the Late Permian of Tanzania in the collections of the Institut und Museum für Geologie und Paläontologie der Universität Tübingen, with special reference to the pristerodontian dicynodonts. – Ph. D. Dissertation, Eberhard Karls Universität Tübingen, Germany, 350 pp.
- MENDREZ, C. H. (1972): On the skull of *Regisaurus jacobi*, a new genus and species of Bauriamorpha WATSON and ROMER 1956 (Scaloposauria BOONSTRA 1953), from the Lystrosaurus zone of South Africa. In: JOYSEY, K. A. & KEMP, T. S. (Eds.): Studies in Vertebrate Evolution, p. 191–212; Edinburgh (Oliver & Boyd).
- MENDREZ-CARROLL, C. H. (1979): Nouvelle étude du crâne du type de *Scaloposaurus constrictus* OWEN, 1876, spécimen jeune, Therocephalia, Scaloposauria, Scaloposauridae, de la zone à *Cistecephalus* (Permien supérieur) d'Afrique australe. – Bulletin du Museum National d'Histoire Naturelle, (C), **1**: 155–201.
- SIDOR, C. A., ANGIELCZYK, K. D., WEIDE, D. M., SMITH, R. M. H., NESBITT, S. J. & TSUJI, L. A. (2010): Tetrapod Fauna of the Lowermost Usili Formation (Songea Group, Ruhuhu Basin) of Southern Tanzania, with a new burnetiid Record. – Journal of Vertebrate Paleontology, **30**: 696–703.
- SIGURDSEN, T., HUTTENLOCKER, A. K., MODESTO, S. P., ROWE, T. B. & DAMIANI, R. (2012): Reassessment of the morphology and paleobiology of the therocephalian *Tetracynodon darti* (Therapsida), and the phylogenetic relationships of Baurioidea. – Journal of Vertebrate Paleontology, **32**: 1113–1134.
- SUN, A. L. (1991): A review of Chinese therocephalian reptiles. – Vertebrate Palasiatica, **29**: 85–94.
- TATARINOV, L. P. (1995): A new ictidosuchid *Karenites ornamentatus* (Theriodontia) from the Upper Permian of the Kotel'nich Locality in the Kirov Region. – Russian Journal of Herpetology, **2**: 18–33.
- VAN DEN HEEVER, J. A. (1994): The cranial anatomy of the early Therocephalia (Amniota: Therapsida). – Universiteit van Stellenbosch Annale, **1994**: 1–59.

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## Appendix

Codings for *Silphoictidoides ruhuhuensis* for the data matrix of HUTTENLOCKER & SIDOR (2016)

100011010000012013001011110121111001010?210111111212111110?11211?10000111?1?2100001111111000111001100??10?0?????1  
?????????1????1