Rediscovery of the holotype of Clelandina major Broom, 1948 (Gorgonopsia: Rubidgeinae) with implications for the identity of this species

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INTRODUCTION
Clelandina is one of the rarest and most unusual gorgonopsians. Like its close relatives Dinogorgon and Rubidgea, Clelandina has an extremely baroque-ornamented skull, with extensive pachyostosis of the skull roof and zygoma, development of supraorbital and supratemporal bosses, and anteroposterior expansion of the postorbital bar. Uniquely among gorgonopsians, however, Clelandina completely lacks postcanine teeth. Reduction in postcanine count is common in Gorgonopsia, and several other taxa have lost the lower postcanines (e.g. Inostrancevia, Leontosaurus, Rubidgea), but only in Clelandina are maxillary postcanines absent as well (Kammerer 2016). In this regard it is similar to the thaitissid theroccephalian Theriongathus microps, which could indicate parallels in feeding style between these distantly-related theriodonts. Only four specimens of Clelandina are known, all of which were found in rocks of the Cistecephalus–Daptocephalus assemblage zones (late Permian) exposed near Graaff-Reinet and Murraysburg.

In his original description of the genus Clelandina, Broom (1948) included two species: the type species C. rubidgei and a referred species C. major. Clelandina rubidgei was based on a poorly-preserved skull with occluded lower jaws and some associated postcranial material found at Adendorp, south of Graaff-Reinet. Clelandina major was based on a dorsoventrally crushed cranium collected by Ben Kitching from Spandau Kop, southwest of Graaff-Reinet. Unfortunately, Broom provided no specimen numbers for the holotypes of C. rubidgei, C. major, or any of the 35 other new species named in his 1948 paper. However, as most of this paper was devoted to describing the specimens in the well-curated collection of Dr Sidney Rubidge, subsequent identification of these specimens has generally been straightforward. There is no question, for instance, that the holotype of Clelandina rubidgei is RC 57, a skull with lower jaws still housed in the Rubidge Collection, and the same is true for nearly all of the other taxa named by Broom (1948). Clelandina major, however, has proven problematic.

The earliest published record listing specimen numbers for the taxa named by Broom from the Rubidge Collection is Haughton & Brink’s (1954) comprehensive catalogue of ‘Karroo Reptilia’, Haughton & Brink (1954) stated that the holotype of Clelandina major is RC 94, which is a dorsoventrally crushed gorgonopsian cranium (Fig. 1A). This specimen also accords with Broom’s (1948) description of C. major having the left maxilla crushed outwards and the right maxilla missing (reconstructed with plaster). All subsequent authors have accepted that RC 94 is the correct specimen number for the holotype of C. major (Sigogneau 1970; Brink 1988; Sigogneau-Russell 1989; Kammerer 2016). However, Sigogneau (1970) suspected that the wrong specimen had been labelled RC 94, and considered the skull with this number in the Rubidge Collection to pertain to a Leontocephalus-like taxon. In the most recent revision of rubidgeine gorgonopsian
taxonomy, Kammerer (2016) also noted that the morphology of RC 94 does not accord with that of Clelandina (among other features, this specimen bears five maxillary postcanines) and instead considered this specimen referable to Aelurognathus tigriceps.

Given Broom’s legendarily tortuous taxonomies, it would be easy enough to write this off as one of his many misidentifications. However, in this case there are several indications that something is awry. Broom’s (1948, p. 591) figure of C. major (Fig. 1B) depicts the zygomatic arches as present, whereas these structures are missing in RC 94. Although Broom’s figures frequently portrayed idealized versions of very poorly preserved fossils, they rarely showed truly missing elements: he generally used dashed lines to indicate missing or damaged edges. Additionally, Broom (1948) gave the dimensions of the C. major holotype as roughly 270 (maximum length) × 245 mm (maximum width), whereas the dimensions of RC 94 are roughly 300 mm (basal length, dorsal skull length ~240 mm) × 135 mm. Although some uncertainty in measuring badly distorted specimens is expected, this is well outside of the margin of error. Finally, and most notably, Broom (1948, pp. 590–591) stated, ‘I can find no trace of any molars’ in the holotype of C. major. Broom was obsessive when it came to ‘molar’ (=postcanine) counts, erecting numerous theriodont taxa based on postcanine count alone and often grinding tooth rows into oblivion just to get a definitive count of the underlying roots. Although the tooth row is damaged in RC 94, the roots of five postcanines are clearly exposed in the maxilla, and definitely would have been recognized by Broom if this was the specimen he was describing as C. major.

Based on this information, it is clear that RC 94 is not the same as the specimen Broom (1948) described as the holotype of Clelandina major. Where, then, is that specimen? Haughton & Brink (1954) believed that the holotype of Clelandina major was housed in the Rubidge Collection, like C. rubidgei and almost all the other taxa described by Broom (1948). There were a few exceptions to this, however. The holotype of the gorgonopsian Cyniscops cooliei ended up in the Bernard Price Institute (currently Evolutionary Studies Institute of the University of the Witwatersrand), where it is now catalogued as BP/1/648. The holotype of the dicynodont Dicynodon robertsi ended up in the Transvaal Museum (currently Ditsong National Museum of Natural History), where it is catalogued as TM 1598. And most intriguingly, several specimens collected by the Kitchings (rather than Sidney Rubidge) ended up in the McGregor Museum in Kimberley (i.e. MMK 5028, holotype of Cyniscops kitchingi, and MMK 5033, holotype of Dicynodon moutonae). During a recent collections visit to the McGregor Museum, I found a specimen (MMK 5031; Fig. 1C) perfectly matching Broom’s (1948) description of Clelandina major. This specimen is marked with a red dot (historically used to indicate type status in South African collections) and affixed with a handwritten label identifying it as ‘Clelandina Major’ [sic]. Here, I affirm that this specimen represents the true holotype of Clelandina major and discuss its taxonomic attribution.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Gorgonopsia Seeley, 1894
Rubidgeiniae Broom, 1938
Rubidgeini Broom, 1938

Clelandina rubidgei Broom, 1948
Clelandina major Broom, 1948 syn. nov.
Tigrisaurus pricei Broom & George, 1950
Dracocephalus scheepersi Brink & Kitching, 1953

Holotype. RC 57, a poorly-preserved, extensively reconstructed cranium and lower jaws from Adendorp, Graaff-Reinet, Eastern Cape Province. Broom (1948) stated that

Figure 1. Clelandina major Broom, 1948. A, RC 94, the skull historically considered to be the holotype of C. major. B, Broom’s (1948) drawing of the holotype of C. major. C, MMK 5031, the specimen here considered to be the holotype of C. major. Scale bars equal 5 cm.
vertebrae and a partial pectoral girdle were associated with this specimen; this material could not be located during recent visits to the Rubidge Collection.

Previously-referred material. BP/1/742 (holotype of Tigrisaurus pricei), a partial cranium and lower jaws from Milton (a.k.a. Swavel Kranse), Murraysburg, Western Cape Province; RC 102 (holotype of Dracoccephalus scheepersi), a distorted cranium and lower jaws from Zuurplaaas, Graaff-Reinet, Eastern Cape Province; UCMP 35437, a dorsoventrally crushed cranium from Waterval, Graaff-Reinet, Eastern Cape Province (Kammerer 2016).

Newly-referred material. MMK 5031 (holotype of Clelandina major), a dorsoventrally crushed cranium from Spanda Kop, Graaff-Reinet, Eastern Cape Province.

Diagnosis. Large gorgonopsian (up to 36 cm basal skull length) distinguished from other rubidgeines by the complete absence of postcanine teeth, presence of an edentulous maxillary ridge, reduced palatal dentition (1–2 teeth on palatal boss), and presence of a depression on the skull roof between parietals and frontals (Kammerer 2016).

DISCUSSION

The specimen MMK 5031 is badly dorsoventrally crushed, extensively restored in plaster, and poorly prepared. Nevertheless, the exposed dorsal surface of the skull closely accords with the reconstruction presented by Broom (1948) of Clelandina major (see Fig. 1). The nasals, frontals, and left maxilla are the best-exposed and most complete elements. Notably, the frontals are excluded from the orbital margins, as is usually the case in rubidgeines (Kammerer 2016). The postorbital bar is anteroposteriorly expanded compared to non-rubidgeine gorgonopsians, and is comparable in proportions to that of RC 57. The bone surface of the skull roof does not show the rugosity present in the specimens BP/1/742 and UCMP 35437, but this is likely attributable to over-preparation, as in RC 57 and RC 102. One point where my examination of the specimen does not concord with Broom’s (1948) reconstruction is his depiction of a narrow prepaerial bone. A prepaerial was originally considered present in several other specimens now referred to Clelandina rubidgei, but as recently discussed (Kammerer 2016), the supposed ‘prepaerial’ in these specimens actually represents a narrow depression on the parietals where they contact the frontal midline. The ‘prepaerial’ of MMK 5031 is this same depression, an important autapomorphy of Clelandina rubidgei. This character, combined with Broom’s (1948) statement on the absence of postcanines in this specimen, allows Clelandina major to be confidently synonymized with C. rubidgei. Regrettably, the ventral surface of this specimen is now largely covered in plaster, obscuring almost all of the maxillae, so it was not possible to confirm the absence of postcanines based on personal observation. Nevertheless, given Broom’s intense focus on postcanine counts his statement of absence can be taken as accurate.

MMK 5031 represents only the fifth recognized specimen of Clelandina rubidgei. Like all other representatives of the species it was collected in a relatively small area of the Karoo Basin, consisting of the region around Graaff-Reinet and the adjoining Murraysburg district. As discussed by Kammerer et al. (2015), a number of Permian therapsid taxa are known only from this region, but the significance of this geographic restriction remains obscure. Possible explanations are that this region exposes rocks from a temporal interval either not preserved or not sampled elsewhere in the basin, that this region preserves a different palaeoenvironment than Cistecephalus (or basal Daptocephalus) Assemblage Zone exposures elsewhere in the basin, or simply that this reflects sampling bias, with more rare taxa recovered as the result of prolonged collection in the area on the part of the Kitching and Rubidge families. Unfortunately, despite such extensive historical collection, the Cistecephalus Assemblage Zone is understudied from a modern, high-resolution stratigraphic standpoint. Faunal change within the biozone is poorly understood, and the first appearances of biostatigraphically-important genera like Dicyonodon and Procynosuchus are poorly resolved (Viglietti et al. 2016). Additional sampling of this biozone is necessary to resolve puzzling distributions like that of Clelandina and to understand the assembly of diversity during the therapsid ‘heyday’ prior to the end-Permian mass extinction.

INSTITUTIONAL ABBREVIATIONS

BP Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg, South Africa.

MMK McGregor Museum, Kimberley, South Africa.

RC Rubidge Collection, Wellwood, Graaff-Reinet, South Africa.

TM Ditsong National Museum of Natural History, Pretoria, South Africa.

UCMP University of California Museum of Paleontology, Berkeley, U.S.A.

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REFERENCES


