Biesiespoort revisited: a case study on the relationship between tetrapod assemblage zones and Beaufort lithostratigraphy south of Victoria West

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The relationship between the tetrapod assemblage zones of the South African Karoo Basin and the lithostratigraphic divisions of the Beaufort Group is well-established, and provides an independent means of dating fossil occurrences. However, this relationship may not be consistent across the basin; a discrepancy exists between the historical tetrapod assemblages in the vicinity of Victoria West, Northern Cape Province, and the expected tetrapod assemblage zones based on mapped geology. In order to examine this disconnect, we collected fossils at two localities close to Biesiespoort railway station, a locality that was visited on a number of occasions by Robert Broom. Our fossil samples support the biostratigraphic determinations of Broom and thus confirm that the stratigraphic extent of the biozones at these localities differs from their type areas further south. The reasons for this are unclear but could be related to the northward younging of the lithological units, implying complex depositional processes, or result from difficulties in mapping. Nevertheless, caution should be exercised when using mapped geology near Victoria West as a guide to the age of fossils found there.

Keywords: *Tropidostoma*, *Cistecephalus*, biostratigraphy, Karoo, Beaufort Group, Victoria West.

INTRODUCTION

In the Main Karoo Basin of South Africa, the use of fossils to differentiate rock strata and correlate sedimentary units across the basin goes back to the earliest stratigraphic work of A.G. Bain (1845, 1856). This is perhaps most evident in the Beaufort Group, which represents a thick sequence of fluvial to lacustrine rocks deposited between the Guadalupian and Middle Triassic (Rubidge *et al*. 2016), and from which A.G. Bain first collected his fossilised 'bidental' (i.e. dicynodont) remains between 1838 and 1844. More extensive palaeontological exploration of the Karoo began after Bain sent a selection of these fossils to the Geological Society of London, bringing the existence of fossil reptiles in South Africa to the attention of the wider scientific community. By the 1890s the number of fossil vertebrates recovered from the Beaufort Group, particularly of synapsids, was sufficient to allow Seeley (1892) to propose a succession of biozones, each characterised by an assemblage of different fossil groups. This biostratigraphic succession, later refined by Broom (1906), was soon paired with lithological observations to define stratigraphic subdivisions of what was then called the 'Beaufort Series' (e.g. Rogers 1903; Rogers & Schwartz 1903; Du Toit 1905; Hatch & Corstorphine 1905, 1909). Because of a lack of reliable lithological marker horizons over much of the basin (Hancox & Rubidge 2001), tetrapod biostratigraphy provided the only reliable means to further subdivide the 5 km-thick lower division of the 'Beaufort Series' until as late as 1976 (Johnson 1976; SACS 1980; Catuneanu & Bowker 2001; Catuneanu & Elango 2001).

Finer lithostratigraphic subdivisions of the lower Beaufort into formations and members were developed in the latter half of the 20th century (Johnson 1976; Keyser & Smith 1979; Stear 1980; Turner 1981; Le Roux 1985; Jordaan 1990), during which time the biostratigraphy was further revised and formally linked to lithostratigraphic units (Kitching 1977; Keyser & Smith 1979; Rubidge 1995). In the southwestern part of the basin, these relationships are based mostly on collections along the Nuweveld Mountains extending west from Beaufort West and south towards the Swartberg Mountains; this was a result of the extensive vertical exposures along the escarpment and the relative ease of correlating horizons, and was also driven by desire for biostratigraphic constraints on the uranium-bearing sandstones of Poortjie Member, which crops out along much of the escarpment. Biostratigraphy remains an important tool for identifying lithostratigraphic horizons across the whole region, but especially north of the Nuweveld Mountains, where they can be difficult to discern in outcrop (Le Roux & Keyser 1988; Cole & Wipplinger 2001).

During research to determine the stratigraphic prove-

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nance of fossil occurrences in the Guadalupian (middle Permian) part of the Beaufort Group, it became apparent that several localities in the Victoria West district (Ubuntu Local Municipality, Pixley ka Seme District Municipality) of the Northern Cape Province demonstrated an unexpected discrepancy between the fossil assemblages reported and those expected based on the mapped lithostratigraphic units exposed. One of these localities, the area surrounding Biesiespoort railway siding on the cadastral farm plot of Nobelsfontein 248 (Fig. 1), has been visited by palaeontologists for more than a century and has produced many holotype specimens of stratigraphic significance (e.g. Broom 1921, 1925, 1935a).

The Geological Survey of South Africa (now the Council for Geoscience) mapped the region around Victoria West between 1977 and 1987 and determined that the entire area of Nobelsfontein 248 (including Biesiespoort station) exposed strata of the Poortjie Member of the Teekloof Formation (Geological Survey 1989). Thus, fossils from the area are expected to belong to the *Pristerognathus* Assemblage Zone (AZ), according to the prevailing biostratigraphic/lithostratigraphic concordance (Smith & Keyser 1995a; see Fig. 2). However, based on fossil content, the Biesiespoort area, including Nobelsfontein specifically, has long been recognised as a predominantly *Cistecephalus* AZ locality (e.g. Broom 1921; Kitching 1977; King 1988; Sigogneau-Russell 1989). Despite this, in the explanation to the geological map of Victoria West (Sheet 3122), the Geological Survey reported that the *Pristerognathus* AZ corresponded to the Poortjie Member and the *Tropidostoma* AZ to the lower majority of the Hoedemaker Member in the area (Le Roux & Keyser 1988). A number of fossils from Nobelsfontein have consequently been attributed to the *Pristerognathus* AZ on the basis of geology, both in the literature (Brink 1986, 1988) and in the catalogues of museum collections.

The discrepancy between the fossil assemblage and the mapped geology raises concerns about the veracity of the geological map, the relation between litho- and biostratigraphy, and/or the accuracy of the locality information attending the collections from the area. It is important to resolve this discrepancy because using lithostratigraphic position as an independent temporal constraint over a relatively small geographic area can be a powerful tool in reconstructing patterns of palaeodiversity (e.g. Day *et al*. 2018), and because fossils from the Victoria West district, collected mostly by the Geological Survey, represent a considerable proportion of late Permian fossil occurrence data from the western Karoo. Because the biostratigraphic succession of the Karoo provides the most complete record for terrestrial vertebrates between the late Guadalupian and the Middle Triassic (Broom 1906; Watson 1914; Kitching 1970; Keyser & Smith 1979; Rubidge 1995; Lucas 1998, 2006, 2017), any confusion over the age (and/or host assemblage zone) of fossils in the Victoria West area has the potential to bias analyses of tetrapod diversity in the mid-late Permian, if these data are included. In order to clarify the situation from a biostratigraphic perspective, we conducted fieldwork in the vicinity of Biesiespoort railway siding and reviewed the published literature to determine the assemblage zones present, as well as their local stratigraphic extent.

Geological context

The area surrounding Biesiespoort station exposes fluvio-lacustrine sedimentary rocks of the lower Teekloof Formation of the Beaufort Group (Fig. 2). Older rocks belonging to the underlying Abrahamskraal Formation are exposed approximately 18 km to the north and on the flats between Hutchinson Station and Victoria West.

According to the geological map (Geological Survey, 1989), the majority of the adjacent farms Modderfontein 228 and Houdenbeck 222 expose mostly Poortjie Member strata, with the exception of the high ground on their northern margins. In the case of Houdenbeck this corresponds to the slopes of a dolerite dyke, where the overlying Hoedemaker Member is allegedly exposed; in the case of Modderfontein, strata of the Hoedemaker and Oukloof members are mapped on the southern slopes of a mountain known as The Horseshoe or Gys Roosberg (Fig. 1).

Palaeontological background

The first vertebrate fossils from the vicinity of Victoria West were found near the town in early 1907 by T.J.R. Scholtz, a student of Robert Broom, of which three were described later that year (Broom 1907). At this time, Broom was under the impression that the Beaufort strata at Victoria West were the terrestrial equivalents of the Early Triassic '*Lystrosaurus* Beds', but by 1909 he had been convinced by A.L. du Toit of the Geological Commission that these rocks were actually in the Lower Beaufort and thus probably equivalent to the middle Permian *Pareiasaurus* (= *Tapinocephalus*) zone (Broom 1909).

The fossils collected by both Scholtz and Broom at Victoria West were all recovered from a kloof or ravine that is now silted up by the municipal dam (Rogers & du Toit 1909: 102; Broom 1921) and were for some years the only fossils from the area. The paucity of fossils persisted until 1920, when Broom collected at Biesiespoort and found there several specimens of sufficient interest to induce him to visit the locality on a number of subsequent occasions. One of his first discoveries was to become the holotype of *Lycaenops ornatus* (Fig. 3A). Broom (1930: 349) writes:

> The beautiful Gorgonopsian skeleton which forms the type of *Lycaenops ornatus* was discovered by me in 1920, by the side of the railway line, about two miles south of Biesjespoort railway station. It lay on a slope of shale, which is weathering so fast that on revisiting the spot two years later it was with great difficulty that the exact spot could be identified.

The approximate position of this locality is easily determined, once one is aware that the course of the railway has changed since Broom's day. The original Cape Government Railways (CGR) line was built through the area in 1883 as part of the great drive to reach the diamond fields of Kimberley. This line took a winding route up the low sandstone terraces west of the dam by Nobelsfontein

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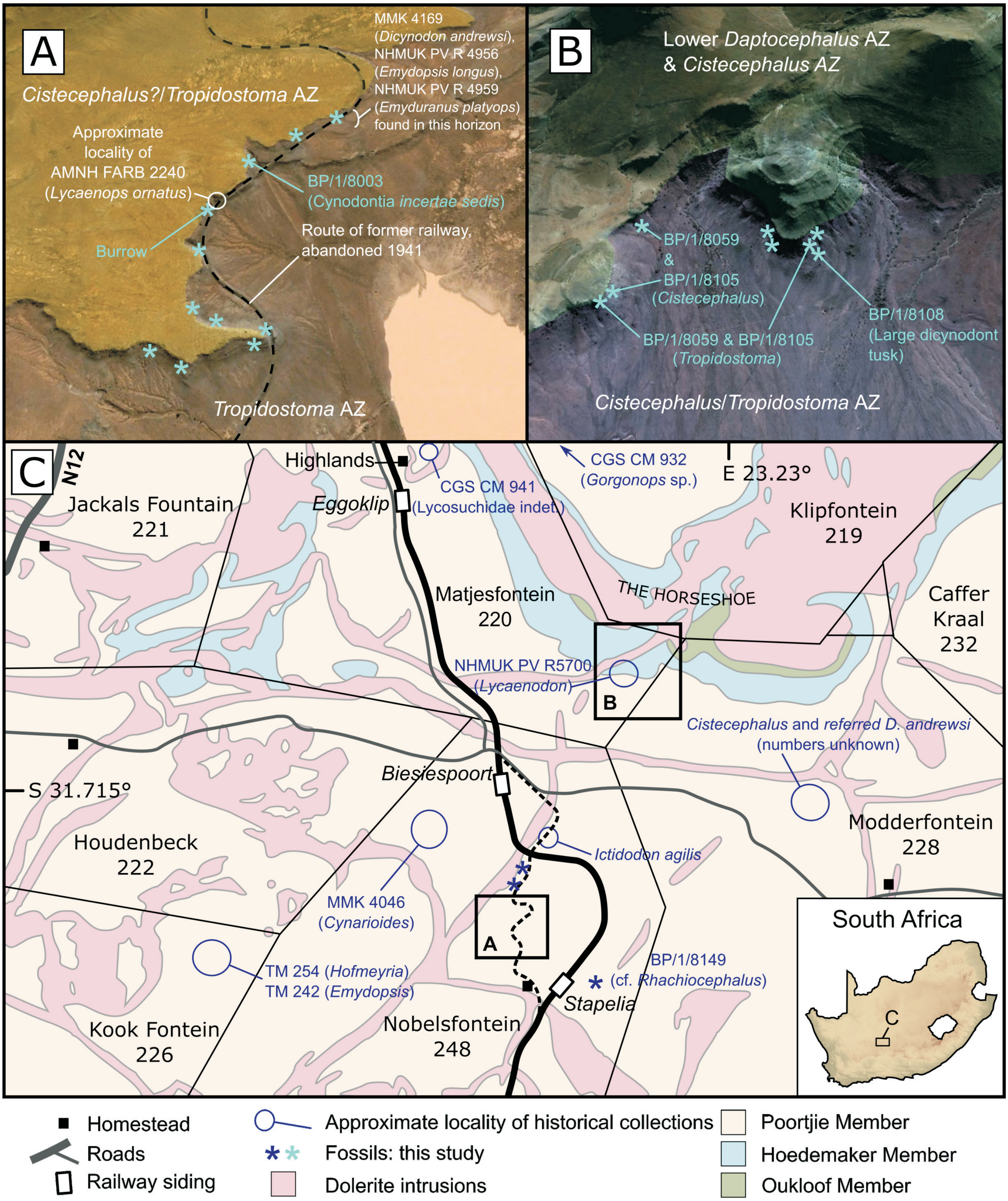

Figure 1. Map showing fossil collections from the Biesiespoort area. A, Aerial view of Nobelsfontein west of the dam along the course of the abandoned railway (images from Google Earth). B, Aerial view of the koppie at the border of Matjesfontein and Modderfontein; at least the lower 50 m of the slopes expose the overlap in the ranges of *Tropidostoma* and *Cistecephalus* (images from Google Earth). C, Map of wider Biesiespoort area showing key historical fossil sites (geology taken directly from Geological Map Sheet 3122 Victoria West (Geological Survey 1989). Asterisks marking fossil localities from this study indicate *Diictodon*, *Emydops*, *Oudenodon* or *Pristerodon* except where stated otherwise (GPS coordinates available from the Evolutionary Studies Institute). CGP, Council for Geoscience, Pretoria.

homestead and necessitated cuttings that provide fine exposures of mud- and siltstone beneath the terrace-forming sandstone (Figs 1A & 4). Today the line runs atop an embankment across the valley floor in a wide curve, where it was moved in 1941 (Lewis 2017), but the original path of the railway is still littered with railway refuse and is bordered by good exposures in the cut bank.

Broom collected many specimens from this bank (see

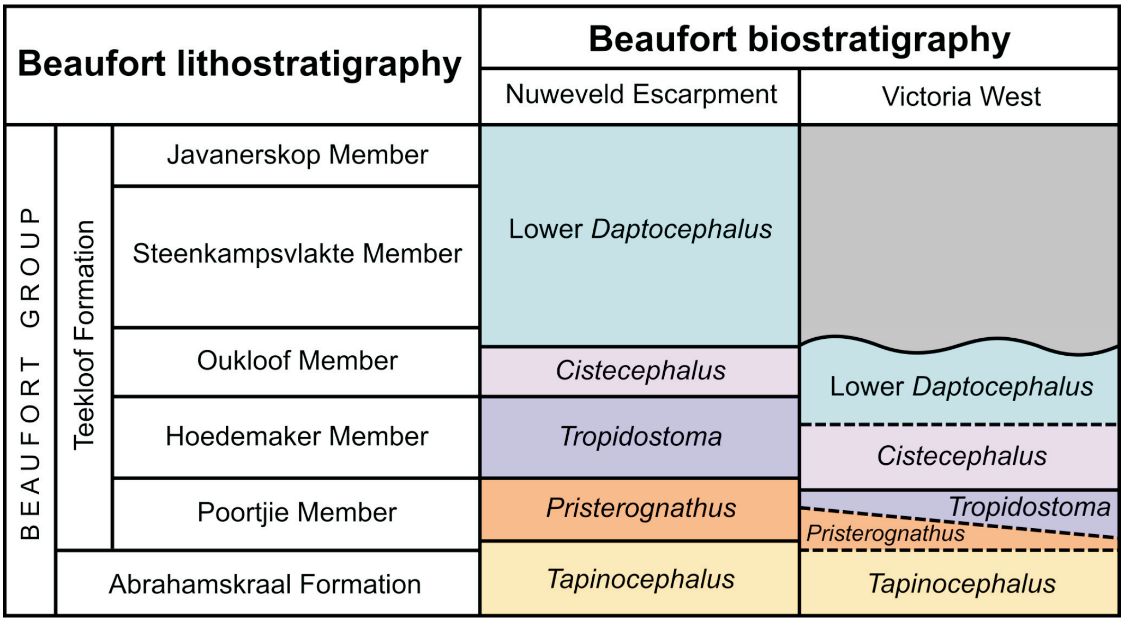

Figure 2. Relationship of Karoo biostratigraphy to the lithostratigraphy along the Nuweveld. Escarpment and in the Victoria West area. Nuweveld relationships based on Rubidge (1995), with amendments from Day *et al*. (2015) and Viglietti *et al*. (2016, 2017).

below), which he identified as the top of the '*Endothiodon* zone' (approximately equal to the modern *Tropidostoma* AZ [see Keyser & Smith 1979]), but he also ventured to explore the flat ground above it and the slopes of surrounding koppies, as well as adjacent farms (Broom 1921). From the collections he made there, he determined that the level of the station itself, and the strata above it, belonged to the *Cistecephalus* AZ (e.g. Broom 1925). He must have visited Biesiespoort several times during the 1920s and possibly the early 1930s, and published on numerous fossils from surrounding farms (Broom 1921, 1925, 1928, 1930, 1935a,b). His discoveries at Biesiespoort also changed his mind again regarding the age of the fossils found previously at Victoria West, given the relatively horizontal orientation of the strata between the two localities (Broom 1921), from the mid-Permian *Tapinocephalus* AZ (Broom 1909) to the late Permian upper *Endothiodon* AZ or *Cistecephalus* AZ; this second change in opinion later led to some confusion (e.g. Haughton & Brink 1954; Kitching 1977; Brinkman 1981). In fact, the fossils from

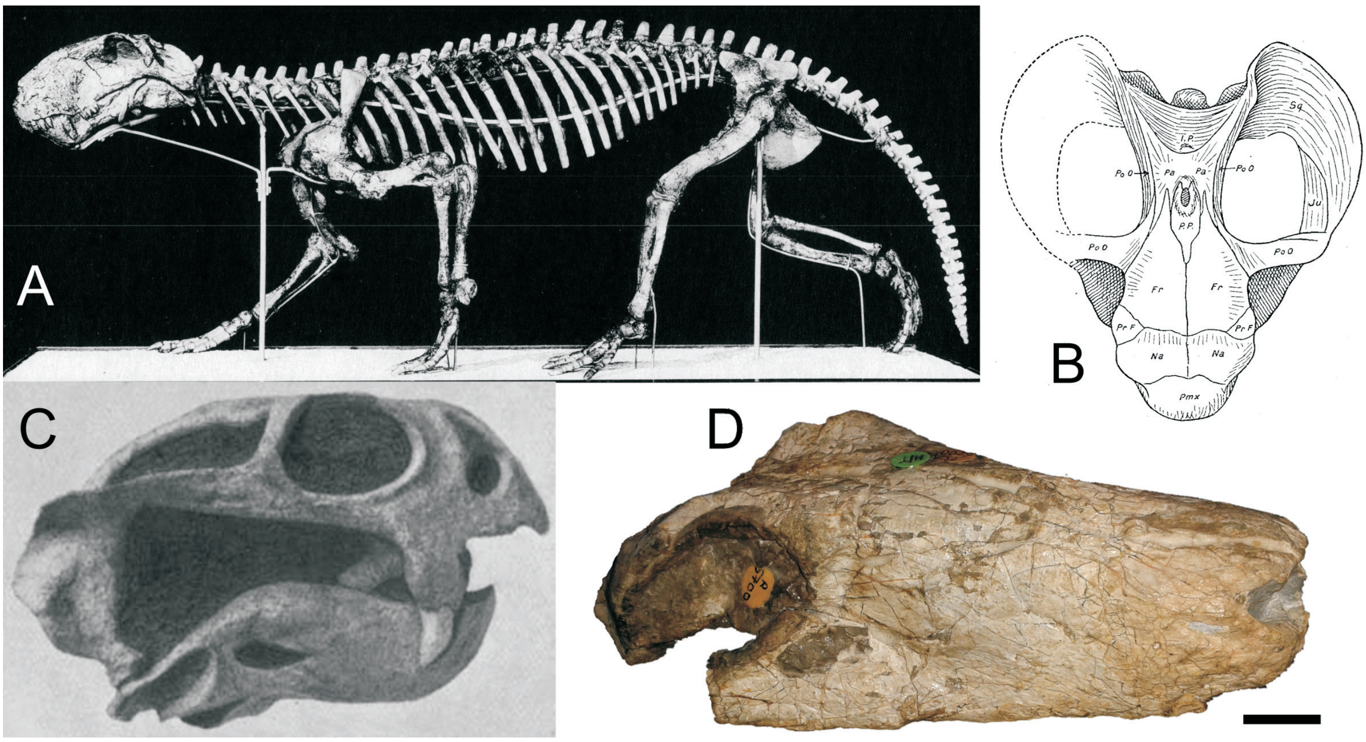

Figure 3. Some historical collections from Biesiespoort area. **A**, Mounted skeleton of the holotype of *Lycaenops ornatus* Broom (AMNH FARB 2240), from Colbert (1948). **B**, Illustration of the allegedly lost holotype of *Bainia peavoti* Broom (MMK 4237; = *'Aulacephalodon' peavoti*), from Broom (1921). **C**, Photograph of referred specimen of *Dicynodon sollasi* Broom (= *Diictodon feliceps*), from Janensch (1952a). **D**, Photograph of the holotype of *Lycaenodon longiceps* Broom (NHMUK PV R 5700). Scale bar equals: 2 cm.

Figure 4. Approximate locality of the holotype of *Lycaenops ornatus*, then and now. **A**, Photograph of the locality during fieldwork in March 2017, looking southwest. **B**, Photograph of the same locality in the early 1930s, taken from the carriage of a train looking north, as it would have looked during Broom's time; photograph courtesy of Pierre de Wet and Charlie Lewis; this site is marked on Fig. 1A.

Victoria West (e.g. *Eosimops newtoni*, *Heleosaurus scholtzi* and *Galechirus scholtzi*) do indeed represent records from the *Tapinocephalus* AZ (Modesto *et al*. 2001; Botha-Brink & Modesto 2007; Reisz & Modesto 2007; Kümmell 2009; Angielczyk & Rubidge 2013).

Broom's work near Biesiespoort attracted others to seek material there, and the area was collected by several generations of palaeontologists, including Friedrich von Huene (in 1924), Werner Janensch (in 1929), Lieuwe Boonstra (in 1931), Sidney Rubidge (in 1938), C. van der Horst and the Kitching brothers (in 1945), James Kitching and Lukas Huma (in 1955–56, 1968, and 1974), and Colin MacRae (in 1986). Fossils collected from the area surrounding Biesiespoort station can today be found in museum collections across South Africa, the U.S.A., the U.K. and Germany.

MATERIALS AND METHODS

In March 2017, we spent two days prospecting for fossil vertebrates in the area of Biesiespoort station, during which we collected 57 therapsid specimens (Table 1). Fossils were collected from Nobelsfontein 248, south of Biesiespoort station, in the area where Broom described the locality of *Lycaenops ornatus*, and on the Highlands portion of the farm Matjesfontein 220, northeast of Biesiespoort (Fig. 1). Fossil material was transported to the Evolutionary Studies Institute (ESI) at the University of the Witwatersrand where it is now curated. If clearly identifiable without preparation, fossil specimens were accessioned into the collections catalogue and stored directly; otherwise, they were mechanically prepared using an air scribe and a stereoscopic optical microscope at the ESI laboratory.

Recent identifications for specimens in existing collections were compiled from the collections catalogues of South African fossil repositories and the Beaufort Fossil Vertebrate database. Specimens curated at the ESI were re-examined if no recent identification existed and a selected number of these underwent additional mechanical preparation. However, many specimens remain unprepared and unidentified. Material from collections outside South Africa was added on the basis of published literature. In total, we recognise 342 specimens collected historically in the vicinity of Biesiespoort (Supplementary Table 1).

RESULTS AND PALAEONTOLOGY

Nobelsfontein 248

Forty specimens were collected on the farm Nobelsfontein; all specimens were recovered from a bank of blue and subordinate maroon silt- and mudstones below a prominent shelf-forming sandstone, along which the former course of the railway climbs up from the base of the valley (Fig. 1). This bank is almost certainly the locality described by Broom (1921, 1925, 1930) as producing the holotypes of *Lycaenops ornatus*, *Cynariops robustus*, *Emyduranus platyops*, *Emydops longus*, and *Dicynodon sollasi*. This horizon was extraordinarily fossiliferous, with a fossil skull being discovered approximately every 10–15 m laterally along the bank.

Of the fossils found at this locality during the study, the vast majority are dicynodonts, and among these *Diictodon feliceps* is by far the most abundant (Table 1). This is in accordance with expectations for the *Tropidostoma* AZ and with the numerous individuals of *'Dicynodon sollasi'*

Table 1. List of specimens collected from the Biesiespoort area in this study.

Specimen	Identification	Locality	Assemblage Zone
BP/1/7990	*Cistecephalus* sp.	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/7992	*Oudenodon baini*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8003	Pareiasaur indet.	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8023	Indet.	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8055	*Diictodon feliceps*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8057	Oudenodontidae indet.	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8059	*Tropidostoma dubium*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8061	cf. *Oudenodon*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8062	cf. *Oudenodon*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8063	cf. *Tropidostoma*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8064	*Cistecephalus microrhinus*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8070	Burrow – unknown occupant	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8083	cf. *Diictodon*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8092	cf. *Oudenodon* or *Tropidostoma*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8102	cf. *Diictodon feliceps*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8105	*Tropidostoma dubium*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/8108	Large tusked dicynodont cf. *Aulacephalodon*	Matjesfontein	*Tropidostoma/Cistecephalus*
BP/1/7983	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/7984	cf. *Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/7986	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/7987	cf. *Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/7988	cf. *Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/7989	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/7991	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/7993	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/7994	Theriodontia indet.	Nobelsfontein	upper *Tropidostoma*
BP/1/7996	cf. *Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/7997	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/7998	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/7999	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8033	Cynodontia *incertae sedis*	Nobelsfontein	upper *Tropidostoma*
BP/1/8034	*Emydops arctatus*	Nobelsfontein	upper *Tropidostoma*
BP/1/8036	cf. *Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/8056	*Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/8060	*Emydops* sp.	Nobelsfontein	upper *Tropidostoma*
BP/1/8065	*Emydops* sp.	Nobelsfontein	upper *Tropidostoma*
BP/1/8066	*Emydops* sp.	Nobelsfontein	upper *Tropidostoma*
BP/1/8068	*Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/8073	Theriodont cf. *Gorgonopsia*	Nobelsfontein	upper *Tropidostoma*
BP/1/8074	Dicynodontia indet.	Nobelsfontein	upper *Tropidostoma*
BP/1/8075	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8076	cf. *Emydops*	Nobelsfontein	upper *Tropidostoma*
BP/1/8077	cf. *Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/8078	cf. Diictodon	Nobelsfontein	upper *Tropidostoma*
BP/1/8079	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8080	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8081	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8082	*Pristerodon mackayi*	Nobelsfontein	upper *Tropidostoma*
BP/1/8084	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8086	cf. *Diictodon*	Nobelsfontein	upper *Tropidostoma*
BP/1/8087	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8090	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8095	*Diictodon feliceps*	Nobelsfontein	upper *Tropidostoma*
BP/1/8098	*Emydops* sp.	Nobelsfontein	upper *Tropidostoma*
BP/1/8099	*Emydops*	Nobelsfontein	upper *Tropidostoma*
BP/1/8100	*Emydops*	Nobelsfontein	upper *Tropidostoma*
BP/1/8109	*Pristerodon mackayi*	Nobelsfontein	upper *Tropidostoma*
BP/1/8149	*Rhachiocephalus magnus*	Nobelsfontein	upper *Tropidostoma*

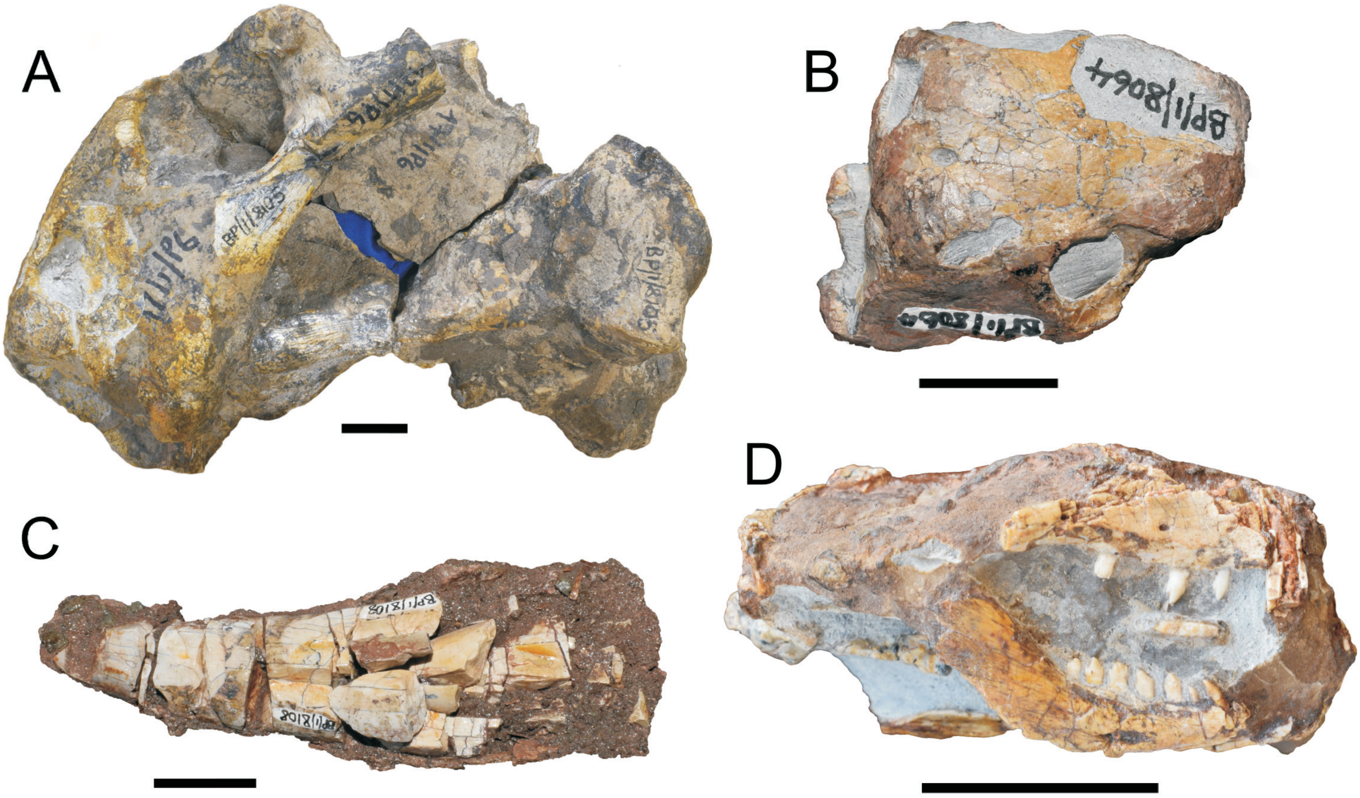

Figure 5. Some new collections from Biesiespoort area. **A**, Left lateral view of dicynodont skull (BP/1/8105). Despite its apparently deep snout, this laterally compressed specimen was identified as *Tropidostoma dubium* as it bears the roots of two large tusks, which are lacking in *Oudenodon bainii*. **B**, Dorsal view of dicynodont skull (BP/1/8064), *Cistecephalus* sp. **C**, Tusk of a large dicynodont (BP/1/8108), cf. *Aulacephalodon* or *Odontocyclops*. **D**, Right lateral view of partial skull (BP/1/8033), Cynodontia *incertae sedis*. Scale bars equal 2 cm.

(= *Diictodon feliceps*) reported by Broom for this horizon. The relative abundances of taxa found in this study are reflected in historical collections from this locality (Supplementary Table 1). The second most abundant genus is *Emydops*, which is represented by seven specimens from our collections (with one additional tentative assignment) and nine from historical collections, of which seven likely come from this horizon. *Pristerodon* is represented by two specimens collected during this study and four from historical collections. It is also likely that at least one specimen of *Oudenodon bainii* (the holotype of *Dicynodon andrewsi*) was found by Broom in this horizon (see Appendix 1).

Other therapsids recovered from this horizon in the course of this study consisted of the femur of a gorgonopsian, an indeterminate theriodont snout, and a small cynodont skull (Fig. 5). This latter specimen is a basal (i.e. non-eucynodont) cynodont of some kind but is poorly preserved. Unusually, however, it displays two postcanine morphs in the lower dentition and may represent a previously unknown taxon (Jasinoski and Abdala, pers. comm. 2017). This specimen will be considered further in a future study and is not described here. Historically, theriodonts from this horizon are represented by several gorgonopsians, including material now identified as *Gorgonops torvus*. Therocephalians have not yet been found this low in section in the area.

A vertebrate burrow was discovered in the siltstones of the railway bank in a small erosional gully. The burrow was almost straight and was exposed along much of its length, causing it to have weathered into six segments (Fig. 6). The deepest part of the burrow was less distinct from the surrounding matrix and was truncated by the gully so its total length could not be measured. No bone was evident within the burrow but the entrance to the burrow was obscured by large nodules that had formed around large vertebrate bones, the identity of which could not be ascertained due to their heavy weathering. On the east side of the farm we found the skeleton of the large dicynodont *Rhachiocephalus magnus* (BP/1/8149), 2 m below the terrace-forming sandstone.

Historically collected fossils from Nobelsfontein that were found above this horizon (i.e. above the sandstone at the top of the railway slope; Fig. 1A), and east of the dolerite dyke that stands between Biesiespoort station and Nobelsfontein homestead, were attributed by Broom to 'the very top of the *Endothiodon* zone, or, just possibly, the base of the *Cistecephalus* zone [because] *Cistecephalus* itself was found by me on a spot about three miles away on what must be very nearly the same horizon' (Broom 1925: 321). Earlier, in reference to a referred specimen of *Dicynodon andrewsi* (= *Oudenodon bainii*), he (Broom 1921: 650) stated that this second individual was collected 'from a locality 3 miles east of Biesjespoort … [where it was] found in near association with a specimen of *Cistecephalus* sp.' These are no doubt the same *Cistecephalus* occurrence. The therocephalian specimen described as *Ictidodon agilis* and the gorgonopsian described as *Cynarioides tenuis* (Broom 1925) are also from strata above the terrace sandstone on Nobelsfontein.

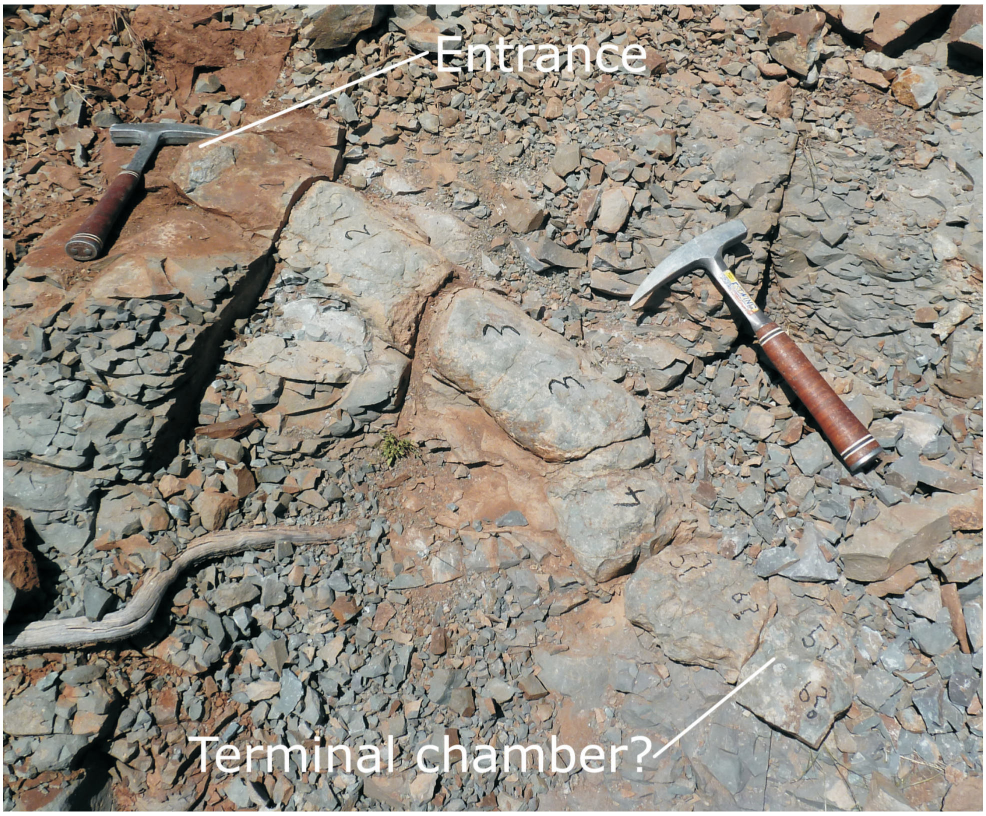

Figure 6. Vertebrate burrow in blue-grey siltstones in the bank of the old railway cutting on Nobelsfontein.

Broom also suggested that the strata on which Biesiespoort station is situated are above the base of the *Cistecephalus* zone, and that the higher slopes 'about 100 feet above the level of Biesiespoort Station, … [are] thus well within the *Cistecephalus* zone' (Broom 1925: 325). Our altitude readings suggest that the flats around the station and the low slopes along the dolerite immediately to the north are around 20–50 m above the terrace sandstone. The taxa he and other palaeontologists collected there (*Oudenodon bainii* and *Cynarioides tenuis*) are not restricted to either the *Tropidostoma* or *Cistecephalus* AZs and cannot be used to distinguish between them; we did not find anything in these horizons. However, we did find fossils of *Cistecephalus* on the farm Matjesfontein 220, 2.5 km to the northeast, at a level approximately 50 m (in altitude) above the level of old Biesiespoort station. Because strata may be dipping very slightly south or southwest in the study area, this should be considered a maximum thickness.

Matjesfontein 220 (Highlands)

Seventeen specimens were collected on the farm Highlands. All fossils were found on the lower slopes of a small spur from the Horseshoe Mountain, on which the exposure of rock is excellent within numerous deep gullies and dongas. The lower part of these slopes is not much higher than Biesiespoort station, and the stratigraphic distance between the foot of the hill and the rich horizon along the railway bank on Nobelsfontein, as estimated from altitude readings, is approximately 70 m. The assemblage we found on these lower slopes includes *Cistecephalus*, *Diictodon* and oudenodontid dicynodonts, with the latter being better represented.

Historical collections from this farm locality are mostly typical of the *Cistecephalus* AZ: dicynodonts include abundant *Cistecephalus*, *Oudenodon*, *Diictodon*, and *Bainia peavoti* (= *Aulacephalodon*), while theriodonts are represented by the therocephalians *Hofmeyria* and indeterminate ictidosuchids, and several gorgonopsians are also present. However, one of the fossils found by James Kitching in 1968 at this locality was a skull of the therocephalian *Theriognathus microps*, while another skull of this species was found during the same trip on the adjacent farm Modderfontein 228. *Theriognathus* is typical of the overlying *Daptocephalus* AZ, and recently its first appearance datum (FAD) has become part of the definition of the base of this zone (Viglietti *et al*. 2016). Kitching (1977: 60) describes the *Daptocephalus* AZ as being present on the upper 500 feet (150 m) of the Horseshoe Mountain and ascribes only *Theriognathus* and the pareiasaur *Pareiasaurus* to this zone. We can therefore reasonably deduce that the specimens of these taxa were found on the upper slopes, and the rest of his collecting was confined to the lower slopes of the mountain.

There is further evidence to suggest that Kitching's collecting was restricted to the southern part of Matjesfontein, closest to Biesiespoort station. This comes from the second aberrant taxon from this locality, a mid-Permian therocephalian tentatively identified as a member of the family Lycosuchidae (CGS CM 941; Abdala, pers. comm. 2016), collected by Colin MacRae. Like other collections made by the Geological Survey, the exact locality of this specimen was plotted on a 1:50 000 topographic map of the area, which shows that it was found on the northern part of Matjesfontein, 5.5 km north of the area collected by us (Fig. 1). Although it occurs at a similar altitude, its occurrence, along with a specimen of attributed to *Gorgonops* sp. (CGS CM 932) from a similar horizon on the neighbouring farm of Klipfontein 219, indicates the presence of the *Pristerognathus* AZ.

DISCUSSION

Biostratigraphy of the Biesiespoort area

The predominance of *Diictodon* in the railway bank on Nobelsfontein is suggestive of the *Pristerognathus* or *Tropidostoma* AZs, as is the secondary abundance of *Emydops* and *Pristerodon*. The presence of *Rhachiocephalus*, the gorgonopsian *Lycaenops ornatus*, and of a small basal cynodont are more consistent with the younger of these units, as the former two genera are known only from the *Tropidostoma* AZ or younger (Smith *et al*. 2012) and the earliest known cynodonts worldwide are from the upper *Tropidostoma* AZ (Botha *et al*. 2007; Kammerer 2016; Jasinoski, pers. comm. 2017). The occurrence on Nobelsfontein of the dicynodont *Oudenodon bainii* (MMK 4169) lends further support to an upper *Tropidostoma* AZ assignment, as this taxon first appears in the upper part of this assemblage zone; Botha & Angielczyk 2007). The lack of the characteristic *Tropidostoma* AZ dicynodont taxa *Tropidostoma dubium* or *Endothiodon bathystoma* at Nobelsfontein is, however, surprising, though *E. bathystoma* (CGS CM 790) has been found in a similar horizon on Modderfontein.

Above this horizon is an interval of <50 m of predominantly silt- and mudstone that were not collected during this study and from which only a few historical specimens have been found. This interval includes the level of Biesiespoort station itself. In the immediate vicinity of the station, known historical finds include the holotypes of the gorgonopsian *Cynarioides tenuis* and the therocephalian *Ictidodon agilis* but these taxa are not biostratigraphically useful (both are probably *nomina dubia*, especially considering that the holotype of *I. agilis* is lost). The only evidence for the biostratigraphy of this interval comes from the alleged specimen of *Cistecephalus* reported by Broom (1921, 1925) from a locality 3 miles to the east in association with a referred specimen of *Dicynodon andrewsi* (= *Oudenodon bainii*). Because the flat ground in the area is covered in soil, exposure is limited to the banks of sandstone terraces and rivulets; this locality could correspond to some outcrops along terraces on the farm Modderfontein 228 three miles east of Biesiespoort, just northeast of the road, which, based on field correlation, expose strata just above and below the sandstone at the top of the bank at Nobelsfontein (see Fig. 1). Our altitude readings suggest this encompasses about 20 m of strata above the terrace-forming sandstone. Alternatively, we cannot rule out that they were found northeast of Biesiespoort on the lower slopes of the Horseshoe Mountain, in which case they would be stratigraphically higher. Although the biostratigraphy of this interval cannot be substantiated at present, the first occurrence of *Cistecephalus* and *Oudenodon* may potentially be as low as the level of the railway bank sandstone.

Above this, our collecting on the lower slopes of The Horseshoe demonstrates that the ranges of the dicynodonts *Tropidostoma*, *Oudenodon* and *Cistecephalus* overlap. Strata of this level also crop out on the slopes surrounding the more pronounced dolerite dykes in the area such as the east–west trending dyke north of the road. The presence of these three taxa would be consistent with an uppermost *Tropidostoma* AZ assignment as currently defined (Smith *et al*. 2012; but see Smith & Keyser [1995b] and Botha & Angielczyk [2007]). The presence of a large dicynodont tusk (BP/1/8108) at this level indicates that at least one large tusked species overlapped with the range of *Tropidostoma* (possibly *Odontocyclops* or *Aulacephalodon*), but its vague identity prevents further analysis. Historical collections from higher on the slopes of the Horseshoe, including *Aulacephalodon* and *Theriognathus* (see Appendix 1), indicate that the *Cistecephalus* AZ and at least part of the Lower *Daptocephalus* AZ are present there.

To the south, a specimen of a scylacosaurid therocephalian cf. *Glanosuchus* (SAM-PK-10544) was found in 1931 on the farm Brakfontein 225, which lies 18 km southwest of Biesiespoort. This is probably attributable to the *Pristerognathus* AZ but the only other fossil known from this farm is the holotype of *Silpholestes jackae* (TM 1608), the skeleton of a small therocephalian that, like many other former members of the 'Scaloposauridae', may be a juvenile of a larger taxon. Evidence for the *Pristerognathus* AZ also comes from the northern part of the farm Matjesfontein 220, where several putative specimens of *Diictodon* (CGS CM 940, CM 942–945) and a specimen referable to the basal therocephalian family Lycosuchidae (CGS CM 941) were found in 1986 on the lower slopes of the northwestern limb of the Horseshoe Mountain (Fig. 1).

Discrepancy between litho- and biostratigraphy

The collection of fossils made during our fieldwork, combined with those made in the past, are consistent with the biostratigraphic assessment made initially by Broom during his earliest visit to the locality in 1920. The relationship between the later mapped lithostratigraphic units and the fossil assemblages present is therefore not consistent with expectations based on the existing paradigm (see Rubidge 1995), whereby the *Tropidostoma* AZ mainly corresponds to the argillaceous Hoedemaker Member of the Teekloof (= Middleton) Formation and the underlying Poortjie Member mainly hosts the *Pristerognathus* AZ.

This is not the only locality in the area where this occurs. Another example is the farm Gemsbokfontein, about 15 km northwest of Victoria West along the R63: the geological map shows this farm to expose the upper Abrahamskraal Formation and the Poortjie Member of the Teekloof Formation, but it has allegedly produced a specimen of *Oudenodon* (BP/1/4172). Yet another is the farm Meltonwold 158, 30 km west of Victoria West, on which *Tapinocephalus* AZ fossils have been found; this farm has also produced at least six specimens of *Oudenodon* (CGS MJF 239, 244, 249, 251–3) from an area that is mapped as exposing the uppermost Poortjie Member and lower Hoedemaker Member (Geological Survey 1989).

Because the relationship between the assemblage zones in question and the lithostratigraphy is mostly based on observations along the Nuweveld Escarpment, one possible explanation is that the lithostratigraphic members of the Teekloof Formation are diachronous, becoming younger to the northeast as the result of the distal migration of these units. Conversely, the uppermost Abrahamskraal Formation at Victoria West has produced an expected *Tapinocephalus* AZ fauna (see above) and a tapinocephalid dinocephalian (BP/1/7287) has been found close to the top of the Abrahamskraal Formation on the farm Montana (Vigilants Dam 100), about 28 km north of Victoria West. The upper Abrahamskraal Formation is therefore not evidently younger than further south (see Fig. 2).

This could be explained by a stratigraphic gap equivalent to part or all of the *Pristerognathus* AZ, but an assemblage consistent with the *Pristerognathus* AZ (including a lycosuchid therocephalian in association with putative *Diictodon*) has been collected from the northern part of Matjesfontein 220, near the Highlands farmstead. This poses a problem for a proposed younging of the Poortjie Member, as it was found close to the top of the Poortjie Member as it is mapped (Geological Survey 1989). If the map is correct, this would suggest that the majority of the member was within the *Pristerognathus* AZ at this locality. The occurrence of a *Pristerognathus* AZ assemblage in the upper Poortjie Member at Highlands would thus indicate that it was in fact *older* than 6 km to the south, where it hosts the uppermost *Tropidostoma* AZ.

An alternative hypothesis is that the lithostratigraphic units are not consistent throughout the region, with sandstone packages recognized further south not having such a wide lateral extent. This could have led to the incorrect lithological correlation and mapping of sandstone units. In this scenario, time-equivalent strata of the Hoedemaker Member (as defined on the Nuweveld Escarpment) in the local area between Victoria West and Biesiespoort would be relatively rich in sandstone, such as to appear part of the Poortjie Member. This may have been a confounding factor contributing to lithostratigraphic offset of the biozones, and would explain the presence of both the *Pristerognathus* and *Tropidostoma* AZs within the Poortjie Member. However, it would not explain why these two biozones would both be present within the upper Poortjie Member, unless local miscorrelation has occurred between the north and south of Matjesfontein 220. Although this is not impossible, the similarity in the position and altitude of the upper contact of the Poortjie Member NE of Biesiespoort and at Highlands is consistent with the apparently low dip in the area. Indeed, Broom (1921: 663) remarked that 'Biesjespoort, which lies about 20 miles south of Victoria West, is very rich in fossils, and is certainly at the base of the *Cistecephalus* zone. For miles the strata are almost perfectly horizontal, and it is hard to believe that the beds at Victoria West can be much lower than those at Biesjespoort.'

Further fieldwork is required to review the lithostratigraphic succession in the area and to determine the stratigraphic extent of the *Pristerognathus* and *Tropidostoma* AZs in the vicinity of Victoria West.

CONCLUSIONS

Our research has revealed that the biostratigraphic assessments made by Broom of the Biesiespoort area were accurate; that is, strata surrounding the Biesiespoort station host Wuchiapingian assemblages assignable to the upper *Tropidostoma* and *Cistecephalus* AZs, rather than the older *Pristerognathus* AZ as would be suggested by the presence of the Poortjie Member. This confirmation, and the clarification of the relationship between lithological horizons and biozone occurrence, has allowed us to reassess the biostratigraphic provenance of specimens collected historically in the local area (Appendix 1). Amongst others, the holotype of *Lycaenops ornatus* can be constrained to the uppermost *Tropidostoma* AZ, rather than the *Cistecephalus* AZ more broadly.

The relationship between the tetrapod biozones and lithostratigraphy in the Victoria West area is offset from that traditionally presented for the Teekloof Formation along the Nuweveld Escarpment, with the presence of the upper *Tropidostoma* AZ within the upper Poortjie Member at Biesiespoort. Distal younging within the Teekloof Formation does not explain these observations as an assemblage likely representing the *Pristerognathus* AZ is present in the upper Poortjie Member 6 km to the north of Biesiespoort. Inconsistency in the regional mapping of the Teekloof Formation may be significant, as well as local miscorrelation on Matjesfontein 220. However the apparently low dip of the strata between Highlands farm (*Pristerognathus* AZ) and southern margin of the Horseshoe (uppermost *Tropidostoma* AZ) and the similar altitude of the Poortjie-Hoedemaker Member contact as mapped are mutually consistent. The change in assemblage zone with relatively little change in stratigraphic horizon could result if the *Tropidostoma* AZ, and possibly the *Pristerognathus* AZ, is locally restricted to a narrow stratigraphic interval due to periods of relatively lower sedimentation rates and/or depositional hiatuses. Evidence for the reduced thickness of these biozones in the study area also comes from other historically collected fossil material on several farms west of Victoria West, including Meltonwold (CGS MJF 127, 239, 244, 249, 251, 252) and Gemsbokfontein (BP/1/4172). Here, fossils reliably identified as *Oudenodon bainii* have been found stratigraphically close to *Tapinocephalus* AZ assemblages. This material is housed at the Council for Geoscience, Pretoria, and the Evolutionary Studies Institute, Johannesburg.

Untangling the situation requires further fieldwork but the current evidence is sufficient for us to advise caution when using the lithostratigraphic provenance, as determined from geological maps, as a means of correlating fossil occurrences between the Victoria West area and the rest of the basin.

INSTITUTIONAL ABBREVIATIONS

AM	Albany Museum, Grahamstown
AMNH	American Museum of Natural History, New York
BP	Evolutionary Studies Institute, Johannesburg
CGS	Council for Geoscience, Pretoria
FMNH	Field Museum of Natural History, Chicago
MB	Museum fur Naturkunde, Berlin
MMK	McGregor Museum, Kimberley
NHMUK	Natural History Museum, London

RC Rubidge Collection, Graaff-Reinet
SAM Iziko South African Museum, Cape Town
TM Ditsong National Museum of Natural History, Pretoria.

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APPENDIX 1

STRATIGRAPHIC PROVENANCE OF HISTORICAL COLLECTIONS

This section includes detailed analysis of the stratigraphic provenance of some historical collections from the area of Biesiespoort. It is primarily aimed at holotypes collected in the early 20th century, for which details of locality are provided in the published literature. A comprehensive list of previously collected specimens from the area is provided in Supplementary Table 1.

UPPERMOST *TROPIDOSTOMA* AZ

This horizon is exposed below Biesiespoort, along the railway south of the station along the mudrock slopes in the valley on Nobelsfontein north of the homestead (Fig. 1C).

Gorgonopsia

AMNH FARB 2240. Holotype of *Lycaenops ornatus*. First described by Broom (1925) and later in more detail by Broom (1930) and Colbert (1948), this genus and species is considered valid (Sigogneau-Russell 1989; Gebauer 2007). The specimen was found in the bank above the first route of the railway on the farm Nobelsfontein, as described in the text.

NHMUK PV R 5743. Holotype of *Cynariops robustus*. This specimen initially formed the basis for the new genus of gorgonopsian (Broom 1925) but was referred to the genus *Scylacognathus* by Sigogneau (1970) as *S. robustus*, a decision upheld by Sigogneau-Russell (1989) and Gebauer (2007). Kammerer *et al*. (2015) synonymized the type species of *Scylacognathus*, *S. parvus* from the *Tapinocephalus* AZ, with *Eriphostoma microdon*, leaving the other referred species of *Scylacognathus* as Gorgonopsia *incertae sedis*. Subsequent research on '*S.*' *robustus* has found it to be a valid species, necessitating resurrection of the genus *Cynariops* (Bendel *et al.* 2018). It was found 'about 100 feet below the horizon of Biesjespoort station' (Broom 1925: 324), which places it in the same horizon as Broom's specimens of *Dicynodon sollasi* and *Lycaenops ornatus*.

MB.R.999. Specimen referred to *Cynariops robustus*. This specimen was tentatively referred to *Aloposaurus* by Janensch (1952b) and *Aelurosaurus* by Bendel *et al*. (2017); however, digital reconstruction of the specimen based on CT-data demonstrates that it is extremely similar to NHMUK PV R 5743 and can be referred to the same species (Bendel *et al*. 2018). Janensch recorded it as having been collected 'in der *Endothiodon*-Zone von Biesjespoort' (Janensch 1952a: 234). This designation is likely from Broom and suggests that this specimen comes from the upper *Tropidostoma* AZ, around the same level as *Lycaenops ornatus*.

Therocephalia

Specimen unknown. Holotype of *Ictidodon agilis* (possibly Ictidosuchidae indet.). Originally described by Broom (1925), this genus has received little subsequent attention. The only references to it (Boonstra 1954; Haughton & Brink 1954; Brink 1988; Fourie 2013) rely on the description and do not mention a number or repository for the specimen, which is apparently lost. The specimen may have belonged to a basal baurioid of the family Ictidosuchidae, given that they are the most common therocephalians from the *Tropidostoma* AZ, but with the holotype specimen missing its affinities remain uncertain. It was found 'in the shales of the railway bank about a mile below Biejespoort Railway Station …The zone of this type is most probably the very top of the *Endothiodon* zone, or, just possibly, the base of the *Cistecephalus* zone' (Broom 1925: 320). It is below the last occurrence of *Tropidostoma* and around the FAD of *Cistecephalus*, so is tentatively considered more likely to belong to the uppermost *Tropidostoma* AZ.

Dicynodontia

SAM-PK-7420. Holotype of *Dicynodon sollasi* (= *Diictodon feliceps*). This species was described by Broom (1921: 648) on the basis of 'a series of over 20 good skulls and many imperfect ones discovered near Biesjespoort … Though many skulls, both males and females, are known, I take as the type one of the best preserved, which I believe to be an adult male'. The species was transferred to the new genus *Pylaecephalus* by van Hoepen (1934), along with several other described species of *Dicynodon* that he considered closely related to *Diictodon*. Cluver & Hotton (1981) assigned the species to *Diictodon* and since the work of King (1993) and Sullivan and Reisz (2005), only one species of *Diictodon* (*D. feliceps*) is recognized. The horizon from which most specimens were found was considered by Broom to be 'at the very top of the *Endothiodon* zone,' but he noted that the genus also 'appears to extend a short way into the *Cistecephalus* zone' (Broom 1921: 649). The main locality almost certainly corresponds to the bank above the old railway line on the farm Nobelsfontein based on Broom's biozone determination, when cross referenced against his locality description for *Lycaenops ornatus* (Broom 1925, 1930) and his reference to a horizon that produced over 20 good skulls of *Dicynodon sollasi* (= *Diictodon feliceps*).

NHMUK PV R 4956–8. Holotype and referred specimens of *Emydopsis longus* (= *Emydops arctatus*). This species of *Emydopsis* was described by Broom (1921) at the same time as *Dicynodon sollasi* and was based on several specimens that were eventually sent to London. *Emydopsis* was synonymized with *Emydops* by Toerien (1953) but retained its status as the species *Emydops longus*, until Keyser (1993) determined that the specimens were referable to *Pristerodon mackayi* and that *E. longus* should become a junior synonym of that species. Most recently, Fröbisch & Reisz (2008) have returned these specimens to the genus *Emydops*, with *E. longus* becoming a junior synonym of *Emydops arctatus*. Broom (1921: 667) describes all specimens as having been found 'in exactly the same horizon as *Dicynodon sollasi*.'

NHMUK PV R 4959. Holotype of *Emyduranus platyops* (= *Pristerodon mackayi*). *Emyduranus* was also described by Broom, for what he regarded as 'a very distinct genus' (Broom 1921: 672). Only brief mention was made of it subsequently and, though it was retained as valid by King (1988), it was later synonymized with *Pristerodon mackayi* by King and Rubidge (1993). Broom discovered this skull near Biesiespoort 'in the deposit which has yielded the very numerous skulls of *Dicynodon sollasi*' (Broom 1921: 670). It is therefore from the farm Nobelsfontein.

TM 241. Holotype of *Emydorhynchus formosus* (possibly *Diictodon feliceps*). This species was described by Broom (1935a) on the basis of a skull. The type species, *E. palustris*, was interpreted to be attributable to the genus *Diictodon* by Cluver and Hotton (1981) but they demurred to comment on the status of *E. formosus* because the type specimen was at that time missing. King (1988) proposed that Broom's original observation of the latter's similarity to *E. palustris* suggested that *E. formosus* was also referable to *Diictodon*, but that the specimen required more preparation before this could be confirmed. Because only one species of *Diictodon* is currently recognized, this specimen likely represents another referred specimen of *D. feliceps*. It was found by Broom 'near Biesjespoort, just below the *Dicynodon sollasi* horizon and thus near the top of the *Endothiodon* zone' (Broom 1935a: 6).

MB.R.984. Holotype of *Storthyggognathus haughtoni* (possibly referable to *Emydops*). This genus was based on a skull collected by Janensch in 1929 and described by him some decades later (Janensch 1952b). King (1988) suggested affinities with the *Tapinocephalus* AZ genus *Chelydontops* but retained it as a separate genus. It was considered to be likely a synonym of *Emydops* by King & Rubidge (1993), with the retention of a species distinction dependent on the authenticity of the absent interpterygoid vacuity. The specimen is described as having been found '*in der oberen (?) Endothiodon-Zone bei Biesjespoort*, *Farm Nobelsfontein (Kapprovinz)*' (Janensch 1952b: 218). As with specimen MB.R.999, the upper *Endothiodon* AZ designation is probably from Broom and suggests that this specimen was found in the railway cutting south of Biesiespoort below the sandstone shelf marking the base of the *Cistecephalus* AZ.

MMK 4169. Holotype of *Dicynodon andrewsi* (= *Oudenodon bainii*). *D. andrewsi* was described by Broom (1921: 650) on the basis of a skull that he found to represent a 'strikingly new' form of dicynodont. Later, the species was considered synonymous with *Oudenodon bainii* by Keyser (1975) and all subsequent authors (e.g. King 1988; Kammerer *et al*. 2011). The holotype was found in 'the same horizon and nearly the same spot at Biesjespoort that yielded the type of *D. sollasi*' (Broom 1921: 650), which suggests that it can be attributed to the uppermost *Tropidostoma* AZ. Broom goes on to state that 'in addition to the type specimen I have two others which I refer to the same species—one from a locality between Murraysburg and Biesjespoort, and the other from a locality 3 miles east of Biesjespoort. As this latter specimen was found in near association with a specimen of *Cistecephalus* sp., it gives us the horizon as the base of the *Cistecephalus* zone.' The fact that the specimen represents *Oudenodon*, which is common in the overlying *Cistecephalus* AZ, probably accounts for Broom's correlation here, even though it contradicts his biostratigraphic assessment of the same horizon for other taxa found in the *D. sollasi*-rich horizon.

TROPIDOSTOMA/CISTECEPHALUS OVERLAP ZONE

This horizon is exposed at the level of Biesiespoort station, the sides of the surrounding koppies, and on the lower slopes of the Horseshoe Mountain to the north.

Biarmosuchia

NHMUK PV R 5700. Holotype of *Lycaenodon longiceps*. This genus and species was also described by Broom (1925) along with the other theriodonts he found in the early 1920s. It remains valid and since the late 1980s has been considered a basal biarmosuchian (Hopson and Barghusen, 1986; Sigogneau-Russell, 1989; Rubidge & Sidor, 2001; Sidor 2003). Broom found this specimen in 'a horizon about 100 feet above the level of Biesiespoort Station, and thus well within the *Cistecephalus* zone' (Broom 1925: 325). The exact area is hard to place based on this description but exposure of this level occurs just to the northeast of old Biesiespoort station, along a dolerite dyke, or perhaps further northeast along the lowest slopes of the various spurs extending out from The Horseshoe Mountain. In either case, this is within the range of both *Tropidostoma* and *Cistecephalus*.

Gorgonopsia

MMK 4046. Holotype of *Cynarioides tenuis*. This specimen was erroneously recorded as MMK 2046 by Sigogneau (1970) and subsequent authors. It was described as the genotype of the new genus *Cynarioides* by Broom (1925), but was referred to cf. *Aloposaurus tenuis* by Sigogneau (1970). This uncertain designation was maintained in subsequent reviews of Gorgonopsia (Sigogneau-Russell 1989; Gebauer 2007), and given the poor preservation of this specimen a definitive identification may not be possible (C. Kammerer, pers. comm. 2018). It was found 'about half a mile west of Biesjespoort Station, and on a horizon which must be about 100 feet higher than that of *Cynariops robustus*, and pretty certainly in the *Cistecephalus* zone' (Broom 1925: 324).

TM 245. Holotype of *Cynarioides laticeps*. This specimen was described by Broom (1935a) as a new species of *Cynarioides* and was synonymized with *Scylacognathus grimbeeki* (formerly *Cynarioides grimbeeki*) by Sigogneau (1970). Gebauer (2007) referred it to the type species of *Scylacognathus*, *S. parvus*. Bendel *et al*. (2018) refer this specimen to *Cynariops robustus*, based on their re-description of MB.R.999. The specimen was found by Broom 'near the top of kopje some miles east of Mr D. Steytler's house on the farm Kookfontein near Biesjespoort' (Broom 1935a: 5). As suggested by Broom, the tops of the koppies in the east of Kookfontein are likely to be just within the *Tropidostoma/Cistecephalus* overlap range based on altitude comparison with neighbouring Nobelsfontein; however, the lack of index taxa from Kookfontein, and the distance from the horizons identified in this study means that this must be considered as tentative.

Therocephalia

TM 254. Holotype of *Hofmeyria atavus*. This genus and species was erected by Broom (1935b: 55) for a skull found 'on the farm Kookfontein, near Biesjespoort'. He does not indicate where on the farm it was collected but the following year, he described the skull in more detail and cited its provenance as 'either at the top of the *Endothiodon* zone, or the base of the *Cistecephalus* zone' Broom (1936: 25). The other specimens found by Broom on Kookfontein in the early 1930s, TM 245 (*Cynarioides laticeps*) and TM 242 (*Emydopsis minimus*), were both found near the top of a koppie in the east of the farm and it is likely that this specimen was also found in this area. Broom's 1936 suggestion of a position close to the base of the *Cistecephalus* AZ supports this interpretation but, as with the other specimens from this locality, the assignment is tentative.

Dicynodontia

SAM-PK-7850. Holotype of *Dicynodon curtus* (= *Oudenodon bainii*). Broom (1921) described *D. curtus* on the basis of a skull and lower jaw and little mention was made of it until it was synonymized with *Oudenodon bainii* by Keyser (1975). It was found 'at Biesjespoort … [in a] horizon [that] is probably about 100 feet above that in which the type of *D. sollasi* was obtained' (Broom 1921: 654), and therefore falls within the range of *Cistecephalus*.

TM 242. Holotype of *Emydopsis minimus* (= *Emydops arctatus*). First described by Broom (1935a), this specimen was referred to *Emydops* by Toerien (1953) as the combination *Emydops minimus*, which was maintained by King (1988). Keyser (1993) later synonymized *E. minimus* with *Pristerodon mackayi* but, most recently, Fröbisch & Reisz (2008) referred TM 242 to *Emydops arctatus*. It was found 'at Kookfontein, Biesjespoort district, very close to the spot where the type skull of *Cynarioides laticeps* was discovered' (Broom 1935a: 5). Its biostratigraphic position is tentative, as with other specimens from Kookfontein.

NHMUK PV R 5763 and NHMUK PV R 5762. Holotype and paratype of *Cistecephalus angusticeps*, respectively. Broom (1932) described the type specimen as a new species of *Cistecephalus* on the basis of its narrower intertemporal region, but *C. angusticeps* was synonymized with the type species *C. microrhinus* by Keyser (1973) as it was interpreted to represent an earlier growth stage of the latter. The locality information provided by Broom (1932: 225) merely states that the type skull was collected from 'the base of the *Cistecephalus* zone at Biesiespoort.' The lack of uncertainty in this assignment suggests it was found at the level of Biesiespoort station or above, based on his opinions of biostratigraphy in other descriptions.

CISTECEPHALUS AZ

In the study area this biozone is exposed only on the slopes of the Horseshoe Mountain, encompassing most of the mountainside excluding the lower 50 m and the upper 100 m or so. The thickness of this assemblage zone is not well defined.

Dicynodontia

MMK 4167. Holotype of *Dicynodon wilmanae*. First described by Broom (1928), this species was transferred to the genus *Oudenodon* by van Hoepen (1934) before eventually being synonymized with the type species, *O. bainii*, by Keyser (1975). It was discovered by Broom 'on the side of the high mountain about 2 ½ miles east of Biesjespoort station and probably about 500 feet above the horizon of the station. As the station is as near as may be at the top of the *Endothiodon* zone, this new species may be regarded as being situated about 500 feet up in the *Cistecephalus* zone' (Broom 1928: 424).

UNKNOWN PROVENANCE

NHMUK PV R 4955. Holotype of *Palemydops platysoma*. Another of Broom's (1921) dicynodonts, *P. platysoma* has remained an enigmatic taxon. Its validity has been doubted but it has not yet been subject to formal review (see Cluver & King 1983; King 1988; Fröbisch 2009). Broom (1921: 665) provides a brief statement of its locality that is insufficient to place it in the area, saying only that it was 'found by me at Biesjespoort.'

MMK 4237. Holotype of *Bainia peavoti* (= *'Aulacephalodon' peavoti*). Broom (1921) initially described this taxon as a new species of *Bainia*, a genus he established in the same publication to accommodate various species of '*Dicynodon*' (*sensu lato*) with broad intertemporal regions and massive nasal bosses. Later (Broom 1932), he recognized that Seeley's (1898) subgeneric name *Aulacephalodon* had priority for this morphotype (though misspelling it as '*Aulacocephalodon*'), and transferred this species to *A. peavoti*. Keyser (1972) suggested that all named species of *Aulacephalodon* may synonymous with *Aulacephalodon bainii* but, most recently, Govender (2008) raised the possibility that '*Aulacephalodon' peavoti* represents a valid species on the basis of its postcranial anatomy. However, her account did not consider the holotype skull, which was reportedly missing at the time, and instead focussed on a referred specimen in the Field Museum of Natural History (FMNH UC 1532). The only portion of the holotype that can currently be located in the McGregor Museum is a partial lower jaw, which is indistinguishable from that of typical *A. bainii* (C. Kammerer, pers. comm. 2018). Broom (1921: 659) wrote that 'this new species is founded on a very fine skull discovered by me at Biesiespoort', but provided no details that could be used to determine where in the area it was found. Nevertheless, our collecting in the area and prevailing biostratigraphic opinion regarding the range of *Aulacephalodon* suggest that it was found no lower than the first appearance of *Cistecephalus*.