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TWO NEW GORGONOPSIAN SKULLS

By A. A. Manten*

ABSTRACT

Two complete and well-preserved skulls are described. One is referred to the species *Gorgonops torvus* Owen. It gives information on several details that are not clear in the type specimen. The second skull is recognized as a new species of *Prorubidgea,* and named *Prorubidgea brinki.*

INTRODUCTION

Among the skulls of fossil Therapsids recently cleaned in the Bernard Price Institute for Palaeontological Research there are two beautiful specimens of Gorgonopsians, each with the lower jaw in situ. As part of my activities during my sojourn of one year at this Institute, these specimens were placed at my disposal for description. One skull is recognized as a *Gorgonops torvus* Owen; the other is made the type of a new species of *Prorubidgea, P. brinki.*

Gorgonops torvus Owen

(Figs. 21B, 22, 24, 25 and 28)

1876, Owen, R., *Cat. Foss. Rept. S. Afr.,* p. 27; pls. xxi, xxii.
1914, Watson, D. M. S., *Proc. Zool. Soc.,* p. 1031.
1921, Watson, D. M. S., *Proc. Zool. Soc.,* p. 39, figs. 4-6.
1932, Broom, R., *Mammal-like Reptiles,* p. 113, fig. 37A.
1934, Boonstra, L. D., *Ann. S. Afr. Mus.,* xxxi, p. 181, fig. 4.
1935, Boonstra, L. D., *Am. Mus. Novitates,* 772, p. 2, figs. 1-3.

Type: Incomplete skull in the British Museum of Natural History (Cat. No. R.1647), from *Endothiodon*-zone beds at Mildenhalls, Fort Beaufort.

The present description is based on a skull found by Mr. J. W. Kitching on the farm Driehoeksfontein in the Murraysburg district. Stratigraphically the beds on this farm belong to the Upper *Endothiodon*-zone. The skull is beautifully complete and extremely well preserved. The lower jaw is present in situ. The skull is numbered 290 in the collection of the Bernard Price Institute.

Revised diagnosis: Skull medium to large. Dental formula i.5, c.1, pc. 4-5. Snout low, broader than high. Orbits directed laterally, but visible in dorsal view. Interorbital width greater than intertemporal width. Frontals form a small part of the supraorbital border. Prefrontals and postfrontals moderately large. Preparietal large and pineal foramen situated rather posteriorly on a small boss. Pterygoid processes at level of middle of skull length. Internal nares large.

Locality.

The specimen was found in the SE. wall of a hill, called Bloukop, on the farm Driehoeksfontein, Murraysburg. In September 1958 the author was enabled to visit the site. The hill has a top layer of sandstone. For the rest it is built up by an

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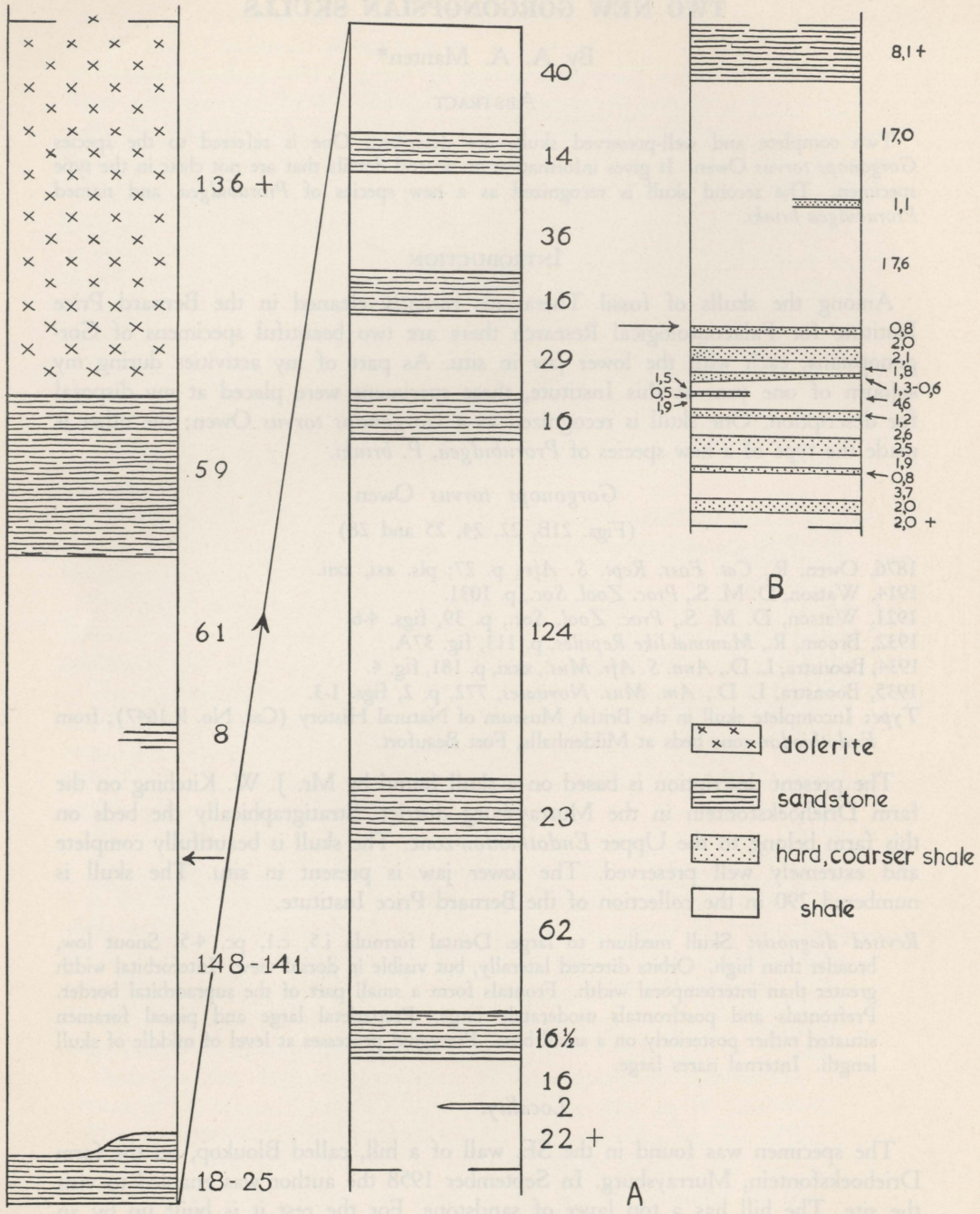


Fig. 21—Stratigraphic columns of the sites where the two described skulls have been found. A. *Prorubidgea brinki,* sp. nov.; B. *Gorgonops torvus* Owen. The figures indicate thickness in feet, the arrows the level on which the skulls have been excavated.

alternation of hard, somewhat coarser, more resistant shales of violet colour and softer shales, finer grained, very crumbly, predominantly bluish gray, partly also violet coloured. The skull was found on the line between a softer and a harder layer, indicated by an arrow in the profile in fig. 21B. The beds belong to the upper part of the *Endothiodon*-zone, but their exact position in the column of this zone has not been established.

The following are some measuremens in mm. of the present skull as compared with those of the type specimen:

		Type
Greatest length	325	—
Length from occipital condyle to premaxilla	305	210
Length from pineal foramen to premaxilla	265	170
Length from pineal foramen to edge of occipital plate	16	14
Length from premaxilla to front of orbit	183	111
Width across squamosals	205?	120?
Interorbital width	70	60
Intertemporal width	85	68?
Width across canines	100?	60
Width across pterygoid processes	150?	72
Height of snout	75	50
Height of occiput	86	45
Diastema	23	14
Incisor series	46	34
Length of lower jaw (along axis of skull)	284	—

Dorsal and lateral aspects.

The snout of this new skull is long and massive and represents slightly more than half of the total length of the skull.

The dentigerous parts of the premaxillae are rather high. They articulate directly with the anterior ends of the maxillae. The dorsal surfaces of the premaxillae are covered by the septomaxillae, which form the lateral halves of the lower margins of the external nares, and anteriorly they are produced upward and backward as deep wedges, penetrating the nasals.

The maxillae reach the nasals, except anteriorly where they form sutures with the facial parts of the septomaxillae. The latter in turn articulate in these areas with the lower margins of the nasals, but on each side the two bones separate at a level well behind the anterior ends of the nasals to surround the external nares. The nares face more laterally than anteriorly. The septomaxillae display rather clearly the nature of the inwardly directed turbinal processes dividing the nares into upper and lower passages.

The nasals are long, more than one third of the total skull length, and are broader in front than behind. They are restricted mainly to the dorsal surface of the skull, hardly contributing to the lateral sloping walls.

The prefrontals and lachrymals are moderately large.

The sides of the snout are not straight. Behind the canines the maxillae are bent

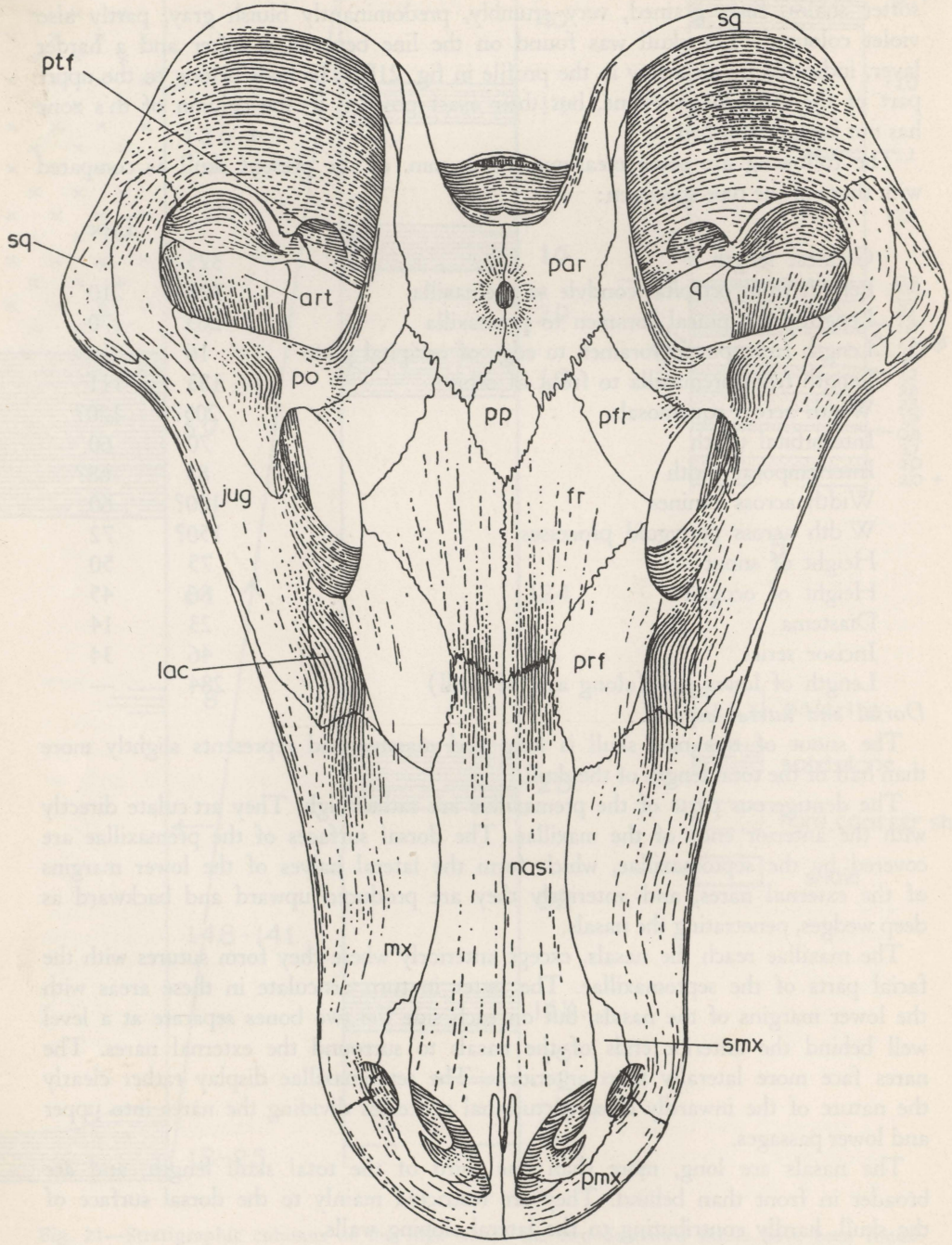


Fig. 22—Dorsal view of the skull of *Gorgonops torvus* Owen, restored half natural size. For abbreviations see end of article.

slightly inward. There is a very marked preorbital depression, extending mainly over the lachrymal area and overhung dorsally by an almost boss-like thickening of the prefrontal, which marks the lateral border of the dorsal surface of the skull in the

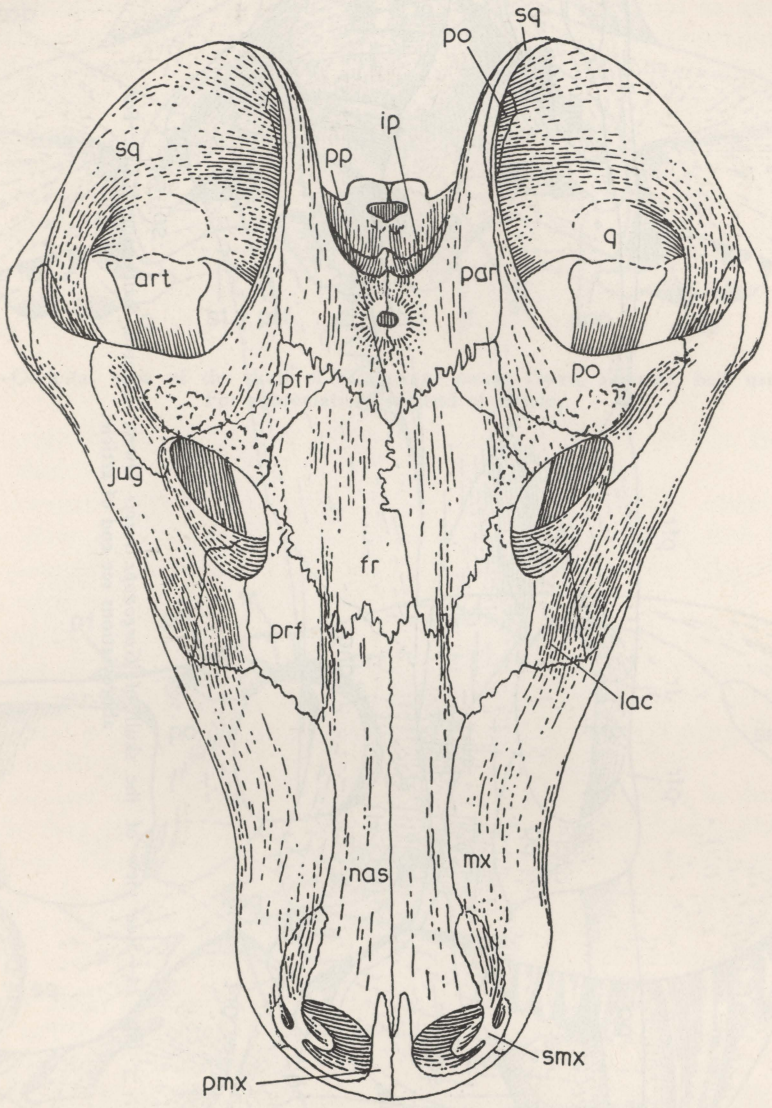


Fig. 23—Dorsal view of the skull of *Prorubidgea brinki* sp. nov., restored half natural size. For abbreviations see end of paper.

region in front of the orbits. In this region of the skull roof, where the nasals articulate with the frontals, there is a depression on each side, with a rather prominent median ridge.

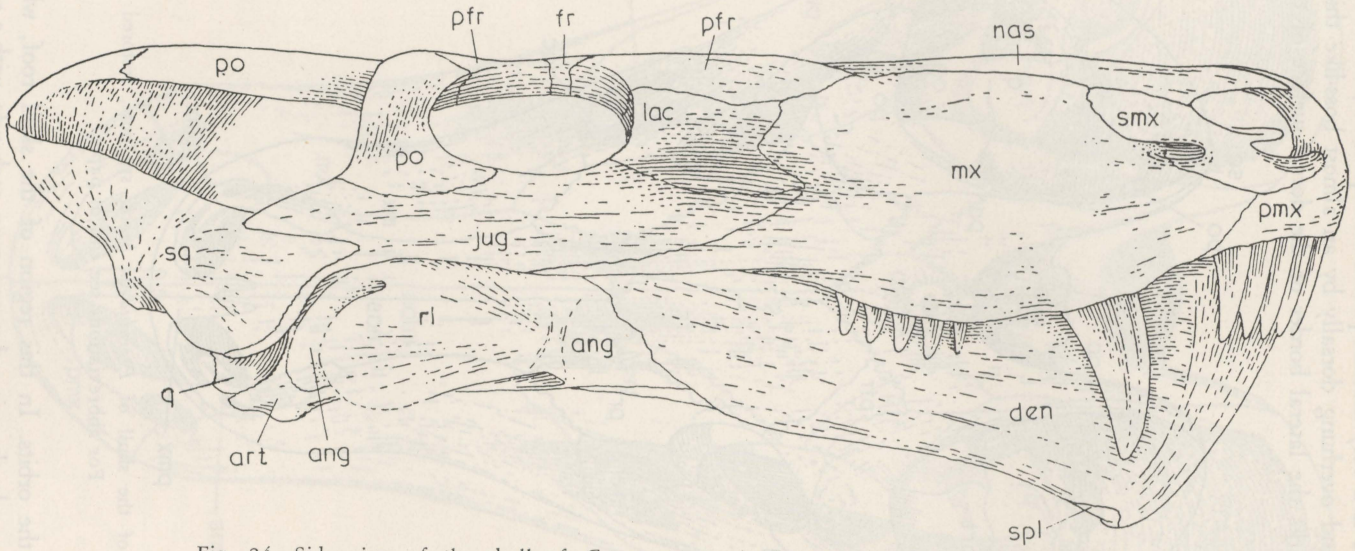


Fig. 24—Side view of the skull of *Gorgonops torvis* Owen, restored, half natural size. For abbreviations see end of article.

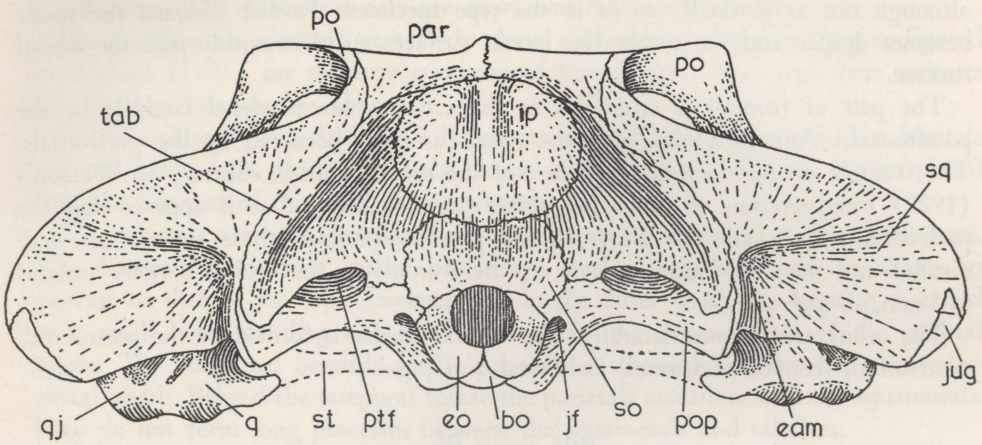


Fig. 25.—Occipital view of the skull of *Gorgonops torvus* Owen, restored, half natural size. For abbreviations see end of article.

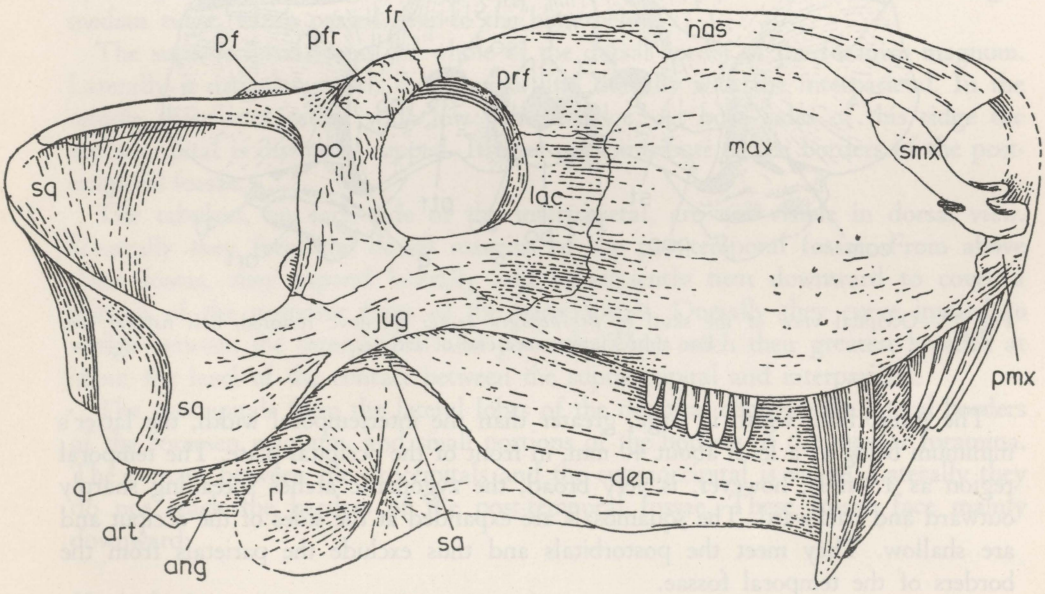


Fig. 26—Side view of the skull of *Prorubidgea brinki* sp. nov., restored, half natural size. For abbreviations see end of article.

Immediately in front of the orbits the snout is more or less square in section, although not as markedly so as in the type specimen. Farther forward the snout becomes deeper and the rather flat lateral surfaces curve smoothly into the dorsal surface.

The pair of frontals is cruciform in shape. They are bordered laterally by the postfrontals. Anteriorly they join the nasals and are bordered by the prefrontals. The frontals do not form a large part of the orbital border, contrary to Watson's (1921) interpretation of the type, which may be incorrect as it appears that the prefrontal sutures are not clear. In the present specimen these sutures are very distinct and the contributions made by the frontals to the orbital borders amount to 5 mm. on each side.

The orbits are directed laterally. The orbital border is formed by the postorbital, postfrontal, frontal, prefrontal, lachrymal and jugal.

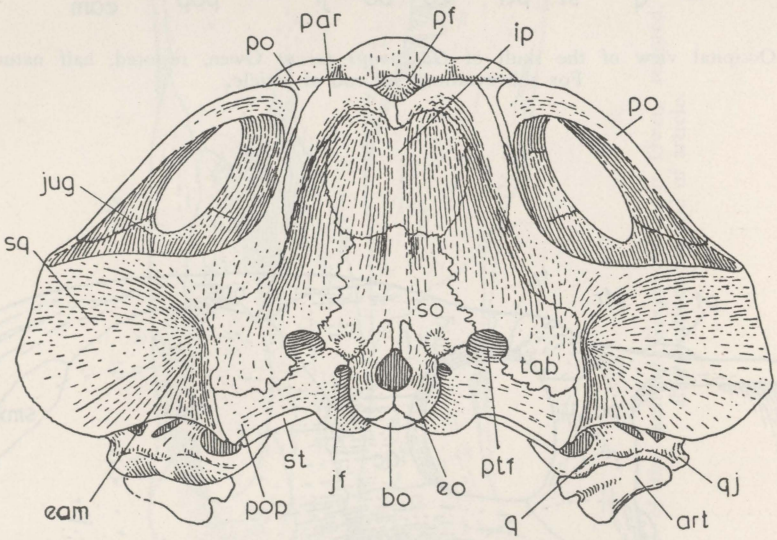


Fig. 27—Occipital view of the skull of *Prorubidgea brinki* sp. nov., restored, half natural size. For abbreviations see end of article.

The interorbital width is large, greater than the intertemporal width, the latter's minimum being at a level about 40 mm. in front of the occipital plate. The temporal region as a whole, however, is very broad, the zygomatic arches spreading sharply outward and backward. The squamosals are expanded at the sides of the occiput and are shallow. They meet the postorbitals and thus exclude the parietals from the borders of the temporal fossae.

The postorbitals form the posterior part of the orbital margins. They also contribute partly to the ventral borders where they have broad fan-like contacts with the jugals. They extend backward dorsally to the temporal fossae, where they

flank the parietals. The postorbitals are about three times as long as they are high in side view. The postorbial bars are short and moderately broad.

The postfrontals, situated posteriorly above the orbits, are not as long as figured by Watson (1921) for the type specimen of *Gorgonops torvus,* and their contacts with the parietals are less abnormal.

There is a large preparietal bone lying between the posterior parts of the frontals and the front ends of the parietals. It lies completely in advance of the pineal foramen, forward of the level of the postorbital bars.

The parietals are well developed. They separate to surround a pineal foramen. This foramen is situated rather posteriorly, and is regularly oval in shape, in contrast to that of the type specimen. As in the latter skull, the opening is raised on a small boss, standing about 3-4 mm. above the general level of the parietal region. The combined breadth of the parietals is distinctly smaller than the inter-orbital width. Behind the temporal fossae the parietals articulate with the squamosals. They do not form long processes between the squamosals and tabulars.

Occipital plate.

The occipital plate is slightly sloping and moderately cupped, and on the average broader than high.

The interparietal is rather indistinct, quite broad and situated entirely on the occipital plate. It does not reach the dorsal border of the occiput, which is formed by the parietals. Although damaged, it is clear that the interparietal had a slight median ridge, which passed over to the bone below.

The supraoccipital forms the whole of the dorsal border of the foramen magnum. Laterally it articulates with the tabulars and dorsally with the interparietal. In the middle there is a rather wide low vertical ridge. At both sides of this ridge the supraoccipital is distinctly cupped. It does not contribute to the borders of the post-temporal fossae.

The tabulars, on each side of the interparietal, are not visible in dorsal view. Ventrally they form the dorsal margins of the post-temporal fossae. From above these fossae, they expand laterally and subsequently turn downward to cover a portion of the posterior faces of the paroccipitals. Dorsally they curve inward to wedge between the interparietal and parietals. They reach their greatest breadth at about the level of the contact between the supraoccipital and interparietal.

The exoccipitals form the lateral lobes of the occipital condyle, the lateral borders of the foramen magnum, and small portions of the borders of the jugular foramina. The contact between the exoccipitals and the supraoccipital is vague. Laterally they do not reach the borders of the post-temporal fossae. These fossae face mainly downward.

Ventral view.

The well-rounded occipital condyle is mainly built by the basioccipital, the exoccipital contributions being less significant. The condyle is directed more ventrally

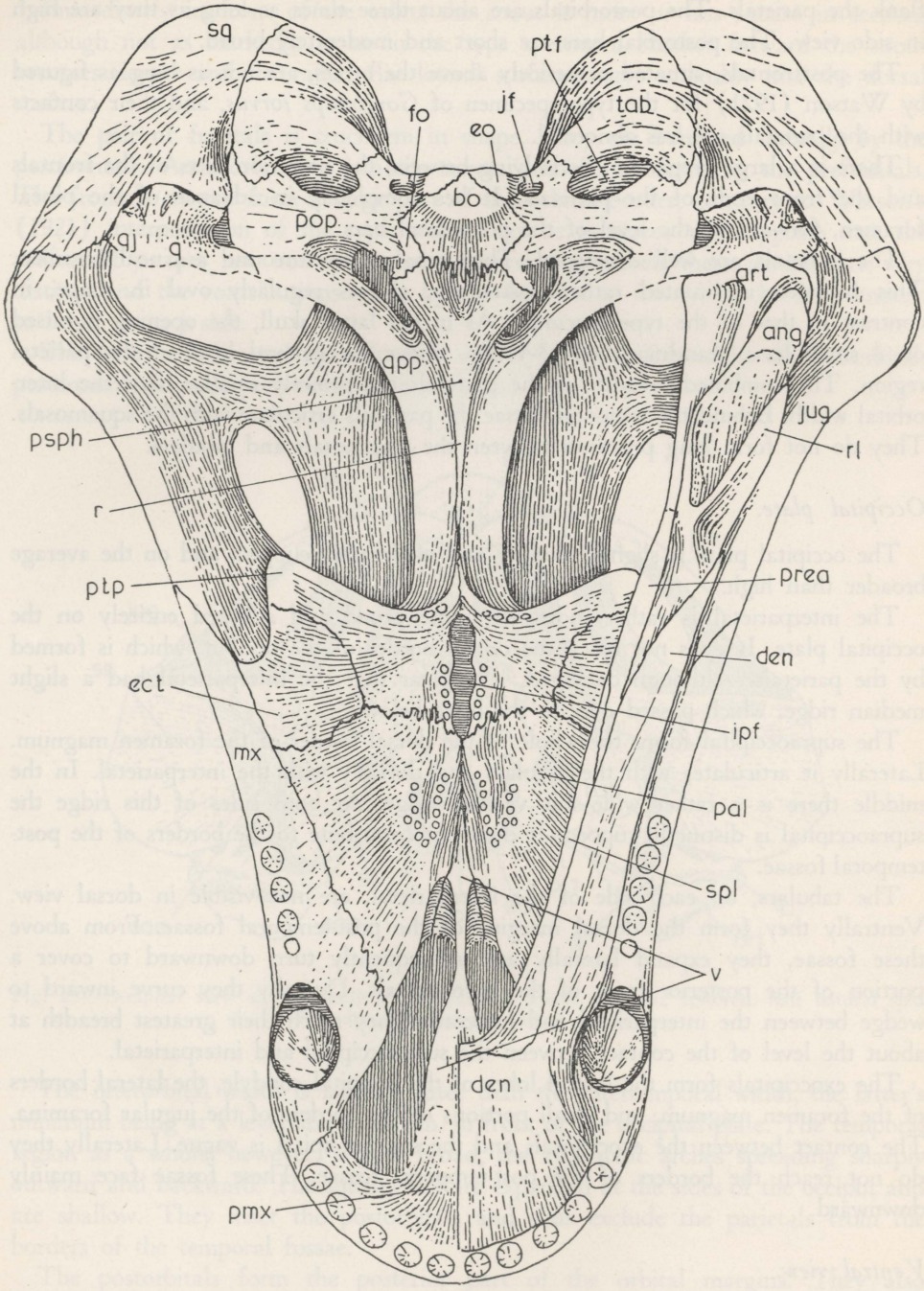


Fig. 28—Ventral view of the skull of *Gorgonops torvus* Owen, restored, half natural size. For abbreviations see end of paper.

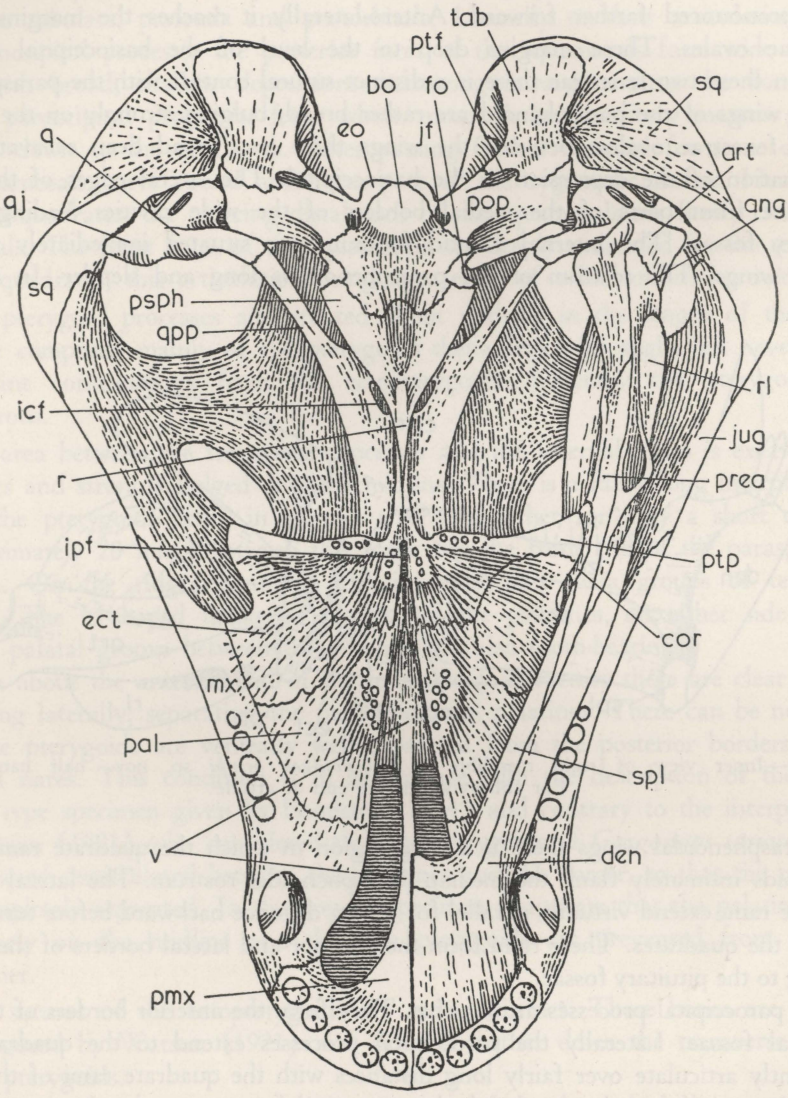


Fig. 29—Ventral view of the skull of *Prorubidgea brinki* sp. nov., restored, half natural size. For abbreviations see end of article.

than posteriorly. The basioccipital does not contribute to the ventral margin of the foramen magnum. Laterally and close to the condyle are the two jugular foramina, but the basioccipital does not contribute to their margins either. In front of the condyle the basioccipital expands laterally and continues forward between the opisthotics, but at a slightly higher level. This area is vaulted, the excavation being more pronounced farther forward. Antero-laterally it reaches the margins of the fenestrae ovales. These margins drop to the level of the basioccipital condyle. Between these two fenestrae there is a distinct sutural contact with the parasphenoid.

The wings of the parasphenoid are rather broad, bulging strongly on the borders of the fenestrae ovales. Between the wings there is a broad deep excavation, the continuation of the depression in the basioccipital. The lateral edges of the wings form the front parts of the medial borders of the wide cavities leading to the pituitary fossae. The internal carotid foramina are situated immediately in front of the wings. The rostrum of the parasphenoid is long and slender. In front of

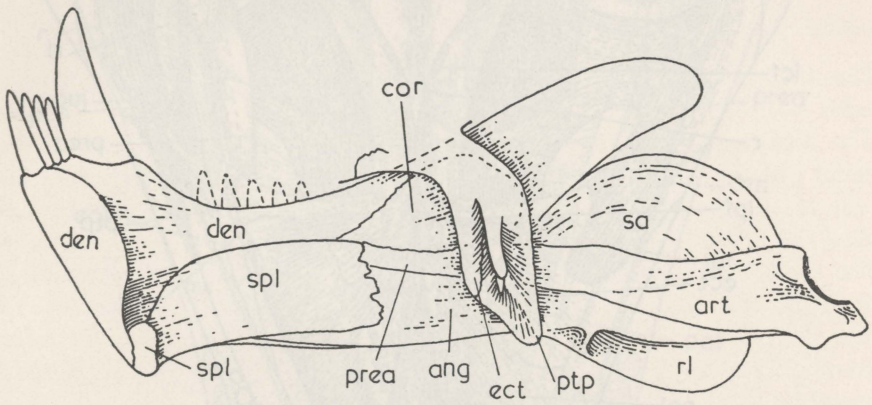


Fig. 30—Inner view of right mandible of *Prorubidgea brinki* sp. nov., half natural size. For abbreviations see end of article.

the parasphenoidal wings there is a long region in which the quadrate rami of the pterygoids intimately flank the median parasphenoidal rostrum. The lateral margins of these rami extend virtually parallel for a long distance backward before turning out to join the quadrates. These rami form the anterior and lateral borders of the cavities leading to the pituitary fossae.

The paroccipital processes are massive. They form the anterior borders of the post-temporal fossae. Laterally the paroccipital processes extend to the quadrates and apparently articulate over fairly long distances with the quadrate rami of the pterygoids. Posteriorly to the quadrates the paroccipital processes abut against folds of the squamosal, which form the medial borders of the auditory meatus grooves.

The quadrates are bones of moderate size. Their anterior margins are thickened to form the condyles for the articulation with the lower jaw. It is likely that the quadrates were streptostyl.

It is not clear to what extent the quadratojugal builds the lateral portion of the quadrate element. The quadrates and quadratojugals are partly overhung by the squamosals, in such a way that much of the height of both bones is hidden in occipital view.

From the quadrates the squamosals extend dorsally and medially to articulate with the tabulars, parietals and postorbitals. Laterally to their articulations with the paroccipital processes the posterior faces of the squamosals form wide fan-like areas with broad, shallow depressions narrowing inward to near the dorsal end of the paroccipital processes, from where more distinct auditory meatus grooves descend down to the quadrates. After passing farther outward for some distance the squamosals curve round and form part of the zygomatic arches. Here, level with the quadrates, the tapering distal ends of the squamosals are firmly clasped by the jugals. The front faces of the squamosals are deeply excavated for the reception of the quadrates, this articulation being apparently of a ball-and-socket nature.

The pterygoid processes are situated about midway in the length of the skull, and are composed mainly of the pterygoids themselves with slight but nevertheless significant contributions from the ectopterygoids. Medially the pterygoids are dentigerous.

The area between the transverse processes and the internal nares is excavated at the sides and strongly bulged near the midline. There is a fairly long interpterygoid fossa, the pterygoids being in contact with each other for only a short distance (approximately 20 mm.) between this fossa and the front end of the parasphenoid rostrum. On the ridges bounding the interpterygoid fossa groups of teeth are present. The U-shaped thickened regions on the palatines, on either side of the median palatal groove between these bones, are also tooth-bearing.

From about the anterior end of the interpterygoid vacuity there are clear sutures extending laterally, separating the pterygoids and palatines. There can be no doubt that the pterygoids are ventrally well separated from the posterior borders of the internal nares. This condition is in accordance with the description of the palate of the type specimen given by Boonstra (1934) and contrary to the interpretation of Watson (1921) who considered that the pterygoids of *Gorgonops torvus* extend far forward, intercalated between the palatines and the vomer, so that the palatines are completely separated. In the present specimen it appears that the palatines meet posteriorly on the midline and that the pterygoids are prevented from meeting the vomer.

The sutures of the ectopterygoids are rather distinct. These bones are broader than figured by Watson (1921) and descend farther down the transverse flanges of the pterygoids.

The internal nares are very large, separated by a bar which lies considerably above the level of the lower edges of the maxillae. This bar is comparatively broad and flat anteriorly and narrow and high behind. In front the nares are bounded by the premaxillae; here they are widest. Somewhat farther back they are constricted by the bulging of the maxillae at the level of the canines. The outer borders are

formed anteriorly by the maxillae and posteriorly by the palatines, the latter also forming parts of the posterior border. The internarial bar (vomer) is continued backward into this part of the palate as a narrow wedge. The actual posterior borders of the internal nares extend transversely at a very high level, well above the ventral surface of the vomer.

Dentition.

The dentition of the upper jaw is well exposed. There are on each side five functional incisors, a long canine and five simple conical cheek teeth. Although the genus *Gorgonops* was defined as having only four postcanines (Haughton and Brink 1954, p. 114), this is not thought to be a valid criterion for placing this specimen in a new genus, the number of these teeth often increasing with the age of the individual. Besides, the postcanines in several Gorgonopsians are so degenerate that apparently their number can even differ within a species in specimens of similar age. The number of incisors may well form a sounder basis for generic distinction.

The incisors are all broken off along the alveolar border. Judging from the sections they were large, cylindrical teeth, slightly compressed transversely. There are no signs of replacement teeth. The left canine is complete, but superficially damaged, while the right one is very fragmentary. The canines are relatively short, with a crown length of about 40 mm.; they are normally curved and directed slightly forward. On the right side the first postcanine tooth is very small and had apparently recently erupted. The second and fourth teeth are missing, leaving empty sockets. The third and fifth teeth are present but the crowns are slightly damaged. On the left side only the first cheeck tooth is missing, but from the nature of the socket it appears to have been as small as its fellow of the opposite side. The crowns of the four subsequent teeth have been variously damaged. All the teeth, excluding the canines, indicate a solid cross section at the level of the alveolar border with only the slightest trace of a pulp cavity in some incisors. Thus it would appear that this specimen is quite advanced in age. However, the damaged left canine shows a very large pulp cavity and both canines are situated loosely in their sockets, more towards the anterior side. It is quite clear that the canines are young, having recently replaced their predecessors. Thus, replacement of the canines in a specimen which otherwise seems to be well advanced in age indicates that there is no limit to the number of replacements, or an arrest at a particular age. This observatio nis contradictory to the hypothesis of Kermack (1956) who supposed that tooth replacement occurred only during the period that the animal grows in size. Each animal would have a number of deciduous dentitions, not perhaps the same number for all the teeth, followed by a final, permanent dentition. (Kermack 1956, p. 129).

There is a step in the alveolar border, in front of the canine, so that the incisors are raised above the level of the canines and cheek teeth. This step, however, is not as high as figured by Watson (1921). This drawing of the dentigerous border seems to be a misinterpretation as a result of imperfect preservation. Over the roots of the canines the maxillae show long and broad swellings.

The lower jaw is so closely in situ that the nature of the lower dentition is difficult to ascertain. On the left side it is barely possible to trace the presence of four incisors between the symphysis and the position of the canine. It is normal in Therapsids to have one incisor less in the dentary than in the premaxilla. A portion of the left canine is exposed on the inside, in front of the choana. Approximately 20 mm. behind this canine two cheek teeth are exposed. They correspond in relative position to the diasteme behind the upper canine.

The excavations on the sides of the dentaries, which allow room for the upper canines, are very pronounced and indicate that the latter teeth are quite large when fully erupted.

Palatal teeth occur on thickened U-shaped regions of the palatines, but they are badly preserved. There are similar teeth on the pterygoids, on either side of the interpterygoid vacuity and on the median parts of the sharp ridges extending to the pterygoid processes.

The lower jaw.

The lower jaw is well preserved. The dentaries form about two-thirds of the length of the jaw. The "coronoid" extensions are weak and extend barely beyond the level of the pterygoid processes. On the inside of the dentaries the splenials are high and flat. They form the ventral margin of the jaw in the region of the symphysis, and they curve outward on the bend at the level of the upper canines so that they are just visible in lateral view. For some distance backward they tend to contribute to the ventral margins of the rami. At this level they reach upward to the alveolar border. The height of the splenials is considerably less in the region of the symphysis. Posteriorly the splenials taper and terminate shortly in front of the level of the pterygoid processes, where highly reduced coronoids are almost completely hidden by these processes.

The prearticulars are firmly wedged between the dentaries and splenials anteriorly. Farther back they are exposed on the inside, except where they are covered by the small coronoids. Laterally they are completely covered by the angulars. The articulars are continuous with the prearticulars and extend back to form the articular facets.

The surangulars are badly exposed and indistinct.

The angulars penetrate forward between the prearticulars and the dentaries. They cover large areas in lateral view, accross the prearticulars, articulars and surangulars. The reflected lamina is large and wide. Posteriorly it lies flat against the main body of the bone but it is inclined to leave a distinct space along the line where it is inserted.

A peculiar feature of the lower jaw is that while the rami are rather slender and not very high along their entire lengths, the symphysial region is still very high. The symphysis is, however, not very thick antero-posteriorly.

Discussion.

There are a number of differences between the new specimen and the type of *Gorgonops torvus* Owen, as described by Watson (1914, 1921) and Boonstra (1934):

The specimen as a whole is considerably larger.
There are five cheek teeth instead of four.
The frontals do not form a large part of the orbital border.
The frontals and postfrontals are smaller.
The pineal foramen is not irregularly shaped.
The ectopterygoids are larger.

The first two differences, however, may be the result of merely a difference in the age of the two individuals, the type specimen being more juvenile. The massive sections of the teeth, with hardly any sign of pulp cavities, show that the present skull is that of a rather old individual. As far as the frontals' participation in the orbital borders is concerned, Watson indicates the prefrontal sutures as indistinct, and it could be that his interpretation is incorrect. The irregular shape of the pineal foramen may be artificial. Furthermore Boonstra admits that the sutures of the ectopterygoids are not clearly visible in the type. There are, therefore, no reasons for making the present skull the type of a new species.

The main morphological features of *Gorgonops torvus* Owen may be summarized as follows:

Primitive: Snout square in section. Tooth row fairly straight. Step in the alveolar border. Marked preorbital depression. Orbits directed outward. Large postfrontals. Preparietal large. Posterior position of the pineal foramen. Small, somewhat laterally directed temporal openings. Slightly sloping occiput. Paroccipital massive. Basioccipital large. Internal nares large.

Advanced: Snout wider than high. Sides of the skull not straight. Frontals do not form a large part of the orbital border. Occiput slightly cupped. Pterygoid flanges not far posteriorly.

From this summary it appears that *Gorgonops torvus* is one of the more primitive Gorgonopsians.

Leptotrachelus eupachygnathus Watson is considered by Watson and Romer (1956) as a member of the family Gorgonopsidae, which includes otherwise only the genus *Gorgonops* and a specimen referred to by Von Huene (1950) as *Lycaenops kingoriensis*. This new interpretation of the relationships of *Leptotrachelus* seems rather unlikely. As part of the family diagnosis, Watson and Romer mention a noticeable square cross-section of the snout in front of the orbits and a very marked "step" in the dentigerous border between the incisors and the canine. Boonstra (1934), however, remarks: (1) that there is no definite evidence of a step in the alveolar border in *Leptotrachelus,* and (2) that the snout is not square in cross-section.

There are also several other differences between *Gorgonops torvus* and *Leptotrachelus eupachygnathus,* e.g. in the latter; (3) The jugals are much deeper in front of the orbits; (4) The frontals are considerably larger; (5) The pineal foramen is more anteriorly situated; (6) The occiput is distinctly more deeply cupped; (7) The basioccipital is very small.

From this it appears that *Leptotrachelus* stands on a higher developmental niveau than *Gorgonops* and is thus more comparable with *Scymnognathus*. Besides, Boonstra (1934) is of the opinion that *Leptotrachelus* is actually very closely related to *Scymnognathus,* and even the description of Watson (1921) indicates only a few small differences between these two genera.

The exaggerated step in the alveolar border, as figured by Watson (1921) for *Leptotrachelus eupachygnathus,* seems to be a misinterpretation as a result of imperfect preservation.

Lycaenops kingoriensis Von Huene, from beds of *Cistecephalus*-zone age in the Tanganyika Territory is also greatly different from *Gorgonops torvus*: (1) It has a thickening of the anterior and dorsal orbital margins; (2) The frontals are considerably larger; (3) The postorbital bars are very broad; (4) The jugals are very deep below the orbits; (5) The pineal foramen is situated on the very edge between the dorsal surface and the occipital plate; (6) The occipital plate is very gradually sloping; (7) There are apparently no teeth on the pterygoids (family diagnosis!). Its relationship to the Gorgonopsidae is, therefore, also extremely doubtful.

The present author is not satisfied with the inclusion of *Leptotrachelus eupachygnathus* in this family, and he also feels that, *Lycaenops kingoriensis* being an uncertain factor, the family diagnosis of the Gorgonopsidae should be revised.

Prorubidgea brinki sp. nov.
(figs. 21A, 23, 26, 27, 29 and 30)

The type specimen is a nearly perfect skull, with both mandibles present and in position. It was found by Mr. E. Kriegel in March 1955, on his farm Ringsfontein, in the Murraysburg district. He disposed of the skull to Mr. J. W. Kitching of the Bernard Price Institute. The skull is catalogued No. 289. Its stratigraphic age is low in the Upper part of the *Cistecephalus* zone.

I propose to name this specimen *Prorubidgea brinki* sp. nov., after Dr. A. S. Brink, scientific officer of the Bernard Price Institute, who gave me valuable assistance during my period of study at the University of the Witwatersrand.

Diagnosis: Skull medium in size. Dental formula of the upper jaw i.5, c.1, m.5. Canines large. Snout relatively narrow and deep at the canines. Orbits small, visible in dorsal view. Interorbital width greater than intertemporal width. Frontals form a small portion of the supraorbital border. Preparietal small or absent. Pineal foramen present, situated rather posteriorly. Postorbitals extending far backward. Quadrates markedly streptostyl. The foramen magnum almost completely surrounded by the exoccipitals, Transverse processes of the pterygoids about mid-way in the skull length and not very massive. Ectopterygoids and palatines relatively large. Palatines meeting posteriorly on the midline, preventing the pterygoids from meeting the vomer. Mandible massive. Front face of symphysis long and sloping.

Locality.

The beds on the farm Ringsfontein belong mainly to the middle part of the *Cistecephalus* zone. A representation of these beds is given in column-form in fig.

21A, measured by the author with the aid of a telescopic alidade in Oct. 1958. On top there is a thick dolerite layer. The underlying 280 ft. of sandstone and shale are considered by J. W. Kitching as belonging to the Upper part of the *Cistecephalus* zone. The type specimen of *Prorubidgea brinki* has been found about 200 ft. underneath the dolerite. A study of the beds on the farm Beeldhouwersfontein, also in the Murraysburg district, has shown that the genus *Cistecephalus* disappears about 530 ft. below the supposed Middle-/Upper *Cistecephalus*-zone border. This disappearance seems to be a rather characteristic line within the *Cistecephalus* zone, which may well be useful to draw the line between the Lower and Middle parts of this zone. Comparison between the two farms shows that *Prorubidgea brinki* was found about 610 ft. above the last *Cistecephalus*-containing layer.

The following is a list of useful measurements:

Greatest length	280 mm.
Length from occipital condyle to premaxilla	240
Length from pineal foramen to premaxilla	205
Length from pineal foramen to edge of occipital plate	12
Length from premaxilla to front of orbit	139
Width across squamosals	203
Interorbital width	65
Intertemporal width	54
Width across canines	88
Width across pterygoid process	147
Height of the snout, measured at the level of the canines	102
Height of the occipital plate	87
Length of the lower jaw (along axis of skull)	221
Height of mentum	68
Height of mandible just behind canines	38

Dorsal and lateral aspects.

The snout of the new specimen has a length of exactly half that of the skull as a whole. It is relatively narrow and deep in the region of the canines, the ratio between width and height being about 1 : 1·16. As there is a tendency among Gorgonopsians to flatten the snout, the majority of *Cistecephalus*-zone forms have a face which is broader than high. A relatively high and narrow snout is found in this zone in such forms as e.g. *Aelurognathus serratidens* Haughton, *Scylacocephalus watermeyeri* Broom, *Lycaenodon longiceps* Broom, and the Rubidgeidae. The sides of the snout bend slightly inward behind the canines, expanding again backwards and passing gradually into the orbital and temporal regions.

The alveolar borders of the premaxillae slope sharply downward from the midline to the canines. The suture marking the extensive overlap of the maxilla over the premaxilla runs sharply forward from the fifth incisor, up to the septomaxilla. The

internarial bridge is missing, but enough is preserved dorsally to indicate that each premaxilla penetrates the nasal of its side, and that these two processes are not inclined to separate the nasals on the midline.

As far as can be ascertained the septomaxillae resemble in broad outline those of other Gorgonopsians. They cover the anterior faces of the premaxillae to a much lesser extent than in *Gorgonops torvus*. The foramen between the septomaxilla and maxilla is also smaller and more superficial; in *Gorgonops* a wide depression leads to this foramen.

The maxillae are short and deep. Their alveolar borders are gently curved. Dorsally the maxillae reach the nasals, except anteriorly, where they articulate with the facial parts of the septomaxillae.

The nasals are long and rather slender, covering about three-sevenths of the total skull length, or more than half the distance from the front of the snout to the edge of the occipital plate. They are wider at the ends than in the middle. They form the dorsal surface of the snout, contributing also slightly to the lateral walls.

The prefrontal is rather large, forming the front half of the dorsal orbital margin. The anterior margin is formed mainly by the lachrymal. This bone is short, about as high as long. There is a slight depression on each lachrymal and a deeper separate depression lower down, covering mainly the anterior part of the jugal.

The suborbital portions of the jugals are not very deep, compared with the forms dealt with above, but deeper and shorter than in *Aelurosaurus*. From here the jugals pass backward and outward to meet the squamosals. There is not a sharp outward swing on the temporal arch, but the downward bend is rather pronounced.

The orbits are directed mainly laterally, but also slightly anteriorly. They are very well visible in dorsal view. The interorbital width is greater than the intertemporal width, the latter being narrowest shortly behind the middle of the temporal openings, at about the level of the occipital condyle.

The frontals are separated on the midline by a rather irregular suture. They only form a small part of the supraorbital border. Anteriorly they articulate with the prefrontals and nasals, posteriorly with the postfrontals and parietals. It is not absolutely clear whether there is a preparietal bone. The anterior parietal suture curves sharply forward on the midline, suggesting that a small preparietal is located in this area. There are, however, no clear sutures separating the preparietal from the parietals. There is clearly no median suture at this level.

The postfrontals, reaching backward from the posterior parts of the supraorbital margins, are comparatively long.

The postorbitals are large and extend very far backward, forming nearly all of the supratemporal borders. They also form the postorbital arches, which are not conspicuously broad or massive. They do not contribute to the ventral borders of the orbits.

The parietals are relatively broad and short. They are well fused along the midline, so that the median suture, although visible, is not very distinct. Laterally

the parietals do not contribute to the dorsal borders of the temporal fossae, being separated from these by the long posteriorly extending processes of the postorbitals, which meet the squamosals and are gradually replaced by them. At this level the parietals also articulate with the squamosals, where they penetrate deeply between the long anterior processes of the latter and the tabulars.

There is a pineal foramen of medium size, situated on a distinct, more or less circular boss about five millimetres high.

Occipital plate

The occipital region inclines forward and bears a low but nevertheless distinct median ridge, extending from the foramen magnum to the pineal boss.

The interparietal is slightly dumbbell-shaped, bordered dorsally by the parietals, laterally for the major part by the tabulars. It is slightly visible in dorsal view, but does not reach the horizontally thickened, concave dorsal occipital border.

The supraoccipital is comparatively narrow and rather conspicuously high. Laterally it articulates with the tabulars and dorsally with the interparietal. It contributes only to a very minor extent to the dorsal border of the foramen magnum, sending here a small process down between the two large exoccipitals. From this process the median occipital ridge arises. On both sides of this ridge the supra-occipital occupies two flat areas, turning backward laterally and leading upward to small, well-defined depressions. Ventro-laterally it forms small portions of the dorso-medial borders of the post-temporal fossae. Between the post-temporal fossae and the occipital condyle on either side the supraoccipital forms a minute boss.

The tabulars are relatively narrow, bordered medially by the supraoccipital, ventrally by the paroccipital processes and laterally by the squamosals. Dorsally they taper between the interparietal and parietals. The tabulars form the lateral and the greater portion of the dorsal borders of the post-temporal fossae. The overlap of the tabulars across the paroccipital processes is broad and elaborate. The post-temporal fossae face backward.

The exoccipitals are large. They form the ventral, lateral and most of the dorsal borders of the foramen magnum, surrounding it almost completely. Dorsally they are separated by a narrow process of the supraoccipital. The exoccipitals also contribute to the occipital condyle. From this specimen it is clear that the occipital condyle as a whole is trough-shaped dorsally, this trough leading horizontally forward to the foramen magnum. The walls of the trough largely represent the exoccipital contributions to the condyle. Where these walls pass over into the surface of the occipital plate on either side of the foramen magnum, the exoccipitals articulate indistinctly with the supraoccipital. The exoccipitals are well separated from the borders of the post-temporal fossae.

Ventral view.

The basioccipital forms the bulk of the single, rounded occipital condyle, the

contributions of the exoccipitals being less significant. When the skull is posed with its long axis horizontally, the condyle is directed more posteriorly than ventrally. The basioccipital does not reach the ventral border of the foramen magnum. Laterally, forward of the condyle are the two jugular foramina, bordered medially and anteriorly by the basioccipital, laterally and posteriorly by the paroccipitals and medially by the exoccipitals. In front of these foramina the basioccipital expands laterally between the paroccipital processes. It reaches its maximum breadth where it borders on the medial margins of the fenestrae ovales. From here it continues for a short distance forward between the posterior wings of the parasphenoid.

The posterior part of the parasphenoid is broad, with broad wings at the sides and a deep groove in the middle. The wings decrease in breadth forward. The narrow rostrum of the parasphenoid is relatively short and wedges forward between the quadrate rami of the pterygoids. This portion of the parasphenoid forms a prominent and very deep keel, dropping to a level below that of the wings farther back. The lateral edges of the parasphenoidal wings form the medial borders of the excavations leading to the pituitary fossae.

The lateral margins of the quadrate rami of the pterygoids are only for a short distance parallel to the long axis of the skull. About 15 mm. behind the transverse processes they start turning outward to join the quadrates but not with sharp curves.

The paroccipital processes are massive. Anteriorly the paroccipitals form the posterior margins of the excavations leading to the pituitary fossae. Posteriorly they form the anterior borders of the post-temporal fossae. Medially to the pituitary excavations the paroccipitals articulate with the basioccipital, where they form the posterior halves of the margins of the fenestrae ovales. Laterally they extend to the quadrates and apparently just articulate with the quadrate rami of the pterygoids on the dorsal side of the distal ends of the stapes.

Posteriorly to the quadrates, the blunt ends of the paroccipitals abut against folds of the squamosals forming the medial borders of the auditory meatus grooves.

The stapes are rather damaged. They extend from the fenestrae ovales to the quadrates, where their distal ends are well held in position by prominent quadrate processes.

The quadrates are well developed with thickened anterior margins, which form the articulation with the lower jaw. The quadrates are streptostyl. They articulate loosely in deep excavations in the anterior faces of the squamosals. It is not clear to what extent the quadratojugals contribute to these elements.

The squamosals are of moderate size, but they form the bulk of the posterior walls of the temporal fossae. Medially the squamosals articulate with the tabulars, dorsally they taper between the post-orbitals and parietals. Laterally to their articulations with the paroccipital processes the posterior faces of the squamosals form wide fan-like areas with broad, shallow depressions, from where more distinct auditory meatus grooves descend down to the quadrates.

The transverse processes of the pterygoids are midway in the length of the skull

and have broad outer surfaces for the support of the mandibles. The medial halves of the sharp crests, extending from the parasphenoid keel to the transverse processes of the pterygoids, are tooth-bearing. The anterior parts of the pterygoids are separated by a small, very narrow interpterygoid fossa. They do not meet the vomer. There are separate groups of teeth on the pterygoids, close to the border of this fossa.

The ectopterygoids are large bones, more or less oval shaped. Each ectopterygoid articulates with the palatine, the maxilla, and the pterygoid. They contribute to a lesser extent to the formation of the transverse pterygoidal flangs than in *Gorgonops*.

The palatines are relatively large, forming the posterior halves of the lateral borders of the internal nares. There are extremely high ridges on both sides of the median palatal groove, which anteriorly are tooth-bearing. Anteriorly and laterally the palatines articulate with the maxillae, which form the anterior halves of the lateral borders of the internal nares. The anterior borders are formed by the premaxillae. The internal nares are widest at the level where the premaxillae articulate with the maxillae.

The vomer forms a deep median plate between the internal nares, its lower margin lying considerably above the level of the palatines. Posteriorly this plate penetrates between the palatines, and terminates in front of the interpterygoid vacuity. The palatines apparently meet just on the midline, so that the pterygoids are barely separated from the vomer.

Dentition.

In the premaxilla there are five functional incisors on each side. Of these only the fifth one on the right side is complete. It is slightly curved, with a crown of about 17 mm. length. All other incisors are broken off. Their sections show clear pulp cavities, from one to three mm. in diameter. This may indicate that, although the individual appears to be fully mature, it had not reached an advanced age.

On each side there is a large canine, the front margin of which is 11 mm. behind the fifth incisor. The base of each canine has an antero-posterior measurement of about 18 mm. The tips of both canines have disappeared, but the length of the canines when complete may be estimated at about 45-50 mm., and the teeth must have extended somewhat below the borders of the mandibles, as is shown in the side view of the skull. In both the incisors and the canines there are no signs of any replacement.

On each side there is a series of five cheek teeth, 13 mm. behind the canine. Of these the first one is complete on both sides, the third and fourth are present only on the left side. Both the fifth molars are represented only by sections at the level of the alveolar border. They are smaller than the others and seem to be rather immature.

There is no clear step in the alveolar border between the incisors and the canine.

As the mandible is in close articulation with the skull the lower dentition cannot

be properly interpreted. There seem to be four incisors and a canine on each side, but the number of postcanines cannot be determined.

Palatal teeth are present on very high ridges on the palatines. Posteriorly these ridges extend on the pterygoids, where their posterior ends are also tooth-bearing, closely on either side of the interpterygoid fossa. Finally, teeth are developed on the median halves of the crests leading to the transverse flanges of the pterygoids. All palatal teeth are badly preserved.

The lower jaw.

The lower jaw is quite well preserved and exposed.

The dentaries are long and less slender than in *Gorgonops*. The symphysial region is very high and well inclined. In front of the canines there are low ridges that sweep into the lower border of the jaw. The coronoid processes are long and slender.

The splenials contribute slightly to the lower symphysial margin. On the symphysis the splenials are not high. On the rami they grow higher, but not as high as in *Gorgonops*. They do not reach to the alveolar borders. Posteriorly they terminate abruptly and bluntly, well in front of the pterygoid processes.

The coronoids are large, situated dorsally. They taper forward and have delicate contacts with the dorsal margins of the splenials. The prearticulars are exposed below the ventral margins of the coronoids and, below them, the angulars penetrate forward massively between the splenials and dentaries.

The angulars are extremely large. Posteriorly they flank the articulars intimately. The reflected lamina extends parallel to this portion, leaving a space of about 3 mm. in between. This space is considerably wider where the reflected lamina leaves the main body of the bone, on the ventral margin of the jaw. On the outer face this position is marked by a prominent ridge. This ridge extends dorsally and slightly anteriorly, but the actual line of contact of the reflected lamina with the main bones runs sharply backward, so that the ridge does not mark the actual line of origin of the fold.

The surangulars are exposed on the inside as large, dorsally curved bones lying above the articulars. Their inside surfaces are smooth.

The articulars are wide and massive. Anteriorly they are indistinguishably continuous with the prearticulars.

Discussion.

During a short visit to the collection of Dr. S. H. Rubidge of Graaff-Reinet the author saw the type specimen of *Prorubidgea maccabei* Broom. There can be no doubt that the present specimen belongs to the same genus, although it is a new species. From the drawings and the very brief description of *Prorubidgea maccabei* by Broom (1940) the following differences can be established: The nasals in *P. brinki* are relatively longer, the frontals distinctly shorter; the lachrymals smaller. The prefrontals are smaller and form less of the supraorbital margins. The preparietal is certainly not as large as figured by Broom for *P. maccabei*. The temporal fossae in

P. maccabei are almost entirely behind the plane of the pineal, in *P. brinki* they extend at least 10 mm. forward of the pineal foramen. The postorbital bars are less massive in *P. brinki.*

Prorubidgea robusta Brink and Kitching is rather different in general appearance from *P. maccabei* and *P. brinki,* especiallly in the posterior half of the skull. It may even be doubtful whether the identification of this species as a *Prorubidgea* is correct. The orbits are less apparent in dorsal view. The frontals are excluded from the orbital margin. The post- and suborbital bars are distinctly more massive. The postfrontals are larger. The preparietal is large and contains the pineal opening. The temporal openings are comparatively small. Unfortunately the palate of *P. robusta* is not visible. There are only three cheek teeth, but as the specimen is quite mature this could be due to loss of the fourth and fifth teeth with advanced age. In both the other *Prorubidgea* species this number is five.

The main morphological features of *Prorubidgea brinki* sp. nov. are:

Primitive: Snout higher than broad. Slight preorbital depression. Postfrontals fairly large. Posterior position of the pineal foramen. Sloping occiput, not cupped. Basioccipital large.

Advanced: Deep maxilla, fairly short. No abrupt step in the dentigerous border, which is distinctly ventrally curved. Anteriorly situated nostrils. Small facial part of the septomaxilla. Section of the snout not square. Sides of the skull not straight. Orbits slightly anteriorly directed. Frontal forming only a small part of the orbital border. Preparietal small or absent. Temporal openings somewhat dorsally directed and rather large in relation to the size of the skull. Pterygoid flanges not far posteriorly.

It is quite clear that, in contrast to *Gorgonops torvus,* this specimen belongs to a family of advanced Gorgonopsians, such as the Rubidgeidae.

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Abbreviations

Angular.	ang
Articular.	art
Basioccipital.	bo
Coronoid.	cor
Dentary.	den
External auditory meatus.	eam
Ectopterygoid.	ect
Exoccipital.	eo
Fenestra ovalis.	fo
Frontal.	fr
Internal carotid foramen.	icf
Interparietal.	ip
Interpterygoid fossa.	ipf
Jugal.	jug
Jugular foramen.	jf
Lachrymal	lac
Maxilla.	mx
Nasal.	nas
Palatine.	pal
Parietal.	par
Pineal foramen.	pf
Postfrontal.	pfr
Premaxilla.	pmx
Paroccipital process.	pop
Preparietal.	pp
Pterygoid process.	ptp
Prearticular.	prea
Prefrontal.	prf
Parasphenoid.	psph
Post-temporal fossa.	ptf
Quadrate.	q
Quadratojugal.	qj
Quadrate process of the pterygoid.	qpp
Rostrum of parasphenoid.	r
Reflected lamina.	rl
Surangular.	sa

Septomaxilla.	smx
Supraoccipital.	so
Splenial.	spl
Squamosal.	sq
Stapes.	st
Tabular.	tab
Vomer.	v