A NEW GOMPHODONT CYNODONT FROM THE CYNOGNATHUS ZONE OF SOUTH AFRICA

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Abstract

This paper describes a somewhat peculiar new gomphodont cynodont from *Cynognathus*-zone beds of the Karroo System of South Africa. It is a fairly good skull, with lower jaw in position, but lacking the anterior portion of the snout. Its peculiarity lies in the fact that while the posterior portion of the dentary is powerfully expanded in true gomphodont style, the zygomatic arch is very weakly developed, unlike the condition in any of its other cynodont contemporaries. It is described as a new genus and species, *Cragievarus kitchingi*, generically after the locality Cragievar and specifically after its collector, Mr J. W. Kitching.

Introduction

In an article on fossil pockets and bone beds in the *Cynognathus*-zone, Mr J. W. Kitching (1963) refers to a locality below and west of the Wonderboomspruit railway bridge on the farm Cragievar some five miles south of Burghersdorp, Cape Province. In March 1962 he recovered from this fossil pocket 26 specimens, eight of which are immature *Diademodon browni* skulls. I referred to these latter skulls in a paper on *Diademodon* (Brink, 1963b) and listed some notes on four of the better preserved specimens.

Amongst the specimens recovered from this site there is a peculiar skull which, although one of the first to be cleaned, has been shelved for description on account of its somewhat unusual structure; I wished to consult the literature as widely as possible and the opinions of other palaeontologists before advancing my own views.

This specimen is a reasonably complete skull with a good lower jaw in position, and there are some fragments of vertebrae associated. The anterior portion of the snout and the left zygomatic arch are missing. The dentition is clearly gomphodont, but the crown structure of every tooth is obliterated through abrasion. Unfortunately the articular regions are badly preserved on both sides.

The peculiarity of the skull lies in the fact that it has the powerful extremely advanced lower jaw structure of a diademodontid, in the elaborate development of the three posterior portions—the coronoid, articular and angular processes. In sharp contrast, however, the zygomatic arch is delicate. In gomphodonts and cynognathids the zygomatic arch is powerful, to cope with the strongly developed masseter muscles suggested by the widely expanded posterior portions of the dentaries, but in this specimen the zygomatic arches are almost procynosuchid-like by comparison.

Delicate in appearance, in structure it is advanced. The jugal interlocks

extensively with the squamosal and, while damaged, there is evidence of an elaborate external auditory meatus groove not unlike that of *Diademodon*. The arch is situated at a high level, as in *Diademodon* and unlike the procynosuchid condition. It is, in fact, a delicate, miniature *Diademodon*-like or *Trirachodon*-like arch, but it lacks evidence of a jugal process.

Although this specimen is from the middle part of the *Cynognathus*-zone in this characteristic at least it predicts a condition which becomes characteristic again of the post-*Cynognathus*-zone cynodonts from the Molteno and Manda beds. In *Luangwa drysdalli* from the Ntawere formation in the Luangwa valley of Zambia (Brink, 1963a) there is also a marked reduction of the breadth of the skull across the zygomatic arches and the arches are shortened even though they still have some appreciable height. In the present specimen the vertical thickness is reduced and the arches are short proportionally, but they still curve widely laterally.

The whole arrangement would appear to lend support to Crompton's views (1963) on the forces exerted and the directions of pull of the jaw muscles to ease the strain on the suspension while the latter is being converted into the mammalian condition; and perhaps the arrangement in the present specimen can be interpreted as one where the articular process of the dentary is in a more advanced stage of interference in the suspension than in other contemporaries. This is only a deduction, because the suspension regions are too badly preserved in this specimen to permit any definite conclusions.

Cragievarus kitchingi gen. et sp. nov.
(Figures 41, 42 and 43)

Type. Reasonably complete skull, lacking the anterior part of the snout and left zygomatic arch, and damaged across the occiput, but with a good lower jaw and including some fragments of skeletal bones, catalogued under Field Number 3776 and Museum Number 368 in the collection of the Bernard Price Institute, derived from the middle of the *Cynognathus*-zone beds on the farm Cragievar in the Burghersdorp district of South Africa.

Diagnosis. Medium-sized gomphodont with unimpressive molariform post-canine teeth; formula i4 : c1 : pc2 + 7? for the upper jaw and i3 : c1 : pc-0 + 7 for the lower jaw; diademodontid in general shape and structure, but with dentaries even more powerfully expanded and with zygomatic arches conspicuously reduced.

Measurements. The following is a comprehensive list of measurements, in millimeters, useful for comparison:

Approximate total length of skull, as reconstructed	142
Approximate maximum breadth of skull across squamosals, as reconstructed	91
Minimum breadth of snout	26

Interorbital breadth	32
Minimum breadth across parietals posteriorly	10
Maximum breadth across parietals anteriorly	17
Antero-posterior length of orbit	24
From level of posterior borders of orbits to interparietal notch	41
Minimum width between postcanines	19
Width between last postcanines	38
From occipital condyles to posterior border of secondary palate	72
Breadth across pterygoid processes	37
Breadth between fenestrae ovales	22
Distance covered by seven molariform upper cheek teeth	27
Distance covered by seven molariform lower cheek teeth	30
Maximum length of dentary	125
Maximum vertical height of dentary	60
Minimum vertical height of dentary	15
Breadth of symphysis	17
Length of symphysis	41

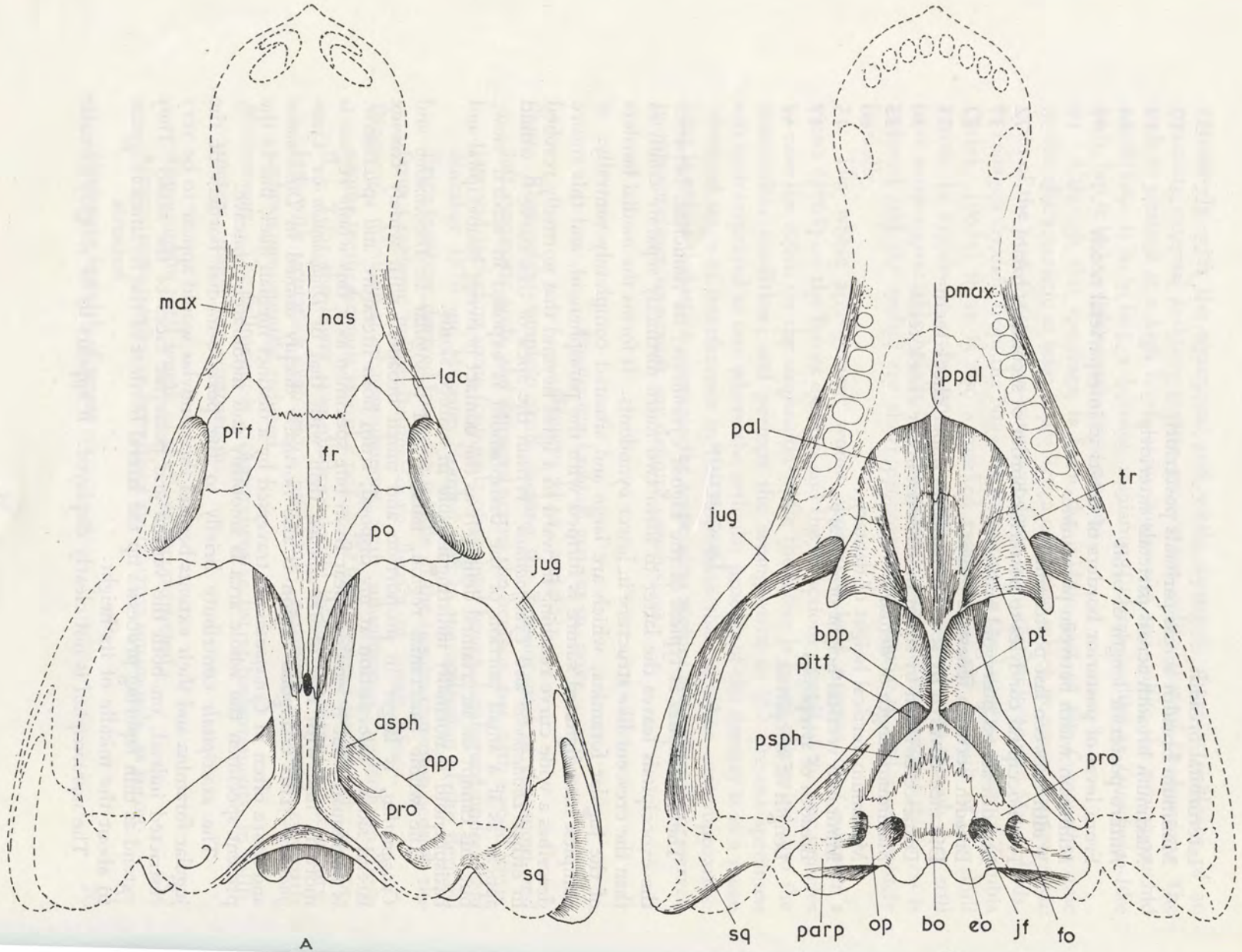
Description

The *basioccipital* is typical of the higher cynodonts; its reduction between the exoccipitals leaves the latter to form two more distinctly separate condyles than the crescent-like structure in lower cynodonts. It forms the medial borders of the jugular foramina, which are large and situated completely ventrally. A complex interdigitated suture is formed with the parasphenoid, and this suture describes a wide curve reaching forward to a level beyond that normally reached in either *Diademodon* and *Cynognathus*. Within the apex of this curve it would appear as if a small portion of the basisphenoid is exposed in ventral view, but this cannot be ascertained definitely as the contact between basioccipital and basisphenoid is normally indistinguishable in mature skulls.

The whole basicranial region, narrow and triangular in *Diademodon* and *Cynognathus*, is larger in proportion and much broader, with widely convex lateral sides. Information at my disposal, from both literature and specimens, is inadequate, but it would appear from one specimen as if this whole region is more in line with that of *Trirachodon* than with that of *Diademodon* or *Cynognathus*. This triangular region is also normally deeply domed in *Diademodon* and more often in *Cynognathus* is traversed by a distinct median keel, but in the present specimen the whole area is smoothly and moderately concave.

The *exoccipitals* contribute briefly to the postero-medial borders of the jugular foramina and their extents beyond the condyles would appear to be very restricted indeed, on both the ventral and posterior faces of the skull. They extend as thin tapering processes up the lateral borders of the foramen magnum to about the middle of its height.

The *supraoccipital* is not clearly displayed. It appears to be roughly circular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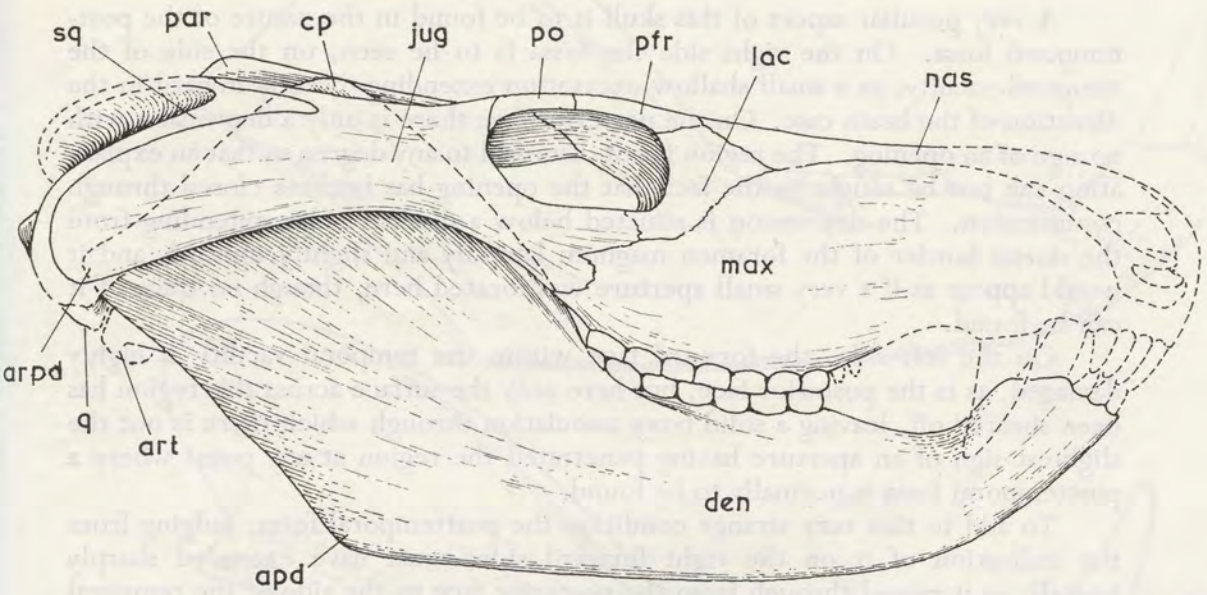

FIG. 42—Side view of the skull of *Cragievarus kitchingi* gen. et sp. nov., natural size. For abbreviations see figure 41.

in outline, forming the dorsal border of the foramen magnum, leaving the portions of the border between itself and the exoccipitals to the opisthotics. In height and size it appears to be similar to the interparietal above, the latter being somewhat broader. Sutures with the interparietal and tabulars are heavily interdigitated.

The *opisthotics* are damaged at their lateral extremities, but on the whole the paroccipital processes are shaped as portrayed in figure 41B. Although reconstructed, they are figured in line with what the specimen conveys. The crest between the posterior and ventral faces is not as sharp as in either *Diademodon* or *Cynognathus*. The arrangement forward over the roof of the middle ear and in the region of the fenestra ovalis is not clear. On the posterior face of the skull the opisthotics are elaborately covered by the tabulars.

◁ FIG. 41—A, Dorsal; and B, Ventral view of the skull of *Cragievarus kitchingi*, gen. et sp. nov., natural size.

Abbreviations: apd—angular process of the dentary; arpd—articular process of the dentary; art—articular; asph—alisphenoid; bo—basioccipital; bpp—basipterygoid process; cp—coronoid process; den—dentary; eo—exoccipital; fo—fenestra ovalis; fr—frontal; jf—jugular foramen; jug—jugal; lac—lachrymal; max—maxillary; nas—nasal; op—opisthotic; pal—palatine; par—parietal; parp—paroccipital process; pitf—pituitary fossa; pmax—palatal plate of the maxillary; po—postorbital; ppal—palatal plate of the palatine; prf—prefrontal; pro—prootic; psph—parasphenoid; pt—pterygoid; q—quadrate; qpp—quadrate process of the pterygoid; sq—squamosal; tr—transverse bone; v—vomer.

A very peculiar aspect of this skull is to be found in the nature of the post-temporal fossa. On the right side the fossa is to be seen, on the side of the temporal vacuity, as a small shallow excavation extending directly inward in the direction of the brain case. On the posterior face there is only a depression with no sign of an opening. The region is not distorted to any degree so that an explanation can not be sought in the fact that the opening has become closed through compression. The depression is situated below a distinct ridge extending from the dorsal border of the foramen magnum laterally and slightly upward, and it would appear as if a very small aperture was located here, though no trace of it can be found.

On the left side, the forward face within the temporal vacuity is highly damaged, as is the posterior face, but here only the surface across this region has been sheared off, leaving a solid bony association through which there is not the slightest sign of an aperture having penetrated the region at any point where a posttemporal fossa is normally to be found.

To add to this very strange condition the posttemporal fossa, judging from the indication of it on the right forward side, must have extended sharply laterally as it passed through from the posterior face to the side of the temporal vacuity, but in both *Diademodon* and *Cynognathus* it extends inward.

The *prootic* of the left side could not be exposed for fear of destroying interesting evidence regarding the posterior region of the dentary, and although exposed on the right side, its outline, exact form and relationship are not clear. In *Cynognathus* and *Diademodon* the prootic is inclined to be small and deeply hidden below the parietal flange, but in the present specimen it is larger and more visible in dorsal view, as in lower cynodonts, but this may be due to displacement of the bone after death.

The *tabulars* overlap the posterior faces of the paroccipital processes quite elaborately, especially laterally. The condition is similar to that described by Broili and Schröder (1935) for *Diademodon mastacus* and very unlike that described by these authors (1934) for *Cynognathus platyceps*.

The *interparietal's* exact extent and outline, especially on the margins of the occipital flanges, can not be ascertained clearly, due to damage. It would appear to be somewhat broader than the supraoccipital below and on the whole its disposition seems to correspond with that of a typical gomphodont.

The *parietals* are also typical of a gomphodont like *Diademodon*, especially in the arrangement around the pineal. Although the occipital flanges are damaged on both sides, the only possible way to reconstruct them is in line with the *Diademodon* condition, perhaps even more in line with that of *Trirachodon* and unlike that of *Cynognathus*. Proportionally the breadth across the brain case is greater than that of *Diademodon* and *Cynognathus*, and more comparable with that of *Trirachodon* and the lower procynosuchid cynodonts. In both *Diademodon* and *Cynognathus*, as well as in *Trirachodon* and the lower cynodonts like *Leavachia*, the parietals have a greater height at the level of the prootic than farther forward at the level of the alisphenoid. In the present specimen the height is greater in

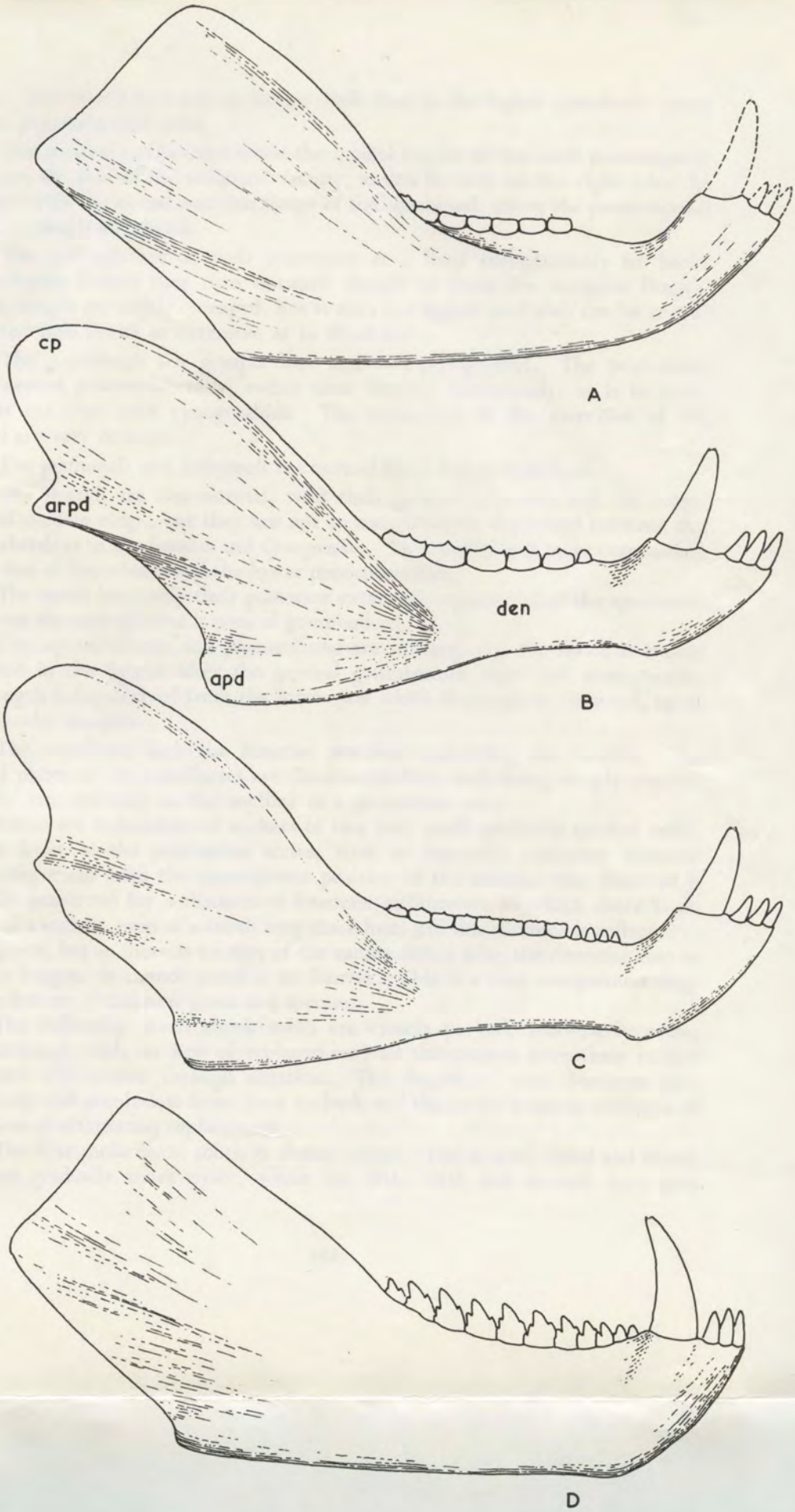

FIG. 43—Side views of dentaries of: A—*Cragievarus kitchingi;* B—*Luangwa drysdalli* (Brink, 1963); C—*Diademodon rhodesiensis* (Brink, 1963b); and D—*Cynognathus platyceps* (Broili & Schröder, 1934). A is natural size and the others are brought to the same size for comparison. For abbreviations see figure 41.

front. The pineal is at a level farther back than in the higher cynodonts, more at the procynosuchid level.

The parietal reaches and forms the medial border of the small posttemporal fossa on the side of the temporal vacuity, as can be seen on the right side. Its contact with the dorsal occipital flange of the squamosal, above the posttemporal fossa, is clearly displayed.

The parietals are at their narrowest at a level conspicuously far back, immediately before they turn outward sharply to form the occipital flanges. These flanges are highly damaged, but it does not appear as if they can be reconstructed into crests as extensive as in *Diademodon*.

The *postorbitals* are gomphodont and not cynognathid. The postorbital bars extend postero-laterally, rather than directly transversely, as is to some extent the case with cynognathids. The extensions in the direction of the pineal are very delicate.

The *prefrontals* and *lachrymals* are normal for a higher cynodont.

The *frontals* are also normal, with their general concavity and the longitudinal median ridge, but they are not as conspicuously depressed between the postorbitals as in *Diademodon* and *Cynognathus*. The condition is more comparable with that of *Trirachodon* and the lower procynosuchids.

The *nasals* have only their posterior extremities preserved in the specimen, and here the arrangement is normal gomphodont.

The *septomaxillaries* and *premaxillaries* are missing, and the snout is reconstructed in the figures after the general gomphodont shape and arrangement, the length being derived from the lower jaw which is complete, forward, up to the alveolar borders.

The *maxillaries* lack the anterior portions containing the canines. The palatal plates of the maxillaries are *Diademodon*-like, each being deeply concave and the two meeting on the midline in a prominent crest.

There are indications of sockets of two very small evidently conical teeth, at the front of the postcanine series, with an unusually extensive diasteme separating them from the approximate position of the canine. The diasteme is actually preserved for a distance of fourteen millimeters in which there is no trace of a socket, even of a tooth long since lost, and this distance is reflected in the figures, but as there is no sign of the canine either side, the diasteme may in fact be longer. It cannot possibly be shorter. This is a very conspicuous diagnostic feature of this new genus and species.

The following seven cheek teeth are closely packed, moderately ovate, flat crowned, with no sign of replacement; all the crowns have their surface structure obliterated through abrasion. The degree of wear becomes progressively and evenly less from front to back and the series bears no evidence of any form of alternating replacement.

The first molariform tooth is almost round. The second, third and fourth become gradually more ovate, while the fifth, sixth and seventh turn pro-

gressively more sectorial. Unfortunately the dentaries are intimately compressed against these posterior teeth.

The *transverse* bone is not visible and is presumably like that of *Diademodon*, entirely confined to the notch between the pterygoid and jugal. The dentaries are intimately pressed into these notches on both sides.

The *jugals* constitute one of the peculiarities of this specimen. Contrary to the condition in other higher cynodonts, both gomphodont and cynognathid, they contribute to a very delicate zygomatic arch which rises with an arc to a high level. Posteriorly the jugal does not bend down as sharply as in *Diademodon*. On the whole the zygomatic arch appears to be completely out of step with the powerful dentaries and if the lower jaw of this specimen had been discovered completely dissociated from the skull, it would have been difficult to discover that they belong to the same species.

The *squamosals* contribute their share to the zygomatic arches, but they do not penetrate nearly as far forward as in *Diademodon* or *Cynognathus*, let alone *Trirachodon* or *Luangwa* where the extent of interlock with the jugals is even greater. Although the zygomatic arch as a whole is, in its delicate nature, reminiscent of a lower cynodont, its structure is in miniature that of a *Diademodon* and its shape that of *Trirachodon*. Less curved, at a higher level, its structure is still typical and although the fold over the external meatus groove is damaged, what remains there is clearly indicative of an arrangement greatly similar to that of *Diademodon*.

The rest of the squamosal, as far as preserved on the right side, seems to be quite typical.

The *quadrates*, *quadratojugals* and *stapes* are missing from both sides and the regions in their environment are highly damaged.

The *vomer* can only be seen against the roof of the internal nares and the arrangement is typical of a higher gomphodont.

The *palatines* and the whole structure behind the secondary palate are very similar to that of *Diademodon*. The palatal plates overlap slightly, obviously due to some distortion. The region immediately behind the secondary palate is wider and more smoothly curved than in *Diademodon*, more like the condition in *Trirachodon*. In *Diademodon* this region is not only narrower but more distinctly square, and the two palatal plates meet firmly in the midline.

The *pterygoids* are also like those of *Diademodon* or *Trirachodon* in general appearance, mostly across the pterygoid processes. These processes are long and delicate, and the concavities on their antero-medial slopes are less conspicuous than in *Trirachodon*. Their posterior faces are not in the same plane as is often the case in *Diademodon*, but incline sharply forward and outward, a tendency shown on a lesser scale by *Trirachodon*.

In both *Diademodon* and *Cynognathus*, and to a slightly lesser extent in *Trirachodon*, the pterygoids remain extremely narrow up to the basipterygoid region and only after the alisphenoids take over, the latter's extensions to the quadrates turn sharply outward. The condition in the present specimen is

more like that of lower cynodonts. The basisphenoid processes are wide and powerful, and the pterygoids tend to reach straight for the quadrates. Although there is clear interference on the part of the alisphenoids farther back, it would appear that the pterygoids themselves still reach the quadrates, as is characteristic of *Protacmon*.

The *alisphenoid* of the right side is exposed over its dorsal region and would appear to be typically diademodontid. Below, it definitely interferes with the pterygoid extension to the quadrate, but it seems as if it does not reach as far laterally.

The *parasphenoid* forms a keel somewhat deeper than in the higher cynodonts, another feature in which this region generally shows affinity with more primitive cynodonts.

The lower jaw is very advanced indeed, but little can be made of the accessory bones; in what little there is to be seen the arrangement seems to be perfectly in line with that of *Diademodon*. The splenial is a very delicate flake of bone and it clearly does not reach the symphysis.

The *dentary* has a few peculiarities, even though it is very typical of an advanced cynodont. The symphysis is extremely long and the jaw is very narrow across this region. On the whole it is *Diademodon*-like, and extremely unlike *Trirachodon* or *Luangwa*, but it lacks the distinct chin of *Diademodon*. The diasteme behind the canine is longer (45 mm) than in any other related form on record, and the dentary is rather slender through this region. By contrast, the dentary is deeper in the region of the cheek teeth than in other gomphodonts, yet not as deep as in the cynognathids. Posteriorly, the general shape of the dentary is more like that of *Cynognathus*, with less conspicuous differentiation between coronoid, angular and articular processes. The articular process reaches farther into the articular region and would appear to have had nearly direct contact with the squamosal.

Literature Cited

Brink, A. S., 1963a. Two cynodonts from the Ntawere formation in the Luangwa valley of Northern Rhodesia. *Palaeont. Afric.*, viii, p. 77.

————, 1963b. Notes on some new *Diademodon* specimens in the collection of the Bernard Price Institute. *Palaeont. Afric.*, viii, p. 97.

Broili, F. and Schröder, J., 1934. Zur Osteologie des Kopfes von *Cynognathus*. *Sitzb. bayer. Akad. Wiss.*, p. 95.

————,1935. Über den Schädel von *Gomphognathus* Seeley. *Sitzb. bayer. Akad. Wiss.*, p. 115.

Crompton, A. W., 1963. On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. *Proc. Zool. Soc.*, 140, 4, p. 697.

Kitching, J. W., 1963. Notes on some fossil pockets and bone beds in the *Cynognathus*-zone in the Burghersdorp and Lady Frere districts. *Palaeont. Afric.*, viii, p. 113.