ON SOME UPPER BEAUFORT THERAPSIDA.

By S. H. Haughton, B.A., D.Sc.

(Published by permission of the Hon. the Minister for Mines and Industries.)

(With Plate XIII and two Text-figures.)

Cynidiognathus longiceps, gen. et sp. nov.

The specimen which forms the type of this new genus was collected on the farm Vaalbank, Albert District, at the foot of the northern slope of the Dreunberg during the course of the geological survey of the area carried out in 1921. It consists of an almost perfect skull with part of the lower jaw, and some fragmentary limb-bones, but the skull only will be described here.

The principal measurements are as follows :—

Maximum length	375 mm.
Dorsal length in mid-line	330 mm.
Maximum width	240 mm.
Width at canines	80 mm.
Interorbital width	51 mm.
Snout to front of orbit	180 mm.
Orbital diameter	50 mm.
Snout to back of pterygoid flange	200 mm.
Maximum height	95 mm.

Premaxilla.—The two bones are separated by well-marked suture. Each bone carries 4 incisors, but at the alveolar edge the facial portion is fairly short. It extends backwards in its lower portion to form the lower border of the external nares, but does not meet the nasal behind the nostril. Above the nostril each premaxilla sends backwards a narrow tapering process to the level of the back of the outer nares, the two processes lying between the front parts of the nasals.

The palatal portion of the premaxilla is partly seen, although the ventral surface has not been fully displayed. On the ventral surface, however, the

premaxilla passes backwards to the level of the back of the canine, appearing in its posterior part as a narrow splint of bone lying medial to the maxilla. The dorsal surface has been almost completely developed. Anteriorly the bone forms the floor and outer side of the nasal opening—no ossified internasal septum being present. Near the front of the nasal floor on each side there is a rounded foramen, and just anterior to this the septomaxilla lies on the premaxilla. Behind the septomaxilla the lateral portion of the premaxilla is a thin inclined plate of bone lying on the maxilla and passing back to the level of the back of the canine. Medial to this plate there is a deep channel which is flanked medially by an upstanding process, somewhat swollen above, which extends from the level of the last incisor to the level of the front of the canine. This palatine process forms the inner wall of the premaxilla and is separated from its neighbour by a deep narrow channel, which is partly divided by a longitudinal thin bony plate not reaching down to the secondary palate. This palatine process of the premaxilla does not seem to be separate from the main body of the bone. The bone is somewhat cracked, and the cracks are filled with red iron oxide ; but the cracks are so unsymmetrical, and no one of them can be matched by a counterpart on the other side, that none can be considered as a suture dividing off the premaxilla from a prevomer.

Broom has mentioned and figured the occurrence of such processes in *Lycochampsa ferox* and Watson in *Gomphognathus polyphagus*, but no adequate description has been given of either.

Septomaxilla.—This bone is only preserved in the right nostril. It lies on the floor and against the lateral portion of the premaxilla and is almost completely separated by that bone from the maxilla, only meeting the latter at its upper corner. The front lower half of the bone is a very thin lamina, concave from above (called the pars horizontalis of the os narialis by Wegner, 1922). Half-way up it thickens considerably and sends inwards a fairly thin turbinal process (processus intrafenestralis of Wegner) which almost reaches the mid-line of the skull. The turbinal process lies wholly in front of the palatine process of the premaxilla. On the floor of the nostril there is a foramen between the front of the septomaxilla and the narial portion of the premaxilla. The septomaxillary foramen is very small.

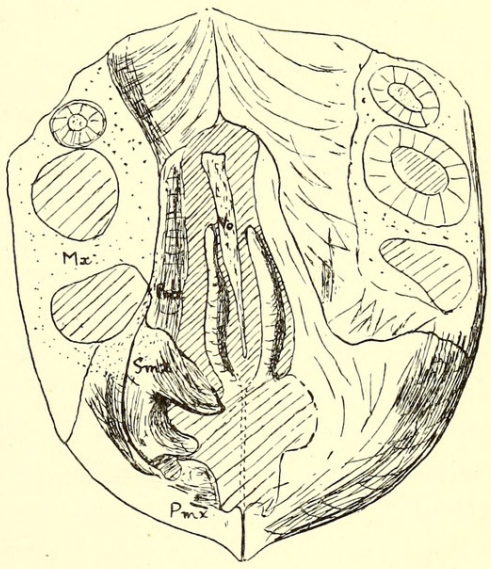
Maxilla.—The maxilla carries 1 large canine and 10 molars. The molar series occupies a length of 103 mm. Only the sockets of the molars are preserved. These are longer than wide, and begin almost directly behind the canine. The last tooth is very small.

Lachrymal.—This bone has contact with the prefrontal, nasal, maxilla, and jugal. In front of the orbit it is excavate as in many Gorgonopsids and is bounded behind by a pronounced ridge which forms here the antorbital border. At the bottom of the excavated portion is the lachrymal foramen

which forms the entrance to a short duct running through the bone whose posterior end opens into the orbit.

The other bones of the face and of the top of the skull are very similar to those of *Cynognathus platyceps*, and their shapes and relationships are adequately displayed in the figure.

"*Vomer.*"—In section anterior to the orbit the vomer is broad, thin, slightly concave downwards, with a ventral median keel and a dorsal median groove flanked by thin upstanding walls. When traced forward in longitudinal section the horizontal plate gradually disappears, the vertical plate becomes higher and its ventral portion swells, so that at the anterior end, between the palatine processes of the premaxillæ, the median plate is sharp-pointed above and rounded below. At the anterior end the bone-mass is certainly single; along its length there may possibly be a suture separating an upper portion from a lower; but the median septum, except in its lower swollen portion, is very thin and much cracked, so that it is not possible to be absolutely certain of the presence of a suture. If a suture *is* present, then the bone between the premaxillæ is the vomer, and the bone which roofs the pharynx is the parasphenoid; or the former is the fused prevomers and the latter the vomer. It is certain that the bone which roofs the pharynx forms the *upper* part of the median septum at least; and that the condition is different from that figured by Broom in *Diademodon*, in that no mesethmoid forms the upper part of the septum. On the other hand, if the bone is single, the changes which take place in it when traced forward from the pharynx are the gradual loss of the horizontal septa, the thickening of the ventral part of the vertical plate, and the complete or almost complete fusion of the walls of the dorsal groove.



Cynidiognathus longiceps.—Htn. Irregular section across snout. Dorsal view. Left septomaxilla not preserved.

Posterior to the line of fracture in front of the orbits, the "vomer" becomes more arched with a ventral median keel and passes rapidly downwards and backwards, forming the front part of the groove in the palate; the hinder portion of this groove is formed by the pterygoids. Broom and Watson have both figured this region in *Diademodon*, and have shown the vomer as forming the whole of this vaulted area of the palate, and Watson

has further figured a large vomer in this position in some Gorgonopsia. I have elsewhere expressed my inability to see a vomer separating the pterygoids in Gorgonopsian skulls which I have examined, and the evidence afforded by this Cynodont skull seems to re-open the whole question of the identity of the bone which forms the median septum of the anterior part of the skull and the roof of the front part of the pharynx.

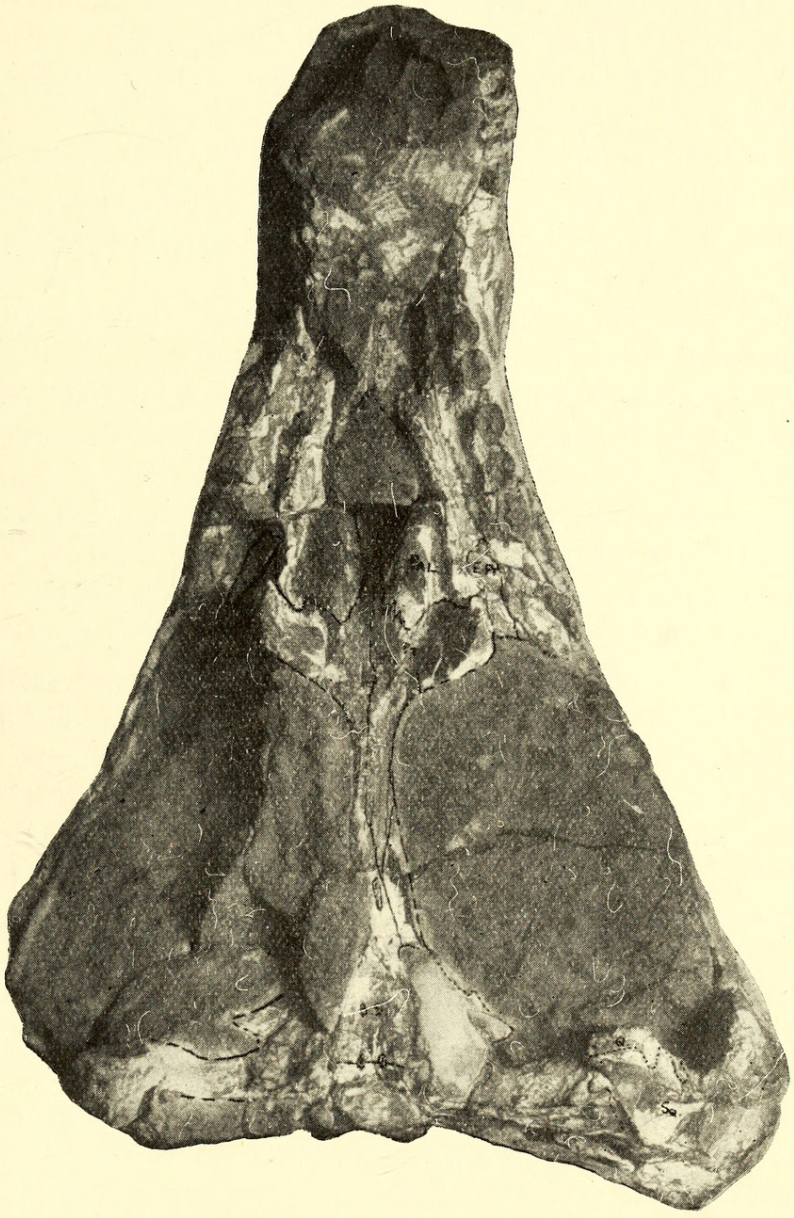
Is it the anterior prolongation of the parasphenoid ? or is it the fused prevomers of the Therocephalia ? Its position in front of, and slightly flanked by, the pterygoids, and between the palatines, would seem to homologise it with the prevomers ; and until further evidence of its actual connection with the parasphenoid is obtained, it would seem best to consider it as the fused prevomers.

Basicranium.—The basicranial region is similar to that of *Cynognathus* in general plan, but there are significant points of difference. The pterygoid is large, the vomer extends back at least to the front of the median bar ; and posteriorly the pterygoids stop some distance in advance of the triangular basisphenoid plate and are separated from each other by an anterior prolongation of the basisphenoid along the median bar. Laterally the posterior portion of the pterygoid is overlapped by the epipterygoid, which has a long articulation with the basisphenoid. Posteriorly the epipterygoid is considerably shortened. It has the same relations with the openings in the brain-case as in other Cynodonts, but it does not extend outwards to articulate with the quadrate, being separated from that bone by a considerable gap and lying as a thin lamina on the mass of the pro-otic. Watson describes a somewhat similar condition in *Protacmon brachyrhinus*, but there the epipterygoid terminates posteriorly in a thickened margin. Anteriorly in our form there is a foramen between the pterygoid and epipterygoid, which continues forward as a groove along the dorsal surface of the pterygoid. This is the opening seen by Broom in *Gomphognathus*, and considered by him to be the internal carotid foramen.

The basioccipital forms most of the floor of the brain-case behind the sella turcica, extending from the condyles to the dorsum sellæ, where a fracture shows it lying on the pro-otics as a thin plate of bone with triangular section. It forms the inner boundary of the internal auditory opening and is perforated on each side by two foramina for the exit of the branches of the XIIth nerve.

Seen in dorsal view the basisphenoid forms the floor of the sella turcica into which the carotid foramina enter. The carotid arteries enter the ventral surface of the basisphenoid far back, and thus pass nearly horizontally forwards through the bone. The side walls of the sella turcica are formed by the anterior superior processes of the pro-otics, which bones lie here between the basisphenoid and basioccipital. Anteriorly to the sella

turcica the basisphenoid is continued forwards as a median bar overlapped laterally by the epipterygoids and then by the pterygoids. The dorsal ridge of this median bar is formed of a thin, high plate.



Cynidiognathus longiceps—Htn.
Photograph of palatal view of type skull.

As in *Diademodon* the foramen jugulare lies just anterior to the occipital condyle and faces downwards ; while the fenestra vestibuli looks forwards and outwards, being separated from the foramen jululare by a thin vertical plate of the periotic mass. The bone above the fenestra, instead of having a vertical face, as in *Diademodon*, is bent horizontally to form an eave

overhanging the fenestra. This eave is deeply notched on its anterior edge. The inner border of the notch is formed by the posterior end of the epipterygoid, the remainder of the border by the pro-otic. This notch must represent the pterygo-paroccipital foramen of *Diademodon*, the retraction of the epipterygoid from the quadrate giving rise to the open form. The foramen for the exit of the VIIth nerve is larger and nearer the pituitary fossa than in *Diademodon*.

The periotic (pro-otic) forms most of the side wall of the brain-case behind the dorsum sellæ, articulating behind with the fused exoccipital and supraoccipital, the latter forming the posterior wall of the canal for the IXth–XIth nerves.

The paroccipital process is quadrangular in section, and not triangular as in *Diademodon*.

Quadrate.—Another feature of interest lies in the quadrate mass. The quadrate is a plate of bone with a slightly hollowed anterior surface, and lies on the anterior face of the squamosal, being furnished with an outer flange which is clasped by the squamosal. It has no pterygoid wing. The quadrato-jugal is lateral to the quadrate. It is bifid in character, consisting of a larger anterior vertical thin plate and a smaller posterior one which clasp the lower edge of the squamosal between them. There is probably a quadrate foramen between the quadrate and the quadrato-jugal. A somewhat similar quadrate complex exists in *Protacmon*, but there the quadrato-jugal spreads inwards between the quadrate and squamosal.

Discussion of the relationship of this type to other Cynodonts is deferred until a more complete account of the fossils of the Upper Beaufort Beds is prepared. It is sufficient here to point to some of the advanced features which this form possesses—the complete loss of the quadrate ramus of the pterygoid, the gap between the quadrate and the epipterygoid, loss of a pterygoid process separating the palatine and vomer, and extreme flattening of the basicranium—all logical results from the evolutionary tendencies traced in the Theriodontia, as pointed out recently by Watson.

The absence of an internasal process of the premaxilla and the usurpation of the functions of prevomers by palatine processes of the premaxillæ—functioning as supports to Jacobson's cartilage—are interesting features which are distinctly mammalian in character. The former is paralleled in a large skull of *Cynognathus* from Winnaarsbaaken, Albert District, now in the South African Museum, in which the premaxillæ form a pillar in front of the nostrils reaching upwards and backwards to the nasals.

Cynidiognathus (?) *broomi*, n. sp.

1911. Broom, *Cynognathus berryi*, Proc. Zool. Soc., pl. xlvi, figs. 1, 2.

The occiput and outer view of the bones of the brain-case of an incomplete skull in the South African Museum collection (Cat. No. 1056) were figured by Broom as *Cynognathus berryi*. Recent examination of the specimen has shown that it possesses 10 molars, and cannot therefore belong to the genus *Cynognathus*. In view of the general agreement between the two forms, as far as their features can be compared, I have tentatively placed it in the newly-erected genus.

Comparison with Broom's figures shows that the division between the two condyles is not quite strong enough in the drawing he gave. Further, it seems doubtful whether the epipterygoid passed back to meet the quadrate as described by Broom. As actually preserved, the suture between the pro-otic and epipterygoid is rather more vertical below the big foramen than in his figure and the broken lower edge of the plate shows an interdigitation between the two bones. Unfortunately, the lower outer corner of the palate figured by Broom no longer appears on the specimen, so that it is impossible to settle the point definitely.

No suture can be seen between the exoccipital and paroccipital ; the features of the region are mainly as in Watson's description of *Diademodon*. The post-temporal fossa is above the level of the foramen magnum. The fenestra ovalis lies lower than in *Diademodon*.

The basisphenoid and basioccipital in ventral view are somewhat hollowed out, not flat, and in the posterior part there is a well-marked, narrow, shallow, median keel flanked by two narrow elongated grooves which pass forward well beyond the level of the tubera basisphenoidalia.

There is a pronounced occipital boss on the upper border of the foramen magnum.

The series of 10 molars occupy a length of 85 mm. The first is immediately behind the canine. In *Cynognathus* and *Lycochampsa* there is diastema between the canine and the first molar, which is relatively largerin the latter.

The frontal is more lozenge-shaped than in *Cynognathus crateronotus*, reaching to within 4 or 5 mm. of the orbital border.

The probable length of the skull is 260–270 mm. ; the interorbital width is 52 mm., and the width at the canines 58 mm.

Ælurosuchus browni, Broom.

1906. Broom, Trans. Phil. Soc. S. Afr., xvi, 4, p. 376, pl. x.

Broom has described all the visible features of the top of the weathered skull and of the postcranial skeleton. Since the type came into the posses-

sion of the South African Museum (Cat. No. 5875) it has been possible to display the general features of the palate and basicranium, and to show that the form must be classed among the Bauriamorpha.

The palatal aspect is similar to that of *Bauria*, except that it is probable that the secondary palate is more fully formed than in that genus. The septum dividing the posterior nares was figured by Broom. There is a large suborbital fossa, bounded posteriorly by the pterygoid and laterally by a bone which expands forwards and is probably the ectopterygoid. The bone substance is very soft and sutures are usually indistinguishable in a sandstone matrix such as this fossil possesses. There is a large cordate interpterygoid vacuity.

The quadrate ramus of the pterygoid meets the quadrate, and between it and the paroccipital there is a very considerable space.

The epipterygoid is a flat bone, fairly narrow in the middle, but expanded at each end, resting on the quadrate ramus of the pterygoid and touching the parietal. It is far more like the epipterygoid of the Therocephalia than that of the Cynodontia.

The basisphenoid is broad, and apparently extends in the middle line to the back of the interpterygoid vacuity. Near the front it is pierced by a single circular foramen, probably the foramen for the carotids. It forms, as usual, part of the border of the fenestra ovale, which is closed by the stapes. The stapes are dumb-bell shaped bones, the outer end lying between the paroccipital, quadrate, articular, and pterygoid.

The paroccipital is shallow—possibly on account of the post-mortem flattening of the skull—but laterally is broad from back to front; its under surface is provided with a broad, shallow groove. Its inner end forms the border of the large foramen jugulare, whilst medial and slightly posterior to the latter is a smaller opening for the exit of the XIIth nerve.

No other details are visible, but enough is seen to place this form in the Bauriamorpha, to which the ill-defined features of the upper surface of the skull would also assign it.

Addendum.

Since the above description of *Cynidiognathus longiceps* was drawn up, Dr Broom has informed me in a verbal communication that the bone hitherto known as basisphenoid in Therapsids (and so described in this paper) is, in his opinion, the parasphenoid. In an immature Gorgonopsian skull from the top of the *Cistecephalus* zone, whose basicranial region he has sectioned, he finds the basisphenoid existing as two small ossifications lying in front of the basioccipital—quite distinct from it and from the bone which sends back a thin plate to underlie the basioccipital and which is anteriorly clasped by the pterygoids, extending forwards above them as a median septum bone

—the parasphenoid or vomer. In later life the basisphenoidal ossifications fuse with the posterior portion of this parasphenoid.

According to this view, only the upper posterior portion of the bone called basisphenoid in such figures as the one published by the writer as a section through the brain-case of *Alopecognathus minor* (Ann. S.A. Mus., xii, p. 211), should be known by that name ; the remainder is the true parasphenoid.

EXPLANATION OF PLATE.

Cynidiognathus longiceps, gen. et sp. nov.

Fig.

1. Top view of type skull.
2. Side view of type skull.
3. Ventral view of basicranium.
4. Dorsal view of floor of brain-case.
5. Anterior view of left quadrate mass.
6. Ventral view of same.

Cynidiognathus broomi, sp. nov.

7. Side view of type skull.
8. Top view of type skull.

Ælurosuchus browni, Broom.

9. Dorsal view of horizontal section through type skull.

B.O., Basioccipital ; B.S., Basisphenoid ; d.s., dorsum sellæ ; Ep.pt., Epipterygoid ; inner vest., inner vestibule of ear ; J., Jugal ; L., Lachrymal ; Mx., Maxilla ; N., Nasal ; P.Mx., Premaxilla ; P.O. (Pro. Ot.), Pro-otic ; Pal., Palatine ; Par. Occ., Paroccipital ; Po.O., Postorbital ; Pr.F., Prefrontal ; Pt., Pterygoid ; Q., Quadrate ; Q.J., Quadratojugal ; Smx., Septomaxilla ; Sq., Squamosal ; St., Stapes ; Tab., Tabulare ; Vo., Vomer.