A NEW SKULL OF THE PROCYNOSUCHID CYNODONT *LEAVACHIA DUVENHAGEI* BROOM

By A. S. Brink

ABSTRACT

This paper describes one of the most excellent, complete, virtually undamaged and undistorted skulls of a Karroo therapsid yet found. It is of exactly the same size as the type specimen of *Leavachia duvenhagei* Broom, housed in the Rubidge Collection. Nearly every detail of the structure of the skull can be traced, except structures on the inside of the cranial cavities and details obscured by the lower jaw which is in good occlusion. It is the third specimen of this species on record and this description renders it the best known specimen of all procynosuchid species. It is pointed out that the genera *Leavachia* and *Procynosuchus* are not readily distinguishable, but this may be due to lack of knowledge of the latter genus.

INTRODUCTION

The species *Leavachia duvenhagei* Broom (genotype) was described by Broom in 1948, based on an excellent specimen in the Rubidge Collection. This specimen includes, besides a good skull, also much of the postcranial skeleton. Broom unfortunately described the specimen in its unprepared state and the author, in collaboration with Mr. J. W. Kitching, decided to clean the specimen and issue a further description (Brink and Kitching, 1953). Dr. Rubidge had in the meantime, however, taken exceptional pride in this specimen, which he quite rightly considers as the most precious in his collection of over 800 therapsids. We therefore promised not to deface the specimen by extensive preparation. Our superficial cleaning improved the general appearance, but exposed little in the line of additional structural detail which could improve on Broom's interpretations.

In the same year Broom and Robinson (1948) described a specimen in the collection of the Bernard Price Institute as *Aelurodraco microps*. Mr. Kitching and I afterwards referred this specimen to the genus *Leavachia*, mentioned a second specimen, and introduced a third new species, *Leavachia gracilis* (Brink and Kitching, 1951), while endeavouring to find a basis for distinguishing between the genera *Leavachia*, *Procynosuchus*, *Galeophrys* and *Galecranium*. Subsequently when we added some notes to our knowledge of *Leavachia duvenhagei* (Brink and Kitching 1953), mentioning also in passing the presence of a second specimen in the Rubidge Collection, we listed additional notes on specimens of *Galecranium liorhynchus*, *Procynosuchus rubidgei* and *Nanictosaurus rubidgei* which were borrowed at the same time.

Three species of *Leavachia* are therefore known at present. *L. duvenhagei* is now represented by three specimens, two in the Rubidge Collection and one in this Institute; *L. microps* has two specimens on record, both in this Institute, while *L. gracilis* is still represented only by the type specimen, also housed in this Institute.

In December 1961 Mr. Kitching quite casually stopped at the town of his birth, New Bethesda, north of Graaff Reinet where, as a child, he discovered his first fossils, and recovered from the river bed inside the town commonage perhaps one of the most excellent skulls of a Karroo therapsid yet found. It was embedded upside down and the erosive action of the seasonal downwash had just exposed the ventral margins of the lower jaw. Damage on the left is negligible; on the right side the articular region is worn down slightly to expose in longitudinal section, most beautifully, the relationship between parts of the post-dentary bones. This, and some wear along the ventral margins of both dentaries, are the only damage the skull suffered. Sutures are remarkably clear and on the whole the skull can be regarded as undistorted. If any, the skull had been very evenly and uniformly compressed dorso-ventrally. Otherwise fine cracks, colouring and artificial surface damage as a result of difficulties encountered with preparation render the specimen superficially less attractive to the eye.

This specimen could immediately be recognised as belonging to the species *L. duvenhagei* on the strength of the size and shape of the nodule, while the ventral margins of the mandibles were the only bony exposures. It is of exactly the same size as the type, but somewhat flatter (see table of measurements).

Leavachia duvenhagei Broom 1948

(Figures 10 and 11)

1948, Broom R., *Trans. Roy. Soc. Edinb.*, lxi, p. 618, figs. 35-43.
1953, Brink, A. S. and Kitching J. W., *S. Afr. J. Sci.*, xlix, p. 312, figs. 1, 2.

Type. Complete skull and much of the postcranial skeleton, No. 92 in the Rubidge Collection, from *Cistecephalus*-zone beds on the farm Doornkloof in the Graaff Reinet district.

Present Specimen. Complete and perfect skull, No. 357 in the collection of the Bernard Price Institute, from *Cistecephalus*-zone beds in the river bed of New Bethesda commonage.

Generic diagnosis. If proportional aspects are discarded as being of little diagnostic significance at the generic level, and the extent to which the postorbitals reach posteriorly is considered as either due to damage or the age of the individual, the genera *Leavachia* and *Procynosuchus* are distinguishable only on their dental formulae as far as our knowledge stands at present. It will be shown, however, that there may be no substantial difference in the dental formula and that these two genera could in fact be synonymous. Moreover, if allowance is made for misinterpretations and the dental formula is accepted as five incisors, three canines and postcanine teeth in the region of ten according to age it would, with the dentition as basis, be difficult to differentiate between the genera *Leavachia*, *Procynosuchus*, *Paracynosuchus*, *Galeophrys* and *Galecranium*, These forms nevertheless appear to be generically different and proper diagnoses can only be formulated when the other genera are better known.

Specific diagnosis. For reasons similar to the above it is difficult to formulate a specific diagnosis until the other species have been analysed to a similar extent. Size seems to be a good basis; specimens of the other species are half the size of the present specimen and those of *L. microps* at least are fully adult. Specific diagnoses of the three species will no doubt eventually rest upon peculiar combinations of several minor characteristics. Casual examples are the shorter and heavier dentary, with a more distinct chin, the depressed interorbital region and the constriction of the parietal crest in front of the much smaller pineal opening, in *L. microps*.

Table of measurements. The following is a comprehensive list of useful measurements, in millimetres; those of the type are based on Broom's (op. cit.) illustrations:

	Present specimen	*Type*
Total length of skull	155	155
Length to occipital condyle	142	143
Length to internal carotid foramina	116	
From premaxillaries to interpterygoid fossa	81	
To posterior border of secondary palate	50	
To level of anterior border of orbits	59	60
To posterior border of orbits	82	78
To pineal foramen	108	98
To interparietal notch	139	139
Length of pineal opening	9	8
Breadth of snout across canines	40	40
Interorbital width	32	32
Maximum width of skull	113	109
Width of parietals at pineal foramen	16	16
Maximum width of secondary palate cleft	10	
Minimum width of secondary palate cleft	5	
Breadth of palate between anterior postcanines	28	
Distance between posterior postcanines	50	

Distance between canines	28	
Distance across pterygoid processes	46	
Minimum breadth across pterygoids at level of interpterygoid fossa	21	
Distance across paroccipital processes	55	60?
Total length of dentary	99	94
Height of dentary at postcanine level	15	19
Height of dentary posteriorly	30	39
Greatest antorbital height	28	38

Structure of the Skull

The *basioccipital* contributes substantially to the condyle structure, its contribution being greater than those of the exoccipitals jointly. The condyle is nevertheless distinctly crescentic or kidney-shaped, as is typical in the procynosuchids, and not trilobed as in the scaloposaurids. The condition is similar in *Procynosuchus* (Broom, 1938), but in the more primitive *Scalopocynodon* (Brink, 1960*a*) the basioccipital is more reduced, tending to produce more distinctly two exoccipital condyles. In the type of *L. duvenhagei* Broom (1948) noticed the kidney shape, but he figures a structure more like a single condyle to which the exoccipitals do not contribute very substantially. While the condition is similar in the present specimen and reasonably different from the more distinct double condyle of *L. microps*, with substantial exoccipital contributions, this aspect could be evaluated as a possible specific diagnostic feature.

The general build of the basioccipital as a whole is comparable with that of *Scalopocynodon*, where the structure is well displayed in a wax model. The two foramina along the midline are proportionally larger in the present specimen and the contacts with the opisthotics anteriorly to the jugular foramina are shorter and more solid.

The *exoccipitals* are somewhat obscured on the occiput by the presence, in situ, of the two proatlas bones (a distinct lateral process of the left proatlas bone extends virtually into the post-temporal fossa and the condition appears to be quite natural). The general structure and relationship of the exoccipitals, as far as can be traced, agree very well with that of *Scalopocynodon*. A conspicuous difference is the greater size of the jugular foramina in the present specimen and their position, farther forward and closer together. The condyle structure therefore appears to expand posteriorly while, by comparison too, the basioccipital is more constricted in the area between the two foramina.

The *supraoccipital* is narrow and high, rather small, and extends dorsally into a very deep depression with a prominent median ridge. The bone is broader dorsally than ventrally. Its restricted breadth is no doubt only superficial and the result of substantial overlapping of the tabulars.

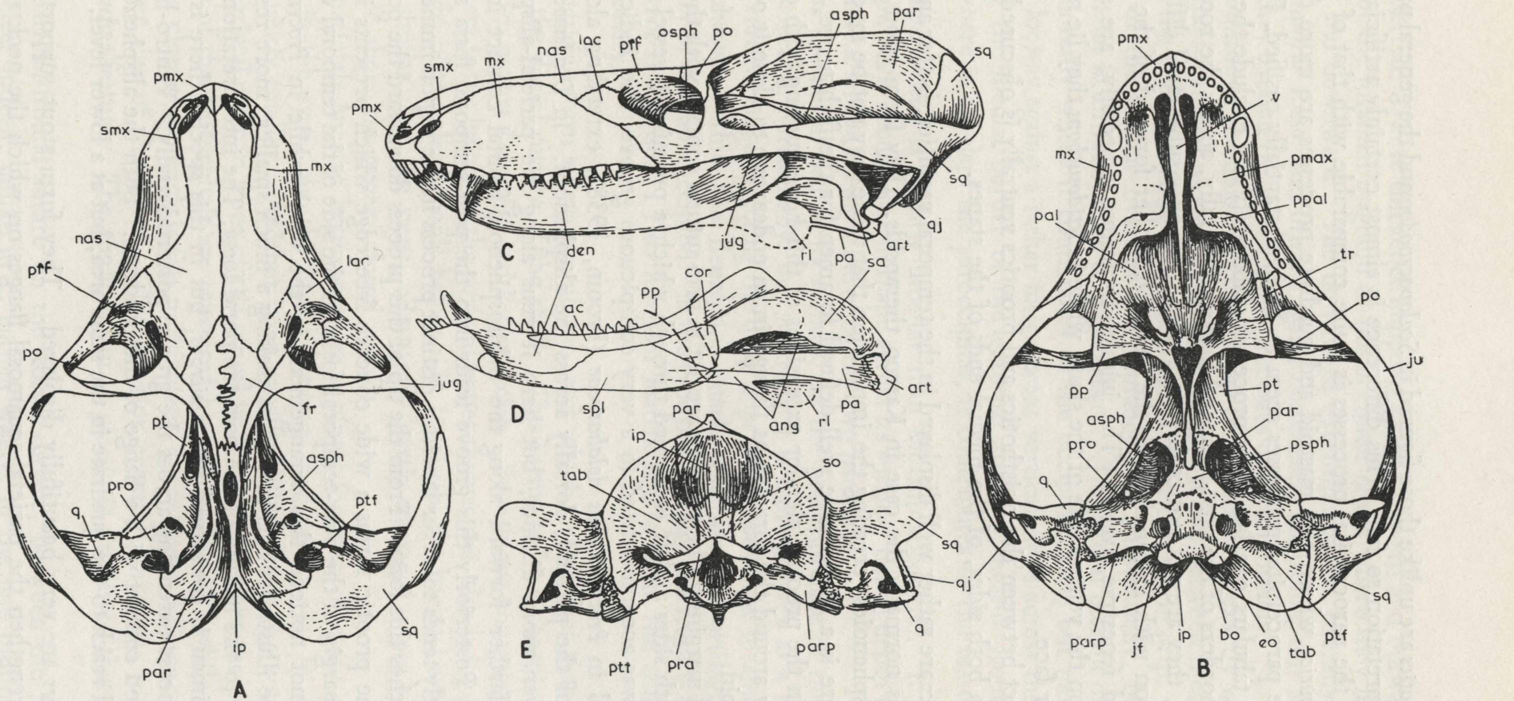

Fig. 10—A, Dorsal view; B, Ventral view; C, Side view; D, Internal view of mandible; E, Occipital view, of skull of *Leavachia duvenhagei*, x$\frac{1}{2}$, For abbreviations see end of article.

The *opisthotics* are unlike those figured in *Scalopocynodon* and the general procynosuchid interpretation so far. This difference is almost certainly artificial. The structure of the paroccipital processes is quite comparable with that of *Ictidosuchops* and *Bauria*, where the mastoid and quadrate processes are more distinct. Laterally the paroccipital processes seem to be insubstantially ossified. Posterodorsally the tabulars overlap these processes elaborately and exclude them from the ventral borders of the post-temporal fossae. Ventrally, across the roof of the middle ears, they are not noticeably excavated. The only substantial difference, by comparison with *Ictidosuchops*, is the situation farther forward of the jugular foramina and fenestrae ovales. The jugular foramina, especially, are situated completely on the ventral side of the skull, while in *Ictidosuchops* they lie more on the posterior face.

The contact between the opisthotics and prootics ventrally is obscured by the presence, on both sides, of the medial ends of the stapes.

The *prootics* are rather well displayed in the temporal vacuities, better and more intact than is normally the case in Karroo therapsids. They form good sutures with the alisphenoids, creating the impression that there may not be much of an overlap. There is a single large well-defined foramen for the fifth nerve, located almost within the prootic, slender extensions of this bone curving both dorsally and ventrally around the foramen as though in an endeavour to close it off from the alisphenoid.

The dorsal margins of the prootics are not in firm sutural contact with the parietals. On both sides a cleft is formed through which a prominent vessel passed. This vessel was accommodated in a very conspicuous groove, also indicated in the type and in *Procynosuchus delaharpeae* (Broom, 1938), extending along the lateral face of the parietal, dorsally across the alisphenoid. In *Diademodon* this groove is even more distinct, but here it runs along the parietal-alisphenoid suture and farther forward along the orbitosphenoid-frontal contact into the nasal cavity. Posteriorly this groove leads into the post-temporal fossa and the prootic merely tends to cover it with a distinct process in the region immediately before it reaches this fossa. From the tip of this process downward the posterior margin of the prootic forms a wide concave free edge which presents itself as the ventral margin of the post-temporal fossa on the side of the temporal vacuity. Broom had not noticed this arrangement in the type, while in *Procynosuchus delaharpeae* he illustrates this margin as making a much smaller, more restricted contribution to the margin of the post-temporal fossa. The interpretation in the present specimen is confirmed in *L. microps*, but in this species there is not as distinct a process extending across the groove posterodorsally. Ventro-laterally there is a good contact with a flange of the quadrate. Both the alisphenoid and the pterygoid reach to the quadrate in the same area, but at a lower level.

The *tabulars* are very beautifully displayed. They form stout supports from behind to strengthen the parietal-squamosal flanges on which the neck muscles were inserted. These thickened supports extend upward and outward from the region of the foramen magnum to the occipital crests where they fan out, both upward and downward. The downward extension curves laterally around the post-temporal fossa, and inward again, completely encircling this fossa. In this region they overlap the paroccipital processes quite elaborately.

The outline of the dorsal portion of the fan corresponds exactly with the outline of the squamosal process directly in front of it and between these two plates of bone the occipital flange of the parietal is clasped in a firm grip. The medial margin of the tabular overlaps the supraoccipital substantially, but with the interparietal it forms an edge to edge suture. The lateral margin of the tabular is free dorsally where it contributes to the occipital crest, but more ventrally it abuts loosely against a rather insignificant vertical ridge across the squamosal, marking the medial border of the external auditory meatus groove. Farther down where it overlaps the paroccipital, it contributes to the mastoid process.

The *interparietal* is slightly broader than the supraoccipital. It is narrower than high, fairly rectangular in shape across its surface, but in depth it appears to extend like a wedge forward between the two parietals.

Across the dorsal half of its surface, on the posterior face of the skull, it is deeply concave, horizontally, but ventrally it is more convex as a result of the median vertical ridge bisecting the deep depression above the foramen magnum. This upheaval within the depression marks the usually cartilaginous dorsal extremity of the supraoccipital. In the type of *L. microps* this ridge is eroded away and matrix is exposed. This lump of matrix falls outside the contour of the cranial cavity.

The *parietals* form a very prominent crest which rises higher than the general level of the dorsal surface of the skull. This seems to be a conspicuous feature of the two genera *Leavachia* and *Procynosuchus*. Even more conspicuous in these two genera is the height of the parietal bones themselves, this being greater than the height of the alisphenoids below. In *L. microps* the parietal arrangement is exactly similar, but the crest, admittedly partly damaged, does not seem to rise much above the general dorsal surface.

The parietals enclose between them a pineal foramen of quite considerable size, as in the type, but the pineal foramen in *L. microps* is, by comparison, conspicuously smaller. Another good specific difference is the constriction of of the parietal crest in front of the pineal in *L. microps*. Here the posterior extensions of the postorbitals are separated by one millimeter, while in *L. duvenhagei* the closest approach is five millimeters, a significant difference in spite of the larger size of the latter. This anterior constriction seems to be more a *Procynosuchus* feature. The condition in *L. gracilis* is similar to that of *L. duvenhagei*.

The parietal-frontal suture on the dorsal surface, between the postorbitals, is very clear indeed, unlike in *L. microps* where, in the one millimeter space, no suture can be traced. In fact, all the sutures in *L. microps* are well closed and fused and there can be no doubt over the substantial maturity of this specimen, representing a species half the size of the one under discussion.

The parietal-frontal contact is more substantial in depth and at a lower level the parietals extend farther forward, almost to the level of the postorbital bars.

The ventral margins of the parietals are not free anteriorly. The alisphenoids support these margins over considerable lengths. Far posteriorly these margins seem to be free, only loosely covered by the prootics, but anteriorly thin, elongated extensions of the alisphenoids accompany the margins up to the level where there is loose contact with the orbitosphenoids. The alisphenoid prolongations actually penetrate some distance forward between the parietals and the orbitosphenoids. Here the canal extending along the lateral face of the parietal from the post-temporal fossa forward above the alisphenoid becomes less distinct, but it is still clear that the vessel it contained followed a course along the orbitosphenoid-parietal contact into the nasal cavity.

Posteriorly the parietals penetrate deeply between the squamosals and tabulars.

The *postorbitals* contribute in the normal manner to rather delicate postorbital bars. In this respect Broom's interpretation in the case of the type is obviously incorrect. Their contribution to the dorsal surface in the interorbital region is not substantial. This observation may provide good ground for distinguishing between this genus and *Procynosuchus*, or even *Galecranium*, where the postorbitals contribute handsomely to the interorbital surface. In *L. microps* these contributions form marked narrow ridges, but in spite of these ridges the interorbital surface is still distinctly depressed. Such ridges are not apparent in the present specimen and the interorbital region as a whole is not depressed. The type seems to be in agreement, as does *L. gracilis*. This feature is, therefore, of diagnostic significance in the case of the species *L. microps*.

The posterior extensions of the postorbitals reach to a level shortly behind the anterior margin of the pineal foramen. This seems to be within the normal reach; it agrees with *Galeophrys* and *Galecranium* and the condition in the type where the postorbitals reach somewhat farther back is no doubt an individual variation or subject to the age of the specimen. In *Procynosuchus rubidgei* Broom (1938) interprets these extensions as being considerably shorter, but it could be the result of damage or an immature feature.

The *frontals* are normal, with the suture between them heavily contorted. The nasals spread widely across their anterior margins and the extent to which they reach back, well beyond the level of the anterior borders of the orbits, is quite a general procynosuchid feature.

The *prefrontals* are in outline similar to those of the type. They form the broad, smoothly rounded dorsal borders of the orbits. This absence of a sharp well defined dorsal border to the orbits also seems to be a general and characteristic procynosuchid feature.

The *lachrymals* are equally typical. Dorsally to the lachrymal ducts they also form indistinct anterior margins to the orbits. At the duct openings the margin becomes sharper, but yet not as clearly defined as in higher cynodonts.

The *nasals* reach far back to level with the most anterior angles of the postorbitals, as in *Galeophrys* and *Galecranium*, In the type and in *L. microps* and *L. gracilis* they reach less far back, but still more than in *Procynosuchus*. Between the posterior ends of the nasals the frontals extend to the level of the anterior borders of the orbits in all procynosuchid specimens described and at hand, but in the present specimen the frontals stop distinctly short of this level.

Anteriorly the nasals are not substantially separated by prolongations of the premaxillaries. The condition in all other procynosuchids is not clear. These premaxillary prolongations are short and stout and penetrate between the nasals for a distance of only about three millimeters. Laterally the anterior ends of the nasals are well flanked by slender extensions of the septomaxillaries; the slenderness of these prolongations seems to be a general procynosuchid feature. The anterior free borders of the nasals slope quite sharply, forming an angle of less than 90° between them.

The *septomaxillaries* are in good condition. They form distinct but very slender thin shelves horizontally across the external nares. These shelves actually form the ventral borders of the external nares. Below these shelves the septomaxillaries are merely excavated to accommodate glands of some description. Below these excavations borders are also formed which are more often regarded as the actual ventral margins of the external nares. To these margins the septomaxillaries do not contribute as extensively as in other non-procynosuchid cynodonts.

Laterally to the external nares, at the junction between the septomaxillaries, premaxillaries and maxillaries, there are the normal conspicuous openings which, as in other procynosuchids, are of quite considerable size. The thickness of the bone between these openings and the external nares is very highly reduced.

The *premaxillaries* are of normal build. The internarial bridge is short and stout. Anteriorly, close to the median suture, immediately above the roots of the first incisors, the foramina penetrating apparently as in *Akidnognathus parvus* (Brink, 1960a) both up to the septomaxillary glands and down into the anterior palate are very distinct and conspicuous.

The premaxillaries carry five incisors as in the type, the fifth being slightly smaller. On the palatal side the extent of the premaxillaries cannot be traced due to the occlusion of the lower jaw. In figure 10B sutures are introduced after the condition in *Procynosuchus delaharpeae* (Broom, 1937). This seems to be quite the normal arrangement and it is doubtful whether the structure in this specimen should be substantially different.

The *maxillaries* display the typical procynosuchid arrangement as far as the secondary palate is concerned. A difference portrayed by the present specimen is the broadening of the cleft between the palatal plates anteriorly. In other procynosuchids, even in *Scalopocynodon*, there is a tendency for the cleft to widen anteriorly, but in the present specimen it is far more pronounced.

There is a substantial overlap between the palatal plates of the maxillaries and the palatines, those of the maxillaries reaching back underneath those of the palatines. The palatal foramen in this suture ventrally appears to pass upward not through a notch in the palatal plate of the palatine but completely encircled by the palatine bone, as is also the case in *Scalopocynodon*.

The maxillaries reach back to well beyond the last cheek teeth, to level with the middle of the orbits. This extension is more slender and reaches farther back than in the type, or in *L. microps*.

There are two small anterior canines, a normal sized anteriorly sloping main canine, and ten post-canine teeth. On the left side the first post-canine tooth follows immediately on the canine, with no diasteme. A space follows which clearly accommodated two teeth and the tip of a replacing tooth is present in the anterior half of this space. The following seven teeth are in good condition, the last being slightly smaller. All the teeth have the additional posterior cups well preserved.

On the right side there are ten teeth, the first behind the canine being replaced. All the teeth are in as good a condition as on the left side.

In this respect there seems to be a substantial difference between the present specimen and the type, where Broom (1948) counted eight post-canine teeth, confirmed by Brink and Kitching (1953). It would appear that certain spaces between teeth had not been carefully excavated to ascertain the presence of additional empty sockets. Compared with the present specimen a first post-canine tooth can fit in the space immediately behind the canine and it would appear that the third is missing too, in Broom's figure 37 (op. cit.), bringing the total to ten. In figures produced by Brink and Kitching (op. cit.) a diasteme is allowed in the place of the first postcanine and counting this as the first tooth, the fourth is indicated as missing on the left side and a sixth tooth is missing on the right. The total would therefore be nine either side. Obviously in both descriptions based on the type great care had not been exercised in ascertaining the exact number by excavating all spaces that could contain extra sockets.

The dental formula can be taken as i5, c3, pc10 for the upper jaw, with apparently four incisors, one canine and up to ten post-canine teeth in the lower jaw. Although fully adult *L. microps* has only eight closely packed post-canine teeth, while *L. gracilis* has a ninth erupting.

Mistakes have been made in distinguishing between incisors and canines in these forms with multiple canines and it is not unlikely that the position in *Procynosuchus* (with ten post-canine teeth) is also five incisors and three canines rather than six incisors and two canines. If this is the case, which appears to be very likely indeed, it would be difficult to find other features on the strength of which these two genera can be differentiated. The present investigation has not brought any such feature to light but it would be unsafe to suggest a synonymy at this stage, before the genus *Procynosuchus* has been investigated to a similar extent.

The *transverse* bones are exposed in front of the pterygoid processes, as figured, but their lateral extents are not clear due to the occlusion of the lower jaw. Important is the cynodont arrangement where the transverse bones do not extend along the pterygoid processes as is more characteristic of the Therocephalia and Scaloposauria. This therocephalian-scaloposaurid arrangement is also found in the primitive silphedestid cynodont *Scalopocynodon*.

The *jugals* contribute in the normal manner to the postorbital bars, unlike Broom's interpretation for the type (Broom, op. cit.). They reach far back to the level of the quadratojugals. They are not as high below the orbits as in the type, or in *L. microps*. Their contacts with the transverse bones cannot be seen, with the lower jaw in situ; the interpretation in figure 10D is based on the general condition in other related forms. In the higher cynodonts like *Diademodon* the jugals reach farther inward in this area, as the transverse bones become correspondingly reduced.

The *squamosals* are best described in terms of their five distinctly separate processes. The most prominent process is the one contributing to the zygomatic arch. This portion is not as high or massive as in the type and it is not concave over its outer surface. It is longer and less curved in the vertical plane than in *L. microps*. Compared with the type it is also at a lower level. This may partly be due to some dorso-ventral compression during fossilization.

A second conspicuous process is the one overlapping the posterior flange of the parietal, above the post-temporal fossa on the side of the temporal vacuity. The shape and outline of this process are interpreted somewhat differently in the present specimen than in the type. There is not a deep notch between these two processes, but rather a wide smooth shallow valley.

A third process, which may conveniently be called the prootic process of the squamosal, extends forward and downward below the post-temporal fossa on the side of the temporal vacuity; the fossa is actually situated in a notch between this and the previous process. The prootic reaches across this process to meet a flange of the quadrate.

A fourth process, apparently not substantially separated from the previous, but with a different superficial relationship, reaches down posteriorly between the quadrate and paroccipital process to the region accommodating the tympanum. This portion may be referred to as the opisthotic process of the squamosal. Normally the external auditory meatus groove extends across this process. In the present specimen this groove is not well defined.

The fifth process is the smallest, but perhaps not the most insignificant. It is a very slender projection of bone penetrating between the quadrate and quadratojugal and tends to support the latter from behind. This projection may be called the quadratojugal process of the squamosal.

The *quadratojugal* is a bone clearly distinguishable from the quadrate. The structure of these two bones is rather comparable with that of *Scalopocynodon*. Although the quadratojugal is lodged in the squamosal well separated from the quadrate, with a distinct squamosal process intervening, it is nevertheless clear that they join firmly in the condyle structure.

The figures illustrate the condition as clearly as can be gathered from the specimen. From this arrangement it is rather apparent that the quadrate in higher cynodonts is a composite bone which incorporates the quadratojugal. The quadratojugal represents the lateral portion which normally forms the deep wedge cutting antero-posteriorly across the transverse squamosal wall. The condition in the present specimen, and apparently all procynosuchids, is substantially different from forms both more advanced and more primitive (*Scalopocynodon*) in that the squamosal contributes no additional support over the lateral face of the quadratojugal. This bone is completely exposed in lateral view.

While the quadratojugal unites with the quadrate at the condyle, it is very clear that it forms no part of the articulation surface. The quadrate condyle extends far laterally and completely excludes the quadratojugal from contact with the articular.

The *quadrate* lies anteriorly to both the prootic and opisthotic processes of the squamosal and a prominent flange reaches across the former process to contact the prootic. Below this contact the pterygoid reaches to the quadrate condyle and the alisphenoid also extends boldly towards near contact with the quadrate, between the prootic and the pterygoid. More laterally, between the opisthotic and quadratojugal processes of the squamosal, the quadrate seems to form a structure more like a condyle than a wedge, which is loosely seated in a deep excavation.

Both *stapes* are represented only by their most medial portions fitting in the fenestrae ovales. Enough is preserved to indicate that the stapedial foramen is of fair size.

The *vomer* forms a vertical wall longitudinally through the ventral part of the nasal cavity. Between the palatal plates of the palatines the ventral edge forms a narrow flat surface. As the cleft widens between the palatal plates of the maxillaries, this surface broadens too. Behind the posterior border of the secondary palate the ventral edge of the vomer becomes sharper and the partition decreases in height while on either side, across the roof of the internal nares, lateral plates spread out to cover the ventral surfaces of the palatines. This part of the vomer also spreads ventrally over the anterior ends of the pterygoids.

The *palatines*, as in *Scalopocynodon*, substantially overlap the maxillaries on the secondary palate. The median edge of the palatal plate is carried back with a curve, as a fairly prominent ridge, across the general ventral surface of the palatine, and across the transverse bone, to the pterygoid process. Posteriorly the palatines contribute substantially, with elongated projections, to the prominent pterygoid bosses anterolaterally of the interpterygoid fossa. This extensive contribution is a good procynosuchid feature. In *Scalopocynodon* the arrangement is nearly similar. On the whole the tendency on the part of the palatines merely to reach towards these bosses seems to be more a cynodont feature, compared with the therocephalian-scaloposaurid condition.

The *pterygoids* have the normal arrangement, with their complex radiating processes. The pterygoid processes guiding the lower jaw project freely downward and somewhat backward, and are not supported by the transverse bones. The ventral transverse edges of these processes curve smoothly backward as they approach the midline to form the ventral edges of the parsaphenoid processes (to the basipterygoid processes) which accommodate between them the interpterygoid fossa.

The two basisphenoid processes of the pterygoids together build a short keel behind the interpterygoid fossa, at the same time clasping between them the anterior end of the parasphenoid keel. Laterally to this keel the posterior margins of the basispheniod processes form broad intimate sutures with the body of the parasphenoid across the basipterygoid region. This contact is narrower in higher cynodonts and in the bauriamorphs, while in certain scaloposaurids, and especially in the more primitive *Scalopocynodon*, there is a looser articulation, suggesting a kinetic structure, or at least a kinetic condition which had recently been lost. Interesting is the fact that in both specimens of *L. microps* at hand, the basipterygoid fusion appears to be less substantial than in *L. duvenhagei* and more like the average condition in the scaloposaurids.

Laterally to the basisphenoid processes of the pterygoids the quadrate processes arise and extend boldly back to the quadrates, while carrying the alisphenoids on their dorsal margins. These processes seem to be more robust than in other nearly related forms and they incline slightly off the vertical plane as usual. It is not clear in the present specimen, but it would appear that the alisphenoids overlap the lateral faces of these processes as is well shown in both specimens of *L. microps*. This contact in *Leavachia*, and apparently the procynosuchids in general, is more solid than in the scaloposaurids, while in *Scalopocynodon* these bones barely come in contact. Another procynosuchid feature is the strong forward projection of the antero-ventral angle of the alisphenoid across the portion of the quadrate process which lies forward of the pituitary fossa. This condition is less conspicuous in *L. microps*.

On the anterior edge of the interpterygoid fossa the two pterygoids jointly form a minute mesial boss, reminiscent of the characteristic boss in *Bauria*.

In *Bauria*, however, the transverse ventral margins of the pterygoid processes extend directly inward to this boss. This small boss is absent in both specimens of *L. microps* and it is not unlikely that the boss in the present specimen is a small foreign element that accidentally landed in this position.

Antero-laterally of the interpterygoid fossa the pterygoids droop conspicuously to form two very prominent posterior palatal bosses, leaning somewhat outward. To these bosses the palatines contribute substantially, as pointed out earlier. In the present specimen these two bosses are well separated; in one *L. microps* specimen they are nearly in contact with each other, while the second *L. microps* specimen illustrates an intermediate condition. In *Procynosuchus* the bosses are also well separated.

The nature of the anterior outlines of the pterygoids is not clear as these margins are extensively covered ventrally by the palatines, transverse bones and the vomer.

The *alisphenoids* appear depressed vertically as a result of the exaggerated height of the parietals above. Their free anterior margins are deeply curved and elongated projections extend forward both along the dorsal margins of the pterygoids and along the ventral margins of the parietals. The latter processes make contact with the orbitosphenoids and actually penetrate between them and the parietals. The posterior margins of the alisphenoids overlap the anterior margins of the prootics and ventrally a bold endeavour is made to reach the quadrates.

The *orbitosphenoids* seem to form typically an elongated vessel supporting the olfactory lobes from below. They lie immediately below the frontals, but extend back to below the anterior ends of the parietals.

The *parasphenoid* encases the *basisphenoid* ventrally. Between the pituitary fossae the basicranium is well constricted and the parasphenoid keel arises abruptly at this narrowest level, in the shape of a boss, from where the more delicate keel extends forward to terminate between the postero-ventral angles of the basisphenoid processes of the pterygoids. The internal carotid foramina penetrate the basicranium closely either side of the keel immediately before reaching the latter processes. Posteriorly to the keel the parasphenoid fans out flatly to the fenestrae ovales. This triangular basicranial surface is more concave in *L. microps*.

Structure of the Lower Jaw

Although the present specimen is of exactly the same size as the type, the skull is quite markedly flatter. This is no doubt to some extent due to very even and direct dorso-ventral compression during fossilization, but such compression cannot account for certain structural phenomena like the more delicate zygomatic arches and, especially, the more slender lower jaw. In view of all the other points of agreement this difference cannot be regarded as of specific value and can provisionally be passed over as an individual variation or perhaps a phenomenon of sexual dimorphism.

The *dentary* has the same general build as in the type, but is on the whole more slender and less high. Its reduced height may also be accounted for by the erosion of the ventral margins while embedded upside down in the river bed. On the left side, however, the ventral margin is genuine up to the level of the fifth postcanine and in this region the depth of the dentary is still reduced, compared with the type, and to a greater extent than can be accounted for by compression.

Posteriorly the dentary reaches to a level less than half way across the length of the temporal vacuity, leaving a substantial space behind for the postdentary bones. It ends rather squarely, suggesting slightly two angles, a coronoid and an articular angle, but both should actually be looked upon as the coronoid process. Differentiation is less marked than in *Scalopocynodon* where there is also a suggestion of an angular process. There is no "chin" angle anteriorly, as in *Scalopocynodon*. The symphysis is also longer, with a slight sign of a "chin", in *L. microps*.

The dentary is characterised, as in the type, by a well defined area or depression in which the masseter muscle was inserted.

The *splenial* is more slender anteriorly than posteriorly and extends into the symphysis. The ventral margin is approximately level with the ventral margin of the dentary. It covers the meckelian canal completely and approximately at the middle of its length at least, where a cross section has been cut, a sharp crest extends into the canal to line its floor. The dorsal margin of the posterior expanded portion of the splenial is in good sutural contact with the coronoid and anterior coronoid. It tapers to a sharp point beneath the pterygoid process and in this area it folds intimately over the anterior end of the angular which penetrates deeply into the meckelian canal from the back.

The *coronoid* is a thin plate of bone covering the area across which the pterygoid process moves when the jaw is in action. It ends bluntly posteriorly, the margin barely showing behind the pterygoid process, but it extends forward as an elongated tapering process penetrating between the splenial and anterior coronoid forming good sutural contacts with both.

The *anterior coronoid* is a separate elongated bone lining the inner alveolar border. It is in contact with the splenial posteriorly, but anteriorly these two bones are well separated.

The anterior coronoid is well known in the pelycosaurs, but in descriptions of therapsids it has been blatantly overlooked. In fact, at the time of writing I have failed to find a single recorded reference to this bone in publications on therapsids. Admittedly the effort was not extensive. In referring to actual specimens in the collection of this Institute, however, it soon transpired that the anterior coronoid is present in dicynodonts, gorgonopsians, therocephalians, scaloposaurids and cynodonts. Its presence is not convincingly clear in the two adequately cleaned specimens of *Bauria* at hand, while our deinocephalian material is inadequate. In all groups excluding the dicynodonts and gorgonopsians the general nature of the anterior coronoid is similar to that of the present *Leavachia* (and that of the pelycosaurs) and the position is perhaps similar in at least the carnivorous deinocephalians.

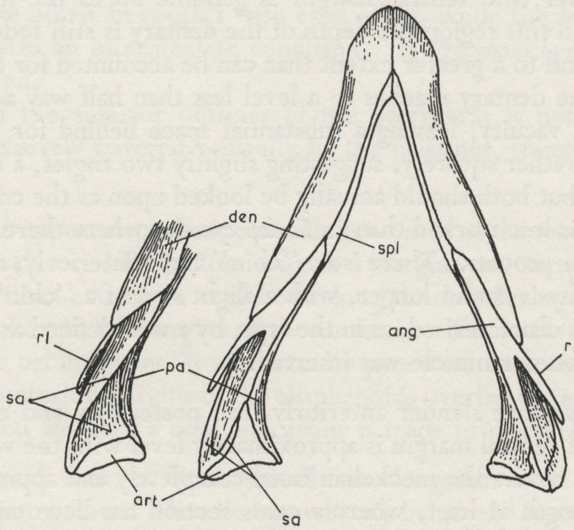

Fig. 11—Ventral view of the lower jaw of *Leavachia duvenhagei*, as preserved. Figure on left shows post-dentary bones in dorsal view. x½.

On referring to the section drawings of *Scalopocynodon* it was discovered that the anterior coronoid is also present in this specimen. It was not figured and described, as it was thought to be a flake that came off the surface of the dentary.

The *prearticular* penetrates forward underneath the coronoid rather than the splenial. It is a thin blade of bone and posteriorly it folds both inward medially to, and outward ventrally around, the articular. It virtually reaches the articular surface.

The *articular* is wedged between the posterior fold of the prearticular medially and ventrally and the posterior ends of the angular and surangular laterally. The surangular also swings around to the dorsal side of the articular.

The *surangular* arises far back intimately alongside the articular and briefly contributes to the articular surface. In this region it is overlapped by the posterior end of the angular. It spreads around to the dorsal side of the articular, but the main body of the bone rises directly from the lateral angle of the articular as a powerful arch across to the coronoid process of the dentary and then plunges deeply beneath the coronoid, above the prearticular. The dorsal edge of this arch is fairly sharp and contrasts conspicuously with the broad and flattened margin in *L. microps*.

The *angular* is quite massive and substantially covers the articular-prearticular laterally, as well as the surangular to some extent. While decreasing in height forward, it becomes very stout and boldly penetrates underneath the posterior end of the splenial, the latter bending ventrally across it with a noticeably thickened margin. Behind the posterior margin of the dentary the reflected lamina extends freely backward. Both reflected laminae are extensively damaged as a result of erosion.

The structure of the lower jaw conforms with the general procynosuchid-cynodont pattern, which agrees rather well with the therocephalian-scaloposaurid arrangement, but differs markedly from the higher cynodont condition.

In other respects too, especially the palate and dentition, there seems to be a marked difference between the lower cynodonts as a whole, which can be grouped under the Procynosuchia, and the higher cynodonts, also as a whole, which can be referred to as the Cynognathia. As suggested in the previous paper (page 39 of this issue), the Synapsida should be elevated to Class status so that the Therapsida becomes a subclass and the Theriodontia an order. The suborder Cynodontia can then accommodate the Procynosuchia and Cynognathia as infraorders, still leaving the rank of superfamily free for a much desired further subdivision. A suggestion is that the Silpholestoidea, Procynosuchoidea and Galesauroidea, at least, be recognised as superfamilies under the Procynosuchia, while the Cynognathia accommodates the superfamiles Cynognathoidea and Gomphodontoidea, clearly separable on dental characteristics.

Summary

1. A rather excellent specimen of a procynosuchid cynodont is described, improving reasonably our knowledge of this infraorder.
2. Various structural details, especially in the lower jaw, support the contention that the suborder Cynodontia clearly comprises two separate infraorders, the Procynosuchia and Cynognathia. Within the former infraorder three superfamilies can provisionally be recognised; the Silpholestoidea, Procynosuchoidea and Galesauroidea, with *Scalopocynodon*, *Leavachia* and *Thrinaxodon* as the best known genera respectively.
3. The most outstanding difference between the Procynosuchia and the Cynognathia is found in the arrangement of the postdentary bones and the differentiation in the latter between distinct coronoid, articular and angular processes to the dentary.

4. The three superfamilies under the Procynosuchia can be differentiated as follows:

Silpholestoidea:	Cleft secondary palate—multiple canines—scaloposaurid affinity.
Procynosuchoidea:	Typical cleft secondary palate—multiple canines—cynodont structure.
Galesauroidea:	Cleft to closed secondary palate—single canines—procynosuchid mandibles.

5. The genera *Procynosuchus*, *Paracynosuchus*, *Leavachia*, *Galeophrys* and *Galecranium* are not satisfactorily separable on definite structural grounds. Synonymy is not suggested while certain genera are still inadequately known.

6. Diagnoses of the three *Leavachia* species are deferred until better material of the two smaller species, *L. microps* and *L. gracilis*, comes to hand.

7. Our general knowledge of a procynosuchid skull is not greatly improved, but the ventral surface of a *Leavachia* skull is described for the first time.

8. This specimen has drawn attention to the fact that an all but inconspicuous bone in the lower jaw, the anterior coronoid, had consistently been ignored in descriptions of specimens belonging to all therapsid groups.

Abbreviations

ac	Anterior coroniod.	pmx	Premaxillary.
ang	Angular	po	Postorbital.
art	Articular.	pp	Pterygoid process.
asph	Alisphenoid.	ppal	Palatal plate of the palatine.
bo	Basioccipital.	pra	Proatlas.
cor	Coronoid.	prf	Prefrontal.
den	Dentary.	pro	Prootic.
eo	Exoccipital.	psph	Parasphenoid.
fr	Frontal.	pt	Pterygoid.
ip	Interparietal.	ptf	Post-temporal fossa;.
jug	Jugal.	q	Quadrate.
jf	Jugular foramen.	qj	Quadratojugal.
lac	Lachrymal.	rl	Reflected lamina.
mx	Maxillary.	sa	Surangular.
nas	Nasal.	smx	Septomaxillary.
osph	Orbitosphenoid.	so	Supraoccipital.
pa	Prearticular.	spl	Splenial.
pal	Palatine.	sq	Squamosal.
par	Pareital.	tab	Tabular.
parp	Paroccipital process.	tr	Transverse bone.
pmax	Palatal plate of the maxillary.	v	Vomer.

References

BRINK, A. S., 1960a, A new type of primitive cynodont. *Palaeont. Afric.*, vii, p. 119.

BRINK, A. S., 1960b, On some small therocephalians. *Palaeont. Afric.*, vii, p. 155.

BRINK, A. S. and KITCHING J. W., 1951, On *Leavachia*, a procynosuchid cynodont from the middle *Cistecephalus*-zone. *S. Afr. J. Sci.*, 47, p. 342.

BRINK, A. S. and KITCHING J. W., 1953, On *Leavachia duvenhagei* and some other procynosuchids in the Rubidge Collection. *S. Afr. J. Sci.*, 49, p. 313.

BROOM, R., 1937, A further contribution to our knowledge of the fossil reptiles of the Karroo. *Proc. Roy. Soc.*, Ser. B, Part 3, p. 299.

BROOM, R., 1938, The origin of the cynodonts. *Ann. Transv. Mus.*, xix, 2, p. 279.

BROOM, R., 1948, A contribution to our knowledge of the vertebrates of the Karroo beds of South Africa. *Trans. Roy. Soc. Edinb.*, lxi, 2, p. 577.

BROOM, R. and ROBINSON J. T., 1948, On some new types of small carnivorous mammal-like reptiles. *Spec. Publ. Roy. Soc. S. Afr.*, p. 29