

THE MAMMAL-LIKE REPTILE
LYCAENOPS

EDWIN H. COLBERT

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INTRODUCTION

THE GORGONOPSIAN GENUS *Lycaenops* was created by Broom in 1925 with *Lycaenops ornatus* Broom as the type species. This species in turn was based upon a rather complete skeleton that had been found by Broom in 1920 at Biesjespoort, Union of South Africa, in beds "that are at the very top of the *Endothiodon* zone."

The original description of *Lycaenops ornatus* was presented by Broom in a preliminary notice published in the Records of the Albany Museum for 1925. Subsequently, in 1930, he published a rather extensive description of the type specimen in the Philosophical Transactions of the Royal Society of London, while reference to this form was made in his book, "The mammal-like reptiles of South Africa," which appeared in 1932. Consequently it will be seen that our knowledge of *Lycaenops ornatus* rests upon a solid basis of published information.

In 1928 the type specimen was acquired from Dr. Broom by the American Museum of Natural History. It was placed in the collections of this Museum, where it remained for some years in essentially the same condition as it had been when received from Dr. Broom. Recently it has been thought advisable to complete the preparation of the skeleton, in order that it might be put in proper condition for exhibiting as a mount. In preparing the skeleton it was apparent that many new morphological characters were coming to light, characters which hitherto had been obscured by the matrix adhering to the bones of the skeleton. Consequently it was decided to attempt a new description of this specimen, in order that all the information obtained as a result of its preparation might be made available.

This will explain why a new and detailed study of *Lycaenops ornatus* has been made, in spite of the fact that Broom has already published on this form at some length. It is thought that a supplementary description and discussion of the specimen are entirely justified, particularly in view of the importance of the fossil to the subject of vertebrate paleontology. While skulls of theriodont reptiles are fairly numerous, complete skeletons

are not at all common, and every such specimen deserves the fullest treatment possible in the literature. This present specimen is of particular importance because it is one of the few relatively complete gorgonopsian skeletons known, and as such gives us much of our knowledge of gorgonopsian structure.

Four previous publications have been devoted to a large degree to fairly detailed elucidations of the postcranial structure in the Gorgonopsia. One of these is the monographic study of the Gorgonopsidae from the Permian of Russia made by Pravoslavlev and published in 1927. This very fine publication, devoted to a detailed description of the skull and skeleton of *Inostrancevia* and *Amalitzkia*, is unfortunately entirely in Russian, with no summary in another language. However, the plates and figures give a fairly adequate idea as to the details of the postcranial skeleton in these Russian gorgonopsians. The second of these papers is Broom's monograph of 1930 on the structure of the Gorgonopsia, a study founded for the most part on the *Lycaenops* skeleton now under consideration. However, as pointed out above, there is much to be added to Broom's description of the skeleton of *Lycaenops*. Incidentally, it might be said in this connection that in Broom's comprehensive book on the mammal-like reptiles, published in 1932, about two pages are devoted to a general discussion of the characters of the postcranial skeleton in the Gorgonopsia. The third paper on the structure of the skeleton in the Gorgonopsia is Boonstra's "Contribution to the morphology of the Gorgonopsia," published in 1934. In this paper Boonstra considers in some detail the postcranial skeleton of the Gorgonopsia, with special emphasis on the genus *Aelurognathus*, of which an exceptionally fine skeleton is known. The fourth paper is that of Broili and Schröder, published in 1935, in which they describe the skeleton of *Scymnognathus*. In this paper a restoration of the skeleton of *Scymnognathus* is presented.

In his paper Boonstra presents a comprehensive list of the several gorgonopsians in which postcranial elements are known. The most complete skeletons are represented in

the genera *Lycaenops*, *Aelurognathus*, and *Inostrancevia*. The *Lycaenops* skeleton is complete except for the cervical vertebrae, most of the caudals, and most of the ribs. The skeleton of *Aelurognathus*, described by Boonstra, lacks the posterior dorsolumbar vertebrae, most of the caudals, the pubes, certain bones in the feet, and presumably the ribs. In *Inostrancevia* the skeleton is complete except for the posterior portion of the tail, the feet, which are completely lacking, and most of the ribs. The skeleton of *Scymnognathus*, described by Broili and Schröder, lacks the cervical vertebrae and all of the caudals, the upper part of the scapula, the manus, the pubes and ischia, certain bones in the pes, and most of the ribs.

Less complete skeletons are known in the genera *Scylacops*, *Hipposaurus*, and *Arctognathoides*, while in *Cynodraco*, *Lycaenodontoides*, and *Amalitzkia* only scattered postcranial elements are preserved. It is upon the basis of comparisons with the above-named genera that this present study of the skeleton of *Lycaenops* will be attempted.

It might be well at this point to call attention to Boonstra's analysis of the causes for the comparative paucity of gorgonopsian skeletons. He says: "The Gorgonopsia were agile beasts of prey that lived on the higher and drier parts of the great Karroo Basin during Upper Permian and Lower Triassic times, so that on death their remains, in order to be entombed in the sediments, had to be transported to the lower-lying areas. During transportation the comparatively slender and more fragile bones of the postcranial skeleton were destroyed, whereas the more compact skull was more often preserved" (Boonstra, 1934, p. 137).

The preparation of the skeleton described in this paper was done by Mr. Jeremiah Walsh of the American Museum of Natural History Paleontological Laboratory, while the mount was made by Mr. Charles Lang, chief of the laboratory. New drawings illustrating this skeleton were made by Mr. John C. Germann of the Department of Geology and Paleontology, the American Museum of Natural History.

MATERIALS AVAILABLE FOR STUDY

THIS STUDY IS BASED primarily upon the type skeleton of *Lycaenops ornatus* Broom. As for other materials at hand, comparisons naturally have been made with such other theriodonts, and especially such other gorgonopsians, as are available in the collections of the American Museum of Natural History. These are, particularly, skulls and jaws belonging to the genera *Gorgonops*, *Aelurosaurus*, *Aloposaurus*, *Scymnognathus*, and *Delphaciognathus*, all of which were redescribed by Boonstra in 1935. Other comparisons are, of course, based upon the literature.

It may be well at this place to review in detail the materials that constitute the type specimen of *Lycaenops ornatus* Broom.

Lycaenops ornatus Broom, A.M.N.H. No. 2240; skeleton found near the railway line, about 2 miles south of Biesjespoort Railway Station, Union of South Africa. The horizon is upper *Endothiodon* zone, Lower Beaufort beds, Beaufort series, Karroo system, Permian. The circumstances of the discovery of this specimen and its conditions at the time of discovery have been described by Broom as follows:

"The beautiful Gorgonopsian skeleton which forms the type of *Lycaenops ornatus* [A.M.N.H. No. 2240] was discovered by me in 1920, by the side of the railway line, about two miles south of Biesjespoort railway station. It lay on a slope of shale, which is weathering so fast that on revisiting the spot two years later it was with great difficulty that the exact spot could be identified. When first discovered only the front end of the pubis was exposed and a part of the femur, but on digging into the shale nearly the whole skeleton was found, for the most part

lying as the animal had probably died. Most of the cervical region and most of the tail had been weathered away. A few phalanges and carpal bones of one hand, and some phalanges of the other and of both feet were not discovered, and some parts of the shoulder girdle are missing and probably were removed before the skeleton was covered by mud, but otherwise the skeleton is practically perfect. As is the case with all Karroo fossils there is some degree of crushing, but most of the bones except the vertebrae are beautifully preserved" (Broom, 1930, pp. 349-350).

Plate 27 of Broom's 1930 paper is here reproduced, to show the position of the skeleton and its condition when it was discovered.

The bones constituting the skeleton may be listed as follows:

Skull and mandible

Left half of atlas arch and lower portion of atlas
Twenty presacral vertebrae, in a continuous series from the sacrum forward

Portions of ribs articulating with some of these vertebrae

Two sacral vertebrae

Sternum

Left scapula, coracoids, humerus, radius, ulna, and manus, the latter with all bones present except those of the fifth digit

Right humerus, radius, ulna, and of the right manus three carpals and three ungual phalanges

Left ilium, ischium, pubis

Right ilium, ischium, pubis

Left femur, tibia, fibula, and pes, the latter with all bones present except for most of the phalanges

Right femur, tibia, fibula, pes, the latter lacking all but the proximal ends of two metatarsals and all but one phalanx

DESCRIPTION AND DISCUSSION

TAXONOMY

ORDER THERAPSIDA SUBORDER THERIODONTIA INFRAORDER GORGONOPSIA

DIAGNOSIS: Carnivorous therapsids of Middle and Upper Permian age. Parietal region very broad; postorbital and squamosal joining above the temporal opening; postfrontal bone present, preparietal bone generally present; large interparietal and tabular; no secondary palate; occipital condyle single; dentary large, but not unduly encroaching on the angular, surangular, and articular; strong mandibular symphysis; postcranial skeleton rather heavily constructed; phalangeal formula generally 2, 3, 4, 5, 3, but with the middle phalanges of the third and fourth digits very much reduced.

FAMILY GORGONOPSIDAE

The characters of the family are essentially the same as those for the infraorder, presented above.

GENUS LYCAENOPS BROOM, 1925

Lycaenops BROOM, 1925, Rec. Albany Mus., vol. 3, p. 323.

Lycaenops ornatus Broom

Lycaenops ornatus BROOM, Rec. Albany Mus., vol. 3, p. 323.

TYPE: A.M.N.H.No.2240, skull and skeleton, listed in detail on page 361.

HORIZON: Upper *Endothiodon* zone, Lower Beaufort beds, Beaufort series, Karroo system, Permian.

LOCALITY: About 2 miles south of Biesjespoort Railway Station, Union of South Africa (for the type, and to date the only known specimen).

DIAGNOSIS: A gorgonopsian of average size. The skull shows the typical broad frontoparietal region of the Gorgonopsia. There is a large preparietal, and the pineal foramen, which is not very large, is raised upon a well-developed boss. The squamosal bone is large

and the quadrate is much reduced, consisting of little more than an articulating surface. The occiput is sloped forward, as is characteristic of many gorgonopsians, and there is a large interparietal. The occipital condyle is single. The dentition consists of five large incisor teeth, of which four are contained within the premaxilla, a very large canine, and four small, simple postcanine teeth. The canine tooth is serrated along its posterior cutting edge. The mandible is deep in the symphyseal region, to form a protection for the large canine, and the dentary is large.

There are probably 27 presacral vertebrae, of which the first seven may be considered as cervicals. The vertebrae are characterized by well-developed transverse processes, and by relatively short neural spines. Intercentra are but feebly developed between the first few vertebrae. Three sacral vertebrae. The tail evidently was relatively short, and probably consisted of about 25 or 30 rather small caudal vertebrae. Ribs were continuous from the skull to the pelvis.

The scapular blade is comparatively small; the coracoids are large. Clavicles well developed and interclavicle slender. A broad and osseous sternum is present. The bones of the fore limb are rather slender. Both ectepicondylar and entepicondylar foramina are present in the humerus. The manus is comparatively short and broad, with 10 well-developed carpal bones. Phalangeal formula: 2, 3, 3, 4, 3.

The pelvis is strong and shows various specializations. There is a short iliac crest. The ischium is very deep, while the pubis is constricted in front of the acetabulum, and expanded anteriorly. The femur is long and slender, and the head is set at an angle to the shaft, so that the bone is brought in beneath the body. The tibia and fibula are relatively short. The pes, in proportions, is like the manus, and is characterized by the large astragalus and calcaneum. Phalangeal formula: 2, 3, 3, 4, 3.

THE SKULL AND MANDIBLE

Broom's original description of *Lycaenops ornatus* was a preliminary notice in which no attempt was made at a comprehensive description of the skull and mandible or of the postcranial skeleton in this animal. In 1930, however, a fairly detailed presentation was made, with accompanying figures of the skull and jaw and of certain elements in the postcranial skeleton. It is the purpose of this present description to present rather fully the anatomical details of the skull and skeleton of *Lycaenops*, to repeat in part the knowledge already made available in Broom's memoir, and to add points that either were omitted by Broom or were unknown to him because of the incomplete preparation of the specimen.

GENERAL PROPORTIONS AND SIZE

Lycaenops is what one might call an "average-sized" gorgonopsian. The skull, after the effects of crushing have been corrected, is about the size of the skull in *Gorgonops*; it is slightly smaller than the skull in *Lycaenoides* and *Scymnognathus*, and as compared with these genera it has a relatively shorter muzzle. The character of particular importance in this regard is the relative depth and narrowness of the skull and mandible, especially in the anterior portions. The contrast between *Lycaenops* and *Gorgonops*, for instance, in this respect is quite striking.

THE MUZZLE

There is nothing in particular to differentiate the premaxilla in *Lycaenops* from the same element in other gorgonopsians. As in other members of this group, it carries four of the so-called incisor teeth. It should be noted here that in Broom's figure of the skull it appears that only three of the "incisors" are contained within the premaxilla. However, the suture between the premaxilla and maxilla definitely reaches the edge of the bone at the posterior edge of the fourth tooth, as shown in the new figure of the skull (fig. 1).

The maxilla is a large bone, forming most of the height of the snout or muzzle in its anterior portion, and extending back ventrally in a process that reaches beneath the jugal to a point about opposite the middle of the orbit.

In this bone are inserted the fifth of the five "incisor" teeth, the "canine" and the four rather small "molar" teeth.

The septomaxilla, a bone that is well developed in many of the therapsid reptiles, is large and prominent in *Lycaenops*. It is an elongated bone, with its posterior end intruded between the maxilla and the nasal. Anteriorly it forms the posteroventral portion of the external nares on either side. At the junction of this bone with the premaxilla and the maxilla there is a large foramen.

As Broom has shown, the lacrimal bone in *Lycaenops* is roughly quadrangular, in which respect it resembles the same bone in various other genera of gorgonopsians. It forms a portion of the anterior border of the orbit and is bounded above and below by the prefrontal and jugal, respectively, and anteriorly by the maxilla. The jugal is an elongated bone with a somewhat expanded facial portion extending dorsally to form a part of the front border of the orbit. It articulates in its middle region firmly with the postorbital, and posteriorly with the squamosal. This latter bone extends forward as a long, thin tongue or process embraced both above and below by the jugal.

The nasals are large bones, transversely expanded both anteriorly and posteriorly, and extending from the upper borders of the external nares, of which they form a part, to points just above the front borders of the lacrimal and the jugal. It should be noted that the nasal does not extend back quite so far as is shown in Broom's figures (1930, fig. 1; 1932, fig. 44). Posteriorly each nasal comes to a point which inserts itself between the frontal on the medial side and the prefrontal on the lateral side.

THE TEETH

At this place it may be advantageous to take up the dentition in *Lycaenops*. The upper teeth, mentioned above, are well shown in the specimen, but owing to the firm interlocking of the lower jaw in position, the lower teeth are not visible. The "incisors," of which four are contained in the premaxilla and one in the maxilla, are long, pointed teeth. Of these teeth the first and fifth in the series are the smallest and about equal to each other in

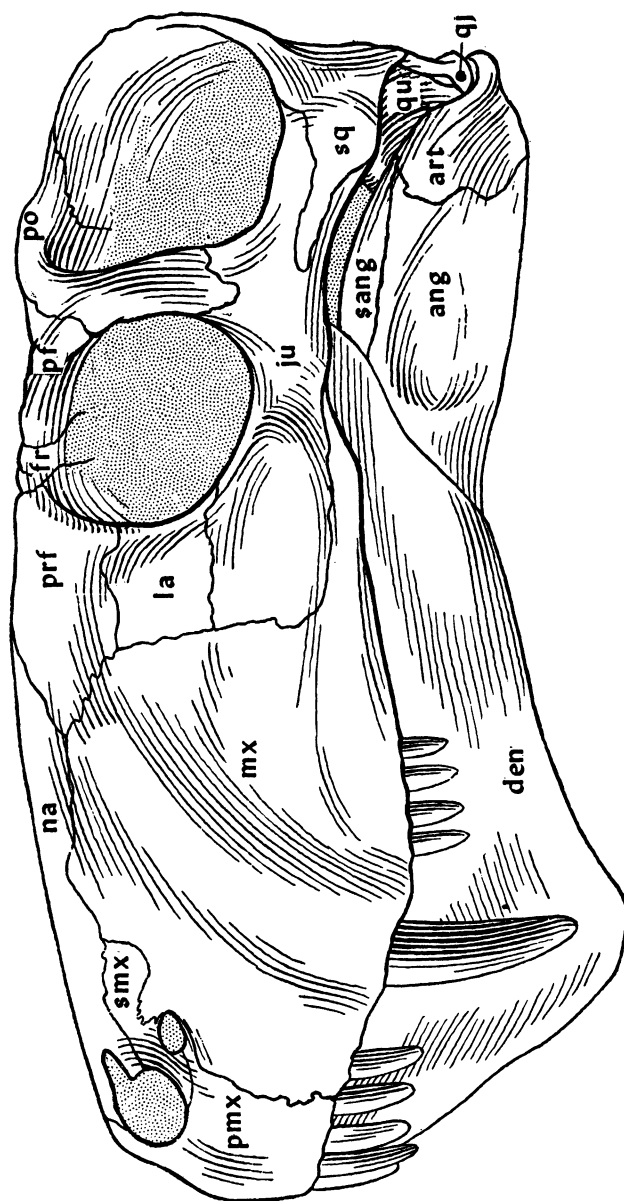


FIG. 1. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, skull and mandible. Left lateral view, $\times \frac{1}{2}$, restored. *Abbreviations:* ang, angular; art, articular; den, dentary; fr, frontal; ju, jugal; la, lacrima; mx, maxilla; na, nasal; pf, postfrontal; pmx, premaxilla; po, postorbital; prf, prefrontal; qj, quadratojugal; qu, quadrate; sang, surangular; smx, septomaxilla; sq, squamosal.

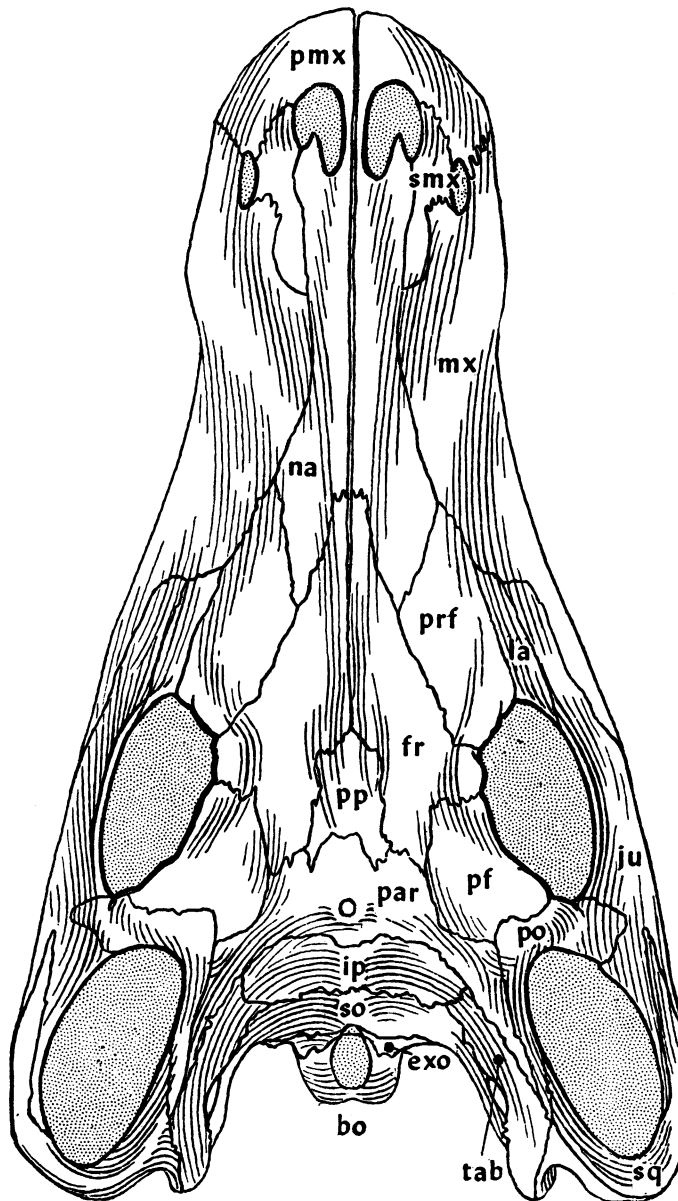


FIG. 2. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, skull. Dorsal view, $\times \frac{1}{2}$, restored. *Abbreviations:* bo, basioccipital; exo, exoccipital; fr, frontal; ip, interparietal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; par, parietal; pf, postfrontal; pmx, premaxilla; po, postorbital; pp, preparietal; prf, prefrontal; smx, septomaxilla; so, supraoccipital; sq, squamosal; tab, tabular.

length. The second tooth is considerably longer than the first, while there is a gradation in length from this tooth to the fifth tooth. The third tooth of the series is considerably thicker and heavier than the other teeth.

In these teeth the anteroposterior diameter is greater than the transverse diameter, and the front border of the tooth is rounded and recurved. The back border of the tooth, however, is compressed into a thin edge which is

rated as in the "incisor" teeth. In this tooth the striations of the enamel are particularly prominent.

The gorgonopsians as a group might be considered as the "saber-toothed" therapsids. Enlargement of the canines is characteristic of the Therapsida as a whole, but it is in the gorgonopsians (leaving out of consideration the highly specialized and rather aberrant dicynodonts) that this trend has reached the

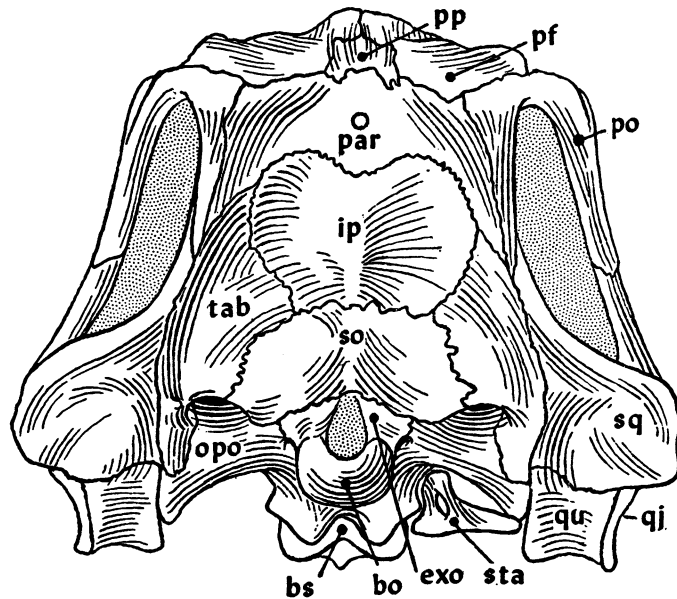


FIG. 3. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, skull. Occipital view, $\times \frac{1}{2}$, restored. Abbreviations: bo, basioccipital; bs, basisphenoid; exo, exoccipital; ip, interparietal; opo, opisthotic; par, parietal; pf, postfrontal; po, postorbital; pp, preparietal; qi, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; sta, stapes; tab, tabular.

approximately straight. This edge is finely serrated or denticulated, as shown in the enlarged figure (fig. 4). It might be pointed out here that Broom evidently failed to see the serrations on the teeth in *Lycaenops*, since he states that "there are apparently no serrations either on the front or posterior edges of the teeth" (Broom, 1930, p. 351). The surfaces of these teeth, as well as of the teeth behind them, are composed of longitudinally striated enamel.

The canine is a very large tooth, generally oval in cross section but with a sharp edge along the back surface, this edge finely ser-

maximum of its development. For in these reptiles not only is the tooth inordinately long, but the front part of the dentary has been deepened to form a protective flange for this tooth, an evolutionary development that is curiously prophetic of what was to take place quite independently at a later date in various lines of mammalian evolution. And of the gorgonopsians, *Lycaenops* appears to be among the most highly specialized genera with regard to this adaptation, comparable to such forms as *Sycosaurus*, *Inostrancevia*, and *Rubidgea*, in which canine enlargement has reached an extreme.

It might be said here that that part of the canine in *Lycaenops* embedded within the alveolus is much longer than the exposed portion of the tooth. In fact, the base of the tooth extends up through the height of the maxilla to a point near the junction of the maxilla with the nasal and prefrontal bones.

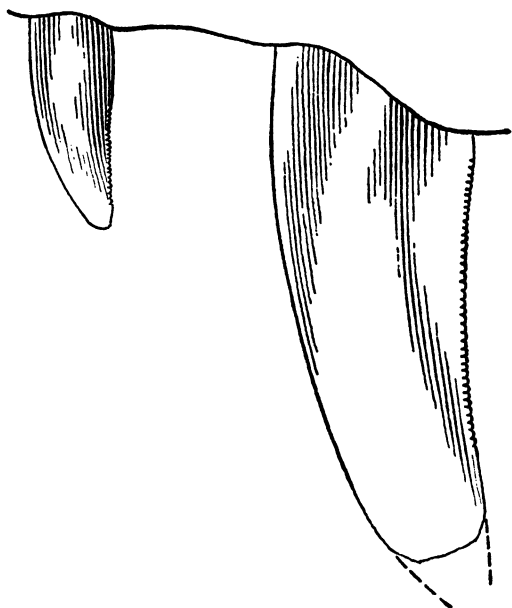


FIG. 4. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, fifth incisor (first maxillary tooth) and canine (second maxillary tooth) of left side. Lateral view, $\times 2$. This shows the serrations along the posterior edge of each tooth.

During the preparation of the specimen, the skull and mandible broke very cleanly across the muzzle behind the exposed part of the canine. This was a lucky accident for it exposed the implanted portion of the tooth, enabling a determination of its course as described above. Moreover, this break afforded us with a fine transverse section of the skull in this region, showing the relationships of the bones to one another and to the teeth. These are shown in figure 5.

Among other things, this break revealed on the left side the presence of a second canine tooth, apparently in the process of developing as a replacement for the functional canine. This replacing tooth is immediately beneath the functional canine, its point being just inside the alveolar border. It is quite

obvious that as growth proceeded this tooth would push forward and down to take the place of the canine now functional. Traces of the functional canine and its replacing tooth are to be seen on the opposite side of the skull, but because of the crushing of this side the break that has exposed these structures crosses near the utmost proximal end of the teeth, so that they are not well shown.

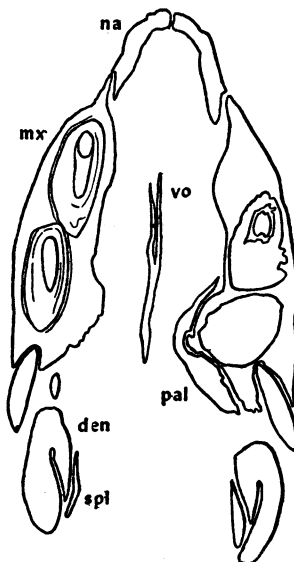


FIG. 5. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, cross section of the skull in the anterior portion, $\times \frac{1}{2}$. Abbreviations: den, dentary; mx, maxilla; na, nasal; pal, palatine; spl, splenial; vo, vomer.

Behind the canines are the four so-called "molars." These are the smallest of the teeth, and evidently were of no very great functional significance, in which respect *Lycaenops* is similar to other specialized gorgonopsians, such as *Aelurognathus*, *Lycaenoides*, and various other genera. These teeth are more nearly round in cross section than are the incisors, and it would seem that the posterior ridge is limited to the proximal portion of the tooth. Moreover, no serrations are to be seen on this ridge.

Evidently the dentition in *Lycaenops* was a biting, slashing mechanism. Animals of this genus, and most of the other specialized gorgonopsians as well, probably were very active hunters, seizing and killing their prey

with the sharp incisors and the long, saber-like canines. There must have been very little chewing of the food; rather it was probably torn into large pieces and swallowed whole.

THE SKULL ROOF

The prefrontal, a rather large and elongated bone, forms the anterodorsal border of the orbit. Its relationships with the bones around it have already been mentioned. The frontal bone is long, pointed in front, and it forms a small portion of the dorsal border of the orbit. Its upper surface is roughened and pitted, as was noted by Broom. Curiously, this roughening of the upper surface is confined largely to the frontals and does not extend in any degree to the other bones of the cranial roof, as might be expected.

Lycaenops, like most of the gorgonopsians, has a large preparietal bone, located at the back of the frontals and the front of the parietals and situated immediately in front of the pineal foramen. The preparietal in this genus appears to be an elongated bone, quite different in shape from the rather rounded preparietal characteristic of *Gorgonops* and of various other gorgonopsian genera. As Broom has shown, this bone is as broad anteriorly as it is posteriorly, so that it has the shape of a long rectangle.

The parietals, which are fused into one bone, are very broad in comparison to their length, probably exceeding in this detail the same bones in any of the other gorgonopsians. This is a correlative of the very broad intertemporal region in *Lycaenops*, in which genus the broadening of the cranial region of the skull, so characteristic of the gorgonopsians, has reached an extreme of development. On either side a long process of the parietal extends back above the temporal opening closely in contact with the postorbital and squamosal externally and the tabular medially. This posterior extension of the parietal will be discussed more fully below. The pineal foramen is small and is raised above the general level of the skull roof upon a small, rounded boss.

The postfrontal bone, a characteristic element in the gorgonopsians, is very large in *Lycaenops*. It forms the posterodorsal portion of the orbital border and extends posteromedially between the frontal and postorbital.

THE TEMPORAL REGION

The postorbital bone consists of two parts, a ventral portion forming the main part of the postorbital bar, and a posterodorsal portion forming the front part of the upper border of the temporal opening. These two processes, one extending down and one extending back, emerge from an expanded part of the bone which occupies the space immediately behind the postfrontal. The expansion of this dorsal horizontal portion of the postorbital is appreciably greater than indicated in Broom's figure of the dorsal surface of the skull (Broom, 1930, pl. 29, fig. 27). The posterior process of the postorbital is pointed, to meet the forwardly extending pointed process of the squamosal.

The squamosal, as seen from the side, is a semicircular bone enclosing the temporal opening posteriorly. Dorsally it extends forward to meet the posterior process of the postorbital, while posteromedially it is overlapped by the large tabular. Posteriorly the squamosal flares widely to form most of the posterior surface lateral to the occiput. This is a gorgonopsian character, well exemplified in the skull of *Gorgonops* itself, but it is probable that in no other member of the group is the posterior vertical surface of the squamosal so widely expanded as it is in *Lycaenops*. Indeed, one might say that this bone is dominant at the expense of the quadrate, which forms hardly more than the articulating surface for the lower jaw, beneath the squamosal. Ventrally the squamosal sends forward a long pointed process that is wedged into a sort of V-shaped slot in the posterior process of the jugal.

The quadratojugal in the specimen under consideration seemingly is quite small, as in other gorgonopsians.

The stapes is a rather short but heavy bone. Proximally the bone is expanded, with a ventral foot plate articulating into the fenestra ovalis and a prominent dorsal process extending up to a position beneath the median portion of the opisthotic or paroccipital bone. It is very probable that the dorsal process had an articulation with the prootic, as Romer has shown for the pelycosaur, but owing to the crushing which the specimen has undergone this point cannot be definitely determined. There is a well-defined stapedia

foramen. Distally the bone is expanded at right angles to its proximal expansion, so that it terminates in a sort of broad, double prong. This distal end of the bone would seem to rest against the inner surface of the quadrate, and it is likely that there was a cartilaginous extra-stapedial process connecting this expanded end of the stapes with the tympanum. There may have been also an elastic ligament forming a connection between the quadrate and that portion of the

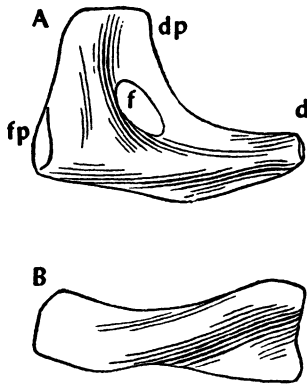


FIG. 6. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, stapes. A. Posterior view. B. Ventral view. Both $\times 2$. Abbreviations: d, distal end of stapes; dp, dorsal process; f, stapedial foramen; fp, proximal portion of stapes that fitted into the fenestra ovalis.

distal end of the stapes which may be homologized as the internal process. Romer suggests a relationship of this sort for *Dimetrodon*.

It is interesting to see the general correspondence between the stapes of *Lycaenops* and the stapes of "gorgonopsian B," described and figured by Olson. The main differences are that in *Lycaenops* the dorsal process is much larger and more pronounced than in "gorgonopsian B," while the internal and external processes of the distal end of the bone are less clearly differentiated than they are in "gorgonopsian B." In these respects the stapes of *Lycaenops* and of the other known gorgonopsians seem to be considerably different from the stapes of *Lystrosaurus*, as recently described by Parrington (1946). In this latter genus the stapes is short and heavy, without a proximal dorsal process and

without a stapedial foramen. On the other hand, there is a strong distal process (designated by Parrington as the "dorsal process") in the stapes of *Lystrosaurus* which appears to have been in contact with the outer end of the opisthotic. Thus, according to Parrington: "This brings the dorsal half of the distal end [of the stapes] opposite the space below the posterior extension of the vertical component of the squamosal. The tympanum must therefore be presumed to have been stretched across this space, in which case it was carried by the squamosal and the quadrate" (Parrington, 1946, p. 629).

THE OCCIPUT

The new, corrected drawing of the occiput of *Lycaenops* brings out in a very striking manner the depth of the skull as seen in this aspect. Indeed, as shown by figure 3, the occiput of this therapsid has a rather definite pelycosaurian appearance by reason of its depth, a fact that perhaps has not been previously appreciated.

On the occipital surface of the skull the interparietal is very large, a gorgonopsian character, and it forms the median dorsal element of the occipital complex. The supraoccipital bone in *Lycaenops* is both broad and high. In this respect it is shaped somewhat differently from the same bone in *Gorgonops*, and it reflects the relatively deep skull of *Lycaenops* as compared with most of the other genera of Gorgonopsia.

The tabulars, forming on either side the outer portions of the occiput, are very large bones. Each tabular articulates laterally with the squamosal and with the posterior process of the parietal, and medially with the interparietal and supraoccipital while ventrally it sends down a process that abuts against the outer end of the opisthotic. At the junction of the tabular, supraoccipital, and opisthotic there is a very large foramen.

The occiput of *Lycaenops* shows a very characteristic gorgonopsian feature in that it slopes strongly forward from the occipital condyle to the skull roof. This slope is so marked in *Lycaenops* and in other gorgonopsians that it results in the occipital surface being depressed with relation to the upper and posterior borders of the lateral temporal fenestrae. Consequently the tabular bone on

the occipital surface, together with the squamosal, postorbital, and the posterior process of the parietal, forms a wall enclosing on either side the depressed occipital region and looking laterally into the temporal fenestra. This development is well shown in the American Museum skull of *Gorgonops torvus*, A.M.N.H. No. 5515, and is particularly striking in the type skull of *Lycaenoides angusticeps*, A.M.N.H. No. 5537. In this latter skull the effect is accentuated by the lateral crushing to which the skull has been subjected; nevertheless, there can be no doubt that in the normal skull of this particular animal the occiput was very much depressed ventrally and anteriorly so that a good half of the diameter of the temporal fenestra is entirely *behind* the occipital surface.

In this connection it might be said that the extreme depression of the occiput in *Lycaenoides* was not recognized until recently, when the skull received some additional preparation that revealed this character. Originally the area between the upper and posterior borders of the temporal fenestrae was filled with matrix, and it had been assumed that the occipital surface was but a short distance beneath the matrix. Preparation of the skull revealed quite a different configuration of the occiput than what had been assumed, a striking example of the importance of complete preparation of fossil materials.

The exoccipitals, forming the lateral walls of the foramen magnum, are quite small. On the outer side of the occipital condyle, between the exoccipital and the opisthotic, is a foramen that served for the exit of the ninth, tenth, and eleventh cranial nerves.

THE BASICRANIUM AND PALATE

The single occipital condyle is formed by the basioccipital, which extends anteriorly to form a portion of the floor of the endocranial cavity. In front of the condyle, on either side, this bone is expanded into a pair of prominent basilar tubercles that served as strong attachments for some of the muscles of the rectus capitis group. These tubercles are continued forward on the next bone, the basisphenoid, a bone broad at the back and carrying the strong basilar tubercles, already mentioned,

but tapering rapidly anteriorly into a thin median ridge. This ridge is inserted into the large and complex pterygoid.

The paired pterygoids are prominent bones in the ventral view of the *Lycaenops* skull, as they are in *Gorgonops* and other related genera. Particularly characteristic of the pterygoids are the large lateral flanges, which served to limit the motion of the lower jaw to a dominantly orthal plane.

It is not possible to make out with any degree of satisfaction other particulars with regard to the palate in *Lycaenops*, but there is every reason to think that this region, and the basicranium as well, are essentially similar in *Lycaenops* to the same regions in *Gorgonops*. The ventral view of the *Gorgonops* skull has been figured by Boonstra (1934) from a very fine skull in the American Museum of Natural History collection. The reader is referred to this figure for the details of structure of the gorgonopsian basicranium and palate.

THE MANDIBLE

As mentioned above, the lower jaw is deep in front, its vertical growth being an adaptation correlated with the large size of the canine teeth, for which it affords a protecting structure. With this great depth in the front portion of the lower jaw, the symphysis is strong, as might be expected. Consequently, the splenial is strong, but so far as can be determined, it is not greatly extended posteriorly.

According to Broom, the lower jaw agrees posteriorly with that of other gorgonopsians, and this would certainly seem to be the case. For instance, the dentary is enlarged as in other gorgonopsians and as in the therocephalians, but it has not reached the extreme enlargement so characteristic of the cynodonts. Therefore, the bones behind it are well developed.

These consist in part of a large angular, and above it a surangular of rather limited extent. The articular seemingly is limited to the region of the articulation, as in other gorgonopsians. On the inner side of the jaw, in front of the articular, is the prearticular, an elongated, thin bone, the anterior extent of which it is not possible to determine with certainty.

ADAPTIVE RADIATION IN THE SKULL OF THE GORGONOPSIA

It is intended in the preceding description and figures to give a rather comprehensive picture of the skull, jaw, and teeth in the gorgonopsian reptile *Lycaenops ornatus*. This leads us now to the large and rather difficult question of the relationships of this form to other gorgonopsians from the Karroo beds of South Africa and from other regions as well.

To say that it is a difficult question does not exaggerate the case. The Karroo system is a thick and complex series of sediments, and in those portions containing gorgonopsian remains, namely, the *Tapinocephalus*, *Endothiodon*, and *Cistecephalus* zones of the Lower Beaufort beds, there are involved many thousands of feet of continental deposits through which fossil gorgonopsians occur at various levels. As a result of discoveries and studies made upon these fossils during past years a considerable number of genera and species have been named and described. And in this multiplicity of forms it is difficult to draw really valid conclusions as to taxonomic relationships, synonymies, and the like.

One certainly gets the impression that there has been an undue multiplication of genera and species, that many of the described forms have been differentiated upon small and relatively insignificant differences. Moreover, there can be no doubt that other species have been based upon evidence that is entirely insufficient. On the other hand, how is one to evaluate the differences seen in fossils that are separated by many hundreds of feet, or even thousands of feet, of sediments? In view of wide vertical separations, are small differences to be given considerable weight in the delineation of species, or are these differences to be lightly regarded, upon the assumption that many forms of generic or even specific rank may have extended over a large vertical range? And in this connection, how much of a time lapse is represented by the sediments of any particular zone in the Karroo system? These are questions to which truly objective answers are difficult to find. Much depends upon the personal bias of the student, so that the results of any given study represent to a large degree the philosophical background and the outlook of the man making the study. Perhaps a brief review of

the South African gorgonopsians may be useful in the present approach to this problem.

The Gorgonopsia of the Karroo system, as said above, are found in the three zones comprising the Lower Beaufort beds. They are not found below the *Tapinocephalus* zone in the Upper Ecca beds. This is not particularly significant, because the Ecca beds are very barren, and fossils are indeed rare in these sediments. At the other end of the scale, the gorgonopsians do not persist beyond the *Cistecephalus* zone, because in the succeeding horizon, the *Lystrosaurus* zone, they are replaced by the more advanced cynodonts. Here it would seem obvious that we see the results of extinction, the disappearance of a phyletic line showing many specializations because of encroachments by a still more highly specialized phyletic line.

The distribution of the Gorgonopsia through the three zones of the Lower Beaufort beds can be represented as in table 1.

This is a formidable list of genera, even though they be distributed vertically through some 5000 feet of sediments. Just how much synonymy and bad taxonomy is involved here it is difficult to say. To arrive at any kind of solution of this problem would involve a protracted study of the various collections which contain gorgonopsians, and even then the solution would be far from satisfactory.

Comparing *Lycaenops* with the large and, one must admit, confusing array of gorgonopsians leads to the conclusion that this genus is a fairly typical representative of the family. It occupies a rather central position in the group, as regards not only its morphological structure but also its stratigraphic position. It is certainly advanced beyond the small primitive forms of the *Tapinocephalus* zone, exemplified by such genera as *Eoarctops* and *Galesuchus*. It is not aberrantly specialized as in the case of some genera such as *Ictidorhinus* from the upper portion of the Lower Beaufort beds. In size it is certainly more or less intermediate between the smaller gorgonopsians and the very large forms such as *Gorgonognathus*.

Yet in spite of its rather central position in the Gorgonopsia, both morphologically and

TABLE 1
STRATIGRAPHIC OCCURRENCES OF THE GORGONOPSIA IN THE LOWER BEAUFORT BEDS

	<i>Tapinocephalus</i> Zone	<i>Endothiodon</i> Zone	<i>Cistecephalus</i> Zone
<i>Aelurognathus</i>		X	X
<i>Aelurosauroides</i>		X - - - - -	X ^a
<i>Aelurosaurus</i>		X	
<i>Aloposaurus</i>		X	
<i>Arctognathoides</i>		X - - - - -	X
<i>Arctognathus</i>			X
<i>Arctops</i>		X	
<i>Broomisaurus</i>	X		
<i>Cerdognathus</i>			X
<i>Cerdorhinus</i>		X - - - - -	X
<i>Chiwetasaurus</i>		X - - - - -	X
<i>Cynarioides</i>		X	
<i>Cynariops</i>		X	
<i>Cyniscodon</i>	X		
<i>Cyniscops</i>		X - - - - -	X
<i>Cynodraco</i>		X	
<i>Cyonosaurus</i>			X
<i>Delphaciognathus</i>			X
<i>Dinogorgon</i>		X - - - - -	X
<i>Dixeya</i>		X - - - - -	X
<i>Eoartops</i>	X		
<i>Eriphostoma</i>	X		
<i>Galerhinus</i>		X - - - - -	X
<i>Galerhynchus</i>		X - - - - -	X
<i>Galesuchus</i>	X		
<i>Gorgonognathus</i>		X	
<i>Gorgonops</i>		X	
<i>Gorgonorhinus</i>		X - - - - -	X
<i>Hipposaurus</i>	X		
<i>Iclidorhinus</i>			X
<i>Leontocephalus</i>		X - - - - -	X
<i>Leptotrachelus</i>		X	
<i>Lycaenodon</i>			X
<i>Lycaenodontoides</i>		X - - - - -	X
<i>Lycaenoides</i>			X
<i>Lycaenops</i>		X	
<i>Pachyrhinos</i>	X		
<i>Prorubidgea</i>		X - - - - -	X
<i>Rubidgea</i>		X - - - - -	X
<i>Scylacognathus</i>		X	
<i>Scylacops</i>		X	X
<i>Scymnognathus</i>		X	
<i>Sycosaurus</i>			X
<i>Tetraodon</i>		X - - - - -	X

* The dashes indicate that the published data are not sufficiently exact to limit the genus in question to the one or the other of the two zones. Undoubtedly some of these genera were so limited in vertical extent, while others may have ranged through both zones.

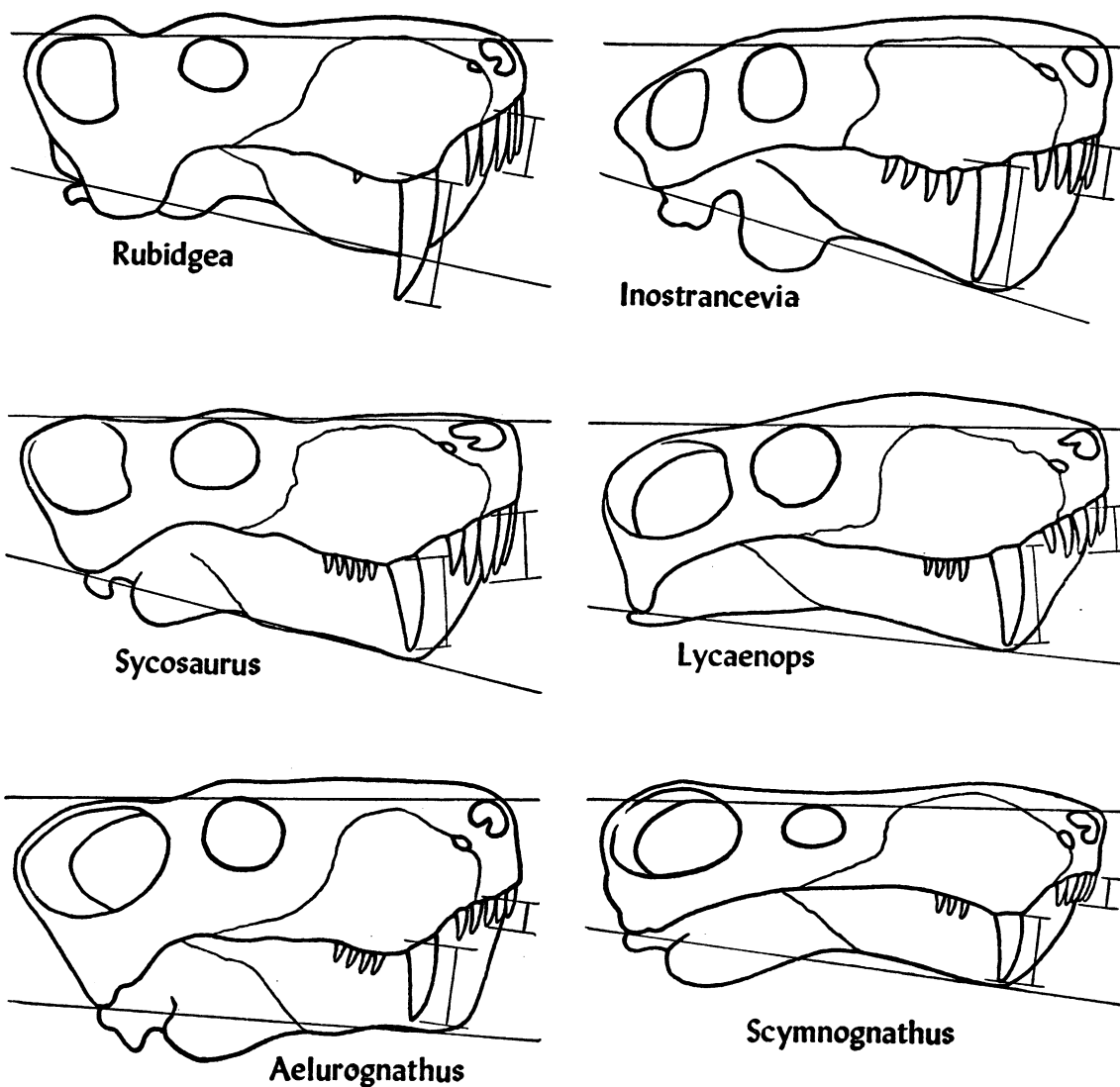


FIG. 7. Comparison of the skull and mandible in certain genera of Gorgonopsia. All drawings reduced to unit length. This shows the relative lengthening of the canine tooth, the relative increase in size of the incisor teeth, and the relative depth of the anterior portions of the skull and mandible, correlative with the development of the anterior teeth.

stratigraphically, *Lycaenops* shows certain specializations that indicate it to be one of the more advanced members of the family. As shown in the skull and jaw, these specializations are, particularly, the relatively great depth and narrowness of the muzzle or anterior portion of the skull, as compared with the unusual breadth of the parietal region.

The narrowness and depth of the muzzle in

Lycaenops are correlated with the development of an especially large canine tooth, making this animal, as pointed out above, one of the "saber-toothed" gorgonopsians. It has reached almost an extreme of development in the family with regard to this character, exceeded in this respect probably only by the genera *Sycosaurus* and *Rubidgea* of South America and by *Inostrancevia* from

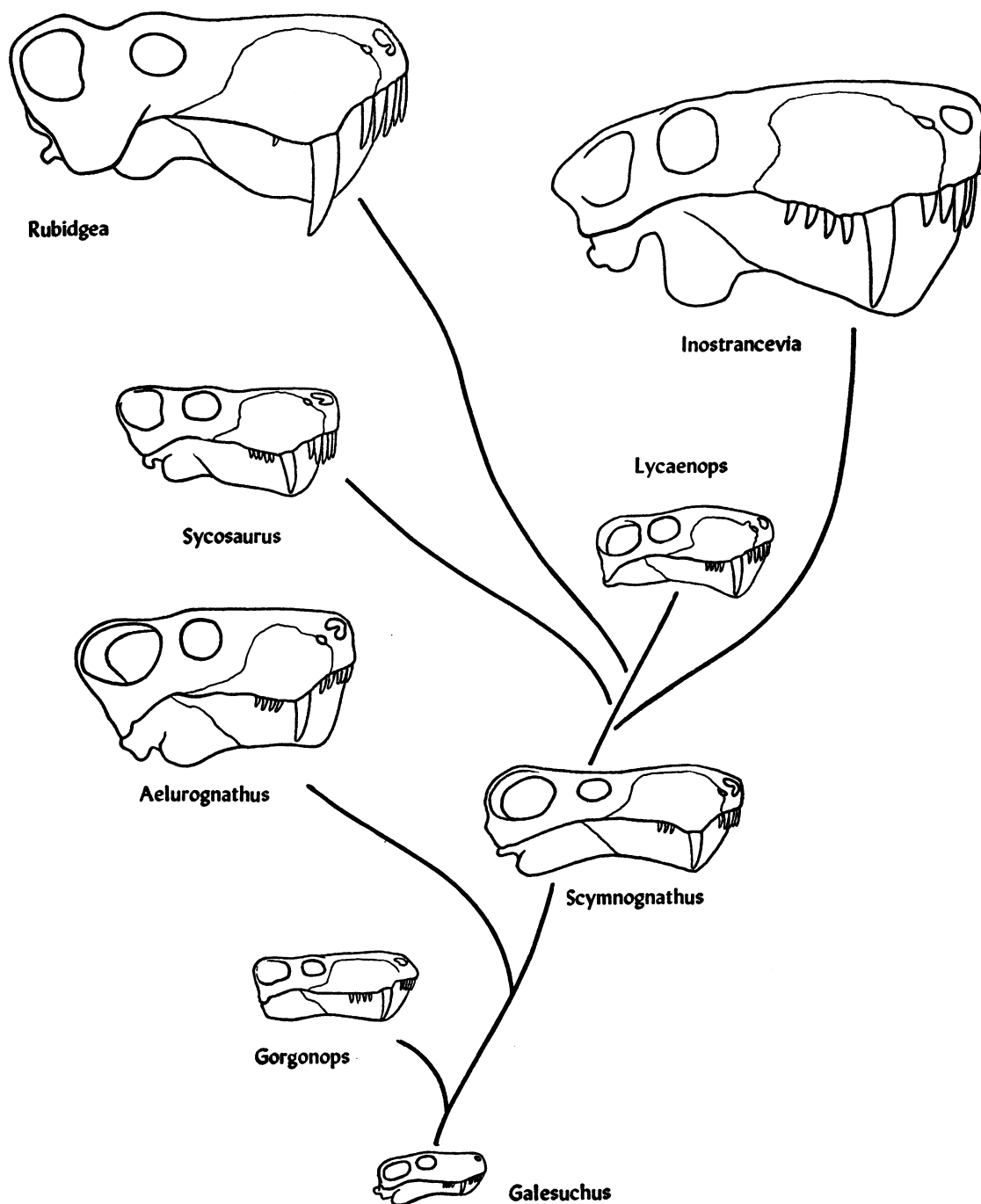


FIG. 8. Suggested phylogenetic relationships of certain genera of Gorgonopsia. All drawings $\times \frac{1}{2}$.

Russia. Since the hypertrophy of the canines with the consequent deepening of the front part of the lower jaw is more advanced in

Inostrancevia and *Rubidgea* than in any of the other saber-toothed gorgonopsians, it would seem logical to regard these giant forms as

representing culminations of this particular line of specialization within the family. Various other gorgonopsians, such as *Aelurognathus* and *Scymnognathus*, while showing a considerable degree of emphasis of the canine teeth are less extremely specialized in this respect than the genera discussed above.

This development of the saber-like canines in *Lycaenops*, *Sycosaurus*, *Rubidgea*, and *Inostrancevia* is further shown by a comparison of the front part with the back part of the skull and jaw in each of these four genera. In these genera the depth of the skull and mandible together in the region of the canine teeth is considerably greater than the depth of the skull and mandible in the temporal region. This is not true of such forms as *Aelurognathus* and *Scymnognathus*, in which these two measurements are essentially equal.

Accompanying the development of the large, saber-like canines in these several genera of gorgonopsians, there has been to a limited degree an enlargement of the incisor

teeth. The correlation here is not complete, because in some of the more primitive gorgonopsians, in which the canine teeth are not so greatly hypertrophied, the incisors are also frequently enlarged. Yet it is a fact that in *Lycaenops*, *Sycosaurus*, and *Inostrancevia*, and especially in *Rubidgea*, the incisors do show an unusual degree of enlargement that can be logically correlated with the development of the saber-tooth habitus.

The "molar" teeth in *Lycaenops* are reduced in number to four, and they are relatively small, but this development cannot be correlated in any certain way with the specialization of the rest of the dentition. The reduction of the postcanine teeth seems to be a general and characteristic development in the Gorgonopsidae, and it can be traced through many of the genera from the less specialized to the more specialized forms, occurring at various levels in the Lower Beaufort beds. In this respect it might be noted that in *Rubidgea*, perhaps the most completely saber-toothed gorgonopsian, the postcanine den-

TABLE 2
COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF THE SKULL, MANDIBLE, AND TEETH

	<i>Lycaenops</i> A.M.N.H. No. 2240	<i>Gorgonops</i> A.M.N.H. No. 5515	<i>Gorgonops</i> ^a B.M.N.H. No. R1647	<i>Lycaenoides</i> A.M.N.H. No. 5537	<i>Scymnognathus</i> (From Broili and Schröder)	<i>Aelurognathus</i> ^a S.A.M. No. 9344
SKULL						
Length, premaxillary-basioccipital	190 (approx.)	246	210	280	270	197
Length, premaxillary-orbit	115	126	111	163	—	105
Width, snout	60	66	60	—	—	60
Width, intertemporal	56	56	68?	—	—	56
Width, quadrates	118	160	—	—	—	99?
Height, snout	66	57	50	90	—	63
Height, occiput	65	54	45	—	—	66
MANDIBLE						
Length	177	—	—	248	—	180?
TEETH (UPPER)						
Length, incisor series	33	31	34	37	34	—
Length, molar series	21	—	—	—	22	9
Length of crown, third incisor	16	—	—	21	—	—
Length of crown, canine	33	—	—	34	—	—
Length of crown, first molar	11	—	—	—	—	—

^a From Boonstra. S.A.M., South African Museum.

tition has been reduced to a single small tooth on either side.

The breadth of the intertemporal region is in great contrast to the narrowness of the nasal region in *Lycaenops*. In this character *Lycaenops* approaches but by no means equals the very highly specialized *Rubidgea*. Certainly in no other gorgonopsians are the parietal bones so broad in comparison with their anteroposterior diameters as in these two

is to be seen in the genus *Sycosaurus*. In both of these genera the temporal region of the skull is quite broad in comparison with the nasal region.

If Broom is correct in his interpretation of the skull of *Sycosaurus*, it is unique in the lack of a preparietal bone. In *Lycaenops* the preparietal is a large and elongated bone, and the same is true in *Inostrancevia*. The bones of the skull roof evidently are so completely

TABLE 3
COMPARATIVE RATIOS AND INDICES OF THE SKULL AND TEETH

	<i>Lycaenops</i>	<i>Gorgonops</i> A.M.N.H.	<i>Gorgonops</i> B.M.N.H.	<i>Lycaenoides</i>	<i>Aelurognathus</i>
$\frac{\text{Snout length}}{\text{Skull length}} \times 100$	61	51	53	58	53
$\frac{\text{Occipital height}}{\text{Snout height}} \times 100$	99	95	90	—	95
$\frac{\text{Quadrate width}}{\text{Skull length}} \times 100$	62	65	—	—	50?
$\frac{\text{Intertemporal width}}{\text{Skull length}} \times 100$	29	23	—	—	28
$\frac{\text{Third incisor}}{\text{Canine}} \times 100$	48	—	—	62	—

genera. *Inostrancevia*, in spite of the great specializations in the front part of the skull and jaws, has a comparatively narrow intertemporal region with elongated parietals, in which respect it resembles some of the more generalized forms such as *Gorgonops*. Except for *Rubidgea*, the nearest approach to this broadening of the parietal bones in *Lycaenops*

coalesced in *Rubidgea* that their boundaries cannot be determined.

So far as the characters of the skull, jaws, and dentition are definitive, the general phyletic relationships of *Lycaenops* to various other gorgonopsian genera may be represented as shown in figure 8.

THE VERTEBRAE AND RIBS

As listed on a preceding page, except for the left half of the atlas arch and the atlantal intercentrum, the cervical vertebrae are missing in this specimen of *Lycaenops*. There are, however, 20 presacral vertebrae preserved in series, and if a sharp distinction is to be made between cervicals and dorsolumbars in the therapsids, the first of these 20 vertebrae may be regarded as the first dorsolumbar vertebrae.

Moreover, since seven vertebrae have been designated as cervicals in other genera of gorgonopsians, such as *Aelurognathus*, *Hipposaurus*, and *Arctognathoides*, it is reasonable to assume that there was a like number in *Lycaenops*. This, therefore, would make a total of 27 presacral vertebrae in this genus, as compared with 26 presacrals in *Inostrancevia*, 27 in *Scymnognathus*, and 28 in *Hipposaurus*.

In this connection, the vertebral formulae as known for several genera of gorgonopsians may be compared as follows:

	CERVICALS	DORSO- LUMBARS	PRESACRALS	SACRALS	CAUDALS
<i>Lycaenops</i>	7 (est.)	20	27	3	—
<i>Aelurognathus</i>	7	—	—	3	—
<i>Scymnognathus</i>	7	20	27	3	—
<i>Hipposaurus</i>	7	21	28	3	26 +
<i>Arctognathoides</i>	7	—	—	—	—
<i>Inostrancevia</i>	7	19	26	4	12 +

As in other Gorgonopsia, the atlantal arch is in two halves, a contrast to the fusion of the atlantal arch into a single structure in the Cynodontia. The atlantal arch in *Lycaenops* (shown in the present specimen by the left half), while generally similar to the same element in other gorgonopsians, differs in certain details of structure so that it is distinctive. Indeed, of the several genera in which the atlas is known, each seems to differ from the others in the shape and the detailed structure of the atlantal arch, a fact that is made clear by a comparative figure (fig. 9). In *Lycaenops* there is no posteriorly extended

lateral spine, as is the case in *Scymnognathus*, *Aelurognathus*, and *Arctognathoides*.

On the lateral surface of the arch there are

two ridges, one directed posterodorsally from the middle region of the bone, the other directed posteroventrally and terminating in the atlantal diapophysis. The condition is made clear by the figure, referred to above. In this respect the atlantal arch of *Lycaenops* differs from the same element in other gorgonopsians, all of which appear to have smooth lateral surfaces.

As would be expected, the atlantal inter-centrum is crescentic, with its anterior articular surface so shaped as to fit closely against the ball-like occipital condyle. The posterior articulating surface, which abuts against the odontoid, is essentially flat, and at its lateral extremities are the small parapophyses.

The dorsolumbar vertebrae are all approximately equal in size. This uniformity is confined not only to size, but it extends also to the general proportions and the structure of these vertebrae, with the result that in most respects they are but little differentiated from one another.

The centra are somewhat compressed; consequently at the ends the vertical dimension exceeds the horizontal dimension, a condition that is well shown in the relatively uncrushed first and second dorsolumbars. There are changes in proportions from the front of the presacral series to the back, so that in the last presacral vertebra the articulating surfaces of the centra are approximately round, as viewed either anteriorly or posteriorly. In the middle region the centra are strongly constricted, and as seen from below each centrum has the "hour-glass" outline typical of many reptiles.

The articulating surfaces are very slightly concave, in which respect *Lycaenops* resembles other gorgonopsians.

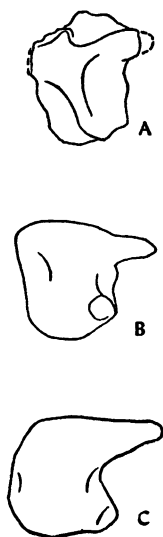


FIG. 9. Comparison of the left atlantal arches in three genera of Gorgonopsia. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240. B. *Aelurognathus microdon* Boonstra, after Boonstra. C. *Arctognathoides breviceps* Boonstra, after Boonstra. Lateral views, all $\times \frac{1}{4}$.

According to Broom "there is only slight evidence of one or two intercentra, but possibly very feebly developed intercentra may have been present between all the vertebrae" (Broom, 1930, p. 352). The indications are that there were very small intercentra between a few of the anterior dorsolumbar vertebrae, but these soon disappear in following the vertebral series caudad. Indeed, it would seem that there are no intercentra behind the fourth or fifth dorsolumbar vertebrae.

The neural spines are relatively short and weak, whereby *Lycaenops* differs markedly from other gorgonopsians in which the vertebrae are well known. For instance, the tallest preserved spine in *Lycaenops*, that of the twelfth dorsolumbar vertebra, is slightly shorter than the vertical diameter of the centrum in the same vertebra. At the same time the anteroposterior diameter of the spine near its base is but slightly greater than half the length of the centrum in the same vertebra.

In *Scymnognathus*, as figured by Broili and Schröder, the spines are generally at least twice the vertical diameters of the centra, while anteroposteriorly their measurements almost equal the length of the centra. In *Aelurognathus*, as figured by Boonstra, the spines are tall and heavy, each spine being more than twice the height of the centrum to which it is attached, while its anteroposterior diameter is equal to that of the centrum. In *Arctognathoides* the spines are heavy, but apparently not so tall as in *Aelurognathus*. In *Inostrancevia* the spines are tall and robust, as would be expected in a large, heavy animal.

The transverse processes are well developed in *Lycaenops*, and they are placed rather high, on a level with the top of the neural canal. The base of each process arises from the side of the neural arch, mostly anterior to the spine, and from this base the process projects horizontally and posterolaterally. Each process is terminated by an articular surface, the diapophysis.

In front of and behind each transverse process there are parapophysial facets on the side of the centrum. These facets, which are paired on adjacent vertebrae, form large articular surfaces for the heads of the ribs. It is

evident that the ribs were double-headed throughout most of the dorsolumbar series, articulating with both the parapophyses and the diapophyses, for a diapophyseal facet is

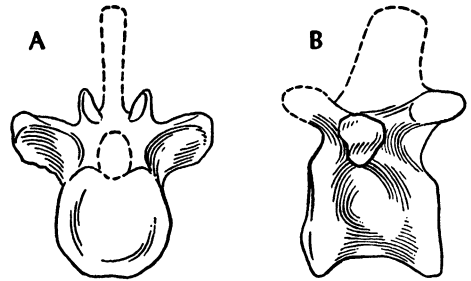


FIG. 10. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, eighth presacral (first dorsolumbar) vertebra. A. Anterior view. B. Left lateral view. Both $\times \frac{1}{2}$.

to be seen on the seventeenth dorsolumbar vertebra. It is quite possible that the last four ribs were single-headed, articulating only on the parapophyses; indeed, there is the proximal end of a single-headed rib in the

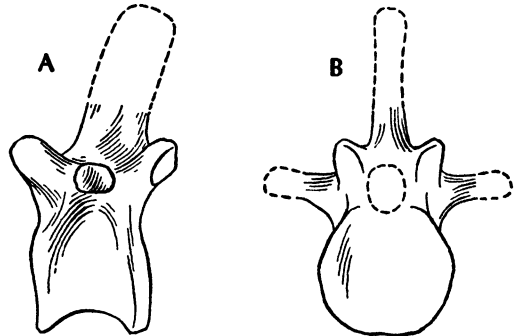
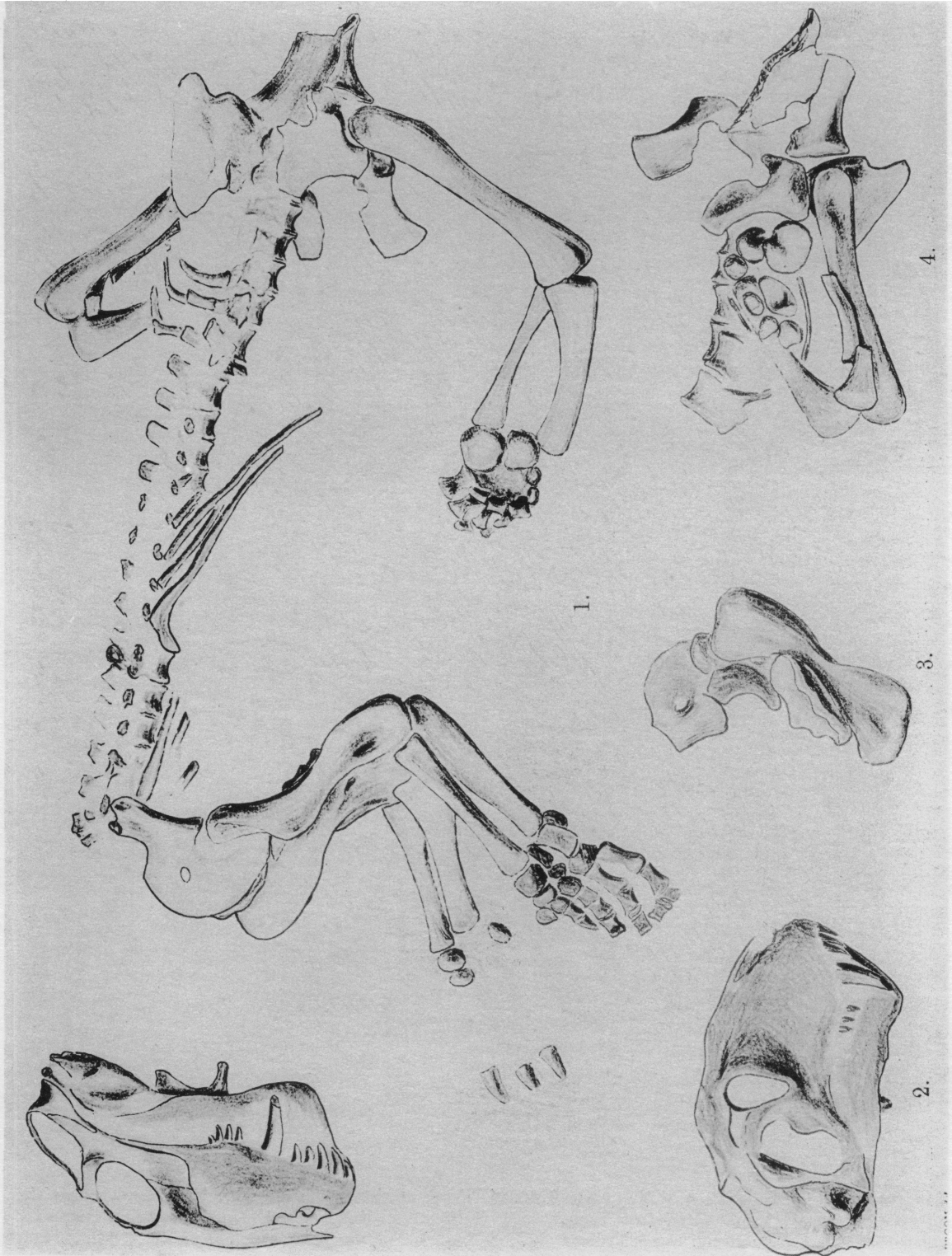


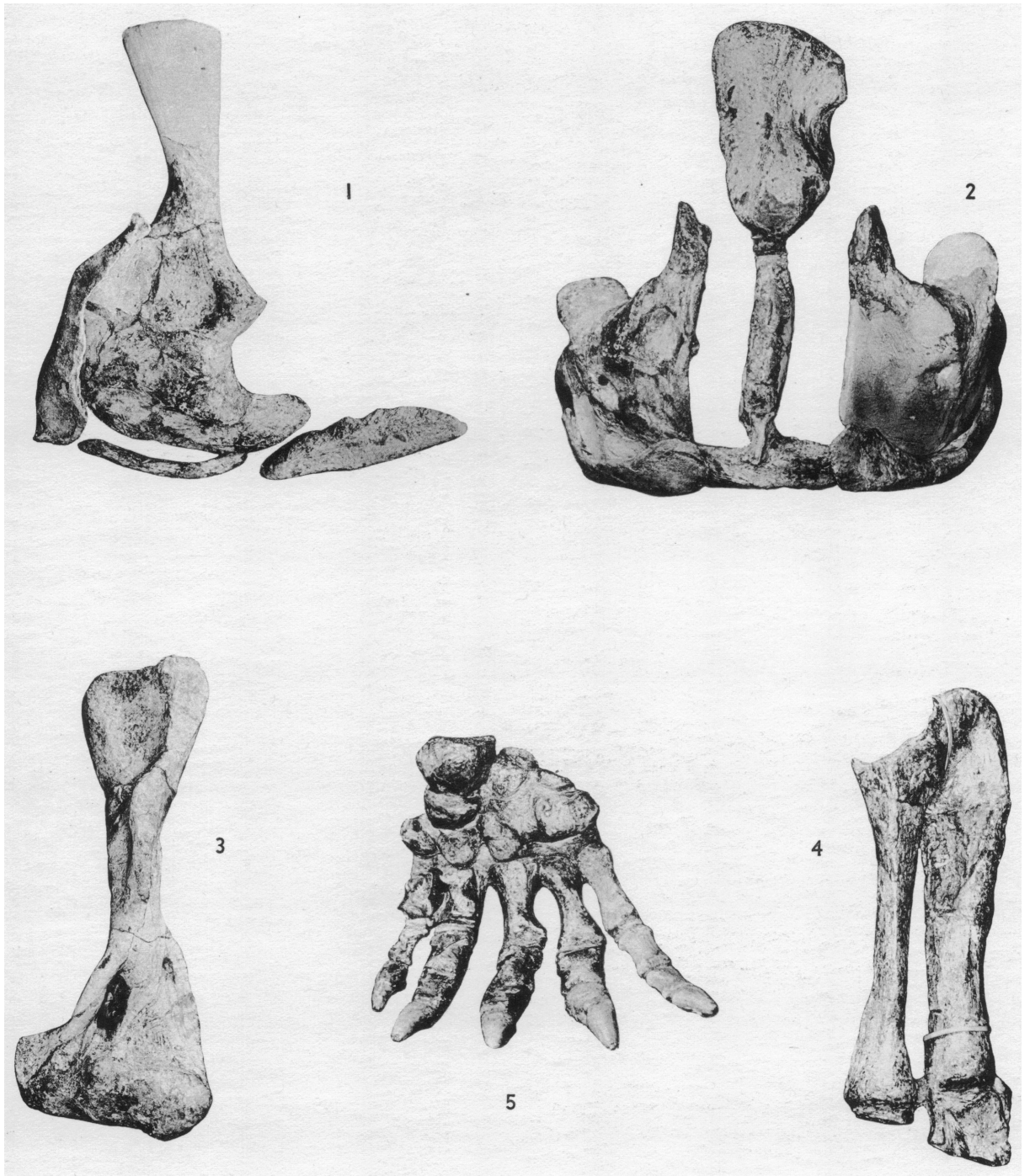
FIG. 11. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, last presacral vertebra. A. Left lateral view. B. Posterior view. Both $\times \frac{1}{2}$.

materials at hand. It is certain that the ribs did continue all the way back to the pelvis, a point concerning which there was some doubt in the mind of Boonstra.

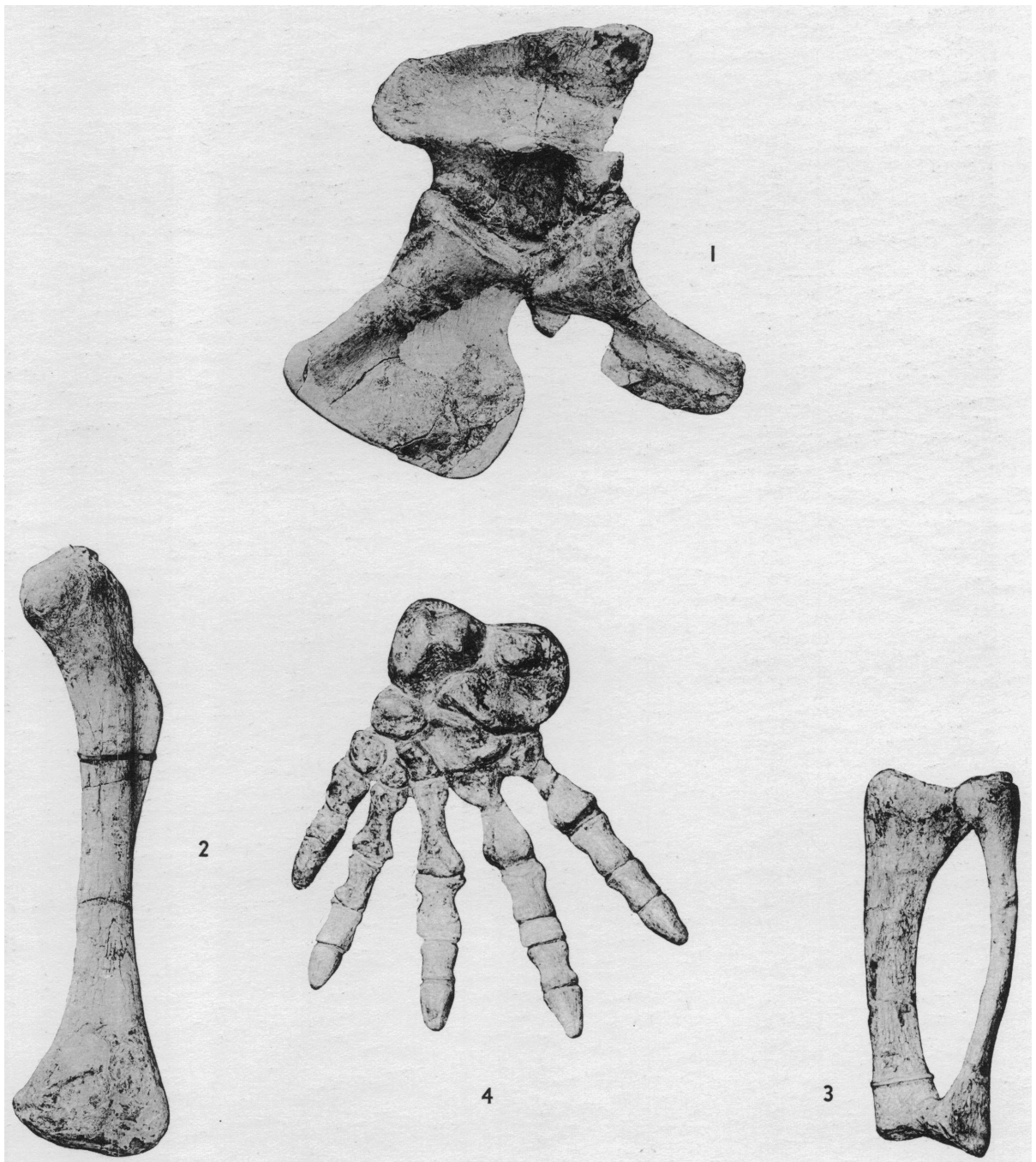
"Although Broom, in his reconstruction of *Lycaenops* (Mammal-like Reptiles, fig. 45), figured ribs right up to the sacrum, I am inclined to think that in the Gorgonopsia the vertebrae immediately anterior to the sacrum carried no ribs. This would be in harmony



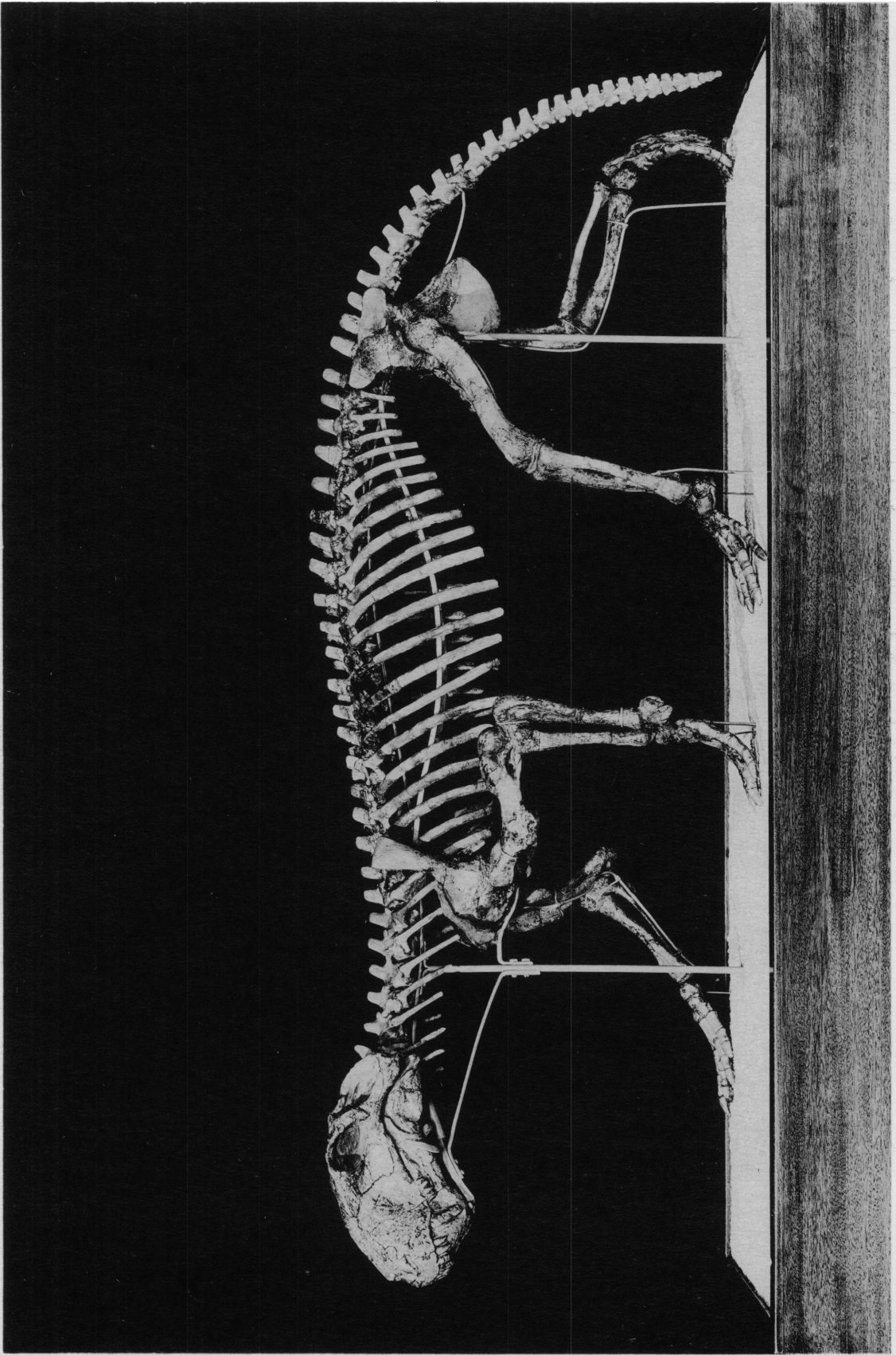
Lycenops ornatus Broom. A.M.N.H. No. 2240. From Broom, 1930, plate 27. 1. Skeleton, as found. About $\times \frac{1}{4}$. 2. Right side of the skull. 3. Remains of the shoulder girdle, sternum, and right humerus, as found. 4. Pelvis with right hind limb, as found



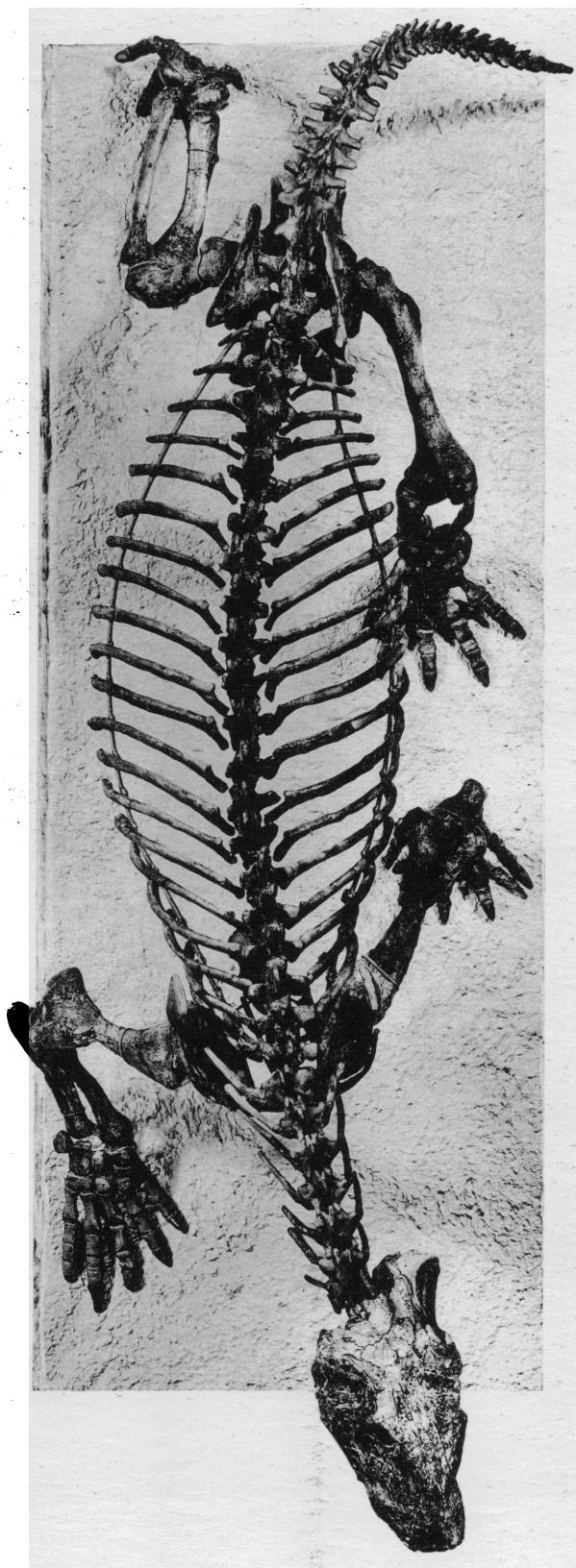
Lycenops ornatus Broom. A.M.N.H. No. 2240. 1. Pectoral girdle showing scapula, coracoids, clavicle, interclavicle, and sternum. Left lateral view, $\times \frac{1}{2}$. 2. Pectoral girdle, showing both scapulae, coracoids, clavicles, interclavicle, and sternum. Ventral view, $\times \frac{1}{2}$. 3. Left humerus, ventral view, $\times \frac{1}{2}$. 4. Left radius and ulna, lateral view, $\times \frac{1}{2}$. 5. Left manus, dorsal view, $\times \frac{1}{2}$



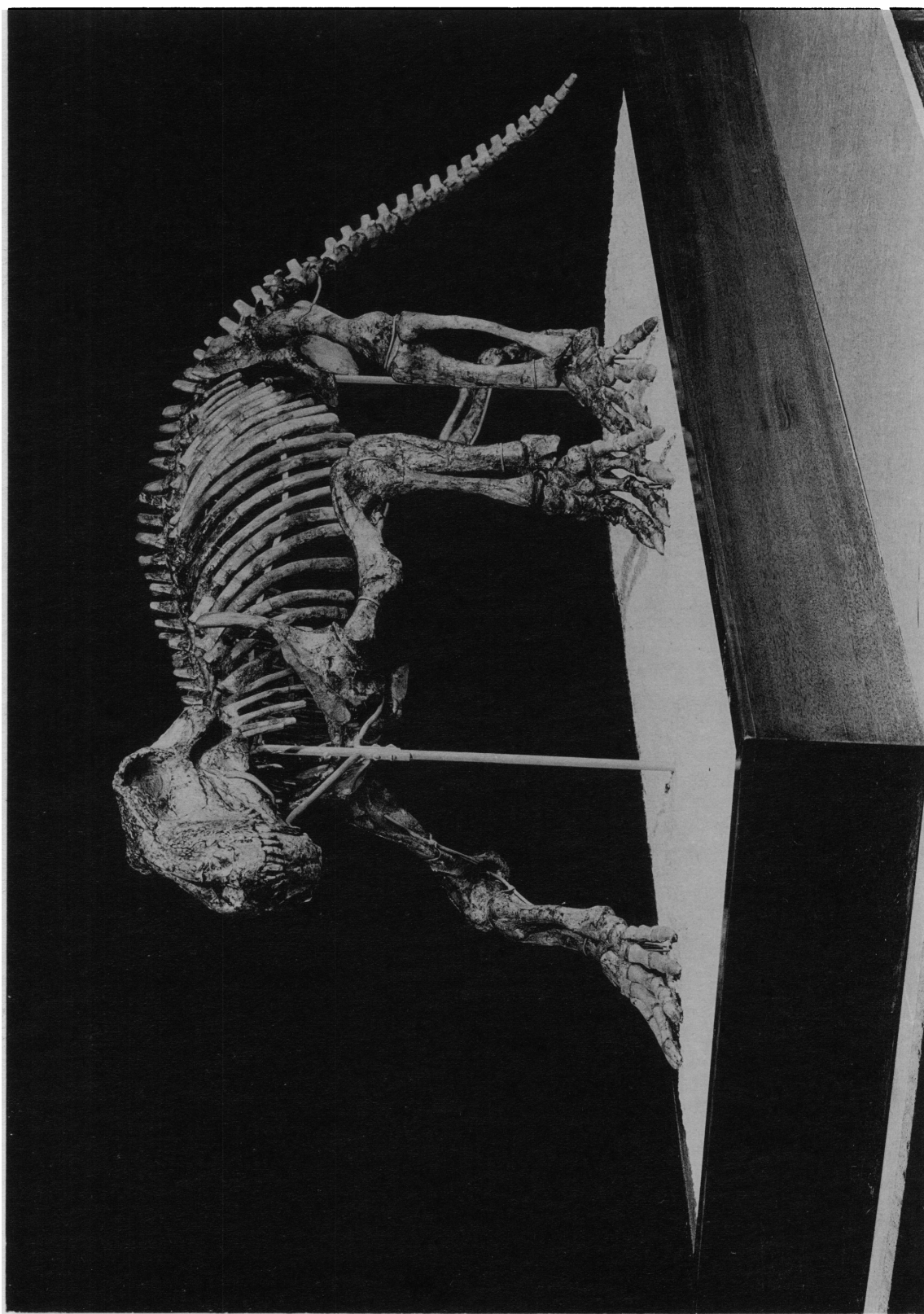
Lycanops ornatus Broom. A.M.N.H. No. 2240. 1. Pelvis, lateral view of right side, $\times \frac{1}{2}$. 2. Left femur, dorsal view, $\times \frac{1}{2}$. 3. Left tibia and fibula, anterior view, $\times \frac{1}{2}$. 4. Left pes, dorsal view, $\times \frac{1}{2}$



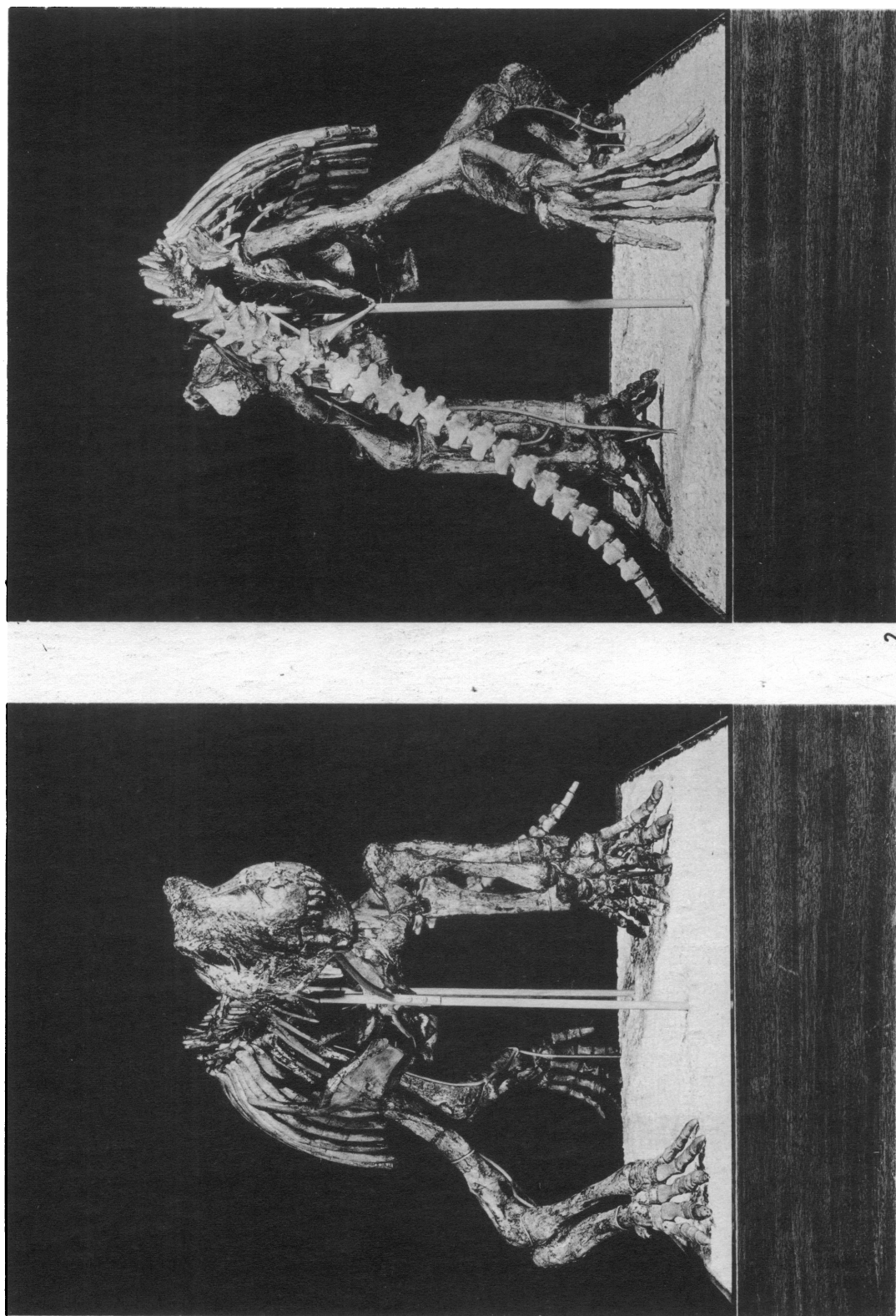
Lycanopsis ornatus Broom. A.M.N.H. No. 2240, skeleton as mounted by Charles Lang. Lateral view of left side, $\times \frac{1}{6}$



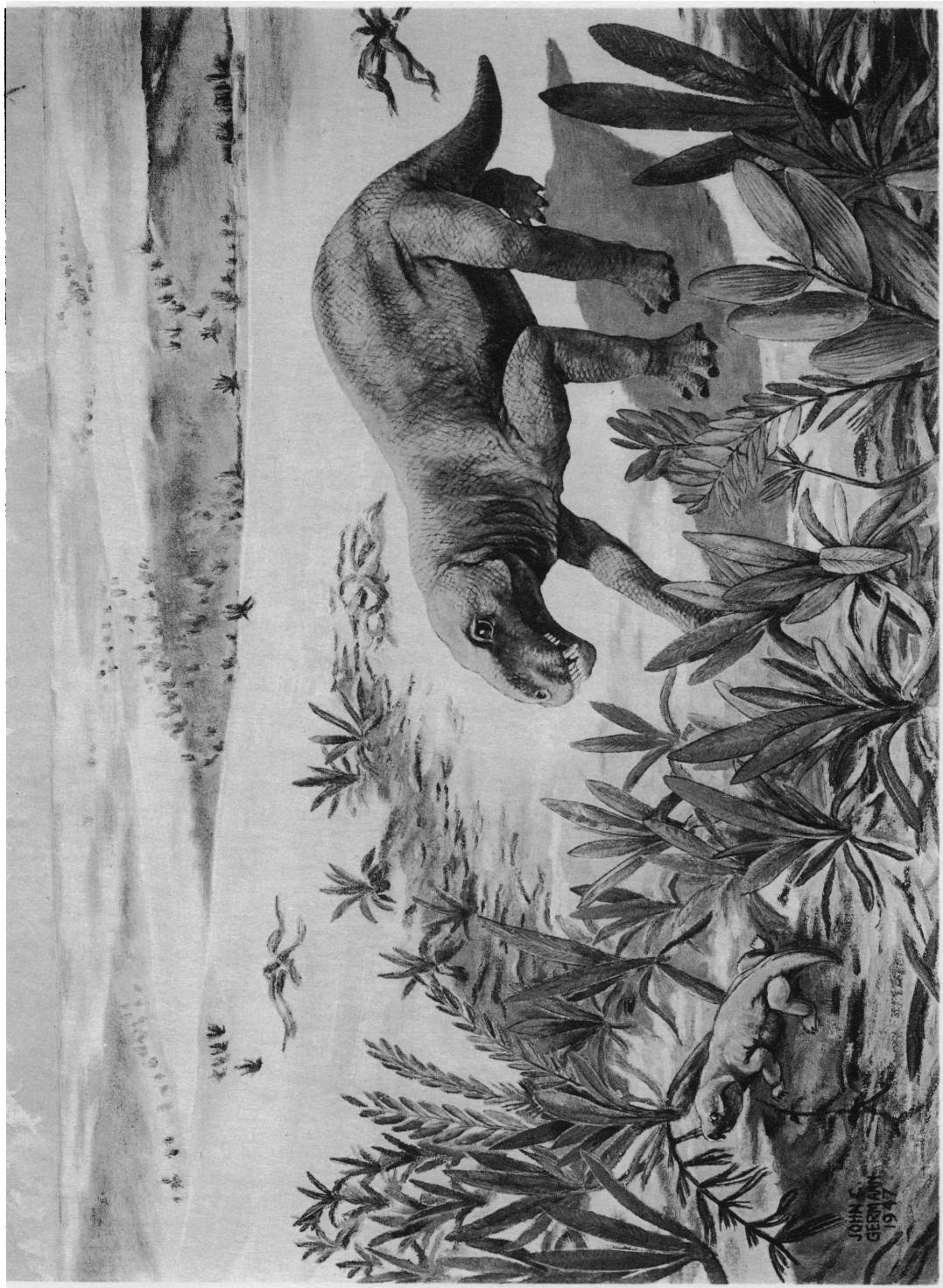
Lycanops ornatus Broom. A.M.N.H. No. 2240, skeleton as mounted by Charles Lang. Dorsal view, $\times \frac{1}{2}$



Lycenops ornatus Broom. A.M.N.H. No. 2240, skeleton as mounted by Charles Lang. Oblique view



Lycuonops ornatus Broom. A.M.N.H. No. 2240, skeleton as mounted by Charles Lang. 1. Anterior view, $\times \frac{1}{2}$. 2. Posterior view, $\times \frac{1}{2}$



Tyrannosaurus ornatus Broom. Restoration by John C. Germann

with the rest of the skeleton, which indicates fairly lightly built animals of considerable agility. The absence of ribs in the lumbar region would greatly increase the flexibility of the back—particularly in lateral direction. If I am correct in this point of view the Gorgonopsia would in this respect approach the condition of some Cynodonts . . . , Cotylosaurs . . . , and Pelycosaurs . . . ” (Boonstra, 1934, p. 151).

The additional preparation that has been done on the *Lycaenops* skeleton since Broom's original study confirms the correctness of Broom's interpretation, in which he indicates the ribs as continuing to the pelvis. It may be, however, that the posterior ribs were not so long as shown by Broom; short ribs in this region would give the added lateral flexibility that Boonstra thinks was characteristic of the gorgonopsian backbone.

The zygapophyses in *Lycaenops* are rather narrow, and they fit together in adjacent vertebrae to form a relatively tight joint.

There are two sacral vertebrae preserved in *Lycaenops*, but it is probable, as Broom suggested, that there were three sacrals in this genus as is common in other genera of Gorgonopsia. Owing to the fact that the sacral vertebrae are not fused to one another, it is quite likely that the third sacral became detached during the process of fossilization and was lost.

These vertebrae are attached to the ilium

by their costal processes. In the first sacral the costal processes are enlarged to form a very broad and strong articulation with the pelvis, while in the second vertebra the processes and their articulating ends are of normal size.

Only three caudal vertebrae are preserved in *Lycaenops*, and these have been tentatively placed as the third, sixth, and eighth in the caudal series. It is evident that the tail was rather short but heavy in this animal, and it has been restored as containing about 25 vertebrae. The articulating surfaces of the caudal centra are set at a considerable angle to the body of the bone. From either side of the centrum in each vertebra there projects laterally a strong transverse process. The neural spines are well developed.

Unfortunately only the proximal ends of a few ribs are preserved in the skeleton of *Lycaenops*. As would be expected in an animal having the diapophyses located on the end of long transverse processes, the head of the rib is far removed from the tubercle and is carried on a long pedicle that projects almost at right angles to the shaft of the rib. Thus the ribs in *Lycaenops* are closely comparable to the ribs in *Aelurognathus*, as figured by Boonstra. In this respect it might be said that in *Lycaenops*, as in *Aelurognathus*, the ribs are slender. As mentioned above, some of the most posterior ribs seemingly were single-headed.

THE PECTORAL GIRDLE

The pectoral girdle in *Lycaenops* is known from the scapula and coracoids, incompletely preserved, from the sternum, and from portions of the clavicle and interclavicle. The cleithrum is unknown. As Boonstra has pointed out, the pectoral girdle in the Gorgonopsia is well known from the evidence afforded by several genera, notably *Hipposaurus*, *Aelurognathus*, *Arctognathoides*, and *Inostrancevia*.

In all of these genera except the last named the blade of the scapula is comparatively small in relation to the combined ventral region plus the coracoids. The same appears to be true of *Lycaenops*. In *Inostrancevia* the blade of the scapula has become enlarged and

expanded at the top, obviously as correlated with the great increase in size of this animal over most of the other gorgonopsians. As in other gorgonopsians the scapular blade in *Lycaenops* would seem to be smooth (its upper portion is missing) and without an acromion process. As seen either anteriorly or posteriorly, the scapular blade has a well-defined curvature, convex externally and concave internally, to fit the shape of the thorax.

Ventrally the scapula is expanded to meet the large coracoids, and posteroventrally it forms the upper portion of the glenoid cavity.

The remainder of the glenoid is formed by the coracoid. The glenoid surface is simple, and it faces posteriorly and somewhat later-

ally. Beneath the glenoid the coracoid is thin, and there is a long, posterior process or hook, extending ventrally behind the glenoid. This posteriorly projecting process of the coracoid is a primitive feature, inherited from the early tetrapods, but retained in many of the therapsids.

Anteriorly the scapula and coracoid articulate with the large, plate-like precoracoid in a manner that is similar to the condition seen

a sort of facet for this articulation can be seen on the surface of the latter bone. From this point the clavicle curves around the front border of the scapula and precoracoid, in a manner similar to what is seen in other gorgonopsians, while its lower end is expanded and flattened to fit over the interclavicle.

What seems to be the posterior end of the interclavicle is preserved in this specimen.

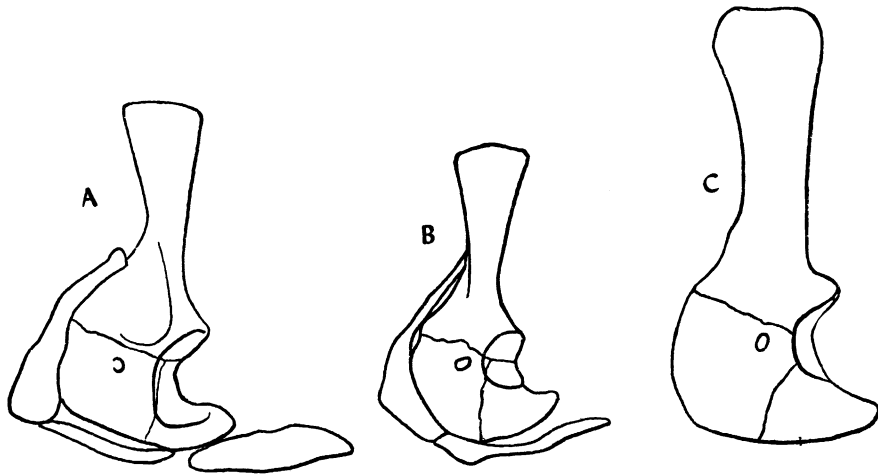


FIG. 12. Comparison of the pectoral girdles in certain genera of Gorgonopsia. Left lateral views. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240, $\times \frac{1}{3}$. B. *Aelurognathus microdon* Boonstra, after Boonstra, $\times \frac{1}{3}$. C. *Scymnognathus* cf. *whaitsi* Broom, after Broili and Schröder, $\times \frac{1}{3}$.

in other genera of Gorgonopsia. Near the suture between the precoracoid and scapula, on the lateral surface, is the well-developed precoracoid foramen, for the passage of the supracoracoid nerve. This foramen leads to a passage that traverses the precoracoid dorsally to emerge on the internal surface of the shoulder girdle entirely within the lower portion of the scapula.

The clavicles of *Lycaenops* are broken and crushed and because of this are rather difficult to interpret. It is quite evident, however, that the clavicles in this genus are very robust. The upper end of the clavicle abuts against the anteroexternal surface of the scapula at the base of the scapular blade, and

This is an elongated, narrow bone, shaped something like the interclavicle in *Aelurognathus microdon*.

The sternum is well preserved, though slightly distorted by crushing. It is well ossified and is elongated and is dished out so that the upper surface is concave and the ventral surface convex from side to side. The anterior end of the bone is somewhat expanded laterally, and there is good reason to think that the anterior edges articulated with the posterior processes of the two coracoids. Facets on the posterior end of the bone indicate the presence of a xiphisternum. On either side are clear indications of articulations for the first three dorsal ribs.

THE FORE LIMB

The humerus of *Lycaenops* would appear to be more slender than the same bone in other gorgonopsians, with the exception of *Hipposaurus*. In this last-named genus the limbs are very slender. Boonstra, in 1934, presented a very thorough comparative discussion of the fore limb in the *Gorgonopsia*, so this description of the fore limb in *Lycaenops* must be considered as supplementary to Boonstra's description.

As Boonstra has shown, the gorgonopsian humerus, though generally rather slender, is none the less comparatively primitive. In

coid. As Boonstra pointed out, the humerus does not stand out horizontally, as in the pelycosaurs, for instance, but rather it points posteriorly to a considerable degree. This is caused by the direction at which the glenoid is directed and the manner in which the head of the humerus fits into the glenoid.

Below the head of the humerus there is a strong deltopectoral crest curving ventrolaterally. This is very pronounced in the gorgonopsians and would indicate that in *Lycaenops*, as in related genera, the pectoral muscles were unusually strong.

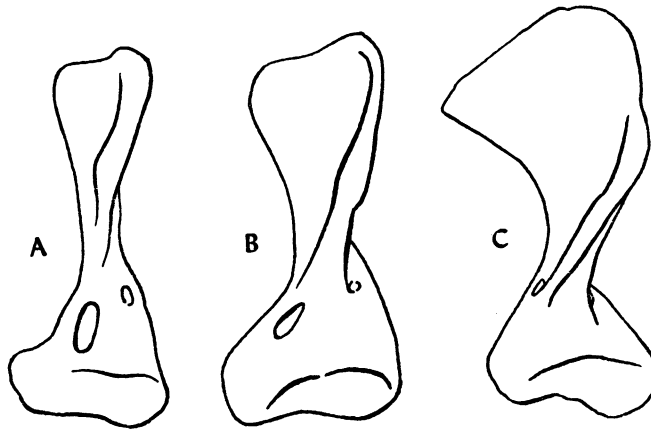


FIG. 13. Comparison of the left humeri in certain genera of Gorgonopsia. Ventral views. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240, $\times \frac{1}{3}$. B. *Aelurognathus tigriceps* (Broom and Haughton), after Boonstra, $\times \frac{1}{3}$. C. *Scymnognathus* cf. *whaitsi* Broom, after Broili and Schröder, $\times \frac{1}{3}$.

Lycaenops as in other gorgonopsians the proximal and distal ends of the bone are expanded and are twisted around the shaft so that they subtend an angle of about 30 degrees. This angle is somewhat smaller than the angle indicated by Boonstra for other gorgonopsians, 40 degrees, but in the case of *Lycaenops* the lesser angle would seem to be real and not due to any appreciable extent to crushing. Perhaps in this particular character the form under consideration is somewhat more advanced than the other gorgonopsians.

The proximal articulating surface of the humerus is elongated, and during the movement of the limb this long surface slid back and forth in the glenoid of the scapulacora-

There are both entepicondylar and ectepicondylar foramina, the latter piercing a strong supinator crest. The entepicondylar crest is also strong, so it is evident that the flexor and extensor muscles in the fore limb of *Lycaenops* were very well developed. Distally the pronounced ectepicondyle is rounded into a capitellum for the articulation of the cup-like proximal articulation of the radius. Immediately medial to this is the trochlea for the articulation of the ulna; it is evident, therefore, that the proximal end of the ulna is inside the radius—a point that will be discussed below. Medial to the trochlear groove is a large entepicondyle.

The radius and ulna in *Lycaenops* are slen-

der and, as Broom has pointed out, but slightly shorter than the humerus. The radius is generally of a rounded cross section, but the ulna is much flattened so that laterally it is quite thin. This bone is distinguished by a well-developed olecranon. Proximally the cup-like articular surface of the radius rides against the rounded capitellum of the humerus,

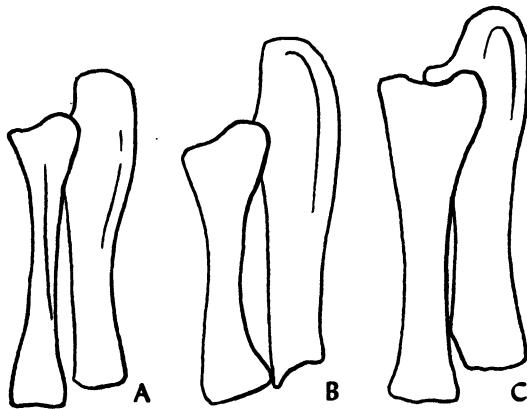


FIG. 14. Comparison of the left radii-ulnae in certain genera of Gorgonopsia. Anterior views. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240, $\times \frac{1}{3}$. B. *Aleurognathus tigriceps* (Broom and Haughton), after Boonstra, $\times \frac{1}{3}$. C. *Scymnognathus* cf. *whaitsi* Broom, after Broili and Schröder, $\times \frac{1}{3}$.

while the broadly crescentic articular surface of the ulna works against a very well-defined trochlear surface on the entepicondylar end of the humerus.

Although the radius and ulna are, generally speaking, parallel, the latter bone being posterior to the former, there is a certain degree of crossing of these bones proximally, so that at their upper ends the ulna is internal to the radius. In this respect, as in so many others, *Lycaenops* resembles other gorgonopsians, because the same relationships of the bones are to be seen in *Aelurognathus* and *Hipposaurus*, as figured by Boonstra. A somewhat similar pose of the fore limb is typical of the earlier synapsids such as the pelycosaurs.

In looking at higher forms, we see this proximal crossing of radius and ulna in primitive mammals, such as the marsupials, a condition that is quite obviously an inheritance from a therapsid ancestry. In the mammals

the articular surface of the ulna has been broadened so that it rides against both entepicondyle and ectepicondyle, a fact that makes the basic proximal crossing of the bones somewhat less obvious than is the case in the therapsids, where the ulna is narrow proximally and has only the inner trochlear articular surface.

Distally the radius and ulna articulate with a large radiale and ulnare, respectively. These bones are described below, in the consideration of the manus.

In the relationships of the bones and the general proportions the manus of *Lycaenops* is very closely comparable to the manus of *Aelurognathus*, which has been figured by Boonstra.

As Boonstra has shown, the gorgonopsian carpus consists of a proximal row containing three bones, the radiale, ulnare, and intermedium, a medial row containing the two centralia, and a distal row containing four or five bones. In *Lycaenops* the radiale is a large, robust element, while the ulnare is elongated and flattened. Between these two elements is a small, elongated, rather rod-like intermedium, while on the posterolateral side of the ulnare, as Broom has shown, is a flattened pisiform. The first centrale, directly beneath the radiale is, as is the bone above it, large and heavy. It might be said here that both radiale and centrale 1 in *Lycaenops*

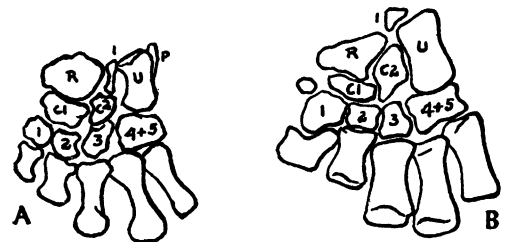


FIG. 15. Comparison of the left fore feet in certain genera of Gorgonopsia. Dorsal views. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240, $\times \frac{1}{3}$. B. *Aelurognathus tigriceps* (Broom and Haughton), after Boonstra, $\times \frac{1}{3}$. See figure 16 for a key to the identifications of the carpal bones.

are definitely more robust than the same bones in the carpus of *Aelurognathus*. Unfortunately the upper surface of the second centrale is missing in *Lycaenops*, but enough

of the bone is preserved in the matrix to show its shape as a rather nodular element.

The distal bones of the carpus are all large, and of these the outside one is very large and articulates with both the fourth and fifth digits. This bone obviously represents a fusion of the two primitive carpal elements articulating with the two lateral digits.

The first metacarpal is quite small, and there is a progressive increase in size from

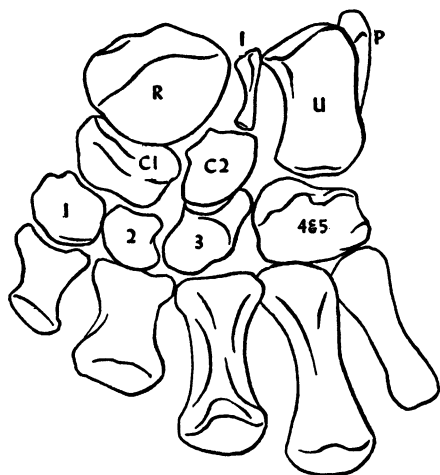


FIG. 16. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, left carpus and metacarpals. Dorsal view, $\times \frac{1}{2}$. Abbreviations: Cl, centrale 1; C2, centrale 2; 1, 2, 3, 4, and 5, carpalia; I, intermedium; P, pisiform; R, radiale; U, ulnare.

this to the fourth metacarpal. The second metacarpal is much broader than the other bones in this series.

The phalanges are not all present. In the first digit there are the usual two phalanges, the ungual being a pointed claw. In the second digit there are two phalanges, and the ungual is missing, while in the third digit there are also two phalanges and a missing terminal phalanx. In the fourth digit, only the proximal phalanx is present, and, as pointed out previously, the fifth digit is completely missing.

Broom, in 1930, figured four phalanges in

the third digit of the manus of *Lycaenops*, showing the second phalanx as a short, disk-like element. Furthermore, he figured five phalanges in the fourth digit, making the second and third phalanges disk-like bones. Thus, according to his interpretation of the manus, the phalangeal formula in *Lycaenops* should be 2, 3, 4, 5, 3—in other words, the primitive reptilian formula.

Boonstra, in 1934, expressed some doubts as to Broom's interpretation of the phalangeal formula in this reptile, and suggested that it should be 2, 3, 4, 4, 3. This was the formula that he found in the manus of *Aelurognathus*.

Further preparation of the manus in *Lycaenops* shows that the short, disk-like second phalanx seen in the third digit of *Aelurognathus* is not present in *Lycaenops*. Instead there are only two phalanges, each of normal length, between the metacarpal and the ungual. Broom, in 1930, in his plate showing the *Lycaenops* skeleton as it was found *in situ*, indicated a disk-like phalanx and, distally to it, another normal phalanx, below the proximal phalanx of the fourth digit of the left manus. There is also another bone, the exact nature of which is indeterminate, shown by Broom as distal to the proximal phalanx. These distal phalanges are not present in the materials now at hand, and it would appear that during the course of time they have been lost.

Since there is no disk-like second phalanx in the third digit of *Lycaenops* it is reasonable to assume that reduction of the phalanges in this reptile has proceeded to such an extent that this bone has been completely suppressed. Therefore it is reasonable to assume that a similar reduction has taken place in the fourth digit so that at least one of the disk-like phalanges has likewise been suppressed. According to this interpretation, the phalangeal formula in the manus of *Lycaenops* should then be 2, 3, 3, 4, 3. On the basis of this evidence it is hereby suggested that the manus in *Lycaenops* is somewhat more specialized towards the mammalian condition than is the manus of *Aelurognathus*.

THE PELVIC GIRDLE

The pelvis in *Lycaenops* is unusually well preserved, a fact that was emphasized by Broom but which perhaps has not been fully appreciated. The right ilium is complete, and the left ilium is preserved in part. The ischia and pubes of both sides, while restored in various places, supplement each other to such an extent that it may safely be said that our knowledge regarding these bones is virtually complete. Complete preparation of the pelvis gives a picture of this part of the skeleton considerably different from that drawn up by Broom on the basis of his observations.

The ilium is short and deep, and the iliac crest extends but slightly in front of the

the ilium is flared out to form a prominent shelf that undoubtedly served to keep the head of the femur from slipping out of the acetabulum. Behind the acetabulum there is a large and well-defined notch in the surface of the ilium, a notch that causes a reëntrant in the acetabular border itself. This same notch is well defined in the pelycosaurs, so that its presence in *Lycaenops* obviously represents the inheritance of a primitive synapsid character. As Romer has shown in his description of the pelycosaur ilium, this notch may be compared with the cotyloid notch in the mammals.

The ilium is very broad anteroposteriorly at the level of the upper border of the ace-

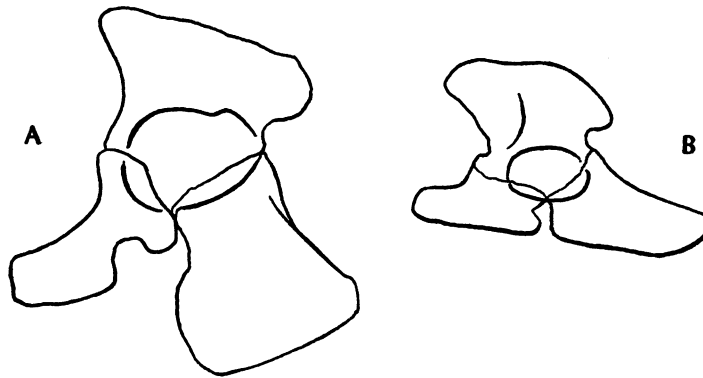


FIG. 17. Comparison of the pelvis in certain genera of Gorgonopsia. Left lateral views. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240, $\times \frac{1}{3}$. B. *Aelurognathus microdon* Boonstra, after Boonstra, $\times \frac{1}{3}$.

anterior border of the acetabulum, and only moderately behind the posterior border. Thus the bulk of the bone in the form of an externally concave vertical plate is located above the acetabulum, which is relatively large in comparison to the pelvis as a whole. Consequently there is a considerable area of attachment for the ilio-femoralis muscle, and this muscle must have been large and powerful as in other therapsids. The iliac crest is thin, but the posterior border of the ilium is thickened, and this may have served in part for the insertion of a strong coccygeo-femoralis muscle.

Along the dorsal border of the acetabulum

tabulum; therefore it does not have any appreciable "neck" such as is seen in many other therapsids and even in many of the pelycosaurs. All in all, this bone in *Lycaenops* bears a close resemblance to the same element in *Aelurognathus*, except that it would appear as if the iliac crest is straighter.

Broom compares the pelvis of *Lycaenops* with that of the pelycosaurs, but this comparison does not hold except in a most general way. Indeed, the differences are so marked between this pelvis and the pelycosaurian pelvis that one is justified in saying that resemblances beyond those of a general nature are in fact few. The ilium certainly is quite

different in shape from the pelycosaurian ilium, while the ischium and pubis are even more divergent from the form of these bones as seen in the primitive synapsid pelvis. Perhaps Broom was misled to some extent by the incomplete preparation of the fossil when he studied it, with consequent errors in his interpretation of its structure. This is particularly apparent in the lower portion of the pelvis—in the ischium and pubis.

Broom figured the ischium as a rather triangular element, one side of which articulates along its entire length with the pubis. As a matter of fact, the ischium is much deeper than it was figured by Broom, and it articulates only in the acetabulum with the pubis.

The ischium forms the posteroventral quarter of the acetabulum. Its upper border, which is thin, sweeps back in a gentle downward curve from the ilio-ischial junction on the back edge of the acetabulum, to terminate in a fairly sharp point far behind the posterior end of the iliac crest. From the ischiopubic junction on the ventral edge of the acetabulum, the anteroventral edge of the ischium, also a thin edge, sweeps back and down in a gentle flexure which carries the bone far down below the ventral limits of the pubis. At their most ventral points the two ischia meet along a very limited symphysis.

The ischium is thus essentially vertical in position, in which respect it appears to resemble the same bone in *Inostrancevia*, and as the two ischia meet they form a very sharp V, when seen in posterior view. Moreover, this great downward extension of the ischium has resulted in the development of an extensive ischial plate below and behind the acetabulum, a plate that is almost vertical and of which the outer surface is somewhat concave. This enlarged plate would have formed a broad surface of insertion for the pubo-ischio-femoralis muscles and for the various adductors, all of which must have been relatively strong in *Lycaenops*.

The pubis, forming the anteroventral quarter of the acetabulum, is constricted in front of the acetabulum. Beyond the constriction, which is indeed very great, the bone

expands into a rhombic plate, largely horizontal in position, the inner edge of which unites with its fellow in an elongated symphysis. As mentioned above, the pubis articulates with the ischium only in the acetabulum.

Just in front of the acetabulum the pubis and that portion of the ilium immediately above it are expanded and roughened, evidently as an insertion for a strong ambiens muscle. At the back of the pubis, immediately beneath the acetabulum, there is a downwardly directed process. Broom supposed that this represented the bone forming the posterior border of an enclosed pubic foramen. On the other hand, Boonstra found that in *Hipposaurus* there was no enclosed foramen, but rather a notch in the pubis, which together with the anterior border of the ischium formed a sort of fenestra. It would appear that in *Lycaenops* the condition is more or less similar to that described by Boonstra in *Hipposaurus*, except that the pubic notch is far enough anterior in position that its back edge is formed by the downwardly pointing process from the pubis, described above.

Ventrally the pelvis is broadly open between the front border of the ischia and the back borders of the pubes.

Dorsally the anterior inner surfaces of the ilia articulate with the sacral ribs.

From this description it can be seen that the pelvis in *Lycaenops* is anything but primitive; indeed, it has specialized to a considerable degree along its own line, a line quite different from that followed by the cynodonts in their pelvic specializations, yet one that is nevertheless far advanced beyond the basic synapsid condition. So far as can be determined, it would appear that the *Lycaenops* pelvis resembles in most respects the pelves of other gorgonopsians, and in particular the pelvis of *Inostrancevia*. In both of these genera the pelves are deep, the ilia are broad, and the ischia are large, vertical, and plate-like. It is too bad that better figures of *Inostrancevia* are not available, to make this comparison of the pelvis between the Russian genus and *Lycaenops* more complete and accurate.

THE HIND LIMB

The femur in *Lycaenops* is long and slender, a gorgonopsian character that is well exemplified in other genera, such as *Aelurognathus* and *Hipposaurus*. There is very little expansion at either end of the bone, and, as Boonstra has shown, the "twisting" of the two ends on the shaft is not great. In the two femora of *Lycaenops* this twisting seems to be on the order of about 20 to 25 degrees—figures somewhat less than what was seen to be characteristic of the humerus. There is no distinct neck separating the head of the femur from the shaft, but the head is nevertheless set at a very noticeable angle to the shaft of

cation of relatively weak muscles running from this portion of the bone to the pelvis.

Distally the two condyles of the femur are confluent on their articulating surfaces and are separated mainly on the posterior or ventral surface of the bone by the popliteal fossa. The internal condyle is much larger than the external one, the latter being elongated and transversely compressed, its long axis set at an angle to the internal condyle. Thus, as seen distally, the articulating surface of the femoral condyles has a very "oblique" set. This is correlated with the action of the femur and of the lower portions of the leg and the foot during locomotion. Although the femur was not thrust laterally, as it was in primitive reptiles, it still was not pulled into a completely fore-and-aft position as is characteristic of the quadrupedal mammals. Therefore, during its back-and-forth swing, the femur maintained a somewhat oblique angle to the median axis of the body; hence the obliquity of the distal condyles, which served to maintain the tibia in a vertical position, as seen from front or back. Otherwise the tibia would have been thrust out during locomotion, with its lower end far outside of its proximal end, and this most obviously would have been mechanically disadvantageous.

The tibia is somewhat shorter than the femur and is strongly bowed inward. Since the fibula is bowed outward, it is evident that there was a large interosseal space between the middle portions of the two bones. Proximally the tibia is greatly expanded to form a broad articulating surface for the femoral condyles. Because of this expansion, it would seem that the major portion, perhaps almost all, of the thrust during locomotion passed from the foot through the tibia and into the femur. The tibia is certainly a strong bone.

Anteriorly there is a weak cnemial crest on the proximal face of the tibia. Distally the tibia is somewhat expanded to articulate with the rounded tibiale.

The fibula is a slender bone, slightly longer than the tibia. As mentioned above, it is bowed away from the tibia. Proximally it is expanded anteroposteriorly, and on the inner

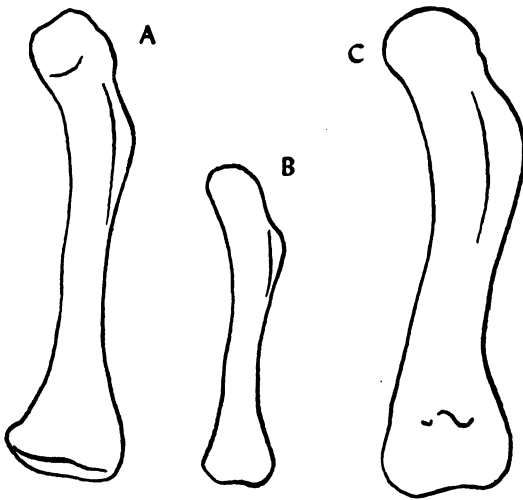


FIG. 18. Comparison of the left femora in certain genera of Gorgonopsia. Dorsal views. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240, $\times \frac{1}{2}$. B. *Aelurognathus microdon* Boonstra, after Boonstra, $\times \frac{1}{2}$. C. *Scymnognathus* cf. *whaitsi* Broom, after Broili and Schröder, $\times \frac{1}{2}$.

the bone. This angle, as seen in anterolateral aspect, amounts to approximately 27 degrees, from which it can be assumed that the femur was rotated towards the midline and was not thrust laterally as is typical of the primitive synapsids. On the posterolateral surface of the shaft, near the proximal end of the bone, there is a low and elongated greater trochanter for the insertion of a well-developed iliofemoralis muscle. As in *Aelurognathus*, the lesser trochanter on the posterior surface of the bone is no more than a low ridge, an indi-

surface of this expanded end there is a facet that articulates with the outer surface of the inner femoral condyle. This facet rode back

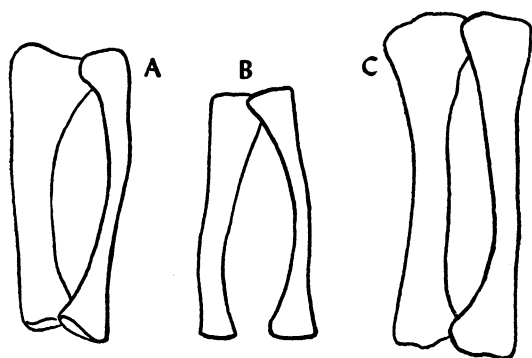


FIG. 19. Comparison of the left tibiae and fibulae in certain genera of Gorgonopsia. Anterior views. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240, $\times \frac{1}{2}$. B. *Aelurognathus microdon* Boonstra, after Boonstra, $\times \frac{1}{2}$. C. *Scymnognathus* cf. *whaitsi* Broom, after Broili and Schröder, $\times \frac{1}{2}$.

and forth across the inner part of the condyle anterolaterally to the tibial articulating surface during the extension and flexion of the leg. Distally the fibula is also expanded to articulate with a rounded surface on the fibulare.

Subsequent to Broom's original studies of *Lycaenops*, the pes in this animal was sub-

"The astragalus is more or less rectangular in shape and is well rounded on its dorsal surface. This area is divided into two parts or articular surfaces by a shallow groove running in a proximodistal direction. The medial articular surface for the tibia is directed in a medial and dorsal direction in the same manner as is the homologous surface on the pelycosaur astragalus. The lateral fibular articular surface is relatively smaller and is in line with the rounded proximal border of the calcaneum, which, of course, also articulates with the joint. The astragalus overlaps the calcaneum to a slight extent proximally and the calcaneum overlaps the astragalus to a greater extent distally. . . . This method of articulation absolutely precluded any possibility of movement between the astragalus and the calcaneum. . . .

"The calcaneum is very similar to that found in *Galechirus*; in other words, it still resembles the primitive therapsid type, being disk-shaped and concave in the middle of the dorsal surface. Its medial border is notched for the reason mentioned above. The proximal border is relatively thicker and the curved surface more extensive than in *Galechirus*." It might be said at this point that the rounding of the proximal articular surface is also much more extensive than is the case in *Aelurognathus*.

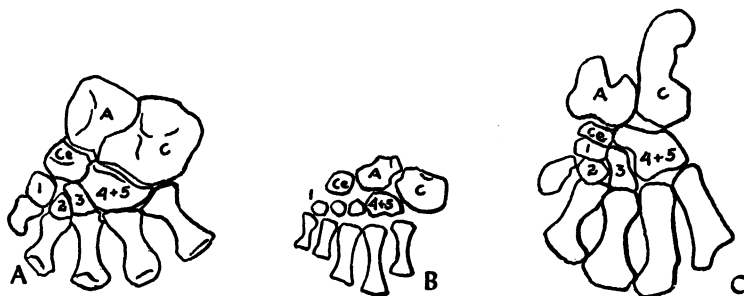


FIG. 20. Comparison of the left hind feet in certain genera of Gorgonopsia. Dorsal views. A. *Lycaenops ornatus* Broom, A.M.N.H. No. 2240, $\times \frac{1}{2}$. B. *Aelurognathus microdon* Boonstra, after Boonstra, $\times \frac{1}{2}$. C. *Scymnognathus* cf. *whaitsi* Broom, after Broili and Schröder, $\times \frac{1}{2}$. See figure 21 for a key to the identifications of the tarsal bones.

jected to a detailed examination by Schaeffer (1941), who described the tarsus in considerable detail. Schaeffer's description is in part as follows:

"In *Lycaenops* there is evidence for the first time that the fibula was able to rotate somewhat on the calcaneum in the vertical plane. . . .

TABLE 4
COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF POSTCRANIAL SKELETON

	<i>Lycaenops</i> A.M.N.H. No. 2240	<i>Scymnognathus</i> (From Broili and Schröder)	<i>Aelurognathus</i> ^a S.A.M. No. 9344	<i>Hipposaurus</i> ^a S.A.M. No. 8950
VERTEBRAE				
Length, presacrals	651	650	660 est.	—
Length, first 7 presacrals	170 est.	160 est.	167	191
Length, caudals	410 est.	—	—	—
Height, axis	50 est.	—	57	37
Height, first dorsal	48	—	81	37
SCAPULA-CORACOIDS				
Height, total	135 est.	165 est.	178	113
Height, glenoid-scapular border	90 est.	110 est.	123	99
Length, precoracoid-coracoid	83 est.	89 est.	90	77
Length, clavicle	90 est.	—	107	78
HUMERUS				
Length	152	160	159	174
Width, mid-shaft	17	21	17	16
Width, epicondyles	65	70 est.	57	44
RADIUS				
Length	111	—	111	127
Width, proximal	29	36	28	23
ULNA				
Length	128	141	123	147
Width, proximal	44	43	38	31
MANUS				
Length, total	130	—	—	—
Height, carpus	43	—	—	—
Width, carpus	62	—	—	—
Length, fourth metacarpal	34	—	—	—
Length, fourth digit	86	—	—	—
PELVIS				
Length, ilium	86	107	102	64
Length, ischium	77	—	82	65
Length, pubis	72	—	—	56
Height, pelvis: total	123	—	—	—
Height of ilium above acetabular border	31	52	49	—
Width at upper acetabular border	81	—	—	—
FEMUR				
Length	177	193	176	167?
Width, mid-shaft	22	25	—	—
Width, distal	38	57	34	33
TIBIA				
Length	129	133	136	159
Width, proximal	45	32	41	26

^a From Boonstra, 1934a. S.A.M., South African Museum.

TABLE 4—(continued)

	<i>Lycaenops</i> A.M.N.H. No. 2240	<i>Scymnognathus</i> (From Broili and Schröder)	<i>Aelurognathus</i> S.A.M. No. 9344	<i>Hipposaurus</i> S.A.M. No. 8950
FIBULA				
Length	131	133	137	162
Width, proximal	29	10?	27	17
PES				
Length, total	138	—	—	—
Height, tarsus	54	—	—	—
Width, tarsus	52	—	—	—
Length, fourth metatarsal	30	42	34	41
Length, fourth digit	83	—	—	—

“The cuboid is transversely elongated, tapering laterally to almost a point” (Schaeffer, 1941, pp. 452–453).

As Schaeffer has pointed out, the navicular barely touches the internal distal tarsal or entocuneiform. The naviculare, however, has very broad contacts with the astragalus or tibiale and with the cuboid. It articulates also with the third of the distal tarsals, but not with the second which is quite small and nodular.

The metatarsals are well developed and show a progressive increase in length from the first of the series to the fourth and fifth, which are approximately equal in size. *Lycaenops* is different in respect to this last character from *Aelurognathus*, for in *Aelurognathus* the fifth metatarsal is definitely smaller than the fourth one. The first metatarsal is broad and robust, the third is relatively slender, and the fourth and fifth are heavier than the middle one. All of the metatarsals except the first are broadly expanded both proximally and distally.

Since all of the phalanges are not preserved the question of the phalangeal formula cannot be definitely answered at the present time. It will be remembered that evidence was offered above to support the idea that the phalangeal formula in the manus is 2, 3, 3, 4, 3, rather than the primitive reptilian formula. While there is no direct evidence afforded by the bones of the pes, there is good reason to think that a phalangeal formula similar to that of the manus was also characteristic of the pes in this genus. In the first

place, if the formula of 2, 3, 3, 4, 3 for the manus is correct, it seems likely that this same formula would hold also for the pes. Second, Boonstra has shown that in *Hipposaurus* the phalanges have been reduced, so that there are four phalanges each in the

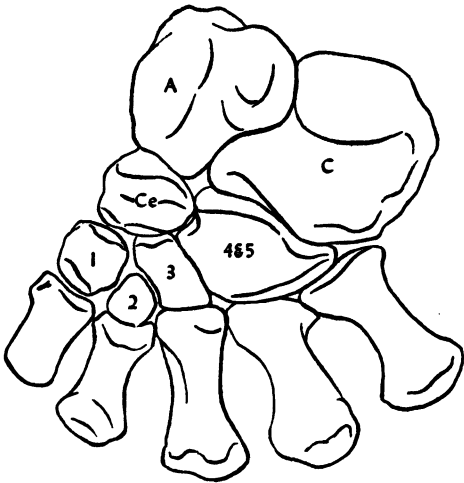


FIG. 21. *Lycaenops ornatus* Broom. A.M.N.H. No. 2240, left tarsus and metatarsals. Dorsal view, $\times \frac{1}{2}$. Abbreviations: A, astragalus; C, calcaneum; Ce, centrale; 1, 2, 3, 4, and 5, tarsalia.

third and fourth digits; therefore, the phalangeal formula for this genus probably is 2, 3, 4, 4, 3. “The 2nd phalanx of the 3rd digit of *Hipposaurus* is much reduced, and it is probable that in the geologically younger form [*Lycaenops*] it is lost, and the phalangeal formula would then be 2, 3, 3, 4, 3” (Boonstra, 1934, p. 170).

TABLE 5
COMPARATIVE RATIOS AND INDICES OF POSTCRANIAL SKELETON

	<i>Lycaenops</i>	<i>Scymnognathus</i>	<i>Aelurognathus</i>	<i>Hipposaurus</i>	<i>Cynognathus</i> ^a
$\frac{\text{Skull length}}{\text{Length of presacrals}} \times 100$	29	41	30	—	46
$\frac{\text{Height scapula-coracoid}}{\text{Length of humerus}} \times 100$	89	103	113	65	130
$\frac{\text{Length of humerus}}{\text{Length of radius}} \times 100$	137	—	143	137	145
$\frac{\text{Length of humerus}}{\text{Length of manus}} \times 100$	117	—	—	—	153
$\frac{\text{Length of femur}}{\text{Length of tibia}} \times 100$	137	145	130	—	116
$\frac{\text{Length of femur}}{\text{Length of pes}} \times 100$	128	—	—	—	117

^a As measured from reconstructed model.

THE SKELETON AS A WHOLE

The skull and the postcranial elements in *Lycaenops* having been considered at some length, it may be useful at this place to make an over-all survey of the skeleton in this genus, to consider it as an integrated and functioning machine. This present discussion will be limited to the skeleton alone—the relationships of the bones to one another and their probable functions. In a subsequent section of this paper there will be a discussion of the musculature of *Lycaenops*, generally limited to a consideration of the larger and more important muscles of locomotion.

The skeleton of *Lycaenops* as shown in figure 22 and plates 30 to 33 has quite a different appearance from the skeleton as restored by Broom in 1932 (Broom, 1932, fig. 45). It will be seen that in this new restoration the animal is made lower in comparison to its height, and in particular that the backbone is given much less curvature than it was in Broom's restoration.

In the first place it might be said that there is felt to be ample justification for

flattening the spinal column; indeed, it is possible that the backbone may have been even straighter than it is shown here. In making this restoration the vertebrae were joined approximately as they are preserved, with the curve resulting as shown. It was felt that any attempt to separate each vertebra from its fellow would be not only extraordinarily time consuming but actually disastrous to the specimen. Consequently in the mounted specimen there is a degree of curvature in the articulation of the last 10 presacral vertebrae that may exceed to some extent what was the normal condition. For instance, the backbone of the posed *Lycaenops* shows more curvature in the posterior presacral region than does the backbone of *Scymnognathus*, as restored by Broili and Schröder, or of *Cynognathus*, as restored by Gregory. It should be pointed out, however, that this curvature in the spinal column of *Lycaenops* is not much different from the curvature seen in the backbone of the alligator during locomotion. (See fig. 22.)

In this connection some mention should be made of the skeleton of *Inostrancevia*, as illustrated by Pravoslavcev (1927, pl. 1). In this skeleton the backbone shows a very marked dorsal curvature, with an anticlinal point about midway between the pectoral and pelvic girdles. It is felt, however, that the curvature in this case may not be entirely natural and probably is controlled to some degree by the preservation of the vertebrae in articulation.

The position of the limbs in the therapsid reptiles has been given considerable attention by various authors, and needless to say differing interpretations have resulted from the studies made.

Gregory and Camp, in their restoration of the *Cynognathus* skeleton, gave a horizontal position to both humerus and femur, with the elbow joint strongly everted and with the knee also everted during the backward push of the hind leg. In this restoration the pes is shown as pointing laterally during the final phases of the stride. In these respects the pose of the skeleton is, one might say, strongly pelycosaurian. The scapula is shown as being tilted forward.

Subsequently Romer, working with Gregory, made a scale model of the *Cynognathus* skeleton, and this was cast in plaster. In this model the humerus and femur are given more vertical positions than is the case in the first restoration by Gregory and Camp. Moreover, the elbow and knee joints are less everted than in the earlier restoration, although the knee is shown as pointing laterally to a great degree during the final phase of the stride. Both manus and pes are at all times forwardly directed. In this model the scapula is tilted forward, and the two scapulae diverge widely so that their upper ends are far apart.

Two other cynodonts have been restored, *Thrinaxodon* by Broom and *Belesodon* by von Huene. In *Thrinaxodon* the skeleton is given a crouching pose, with the upper and lower limbs at very acute angles to each other. The elbow appears to point back and the knee to point forward, and the feet also point forward. The scapula is tilted forward. In *Belesodon* the humerus is shown as being almost horizontal and the elbow is strongly everted, much as in the earlier restoration of

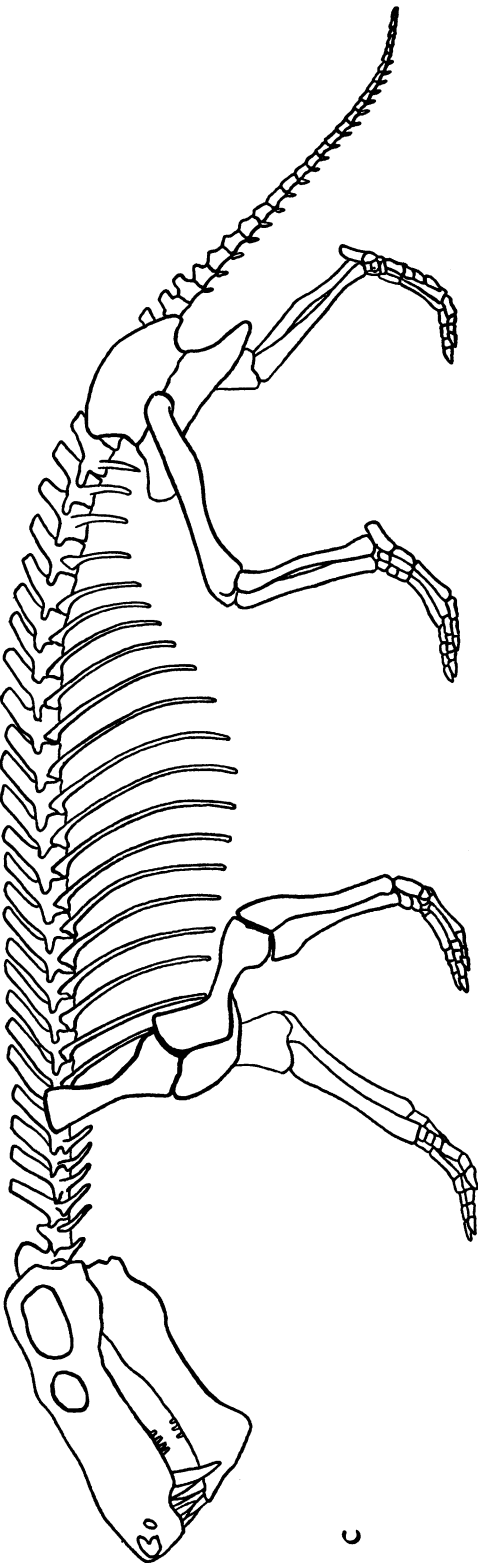
Cynognathus. The femur is also horizontal, with the knee everted. However, the feet all point forward. The scapula is tilted forward, and in relation to the midline it is essentially vertical.

Turning now to the gorgonopsians, we see that in the restoration of *Scymnognathus* by Broili and Schröder, the humerus and femur are less horizontal than in the earlier restoration of *Cynognathus*, and it would appear that the elbow and knee joints are not strongly everted. The feet all point forward, while the scapula is tilted forward.

As a comparison with this restoration, the figured skeleton of *Inostrancevia* shows the humerus and femur in relatively vertical positions, with the elbow everted to some extent and the knee apparently to a lesser extent. The feet are not known and have not been restored in this skeleton, but the scapula is present and is given a backward, rather than a forward tilt. In this skeleton the scapula appears to be essentially vertical, as seen from the front, and the same would seem to be true in the restoration of the *Scymnognathus* skeleton.

In the skeleton of the bauriamorph *Eriaciolacerta*, as restored by Watson, a quite different pose is shown. The elbow and knee joints appear to be directed backward and forward, respectively, but the humerus is horizontal and the femur is directed *up* from its articulation with the pelvis, so that the knee is higher than the acetabulum. The feet are pointed forward, and the animal is given a rather digitigrade pose, which incidentally is true of the pose given by Broili and Schröder to *Scymnognathus*. In *Eriaciolacerta* the scapula is tipped forward, and it appears to be almost vertical in relation to the medial line of the body.

In articulating the fore limb of *Lycaenops* one comes to the inescapable conclusion that the elbow joint in this animal was not strongly everted, which is in line with the restoration of *Scymnognathus* by Broili and Schröder and at variance with the restoration of *Cynognathus* by Gregory and Camp. Indeed, during the final phase of the fore limb stride, the humerus was almost parallel to the midline of the animal, with the elbow close against the body; only during the forward reach of the fore limb was the elbow swung



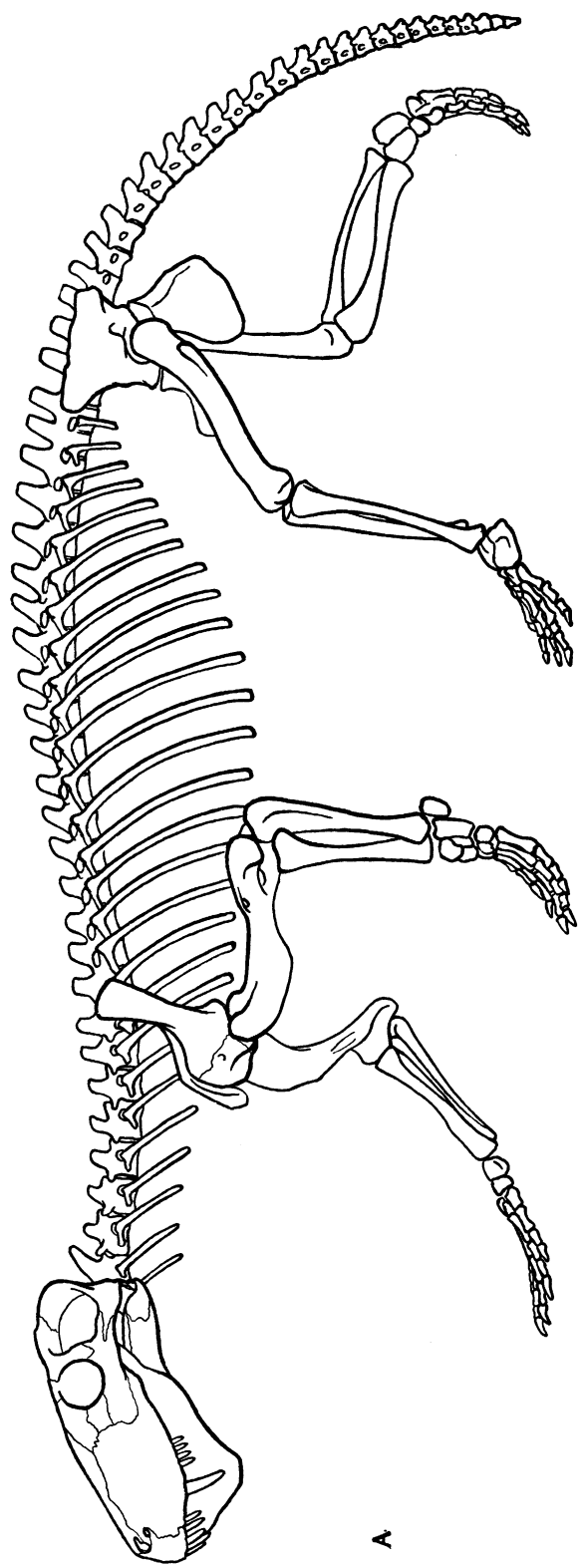


FIG. 22. The skeleton of *Lycanops* in walking pose, as compared with the recent *Alligator* and with the skeleton of *Scymnognathus*. A. *Lycanops ornatus* Broom. A.M.N.H. No. 2240, skeleton as mounted. Approximately $\frac{1}{3}$ natural size. B. *Alligator mississippiensis* Daudin. Traced from a photograph taken by Edwin H. Colbert, 1944. C. *Scymnognathus* cf. *whitaii* Broom. After Broili and Schröder. Approximately $\times \frac{1}{4}$.

out. In these respects the swing of the humerus may be compared to that observed in the modern alligator during locomotion.

It is interesting to observe that while the swing of the humerus during one stride is approximately the same in *Lycaenops* and in the alligator, the limits of the movement of this bone are somewhat different in the two genera. For instance, from the motion pictures of a young alligator walking, made by Schaeffer, it can be established that during the forward reach of the fore limb the humerus swings forward past a right-angle line, so that in its ultimate forward position, as seen in dorsal view, it makes an angle of about 70 degrees with the midline. During the farthest back reach of the fore limb, the humerus makes an angle of about 25 degrees with the midline. Consequently, the swing of the humerus during locomotion is approximately 85 degrees, as measured from a dorsal aspect.

In *Lycaenops* the angle of the humerus to the midline during the forward reach of the fore limb probably was not greater than about 90 degrees, as seen in dorsal aspect, but during the back reach of the fore limb the humerus swung in close to the body to make an angle of no more than 10 degrees. This gives to the humerus a swing of about 80 degrees, as seen from a dorsal viewpoint, during locomotion. Consequently, it may be seen that while the swing of the upper arm in the two forms is about the same, there is a difference in the relation of the arc of swing to the midline of the body. This is shown by the diagram, figure 23.

In this connection it might be said that the question of the movement of the humerus with relation to the shoulder girdle is a vexing one in *Lycaenops*. Nor is the problem limited to *Lycaenops*, because Romer, in his studies of *Cynognathus*, was bothered by the same difficulties. In *Lycaenops* the glenoid cavity of the shoulder girdle is directed posteriorly. Thus, when the humerus points back, as it did during the final phases of the stride, its head fits into the glenoid very nicely. On the other hand, when the humerus is swung forward, as it would have swung during the beginning phases of the stride, its head rolls out of the glenoid cavity. The surface of the glenoid is continued around to the lateral

face of the coracoid, so it would seem that the head of the humerus must have followed this surface around to a limit such that the humerus was at about a right angle to the midline. This, as said above, swings the head of the humerus largely out of the glenoid and seemingly makes for a weakness in the articulation, but there seems to be no other way to allow for an adequate stride in this animal.

In the alligator, the glenoid cavity of the scapula-coracoid is directed laterally, which allows the humerus to swing through its arc without the dislocation that is apparent in *Lycaenops*.

Of particular importance is the fact that the scapula in *Lycaenops* is strongly oblique in its relation to the midline of the animal, not vertical as it has been restored by various authors in other theriodont reptiles. This position of the scapula is determined by the articulation of the head of the humerus in the glenoid and by the relationships of the coracoids to the interclavicle and the midline.

In the description of the femur of *Lycaenops* it was pointed out that the head of the femur was set at a considerable angle to the shaft of the bone. This means that the knee was pulled in medially, so that during locomotion the swing of the hind leg must have been similar to what it is in a mammal. Here again we see a condition that is found in other advanced reptiles, such as the crocodilians. A comparison between *Lycaenops* and the alligator of the arc through which the femur is rotated during locomotion can be made, similar to the comparison made above for the humerus in the two forms.

As determined from the motion pictures made by Schaeffer, the femur reaches forward in the alligator to make an angle of about 35 degrees with the midline, as seen from above, while during the final phase of the hind limb stride the angle of the femur to the midline is about 50 degrees. Consequently the upper leg in this animal swings through an arc of about 95 degrees, as measured from above.

In *Lycaenops* the femur apparently reached farther forward; it was swung closer in towards the midline during the initial phase of the hind limb stride than it is in the alligator. Consequently in its forward position it

was at an angle of 20 degrees or less to the midline. One cannot say exactly how far back the femur swung during the final phase of the stride, because the articulation of the head of the femur in the acetabulum allows for very free motion. The limiting factor here probably was in the attachments and relationships of the muscles. By analogy with the

medial axes of the bones to an imaginary horizontal plane, located above the animal.

Actually the movements of the humerus and the femur are rather complex during locomotion and cannot be adequately represented on a plane surface. In the fore leg the humerus is swung in a rotary motion during a single stride—forward and out, back and

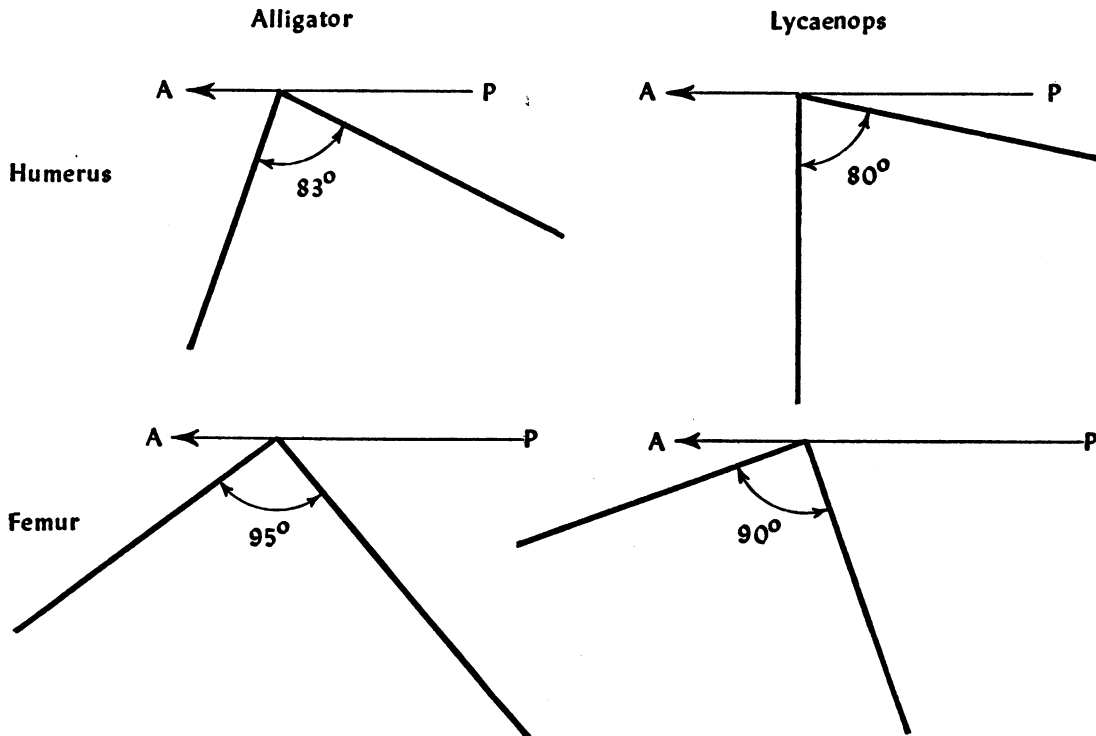


FIG. 23. Arcs of rotation of the humerus and femur, as viewed from above, in relation to the median axis of the body in *Alligator* and *Lycaenops*. Data on *Alligator* taken from photographs, on *Lycaenops* from studies of the skeleton. A. Anterior. P. Posterior.

alligator, it may be supposed that the swing of the upper leg was through an arc slightly greater than that for the upper arm. At any rate, as in the fore limb, the relationship of this arc to the midline was slightly different from what it is in the alligator, as may be seen by figure 23.

The foregoing discussion has been concerned with movement as seen from above and as measured from above. It must not be supposed from the diagram that the angles measured represent horizontal movements of the two bones, the humerus and the femur. Rather, these are projections up from the

in. This is true of the alligator, and almost certainly was true in *Lycaenops*. On the other hand the movement of the femur in both animals is simpler—forward and back, with very little lateral swing.

Schaeffer (1941) has shown that during all phases of locomotion in the primitive amphibians and reptiles the feet are kept pointing essentially forward while in contact with the ground. This is certainly true of the alligator, as shown by observations made by the writer on living alligators. (Schaeffer found that during the final pushing phase with the hind foot, there was an eversion of

the pes. It is probable, however, that this was not entirely natural, for his animals were walking on a glass plate, and it is likely that there was enough slipping of the foot to cause it to pivot at the ankle joint in that phase of the stride when the greatest pressure was being applied. The writer, while observing half-grown and adult alligators walking over a rough surface, saw no such eversion of the pes.) There is every reason to think that in *Lycaenops*, and in other mammal-like reptiles as well, the feet maintained their forward direction at all times and were never turned out as shown by Gregory and Camp in their restoration of *Cynognathus*. The analogies here are with the Crocodilia, not with the Lacertilia.

In many of the restorations of theriodonts the feet are shown as digitigrade. It is probable, however, that the gait was more plantigrade than digitigrade, a point that has been emphasized previously by Schaeffer (1941, p. 463). Here again comparisons can be made with the alligator. As can be seen from the figure, the "heel" of the hand is put against the ground when the fore limb is extended at the beginning of the stride, and likewise the heel of the foot is flat on the ground during the forward extension of the hind limb. Naturally, during the final phase of the stride, the back part of both manus and pes are lifted *before* the toes lose contact with the ground.

The gorgonopsians are characterized, on the whole, by the relative length and slenderness of their limbs. So in the faunas of their days they must have been comparatively swift runners. This fact is well exemplified in the skeleton of *Lycaenops*, in which the limbs are long and slender, probably more so than is the case in *Scymnognathus*. *Lycaenops* shows a close resemblance to *Inostrancevia* in this respect. Except for the difference in size the two genera show many similarities in the proportions of their postcranial skeletons.

It is probable that the reduction of the phalangeal formula from the primitive reptilian condition to 2, 3, 3, 4, 3 in *Lycaenops* is correlated with other adaptations in this animal for comparatively rapid locomotion. Such a reduction would tend to make the foot rather symmetrical on either side of the

midline, thereby increasing its efficiency for swift, mammal-like movements.

A distinctive character of the theriodont reptiles is the large size of the head in comparison with the skeleton as a whole. This is particularly marked in *Cynognathus*, in which animal as restored by Gregory and Camp the length of the skull is approximately half the length of the presacral series of vertebrae. In fact the head of *Cynognathus* is so inordinately large that it appears to be out of proportion to the body as a whole, yet the restoration by Gregory and Camp is based upon careful measurements of the associated material first described by Seeley.

In other forms the skull, while large, is not so extremely large as it is in *Cynognathus*. In the restoration by Broili and Schröder of *Scymnognathus*, for instance, the length of the skull is approximately 40 per cent of the length of the presacral vertebrae, while in *Lycaenops* and *Inostrancevia* this figure is reduced to approximately 30 per cent. Even so, these two latter genera give the impression of being large-headed animals.

The skull was carried at the end of a relatively straight and horizontal neck, and in its normal pose it is probable that the head was carried with the nose tipped down somewhat, dog-fashion.

As pointed out in a preceding portion of this paper, the gorgonopsians are essentially "saber-toothed" theriodonts, showing adaptations that precede the similar and parallel adaptations among the saber-toothed carnivorous mammals in later geologic ages. There can be no doubt that these reptiles were active hunters, probably pursuing and dragging down their prey in a fashion analogous to that used by the predatory mammals of Cenozoic times. Of course, being reptiles, the gorgonopsians and the other theriodonts certainly were not capable of the rapid and sustained efforts that are characteristic of the carnivorous mammals, so that their hunting activities were very probably characterized by short and swift dashes or sorties to seize and overcome their victims. On the other hand it must be remembered that the victims themselves were not capable of the rapid and sustained flight that is characteristic of modern mammals. Consequently, if the predatory power of the theriodont was

comparatively much less than that of a modern mammal of comparable size and adaptations, so was the power of escape or of defense by the victim much less than is the

case among the modern mammals. It is the old story of hunter and hunted, but on a scale much slower and more imperfect than at the present time.

THE MUSCLES

An attempt was made, when the skeleton of *Lycaenops* was being restored and posed, to work out the attachments and directions of some of the larger and more important muscles, especially in the postcranial region. It was felt that by such a study a better understanding of the relationships of the bones to one another could be obtained. The results of this attempt to reconstruct in part the myology of *Lycaenops* are shown by the accompanying figures. As can be seen, in these figures the myology of *Lycaenops* has been simplified and formalized to a diagrammatic treatment, whereby only the principal areas of attachments and the directions of the muscles are shown. In this way, the skeleton is not hidden, and the relationships of the larger muscles to the skeleton as a whole may be seen. It was felt that in view of the rather detailed treatment of the musculature of *Cynognathus* by Gregory and Camp (1918), a more elaborate handling of the subject at this place is not necessary.

It may be helpful to consider briefly the relationships of some of the muscles in *Lycaenops*, particularly as they can be compared with the same muscles in *Cynognathus*, in the the alligator, in other reptiles, and in mammals.

MUSCLES OF THE HEAD

In *Lycaenops* the muscles of the skull and jaws probably were generally similar to the muscles in *Cynognathus*, which in turn may be compared broadly with the musculature seen in the modern crocodilians.

The complex group of adductor mandibulae muscles, corresponding to the temporal and masseter muscles of the mammals, was well developed and strong in *Lycaenops* as was the case in *Cynognathus*. The very large temporal fenestra in *Lycaenops* indicates particularly space for the bulging of exceptionally strong medial and internal portions of the adductor mandibulae muscles. These

muscles are very strong in the modern crocodilians, which accounts for the tremendous power for closing the jaws that is so characteristic of these recent reptiles.

The pterygoid muscles also were well developed in *Lycaenops*.

If there was a depressor mandibulae in *Lycaenops*, and in other therapsids as well, it must have been very weak. In these reptiles there is no postarticular process in the mandible, whereas in the crocodilians this process for the insertion of the depressor mandibulae is very strong. It is possible that the depressor mandibulae in *Lycaenops* and in other therapsids was inserted on the inner surface of the mandibular ramus, beneath the articular glenoid in the articular bone.

MUSCLES OF THE FORE LIMB

The trapezius evidently was a large muscle in *Lycaenops*, its origin extending from the back of the skull and the ligamentum nuchae well back on the spines of the dorsal vertebrae. It was inserted upon the expanded acromial region of the scapula and upon the large and robust clavicle.

The rhomboideus, arising on the fascia above the cervical and the anterior dorsal vertebrae, was inserted along the inner surface of the vertebral border of the scapula. In *Lycaenops* the upper portion of the scapula is comparatively small, which would mean that there was a restricted area for the insertion of this muscle. Perhaps the condition in *Lycaenops* was similar to that seen in the recent crocodilians, where the upper portion of the scapula also is rather small.

Also inserting upon the upper portion of the scapula was the levator scapulae, which has its origin on the cervical ribs. Since the cervical ribs are rather large in *Lycaenops*, this must have been a fairly strong muscle. Gregory and Camp indicate this muscle in *Cynognathus* as inserting upon the cartilaginous suprascapula, as well as upon the bone

itself, and it is probable that the same was true in *Lycaenops*.

In the mammals and even in *Cynognathus* the deltoid muscle has its origin upon the spine of the scapula and runs from there to the deltoid crest of the humerus. But in *Lycaenops* there is no scapular spine; this reptile had not evolved so far in the direction of the Mammalia as had *Cynognathus*. Therefore it is probable that the muscle in *Lycaenops* that may be regarded as the dorsalis scapulae had its origin largely along the anterior edge of the scapula.

The serratus muscle, arising on the anterior ribs, was inserted along the posterior edge of the scapula.

The infraspinatus, arising on the outer surface of the scapula and inserting upon the greater tuberosity of the humerus, probably was comparatively small in *Lycaenops*, particularly in view of the rather restricted area of origin available.

On the other hand, the biceps and triceps muscles seemingly were powerful opponents in *Lycaenops*. The former of these two muscles had a greatly expanded area of origin on the large precoracoid, the latter an expanded origin on the coracoid, beneath the glenoid. These muscles were inserted upon the proximal ends of the radius and ulna respectively. There is a strong olecranon process on the ulna in *Lycaenops* for the insertion of the triceps.

In this reptile there was the usual development of extensor and flexor muscles in the lower leg. It is interesting to see the presence of a large pisiform in the manus, which served to provide a fulcrum for the flexors, thereby adding to the propulsive power of the foot.

MUSCLES OF THE PELVIS AND THE HIND LIMB

As in so many reptiles, the pelvis of *Lycaenops* served as a pivot for many strong muscles directed anteriorly, posteriorly, outwardly, and ventrally. These muscles served not only to activate the hind limb, but also to control and give power to the body and the tail.

Running forward from the pelvis were several sets of strong muscles, along the backbone, to the ribs and along the ventral portion of the body. Of these the sacrospinalis, arising from the ilium, probably extend-

ed far forward along the vertebral column and on the side of the thorax to the anterior ribs. This muscle was important in arching the back.

Beneath the sacrospinalis was the large obliquus abdominus, which has an extensive origin over the lateral and ventral portions of the middle and posterior ribs and was inserted on the pubis. The rectus abdominus occupied the usual position along the ventral portion of the body, running from the pubis far forward to the sternum.

An important series of muscles in the crocodilians is the pubo-ischio-femoralis complex, which includes a group of muscles in the pelvic and femoral regions. Gregory and Camp indicated in *Cynognathus* a quadratus lumborum, originating on the ventral surfaces of the posterior presacral vertebrae and ribs and inserting in the sacro-iliac region. This is the muscle which Romer has called the pubo-ischio-femoralis internus, part 2, and which in the crocodilians runs from the ventral surfaces of the posterior presacral vertebrae to the proximal end of the femur. The possibility for such an insertion for this muscle in *Cynognathus* was recognized by Gregory and Camp, and it would seem probable that similar relationships held for *Lycaenops*. A deeper portion of the muscle in the crocodiles arises from the internal portion of the ilium and ischium and the sacral ribs, and runs out and down to insert near the more superficial muscle mass, described above. The same relationships have been indicated for *Lycaenops*. These muscles acted powerfully on the femur to pull it forward.

Working correlatively with the dorsal pubo-ischio-femoralis described above are the ventral muscles belonging to the externus group in the crocodilians. These ventral muscles arise on the pubis and ischium and are inserted proximally upon the femur near the insertion of the dorsal muscles. In *Lycaenops* the muscles of the externus group probably were short but powerful. It is doubtful whether there was any extensive area of origin on the ischium, possibly none at all.

Opposed to these muscles are those of the coccygeo-femoralis group, which in *Lycaenops* apparently were well developed. These muscles arose on the back of the ilium and the

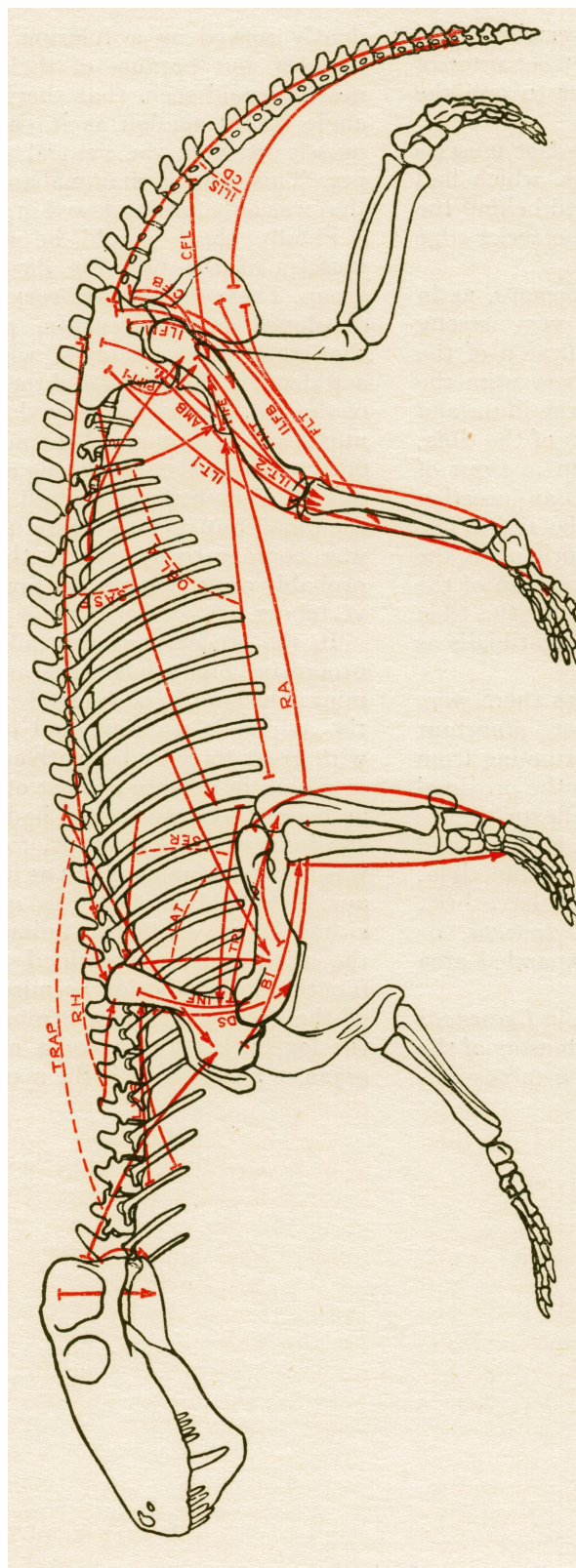


FIG. 24. Origins, insertions, and courses of certain locomotor muscles as restored in *Lycaenops ornatus* Broom. *Abbreviations:* AMB, ambiens; BI, biceps; CFB, coccygeo-femoralis brevis; CFL, coccygeo-femoralis longus; DS, dorsalis scapulae; FLT, flexor tibialis; FMT, femoro-tibialis; ILFB, ilio-fibularis; ILFM, ilio-femoralis; ILISCD, ilio-ischio-caudalis; ILT 1, ilio-tibialis, 1; ILT 2, ilio-tibialis, 2; INF, infrapinatus; LAT, latissimus dorsi; LVS, levator scapulae; OBLA, obliquus abdominis; PIFI 1, pubo-ischio-femoralis internus 1; PIFI 2, pubo-ischio-femoralis internus 2; PIFE, pubo-ischio-femoralis externus; RA, rectus abdominis; SASP, sacrospinalis; SER, serratus; TRAP, trapezius; TRI, triceps.

more anterior of the caudal vertebrae and were inserted upon the fourth trochanter of the femur. They acted together to pull the leg back.

Associated in action with the last muscles described was the ilio-femoralis, which had its origin on the ilium, above and behind the acetabulum. It inserted on the posterior edge of the femoral shaft.

It would appear that in *Lycaenops*, as in the crocodilians, there were very strong muscles for the extension and flexion of the hind limb. Of the extensors, there were the ilio-tibialis muscles, arising on the ilium and inserted on the proximal portion of the tibia, and the ambiens, with an origin in front of the obturator foramen and with an insertion also on the proximal end of the tibia. The femoro-tibialis, which had its origin on the shaft of the femur, joined one portion of the ilio-tibialis to insert proximally on the tibia and to act in concert with the ilio-tibialis as an extensor of the lower limb.

As opposed to these extensors there were the flexors, of which the most important muscles were the ilio-fibularis, running from the back portion of the ilium to the proximal part of the fibula, and the flexor-tibialis group, arising broadly on the ischium and inserting on the proximal end of the tibia. This last series of muscles must have been extraordinarily powerful in *Lycaenops*, as indicated by the very much expanded area of origin.

As in the fore limb, there were in *Lycaenops* the characteristic flexors and extensors of the foot. The proximal bones of the tarsus evi-

dently served as a fulcrum for the flexor muscles, but because of their relative flatness it would seem that there was no sharp angle in the tendon as it passed from the muscle mass to the ventral portion of the pes. This was a mammalian development that was only foreshadowed in the therapsids.

Finally there should be mentioned the muscles of the tail, the ilio-ischio-caudalis group. These muscles are very large and well developed in the reptiles, particularly in the crocodilians, animals which are characterized by the length and the great strength of the tail. There can be no doubt that these muscles were strong in *Lycaenops*, but apparently not relatively so strong as in the crocodilians. Very little of the tail is preserved in the fossil, but there is reason to think that it was comparatively short, that is to say, probably not so long as the presacral series of vertebrae.

In the crocodilians the tail is a powerful propulsive organ when the animal is swimming. On land it is dragged passively while the animal is walking, and it can be used with great force and effectiveness as a whip or a club in defense against other large land animals. Certainly the tail had a quite different function in *Lycaenops*, for it obviously was not a swimming organ as in the crocodilians. It probably was not used much in defense either. However, in this animal, as in all of the therapsids, it retained an important function in locomotion because of the action of the coccygeo-femoralis muscle in pulling the leg back. It was not a mere balancing organ or a switch, as is the mammalian tail.

CONCLUDING REMARKS

IN THE FOREGOING DESCRIPTION and discussion an attempt has been made to present the details of the osteology of a gorgonopsian theriodont, *Lycaenops*. Moreover, from the osteology of this animal certain interpretations regarding the musculature are presented, while speculations regarding the habits and the relationships of *Lycaenops* are set forth.

Lycaenops ornatus, the type of which is one of the most complete and best preserved of the known theriodont skeletons, is a typical gorgonopsian, and a study of this specimen affords a fairly adequate idea as to the anatomy in the Gorgonopsia as a group. Moreover, in looking at the skull and skeleton of *Lycaenops ornatus* we are enabled to obtain a general impression as to the anatomy, the adaptations, and by interpretations from them, the habits, of the theriodonts as a whole.

The gorgonopsians represent one large group of theriodonts, the other groups being the therocephalians (including the bauriamorphs) and the cynodonts. These groups, which may be given the rank of infraorders, are in some ways successive and in some ways parallel to one another. If they are looked at in a broad way, it may be said that the differences separating them from one another are differences in detail, so that generalizations can be made upon the basis of a member of one of these groups that will apply pretty well to the entire suborder of the Theriodontia. On the other hand, a closer study of the theriodonts illustrates the fact that, although the differences between them are those of details, they are none the less sufficiently large to differentiate the infraorders and within them the families and lesser categories. Consequently generalizations based upon a single representative form cannot be applied beyond a certain point. The situation here is analogous to that of the mammalogist who wishes to discuss among the artiodactyls such animals as camels, deer, giraffes, and cattle.

But if we keep these facts in mind, we are able to see in *Lycaenops* the adaptations characteristic of a gorgonopsian, and beyond that those characteristic of a theriodont.

Lycaenops, as was pointed out in the dis-

cussion, was a highly carnivorous reptile, and within the limitations of reptilian physiology a very active animal. It was a hunter and probably to a considerable extent a feeder upon carrion. The emphasis in the dentition upon the incisors and particularly upon the canine tooth in this animal suggests the probability that it was able to track down and kill other active reptiles, in a manner analogous to that in which the saber-toothed cats of later geologic periods were able to track down and kill active mammals. It was a reptile with a sharp, stabbing dagger on either side of the skull, a dagger that must have been used with great effectiveness. To judge from the relative increase in size of these sabers during the evolutionary history of the gorgonopsians, it may be presumed that as time went on ever greater reliance was placed upon these weapons for the purposes of hunting and defense. Perhaps the disappearance of the gorgonopsians at the top of the *Cistecephalus* zone is comparable to the later extinction of the saber-toothed cats near the end of Pleistocene times; in both cases the animals had become highly specialized and may have been unable to adapt themselves to changing conditions, particularly to changing food supplies.

We can see the extent of specialization in the gorgonopsians, again as exemplified by *Lycaenops*, in the reduction of the postcanine teeth. And again here is an adaptation paralleled in later ages by the saber-toothed cats. In this respect the gorgonopsians may be contrasted with other theriodonts, in which the postcanine teeth were well developed for purposes of mastication or comminution of the food.

In spite of these several specializations in the teeth, which are to be correlated with specializations in habits, the gorgonopsians are in many respects the most primitive of the theriodonts, a point that has been previously emphasized by various authors. This is seen in many details of the skull, such as the exclusion of the parietals from the temporal fenestra, the incipient secondary palate, and the like, and in the postcranial skeleton in such characters as the lack of an acromion and shape of the ilium. On the

other hand, *Lycaenops* is rather advanced in the development of the feet, especially in the reduction of the phalanges. Evidently this was a cursorial animal, if it can be said that a reptile such as this was cursorial, so that the feet became symmetrical as an adaptation to walking and running.

That *Lycaenops* was an animal well adapted to walking and running over hard ground is indicated by the development of the limbs. In some ways the limb bones are crocodilian-like, and there is good reason to think that progression was similar to that of a crocodilian when walking. The belly was carried well off the ground. The legs were in close to the body, especially the hind legs. The feet pointed forward.

Yet in spite of this approach to a mammal-

like pose, the progression of *Lycaenops* was not truly mammalian in its nature, for this animal moved the limbs as does a highly advanced reptile. The muscles utilized in giving power to the stride were the muscles used by other reptiles in walking and running. The difference from mammalian locomotion in this respect was particularly apparent in the movements of the hind limb, where the tail formed an important base for the attachment of muscles to propel the legs.

Such were the adaptations of *Lycaenops* and such were the adaptations in the gorgonopsians as a group. Moreover, in a general way such were the adaptations of the theriodonts. They were mammal-like, but still they were reptiles.

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