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ON THE CLASSIFICATION OF THE GORGONOPSIA

by D. Sigogneau[1]

The work here summarized represents an attempt to review the South African Gorgonopsians, an attempt based on a re-examination of the cranial anatomy of the type material and a comparison of all the specimens available[2]. The possible origin of the group from the Russian eotheriodonts is discussed in conclusion.

When one realizes what a tremendous amount of material Broom had to deal with, one cannot help but be impressed by the synthesis at which he was able to arrive and which remains to-day largely valid. He masterfully recognized the major taxonomic boundaries and their significance, perceiving within each group the affinities uniting the different constituents.

However, his inner feeling that it was his duty to make known each and every specimen examined by him led him to neglect somewhat their preparation and to establish types insufficiently described or justified. Quite apart from that, the number of specimens accumulated for over a hundred years naturally demanded a re-organization of the different infra-orders; I was offered by Dr. A. S. Brink, former Assistant Director of the Bernard Price Institute for Palaeontological Research of Johannesburg, the opportunity to disentangle the Gorgonopsians. After four years of reflection I emerged in 1967 with a provisional classification, the sole pretention of which being to present some new morphological data. The material consists of about 150 specimens, formerly distributed in 67 genera and 108 species. Except for the North American material, every specimen has been re-examined, often further prepared, and drawn and photographed.

This activity was made possible firstly by the Bernard Price Institute for Palaeontological Research, which offered me the counsel of Dr. A. S. Brink and the multifarious aid of Mr. J. W. Kitching, by the collaboration of many other institutions both in South Africa and in Europe, as well as by the co-operation of Dr. S. H. Rubidge and his family. It was also made possible by the aid of the Centre National de la Recherche Scientifique, and the direction of Professors J. Piveteau and J.-P. Lehman.

My first idea was to sort out a few principal structural types and to rearrange the main bulk around them. But I soon discovered what an astonishing homogeneity reigned within the infra-order; this, combined with the fact that many of the nomenclatorial types—being among the first mammal-like reptiles discovered—were in a rather poor state of preservation, hindered the achievement of this idea.

However, out of the mass of nearly identical forms I soon noticed, as had Broom and others, that a few specimens emerged rather sharply. For these I

maintained the family Ictidorhinidae created by Broom, even though I have lately come to doubt the familial status of the group; this will be discussed later.

In this view, the rest of the Gorgonopsians had to be united in a single family, the Gorgonopsidae, and any subdivision within them had to be infra-familial since the anatomic divergences that could be picked out among them were always less in degree than those between them and the Ictidorhinidae. I have therefore been led to distinguish two subfamilies, the Gorgonopsinae and the Rubidgeinae.

Haughton and Brink were the first authors to give generic diagnoses which took into account, in the Gorgonopsidae, the shape of the skull, the particularities of the frontal and the prearietal, the morphology of the palate and the number of post-canines. In a previous article I have already stated the necessity for more criteria, but a few complementary remarks are needed here. It is obvious that, as far as shape is concerned, post-mortem deformation has to be considered, but it is possible that the present shape is more indicative than previously thought; indeed, one may presume that a skull will not generally be deformed in just any manner, but that a narrow skull will be compressed laterally while a wider one will see its width accentuated. Still on the subject of shape, we do not know for sure what modifications are to be expected between juveniles and adults; no more do we know the amplitude of individual variation in this and other characters.

I eventually accorded a generic value to the following ensemble of characters; the general shape of the skull, the size and shape of the temporal fossae, the ratios of the inter-orbital and inter-temporal widths, the shape of the post-orbital, sub-orbital and zygomatic arches, the relation of the frontal to the supra-orbital rim, the presence of the prearietal, the dimensions of the post-frontal and lacrymal, details of the occiput, the degree of ossification of the braincase wall, and the relative position of the pterygoid transverse apophyses. In spite of the number of criteria utilized, it was often difficult to decide to which genus a specimen should be referred, and some of them even did not fit at all into this scheme. One of the reasons for this difficulty is, of course, the fact that as yet very rarely are post-cranial elements known, and this accentuates the artificial character of this classification.

Nevertheless, I arrived, for the family Gorgonopsidae, at a total of 22 genera; these shall be quickly reviewed.

Three of them—*Broomisaurus* Joleaud, *Galesuchus* Haughton and *Eoarctops* Haughton, all monotypic and represented by a single specimen—are among the oldest South African gorgonopsids known, since they come from the bottom of the *Tapinocephalus* zone of the Beaufort series[3]. Unfortunately, they all are in a rather bad state of preservation (one of them is even reduced to a weathered snout), but they show rather clearly that the gorgonopsid structural type was already fully established at this time. Moreover, they do not appear as the most primitive members of the family, if one takes as a point of reference their sphenacodont ancestors. From the same zone, Dr. L. D. Boonstra has collected,

and generously lent to me, other specimens which possess with the above genera a number of common characters, thus making the "*Tapinocephalus* assemblage" a rather homogeneous one. It was therefore tempting to group these specimens in a subfamily, the Galesuchinae. But, for one thing, its definition would not have been really in opposition to that of the two other subfamilies; furthermore there remains the question of what to do with the genera which begin in this zone as "Galesuchinae" (*Aelurosaurus felinus*[4], for example) and continue into the following zone as Gorgonopsinae (*Aelurosaurus wilmanae* (Broom), for example). From these considerations came my decision to maintain this assemblage within the Gorgonopsinae.

Indeed, the genus *Aelurosaurus* Owen, in the form of its type-species, *A. felinus*, would fit perfectly well in the "*Tapinocephalus* assemblage". There is even a good similarity between this species (known only by snouts) and the only species of *Galesuchus*, both in proportions and in details of the bones, and it is not impossible that the two species belong to the same genus; but there remain uncertainties in the palate of *G. gracilis* and in the posterior part of the skull of *Aelurosaurus felinus*; moreover I have now extended the genus *Aelurosaurus* to a number of later species. Thus conceived, it appears as a rather primitive form of small size, as the first representatives of the infra-order might be expected to be; the skull is lightly built, the skull roof relatively narrow, but the snout is already short. The preparietal, anteriorly situated in the type-species, underwent some backward displacement in the two latest species; the facial part of the lacrymal is short and the cheek dentition has begun a reduction, but the transverse apophyses are still found rather posteriorly. Besides the species individualized by Broom, and which I have for the most part maintained, the genus comprises now two other species: *Aelurosaurus* ("*Aelurosauropsis*") *wilmanae* (Broom) and *A.* ("*Galerhinus*") *polyodon* (Broom), as well as an uncertain third, *A.*? ("*Scylacocephalus*") *watermeyeri* (Broom), whose affinities tend also toward *Cyonosaurus*.

Morphologically very close to the preceding comes the genus *Arctognathus* Broom. The differences noted between the two genera are often due to a simple progression: the small forms of the beginning would have increased in size, their snout shortened even more; the frontals would have reduced their participation in the supra-orbital rim, and the preparietal would have become smaller; at the same time the transverse apophyses would have become edentulous. However, one would not have expected, of forms so late, a braincase so little ossified, no more than one would expect, in the course of evolution, the accentuation of the sinuosity in the maxillary alveolar border and the retreat of the pterygoid transverse apophyses. The existence of a specimen attributed to *Arctognathus* in the *Tapinocephalus* zone would seem to confirm my hypothesis that a separation of the two genera has taken place early. "*Lycaenodontoides bathyrhinus*" Haughton is definitely a synonym of the type-species, *Arctognathus curvimola*. It is less sure that "*Arctognathoides*" *breviceps* (Boonstra) finds its place here. As for the inclusion in the genus *Arctognathus* of "*Dixeya*" *nasuta* (von Huene), this remains somewhat

open to discussion, all the more since the details of the cranial roof of this species are not known.

It is not impossible that the small "*Galerhinus*" *rubidgei* of Broom should be, like the type-species "*Galerhinus*" *polyodon*, incorporated in the genus *Aelurosaurus*. But in order to decide it would be necessary to know the modalities of differential growth, for it is perhaps a juvenile form. This uncertainty obliged me—since I had suppressed the type-species—to create for this small skull a new generic name, according to a rule of nomenclature which does not always appear defensible.

The affinity which unites *Aelurosaurus* to *Scylacognathus* Broom (another genus beginning in the *Tapinocephalus* zone) is not less probable, but it occurs on another plane than for *Arctognathus*: it is a question here of two contemporaneous forms not long detached from a common stock. One finds again the short snout and the preparietal anteriorly situated, but a beginning of specialization would appear in the frontal tending to become isolated from the supra-orbital rim, in the inter-orbital roof enlarging, and the post-canines reducing even more in number. Beside synonymizing the two species of Broom, *Sc. parvus* and *Sc.* "*major*", I introduced into the genus the stocky "*Cynariops*" *robustus* (Broom) and the three species "*Cynarioides*" *gracilis* (Broom), *grimbeeki* (Broom) and *laticeps* (Broom).

It seems that *Scylacops* Broom is to *Scylacognathus* what *Arctognathus* was to *Aelurosaurus*. In the course of evolution there would have been an increase in size, an attenuation of the ventral sinuosity of the skull, complete elimination of the frontal from the supra-orbital rim, and forward displacement of the transverse apophyses. These modifications make of *Scylacops* a somewhat evolved genus, even though its prootic remains apparently little ossified. The incorporation of "*Sycocephalus*" *bigendens* (Brink and Kitching) into *Scylacops* has the merit of underlining the resemblance that exists between this genus and *Gorgonops*, a resemblance which does not however, in my opinion, correspond to a close relationship.

Gorgonops torvus, the first Gorgonopsian species to be described, by Owen in 1876, was based on a rather poorly preserved skull. At present the species is represented by four specimens (a fifth one has been serially sectioned), of which only one comes from the *Cistecephalus* zone. Like *Scylacops*, it is a middle-sized form (the type was thought to be juvenile, but further studies and comparisons do not confirm this hypothesis) and, contrary to what was supposed until now, does not appear very primitive. It is true that the snout is still long, the preparietal and the lacrymal well developed, the frontal largely open on to the orbit, the palate provided with an abundance of teeth, and the transverse apophyses remain posterior. But the shape of the skull, the inter-orbital width, the number of post-canines and above all the degree of ossification of the prootic (of which the dorsal and ventral processes close in front of the fifth nerve) testify already to a certain degree of evolution. Furthermore, the most recent specimen of the species is distinguished by a reinforcement of the divers arches, an inter-temporal enlargement, and a reduction of the preparietal and the supra-orbital frontal,

all of which are advances tending to fill in the space between *Gorgonops torvus* and *G. whaitsi*.

The latter constituted previously the type of the genus "*Scymnognathus*" Broom. This form was represented by five specimens, unhappily very fragmentary and poorly preserved, of which three are at present in the collections of the American Museum of Natural History, New York, and were, in consequence, not examined. When Broom created the species, he said that he hesitated to distinguish it generically from *Gorgonops torvus*, and he did not in fact justify his ultimate distinction. However, according to Boonstra, it is a form clearly more evolved than *G. torvus*. A detailed analysis led me back to the first opinion of Broom. For example, going back to the arguments given by Boonstra, one sees that the snout is in fact equally rounded in both cases, the temporal fossae are scarcely more developed in *G. whaitsi*, while the orbits are relatively a little smaller; the tooth row was probably convex in both species, and the ossification of the prootic has progressed equally in the two forms; lastly, the supra-orbital frontal appears a little narrower in *G. whaitsi*, but, as noted above, it is tending toward reduction in the last specimen of *G. torvus*. It is true that there are real differences, such as a great disparity in size and perhaps in the position of the transverse apophyses, but these differences do not, in my view, exceed a generic level. As a matter of fact, the two species appear to be very close to each other, with *G. torvus* remaining slightly retarded. I have considered it possible to include as well in this genus the large "*Gorgonognathus*" *longifrons* (Haughton), whose differences with respect to *G. whaitsi* are only of degree and which, according to its author himself, would only be an advanced form of the latter. I have also adopted Boonstra's opinion according to which "*Leptotrachelus*" Watson would be close to "*Scymnognathus*". The inclusion of "*Chiwetasaurus*" *dixeyi* Haughton in this genus is perhaps more disputable. On the other hand, "*Pachyrhinos*" *kaiseri* (Broili and Schroeder), from the top of the *Tapinocephalus* zone, seems rather clearly related to *G. whaitsi*, even though its type and only specimen is too incomplete for certainty, and though a resemblance between it and *Aloposaurus*? ("*Aloposauroides*") *tenuis* (Brink and Kitching) has been noted: they both show the same particularities of the snout, of the orbits and of the post-orbital arches. But the amplitude of the posterior widening and the position of the transverse apophyses are not known in *G. kaiseri* where, moreover, the post-canines are much larger.

The genus *Aloposaurus* Broom itself remains rather poorly defined, the type-specimen, which I have not seen, being apparently very badly preserved. Its affinities appear to be divided between *Gorgonops* and *Scylacops*.

It is not impossible that there exists also a relationship between the same genus *Gorgonops* and *Leontocephalus* Broom, at least as regards the type-species, *L. cadlei* Broom. But for the time being the affinities of this snout, and the reference of the two other species to this genus, *L.* ? (*Aelurognathus*) *haughtoni* (von Huene), remain doubtful.

Situated more or less at the heart of the Gorgonopsians is the genus *Cyonosaurus* Olson[5]. This essentially replaces the genus *Cyniscops*, established three months later by Broom on a different number of incisors; this number having since been shown to be identical[6] in the two cases there is no longer any reason to separate *Cyonosaurus longiceps* and *Cyniscops longiceps*. We are dealing here with one of the best represented species of all the Gorgonopsians, as well as one of the most primitive. This middle-sized animal has retained, cranially, a long snout; the temporal fossae are also elongated, but not extended posteriorly by ample squamosal wings; the gracility of the arches, like the proportions of the cranial roof, are certainly original, confirmation of which can be seen in the large size of the frontal, preparietal and lacrymal; the same thing applies to the posterior position of the toothed transverse apophyses and the feeble degree of ossification in the prootic; lastly, it is the species which, after "*Galerhinus*" *rubidgei*, has retained the greatest number of small post-canines. Only the downward extension of the lateral postorbital appears evolved in this species, along with the elongated temporal fossae. Two of the other species formerly included in this genus, *Cyonosaurus rubidgei* (Broom) and *C. kitchingi* (Broom) (with which "*Alopecorhynchus rubidgei*" Brink and Kitching has been synonymized), are somewhat more specialised. Of the two others, "*Cyniscops*" *cookei* (Broom) and "*Cyniscops*" *broomianus* (von Huene), the first is now referred to *Arctognathus*, the second synonymized with "*Scylacocephalus*" *watermeyeri* and therefore included with it in *Aelurosaurus*. As has been noted above, the distinction between this genus and *Cyonosaurus* remains, with respect to the latter species, a little vague.

Lycaenops ornatus Broom is almost as primitive as *Cyonosaurus*; in fact, the general shape of the skull appears more sphenacodont-like than that of *Cyonosaurus longiceps*, but the palate is undoubtedly more evolved and the cheek dentition already somewhat reduced. The two other species, *Lycaenops* ("*Lycaenoides*") *angusticeps* (Broom) and *L.* ("*Tigricephalus*") *kingwilli* (Broom), form with the type-species something of a morphological succession by a progressive increase in size, in general massiveness, and a reduction of the preparietal. On the contrary, the three other species remain as primitive as the type. But all three are questioned, *L.?* ("*Tangagorgon*") *tenuirostris* (Boonstra) because of its affinities with *Cyonosaurus*, *L.?* (*Aelurognathus*) *minor* (Brink and Kitching) and *L.?* (*Aelurognathus*) *microdon* (Boonstra) because of their affinities with *Aelurognathus* (Broom and Haughton).

This last genus retains, like *Lycaenops*, a convex dorsal profile and temporal fossae lacking a posterior extension; the prootic is scarcely more evolved and the details of the bones differ little in the two cases. Only a greater massiveness, both general and local, can be noted in *Aelurognathus*, but the basic affinity is indisputable. Besides the synonymization of *A. nyassaensis* Haughton with *A. tigriceps* Broom and Haughton and the suggested exclusion of *A. microdon* and *A. minor*, the principal innovation concerning this genus resides in the incorporation of "*Dixeya*" *quadrata* (Haughton). This species is now well represented and responds in a satisfactory manner to the definition of the genus *Aelurognathus*.

One finds in *Arctops* Watson the general massiveness of *Aelurognathus*, together with the primitive characters of *Lycaenops*. In addition, the cranial roof proportions of *Arctops* seem to me directly inherited from the sphenacodonts, the prootic remains very short anteriorly, and the palate itself has evolved but little: one of the most primitive genera of the Gorgonopsidae is the result. I have thought it possible to include in the type-species, based on the posterior part of the skull, *A.* "*watsoni*" Brink and Kitching, as well as another skull, undescribed. "*Gorgonorhinus*" *minor* (Broom) follows most of the definition of *Arctops*. This genus contains the only new species here proposed of the Gorgonopsidae; the specimen upon which it is based was previously classed in *Aelurognathus minor*, but it seems more comfortably situated in the genus *Arctops*, mostly because of the morphology of the ventral surface of the skull. The above discussion stresses the affinity which unites *Arctops* and *Aelurognathus*.

The species *Arctops?* ("*Smilesaurus*") *ferox* (Broom) (="*Pardocephalus*" Broom) offers another testimony to this affinity; indeed it allies not only *Arctops* to *Aelurognathus* but both of them to *Lycaenops*, morphologically extending just beyond *L. kingwilli* in the sequence already mentioned (*L. ornatus*, *L. angusticeps*, *L. kingwilli*). At the same time *Arctops? ferox* considerably evokes *A. willistoni*, by its form, its massiveness (increased here), its posterior width, the proportions of the cranial roof, and the large size of the post-canines (fewer in number); the palate, on the contrary, is like that of *Aelurognathus*. The choice of *Arctops* for this species derives from the fact that the only difference between this genus and "*Smilesaurus*" is one of an order of evolution (advancement of the pterygoid transverse apophyses), whereas in order to go from *Aelurognathus* or *Lycaenops* to "*Smilesaurus*", one must imagine a "regression" (inter-orbital shrinking for the first, inter-temporal widening for both). But it would perhaps have been preferable to simply retain the genus "*Smilesaurus*", all the more since the Russian *Inostrancevia* Amalitzki seems to have affinities with this form.

Within this ensemble, restricted to a narrow evolutionary framework, was however born another survival attempt in the form of the Rubidgeinae. This attempt consisted essentially in an increase of the power of aggressivity, manifested by larger size, the reinforcement of the snout and the development of the anterior dentition at the expense of the post-canines. The widening of the cranial roof and of the diverse arches must have corresponded to more extensive muscle insertions, as did, presumably, the hollowing of the occiput. Perhaps the tendency toward closure of the cerebral wall by the coming together of the prootic and the orbitosphenoid could be interpreted in the same sense (it should be noted that the epipterygoid not only remains always exterior to the wall, but that it never manifests any tendency to widen). At the same time and as in all the large forms, one is confronted with a reduction of the preparietal and a retreat of the frontal from the supra-orbital rim.

This attempt appears timidly in *Sycosaurus* Haughton, is expressed more or less clearly in *Prorubidgea* Broom and *Clelandina* Broom, and attains its full

development in *Dinogorgon* Broom and *Rubidgea* Broom; the succession thus evoked remains for the most part purely morphological.

Sycosaurus somewhat brings to mind *Scylacops*, with its snout scarcely as high as wide and narrowed anteriorly, and with the posterior broadening of the skull. But the large size of the post-canines and the posterior situation of the transverse apophyses also remind one of *Arctops*. Be that as it may, the specialization of the cranial roof has already advanced and one can note an incipient zygomatic widening in *Sycosaurus laticeps* and *S.* ("*Leontosaurus*") *vanderhorsti* (Broom), but less clearly in *S.*? (*Lycaenops*) *kingoriensis* (von Huene). As for the species "*Sycosaurus*" *brodiei* Broom, it seems to me to participate more directly in the following genus.

Prorubidgea Broom appears derived more or less directly from a form close to *Aelurognathus*: one finds again the elevated shape of the skull with its rounded snout, the small orbits and the transverse apophyses anteriorly situated (with one exception). The zygomatic arches and the cranial roof, while more evolved than in *Aelurognathus*, are less so than in *Sycosaurus*, which might explain the exclusion of *Prorubidgea* from the Rubidgeidae by Haughton and Brink (but not Watson and Romer). The various species of this genus have diversely developed the generic plan, but their affinities with each other seem to me difficult to question.

From a strictly morphological point of view, *Dinogorgon* Broom prolongs in a very satisfactory fashion *Prorubidgea*. Not only is the shape the same and the orbits of similar proportions, but the only differences that one can find constitute evolutionary advances with respect to *Prorubidgea*: the cranial roof is barely enlarged and there are still five post-canines, but neither a preparietal nor a supra-orbital frontal exist any longer; the ventral zygomatic apophyses are strongly developed, and the pterygoid transverse apophyses are placed even more anteriorly. Lastly, an elongate swelling is formed, increasing the thickness of the supra-orbital rim, which extends onto the post-orbital arch in the form of an oblique ridge.

It seems to me that there is an identity between the three species previously attributed to this genus. I would go even further and consider this single species as referable to the genus *Rubidgea* Broom. But *Dinogorgon* was created first and on a snout in rather poor condition; the synonymy of the two genera would lead me to base all this assemblage on an incomplete specimen, a deed that would always be open to suspicion. Consequently, *Rubidgea* is maintained.

This genus *Rubidgea* prolongs in turn (especially in the form of *R. atrox*) the *Dinogorgon* "stage"; the maximum of force developed in the Gorgonopsians is attained here. The development of the cranial roof is such that the small orbits are practically invisible dorsally, and the zygomatic projection is so developed that it constitutes the most ventral point of the skull; the post-canines are reduced to one or two and the palatine teeth tend to disappear. The divergences that are visible between the three principal specimens do not seem easily attributable to individual variation. As for the skull of "*Tigrisaurus*" *pricei* Broom, this appears to me too incomplete to permit its attribution to any of the three recognized species.

It remains to discuss, in this subfamily, two forms which are rather exceptional by the width of their skull: this width is only extreme in the small *Clelandina rubidgei* Broom and *C.* (''*Dracocephalus*'') *scheepersi* (Brink and Kitching); it becomes extraordinary in *Broomicephalus laticeps* Brink and Kitching (= *Rubidgea laticeps* Broom) since here it exceeds the skull length. The last-named species has attained a level of specialization identical to that of the other *Rubidgea* and was previously classified in the same genus. However, I have tried to maintain a consistency with the rest of this classification by following Brink's suggestion and by placing it in a parallel genus.

It does appear that this specialization of the Rubidgeinae was fatal; there, where suppleness and invention were needed in order to adapt to ecologic change, they reacted with a deploying of force and an increase in power and aggressiveness. It is perhaps not just due to chance that the only Gorgonopsian found in the *Lystrosaurus* zone belongs to the genus considered as the most primitive, *Cyonosaurus*.

The Ictidorhinidae still remain very poorly known; at present only nine specimens are available[7]. They contrast with the Gorgonopsidae in the shape of the skull (very convex in dorsal profile), in the small size of the temporal fossae and the large size of the orbits, in the constitution of the basicranium, in the stage of evolution of the mandible (lack of a coronoid apophysis, reflected lamina of the angular reaching posteriorly to the articular region), and in the persistence of numerous and small post-canines. One notes, however, that a certain number of characters as significant as the position of the vomer and its shape, the position of the nostrils, and the nature of the teeth are not constant within the group. And even characters common to all the specimens (like the inter-temporal width, the proportions of the orbits and the temporal fossae) may in fact have a different significance according to the case. It thus appears probable that in an early form like *Hipposaurus* (from the base of the *Tapinocephalus* zone) these particularities, exemplified in moderation, only testify to an especially primitive state. On the contrary, in forms like *Lemurosaurus* Broom or *Ictidorhinus* Broom (which are as late as *Rubidgea*) these traits, which are here particularly evident, could indicate a specialized state. Under these conditions one can wonder if the status of this group is really taxonomically equivalent to that of the Gorgonopsidae (the generic criteria are not only different in the two cases but of inequal value), or if we are dealing with an infra-ordinal unit; the presence of a preparietal and the absence of a parietal crest do not require *ipso facto* a gorgonopsian identification.

But for the time being, this ''family'' comprises the four genera previously recognized, to which must be added the type of the infra-order Rubidginoidea, *Rubidgina* Broom. Of these five forms, as we have already noted, *Hipposaurus* appears as the least specialized; it seems also that the genus tended toward the gorgonopsid structural type: its vomer appears to have been already deeply situated (but its shape remains incompletely known) and the septomaxillary presents a transversal blade dividing the nostril into two compartments. What is more, an undescribed specimen (generously put at my disposal by Boonstra) that

I have referred to this genus differs from the type-species by the greater size of the temporal fossae and the beginning of a flattening of the cranial profile, accompanied by a correlative displacement of the nostrils; there is also a retreat of the mandibular and occipital articulations. These are all advances which make of it an intermediary between *Hipposaurus boonstrai* and the Gorgonopsidae. One may, however, object to this reasoning, based mostly on the generic identification of S.A.M. 122252 (object all the more since the anterior position of the occipital condyle is probably not an eo-gorgonopsid character). Recent information from Boonstra indicating that the stapes of *H. boonstrai* lacks a stapedial foramen contributes to this ambiguity.

Lycaenodon longiceps Broom (''*Hipposauroides rubidgei*'' Broom), known only by two anterior skull portions, approaches *Hipposaurus* by the proportions of the orbits and the temporal fossae. But the skull must have been wider and lower, evoking somewhat the Russian brithopodid *Syodon*. In fact, a certain parallelism with this family is found here in the length of the dorsal premaxillary processes, the constitution of the septomaxillary, the superficial position of the vomer and its concave form, in the reduction of the palatal tuberosities and in the position and form of the canines. However, it does not seem that one has here even an incipient indication of the inter-temporal constriction and the post-orbital twisting characteristic of this family.

The present position of the nostrils in the single specimen of *Ictidorhinus martinsi* Broom seems extremely suspicious, all the more since the septomaxillary appears to be of the same type as in *Lycaenodon* and that the vomer retains the same position and form. But the inter-orbital roof is here so wide posteriorly that the enormous orbits are masked in dorsal view, and the length of the temporal fossae is reduced to one third of the orbits. The opisthotic-quadrate contact is wide in posterior view (from which one may deduce that there was no coronoid process in the lower jaw). Nothing is known of the cheek dentition of the genus.

In *Lemurosaurus pricei* Broom one observes the same development of the orbits and the cranial roof, but, as in *Hipposaurus*, the vomer would occupy a dorsal position while the occipital condyle and the quadrate would be slightly displaced anteriorly. The great particularity of this skull (if one does not dwell upon the strange formation which covers the bone) resides in its dentition: its first anterior elements intermesh with corresponding teeth of the lower jaw and develop an incipient lingual talon. The post-canines themselves are more symmetrical and more coarsely denticulated than is usual in Gorgonopsians. The dental particularities bring to mind the condition in the Brithopodidae and the Dinocephalia.

If there is no doubt that *Rubidgina* can be integrated within this assemblage, it is less certain that it would not belong to the genus *Lemurosaurus*. The proportions of the orbits and the temporal fossae are similar, the upper and lower anterior incisors must have intermeshed, and the post-canines present a comparable morphology. But the details of the dentition in the other genera are not

known; moreover, the palatal dentigerous tuberosities are here much longer than in *Lemurosaurus*, and the proportions of the snout and of the inter-orbital roof are different. This could be only an effect of its small size or it could indicate a juvenile state (contradicted, though, by the size of the foramen magnum). However that may be, there do not seem to have been sub-orbital vacuities on the palate, as Broom suggested.

There remains a very small, hitherto undescribed, snout that I have referred to this family. The intermeshing of the first incisors and their incipient talon induced me to refer it at first to *Lemurosaurus*. However, the shape of the snout, for one thing, and of the palate (vomer and palatal tuberosities) for another, are very similar to those of *Lycaenodon*, but it should be kept in mind that the dental morphology is unknown in this genus.

The multiplicity of combinations of primitive and specialized characters would not be surprising did they not concern points as important as those cited above. But perhaps, morphologically, we are here at the heart of the great theriodont-anomodont subdivision; the resemblances of the Ictidorhinidae to the Russian eotheriodonts (*sensu lato*) would tend to confirm this interpretation. These resemblances left us also with the hope of finding there the origin of the Gorgonopsians.

Biarmosuchus Chudinov, one of the genera from the base of the Russian late Permian, strangely resembles the genus *Hipposaurus*. They both display the same cranial shape, the same proportions of the orbits and the temporal fossae, the same relation between the inter-orbital and the inter-temporal widths, the same position of the nostrils, the same orientation of the occiput, the same length of the prefrontals and lacrymals, the same position of the suspensorium, the same degree of evolution of the palate and the common persistence of numerous post-canines. The mandible in both cases is also very similar (absence of a coronoid process, posterior position of the reflected lamina of the angular). Lastly, the elements of the skeleton present the same gracility in the two genera. However, not only does *Biarmosuchus* lack those specializations of the Gorgonopsians already developed in *Hipposaurus*, but it has developed others, which orient it more in the direction of the brithopodids. We cite in particular the beginning of twisting in the post-orbital arch, with, correlatively, an incipient opening of the inter-temporal roof. The fact that the vomer is already deep and the stapes perforated is not in opposition to this interpretation; it only indicates that, on the brithopodid stem, a parallel, if not ancestral, line to ictidorhinids[8] would have rapidly developed.

The two other principal Russian eotheriodont genera, *Eotitanosuchus* Chudinov and *Phtinosuchus* Efremov, do not seem to provide us with more fruitful results. I have seen on these two skulls the same beginning of torsion of the post-orbital arch which, it seems to me, immediately isolates them from the gorgonopsian path. But, for *Eotitanosuchus* at least, evolution would have paralleled the gorgonopsids rather than the ictidorhinids.

The conclusion of this research on gorgonopsian origins remains therefore still rather negative. There is, however, no doubt that it is in detailing and enriching our knowledge of these intermediary forms—the ictidorhinids and the eotheriodonts—that the untangling of the threads of this evolution will be accomplished. All that can be said at present, in agreement with Boonstra, is that this theriodont branch became individualized early and quite probably rather rapidly. It thus arrived at a structure which was later but little modified and which found in this very precociousness the cause of its evolutionary sterility.

I

GENERA RETAINED*

Aelurognathus	Aelurosaurus
Aloposaurus	Arctognathus
Arctops	Broomicephalus
Broomisaurus	Cerdorhinus
Clelandina	Cyonosaurus
Dinogorgon	Eoarctops
Galesuchus	Gorgonops
Leontocephalus	Lycaenops
Prorubidgea	Rubidgea
Scylacops	Sycosaurus
Hipposaurus	Ictidorhinus
Lemurosaurus	Lycaenodon

Rubidgina

* Only type-species are considered here.

II

GENERA SYNONYMIZED*	WITH

1—*Gorgonopsidae*

Aelurosauroides	Aelurosaurus
Aelurosauropsis	Aelurosaurus
Alopecorhynchus	Cyonosaurus
Aloposauroides	Aloposaurus?
Arctognathoides	Arctognathus
Chiwetasaurus	Gorgonops
Cynarioides	Aloposaurus?
Cynariops	Scylacognathus
Cyniscops	Cyonosaurus
Cyniscopoides	Cyonosaurus
Dixeya	Aelurognathus
Dracocephalus	Clelandina
Galerhinus	Aelurosaurus
Galerhynchus	Cerdorhinus?
Gorgonognathus	Gorgonops
Leontosaurus	Sycosaurus
Leptotrachelus	Gorgonops
Lycaenodontoides	Arctognathus
Lycaenoides	Lycaenops
Nanogorgon	Aelurosaurus?
Pachyrhinos	Gorgonops
Pardocephalus	Arctops?
Scylacocephalus	Aelurosaurus?
Scymnognathus	Gorgonops
Smilesaurus	Arctops?
Sycocephalus	Scylacops
Tangagorgon	Lycaenops?
Tigricephalus	Lycaenops
Tigrisaurus	Rubidgea

* Only type-species are considered here.

2— *Ictidorhinidae*

Hipposauroides	Lycaenodon

III

UNCERTAIN GENERA

Arctosuchus
Cyniscodon
Delphaciognathus
Genovum
Lycosaurus
Cerdognathus
Cynodraco
Eriphostoma
Gorgonorhinus
Tetraodon

Tigrisuchus

1 Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris.

2 Exception made of those in the collections of North America.

3 In fact six genera are known from this zone, but the three others, continuing into the upper zones, will be discussed further on.

4 In the form of "*Aelurosauroides watsoni*" Boonstra.

5 Which I consider as homologous to *Cerdorhinus* Broom; but the law of priority would have demanded the abandonment of *Cyonosaurus* and the acceptance of *Cerdorhinus*, which I could not compel myself to do.

6 It still seems doubtful that any Gorgonopsian has less than five incisors.

7 Not counting the type of *Pseudohipposaurus kitchingi* Broom, which I was not able to locate.

8 It is not impossible that there was in *Biarmosuchus* some intermeshing of the incisors.