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Researches on the Structure, Organisation, and Classification of the Fossil Reptilia. Part IX., Section 1. On the Therosuchia

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XXI. *Researches on the Structure, Organisation, and Classification of the Fossil Reptilia.*—Part IX., Section 1. *On the Therosuchia.**

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[Plate 88.]

Contents.

Definition of Theriodontia.

The extinct order of fossil Reptilia named Theriodontia by Sir R. Owen in 1876,† has already been extended so as to comprise animals which are not included by the original definition.‡ It was founded upon skulls and fragments of skulls from South African rocks, chiefly obtained from localities near Fort Beaufort, the Sneeuwberg, and the Rhenosterberg. No other portion of the skeleton was known, except an isolated humerus referred to the genus *Cynodraco*, which cannot be proved to be part of the same animal as the skull fragment with which it was associated.

This order of animals was defined (*loc. cit.*, p. 15) in the following terms: "Dentition of the carnivorous type; incisors defined by position, and divided from molars by a large laniariform canine on each side in both upper and lower jaws, the lower canine crossing in front of the upper, as in Mammalia." This character had not previously been recognized among the Reptilia as having ordinal importance in classifica-

* This name does not refer in any way to the genus of Purbeck Crocodilia named *Theriosuchus* (Ow.); but indicates animals with a combination of saurian and mammalian character.

† 'Descriptive and illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum,' 4°, 1876.

‡ Zittel, 'Handbuch der Palæontologie,' vol. 3, p. 572.

tion, being only known as a mammalian character found in many different orders, such as Primates, Carnivora, Insectivora, Cheiroptera, Marsupialia, and certain ungulates. The fact that the character is not sufficient to define an order of mammals, has led me to doubt whether it is sufficient to define the animal group which some writers have named Theriodontia. Sir R. Owen did not adhere closely to the definition, since *Procolophon* was included under it, and in that genus there is no indication of such differentiation of the teeth, which are uniform in size, and conical.

As the order was at first constituted, it included animals showing some diversity of structure. It is, therefore, convenient to endeavour to fix the type which may be regarded as representative of the group ; and for that purpose I propose to take the genus which the author placed first upon his list. He divided the order into three families, and arranged the genera in groups in the following sequence :—

Binarialia with *Lycosaurus* and *Tigrisuchus*.

Mononarialia with *Cynodraco*, *Cynochampsa*, *Cynosuchus*, *Galesaurus*, *Nythosaurus*, *Scaloposaurus*, *Procolophon*.

Tectinarialia with *Gorgonops*.

I infer that *Lycosaurus* was regarded by the author as the type of the Theriodontia, because no reference is made to the family Cynodontia, formed in 1860 by Sir R. Owen for the genus *Galesaurus*.*

Dr. Zittel regards these three families as sections of the family Cynodontia, for which he takes as type the American genus *Clepsydrops* (Cope), which would thus become the type of the Theriodontia. But if the order is to be defined at all, its type can only be either *Lycosaurus*, which stands first on the list of constituent genera ; or *Galesaurus*, which was the type of the older family Cynodontia, which is absorbed in the larger group Theriodontia.

The difficulty in defining the order is the more evident since Dr. Zittel places in it the families Cynodontia, Pariotichidæ, Diadectidæ, and Endothiodontidæ, thus implying a community of structure, and since Mr. R. Lydekker† includes in the order the families Galesauridæ, Tapinocephalidæ, Diadectidæ, and Clepsydropidæ, placing *Galesaurus planiceps* first upon the list.

If the three types thus taken by different writers to represent the Theriodontia were known from complete skeletons or skulls, or were obviously members of the same family group, no inconvenience would follow. But the type species of *Lycosaurus* has the skull badly preserved, and the only well preserved skull is referred by Mr. R. Lydekker to the genus *Ælurosaurus*. The type of *Galesaurus* is so preserved that details of structure of the teeth are not shown. The essential parts of the skull in *Clepsydrops* are imperfectly known, though, in dental character,‡ it does not appear to differ substantially from *Lycosaurus*. It has therefore seemed

* 'Quart. Jour. Geol. Soc.,' vol. 16, p. 58.

† 'Cat. Foss. Rept. and Amphib., Brit. Mus.,' Part IV., 1890.

‡ Cope, 'Trans. Am. Phil. Soc.,' 1892, Plate 2, fig. 6.

desirable to re-examine the types of *Lycosaurus*, *Ælurosaurus*, and *Galesaurus*. The result is that several distinct animals appear to have been comprised in *Galesaurus planiceps;* that the generic distinctness of *Ælurosaurus* is evident, the genus being well differentiated from *Lycosaurus;* and that *Lycosaurus curvimola* supplies for the first time the means of defining the order Theriodontia by characters of the palate. The evidence on which these conclusions rest is now given.

The palate, and types of dentition in the Theriodontia.

I. *Galesaurus.*

In 1860, *Galesaurus planiceps* was the only South African reptile known to possess incisor, canine, and molar teeth. No molar tooth in the type specimen of that genus has the summit of the crown preserved. What remains shows the crowns to be flattened at the side and somewhat wide. In Sir R. Owen's 'Palæontology,' 2nd ed., 1861, p. 268, it is stated that "twelve close-set conical sub-compressed teeth succeed the canine in both jaws, holding the place of the molar series; they are of nearly equal size, but much less than the canines; those of the upper jaw pass external to the lower molars when the mouth is shut." "The canines have the same relative positions to each other, as in mammals, the lower passing in front and on the inner side of the upper when the mouth is shut." "Both the upper and lower incisors are arranged in contact or close order, as in mammals."

In this specimen no indication is recorded of lateral cusps to the molar teeth, and therefore there is no difference from *Lycosaurus* in dental type which is evident. So that all the genera included in the Theriodontia in 1876 were characterized, so far as known, by having simple conical pointed teeth without cusps, except that *Nythosaurus* is said to show indications that the laterally compressed crowns of the upper molars are notched at their somewhat expanded borders. It is added: the molars in *Galesaurus* are too mutilated to show such character, if it existed. There is no doubt expressed till 1887 concerning the Theriodont type of the molar tooth of *Galesaurus*. The group was enlarged in 1876 by recognition of Theriodonts in the Permian rocks of Russia; but the teeth of *Deuterosaurus* were compared to those of *Lycosaurus** and *Cynodraco*. *Titanosuchus ferox*, described by Sir R. Owen in 1879, made known a large animal in which the crowns of the teeth are lost, but transverse sections show no specialization of the numerous and relatively small molars† which succeed the large canine. The description of *Ælurosaurus* in 1881‡ showed small and pointed molar teeth which make no deviation from the Lycosaurian type (p. 992).

Sir R. Owen's last memoir on "South African Reptilia," in 1887, is professedly an

* 'Quart. Jour. Geol. Soc.,' vol. 32, p. 352.
† 'Quart. Jour. Geol. Soc.,' vol. 35, p. 189.
‡ 'Quart. Jour. Geol. Soc.,' vol. 37, p. 261.

account of the skull and dentition of *Galesaurus planiceps*.* This second specimen has been accepted by myself ('Phil. Trans.,' 1889) and subsequent writers, as the type of *Galesaurus*. It made known among Theriodonts the palate, and the form of molar teeth, with lateral cusps, which had been imperfectly suggested by *Nythosaurus*. This fossil from Thaba-chou, Basutoland, gave the genus a different aspect in 1887 from what it had in 1860 on the evidence of the Rhenosterberg specimen.

The two skulls are similar in size and general aspect, but when critically compared, they show differences which may be of generic value.

The obvious differences between them are that (1) in the type specimen of 1859–60, the occipital plate is exposed as a large inclined surface which extends forward, with the bifurcation of the parietal crest, between the temporal vacuities for more than a third of their length; in the second specimen of 1887 the occipital plate is not exposed, but was manifestly more nearly vertical, and the bifurcation of the parietal bones only slightly indents the back of the skull. (2) In the type the parietal foramen is one-third of the length of the temporal vacuity from its anterior border; in the second specimen this foramen is in the middle length of the temporal vacuity. (3) In the type, the temporal vacuities are narrow, oblique, and have the aspect of their long axes converging forward; in the other specimen they are longitudinally ovate, and the long axes are nearly parallel to each other. (4) The width of the cerebral region at the parietal foramen in the second specimen is seven-tenths of its width in the type. (5) In the type the orbits are sub-triangular; in the other specimen they are circular. (6) In the type the frontal bone has a median suture; in the other skull the median suture is absent or obliterated. (7) The dental formula seen in the type is $I\frac{4}{4}.c\frac{1}{1}.m\frac{10}{12}$; while in the other skull it is $I4.c1.m6$, and the molar teeth of the second specimen have a lateral cusp on each side of the median cusp, which is conical. I regard generic difference between these fossils as being probably established by these characters. The palate of the 1859–60 specimen is unknown.

There appear to be two other genera with cuspidate molars, *Scaloposaurus* and *Nythosaurus;* the latter known only from a cast of the skull from which the teeth are lost. *Scaloposaurus* has the skull of different form; and though the teeth are tricusped they are more slender and more numerous. I formerly identified the second type of skull (1887) with *Nythosaurus*. In that genus no evidence of the incisors is preserved, and the number of molars behind the canine is eight in the upper jaw, and seven in the mandible. These teeth are wide, close-set, in sockets, with a distinct cingulum at the base of the crown. The pre-molar teeth have three nearly equal cusps, and the molar teeth have five nearly equal cusps. In its smaller number of teeth *Nythosaurus larvatus* is distinct from the type of *Galesaurus planiceps;* and in the greater number of cusps and larger size of the

* 'Quart. Jour. Geol. Soc.,' vol. 43, p. 1.

more numerous teeth *Nythosaurus larvatus* is also distinct from Sir R. Owen's second type of *Galesaurus*, described in 1887. It is not impossible that the teeth of the type of *Galesaurus planiceps* may have had the three and five-cusped crowns seen in *Nythosaurus larvatus*, but at present, proof of their generic identity is not known. The five-cusped molar is probably a generic difference from the three-cusped molar. Hence I arrive at the result that there is no ground for referring the Galesauroid skulls, which the British Museum obtained from Dr. Exton, from Basutoland and the Orange Free State, to either *Galesaurus* or *Nythosaurus*, supposing those genera to be distinct. I suggest for the genus ('Quart. Jour. Geol. Soc.,' vol. 43, plate 1) the provisional name *Thrinaxodon;* the species may be known as *T. liorhinus*. It is thus evident that besides types with simple pointed or serrated molar teeth, the Theriodontia includes a group of genera with laterally cuspidate molars. These groups of animals may be separated as distinct families, if not sub-orders of Theriodontia, by many characters of the skull and dentition. Yet in describing *Thrinaxodon liorhinus*, in 1886–7, Sir R. Owen refers to *Galesaurus planiceps* as the type of the order. The evidence of dentition in *Galesaurus* remains what it was in 1859–60, and there is no proof whether the teeth had any cusps, or three, or five; so that there is no ground for transferring the type of the order from *Lycosaurus* to *Galesaurus*. It is probable that *Galesaurus* was like *Thrinaxodon* and *Nythosaurus* in molar dentition. Hence it may be convenient to retain the name Cynodontia,* to distinguish the genera with laterally cuspidate molars, since other genera occur with similar teeth, divided from the incisors by canines.

Fig. 1.

Comparison of the molar teeth of (*a*) *Nythosaurus larvatus*, and (*b*) *Thrinaxodon liorhinus*.

II. *Ælurosaurus.*

Ælurosaurus closely resembles *Lycosaurus* in its dentition, especially the species *Lycosaurus curvimola*. On that resemblance, apparently, Mr. R. Lydekker† removed the *Lycosaurus curvimola* to the genus founded on *Ælurosaurus felinus*. As the skulls are dissimilar, I submit the following further evidence of the nature of *Ælurosaurus*, based upon the original specimen described by Sir R. Owen.

The skull has lost the occipital and parietal regions, but the missing part is inferred to have been short from the circumstance that the squamosal bone descends to form the articulation for the lower jaw, in a way which may be compared with that shown

* Cynodont molar teeth are drawn in Plate 88, fig. 6.

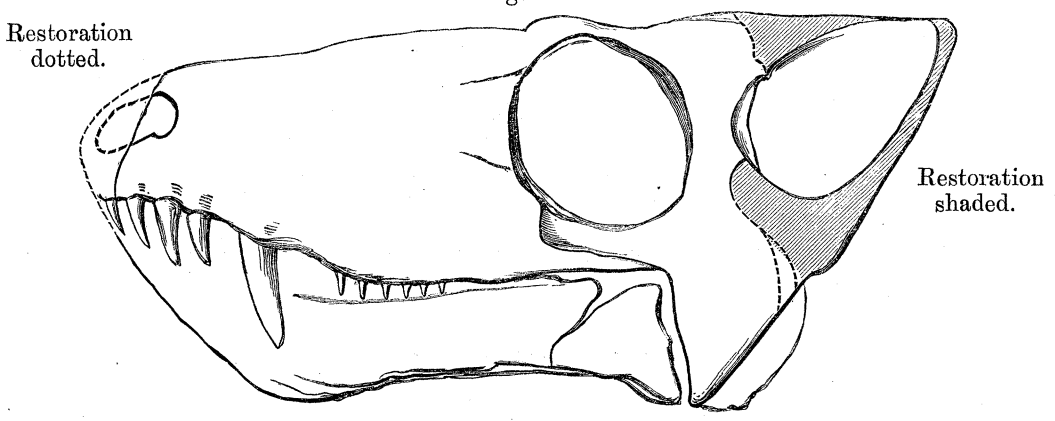
† 'Cat. Foss. Rept. and Amphib., Brit. Mus.,' Part IV., 1890 p. 77.

in *Delphinognathus conocephalus* (' Quart. Jour. Geol. Soc.,' 1892, vol. 48, p. 470), in which, also, the articulation for the lower jaw is below the back of the orbit. On this basis I offer a restoration of the skull of *Ælurosaurus felinus*, from which it seems probable that the proportions of the parts of the head must have been dissimilar in *Ælurosaurus felinus* and *Lycosaurus curvimola*.

The lower jaw shows some distinctive features. The suture between the rami is persistent, notwithstanding the great depth of the symphysis. The whole length of the dentary bone is flanked internally by a large sphenial bone, and the suture is manifest along the inferior edge of the jaw. The sphenial bones unite anteriorly. Behind the dentary bone externally is a large thin sub-triangular bone, which abuts against the articular part of the squamosal, and covers an area of the lower jaw which is excavated in all known Cynodontia. This bone is hence likely to be the sur-angular, an element which I have not seen in that form or position in any other skull; yet affinity with *Delphinocephalus* would not support that interpretation.

The matrix has been slightly removed at my suggestion from the palate, which shows a typically Theriodont plan of construction in the development of plates, which extend transversely outward and downward from the back of the palatine region to abut against the lower jaw (Plate 88, fig. 2*t*), in a position which is below the orbits. Upon this transverse-palatine ridge is a row of small teeth, indicated by their circular bases.

Fig. 2.



Left side of the skull of *Ælurosaurus felinus*, restored.

In advance of the compressed transverse plates there is evidence of a horizontal plate, which may be vomerine, upon which there are placed laterally symmetrical groups of small cylindrical teeth, which appear to have the crowns rounded hemispherically.

There is a posterior patch of about fifteen teeth on each side of this area, rather more densely grouped, in three rows. Anterior to these teeth appear to be three other rows less dense, with the rows more elongated, and having the external series of the palatal teeth somewhat larger (Plate 88, fig. 2*v*).

Posterior to the transverse palatine processes is the vertically compressed median keel of the sphenoidal region (fig. 2*ps*), which appears to be developed as in all Theriodonts from South Africa, in which the palate is known.

The development of teeth upon the palate finds no parallel in *Lycosaurus curvimola*. It indicates some approximation to the condition seen in *Procolophon* and *Pareiasaurus*, and demonstrates that a Theriodont may have the palate covered with teeth. Neither *Pareiasaurus* nor *Procolophon* have the transverse palatine processes developed downward, in the way found in Theriodonts; but they are strongly developed in *Pareiasaurus*, carry teeth, are truncated externally, and when the lower jaw is closed they extend between the rami of the mandible in a way which establishes a close affinity between the Theriodontia and Pareiasauria. Until the palate is known in the allies of *Tapinocephalus*, it cannot be regarded as established that the systematic position of *Ælurosaurus* is with the Lycosauria.

III. *Lycosaurus*.

The specimen No. 47,339 in the British Museum, named *Lycosaurus curvimola* (Owen), from Kugaberg, near Stewart's Farm, was presented by Mr. A. G. Bain. I see no reason to doubt its generic association with the less perfectly preserved skull fragments referred to the same genus. *Lycosaurus pardialis* and *Lycosaurus tigrinus* are both too much crushed and too imperfect to admit of the necessary work of development with the chisel to display the skull structure, and I therefore propose to regard *Lycosaurus curvimola* as the type of *Lycosaurus*.

The palate of this type, like that of every other described African Theriodont, except *Thrinaxodon*, has hitherto been unknown. But it is upon the characters of the palate that the order will be established, as distinct from the Bidentalia or Dicynodontia. The palate has therefore been excavated at my request, in the workshops of the British Museum, by Mr. Richard Hall. It now shows the striking fact that this type, with small and slender conical curved molar teeth, does not differ in essential characters of palate structure from the Cynodontia, which I obtained at Lady Frere. The sphenoidal bar is long and slender (Plate 88, fig. 1), and its most dictinctive feature appears to be an angular bend which it makes with the anterior part of the palate where the transverse palatine processes *t* are developed downward. The posterior sphenoidal region (*bs*) makes but a small angle with a part of the occipital region which is preserved. This is a slight approximation to the condition of the sphenoidal region found in *Rhopalodon* and *Deuterosaurus* from the Permian rocks of Russia. The palate is vaulted in the region of the palato-nares, and this concavity is prolonged backward as a narrow channel defined laterally by short, strong, compressed ridges, which approximate posteriorly. At the back of this groove the processes of the palatine and transverse bones (the sutures are not seen) which diverge transversely outward and down-

ward, abut against the inner side of the lower jaw and descend to its base (*t*), in a line which appears to correspond with the back of the orbit, though the skull is distorted. These processes are compressed from front to back, and terminate inferiorly in a sharp ridge which forms a concave arch, as it extends from side to side at the back of the palate. These processes are one of the most distinctive ordinal characters of the Theriodontia, which they share with other Therosuchia.

Behind the intramandibular processes is the long sharp laterally compressed pre-sphenoid keel, which widens posteriorly into the obliquely truncated triangular mass, which I regard as the basi-sphenoid. It closely resembles the basi-sphenoid of a Chelonian, though it is nearly in the same plane with the back of the skull. The median sphenoidal bar in front terminates inferiorly in a sharp ridge, which is flanked by the pterygoid bones. These bones are compressed from above downward, are in contact with the sphenoidal keel, but in a plane at some height above its base. As they extend backward they widen transversely, and are prolonged horizontally outward (*pt*), so as to be separated from the opisthotic region at the base of the occipital plate, by a transverse inferior foramen like that seen in *Cynognathus*. The external bar of the pterygoid is slender and thin, and the union which it may be supposed to have made with the quadrate bone is not seen. The triangular surface of the basi-sphenoid between the pterygoid bones is a little wider than long.

The foramen magnum is small and vertical. There do not appear to be any occipital condyles preserved.

The palate now described is similar to that of *Cynognathus*, which may be regarded as typical of the Cynodontia, so as to prove that both forms of skull and dentition may be included in the order Theriodontia. *Lycosaurus* may therefore be both the type of the order Theriodontia, and the type of the division of it characterised by simple conical compressed molar teeth (Plate 88, fig. 1*m*), which may be termed Lycosauria.*

In illustration of known variation in incisor teeth in skulls of this Lycosaurian type, I append here a note on the snout of *Pristerognathus polyodon*.

Pristerognathus polyodon (Seeley). Plate 88, fig. 3.

At a locality known as Cypher, to the east of Tamboer Fontein, I found the weathered extremity of a snout of a Theriodont. It is the only example of an animal with that type of dentition which I met with in the lower Karroo rocks, though not the only Theriodont which they have yielded. It is in bad preservation, having been long exposed to the solvent and disintegrating action of the atmosphere; and is a

* I formerly used the term Gennetotheria for this group, when its distinctness from the Cynodont type was recognized ('Phil. Trans.,' 1889). But as that name had been associated with *Propappus*, it is now relinquished in favour of Lycosauria.

little distorted by oblique compression, like most of the Karroo fossils. As it appears to indicate a different genus from any of the types hitherto defined, characterized by its incisor dentition, I describe its distinguishing characters. Many of the types described by Sir RICHARD OWEN are known from similarly imperfect materials, and therefore it admits of definite comparison with them. Among such genera are *Cynochampsa*, *Cynodraco*, *Tigrisuchus*.

The dental formulæ of these types, as determined by Sir R. OWEN, are given in the following tabular statement, and I have added to them the tooth formula of *Cynosuchus* and *Lycosaurus*, all of which types I suppose to have possessed molar teeth of simple conical form, like those seen in the jaws of *Ælurosaurus* and *Lycosaurus*, but the crowns of the molars are known only in those genera.

Pristerognathus	I. $\frac{6-6}{3-3}$	c. $\frac{1-1}{1-1}$	m. $\frac{4+-}{}$
Ælurosaurus	I. $\frac{5-5}{5-5}$	c. $\frac{1-1}{1-1}$	m. $\frac{5-5}{5-5}$
Cynodraco	I. $\frac{5-5}{4-4}$	c. $\frac{1-1}{1-1}$	m. ?
Titanosuchus	I. $\frac{5-5}{4-4}$	c. $\frac{1-1}{1-1}$	m. $\frac{11-11}{10-10}$ (or 11)
Cynochampsa	I. $\frac{4-4}{3-3}$	c. $\frac{1-1}{1-1}$	m. ?
Cynosuchus	I. $\frac{4-4}{}$	c. $\frac{1-1}{}$	m. $\frac{7-7}{}$
Tigrisuchus	I. $\frac{3-3}{}$	c. $\frac{1-1}{}$	m. ?
Lycosaurus	I. $\frac{4-4}{3-3}$	c. $\frac{1-1}{1-1}$	m. $\frac{5-5}{5-5}$

It is thus evident that *Pristerognathus* differs from all Theriodonts hitherto known, first in the large number of its superior incisors, which is greater than in any previously known genus, and exceeds the number in Opossums; and, secondly, in the relatively small number of the incisors in the lower jaw.

The fragment is $3\frac{1}{2}$ inches long and $2\frac{1}{4}$ inches wide external to the canines, with the anterior alveolar border convexly rounded in front, and rising in the usual way, a little in advance of the teeth, in a manner which characterizes most, if not all, Theriodont genera. The lower jaw fits within the canines and incisors of the upper jaw in the usual way, and the inferior canines pierce through the maxillary bones into the skull as in all known Theriodonts.

The rami of the mandible are entirely separate, the suture persisting with a distinctness which is not seen in other genera (fig. 3). Their anterior surface is rounded from side to side, and the chin retreats as it descends. Only about $1\frac{3}{10}$ inch of its depth is preserved. The least transverse width below the maxillary canines is $1\frac{3}{10}$ inch, while

external to the mandibular canines the width exceeds $1\frac{1}{2}$ inch. This anterior surface is marked with numerous small vascular foramina. The rami diverge at an angle of about 40°. The dentary bone behind the symphysial area is about $\frac{3}{10}$ inch thick, and is not in close contact with the thin splenial bone, which extends along its inner side, as in other Theriodonts.

The large mandibular canine is only exposed on the right side, except that the roots are shown by the inferior fracture of the base of the jaw to be quite close to its antero-lateral angle, while the alveolar border is about an inch behind its anterior extremity. This canine is ovate in section, and apparently has sharp cutting margins back and front. It is almost or entirely in front of the maxillary canine, and large, but its entire width is not exposed.

The dentary incisors have their crowns preserved on the right side. They are three in each dentary bone, placed in sockets so as to occupy the space in front of the canine. The roots appear to be ovate. The crowns decrease in size from the first to the third. They are long, curved backward, convex externally, terminating laterally in sharp curved finely serrated margins. No indications are preserved of teeth behind the canines. The three incisors and their interspaces occupy a width of $\frac{7}{10}$ inch.

The anterior nares show no trace of median division, but as the preservation is unsatisfactory, it is impossible to affirm that there was but one aperture. Further back, at the posterior fracture, there is a strong median division separating the chamber above the palate into two lateral parts. It appears to be formed by bones which diverge in a broad Λ-shape extending outward to the maxillary. They are apparently the palatines.

The nasals, which form the median roof bones of the skull, are crushed, so that their width cannot be measured, though it exceeded one inch.

The maxillary bones, which form the side of the jaw, and ascend somewhat convexly to the upper surface, are sculptured with a fine sub-crocodilian ornament. The anterior border of the bone extends forward by squamous overlap upon the premaxillary alveolar border, as in Deuterosauria, so that the premaxillary bones extend further backward than is shown by the external position of the suture. All the incisor teeth are in the premaxillary bone, but there is no evidence whether it forms part of the socket for the canine. The incisors are six in number in each premaxillary. The crowns are lost (fig. 3, 1–6). The roots show the first to have been circular, but all others are ovate, with the long axes in longitudinal sequence. The second to the fifth are nearly uniform in size, but the sixth is smaller. The measurement from the first to the sixth is $1\frac{4}{10}$ inch. The transverse measurement over the palate at the sixth is $1\frac{9}{10}$ inch. The front pair of incisors is in near contact, so that they are between the larger front pair of mandibular incisors, though externally in advance of them. The anterior margin of the root of the canine (c) is $1\frac{8}{10}$ inch behind the median premaxillary suture. It is broken away, but enough remains to show that the crown was ovate in section, $\frac{11}{20}$ inch wide, $\frac{3}{10}$ inch thick, rounded on the anterior border,

compressed on the posterior border to a sharp edge, which is serrated. The molar teeth indicated, rather than preserved, have lost their crowns, and the few sections of their roots appear to be rather more circular than those of the incisors, and if not smaller, were not larger.

The genus is defined by having the twelve incisor teeth in the upper jaw ovate in section, compressed from within outward; and the six incisor teeth in the mandible have the curved crowns compressed to sharp serrated edges, and decrease in size from the median line. The mandibular canines appear to be completely hidden when the jaw is closed.

Thus the Theriodontia, as originally defined, included first a group of animals with skulls formed on the type of *Lycosaurus;* secondly, a group with skulls formed on the type of *Thrinaxodon*, and these groups with similar "Theriodont" dentition are united by a community of structure of the palate which distinguishes them from the Dicynodonts. This is the most important difference known between these groups.

Professor E. D. Cope has stated,* "It is evident that the Anomodontia differ from the Theriodonta in the absence of a zygomatic arch, and in the presence of a supratemporal arch, which is separated from the parietal bone by a supratemporal foramen." I cannot admit this distinction, if it is intended to imply a structural difference in the groups. I can find no difference in the character of the arch in the two groups, except that in the Theriodont the malar bone has a greater external backward development than in Dicynodonts; and that in Dicynodonts the squamosal bone has a greater downward development than is usually seen in the Cynodontia; but the difference between the groups is not due to any difference in the nature of the arches, but to a less development of the quadrate bone in the Theriodontia, which has resulted in a diminution (*Ælurosaurus* and *Lycosaurus*) or atrophy (*Thrinaxodon*) of the descending pedicle of the squamosal bone.† I therefore find no facts to support Professor Cope's arrangement of the Permian Reptilia, which he classifies by theoretical interpretations of this arch.

The two orders, Dicynodontia and Theriodontia, are absolutely distinct in palatal characters, but there is no manifest distinction in the post-orbital arch. It will be

* 'Trans. Am. Phil. Soc.,' vol. 17, p. 16, 1892.

† Professor Cope ('Proc. Am. Assoc. Adv. Sci.,' vol. 33, p. 473, 1885) describes the quadrate bone in *Clepsydrops* as consisting of two portions, one vertical, the other transverse; and adds: "This horizontal ramus of the quadrate is nothing more than the zygomatic process of the squamosal bone of the mammalia, forming with the malar bone the zygomatic arch:" "hence we have here a reptile with a zygomatic arch attached to the distal extremity of the quadrate bone." This condition is not evident in Professor Cope's figures of *Clepsydrops* and other genera given in 1892 ('Trans. Am. Phil. Soc.'), where a large horizontal bone in some genera (lettered Z) is described as "zygomatic (quadrato-jugal)." No such condition is seen in true Theriodonts, in which the zygoma is formed by the horizontal branch of the squamosal bone and the malar bone, though the external bar of the squamosal has the aspect of being divided by a vertical fracture or suture in one or two specimens of South African Theriodonts.

shown that there is a foramen in the post-orbital arch of one species of *Cynognathus*, but it is wanting in another species of the same genus.

I am unable to find any justification for Professor Cope's suggestion to replace the group Pareiasauria by the Cotylosauria,* based upon American types. In his second contribution to the "History of the Permian Vertebrata of Texas," ('Proc. Am. Phil. Soc.,' 1880, vol. 19, p. 45), it is mentioned that the author felt justified in proposing a new division of the Theromorpha ('Am. Nat.,' 1878), to include the Diadectidæ, to be called Cotylosauria ('Am. Nat.,' 1880, p. 304). I believed that group, with *Empedias* as its figured type, to conveniently define animals with teeth of a transverse insectivorous type ('Proc. Am. Phil. Soc.,' 1878, p. 516; 1880, p. 634; vol. 19, Plate 5, 1881). In the side view of the skull three fragments appear to be known; and in the restoration which connects them a considerable temporal vacuity is shown. In 1892, Professor Cope defined the Cotylosauria as distinguished by having the temporal vacuities entired roofed over: the group is then made to comprise the genera *Chilonyx*, *Pantylus*, and *Pariotichus* in America, probably *Pareiasaurus* from South Africa, and *Phanerosaurus* from the Permian of Germany. It is therefore evident that the Cotylosauria of 1892 (Cope) has no obvious relation to the group so named by him in 1881. I make this statement in this place in illustration of difficulties in attempting to correlate unfigured American genera with the materials from South Africa; and without examining the specimens it would be impossible to say whether the unfigured genera can be referred to European or African groups of animals.

Whatever may prove to be the systematic position of the genera *Chilonyx*, *Pantylus*, *Pariotichus*, *Edaphosaurus*, *Clepsydrops*, *Naosaurus* and *Diopeus*, I gather from Professor Cope's figures ('Trans. Am. Phil. Soc.,' 1892) that so far as the teeth are concerned, there appears to be a close resemblance of *Clepsydrops* to *Lycosaurus*. This may possibly extend to *Naosaurus*, though the canines and incisors do not appear to be preserved. *Pantylus* appears to have a canine dividing incisors and molars, but in *Edaphosaurus* and *Pariotichus* there is no evidence of a functionally developed canine, and there is no evidence from the figures that the teeth are preserved in *Chilonyx* and *Diopeus*. The original description of *Chilonyx* ('Proc. Am. Phil. Soc.,' 1883, p. 631) indicates for that genus, apparently, teeth of the type seen in *Empedias*, which makes it impossible to place the transversely wide crushing teeth of this type in the same family with *Clepsydrops*, which has piercing and tearing teeth.

There are similar difficulties with the classification of African types, due partly to imperfection of evidence, and partly the result of diversity of character. They raise the question whether the original dental definition of the Theriodontia should be retained or abandoned.

There is a third group of true Theriodonts, which falls within Sir R. Owen's

* 'Trans. Am. Phil. Soc.,' vol. 17, 1892, pp. 13, 16.

definition, the Gomphodontia, comprising the allies of the new genera *Gomphognathus* and *Trirhachodon*, which shows but little difference from the Cynodontia in the form of the skull or the structure of the palate, but has the molar teeth modified for grinding.

These three groups are so far parallel to certain types of placental and marsupial mammalia as to suggest the possibility of further dental variation, by the suppression of the incisor teeth, of the canines, or of the molars. The evidences of such modifications of the dentition among fossils from South Africa are not complete. But if it can be shown that the palate retains the same type of structure as in the Lycosauria there may be sufficient reason for associating any such family with the Theriodontia as a parallel group, even though it does not conform to the original definition of the order. But its inclusion in the Theriodontia would necessitate a new definition for the extended group, which, by absorbing the Theriodontia, would substitute for it another group of animals.

So long as there is evidence that the plan of a natural group is the same, there should be no more difficulty in comprising within it closely allied minor groups of animals than there is in including diverse dental types among the Marsupialia or Lacertilia. It would be impossible to use the name Theriodontia for such an enlarged group, if the Theriodontia were retained in the terms of Sir R. Owen's original definition. Thus, in the genus *Deuterosaurus*, from the Permian of Russia, the molar teeth are apparently reduced to a single tooth on each side. It is therefore conceivable that the molar teeth might disappear entirely. There is some reason for thinking that such a type exists. Sir R. Owen described several genera, such as *Cynodraco*, *Cynochampsa*, *Tigrisuchus*, in which no molar teeth are recorded. That condition, however, is associated with fracture of the snout; and there is no evidence that those genera are not allied to *Lycosaurus* or to *Ælurosaurus*, though they may be allied to *Gorgonops*, which is not so obviously Theriodont in dentition. In that genus the head is elongated, without evidence of posterior transverse expansion which is usually seen in Theriodonts. The temporal vacuities are roofed over with bone, as in *Pareiasaurus*, and the bone is smooth. The condition of roofing of the skull however is unlike *Pareiasaurus*, because the roof-bones are continuous with the vertical occipital plate, closing in the back of the skull, as in *Kistecephalus*. There is no indication that the articulation for the lower jaw descended below the level of the palate, or that the transverse-palatine processes were developed downward between the mandible, and it is on this character that the inclusion of the Gorgonopsia in the same group with the Theriodontia would depend. This condition however results from the state of preservation* of the specimen. It is evident that those processes, which are now broken away, attained a considerable downward development, but it is not evident that they terminated externally in the thickened lateral truncated surfaces seen in typical Theriodonts. Enough however remains to

* 'Cat. Foss. Rept. South Africa,' Plate 21, fig. 2.

justify the association of the Gorgonopsia with the Theriodontia in one larger group, so far as palatal characters are concerned. There are incisor teeth and canines, but I am unable to recognize molars; of which Sir R. Owen thought there were one or two doubtful indications, which are not shown in his figure. The nares are crushed and have a transverse dumb-bell like form, as preserved, which led Sir R. Owen to place the genus in a distinct family, Tectinarialia. I attach no importance in classification to this form of nostril, or to the single or divided nares of other genera. For the nares in all typical Theriodont animals being terminal, the existence or width of the inter-nasal septum is difference of degree, not of kind, and is influenced by its state of preservation.

South African groups of Reptilia which approximate to Theriodontia in structure of the palate, but differ in dentition and structure of the skull.

Very little importance can be attached to the complete roofing of the skull. In the Museum of the Royal College of Surgeons, there has long been a skull of a recent Crocodile in which there are no supra-temporal vacuities. The roofing of the skull of *Pareiasaurus* is essentially comparable to the condition in certain Chelonia, for the roof is distinct from the back of the brain case. I therefore suppose it might be similarly absorbed in both groups. And such a difference as distinguishes the roof of the skull of *Chelone* from *Testudo*, defines the difference in this respect between the skulls of *Pareiasaurus* and the typical Theriodonts. There are many other differences, however, in the skull. The large single sub-ovate occipital condyle of *Pareiasaurus* with its central concavity is unparalleled in any known Theriodont. The posterior nares are carried further back on the palate. There is no median keel to the presphenoid exposed behind the posterior nares, and therefore no extension of the pterygoid bones along the margin of that keel. The quadrate bones attain a development unknown in typical Theriodonts. And the transverse truncated processes of the palate, which abut against the lower jaw, are directed forward and downward, owing to the backward position of the palato-nares. There is no conspicuous coronoid process to the lower jaw. It is not obvious that the differences of this type of skull from *Ælurosaurus* and *Gorgonops*, are of the same order as those which separate it from the Lycosauria, Cynodontia, and Gomphodontia. If the Theriodontia is limited to the latter three closely allied groups, there can be no doubt that the Pareiasauria lies entirely outside the Theriodontia. But with the affinity of the skeleton between *Pareiasaurus* and the Deuterosauria on the one hand, and between *Pareiasaurus* and *Theriodesmus* on the other hand, it is obvious that the relationship between *Pareiasaurus* and the Theriodont type of animal is closer than might have been suspected from the skull. Both are not improbably closely related constituent members of a larger group of animals. The peculiar laterally cuspidate structure of all the teeth of *Pareiasaurus*, and the unvaried condition of the teeth from front to back, demonstrates that the canine

tooth is not unrecognized on account of small size, as it might be in a Lycosaurian, but that no canine tooth or incisor was ever differentiated. Therefore a difference, which is possibly subordinal, separates the Pareiasaurian dentition, which may be conveniently distinguished as Homalodont, from the Theriodont specialization of teeth.

Another dental type from South Africa is that in which the incisor or other alveolar teeth are lost, and the palate retains evidence of Theriodont construction. This group may apparently develop canine teeth, and possibly other kinds of teeth, so that the Endothiodont dentition may not be so exceptional as it at first appeared to be.

Endothiodontia.

The only genus of this group hitherto defined is *Endothiodon*, of which the type is *Endothiodon bathystoma*. I, at present, know of no other species which can be included in the same genus. This type is known from the anterior parts of the lower jaw and skull from the Oude Kloof, on which Sir Richard Owen founded the genus, and the complete ramus of the lower jaw and zygoma given me by Mr. T. Bain,* now presented to the British Museum. On these materials the genus *Endothiodon* may be defined as devoid of teeth in the anterior part of the jaws; with the mandibular teeth in parallel rows, each tooth having a long crown, compressed and serrated on both the front and back margins. There is no ascending coronoid process to the lower jaw. There is a smaller perforation in the jaw than in *Dicynodon*. There is a large excavation on the external side of the mandible, in front of the terminal articulation. The nares are lateral and terminal, and the palato-nares deeply excavated, forming a channel behind the narrow vomerine bones in front, margined laterally by the palatine bones, which are strongly developed on their external border, descending between the rami of the mandible. There is no trace of division of the palato-nares.

It thus appears that the Endothiodontia parallel the Edentata in the absence of teeth in the front of the jaws. They are characterized by having teeth which are removed from the usual marginal position on the jaws.

A second genus, which may possibly find a place in this group, is *Pristerodon*, described in 1868, by Professor Huxley, from specimens obtained by Mr. McKay, of East London.† It has a depressed form of skull, somewhat Dicynodont in aspect, with a moderately wide flat area between the temporal vacuities, and, so far as can be seen, is without any conspicuous descending process in the squamosal region for articulation with the lower jaw. The materials are not well-preserved, but apparently there are no teeth in the front of the jaw. All the teeth in the maxillary region are characterized by long compressed crowns, with a smooth sharp anterior border, and a serrated posterior border. Besides the principal external row of teeth, there are on the

* 'Quart. Jour. Geol. Soc.,' 1892, vol. 48, p. 476.

† 'Geol. Mag.,' 1868, p. 201, Plate 12.

inner side other teeth at a lower level; and, although too few are preserved to indicate parallel rows in the lower jaw like those of *Endothiodon*, they seem to me as likely to indicate portions of parallel rows compressed together, as to be successional teeth in stages of development. If this genus is rightly referred to this group, it is the only specimen which shows the external structure of the superior part of the skull.

In 1879, Sir R. Owen described as a second species *Endothiodon uniseries*,* known from the anterior part of the skull, which exhibits the structure of the palate. The teeth are far removed from the sharp external margin of the jaw, and form a single series. I regard this fossil as the type of a distinct genus, which I propose to define as *Esoterodon*. This genus is devoid of teeth in the front of the jaw, like all known Endothiodonts. The teeth form a single series upon the maxillary bone, with the rows divided from each other by the vomera. The teeth are parallel to the cutting margin of the jaw. Their crowns were probably conical and pointed, but are not preserved. The anterior nares are lateral, the palato-nares are exposed in a deep groove with sharp lateral margins bounded by the palatine bones as in *Endothiodon*, and as in the Cynodontia.

Cryptocynodon simus. Plate 88, figs. 4, 5.

A modification of the dental type of *Esoterodon* may be indicated by a small fossil, which I found in soft green shales at Molteno Pass, in the Nieuwveldt range. This specimen is in bad preservation, and only known from the anterior half of the skull. It is about two inches long, and does not show the back of the orbit. It agrees with *Esoterodon uniseries* (Owen) in the toothless condition of the front of the jaw, which is concavely excavated in a similar way, but it appears to differ in having a single minute canine tooth upon the alveolar border. This may be associated with other differences of a generic character, difficult to define on account of the condition of preservation. I have suggested a distinct generic name for the fossil, which is the more interesting as combining in a Theriodont type of skull, the palatal teeth of *Esoterodon*, with canines situate like those of *Dicynodon*. I believe it belongs to the Endothiodontia, but it is the only Endothiodont with canine teeth. *Cryptocynodon simus* is interesting from the circumstance that the maxillary teeth form a row of about six or seven close set cylindrical crowns which appear to commence behind the middle of the palate, and diverge to the hinder external angle of the maxillary bone, so that the canine is external in position to the front tooth. This is only an extreme modification of the condition of the canine in *Titanosuchus ferox* (Owen) ('Quart. Jour. Geol. Soc.,' vol. 35, Plate 11), which, with other evidence, led me to regard the incisors, canines, and morals of Theriodonts as representing three or more parallel rows of teeth, not all developed simultaneously, which

* 'Quart. Jour. Geol. Soc.,' 1879, vol. 35, p. 557, Plate 27.

may be compared with the parallel rows of teeth in the mandible of *Endothiodon*. The type specimen is somewhat distorted.

The palate is arched in front, with the sides of the maxillary bones apparently parallel. The maxillary passes in front of the premaxillary, and extends forward to the base of the nasal aperture. The exact extent of the premaxillary is not manifest. So far as can be judged from the condition of the specimen, there is no evidence that it was divided, but the condition of the fossil has not allowed of excavation of the palatal surface. The entire length from the back of the maxillary to the front of the premaxillary is $1\frac{1}{2}$ inch, and the width of the bone at the back of the maxillary region is $1\frac{2}{10}$ inch as preserved. The canine tooth (fig. 4, *c*, *c*) is upon a sharp alveolar border, and is distant $\frac{9}{10}$ inch from the median anterior extremity. The whole of this anterior space appears to be concavely excavated, and its anterior margin seen from the front is vaulted exactly as in *Ptychognathus*. From the base of the canine tooth a convexity ascends curving backward towards the orbit. The alveolar margin appears to extend for about $\frac{6}{10}$ inch behind the socket for the canine tooth. The palate is divided by a median ridge sharply elevated, presumably formed by the vomer, and it indicates division of the palato-nares. These vacuities are deeply excavated and margined externally behind by the palatine bones, which form sharp ridges on their outer borders. The width of the palato-nares at the posterior fracture exceeds half an inch. On the maxillary bone, apparently midway between its external border indicated by the canine and the vomerine ridge in front of the palatine, is the row of palatal teeth (fig. 4 and fig. 5*mt*). They have been broken from their roots, which are in most cases also exposed, and show the crowns to be comparatively high and sub-cylindrical with a tendency to be ovate in section, slightly expanded on the summit, which is enamelled, and in some cases, especially the last tooth, marked with ridges. One specimen on the right side indicates a tooth which terminates in a point. Only four teeth are clearly demonstrated on each side, but I suppose that six or seven are indicated on the left side. There is no trace of serrations upon the crowns of the teeth.

Seen from the side, the maxillary region is deep, and the bone apparently ascends to a level with the flattened top of the skull (fig. 5), being fully $\frac{8}{10}$ inch high at the canine tooth, and about $1\frac{3}{10}$ inch long on the alveolar border. The nares (*n*, *n*,) are lateral, looking outward and very slightly forward, separated by an interspace of about $\frac{7}{20}$ inch. This flat nose has suggested the specific name. This measurement is about equal to the height of the nasal vacuity, which is somewhat longer, though owing to the encrusting matrix its length on the left side exceeds that on the right side. The length of the interspace between the narine and the orbit appears to differ on the two sides of the head, but was about $\frac{7}{10}$ inch. The orbits (*o*, *o*,) were large and lateral, the width of the interspace between them as preserved is about $\frac{9}{10}$ inch. Their superior border was formed by the post-frontal and pre-frontal bones in the usual way. The post-frontal is broken away from the back of the orbit, as is the malar; but

the posterior fracture of the frontal bones shows that their descending lateral walls were ossified. A median plate descends towards the palate; but there is no evidence of a complete interorbital septum, or that the cavity enclosed between the region of the post-frontals is the anterior termination of the brain case. There is nothing in the external aspect of the specimen to suggest the structures which its palate* shows.

There is another group of South African reptiles which is perhaps less obviously allied to the Theriodontia, indicated by the imperfect skull of the genus *Delphinognathus*.† It is allied to the Gorgonopsia in the great breadth and shortness of the parietal region of the skull and has small lateral temporal vacuities. It has a squamosal pedicle descending to the articulation with the lower jaw, which extends forward, and appears to imply a short sphenoidal region to the palate, in which it resembles *Ælurosaurus*. Its molar teeth are imperfectly known, but appear to be simple and conical, without cusps. There is some evidence, from specimens which I obtained, that this group includes more than one type of dentition. The complete skull will be evidenced by *Tapinocephalus*. That genus has a single occipital condyle. Its teeth give no indication of functional canines, or of difference of size of molars and incisors; but the crowns are of a type previously unknown in South African reptiles. With these animals is associated an imperfect skull of similar type, to be distinguished as *Dinocephalus*, which has the largest canine teeth found in any South African fossil, associated with small molars. If *Ælurosaurus* should find a place in this group it would add to its dental diversity. The fact that the principal genera have similar types of skull, but differ in types of dentition, suggests that the group may possibly be a primary division of the Anomodont alliance, though its palate indicates Theriodont affinities. It may be referred to as Dinocephalia. There are thus four groups of fossil reptiles distinguished by their dental types, the

* The back of the skull is unknown in every Endothiodont. I have long suspected that the skull of *Tropidostoma Dunni* ('Phil. Trans.,' 1889, Plate 12), which has the Therosuchian type of sphenoid, dividing the pterygoid bones, may be an Endothiodont skull. I base this suggestion upon the presphenoid keel, the cup-shaped excavation of the occipital plate, the absence of developed occipital condyles. None of these characters are known in Dicynodonts, all are found in Theriodonts. The back of the skull is not of a known Therosuchian type, differing in the elevated position of the Zygoma and other characters which approximate to Dicynodonts. The unknown Therosuchian type of skull may be Endothiodont. Mr. R. Lydekker ('Cat. Foss. Rept. Brit. Mus.,' Part 4, p. 36) regards *Tropidostoma Dunni* ('Phil. Trans.,' 1889, Plate 12) as a synonym of *Dicynodon microtrema* (*loc. cit.*, Plate 11), notwithstanding the ordinal differences of structure which the specimens show. They are combined under the genus *Ptychosiagum* (Lyd.); but so far as I can judge from the figures of specimens ('Rec. Geol. Surv. India,' 1890) it is probable that that Indian genus belongs to the Therosuchia, if it is not Theriodont, since the scapula, ilium, vertebræ, are Therosuchian, while I recognize no Dicynodont character in any of the figures.

† 'Quart. Jour. Geol. Soc.,' 1892, vol. 48, p. 469.

homalodont Pareiasauria; the Theriodont, comprising Lycosauria, Cynodontia, and Gomphodontia; the edentate Endothiodontia; and the heterodont Dinocephalia, under which the Gorgonopsia may perhaps be included. In the absence of knowledge of the post-orbital region of the skull, and in view of the remarkable difference of the lower jaw of *Endothiodon bathystoma* from that of a Theriodont, it seems impossible that it can be included in the same order with the true Theriodonts. While in view of some resemblance of plan in the back of the skull between *Tapinocephalus* and *Gorgonops*, and the forward position of the palato-nares in both, I hesitate, for the present, to regard those genera as representative of groups which are both of equal value.

It is possible that another South African group may hereafter be based upon the reputed mammal *Tritylodon*, in which there is a close resemblance to typical Theriodont dentition; and with that genus may be associated the teeth which are described under the name *Diademodon*. But as the post-orbital region of the skull is unknown it is impossible to define the group, or prove that it is distinct from the Gomphodontia which the animals resemble in details of skull structure.

European Fossil Reptiles which approximate to the Theriodontia.

Some of the Permian reptiles of Europe have obvious and near affinity with these South African groups, and Sir R. Owen proposed to include the Russian genera in the Theriodontia. I have rather inclined to refer *Deuterosaurus* and *Rhopalodon* to a separate group under the name Deuterosauria, (1) because the palato-nares open by two distinct completely exposed vacuities, without any arch below them of a hard palate truncated posteriorly, such as characterises all true Theriodonts which I have examined; (2) because the sphenoido-pterygoid region makes an angular bend with the palate, so as to be in the same plane with the occiput; and (3) because the quadrate bones attain a large vertical downward development unknown in the Theriodontia. With these differences are associated a simpler pelvis, and limb bones which show some resemblances to those of *Pareiasaurus*, and are unlike those of any known African Theriodont. The type to which the skull approaches nearest appears to be *Lycosaurus*. It is possible that the Deuterosauria may include *Placodus*.

A European type which approximates to the Theriodonts is indicated by the remains described by Professor Albert Gaudry as *Stereorachis dominans*.*

The only part of the skull known is the premaxillary and maxillary bones. They show three incisors, of which the first two are large; no canine; and six pointed molars. In the dentary bone the three incisors are larger; there is no canine, but the pointed molars are ten in number. The other parts of the skeleton preserved

* 'Les Vertébrés Fossiles des Environs d'Autun,' 1888, from the lower Permian of Autun in France.

include vertebræ and ribs, inter-clavicle, clavicle, scapula, coracoid, and humerus. M. Gaudry has remarked on the resemblance of the humerus with that of monotreme mammals, and with *Cynodraco*, *Platypodosaurus*, and *Brithopus* (= *Deuterosaurus*). The humerus is probably more mammalian than that of any known fossil reptile, and at the same time more like the Theriodont type of Africa than anything previously figured. The humerus is in harmony with the bones of the shoulder girdle in their monotreme characters; while the humerus in Theriodonts seems to me more marsupial in type. The absence of canine teeth in both jaws excludes the type from the Theriodontia; and I propose to use that character in defining the Stereorachia provisionally, till the hinder part of the skull is known. The only European animals which the remains at all resemble is the Protorosauria; and it is possible that the Stereorachia may be included in that group. The data for comparison are scanty. And if the teeth suggest some degree of approximation, which may be supported by the structure of the shoulder girdle, there are greater differences in the humerus than would be anticipated in members of the same group. There are features of the dentition or skeleton in which the Stereorachia can be compared with the Deuterosauria.

It further appears to be not improbable that the Protorosauria may be more nearly related to the groups of animals which I have here indicated than to other known fossils. In the skull the extremity of the snout is unknown, and it now seems to me more likely that the anterior nares were terminal, than that they were situate in advance of the lachrymal bone. Owing to the squamous overlap of the maxillary upon the premaxillary bones, the definition of the premaxillary is not always clear in Anomodonts, Ornithosaurs, and Plesiosaurs, and there is still no indication of the anterior nares in *Protorosaurus*. There is probably but a single post-orbital arch; and the upper and under surfaces of the skull show resemblances in the forms and proportions of the bones to animals allied to Theriodonts, which were not obvious formerly because the evidence was not available. The clavicular arch described by Professor H. Credner is an important resemblance to Anomodonts. The humerus finds a parallel in form in the Deuterosauria. The femur is Anomodont in its modification at the proximal end. The pelvis appears to be intermediate between that of known Anomodonts, and the types seen in Ornithosaurs and the Cetiosaurian Saurischia. But with these Anomodont resemblances there are differences, such as the hollow limb bones of *Protorosaurus*; but as I have a vertebra from South Africa which I believe to be Anomodont, which is apparently pneumatic, that difference may not be more than sub-ordinal. I therefore would place the Protorosauria in association with the foregoing groups provisionally, but there is no evidence figured that the shoulder girdle is Anomodont in having a pre-coracoid bone.

I am not aware of many characters which unite these orders or sub-orders together, which do not equally unite them with the other South African Anomodonts, toothed and toothless. So far as known all have substantially the same type of pelvis,

shoulder girdle, and clavicular arch. The differences in the larger limb bones are chiefly dependent upon their length and function. The differences in the vertebræ do not give grounds for distinction. In the carpus, tarsus, and digits there is evidence of variation, but this does not allow of the types just considered being grouped together, for those regions of the skeleton are known in a few only of the groups. Many groups show in the skull the development of the transverse palatine, intra-mandibular arch, into which the transverse bone appears to enter, which is not known in the Bidentalia of BAIN (= Dicynodontia). That arch is not at present known to exist in the Stereorachia, of which the palate is unknown. And it has not been recognized in the single imperfect skull of *Protorosaurus*, which has the bones of the palate displaced. It serves to unite apparently the Pareiasauria, Gorgonopsia, Dinocephalia, Deuterosauria, Endothiodontia, and Theriodontia, under which are comprised Lycosauria, Cynodontia, and Gomphodontia. This larger group I would propose to distinguish as the Therosuchia, since it comprises animals which, while essentially Reptilian and almost Rhyncocephalian in some fundamental characters, make transitions towards the lower Mammalia in every part of the skeleton.

American Permian Reptiles which are allied to the Theriodontia.

The American Permian Reptilia from Texas, described by Professor E. D. COPE since 1876, were referred in 1878 to a group or order of animals named Pelycosauria ('Proc. Am. Phil. Soc.,' 1878, vol. 17, p. 529).

The author states that the division Pelycosauria is established primarily on the genera *Clepsydrops* and *Dimetrodon*. In 1892 ('Trans. Am. Phil. Soc.,' vol. 17, Plate 2, fig. 6) an outline figure was given of the lateral aspect of the skull of *Clepsydrops*. In describing the dentition in 1878 the teeth are said to be "of different sizes, and the premaxillaries and the canines are distinguished from the others by their proportions." All have "more or less defined anterior and posterior cutting edges." In 1892 it is added: "No indication of the supra-temporal foramen can be found in the rather mutilated specimen. I think it was not present." Many parts of the skeleton were known, showing Rhyncocephalian characters; but, from the absence of the quadrato-jugal arch, the genus is referred to a distinct sub-order named Pelycosauria.

In *Dimetrodon* the superior dentition does not differ from that of *Clepsydrops*, according to Professor COPE; and the animal is distinguished chiefly by other portions of the skeleton. It is said to be allied to *Deuterosaurus*, which the author quotes from OWEN's figure in the 'Journal of the Geological Society' in 1876. It is stated to more closely resemble *Lycosaurus*, in which, however, the enlarged anterior incisor teeth of *Dimetrodon* are not found.

Professor COPE considered it probable that other genera, which he had named *Ectocynodon*, *Pariotichus*, and *Bolosaurus*, should be placed in this group, and

subsequently the number of genera was increased. Since Professor Cope recognized the close resemblance of some of the American genera to those on which Sir R. Owen founded the order Theriodontia in 1876, it may be convenient to quote the following passage ('Proc. Am. Phil. Soc.,' 1878, p. 529): "Professor Owen has named a group of Triassic and Permian reptiles the Theriodontia, characterized by the mammal-like differentiation of the incisor and canine teeth. The animals thus referred by Professor Owen probably enter my sub-order, Pelycosauria; though the structure of their pelvis remains to be ascertained. If so, they correspond with my Clepsydropidæ, since Professor Owen does not include herbivorous forms in his division. As it is plain that the herbivorous and carnivorous types belong to the same order, and probably sub-order, it becomes necessary to sub-ordinate the term Theriodontia to that of Pelycosauria. To another division of reptiles from the South African Trias typified by the genus *Pareiasaurus* (Owen) he gives a special name, expressive of the deeply-impressed surfaces of the centra occupied by the remains of the chorda dorsalis. As this, or the perforate condition, is characteristic of all the Pelycosauria, it is probable that it is present in Professor Owen's Theriodontia also.* It is also evident that, since the dental characters of *Pareiasaurus* do not serve to distinguish it as an order from the genera with distinct canine teeth, this group also must be looked upon as a sub-division, perhaps of family value, of the Pelycosauria† or other parts of the Rhyncocephalous order." Prior to the foundation of the Theriodontia Professor Cope had referred these American fossils to the Rhyncocephalia.

This passage shows that the Pelycosauria was not clearly defined by any character, such as that used by Sir R. Owen in characterizing the Theriodontia. That it was a hypothetical group based chiefly upon an assumed vertebral character, which has, I believe, no ordinal value, for the double cones or funnel-shaped articular faces of the centrum characterize some species and genera of Sauropterygia, while in other species and genera the articular faces are perfectly flat, or even have a tendency to a plano-convex condition. When Professor Cope wrote in 1878, no vertebra of a typical African Theriodont was described; and therefore the predicated vertebral character was hypothetical for the Theriodontia, and has not been substantiated by

* In 1878 *Pareiasaurus* was only known from the specimens figured by Sir R. Owen in his 'Catalogue of South African Reptilia,' 1876. This passage, quoted from Professor E. D. Cope, is the basis for the statement by Mr. R. Lydekker ('Cat. Foss. Rept. Brit. Mus.,' Part 4, p. 112):—"The typical members of this group (Pareiasauria) were regarded by Owen as referable to the Dinosauria, under the name Tretospondyli, but their Anomodont character was first pointed out by Cope (*loc. cit.*, 1878), who included them in his Pelycosauria." I am unaware of evidence that the vertebra figured by Sir R. Owen (*loc. cit.*, Plate 11) belongs to *Pareiasaurus*. Professor G. Baur ('Journ. Morph.,' vol. 1, p. 101) in 1887 thought that the exact position of these animals could not be determined with the material then known. He says *Pareiasaurus* shows characters of the Sauropoda; *Anthodon* of the Stegosauridæ, as Professor O. C. Marsh urged in 1889 ('Geol. Mag.,' p. 207).

† I do not follow Professor Cope's argument that the dental characters of *Pareiasaurus* do not distinguish it as an order from the genera with distinct canine teeth.

the specimens obtained by myself. It is also clear that Professor Cope was aware of no cranial character by which the genera *Clepsydrops* and *Dimetrodon* could be separated from the Theriodontia. And the only ground for instituting the Pelycosauria was the hypothesis that it included the Theriodontia, and a herbivorous type of animal which was distinct from the Theriodontia, but which Professor Cope could not put into a separate sub-order. That herbivorous type was not specified, but was presumably indicated by *Bolosaurus*, in which the teeth are transverse to the axis of the jaw, formed of a ledge and cusp, but without enlarged canine or incisor teeth. It may also have comprised *Diadectes*, in which the molar teeth are of similar type and worn, and in which a distinct canine is found (1880). At that time *Empedocles* (afterwards *Empedias*) was only known from vertebræ. This supposed herbivorous type was not defined, nor was a name—Cotylosauria—suggested for it till 1880 ('Proc. Am. Phil. Soc.'). To this day no name has been suggested for the carnivorous type indicated by *Clepsydrops*.

In 1889 ('Am. Nat.,' p. 865), Professor Cope proposed to combine the Diadectidæ with the Pareiasauria to form the Cotylosauria. At that time the Pelycosauria included the families Clepsydropidæ, Pariotichidæ, and Bolosauridæ ('Trans. Am. Phil. Soc.,' 1886). But in 1892 ('Trans. Am. Phil. Soc.'), although the Diadectidæ is not mentioned and *Pareiasaurus* remains, Professor Cope proposed to include the carnivorous types in the Cotylosauria, among them *Chilonyx*, which has no conspicuous canine, *Pantylus* which has a canine developed, *Pariotichus* which has the canine undeveloped. The reason for this change appears to be that those genera prove to have the temporal vacuities entirely roofed over. Professor Cope at the same time expressed his belief that the same condition is found in *Clepsydrops*. If I understand this change of nomenclature, it is a replacement of the term Pelycosauria by Cotylosauria, though this is not stated; and the way in which the change has been brought about shows that the author no longer attaches importance to the dentition as herbivorous or carnivorous, as defining a natural group of animals. Therefore, the original ground for using the name Pelycosauria in preference to Theriodontia disappears. But Professor Cope having placed the supposed herbivorous Cotylosauria outside the Theriodontia in 1880, apparently combines with them, first, the Pareiasauria in 1889, and, subsequently, the carnivorous Pelycosauria in 1892, which had previously been in no way distinguished from Theriodonts; defining the group in 1892 as having the temporal vacuities roofed by bones, which, in the figures given of carnivorous genera, include the supra-temporal bone. I have no means of judging whether the specimens support this grouping; for while the temporal vacuities are roofed in the Pareiasauria, the roof is like the parietal roof of the genus *Chelone*; whereas, in Professor Cope's figure of *Empedias* ('Proc. Am. Phil. Soc.,' vol. 19, Plate 5), which gives the only representation of the back of the skull in an American genus, the skull appears to be closed behind as in Gorgonopsia.

It has not yet been clearly proved that the character upon which the Cotylosauria

was established in 1880 (the two occipital condyles widely separated from each other) is a true interpretation of the specimen of *Empedias molaris*, or that the character is found in all members of the group. If the order is so defined, the genus *Dimetrodon* and its allies would appear to belong to a different group, since Professor COPE states that "the occipital condyle is not perforated, nor divided by sutures." The association of the Diadectidæ and the Pareiasauria in one group is not supported by evidence, for the large concave occipital condyle of *Pareiasaurus* is not comparable with the two condyles attributed to *Empedias*; nor has any evidence been brought forward to favour the idea of both animals being members of a natural group. But while the Cotylosauria of 1889 is a mere name, so far as I can judge from my knowledge of *Pareiasaurus* and Professor COPE's memoirs, the Cotylosauria of 1892 has no more certain basis than the original Pelycosauria, for the definition is insufficient. It has not been shown that any character figured or described in the back or base of the skull of *Pareiasaurus* is also present in the genera *Chilonyx*, *Pantalus*, and *Pariotichus*, which would suggest the possibility of combining those animals, one with Homalodont dentition, and the other with Theriodont dentition, as a natural group of animals.

There is another aspect of the nomenclature of these American Permian fossils; for in December, 1878 ('Am. Nat.,' p. 829), Professor COPE, having defined the Anomodontia and the Pelycosauria, united them in a larger group named Theromorpha, which the author has since proposed to change to Theromora. It is stated that the scapular arch of this order consists of scapula, coracoid, and epi-coracoid closely united, that the three pelvic bones close the obturator foramen and the acetabulum. The group is said to want the quadrato-jugal arch. The Theromora has been accepted by Dr. GEORGE BAUR, Dr. ZITTEL, and other naturalists; but so far as I can judge from descriptions and figures, no characters were ever advanced and defined by Professor COPE which would sustain either the Pelycosauria or Theromora. In 1892 the Pelycosauria has entirely disappeared, Professor COPE closing his remarks with the statement that there are four types of crania represented in the Permian Reptilia, which are distinguished as Cotylosauria, Theriodonta, Diopeus, and Anomodonta. It is not evident that the Theromora disappears with the Pelycosauria, since it is referred to in the author's latest memoir (1892). It is quite possible that the American genera made known by Professor COPE belong to new groups distinct from African types, capable of being clearly defined, and even of being combined with the African types; but it does not necessarily follow that a new group had to be formed to receive the American and African sub-orders, for the evidence has never been set out up to the present time.

Classification of the Anomodontia.

Between 1860 and 1870 there was no more authoritative summary of the classification of the South African Reptilia in use than that given by Sir R. OWEN in his

'Palæontology.' He divided the order Anomodontia into three families—Dicynodontia, which have a canine tooth in each maxillary bone; Cryptodontia, with the jaws edentulous, or teeth imperfectly developed; and Cynodontia, in which the dentition, exemplified in the genera *Galesaurus* and *Cynochampsa*, was fully developed as in the type of carnivorous Mammals. The first variation from this classification occurred when Professor HUXLEY, disregarding the Cynodontia, proposed in 1871 ('Manual Anat. Vert. Animals') to combine *Dicynodon* and *Oudenodon* into the order Dicynodontia, which stands in place of Anomodontia in Professor HUXLEY's classification. But the change left the Dicynodontia and the Cynodontia as two constituent members of the order Anomodontia.

In 1876, Sir R. OWEN obtained the first bone of the skeleton, other than skull, of the Cynodont type, and with it evidences of new genera which resemble mammals in dentition. The Cynodontia then disappeared, its genera were absorbed in the new order named Theriodontia. But the definition of the Theriodontia was made in the same words which had defined the Cynodontia. When Sir R. OWEN made his important generalization, the Dicynodontia, which had already been regarded as an order by Professor HUXLEY, were re-described under the name Anomodontia which had been applied originally to both the Dicynodont and Theriodont groups of animals. When once issued names cease to be possessions of their originators and, as instruments of research, are the common property of science. The circumstance that Sir R. OWEN, prior to 1876, placed the same group of animals within the Anomodontia and afterwards placed it external to the Anomodontia, appeals to subsequently obtained evidence for support or refutation. It is not possible to avoid the conclusion that, although the Dicynodontia was abandoned by Sir R. OWEN, in 1876, when he adopted the early name Bidentalia of A. G. BAIN, under which those animals were first made known by their discoverer, the name Dicynodontia has obtained general recognition and use.

For some time I doubted whether the Theriodontia should form a separate order, and grouped it as parallel to the Dicynodontia in the Anomodont order. If the Anomodont order is retained as dating from 1859, there can be no doubt that it is wide enough to include all the diversities of skull structure and dentition of animals which have the shoulder girdle and pelvis developed substantially on the plan seen in *Dicynodon*.

I have already endeavoured to show that the Theromora was founded in error; and it is not till 1892 that Professor COPE attempted a new definition of constituent groups to form it, although a new classification had been proposed in 1889. The attempt to distinguish the order Theriodontia from the Dicynodontia which Professor COPE makes is fallacious, because he regards the post-orbital arch as differently constructed in the two groups, not realizing that there is no essential difference between the arches, except that which results from the greater production

downward of the squamosal bone in Dicynodonts below the zygoma, and the less production of the malar bone backward upon the outer side of the horizontal part of the squamosal bar. As the structure of the post-orbital arch is the only differential character mentioned by Professor Cope, his distinction between the Theriodonts and Anomodonts fails. There is no evidence in the diagram figure that the genus *Diopeus* possesses the superior and inferior temporal arcades which the figure indicates. Reasons have already been advanced for doubting the existence of the Cotylosauria as a natural group, so that there is some ground for regarding the Theromora as resting more on imagination than evidence. It is not difficult to combine groups of animals together and give a name to the assemblage; but names have no value without a definition or description of the groups, which shows that their structures have been recognized by naturalists who have used the terms. In 1889 ('Am. Nat.,' p. 863) Professor Cope regarded the Theromora as including six sub-orders, Placodontia, Proganosauria, Parasuchia, Anomodontia, Pelycosauria, and Cotylosauria. In 1888 I had ('Proc. Roy. Soc.,' p. 383) proposed to include under the order Anomodontia the Pareiasauria, Procolophonia, Dicynodontia, Gennetotheria (now named Lycosauria and combined with the Theriodontia), Pelycosauria, Theriodontia, Cotylosauria, and Placodontia. So that the only new points in Professor Cope's classification were that he substituted the name Theromora for the older Anomodontia; combined the Procolophonia, Palæohatteriidæ, Homœosauridæ, Protorosauridæ, Rhynchosauridæ, and Mesosauria, as the Proganosauria, without evidence of community of structure; combined the Pareiasauria and Cotylosauria, equally without evidence; and included the Parasuchia, stated to comprise the Belodontidæ and probably the Aëtosauridæ, but without finding the precoracoid bone, or showing how the pelvis differed from that of the Saurischia, which alone could justify the grouping.

I think that the American fossils forming the Diadectidæ fall within the definition of the Therosauria, being parallel to the Gomphodontia of Africa, but distinct from the Therodontia as a sub-order on the evidence of the structure of the palate, the back of the skull, and possibly the roof of the brain case; and I am aware of no valid reason why the name Cotylosauria should not be retained for this group in the sense in which it was originally given, to the exclusion of its later applications. In the same way the genera which are allied to *Clepsydrops*, which have been placed in the Pelycosauria, should, I think, retain that name, unless it can be proved that they can be comprised in the Lycosaurian division of the Theriodontia; in favour of which no evidence is available. There is no proof that they have the palatal characters of the Therosuchia, though this is probable from their affinity with the Diadectidæ.

The following is a summary of the Classification :—

ANOMODONTIA.

Extinct Reptilia in which the precoracoid is developed and unites by suture with the coracoid and scapula to form the shoulder-girdle. The clavicular arch includes interclavicle and clavicles. The pelvic acetabulum is closed; the pubis smaller than the ischium, and the ilium usually developed both in front of and behind the acetabulum. There is a ventral symphysis of the pubes and ischia. The articular faces of the centra are biconcave or flat. The pterygoid bones join the sphenoid by suture. There is a single post-orbital arch which may be masked by the temporal vacuities being roofed over.

The Anomodontia includes two principal orders, Therosuchia and Therochelonia, and apparently the Mesosauria. It is nearly related to Protorosauria and Nothosauria; as well as to Ornithosauria and Saurischia.

Therosuchia comprise—
- Pareiasauria,
- Procolophonia,
- Gorgonopsia,
- Dinocephalia,
- Deuterosauria,
- Placodontia,
- Theriodontia { Lycosauria, Cynodontia, Gomphodontia,
- Endothiodontia,
- [Theromora*] { Pelycosauria, Cotylosauria

Therochelonia comprises—
- Dicynodontia,
- Kistecephalia.†

Mesosauria or Proganosauria.

Nothosauria ?

THEROSUCHIA.

The palatine and transverse bones of the palate are produced outward and usually downward, in an arch, which abuts against the inner side of the mandible. This character defines the order from the Dicynodonts, Mesosaurs, Nothosaurs, and all fossil groups of reptiles. There are more or less completely divided heads to dorsal ribs.

* This group has no authority at present, and is subject to future definition.

† The palate is undescribed.

A foramen of variable size occurs between ischium and pubis. The crest of the ilium extends on both sides of the acetabulum.

Sub-order—Pareiasauria.

Temporal vacuities of the skull roofed over as in *Chelone;* a large single (concave) occipital condyle; sphenoidal region short; transverse palatine processes directed out and forward. Teeth conical or with compressed cuspidate crowns, not divided into incisors, canines, and molars. Ribs with the heads deep and occasionally divided. *Procolophon* appears to be the type of a division of the order.

Types :—*Pareiasaurus* and *Procolophon.*

Sub-order—Gorgonopsia.

Temporal vacuities roofed over, with the broad brain-case closed behind, as in *Kistecephalus*, by a vertical occipital plate. Skull bones thin, enclosing an interior cartilage. The palato-nares are placed far forward, without any indication of a hard palate forming a platform in front of them. The teeth appear to have been pointed. [At present only incisors and canines are known.]

Types :—*Gorgonops.**

Sub-order—Dinocephalia.

Temporal vacuities small. Cerebral region between them wide, and usually expanded above the brain-case. Skull bones are enormously thick; no interior cartilage to the brain-case. Palato-nares placed far forward. Occipital condyle single, convex. Teeth with canines sometimes developed. Molar teeth pointed, convex in front, concave behind, with serrated borders, and a transverse inwardly developed ledge.

Types :—*Delphinognathus* and *Tapinocephalus.*

Sub-order—Deuterosauria.

The palato-nares are ovate vacuities divided by the vomerine bones opening in the palate as in *Nothosaurus.* The sphenoid bar makes an angular bend with the palate,

* Mr. R. Lydekker states that, "in the roofing of the temporal fossa *Gorgonops* agrees with *Chilonyx*, and also with the Pareiasauridæ" ('Cat. Foss. Rept. Brit. Mus.,' Part 4, p. 111). *Pareiasaurus* is only roofed in the sense in which Chelone is roofed, while in *Gorgonops* there appears to have been a large cartilaginous envelope to the brain as in *Kistecephalus* ('Phil. Trans.,' 1889, B., Plate 9, fig. 1), which was completely covered with bone, not only above but behind also. I have no evidence whether *Chilonyx* agrees with either type.

and is in the same plane with the occiput. The incisor teeth are strongly developed in some types; the molar teeth are strongly developed in others. The bones of the shoulder-girdle and principal limb bones resemble those of *Pareiasaurus* and Dicynodonts. The horizontal processes of the ilium are but slightly developed. The Placodontia form a division of the order.

Types :—*Deuterosaurus* and *Rhopalodon*.

Sub-order—Theriodontia.

The occipital plate is usually concave. The parietal crest is narrow with large temporal vacuities, and a zygoma into which the malar bone enters. The anterior nares are terminal; the palato-nares are defined by a hard palate. The teeth resemble incisors, canines, and molar teeth of mammals in form and position. The order comprises :

(1.) Lycosauria, with small pointed molars without cusps, but usually serrated; and the squamosal pedicle of the skull descends behind the lower jaw.

(2.) Cynodontia, in which the large molar teeth have a few lateral cusps like those of carnivorous mammals. The quadrate bone is small. The occipital condyle is V-shaped, consisting of two parts, connected below, so as to have the aspect of two condyles when seen from above.

(3.) Gomphodontia, in which the molar teeth are more or less transverse with transverse ridges, on which there may be cusps, tubercles, or crenulations, which are worn down with use. Occipital condyle V-shaped in two lateral parts.

Types :—(1) *Lycosaurus*, (2) *Cynognathus*, (3) *Gomphognathus*.

Sub-order—Endothiodontia.

The posterior nares are bordered in front by the hard palate, but the palatine bones do not meet in the median line below them, as those bones meet in the Theriodontia. There are no incisor teeth. When teeth are developed on the palate they may be arranged in series or irregularly scattered. The lower jaw does not develop a coronoid process. It is excavated externally in front of the articulation, apparently by the masseter muscle.

Type :—*Endothiodon*.

Sub-order—Theromora.

No characters have been given to define this group by structure of the skull. I take it as including the genera enumerated in Professor Cope's systematic catalogue ('Trans. Am. Phil. Soc.,' 1886). It is retained provisionally to comprise the American

Pelycosauria, 1878, and Cotylosauria, 1880; but no characters have been found to unite those groups; and there is no published evidence to show that both have the palate of the Therosuchia. Pelycosauria was defined in 1889 as having the ribs two-headed, and vertebral centra generally Notochordal. To this may be added occipital condyle single. The Cotylosauria was defined at the same time as having the ribs single-headed, with the temporal vacuities of the skull roofed over. There appear to be two occipital condyles; but the character has not been confirmed.

Types:—*Clepsydrops* and *Empedias*.

Therochelonia.

In this order of animals there is general resemblance in the plan of the palate to the Chelonia, which distinguishes it from the Therosuchia, while some parts of the skeleton approximate towards mammals. The pterygoid bones meet in the middle line of the palate behind the posterior nares without being divided by an intervening sphenoidal keel or bar. The palatine bones are not developed transversely outward and downward to form an arch behind the palato-nares. There is no platform of a truncated hard palate covering the front of the posterior nares. The external occipital plate is more or less vertical. The single occipital condyle is often tripartite. The large quadrate bones, covered externally by the squamosal, form the articulation for the lower jaw.

Sub-order—Dicynodontia.

Premaxillary bone single without teeth. Nares never extending in advance of the anterior extremity of the palate. No developed coronoid process to the lower jaw. Squamosal bone produced below the zygomatic arch. The only teeth known at present are canine teeth in the skull. Articular faces of vertebræ flat.

Type:—*Dicynodon*.

Kistecephalus may be the type of a second sub-order. The skull bones are thin, enclosing a large cartilage. The palate is imperfectly known.

Proganosauria or Mesosauria.

The palate is closed in the median line. The palato-nares open as in *Nothosaurus*. The sutures of the shoulder-girdle are obliterated. The neck includes more than nine vertebræ. The humerus has a form seen in some Edentata, with an entepicondylar foramen.

Types:—*Stereosternum* and *Mesosaurus*.

There is no proof that either of the following groups can be included in the Anomodontia, but they approximate to the type in opposite ways.

Nothosauria.

The palato-nares open as in Dicynodontia and Mesosauria, except that they are entirely divided by the vomerine bones and have the palatine bones chiefly developed behind them. There is a similar transverse constriction of the flattened pterygoid region, and similar conditions of the occiput, occipital condyle, and quadrate bone. The vertebræ are single-headed; the neck is elongated. The humerus indicates both ect- and ent-epicondylar perforations. There is a foramen between the pubis and ischium, a posterior notch in the pubis; and the ilium appears to be but slightly developed. The pre-coracoid is not ossified, but its place is indicated by a vacuity between the scapula and coracoid. The Neusticosauria are probably to be placed in near association with the Nothosauria, and they may eventually prove to form with the Proganosauria, the group Mesosauria.*

Type :—*Nothosaurus.*

Protorosauria.

This group is not represented by any genus in which the palate and back of the skull are known from well-preserved evidence. It is, therefore, impossible to affirm that it can be extended to include the Stereorachia and Palæohatteria as appears to be not improbable. *Protorosaurus* has the larger limb-bones hollow. Its affinities in the clavicular arch, and forms of the humerus and femur, to described Anomodontia, make its reference to that group not improbable. These resemblances suggest that the anterior nares were in the extremity of the snout which is lost.

Type :—*Protorosaurus.*

The relations of the Protorosauria and Nothosauria to the Anomodontia are expressed in the following arrangement of the Sauromorpha.

Sauromorpha.
- Rhynchocephalia.
- Protorosauria.
- Anomodontia.
- Nothosauria.
- Sauropterygia.
- Chelonia.

* 'Quart. Jour. Geol. Soc.,' 1892, vol. 48, p. 586.

Explanation of Plate.

PLATE 88.

Fig. 1. Palatal aspect of the skull of *Lycosaurus curvimola:* the original type specimen, 47339, in the British Museum. It shows the Lycosaurian dentition of incisor (*i.*), canine (*c.*), and (*m.*) molar teeth. Within the mandible the palato-nares are exposed. Extending laterally behind the palato-nares is the transverse palatine arch (*t.*) which abuts against the inner sides of the mandible; and behind this arch is the compressed, sharp, pre-sphenoid keel, flanked on each side by (*pt.*) the pterygoid bones. Behind the pre-sphenoid keel is the concave area of the basi-sphenoid. Natural size.

Fig. 2. The palatal region of *Ælurosaurus felinus.* The area within the mandible is drawn from the original type specimen, R. 339, British Museum. The pre-sphenoid keel (*ps.*) may be compared with that of *Lycosaurus*, as may the transverse palatine arch (*t.*), on which teeth are developed. There are patches of teeth on the palatine bones (*pl.*); the larger teeth in front are regarded as vomerine. The figure is twice natural size.

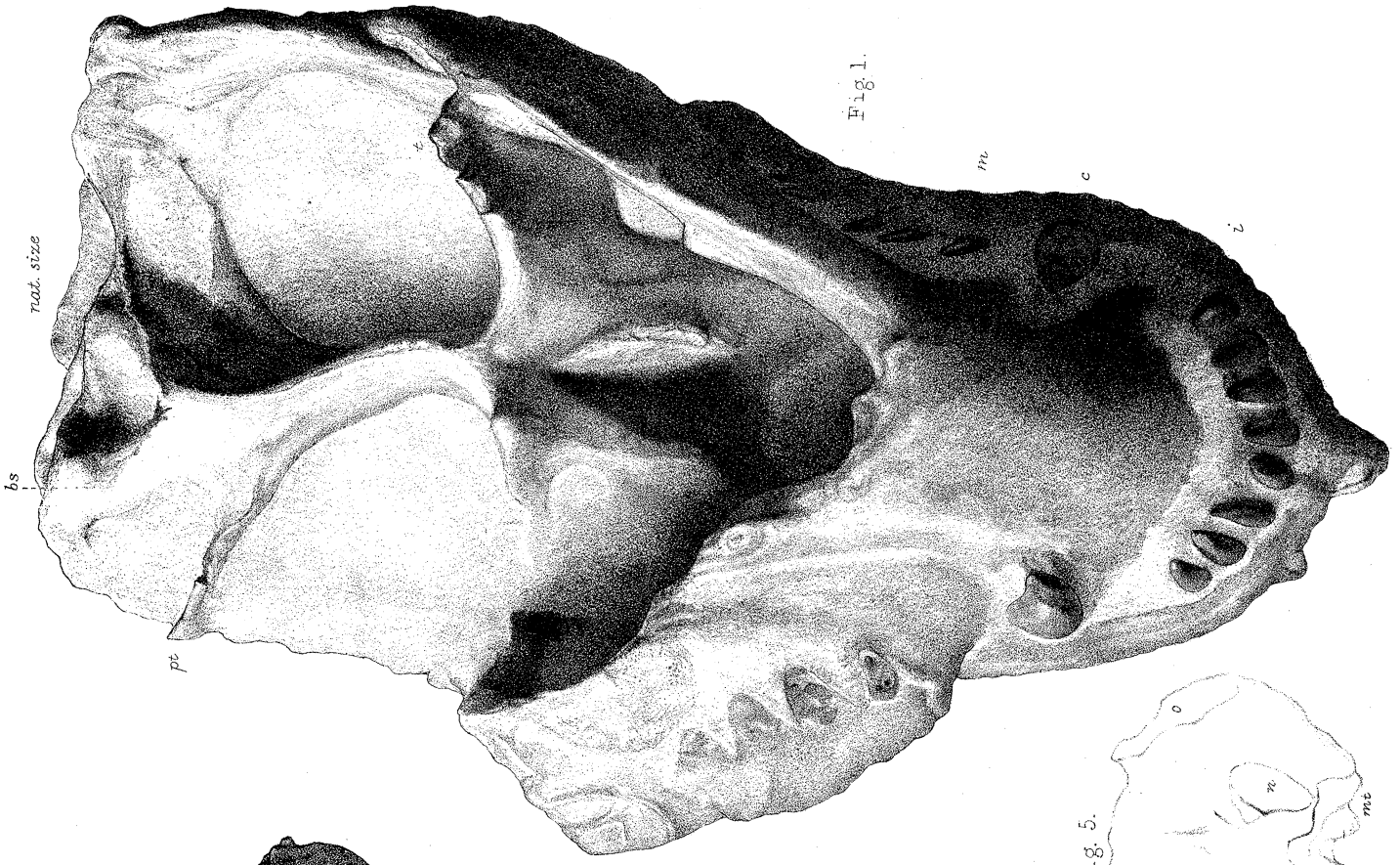
Fig. 3. Palatal aspect of the anterior part of the skull of *Pristerognathus polyodon*, showing the incisor teeth, one to six in each pre-maxillary bone, the canines (*c.*), and pre-molars (*pm.*). Within these teeth is the mandible, with the two rami formed of the dentary bones, which are not united by synostosis at the symphysis. The hind splint of the splenial bone lies within the dentary bone. Incisors are seen at the extremity of the mandible, and the roots of the mandibular canine are exposed behind the symphysis by abrasion. Natural size.

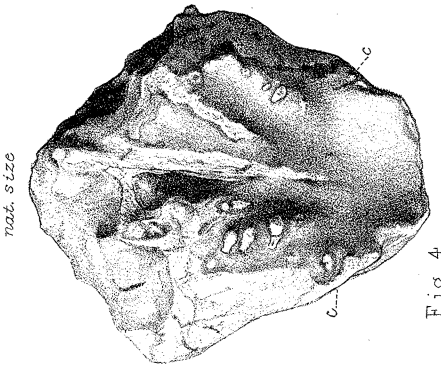
Fig. 4. Palatal aspect of the anterior part of the skull of *Cryptocynodon simus*, showing (*c.*) the immature canine teeth; behind and internal to which is the single row of teeth on the palate. Natural size.

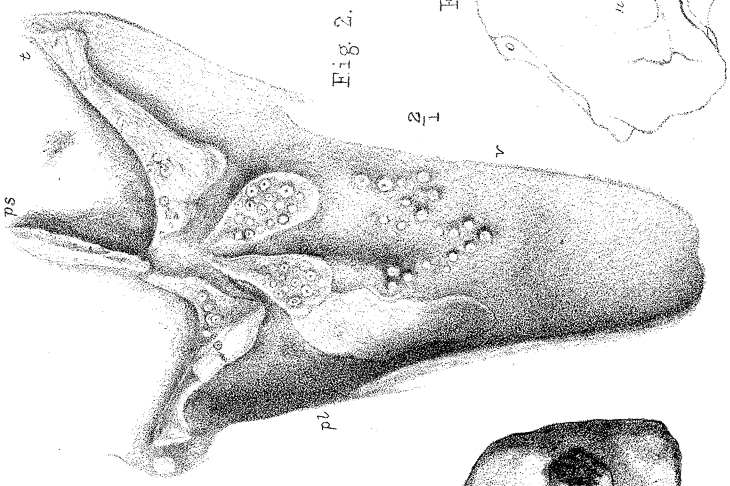
Fig. 5. Outline of the anterior aspect of the same skull. The anterior nares (*nn.*) are well separated in front, and the orbits (*oo.*) are widely separated behind. Within the anterior arch of the mouth the teeth upon the palate are indicated (*mt.*). Natural size.

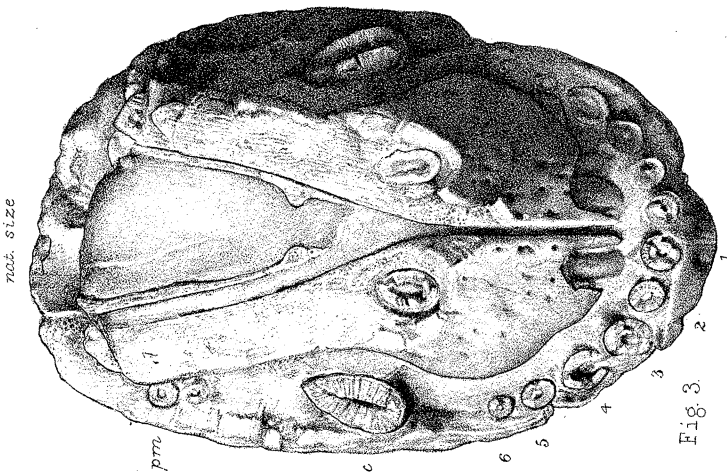
Fig. 6. Internal aspect of the dentary bone of *Tribolodon* from Lady Frere, showing the angle of the jaw, and the coronoid process. The other bones which compose the lower jaw are lost from the slightly grooved surface exposed. The teeth are remarkable for their distance from each other, and height above the alveolar margin. Natural size.

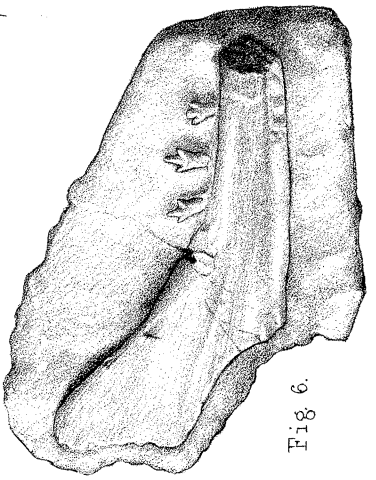
Fig. 7. A single tooth of *Tribolodon* enlarged, showing its aspect from the inner side of the jaw.











G.M.Woodward del. et lith.

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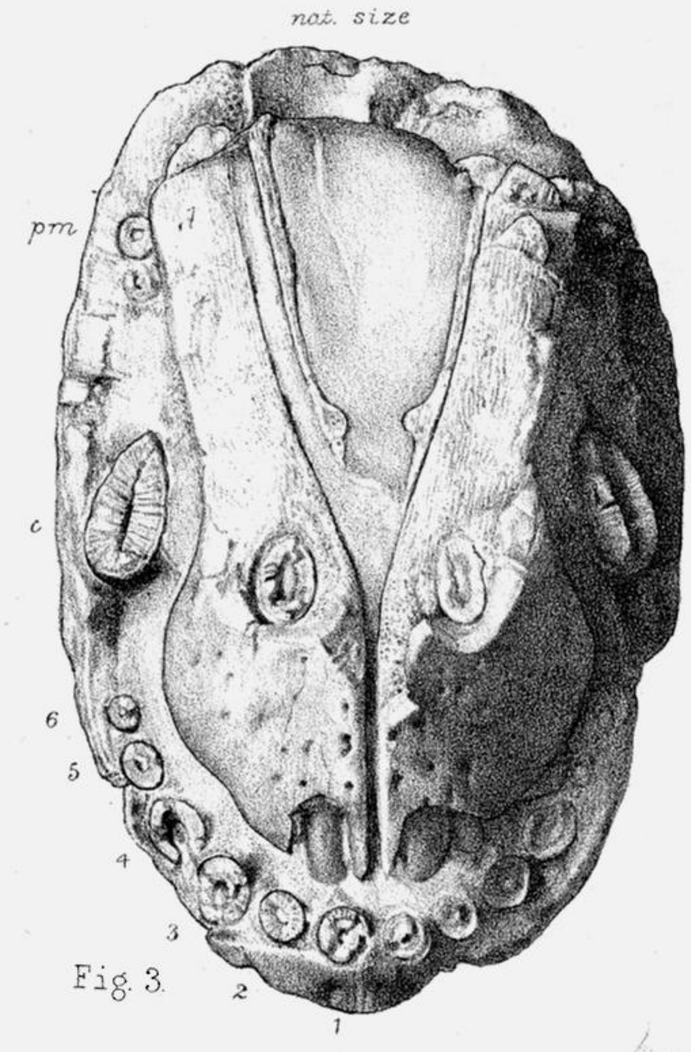

Fig. 3.

Fig. 7.

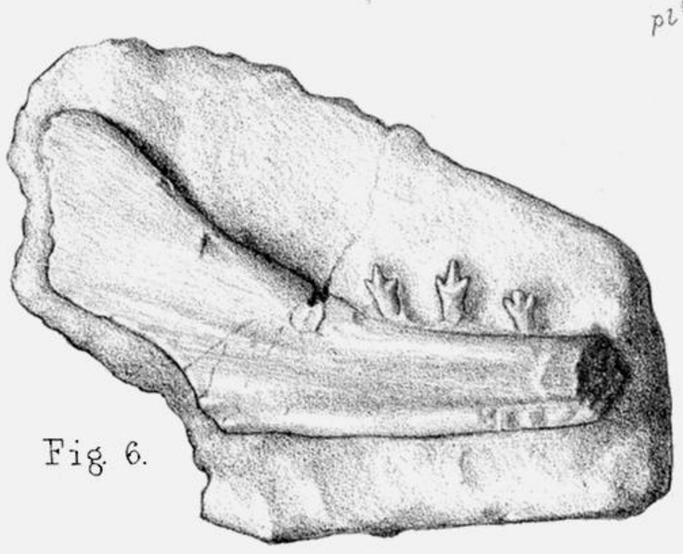

Fig. 6.

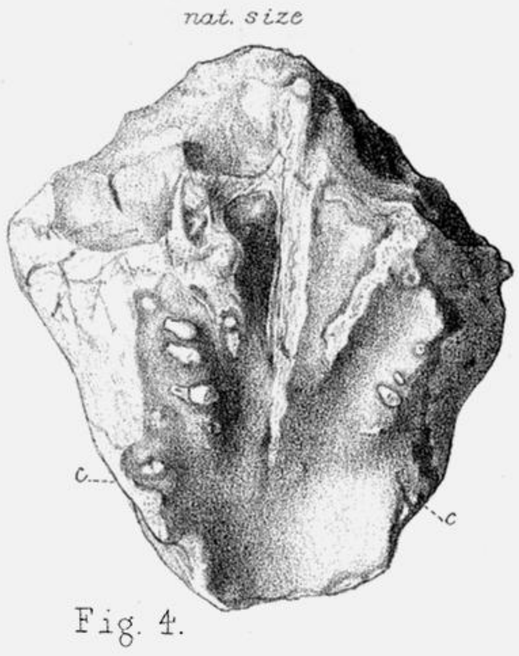

Fig. 4.

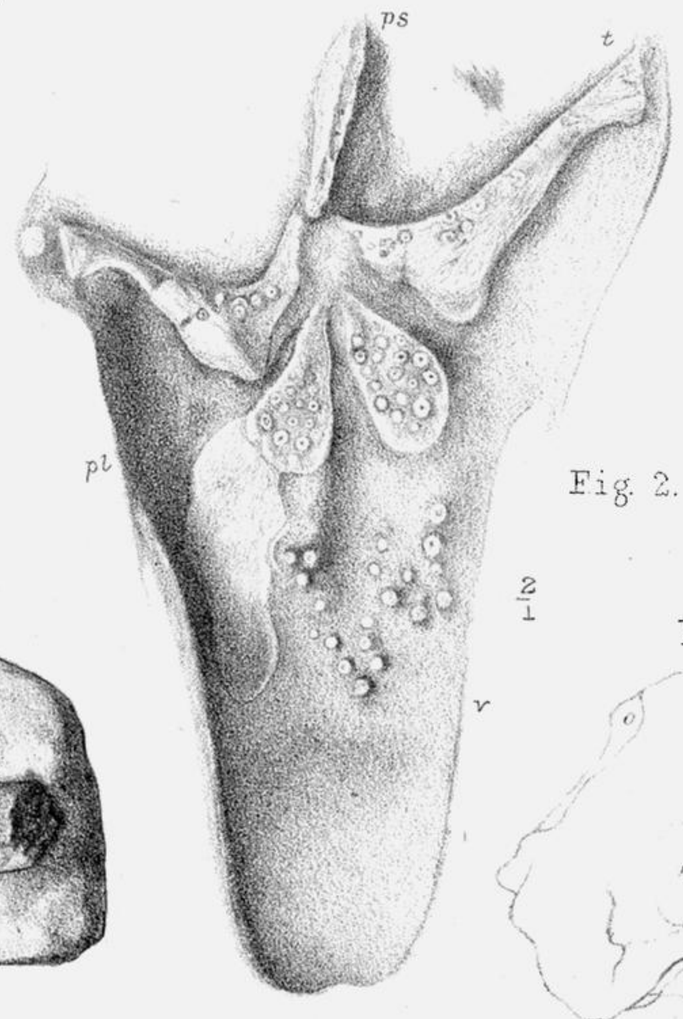

Fig. 2.

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Fig. 5.

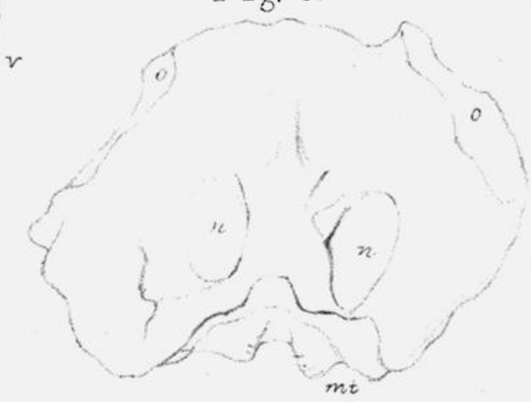

Fig. 1.

PLATE 88.

Fig. 1. Palatal aspect of the skull of *Lycosaurus curvimola:* the original type specimen, 47339, in the British Museum. It shows the Lycosaurian dentition of incisor (*i.*), canine (*c.*), and (*m.*) molar teeth. Within the mandible the palato-nares are exposed. Extending laterally behind the palato-nares is the transverse palatine arch (*t.*) which abuts against the inner sides of the mandible; and behind this arch is the compressed, sharp, pre-sphenoid keel, flanked on each side by (*pt.*) the pterygoid bones. Behind the pre-sphenoid keel is the concave area of the basi-sphenoid. Natural size.

Fig. 2. The palatal region of *Ælurosaurus felinus*. The area within the mandible is drawn from the original type specimen, R. 339, British Museum. The pre-sphenoid keel (*ps.*) may be compared with that of *Lycosaurus*, as may the transverse palatine arch (*t.*), on which teeth are developed. There are patches of teeth on the palatine bones (*pl.*); the larger teeth in front are regarded as vomerine. The figure is twice natural size.

Fig. 3. Palatal aspect of the anterior part of the skull of *Pristerognathus polyodon*, showing the incisor teeth, one to six in each pre-maxillary bone, the canines (*c.*), and pre-molars (*pm.*). Within these teeth is the mandible, with the two rami formed of the dentary bones, which are not united by synostosis at the symphysis. The hind splint of the splenial bone lies within the dentary bone. Incisors are seen at the extremity of the mandible, and the roots of the mandibular canine are exposed behind the symphysis by abrasion. Natural size.

Fig. 4. Palatal aspect of the anterior part of the skull of *Cryptocynodon simus*, showing (*c.*) the immature canine teeth; behind and internal to which is the single row of teeth on the palate. Natural size.

Fig. 5. Outline of the anterior aspect of the same skull. The anterior nares (*nn.*) are well separated in front, and the orbits (*oo.*) are widely separated behind. Within the anterior arch of the mouth the teeth upon the palate are indicated (*mt.*). Natural size.

Fig. 6. Internal aspect of the dentary bone of *Tribolodon* from Lady Frere, showing the angle of the jaw, and the coronoid process. The other bones which compose the lower jaw are lost from the slightly grooved surface exposed. The teeth are remarkable for their distance from each other, and height above the alveolar margin. Natural size.

Fig. 7. A single tooth of *Tribolodon* enlarged, showing its aspect from the inner side of the jaw.