INTRODUCTION

During the last three decades I have studied the fauna of the *Tapinocephalus* zone. Hitherto the emphasis has fallen mainly on the three aspects, viz. faunistic, morphological and taxonomic. In this contribution I would like to present some phylogenetic considerations. Here I am confining myself to the chief element of the fauna—the Therapsids. The only other important element is the Pareiasaurs, on which I have already written. Most students are agreed, in general terms, that the order Therapsida, constituting a well-defined group of mammal-like reptiles, arose from a group with a morphological set up as exemplified by the sphenacodont Pelycosaur. Recent discoveries enable one to be a bit more specific as to the connecting links. It is now, moreover, possible to trace some of the earlier divergences within the Therapsids stem.

THERAPSIDS OF THE *TAPINOCEPHALUS* ZONE IN SOUTH AFRICA

In South Africa the earliest Therapsids occur in the lowest zone of the Beaufort Beds. This—the *Tapinocephalus* zone—lies conformable on the underlying Ecca Beds, which have as yet yielded no Therapsid remains.

The *Tapinocephalus* zone has as yet not been adequately surveyed and its geographical distribution can only by roughly indicated in the form of a sketch map. (Fig. 1).

The area involved is well over 20,000 sq. miles.

In the geologically adequately surveyed parts, officers of the Geological Survey have determined a greatest thickness of 7,000 ft., consisting mainly of mudstones and sandstones deposited in the form of overlapping lenses of various sizes. The presence of two bands of Cherts has enabled them to subdivide the zone into three horizons—lower, intermediate and upper.

The fauna is already well established in the lower horizon, and the large collections that have been made come mainly from an area of concentration in the west known as the Koup. No specimens have as yet been found east of 22° 50' longitude or north of 31° 25' latitude.

Over 2,000 specimens have already been collected from the *Tapinocephalus* zone and 137 species have been described. Although it would be rash to state that the collection in the zone has been exhaustive, I nevertheless believe that the present collections give a good picture of the composition of the fauna and that further discoveries are not likely to add more than additional details faunistically, but better preserved specimens can add a lot to our knowledge of the structure of many of the known forms and a number of the present "species" may prove to be synonyms. A fuller morphological knowledge will undoubtedly affect our ideas of the phyletic relationships. Nevertheless the available facts enable us to make quite interesting phyletic deductions. The composition of the Therapsid part of the fauna is here shown in tabulated form. Only adequately known genera are listed.

ORDER THERAPSIDA (FIGS. 2-5)

1. Sub-Order Anomodontia,
   Infra-Order Dinocephalia
   Family Anteosauridae with 3 genera
   Dianoccephalidae with 4 genera
   Tapinocephalidae with 16 genera
   Infra-Order Dicynodontia
   Family Endothiodontidae with 4 genera
   Dicynodontidae with 2 genera
   Infra-Order Dromasauria
   Family Dromasauridae with 2 genera

2. Sub-Order Theriodontia
   Infra-Order Gorgonopsia
   Family Galesuchidae with 5 genera
   Hipposauridae with 1 genus
   Infra-Order Theroccephalia
   Family Priesterognathidae with 11 genera
   Lycosuchidae with 4 genera
   Alopecodontidae with 4 genera
   Scaloposauridae with 2 genera

Contemporary with these Therapsids are two inadequately known Pelycosaur genera,
which are of phyletic interest, and then there are the well represented Pareiasaurs with 6 genera, which are of ecological importance. The two Amphibians and one Chelonian are not in the present context of importance phyletically or ecologically.

Ecologically the *Tapinocephalus* zone fauna appears to have been well established and well balanced consisting as it does of:

- **Herbivores** — Pareiasaurs, Dicynodonts, Tapinocephalids, Titanosuchids, Styracocephalus and probably also the Dromasaurids.
- **Carnivores** — Gorgonopsia, Therocephalia and Anteosaurids.

Of the herbivores the large and bulky Pareiasaurs occur abundantly in the two lower horizons, as do also the Tapinocephalids and Titanosuchids, whereas the small Dicynodontia occur in large numbers in the upper two horizons. Of the carnivores the Gorgonopsia are rare throughout the zone; the Therocephalia — ranging from small to quite large forms — and the large Anteosaurids are well represented in the lower two zones.

The Distribution of the Therapsids within the *Tapinocephalus* zone.

<table>
<thead>
<tr>
<th>Anteosauridae</th>
<th>Low</th>
<th>Mid</th>
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<tbody>
<tr>
<td>Anteosaurus</td>
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<td>Parantoeosaurus</td>
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<td>Micranoeosaurus</td>
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<td>Scapanodon</td>
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<td>Jonkeria</td>
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<td>Styracocephalidae</td>
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<td>Tapinocephalidae</td>
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<td><em>Tapinocephalus</em></td>
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<td><em>Mormosaurus</em></td>
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<td><em>Phocosaurus</em></td>
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<td><em>Keratocephalus</em></td>
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<td><em>Struthionops</em></td>
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<td><em>Struthiocephalus</em></td>
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<td><em>Riebeekosaurus</em></td>
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<td><em>Mochops</em></td>
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<td><em>Delphinognathus</em></td>
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<td><em>Crocophalus</em></td>
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<td>Endothiodontidae</td>
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<td><em>Koupia</em></td>
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<td><em>Robertia</em></td>
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<td>Dicynodonta</td>
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<td><em>Dicynodon</em></td>
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<td><em>Oudenodon</em></td>
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<td><em>Pristerognathoides</em></td>
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<td><em>Trochosuchus</em></td>
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<td>Scaloposauridae</td>
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<td><em>Icticephalus</em></td>
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<td><em>Blattoideolestes</em></td>
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Of the 57 adequately known genera 49 are already present in the lower horizon of the Tapinocephalus zone. Fifteen are present in the lower and the intermediate horizons and 6 occur throughout the zone. Five first appear in the intermediate horizon; and of these 5, none continue into the upper zone. Three only occur in the upper horizon. In the upper horizon the whole fauna becomes reduced, with only 9 genera represented.

In the Anteosauridae the forms from the intermediate horizon are not more advanced than those of the lower zone, and in the lower zone the more primitive *Paranteosaurus* occurs with the more advanced *Anteosaurus*. In the Titanosuchidae no advance can be seen in the forms from the intermediate horizon beyond those from the lower horizon. But *Styracocephalus*, from the intermediate horizon is undoubtedly a highly specialised form and could have arisen from a primitive Titanosuchid.

In the Tapinocephalidae, *Tapinocephalus* and *Phocosaurus* range unchanged from low to high in the zone. The lower and intermediate specimens of *Keratocephalus*, *Struthiocephalus* and *Delphinognathus* show no morphological advance. The Moschopines *Moschops*, *Avenantia* and *Crocophalus*, although all from the lower horizon show primitive and advanced features. But *Agnosaurus* from the intermediate zone is still primitive. *Riebeekosaurus* from the middle horizon shows definite advanced features in the intertemporal region.

But *Moschops*, which has as yet only been found high up in the zone is morphologically more primitive than any of the lower horizon Tapinocephalids.

In the Dicynodontia the more primitive *Broilius* occurs later than the more advanced *Brachyuraniscus*, *Koupia* and *Robertia*. In the Gorgonopsia the late *Pachyrhinos* could be derived from one of the earlier Galesuchids. In the Therocephalia the primitive Pristerognathids and Lysosuchids occur together with the more advanced Alopecodontids and one Scaloposaurid, but *Blattoideolestes* with some cusped postcanines, occurring in the middle zone, is derivable from the older *Icticephalus*.

From the above it is thus evident that the Therapsids of the Tapinocephalus zone diverged from each other before Tapinocephalus zone times, and during the time the 7,000 ft. deposits were laid down each group remained very stable, with only small advances in a few cases and these of little phyletic significance.
Fig. 2.—Synapsids of the Tapinocephalus zone. Representative skulls of the families shown in lateral view and brought to approximately the same basal length. Arranged to show their relationships.

a. Pelycosaur; b. Galesuchid; c. Hipposaurid; d. Pristerognathid; e. Lycosuchid; f. Scaloposaurid; g. Dicynodontid; h. Endothiodontid; i. Dromasaur; j. Anteosaurid; k. Titanosuchid; l. Styraccephalid; m. Tapinocephalid.
This stagnation during the formation of such a thick deposit—7,000 ft.—must be considered remarkable.

In the accompanying text figures (Figs. 2-5) series of cranial figures of the Synapsids of the *Tapinocephalus* zone, with each sketch representing a family, are given and arranged to show the relationships. The motivation for the indicated relationships is given in later sections of this paper.

As the *Tapinocephalus* zone presents us with a Therapsid fauna already diversified and which during its duration undergoing little phyletic development, and the beds lying conformable under it being barren we must for the elucidation of the origin of this fauna look elsewhere, if we are not content to rely wholly on the methods of pure comparative morphology.

The Dinocephalia become rare in the upper horizon and do not continue into the *Endothiodon* zone.

The Dicynodontia, little developed in the *Tapinocephalus* zone, get really into their

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*Fig. 3.—Synapsida of the Tapinocephalus zone. Representative skulls of the families shown in dorsal view and brought to approximately the same basal length. Arranged to show their relationships.*

- a. Pelycosaur; b. Galesuchid; c. Hipposaurid; d. Pristerognathid; e. Lycosuchid; f. Dicynodontid; g. Endothiodontid; h. Anteosaurid; i. Titanosuchid; j. Styracocephalid; k. Tapinocephalid.
stride in the *Endothiodon* zone. This also applies to the Gorgonopsia. In the higher zones the primitive Therocephalia, well developed in the *Tapinocephalus* zone, peter out and their place is taken by the more specialised families.

THE EARLY THERAPSIDS OF RUSSIA

Elsewhere than in South Africa a fauna of early Therapsids is known only from Russia. Here occurs a Permo-Triassic sequence, which had been divided into 6 palaeontological zones. Only the fauna from the lower two of these zones need be considered here. Their age is still in dispute but some workers are convinced that the lowest zone, at least, is older than the *Tapinocephalus* zone of South Africa. I am not competent to discuss the stratigraphy. But let us consider the fauna of early Therapsids from these Russian Beds.

The composition of the Therapsid fauna is given here in tabulated form and only adequately known genera are listed.

**ORDER THERAPSIDA**

1. **Sub-order Eotitanosuchia**
   Family Eotitanosuchidae (3 genera)
   " Phthinosuchidae (2 genera)

2. **Sub-order Anomodontia**
   Infra-order Dinocephalia
   Family Brithopidae (4 genera)
   " Anteosauridae (3 genera)
   " Estemmenosuchidae (1 genus)
   " Tapinocephalidae (1 genus)
   Infra-Order Dicynodontia
   Family Otsheridae (1 genus)
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**THE EARLY THERAPSIDS OF RUSSIA**

[Diagram of Therapsid skulls]

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2. **Sub-order Anomodontia**
   Infra-order Dinocephalia
   Family Brithopidae (4 genera)
   " Anteosauridae (3 genera)
   " Estemmenosuchidae (1 genus)
   " Tapinocephalidae (1 genus)
   Infra-Order Dicynodontia
   Family Otsheridae (1 genus)
   " Venjukoviidae (1 genus)
3. Sub-order Theriodontia
   Infra-order Therocephalia
   Family Pristerognathidae (2 poor genera)

Associated with these are some limb-bones of three genera assigned to the family Phreatosuchidae, probably Pelycosaurian.

The above list shows that the early Russian Therapsid fauna is, as far as our present knowledge goes, much poorer than the equivalent South Africa fauna. Further collecting in Russia will undoubtedly change this picture, notwithstanding the differences in collecting conditions.

Whereas the Tapinocephalus zone in South Africa extends over a large continuous area in an arid climate with the strata very well exposed and accessible, in Russia the two lower zones of their succession are poorly exposed in difficult terrain and the collections hitherto made have been recovered from old now disused copper mines and a few patches of unconnected exposures. The known collections can thus hardly be considered as truly representative of the Russian fauna.

Where the South African fauna, as known, consists of 57 adequately preserved genera and the 137 described species are based on over 2,000 specimens, the Russian fauna consists of 16 adequately preserved genera and the 25 described species are based on a number of specimens little more than a small multiple of the described species.

The early Russian Therapsid fauna has the following ecological composition:

Herbivores — a couple of specimens of a Tapinocephalid, three specimens of Dicynodontia and an assemblage of skeletons of Estemmenosuchus.

Carnivores — fragments of two Therocephalia, four skulls of Eotitanosuchia, four genera of Brithopids and a few specimens of 3 genera of Anteosaurids.

The preponderance of carnivores shows the imbalance of the fauna as known at present. Remarkable is the absence of typical Titanosuchids and the paucity of Therocephalia. In contrast to the South

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Fig. 5.—Therapsids of the Tapinocephalus zone. Representative lower jaws of the families in lateral view. Scale on the basis of approximately the same basal skull length.

a. Galesuchid; b. Hipposaurid; c. Lycosuchid; d. Pristerognathid; e. Scaloposaurid; f. Dicynodontid; g. Endothiodontid; h. Dromasaur; i. Anteosaurid; j. Titanosuchid; k. Tapinocephalid.

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African faunistic composition, Pareiasaurs in the two lower Russian zones are represented by only a few fragments, whereas in the Tapinocephalus zone complete Pareiasaur skeletons are abundant.

Nevertheless, the known early Russian Therapsids are of great interest.

I have recently had the opportunity of examining all this Russian material and found it extremely interesting, particularly from a phylogenetic point of view. I am incorporating the evidence in a later section of this paper, but a preliminary tabulation will at this stage be useful.

For the determination of the origin and relationships of the Dinocephalia and Gorgonopsia the Eotitanosuchian genera Eotitanosuchus, Biarmosuchus, Biarmosaurus, Phthinosuchus and Phthinosaurus are of great importance, linking up as they do the primitive Brithopids (Archaeosyodon, Syodon, Titanophoneus) with the Sphenacodonts and showing possible relations with the primitive Gorgonopsians. The Brithopids gave us an insight into the early stages of the Anteosaurid development. The Dicynodontia genera Otsheria and Venjukovia take us a step back into the history of the Dicynodontia.

Ulemosaurus being less primitive than some South African Tapinocephalids is less important.

Estemmenosuchus is of interest mainly due to its mixture of characteristics and specialisations, and this chiefly because of the fact that no typical Titanosuchidae have as yet been found in the Russian assemblage.

ORIGIN AND EARLY DEVELOPMENT OF THE THERAPSID STEM

In order to attempt to link up the mammal-like Therapsida with the primitive reptile groups we may begin our story at the Captorhinid level.

By at first only taking into consideration certain morphological highlights the main theme should become apparent. Details can be considered later.

A. In the Captorhinid skull we have:
1. A closed anapsid skull roof, with the adductor muscles of the jaws originating from the under surface of the temporal roof bones.
2. The undifferentiated adductor muscle is inserted in the adductor fossa of the lower jaw.
3. The pterygoid has a movable articulation with the cranial base; the connection between the pterygoid and quadrate is firm and strong; the connection between the occiput and the quadrate and also with the squamosal is weak.
4. The quadrate is situated far posteriorly and lies in the same plane as the alveolar border of the upper jaw.
5. The vomer lies in the general plane of the palate.
6. The quadratojugal is a bone of the lateral surface supporting the quadrate.

B. In the Sphenacodont skull (Fig. 6, 1) we have:
1. The skull roof has become fenestrated (synapsid) but the origin of the adductor muscles remains fairly primitive, still arising from the under surface of the roof bones (parietal and postorbital), which widely overhang the temporal fossa.
2. The adductor mass has become differentiated, with the inner part primitively inserted mainly in the adductor fossa, but the outer part (masseter) is inserted on the dorsal border of the lower jaw.
3. The pterygoid, quadrate and vomer remain primitive.
4. The quadratojugal becomes weaker in some cases.

C. A postulated Eo-Therapsid (Fig. 6, 2):
The next stage known concretely is that found in the early Therapsids. But since the earliest known Therapsids, already show divergent developments well established, intervening stages must be postulated.

In a first stage the skull would have:
1. The temporal fossa increased in size; with the outflaring of the post-temporal bar posteriorly as well as of the subtemporal bar laterally, the two components of the adductor mass

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show a further differentiation. The origin of the temporal part now lies further posteriorly and the direction of its pull shifts from the vertical to a diagonal direction. The origin is still chiefly from the under surface of the parietal and postorbital.

2. The insertions are still in the adductor fossa and the dorsal border of the lower jaw.

3. The basal articulation is lost. Together with the fusion of the pterygoid to the cranial base there is a strengthening of the connection between the occiput and the quadrate and squamosal. The quadrate ramus of the pterygoid and its connection with the quadrate remains strong and firm.

4. The changes in the temporal fossa, associated with the changes in the direction of pull of the adductor muscles, is also accompanied by changes in the jaw articulation. An important feature in this connection is the downward shift of the quadrate, which now lies below the level of the alveolar border of the upper jaw.

5. The vomer still lies in the primitive level.

6. The quadratojugal is moving away from the outer surface and becoming functionally unimportant.

Such a skull would conform to the definition of a Therapsid and represent a first step beyond the Sphenacodont condition.

D. Origin of the Sub-orders Theriodontia and Anomodontia.

After this hypothetical stage a split must have occurred in the Therapsid stem. Evidence of this is afforded by the Eotitanosuchia (Fig. 6, 4). In this group, comprising 5 genera — Eotitano suchus, Biarmosuchus and Biarmosaurus, Phthinosuchus and Phthinosaurus—we find features met with in the Gorgonopsia (a Theriodont infra-order) and the Dinocephalia (an Anomodont infra-order).

The primitive Theriodont characters are:

1. Upper part of the postorbital still a bone of the dorsal surface from whose under surface and edge the temporal part of the adductor mass originated. The intertemporal region is still broad with the parietal and postorbital overhanging the temporal fossa.

2. The quadrate is posteriorly situated.

3. The choanae are still long and anteriorly situated.

4. The nares are still terminal.

The Dinocephalian characters are:

1. The dorsal process of the premaxilla prolonged in the dorsal median surface intercalated for a long distance between the nasals.

2. The quadrate ramus of the pterygoid strong and with a firm connection with the quadrate.

3. No preparietal.

4. No coronoid process to the dentary.

But an advanced Gorgonopsian character is the shifting of the vomer to a higher level. Eotitanosuchia.

This sub-order contains two families.

Eotitanosuchidae. A family of primitive Therapsids from Russia with 3 genera showing affinities to the early Dinocephalia. Long dorsal process of the premaxilla, robust quadrate ramus of the pterygoid, the postorbital shows an incipient encroachment of the adductor muscles onto its lateral face. Short postcanine series, sloping occiput. No coronoid process on the dentary. Moderate entry of frontal onto the orbital border. Vomer lies above general palatal level as in later Gorgonopsians.

Phthinosuchidae. A family of primitive Therapsids from Russia with 2 genera, showing affinities to the early Gorgonopsia. Short posterior process to the postorbital which is met by a high dorsal process of the squamosal forming a lappet overhanging the temporal fossa. Adductor originated from under surface of roof bones. Long postcanine series, upright occiput. Incipient coronoid process. Large entry of frontal into orbital border. Vomer lies above general palatal level as in Gorgonopsians.
Fig. 6.—Diagrammatic scheme illustrating the origin of the three Therapsid suborders and the four infra-orders.

I thus aver that the Eotitanosuchia are a relict infertile branch not ancestral to either the Theriodontia or the Anomodontia, but morphologically near the level from which these two sub-orders commenced their distinct lines of development.

At this level the primitive Therapsid (Fig. 6, 2) had a skull with:

1. A wide intertemporal region with the upper part of the postorbital a surface bone overhanging the temporal fossa.
2. The quadrature ramus of the pterygoid strong and firmly attached to a robust quadrature.
3. Lower jaw without a definite coronoid process.

With the development of a coronoid process to the dentary the temporal muscle definitely became a distinct muscle, and the direction of its pull horizontal, with its point of origin lying posterior to its point of insertion. This reduced the stress at the jaw hinge, which resulted in a weakening of the quadrature and the connection of this bone with the quadrature ramus of the pterygoid, which became a weak bar of bone.

These developments gave rise to the first Theriodonts (Fig. 6, 3).

Where no coronoid process was developed the adductor muscles continued to pull upwards and the stress on the quadrature at the jaw hinge remained great. In developing a greater efficiency of the adductor mass, without a coronoid process, the quadrature moved anteriorly. With the insertions of these muscles on the lower jaw appears to have developed on much the same lines. The difference lies in the origin of these muscles. The primitive area of origin, viz. mainly from the under surface of the parietal and postorbital, is to a great extent retained in the Gorgonopsia, which accounts for the continued presence of a broad intertemporal region and a well developed postorbital which has its upper part lying horizontally in the surface of the skull table.

With the shifting of the area of origin of the temporal muscle medially the intertemporal region narrowed, culminating in the formation of a median sagittal crest and a reduction of the upper part of the postorbital to a mere process lying vertically flanking the lateral face of the parietal, from which bone the muscle mainly originated. This is the basic Therocephalian condition.


Apart from the weakened pterygo-quadrature complex the, as yet undifferentiated, Theriodont stem had certain other characters. A character retained from the Sphenacodont ancestors was the broad intertemporal region in which the postorbital formed a horizontal overhanging rim above the temporal fossa.

This condition we find retained in the Gorgonopsia. (Fig. 6, 6).

This condition is lost in all the known Therocephalia (Fig. 6, 7).

This splitting of the ways can be attributed to a differential further development of the adductor muscles. The insertions of these muscles on the lower jaw appears to have developed on much the same lines. The difference lies in the origin of these muscles. The primitive area of origin, viz. mainly from the under surface of the parietal and postorbital, is to a great extent retained in the Gorgonopsia, which accounts for the continued presence of a broad intertemporal region and a well developed postorbital which has its upper part lying horizontally in the surface of the skull table.

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F. Origin of the Dinocephalia and Dicynodontia.

In the Anomodont stem (Fig. 6, 5) soon after the hiving off from the Theriodonts, developments in the general jaw mechanism also took place.

The initial primitive wide intertemporal region became reduced and the postorbital no longer forms an overhanging rim over the temporal fossa, when the area of origin of the adductor muscles moved medially. But the insertion on to the lower jaw remained fairly primitive, without the development of a coronoid process to the dentary.

This common development within the stem soon gave the way to differentiation.
In one group the primitive strong pterygo-quadrate complex was not only retained but strengthened. This group constitutes the Dinocephalia (Fig. 6, 9).

Another group retains the strong robust quadrate, but the support from the quadrate ramus of the pterygoid becomes weakened and in its place a strong paroccipital brace to the quadrate becomes established. This group constitutes the Dicynodontia. (Fig. 6, 8).

The origin of the above four infra-orders of the Therapsida must have taken place early in the Ecca times.

Between this and the beginning of Beaufort times further diversification took place giving rise to the various families we find developed at the base of the Tapinocephalus zone.

FURTHER DEVELOPMENTS IN THE THERAPSID INFRA-ORDERS

Families of the Gorgonopsia.

At the beginning of Tapinocephalus zone times at least two distinct families were already developed.

1. Galesuchidae. A primitive family with at least five adequately known genera from South Africa. The temporal fossa is of moderate size with the squamosal not flaring posteriorly; large frontal entry into the orbital border; premaxillary alveolar border horizontal; a short postcanine series; with quadrate slightly below the maxillary alveolar border. Moderate coronoid process.

2. Hipposauridae. With one genus. The temporal fossa is small, with a very broad intertemporal region, but the squamosal flares posteriorly. Large frontal entry into the orbital border; short postcanine series; with quadrate very far below the maxillary alveolar border; strong dorsal curvature of skull; occiput upright but deeply concave from side to side; premaxillary border horizontal. Moderate coronoid process.

Families of Therocephalia.

At the beginning of Tapinocephalus zone times there were at least four distinct families of Therocephalia developed.

1. Pristerognathidae. With at least eleven adequately known genera. Temporal fossa long and broad, with narrow elevated inter-temporal region (parietal crest), and posteriorly and laterally flaring squamosals; frontal entry into orbital border moderate or excluded; postcanine series varies from very short to moderately long; quadrate just below alveolar border, occiput upright and deeply concave from side to side; large suborbital fenestrae; postdental part of mandible strong; a single canine; 5-6 incisors; epipterygoid narrow. Strong coronoid process.

2. Lycosuchidae. With four good genera. Essentially as in Pristerognathids, but the postcanine series is short, there are two upper canines; the skull is shallower, the epipterygoid widened and the basisphenoidal tubera strong.

3. Alopecodontidae. With four genera. With small maxillary teeth anterior to the canine; postcanine series short to quite long.

4. Scaloposauridae. With two inadequately known genera. With broad parietal region; long slender curved dentary; fairly numerous postcanines, some of which are cuspised; small additional canines anterior to the main canine; postorbital bar weak.

Families of the Dinocephalia.

When the Dinocephalian stem diverged from the Dicynodontian stem early in Ecca times the morphological level of these ancestral Dinocephalians can be diagnosed as follows:

The quadrate ramus of the pterygoid and the quadrate was strongly developed; the quadrate still occupied a posterior position and was still not descended much below the level of the maxillary alveolar border, the intertemporal skull table was broad, with the dorsal part of the postorbital lying fairly horizontally in the dorsal surface slightly overhanging the temporal fossa; the temporal fossa, although short, extended down to a level just above that of the alveolar border; the lower jaw was without a coronoid process. Both the origin and insertion of the adductor muscles thus show a fairly primitive condition. The postcanine series was long and the alveolar border of the premaxilla was horizontal.

Brithopidae. At the next stage we find the following development. The quadrate has moved forwards to a plane just anterior to that in which the occipital condyle lies and
is situated well below the level of the alveolar border. The inter-temporal part of the skull roof is reduced in width, with the dorsal part of the post-orbital lying at a slant below the general level of the skull roof. The temporal fossa extends far ventrally and the squamosal flares posteriorly. A definite change in the area and nature of the origin of the adductor muscles has thus taken place.

The three Brithopid genera, Archaeosyodon, Syodon and Titanophoneus, although from a high horizon, exemplifying this stage of development very well.

**Anteosauridae.** A skull like that of Titanophoneus developing as follows: the dorsal part of the postorbital shifting to a vertical position to lie flanking the parietal; the squamosal flaring greatly laterally as well as posteriorly; the quadrate shifting further ventrally as well as anteriorly; the postfrontal swelling so as to exclude the frontal from the orbital border; increasing upward slant of the premaxillary border, with a lengthening of the incisors and a pachyostotic thickening of the roof bones would produce a typical Anteosaurus. I thus conclude that the Anteosaurids are a direct development from the Brithopid level.

**The Titanosuchid-Tapinocephalid Stem.** When the Brithopids and their descendants, the Anteosaurids, hived off the other Dinocephalian stem was at the following morphological level:

In the skull the temporal fossa was large, with the postorbital flanking the parietal; the postcanine series was long and the alveolar border of the premaxilla horizontal; the incisors, canines and postcanines were simple conical teeth; no pachyostotic developments; the snout comparatively short and high; the dorsal premaxillary process moderately long and the quadrate was situated far forward and ventrally. Further developments in this stem were: the incisors developed a talon-and-heel structure; the snout lengthened and became shallower; the dorsal premaxillary process increased greatly in length and the quadrates moved still further anteriorly as well as ventrally.

**Titanosuchidae.** In this branch the strong canine was retained; the talon-and-heel incisors became strongly developed, and the postcanines developed spatulate crowns and increased in number in posterior direction; the snout became greatly lengthened and reduced in height and little pachyostosis took place. From this line of development Styracocephalus arose as a late off-shoot.

**Tapinocephalidae.** In this branch the canine was lost as such and all the teeth developed crowns with a talon-and-heel; the snout became only moderately long and remained fairly high. This line of development produced an ancestral Tapinocephalid looking very like Moschosaurus. From such a level as exemplified by Moschosaurus the various groups of the Tapinocephalids branched out in a last fling of digitation. For instance: Riebeeckosaurus decreased its intertemporal width to a sharp parietal crest; Moschosaurus and its related genera have their snouts greatly shortened, with the dorsal skull contour forming an even curve; the intertemporal region becomes secondarily widened and the temporal fossa greatly reduced in size. In Struthiocephalus and its allied genera a prominent naso-frontal horn-like boss develops. In Tapinocephalus and its allies the pachyostosis becomes enormous and the snout very weak.

**Estemmenosuchidae.** The salient features in the Russian genus Estemmenosuchus are, the broad inter-temporal region with the upper part of the postorbital lying on the dorsal surface overhanging the temporal fossa. The presence of these features indicate that the forebears of Estemmenosuchus hived off from the Dinocephalian stem before the Brithopids.

**Estemmenosuchus** parallels both the Titanosuchids and Tapinocephalids in the great downward and forward shift of the quadrates and the development of a long series of postcanines. The temporal fossa remained large, but in the general pachyostosis and the extraordinary development of bosses and hornlike processes there is a parallelism with the Tapinocephalids. Its canines and incisors parallel those of the Brithopids. The quadrate ramus of the pterygoid is very like that of Jonkeria.

In short Estemmenosuchus developed characters of each of the Dinocephalian groups.

In its palate it retained a shagreen of teeth reminiscent of some early Sphenodonts.
MORPHOLOGICAL SERIES

To illustrate the foregoing evolutionary story I have arranged sketches of the relevant Synapsid skulls in series. By doing this concordant, but also discordant, features become apparent, which are discussed in the following explanatory notes.

The Series Dimetrodon — Anteosaurus

(A, B, E, F, G, H and I — Fig. 7)

A comparison of the skulls seen in lateral view brings out the following morphological points:

The small temporal opening of the Sphenacodonts becomes enlarged at the first step as exemplified by *Eotitanosuchus* and then increases step by step to culminate in the large temporal fossa of *Anteosaurus*. The posterior limb of the postorbital lies horizontally in the roof of the skull of *Dimetrodon* and retains practically the same position in *Eotitanosuchus*; from *Syodon* the postorbital commences to descend from the surface of the skull roof and its surface begins to lie at a slant; this process is continued in the series, step by step, until the condition is reached in *Anteosaurus*, where the upper part of the postorbital has its morphological median edge directed dorsally and its morphological dorsal facing laterally and thus from a roof-bone becomes a bone lining the inner face of the temporal fossa.

The forward shift of the quadrate and the concomitant shortening and increase in massiveness of the lower jaw can be seen to have been progressive. Progressive also is the reduction of the postcanine series, the upward slant of the alveolar border of the premaxilla and the lengthening of the incisors.

The lacrimal is shortened at the first step (in *Eotitanosuchus*) and then remains consistently short throughout the series, this also applies to the lengthening of the dorsal process of the premaxilla.

The primitive anterior position of the nostril is retained in *Eotitanosuchus*, but from *Syodon* shifts more and more dorsally and posteriorly.

The pachyostosis can be followed step by step, so also the gradual outsting of the frontal from the orbital border — complete in *Doliosaurus*—culminating in the development of the prominent boss-like postfrontal of Anteosaurus and a decrease in size of the orbit, which is, step by step, removed lower down in the skull away from the skull roof. The angular boss commences its development late — in *Doliosaurus* — and is massive in *Anteosaurus*.

The Series Dimetrodon — Hipposaurus

(A, B, C and D, Fig. 7)

This series from Sphenacodont to Gorgonopsian is less convincing.

The temporal fossa is increased in size in *Eotitanosuchus* and *Phthinosuchus*, small in *Hipposaurus* and then enlarged in all later Gorgonopsians.

The posterior limb of the postorbital remains a surface bone overhanging the temporal fossa in the Gorgonopsia, but in *Phthinosaurus* the upward growth of the squamosal is a discordant step. The well developed postcanine series in *Phthinosuchus* is also out of step. The incipient development of a coronoid process to the dentary in *Phthinosuchus*, is however a forerunner of the well developed process in all later Gorgonopsians.

In the whole series the nostril remains terminal and no pachyostosis occurs. But the elongated dorsal premaxillary process in *Eotitanosuchus* and *Phthinosuchus* is incongruous in this series.

The Series Dimetrodon — Anteosaurus in Dorsal View (Fig. 8)

(A, B, E, F, G, H and I)

This series commences with, in *Dimetrodon*, a broad intertemporal region, small temporal fossa, the posterior process of the postorbital a surface bone overhanging the temporal fossa and the occiput sloping forwards; the dorsal premaxillary process still short and the lacrimal long.

In *Eotitanosuchus* the intertemporal region is still broad, the postorbital has not changed and the occiput is still sloping. But, the shortening of the lacrimal has taken place in one step; the premaxilla process has lengthened; the temporal fossa has started to enlarge and the supra-temporal lost.

In *Syodon* the occiput becomes upright and this feature remains constant throughout the series. The upper surface of the postorbital commences to move downwards
Fig. 7.—Morphological Series of Skulls in lateral view brought to approximately the same basal length. Gorgonopsid Series: a. Dimetrodon; b. Eotitanosuchus; c. Phthinosuchus; d. Hipposaurus. Anteosaurid Series: a. Dimetrodon; b. Eotitanosuchus; c. Syodon; f. Titanophoneus; g. Deuterosaurus; h. Doliosaurus; i. Anteosaurus.
away from the dorsal roof surface and begins to lie at a slant; the parietal table decreases in width and a tendency to a median parietal crest becomes apparent.

From Titanophoneus to Anteosaurus the postorbital progressively becomes a bone lying more and more below the surface of the skull roof and situated more and more vertical to form a facing to the lateral face of the parietal and lining the median surface of the temporal opening. The posterior and lateral flaring of the squamosal with increase of the size of the temporal fossa is progressive. With the increased pachyostosis less and less of the orbit faces upwards and the postfrontal boss becomes more and more prominent.

This morphological series gives a very good picture of the probable history of the development in the Anteosauridae.
The Series Dimetrodon — Hipposaurus (Fig. 8, A, B, C and D).

In this series the broad intertemporal region is retained and even increased with the upper part of the postorbital lying on the dorsal surface as a surface bone throughout, giving origin to the adductor muscles from its under surface. The lappet of the squamosal overhanging the temporal fossa is a peculiarity of Phthinosuchus. The nostrils remain terminal throughout, but the lengthening of the premaxillary process seen in Eotitanosuchus is later reversed indicating that this form does not lie on a direct ancestral line.

The Series Dimetrodon — Anteosaurus in Ventral View (Fig. 9) (A, B, C, D and E).

It will be immediately noticed that here Eotitanosuchus is not included in the series leading to Anteosaurus because of discordancy. It is, however, concordant in the Gorgonopsian series. In this series the crucial change from Sphenacodont to Therapsid is apparent in the first step, namely the moveable basal joint of Dimetrodon is lost in Archaeosyodon. The anterior process of the pterygoid is long in Dimetrodon and at the first step in Archaeosyodon becomes short and remains constantly short throughout. Both these developments are paralleled in the Gorgonopsian series.

From Titanophoneus the choanae have shifted backwards and from Archaeosyodon decreased in length. The vomer lies in the general plane of the palate throughout the series, but from Archaeosyodon becomes stouter. The lateral flange of the pterygoid becomes greatly strengthened and progressively more prominent. In the relation of choana to palatine the condition in Archaeosyodon appears to be discordant.

The Series Dimetrodon — Hipposaurus (Fig. 9) (A, F, G, and H).

In this series, which includes Eotitanosuchus, the long anteriorly situated choanae remain constantly narrow throughout and the vomer never becomes massive. At the first step, in Eotitanosuchus, the vomer shifts to a higher plane and remains in this position throughout the Gorgonopsia.

Dicynodontia.

At the Dicynodont divergence from the Dinocephalian branch the structural level can be high-lighted as follows: the intertemporal surface is fairly narrow and is formed by the parietals, with the dorsal part of the postorbital forming little more than just the dorsal edge of the temporal fossa; the temporal fossa is fairly wide but still short, notwithstanding the posterior flaring of the squamosals; the quadrates lie just anterior to the plane of the occipital condyle and a short distance ventrally; the pterygoid-
quadrate ramus is fairly strong and the paroccipital-quadrate brace is strengthened; the subtemporal bar moves dorsally so that the squamosal develops a ventral stalk to meet the quadrate.

The teeth are fairly simple conical with a reduction in size of the canine. The palatal teeth are reduced. The vomer still lies on the same level as that of the palate generally. The lateral flange of the pterygoids still prominent. The dorsal process of the premaxillaries are still fairly long. The occiput is sloping with the pineal foramen near its edge. There was no preparietal.

Dromasauria.

It appears probable that at this morphological level the inadequately known Dromasauria branched off.

Venjukoviidae.

The skull of Venjukovia is incompletely known, but it appears to represent a specialised form of a group which branched off from the Dicynodont stem fairly early. It shows primitive and specialised features. Primitive are: the long snout; the long dorsal processes of the premaxilla; the long lacrimal; the elongated choanae; the presence of incisor teeth and a fairly long row of maxillary teeth.

Advanced are: the reduction of the lateral pterygoid flanges; the extensive palatal face of the premaxilla; the meeting of the palate and premaxilla thus excluding the maxilla from the choanal border; the vomer lying at a higher level than the palate generally; the posterior position of the choanae. The teeth still lie on the alveolar edge, but have become specialised, particularly the chisel-shaped incisors. In the dentary the teeth have moved away from the outer edge. The peculiar pachyostosis is highly specialised.

Otsheridae.

The skull of Otsheria is known from a single skull from near Eshevo, Perm, Russia. This highly interesting form already has the typical greatly shortened Dicynodont snout with a very short lacrimal, a large orbit and the subtemporal arch has moved upwards so that the squamosal has a stalk-like process to meet the quadrate; the palatal face of the premaxilla is increased and the choanae moved posteriorly. But it still retains the following primitive characters: the dorsal process of the premaxilla is long, intercalated between the nasals; there is no prefrontal; the intertemporal region is still fairly wide with the postorbital overhanging the temporal fossa which, is still moderately small.

In the palate the lateral pterygoid flange is still laterally directed and prominent, the vomer still lies in the general palatal level and the relations of vomer, palate and transversum are still primitive. The palate does not meet the premaxilla. The quadrate ramus of the pterygoid is still well developed and strong. The teeth in the premaxilla and maxilla lie on the alveolar edge.

Morphologically Otsheria lies on the direct line of development of the later Dicynodonts, but because of its stratigraphical position cannot be a direct ancestor.

Endothiodontidae and Dicynodontidae.

Before the Dicynodontia stem split into two branches — Endothiodontidae and Dicynodontidae—a higher morphological level was reached.

The lateral pterygoid flange is all but lost, is directed anteriorly and incorporated in the general palatal surface; with it the transversum is also greatly reduced; the pterygoid forms a median girder and the quadrate ramus becomes weak. The temporal fossa becomes greatly lengthened, but the postorbital becomes a strong element flanking the parietals. With radical changes in the function of the temporal muscles the squamosal becomes highly specialised with the formation of an outer horizontal ledge from whose underside a strong outer masseter originates. The septo-maxilla is confined within the nostril. The palatal face of the premaxillaries is greatly increased; the choanae shifted well back and reduced. The vomer shifted to a higher plane and the whole palate, vomer, maxilla, transversum relationship highly modified.

All premaxillary teeth are lost and the molar teeth shifted away from the outer maxillary edge.

In the Endothiodont-Dicynodont split the chief feature concerned is the retention of very modified molars by the Endothiodonts.
and their total loss by the Dicynodonts. I need not discuss the Endothiodont-Dicynodont relation here as this has recently been done by Toerien.

The Series Dimetrodon — Dicynodontia (Fig. 10)

Here it is clear that Venjukovia (D) with its long snout, long lacrimal, long dorsal premaxillary process and posteriorly shifted nostril represents an offshoot away from the main Dicynodont line. But its reduced lateral pterygoid flange shows how this feature developed in Dicynodonts.

Otsheria (B) with its shortened snout and lacrimal and its dorsally shifted subtemporal bar is a probable intermediate stage between Sphenacodonts and the Dicynodontia (C). But the lengthened dorsal premaxillary process is an incongruity.

The Series of Palates — Dimetrodon to Dicynodontia (Fig. 11)

The palates of both Venjukovia (E) and Otsheria (B) can be derived from some such form as Dimetrodon (A). In both the choanae have shifted backwards with the increase of the palatal face of the premaxillaries, the anterior pterygoid process reduced in length and the lateral pterygoid flanges shifted anteriorly. The reduction of the lateral pterygoid flange has proceeded further in Venjukovia than in Otsheria. But in Venjukovia the choanae have remained long, the vomer has developed a large spatulate posterior end and the meeting of the palatine and premaxillar excludes the maxilla from the choanal border. These features together with the highly specialised nature of the dentition and the pachyostis exclude Venjukovia from the line leading to the Docynodontia.

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**Fig. 10.**—Morphological Series of Skulls in lateral view brought to approximately the same basal length.

a. Dimetrodon
b. Otsheria
c. Dicynodon
d. Venjukovia

**Fig. 11.**—Morphological Series of Palates.

a. Dimetrodon
b. Otsheria
c. Dicynodon
d. Robertia
e. Venjukovia

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From a form like Otsheria the Dicynodont palate is easily derived.

Before the branching of the Dicynodontidae from the Endothiodontidae a common development would be: a reduction of the marginal teeth and their medial movement; reduction of the prominent lateral pterygoid flange; posterior shift and reduction of the size of the choanae; dorsal shift of the vomer with its entry into the anterior border of the interpterygoid vacuity. Then in the Endothiodontidae (D) some maxillary teeth remain and the palatine meets the premaxilla, whereas in the Dicynodontidae (C) all but the canines are lost and the palatine fails to meet the premaxilla.

CONCLUSION (FIG. 12)

The accompanying tree summarises our conclusions graphically.

1. The Therapsid stem gives off three branches, an Anomodont, a Theriodont and an Eotitanosuchian branch.

2. The Theriodonts split into Gorgonopsia and Therocephalia.

3. The Anomodonts split into Dicynodontia, Dromasauria and Dinocephalia.

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