

# PHILOSOPHICAL TRANSACTIONS.

## I. CROONIAN LECTURE: *On the Origin of Mammals.*

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### INTRODUCTORY.

Since in the last 50 years the belief in the descent of all higher forms of life from earlier types has become universal, the desire to discover the origins of things has grown strong and there is probably no group in whose origin we are more interested than that to which we ourselves belong. The problem is fascinating not only because of our personal interest, but perhaps nearly as much on account of its difficulty. The living mammals differ so very markedly from all other living vertebrates that there is no group to which they seem nearly related, and none which is manifestly ancestral to them. With many marvellous specialisations and many peculiar degenerations, they retain a host of primitive characters. In some features they resemble the lizards; in others more strikingly do they agree with *Sphenodon*. In the possession of a secondary palate and in some other characters they seem to have some Crocodilian affinity; in developing with a primitive streak and in one or two other points they agree with the birds. In the simple character of the bones of the skull, in the relation of certain blood-vessels, and in certain points in the ontogeny the affinities seem nearer to the amphibians than to the living reptiles; and a few characters even seem to suggest an origin directly from some group of fishes.

For the solution of the problem we seem to be restricted to three lines of research—Comparative Anatomy, Embryology and Palæontology—and unfortunately all three are subject to serious limitations.

When we have a large series of connected forms it is a simple matter to trace a

structure down and to homologise it with the corresponding in lower types, but when the gap is as great as it certainly is between mammals and living amphibians or reptiles the tracing of homologies becomes a matter of difficulty and doubt. Structures which seem to correspond may be merely analogous, and our conclusions become for the most part guesses more or less probably true. While most valuable work has been done in vertebrate comparative anatomy there is probably no investigator in this field who will not be ready to admit that the conclusions to which his researches on the origin of mammals lead are vague and uncertain.

The second line of research may be regarded as in part a branch of the first. There is no question that later embryos show characters of the immediate ancestors. For example, the foetal marsupial is seen to have a shoulder girdle of the Monotreme type, and the ostrich chick embryo shows four digits in the manus and five in the pes. But if we look for a recapitulation of the characters of more remote ancestors, we find them, if at all, so obscured by others that are manifestly not ancestral that we cannot disentangle them. Still by this method and in combination with comparative anatomy, workers such as KITCHEN PARKER and GAUPP have shown what valuable results may be obtained.

The other branch of embryology, which studies the mode of development of the ovum and germinal layers, while a branch of study of great interest, is one whose results are extremely difficult to interpret. Animals that are manifestly closely allied differ greatly in their early development, while others that are widely apart agree closely in many points in their early ontogeny.

The third mode of research is the study of the extinct forms as we find them preserved in the rocks. If we had in our museums one good specimen representative of even every family that has lived in the past we should be able to trace with absolute certainty the evolutionary history of every type of vertebrate that has a skeleton that would be preserved as a fossil. We should further be able to trace back to its origin every bone and to compare the skulls of each type and say with confidence which bones are homologous and which are not. Needless to say we are very far from this at present. Until about 40 years ago the results that palæontology had to show were very meagre. Museums were found to be content too often with scraps of bone, and whole orders were frequently represented by isolated teeth or fragmentary limb bones or vertebræ. Practically a new era originated with MARSH and COPE, and the researches of these brilliant scientists, ably continued by a large number of later workers in America, have shown what results palæontology can yield. With only a very few blanks the evolutionary history of the mammals during the Tertiary period can be written with confidence. And though there is some reason to fear that it may be long before the complete history of mammals during Jurassic and Cretaceous times can be written, we may quite safely predict that palæontology within the next 100 years will be able to give a very full account of the evolutionary changes in the land vertebrates during the 3,000,000 or so of years representing the

Permian and Triassic times and to reveal very fully most of the history of the origin of mammals. In the present lecture an endeavour will be made to show that even now a good deal is known, and that though many details are still left in doubt we can indicate the main stages at least by which the mammals arose.

#### HISTORICAL.

As it is mainly the palæontological evidences that will be here dealt with, it will only be necessary to review briefly the work of those few who have previously approached the problem from the palæontological standpoint.

When OWEN in 1844 (OWEN, 1) first received specimens of Dicynodont reptiles from South Africa he noted a number of mammalian characters in them, and when in 1853 and 1858 he received specimens with teeth differentiated as in mammals into incisors, canines, and molars, these striking mammal-like features were pointed out. It appears, however, to have been only as lately as 1876 that he first hinted that the mammals might have arisen from an ancestor like one of these extinct reptiles. In 1880 when describing (OWEN, 3) the girdles and limb bones of the large Anomodont which he named *Platypodosaurus robustus*, but which we now have reason to believe to be a species of *Dicynodon*, probably, *D. magnus*, he stated much more clearly his belief in the descent of mammals from a reptile such as he was describing. The paragraph deserves to be quoted in full. "From the number of correspondences presented by parts of the skeleton of *Platypodosaurus* with homologous ones in the skeletons of the two existing genera of Monotrematous mammals, one is led to relieve the dry work of comparison by speculations on the vast number and variety in gradually advancing structure of air-breathing vertebrates, off-springs of the strange reptilian forms exemplified by their remains in Cape localities—but which, of old, may have spread over lands extending thence northward and eastward, now in great part submerged and of whose inhabitants a remnant still survives and lurks in the burrows and waters of Australia. One may also conjecture, on the derivative hypothesis, that the higher class of vertebrates, as represented by the low ovoviviparous group now limited to Australia, may have branched off from a family of Triassic Reptilia represented and at present known only by the fragmentary evidences of such extinct kinds as that which forms the subject of the present communication."

About the same time COPE, working with the fossil reptiles from Texas, recognised Monotreme affinities in the Pelycosaurs. In 1884 he (COPE, 2) wrote as follows:—"The question as to the origin of the Mammalia has remained unsettled and speculations have been divided as to whether the class has arisen by a modification of the Batrachia or of the Reptilia. Although there are cogent reasons why the descent should be from the former class, the evidence obtained up to this time from palæontology is in favour of the hypothesis of derivation from the Reptilia. . . . Most of the characters of the Batrachia, which have been cited by HUXLEY as

indicative of the descent of Mammalia from that class, are found in the Pelycosaurian Reptilia." In later years COPE consistently maintained the reptilian ancestry of the mammals, holding the Pelycosaurs to be, if not ancestral, at least distinctly related to the forefathers of the mammals.

BAUR, the brilliant young palæontologist who died when his work was little more than commenced, while he differed from COPE in regard to the affinities of the Pelycosaurs agreed with him and with OWEN that the mammalian ancestor was a reptile allied to some of the forms known from South Africa. In 1897, writing conjointly with CASE (BAUR and CASE, 1), he said :—" We are fully convinced that among these South African forms . . . we have those reptiles which might be considered as ancestral to the mammals, or at least closely related to their ancestors."

OSBORN (OSBORN, 1-5), in numerous papers since 1888, has also steadily maintained a view similar to that of BAUR and OWEN. In 1898 (OSBORN, 3) he discussed the palæontological aspect of the question at length, and concluded that " the Theriodontia constitute a group which contains practically all the primitive characters of the Mammalia in the skeleton and teeth, and that no other reptiles or amphibians approach so near the hypothetical promammal. The explanation of the presence of amphibian characters in the soft parts of the existing Mammalia appears to be that the promammal sprang from primitive reptiles which preserved a number of still more primitive amphibian or stegocephalian characters." He further states his belief " that the Theriodontia are the Hypotheria or Promammalia, because it appears that within the order may well have existed some small insectivorous types, far less specialised in tooth structure than either the carnivorous Cynodonts or herbivorous Gomphodont, as one of those conservative spurs of adaptive radiation which form the focus of a new progressive type."

In 1888 SEELEY (SEELEY, 1-12) took up the study of the South African mammal-like reptiles, and from this year till his death, but chiefly between 1888 and 1895, he published a number of important papers, which greatly increased our knowledge of these fossil forms. His most valuable work is his description of the skeleton of *Pareiasaurus*, of good skulls, and much of the skeleton of *Cynognathus*, and of beautifully preserved skulls of *Gomphognathus*, *Trirachodon*, and other allied forms. The resemblance of many of these forms to mammals is so striking that it could not escape one. In 1888, in describing *Pareiasaurus*, he states: " The Mammalia and Reptilia . . . appear to have a common origin, to which *Pareiasaurus* approaches nearer than any animal hitherto known." It is, however, very difficult to get from SEELEY's papers very clear ideas as to the relations of the Theriodonts, Anomodonts and *Pareiasaurus* to each other, or to mammals. The mammalian resemblance he clearly saw. The limb, for example, of *Theriodesmus* (nearly certainly a Gorgonopsian and possibly the same as *Ælurosaurus*), which he described in 1888, he regarded as that of a " Bunotheroid type which lies between the



Lemurs and Carnivora." In 1894 (SEELEY, 7), he described *Diademodon*, with its wonderful broad crowned, cusped teeth, and mentioned that had the teeth been discovered alone it would have been legitimate to have referred them to mammals and spoke of the close approximation between mammals and reptiles and how few characters there were to distinguish them. In 1895, he regarded the Monotremes as so closely allied to the Anomodonts that he proposed to unite the two into one group, the *Theropsida*. In 1898, he expressed the opinion that "Anomodonts are not the parents of Mammals, but a collateral and closely related group. The common parent of both may be sought in rocks older than Permian, perhaps in Silurian or Devonian strata." The apparent contradiction here is explained by SEELEY's later acceptance of the very remarkable view of MIVART, that the Monotremes arose from Sauropsidan ancestors, while the higher mammals, marsupials and placentals, sprang independently from amphibian-like stem forms.

Almost the only recent work dealing with the palæontological evidence of the origin of mammals has been the work by WATSON and by myself, some points of which will be discussed later on.

#### SOUTH AFRICAN KARROO DEPOSITS.

For the appreciation of the various groups of the mammal-like reptiles, their environment and the associate faunas, some brief account will be necessary of the geological formations in which the remains occur.

The Karroo deposits cover an area of about 200,000 square miles. They are composed mainly of shales and mudstones, with numerous layers of sandstone for the most part a few feet in thickness, but in a few instances 200 or 300 feet. Most of the deposits have either been formed in shallow water or by wind on land. The present facts seem to lead to the conclusion that a huge river, comparable in size to the Nile or Mississippi, flowed south-west towards the middle of what is now Cape Colony. Here it turned towards the east and spread over a huge plain extending for nearly 1000 miles. During the greater part of Permian and Triassic times this great plain was steadily sinking, and as it sank the mud brought down by the river became deposited and retained in the basin. Though, of course, the conditions may have varied very considerably during the 3,000,000 or so years represented by the Permian and Triassic epochs, the conditions, on the whole, were probably not unlike those of Egypt of to-day. Away from the river there were probably sandy deserts, but where watered by the river and its inundations there was a rich *Glossopteris* flora. The shales and mudstones are probably the remains of the inundations—frequently rearranged by local denudation and as often dried, crumbled up, and redeposited by the wind. The sandstones are in most cases formed of wind-blown sand. Land vertebrates flourished in abundance along the fertile tracts, and their bones are, for the most part, preserved in the mudstones. The presence of a large number of remains in a limited area is probably to be

explained by such areas alone in a large tract retaining water during a drought. As examples of such localised areas, with abundant and very varied fossil remains, might be cited the south-west part of Beaufort West commonage, the village of New Bethesda, and the native location at Pearston. Complete skeletons, except of the large animals, are rare, and even then the bones are usually considerably scattered, presumably by carnivorous reptiles.

The entire thickness of the deposit at its maximum is about 17,500 feet, though in no single locality is there probably a thickness of more than 6,000 or 8,000 feet. In many places hundreds, even thousands of feet, are practically unfossiliferous, and only a few spots are rich. Yet, with the exception of the older deposits, fossils are known from practically all horizons, and a very fair idea can now be obtained of the faunas that lived at the different periods.

The following table gives a general classification of the various sections of the system, with the more characteristic fossil forms met with :—

Cave Sandstone	...	Theropoda ( <i>Gyposaurus</i> ); Crocodilia ( <i>Notochampsia</i> ).
Red Beds	... ..	Theropoda ( <i>Euskelesaurus</i> , <i>Massospondylus</i> , etc.); Pre- dentata ( <i>Geranosaurus</i> ); Crocodilia ( <i>Notochampsia</i> ); Cynodontia ( <i>Tritheledon</i> , <i>Pachygenelus</i> ); Mammalia ( <i>Tritylodon</i> ).
Molteno Beds	... ..	Rhœtic plants. Reptilian remains very rare; no identi- fiable remains known.
Burghersdorp Beds or Cynognathus zone.	or	Thecodontia ( <i>Erythrosuchus</i> , <i>Euparkeria</i> , etc.); Anomo- dontia ( <i>Kannemeyeriä</i> ); Cynodontia ( <i>Cynognathus</i> , <i>Diademodon</i> , <i>Bauria</i> , etc.); Rhynchocephalia ( <i>Pala- crodon</i> ); Stegocephalia ( <i>Cyclotosaurus</i> , <i>Batracho- suchus</i> , <i>Capitosaurus</i> , etc.).
Procolophon zone	...	Thecodontia ( <i>Proterosuchus</i> ); Lacertilia ( <i>Paliguana</i> ); Anomodontia ( <i>Lystrosaurus</i> ); Cynodontia ( <i>Nytho- saurus</i> , <i>Galesaurus</i> , <i>Ictidopsis</i> ); Cotylosauria ( <i>Sauro- sternon</i> , <i>Procolophon</i> ); Stegocephalia ( <i>Bothriceps</i> , <i>Micropholis</i> ).
Lystrosaurus zone	...	Anomodontia ( <i>Lystrosaurus</i> , <i>Dicynodon</i> ). Land reptile remains very rare.
Cistecephalus zone	...	Thecodontia ( <i>Youngina</i> ); Anomodontia ( <i>Dicynodon</i> , <i>Ciste- cephalus</i> , <i>Emydorhynchus</i> ); Gorgonopsia ( <i>Scymno- gnathus</i> , <i>Tigrisuchus</i> , <i>Cynosuchus</i> , <i>Scylacops</i> , <i>Ictido- rhinus</i> ); Therocephalia ( <i>Ictidognathus</i> , <i>Scaloposaurus</i> ); Cotylosauria ( <i>Propappus</i> , <i>Anthodon</i> ); Stegocephalia ( <i>g. indet.</i> ).

Endothiodon zone	...	Anomodontia ( <i>Dicynodon</i> , <i>Endothiodon</i> , <i>Dicelurodon</i> , <i>Cryptocynodon</i> , <i>Diictodon</i> ); Gorgonopsia ( <i>Scymnognathus</i> , <i>Gorgonops</i> , <i>Ælurosaurus</i> , <i>Aloposaurus</i> , <i>Cynodrac</i> ); Therocephalia ( <i>Ictidognathus</i> , <i>Ictidosaurus</i> , <i>Ictidosuchus</i> ); Cotylosauria ( <i>Propappus</i> , <i>Saurosternon</i> ); Stegocephalia ( <i>g. indet.</i> ).
Pareiasaurus zone	...	Anomodontia ( <i>Dicynodon</i> ); Gorgonopsia and Therocephalia ( <i>Alopecodon</i> , <i>Scylacosaurus</i> , <i>Pardosuchus</i> , <i>Glansuchus</i> , <i>Arnognathus</i> , <i>Trochosaurus</i> , <i>Hyenasuchus</i> , <i>Lycosuchus</i> ); Dinocephalia ( <i>Moschops</i> , <i>Delphinognathus</i> , <i>Tapinocephalus</i> ); Dromasauria ( <i>Galepus</i> , <i>Galechirus</i> , <i>Galeops</i> ); Incert. sed. ( <i>Titanosuchus</i> ); ?Chelonia ( <i>Eunotosaurus</i> ); Cotylosauria ( <i>Pareiasaurus</i> ); Stegocephalia ( <i>Rhinesuchus</i> ).
Upper Ecça beds	...	No vertebrates known, though possibly <i>Moschops</i> belongs to this zone.
Middle Ecça beds	...	Dinocephalia ( <i>Eccasaurus</i> ); Incert. sed. ( <i>Archæosuchus</i> ).
Lower Ecça beds	...	No vertebrates known.
Upper Dwyka beds	...	Mesosauria ( <i>Mesosaurus</i> , <i>Noteosaurus</i> ).
Dwyka tillite	...	No vertebrates known.
Lower Dwyka beds	...	No vertebrates known.

In the entire absence of marine shells and the uncertainty of the age of certain European beds containing somewhat similar remains, it is impossible to fix the age of all the various beds with certainty, but as we can be fairly sure about one or two we cannot be very far out in estimating the age of the others.

The Cave sandstone and Red Beds may with practical certainty be regarded as Lower Jurassic. The Molteno are undoubtedly Rhætic. The Burghersdorp, *Procolophon* zone and the *Lystrosaurus* zone probably represent Upper, Middle, and Lower Triassic, while the *Cistecephalus*, *Endothiodon*, and *Pareiasaurus* zones represent the Upper and Middle Permian. Whether the Dwyka is also Lower Permian or in part Carboniferous is a point which cannot at present be settled, and which does not seriously concern the present subject of discussion.

From a glance at the table of the strata it will be seen that we have a pretty fair knowledge of the faunas of Middle and Upper Permian and of Middle and Upper Triassic, but that our knowledge of the animals of Lower Permian and Lower Triassic is very poor. Every year, however, is adding to our knowledge, and many of our present blanks we may confidently expect soon to be filled. In the meantime, though we cannot trace with certainty the lines of evolution resulting in the different groups of the mammal-like reptiles and the early mammals themselves, the study of

various types of Therapsida now known enables us to see, if as yet dimly, something of the origin of mammals.

Before considering in detail a number of the problems in the structure of mammals, it will be well to look, in some cases briefly, in others with more minuteness, into the structure of the different sub-orders of the Therapsida or mammal-like reptiles, and of the even more primitive groups which are, perhaps, ancestral to the Therapsida.

As in South Africa we have few remains of importance before the Middle Permian, we must look elsewhere for the earlier types, and the only satisfactory deposits at present known which reveal land forms of the period we want are the American beds in Texas and New Mexico, which have yielded the Cotylosauria and Pelycosauria, chiefly known through the researches of COPE, WILLISTON, and CASE.

### *Cotylosauria.*

This Order or Super-order, first established by COPE for *Diadectes* and allied forms, is now very conveniently taken to include all the early type of reptiles with the temporal region completely roofed. It is subdivided into a considerable number of sub-orders, and though the differences in the various types are considerable it seems probable that all have come from a common ancestor and that the group is a natural one.

The skull in some types, such as *Seymouria*, agrees strikingly with that of the large Carboniferous Stegocephalians such as *Loxomma*, and there can be little doubt that the Cotylosaurs are directly descended from such Carboniferous forms, as these latter have themselves sprung from Devonian Crossopterygians as maintained by WATSON. In many Cotylosaurs the cranial structure is simplified by the loss of one or more of the bones, and there are numerous specialisations of the teeth, but there are many types sufficiently generalised and primitive to have been the ancestors of any of the later reptiles. These later reptiles may have arisen by as many as five or six different lines from Cotylosaurian ancestors, but there is no reptile known which is too primitive to have had a Cotylosaurian ancestor. As we are only dealing at present with the mammalian origins, it is unnecessary to look at the Cotylosauria farther than as the starting point of the mammal-like reptiles.

When COPE first studied the order he was struck by the many resemblances between the Cotylosaurs and the more mammal-like Pelycosaurs, and included both in his group the Theromorpha or Theromora. Though the more typical later reptiles can be traced back to Cotylosaurian ancestors, the Therapsida have retained more of the early characters, and hence the resemblances between these latter and the Cotylosaurs are the more striking. The Pareiasaurs are strikingly Therapsid-like in the girdles and limbs, but this is probably largely due to convergence, and it will, I think, be necessary to look for the Cotylosaurian root of the mammalian stem in some small form a little like *Captorhinus*, but more primitive and, perhaps, one more closely allied to *Limnoscelis*, but less specialised. When we consider that the

Cotylosauria flourished for possibly 5,000,000 years and were probably world wide in their distribution, and that the 20 or so genera that we know probably do not represent 1 in 1000 of those that existed, we shall see how unlikely is the discovery of the precise animal through which any line has passed, and we ought to be satisfied if we can find a representative of even the family.

*Pelycosauria.*

This group of reptiles, principally known from the Carboniferous and Lower Permian rocks of America, but also found in Europe, is the order whose fundamental resemblances to Monotremes struck COPE so forcibly that he regarded them as closely allied to the ancestor of, if not ancestral to, the mammals. For many years most people were inclined to regard COPE'S view as erroneous, but with fuller knowledge of the group we now know that not only was he right in regarding the Pelycosaurs as having marked affinities with the Cotylosaurs, but also that they are not very far removed from the ancestral Therapsid types. No one would, of course, think of suggesting the descent of the later Therapsids from forms such as *Dimetrodon* with its peculiarly specialised spines. But if we look at the essential structure of the group we find it almost impossible to give a definition of the Pelycosauria that will exclude the Therapsida, or of the Therapsida that will exclude the Pelycosauria. Every element of the Pelycosaurian skull is found in similar position in the early Therapsids. There is a large temporal vacuity formed as in the Therapsids mainly between the postorbital and the squamosal, and the zygomatic arch is mainly formed as in Therapsids and mammals by the squamosal and jugal. So far as is known the only important difference is that in the Pelycosaurs the front of the skull is, as in *Sphenodon* and lizards, more or less movable on the basispheno-occipital segment, whereas in all known Therapsids no movement is possible. The girdles, limbs, and vertebræ differ little except in details from those of the Therapsids, and are even already pro-mammalian. The shoulder girdle has the precoracoid well developed and a small cleithrum. The carpus and tarsus are practically as in Therapsids and almost as in mammals. As the Pelycosaurs were lizard-like in habit they retained the primitive Cotylosaurian digital formula of 2, 3, 4, 5, 3-4.

Included at present in the Pelycosauria are a number of forms that are not very closely allied to the types such as *Dimetrodon*, and these may later be placed in distinct sub-orders. Their interest for us at present is the evidence they show that succeeding the Cotylosaurs there was a second large and varied group more lightly built and with a single large mammal-like temporal opening. This group doubtless contained the ancestors of the succeeding mammal-like reptiles, though at present all the forms known are too specialised. Remains of large animals are always much more frequently preserved as fossils than of the small; and it is the small we must have as ancestors—the large being always too specialised. The large, however, give us very clear indications as to the characters of the small which are so often lost.

*Dinocephalia.*

The gap between the Lower Permian of America and the Middle Permian of South Africa is a considerable one, but the first rich Karroo fauna, though in general appearance very unlike the American, is in fundamental characters manifestly related. In the American Lower Permian are four or five types of mammal-like reptiles: in the South African fauna of the *Pareiasaurus* zone we have four or five other groups of mammal-like forms—all different from those known in the Lower Permian of America and all so distinctly more mammal-like that it is convenient to group them together as the Therapsida. Though the lowest Therapsids are more nearly allied to the American types than they are to the higher Therapsids, to prevent the groups becoming too large a line must be drawn somewhere, and at present it is handiest to keep the American groups by themselves and to call the South African types Therapsids.

The most primitive known Therapsid sub-order is the Dromasauria, but it will be more convenient to consider first two other sub-orders distinctly off the mammalian line of descent—the Dinocephalia, on account of their affinities with the American Pelycosaurs, and the Anomodontia, on account of the clear indications they afford as to the structure of the early mammalian ancestors.

The Dinocephalia is a group of large reptiles, the smallest known being about as large as a wild boar and the largest probably as large as a rhinoceros. They are the oldest really powerful-limbed animals. Though the skull is much specialised in having the cranial bones enormously thickened, in essential structure it agrees closely with the Pelycosaurs. All the cranial bones appear to agree. There is a well developed quadratojugal and a large tabulare. The internal structure of the skull is not yet well known.

The vertebræ are on the whole very similar to those of the Pelycosaurs, most of the ribs having two heads widely apart.

The shoulder girdle has a large scapula, a short coracoid and a long precoracoid. There is a delicate cleithrum and a large clavicle and interclavicle.

The humerus is extremely well developed. In some forms it is very massive: in others relatively long. In most forms it is considerably longer than the skull.

The ulna has a very distinct olecranon process. The structure of the carpus and the phalangeal formula are unknown.

The pelvis is large and deep. The ilium has both a preacetabular and post-acetabular development. The pubis and ischium are modifications of the plate-like type, but both are deeper than long antero-posteriorly.

The femur is long; the tibia and fibula relatively short.

The tarsus is probably similar in structure to that in the Dromasauria.

There are no indications of abdominal ribs.

For further details of the skeleton see Plates 1 and 2, figs. 1–28, and the descriptions of the same, pp. 40–42.

*Anomodontia.*

This sub-order was not only the first sub-order of the mammal-like reptiles to be studied, but is the only one that we may say is thoroughly known. Anomodonts occur in South Africa from the Middle Permian to the top of the Triassic and they are by far the commonest of the forms met with. Of every ten fossil vertebrate specimens found in the Karroo, nine are remains of Anomodonts, and this notwithstanding the fact that they are not common in the *Pareiasaurus* zone and rare in the *Procolophon* zone.

*Dicynodon*, with its female *Oudenodon*, may be taken as the type of the order, and so homogeneous is the group that the more aberrant genera such as *Endothiodon* or *Cistecephalus* only differ but slightly from the typical form.

Over 40 well marked species of *Dicynodon* are already known, varying in size from forms little larger than a rat to others about as large as a tapir.

Though the Anomodonts are quite off the mammalian line they nevertheless give us more important clues as to the remote mammalian ancestors than do almost any others except the Cynodonts. Yet quite manifestly, though they are peculiarly specialised, they are not far off the main trunk. They may be looked on as the "Edentata" of the Therapsida. Some genera have canines and no molars; some molars and no canines. Others have canines and molars. But all agree in having no incisors, and in probably all the front of the beak at least had a horny edge.

The Anomodont skull is essentially mammalian in structure. It is composed of the following bones:—Premaxilla, maxilla, septomaxilla, nasal, lachrymal, prefrontal, frontal, postfrontal, postorbital, preparietal, parietal, jugal, squamosal, quadrato-jugal, quadrate, vomer, prevomer, palatine, transpalatine, pterygoid, ethmoid, basisphenoid, epipterygoid, proötic, paroccipital, basioccipital, exoccipital, supraoccipital, tabular, interparietal and stapes. Of these only prefrontal, postfrontal, quadrato-jugal, and tabular are unknown in any mammalian skull, and, apart from neomorphs in connection with horn cores, the only bones found in the mammalian skull and not in the Anomodont are further ossifications of the cartilaginous elements—turbinals, orbito-sphenoid and presphenoid.

In the skull there are many interesting mammalian resemblances. The zygomatic arch is formed by the large squamosal and the jugal, the latter extending far back. Between the supraoccipital and the parietals is a large interparietal. There are a pair of well developed prevomers, fused together as in *Ornithorhynchus* and *Miniopterus*, lying behind the premaxillæ and forming in part a roof to the posterior nares. Above the fused prevomers lies a large true vomer or parasphenoid. This extends from the basisphenoid almost to the premaxilla in front. The relations of these bones will be dealt with at greater length in a later section. The quadrate is fixed to the squamosal and paroccipital. The stapes is large.

The lower jaw is composed of a large dentary and the following other bones—angular, splenial, surangular, prearticular and articular. There appears to be no coronoid.

The atlas and axis are as in the Dinocephalia. The odontoid is attached to the axis, and the arch of the atlas is in two separate pieces. There is a distinct proatlas. The dorsal vertebræ resemble those of mammals considerably. There are apparently in all Anomodonts seven cervical vertebræ, and the whole number of presacrals varies from 25 in *Lystrosaurus* to 28 in *Endothiodon*. There are from four to seven sacral vertebræ.

The shoulder girdle is primitive in retaining in some genera at least (*Dicynodon*, *Cistecephalus*) a small cleithrum. There is a well developed acromion. The coracoid and precoracoid are both large. There is an ossified sternum.

The humerus has a very large deltopectoral crest and an entepicondylar foramen. The ulna has a small olecranon.

The carpus has two centralia and the fifth distal carpal is retained, but otherwise it resembles the mammalian carpus considerably.

The phalanges are arranged on the mammalian formula of 2, 3, 3, 3, 3.

There are no abdominal ribs.

The pelvis is very mammal-like, in that the ilium has an expanded crest, and is mainly directed forward from the acetabulum. The pubis and ischium are narrow and directed downwards and backwards, and between them is a well marked obturator foramen, doubtless formed by the increase of the pubic foramen. There is some evidence of there having been a prepubic cartilage.

The femur, tibia, and fibula do not present any remarkable features, except that the fibula has the upper end expanded, as in Monotremes and many Marsupials. The tarsus has a large tibiale and fibulare, a small, frequently unossified, navicular and four distal tarsals.

The phalanges are, as in the manus, arranged on the formula 2, 3, 3, 3, 3.

#### *Dromasauria.*

The Dromasauria is an aberrant group of small primitive Therapsids. Though those few that are known are too specialised to have been in the direct mammalian line, the group is particularly interesting, as giving us not only a fair idea of the structure of the primitive Therapsids, but also as showing an independent development of a few mammalian characters by convergence. Only three genera have so far been described, and of these only one has been described in any detail. It therefore seems advisable to give a somewhat fuller account of the group than has been given of the others.

*Galechirus Scholtzi*.—This form (fig. 29) was described from two specimens from Victoria West, and no other specimens have been discovered. The type specimen was figured by me in 1907, and restorations given of the skull, shoulder girdle, and pelvis. In the restoration of the skull I assumed that there was probably much of the lower jaw missing in front, and that the back of the skull was proportioned as in Therocephalians. The evidence afforded by *Galepus* and *Galeops*, and a further



study of the specimen, shows that this is not so. The mandible is short and the articulation is below the back of the orbit. The second specimen of *Galechirus Scholtzi* has been developed to show the structure of the pes. As the manus is beautifully shown in the type specimen, and nearly as well in this second specimen, it seemed justifiable to sacrifice one of the two hands in this specimen for the sake of getting the structure of the foot.

The pes is shown in almost perfect condition. There are two bones in the proximal row of the tarsus—a fairly well developed tibiale, and a very much larger fibulare. There is a single centrale placed exactly like the navicular of the mammal, while the distal tarsal row has four bones, there being no trace of a fifth tarsal. The digits are slender and the digital formula is 2, 3, 3, 3, 3.

*Galepus Jouberti*.—This little Dromasaurian is fairly similar in size to *Galechirus Scholtzi*, and is much better preserved (fig. 28). With the exception of the palate, there is hardly a single point in the skeletal structure that is not revealed.

A preliminary description of the skull was given four years ago with a figure of a restoration. As the bone has been entirely weathered away, the sutures can only be traced from the delicate ridges left on the matrix. Fortunately many of the sutures can be clearly made out, and the sutures, as they appeared in the outer surface of the skull, are not likely to have differed much in position from those indicated on the cast, and in any case we can make out the various cranial elements.

The frontals are fairly large, but are nearly excluded from the orbits by the prefrontals and postfrontals. The nasals are also large, and form most of the upper borders of the large nostrils. Between the nostril and the orbit there lie a fairly large septomaxillary and lachrymal, which completely separate the nasal from the maxillary. The maxillary is thus, as in most Lower Permian reptiles of America, comparatively narrow. It has a single row of subequal teeth, which, however, are only very imperfectly represented in the specimen. Pretty certainly there is no greatly enlarged canine as in most later Therapsida. The jugal is long and slender, as shown in the figure (fig. 31). The postfrontal and postorbital bones are apparently both well developed, as shown in fig. 32, the latter forming the slender postorbital arch. The parietal region is broad, but the parietal itself relatively small, much of the roof being formed by the postorbital, squamosal, and probably interparietal. Not improbably there is a preparietal resembling that of Anomodonts, but the condition of the specimen makes it impossible to be quite certain on this point. There is a fairly large pineal foramen.

The squamosal is large and has a very well developed descending portion, which passes as far below the horizontal zygomatic portion as the ascending part does above. Posteriorly the squamosal forms much of the occipital surface, the whole occiput being not unlike, so far as can be made out, that of the Anomodont. I fail to detect any quadrato-jugal. If one be present it must be very small. Most probably it is quite absent. The quadrate is small.

The structure of the lower jaw cannot be fully made out, but, so far as can be seen, it agrees fairly closely with that of the *Anomodont*.

The vertebræ are fairly preserved in the dorsal and caudal regions. They are notochordal, and the arches are not anchylosed to the centra. The upper dorsal ribs are double headed, and probably the transverse processes of the vertebræ are not unlike those of the *Dinocephalians*. There are probably 28 presacral vertebræ. The number of sacrals cannot be made out, but from the size of the ilium it seems probable that there were not more than two, or possibly three.

The shoulder girdle is well preserved. Fig. 33 is a slightly restored view. Part of the interclavicle is represented as cut away to show the full size of the coracoid and precoracoid. The interclavicle and clavicles are well developed, but the specimen does not show whether or not there was a cleithrum, but as there is certainly no cleithrum in *Galeops*, and most probably not in *Galechirus*, it is most likely to have been absent in *Galepus*. The coracoid is considerably longer than in *Galechirus*. The scapula has a narrower lower end than in *Galechirus*.

The humerus as in *Galechirus* is long and slender. There is an entepicondylar foramen, and a short but well marked pectoral ridge. The radius and ulna are also both long and slender. The olecranon is not well developed.

The carpus and phalanges are only imperfectly seen, but are probably as in the allied *Galechirus*.

The pelvis is well seen. The pubis and ischium are of the usual primitive plate-like type. The pubic foramen is unusually large. The ilium has a longer crest than in *Galechirus*, and is directed more backwards from the acetabulum than in that genus.

The femur is long and slender, as are also the tibia and fibula. Though these bones are not seen in the specimen as figured, they are fully shown in a transverse fracture in front of the two feet. The tarsus is only imperfectly seen, but appears to be essentially similar to that of *Galechirus*, there being a large tibiale and larger fibulare, a small centrale and four distal tarsals. The metatarsals are relatively rather longer than in *Galechirus*, but, as in that genus, they increase in length from the first to the fourth, with the fifth only slightly longer than the third. The phalangeal formula is 2, 3, 3, 3, 3, and the claws are feeble and only slightly curved.

*Galeops Whaitsi*.—This Dromasaurian, which differs from *Galechirus* and *Galepus* sufficiently to justify perhaps its being placed in a distinct family, is represented by the anterior half of the skeleton. The matrix in which the specimen is preserved is extremely hard and the bone too brittle to admit of much in the way of development, but fortunately the specimen has been fractured in such a way as to reveal most of the structure.

The skull has already been described.\* It agrees with that of *Galechirus* and *Galepus* in having the squamosal descending well below the level of the zygoma, though here the articulation for the jaw is almost under the postorbital arch. The

\* 'Zool. Soc. Proc.,' 1912, p. 860.

whole skull is relatively shorter and deeper. The most striking difference in the skull of *Galeops* is the entire absence of teeth. The beak had probably a horny covering as in the Anomodonts. In general structure the mandible agrees closely with that of the Anomodont but has a suggestion of a coronoid process.

The structure of the vertebræ cannot be made out but quite manifestly they are notochordal.

The shoulder girdle is fairly well preserved. The scapula has a very broad lower end and a long narrow upper part. The coracoid is relatively small, and the precoracoid large. The restoration shown in fig. 34 is founded on the elements of the two sides. In the specimen as shown in fig. 30 the coracoid and precoracoid of the right side are seen to be fairly well preserved, and much of the coracoid and precoracoid of the left side. The interclavicle is moderately large and the clavicle well developed, but there is no cleithrum. The humerus is long and slender, as are also the radius and ulna. Only a few bones of the carpus are preserved, the radiale, intermedium, ulnare, and one of the centralia.

*Galesphyrus capensis*, g. et sp. nov.—This new species is founded on a very imperfect skeleton which probably represents a new type of Dromasaurian. The specimen consists of the greater part of the dorsal region with much of the manus and the hind limbs. Most of the specimen is badly weathered, but one pes is in nearly perfect preservation. It differs from that of *Galepus* in having a relatively much larger tibiale and a relatively much smaller fibulare and in retaining the fifth tarsale.

#### THEROCEPHALIA, GORGONOPSIA, AND OTHER PRIMITIVE CARNIVOROUS THERAPSIDA.

In the matter of classification the palæontologist is always at a great disadvantage as compared with the worker on living groups in that the majority of his specimens are very imperfectly preserved, and while it may be easy enough to arrange the well preserved types, all classifications which endeavour also to classify the fragmentary types must necessarily be only tentative. The classification of even the living mammals has been a troublesome enough matter, and even yet we have probably not reached finality with such groups as the "Insectivora" and "Edentata," but one can readily realise how difficult the problem would be if all mammals had simple uncusped molars like the dolphin and the systematist were given only imperfect jaws and snouts to deal with.

In 1876 OWEN (2) placed all the carnivorous mammal-like reptiles in the order *Theriodontia*, which he sub-divided into three groups according to the conditions of the nostrils. Twenty years later SEELEY sub-divided the carnivorous forms into other groups, but as both these palæontologists had only for the most part very fragmentary specimens to deal with, it is not surprising that neither of the classifications has stood the test of extended research.

In 1902 I (BROOM, 7) examined the first really good skull of an early carnivorous

Therapsid, and the following year (BROOM, 8), finding that the early types had a Rhynchocephaloid palate and differed in many ways from the better known Upper Triassic types, I placed those early forms in the order Therocephalia and retained OWEN'S term Cynodontia for the more mammal-like Triassic forms. This division has formed a good working arrangement for 10 years, but as the number and variety of types are steadily multiplying and our knowledge of them increasing, it has been found that the carnivorous Therapsids which we were placing together in the Therocephalia really belong to quite a number of well marked groups. It would seem as if the Therapsida formed a class with as many and as varied orders as the Mammalia, and even those primitive carnivorous types which we had grouped as the Therocephalia probably represent groups as widely different as, or more widely different than, Polyprotodont Marsupials, Triconodonts, Insectivores, Creodonts, and Carnivores.

Perhaps the oldest group of carnivorous Therapsids met with in Africa is that represented by the Lower Permian *Archæosuchus* and the Mid-Permian *Titanosuchus* and *Scapanodon*. The affinity of these forms is very doubtful, as they are only known by imperfect jaws and a few limb bones and vertebræ. All are large animals, no known later carnivorous Therapsid having ever equalled *Titanosuchus* or *Scapanodon* in size. The humerus bears sufficient resemblance to that of the Dinocephalian to suggest that the group will ultimately have to be placed in a distinct sub-order.

The Therocephalia was founded on the types *Scylacosaurus* and *Lycosuchus*, and it will cause, perhaps, least confusion to restrict it to these and similar types.

The Therocephalian skull is tolerably well known. In *Scylacosaurus* and *Lycosuchus*, it differs from the later carnivorous types which are placed in the Gorgonopsia in the following characters:—The parietal region is narrow, the postorbitals relatively small, the frontals large and form the orbital margins, no preparietal, prevomers large and separate, palate with a large suborbital vacuity, mandibles with a loose symphysis, and a number of other minor points. Very little is known of the postcranial skeleton.

The genus *Ictidosuchus*, and the less known *Arnognathus*, certainly represent a very distinct family and, perhaps, a distinct sub-order. Till more is known of the typical Therocephalians it will be safest to place *Ictidosuchus* in a distinct family of the Therocephalia, the *Ictidosuchidae*. The skull of *Ictidosuchus* resembles that of the Dromasaurians in the slenderness of the arches and in having the articulation for the jaw much below the level of the zygoma, but differs from them, and resembles the typical Therocephalians, in the large size of the temporal opening. The parietal region forms a narrow crest. The upper canine is single and relatively small, and there appears to be no lower canine at all. The symphysis is a loose articulation, and the dentary is a long slender bone, with a very large ascending coronoid process. The shoulder girdle resembles closely that of the Dromasaurian *Galeops*. The humerus has the deltopectoral crest fairly well but not greatly developed.

Another group of the carnivorous Therapsids is represented by a number of small forms of which *Scaloposaurus* and *Ictidognathus* may be regarded as the types. They most probably represent a distinct sub-order, but till something is known of the postcranial skeleton they may be placed in the family *Scaloposauridae*. They are at present only known from the *Endothiodon* and *Cistecephalus* zones of the Upper Permian.

The best preserved skull is that of *Scaloposaurus constrictus* described by OWEN in 1876. In 1909, Dr. SMITH WOODWARD very kindly, at my suggestion, had the back part of the palate cleared of matrix, and in figs. 41 and 42 I have given slightly restored views of the upper and under sides of the skull. The upper side shows quite a number of remarkable characters. The zygomatic arch is very slender and the postorbital arch imperfect. The nasal is large and very mammal-like. The frontal is large and forms much of the orbital border. There is no postfrontal. The postorbital does not extend far back. The parietal is broad and there is no preparietal. There is no pineal foramen. There is a large interparietal, but apparently no tabulare. The base of the skull shows features as remarkably aberrant. There is a single occipital condyle formed by the basioccipital and two exoccipitals. A little in front of the base of the condyle is a large jugular foramen, and a little farther in front a foramen which is evidently the fenestra ovalis. A pair of foramina near the front of the basisphenoid are evidently for the carotids. The pterygoids are well developed, but of unusual form. There is a large rounded suborbital vacuity, whose outer border is formed by the transpalatine, and of which the pterygoid forms the posterior and inner borders. The transverse process of the pterygoid is long and slender and fairly straight. The anterior process of the pterygoid is comparatively short and apparently articulates in front with the palatine. Posteriorly, there is a long slender process passing to the quadrate and a shorter process articulating with the basisphenoid. Between the pterygoids is a large interpterygoid vacuity. The anterior part of the palate is not seen in the skull of *Scaloposaurus constrictus*, but it is probably somewhat similar to that seen in a small undescribed species. There is in front a long narrow pair of prevomers anchylosed together, and on either side a rudimentary secondary palate formed by maxillaries and palatines. Nothing is known of the postcranial skeleton.

*Gorgonopsia*.—When OWEN described the skull of *Gorgonops torvus* in 1876 (OWEN, 2), he recognised a number of characters in which it seemed to differ from the other Theriodonts, and made it the type of a distinct group, the *Tectinaria*. LYDEKKER and SEELEY also believed that it differed from the other Theriodonts in having the temporal region roofed, and SEELEY made it the type of an order, the *Gorgonopsia*. In 1909, I showed that, though the parietal region is wide, there are distinct temporal openings. Since then, a number of well preserved skulls have been found of *Gorgonops* and allied forms, and the structure is now fairly well known. The skull differs from that of the Therocephalia proper in the following

characters :—The frontals are shut out from the orbital margins by the prefrontals and postfrontals; there is a distinct preparietal; the parietal is shut out from the temporal fossa by the postorbital; there is no suborbital vacuity; there is no interpterygoid vacuity; the internal nares are divided by a median bone (? true vomer or fused prevomers); the pineal foramen is small.

The shoulder girdle has a long scapula, and relatively small coracoid and precoracoid. There is no acromion process and no cleithrum, though the clavicle and interclavicle are well developed. The humerus is elongated and with a moderately developed deltopectoral ridge. The carpus is of the usual Therapsid type. The phalangeal formula is 2, 3, 4, 5, 3, though in the third toe one, and in the fourth toe two, phalanges are very much shortened. The pelvis is a modification of the plate-like type, but it is not well known, and the pes is also imperfectly known.

### *Cynodontia.*

All the carnivorous Therapsids at present known from the Triassic beds of South Africa differ from the Permian types in having a well developed secondary palate as in mammals, and are placed in the distinct order Cynodontia. But, though most of the better known forms are manifestly allied and form a natural group, there are others that differ so considerably that it is uncertain whether they are ancestral aberrant forms, or whether they have merely acquired Cynodont characters by convergence.

The most troublesome genus to place is the primitive *Bauria*. This form occurs in the lower beds of the *Cynognathus* zone. It is only known by three skulls. It agrees with the typical Cynodonts in having a well formed secondary palate and in having a large median unpaired vomer, but differs in having a single occipital condyle only imperfectly divided, in having the pterygoids extending back to the quadrates, in having the quadrates large and fixed, in having the angular and surangular of large size, in having an epipterygoid like that of the Therocephalians, and in a number of other minor characters. We are thus left in considerable doubt as to whether *Bauria* is an aberrant primitive Cynodont, or a type which has sprung from quite a different carnivorous ancestor and has acquired a secondary palate by convergence. Something can be said in favour of both. On the whole, *Bauria* seems nearer to the higher Therocephalians, such as *Scaloposaurus*, than to the typical Cynodonts, but until something is known of the skeleton we may provisionally retain it with the Cynodonts where it was originally placed. Though *Bauria* has not nearly so many mammalian characters as the typical Cynodonts, it is interesting to note that most of the characters in which it differs from the Therocephalians are mammalian characters.

Another Cynodont which seems allied to *Bauria* is *Microgomphodon*. This genus is only certainly known by a single skull, but as this is fairly well preserved the more important points of structure can be made out. The palate resembles considerably

both that of *Bauria* and that of *Scaloposaurus*. On the other hand if the skeleton which SEELEY makes the type of *Microgomphodon eumerus* be rightly referred to *Microgomphodon*, then it is pretty certainly a true Cynodont. Until more is known of *Microgomphodon* one need not speculate on its possible affinities. It retains the pineal foramen which is lost in *Bauria* but found in most other Cynodonts. Notwithstanding the number of features in which *Microgomphodon* resembles *Bauria*, I do not feel satisfied that it belongs to the family Bauridæ.

A very important group of Cynodonts is represented by the genera *Sesamodon* and *Melinodon*, of which, however, only the first named is at all well known. Though no doubt true Cynodonts they are considerably removed from the group represented by *Cynognathus*, and on the whole they are considerably more mammal-like. The teeth are uncusped, and the wearing shows that there must have been some slight antero-posterior movement of the lower jaw, but whether this was effected by a movement between the dentary and the posterior bones of the jaw, or between the articular and the quadrate, or by a loose attachment of the quadrate, is at present unknown. A remarkable mammal-like character is the passing of the lower canine outside the edge of the maxillary bone. In a number of characters such as the development of the septomaxillary, the shape of the nasals, the fact of the frontals entering the orbital margins, the apparent absence of a pineal foramen and the structure of the teeth, an affinity with *Bauria* is suggested. On the other hand *Sesamodon* differs markedly from *Bauria* in the shape of the lower jaw, in the structure of the squamosal, in the mode of articulation of the lower jaw, in having a feebly developed vomer, and in the general structure of the back of the skull. *Sesamodon* also differs markedly from the typical Cynodonts of the *Cynognathus* group in a number of characters and in most of these it agrees with the mammalian condition.

Unfortunately nothing is known of the postcranial skeleton of *Sesamodon* or *Melinodon*.

Probably two other distinct families of Cynodonts are represented by the two supposed Cynodonts from the lower Jurassic Red Beds. One is represented by an imperfect upper jaw; the other by an imperfect lower. *Tritheledon* has numerous molars with narrow transverse crowns with 3 or 4 cusps, a structure quite unlike that of any known Cynodont or mammal.

By far the best known group of Cynodonts is that represented by the genera *Cynognathus*, *Diademodon* and *Nyctosaurus*. Possibly each of these might be regarded as the type of a distinct family, yet all are manifestly pretty closely related to each other and can conveniently be considered together. *Nyctosaurus* occurs in earlier beds than the others and is more primitive in a number of characters. The septomaxillary forms part of the facial surface, the zygomatic arch is less specialised than in the later types, the molars are less cusped, and the posterior bones of the mandible are less reduced.

*Cynognathus* and *Diademodon* are the best known Cynodont types. The former is

known by two good and two or three imperfect skulls and by the fairly complete skeleton of *C. crateronotus*. *Diademodon* and the allied if not generically identical *Gomphognathus* is known by about half a dozen good skulls and a fair number of other bones of the skeleton. Moderately good skulls are also known of the allied *Trirachodon*.

The skull type seen in *Cynognathus* and *Diademodon* is probably a further development and specialisation of the type seen in *Nyctosaurus*, and differs chiefly in the greater development of the postorbital and zygomatic arches, in the greater development posteriorly of the dentary, with a corresponding reduction of the angular and surangular, and in the more highly developed condition of the molars.

The following are the more important cranial characters of this group of Cynodonts :—

1. Septomaxillary small, mainly inside the nose (on face in *Nyctosaurus*).
2. Lachrymal large.
3. Postorbital arch well developed, formed by postorbital and jugal.
4. Frontals small, shut out from orbital margins by prefrontals and postorbitals
5. Parietals narrow, with small pineal foramen.
6. Squamosal large, forming much of zygomatic arch, and meeting postorbital in most genera.
7. Large tabulars.
8. Two occipital condyles.
9. Relatively small quadrate, loosely articulated to squamosal.
10. A long stapes, strongly developed and apparently perforated (*Cynognathus*), or very slender and imperforate (*Trirachodon*).
11. Alisphenoid large, forming much of the cranial wall, and on the palatal surface connecting the pterygoid with the quadrate.
12. Pterygoid forming a large pterygoid process, but not passing back to the quadrate as in most reptiles and also in *Bauria*.
13. A small transpalatine appears to be present in some genera (*Diademodon*)—perhaps it is present in all but has not yet been detected.
14. The vomer is a large median bone which extends from the basisphenoid to the premaxillary region.
15. In some genera (*Lycognathus*) there are palatine processes to the premaxillaries.
16. In some genera (*Gomphognathus*, *Cynognathus*), there appear to be a pair of small distinct prevomers.
17. In most genera the angular, surangular and coronoid are much reduced, and the dentary extends back nearly to the articulation.
18. There are usually 4 upper incisors (rarely 3 or 5), 1 canine, and 7 to 9 molars (rarely 12 or possibly 14).
19. In *Diademodon*, and possibly in all genera, the incisors, canines, and first four molars appear to be replaced.



In *Cynognathus* there are 28 presacral vertebræ, of which seven are probably cervicals. The atlas has the two sides of the arch united, but the arch is not ankylosed to the intercentrum. The axis has the odontoid process ankylosed to its centrum. Most of the vertebræ have double-headed ribs. In the lower dorsal or lumbar region the ribs are short and resemble somewhat in appearance the broad transverse processes seen in some mammals.

The scapula has a small acromion. There is always a well developed precoracoid and coracoid. There is no cleithrum, but the clavicle and interclavicle are well developed.

The carpus in *Cynognathus* has two centralia and four distal carpalia and the digital formula is 2, 3, 3, 3, 3.

The pelvis has an ilium with a large crest. The pubis and ischium have between them a large obturator foramen. A cartilaginous prepubis was probably present.

The pes is not well known but appears to agree essentially with the mammalian type, and like the manus it has a digital formula of 2, 3, 3, 3, 3.

#### THE RELATIONS OF THE THERAPSID GROUPS TO EACH OTHER AND TO MAMMALS.

As there is at present no general agreement as to the phylogenetic relationships of the orders of living mammals, it is hardly to be expected that any attempt to arrange the extinct Therapsid groups, many of which are imperfectly known, can be more than tentative. Nevertheless a consideration of the apparent affinities seems to throw some light on the origin of mammals, and even if we cannot yet trace beyond question the whole line we can at least suggest how the line may have run.

The Dinocephalia are so manifestly off the mammalian line that we need not devote much time to the consideration of the group. They are principally of interest through their having distinct relationship with the later Therapsids, and also with the earlier American types.

The Dromasaurians are a much more instructive group. In many respects they are so mammal-like as to suggest the question whether the ancestral mammal may not have been a Dromasaurian. If we knew nothing of Therocephalians, Anomodonts or Cynodonts we might readily conclude that such a type as *Galepus* might be the mammalian ancestor. The hand and foot are practically mammalian, and though the shoulder girdle and pelvis differ considerably there is nothing in their structure that would preclude them from being ancestral mammalian types. The skull is certainly very much more primitive than the mammalian and seems a little too specialised in the articular region to have been ancestral, yet it is difficult to point to a single feature that would prove that it could not have been so. The Gorgonopsians have the digital formula 2, 3, 4, 5, 3, and it is probable that the Therocephalians had a similar formula. If so the Dromasaurians could not have been ancestral to them, and if the mammals arose from a Dromasaurian all the more mammal-like characters found in the Therocephalians, Gorgonopsians and apparently in the Anomodonts and Cynodonts

must be accounted for by convergence. It seems easier, however, to account for the digital formula of the Dromasaurians as being due to convergence than the large number of mammalian characters met with in Cynodonts. On the present evidence I consider the Dromasaurians to be a group allied to the common ancestor of the Anomodonts and Therocephalians, but having early acquired an active running habit, possibly to capture winged insects, the hand and foot came to resemble that of the later Anomodonts, Cynodonts and mammals.

The Anomodonts though having a much specialised skull have the postcranial skeleton remarkably mammal-like. It is interesting to note that while OWEN was principally impressed by the Lacertilian and Chelonian characters of the Anomodont skull, when he examined the skeleton of *Platypodosaurus*, not knowing it to be the skeleton of probably a species of *Dicynodon*, he believed the affinities to be mainly with the Monotremes.

In spite, however, of the specialisation of the beak the Anomodont skull is in many ways remarkably mammal-like. The suborbital and zygomatic arch formed by the maxilla, jugal, and squamosal is essentially mammalian. There is a rudimentary secondary palate formed by the maxilla and palatine, and as will be seen by the figures given there is a long true mammal-like vomer which lies above the fused prevomers. There is a short columnar stapes closely articulated at its outer end with the quadrate in a manner very suggestive of the articulation of the stapes with the incus in mammals.

There are, on the other hand, besides a number of specialisations peculiar to the group, a considerable number of primitive characters retained which have been lost in the mammals, such as the separation in many species of the maxilla from the nasal by the meeting of the septomaxilla and the lachrymal, the presence of prefrontal, post-frontal, postorbital, preparietal, quadrato-jugal, and tabular bones, the epipterygoid developed as a slender columella cranii, and the single occipital condyle.

The postcranial skeleton is more strikingly like that of the mammal than is the skull. The scapula with its acromion, the digital formula of 2, 3, 3, 3, 3, and the shape of the pelvis, all look as if they indicated a relationship to the mammals, but since in *Pareiasaurus* we have similar developments of the scapula and pelvis and a reduced digital formula of 2, 3, 3, 4, 3, it seems probable that these mammal-like characters are to be explained as cases of convergence. The Anomodonts are, I believe, primitive mammal-like reptiles descended from a form which was near the common ancestor of the Dromasaurians and Therocephalians, and, having gradually become vegetarians, browsing among the plants of the Karroo swamps, the teeth of the front of the jaws became replaced by a horny beak, and the molars modified and ultimately lost. The walking and probably digging habits resulted in those modifications of the girdles and limbs which so strikingly resemble characters seen in living mammals. But while most of the Anomodont characters are specialisations, and of those that are mammal-like a number are due to convergence, there can be

little doubt that the primitive Therapsid which was the common ancestor of the Dromasaurians, the Therocephalians and Anomodonts would also be the remote ancestor of the mammal.

This primitive Therapsid, which we may regard as the common ancestor of all the Therapsids, except probably the Dinocephalians, would have a skull like the Dromasaurian *Galepus*, but with the arches stronger, and with a suspensorial region more like that of the Therocephalians. The arches would also be Dromasaurian in type, but the limbs would be much shorter and stouter, and the digital formula would be 2, 3, 4, 5, 3. The vertebræ and ribs would be similar to those in the Anomodonts. Such a type, which doubtless lived in Lower Permian times, would answer all the requirements of the remote ancestor of the mammals, and while it is quite conceivable that the evolution of the mammal from such a primitive type may have taken place during Permian and Triassic times in some part of the world that has hitherto yielded no fossil land vertebrates, it seems more probable that in the rich Permian and Triassic faunas of South Africa we should get some indications of the evolving forms.

Though a large number of different carnivorous Therapsids are known from the Permian beds, few are known by more than imperfect skulls, and, though there is considerable reason for believing that the lines resulting in both the Cynodonts and mammals have passed through Therocephalian ancestors, too little is known to indicate at all clearly what forms may have been ancestral. The Therocephalians and the allied carnivorous Permian types differ from all earlier forms, in having a large coronoid process formed by the dentary. In most families the canines are large, though it is apparently the second maxillary tooth that becomes enlarged, and even where there is no small anterior tooth it seems probable that the single canine in later forms is the homologue of the Therocephalian second maxillary tooth. The Gorgonopsians cannot be descended from any of the Therocephalian types at present satisfactorily known. The structure of the palate differs very considerably, and the bones of the parietal and frontal regions must have been derived from somewhat more primitive types. We are probably justified in believing that the Gorgonopsians have originated from an early Therocephalian type of Middle or Lower Permian age at present unknown. The occurrence of the undoubted Gorgonopsian *Scylacognathus* in the Middle Permian *Pareiasaurus* zone shows that the group is tolerably ancient. The Gorgonopsians also show very marked affinities in one or two respects with the Anomodont. Nevertheless, they are nearer to the Therocephalians.

The small Therocephalians, such as *Scaloposaurus* and *Ictidognathus*, form a fairly well marked group by themselves, which have also probably been derived from a Middle Permian Therocephalian, but from a later type than gave rise to the Gorgonopsians. Though in some respects, such as the structure of the palate and the occurrence of a rudimentary secondary palate, they foreshadow some of the Cynodonts, e.g. *Bauria*, they certainly cannot be ancestral to Cynodonts of the

*Nythosaurus* or *Cynognathus* types, and I think it very doubtful whether the resemblances to *Bauria* are more than the result of convergence.

The typical Cynodonts have probably been derived from an early type of Therocephalian, such as gave rise to the Gorgonopsians, though at present nothing is known of the immediate Cynodont ancestors of Upper Permian and Lower Triassic times unless we assume *Bauria* to be a modified intermediate form. If we derive *Bauria* from a Therocephalian like *Scaloposaurus*, we must conclude that the Cynodontia is diphyletic in origin, or that *Bauria* ought not to be placed with the Cynodonts, but in a distinct sub-order. Such a Cynodont as *Nythosaurus* cannot have been evolved from a Therocephalian like *Scaloposaurus* or *Ictidognathus*, but must have arisen from a more primitive, and probably more Gorgonopsian-like, ancestor. In the present state of knowledge I am inclined to the view that all the Cynodonts have come from a single primitive type, and that *Bauria* is an intermediate form which has become considerably specialised, and that its resemblances to the small later Therocephalians is probably due to convergence.

When we come to consider the Mammalia we are in much the same difficulty as with the Cynodonts. There is always the tendency to derive aberrant types independently from remote ancestors. Notwithstanding the striking resemblances between man and the higher Anthropoids there are some who would derive man quite independently from an Eocene or pre-Eocene Lemuroid. And a number of very eminent scientists have argued in favour of a diphyletic origin of the mammalian class. The Monotremes and Marsupials differ strikingly in a number of important characters, and it has been held by some that the two groups had a common ancestor only in Devonian or Silurian times. Yet embryology shows that they are possibly as nearly allied to each other as are the Marsupials and the Edentata. As with the mammals so with the Cynodonts the difficulty is to know how far resemblances are due to convergence, and how far real affinities are obscured by specialisations due to change of habit. But while in the mammals we have a number of characters in the soft parts that are very reliable guides to affinity, in the Cynodonts we have to rely exclusively on the more variable skeletal structures.

Assuming that the common ancestor of all mammals was a small generalised insectivorous type with a skull somewhat resembling that of *Marmosa* or *Ptilocercus*, but with a small frontal and a shoulder girdle with a large coracoid and an inter-clavicle, the problem resolves itself into the determination of whether this ancestral mammal originated from a pre-Therocephalian Therapsid, a Therocephalian, or a Cynodont. Numerous arguments might be advanced in favour of each of these three positions, but the evidence in favour of the ancestor having been a Cynodont seems to me so much the stronger that I still favour this opinion as I did 15 years ago. I am aware of no character in the mammalian skeleton that could not as readily have been derived from a Cynodont ancestor as from a Therocephalian by specialisation or degeneration, and the few Cynodonts we know exhibit so many

mammalian characters that are not found in Therocephalians that it seems easier to believe that there is a genetic relationship with the Cynodont than that these Cynodont mammal-like characters are all the result of convergence.

The following is a list of mammalian characters which are found in Cynodonts but which are not known to occur in any Therocephalian :—

1. Large infraorbital foramen (*Sesamodon*).
2. Mammal-like relationship of lachrymal and squamosal.
3. Reduced quadrate slipping out from main jaw articulation.
4. Mammal-like secondary palate.
5. Large median vomer which extends back to basisphenoid.
6. Premaxilla with palatine processes (*Lycognathus*).
7. Large alisphenoids which extend outwards towards the articular region.
8. Pterygoid not extending to the quadrate.
9. Two occipital condyles.
10. Mandible mainly formed by the dentary, the articular, prearticular and angular being much reduced.
11. A mammal-like dental formula (*Galesaurus* i5, c1, m12; *Nythosaurus* i4, c1, m7; *Cynognathus* i4, c1, m9; *Ælurosuchus* i5, c1, m7).
12. A mammal-like dental succession in incisors, canines and four premolars (*Diademodon*).
13. An obturator foramen and no pubic foramen.

If instead of this large series of mammalian characters there were only three or four one might readily hesitate before assuming that they indicated affinity, but this large assemblage of very exceptional characters seems to render the case so strong against convergence as to force us to assume in the absence of any evidence to the contrary that the mammalian ancestor was a small primitive Cynodont.

#### ON SOME DISPUTED POINTS IN MAMMALIAN AND THERAPSID STRUCTURE.

##### 1. *The Pterygoid Question.*

The discovery by GAUPP (GAUPP, 2) a few years ago of two membrane bones in the pterygoid region of the skull of the embryo *Echidna*, and his conclusion that while the outer is the bone usually called pterygoid in the adult *Echidna* the smaller is really the homologue of the pterygoid of the higher mammals, has placed the question of pterygoid homologies in considerable confusion. He believes the "Echidna-ptyergoid" to be the homologue of the reptilian pterygoid and the "Eutherian-ptyergoid" to be the homologue of the lateral part of the parasphenoid of the lizard and some other reptiles.

Were this conclusion of GAUPP's confirmed it would result in very serious confusion of nomenclature. The bone that for years in reptiles, amphibia, and fishes has been

called parasphenoid would have to be called pterygoid and a new name given to the bone in the lower vertebrates which is at present called pterygoid.

Through the kindness of Profs. J. T. WILSON and J. P. HILL I have been enabled to examine the condition of affairs in embryos of *Ornithorhynchus*, and so far as the facts are concerned I feel compelled to agree with GAUPP's observations. In *Ornithorhynchus* as in *Echidna* there are two "pterygoid" elements. On the other hand I feel inclined to differ from GAUPP's conclusions as to the homologies of the elements.

The two "pterygoid" elements are even more strikingly distinct in *Ornithorhynchus* than in *Echidna*. Near the back part of the palatine there is seen a distinct bony element of considerable size lying above it and forming the outer wall of the air passage. The condition is very similar to that figured by GAUPP in *Echidna*, as will be seen by comparing his figure with mine. Farther back the palatine ends rather abruptly, and its place is taken by the large so-called "pterygoid." The smaller upper element becomes much reduced on passing backwards. In the figures I give its relations to the "pterygoid" are seen (Plate 7, figs. 81-84).

GAUPP has argued at length that the small upper element is the pterygoid of the higher mammal, and my observations confirm this view. Fortunately I have been able to find in a marsupial a rudiment of the "Echidna-pterygoid," to use GAUPP's term. This I have discovered in examining some sections of Prof. J. P. HILL's of an embryo of *Petrogale penicillata*, 25 mm. in length. Here we find two "pterygoid" elements pretty certainly corresponding to the two in *Echidna* and *Ornithorhynchus*. Unfortunately I have only been able to study one stage, but in this it looks as if the lower element was in process of absorption. It is really a larger element than the upper but extends neither so far forward nor so far backwards as the upper. The upper element extends through Sections Nos. 18 to 42; the lower element from Sections 31 to 39. The figure I give (fig. 88) is of Section 34, where the lower element is seen at its greatest size. I am inclined to think that in later development it becomes completely absorbed: possibly it may become anchylosed to the upper. Whatever be its fate, there is I think little doubt that the upper is the pterygoid of the higher mammal and the lower the "pterygoid" of *Echidna*.

In two genera of Edentates, *Tatu* and *Tamandua*, I have been fortunate in discovering what appears to be both the "Echidna-pterygoid" and the "Sauger-pterygoid" in a well developed condition, and possibly both elements are present in some other genera.

In the collection of the American Museum of Natural History of New York there is a beautifully prepared skull of a foetal armadillo, *Tatu novemcinctum*, measuring 40 mm. The molar teeth are already calcified and all the bones are ossified. The condition of the bones of the palate is particularly interesting. The palatine is

moderately large; behind it is situated a small bone which at first sight appears to be the pterygoid. It carries the posterior nares  $1\frac{1}{2}$  mm. farther back, but has no manifest pterygoid process. Above it is a second bone which almost completely separates it from the base of the alisphenoid. This second bone has an antero-posterior length of about  $3\frac{1}{2}$  mm., and is about 1 mm. in width. On the right side the upper bone is completely distinct from the lower, but on the left the two bones are partly anchylosed. It seems most probable that the upper bone is the true mammalian pterygoid, the lower one being the *Echidna*-pterygoid. In another skull of *Tatu*, nearly full grown and measuring 90 mm., an almost similar condition is found. Here the lower bone is quite distinct from, but might almost be regarded as part of, the palatine. The upper bone completely separates it from the alisphenoid. In adult specimens of *Tatu* it is difficult to see the sutures between those bones.

Another Edentate shows a different variation of the palatal structure. In *Tamandua tetradactyla*, the posterior nares are carried far back by a bone which seems to be pterygoid. I have examined a large series of young skulls, but have not found any specimens in which this bone is completely distinct from the alisphenoid. One may assume that it probably has a distinct centre of ossification, and that at a very early period it becomes anchylosed to the alisphenoid, and also shortly afterwards to the basisphenoid. Near the point of union of the large palatine with this large pterygoid, at the outer corner, there is usually a distinct small scale-like bone. In most specimens this becomes lost in cleaning. In a few skulls it is wedged in between the palatine and pterygoid, and in many specimens it forms part of the wall of the posterior nares, so that, when lost, an opening is here left in the passage. In the light of the condition seen in the Marsupial *Petrogale*, and the Edentates *Tatu* and *Tamandua*, we may conclude that the upper bone is, as in *Echidna*, the true pterygoid, and that the lower bone is that which forms the so-called pterygoid in the Monotremes. We are also, I think, justified in concluding that the lower bone is the reptilian transpalatine. The relations of the palatine, pterygoid and transpalatine to each other in the Anomodonts, Therocephalians and Cynodonts, is not very dissimilar to the relations of those three bones in the lower mammals, and we are probably right in concluding that they are homologous.

## 2. *The Vomer Question.*

The very large majority of comparative anatomists have agreed in regarding the pair of bones in the anterior part of the palate in lizards and snakes as together homologous with the vomer of mammals. In amphibians there is a pair of vomerine bones; in Teleostean fishes the vomer seems to be a single median element, which seems to develop from a single centre of ossification. And it would not, therefore, seem so very remarkable that the mammalian vomer should also develop from a single centre

The first to cast doubts on the homology of the lacertilian paired vomers with the mammalian vomer were ALBRECHT, SUTTON, and KITCHEN PARKER, who seem to have independently come to the conclusion that the paired vomers of reptiles are more probably homologous with the mammalian palatine processes of the premaxillæ.

In 1895, while studying the comparative anatomy of the organ of Jacobson, I was led to the conclusion that the pair of bones which in *Ornithorhynchus* fuse to form the "dumb-bell bone" are the true homologues of the lacertilian paired "vomers," and that as these are quite distinct from the median vomer, which is also well developed in *Ornithorhynchus*, a new name was required for the paired bones, and I proposed "prevomers" for them.

In the large majority of mammals the prevomers are lost, their place being taken by the palatine processes of the premaxillæ. But in the bat *Miniopterus* a pair of prevomers is present, and in the adult these are fused as in *Ornithorhynchus*. In both *Miniopterus* and *Ornithorhynchus* the prevomers develop in close relationship with the paraseptal cartilages. There seems to be little doubt that the paraseptal cartilage itself is retained for the support and protection of Jacobson's organ, and we may conclude further that the little protective splint bones serve as further protection. There can, I think, be no question that the paraseptal cartilage of the reptile is exactly homologous with the similarly situated cartilage in the mammal, and we seem justified in concluding that the splint bones formed in connection with those cartilages are also homologous.

As the mammalian vomer does not seem to be homologous with the so-called reptilian vomers, a search for its homologue seems to lead to the conclusion that it is represented in the lower forms by the median bone which is usually called parasphenoid. In most reptiles the parasphenoid is a feeble element which originates near the opening for the hypophysis. In some forms it is well developed, as in the snake; in others it is quite rudimentary. In most amphibians it is large.

The palæontological evidence of the phylogeny of the vomerine bones has not hitherto been as complete as could be desired, but recent evidence throws much new light on the subject. The large majority of Lower Permian reptiles have a distinct and often well developed median parasphenoid and a pair of well developed prevomers. In the very primitive *Ophiodeirus* the parasphenoid is extremely well developed. In later forms with the great development and the median union of the pterygoids the parasphenoid becomes much reduced and in Pelycosaurs and Therocephalians it is often difficult to recognise the parasphenoid at all. In *Lycosuchus* WATSON has discovered a distinct median parasphenoid between the pterygoids and also a pair of large prevomers in front. In the small Upper Permian Therocephalians such as *Ictidognathus* we find the prevomers much reduced. They form two little scrolls closely attached one to the other and frequently anchylosed. There can be little doubt that they lodged the organs of Jacobson. The figures given show the cross-sections of the prevomers (Plate 6, figs, 73, 74, 75, 76). In the Anomodonts we



find what looks like a single median vomer, but the bone that appears on the palate between the palatines and pterygoids is unquestionably homologous with the fused prevomers of *Ictidognathus*. Lying dorsal to the fused prevomers, however, there is a well developed median true vomer. This extends from the basisphenoid behind nearly to the premaxilla in front and it seems highly probable that it is this bone that is the homologue of the mammalian vomer and not the fused prevomers that lie below it. There can further be little doubt that this bone, which in its structure and relations so exactly agrees with the mammalian vomer, agrees equally closely with the reptilian parasphenoid. In fig. 46 the prevomer and vomer of *Dicynodon* are seen in median section and in undisturbed relationship. The posterior part of the vomer is seen anchylosed to the basisphenoid. In figs. 47, 48, 49, 50, and 51 transverse sections of the vomer and prevomer are seen. Figs. 52-61 represent a series of transverse sections through the skull of the small Anomodont *Emydorhynchus palustris* in which the bones are less completely ossified than in other known genera. These sections show conclusively that the bone which I regard as the vomer is quite separate from the basisphenoid.

In the Gorgonopsia it is difficult to be quite certain of the homology of the vomerine bone. In the section through the snout of the early Gorgonopsian *Scylacognathus parvus* the structure and relations of the bone are such as would suggest that it is a true vomer. In the later Gorgonopsians the vomer is an unpaired structure, though possibly it may have resulted from the fusion of two parts. By WATSON it has been regarded as the fused prevomers: by myself it has been described as a true unpaired vomer. Till further specimens are studied it will be impossible to settle the question conclusively.

In Cynodonts there is always a large median vomer which pretty certainly is the homologue of the mammalian vomer. The figures given (figs. 63, 64, 68, 69, 70, 71, 72) represent sections across the vomers of various Cynodonts. The section of the vomer in *Bauria* (fig. 68) suggests a possible homology with the prevomer of *Dicynodon*, but the anterior extension of the bone seems to render it more probable that, like the vomer of the higher Cynodonts, it is the homologue of the mammalian vomer. In the higher Cynodonts the vomer is a very large bone which extends from the basisphenoid nearly to the front of the snout. In *Gomphognathus* and *Cynognathus* there appear to be a pair of small distinct prevomers in the anterior part of the floor of the nose. Whether it ultimately turns out that the mammalian vomer is homologous with the paired vomers of most reptiles and the mammalian prevomer a neomorph, or that the dumb-bell bone of *Ornithorhynchus* is the homologue of the lacertilian vomers there can I think be little doubt that the Cynodont vomer is the homologue of the true vomer of the mammal. Further research on the Therapsida will probably yet settle the question.

### 3. *The Alisphenoid Question.*

Until comparatively recently the alisphenoid has been regarded as an element of the cranial wall, and in mammals it forms a considerable part of the brain case. When in 1896 I first examined the marsupial chondrocranium I was somewhat surprised to find the alisphenoid developing as a short rounded rod lying far outside of the cranial wall and having apparently little to do with it. From its relations to the Gasserian ganglion and to the palatine and pterygoid bones it seemed to represent a modification of the cartilaginous bar which in lizards gives rise to the epipterygoid.

GAUPP also came quite independently to the conclusion that the mammalian alisphenoid was not originally an element of the cranial wall. He believes that it is a modified development of a structure homologous with the basipterygoid process of the lizard, and further concludes that the mammalian alisphenoid is not represented as such in the reptile skull.

The study of this region of the skull in the Therapsids throws considerable light on the question.

In the Stegocephalian *Eryops* there is a well developed epipterygoid, and probably one will be discovered in all the higher Stegocephalians and in all the Cotylosaurs. A short epipterygoid is known in *Diadectes* and a long lizard-like columella cranii is met with in *Procolophon*. A short epipterygoid occurs in the Pelycosaur *Dimetrodon*.

In Anomodonts the epipterygoid is present as a long slender rod—in some species rounded and in others much flattened. It extends from the parietal above to the pterygoid below, and its lower end is considerably expanded anteroposteriorly, giving it a long suture with the pterygoid.

In Gorgonopsians the epipterygoid is a long, much flattened rod which inferiorly has probably similar relations to the pterygoid as seen in the Anomodonts.

In the Therocephalians the epipterygoid is only satisfactorily known in *Scylacosaurus*. Here, as may be seen in fig. 43, it is a relatively short, flattened structure with a very wide base which lies along the pterygoid.

In the Cynodonts, at least in the higher forms as exemplified by *Diademodon* and *Cynognathus*, in the region occupied by the epipterygoid in the Therocephalians there is a very much larger bone which there can be little doubt is also an epipterygoid development. The upper part is greatly expanded antero-posteriorly and forms much of the cranial wall. The lower portion of the bone is so much more developed than in the Therocephalian that it completely replaces the posterior part of the pterygoid, as can be seen in fig. 45, and extends outwards as far as the quadrate. There can be little doubt that while this bone is homologous with the epipterygoid of the lower forms, it is also the homologue of the mammalian alisphenoid.

The condition in some reptiles, *e.g.* *Belodon*, would seem at first sight to be opposed to this theory, for here there appears to be both an epipterygoid and an alisphenoid. But there is good reason to believe that the bone which in birds, crocodiles, and

dinosaurs has been called alisphenoid is not homologous with the mammalian alisphenoid.

In reptiles there is, apart from the epipterygoid, a lateral cartilaginous cranial wall which in lizards and *Sphenodon* remains unossified as a network of feeble cartilage bars. In mammals the lateral wall is represented by an upper broad bar of cartilage which becomes ossified as the orbitosphenoid, and a lower bar usually aborted but which remains fairly well developed in the Monotremes and forms the tænia clino-orbitalis. The so-called alisphenoid in birds and crocodiles appears to be an ossification in a structure probably homologous with the tænia clino-orbitalis, and as it is evidently not the mammalian alisphenoid the name "*Oto-sphenoid*" may be applied to it.

In *Bauria* the epipterygoid appears to resemble that of the Therocephalians rather than that of the higher Cynodonts. In fig. 44 this region is seen in section. The long epipterygoid is seen resting inferiorly on the pterygoid.

#### CONCLUSIONS.

That the mammals arose from an ancestor which belonged to one or other of the Therapsid sub-orders seems to be beyond question, and the more generalised types all show skeletal structures such as we should expect in a near or remote ancestor of the mammal. The case for the ancestor having been a Cynodont, while fairly strong, is less conclusive. If, on further investigation, *Bauria* proves to be a true Cynodont it will be difficult to avoid the conclusion that the mammalian ancestor was also a Cynodont. But if *Bauria* proves to be derived from a higher Therocephalian which has independently acquired the secondary palate and other Cynodont characters, the case will be nearly as strong for the mammalian ancestor having been a higher Therocephalian. On the present evidence the most satisfactory conclusion seems to be that the immediate ancestor was a primitive Cynodont in type somewhat between the specialised *Bauria* and the more typical early Cynodonts such as *Ælurosuchus* or *Nythosaurus*. In any case we may safely assume that the line of mammalian descent passed from the Cotylosauria through some primitive Therapsid sub-order allied to the Dromasauria, and that in Middle Permian times the mammalian ancestors were Therocephalians. In Triassic times the ancestors were either Cynodonts or Cynodont-like Therocephalians, more probably the former.

Having determined roughly the line of descent, it is interesting to look for any agencies that may have brought about the evolution. In the first place there can be little doubt that the peculiarities of the shoulder girdle, pelvis, limbs, and some other points in the structure of the Therapsida are directly related to the habit of walking with the body off the ground. All the Cotylosaurs and Pelycosaurs of the Upper Carboniferous and Lower Permian of North America were crawling animals with a lizard-like or salamander-like gait. In the Middle Permian of South Africa we find the Pareiasaurs, allies of the American Cotylosaurs, and the Dinocephalians, Droma-

saurians, Therocephalians, and Anomodonts, allies of the Pelycosaur, all provided with well developed limbs which enabled the animals to walk with a mammal-like gait with the body well supported off the ground. It has been suggested that the alteration in gait was the result of a special evolution of the brain, but as we have a similar evolution brought about in at least two groups not at all closely connected it seems more probable that some environmental condition induced the changed habit and that the evolution of the brain was secondary. In Anomodonts and Cynodonts we know that there has been a remarkable development of the cerebellum, and it seems probable that this has been one result of the walking gait.

Other and more important results that followed were due to the greatly increased activity that became possible with the new gait. The herbivorous Dinocephalians and Anomodonts seem to have remained content with the degree of evolution they had acquired, the larger forms probably retreating into the swamps when in danger, the smaller possibly digging into the sand and mud like the *Echidna* of to-day. The insectivorous and carnivorous types became active running forms. The small Dromasaurians are the oldest known really very active four-footed animals. They were probably much more active than any of the Therocephalians, and possibly had the jaw been further evolved they might have given rise to an early warm-blooded type which might have survived. For some unknown reason the group only lasted a very short time.

In the Therocephalians we find the evolution taking a different line. With apparently abundant food in the numerous varieties of the Anomodonts great speed was unnecessary, and the modifications which we find taking place are of even greater promise for the future. The anterior maxillary teeth have become greatly developed as canines for killing, and the temporal muscle correspondingly greatly developed. The dentary bone has become by far the largest element in the mandible and for the first time a well-developed coronoid process is present.

Most of the changes seen in the Cynodonts appear to be the result of a further evolution along the lines started in the Therocephalians. The dentary becomes relatively so much more developed as to form nearly the whole jaw, and the teeth become more specialised. The increased development of the dentary and teeth, with the narrowing and deepening of the snout, is the probable origin of the secondary palate.

The first mammals, whether derived from higher Therocephalians or early Cynodonts, are evidently the result of further increased activity. The Therocephalians doubtless preyed on the Anomodonts, and the larger Cynodonts of the Upper Trias also probably found their principal food in the large Anomodont *Kannemeyeria*. In Middle Triassic times the smaller Cynodonts probably lived mainly on *Procolophon* and similar lizard-like Cotylosaurs, but in Upper Triassic times these lowly organised types became extinct, and the small Cynodonts were probably forced to hunt the much more active Pseudosuchians such as *Euparkeria*, and other agile reptiles like *Howesia* and

*Mesosuchus*, and it seems probable that it was the increased activity necessary that ultimately resulted in the development of the mammal.

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## REFERENCES TO PLATES.

*A.S.*, alisphenoid; *B.o.*, basioccipital; *B.S.*, basisphenoid; *c.*, centrale; *E.O.*, exoccipital; *E.Pt.*, epipterygoid; *F.*, fibula; *f.*, fibulare; *Fr.*, frontal; *i.*, intermedium; *I.P.*, interparietal; *Ju.*, jugal; *L.*, lachrymal; *M.C.*, Meckel's cartilage; *Mx.*, maxilla; *Na.*, nasal; *O.S.*, orbitosphenoid; *Ot.S.*, otosphenoid; *Pa.*, parietal; *Pal.*, palatine; *Per.*, periotic; *Pmx.*, premaxilla; *Po.F.*, postfrontal; *Po.O.*, postorbital; *P.S.*, presphenoid; *Pt.*, pterygoid; *P.Vo.*, prevomer; *Q.*, quadrate; *R.*, radius; *r.*, radiale; *S.E.*, sphenethmoid; *S.P.*, sclerotic plate; *Sq.*, squamosal; *T.*, tibia; *t.*, tibiale; *T.C.O.*, tænia clino-orbitalis; *T.P.*, transpalatine; *Ty.*, tympanic; *U.*, ulnar; *u.*, ulnare; *Vo.*, vomer.

The specimens marked Am. Mus. are in the collection of the American Museum Nat. Hist., New York.

## PLATE 1.

- Fig. 1.—Left shoulder girdle of the Dinocephalian *Moschops capensis*, Broom. Side view. About 1/5 nat. size. Am. Mus.
- Fig. 2.—Left shoulder girdle of *Moschops capensis*, Broom. Viewed from behind. About 1/5 nat. size. Am. Mus.
- Fig. 3.—Top of right scapula of *Moschops capensis*, Broom. Outer view showing top and greater part of the cleithrum in position. About 1/5 nat. size. Am. Mus.
- Fig. 4.—Interclavicle of *Moschops capensis*, Broom. Viewed from the left side. About 1/5 nat. size. Am. Mus.
- Fig. 5.—Interclavicle of *Moschops capensis*, Broom. Pectoral view. About 1/5 nat. size. Am. Mus.
- Fig. 6.—Left humerus of *Moschops capensis*, Broom. Front view. About 1/5 nat. size. Am. Mus.
- Fig. 7.—Left humerus of *Moschops capensis*, Broom. Outer view. About 1/5 nat. size. Am. Mus.
- Fig. 8.—Left ulna of *Moschops capensis*, Broom. Front view. About 1/5 nat. size. Am. Mus.
- Fig. 9.—Left ulna of *Moschops capensis*, Broom. Inner view. About 1/5 nat. size. Am. Mus.
- Fig. 10.—Left radius of *Moschops capensis*, Broom. Front view. About 1/5 nat. size. Am. Mus.
- Fig. 11.—Left radius of *Moschops capensis*, Broom. Inner view. About 1/5 nat. size. Am. Mus.

## PLATE 2.

Fig. 12.—Right view of pelvis of *Moschops capensis*, Broom. About 1/5 nat. size. Am. Mus.

Fig. 13.—Front view of right side of pelvis of *Moschops capensis*, Broom. About 1/5 nat. size. The large first sacral rib is shown in position in dotted line. The views of the pelvis are, in part, restorations. No specimen is known with all the bones in natural articulation, but as six specimens of ilia, three specimens of the pubis, and four of the ischium are known, almost every detail can be relied upon. In one specimen both ischia are present in articulation with the two ilia, and both ilia in articulation with the sacrum. No specimen is known with the pubis in articulation with the ischium, and, as in all specimens of the pubis the posterior border is imperfect, there is a slight doubt as to the length of the pubic symphysis. It is pretty certainly short and probably as drawn. Am. Mus.

Fig. 14.—Left femur of *Moschops capensis*, Broom. Front view. About 1/5 nat. size. Am. Mus.

Fig. 15.—Left femur of *Moschops capensis*, Broom. Inner view. About 1/5 nat. size. Am. Mus.

Fig. 16.—Left femur of *Moschops capensis*, Broom. Back view. About 1/5 nat. size. Am. Mus.

Fig. 17.—Right fibula of *Moschops capensis*, Broom. Outer view. About 1/5 nat. size. Am. Mus.

Fig. 18.—Right tibia and fibula of *Moschops capensis*, Broom. Front view. About 1/5 nat. size. Am. Mus.

Fig. 19.—Right tibia of *Moschops capensis*, Broom. Inner and back view. About 1/5 nat. size. Am. Mus.

Fig. 20.—Atlas, axis, and intercentra of *Moschops capensis*, Broom. Side view. About 1/5 nat. size. The arch of the atlas is drawn in true side view and correctly orientated to the axis but moved a short distance forward to show zygapophysis and the odontoid of the axis. Am. Mus.

Fig. 21.—Left arch of the atlas of *Moschops capensis*, Broom. Viewed from the under side and showing the three facets, the front one for the occipital condyle, the lower one for the intercentrum and the upper and posterior one for the odontoid. Am. Mus.

Fig. 22.—Front view of the odontoid of *Moschops capensis*, Broom. About 1/5 nat. size. Am. Mus.

Fig. 23.—Side view of a cervical vertebra, probably the 6th, of *Moschops capensis*, Broom. About 1/5 nat. size. Am. Mus.

- Fig. 24.—Sixth right cervical rib of *Moschognathus Whaitsi*, Broom. About  $\frac{1}{5}$  nat. size. *Moschognathus whaitsi* is a Dinocephalian closely allied to *Moschops*. Am. Mus.
- Fig. 25.—Back view of dorsal vertebra, probably 8th, of *Moschops capensis*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 26.—Side view of dorsal vertebra, probably 8th, of *Moschops capensis*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 27.—Front view of 5th dorsal rib of *Moschognathus Whaitsi*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 27A.—Under side of sacrum of *Moschops capensis*, Broom. From an animal not quite fully grown. About  $\frac{1}{5}$  nat. size. Am. Mus.

## PLATE 3.

- Fig. 28.—Skeleton of *Galepus Jouberti*, Broom. Nat. size. The specimen is the almost perfect skeleton of a Dromasaurian. The bones are completely weathered out, but are represented by perfect casts. The greater part of the skeleton lies in one plane, but the skull is bent considerably to the side, and is represented in the drawing obliquely. The whole of the right femur, tibia and fibula are preserved and shown in a cross fracture, but cannot be represented in the drawing. The right pes is folded in under the tibia and fibula. Am. Mus.
- Fig. 29.—Imperfect skeleton of *Galechirus Scholtzi*, Broom. Nat. size. The specimen consists of the natural casts of the left anterior and posterior limbs with much of the girdles, and other remains. The specimen is from the same locality as the type. Am. Mus.
- Fig. 30.—Imperfect skeleton of *Galeops Whaitsi*, Broom.  $\frac{5}{6}$  nat. size. In this Dromasaurian skeleton most of the bones are broken across with the fracture of the stone. The skull is moderately complete, and the lower jaw almost perfect. Of the shoulder girdle there are preserved the complete right scapula and most of the right coracoid and precoracoid and the right clavicle. Much of the interclavicle is shown, with a large part of the left coracoid and precoracoid. The two other bones shown between the coracoid and the point of the lower jaw are portions of the head of the left humerus. The right humerus, radius, and ulna are nearly perfect. The vertebræ are not well preserved, but are seen to be notochordal. Am. Mus.

## PLATE 4.

- Fig. 31.—Side view of the skull of *Galepus Jouberti*, Broom. About  $1\frac{1}{2}$  nat. size. Slightly restored. The specimen shows the casts of the inner sides of the bones. Am. Mus.

- Fig. 32.—Upper view of the skull of *Galepus Jouberti*, Broom. Nat. size. Slightly restored. Am. Mus.
- Fig. 33.—Pectoral girdle of *Galepus Jouberti*, Broom. Nat. size. Part of the interclavicle is represented as cut away to show the inner edges of the coracoid and precoracoid. Am. Mus.
- Fig. 34.—Right scapula, coracoid and precoracoid of *Galeops Whaitsi*, Broom. Nat. size. The drawing is a restoration from the remains seen in fig. 30. Am. Mus.
- Fig. 35.—Restoration of scapula, coracoid and precoracoid of *Galechirus Scholtzi*, Broom. Nat. size. The scapula is from the specimen shown in fig. 29, and the coracoid and precoracoid from the type specimen. Am. Mus.
- Fig. 36.—Left side of pelvis of *Galepus Jouberti*, Broom. Nat. size. Am. Mus.
- Fig. 37.—Restoration of the left side of pelvis of *Galechirus Scholtzi*, Broom. Nat. size. Am. Mus.
- Fig. 38.—Right manus of *Galechirus Scholtzi*, Broom. Nat. size. S.A. Mus., Capetown.
- Fig. 39.—Right pes of *Galechirus Scholtzi*, Broom. Nat. size. Am. Mus.
- Fig. 40.—Right pes of *Galesphyrus capensis*, Broom. Nat. size. S.A. Mus., Cape Town.
- Fig. 41.—Upper side of skull of *Scaloposaurus constrictus*, Owen.  $1\frac{1}{2}$  nat. size. The drawing is a slightly restored view of the British Museum type. B.M., R. 1723.
- Fig. 42.—Palate of *Scaloposaurus constrictus*, Owen.  $1\frac{1}{2}$  nat. size. The posterior half is drawn from the British Museum type; the front half is an attempted restoration founded on the palates of allied forms. B.M., R. 1723.
- Fig. 43.—Epipterygoid of *Scylacosaurus Sclateri*, Broom. Nat. size. B.M., R. 4055.
- Fig. 44.—Transverse section through the skull of *Bauria cynops*, Broom, immediately in front of the proötic. The basisphenoid shows the deep median keel. The epipterygoid is broken in the middle. Its lower end covers over the pterygoid. The brain case is partly walled by a feeble ossification which is probably homologous with the posterior part of the cartilaginous structure seen in the side of brain case in *Sphenodon* and lizards. As the epipterygoid is, in my opinion, the homologue of the mammalian alisphenoid this element requires a new name, and I have ventured to propose "otosphenoid." It is most probably the homologue also of the tænia clino-orbitalis of *Ornithorhynchus* and probably also of the so-called "alisphenoid" of the crocodile and bird. Am. Mus.
- Fig. 45.—The right side of the posterior part of the base of the skull of *Diademodon minor*, Broom. Nat. size. The specimen shows the lower part of the alisphenoid articulating with the pterygoid in front and the proötic behind.

The quadrate shows the two processes which fit into grooves in the squamosal. As the quadrate is considerably displaced to the front without any fracturing of the elements it is manifest that considerable movement between the quadrate and squamosal was possible. B.M., R. 3587.

## PLATE 5.

Fig. 46.—Median section of the prevomer, vomer, and basisphenoid of *Dicynodon platyceps*, Broom. The specimen shows the large bone which has usually been regarded as vomer but which from comparison with the condition in the smaller Therocephalians can be confidently stated to be the prevomers fused. Above it, and lying in a groove on its upper surface, is a median bone so strikingly like the mammalian vomer in character and relations that little doubt exists as to its being the true vomer. Posteriorly it is in intimate association with the basisphenoid. It is manifestly a membrane bone.  $\frac{2}{3}$  nat. size. Am. Mus.

Fig. 47.—Transverse section of the same specimen, as shown in fig. 46, made in the neighbourhood of the letters "vo." The relations of the vomer to the prevomer are well shown, as also the bones of the palate. Above the vomer is seen in section the median cartilage bone. There is some doubt as to whether the element is the mesethmoid or presphenoid of the mammal, and, as I think there is good evidence for regarding it as homologous with the median bone in *Eryops*, which is pretty manifestly the sphenethmoid of the frog, I have called this bone in *Dicynodon*, sphenethmoid.  $\frac{2}{3}$  nat. size. Am. Mus.

Fig. 48.—Transverse section of the same prevomer and vomer of *Dicynodon platyceps*, Broom. Nat. size. Am. Mus.

Fig. 49.—Transverse section through snout of *Dicynodon* sp. Nat. size. Though a different species from that shown in fig. 47, there is a close agreement between the sections. The sphenethmoid is cut slightly farther forward in fig. 49, and the olfactory nerves have each an independent passage. The vomer is seen to be here much more highly developed. Am. Mus.

Fig. 50.—Transverse section across the snout of *Dicynodon feliceps*, Owen. Nat. size. The section is cut obliquely from the front of the orbit towards the back of the posterior nares. The prevomer and vomer and the sphenethmoid have similar relations to those in the specimen represented by fig. 49. Am. Mus.

Fig. 51.—Transverse section of the skull of another specimen of *Dicynodon feliceps*, Owen. Nat. size. This section shows the posterior part of the prevomer and the vomer a very short distance in front of the basisphenoid. Am. Mus.

Figs. 52–61.—A series of transverse sections of the skull of *Emydorhynchus*



*palustris*, Broom, showing the relations of the prevomer and vomer in one of the small and feebly ossified Anomodonts. All sections are four times nat. size. Am. Mus.

Fig. 52.—A section about midway between the nostril and the orbit. It shows the broad flat palatal plate of the premaxilla, with the ascending median ridge.

Fig. 53.—A section across the anterior part of the orbit, and 2.5 mm. behind the section shown in fig. 52. The palatal portion of the premaxilla is still very broad. The median crest is cut near the point where it articulates with the prevomer. The large antral-like space, mainly enclosed by the maxilla, is shown.

Fig. 54.—A section 2.5 mm. behind that shown in fig. 53. The front of the prevomer is shown riding on the crest of the premaxilla.

Fig. 55.—A section 2.5 mm. behind that shown in fig. 54. The prevomer still bears similar relations to the premaxilla seen in the other section. The palatal plate of the premaxilla is rapidly narrowing.

Fig. 56.—A section 3.5 mm. behind that shown in fig. 55. Figs. 52 to 55 are drawn from the posterior surfaces of the slices of the fossil: figs. 56 to 61 from the anterior surfaces. The sections are, however, so nearly transverse and the two sides so similar that this reversing may be regarded as negligible. Section fig. 56 is behind the premaxilla and through the largest part of the prevomer. Here it is seen largely overlapped by the palatines. There is no evidence that the median cartilage fitted into the upper surface either here or farther forward. Doubtless the median cartilage was close above it, but nowhere has it been moulded round the base of the cartilage as is the mammalian vomer.

Fig. 57.—A section 3 mm. behind section fig. 56. The prevomer is seen here in two parts, the posterior end sending out lateral processes. The true vomer is seen considerably displaced to the left side, and cut somewhere near its anterior end. Exactly how much farther forwards it extends is unknown. It is seen on the posterior side of the preceding slice, but not on the anterior side. We thus know that it extends 0.5 mm. farther forwards but not 3 mm.

Fig. 58.—A section 5.5 mm. behind section fig. 57. The true vomer is here seen cut across its largest part. It undoubtedly has been moulded round the base of the median cartilage in exactly the same way as is the mammalian vomer.

Fig. 59.—A section 2 mm. behind section fig. 58. The vomer is here seen to have rapidly decreased in size and to be represented merely by a spur of bone which is a prolongation backwards from the right side of the vomer. The median cartilage is here replaced by the ossified anterior plate-like portion of the basisphenoid. The sections of this small Anomodont were cut

mainly to find if the bone which I believe to be the true vomer is really distinct from the basisphenoid, and the sections prove beyond question that this is the case.

Fig. 60.—A section 1 mm. behind fig. 59. The posterior bony spur of the vomer is still seen quite distinct from the basisphenoid. A thin bony flake by the side of the basisphenoid is evidently a sclerotic plate.

Fig. 61.—A section 2.5 mm. behind fig. 60. The vomer is no longer seen and the median plate of the basisphenoid has sunk down and the bone become greatly broadened out.

#### PLATE 6.

Fig. 62.—Diagrammatic view of the front of the palate of *Lycognathus ferox*, Broom, a Cynodont reptile allied to *Cynognathus*. It will be seen there is a typically mammal-like palatine process to the premaxilla. Am. Mus.

Fig. 63.—Transverse section across the snout of *Lycognathus ferox*, Broom. Though the vomer is represented in two parts it is moderately certain that this is due to a longitudinal fracture. The tip of one of the palatine processes of the premaxillæ is shown; the other ends anterior to the section. Am. Mus.

Fig. 64.—Transverse section of the snout of *Lycognathus ferox*, Broom, posterior to that shown in fig. 63. The vomer here is also shown divided by a longitudinal fracture. Am. Mus.

Fig. 65.—Semi-diagrammatic section across the snout of *Scylacognathus parvus*, Broom—a small Gorgonopsian. About twice nat. size. The actual specimen has the bones much crushed together and distorted, but there is practically no doubt about the elements or their relations. Am. Mus.

Fig. 66.—Section across the anterior portion of the snout of *Scymnognathus tigriceps*, Broom and Haughton. About  $\frac{1}{2}$  nat. size. The supposed vomer is represented by an extremely delicate median plate, which at its base expands into a thick bone. Am. Mus.

Fig. 67.—Section across the snout of the small but highly specialised Gorgonopsian *Ictidorhinus Martinsi*, Broom. About  $1\frac{1}{2}$  nat. size. The supposed vomer is not unlike that of *Scymnognathus tigriceps* seen in fig. 66. Am. Mus.

Fig. 68.—Section through the posterior part of the supposed vomer of *Bauria cynops*, Broom. Nat. size. The specimen is a little crushed. The supposed vomer agrees with the prevomer of *Dicynodon* in its relations, as seen in fig. 49, so closely as to suggest that this is also a prevomer. On the other hand, the anterior part of the bone is fairly similar in its relations to the vomer of the *Diademodon*. A very short distance behind the

plane of the section figured, the supposed vomer dips down below the pterygoids, which, meeting above it, completely remove it from further relations with the median cartilage elements. In its anterior part the "vomer" of *Bauria* thus resembles the higher Cynodonts; in its middle region it resembles the prevomer of *Dicynodon*; and in its posterior relations it resembles the "vomer" of the Gorgonopsians. Am. Mus.

Fig. 69.—Section across the anterior part of the vomer in *Diademodon* sp. Nat. size. Am. Mus.

Fig. 70.—Section across the posterior part of the vomer in *Diademodon* sp. Nat. size. Am. Mus.

Fig. 71.—Section across the snout of *Sesamodon browni*, Broom. About  $1\frac{1}{2}$  nat. size. The bone has a loose cancellous texture and the elements in the palatal region are so anchylosed that it is impossible to see any sutures. The vomer can, however, readily be made out. Am. Mus.

Fig. 72.—Section across the posterior part of the vomer in *Sesamodon browni*, Broom. About  $1\frac{1}{2}$  nat. size. Am. Mus.

Fig. 73.—Section across the snout of the Therocephalian *Pristerognathus platyrhinus*, Broom. Nat. size. Here there are seen to be two prevomers very clearly separated one from the other. Am. Mus.

Fig. 74.—Section across the prevomer of a small undescribed Therocephalian. About 4 times nat. size. The prevomers are fused but are interesting from the shape of their lower borders, which are scroll-like, doubtless to support an organ of Jacobson. The section is strikingly like a section through the dumb-bell bone of *Ornithorhynchus*. Am. Mus.

Fig. 75.—Section across the prevomer of the small Therocephalian *Ictidognathus parvidens*, Broom. About twice nat. size. Am. Mus.

Fig. 76.—Section across the prevomers of the small Therocephalian *Ictidognathus hemburyi*, Broom. About twice nat. size. The condition here is very similar to that seen in fig. 75, but the two prevomers are, though close together, quite distinct. Am. Mus.

#### PLATE 7.

Fig. 77.—Posterior portion of the base of the skull of a large foetus of *Tatu novemcinctum*, Linn., head length 44 mm. On the right side the large transpalatine is seen quite distinct from the pterygoid lying dorsal to it. On the left side the transpalatine and pterygoid are, in part, anchylosed already. Am. Mus.

Fig. 78.—Portion of the base of the skull of a  $\frac{2}{3}$  grown *Tatu novemcinctum*, Linn., showing the later condition of the transpalatine. Am. Mus.

Fig. 79.—View of the same specimen with the transpalatine and part of the palatine removed, so as fully to expose the pterygoid.

Fig. 80.—Back of the palate of *Tamandua tetradactyla*. Slightly enlarged. The small transpalatine is seen on the right side. It varies greatly in different specimens; and in most it is so loosely attached that it is removed and lost when the skull is cleaned. Am. Mus.

Figs. 81–86.—Sections across the palato-pterygoid region in a very young *Ornithorhynchus anatinus*, Shaw.

Fig. 81 shows the large palatine with the true pterygoid above it and very distinct from it.

Fig. 82 is a similar section a little farther back.

Fig. 83 shows the anterior end of the transpalatine and the posterior end of the pterygoid.

Fig. 84 a similar section to 83.

Figs. 85 and 86.—Sections across the more posterior regions of the transpalatine. Coll. Prof. J. P. Hill.

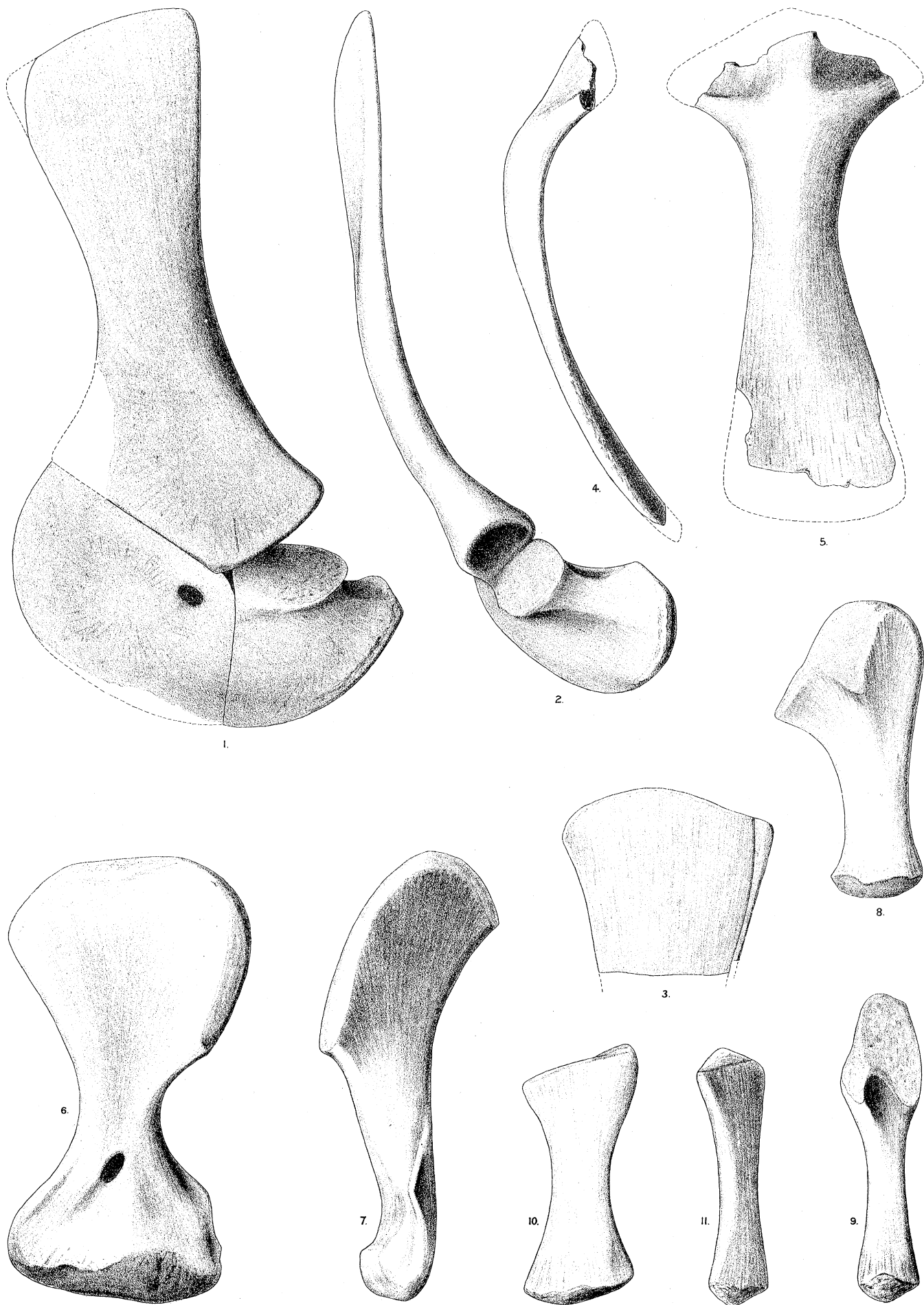
Figs. 87–89.—Sections across the palatine and pterygoid of a mammary foetus (25 mm.) of *Petrogale penicillata*.

Fig. 87 shows palatine near its posterior end.

Fig. 88 shows the pterygoid and the feebly ossified transpalatine.

Fig. 89 shows the pterygoid alone. Coll. Prof. J. P. Hill.

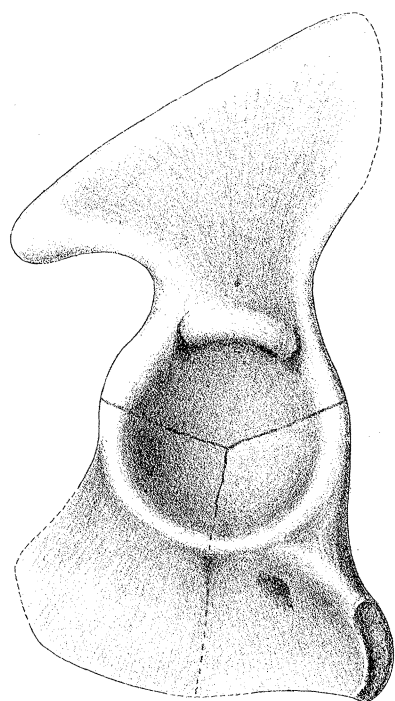
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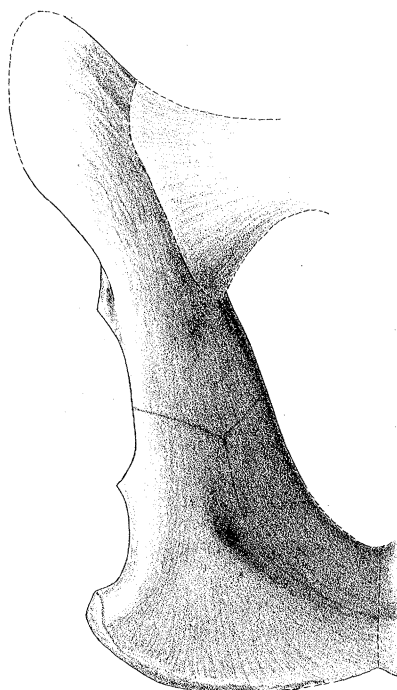
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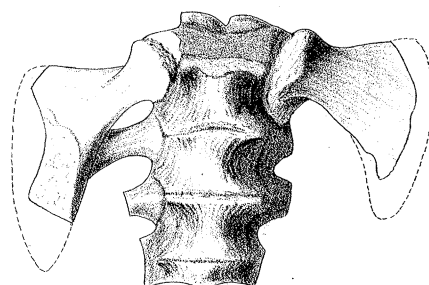
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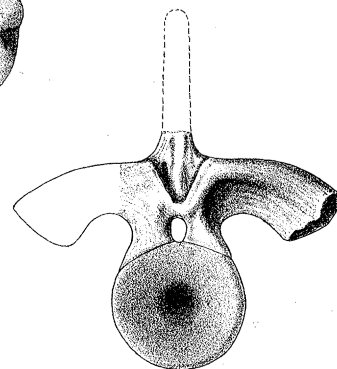
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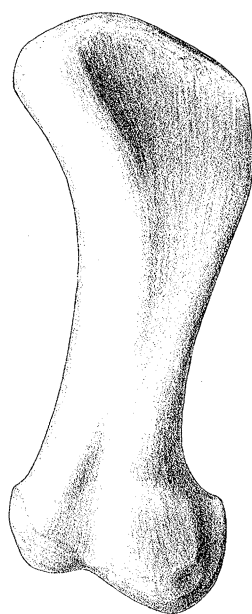
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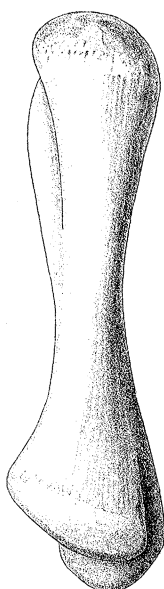
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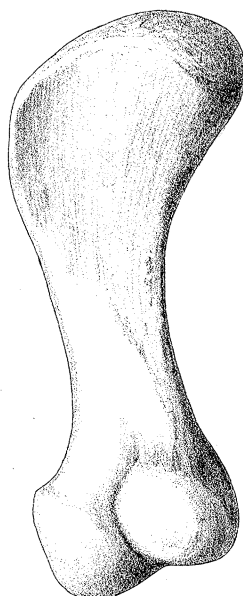
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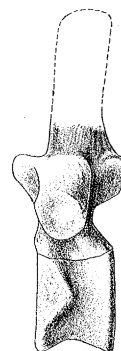
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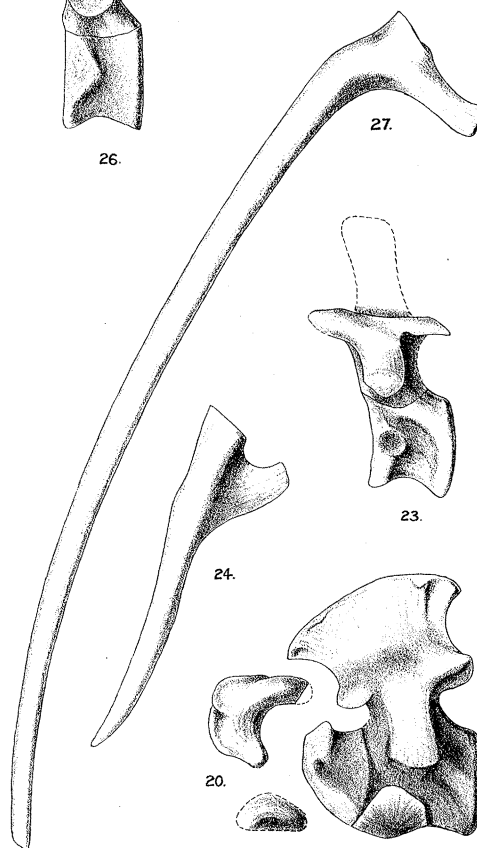
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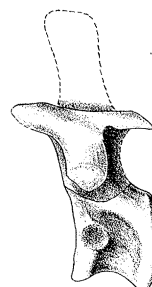
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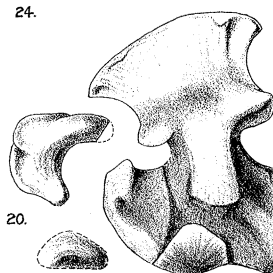
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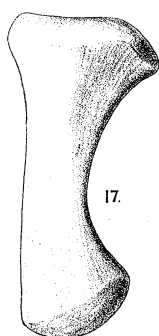
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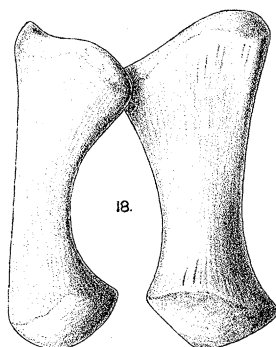
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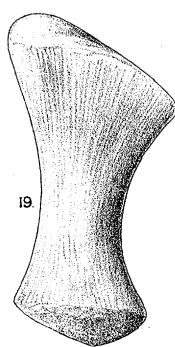
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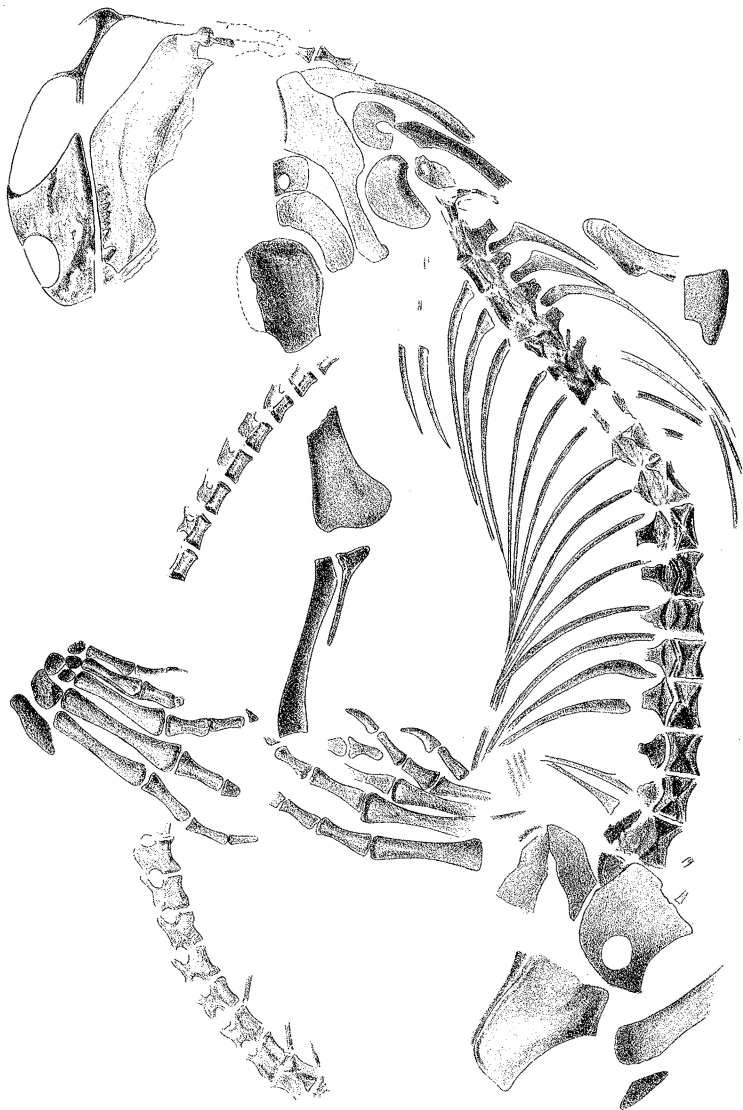
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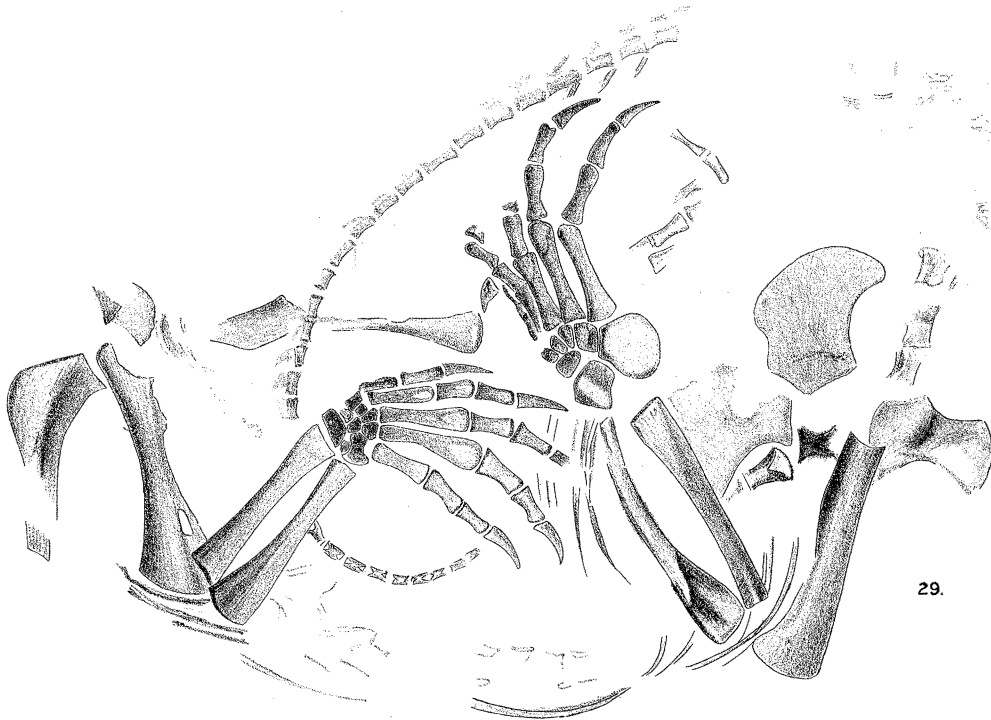
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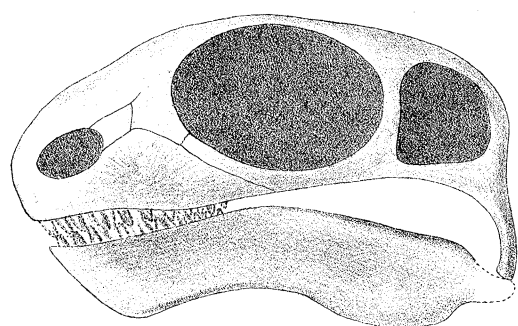
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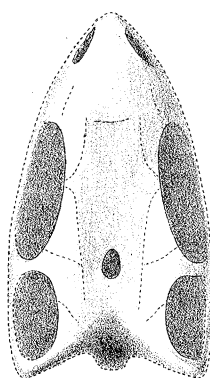
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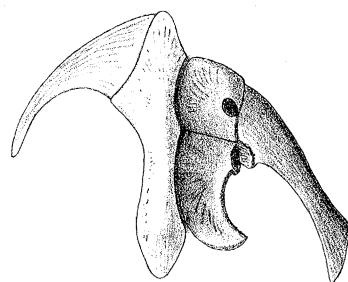
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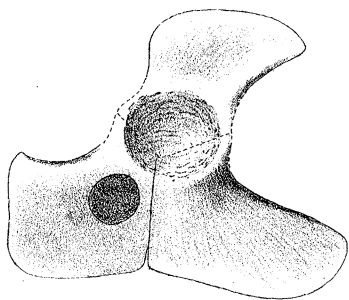
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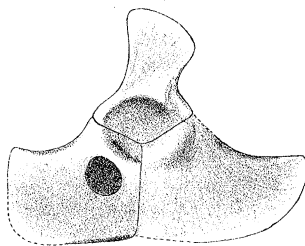
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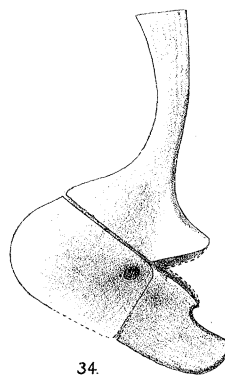
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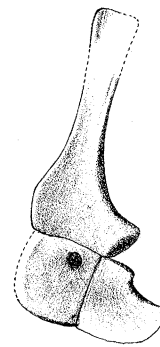
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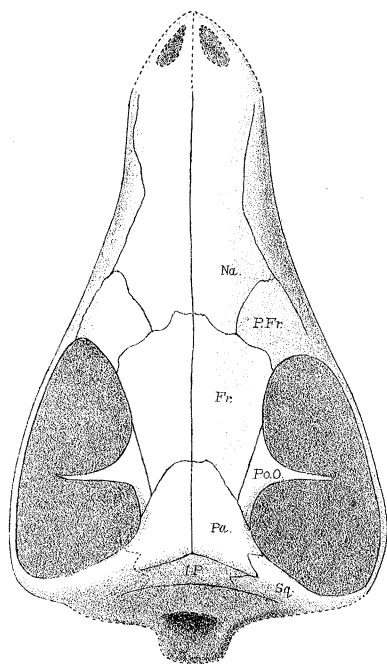
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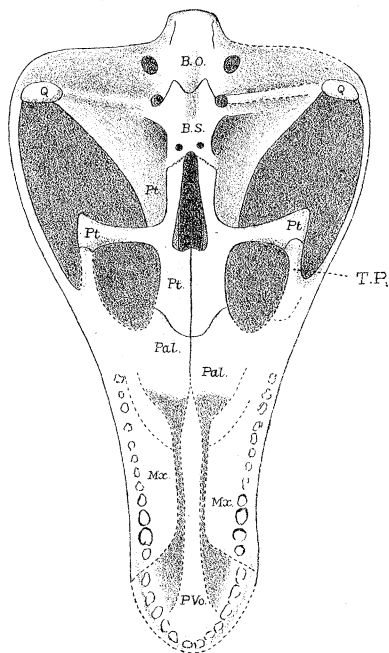
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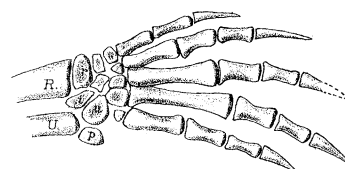
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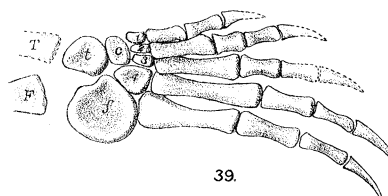
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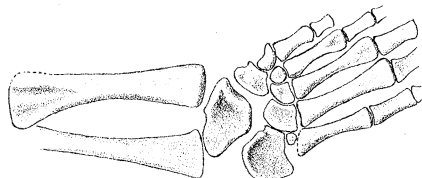
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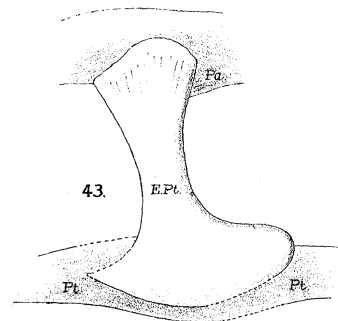
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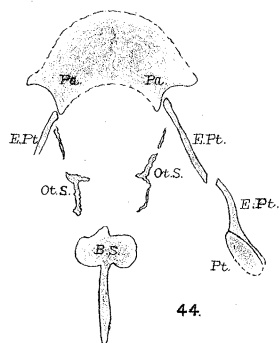
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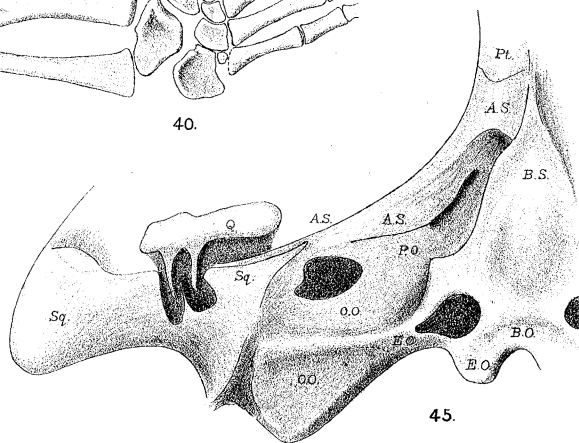
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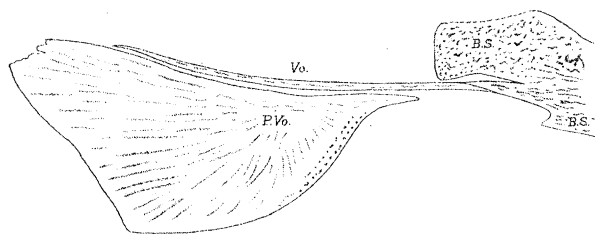


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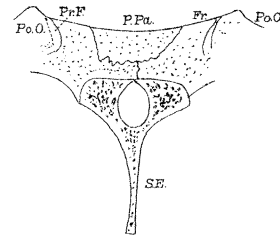


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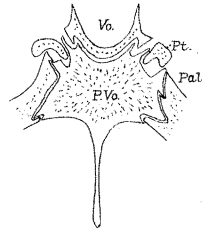




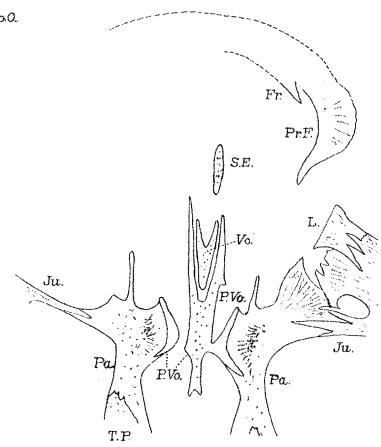
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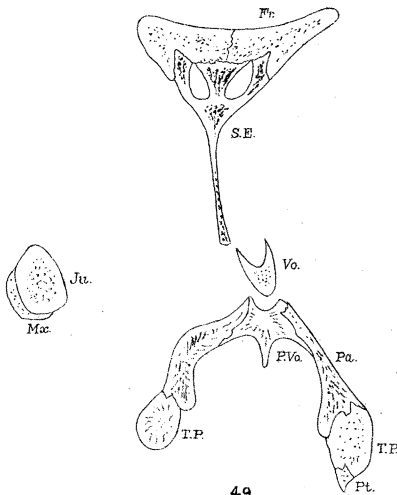
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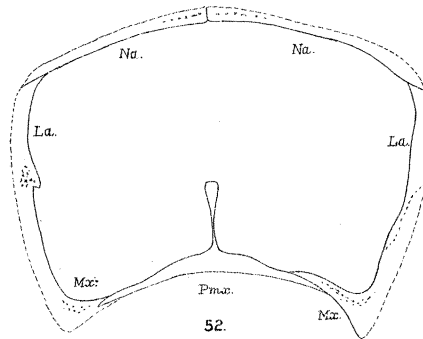
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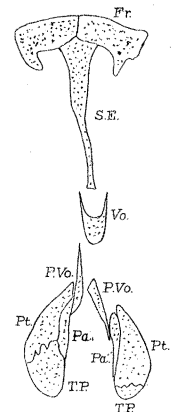
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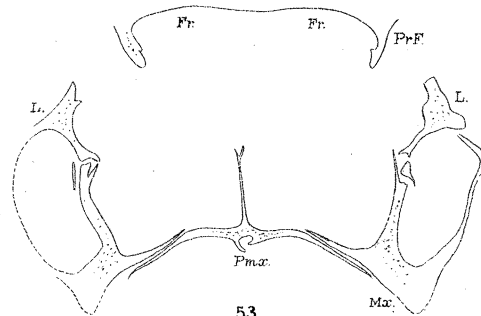
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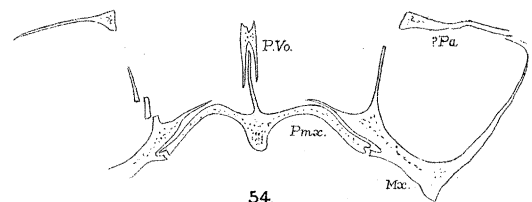
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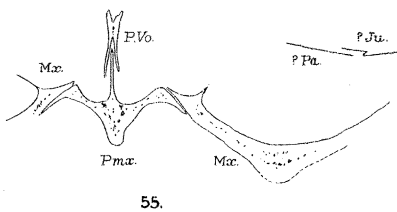
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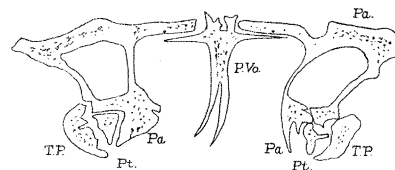
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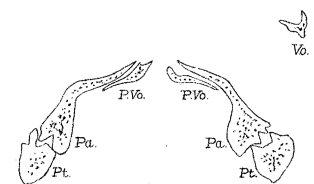
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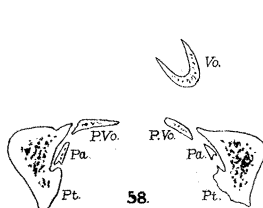
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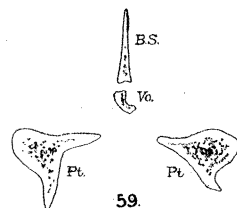
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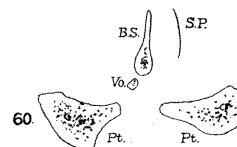
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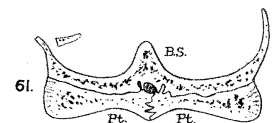
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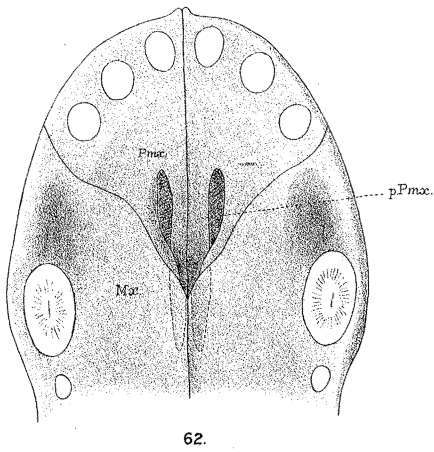
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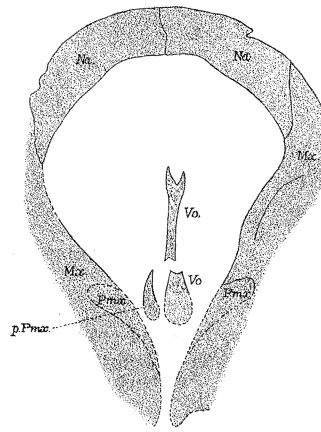
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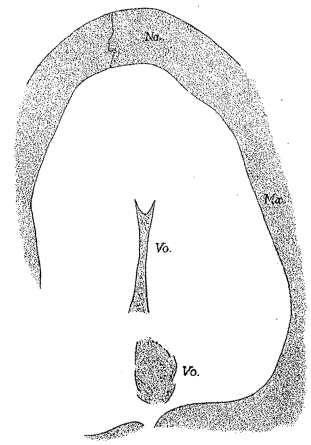
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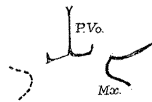
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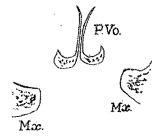
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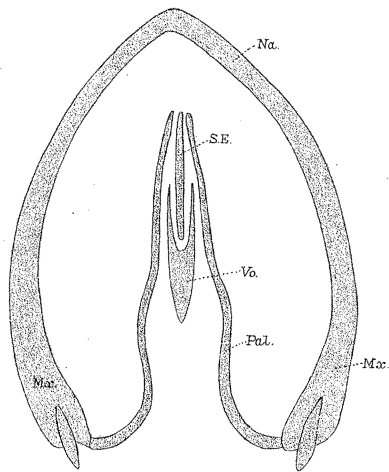
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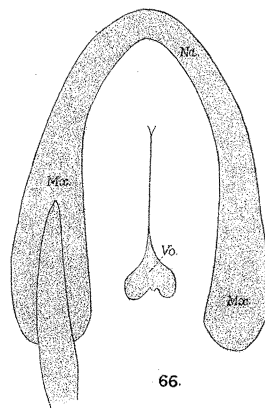
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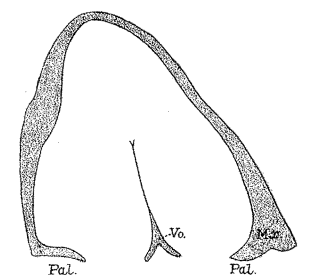
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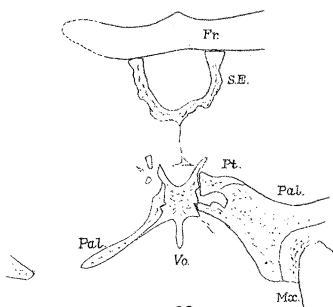
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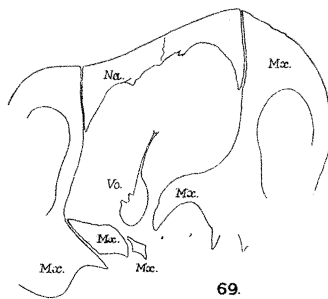
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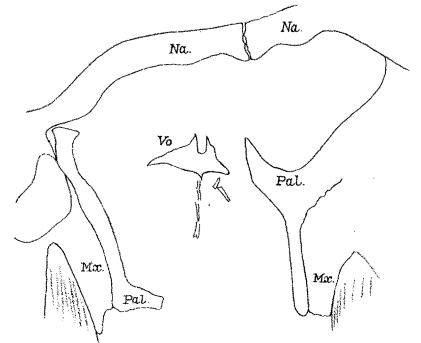
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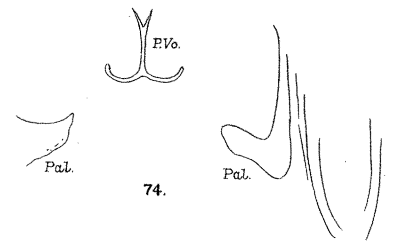
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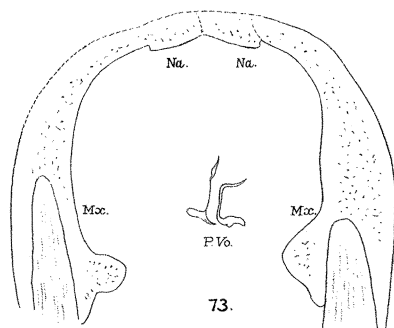
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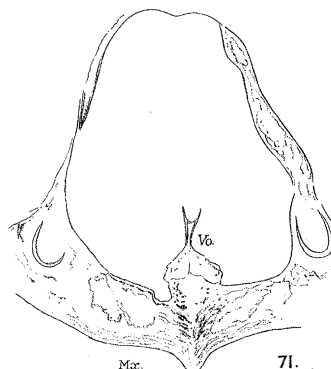
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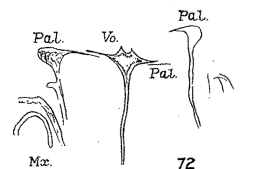
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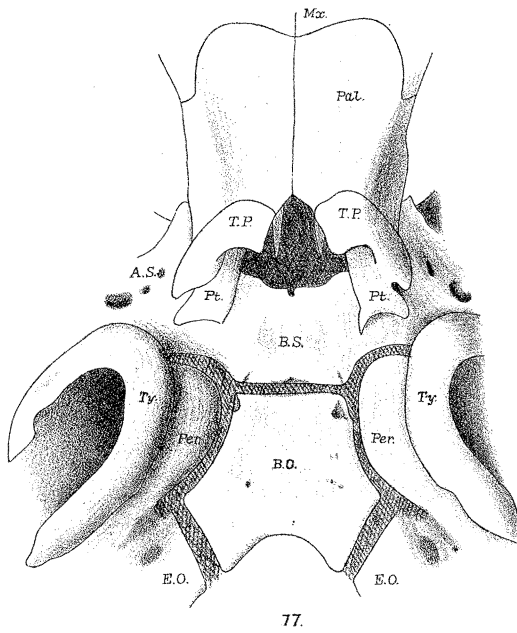
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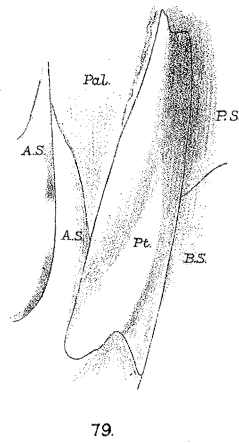
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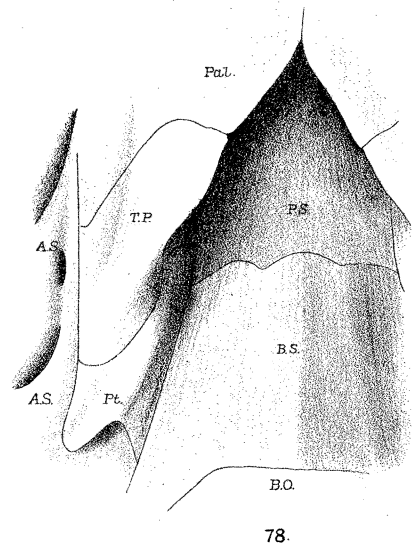
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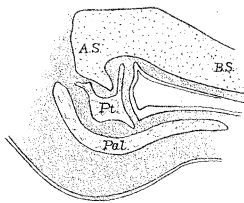
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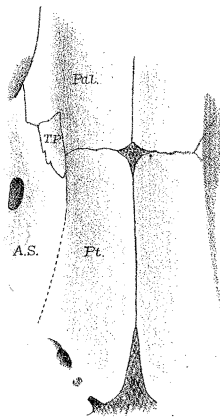
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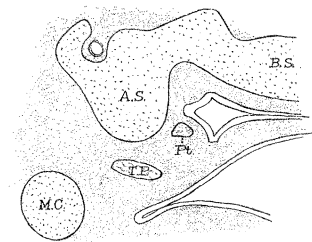
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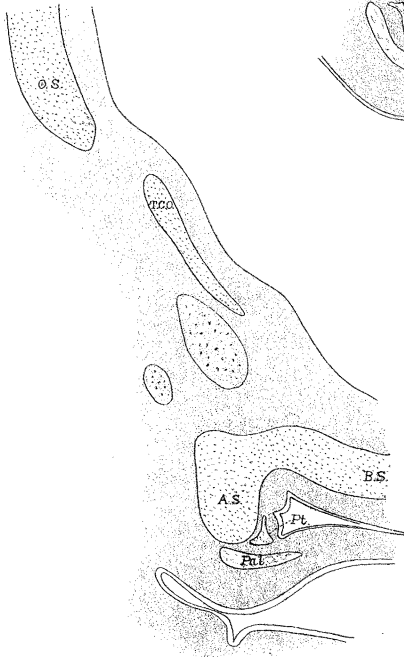
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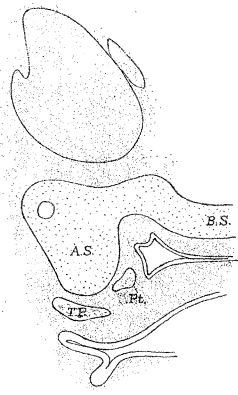
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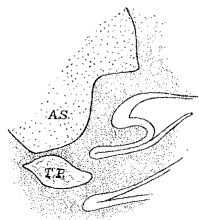
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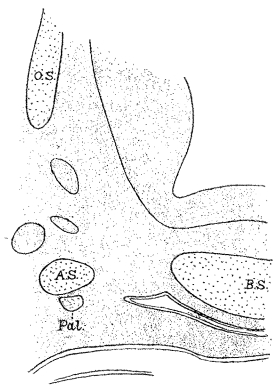
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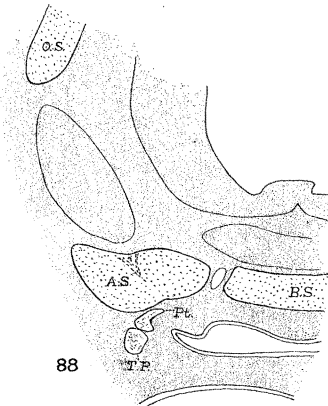
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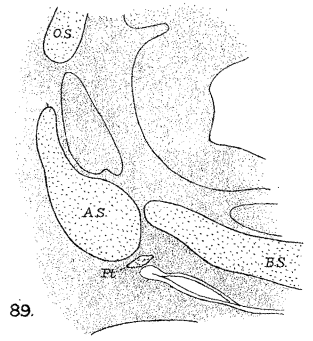
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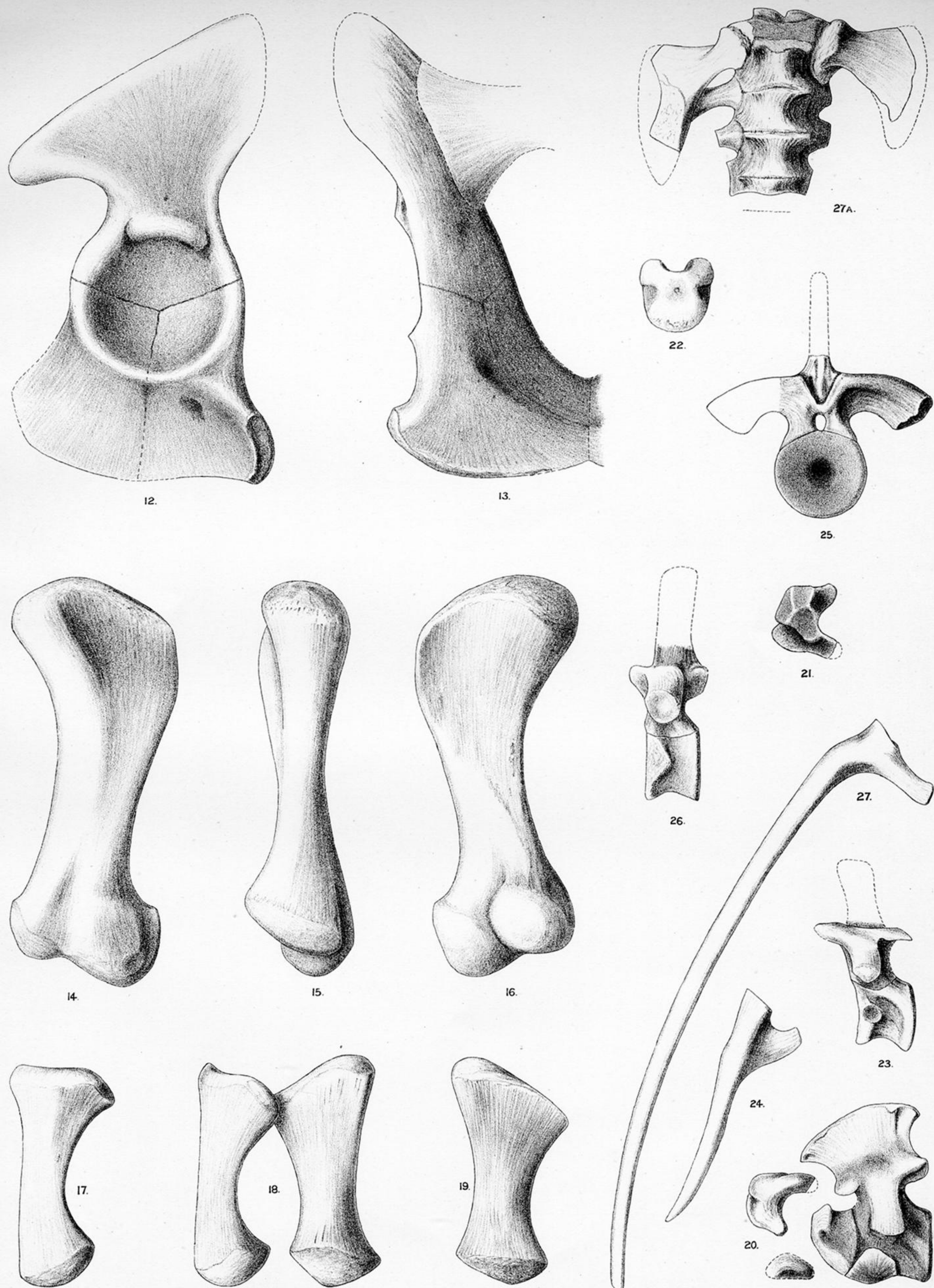


BONES OF DINOCEPHALIAN MOSCHOPS.

PLATE 1.

- Fig. 1.—Left shoulder girdle of the Dinocephalian *Moschops capensis*, Broom. Side view. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 2.—Left shoulder girdle of *Moschops capensis*, Broom. Viewed from behind. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 3.—Top of right scapula of *Moschops capensis*, Broom. Outer view showing top and greater part of the cleithrum in position. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 4.—Interclavicle of *Moschops capensis*, Broom. Viewed from the left side. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 5.—Interclavicle of *Moschops capensis*, Broom. Pectoral view. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 6.—Left humerus of *Moschops capensis*, Broom. Front view. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 7.—Left humerus of *Moschops capensis*, Broom. Outer view. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 8.—Left ulna of *Moschops capensis*, Broom. Front view. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 9.—Left ulna of *Moschops capensis*, Broom. Inner view. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 10.—Left radius of *Moschops capensis*, Broom. Front view. About  $\frac{1}{5}$  nat. size. Am. Mus.
- Fig. 11.—Left radius of *Moschops capensis*, Broom. Inner view. About  $\frac{1}{5}$  nat. size. Am. Mus.





BONES OF DINOCEPHALIANS, MOSCHOPS AND MOSCHOGNATHOS.

PLATE 2.

Fig. 12.—Right view of pelvis of *Moschops capensis*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 13.—Front view of right side of pelvis of *Moschops capensis*, Broom. About  $\frac{1}{5}$  nat. size. The large first sacral rib is shown in position in dotted line. The views of the pelvis are, in part, restorations. No specimen is known with all the bones in natural articulation, but as six specimens of ilia, three specimens of the pubis, and four of the ischium are known, almost every detail can be relied upon. In one specimen both ischia are present in articulation with the two ilia, and both ilia in articulation with the sacrum. No specimen is known with the pubis in articulation with the ischium, and, as in all specimens of the pubis the posterior border is imperfect, there is a slight doubt as to the length of the pubic symphysis. It is pretty certainly short and probably as drawn. Am. Mus.

Fig. 14.—Left femur of *Moschops capensis*, Broom. Front view. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 15.—Left femur of *Moschops capensis*, Broom. Inner view. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 16.—Left femur of *Moschops capensis*, Broom. Back view. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 17.—Right fibula of *Moschops capensis*, Broom. Outer view. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 18.—Right tibia and fibula of *Moschops capensis*, Broom. Front view. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 19.—Right tibia of *Moschops capensis*, Broom. Inner and back view. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 20.—Atlas, axis, and intercentra of *Moschops capensis*, Broom. Side view. About  $\frac{1}{5}$  nat. size. The arch of the atlas is drawn in true side view and correctly orientated to the axis but moved a short distance forward to show zygapophysis and the odontoid of the axis. Am. Mus.

Fig. 21.—Left arch of the atlas of *Moschops capensis*, Broom. Viewed from the under side and showing the three facets, the front one for the occipital condyle, the lower one for the intercentrum and the upper and posterior one for the odontoid. Am. Mus.

Fig. 22.—Front view of the odontoid of *Moschops capensis*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 23.—Side view of a cervical vertebra, probably the 6th, of *Moschops capensis*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 24.—Sixth right cervical rib of *Moschognathus Whaitsi*, Broom. About  $\frac{1}{5}$  nat. size. *Moschognathus whaitsi* is a Dinocephalian closely allied to *Moschops*. Am. Mus.

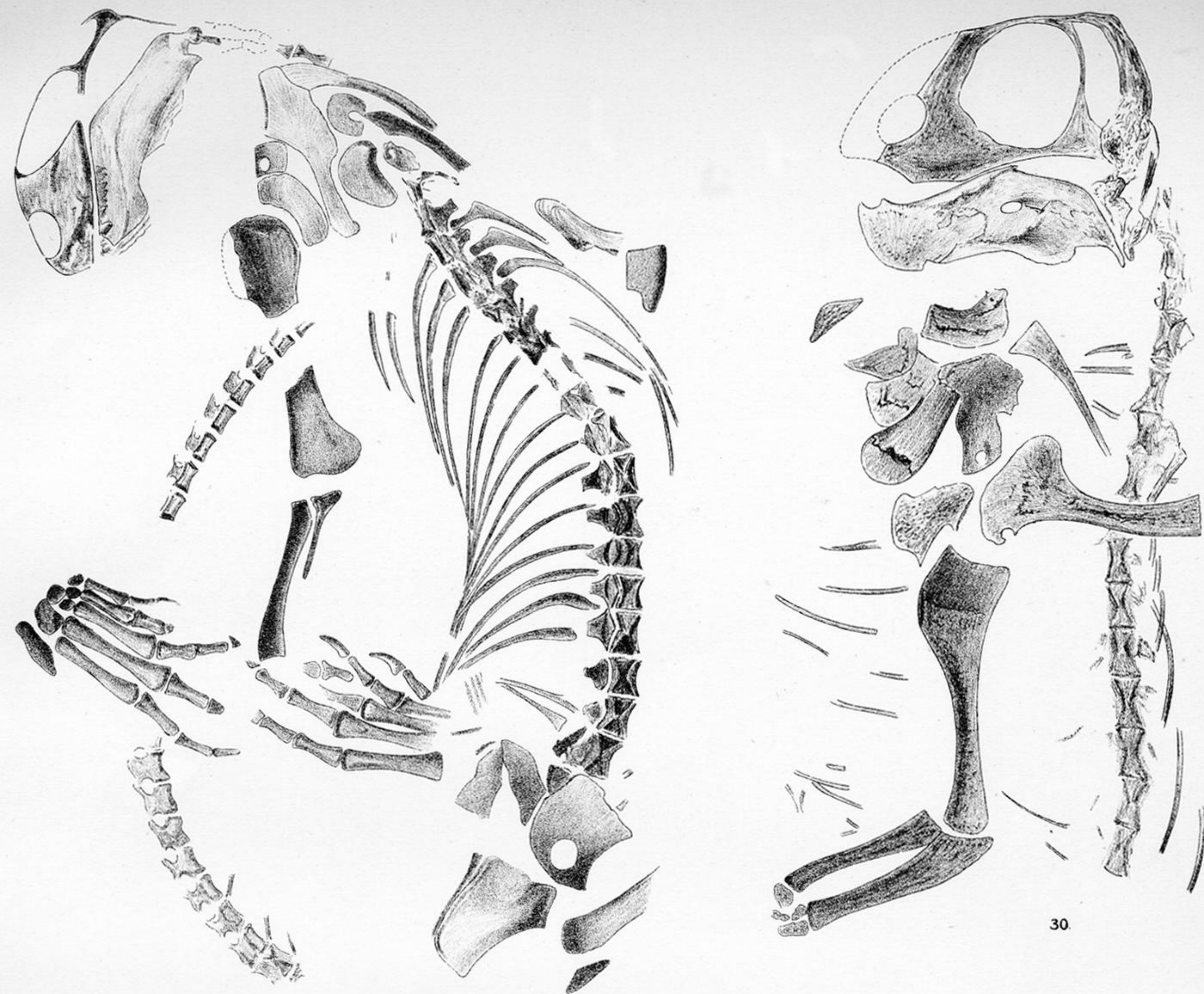
Fig. 25.—Back view of dorsal vertebra, probably 8th, of *Moschops capensis*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 26.—Side view of dorsal vertebra, probably 8th, of *Moschops capensis*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.

Fig. 27.—Front view of 5th dorsal rib of *Moschognathus Whaitsi*, Broom. About  $\frac{1}{5}$  nat. size. Am. Mus.

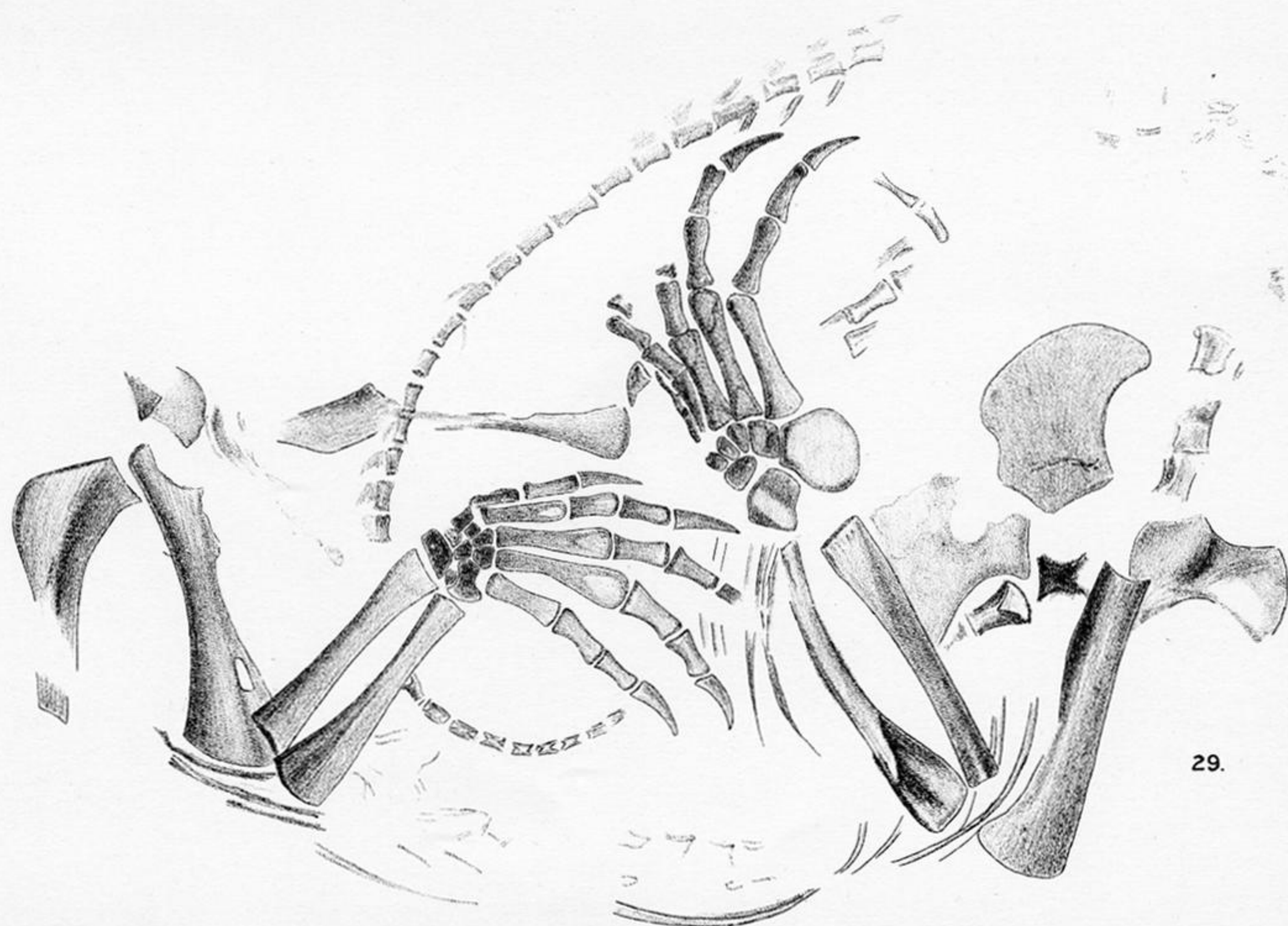
Fig. 27A.—Under side of sacrum of *Moschops capensis*, Broom. From an animal not quite fully grown. About  $\frac{1}{5}$  nat. size. Am. Mus.





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# DROMASAURIANS.

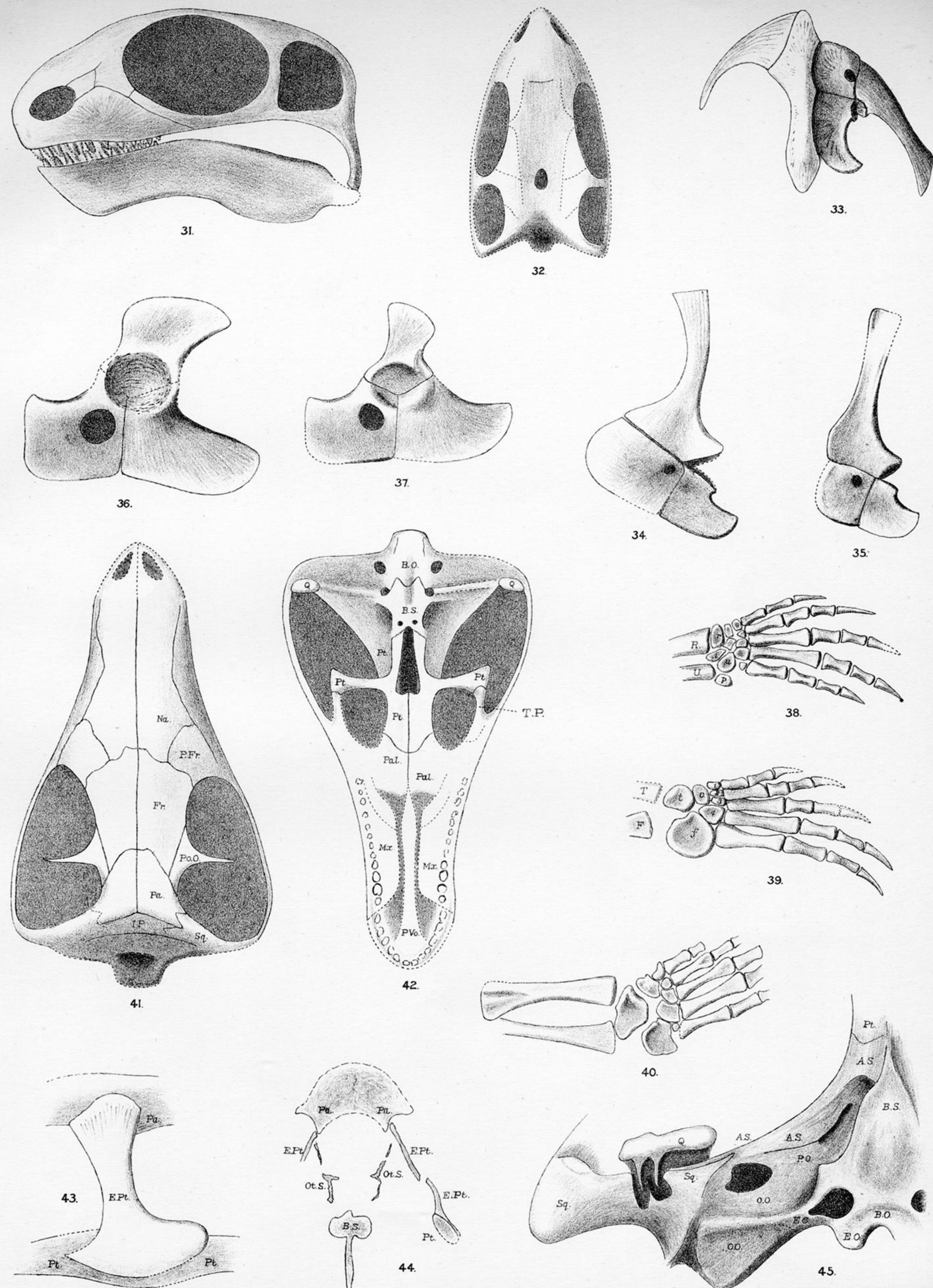
## PLATE 3.

Fig. 28.—Skeleton of *Galepus Jouberti*, Broom. Nat. size. The specimen is the almost perfect skeleton of a Dromasaurian. The bones are completely weathered out, but are represented by perfect casts. The greater part of the skeleton lies in one plane, but the skull is bent considerably to the side, and is represented in the drawing obliquely. The whole of the right femur, tibia and fibula are preserved and shown in a cross fracture, but cannot be represented in the drawing. The right pes is folded in under the tibia and fibula. Am. Mus.

Fig. 29.—Imperfect skeleton of *Galechirus Scholtzi*, Broom. Nat. size. The specimen consists of the natural casts of the left anterior and posterior limbs with much of the girdles, and other remains. The specimen is from the same locality as the type. Am. Mus.

Fig. 30.—Imperfect skeleton of *Galeops Whaitsi*, Broom.  $\frac{5}{6}$  nat. size. In this Dromasaurian skeleton most of the bones are broken across with the fracture of the stone. The skull is moderately complete, and the lower jaw almost perfect. Of the shoulder girdle there are preserved the complete right scapula and most of the right coracoid and precoracoid and the right clavicle. Much of the interclavicle is shown, with a large part of the left coracoid and precoracoid. The two other bones shown between the coracoid and the point of the lower jaw are portions of the head of the left humerus. The right humerus, radius, and ulna are nearly perfect. The vertebræ are not well preserved, but are seen to be notochordal. Am. Mus.



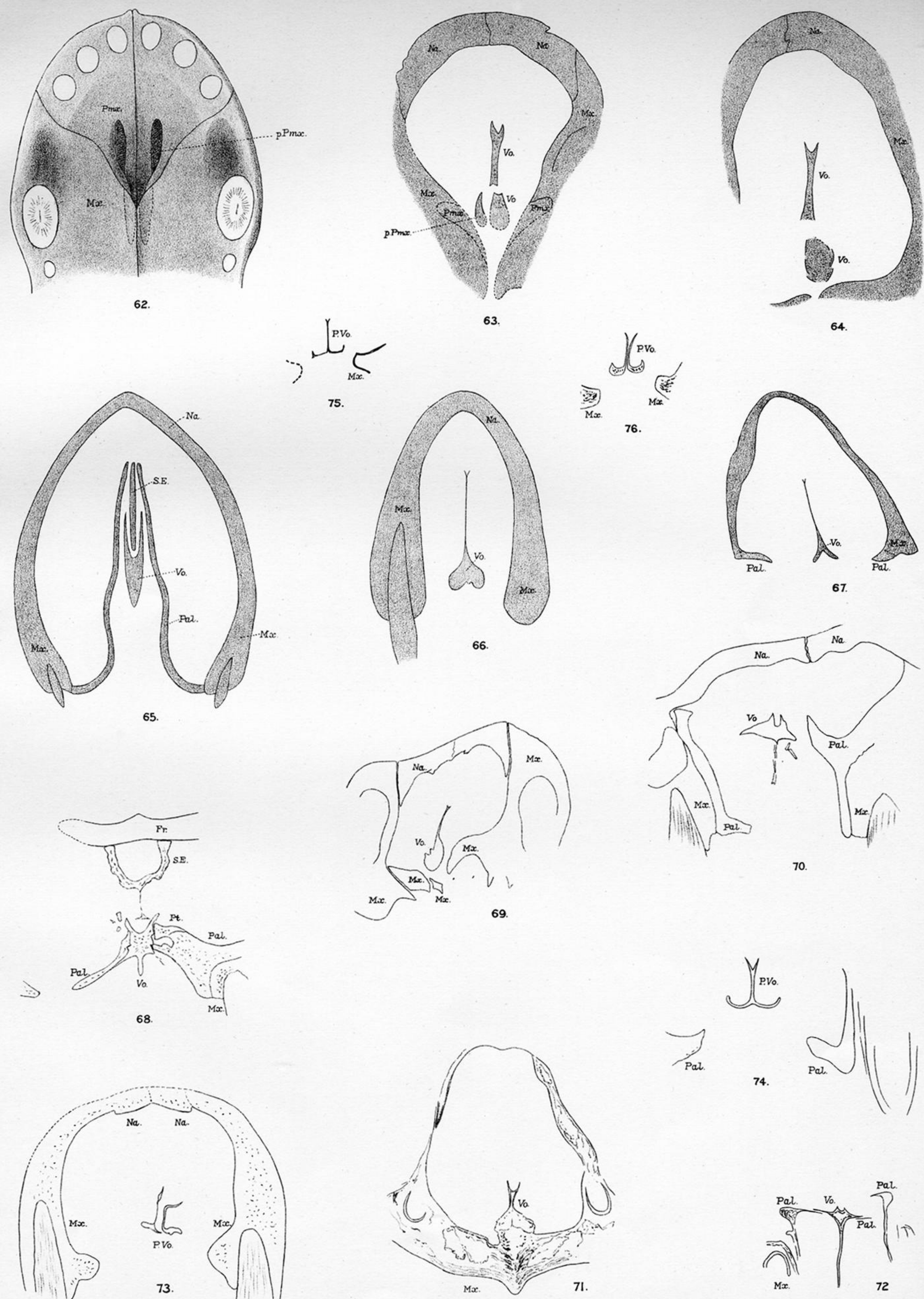


DETAILS OF DROMASAURIANS, THEROCEPHALIANS, AND CYNODONTS.

PLATE 4.

- Fig. 31.—Side view of the skull of *Galepus Jouberti*, Broom. About  $1\frac{1}{2}$  nat. size. Slightly restored. The specimen shows the casts of the inner sides of the bones. Am. Mus.
- Fig. 32.—Upper view of the skull of *Galepus Jouberti*, Broom. Nat. size. Slightly restored. Am. Mus.
- Fig. 33.—Pectoral girdle of *Galepus Jouberti*, Broom. Nat. size. Part of the interclavicle is represented as cut away to show the inner edges of the coracoid and precoracoid. Am. Mus.
- Fig. 34.—Right scapula, coracoid and precoracoid of *Galeops Whaitsi*, Broom. Nat. size. The drawing is a restoration from the remains seen in fig. 30. Am. Mus.
- Fig. 35.—Restoration of scapula, coracoid and precoracoid of *Galechirus Scholtzi*, Broom. Nat. size. The scapula is from the specimen shown in fig. 29, and the coracoid and precoracoid from the type specimen. Am. Mus.
- Fig. 36.—Left side of pelvis of *Galepus Jouberti*, Broom. Nat. size. Am. Mus.
- Fig. 37.—Restoration of the left side of pelvis of *Galechirus Scholtzi*, Broom. Nat. size. Am. Mus.
- Fig. 38.—Right manus of *Galechirus Scholtzi*, Broom. Nat. size. S.A. Mus., Capetown.
- Fig. 39.—Right pes of *Galechirus Scholtzi*, Broom. Nat. size. Am. Mus.
- Fig. 40.—Right pes of *Galesphyrus capensis*, Broom. Nat. size. S.A. Mus., Cape Town.
- Fig. 41.—Upper side of skull of *Scaloposaurus constrictus*, Owen.  $1\frac{1}{2}$  nat. size. The drawing is a slightly restored view of the British Museum type. B.M., R. 1723.
- Fig. 42.—Palate of *Scaloposaurus constrictus*, Owen.  $1\frac{1}{2}$  nat. size. The posterior half is drawn from the British Museum type; the front half is an attempted restoration founded on the palates of allied forms. B.M., R. 1723.
- Fig. 43.—Epipterygoid of *Scylacosaurus Sclateri*, Broom. Nat. size. B.M., R. 4055.
- Fig. 44.—Transverse section through the skull of *Bauria cynops*, Broom, immediately in front of the proötic. The basisphenoid shows the deep median keel. The epipterygoid is broken in the middle. Its lower end covers over the pterygoid. The brain case is partly walled by a feeble ossification which is probably homologous with the posterior part of the cartilaginous structure seen in the side of brain case in *Sphenodon* and lizards. As the epipterygoid is, in my opinion, the homologue of the mammalian alisphenoid this element requires a new name, and I have ventured to propose "otosphenoid." It is most probably the homologue also of the tænia clino-orbitalis of *Ornithorhynchus* and probably also of the so-called "alisphenoid" of the crocodile and bird. Am. Mus.
- Fig. 45.—The right side of the posterior part of the base of the skull of *Diademodon minor*, Broom. Nat. size. The specimen shows the lower part of the alisphenoid articulating with the pterygoid in front and the proötic behind. The quadrate shows the two processes which fit into grooves in the squamosal. As the quadrate is considerably displaced to the front without any fracturing of the elements it is manifest that considerable movement between the quadrate and squamosal was possible. B.M., R. 3587.



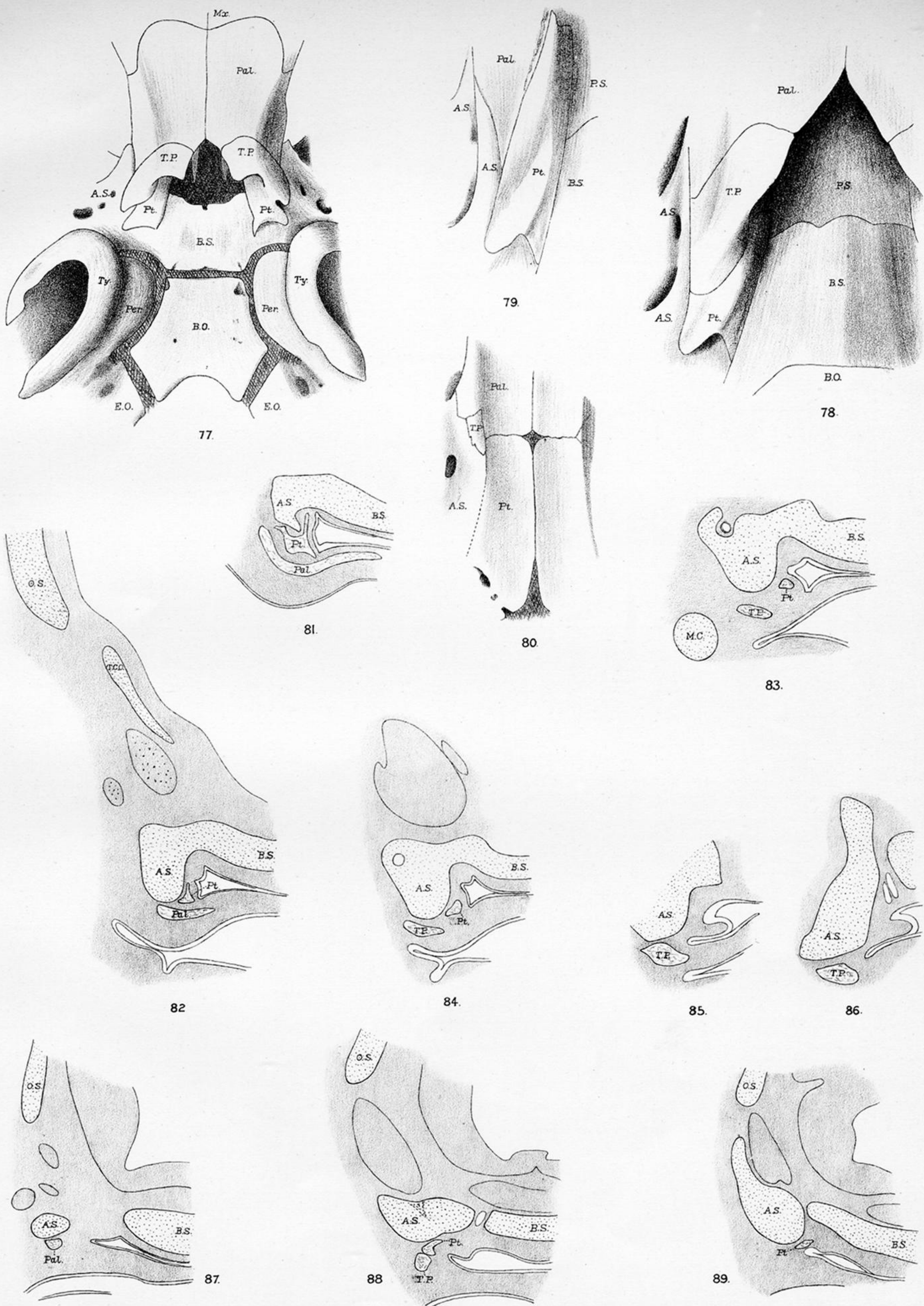


# PREVOMERS AND VOMER IN CARNIVOROUS THERAPSIDS.

## PLATE 6.

- Fig. 62.—Diagrammatic view of the front of the palate of *Lycognathus ferox*, Broom, a Cynodont reptile allied to *Cynognathus*. It will be seen there is a typically mammal-like palatine process to the premaxilla. Am. Mus.
- Fig. 63.—Transverse section across the snout of *Lycognathus ferox*, Broom. Though the vomer is represented in two parts it is moderately certain that this is due to a longitudinal fracture. The tip of one of the palatine processes of the premaxillæ is shown; the other ends anterior to the section. Am. Mus.
- Fig. 64.—Transverse section of the snout of *Lycognathus ferox*, Broom, posterior to that shown in fig. 63. The vomer here is also shown divided by a longitudinal fracture. Am. Mus.
- Fig. 65.—Semi-diagrammatic section across the snout of *Scylacognathus parvus*, Broom—a small Gorgonopsian. About twice nat. size. The actual specimen has the bones much crushed together and distorted, but there is practically no doubt about the elements or their relations. Am. Mus.
- Fig. 66.—Section across the anterior portion of the snout of *Scymnognathus tigriceps*, Broom and Haughton. About  $\frac{1}{2}$  nat. size. The supposed vomer is represented by an extremely delicate median plate, which at its base expands into a thick bone. Am. Mus.
- Fig. 67.—Section across the snout of the small but highly specialised Gorgonopsian *Ictidorhinus Martinsi*, Broom. About  $1\frac{1}{2}$  nat. size. The supposed vomer is not unlike that of *Scymnognathus tigriceps* seen in fig. 66. Am. Mus.
- Fig. 68.—Section through the posterior part of the supposed vomer of *Bauria cynops*, Broom. Nat. size. The specimen is a little crushed. The supposed vomer agrees with the prevomer of *Dicynodon* in its relations, as seen in fig. 49, so closely as to suggest that this is also a prevomer. On the other hand, the anterior part of the bone is fairly similar in its relations to the vomer of the *Diademodon*. A very short distance behind the plane of the section figured, the supposed vomer dips down below the pterygoids, which, meeting above it, completely remove it from further relations with the median cartilage elements. In its anterior part the "vomer" of *Bauria* thus resembles the higher Cynodonts; in its middle region it resembles the prevomer of *Dicynodon*; and in its posterior relations it resembles the "vomer" of the Gorgonopsians. Am. Mus.
- Fig. 69.—Section across the anterior part of the vomer in *Diademodon* sp. Nat. size. Am. Mus.
- Fig. 70.—Section across the posterior part of the vomer in *Diademodon* sp. Nat. size. Am. Mus.
- Fig. 71.—Section across the snout of *Sesamodon browni*, Broom. About  $1\frac{1}{2}$  nat. size. The bone has a loose cancellous texture and the elements in the palatal region are so ankylosed that it is impossible to see any sutures. The vomer can, however, readily be made out. Am. Mus.
- Fig. 72.—Section across the posterior part of the vomer in *Sesamodon browni*, Broom. About  $1\frac{1}{2}$  nat. size. Am. Mus.
- Fig. 73.—Section across the snout of the Therocephalian *Pristerognathus platyrhinus*, Broom. Nat. size. Here there are seen to be two prevomers very clearly separated one from the other. Am. Mus.
- Fig. 74.—Section across the prevomer of a small undescribed Therocephalian. About 4 times nat. size. The prevomers are fused but are interesting from the shape of their lower borders, which are scroll-like, doubtless to support an organ of Jacobson. The section is strikingly like a section through the dumb-bell bone of *Ornithorhynchus*. Am. Mus.
- Fig. 75.—Section across the prevomer of the small Therocephalian *Ictidognathus parvidens*, Broom. About twice nat. size. Am. Mus.
- Fig. 76.—Section across the prevomers of the small Therocephalian *Ictidognathus hemburyi*, Broom. About twice nat. size. The condition here is very similar to that seen in fig. 75, but the two prevomers are, though close together, quite distinct. Am. Mus.





PALATINE, TRANSPALATINE, AND PTERYGOID IN LIVING MAMMALS.

PLATE 7.

Fig. 77.—Posterior portion of the base of the skull of a large foetus of *Tatu novemcinctum*, Linn., head length 44 mm. On the right side the large transpalatine is seen quite distinct from the pterygoid lying dorsal to it. On the left side the transpalatine and pterygoid are, in part, anchylosed already. Am. Mus.

Fig. 78.—Portion of the base of the skull of a  $\frac{2}{3}$  grown *Tatu novemcinctum*, Linn., showing the later condition of the transpalatine. Am. Mus.

Fig. 79.—View of the same specimen with the transpalatine and part of the palatine removed, so as fully to expose the pterygoid.

Fig. 80.—Back of the palate of *Tamandua tetradactyla*. Slightly enlarged. The small transpalatine is seen on the right side. It varies greatly in different specimens; and in most it is so loosely attached that it is removed and lost when the skull is cleaned. Am. Mus.

Figs. 81-86.—Sections across the palato-ptyergoid region in a very young *Ornithorhynchus anatinus*, Shaw.

Fig. 81 shows the large palatine with the true pterygoid above it and very distinct from it.

Fig. 82 is a similar section a little farther back.

Fig. 83 shows the anterior end of the transpalatine and the posterior end of the pterygoid.

Fig. 84 a similar section to 83.

Figs. 85 and 86.—Sections across the more posterior regions of the transpalatine. Coll. Prof. J. P. Hill.

Figs. 87-89.—Sections across the palatine and pterygoid of a mammary foetus (25 mm.) of *Petrogale penicillata*.

Fig. 87 shows palatine near its posterior end.

Fig. 88 shows the pterygoid and the feebly ossified transpalatine.

Fig. 89 shows the pterygoid alone. Coll. Prof. J. P. Hill.