IX. *On the Skulls of Early Tertiary Suidæ, together with an Account of the Otic Region in some other Primitive Artiodactyla.*

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Stehlin in his classic monograph on the " Geschichte des Suiden-Gebisses "* has left little room for further descriptive work on the fossil forms of this group of mammals. I have followed his footsteps around most of the great palæontological collections of Europe, and have found no specimen of interest which has not received his careful consideration. All that I am proposing to do in this paper is to enquire anew into the relationships of some of the early members of the group. Stehlin's main interest, as the title of his work indicates, lay in the dentition. He dealt carefully with the skeletal characters, but he came to them last. By reversing the process, and making skull characters my starting point, I am confining myself to a very small corner of the field, because valuable skull fragments are extremely rare and very unevenly distributed among the known genera. The consideration of big, indisputable morphological differences is alone possible : differences such as those by which we are accustomed to separate into families and genera the animals living to-day. The fossil forms can by these be divided into several well-defined and more or less nearly related groups. Any attempt to trace the phylogenetic relationships of the species within these groups is impossible on skull characters alone.

There are certain families of early Tertiary Mammals which have often been regarded as allied or even ancestral to the Suidæ owing to the similarity of their dentition. In seeking what further evidence their skulls might afford, I have been led very far from the true Suidæ into a study of the skulls of all the early Tertiary Artiodactyls in which these are known. The inadequacy of dentitional characters alone to solve the confused problems of Artiodactyl relationships has become more and more evident to me. The basicranial characters of the skull on the other hand, as being the most complex and the most conservative, the least likely to respond quickly to environmental changes, appear to form one of the surest guides—just as they have been found to do in the lower vertebrates, where they have been so much more carefully studied.

The notes and illustrations in the second half of this paper are an attempt to make clear what are the peculiar characteristics of the basicranial region of the various animals

* H. G. Stehlin, 'Abhandlungen der Schweizerischen Paläontologischen Gesellschaft,' vols. 26, 27, 1899 to 1900.

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dealt with, how far they fundamentally resemble or differ from one another, and thus how far we are justified in placing them together or apart in classification—in other words, how far back we must expect to look for a common origin. This I hope will be a help in laying firmer foundations for future Artiodactyl classification, a re-study of all the other skeletal parts available being necessary before any new attempt is likely to be profitable.

I. Old and New World Suidæ: the Suinæ and the Dicotylinæ.

One of the most interesting stories in the history of the evolution of the Suidæ is that of the divergence of the peccaries of the New World from the true pigs of the Old World. Although essentially a pig-like animal in its general appearance and, from what travellers tell us, in its habits, the peccary of Central and South America of to-day has certain firmly established skeletal characters which divide it from all the Old World pigs, aberrant forms such as *Babirussa*, *Hydrochœrus*, and *Potamochœrus* included. This is often recognised by the separation of the peccaries into a second family, the Dicotylidæ, though it is more convenient to regard them as only of sub-family rank.*

A number of the characters in which the skull of *Dicotyles* differs from that of *Sus* seem to be in connection with one another and with the different ways in which these animals must be able to move their jaws. In all the Old World Suidæ the canine tusks are turned outwards and upwards. This provides the male with a powerful weapon, but it also permits great freedom of movement to the lower jaw, which can be swung both sideways, and backwards and forwards. The glenoid surface is flat and the parts around it arranged so as not to hinder these movements. In *Dicotyles* the upper canine tusks are directed vertically downwards and the lower canines fit tightly into a niche between the upper canines and the posterior incisors; up-and-down movement of the mandible alone is possible, and this is further enforced by the concave glenoid surface, which neatly grasps the cylindrical surface of the condyle. In two forms whose jaws move so differently, further differences are naturally to be found in the shape of all those parts of the skull intimately connected with the arrangement and mode of action of the jaw muscles. These differences are easy to see, but the complex mechanism of jaw action is not so easy to interpret with certainty. Certain suggestions may be tentatively offered however.

The paroccipital process of *Sus* is very long and directed downwards and forwards, while that of *Dicotyles* is a comparatively short stump directed downwards and *backwards*. In *Sus* (as I know from my own dissections) the *digastricus* is the only muscle which takes origin from the distal part of the paroccipital process: it passes from the tip of this process on to the inner surface of the mandible and lies in a plane which is practically parallel with that of the palate, so that its contraction would presumably draw the mandible

* See, for instance, Lydekker, 'Catalogue of the Ungulate Mammals in the British Museum (Natural History),' vol. 4, 1915.

backwards on the upper jaw. In *Dicotyles*, on the other hand, if the lower jaw be articulated, we see that the *digastricus*, in passing from the tip of the paroccipital process to its place of insertion on the mandible, must lie at an angle to the plane of the palate and be directed downwards as well as forwards. Furthermore it is a long muscle compared with that of *Sus* and probably comparatively slender and not very powerful. Since the glenoid surface of *Dicotyles* is concave and grinding movements practically impossible, such a muscle would be used to lower the mandible as it is in a carnivore.

In *Sus* the glenoid surface of the squamosal is practically on the same level as the base of the cranium. In *Dicotyles* the squamosal is prolonged downwards in this region until the glenoid surface lies far below the base of the cranium, almost at palate level. MATTHEW, when contrasting the jaw action of the Felidæ and the Machairodonts,* has shown how such a position of the glenoid may be correlated with a long and comparatively slender temporal muscle permitting the mouth to be opened wide and the canine tusks to have free play. It therefore seems not improbable that the depressed glenoid of *Dicotyles* is also associated with its downwardly directed canine tusks.

In grinding movements of the mammalian jaw the muscles which are usually of principal importance are the pterygoids. A comparison of the pterygoid regions and of the mandibles in the skulls of *Sus* and *Dicotyles* suggests that in the latter the internal pterygoid muscle is again weak and long and is used simply for closing the widely opened jaw rather than for grinding movements with the jaw nearly closed. For in *Dicotyles* the insertion of this muscle on the angle of the jaw is at a lower level compared with its origin in the pterygoid fossa than in *Sus*, firstly because of the low position of the glenoid, and secondly because the angle itself projects downwards in a big curve below the rest of the ventral border of the ramus. In *Sus* the high glenoid, the comparatively straight lower border of the mandible, and the projection of the pterygoid region outwards and downwards towards the angle, all tend towards making the internal pterygoid a shorter muscle than in *Dicotyles*, while its superior strength is attested by the size of the pterygoid fossa and the prominent, roughened area of origin immediately in front of this.

The depressed glenoid and outcurved angle of *Dicotyles* speak also for a longer masseter muscle. In *Sus* the jugal bone, deep but thin, passes right back along the side of the glenoid surface, projecting below it so as to conceal the mandibular condyle in the articulated skull. The posterior, deeper and shorter part of the masseter, used for pulling the mandible upwards and backwards at close quarters and powerfully pressing the teeth against one another, takes origin from the ventral and inner surface of the zygoma as far back as the very tip of the jugal. In *Dicotyles* the jugal has not a sharp ventral edge posteriorly as in *Sus* but a broad and flat one from which no doubt the masseter takes origin: but the hinder, backwardly-pulling part of this muscle must be much curtailed, for the jugal ends abruptly in front of the obliquely placed, concave glenoid surface, a buttress against its anterior slope. Further forwards on the ventral

* W. D. MATTHEW, "The Phylogeny of the Felidæ," 'Bull. Am. Mus. Nat. Hist.,' vol. 25, p. 289, 1910.

surface of the *Dicotyles* zygoma the masseter origin becomes very broad and important, and it extends on to the maxilla as far forwards as the first molar. Thus it seems that the masseter muscle also is longer in *Dicotyles* than in *Sus*, pulling upwards and slightly forwards in counteraction to the digastric and temporal, but still admitting a wide gape.

The Suinæ and Dicotylinæ of the early Tertiary.

A. OLIGOCENE.—In the Oligocene and Aquitanian we have skulls of only three genera showing undoubted relationship to the recent Suinæ and Dicotylinæ. These three genera are *Palæochœrus* of the European Aquitanian, *Doliochœrus* of the Phosphorites du Quercy, and *Perchœrus* of the North American Upper White River and John Day beds, which latter are usually considered as two successive stages corresponding to the earlier and later Aquitanian of Europe. Of these genera *Palæochœrus* is considered by STEHLIN as an ancestral stage in the evolution of the typical Suinæ, while American workers regard *Perchœrus** as a similar stage in the evolution of the Dicotylinæ. Of the skull of *Doliochœrus* there is only one rather poor fragment offering sufficient characters for comparison, and for this STEHLIN has suggested affinities with the Dicotylinæ.

I will first begin with a comparison of the skulls of *Palæochœrus* and *Perchœrus*, pointing out the characters which justify us in assigning them to the roots of two different stocks, and I will then return to *Doliochœrus* and show how what we have learnt from the other two genera helps us to confirm STEHLIN'S opinion of its affinities.

1. *Palæochœrus* and *Perchœrus*.

Of *Palæochœrus* there are two skulls in the Paris *Muséum National.* These are the two from St.-Gérand-le-Puy described and figured by FILHOL as "*Hyotherium Waterhousi.*"† One of these, that of an adult animal, might be thought from FILHOL'S figures to be a particularly complete and beautiful specimen, but in reality its snout and palate are modelled in plaster: there is a little bone in the premaxillary region and around the roots of the cheek teeth, and that is all. Furthermore the shape of the orbit is entirely unreliable and the occiput is broken into several jagged pieces held together by the rather indiscriminate use of a quantity of wax. Wax and plaster are grey, the colour of the bone, and it is difficult to be sure how much of the latter is really present. The other skull, that of a young animal, has been comparatively little tampered with, but it lacks the basiotic and pterygoid regions, the zygomatic bars of the squamosals, the supraoccipital, and part of the left wall of the brain-case.

* In which genus may be included MARSH'S "*Thinohyus*," COPE'S "*Bothriolabis*" and "*Chœnohyus*," SCOTT and OSBORN'S "*Hyotherium americanum*," see MATTHEW, 'Bull. Am. Mus. Nat. Hist.,' vol. 23, p. 216, 1907, and PEARSON, ditto, vol. 48, p. 61, 1923.

† H. FILHOL. "Étude des Mammifères fossiles de Saint-Gérand-le-Puy (Allier)," 'Ann. d. Sci. Géologiques," vol. 11, 1881.

In some ways more interesting than either of these are some fragments in the *Bayerische Staatssammlung* in Munich, from the Aquitanian of Tréteau, Allier, and from the Litorinellenkalk of Budenheim near Mainz. The pieces from Tréteau (Munich No. 1896. vii, 15) —a squamosal, part of the skull cap, part of a premaxilla, part of the zygoma—are in very beautiful condition, showing clearly every detail. The Budenheim fragment (Munich No. 1880, 11, 3) is in bad condition, but shows the shape of the bulla and its relation to the glenoid and postglenoid parts of the squamosal; with it are associated some displaced molars. For the comparison of this material with *Perchœrus*, I have had to rely on my own observations made four years ago on several very good skulls of that genus in the American Museum of Natural History.* These skulls come from the Protoceras beds of the White River Formation, Cheyenne River, South Dakota, and the Diceratherium beds of the John Day Formation, Oregon.

We have seen that the skull of *Dicotyles* is distinguished from that of *Sus* by certain characters apparently correlated with a different type of canine and a different method of mastication. The glenoid surface is much lower than the *basis cranii* and is concave instead of flat; the jugal is differently related to the glenoid. At first glance the glenoid regions of *Perchœrus* and *Palæochœrus* appear very similar to one another, they resemble one another so much more than either resembles that of a *Dicotyles* or that of a *Sus*, but a closer study shows that in *Perchœrus*, at any rate in some species (*e.g. P. rostratus*, American Museum No. 7395), there is already a tendency to lower the level of the glenoid, and its surface is already slightly concave.†

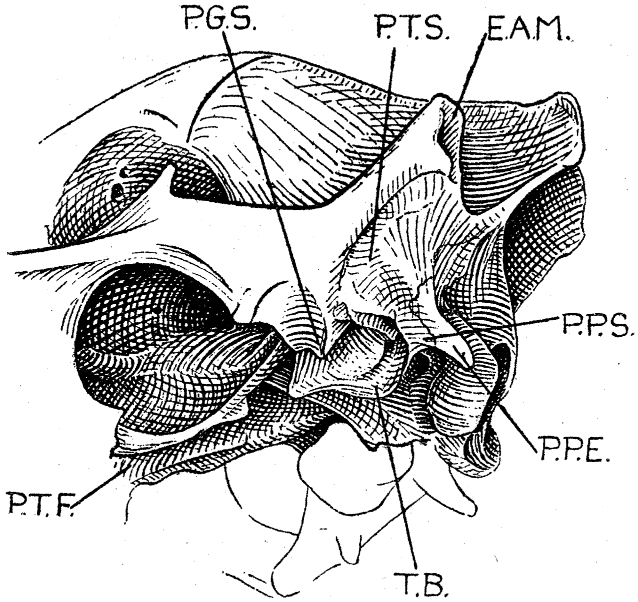
Let us examine in more detail what is happening. We may speak of three processes of the squamosal in the otic and post-otic region of the Suid skull. The first is the postglenoid process. The second may be called the post-tympanic process: it is a flat sheet of bone, which together with the first ensheathes the "neck" of the tympanic bone and the tubular external auditory meatus. The third, since it rests against the face of the paroccipital process of the exoccipital, may be termed the paroccipital process of the squamosal.

In *Dicotyles* the postglenoid process is very prominent. It is because its surface forms a continuous curve with the glenoid that the lower jaw is prevented from slipping backwards on the latter. Furthermore, owing to the lowering of the glenoid as a whole, this process projects a long way below the post-tympanic plate, which is applied to the back of it (see fig. 1). In *Perchœrus* the postglenoid process of the squamosal also projects below the post-tympanic process, but only for a very short distance since the lowering of the glenoid is only commencing. In the Suinæ, on the other hand, the postglenoid process has grown steadily less and less important, until in the recent forms (where the sutures can only be seen in a very young skull) it has practically disappeared. Its place has to some extent been taken by a compressed plate of the tympanic bone,

* Pearson, 'Bull. Am. Mus. Nat. Hist.,' vol. 48, p. 61, 1923.

† Pearson, *loc. cit.*, pp. 67, 78, 89, and figs. 13 and 9.

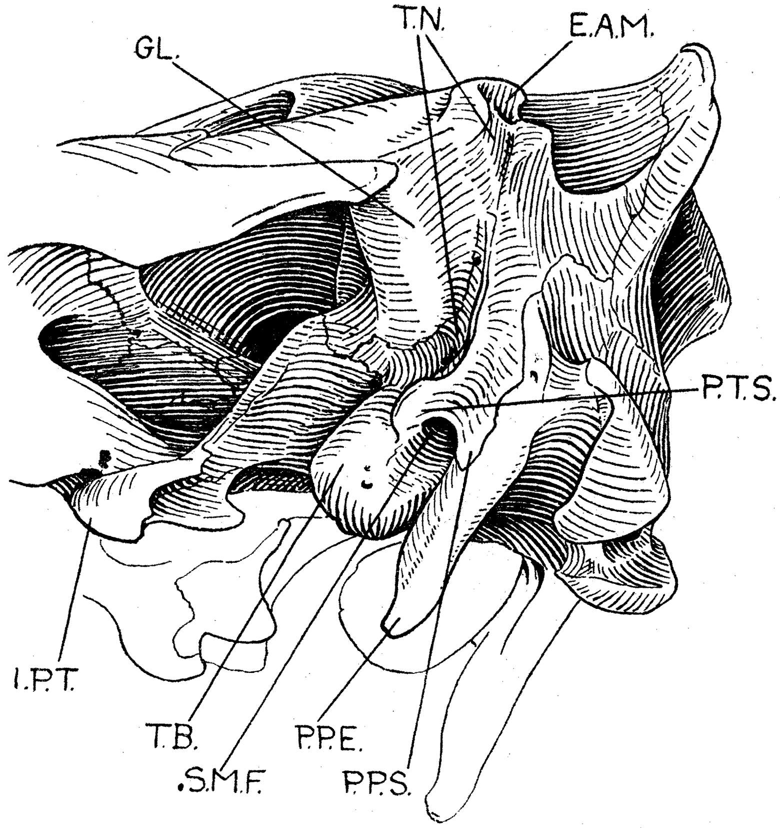
all that is left of the tympanic "neck," but the anterior surface of this, instead of curving down in continuity with the glenoid surface as in the Dicotylinæ, is separated from that surface by a triangular area which in the recent *Sus* faces posteriorly and is completely covered by the articular capsule. It is this arrangement of the squamosal



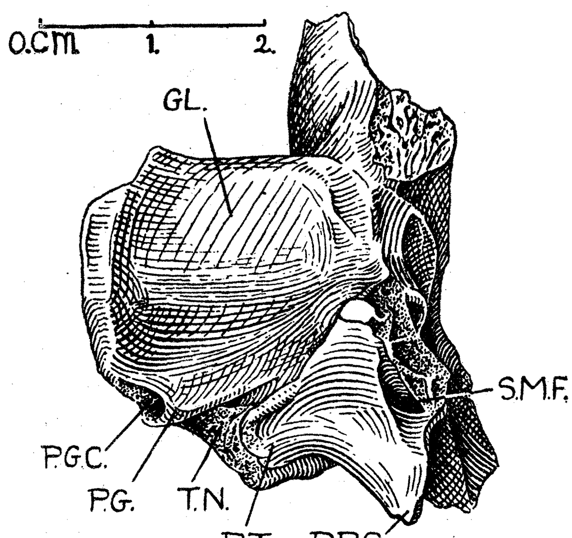
TEXT-FIG. 1.—Oblique view of otic and glenoid region of skull of *Dicotyles* (*Pecari tajacu*). E.A.M., opening of external auditory meatus; P.G.S., P.P.S., and P.T.S., postglenoid, paroccipital and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital; P.T.F., pterygoid fossa; T.B., tympanic bulla.

which permits the Old World forms to slide their lower jaw backwards, since instead of resistant bone behind the condyle there is only a thick mass of elastic tissue (see fig. 2). In *Palæochœrus*, where the tubular external auditory meatus is not so long nor directed so dorsally as in the modern Suinæ, this triangular area is not nearly so extensive, but is represented by a hollowed surface facing ventrally rather than posteriorly (fig. 3). The crest formed by the compressed tympanic neck is thus nearer to the glenoid surface; it is also more prominent,* while the true postglenoid process, pressed against the front of it, is much less reduced: hence that resemblance to *Perchœrus* which at first strikes us. The groove which may in the *Perchœrus* skull be seen curving upwards on to the outer surface of the zygoma from the postero-lateral corner of the glenoid represents the hollow which in *Palæochœrus* looks ventrally and separates the articular surface of the glenoid from the postglenoid; but owing to the descent of the glenoid in *Perchœrus* the relations of this groove to the surrounding parts are quite different,

* In *Palæochœrus* this crest is a continuous ridge extending along the whole length of the external auditory meatus from the bulla to the lateral surface of the zygoma. In recent Suinæ the medial end of this crest has disappeared, but the outer end is still faintly suggested in *Sus* and is well-marked in *Potamochœrus*.



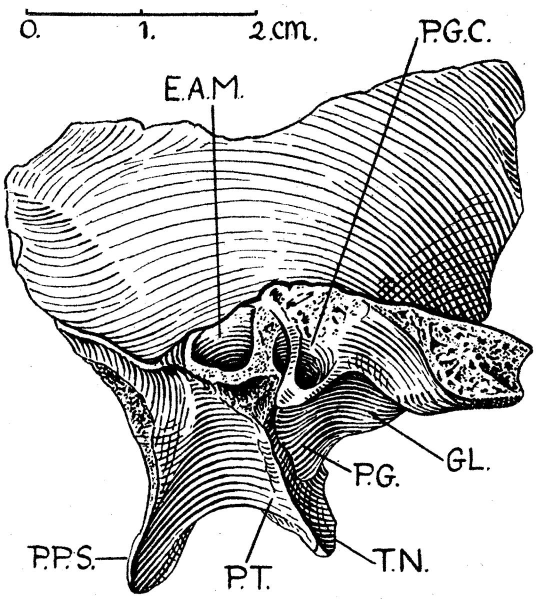
TEXT-FIG. 2.—Oblique view of otic and glenoid region of skull of *Sus scrofa*. E.A.M., opening of external auditory meatus; GL., glenoid surface; I.PT., tuberosity for internal pterygoid muscle; P.P.E., paroccipital process of exoccipital; P.P.S., paroccipital process of squamosal; P.T.S., post-tympanic process of squamosal; S.M.F., stylomastoid foramen; T.B., tympanic bulla; T.N., tympanic neck.



TEXT-FIG. 3.—Ventral view of right squamosal of *Palæochœrus* from Tréteau, Allier. (Bayerische Staats-sammlung, 1896, vii, 15.) GL., glenoid surface; P.G., postglenoid process; P.G.C., postglenoid canal; P.P.S., paroccipital process of squamosal; P.T., post-tympanic process of squamosal; S.M.F., stylomastoid foramen; T.N., tympanic neck.

and the glenoid surface, as in *Dicotyles*, smoothly curves down on to the face of the postglenoid process. In *Dicotyles* itself all traces of this groove have gone and the glenoid surface is marked off by a sharp ridge from the lateral surface of the zygoma.

In *Palæochœrus* there is no tendency to lower the glenoid. The post-tympanic plate of the squamosal, although it fails to meet the postglenoid and thus to conceal the tympanic "neck," yet extends down almost as far as the crest formed by the compression of that "neck," that is to say further than the postglenoid process—a contrast to the condition in *Perchœrus* (text-fig. 4).

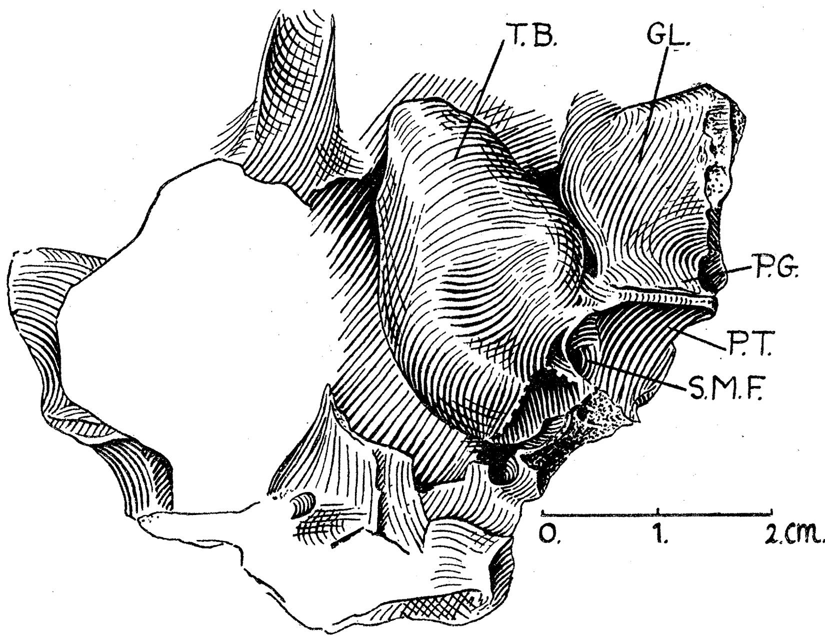


TEXT-FIG. 4.—Lateral view of right squamosal of *Palæochœrus* from Tréteau, Allier. (Bayerische Staatssammlung 1896, vii, 15.) E.A.M., opening of external auditory meatus; GL., glenoid surface; P.G., postglenoid process; P.G.C., postglenoid canal; P.P.S. and P.T., paroccipital and post-tympanic processes of squamosal; T.N., tympanic neck.

Paroccipital process.—The paroccipital process of the exoccipital is present in both the Paris skulls of *Palæochœrus*. The great length of this process in later Suinæ is already foreshadowed here, since its tip is well below the level of the exoccipital condyles—again in contrast to *Perchœrus*, where the tip is hardly if at all below that level. Similarly the paroccipital process of the squamosal, of which mention was made above, is already longer in *Palæochœrus* than in *Perchœrus*. A first glance, however, again gives the impression that these two genera are very like one another, for in *Palæochœrus* this little process of the squamosal is directed well backwards as it is in *Perchœrus*, so that there is a broad area between it and the post-tympanic process (text-fig. 4). This condition is typical of all Dicotylinæ and is very different from that in *Sus*, where the whole paroccipital process has a more forward direction and lies much closer to the post-tympanic plate.

Tympanic bulla.—Like the other parts of the skull the tympanic bullæ of these Oligocene genera have advanced only a little way along their two divergent paths. That of *Perchœrus* is the smaller and simpler; it is not yet filled with cancellous tissue, though that is foreshadowed by a honeycomb of delicate bony ridges on its inner surface. That of *Palæochœrus* is more definitely pear-shaped and relatively somewhat larger, being swollen out with cancellous bony tissue (which would thus seem to have developed independently in the two lines); the groove on its ventral surface, where the stylohyal with its ensheathing muscles rested, is probably connected with this increase in size (text-fig. 5). The Munich fragment from Budenheim, the only *Palæochœrus* I know of in which the bulla is preserved, is badly crushed, so that the angle which the long axis of the bulla made with the *basis cranii* cannot be certainly determined, but it appears to have been directed forwards in the primitive manner rather than obliquely downwards in the manner characteristic of recent Old World pigs.

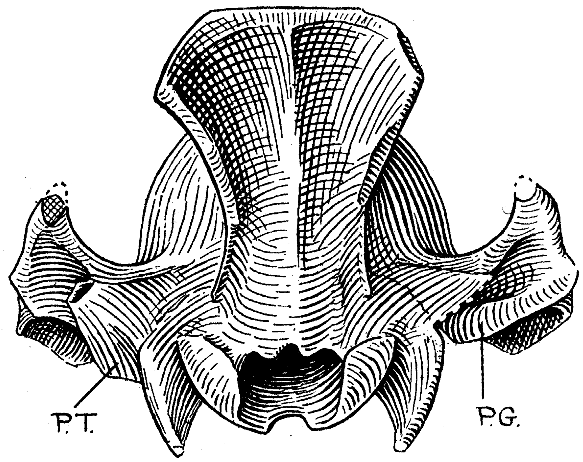
Two other small differences between *Perchœrus* and *Palæochœrus* may be mentioned before leaving the oto-glenoid region. First, that the narrow tunnel, or "postglenoid canal," which in *Perchœrus* pierces the postglenoid ridge along its whole length, is in



TEXT-FIG. 5.—Ventral view of fragment of otic region of *Palæochœrus* from the Litorinellenkalk of Budenheim bei Mainz. (Bayerische Staatssammlung, 1880, ii, 3.) GL., glenoid surface; P.G., postglenoid process; P.T., post-tympanic squamosal; S.M.F., stylomastoid foramen; T.B., tympanic bulla.

Palæochœrus restricted to the outer end of that ridge, there being no sign of its mesial opening near the bulla. This tunnel may still be seen in *Dicotyles*, but in *Sus* it has entirely disappeared. The second small difference is in connection with the stylomastoid foramen. *Perchœrus* agrees with *Palæochœrus* and the Old World pigs, and differs from *Dicotyles*, in retaining the primitive contact between the paroccipital process and the posterior end of the bulla. Owing to this contact the stylomastoid foramen is completely shut off from the *foramen lacerum posterius*, but whereas in *Palæochœrus*, as in more recent Suinæ, the groove into which the stylomastoid foramen opens is a straight, downwardly directed canal whose mouth is delimited laterally by a sharp ridge of squamosal, in *Perchœrus* we find the *Dicotyles*-like condition of a groove smoothly continuous with the squamosal surface lateral to it—*i.e.*, with that broad area of squamosal mentioned above as connecting post-tympanic process with paroccipital.

Occiput.—While *Palæochœrus* resembles the Suinæ in having an occiput with a flat top drawn out laterally into prominent angles (text-fig. 6), *Perchœrus* has the round-topped occiput characteristic of Dicotylinæ. *Palæochœrus* is peculiar in that the lateral occipital crest is not continuous with the dorsal edge of the zygomatic arch, thereby sharply separating temporal from occipital surfaces, as in *Perchœrus* and all recent Suinæ and Dicotylinæ. It agrees with *Perchœrus*, on the other hand, in the possession of a crest lying more posteriorly and bounding with its fellow a well-defined central occipital area ; this crest is continuous with the dorsal occipital crest above and ends freely below at a little distance above the occipital condyle. The remains of this crest, much reduced, may be seen in the skulls of some recent peccaries, but I have never observed it in any of the recent Suinæ.

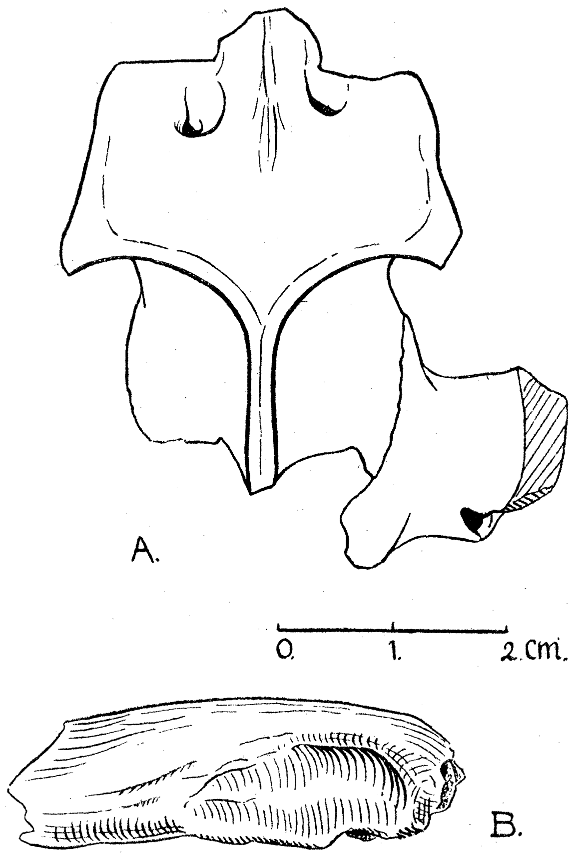


TEXT-FIG. 6.—Occiput of FILHOL'S figured skull of *Palæochœrus* from St.-Gérand-le-Puy, Allier. (Paris, Muséum National, slightly reconstructed.) About three-quarters actual size. P.G., postglenoid process ; P.T., post-tympanic process of squamosal (broken on right side).

Pterygoid region.—This region is not well preserved in any of the *Palæochœrus* material, but enough of it is present in the Paris skulls to show that it was no more powerfully developed in the Suinæ than it was in contemporary and later Dicotylinæ. The pterygoid fossa was not deep and there was no prominent roughened projection in front of this fossa for the origin of the internal pterygoid muscle.

Zygomatic and snout muscle areas.—The anterior end of the masseter origin is well marked on the zygomata of the Oligocene genera (text-fig. 7). There are no deep depressions for the snout muscles on the side of the face, but in the young Paris *Palæochœrus* a little ridge runs forwards from the upper edge of the masseter origin in the position of the better developed one which in *Sus* separates the origins of the *levator* and *depressor rostri* muscles.

Precanine niche.—STEHLIN has pointed out that the presence of a niche in the alveolar border in front of the upper canine, where the lower canine rests when the jaws are shut, is not confined to the Dicotylinæ. Among fossil forms, it is present in *Perchœrus* and in some species, though not all, of *Palæochœrus*. For instance, in the type specimen of *Palæochœrus typus* from St.-Gérand-le-Puy (in the Lyons Musée d'Histoire Naturelle) there is a diastema of about half a centimetre between the third upper incisor and the canine, and a slight depression here in the margin of the jaw, but nothing that could really be called a niche. Another skull from the Aquitanian of Allier, also labelled *Palæochœrus typus*, No. 3496*a* in the British Museum (Natural History), has quite a



TEXT-FIG. 7.—A, Part of skull roof and right squamosal; B, anterior end of right zygoma (ventro-lateral view), of *Palæochœrus* from Tréteau, Allier. (Bayerische Staatssammlung, 1896, vii, 15.)

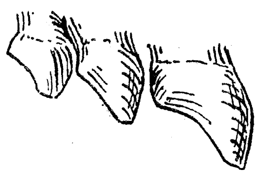
well defined niche, very much like that of *Dicotyles* on a small scale. This is what one might expect to find in view of the fact that certain Miocene Suinæ* possessed a niche as well developed as in *Dicotyles*, or even better.

Dentition.—STEHLIN has dealt with this so fully, that I will only give here a summary of the more important points.

Incisors.—In the upper jaw i^1 of *Palæochœrus* is already a much larger, stronger tooth

* *Hyotherium simorrense*, see below p. 405, and more particularly a small pig from the Chinese Hipparion fauna, of which I hope shortly to give an account in the "*Palæontologia Sinica.*"

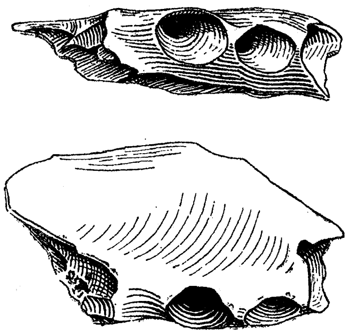
than i^2 and i^3 (figs. 8 and 9). In *Perchœrus* it is only slightly larger than i^2. i^3, the tooth which tends to disappear in both Old World and New World groups, is still well developed in both Oligocene genera. In the lower jaw of *Perchœrus* i_3 is already smaller in comparison with i_1 and i_2 than in *Palæochœrus*, just as in *Dicotyles* it is smaller than in *Sus*.



TEXT-FIG. 8.—Right incisors of FILHOL's figured skull of *Palæochœrus* ("*Hyotherium Waterhousi*") from St.-Gérand-le-Puy, Allier. Actual size.

Canines.—The upper canines of *Perchœrus* were already Dicotyline in shape and proportions: "prominent, downwardly-directed, flattened anteriorly and rounded or with a more or less sharp edge posteriorly."* Those of *Palæochœrus* have proportionately very much shorter, thicker crowns and are of the type whose gradual transition into the out-turned tusks of a typical wild boar has been traced in the Miocene of Europe. The lower canines of the two genera were also differentiated.

Cheek teeth.—There seem to be really no tangible differences between the cheek teeth of *Perchœrus* and *Palæochœrus*. The former as yet showed no tendency to molarisation of its premolars.



TEXT-FIG. 9.—Right premaxilla of *Palæochœrus* from Tréteau, Allier. (Bayerische Staatssammlung, 1896, vii, 15.) Actual size.

2. *Doliochœrus.*

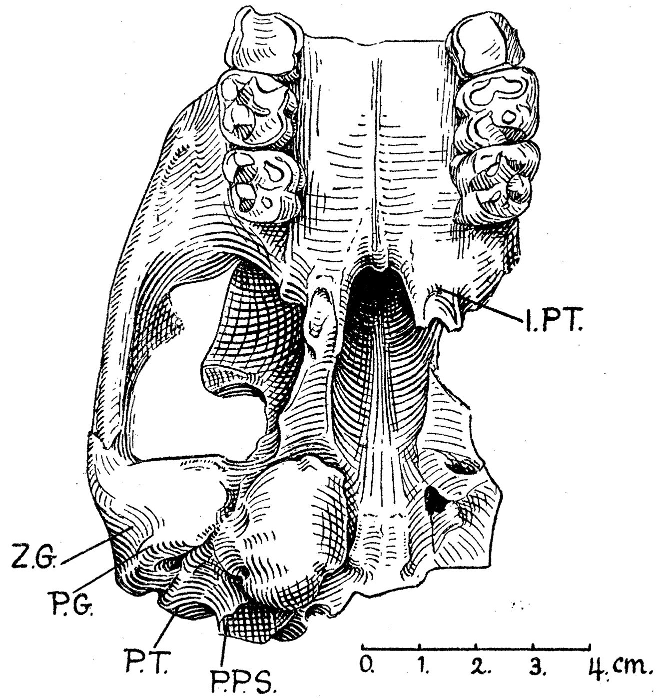
The only skull of *Doliochœrus* which lends itself to comparison with those of the two genera just discussed is FILHOL's type of *Doliochœrus quercyi*† from the Phosphorites du Quercy, now in the Muséum National, Paris. The anterior end of the skull is broken off in front of the first molar tooth. FILHOL gives a restoration of the hinder part, but, as may be seen in figs. 10 and 11 of this paper, the condyles and the paroccipital processes, besides most of the left oto-glenoid region, are in reality missing. On the right side however, we find a glenoid surface very considerably lower than that of the *basis cranii*, a postglenoid process projecting correspondingly below the post-tympanic process, a complete concealment of the tympanic "neck" by the meeting below it of these two processes,‡ and a broad groove curling upward from the postero-lateral corner of the glenoid on to the outer surface of the zygoma. All these characters seem to me to relate *Doliochœrus* rather with *Perchœrus* and the peccaries than with *Palæochœrus* and the true

* H. S. PEARSON, "Some skulls of *Perchœrus* (*Thinohyus*) from the White River and JOHN DAY Formations," 'Bull. Am. Mus. Nat. Hist.,' vol. 48, 1923, p. 72.

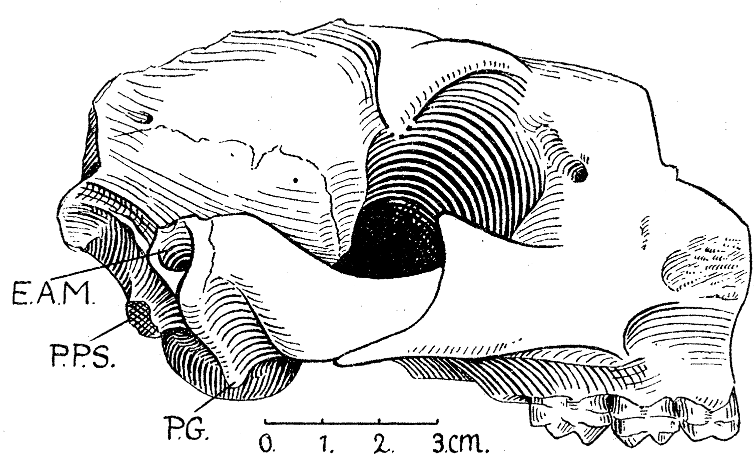
† H. FILHOL. "Observations relatives à des Mammifères Fossiles Nouveaux provenant des Dépôts de Phosphate de Chaux du Quercy," 'Bull. Soc. Sci. Phys. Nat. Toulouse,' vol. 5, 1882.

‡ What is possibly a small piece of the tympanic "neck" appears quite laterally at the opening of the external auditory meatus. The bone is injured here, however, so that its exact structure is unclear.

pigs. Further than this, I think that if the figures of *Doliochœrus* given in this paper be compared with those of *Perchœrus* in my paper of 1923, a very close affinity between these two genera must be admitted, especially striking when it is remembered that the American skulls come not only from a different continent but probably from later deposits : it is to be regretted, however, that the earlier figures do not show as clearly as



TEXT-FIG. 10.—Ventral view of FILHOL's type skull of *Doliochœrus quercyi* from the Phosphorites du Quercy (Paris, Muséum National). I.P.T., tuberosity for internal pterygoid muscle ; P.G., postglenoid process ; P.P.S., paroccipital, and P.T., post-tympanic processes of squamosal ; Z.G., groove on lateral surface of zygoma.



TEXT-FIG. 11.—Lateral view of FILHOL's type skull of *Doliochœrus quercyi* from the Phosphorites du Quercy. (Paris, Muséum National.) E.A.M., opening of external auditory meatus ; P.G. postglenoid, and P.P.S., paroccipital processes of squamosal.

I could wish now those characters of the oto-glenoid region that I have been laying stress on. The post-tympanic process of the squamosal seems in *Doliochœrus* to be even shorter in relation to the postglenoid process, and the entrance to the postglenoid canal seems rather differently placed. Tympanohyal pit and stylomastoid foramen correspond well, the latter truly Dicotyline in its lack of sharp lateral boundary. The crest which in *Perchœrus* joins the dorsal edge of the zygoma with the lateral occipital crest is in *Doliochœrus* possibly not so strongly developed, but the crest which lies behind and median to this on the occiput, although broken above, appears ventrally as a powerful freely-ending projection of the *Perchœrus* type.

The pterygoid region is also very similar to that of *Perchœrus*, except that in front of the pterygoid fossa there is a well defined roughened area for the anterior fibres of the internal pterygoid muscle—rather a curious feature, since such an area, present in *Sus*, seems to be lacking in both *Perchœrus* and *Palæochœrus*.

On the ventral edge of the zygoma the masseter origin is well marked. As in *Perchœrus pristinus*, but not in *P. rostratus*, the jugal reaches back almost to the glenoid.

None of the measurements which it has been possible to take on this imperfect skull fall very far outside the possible range of variation in the known species of *Perchœrus*. The distance between the condylar foramina may be estimated as about 20 mm., rather smaller than in any of the adult skulls of *Perchœrus* in New York. The length of the tympanic bulla is 27 mm., a millimetre or two longer than in the longest New York bulla—a difference quite insignificant in view of the great variability of this measurement. The width of the palate would seem well within the *Perchœrus* range. As regards dental measurements, the combined length of the three molar teeth is only 35 mm., as contrasted with the series 41, 43·5, 45 and 48 mm. given by the *Perchœrus* skulls in New York. This seems to be partly because all three teeth are shorter in *Doliochœrus*, and partly because the third molar has so short a talon that it can hardly be called more than a broad posterior cingulum. Personally I do not think that these measurements can be regarded as of great significance; we know too inexactly how much variation to expect between races of the same genus living in more or less widely separated localities. There were smaller species of *Perchœrus* living in North America at the same time as those represented by the skulls in the American Museum—isolated teeth in New York and at least one skull fragment in Princeton bear witness to this—and some of these I think would be found to have as poorly developed a talon to their third upper molars as *Doliochœrus* itself. The important point is, that the only skull of a true Suine that we have from the European Phosphorites du Quercy is that of an animal practically identical with the American Oligocene Dicotylinæ, at that date already divergent from the rival European sub-family of Suinæ.

Note on the existence of a genus Propalæochœrus.

STEHLIN believed *Doliochœrus* to be Dicotyline. Other remains from European horizons earlier than the Aquitanian he believed to belong to representatives of the Suine group, the ancestors of *Palæochœrus* of the Aquitanian. These he proposed to call *Propalæochœrus*. As far as the Phosphorites du Quercy are concerned, it does not seem possible from existing material to prove that *Propalæochœrus* existed side by side with *Doliochœrus*. I know of no canine from these deposits, and cheek teeth afford no evidence. That a primitive Suine existed in Stampian times, however, seems evident from a palate and mandible from the Sables de Marseille of St. André, now in the Faculté des Sciences in Lyons, the lower canine of which is of undisputable Suine type.

B. *Miocene.*—It is not until the Middle Miocene that we can again get information about the skulls of the Suidæ of the Old World. These are now represented by three new genera: *Hyotherium, Listriodon and Chœrotherium. Chœrotherium* is apparently a new arrival in Europe. *Listriodon* was already established there in the Burdigalian,* *Hyotherium* would seem to be the direct descendent of *Palæochœrus*,†—there are numerous teeth from the Burdigalian locality Baigneaux which could equally well be assigned to either genus, while in other localities of the same age *Palæochœrus* is represented by the very small species *P. aureliensis*.

3. *Hyotherium.*

Of the species *Hyotherium Sœmmeringi,* which from its dental characters appears to have conserved most nearly the characters of *Palæochœrus,* I have been unable to find any skull material of the slightest value. Of the aberrant *Hyotherium simorrense,* however, there are, in the Stuttgart Naturaliensammlung, the fragments of two skulls from the Vindobonian of Steinheim. *Hyotherium simorrense,* it will be remembered, is the pig in which the third and fourth premolars are strikingly enlarged in both jaws. Owing to this enlargement of its premolars and to other dental characters, which, as STEHLIN had already pointed out in 1899,‡ would seem to ally it with the curious *Tetraconodon* of the Indian Siwaliks, PILGRIM has recently§ placed this pig in the new genus *Conohyus*, and regards it as on an entirely different line of development from *Palæochœrus* and *Hyotherium Sœmmeringi.*

In one of the two Stuttgart fragments (bearing the numbers 12770 and Ph. 1910) the parietal crests are only indicated by faint ridges which meet one another posteriorly, while the permanent molars are still uncut and the deciduous molars show no signs of wear. It therefore clearly belonged to a very young individual. Of this skull all the occipital bones are missing, the snout is broken short in front of the second deciduous molar, and all that remains is badly crushed. The mandible is also only a fragment. Nevertheless, the affinities of this specimen with the recent Suinæ and with *Palæochœrus* are clearly recognisable, and many interesting advances on the latter genus may

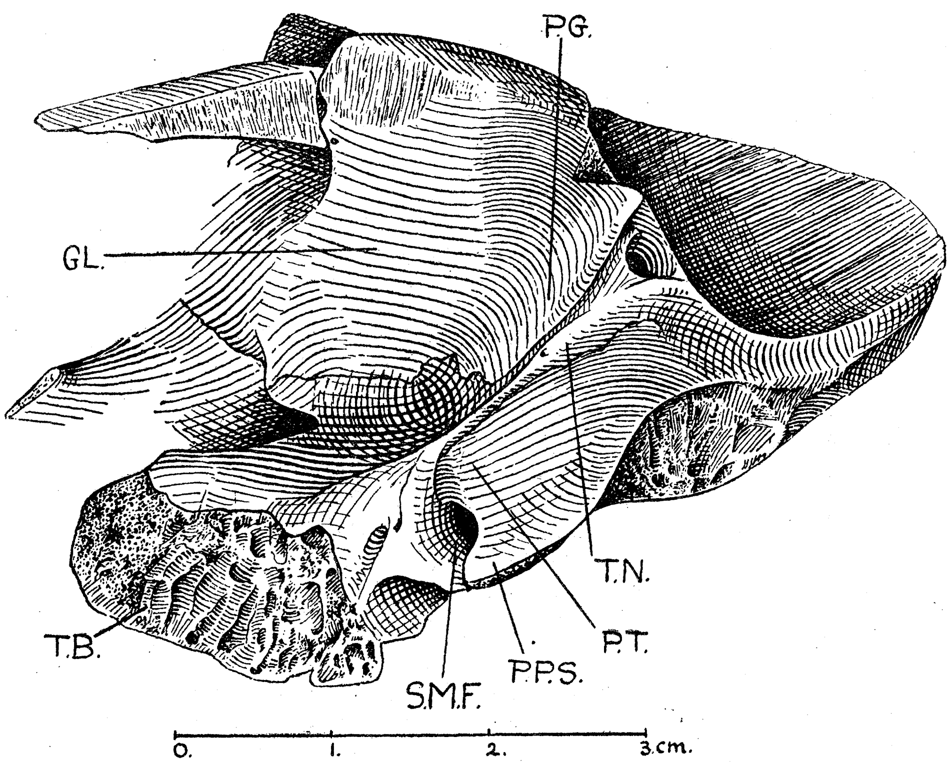
* STEHLIN, "Suiden-Gebiss," p. 83 ff.

† *Ibid., loc. div.*

‡ H. G. STEHLIN, "Suiden-Gebiss," p. 52.

§ G. E. PILGRIM, "The Fossil Suidæ of India," 'Palæontologia Indica,' New Series, vol. 8, 4, 1926.

be detected. Owing to the extreme youth of the animal the sutures of the postglenoid region are especially well shown, and the postglenoid and post-tympanic processes of the squamosal can be clearly distinguished from the compressed crest of tympanic "neck" which projects between them (see fig. 12). We find that the postglenoid process has practically disappeared and that the post-tympanic plate is reduced in width and has only a very short paroccipital process, the mouth of the stylomastoid groove at the same time having become narrower. The tympanic bullæ, although crushed out of recognisable shape, evidently projected more than in *Palæochœrus*. The

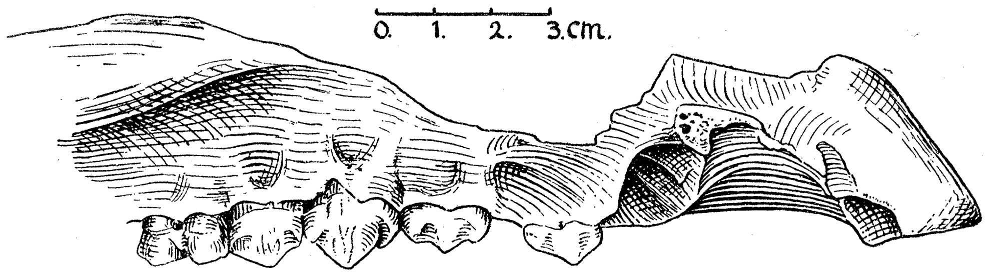


TEXT-FIG. 12.—Oblique view of otic and glenoid region of young skull of *Hyotherium simorrense* (*Conohyus simorrensis*) from Steinheim. (Stuttgart Naturaliensammlung, 12770, Ph. 1910.) Scale approximately as given. GL., glenoid surface; P.G., P.P.S., and P.T., postglenoid, paroccipital and post-tympanic process of squamosal; S.M.F., stylomastoid foramen; T.B., tympanic bulla; T.N., tympanic neck.

glenoid surface is roughened along its lateral border, suggesting that the jugal rested here. The muscle area anterior to the pterygoid fossa, the origin of the anterior part of the internal pterygoid muscle, is well marked.

These are all advances in the direction of the recent Suinæ of the Old World—be it *Sus*, *Potamochœrus*, *Phacochœrus*, *Hydrochœrus* or *Babirussa*—and even if *Conohyus simorrensis* is not in the *direct* line of ancestry of any of these recent genera, it is certain that all of them must have passed through a similar stage in the evolution of their paroccipital, otic, glenoid and pterygoid characters.

The other fragment in Stuttgart is that which FRAAS described in 1885 under the name of "*Chœropotamus Steinheimensis*."* It is the palate of an adult skull in which the canines and incisors are represented only by their empty sockets (fig. 13). It shows the interesting point, to which STEHLIN has already drawn attention,† that in front of



TEXT-FIG. 13.—Lateral view of FRAAS' figured palate of *Hyotherium simorrense* (*Conohyus simorrensis*) from Steinheim. (Stuttgart Naturaliensammlung.)

the upper canine there is a long diastema, and that the alveolar border here curves upwards to form a niche for the lower canine like that which I have described above in some species of *Palæochœrus* (p. 399) only on a much larger scale.

4. *Listriodon*.

The skull of *Listriodon splendens* in Paris, described and figured by FILHOL,‡ is except for the teeth very poorly preserved. The structure of its otic region and occiput, as far as it can be interpreted, indicates that it belongs to the true Old World Suine stock. This I gather to have been also the opinion of STEHLIN.§

5. *Chœrotherium*.

Chœrotherium is represented in the Vindobonian by at least two species, *C. sansaniense* from Sansan and the smaller *C. pygmæum* from Steinheim. Of the former there is the skull now in Paris which FILHOL figured in 1891,|| of the latter there are in Stuttgart the young skull with milk dentition figured by FRAAS in 1885¶ under the name of "*Cebochœrus suillus*," and a less complete fragment of an adult skull which has been added to the same collection later.

The young skull of *Chœrotherium pygmæum*, which has a matrix of very soft sand, is badly broken and the parts are displaced in relation to one another. It is possible, however, to interpret most of the fragments, and with the kind permission of

* O. FRAAS "Beiträge z. Fauna von Steinheim," 'Jahreshefte des Ver. f. vaterl. Naturk. in Württemberg,' Jahrg. 41, pp. 313-326, 1885.

† STEHLIN "Suiden-Gebiss," p. 271, etc.

‡ FILHOL, "Études sur les Mammifères Fossiles de Sansan," 'Ann. d. Sci. Géol.,' vol. 21, 1891.

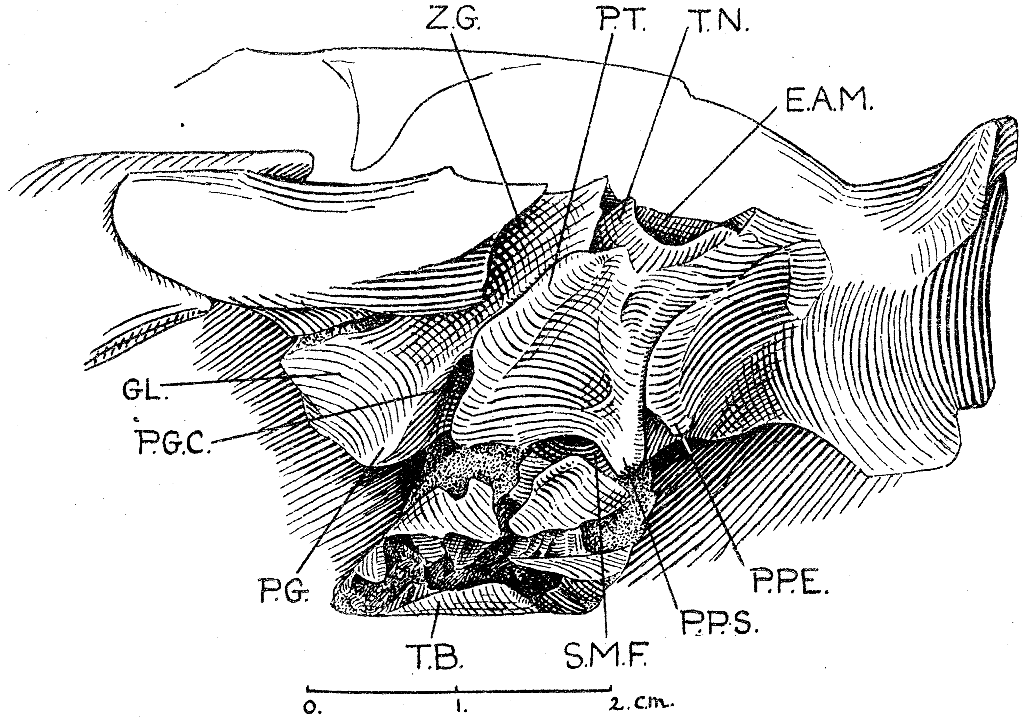
§ STEHLIN, "Suiden-Gebiss."

|| FILHOL, "Études sur les Mammifères Fossiles de Sansan," 'Ann. d. Sci. Géol.,' vol. 21, 1891.

¶ FRAAS, "Beiträge z. Fauna von Steinheim," 'Jahreshefte des Ver. f. vaterl. Naturk. in Württemberg.' Jahrg. 41, 1885.

Dr. BERCKHEMER, I was able to clean away some more of the matrix and bring to light a good deal that had hitherto been hidden (text-fig. 14).

The left glenoid appears to be very much in its right position with regard to the *basis cranii*—a position much ventral to the latter. There is a well defined little postglenoid process standing up at the back of the postero-internal corner of the glenoid surface, making with the latter a smooth continuous concave curve, and projecting well ventrally to the post-tympanic process. Just in front of the glenoid the zygoma is broken, but the fragments are still there, a little out of place but complete. It can be seen that a

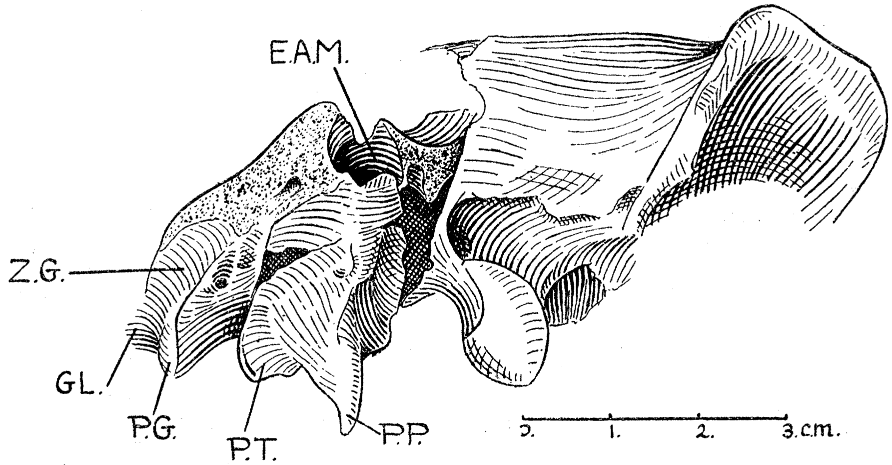


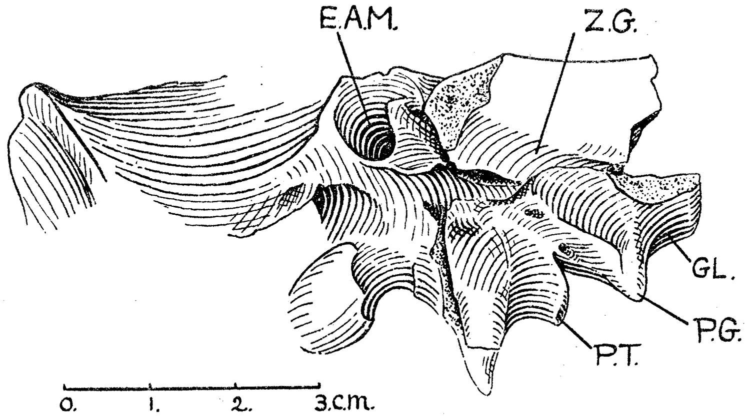
TEXT-FIG. 14.—Oblique lateral view of otic and glenoid region of FRAAS' figured skull of *Chœrotherium pygmœum* from Steinheim. (Stuttgart Naturaliensammlung.) E.A.M., external auditory meatus; GL., glenoid surface; P.G., postglenoid, P.P.S., paroccipital, and P.T., post-tympanic processes of squamosal; P.G.C., postglenoid canal; P.P.E., paroccipital process of exoccipital; S.M.F., stylomastoid foramen; T.B., tympanic bulla; T.N., tympanic neck; Z.G., groove on lateral surface of zygoma.

shallow groove led upwards from the postero-external corner of the glenoid surface on to the outer surface of the zygoma. It can also be seen that the jugal ended ventrally in a blunt point just anterior to the glenoid surface. Immediately behind the postglenoid process there is an open channel separating it from the post-tympanic process, but more laterally the ventral edge of the post-tympanic curls forwards and encloses this channel to form a typical postglenoid canal. The latter opens above close in front of the opening of the external auditory meatus, surrounding which can be seen the distal end of the tympanic "neck:" between this region and the bulla the "neck" is completely hidden between the glenoid and the post-tympanic squamosal. The squamosal has a well developed paroccipital process, but of the corresponding process of the exoccipital only a small piece remains and the suture between the two is widely open. The tympanic bulla is badly squashed but was evidently pointed anteriorly and filled with cancellous bony tissue.

In view of what I have tried to demonstrate concerning the fundamental differences between pigs and peccaries, are not these characters of *Chœrotherium* peculiarly significant ? To my mind at least, the possibility that *Chœrotherium* is Dicotyline rather than Suine is at once suggested ; but let us first see what the Paris skull has to show us of these same characteristics and then proceed to examine the other evidence.

In the Paris skull of *Chœrotherium sansaniense** the glenoid surface and the postglenoid process are similar in shape and position to those in *C. pygmæum* (text-figs. 15 and 16).



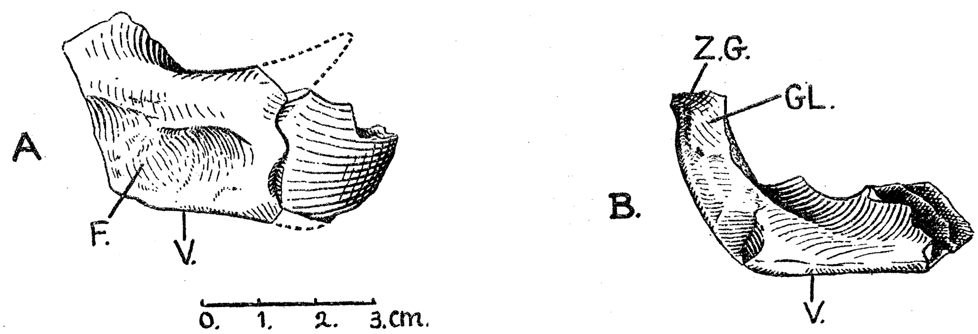


TEXT-FIGS. 15 and 16.—Right and left lateral views of otic and glenoid region of FILHOL's figured skull of *Chœrotherium sansaniense* from *Sansan*. (Paris, Muséum National.) Tip of paroccipital process reconstructed in fig. 16. E.A.M., external auditory meatus ; GL., glenoid surface ; P.G., and P.T., postglenoid and post-tympanic processes of squamosal ; P.P., paroccipital process ; Z.G., groove on lateral surface of zygoma.

* FILHOL's drawing of this skull ("Études sur les Mammifères Fossiles de Sansan," Paris 1891.—Plate xx.) is as usual much too good to be true. The skull is extremely crushed and broken, and affords no evidence for the outline of the parietal crest and for the peak of squamosal over the external auditory meatus.

A similar groove runs upwards from the postero-external corner of the glenoid surface on to the lateral surface of the zygoma. The post-tympanic plate of the squamosal has the same free ventral edge; that the lateral edge of the plate does not overlap the postglenoid region as much as in the Steinheim skull is probably because in the adult animal the glenoid has descended further. Probably also, it is for similar reasons that the postglenoid canal of the Steinheim skull is not represented here, since it is absent in the fragment of an adult skull of *C. pygmæum* in the Stuttgart collection—indeed this adult Steinheim skull resembles the Sansan skull in several small details in this region where the young skull differs.

STEHLIN has referred to the peculiar shape of the zygomatic arch of *C. sansaniense.* This is not like that of any other member of the Suidæ in which it is known. The anterior portion has a very broad edge dorsally, a sharp edge ventrally, and a shallow fossa occupying most of its external surface (see fig. 17). Unfortunately, in both the



TEXT-FIG. 17.—Fragment of left zygoma of FILHOL'S figured skull of *Chœrotherium sansaniense* from Sansan. (Paris, Muséum National.) A, lateral view; B, ventral view. F., shallow fossa; GL., edge of glenoid surface; V., sharp ventral edge; ZG., extremity of groove that runs up on to lateral surface of zygoma.

Paris and the Stuttgart skull this portion of the zygoma is broken away from the skull, on to which its anterior end can no longer be made to fit. Thus it does not seem possible to determine whether the shallow fossa was for a backward extension of the *levator rostri* muscle, usually confined to the side of the snout, or whether it was for an upward extension of the masseter. In *Sus* the ventral edge of the zygoma is narrow and the masseter does not extend upwards on to its outer surface. In *Dicotyles* and all the Oligocene genera there is a broad surface for the masseter towards the ventral border of the anterior end of the zygoma (see text-fig. 7, B); it faces a little outwards, but mostly downwards, thus making the ventral edge of the zygoma here look very thick in contrast to that of *Sus*. In *Chœrotherium* it is just possible that the shallow fossa in question is a very broad masseter surface facing entirely outwards and not at all downwards. Whether much stress need be laid on this peculiarity I think is doubtful, especially since a comparison of the two sub-genera of *Dicotyles* (*Pecari* and *Tayassu*) shows how different this part of the skull may be in two not very distantly related forms. In the Steinheim skull the fossa is much less deeply marked, as might be expected in so young an animal, but otherwise the zygoma is shaped like that of *C. sansaniense.* It shows furthermore, that the place where the zygoma of the Paris skull is broken across (and stuck together again) corresponds almost exactly with the suture between the jugal and the squamosal, and that the jugal has a long, slender, pointed post-orbital process, shaped much as I have restored it in fig. 1. Ventrally the jugal ends in a short point anterior to the glenoid, again rather as in *Dicotyles*, but not forming quite the same long, downwardly curving strut beneath the squamosal as in that genus—probably because the glenoid has not descended so far.

Chœrotherium, Dicotyles and Doliochœrus.

STEHLIN in his " Geschichte des Suiden-Gebisses " pointed out certain resemblances between *Chœrotherium* and *Dicotyles* : in the shape of the temporal crests, of the mandibular condyle, and of the canine teeth, and in the reduction of the incisor dentition. In his opinion these resemblances are not sufficiently exact to indicate relationship—they are only parallelisms—and he concludes that an independent Eocene origin must be sought for *Chœrotherium,* its line of development being quite different both from that of the peccaries and from that of the true pigs.

In this paper I have tried to show that a study of the glenoid and otic regions of the Chœrotherium skull brings out still more points of resemblance to the *Dicotylinœ.* These may be summarised as follows :—

1. A low glenoid.

2. A well developed though narrow postglenoid process, placed postero-medial to the glenoid surface. (Correlated with the *Dicotyles*-like mandibular condyle.)

3. A postglenoid process projecting a long way below the post-tympanic process. (Correlated with (1) above.)

4. A groove on the lateral surface of the hinder end of the zygoma above the glenoid. (Present in *Doliochœrus*, but not in *Dicotyles.*)

5. A jugal ending anterior to the glenoid surface.

6. A weak pterygoid region without a tuberosity for the internal pterygoid muscle, the pterygoid fossa being divided from the palate by only the slightest suggestion of a bounding ridge.

7. A short pointed paroccipital process with a wide base.

8. A paroccipital process lying posterior to instead of almost lateral to the glenoid ; it is directed downwards, and if not as much backwards as in *Dicotyles* at least not forwards as in *Sus.*

It is probable that most of these characters hang of necessity together and are connected with the downwardly directed *Dicotyles*-like upper canine. Further, it is quite true that when any of them are examined in detail, they can be shown not to correspond *exactly* with conditions in the Dicotylinæ. It is clear that *Chœrotherium* can neither be the direct descendant of *Doliochœrus,* than which it is throughout of a more delicate build, nor the direct ancestor of *Dicotyles*, but the very fact that most of its tendencies are so Dicotyline—that the course of its evolution has been so parallel to theirs—seems to me to indicate an initial relationship. Certain other tendencies peculiar to the genus were clearly at work: the teeth are extremely simple, the upper molars without intermediate conules, m^3 with practically no talon, p^4 has not taken on the characters of a molar (although in outline surprisingly Dicotyline owing to the forward position of the inner cone with a broad postero-internal cingulum behind it), p_4 has but a single main cusp, and the lower incisors are without the characteristic ridges* of other Suidæ. Most of these characters it seems possible to regard as a reduction and simplification of an earlier more typically Dicotyline condition. If it were certain that *Doliochœrus* and *Perchœrus* were in the direct ancestral line of *Dicotyles*, then it could be asserted that *Chœrotherium* must have split off from that line at a period earlier than the Oligocene beds in which these make their appearance, but still this would not prevent *Chœrotherium* from being a true member of the Dicotylinæ, and in the incomplete state of our knowledge of the evolutionary history of the group the assertion seems premature.

II. The Cebochœridæ.

In the Middle and Upper Eocene of Europe are found a number of small mammals whose bunodont molar teeth have a certain resemblance to those of the Suidæ. These are the genera *Cebochœrus*, *Chœromorus*, *Acotherulum* and *Leptacotherulum* of various authors. They are commonly included in the family Suidæ, and regarded as primitive and perhaps ancestral members. It has also been suggested that they may form a link between the more typical Suidæ and the Anthracotheres.

Stehlin, surveying the material in his characteristically thorough manner,† concludes from the evidence of the dentition that there is probably little reason for separating *Acotherulum* and *Leptacotherulum* generically from *Cebochœrus*, and that in any case all three are on an entirely distinct line from the Suidæ. An examination of the very excellent skull material in Paris serves, it seems to me, only to emphasise this opinion.

In the case of the remaining genus, *Chœromorus*, Stehlin still finds a possible loophole for Suid ancestry, as regards which we are otherwise left quite in the dark. This loophole, and indeed the possibility of separating *Chœromorus* from *Cebochœrus* at all, is to be found in a certain isolated lower canine tooth among the material in Basel from the Eocene of Mormont. Such a canine Stehlin points out, with its long curling root, could not have fitted into a jaw already furnished with the enlarged first premolar that is characteristic of *Cebochœrus*. From the Middle Eocene of Egerkingen comes another such canine, also unassociated with cheek teeth. If the molars were found, however, would they really be indistinguishable from those of Cebochœrids from the same beds. And, furthermore, are the canines in question really those of true Suidæ ? Stehlin thinks

* Stehlin, "Suiden-Gebiss," p. 330.

† H. G. Stehlin, "Die Säugethiere des Schweizerischen Eocaens," Th. 5, p. 696 ff. 'Abhand. d. Schweiz. Paläont. Gesell.,' vol. 35, 1908.

so, and as the best solution of the problem describes a number of *Cebochœrus*-like molar teeth from Egerkingen under the title "*Cebochœrus helveticus* or *Chœromorus jurensis*."

All that I will say here is that the skulls of Cebochœrids, known in a good state of preservation only from the Phosphorites du Quercy, are very clearly all of one well-defined type, a type very remote from that of contemporary Suidæ, and that this can be demonstrated whether canines and first premolars are present or not.

The best material for such a demonstration is in Paris, and I am extremely indebted to Prof. MARCELIN BOULE for the use he has allowed me to make of it. First there is a skull of the large species *Cebochœrus lacustris* Gervais*—a very beautiful skull but regrettably embellished with plaster, like so much that has passed through FILHOL's hands. It has the typically enlarged first premolar separated from the canine by a shallow niche, which no doubt received the correspondingly enlarged first lower premolar. The canines have been broken and that of the left side unreliably patched up.† Then there is the small skull described and figured by FILHOL as "*Acotherulum saturninum*."‡ STEHLIN has given reasons against FILHOL's *A. saturninum* being the same as GERVAIS' type species, a jaw from La Débruge, and renames it *Cebochœrus quercyi*. A third skull in Paris bears the mistaken label "*Dichobune leporinum*": its proportions differ a little from those of FILHOL's figured skull of *C. quercyi*, since it is rather more lightly built, but I think it may be placed provisionally in the same species. Its dentition is more complete, and its palate, zygomata, and basiotic region are in more perfect condition, but the snout, although a greater length of it is preserved, is badly squashed dorsally. In neither of these last two skulls is a canine or first premolar present, and the palate of a third individual of apparently the same species also tells us nothing of the teeth in front of the second premolar. Lastly there is a very delicate and particularly beautiful little skull considerably smaller than those just mentioned and with certain other small differences to which I will return later. Dr. TEILHARD DE CHARDIN makes the very likely suggestion that this may be the skull of which FILHOL published a brief note in 1877,§ naming it "*Leptacotherulum*." If so, some accident has occurred to it since STEHLIN saw it in 1898,|| for the canine tooth which both he and FILHOL speak of is missing; there is evidence in favour of such a supposition.

* STEHLIN, "Eocaene Säugethiere," p. 694.

† My figures give only a rough indication of this patchwork, which makes the tooth appear equal in size to the enlarged p^1. This would not be improbable in view of the long, trenchant, upper canine of the skull from Euzet-les-Bains described by DEPÉRET as *Cebochœrus minor* ('Ann. de l'Université de Lyon,' Nouv. sér. I, 40, 1917), and of the enlarged canine said to have been present in "*Leptacotherulum*" (see below p. 421). "*Leptacotherulum*" is not reported to have had an enlarged $p.m.^1$ as well, but in DEPÉRET's skull this tooth, although not to be compared in size with that of *C. lacustris*, is at least as large as $p.m.^3$ and has roots projecting well from the alveolar margin like those of the enlarged teeth of other species.

‡ H. FILHOL, "Recherches sur les Phosphorites du Quercy," 'Ann. d. Sci. Géolog.,' viii, 1877.

§ H. FILHOL, "Considérations sur la découverte de quelques mammifères fossiles . . .," 'Bull. Soc. Philom. de Paris' (7), vol. 1, 1877, p. 53.

|| H. G. STEHLIN, "Eocaene Säugethiere," p. 697.

The only other Cebochœrid skull material that I have come across consists of two comparatively poor fragments in the Musée d'Histoire Naturelle of Montauban. One of these is of the size of *C. quercyi*, the other rather larger.

The Cebochœridæ and the Suidæ.

In comparing *Palæochœrus* with *Perchœrus* I laid stress on the differences which separated these two genera, differences which became more and more marked in their descendants of the later Tertiaries, until to-day the representatives of the two lines are often placed in two different families. In naming these two families the Suidæ and the Dicotylidæ respectively we are faced with a difficulty however. What are we to call that group of primitive pig-like animals of the Oligocene which included not only forms that we know, such as *Palæochœrus*, *Perchœrus* and *Doliochœrus*, but also many yet unknown forms, possibly the more direct ancestors of certain later types ? It is the difficulty which always arises in tracing back to their origin any two or more related phyla nowadays separated by characteristics of " family " degree, then only by those of " generic " or perhaps " specific " degree. The problem is not solved by lowering the Dicotylidæ to sub-family rank, as I have done in the earlier pages of this paper, but it permits one to employ the family name *Suidæ* when treating the Oligocene forms as a single group, and it is in this sense which I shall employ it henceforward.

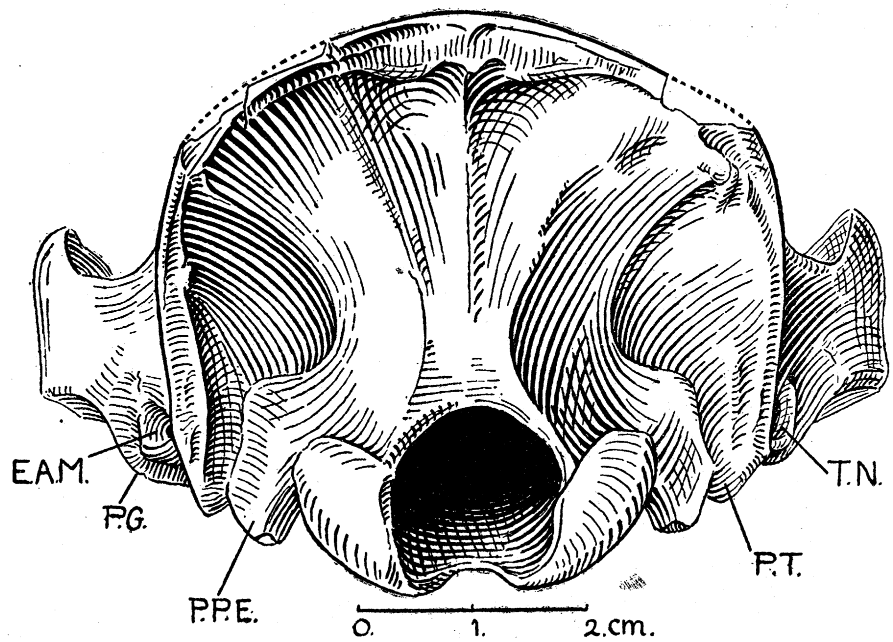
It will be well, perhaps, before comparing the skull of these Oligocene Suidæ with that of other contemporary families, to set down clearly what are the cranial characters which justify us in uniting the several genera together at all. They are the characters which are still to be found uniting the pigs and peccaries of to-day.

1. The most striking of these characters is the shape of the skull when viewed from behind. The occiput is high and narrow above, but at the back of the zygomatic arches, above the external auditory meati, the squamosals are drawn up into curious pointed ear-like projections which do indeed support the cartilages of the outer ears.

2. The external auditory meatus is a long tube running upwards and outwards from the tympanic cavity. Behind it the squamosal sends down an extensive but thin plate of bone which beneath the meatus is pressed forwards against the postglenoid process, either actually joining this process or only separated from it by a very thin crest of tympanic bone, all that can be seen of the tympanic " neck."

3. From the back of this thin post-tympanic plate or process of the squamosal arises a secondary process, which projects backwards away from it to rest against the face of the paroccipital process of the exoccipital, and which I have therefore called the paroccipital process of the squamosal. In this way the squamosal takes the place of a *pars mastoidea* of the periotic bone, which is shown in disarticulated skulls of recent young Suidæ to be in these entirely lacking.

Turning now to the Cebochœridæ we find in contrast the following characters. The occiput is broad and low and is framed by a nearly semicircular crest which terminates ventrally on either side just behind and below the external auditory meatus. The dorsal rim of the broad zygoma meets the cranium just anterior to this crest at about half

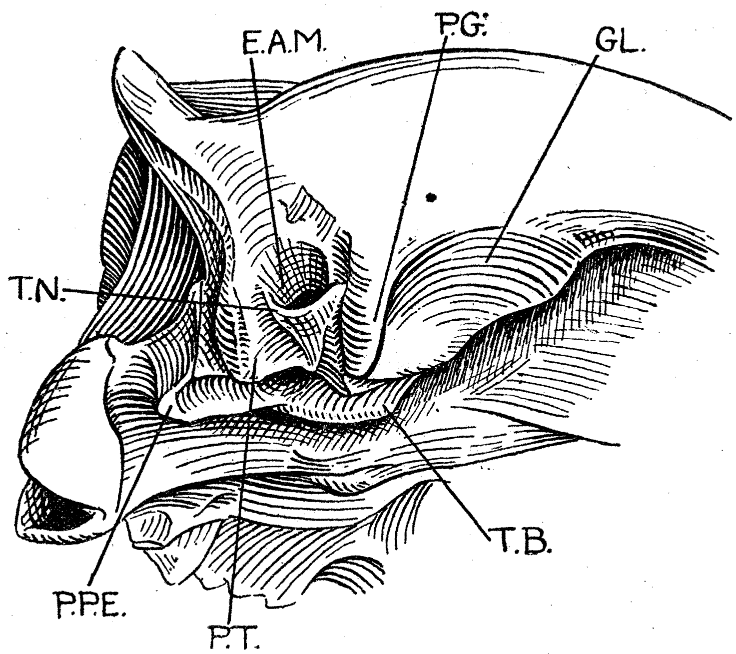


TEXT-FIG. 18.—Occipital view of the skull of *Cebochœrus lacustris* from the Phosphorites du Quercy, Memerlein. (Paris, Muséum National.) E.A.M., opening of external auditory meatus; P.G. and P.T., postglenoid and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital; T.N., tympanic neck.

the height of the occiput. From the occipital region the rim passes outwards and forwards in a gentle curve. Nothing could be much less helpful than this construction if we are seeking to understand the origin of the peculiarly shaped occiput of the Suidæ and of the still more peculiar ear-like projections at the hinder end of their zygomata.

The external auditory meatus of *Cebochœrus*, instead of being a long tube running up at the back of the zygoma, is a very short tube measuring only half the breadth of the glenoid surface. The tympanic neck which forms its wall lies clearly exposed to view between the postglenoid and the post-tympanic processes of the squamosal. The latter, instead of being a thin plate sloping forwards towards the postglenoid process, is a very thick plate which projects well below the level of the tympanic neck, but leans away from this towards the paroccipital process. Between the latter, which is composed of exoccipital, and this thick plate of the squamosal no room is left for a separate little paroccipital process of the squamosal or for that broad sweep of bone which in all the earlier Suidæ and in the living Dicotylinæ lies lateral to the stylomastoid foramen and separates these two squamosal processes.

These characters of *Cebochœrus* are, I think, sufficient proof of how wide and how fundamental are the differences between the Cebochœridæ and the Suidæ. That it is not merely a question of the Cebochœrid condition being the more primitive and the Suid derivable from it, I think becomes especially clear when an attempt is made to imagine how such a derivation might have taken place. Nor even does it seem to me possible that the Cebochœridæ of the Middle Eocene, of whose skulls we know nothing, would



TEXT-FIG. 19.—Oblique view of hinder end of skull of *Cebochœrus lacustris* from the Phosphorites du Quercy, Memerlein. (Paris, Muséum National.) E.A.M., opening of external auditory meatus ; GL., glenoid surface ; P.G. and P.T., postglenoid and post-tympanic processes of squamosal ; P.P.E., paroccipital process of exoccipital ; T.B., tympanic bulla ; T.N., tympanic neck.

have been more helpful in the matter—the divergence in the Upper Eocene is too great. We know so much nowadays of the history of many other groups of mammals that we look for nothing but an immensely slow continuity in the evolution of such skeletal characters as are in question here.

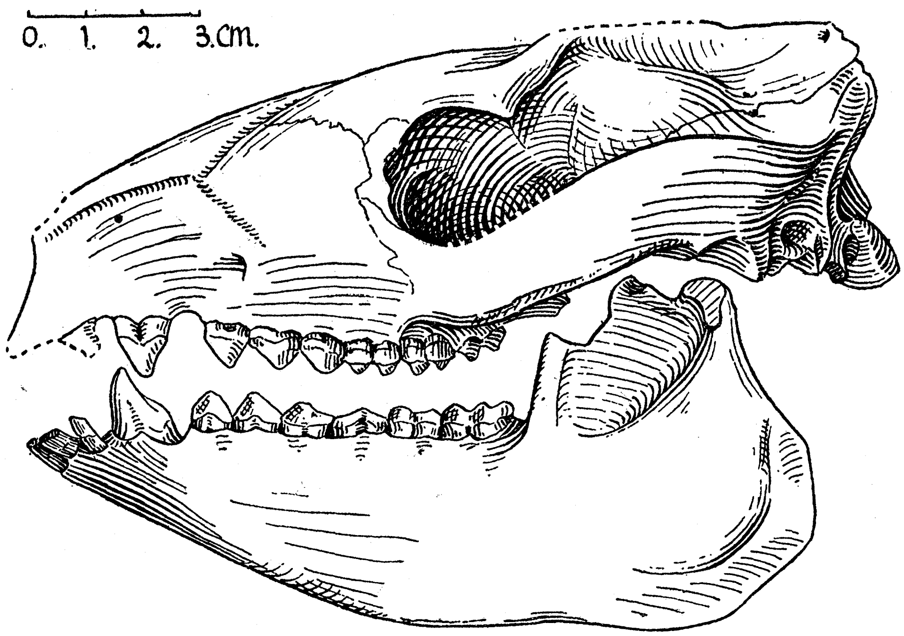
The Skulls of Cebochœrus in Paris.

Since the skull of *Cebochœrus* has never yet been adequately described* it may be worth while to add a little more about it here. I will base my description on the skull of the large species *C. lacustris* and point out afterwards how it differs from the smaller species.

It is a solid, massive little skull with rather a short snout and a very deep mandible. The broad temporal fossæ, surrounded by prominent crests and very broad, strong

* CHARLES EARLE gave a brief description of the Paris skull of *C. lacustris* in his "Notes on the Fossil Mammals of Europe," in the 'American Naturalist,' 1896-98.

zygomata, tell of a powerful musculature capable of pressing the heavy lower jaw firmly against the upper. The glenoid surface is broad and flat in front, while behind it curls gradually and smoothly down on to the face of the short, stout postglenoid process. The condylar surface of the mandible is a flattened cylinder fitting this glenoid surface. It is clear from this that backward and forward jaw movements would have been impossible, but that a limited amount of sideways movement probably took place during mastication, as is also suggested by the bunodont and often well worn molar teeth. The enlarged caniniform first premolars characteristic of both jaws would in any case hinder the mandible from sliding backwards and forwards when its grinding teeth were in contact or nearly in contact with those of the maxilla.

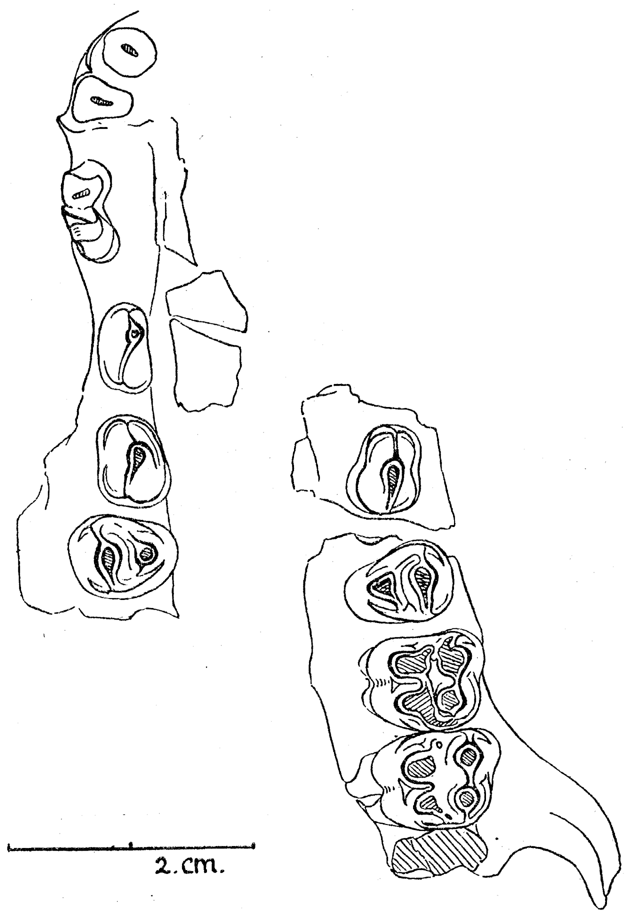


TEXT-FIG. 20.—Lateral view of skull of *Cebochœrus lacustris* from the Phosphorites du Quercy, Memerlein. (Paris, Muséum National.) Upper first premolar partly restored from other side of skull.

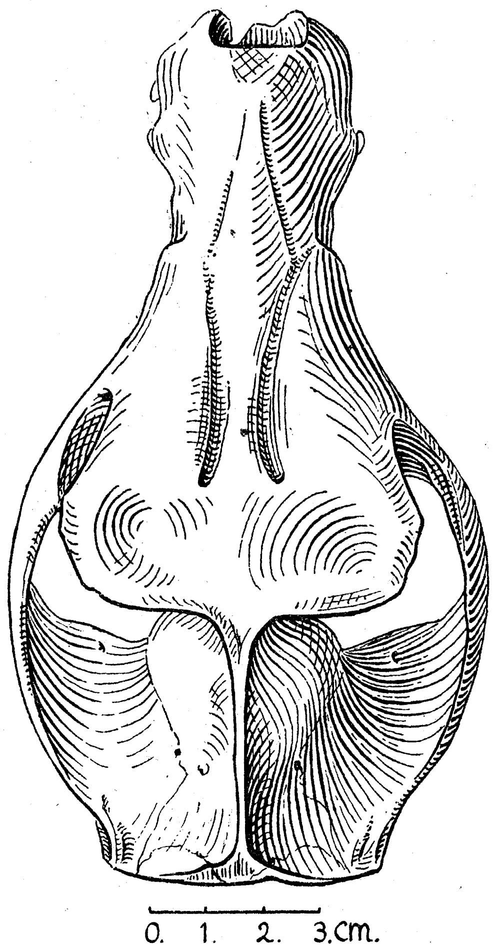
The neck muscles were evidently as powerful as those of the temporal region (see text-fig. 18). The crest encircling the occiput continues down behind the zygoma—and thus quite independent of the temporal fossa—until it merges with the edge of the post-tympanic plate of the squamosal. A low median crest passes downwards from the occipital crest above. Near to the centre of each half of the occipital surface is a depressed area, amounting in the smaller skulls to a deep and elongated pit.

In viewing the skull from above one is struck by the extreme narrowness of the brain case, especially in the cerebral region at the back of the orbit. The post-orbital flanges of the frontals are in contrast very broad: each has a shallow hollow on its dorsal surface. Just in front of these hollows and medial to them are the two supra-orbital foramina, from which a pair of well marked grooves lead forward to a point above the infra-orbital foramen and there divide into one branch that continues forwards towards the tip of the nasals and another passing downwards and backwards.

Of post-orbital processes of the jugal I can find no trace. The zygomatic process of the maxilla arises from the snout just lateral to the last two molars and so close above the roots of these that no space is left for snout muscles such as those that take origin



Text-fig. 21.—A fragment of the upper dentition *Cebochœrus* (*lacustris ?*) from the Phosphorites du Quercy, showing on the right side the stumps of i^3 and *c*, a broken enlarged p^1, and p^2 to p^4, on the left side p^3 to m^2. (Montauban, Musée d'Histoire Naturelle.) The scale is approximate.

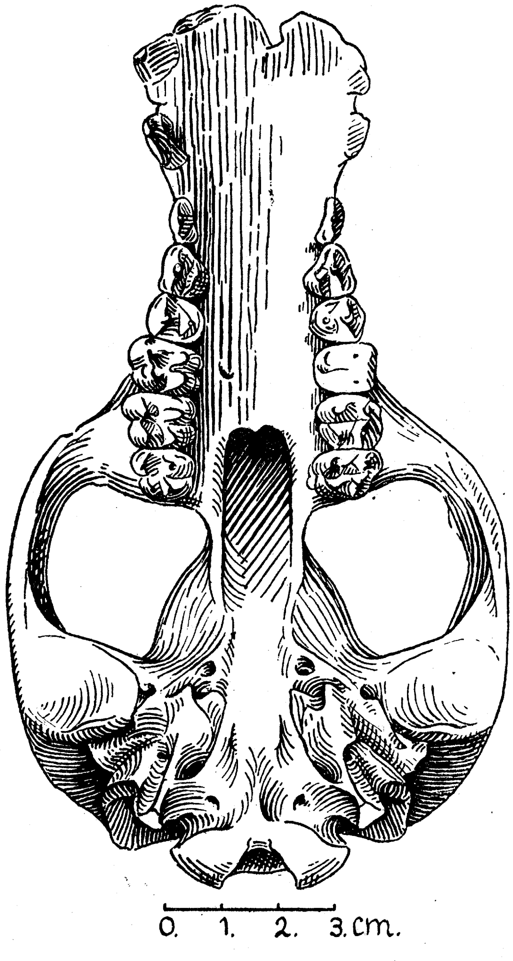


Text-fig. 22.—Dorsal view of skull of *Cebochœrus lacustris* from the Phosphorites du Quercy, Memerlein. (Paris, Muséum National.)

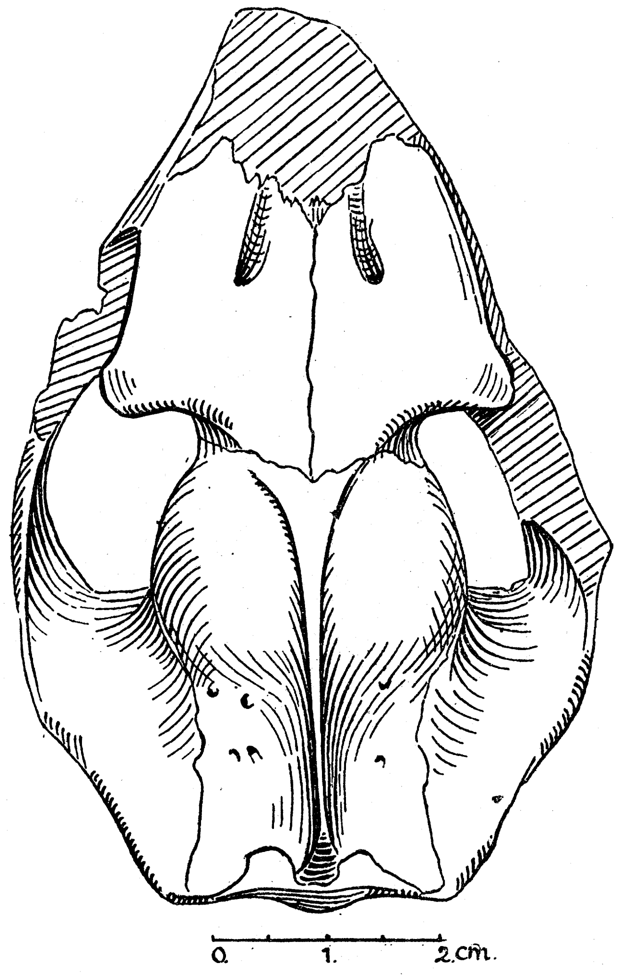
here in the Suidæ. (This condition may be contrasted with that in *Perchœrus*, which already in the Oligocene had a broad space for these muscles.)

The palate offers little to remark upon. It is very straight posteriorly, the cheek teeth forming nearly parallel rows. In the canine and incisor region it broadens a little, but is badly damaged here in all the skulls. There are short diastemata both behind and in front of the enlarged first premolar; that in front of it shows a very slight elevation of the alveolar border, the resting place of the correspondingly enlarged first lower premolar. The hinder end of the palate is opposite the roots of the second molars. The pterygoid laminæ of the palatine and alisphenoid bones are not complete, but they were evidently not very powerful and a pterygoid fossa was probably lacking; this would indicate that the pterygoid muscles were not of such importance as the temporal and the masseter.

Returning once more to the otic region we find that the tympanic bulla is small, flat rather than globular, and with thick walls: its anterior end just behind the *foramen*



TEXT-FIG. 23.—Ventral view of skull of *Cebochœrus lacustris* from the Phosphorites du Quercy, Memerlein. (Paris, Muséum National.)

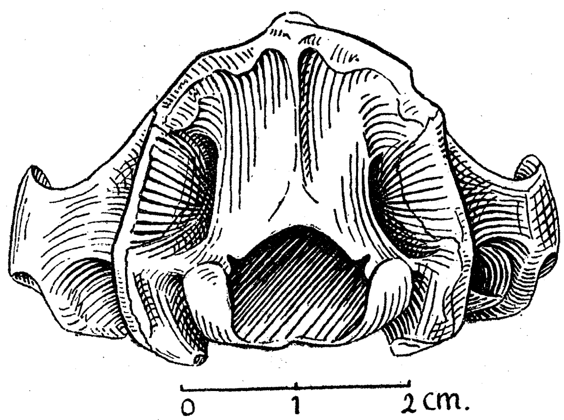


TEXT-FIG. 24.—Dorsal view of skull of *Cebochœrus quercyi*, FILHOL's type of "Acotherulum saturninum"), from the Phosphorites du Quercy. (Paris, Muséum National.)

ovale is drawn into a point, but more medially it allows a large piece of the periotic bone to emerge from beneath it. Where the tympanic neck joins the bulla there is a triangular elevation or fold on the ventral surface of the bone, rather reminiscent of that which I shall describe presently in the Anthracotheres; the appearance of this elevation is different on the two sides of the skull, however, and it is hard to say how much may be due to the bone here having been crushed. Posteriorly the bulla sends out a narrow rib which passes backwards between the stylomastoid and posterior lacerate foramina to join the paroccipital process. The latter is short and stout and its face is deeply grooved from the mouth of the stylomastoid foramen downwards. The outer wall of this groove is formed by the thick post-tympanic plate of the squamosal, which is wedged in between the posterior, exoccipital part of the paroccipital process and the tympanic neck.

The skull of Cebochœrus quercyi ("*Acotherulum saturninum*," FILHOL).

The small skull which FILHOL described as "*Acotherulum saturninum*" and the rather similar one which I have mentioned above as probably belonging to the same species, differ from one another in the following characters. FILHOL'S skull is more massively built and appears to have a broader brain case. Its occiput is also broader from side to side in proportion to its height, while the pits on the back of the occiput are less accentuated. Less accentuated also is the groove that passes upwards and backwards on the zygoma above the external auditory meatus. The molar teeth of this skull of FILHOL'S have always been reported to have the tips of their two outer cusps unusually close to those of their two inner cusps. This seems to me to be due to the angle at which these cusps are leaning inwards towards one another: a very little wear across the tips such as one finds in the other skull would make one lose sight of this characteristic, which I believe is really shared by most *Cebochœrus* molars. FILHOL'S skull has lost all its anterior teeth, so that no further comparison of the dentition can be made.



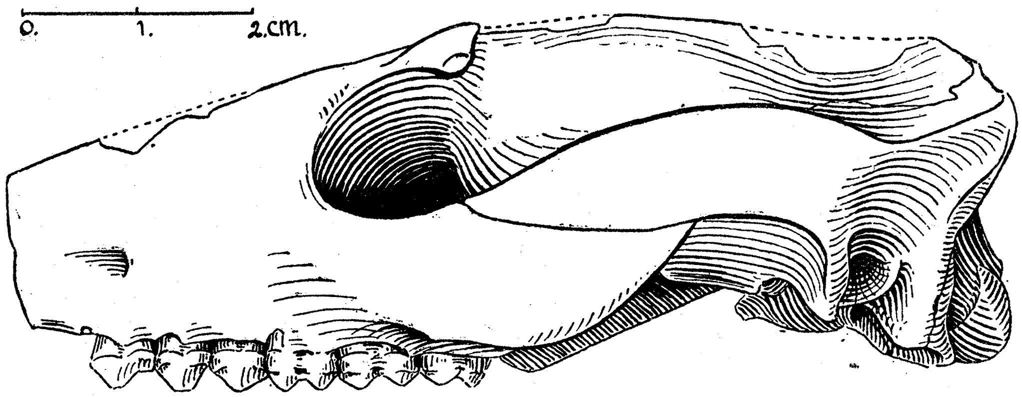
TEXT-FIG. 25.—Occipital view of another skull of *Cebochœrus quercyi* from the Phosphorites du Quercy. (Paris, Muséum National.)

Turning now to a comparison of these skulls with that of *Cebochœrus lacustris* already described, we are at first struck by the inferior size of the brain case of the latter in proportion to the rest of its skull. This, however, is simply in accordance with the now well recognised principle that, within any genus, the increase in size of the brain case of a species does not equal that of the outlying parts of the skull. The more massive the skull the more extensive is the area needed for muscle attachment, and therefore we find in *C. quercyi* that the parietal crests are comparatively feebly developed, the dorsal edge of the zygoma does not meet the occiput at so high a level, and the post-tympanic plate of the squamosal is proportionately less thick. The post-orbital processes also are narrower and there are no depressions on their dorsal surfaces.

In C. *lacustris* the glenoid surface, though of similar shape, is a little lower in relation to the tympanic and the *basis cranii*: its inner border, instead of being quite dorsal to the bulla, overlaps the little triangular fold of tympanic (absent in *C. quercyi*) which lies in the angle between the bulla and the neck: its anterior border is directed a little forwards as it passes out to meet the zygoma.

The shape of the tympanic bone and its relations to the post-tympanic and paroccipital processes are essentially similar in the larger and smaller skulls. The tip of the periotic is in both cases to be seen emerging from beneath its anterior extremity. This extremity, however, appears to divide in *C. quercyi* into two points, whereas in *C. lacustris* only the more lateral of these points is present.

The only very obvious difference in the dentition, as far as it is present in these skulls, is in the third upper premolar. In *C. quercyi* this has a well-developed inner cusp



TEXT-FIG. 26.—Lateral view of same skull as in fig. 25.

placed directly opposite the main outer cusp, and thus resembles p^4, whereas the *C. lacustris* skull is quite different from p^4 and has a broad postero-internal basin-shaped cingulum more like that of the Suidæ, where an internal cusp can hardly be said to exist. Other material shows, however, that the shape of this tooth is very apt to vary, both in the larger and in the smaller species.

One or two other such small differences are probably to be found, but there is nothing, it seems to me, that prevents us from very emphatically subscribing to STEHLIN's opinion that "*Acotherulum saturninum*" FILHOL is really a species of the genus *Cebochœrus*.

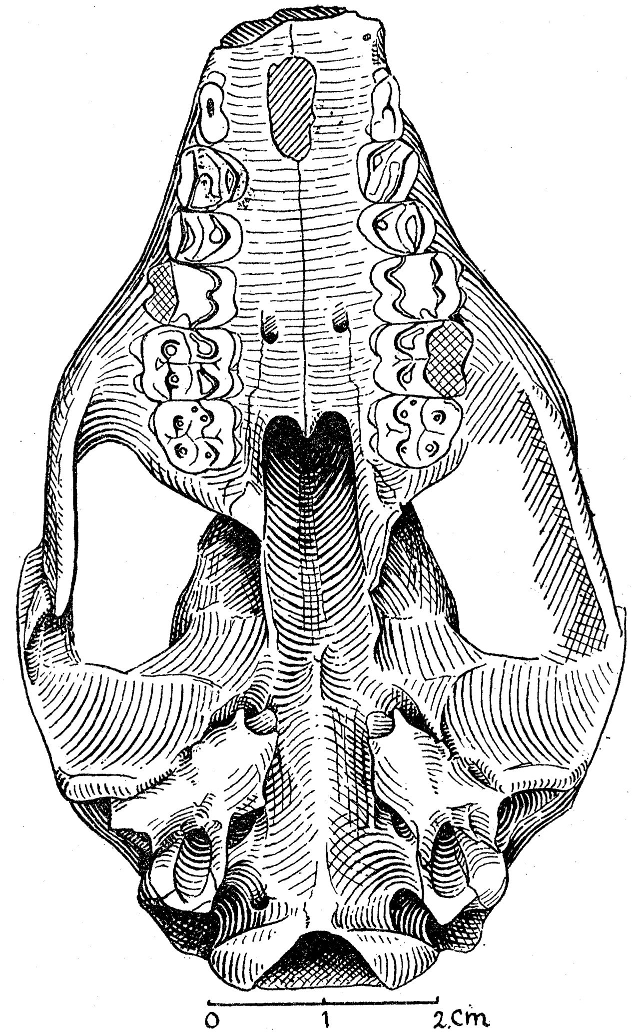
The Skull of "Leptacotherulum" FILHOL.

The small skull which there is reason to think is that described by FILHOL* under the name of "*Leptacotherulum*" differs from the two skulls just described in very much the same way that they differ from *C. lacustris*. It is rather smaller than they are and correspondingly more delicate, the parietal and occipital muscle crests still less strongly

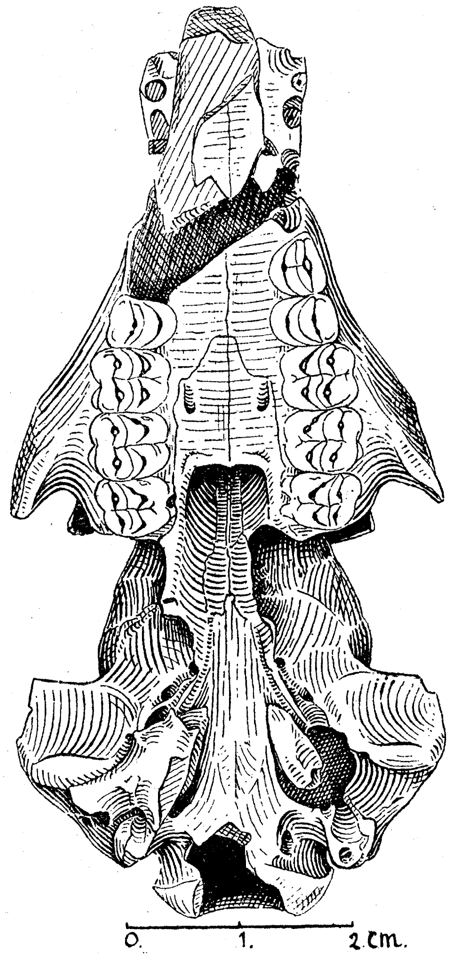
* H. FILHOL. 'Bull. Soc. Philomath., Paris,' 7 ser., vol. 1, 1877.

developed, the post-orbital processes of the frontals strikingly less important. The glenoid surfaces are still higher when compared with the *basis cranii* and the bulla, the latter forming a medial wall to the glenoid cavity. The postglenoid process is very prominent.

The teeth are very little worn, so that the molars appear with their inner and outer cusps closely approximated. It is hard to say whether the very clearly marked crests



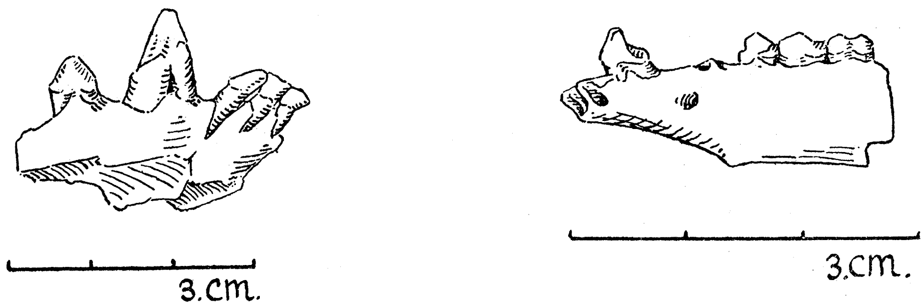
TEXT-FIG. 27.—Ventral view of same skull as in figs. 25 and 26.



TEXT-FIG. 28.—Ventral view of skull of "*Leptacotherulum*" FILHOL (?) from the Phosphorites du Quercy. (Paris, Muséum National.)

on the cusps are also due to this freshness of the teeth or are really a specific difference: they make the inner cusps appear almost selenodont. m^2 and m^3 each have a very small protoconule, on m^1 I cannot detect one. p^4 has a very small postero-external cusp close behind its main outer cusp. p^3 is rather longer, in the antero-posterior direction, than p^4, and agrees with *C. quercyi* in having an inner cusp which, like that of p^4, is not much smaller than the main outer cusp and is placed opposite or a little anterior to it, The crescentic crest of which this inner cusp forms the centre, is curious in having a notch just posterior to the apex, and creating what is practically a second little cusplet behind the main one. I have not met this condition in any other Cebochœrid premolar and I take it for a 'sport.'

Anterior to this the snout has been broken, and although the alveoli of i^3, c, p^1, and p^2 can be seen on the right side they give no information as to what these teeth were like or as to whether p^1 was enlarged. FILHOL describes the canine of *Leptacotherulum* as ". . . . forte, aplatie par ses faces latérales, tranchante par son bord postérieur." He continues: "Elle a beaucoup d'analogies avec celles des *Metadichobune Campichii** et des *Ragatherium*; seulement elle n'est pas due à une modification de forme des prémolaires." That this enlarged tooth was really the canine is confirmed by STEHLIN† who saw the skull before it was broken.



TEXT-FIG. 29.—Left: anterior end of mandible of large species of *Cebochœrus* (*lacustris ?*) from Phosphorites du Quercy, Lamandine, showing two incisors, canine, enlarged p_1 and p_2. Right: anterior end of mandible of smaller species of *Cebochœrus* (*quercyi ?*) from Phosphorites, Bach, showing enlarged p_1, p_3 to m_1 and alveoli of two incisors, canine and p_2. (Both in Montauban Musée d'Histoire Naturelle.) The scale is approximate.

STEHLIN himself suggests that *Leptacotherulum* may represent a stage morphologically more primitive than the larger Cebochœridæ, and through which these must have passed at an earlier period of their evolution. The evidence from the skull seems to be entirely in agreement with this suggestion. *Cebochœrus quercyi* is morphologically a good intermediate between *C. lacustris* and *Leptacotherulum*. It then becomes merely a matter of taste whether we leave the latter as a separate genus or find a place for it within the genus *Cebochœrus*. To the family Cebochœridæ it unquestionably belongs.

III. THE ANTHRACOTHERIIDÆ.

I have tried to show that the Cebochœridæ tell us nothing of the Eocene history of the Suidæ. Were these small bunodont animals more closely related to the Anthracotheres?

Good skulls of Anthracotheres are especially rare in European museums. Among those which I have myself been able to examine the following are the best.

* *I.e.*, to the enlarged lower first premolar of the type mandible of the little *Cebochœrus Campichii*.

† H. G. STEHLIN. "Eocaene Säugethiere," p. 697.

1. In the Geologische Reichsanstalt in Vienna are the two skulls which TELLER described and figured in 1884.* The smaller of these TELLER called *Prominatherium dalmatium*, after Monte Promina in Dalmatia where it was found. DEPÉRET† and STEHLIN,‡ finding no reason for making a new genus of this skull, refer it to *Anthracotherium*. It is uncertain whether the Monte Promina beds are Upper Eocene or Lower Oligocene, but the latter seems more probable.

2. The other skull in Vienna comes from the Oligocene of Trifail in Styria and is of gigantic proportions. It was called by TELLER *Anthracotherium illyricum*, but STEHLIN‡ concludes that it is " Kaum mehr als ein Lokalschlag des *A. magnum*."

Both these skulls are very crushed, but rather more can be made out of them than appears in TELLER's plates : his drawing of the big skull is especially misleading, as his shading gives quite a wrong impression of the relief.

3. In Paris there is a skull of the little *Anthracotherium minimum* (*Microbunodon* DEPÉRET, see STEHLIN, *loc. cit.*, p. 166). This skull, in which the canine stumps, p^2, p^4, and the three molars are present on each side, has unfortunately lost its basi- and exoccipital bones. It is about the same size as the skull of *Cebochœrus lacustris* which I have figured above.

4. A similar loss of the basi- and exoccipital bones has occurred in a young skull of a North American *Ancodus* in Munich. This is stated to come from the Titanotherium beds of White River age in Nebraska and is labelled *Ancodus americanus* LEIDY.

5. The skulls most frequently to be found in European collections are those of *Ancodus velaunus* from the Sannoisian of Ronzon. Unfortunately, these are nearly always so badly crushed and flattened, that the cranial structure is lost. There is a nearly complete skull in Munich, however, in which a great deal has been preserved, and in the same museum there is an even better preserved fragment of a *basis cranii* ; after studying these, I have been able to trace the similarity of some of the other specimens.

6. Prof. DEPÉRET has, in his collection in the University of Lyons, several hitherto undescribed skulls of *Brachyodus borbonicus* GERVAIS from the Upper Stampian of St. André (*argiles de Marseilles*).

7. By far the best cranial fragment of an Anthracothere that I have been able to find is that of *Brachyodus Gorringei* Andrews in Stuttgart. It is one of the three *Brachyodus* species from the Fâyum, the skulls of which were described and figured by MARTIN SCHMIDT in 1913.§ The skulls of SCHMIDT's other two Fâyum species—

* F. TELLER, " Neue Anthracotherienreste aus Südsteiermark und Dalmatien," 'Beiträge zur Paläontologie Oesterreich-Ungarns und des Orients,' Wien, 1884.

† C. DEPÉRET. " L'histoire géologique et la phylogénie des Anthracothéridés," 'Comptes Rendus Aca. Sci.,' vol. 146, p. 158, 1908.

‡ H. G. STEHLIN. " Zur Revision der Europäischen Anthracotherien," 'Verhandl. der Naturf. Gesell. in Basel,' vol. 21, 1910.

§ MARTIN SCHMIDT. " Ueber Paarhufer der Fluviomarinen Schichten des Fajum," 'Geolog. u. Palaeontolog. Abhandlungen,' Neue Folge, 11, 1913.

Brachyodus Fraasi and the small *Brachyodus parvus*—also in Stuttgart, are much less perfectly preserved.

In spite of the unsatisfactory state of preservation of most of this varied material, an idea can yet be obtained from it of the direction towards which cranial specialisation in the Anthracotheres was tending.* The genera *Anthracotherium*, *Microbunodon*, *Brachyodus* and *Ancodus* are held to represent different branches of the Anthracothere stock.† The complex interrelationships of their species have not yet been satisfactorily worked out, but in the hinder part of the skull of all of them we find in a more or less marked degree certain very distinctive characters which unite them together as a family and serve as a test of the correctness with which Anthracotherid relationship has from time to time been attributed to certain other primitive Artiodactyls.

In the Anthracotheres as in the pigs there seems to have been a need for the mandibular articulation to be shifted backwards on the skull, this leading to a compression of those parts lying between the glenoid surface and the occiput. This compression had already gone much further in the Anthracotheres of the Oligocene than in the contemporary Suidæ. In the latter, as already described, that part of the squamosal which lay between the external anditory meatus and the exoccipital was forked at its ventral extremity, the anterior part of the fork consisting of a post-tympanic plate, the posterior part forming a little paroccipital process sloping backwards against the corresponding process of the exoccipital. In the Anthracotheres there is no paroccipital process of the squamosal, but simply a flat post-tympanic plate tightly wedged in between the neck of the tympanic and the exoccipital, its thickened border appearing ventrally between the two. The exoccipital bone forms another plate splayed out against the back of the squamosal but projecting ventrally into a rather powerful, downwardly directed paroccipital process. Dorsal to the exoccipital the squamosal appears on the occiput and is here hollowed out into a deep concavity.

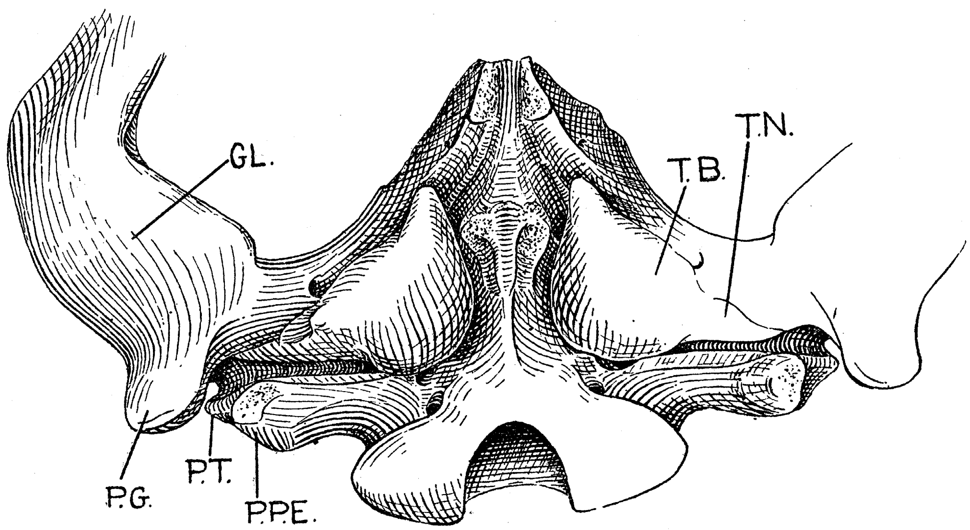
Although the compression of the parts posterior to the glenoid is more accentuated in the Anthracotheres than in the contemporary Suidæ, it has not resulted, as already in the early Dicotylinæ, in the complete concealment of the tympanic neck. This still appears as a more or less flattened strip of bone between the postglenoid process and the post-tympanic plate.

The glenoid articulation not only tends to move backwards in the Anthracotheres, it also tends to move outwards and downwards. This has reached an extreme in *Ancodus velaunus*, where the compression of the parts posterior to it is also the most marked. Here the glenoid lies quite lateral to the opening of the bony external auditory meatus, (although the meatus is also very long) and some way ventral to it, so that it is separated

* W. B. Scott ('Journ. Acad. Nat. Sci. Phil.,' 2nd ser., vol. 9, 1895) has given an account of the osteology of the American *Ancodus brachyrhynchus* with figures of the skull. His figures, however, do not give in detail the points which I would like here to lay stress upon, and his description also is more concerned with the general shape of the skull, though he mentions many points to which I also shall refer.

† C. Depéret, 'Comptes Rendus,' *loc. cit.*, and H. G. Stehlin, "Eocaene Säugethiere," p. 796.

from the bulla by a long bar of squamosal. In TELLER's giant *Anthracotherium* skull the glenoid is also far out to the side, and at least a little depressed, though it is difficult to tell how much so because of the crushing. It is interesting to find the glenoid in this similar position in two forms which clearly represent two quite different lines of development within the Anthracothere family: on the one hand *Anthracotherium magnum* with its gigantic, heavy skull and powerful, crushing dentition: on the other hand *Ancodus velaunus* with its slender, graceful skull typified not only by the extremely long snout with long diastemata on either side of the rather slender canine, but also by the extreme compression of the crescents of its selenodont molar teeth. In *Ancodus velaunus* the movement of the mandible clearly seems to have been that of a ruminant: this is not only suggested by the sharpness of the crescents and the backward and outward

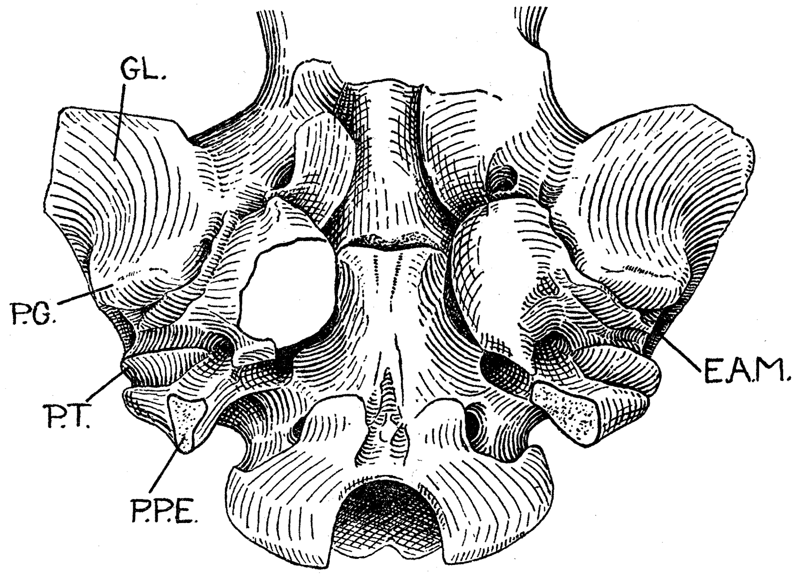


TEXT-FIG. 30.—Ventral view of hinder end of skull of *Ancodus velaunus* from Ronzon, Haute Loire. (Reconstructed from two specimens in the Bayerische Staatssammlung.) Rather less than three-quarters actual size. GL., glenoid surface; P.G., and P.T., postglenoid and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital; T.B., tympanic bulla; T.N., tympanic neck.

direction of the clear cut grooves between them, but also by the convexity of the broad glenoid surface and the freedom of movement given to the mandibular condyle by the extension of that surface lateral to the postglenoid process.

At the same time as the glenoid surface passes out to the side, away from the otic region, the post-tympanic plate of the squamosal extends outwards behind it, broadening from side to side. The external auditory meatus becomes of necessity longer, and with it the neck of the tympanic which ensheathes it from below. In *Ancodus velaunus* I had at first some difficulty in finding the outer opening of the meatus. In this form the tympanic neck appears ventrally as a thin crest of bone pressed against the long bar of squamosal which separates the glenoid from the bulla. Along the back of this crest, bounded behind by the post-tympanic plate of the squamosal, a groove runs outwards from the mouth of the stylomastoid foramen. This thin crest of bone and this groove extend laterally until almost under the shadow of the postglenoid process: then they curve upwards until at right angles to their former position. The outer opening of the meatus, a very small one, is thus carried dorsally just as it is in the Suidæ but by a rather different method.

With the exception of *Anthracotherium magnum*, of which I have seen no better preserved material than Teller's skull referred to above, the other Anthracotheriidæ that I have examined have their glenoid surfaces, either close against the tympanic bulla or only a little way lateral to it, and their external auditory meati correspondingly shorter. *Microbunodon minimum*, in spite of its late geological horizon, is in some ways the least specialised of all: the tympanic neck is not only very short but is very little compressed, although narrow and partially hidden from below by the forwardly sloping post-tympanic plate. Here, however, the glenoids are below the basicranial level and some little way out to the side. In *Brachyodus Gorringei* and *Anthracotherium dalmatium* the glenoids

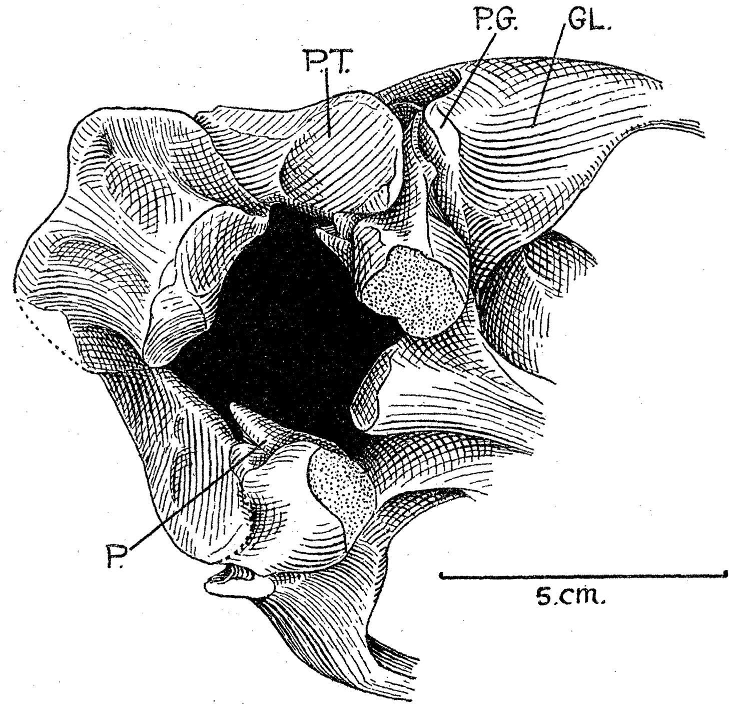


TEXT-FIG. 31.—Ventral view of hinder end of skull of *Brachyodus Gorringei* from the Fâyum. (Stuttgart, Naturaliensammlung.) About three-quarters actual size. E.A.M., opening of external auditory meatus; GL., glenoid surface; P.G. and P.T., postglenoid and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital; T.N., tympanic neck.

are distinctly below the basicranial level, but are quite close in against the bulla. In the former the tympanic neck extends out beyond the postglenoid process and is separated at its distal end from the back of the glenoid by a groove, the entrance to a postglenoid foramen; the neck is almost as much compressed as in *Ancodus velaunus*, consisting as there of a ventral crest with a groove between it and the post-tympanic plate of the squamosal. The *Brachyodus borbonicus* from St. André has a skull of lighter build than that of *B. Gorringei*,* just as its teeth are more selenodont. Without direct comparison of the two skulls it is very difficult to be sure of the differences in the details

* DEPÉRET places *B. Gorringei* on his branch line "*Bunobrachyodus*."

of the basiotic region, especially as the different conditions of preservation may account for much. The compression of the parts behind the glenoid is, I think, slightly greater in *B. borbonicus*, the paroccipital process lying very near to the postglenoid and not so much of the tympanic neck being exposed; at the same time the postglenoid and paroccipital processes are slenderer and the post-tympanic plate thinner. The glenoids are below the level of the basisphenoid, but not projected out to the side. The tympanic neck is shorter than in *B. Gorringei*. The young skull of *Ancodus americanus* in Munich, from the Titanotherium beds of the White River, is in very much the same stage



TEXT-FIG. 32.—Oblique view of otic and glenoid region of skull of *Ancodus americanus* from the White River Titanotherium beds. Basi- and exoccipitals are missing. (Bayerische Staatssammlung.) The scale is approximate. GL., glenoid surface; P., periotic; P.G. and P.T., postglenoid and post-tympanic processes of squamosal.

of specialisation as these European *Brachyodi* and compares especially well with *B. borbonicus*.* The skull is further of interest because the exoccipital bones have dropped off, so that the post-tympanic plates of the squamosals are exposed at the back of the skull and a clear idea can be gained of their shape and relationships; their hinder surfaces are slightly hollowed where the exoccipitals lay.

According to MATTHEW† *Ancodus americanus* is the earliest of a series of four American species of *Ancodus* in which the snout undergoes progressive shortening. These four

* The molar teeth of *Brachyodus borbonicus* also are very similar to those of the American species. Both have attained about the same degree of selenodont compression: that is to say, considerably more than *Brachyodus Gorringei* and considerably less than *Ancodus velaunus*.

† W. D. MATTHEW, "Observations upon the genus *Ancodon*," 'Bull. Am. Mus. Nat. Hist.,' vol. 26, 1909.

species come from four successive levels of which the geological sequence is beyond doubt. They are not in absolute genetic sequence, but nearly so. Among the skulls which I have described of European Ancodonts and Brachyodonts, on the other hand, it seems clear that it is the shorter skulls in which the specialisation of the otic and glenoid region has gone least far. Their geological age is rarely as indisputable as in the case of the American species, but it is pretty clear that this kind of specialisation can only have proceeded in one direction, whatever may have happened to the snout. There is, however, no question of the European species forming anything like a genetic sequence, and it is quite possible that certain of the phyla so inadequately represented may have undergone a shortening of the snout while still retaining a highly specialised otic region.

IV. Mixtotherium.

Before passing to a comparison of the Anthracotheriidæ and the Cebochœridæ it will be convenient to deal with the skull of another form, already described and figured by Stehlin*: that of *Mixtotherium* Filhol.

The very complete skull described by Stehlin comes from the Phosphorites du Quercy and is in the Musée d'Histoire Naturelle in Montauban. When working in this museum last year, I had the good luck to find there, in quite a different case from the rest of the Phosphorites collection, the hinder part of another skull of the genus, without a label but also clearly from the Phosphorites. This fragment shows the details of the oto-glenoid region better than that figured by Stehlin, which is much more heavily mineralised and has rather a rubbed appearance; it is approximately the same size, and the structural details differ only in such very small particulars as might well be expected in different individuals.

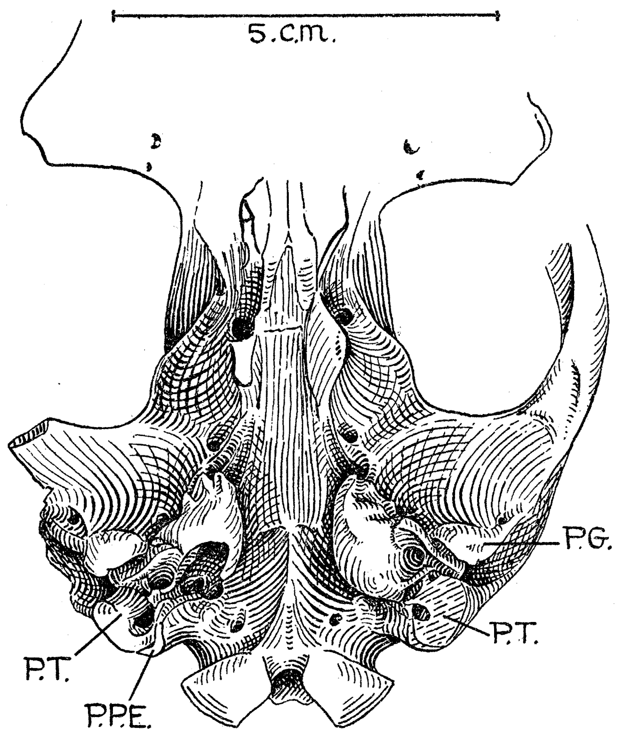
Besides these Montauban skulls there are two others in Paris apparently belonging to a smaller species. One of these, with p^1 to m^3 of either side and part of the left canine, is very crushed and poorly preserved, though it has the better sagittal crest. The other, with p^4—m^3 of either side and a broken left p^3, has the oto-glenoid region and occiput in good condition, and has also kept its long downwardly and backwardly directed paroccipital process, broken short in all the other skulls. The teeth of these two Paris skulls are smaller than those of Filhol's type of *Mixtotherium cuspidatum*† but very

* H. G. Stehlin, "Eocaene Säugethiere," p. 799 ff.

† Filhol occasionally made a type out of two specimens, and these two specimens were not always alike. This is the case here. I have recently examined in Paris the two fragments which he figured as *Mixtotherium cuspidatum* ("Mém. sur quelques Mammifères fossiles des Phosph. du Qu.," 'Ann. Soc. Sci. Phys. et Nat.,' Toulouse, 1882, pp. 92-96, pl. ix, figs. 1-7). They are: (*a*) the fragment of a skull with three molars—the teeth very freshly cut and not well preserved; (*b*) the fragment of an upper jaw with the incisor alveoli and *c* to m^1. At first sight the two first molars, the only teeth present in both specimens, appear to be of about the same size, but a closer examination seems to me to reveal that the badly preserved m^1 of (*a*) is really broken, for the accompanying m^2 and m^3 are so much too big for an animal with an m^1 of the size of that in (*b*). All the teeth of (*b*) agree very well in size and structure with those from the Phosphorites in the Montauban Museum, which Stehlin has figured ("Eocaene Säugethiere," p. 800, fig. cxvii) as *M. cuspidatum*, but the m^2 and m^3 of this latter are *much* smaller than those of Filhol's type specimen (*a*).

similar in pattern, the protoconule only just to be seen on m^1, while on m^2 and m^3 it is practically not to be distinguished.

After what we have learnt of the basicranial peculiarities of the Anthracotheriidæ an examination of the skull of *Mixtotherium* at once shows us that we are dealing here with a similar type of development.* Again we have a skull in which the external auditory meatus and the neck of the tympanic bone ensheathing it are compressed



TEXT-FIG. 33.—Ventral view of hinder end of skull of *Mixtotherium* sp. from the Phosphorites du Quercy. (MONTAUBAN, 'Musée d'Histoire Naturelle.') Bulla of left side partly restored from that of right. The scale is approximate. P.G. and P.T., postglenoid and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital.

by an approximation of the postglenoid and post-tympanic processes of the squamosal. Again all that we can see of the tympanic neck is a thin ventral crest with a groove behind it. And again, there is no mastoid exposure of the periotic bone, but the paroccipital process of the exoccipital is pressed tightly against the back of the post-tympanic process of the squamosal.

In this region of its skull *Mixtotherium* differs from the Anthracotheres principally in being less specialised. The postglenoid compression is not so extreme, the glenoid surface is slightly *dorsal* to the basisphenoidal level and shows no tendency to shift

* MARTIN SCHMIDT in his paper "Ueber Paarhufer der Fluviomarinen Schichten des Fajum" (Geolog. u. Palaeontolog. Abhandl., Neue Folge, Bd. xi, Heft 3, p. 21) has already pointed out that the Anthracothere *Brachyodus Gorringei* resembles *Mixtotherium* in many characters of the otic region.

laterally, the external auditory meatus remains short, and in correspondence with this the post-tympanic squamosal is not so broad nor the exoccipital splayed out in such a broad shoulder behind it.

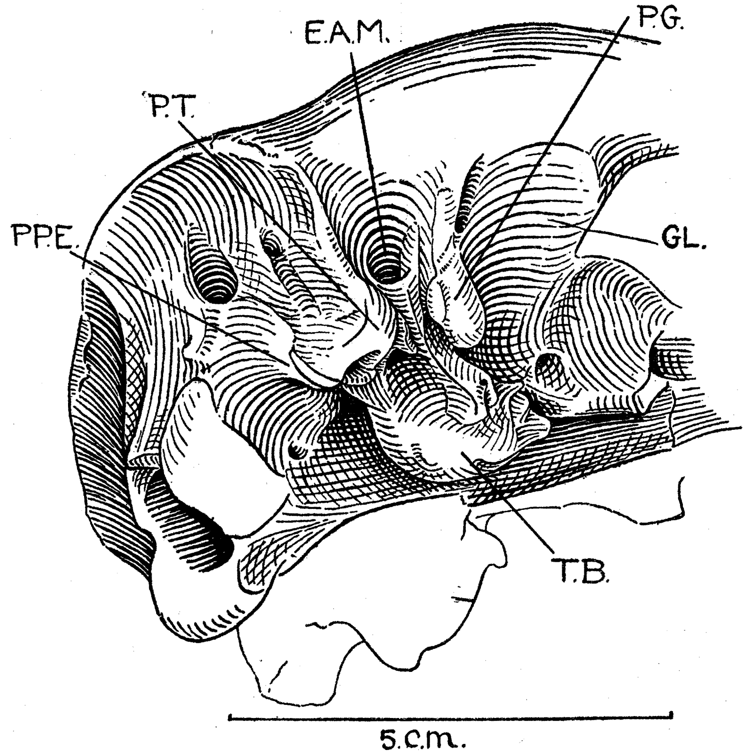
One noteworthy feature of the Montauban fragment of *Mixtotherium* is the very great thickness of the post-tympanic process of the squamosal. It is true that in those Anthracotheres where the postglenoid compression is not so great—as for instance, in *Brachyodus Gorringei*—it is a fairly thick plate, but the shoulder of exoccipital pressed forwards behind it towards the tympanic neck is always of greater importance. Here, however, instead of being as there a wide plate, it is a very thick pillar widely separating the paroccipital and the tympanic neck. A stout post-tympanic process of the squamosal is probably a primitive feature,* and the fact that it is much less massive in the smaller species of *Mixtotherium* in Paris, which in nearly all its other characters is more primitive than the Montauban skull, may be attributed to the Paris skull being altogether smaller and less massive, with occipital and zygomatic crests far less strongly developed, and the postglenoid as well as the post-tympanic process less powerful.

In the Montauban fragment some of the oto-glenoid characters are so much better shown than in the skull figured by STEHLIN that I will give a short description of them here.

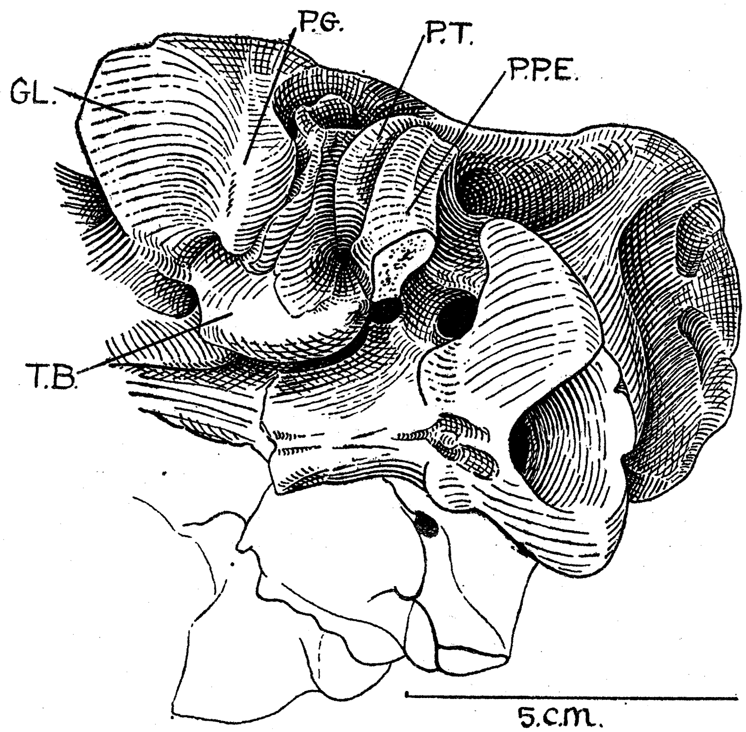
The postglenoid process is very long and pendent, rather narrow, but thick at the tip. Between it and the tympanic neck is a very narrow groove which leads medially into a small postglenoid foramen.† This groove corresponds to the one described above in *Brachyodus Gorringei*, where, however, only the outer end is left open, the tympanic neck being pressed, more medially, tightly against the back of the postglenoid process. The tympanic bulla is large and swollen; anteriorly its tip bears several little bony excrescences, posteriorly it reaches back so as to cover the posterior lacerated foramen. The ventral crest of the neck extends inwards on to a raised area of bone that rests like a flap against the rounded surface of the bulla; this is very reminiscent of the condition in *Brachyodus Gorringei* (compare text-figs. 34 and 35), as is also the position of the tympano-hyal pit immediately behind this raised area in the angle between neck and bulla. In *B. Gorringei* the pit appears to rest directly against the inner end of the post-tympanic squamosal, and the stylomastoid foramen would seem to have been confluent with it, but in *Mixtotherium*, where the compression is less great, the pit can be seen to be completely surrounded by tympanic, a narrow bridge of that bone passing round behind it from the bulla to the neck, while the stylomastoid foramen is a narrow cleft lying between this bridge and the post-tympanic squamosal. From the mouth of the

* See the last section of this paper.

† In the Paris skull this groove is almost completely closed over on the right side by fusion of an outgrowth from the tympanic neck with the postglenoid process. On the left side it is only partly covered by a narrow bridge of bone. Similar outgrowths from the tympanic neck to the postglenoid are commonly found in quite unrelated groups of Artiodactyls where no compression occurs, as will be described below; they are a character which varies much in different individuals.



TEXT-FIG. 34.—Oblique view of hinder end of skull of *Mixtotherium*, reconstructed from two specimens in the Musée d'Histoire Naturelle, Montauban. E.A.M., opening of external auditory meatus; GL., glenoid surface; P.G. and P.T., postglenoid and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital; T.B., tympanic bulla.



TEXT-FIG. 35.—Oblique view of hinder end of same skull of *Brachyodus Gorringei* as in fig. 31. GL., glenoid surface; P.G. and P.T., postglenoid and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital; T.B., tympanic bulla.

tympano-hyal pit a narrow groove runs outwards between the post-tympanic squamosal and the crest of the tympanic neck : it is joined by another little groove from the mouth of the stylomastoid foramen ; these are the grooves which become pressed together to form the single groove found in this position in the Anthracotheres. The sinus which appears in my figures as a dark space in the substance of the post-tympanic squamosal is only seen because the bone here is worn away.

Mention may here be made of a very well-marked shelf with concave ventral surface which runs forwards on the lateral wall of the cranium from the anterior border of the glenoid. This would appear to be the dorsal boundary of the origin of the external pterygoid muscle, and suggests that this muscle was a powerful one. Little else of the pterygoid region remains and nothing of the palate or of the greater part of the snout. The occipital crest is broken, but the two characteristic pits are present on either side of the occiput.

The Anthracotheriidæ, the Mixtotheriidæ and the Cebochœridæ.

Battle has already been waged over the resemblance between the skulls of *Mixtotherium* and *Cebochœrus*, and its meaning. CHARLES EARLE,* who in Paris had the actual material in front of him, was sufficiently impressed by this resemblance to claim relationship. STEHLIN† later insisted that they resembled one another only in such superficial characters as the general shape of the skull and the smallness of the brain case, while the basis cranii, the bullæ, the otic region, the paramastoid process tell in detail another story : that we have to do with two unconnected lines of cranial development. To me it seems that both writers are to some extent right. There is no doubt that the two animals are on different lines of development ; the difference in their dentition makes that at once obvious ; but unconnectedness, like distance, is always only comparative, and I believe that here it is not so great as between many lines of development which STEHLIN allows to be linked to one another.

The evidence from the basiotic region, so far from damning EARLE's contention, seems to me to be in favour of it, and this by virtue of the possession by both genera of just those characters in which, as I have tried to show, *Mixtotherium* resembled the Anthracotheres : namely, the tendency to compression of the parts behind the glenoid, the tendency to lengthen the external auditory meatus, the absence of a mastoid exposure of the periotic, and the possession of a powerful post-tympanic process of the squamosal. Just as in *Mixtotherium* the compression and lengthening of the tympanic neck has gone less far than in the Anthracotheres, so in *Cebochœrus* it has gone less far still.

Cebochœrus, *Mixtotherium*, and the Anthracotheres do not form a series, however, for while *Mixtotherium* possesses many Anthracotherid characters which *Cebochœrus*

* C. EARLE, "Notes on the Fossil Mammals of Europe," 'American Naturalist,' 1896-98.

† H. G. STEHLIN, "Eocaene Säugethiere," p. 815.

does not, *Cebochœrus* also possesses certain Anthracotherid characters which *Mixtotherium* does not. Among the former may be mentioned the swollen bulla and the narrow, pendent postglenoid process; among the latter the tendency to lower the glenoid surface, the forward direction of its outer end, and the plate-like post-tympanic process of the squamosal.

Of either genus being in the ancestral line of the Anthracotheres there has never been any question. All that I wish to advocate here is, that they are both members of a big group, to which the Anthracotheres also belong by virtue of common ancestry; that owing to the comparative conservatism of their basiotic region, they throw light on what we must expect to find in the as yet undiscovered ancestral Anthracothere; and that *Cebochœrus* shows the greater conservatism in respect of most of the common trends.

Presently I shall try to establish the claims of *Cebochœrus* to be more nearly in the ancestral line of *Hippopotamus*—a view which STEHLIN thinks not improbable.* Now *Hippopotamus* is so close a parallel to the Anthracotheres in cranial development, that one cannot but believe the kinship to be a near one. If then *Cebochœrus* can give origin to an animal so Anthracothere-like as *Hippopotamus*, surely it must itself have been very similar to the animal which gave origin to the Anthracotheres.

It may be well to recall here those trends of the Cebochœrid family, noted above in the description of the different species, which do not point in the direction of the true Anthracotheres. These are: (1) the broadening of the postglenoid process from side to side, its thinning out antero-posteriorly, and its reduction in height so that the glenoid cavity becomes shallower; (2) the changing of the third upper premolar from a tooth with inner and outer subequal cusps into a tooth with one main cusp, and a postero-internal cingulum; (3) the enlarging of p^1 into a caniniform tooth; (4) the development of more bunodont cheek teeth. These trends are comparable with the peculiar trends of the Mixtotherid family, namely the thickening of the post-tympanic squamosal and the molarisation of the premolars. Peculiar to the Anthracotheres are the passing out to the side (not only downwards) of the glenoid, and the ruminant-like specialisation of the molar teeth in *Brachyodus* and *Ancodus*.

Since EARLE has been criticised for neglecting essentials in comparing the skulls of *Cebochœrus* and *Mixtotherium* it may be wise to give a detailed comparison here. For this purpose I will use the Paris skull of *Cebochœrus lacustris* (which was also that described by EARLE) and the larger species of *Mixtotherium*, these being so very similar in size and proportions. Figs. 23 and 33 illustrate best this comparison.

In the otic region the most striking difference lies in the shape of the tympanic bulla. Whereas in *Mixtotherium* this is large and swollen, making the basioccipital look narrow, completely concealing the periotic bone, and covering in the posterior lacerated foramen, in *Cebochœrus* it is small and rather flattened, allows a broad corner of periotic to appear in front of it and the posterior lacerated foramen to open widely behind it, while the

* H. G. STEHLIN, "Eocaene Säugethiere," p. 751.

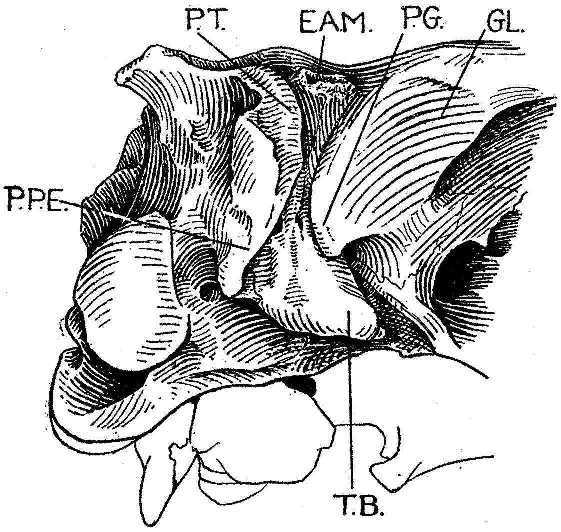
basioccipital exposure is wide. The hinder part of the bulla in *Mixtotherium*, overhanging the posterior lacerated foramen and almost touching the paroccipital process, is represented in *Cebochœrus* by a long and narrow bridge of bone passing between this foramen and the stylomastoid foramen to join the paroccipital. The paroccipital process itself, though it usually seems in *Cebochœrus* to be broken at the tip, was probably never as long as in *Mixtotherium*; it is much stouter than in the latter however, with a broad groove leading down its anterior surface from the mouth of the stylomastoid foramen. These characters of the *Cebochœrus* paroccipital may be interpreted as a lesser degree of compression, and therefore as probably nearer to the primitive condition of the Anthracothere group. Tympanohyal pit and stylomastoid foramen seem to be confluent in *Cebochœrus* as in the Anthracotheres. The neck of the *Cebochœrus* tympanic appears at first sight to be longer than that of *Mixtotherium*, but I think this is only in comparison with the size of the bulla; it is certainly less compressed, though it bears a trace of the ventral crest and flap so characteristic of both *Mixtotherium* and the Anthracotheres (but lacking, it should be remembered, in the smaller, more primitive species of *Cebochœrus* where the "neck" is little if at all compressed). The glenoid surface of both genera is flat, sloping up gradually on to the face of the postglenoid process. This process is stout in both genera, but in *Mixtotherium* it is narrower from side to side, in *Cebochœrus* thinner from behind forwards.

As regards the rest of the skull, in most ways so strikingly alike in these two animals, it may be noted that the snout of *Cebochœrus* is slightly longer, the teeth not being so crowded on one another. The dorsal edge of the zygoma joins the occipital crest much higher up in *Cebochœrus* than in *Mixtotherium*, making with it a long drawn out, sharp angle instead of something like a right angle. Finally the maxillary attachment of the zygoma is not so broad in *Cebochœrus*, joining the alveolar border at about the level of the first molar, whereas in *Mixtotherium* it joins it as far forwards as the third premolar. These are insignificant differences, however, such as may be expected to vary even in individuals of the same genus. What is so strikingly similar in both is the arrangement of the powerful muscle attachments, especially those bordering the temporal fossa: the sagittal and occipital crests are strong, the latter continuing right down on to the post-tympanic squamosal, the zygomata are broad, the post-orbital processes of the frontals are heavy, and there are deep muscle pits and well marked muscle ridges on the occiputs. The smaller, more primitive species of both genera are weaker in all these respects, and the attainment of this greater muscularity by such identical methods (accompanying of course, an increase in size) seems to me in itself to be a point in favour of a not very distant common origin for the two races.

Cebochœrus, Hippopotamus, and the Anthracotheres.

A comparison of fig. 36 with figs. 31 and 35 will show how much the otic region of *Hippopotamus* resembles that of the Anthracotheres. In both the posterior position of the glenoid has led to the approximation of the postglenoid process to the post-tympanic parts of the skull and to the compression of the tympanic neck into a thin vertical crest with only a groove between it and the post-tympanic squamosal. The external auditory meatus has become correspondingly narrow and its outer opening carried up high on to the side of the skull. The post-tympanic squamosal is, in each case, a flat plate without the additional little paroccipital process of the Suidæ.

The occiput in *Hippopotamus* is again strikingly like that of the Anthracotheres, though even broader from side to side in comparison with its height. There are shallow depressions on either side of the middle line, and the exoccipital is splayed out into a broad shoulder at the back of the postglenoid region, its little downwardly directed paroccipital process lying directly behind the postglenoid process.



TEXT-FIG. 36.—Ventral view of hinder end of skull of a West African Pigmy Hippopotamus (*Chœropsis liberiensis*).*

In a more detailed comparison we find several very important differences however. The glenoid surface of *Hippopotamus* is quite differently shaped, broad from side to side and sloping downwards very gradually on to the face of the postglenoid process. The glenoid has neither passed downwards very far in relation to the *basis cranii* nor yet out to the side. The paroccipital process has come to lie in the same transverse plane as the post-tympanic squamosal, the shoulder of the exoccipital forming with the latter a single flattened plate, from the ventro-medial corner of which the small paroccipital process projects downwards.

In all these points *Cebochœrus* would form a better ancestor for *Hippopotamus* than would any of the Oligocene Anthracotheres. *Cebochœrus* had the same type of low post-glenoid process making a very gradual slope with the glenoid surface, though this was

* Skull made available through the courtesy of Mr. R. H. BURNE, of the Royal College of Surgeons.

not at that stage so broad. The position of its glenoid was furthermore conservative in relation to the *basis cranii*. There was as yet little compression of the postglenoid parts, and the post-tympanic plate of the squamosal lay antero-lateral to the paroccipital process instead of directly anterior to it, as in the Anthracotheres : compression in such a skull might well result in the *Hippopotamus*-like condition of the two lying side by side.

Thus while the Anthracotheres advanced very fast along their own line of postglenoid compression and of lateral shifting of the glenoid, and had already reached an extreme in the Oligocene, the as yet unknown Oligocene *Hippopotami*, possessing similar tendencies, were developing them rather more slowly and also along peculiar lines of their own. These lines resembled those of the conservative little Upper Eocene Cebochœridæ more than of any other extinct forms that we know.

One other *Hippopotamus*-like tendency of *Cebochœrus* was the tendency to thicken and broaden the supraorbital plate and postorbital process of the frontal bone.

V. Chœropotamus.

In Paris there are two skulls of this genus from the Upper Eocene, that from the Paris Gypse, which was figured by Cuvier in the "Ossemens Fossiles,"* and another from La Débruge. A third skull coming from the Upper Eocene of Mormoiron, Vaucluse, is in Lyons (Faculté des Sciences) and has recently been described and figured by Roman.† All three of these are very incomplete and help us but little to understand the affinity of the animal.

Like the forms which I have been describing, *Chœropotamus* clearly has no *pars mastoidea* of the periotic bone, but the compression of the parts behind the glenoid is not very great. The gap for the external auditory meatus between the postglenoid and post-tympanic processes of the squamosal is a wide one, and the long paroccipital process of the exoccipital projects backwards away from the latter, instead of being pressed forwards tightly against it as in the Anthracotheres. Whether an ossified tympanic were ever present is not clear. The post-tympanic squamosal is of about the same thickness as in *Cebochœrus*, the postglenoid low and stout, but longer and with more of a tendency to hook forwards than in that genus. Other marked differences from *Cebochœrus* are in the flat, spherical glenoid surface, the extremely low dorsal edge of the zygoma (correlated with the narrowness of the zygomatic arch itself), and the very narrow occiput combined with an extremely high parietal crest.

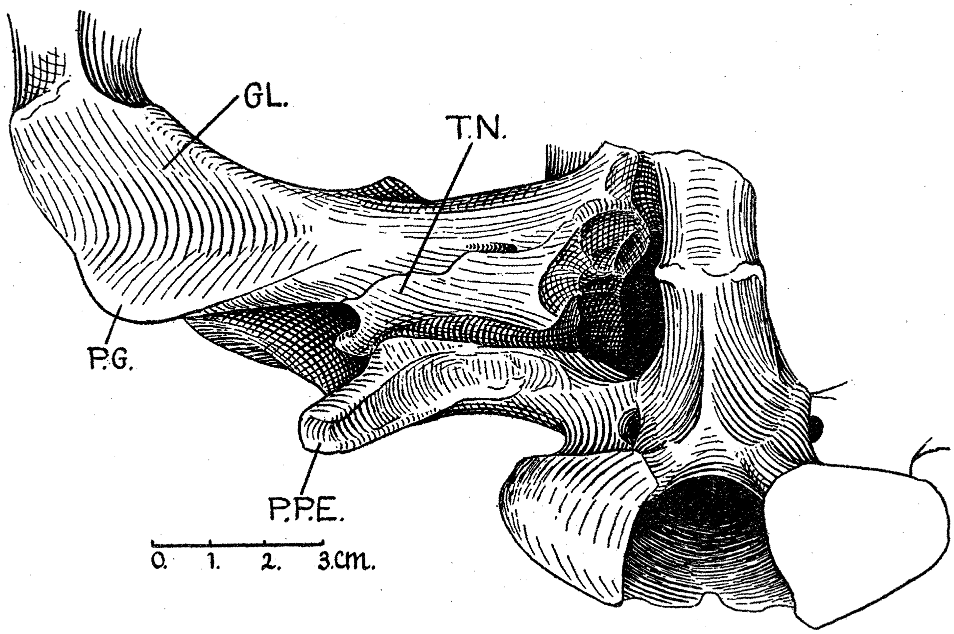
Chœropotamus would thus seem to belong to an early offshoot of the Anthracotherioid stock, which developed along special lines of its own quite independently of those other offshoots represented in the Upper Eocene by *Cebochœrus* and *Mixtotherium*.

* G. Cuvier, "Recherches sur les Ossemens Fossiles," 4th ed., plate 149.

† F. Roman, "Monographie de la Faune de Mammifères de Mormoiron (Vaucluse)," 'Mém. de la Soc. Géol. de France,' vol. 25, 1922.

VI. Entelodon.

On the affinities of this other much disputed genus, I am also unable to throw much new light. Scott* has long since given a clear figure of the basicranial region of one of the American species, and that which I give here—from a skull in Munich, bearing the old label "*Elotherium Mortoni* Leidy, White River, Oreodon beds, Land Creek, Nebraska"—shows essentially the same structure (text-fig. 37).



Text-fig. 37.—Ventral view of basiotic region of skull of *Elotherium Mortoni* from the White River, Oreodon beds, Land Creek, Nebraska. (Bayerische Staatssammlung.) GL., glenoid surface; P.G., postglenoid process; P.P.E., paroccipital process of exoccipital; T.N., tympanic neck.

That its relationship to the Suidæ can have been but a remote one is now generally accepted. Its basicranial structure is in favour of the view that it lies on the whole nearer to the Anthracotheres. Thus the postglenoid compression, which is present in an extreme form, has been brought about in a strikingly similar fashion and is associated with a passing out to the side of the glenoid which is also extreme. The tympanic neck, just as in *Ancodus velaunus*, appears as a thin strip of bone flattened against the back of that long bar of squamosal which separates the glenoid from the bulla; it does not reach as far laterally as the glenoid. Along the back of this strip of bone runs a groove leading inwards to what must have been the mouth of the stylomastoid foramen. The paroccipital process is pressed tightly against the back of the tympanic neck—so tightly, that the ventral edge of the post-tympanic squamosal is apparently not visible between them. The paroccipital is very differently shaped from that in Anthracotheres however.

* W. B. Scott, "The Osteology of Elotherium," 'Transactions of the American Philosophical Society,' vol. xix, p. 273, 1898.

There we found a flat plate overlying the back of the post-tympanic plate of the squamosal and from it a stout ventral process projecting freely downwards. Here there is no such distinction into shoulder and process, there is simply a stout bar passing outwards along the back of the tympanic neck, its distal end projecting freely behind the outer opening of the external auditory meatus. Whether, as SCOTT reports, but does not show in his figure, there is really an exposed surface of periotic bone in the occipital hollow above this bar, cannot be determined from the Munich skull, where the periotics have fallen out; there is certainly a small gap here which they may possibly have filled, but in any case this would not be the right position for a *pars mastoidea*. The squamosal clearly carries the whole of the lateral occipital crest and is flattened down on to the occipital surface of the skull above and lateral to this gap.

It is interesting that the lateral occipital crests pass below into the dorsal edges of the zygomata around the borders of enormous flaps or hoods of bone, that rise up from the back of the glenoids and overhang the lateral openings of the external auditory meati—interesting, because of the resemblance of these hoods to the characteristic, though much less magnificent hoods in the Suidæ, and in view of the fact that in more primitive Suidæ, such as *Palæochœrus* and *Perchœrus*, they are larger than in the recent forms.

The glenoid itself and the postglenoid process are in no way Anthracothere-like; the latter is broad from side to side and very low, the former curving gently down on to its face, so that the resulting surface is the section of a cylinder, rather like that in Dicotyles and probably permitting no greater freedom of movement to the mandibular condyle.

SCOTT did not, in the paper just referred to, compare *Entelodon* with the Anthracotheres. He compared it with *Hippopotamus* however, pointing out resemblances both superficial and deeper seated. These latter, it seems to me, are equally shared with the Anthracotheres. The Suidæ appear to be rather more remote. But there are certain characters which tend to appear in all these forms, linking them all together as the descendants of a common, if distant, stock that separated very early from the other Artiodactyls.

Note on Kowalevsky's Skull of "Entelodon."

The cranial fragment from the Phosphorites du Quercy which KOWALEVSKY described and figured* as the European *Entelodon* is in the Museum of the Faculté des Sciences in Toulouse. It lies there without a label, and when I myself examined it, not long after studying the American *Entelodon* skull in Munich, it never for a moment occurred to me that it could belong to the same type of animal. Later I discovered its identity with KOWALEVSKY's figures. Its exoccipital bones have downwardly directed paroccipital processes, not horizontal ones as in the true *Entelodon*. On the edge of the occiput between the exoccipitals and the squamosals there is a triangular gap, which together with the broad facet on the face of the paroccipital appeared to me to be the resting place of

* W. KOWALEVSKY, "Osteologie des Genus *Entelodon* Aym." 'Palæontographica,' vol. 22, p. 415, 1876.

a powerful periotic mastoid. The whole fragment is shaped very much like the corresponding region of an Anoplothere skull, though too large for *Anoplotherium commune*. In any case it is extremely hard to make a mental restoration of the fragment that would in any way approach it to the *Entelodon* of America. From the account given by KOWALEVSKY of its discovery, there would seem to be a loophole for doubting the correctness of its association with *Entelodon* teeth.

Two Types of Artiodactyl Skull.

All the animals with which we have so far been dealing are characterised by the absence of a *pars mastoidea* of the periotic bone, or at any rate by its failure to appear on the outer surface of the skull. The post-tympanic process of the squamosal to some extent takes its place, but there is a tendency to compress all the parts behind the glenoid. In some cases, but not in all, there is a tendency to lower the level of the glenoid, and sometimes to shift it out to the side, thus widening simultaneously the temporal fossa and the occiput. There is also a tendency to develop heavy lower jaws, powerful sagittal and temporal crests, and a wide zygoma. The incisor teeth are usually well developed, evidently playing an important part in nutrition. The canines tend to become enlarged as tusks.

When we turn to the other Upper Eocene genera of which the skulls are known, we find ourselves at once very far away from any of the families with which this paper has hitherto been dealing. In all of them, there is a *pars mastoidea* of the periotic bone exposed on the surface of the skull between the exoccipital and the squamosal, while the post-tympanic process of the squamosal is small and does not approach the post-glenoid process. Furthermore, the glenoid surface is always close to the cranium, the occiput is narrow, the muscle crests are usually weakly developed, the zygoma is weak, the lower jaw slender, the canine tooth not strongly differentiated from the incisors and the premolars.

VII. HAPLOBUNODON.

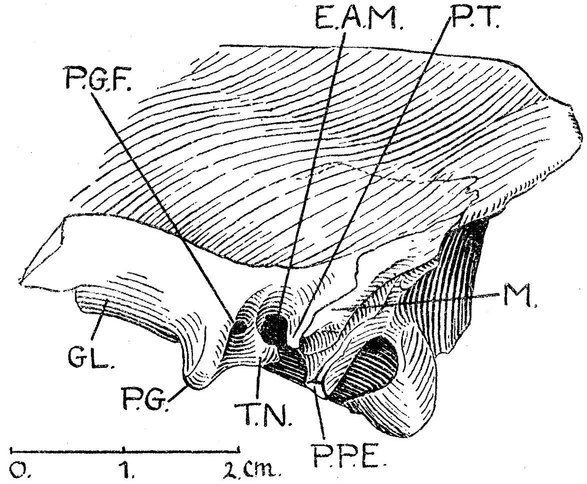
The little skull in the British Museum from the Upper Eocene beds of Hordwell, Hampshire, named by LYDEKKER* "*Anthracotherium Gresslyi*," must now be called *Haplobunodon Lydekkeri*.† Although LYDEKKER only figured the jaws, half of the occiput and the basiotic region of the left side are in good condition, and these I have represented here in text figs. 38 to 40.

It can be seen from text-fig. 38, that the *pars mastoidea* of the periotic is a strip of bone wedged in between the squamosal and the exoccipital at the hinder edge of the skull. Its lower end is grooved at the mouth of the stylomastoid foramen. The post-tympanic part of the squamosal is a small bluntly pointed process projecting just a little

* R. LYDEKKER, "Note on three genera of fossil Artiodactyla," 'Geolog. Mag. (3),' II, p. 69, 1885.

† H. G. STEHLIN, "Eocaene Säugethiere," p. 752, and C. DEPÉRET, 'Comptes Rendus,' vol. 146, 1908, p. 4.

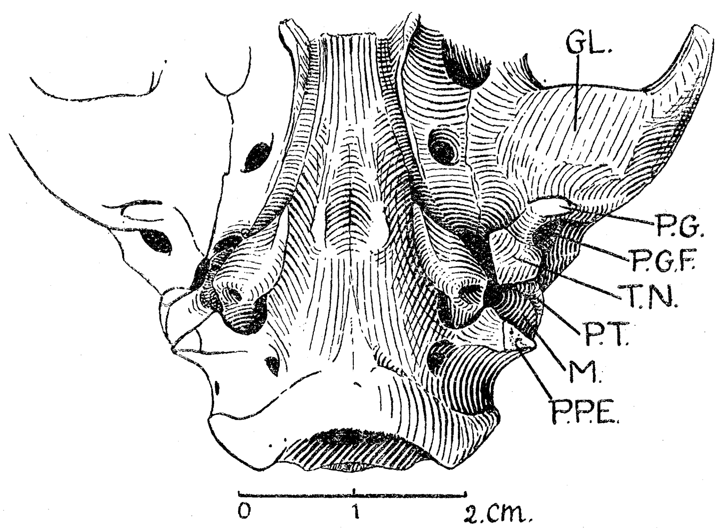
below the mastoid and widely separated from the postglenoid process. The exoccipital, having no broad post-tympanic plate of the squamosal in front of it, is not splayed out



TEXT-FIG. 38.—Lateral view of hinder end of skull of *Haplobunodon Lydekkeri* from Hordwell, Hampshire. (No. 29051 British Museum, Natural History.) E.A.M., outer opening of external auditory meatus ; GL., glenoid surface ; M., mastoid ; P.G. and P.T., postglenoid and post-tympanic processes of squamosal ; P.G.F., postglenoid foramen ; P.P.E., paroccipital process of exoccipital ; T.N., tympanic neck.

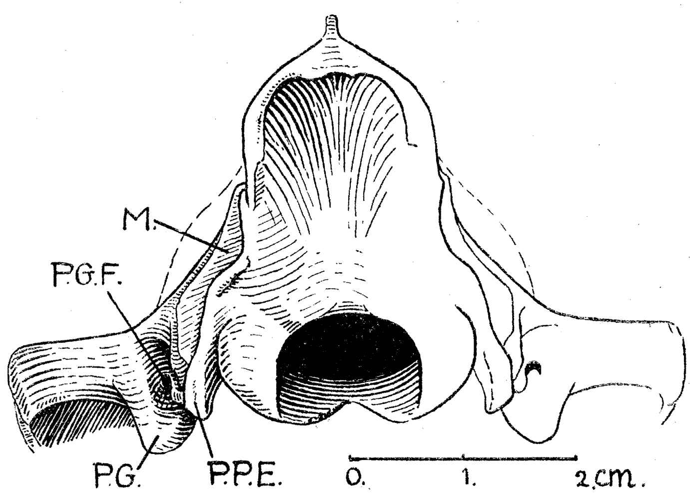
against the back of the tympanic region as in the forms hitherto described ; it has a paroccipital process of moderate length.

The condition of the tympanic bone is an interesting one (text-fig. 39). There is



TEXT-FIG. 39.—Ventral view of hinder end of skull of *Haplobunodon Lydekkeri* from Hordwell, Hampshire. (British Museum, Natural History.) GL., glenoid surface ; M., mastoid ; P.G. and P.T., postglenoid and post-tympanic processes of squamosal ; P.G.F., postglenoid foramen ; P.P.E., paroccipital process of exoccipital ; T.N., tympanic neck.

no ossified bulla, the periotic being freely exposed from ventral view, but fused with the back of the postglenoid process is a small curved piece of bone projecting beneath the external auditory meatus, to which its upwardly facing concave surface forms an incomplete floor—incomplete because its hinder edge fails to meet the post-tympanic process of the squamosal, there being a wide gap between the two. Both this hinder edge and the medial edge have smooth surfaces, showing that there was never more bone present. This piece of bone represents what I have called in this paper the "tympanic neck"; we may imagine that it has arisen by the outward extension beneath the external auditory meatus of ossification from a primary tympanic ring or half ring, no inward extension having taken place such as in bullate forms produces the bulla.*



TEXT-FIG. 40.—Occipital view of same skull of *Haplobunodon Lydekkeri* as in text-figs. 38 and 39. Lettering as before.

The postglenoid process, pierced behind by a big postglenoid foramen, is narrow from side to side, while the glenoid surface is broad and slightly convex.

There is a very high sagittal crest and this is correlated with a high, narrow occiput, with moderately well developed lateral occipital crests running down on to the paroccipital processes, and with very wide temporal fossæ embraced by rather stout zygomata.

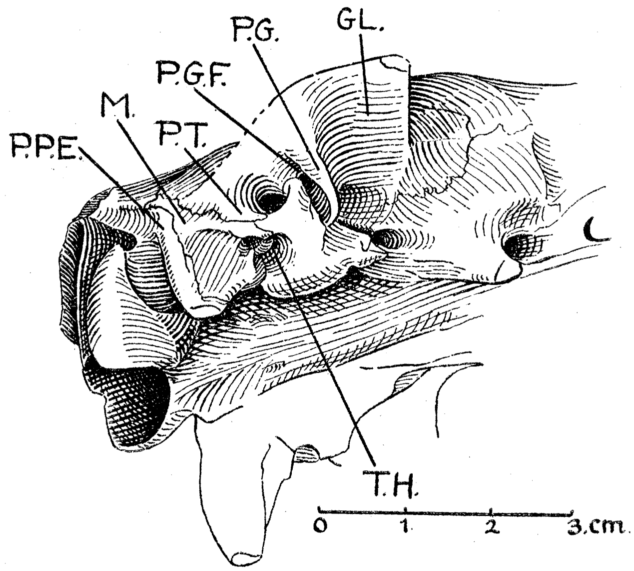
VIII. DACRYTHERIUM AND THE ANOPLOTHERES.

Although both STEHLIN and CHARLES EARLE have insisted on the difference between *Dacrytherium* and *Mixtotherium*, which the old authors were inclined to confuse owing to the great similarity of the molar teeth, I do not think they have done so with sufficient emphasis. EARLE still believed that *Mixtotherium* is intermediate in type between the Anoplotheres and the Suidæ, and that it demonstrates how closely these are related to one another. STEHLIN still separates *Dacrytherium* from *Anoplotherium* and *Diplobune*, and places it with *Mixtotherium* in his group of "Eocene Hyopotamidæ." Good skull material of *Dacrytherium*, of *Diplobune* and of *Anoplotherium* is to be found

* P. N. VAN KAMPEN, "Die Tympanalgegend des Säugetierschädels," 'Morphologisches Jahrbuch,' 1905, vol. 34, p. 358, etc.

however—in Paris, in Munich, and in London—and I think shows indisputably that even if they do not belong to the same family, still they fall very naturally into a single group of which *Dacrytherium* is in most of its characters the least specialised member, and with which *Mixtotherium* has no connection whatever.

First of all *Dacrytherium* has a very broad mastoid. This completely separates the exoccipital from the squamosal, commencing above as a narrow strip of bone on the edge of the occiput at the level of the parieto-squamosal suture, and broadening ventrally as it passes down on the anterior face of the long, laterally compressed paroccipital process. It is divided into upper and lower portions by a sharp ridge, a division marking the remains of the old primitive forking into exoccipital and squamosal portions. This ridge is close behind the suture of the mastoid with the very small post-tympanic process



TEXT-FIG. 41.—Oblique view of hinder end of skull of *Dacrytherium* from the Phosphorites du Quercy (Paris Muséum National.) GL., glenoid surface; M., mastoid; P.G. and P.T., post-glenoid and post-tympanic processes of squamosal; P.G.F., post-glenoid foramen; P.P.E., paroccipital process of exoccipital; T.H., tympanohyal in pit.

of the squamosal: at its anterior end there lies between it and the lower paroccipital part of the mastoid the groove which leads up to the stylomastoid foramen. Immediately in front of that foramen, and thus bounded behind by the mastoid, is the tympanohyal pit, lying in the angle between the tympanic neck and the hinder part of the bulla and containing a bony tympanohyal plug. The mastoid thus occupies in *Dacrytherium* the place which in the amastoid Artiodactyla was held by the post-tympanic process of the squamosal. Although the latter is in *Dacrytherium* insignificant, the mastoid is so broad that the paroccipital process is separated much more widely from the neck of the tympanic than in any of the amastoid forms except perhaps the early

Suidæ, which it will be remembered were peculiar in having a backwardly directed paroccipital process of the squamosal.

Thus in *Dacrytherium* there is not the slightest tendency to concealment or compression from behind of the tympanic neck, which in itself is broad and rather short, the external auditory meatus therefore short and wide. In front, it is separated by a deep groove from the rather thin postglenoid process, and at the bottom of this groove lies a post-glenoid foramen. The tympanic bulla is flattened ventrally and drawn into a long point in front. The flat glenoid surface is at a little higher level than the *basis cranii*: at its postero-lateral corner it curves smoothly upwards into continuity with the outer surface of the zygoma.

The articular surfaces of the occipital condyles are extended on to little projections on either side of the basioccipital. The occiput is high and bounded above by a moderately powerful occipital crest, but this does not continue downwards on to the zygoma as in amastoid forms such as *Mixtotherium* and *Cebochœrus*, where the temporal fossa is completely walled off from the occiput, this latter tending always to become broader in comparison with its height. The occiput of *Dacrytherium* thus appears constricted in the middle: more ventrally, at condylar level, it widens again into the paroccipital processes. Though the central part of the occiput is more prominent than the parts lateral to it, these are not excavated into deep pits.

The zygomatic arches, usually broken, are slender. The brain case is elongate and the whole skull rather elegant. The presence of a deep preorbital fossa has often been remarked upon as a peculiarity of the genus.

STEHLIN, anxious to show that *Diplobune* and *Anoplotherium* cannot be descendants of the Dacrytheres, has placed the latter in a different family. He nevertheless admits that the Dacrytheres undoubtedly approach the Anoplotheres more nearly than do any other known Middle Eocene Artiodactyls. "Dass die Dacrytherien von allen bis jetzt bekannten mitteleocaenen Artiodactylenstämmen den Anoplotheriden weitaus am nächsten stehen ist freilich unbestreitbar; es mag auch sein, dass die letztern auf mitteleocaene Vorfahren zurückgehen, welche sich von den gleichaltrigen Dacrytherien craniologisch und odontologisch nicht viel anders als durch das Fehlen der Praeorbitalgrube und durch die vollständige Trennung der vordern Innenhügel ihrer Mandibularmolaren unterscheiden. Aber Tiere von diesem Typus sind keine Dacrytherien."*

To my mind the complete separation of *Dacrytherium* from the Anoplotheres on the strength of such differences as the presence of a preorbital fossa and the possession of lower molar teeth in which the antero-internal cusp is fully fused, tends to obscure unnecessarily this really very close approach. Even if *Dacrytherium* has these peculiarities, the main plan of its skull still remains that of *Anoplotherium* and *Diplobune*: in most of the details it differs from these simply by being less specialised. Most of the

* H. G. STEHLIN, "Eocaene Säugethiere," 1910, p. 956.

characters which I have given above are found in these two genera also, but inasmuch as these latter are larger animals, *Anoplotherium* much larger, their skulls are more muscular: that is to say, with the muscle crests better developed, with processes such as the postglenoid and paroccipital stouter and stronger, and the whole structure of a heavier build. These are differences such as separate the skull of *Cebochœrus* from that of "*Leptacotherulum*," the *Mixtotherium* skulls in Montauban from the little *Mixtotherium* in Paris, or the skull of a tiger from that of a cat.

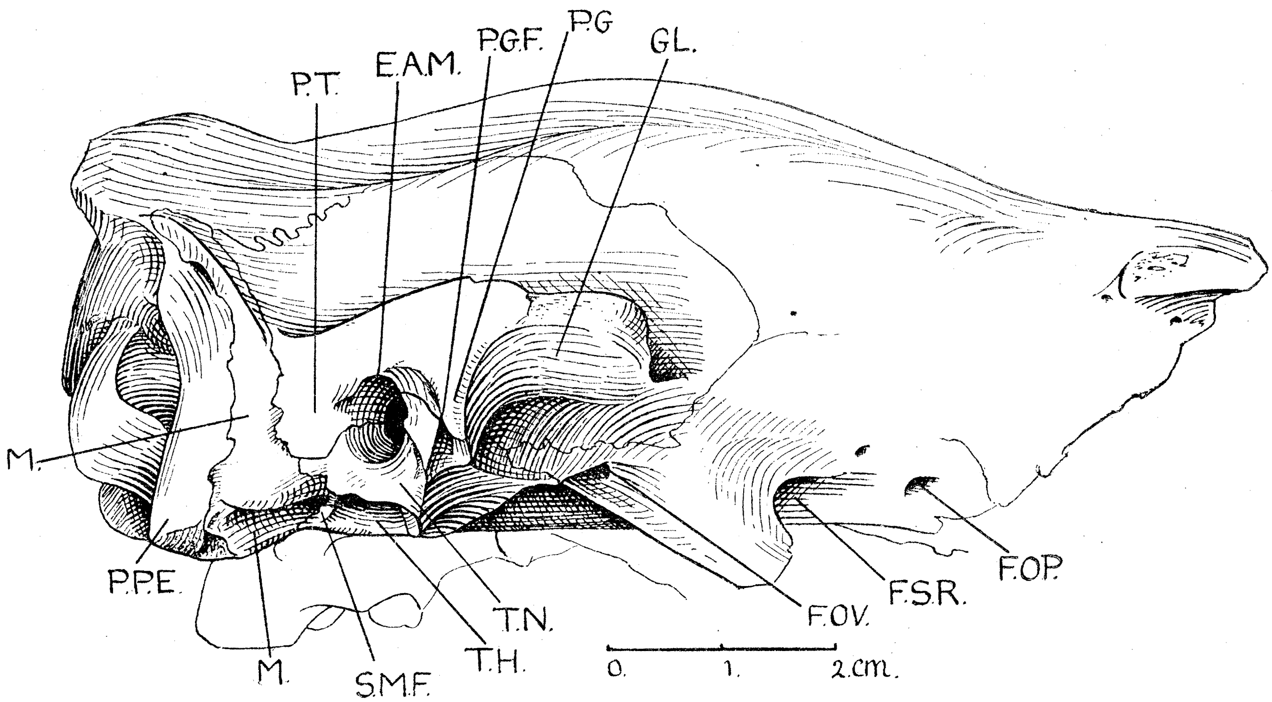
Besides the well-known plates of *Anoplotherium* in CUVIER'S "Ossemens Fossiles" there are some pen and ink drawings by PALMER* of a good cranial fragment from the Phosphorites du Quercy in the British Museum. The following description is based on material in Paris from the Phosphorites and from the Gypse de Montmartre.

In the otic region of *Anoplotherium*, immediately ventral to the opening of the external auditory meatus, the tympanic neck is flattened into a vertical plate of bone separating that opening from the very large trough for the tympanohyal. In *Dacrytherium* this vertical plate is much less deep and the trough much smaller in proportion to the size of the skull. *Anoplotherium* has further a very prominent crest projecting down from the ventral surface of the tympanic neck. This crest is lacking in *Dacrytherium*, where the ventral surface of the neck is not very much lower than the tip of the postglenoid process. The shape of the bulla is very similar: it is flattish, runs to a long point anteriorly, and meets the paroccipital internal to the tympanohyal trough, while the vertical plate described above meets it external to that trough. The arrangement of the mastoid and paroccipital region is so similar to that in *Diplobune*, which I am describing below, that I will not repeat the description here. The glenoid surface is still higher in relation to the *basis cranii* than in *Dacrytherium*. The occiput is of the same narrow type, narrowing especially just above the condyles, where its lateral crests end, instead of continuing forwards into the dorsal edges of the zygomata as in the typical amastoid forms; these lateral crests are much more prominent than in *Dacrytherium* however, and there is also a powerful median crest, very high at its upper end, but gradually lessening as it approaches the *foramen magnum*. High up on either side of the occiput are two small knobs for muscle attachment.

Diplobune, intermediate in size between *Anoplotherium* and *Dacrytherium*, is also intermediate in most of these characters, though nearer to *Anoplotherium*. There are two skulls of this genus in Munich: the one that I have figured (text-figs. 42 and 43), labelled *D. bavaricum* FRAAS, from the Phosphorites of Escamps near Lalbenque, Lot, and another from the Bohnerz of Eselsberg near Ulm. The latter is bigger and is clearly of a different species. In it the hinder margin of the basioccipital is more convex; the position of the condylar foramen is different; the arrangement of the muscle areas on the basioccipital is also different (never a dependable specific character however);

* PALMER, "The Brain and Brain-Case of a Fossil Ungulate of the genus *Anoplotherium*," P.Z.S., 1913, p. 878. PALMER'S figures do not show correctly the arrangement of the sutures in the mastoid region.

the postglenoid process is stouter and projects down further; the ventral edge of this process is met by a projection from the neck of the tympanic, so that the postglenoid groove is converted into a tunnel opening at both ends*; the groove on the face of the paroccipital process opposite the mouth of the stylomastoid foramen, is not so long; there is a very pronounced median crest on the occiput (but the Quercy skull is possibly worn here). In the present discussion, these details are principally of interest as demonstrating what characters of the basicranial region are of little value in the attempt to trace wider relationships or affirm their absence.

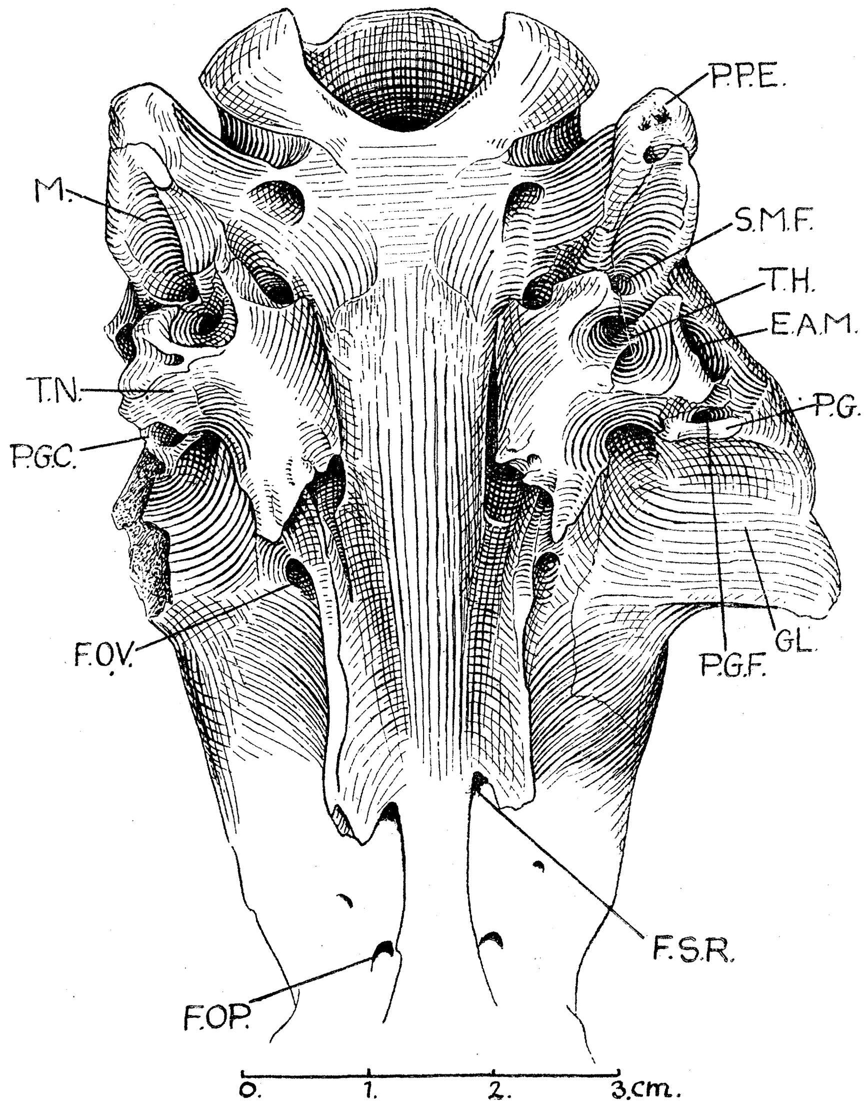


TEXT-FIG. 42.—Slightly oblique lateral view of hinder end of skull of *Diplobune bavaricum* FRAAS from the Phosphorites of Escamps near Lalbenque, Lot. (Bayerische Staatssammlung, 1879, xv.) E.A.M., outer opening of external auditory meatus; GL., glenoid surface; F.OP., *foramen opticum*; F.OV., *foramen ovale*; F.S.R., foramen spheno-rotundum; M., mastoid; P.G. and P.T., post-glenoid and post-tympanic processes of squamosal; P.G.F., postglenoid foramen; P.P.E., paroccipital process of the exoccipital; S.M.F., stylomastoid foramen; T.H., tympanohyal pit; T.N., tympanic neck.

In both these skulls the tympanic neck is thickened as in *Anoplotherium*, projecting vertically downwards below the opening of the external auditory meatus as a great crest of bone whose posterior surface is part of the anterior wall of the large tympanohyal pit. The paroccipital processes are broken short; at their bases they are not so laterally compressed as in *Dacrytherium*, but thick from side to side and from back to front, the broad stylomastoid groove facing directly forwards. The stylomastoid foramen itself

* An interesting parallel to the condition in *Amphimeryx*, see below.

is small, the tympanohyal pit unusually large ; the two are separated by a bony wall of mastoid. In the formation of the paroccipital process the mastoid, as in *Dacrytherium*, plays almost as great a part as the exoccipital, completely excluding the latter from the stylomastoid groove. Again, as in *Dacrytherium*, there is a narrow dorsal portion of the mastoid which carries the feebly developed lateral occipital crest and separates the

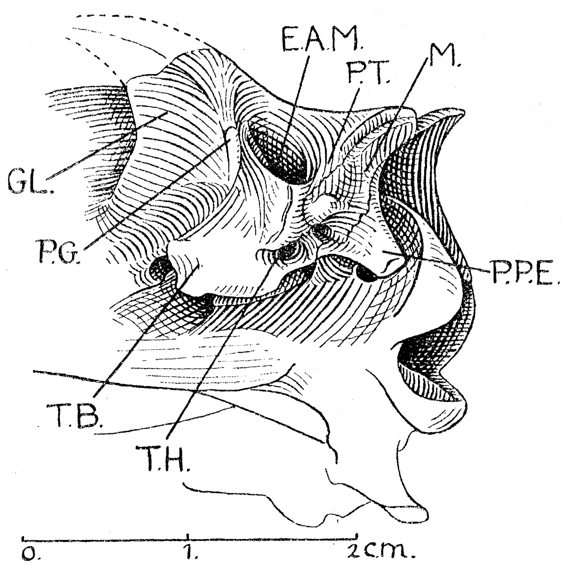


TEXT-FIG. 43.—Ventral view of hinder end of same skull as in text-fig. 42. The scale is approximate. P.G.C., postglenoid canal. Other lettering as before.

exoccipital from the squamosal. The glenoid surface is again well dorsal to the *basis cranii*. The postglenoid foramen leads from the postglenoid groove or canal into a chamber lying at the back of the glenoid ; from this chamber a horizontal canal passes forwards dorsal to the glenoid surface to open just behind its anterior border.

IX. Tapirulus.

Tapirulus (text-fig. 44) has a true mastoid, well exposed on the outer surface of the skull. It lies at the edge of the occiput and separates the exoccipital completely from the squamosal. Its ventral extremity is grooved opposite the stylomastoid foramen. The part of the mastoid in front of this groove is a prominent knob which rests against the back of the tympanic neck behind and below the very small post-tympanic process of the squamosal. The part of the mastoid behind the groove is a flat strip of bone resting against the anterior face of the paroccipital process, but much shorter than the corresponding strip in *Dacrytherium*. The paroccipital process, which is thus formed almost entirely by the exoccipital, is slender and compressed, leaning very decidedly backwards away from the tympanic region. The tympanic neck is very short and broad; it carries a crest along its postero-ventral surface. The bulla is flattish, and in front ends rather squarely in two blunt points. A strip of periotic bone is exposed between the bulla and the *basis cranii*. The glenoid surface is flat in front and behind slopes up very gradually on to the low, unimportant postglenoid. The zygoma is slender. The crests which bound the occiput are, like the sagittal crest, very feebly developed, so that above the level of the *foramen magnum* the occipital surface is higher than broad. The whole skull is characterised by its elongate, elegant shape, due partly to this weakness of its muscle crests and also to its long cranial region and tapering snout.



Text-fig. 44.—Oblique view of hinder end of skull of *Tapirulus* from Phosphorites of Pourrouyon. (Paris, Muséum National.) Zygoma restored from right side. The scale is approximate. E.A.M., outer opening of external auditory meatus; GL., glenoid surface; M., mastoid; P.G. and P.T., postglenoid and post-tympanic processes of the squamosal; P.P.E., paroccipital process of the exoccipital; T.B., tympanic bulla; T.H., tympano-hyal pit (with stylomastoid foramen just behind it).

Here then we have a skull very similar to that of *Dacrytherium* and differing from the amastoid Artiodactyla in nearly all those characters in which *Dacrytherium* differs from them. Of any affinity with the Suidæ there is not the faintest indication.

Charles Earle was also struck by the similarity between *Tapirulus* and *Dacrytherium* and pointed out* how easily the peculiar bilophodont molars of the former might be derived from a more primitive type with an anterior row of three cusps and a posterior row of two. Among the cranial differences which separate the two genera may be mentioned the difference in shape of the ventral extremity of the mastoid, of which the anterior, post-tympanic limb is bigger in *Tapirulus*, the posterior, paroccipital limb

* C. Earle, "Notes on the Fossil Mammalia of Europe," 'American Naturalist,' 1896, vol. xxx, p. 308.

inconspicuous. The paroccipital process of *Tapirulus* is flattened on its antero-lateral surface, that of *Dacrytherium* more laterally. The anterior end of the *Tapirulus* tympanic bulla ends squarely in two points, that of *Dacrytherium* in one drawn-out point. In *Tapirulus* the tympanohyal pit is more remote from the external auditory meatus than in *Dacrytherium*, where there may be already observed the tendency so marked in the larger Anoplotheres to enlarge this pit and place it right in the middle of tympanic neck encircled by bony crests. *Tapirulus* lacks the postglenoid groove and foramen which *Dacrytherium* shares with so many other primitive mammals of diverse relationship. The bend between the glenoid surface and the postglenoid process is in *Tapirulus* very gentle, in Dacrytherium almost a right angle. The glenoid surface in *Tapirulus* is marked off laterally and postero-laterally from the lateral surface of the zygoma by a sharp ridge; in *Dacrytherium* there is no such ridge postero-laterally, but the two surfaces are smoothly continuous. The occipital crests of *Dacrytherium*, though feebly developed compared with those of such amastoid forms as *Mixtotherium* and *Cebochœrus*, are stronger than in *Tapirulus*, giving the occiput that constricted appearance which is yet more pronounced in the larger Anoplotheres.

These characters separating *Tapirulus* from *Dacrytherium* seem to me of a type likely to have been much more recently established than those which they hold in common and which separate them both from any amastoid Artiodactyl.

Skulls of *Tapirulus* from the Phosphorites du Quercy are to be found in Basel and Paris. That in Basel has been fully described and figured by STEHLIN.*

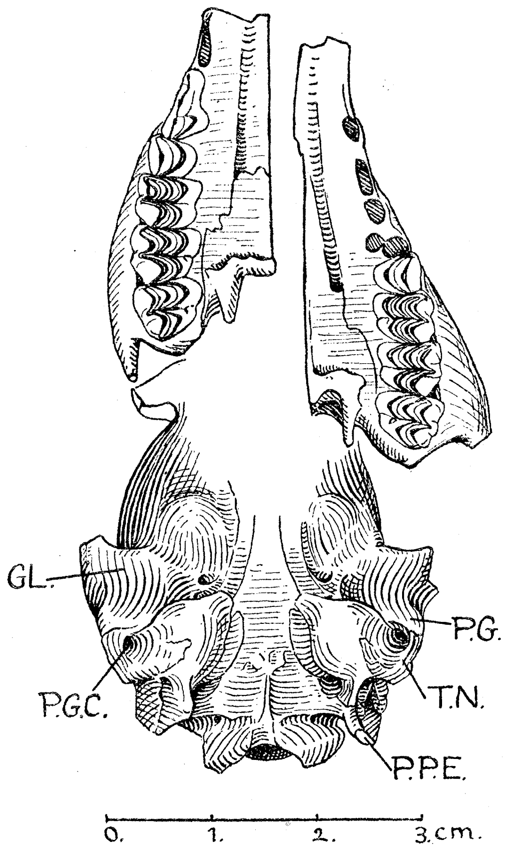
X. AMPHIMERYX.

Amphimeryx is again an Artiodactyl with a mastoid process of the periotic and with many resemblances to *Dacrytherium* and *Tapirulus*. A complete skull has never yet been described, although it is not one of the rarest of the Phosphorites genera. There is a skull in Munich (text-fig. 46), one and a fragment of one in Montauban (text-fig. 45), and two (labelled *Xiphodontherium primævum* FILHOL) in Paris. One of these latter appears to be the form which STEHLIN calls *Pseudamphimeryx*: it is smaller than the other and its occipital crest is not so strongly developed, so that the occiput looks low in comparison to its breadth; there is not so long a diastema behind p^1; the postglenoid groove is open below instead of closed in to form a canal; and the anterior crests of the selenodont molar protocones are cut short. It is this last character, coupled with the shape of the ventral border of the lower jaw,† that STEHLIN gives as separating

* H. G. STEHLIN, "Eocaene Säugethiere," 1910, p. 1065 ff.

† According to STEHLIN's definition this ventral border should be straight in *Amphimeryx*, curved in *Pseudamphimeryx*. The Paris skull with teeth of the latter type is mounted with a lower jaw of straight ventral border, but the fit is not good and the teeth are of a different colour, so perhaps the two are not really associated. One of the Montauban fragments has an associated lower jaw but I do not recollect its shape. In any case, however, *Amphimeryx* and *Pseudamphimeryx*, though clearly distinct species (whether or no we like to regard them as distinct genera), are of such a very similar type that for the purposes of this paper they may be considered as one.

Pseudamphimeryx from *Amphimeryx*. Further, STEHLIN figures the snout of a *Pseudamphimeryx* skull which has a preorbital fossa. There is no such fossa present in the larger of the two Paris skulls with the *Amphimeryx* type of dentition, so that this may be another distinguishing character. The smaller Paris skull and that in Montauban are broken here.



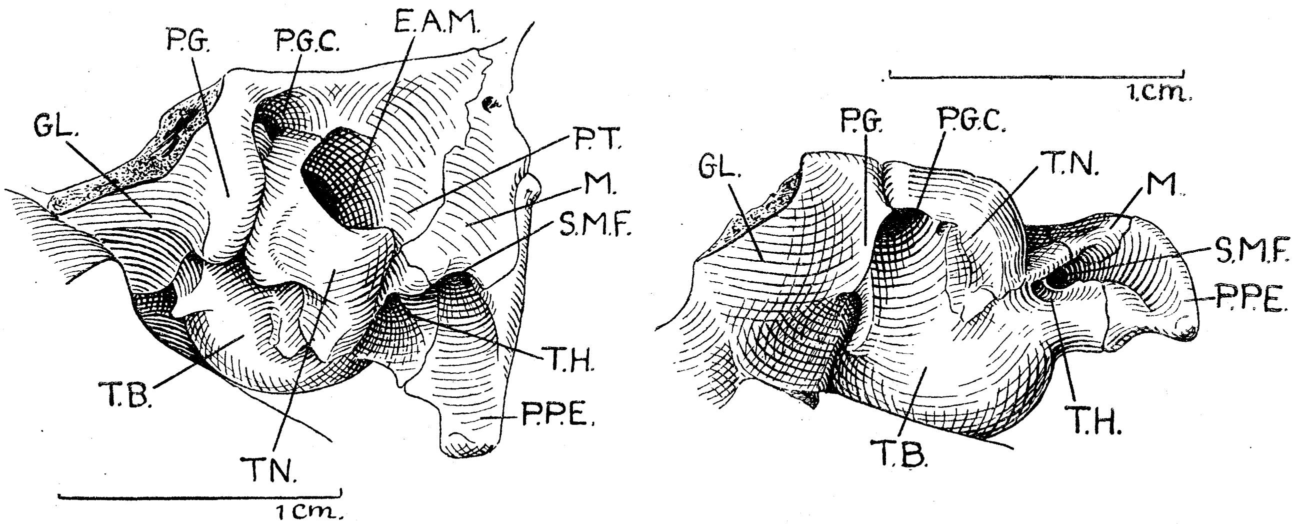
TEXT-FIG. 45.—Ventral view of broken skull of *Amphimeryx* from the Phosphorites du Quercy. (Montauban, Musée d'Histoire Naturelle.) The two halves of the palate are actually displaced more than shown in the figure. The scale applies to cranium and right maxilla—left maxilla is drawn to slightly smaller scale. GL., glenoid surface; P.G., postglenoid process; P.G.C., postglenoid canal; P.P.E., paroccipital process of exoccipital; T.N., tympanic neck.

Not only have *Amphimeryx* and *Pseudamphimeryx* completely selenodont molars, but their basicranial characters have also not a little of the ruminant about them. Their glenoid surface, instead of being flat as in most primitive Artiodactyls, is slightly convex; its level is a little higher than that of the *basis cranii*. On the upper surface of the glenoid region is a hollow depression, facing forwards, and resembling that in the ruminants; *Dacrytherium* and *Diplobune* have no such hollow.

The mastoid completely separates the squamosal from the exoccipital, but does not continue down on to the face of the paroccipital process, this being formed of exoccipital alone. Indeed the primitive forking of the ventral end of the mastoid is almost lost; the stylomastoid groove no longer lies embraced by the fork, but has exoccipital on its inner side and behind it, tympanic in front of it, and the mastoid playing only a small part in its lateral wall. The tympanohyal pit, placed immediately in front of the stylomastoid foramen, is very small and in no way influences the shape of the bulla. As in *Dacrytherium* and *Tapirulus*, the post-tympanic process of the squamosal is so reduced that it does not pass down behind the tympanic neck at all, this being in direct contact with the mastoid. The tympanic bulla is globular, but is drawn into a blunt point anteriorly; a broad strip of periotic is left exposed between the bulla and the *basis cranii*. The tympanic neck is short and broad, its ventral surface bearing little pointed excrescences in *Amphimeryx*, but not in *Pseudamphimeryx*. In *Amphimeryx* also a wide postglenoid canal, open at either end, is enclosed between the back of the postglenoid process and a broad flange of bone which arises from the centre of the tympanic neck. The postglenoid process is broad, but not very high. The pit in the angle between the tympanic bulla and the glenoid surface is very small.

The occiput of *Amphimeryx* is very similar to that of *Tapirulus*, but even narrower dorsally, as the occipital crest is even less developed; there are no deep pits on either side of the middle line. The zygoma is slender, the snout narrow and tapering, the postorbital processes of the frontals feebly developed.

Here then we have a skull which has much in common with those of *Dacrytherium* and *Tapirulus*, agreeing sometimes more with the one, sometimes more with the other, sometimes more with that of a primitive ruminant such as *Dremotherium*, but retaining



TEXT-FIG. 46.—Two views of the left otic region of another skull of *Amphimeryx* from the Phosphorites du Quercy, Escamps, Lot. (Bayerische Staatssammlung.) The right-hand view is more from below and in front. E.A.M., outer opening of external auditory meatus; GL., glenoid surface; M., mastoid; P.G. and P.T., postglenoid and post-tympanic processes of squamosal; P.G.C., postglenoid canal; P.P.E., paroccipital process of exoccipital; S.M.F., stylomastoid foramen; T.B. and T.N., tympanic bulla and neck; T.H., tympanohyal pit.

at the same time its own individual peculiarities. This is just what a study of its dentition might lead us to expect. Affinity with *Tapirulus* has already been suggested by SCHLOSSER, who in ZITTEL's "Grundzüge der Paläontologie" (4th ed., 1923) places both in the same family of Xiphodontidæ.

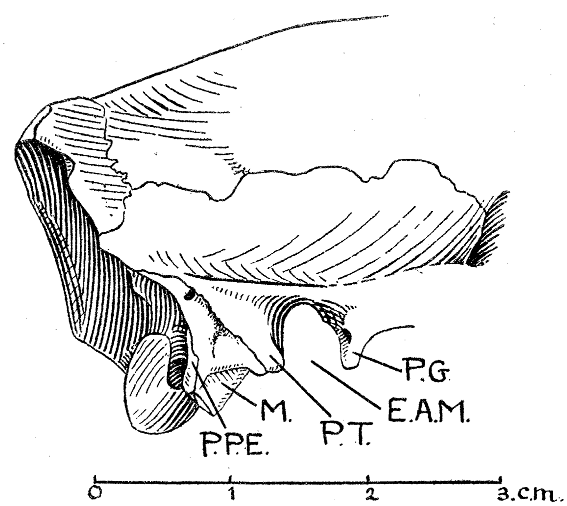
XI. THE DICHOBUNIDÆ.

Dichobune.—After studying in Paris a skull of *Dichobune* from the Phosphorites du Quercy* (text-fig. 47) and comparing it with the other Artiodactyl skulls that I have just been describing, I came to the conclusion that too much stress had been laid on the possession of a hypocone by this genus. This character alone does not seem to me

* A complete account of another skull of *Dichobune* from the Phosphorites, with drawings from all points of view, has been given by STEHLIN in the "Eocaene Säugethiere," 1906, p. 603, ff.

sufficient to justify the isolation of *Dichobune* in a separate sub-order, the "Hypoconifera" of STEHLIN. The association of *Entelodon* with *Dichobune* in this sub-order is still more inadmissibly artificial—as indeed STEHLIN himself admitted it might prove to be. *Entelodon,* as we have seen, is a very highly specialised amastoid form. *Dichobune's* affinities are with the mastoid types just described. First of all it has a well-developed mastoid. Secondly, there is no tendency whatever to compression of those parts of the skull posterior to the glenoid. Thirdly, there is no tendency for the glenoid surface to be lowered or carried out to the side. Fourthly, the muscle crests are weakly developed, the occiput is narrow, the zygomata and the lower jaw are slender. Fifthly, the incisors, canines and cheek teeth form an even series uninterrupted by diastemata and with the canines no longer than the rest.

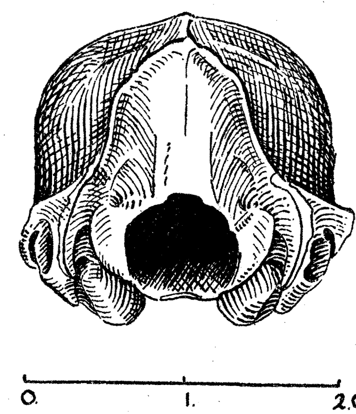
In the basiotic region, the absence of an ossified tympanic bone attached to the skull is probably the retention of a primitive character. The paroccipital process is directed backwards, away from the otic region, and, as in *Dacrytherium,* the mastoid appears to



TEXT-FIG. 47.—Lateral view of hinder end of skull of *Dichobune leporinum* from the Phosphorites du Quercy. (Paris, Muséum National.) The scale is approximate. E.A.M., external auditory meatus; M., mastoid; P.G. and P.T., postglenoid and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital.

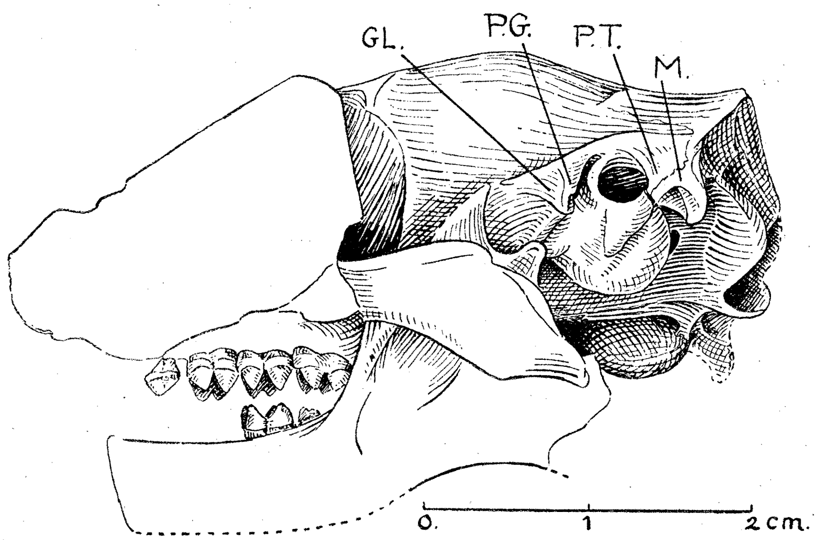
have extended nearly to its tip (though this is, I think, in all cases broken). The primitive forking of the lower end of the mastoid into this paroccipital limb and into an anterior post-tympanic limb is better shown here than in any other Upper Eocene Artiodactyl skull that I have seen, while the post-tympanic process of the squamosal is stout and the paroccipital process of the exoccipital weak, both of which characters I shall presently try to show are also primitive.

Mouillacitherium.—In Paris there is an incomplete skull from the Phosphorites du Quercy of this small Dichobunid (text-figs. 48 and 49). As would be expected in a so much smaller animal, the muscle attachments are much less strongly developed than in *Dichobune*, the sagittal and occipital crests being insignificant and the paroccipital process weak. The mastoid has much the same relations as in *Dichobune*; it is a forked structure embracing the stylomastoid foramen and tympanohyal pit; the hinder limb of the fork constitutes the greater part of the paroccipital process, the exoccipital contribution being small. The post-tympanic process of the squamosal is much feebler than in *Dichobune* and the postglenoid process also very small and narrow from side to side.



TEXT-FIG. 48.—Occiput of skull of *Mouillacitherium elegans* from the Phosphorites du Quercy, Memerlein. (Paris, Muséum National.) The scale is approximate.

It is interesting to find in *Mouillacitherium* a well developed tympanic bulla completely covering the periotic, since there is no trace of this in either of the *Dichobune* skulls known. It is a little spherical bulla with a short neck. The latter has a triangular bony protuberance on it, similar to that in *Amphimeryx*, but no flange joining it with the postglenoid process, from which it is separated by a wide cleft. Facing into this cleft on the back of the postglenoid process, there is a broad vertical channel leading upwards into a postglenoid foramen. Medial to the postglenoid process the edge of the

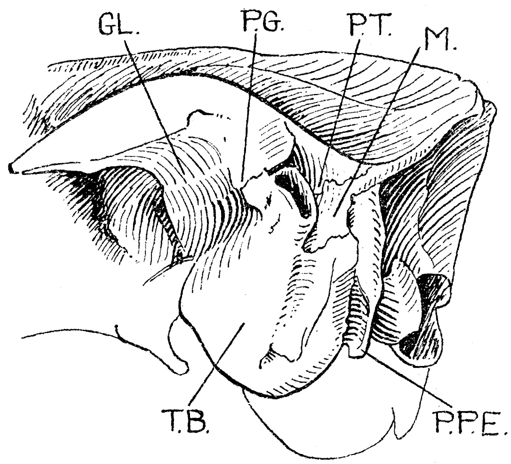


TEXT-FIG. 49.—Oblique lateral view of skull of *Mouillacitherium elegans* from the Phosphorites du Quercy, Memerlein. (Paris, Muséum National.) Partly restored from opposite side. The scale is approximate. GL., glenoid surface; M., mastoid; P.G. and P.T., postglenoid and post-tympanic processes of squamosal.

glenoid surface is bent downwards in front of the bulla, from which it is separated by a shallow groove.

XII. The Cainotheriidæ.

The Cainotheriidæ, like the Dichobunidæ, are usually regarded as a group very much apart from all other Upper Eocene Artiodactyls on account of the peculiarity of their molar teeth. Their skull also is undoubtedly of a very distinct type, but nevertheless it is easy to trace in it the typical ground plan of a primitive mastoid Artiodactyl.* The chief peculiarity of the skull is its very large tympanic bulla. In most Artiodactyls a process of the tympanic bone extends backwards from the bulla to join the paroccipital process and form a wall between the more medial *foramen lacerum posterius* and the more lateral stylomastoid foramen. In the Cainotheres the bulla itself is so big that it presses right back against the anterior face of the paroccipital process, leaving no room for the trough in which usually lie the stylomastoid foramen and the tympanohyal pit. Consequently, the mastoid, which under more primitive conditions would form the lateral wall of such a trough, is here plastered flat against the surface of the hinder part of the enlarged bulla: all that is to be seen of the original trough is a minute pit dinting the lateral surface of the bulla a little way below the ventral edge of the flattened mastoid. The paroccipital process of a Cainothere, although longer than the mastoid, is a comparatively weak little thing, which does not, as in the more typical mastoid forms, project at the lower corner of the occiput as a prominent ridge, continuous above with the lateral occipital crest. The post-tympanic process of the squamosal is practically non-existent. Whereas the tympanic bulla is large, its neck is short and rather narrow; it is drawn out into a flange, which is directed forward to meet the tip of the post-glenoid process, a postglenoid canal being enclosed between the two. The postglenoid process is narrow and dumpy, and restricted to the postero-external corner of the flat glenoid surface. This surface is very high above the level of the *basis cranii*, the tendency towards raising it, which is characteristic of the mastoid Artiodactyls as a group, being here carried much further than in any of the other members already described.



Text-fig. 50.—Oblique view of hinder end of skull of *Cainotherium* from the Phosphorites du Quercy. Enlarged considerably. (From a skull in Paris and another in London.) GL., glenoid surface; M., mastoid; P.G. and P.T., postglenoid and post-tympanic processes of squamosal; P.P.E., paroccipital process of exoccipital; T.B., tympanic bulla.

The zygomata are narrow, the lower jaw slender, and the skull as a whole delicate

* The Cainotheriidæ of the Upper Oligocene are in several ways more specialised than those of the Phosphorites du Quercy on which I have based my description.

with very feebly developed muscle crests, as would be expected from its small size. The occiput is shaped much as in *Amphimeryx* or *Mouillacitherium*, being narrow above, without deep pits, and broadening below in the paroccipital region.

XIII. Pleuraspidotherium, and the Evolution of the Mastoid Region in the Artiodactyla.

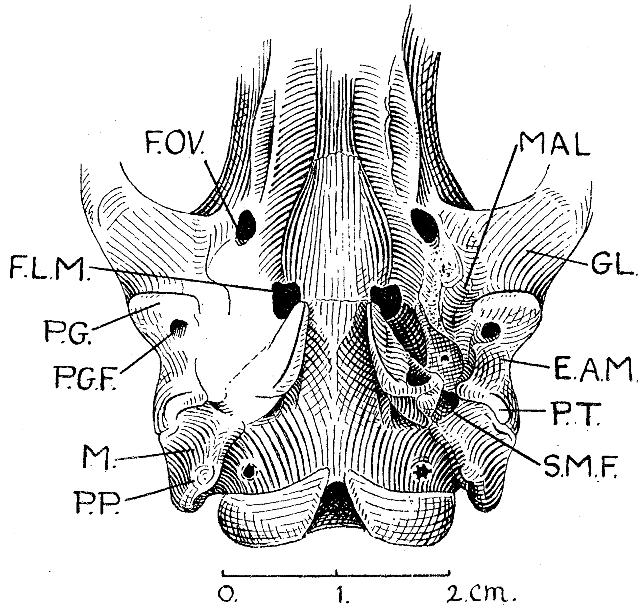
Pleuraspidotherium aumonieri Lemoine is a supposed Condylarthran from the Cernaysian of Rheims. There are a number of teeth and some fragmentary skulls of this interesting little animal in the Muséum National, Paris, and a new account of it with a discussion of its affinities has recently been given by Teilhard de Chardin.*

The only teeth which are quite definitely associated with the skulls are p^3 to m^3. In front of p^3, which like p^4 is tending to become molariform, there is always a diastema, and here the snout is broken short. The anterior end of the snout in the two best preserved skulls has been plastered on artificially, one does not know with what veracity: in one case, the incisor region appears to have been reduplicated and in no case are the incisors *in situ*. I have not myself seen a specimen in which the canines and specialised incisors described by Teilhard de Chardin are definitely associated with the quinquetubercular molars. Furthermore, as he says, none of the isolated bones that have been attributed to *Pleuraspidotherium* are certainly associated with the teeth: association is assumed owing to the commonness of both in the same beds.

Since the back of the skull would thus seem to be the only part of the skeleton undoubtedly associated with the molar teeth, and since it is a part of the highest value in determining relationships, I propose to describe it in detail here before discussing the light which its structure throws on the more particular problem of this paper—the evolution of this part of the skull in the Artiodactyla. Text-figs. 51, 52, and 53A are reconstructions from the two best specimens in Paris, which together give all the details quite clearly.

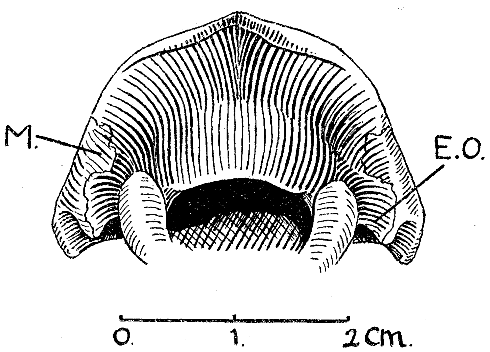
There is no ossified tympanic bone to cover in the periotic, which has a sharp ventral keel. The postglenoid process is stout, but narrow from side to side compared with its length: it does not curl forward over the glenoid surface, which is flat, and it is separated by a wide, shallow groove and a rather broad wall of bone from the *foramen ovale* and *foramen lacerum medium*. This groove continues back medial to the postglenoid process and there curves upwards into the middle ear cavity. It evidently lodged the *chorda tympani* nerve, the handle of the malleus, and the hinder end of the *tensor palati* muscle taking origin from the latter: its unusual breadth is probably a primitive character. Into the back of the postglenoid process leads a large round postglenoid foramen, and behind it there is a wide external auditory meatus unprotected by any ring of tympanic. The squamosal projects down again behind the external

* P. Teilhard de Chardin, "Les Mammifères de l'Éocène Inférieur Français et leurs Gisements," 'Annales de Paléontologie,' vol. 11, 1922, p. 37.



TEXT-FIG. 51.—Ventral view of hinder end of skull of *Pleuraspidotherium aumonieri* LEMOINE, from Cernay, Rheims. (Paris, Muséum National.) Reconstruction of best specimen with help of two others. Position of condylar foramina not certain. E.A.M., external auditory meatus; F.L.M., *foramen lacerum medium*; F.OV., *foramen ovale*; GL., glenoid surface; M., mastoid; MAL., groove for handle of malleus, *chorda tympani* and *tensor palati* muscle; PG., postglenoid process; P.G.F., postglenoid foramen; P.P. paroccipital process; P.T., post-tympanic process of squamosal; S.M.F., stylomastoid foramen.

auditory meatus as a very stout, thick post-tympanic process. Behind this, again, there is a very broad mastoid which forks ventrally into an anterior limb, backing the post-tympanic process, and a posterior limb forming the greater part of the paroccipital process; medial to the convex surface between these two limbs lies the stylomastoid groove. The exposed surface is twisted so that its upper half faces posteriorly, lying on the occiput above the very small paroccipital part of the exoccipital. The paroccipital process is very short, indeed shorter than the post-tympanic, and its summit is formed entirely by the mastoid. The occiput is low and excavated by no muscle pits; its breadth at the back of the ear is considerably greater than its height above the *foramen magnum.* The lateral occipital crests are not continuous with the sharp dorsal edge of the zygoma, but dwindle out in the mastoid region.



TEXT-FIG. 52.—Occipital view of skull of *Pleuraspidotherium aumonieri* LEMOINE, from Cernay, Rheims. (Paris, Muséum National.) Reconstruction of best specimen; relief of occipital surface probably not exact. The scale is approximate. E.O., exoccipital; M. mastoid.

The few published figures of American Condylarthra do not show this hinder part of the skull sufficiently clearly for comparison with *Pleuraspidotherium.* The characters of this genus just described are, however, such as we might reasonably expect to find in a Condylarthran. There is a strong underlying resemblance to the primitive Carnivora, but instead of the cylindrical glenoid always associated with a carnivorous dentition, the glenoid surface is flat and the postglenoid process stands vertically behind it.

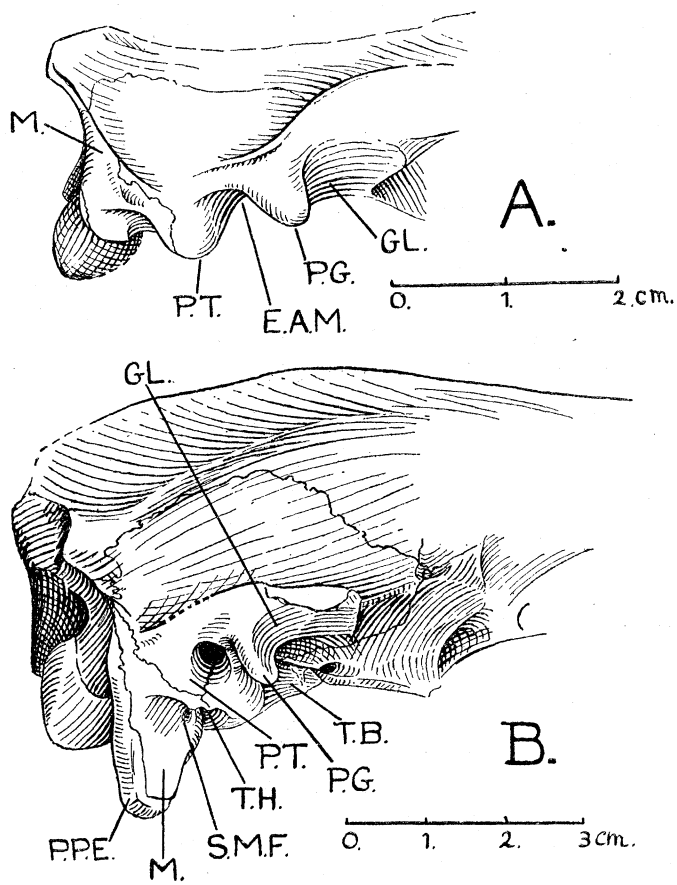
The ventral forking of the mastoid is a character shared by primitive Carnivores and some Insectivores, but whereas in the latter* the mastoid may face entirely backwards as a part of the occiput (*e.g. Centetes*), in Carnivores as in *Pleuraspidotherium* its ventral extremity has come to face laterally.

In reptiles, the mammalian mastoid is represented by the "paroccipital process" of the opisthotic, which lies entirely on the occipital surface, a strut between the occipital bones on the one hand, and the squamosal and hinder end of the palato-quadrate apparatus on the other. This is not a paroccipital process in the mammalian sense, that is to say a free projection for muscle attachment at the lateral border of the exoccipital, formed either by the exoccipital alone or by exoccipital and mastoid together. The development of such a projection is one of several tendencies at work in the Mammalia; another is the enlargement of the exoccipital on the occiput and the shifting of the mastoid on to the lateral surface of the skull; another is the reduction of the mastoid, leading sometimes to its complete disappearance from surface view and to the approximation of the exoccipital to the squamosal. All this is probably correlated with the pushing out of the lateral wall of the brain case to make more room for the gradually swelling brain: also with the reduction of the hinder end of the palato-quadrate apparatus and the changed articulation of the lower jaw.

Thus it seems that mammals such as *Centetes* with a backwardly facing mastoid come nearest to retaining the reptilian condition of that part of the skull. In other Insectivores the mastoid is lateral and extremely like that in primitive Carnivores. In these latter again, it is very like that in the primitive Ungulate *Pleuraspidotherium*, which itself forms a good morphological starting point for the early mastoid Artiodactyla described in this paper (text-fig. 53). Among these latter *Dichobune* has retained the most primitive mastoid region. The mastoid, though now nearly completely lateral, is less reduced than in any of the other forms still possessing it. The paroccipital process, although well developed, is formed more by the mastoid than by the exoccipital. The post-tympanic process of the squamosal is comparatively large. *Mouillacitherium* is in much the same stage as *Dichobune*, but the post-tympanic squamosal is more reduced. In *Dacrytherium* we find a big reduction in the size of the post-tympanic process of the squamosal, an increase in the paroccipital process of the exoccipital, and a mastoid in which the anterior limb is all but vestigial. In *Diplobune* conditions are very similar to those in *Dacrytherium*. In *Tapirulus* the post-tympanic process of the squamosal is yet smaller and the mastoid does not extend down on to the paroccipital process at all, but has still a rather well developed anterior limb. In *Amphimeryx* and the

* See also W. D. MATTHEW, "The Carnivora and Insectivora of the Bridger Basin." 'Mem. Amer. Mus. Nat. Hist.," vol. 9, part vi, 1909, p. 505.

modern Ruminants the post-tympanic process of the squamosal is again insignificant, the paroccipital process is formed wholly by the mastoid, and there is only the barest trace left of the primitive forking of the latter. *Cainotherium* shows a still further reduction of this condition, but stands a little apart because of its enlarged tympanic



TEXT-FIG. 53.—Lateral views of hinder ends of skulls of (A) *Pleuraspidotherium aumonieri* from Cernay, Rheims (reconstruction from two sides of the best specimens with help of another) and (B) *Dacrytherium elegans* from the Phosphorites du Quercy. (Paris Muséum National.) The scales are approximate. E.A.M., external auditory meatus; GL., glenoid surface; M., mastoid; P.G., postglenoid process; P.P.E., paroccipital process of exoccipital; P.T., post-tympanic process of squamosal; S.M.F., stylomastoid foramen; T.B., tympanic bulla; T.H., tympano-hyal pit.

bulla. *Haplobunodon* has retained a rather longer post-tympanic process of the squamosal and the forking of its mastoid is still quite clear, but the latter is, on the other hand, very highly compressed, and its posterior limb is too short to form any part of the paroccipital process.

Turning now to what I have grouped together above as the amastoid Artiodactyla and especially to the least specialised among them, *Cebochœrus* and *Mixtotherium*, one is tempted to the conclusion that they arose quite independently from a mammal in which the mastoid lay wholly on the occiput, the lateral occipital crest was carried by the squamosal, and the paroccipital process of the exoccipital was small. In them a wide strip of squamosal appears on the occiput, while the post-tympanic process of the squamosal is very large and bears the same relations to the tympanohyal and stylomastoid foramen that the mastoid does in other forms. The paroccipital process of the exoccipital, though it becomes important in the later members of the group, was not initially prominent and never comes to lie at the posterior corner of the skull.

It is at any rate clear, that these amastoid forms must have passed through a very long period of evolution since they lost their mastoid, and also that the different families into which they are divided at our earliest knowledge of them must have already been long since separated from the common stock—if such a stock ever really existed as I have been tempted to believe.

The mastoid Artiodactyla of the European Upper Eocene on the other hand, except perhaps for *Haplobunodon*, hang together much more closely, not only in the characters of the otic region, but in the general shape of the skull and in the even dental series. STEHLIN* objects to grouping them all together under the old name "Anoplotheriidæ,"† because, he says, a closed dental series and premolariform canines were probably once possessed by all Artiodactyla. It is true that they can no longer all be classed in one family and that *Anoplotherium* is in any case one of the most aberrant forms among them; but it is by no means certain that even these dental characters were really once shared by all Artiodactyla, and, as I have tried to show, there is still more doubt in the case of the characters of the mastoid region. To me they seem to be primitive members of their own well-defined group, a group from which in post-Eocene times arose the modern Ruminants, the Camels and the Tragulids, besides the extinct Hypertragulids and Oreodonts‡—just as the Pigs, Hippopotami and Anthracotheres are the post-Eocene members of an amastoid group which, in the Upper Eocene, is at present imperfectly known to us through *Cebochœrus*, *Mixtotherium* and *Chœropotamus*.

Haplobunodon alone among the European mastoid forms is a little difficult to place in the mastoid group. Probably in correlation with an enlarged canine, it has a very high sagittal crest, an occiput which is narrow yet with well developed lateral occipital crests, a fairly stout zygoma bending outwards round a wide temporal fossa, and a long premolar diastema, while its anterior molars show no tendency to compression and

* H. G. STEHLIN, "Eocaene Säugethiere," 1910, p. 937.

† CUVIER ("Ossemens Fossiles," 4th ed., 1835, vol. 5, p. 431) indeed included *Anoplotherium*, *Diplobune*, *Dichobune* and *Xiphodon* all in the same genus "*Anoplotherium*" on the strength of the following characters: "*Dentes* 44. *Serie continuâ; Primores utrinque* 6; *Laniarii primoribus similes, cæteris non longiores; Molares* 28, *utrinque* 7. *Anteriores compressi; Posteriores superiores quadrati, inferiores bilunati; Palmæ et plantæ didactylæ, ossibus metacarpi et metatarsi discretis; digitis accessoriis in quibusdam.*"

‡ The typical Oreodonts of the White River Oligocene were just beginning to show signs of the tendencies which gave to *Promerycochœrus* and *Merycochœrus* of the Miocene a certain superficial resemblance to earlier forms of the "amastoid" type.

antero-posterior elongation. The idea that it may be a primitive Anthracothere, based on the characters of the molar teeth with their well developed mesostyles, is thus not without further justification; but as STEHLIN has maintained in regard to the teeth, so also with regard to the cranial characters, it is simultaneously too late in time and too specialised along its own independent line to be really ancestral to the Oligocene Anthracotheres. I should suggest that it came from a very early offshoot of the mastoid stock, at a time when the mastoid was already shifted laterally and the post-tympanic squamosal beginning to be reduced, but before the tendency to premolar compression was established: it then developed independently, and after its own pattern, a crested skull, enlarged canines, and molar mesostyles. It is possible that a more perfect knowledge of the skull of the North American "Dichobunidæ"* will bring to light affinities between *Haplobunodon* and those Lower Eocene bunodont forms.

XIV. SUMMARY.

1. *Palæochærus* of the European Aquitanian and *Perchærus* of the North American Aquitanian, although strongly resembling one another in their cranial characters, are nevertheless already quite distinctly differentiated, the one into primitive pig, the other into primitive peccary.

2. *Doliochærus* of the Phosphorites du Quercy is of peccary affinities and very close to *Perchærus*.

3. *Hyotherium simorrense* (*Conohyus simorrensis* PILGRIM) of the European Vindobonian is intermediate in cranial characters between *Palæochærus* and recent pigs.

4. The affinities of *Chærotherium* of the European Vindobonian are with the peccaries and not with the pigs.

5. "*Acotherulum*" and "*Leptacotherulum*," of the Phosphorites, may both be placed in the genus *Cebochærus*. The Cebochœridæ are not primitive Suidæ or nearly related to them. They were probably closely related to the as yet unknown Eocene Anthracotheres, as were also the genera *Mixtotherium* and *Chæropotamus*. They were probably yet more closely related to the ancestors of *Hippopotamus* if not themselves ancestral.

6. Of the European Anthracothere skulls in which the basicranial region has been preserved, *Ancodus velaunus* has attained the highest degree of specialisation in respect of the common tendencies of the group.

7. *Chæropotamus*, *Cebochærus*, *Hippopotamus*, the Anthracotheriidæ, *Mixtotherium*, *Entelodon*, and the Suidæ appear to belong to one group of Artiodactyla, while the Dichobunidæ, *Dacrytherium*, the Anoplotheriidæ, *Tapirulus*, *Amphimeryx*, the Cainotheriidæ, together with remaining post-Eocene families, form another. These may conveniently be termed the "amastoid" and the "mastoid" Artiodactyla respectively,

* W. J. SINCLAIR, "A Revision of the Bunodont Artiodactyla of the Middle and Lower Eocene of North America," 'Bull. Am. Mus. Nat. Hist.,' vol. 33, 1914, p. 267.

the presence or absence of a *pars mastoidea* of the periotic bone being a conspicuous distinguishing feature.

8. The mastoid Artiodactyla show a progressive reduction in the size of the mastoid, all stages of compression being represented in the Upper Eocene. From its complete absence in the Upper Eocene genera *Cebochœrus, Mixtotherium,* and *Chœropotamus,* and from other skull peculiarities, it is probable that mastoid and amastoid Artiodactyla were separated from one another at a very early date.

9. The cranial characters of the Cernaysian genus *Pleuraspidotherium* may well be those of a Condylarthran. At the same time, they give some useful hints as to the probable course of evolution of the hinder end of the Artiodactyl skull.

It is now my pleasant task to acknowledge the very hospitable treatment which I have received in all the lands that I have visited during the course of these studies. Permission to handle valuable specimens and to make drawings of them for publication, has been freely granted to me on all sides. In overcrowded museums with hardly the working space for their own staff and students, I have nevertheless been allotted most comfortable quarters. Among the most valued of my experiences have been talks with the distinguished palæontologists directing some of these museums, and an insight into their methods. I would like most particularly to thank them for the generous way in which they found time to give all manner of help, advice, and encouragement.

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