THE PHYTOSAURIA OF THE TRIAS

MAURICE G. MEHL University of Wisconsin

Some time ago the writer gave a brief notice of a new genus of phytosaurs of which *Angistorhinus grandis* Mehl was the type.^t It is the purpose of this paper primarily to give a fuller description of this form and of another specimen mentioned in the above paper which further study has shown to be a new species of the same genus.

Angistorhinus grandis MEHL

The general characteristics of the specimen upon which this form is based were set forth in the previous paper and deserve but brief mention here. The skull is elongate with the rostrum produced into a long, slender, depressed snout and the nares elevated on a prominence at its posterior end. It is among the largest of the phytosaurian skulls, with a total length of about 977 mm. The squamosals extend a considerable distance beyond the posterior border of the quadrates and are produced downward into stout, hooklike processes. The supratemporal vacuities are closed posteriorly by a well-developed parieto-squamosal arcade that lies in the plane of the roof of the cranium. A marked depression is seen on the dorsal surface surrounded by the orbits and supratemporal vacuities. The irregular pitting of the surface is confined almost entirely to the lateral and posterior sides of the prominence upon which the nares are situated, and the flat dorsal surface of the cranium back of this, and in front of the supratemporal vacuities. In a lateral view the skull resembles that of Mystriosuchus Fraas² more than any of the other phytosaurs.

¹ Jour. Geol., XXI (1913), 186.

² Die Schwabischer Trias-Saurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt (1896), p. 16, Pl. V.



This content downloaded from 206.212.9.211 on Tue, 10 Mar 2015 15:50:24 UTC All use subject to JSTOR Terms and Conditions

OPENINGS OF THE DORSAL SURFACE OF THE SKULL

The *external nares* are situated on a prominence at the beginning of the rostrum and rise fully 18 mm. above the level of the general surface of the cranial roof. The thin, vertical, median septum separating the nares does not rise to the same height as that of the posterior and lateral borders and thus the nares are given the appearance of a single opening with rounded posterior and acute anterior border. In length they are about 62 mm. and the greatest width of the seemingly common opening is 40 mm. The anterior border is about even with the anterior borders of the antorbital vacuities and 590 mm. from the tip of the rostrum. The region about the anterior border of the nares is somewhat abraded, and the sutures are not distinguishable. No septomaxillae have been distinguished, but as they are present in another specimen to be described later they probably have about the same position here and form the anterior border of the nares.

The *antorbital vacuities* are large, oval in outline, with rather acute anterior and posterior extremities. Their greater diameter is fully 130 mm. and the lesser diameter about 55 mm. Their size is accentuated by an abrupt depression or excavation of the bone along their posterior and upper borders.

The large *orbits* are somewhat elongate antero-posteriorly, about 89 mm. long and 55 mm. wide. Their planes are directed outward and a little less upward, perhaps. The interorbital width is about 68 mm. Only a narrow bar, not over 9 mm. in width, separates the orbit from the lateral temporal fenestrae.

The sides of the *lateral temporal fenestrae* form rough parallelograms with unequal diagonals. The greater diagonal is 171 mm. and the lesser, which is almost perpendicular to the plane of the palate, is about 113 mm. The greatest width of these openings is about 87 mm. There is an excavation for a short distance about their lower anterior borders similar to that of the upper posterior border of the antorbital vacuities.

The *supratemporal fenestrae* are oval in outline with an anteroposterior diameter of 84 mm. and a width of 46 mm. Their plane is directed upward. They are peculiar in that they are closed behind by a well-developed parieto-squamosal arcade that lies in



This content downloaded from 206.212.9.211 on Tue, 10 Mar 2015 15:50:24 UTC All use subject to JSTOR Terms and Conditions

the plane of the dorsal surface of the cranium. This will be discussed more fully in connection with the posterior aspect. No *parietal foramen* is present.

THE SEPARATE BONES OF THE DORSAL SURFACE

The *parietals* are united along the median line for a distance of about 100 mm. Posteriorly they are separated for a short distance by a deep, rounded notch. In spite of this deep incision, however, the occipital condyle is not visible in a dorsal view. Their anterior ends form an acute angle that separates the frontals for a short distance. The greatest width of the parietals, a little in front of the anterior border of the supratemporal fenestrae, is about 42 mm. for each element. The parieto-squamosal suture is not clearly distinguishable; apparently these elements meet on the inner posterior borders of the supratemporal fenestrae.

The squamosals form the posterior and half of the lateral borders of the supratemporal fenestrae and the upper posterior borders of the lateral temporal fenestrae. They are bent abruptly downward at a point on the antero-posterior line of the bar separating the supratemporal and lateral temporal fenestrae, the downward extension being produced into a hooklike process similar to that of *Mystriosuchus* but with greater development. These hooklike angles extend below the dorsal surface of the skull a distance of about 104 mm. This part of the squamosal and the lower posterior surface of the quadrate as well was weathered away, but a perfect natural mold in the matrix made possible a very accurate restoration.

The *postorbitals* form a part of the antero-lateral borders of the supratemporal fenestrae and the postero-lateral borders of the orbits. They extend down and forward to meet the upper posterior process of the jugal, and the two form narrow bars that separate the orbits and the lateral temporal fenestrae. The inner boundaries of the postorbitals are formed by the postfrontals and the parietals which meet near the middle of the postorbitals' length.

The *postfrontals* are rather small, approximately quadrangular elements that form the posterior half of the upper borders of the



orbits. They are bounded on the inner side from front to back by the frontals, the parietals, and the squamosals. The anterior sutures of the frontals are not evident.

The *frontals* appear to extend forward to within 68 mm. of the nares. This would give them a length along their median union of about 68 mm. They form the upper borders of the orbits and join the prefrontals and nasals in front. Their anterior margin seems to form a slight concavity into which the posterior ends of the nasals extend.

The *prefrontal* sutures are not certain; these elements seem to be small, approximately quadrangular in outline, and form the upper anterior borders of the orbits.

The *lachrymals*¹ unite with the maxillae to exclude the nasals from taking part in forming the borders of the antorbital vacuities. Their downward extent and union with the maxillae are uncertain.

The *jugal* forms the lower postero-lateral border of the skull. At its anterior end the jugal sends forward a splinter-like process that forms the lower posterior border of the antorbital vacuity. It also sends back from the anterior upper side a process that unites with the lachrymal in front and the postorbital behind, and thus forms the lower anterior border of the orbit and the anterior half of the lower temporal fenestrae boundaries.

The quadratojugal connects broadly with the jugal below. Its suture with the squamosals is not distinguishable. The sutures between the nasals, the septomaxillae, the maxillae, and the premaxillae cannot be determined with certainty. In all probability the relations are much the same as in another form to be described later (see Fig. 4).

The *premaxillae* are produced into a long, slender, subcylindrical snout much like that of *Mystriosuchus*. Viewed dorsally it tapers gradually from the cranium proper to a point near the extremity, from a width of 94 mm. at a distance of 140 mm. in front of the antorbital vacuity, to 47 mm. Near the tip the rostrum expands

¹ E. Gaupp has attempted to show that the so-called "prefrontal" of reptiles is homologus with the mammalian lachrymal and has suggested the name "adlachrymal" for the element previously called the lachrymal in reptiles (*Anatom. Anz.*, XXXVI, 1910). According to Gregory (1913), however, this homology is in nowise proven. In this paper the writer adheres to the old nomenclature. gradually, attaining finally a width of 84 mm. The anterior extremity is bent abruptly downward and reaches a distance of 39 mm. below the plane of the ventral surface.

THE PALATE

Within the line of the alveoli on the ventral surface is a prominent rounded ridge on either side, as is noted in *Palaeorhinus bransini* Williston¹ and *Mystriosuchus*. It crowds close along the alveoli throughout the entire length of the premaxillae and gradually flattens



FIG. 4.—Angistorhinus gracilis, lateral view showing apparent arrangement of bones about the narial region, one-third natural size.

out on the maxillae. The teeth have all dropped from the alveoli except in the down-curved portion of the rostrum. Here four large ones are to be seen broken off close up to the premaxillae, two on each side. They are all round in section and measure about 15 mm. in diameter. If one may judge from a similar specimen in which these terminal teeth are preserved, they reached a length of from 80 mm. to 90 mm. or more in this form. In the premaxillae there are 23 alveoli on each side. These, with the exception of the two anterior ones described above, are approximately of one size, aver-

¹ J. H. Lees, "The Skull of Palaeorhinus," Jour. Geol., XV (1907), 124.

aging about 11 mm. in diameter. The third tooth of the premaxillae series crowds close upon the down-curve portion of the rostrum. Back of this they are quite regularly spaced, averaging about 8 mm. between adjacent alveoli. A break across the rostrum near the maxilla-premaxilla union exposed an unerupted tooth very similar to that shown in Fig. 9.

The *maxillae* have their greatest extent along the lateral margins of the skull, where they reach a length of about 340 mm. They connect with the jugals near the middle of the antorbital vacuities and form the lower anterior borders of these openings. Above they



Fig. 5.--Angistorhinus grandis, posterior view of skull, two-sevenths natural size

connect slightly with the long anterior projections of the lachrymals and more broadly with the nasals. They contain about 19 alveoli each, of about the same diameter as those of the premaxillae. The spacing is much the same with the exception that in the posterior ones there is a slight diminution of the interalveolar space. Although little can be said with certainty concerning the crowns of the premaxilla-maxilla teeth, they probably ranged from those with nearly round sections, in the anterior part of the rostrum, to those that are laterally compressed with sharp, serrate anterior and posterior cutting edges. A great many of these sorts are found associated with the phytosaur remains and some of the laterally compressed ones were found in a fragment of a skull that very closely resembles the form here described. These teeth will be more fully discussed farther on. The *palate* is somewhat crushed and distorted and most of the sutures are indistinguishable. Still a fairly good idea of its configuration and the general relations of the bones can be gained. It is quite highly arched along the median line and especially so in the region of the nares. The low, rounded arch along the median line of the premaxilla and maxilla, formed by the ridges parallel to the alveoli, increases gradually in height and width posteriorly, the increase being more rapid as the nares are approached, till at the posterior margin of the nares the arch is about 82 mm. wide at the general level of the palate surface and rises to a height of about 42 mm. from that plane. Behind this point the arch attains a still



FIG. 6.—*Mystriosuchus planirostris*, posterior view of skull, two-sevenths natural size. Outlines and sutures after J. H. McGregor.

greater width before it again rounds in posteriorly. The internal nares are a little back of the external nares, 10 mm. perhaps. The forward ends of these openings are still covered by the matrix. Their exact extent in that direction cannot be told, but they are probably about 48 mm. long. The width between their lateral borders is 34 mm. The median partition is slightly wider on the palate surface than it is between the external nares. A line connecting the anterior borders of the *post-palatine foramina* crosses the internal nares a little in front of the posterior border. From this line the foramina extend back and inward a distance of 60 mm. They are about 8 mm. wide, are slightly curved, concave inward, and have rounded anterior and posterior borders. Their anterior extremities are 190 mm. apart and their posterior ends some 120 mm. In size they are similar to those of *Mesorhinus fraasi* Jaekel,¹ a little larger, however, and more slitlike. In both of these forms the post-palatine foramina are considerably larger than in most of the other phytosaurs. The inter-pterygoid vacuity is notable in this form for its antero-posterior extent, being about 103 mm. long. It gradually diminishes in width from 35 mm., its greatest lateral extent, near its posterior boundary, to a very acute angle about 30 mm. back of the posterior border of the nares.

THE SEPARATE BONES OF THE PALATE

The posterior extension of the *premaxilla* is indeterminate; apparently it lacks quite a little of reaching the anterior border of the nares.

The *vomers* seem to have little lateral extent. The exact condition cannot be seen, however, as none of the boundaries is distinguishable. In all probability they unite broadly in front with the premaxillae and form most of the anterior border of the nares as well as their median borders. They probably do not extend as far back as the posterior end of the nares, certainly they cannot extend any considerable distance beyond.

Apparently the maxillae do not enter the nares at all. This is a condition suggested by Lees in *Palaeorhinus bransoni* (*op. cit.*, Fig. 2). If they do take part in the boundaries of these openings it is very slight and along the antero-lateral borders. The pterygopalatine sutures are also more or less hypothetical.

The *palatines* reach far forward, forming most or all of the lateral borders of the nares. They seem to join the pterygoids posteriorly about the middle of the posterior palatine foramina. At the anterior ends of these openings they connect very slightly with the transverse (ectopterygoid) bones, if at all. On the general plane of the palate their greatest width is about 52 mm. along a line connecting the anterior ends of the posterior palatine foramina. At this width they are bent almost vertically upward in an anteroposterior direction.

The *pterygoid bones* form the walls and roof of most of the spacious palate arch back of the nares. Only a small triangular

¹ "Über einen neuen Belodonten aus dem Buntsandstein von Bernburg," *Sitzungsberichten der Gesellschaft naturforschender Freunde*, No. 5, Jahrgang, 1910, p. 209, Fig. 5.

portion of them is to be seen on the general plane of the palate surface. They seem to form the posterior half of the inner boundaries of the posterior palatine openings. Near the anterior limit of the basisphenoid they bend abruptly upward from the roof of the broadly rounded palate arch and extend above the parasphenoid. Anteriorly they approach each other till they embrace the para- and presphenoid and, still farther forward, close together below them. They meet the transverse bones broadly at the posterior ends of the posterior palatine foramina, the suture being directed backward from this point and a little inward. Posteriorly they close with ample and firm contact on the basi-pterygoid process. From this union the pterygoids send back and outward narrow processes which meet like processes of the quadrates about midway between the quadrates proper and the pterygo-sphenoid union. Their relations with the various elements seen in a posterior view will be discussed below.

The *transverse bones*, seen from below, present an approximately triangular outline. They form the lateral borders of the posterior palatine foramina and the anterior borders of the post-temporal vacuities. The broad pterygo-transverse sutures run back and inward from the posterior ends of the posterior palatine openings toward the basi-pterygoid process. Along the outer anterior side the transverse bones unite with the maxillae for a distance of about 40 mm. and at a somewhat less distance with the jugals. The postero-lateral corners are bent downward along a line running from their inner posterior angles obliquely outward from the direction of the posterior palatine openings and extend some 14 mm. below the general ventral plane of the skull.

The ventral surface of the *parasphenoid* is exposed the entire length of the inter-pterygoid vacuity and both the para- and the presphenoid are free from the matrix for some distance along one side. Their union is clearly indicated by a shallow longitudinal groove. At their union with the basisphenoid they form a thin, vertical plate which gradually thickens anteriorly very slightly and becomes rounded below. They are visible from below for a distance of 95 mm. Anteriorly at this distance, about 42 mm. back of the posterior border of the nares, the pterygoids meet below these elements and hence their full anterior extent cannot be determined. At their point of disappearance, however, they still maintain their full thickness and must extend farther forward for some distance. Viewed from below, the postero-lateral processes of the sphenoid, the greater wings, form a high, transverse, rather sharp ridge slightly depressed at the middle and somewhat thickened at the extremities. This is about 76 mm. long and at the middle extends



FIG. 7.—Angistorhinus grandis? Cojoined basioccipital and basisphenoid, natural size.

down 44 mm. below the lower edge of the presphenoid. The anterior face of the pterygoid processes of the sphenoid reaches forward about 35 mm. from this ridge and extends down about even with it. These processes are quite stout and are separated from the posterior wings by a narrow but deep channel. The posterior part of the basisphenoid has been considerably abraded in this specimen and a portion of the occipital condyle is missing. Another specimen is present in the collection, however, a co-ossified basioccipital and basisphenoid (see Fig. 7) that resembles this form very closely, and this has aided materially in the interpretation of the specimen at hand. On the posterior side of the transverse plate formed by the greater wings of the sphenoid is a circular excavation 26 mm. in diameter. Although shallow the depth of the excavation is accentuated by a prominent curved ridge on either side springing from the base of the occipital condyle.

THE POSTERIOR ASPECT

In a posterior view Angistorhinus resembles in the general form Lophoprosopus¹ (Phytosaurus) kapffi H. von Meyer² or Mesorhinus Fraasi. It is depressed in appearance as the skull is over twice as wide as high. From the lowest point of the quadrates to the plane of the dorsal surface it measures about 166 mm. Between the lower, lateral angles of the quadrates the width is about 386 mm. The post-temporal fenestrae are exceptionally large, perhaps larger than in any other form. Those in Lophoprosopus kapffi (see reference above) are about 32 mm., while in A. grandis they measure nearly 40 mm. The width is about 11 mm. From the outer extremities of these openings, which are about 180 mm. apart, they are directed inward and slightly down. The foramen magnum is smaller than in most of the phytosaurs, about 20 mm. in diameter. The quadrate foramina lie between the quadratojugal-quadrate union, about 46 mm. above the lower face of the quadrates. They are oval in shape, the vertical diameter being 23 mm., the lesser diameter about 11 mm. The outer border of these foramina is formed by the quadratojugals, the inner border apparently by the quadrate alone. One of the most remarkable features seen in the skull of A. grandis is the difference between this form and most of the other phytosaurian genera in the upper posterior border of the skull. In Lophoprosopus, Mystriosuchus, and other forms, perhaps, the parietosquamosal arcade, bounding the upper temporal vacuity posteriorly, is considerably reduced and depressed. Quoting McGregor on this point in Mystriosuchus planirostris Fraas:³

A casual observation of the dorsal surface of the skull might lead the observer to think that the supratemporal fenestra was incomplete posteriorly,

¹ The substitution of *Lophoprosopus* for *Phytosaurus* is explained in the appended list of genera and species.

² McGregor, Memoirs of the Amer. Mus. Nat. Hist., Vol. IX, Part II (1896), p. 45, Fig. 4.

³ Ibid., p. 46.

though its outer, anterior, and inner margins are normally represented by the highly sculptured squamosal, postorbital, and parietal. The median posterior portion of the parietal seems to end suddenly over the occiput, and the parieto-squamosal arcade appears to be lacking. In fact, Marsh has stated (1896) that "the skull of *Belodon* [*Phytosaurus*] shows that the supratemporal openings, characteristic of the true crocodillians are wanting."

Again, in characterizing the Phytosauria, McGregor says:¹ "Post-temporal (parieto-squamosal) arcade greatly depressed, reduced, and covered by muscles." In Angistorhinus grandis, however, this is not the condition. A comparison of the posterior view of A. grandis with that of Mystriosuchus planirostrus (Figs. 5 and 6) will serve well to show the differences. In the former the posttemporal arcade is well developed and borders the supratemporal vacuities in the same plane that extends over the roof of the cranium. The posterior extension of this parieto-squamosal arcade forms an overhanging shelf that in a dorsal view hides all the bones of the posterior side of the skull. The *parietals* seem to have a comparatively small lateral and downward expansion on the posterior surface and but slight contact with the supraoccipital. The squamosals, on the contrary, send down broad, platelike extensions from the posterior borders of the supratemporal vacuities that connect broadly with the supraoccipital at their inner edges. They form the upper and outer borders of the post-temporal vacuities and connect broadly with the upper inner ends of the opisthotics. As the specimen is now prepared, a large fenestra pierces this element on either side of the skull just over the post-temporal vacuity. This opening is, however, undoubtedly due to the abraded condition of the bone as the matrix beneath indicated an uninterrupted bone surface. The lateral, downward-directed angles or hooklike processes of the squamosals, mentioned above, extend some 23 mm. below the lower borders of the opisthotics. The boundaries of the supraoccipital are not distinct; it seems to be a small, approximately triangular element forming a considerable portion of the upper border of the foramen magnum. Its greatest width is probably not over 31 mm. The exoccipitals and opisthotics are thoroughly co-ossified. The *exoccipitals* form the lateral and probably most of

¹ Ibid., p. 92.

the lower border of the foramen magnum. The part they take in the formation of the occipital condyle, I take it, is slight. The opisthotics are rather stout and widen considerably toward their lateral extremities. Just before they reach the hooklike processes of the squamosals their vertical measurement is about 38 mm. From this point they rapidly taper off in each direction. They form the lower and apparently the inner borders of the posttemporal vacuities. The relations of the pterygoids with the quadrates seem to be much the same as in *M. planirostris*, according to McGregor's interpretation. Their lateral extent on the posterior surface of the skull seems to be comparatively slight. There is no possibility of their taking part in the borders of the quadrate foramina as they do in Belodon¹ (Mystriosuchus) plieningeri H. von Meyer sp., according to F. von Huene.² In the specimen herein described the lower lateral portion of the quadrate was broken away, leaving, however, a good impression of the inner surface. From this and the natural mold in the matrix, of the outer surface, and with the aid of a separate quadrate found in the same locality, an accurate restoration was possible. It has an articular face of about 75 mm. lateral extent. There is an offset in the quadrate along a vertical line through the inner limit of this articular face. From this offset it extends toward the median line in a thin plate. Its inner edge meets the pterygoid and the two floor over a depression, the outline of which is a parallelogram with the greater diagonal directed upward and inward. This depression is bounded above by the opisthotic, on the outer side by the raised portion of the quadrate, below by the raised barlike portion of the cojoined quadrate and pterygoid, and on the inner side by the exoccipitals and the basisphenoid.

THE MANDIBLE

The mandible of this species is massive throughout. This is especially noticeable in the posterior symphysial region; here the

¹ For an explanation of the substitution of *Belodon* for *Mystriosuchus* see the appended list of genera and species.

² "Beiträge zur Kenntnis und Beurteilung der Parasuchier," *Geologische und palaeontologische Abhandlungen*, Neue Folge, Band X, Heft I (1911), p. 8, Fig. 3.

rami have a thickness of 40 mm. The smallest width of the mandible is 41 mm., at a point about 60 mm. back of the anterior end. From here the width increases gradually to about 90 mm. at the posterior end of the symphysis. The anterior end is considerably enlarged for the reception of the large terminal teeth. The greatest width of this expanded portion is 73 mm. The lateral margins are upturned so as to form a very conspicuous anterior-posteriorly directed groove along the median line. This is 31 mm. wide at the top and is broadly excavated to a depth of 9 mm. From the tip of the mandible to the posterior end of the symphysis the length is about 430 mm. The total length is about 930 mm. The external maxillary fenestra is about 200 mm. long and 44 mm. wide, with rounded anterior and posterior borders. Only the *alveoli* remain in the lower jaw upon which to base a description of the teeth. About 36 of these are present now on one side. There were probably 10 more present in the fragment which is now missing above the anterior end of the external maxillary fenestra, making about 46 alveoli in all. Three of these are placed in the expanded upturned anterior portion of the jaw. They are circular in section, as are all the alveoli, and greatly enlarged. The anterior one on each side is 12 mm. in diameter, the next two are of about equal size and measure 16.5 mm. in diameter. If the supposition that the tooth shown in Fig. 8 is one of these anterior teeth of this or a similar species is correct, we may assign a length of some 45 mm. or more to the teeth of the terminal expansion. The two anterior alveoli which are separated by the median channel mentioned above are about 24 mm. apart. Between the first and second and the second and third teeth only a thin film of bone intervenes. Between the last tooth of the terminal, enlarged series and the following one, the fourth, there is a space of about 15 mm. The alveoli back of the three large anterior ones vary considerably in diameter, ranging from 8 mm. to 16 mm. In a general way they increase in size posteriorly, but this is irregular, some of the largest being placed near the middle of the row. In consequence of this irregularity in the size of the alveoli there is an irregularity in the intervening spaces. These spaces range from a thin film to about 8 mm. in width, the greater spaces being, in general, in the anterior portion of the mandible. This irregularity of size and spacing of the alveoli is probably largely due to the different ages of the teeth; that is, to loss and replacement of some. Well-developed, rounded ridges, such as are seen on the ventral surface of the rostrum, are present just within the lines of alveoli. In this specimen they are prominent anteriorly, combining near the anterior end and gradually spreading posteriorly. They become less prominent toward the posterior end of the symphysis and are entirely wanting before this point is reached.

The second specimen referred to in the preliminary notice of *Angistorhinus grandis*^I would, it was hoped, when worked up, furnish a complete skeleton of that form. It was found, however, that the matrix was a hard, extremely tough sandstone and almost impossible to free from the bone, as the latter was in every case found to be softer than the matrix and extremely brittle. For these reasons a further attempt to prepare a skeleton has been abandoned, for the present at least. Aside from the skull, a portion of the posterior border of which is missing, and the lower mandible, which also lacks a little of the posterior extremities, only a single dorsal vertebra, several abdominal ribs, and quite an assortment of unassociated teeth are available for description. These serve well, however, to set the specimen off as a species distinct from A. grandis.

Angistorhinus gracilis Sp. Nov.

This skull, which I take to be that of an adult individual, probably had a length of about 985 mm., somewhat greater than that of the specimen of *A. grandis*. The greatest length preserved, which does not quite include the quadrate, is 920 mm. This is somewhat greater than the same measurement of *A. grandis*, but in spite of this the latter is the more massively built skull, a point that is especially noticeable in the form of the mandible to be discussed farther on.

OPENINGS OF THE SKULL

The supratemporal fenestrae are missing, but from the close resemblance of the skull to A. grandis in other respects these open-

¹ Jour. Geol., XXI (1913), 190.

ings were probably about the same in both forms. That is, the parietal-squamosal arcades are well devleoped and in the same plane as the dorsal surface of the cranium. The upper posterior border of the lateral temporal fenestra is also wanting. Its width of 80 mm., however, which is greater than that of A. grandis, would indicate at least an equally large fenestra in A. gracilis. Contrary to what might be expected from this greater width of the lateral temporal fenestra, the bar of bone left between it and the orbit is much more massive than in A. grandis. The orbits are somewhat smaller than in this latter genus, about 45 mm. wide and 75 mm. long. Some 30 mm. below the orbit, in the jugal bar, midway between the lateral temporal fenestra and the antorbital vacuity, is a large, well-defined foramen, probably for the enervation of the powerful cheek muscles as in the modern Gavial. This was not noted, but probably was present in the specimen representing A. grandis. The nares are elevated on a considerable prominence, about 31 mm. above the general level of the roof of the cranium. As in A. grandis, they are separated by a thin median partition that does not rise to the same elevation as the posterior and lateral borders of the nares. Thus the nares form, in a way, a common opening about 35 mm. wide and 55 mm. long. The exact length cannot be told, as the anterior borders are weathered away. The state of preservation is such that few of the sutures are distinguishable. Hence a description of all the separate elements of the skull is impossible. Special attention was paid to the region bordering the nares in the hope that the relations of the septomaxillary bones could be determined. With but a few exceptions the students that have worked with the phytosaurs have overlooked these elements. According to F. von Huene they are present in all of the phytosauria. "Vor dem Nasenlöcher schliessen die Nasalia nicht To quote:¹ zusammen. Hier tritt ein ungewöhnlicher Knocken, das Septomaxillare (bei allen Phytosauriern) dazwischen."

A diligent search on the specimen representing A. grandis and also Palaeorhinus bransoni failed to show these elements. However, one is forced to conclude that the failure to locate the sutures of such elements is due to the state of preservation of the specimen

¹ Op. cit., p. 11. The reference is to Belodon (Mystriosuchus) plieningeri.

and not to their absence, as the septomaxillary bones are apparent in the specimen of A. gracilis. In all probability the region about the anterior border of the nares in many of the phytosaurs was always more or less cartilaginous. In many of the specimens that the writer has studied, either from figures or from the original, this anterior border is ill defined, extending forward in a sort of slit. In A. gracilis the septomaxillae evidently unite along the median line and form the anterior border of the nares. Their extent in front of the nares along this line is 45 mm. What part they take in the median septum in separating the nares cannot be determined. Their greatest width is about 27 mm. on a line through the anterior border on the nares. In front the premaxillae dovetail into them and form their anterior border. The nasals meet the premaxillae far forward along the lateral border of the septomaxillae and form the lateral boundaries of those elements. The relations of these various elements are diagrammatically shown in Fig. 4.

The rostrum in this species is much more slender than that of A. grandis. From the tip to the anterior border of the nares is a distance of 670 mm., or about 610 mm. to the anterior border of the antorbital vacuity. In A. grandis these measurements are 650 mm. and 585 mm. respectively. The width of the rostrum just back of the terminal expansion is 34 mm., at about midlength 44 mm., and at a point 140 mm. in front of the antorbital vacuity, 56 mm. These respective measurements in A. grandis are 42 mm., 65 mm., and 94 mm. In the latter species the rostrum, seen in a lateral view, tapers down much less abruptly from the cranium proper than in the former. The terminal expansion of A. gracilis starts abruptly at a distance of 68 mm. from the end of the horizontal portion, increasing from a width of 34 mm. to 51 mm. This width it maintains, with only a very slight increase, to the tip. The extremity is bent abruptly downward and extends approximately 44 mm. below the ventral surface of the rostrum. The rostrum as a whole is curved, concave upward, but this is probably a result of deformation. As seems to be the usual case in phytosaurian remains, most of the teeth have dropped from the alveoli. Only the first, second, and fourth of the right premaxilla teeth are preserved in this specimen but these are entire and well preserved. The first and second are in the down-curved tip of the rostrum. The fourth is probably the last of the long rakelike teeth, for it is the last tooth in the anterior expanded portion. The first tooth, the anterior one, is nearly complete, about 35 mm. long and 9 mm. in diameter at the base. This is probably a substitute for an earlier tooth, as the section of the corresponding tooth on the opposite side, which is broken off close up to the surface of the rostrum, indicates a tooth as large as those that follow. The second tooth is considerably larger and still preserves the sharp point. It is 78 mm. in length and has a diameter of 12 mm. at the base. The third tooth is broken off at the base but the section indicates a size for it equal to the fourth. This tooth is 60 mm. long and 0 mm. in The section of all of these anterior teeth is round with diameter. no indications of trenchant edges or fluting. The space between these teeth of the expanded anterior portion is somewhat greater than those between the remaining teeth. Between the two anterior teeth is a space of fully 18 mm. Between the first and second, the second and third, and the third and fourth the spaces are approximately 12 mm., 9 mm., and 10 mm., respectively. The number of teeth in the rostrum back of these cannot be told accurately. It is probably slightly greater than in A. grandis, however, as there are about 38 in the space from the tip to the anterior border of the antorbital vacuity in the former and 34 in the space of the latter. This is inclusive of those of the expanded anterior portion. In A. gracilis the alveoli back of the expanded portion are subequal, averaging about 10 mm. in diameter, and all are round. There is a slight increase in diameter from the anterior end of the series backward. The spacing is rather irregular, varying between 4 mm. While the crowns of none of these posterior teeth are and o mm. preserved in place, they can be described with some degree of certainty. From the locality where the skulls herein described were collected nearly all the vertebrate remains were phytosaurian. Many loose teeth were picked up as well as several associated with skulls. There is no group of animals from this locality other than the phytosaurs to which the teeth can be ascribed with certainty. A selected series of these teeth is shown in Figs. 8–16. One specimen (not here figured), a fragment of a skull in which some of the

149

teeth of the margin below the antorbital vacuity are still preserved, forms a part of the collection. This fragment is undoubtedly Angistorhinus sp. The crown of one of these teeth is well preserved and is almost identical with that shown in Fig. 16, which is one of several teeth found loose in the matrix close to the skull of A. The crown of this tooth is 25 mm. long, 20 mm. wide at gracilis. its greatest width, which is just above the alveolus, and at this same point has a thickness of about 12 mm. The anterior and posterior edges are sharp and very finely serrate, there being three serrations to one millimeter. Of the other teeth figured all but that in Fig. 9 have sharp anterior and posterior cutting edges with serrations numbering from fifteen to twenty in five millimeters. In that one, while the anterior and posterior edges are not sharp, the section is oval and it is further differentiated from the others by indications of fluting. In general it resembles the unerupted tooth seen in a section through the rostrum of A. grandis mentioned above. Just where this tooth found its place in the dentition cannot be told. It is the presumption, however, that it is one of the anterior teeth. While the ends of any series that can be formed of these teeth differ widely, they grade into each other in such a way that one would probably not be justified in supposing that such a series could not be found in the jaws of a single individual. Fig. 8, for instance, might well be the anterior tooth in the lower jaw of A. grandis; Fig. 10 is much the same sort of a tooth, but somewhat smaller. Fig. 12 is probably one of the premaxillary teeth, Figs. 11, 14, and 16, the middle or posterior maxillary teeth, and Fig. 15, one of the last in the series. The sections of Fig. 13 show well how the approximately circular root suddenly expands into the trenchant edged crown. Such variations as those above show the uncertainty encountered in basing species on a few isolated teeth with our present fragmentary knowledge of the dentition of these forms.

THE MANDIBLE

The posterior extremity of each ramus is missing, probably about 200 mm. The part present shows the same characteristics as does the skull when compared with *A. grandis*, viz., a greater length and more delicate build. The length of the symphysis is approximately 500 mm., considerably greater than in *Belodon* (Mystriosuchus) plieningeri or Lophoprospus (Belodon kapfi). In these two latter forms, according to F. von Huene,^I the length is 290 mm. and 280 mm. respectively. The end of the mandible swells rapidly at a point about 51 mm. from the tip into a disklike expansion with a width of some 68 mm. This terminal expansion



FIGS. 8-16.—Phytosaurian teeth, presumably from the genus Angistorhinus. Figs. 8 and 10, teeth of the anterior terminal expansion of the lower jaw? Fig. 9, probably one of the anterior premaxillary teeth. Figs. 11, 14, 15 and 16, posterior maxillary teeth? Fig. 12, probably one of the anterior premaxillary teeth. Fig. 13, root and part of crown of one of the posterior teeth, showing the sudden transition from round to compressed section. All a little under natural size.

¹ Op. cit., p. 27.

differs from that of *A. grandis* in that the upper surface is a plane instead of being deeply grooved along the median line. Below the expansion there is a considerable convexity for the accommodation of the roots of the large terminal teeth. Just back of the expansion the mandible measures 29 mm. and has a thickness of about 17 mm.

Posteriorly the width increases gradually to 99 mm. at the posterior end of the symphysis or about 9 mm. more than the same measurement in A. grandis. It measures 25 mm. in thickness at this point, while this measurement is 41 mm. in A. grandis. These differences of measurement of the posterior end of the symphysis may be partially due to crushing in the former specimen but there is little evidence of this. Of the lower jaw none of the teeth is complete; the few that remain are broken off close up to the mandible and add little to our knowledge of the dentition except as to the relative size and spacing of the teeth. The alveoli are all more or less circular in outline but vary somewhat in size. In the expanded portion of the anterior end are placed three large teeth of approximately equal sections. They are apparently antero-posteriorly compressed, but this is probably an oblique section, a horizontal section through an outward-directed tooth. The average anteroposterior diameter is about 10 mm., considerably less than that of A. grandis. The two anterior teeth are separated by a space of 24 mm., while the other teeth of the expanded portion are crowded close together. The four teeth of the down-turned extremity of the rostrum evidently met close in front of the lower mandible, thus causing its large terminal teeth to close three on either side of the rostrum. The alveoli immediately back of the expansion are considerably smaller than the anterior ones and somewhat smaller than the teeth in the same region of A. grandis. They average about 5 mm. in diameter and are separated by a space of about 6 mm. From 4 mm. they increase guite regularly to 8 mm. or 9 mm. in the posterior ones and all are approximately 6 mm. or 7 mm. apart. In this species the teeth of the lower mandible are more numerous than in A. grandis, about 40 on each side.

THE VERTEBRAE

The single vertebra freed from the matrix is a little distorted and has lost the upper part of the spine but it shows the essential features well. It is a dorsal vertebra, one of the most anterior. It corresponds in a general way with those of the same region in Rhytiodin carolinensis Emmons and may therefore be compared with one of the anterior thoracics of that form figured by McGregor.¹ The vertebra of Angistorhinus gracilis is considerably the larger and the proportions are somewhat different. The centrum is very much constricted laterally, measuring but 20 mm. in the middle. The posterior face of the centrum is approximately circular, measuring about 54 mm. in diameter. The transverse diameter of the anterior face is somewhat greater than the vertical diameter, due to the enlarged articulation for the tuberosity of the rib. These diameters measure 68 mm. and 69 mm. respectively. The diapophyses form heavy transverse processes extending horizontally at the level of the neural canal and expanding distally. They are approximately triangular in section with one vertex directed downward. The centrum is considerably excavated below the base of the diapophyses, leaving them supported for a short distance laterally by two thin buttresses which are confluent below with the anterior and posterior rims of the centrum. The capitular articulation (if it be the true articular surface) is slightly concave. The articulation for the tuberosity is low down on the anterior border of the centrum, is convex, and as large as the capitular articulation. The posterior zygopophyses are missing. The anterior zygopophyses have a considerable anterior prominence. They are large, are directed up and inward at an angle of about 45° from the horizontal, and, though this measurement may be exaggerated by distortion, measure 44 mm. between the center of the articular faces. The spine is broken off about 31 mm. above the neural canal. The total height of the vertebra must have been at least 150 mm., however, and probably more. The following table of measurements will serve to show some of the differences in the two forms:

Rhytidodo	n carolinensis	Angistorhinus	gracilis
Length of centrum	mm	45 mm	
Height of centrum	mm	54 mm	•
Total height	mm(at least) 150 mm	•
Width across diapophyses104	mm	156 mm	•

¹ Op. cit., p. 66, Figs. 15, 15a, and Pl. 8, Figs. 10, 10a.

VENTRAL RIBS

Weathered out about the specimen were many fragments of ventral ribs. Several of these ribs have been restored and all show a length of 260 mm. or more. Most of them are almost straight for half their length, whence they curve gently to the extremity. At the middle they are somewhat flattened, having greater and lesser diameters of about 16 mm. and 12 mm. respectively. They taper slightly to the extremities and here the section is almost round. These are probably lateral ribs of the ventral series. One of the ribs differs considerably from the others in the amount of curvature. It is broadly curved at the center with the extremities bent nearly at right angles. This is possibly one of the median ventral series.

COMPARISON OF A. grandis AND A. gracilis

A brief review of some of the salient features of these two specimens will serve to show the distinctness of the two species:

- 1. Terminal expansion of rostrum taking place gradually and increasing in width to the tip.
- 2. Rostrum 94 mm. wide at a point 140 mm. in front of the antorbital vacuity.
- 3. Terminal expansion takes place in front of third tooth.
- 4. Greatest length of skull is 977 mm.
- 5. Length from anterior border of orbits to tip of rostrum 755 mm.
- 6. Interorbital width 68 mm.
- Terminal expansion of lower jaw upturned along lateral margins to form a median antero-posterior grove.
- 8. Rounded ridges along inner side of alveoli prominent.
- 9. Number of teeth in lower jaw about 46 on each side.
- Diameter of alveoli of lower jaw, exclusive of the large anterior ones, ranging between 8 mm. and 16 mm.

- 1. Terminal expansion of rostrum taking place suddenly and retaining the same width to the tip.
- 2. Rostrum 56 mm. wide at a point 140 mm. in front of the antorbital vacuity.
- 3. Terminal expansion takes place in front of fifth tooth.
- 4. Greatest length of skull is about 985 mm.
- 5. Length from anterior border of orbits to tip of rostrum 750 mm.
- 6. Interorbital width 68 mm.
- 7. Terminal expansion of lower jaw in a plane.
- 8. Rounded ridges along inner side of alveoli not prominent.
- 9. Number of teeth in lower jaw at least 49 on each side.
- Diameter of alveoli of lower jaw, exclusive of the large anterior ones, ranging between 5 mm. and 8 mm.

A COMPARISON OF THE GENUS Angistorhinus with other Genera

Angistorhinus is one of the largest forms known. The skull is longer than any other except perhaps that of Lophoprosopus (Belodon) kapffi. The most striking difference seen between these two forms is in the rostrum. In Lophoprosopus there is a high, vertical swelling or crest extending almost the entire length, while in Angistorhinus the rostrum is low and slender. In this form, too, the anterior extremity is abruptly turned down, much more so than



FIGS. 17-18.—Angistorhinus gracilis, anterior and lateral views of one of the anterior thoracic vertebrae, about one-third natural size.

in Lophoprosopus. Another important difference is seen in the well-developed parieto-squamosal arcade lying in the plane of the dorsal surface of the cranium of Angistorhinus and the much-reduced, depressed post-temporal arcade of Lophoprosopus that gives the supratemporal fenestra the appearance of being open behind.

From *Mystriosuchus* the genus differs, not only in the development of the post-temporal arcade in the manner mentioned above, but also quite radically in the teeth. In *Mystriosuchus* there are 94 of these in the upper dentition and not more than 84 in the upper dentition of *Angistorhinus*. In the latter genus, as pointed out above, the posterior teeth are laterally compressed with sharp anterior and posterior cutting edges. In the former genus, on the other hand, as shown by Dr. E. Fraas,¹ all the teeth are circular in section. In *Angistorhinus* the anterior end of the rostrum is much more abruptly down-turned and the downward extent is considerably greater than in *Mystriosuchus*. In the former genus, too, the posterior palatine foramina are much longer and more slit-like. In a lateral view the cranium proper of *Angistorhinus* is seen to make up a greater portion of the entire length of the skull than is the case in *Mystriosuchus*.

Rutiodon, of which R. carolinensis is the type, probably resembles Angistorhinus in general form more than any of the other genera. The differences found in the vertebrae have been pointed out above and it was shown that those of Angistorhinus were considerably the larger. The skulls, too, bear out this difference in size. The total length has not been determined for Rutiodon but the indications are that it was about that of Mystriosuchus, viz., 820 mm.,² while that of Angistorhinus is from 977 mm. to 985 mm. or more. The distance from the anterior border of the nares to the tip of the rostrum in the former is 510 mm.; in the latter genus the same measurement is 500 mm. Although a direct comparison of the dentition of the two forms is impossible, the teeth of *Rutiodon* at the middle of the rostrum seem to be considerably larger than those of Angistorhinus. The post-temporal arcade of the latter is greatly developed (in this it seems to differ from all other genera except perhaps *Palaeorhinus*) and the posterior palatine foramina are quite different. In the former genus they are almost round and probably not over 15 mm. in diameter, while in Angistorhinus they are about 60 mm. long and about 8 mm. in diameter.

Besides the much more anterior position of the nares in *Palaeo-rhinus* and the but slightly down-curved tip of the rostrum, this form differs from *Angistorhinus* in that the skull is much smaller and the slender rostrum makes up but about one-half the entire length. *Palaeorhinus* also has a less backward extension of the upper posterior border of the skull, much less developed "squamosal hooks," and the opisthotics are less massive, thinner, and more spatulaform than in *Angistorhinus*. The anterior extent of the

¹ Op. cit., p. 16. ² McGregor, op. cit., p. 58.

pre- and parasphenoid and of the inter-pterygoid vacuity is apparently considerably less in the former genus, and the pterygoid process of the basisphenoid is less massive and more separated from the greater wings than in the latter. The number of teeth in the upper mandible of *Palaeorhinus* is about 72, while in *Angistorhinus* they number 84. In all probability the post-temporal arcade is somewhat the same in both forms. Of this more will be said later in the special reference to *Palaeorhinus*.

The anterior part of the rostrum of *Mesorhinus fraasi* is missing. The rostrum therefore affords little material for comparison. What remains of it, however, suggests a form between *Angistorhinus* and *Lophoprosopus*. The external nares are much more anterior in *Mesorhinus* than in *Angistorhinus*, and the former, according to Jaekel, possess a parietal foramen. There is also apparently a difference in the elements about the anterior border of the nares in the two forms. Jaekel says:¹

Zwischen den vordern Enden der Nasenlöcher stehen zwei vertikale schmale Knochenleisten, die ich unbedenklich als Teile der Prämaxillaris angesprochen haben würde, wenn nicht Herr v. Huene ähnliche Gebilde bei anderen Belodonten eben als besondere Elemente, als Septomaxillaria beschrieben hätte.

F. von Huene, however, in a later paper, considers these as the ends of the premaxillae.² If we accept the interpretation of the latter, the difference between the two forms in this respect is evident. In *Angistorhinus* the septomaxillary bones seem to unite in the median line in front of the nares and exclude the premaxillae from that opening, while the premaxillae of *Mesorhinus* supposedly form the anterior and much of the lateral borders of the nares. While the parieto-squamosal arcade seems to be developed somewhat similar in the two forms, if one may judge from the figures of *Mesorhinus*, its posterior extent is not so great in the latter.

Palaeorhinus bransoni WILLISTON

This genus and species was briefly described by Dr. S. W. Williston in 1904.³ In 1907, after a detailed study of the type specimen, Mr. J. H. Lees published a much fuller description of

¹ Op. cit., p. 201. ² Op. cit., p. 50. ³ Jour. Geol., XII (1904), p. 696.

this form. Several new features were presented in this paper. To quote:

The new features which the present study has disclosed may be here summarized: The presence of the otic capsule and its relations and dimensions have been delineated. The sutural relations of the palatines, pterygoid, and vomer have been more clearly delineated and the unsuspected posterior extension of the latter elements as far as the presphenoidal vacuity demonstrated.

And again (p. 147):

In Mystriosuchus the parietals extend backward between the supratemporal openings at the level of the top of the skull for a little less than one inch, while in *Palaeorhinus* they extend in this direction two and one-fourth inches, are widely separated as already described, and meet the squamosals posteriorly to inclose the supratemporal at the upper level of the skull.

With these particular things in mind, viz., the posterior extent of the vomers, the otic opening, and the parieto-squamosal arcade, the writer has made a careful examination of the material representing this form. The skull is very much crushed, especially the palate, and few of the sutures are discernible. As the specimen is now prepared the articular face of the quadrate is turned almost directly outward instead of down, thus greatly exaggerating the posterior width of the skull. Basing the outline of a posterior view of Palaeorhinus on either Mystriosuchus or Angistorhinus, the greatest width would probably be not over 240 mm. in an uncrushed condition, or but little if any greater than that of M. planirostrus. In 1911, in a paper cited above, Jaekel mentioned the peculiar relations and development of the vomers in Palaeorhinus and presented figures showing what he considered a more likely interpretation of the palate. Jaekel's interpretation is certainly more phytosaurian. However, with the present state of the specimen one can only say that it is probably not justifiable to consider the vomers as extending back and forming the anterior border of the "presphenoidal vacuity." Concerning the otic capsule little can be said. The opening is present on the right side of the specimen; the left side is restored. This region was restored in Angistorhinus grandis from the impression of the inner surface of the bone. A thin film of the bone was still present and showed no indications of such an opening. Indeed, to the writer's knowledge, Palaeorhinus

158

is the only form in which the opening has been noted. In conversations with him, Dr. Williston has expressed the opinion that the opening is accidental in this case. One should probably not lay too much stress on its presence in this form till it has been found in other members of this genus. The parieto-squamosal arcade is crushed and largely broken away, giving an appearance to the supratemporal fenestra much like that of *Mystriosuchus planirostrus*. Whether this is the true condition or whether the form is like



FIGS. 19-20.—Ilia of a new, unnamed form. The ilium shown in Fig. 19 was referred by Lees to *Palaeorhinus bransoni*. Both figures about one-half natural size.

that of *Angistorhinus* as described above is not certain. The writer is inclined to agree with Lees, however, in assigning to it the form of the latter, but this view should probably also be held as tentative.

It has been impossible to ascertain the association of the ilium figured with the skull of *Palaeorhinus*.¹ Material has recently come into the hands of the writer which shows that the ilium is not that of *Palaeorhinus* as Mr. Lees supposed, but belongs to an entirely different group of reptiles. Fig. 19 is of the same ilium figured with

¹ Lees, *op. cit.*, Fig. 8.

Palaeorhinus, with slightly different orientation to bring out its similarity with another specimen, Fig. 20. This second specimen is somewhat crushed laterally and is slightly smaller and more slender than the first. They probably represent two different species but the figures indicate that they are generically the same, or at least should be so considered till evidence to the contrary is forthcoming. A brief notice of this new form follows:

NEW GENUS?

The material upon which this form is based consists of several extremities (both proximal and distal) of limb bones, several vertebrae from various regions of the body, and many other fragments, besides the ilium figured above (Fig. 20). The specimen is a part of the collection of the University of Chicago expedition of 1904 and comes from the Popo Agie River region of the Trias of Wyoming.

One of the vertebrae has been freed from the matrix and shows characteristics not at all like those of the phytosaurs. It is a middle or anterior thoracic vertebra with the capitular articulation in a transitional stage in its elevation from the centrum to the arch. The centrum is spool- or hourglass-shaped with anterior and posterior faces slightly concave and is much constricted laterally along its midlength. It is 54 mm. long and 10 mm. wide at the center (this width is probably lessened by pressure). The articular faces are slightly oblong in outline, about 32 mm. wide and 30 mm. high. The diapophyses are in the form of thin horizontal plates confluent anteriorly with the articular faces of the zygapophyses and widening regularly posteriorly. Suddenly, near the posterior ends, they thicken below into the articulation for the tuberosity. At this point the diapophyses are about 56 mm. from tip to tip. They are supported at the posterior end by two thin diverging buttresses, one directed toward the upper posterior articular face of the centrum but not reaching this point, the other confluent with the capitular articulation on the upper anterior articular face of the centrum. The distance between the articular faces for the tuberosity and that of the capitulum is some 30 mm. The total height of the vertebrae is 96 mm. The upper portion of the spine is

missing, however—probably no small portion. At the base the spine is thin, not over 5 mm. in thickness, and has a width of 43 mm.

Several forms have been described from the region where these remains were found, all based on more or less fragmentary material.^T The indications all point to their distinctness from the form herein described, but as yet not enough is known to warrant its being given a new generic name. The writer expects soon to make a series of thorough collections in the western Trias and hopes to add to the knowledge of this and other forms that are little known. A fuller description of the material here mentioned and a discussion of its relationships will follow.

All who have worked with the phytosaurs have felt, I am sure, that we have been too zealous in our efforts to place all the fragments that have been referred to this group in the various schemes of classification. Too often we have proposed new species and even new genera for a few tooth fragments or a few imperfect limb bones.

The following list consists of those forms that, in the writer's opinion, have been fairly well established. In the arrangement of these forms no attempt is made to show the genetic relationship. 1. *Phytosaurus Jaeger*²

P. cylindricon Jaeger

In 1861 H. von Meyer attempted to show that *P. cylindricon* and *P. cubricon* Jaeger were in reality described from different regions of the jaw of one individual and that this form was the same as his *Belodon kapffi.*³ This being the case, the name *Phytosaurus* has priority, and McGregor has so used it (1906) referring to that genus the forms that had previously been placed in the genus *Belodon*. The material upon which the genus *Phytosaurus* was based, however, is in such an exceedingly poor state of preservation

¹ For a description of *Dolichobrachium gracile* Williston, *Eubrachiosaurus browni* Williston, and *Brachybrachium brevipes* Williston, see *Jour. Geol.*, XII (1904), 688–94.

² G. F. Jaeger, Über die fossil Reptilien welche in Württemberg aufgefunden worden sind. Stuttgart, 1828.

³ "Reptilien aus dem Stubensandstein und Keuper," *Palaeonlographica*, VII 253-346.

that one can never safely refer other material to it.^I The species *P. cylindricon*, then (the form first described), is the type and only species of this genus, and the form described by von Meyer as *Belodon kapfi* should be considered distinct.

2. Belodon von Meyer

B. plieningeri von Meyer

B. (Mystriosuchus) rutimeyeri F. von Huene

The genus *Belodon*, of which *B. plieningeri* is the type, was proposed in 1842^2 for a form with a slender rostrum and laterally compressed, arrowhead-shaped posterior teeth.

3. Mystriosuchus E. Fraas

M. (Belodon) planirostris H. von Meyer

This form differs from the genus *Belodon* chiefly in that the teeth of the former are all round in cross-section.

4. Rutiodon Emmons³

R. carolinensis Emmons

R. manhattanensis von Huene

The writer has followed McGregor in uniting in the first species most of the many specimens that have been described from the Trias of the eastern United States under the following names:

Clepsysaurus pennsylvanicus I. Lea. Centemodon sulcatus I. Lea. Omosaurus perplexus J. Leidy. Palaeosaurus sulcatus E. Emmons. Palaeosaurus carolinensis E. Emmons. Compsosaurus priscus J. Leidy. Clepsisaurus leaii E. Emmons. Eurydorus serridus J. Leidy. Belodon carolinensis E. D. Cope. Belodon priscus Cope. Belodon lepturus Cope. Belodon leaii Cope. Rhytiodon rostratus O. C. Marsh. (?) Beldon validus Marsh (doubtful, never figured).

¹ Although the writer has not seen this material, he has been informed by no less an authority than Dr. S. W. Williston, who has recently had the opportunity to examine the type remains, that the preservation is such that one can in nowise be certain of its generic identity.

² Von Meyer, Neues Jahrb. f. Mineralogie.

³ Geological report on the midland counties of North Carolina.

5. Lophoprosopus gen. nov.

L. (Belodon) kapffi von Meyer

(?) L. buceros Cope¹

The generic value of the form represented by *Belodon kapffi* von Meyer is well established. The name *Lophoprosopus* is here substituted because, as pointed out above, both *Belodon* and *Phytosaurus* are preoccupied.

In the past several species have been based on very doubtful material and referred to the group represented by *L. kapffi*. These deserve, perhaps, brief mention here:

Belodon (Zanclodon) arenaceus E. Fraas, a fragment of a mandible that resembles L. kapffi and may well belong to that species.

Belodon ingens E. Fraas, a single skull very similar to that of L. kapffi and probably the same.

Belodon scopax E. D. Cope. Judging from the snout this form may well belong to the genus Palaeorhinus.

Belodon superciliosus E. D. Cope. This species is based on a few skull, teeth, and scute fragments and is very doubtful.

Heterodontosuchus ganei F. A. Lucas. The fragment of a mandible upon which this species was based was originally described as a Triassic crocodile. According to McGregor² we may expect to find this to be identical with L. (*Phytosaurus*) buceros when better material is at hand.

6. Palaeorhinus Williston

Palaeorhinus bransoni Williston

- (?) P. scopax (see the reference to this species under the genus Lophorhinus)
- 7. Angistorhinus Mehl
 - A. grandis Mehl
 - A. gracilis Mehl

¹ Some question arises as to whether this form belongs here. To quote Dr. O. Jackel (*Sitzungsberichten der Gesellschaft naturforschender Freunde*, No. 5, Jahrgang 1910, pp. 210-20): "Durch die Gesamtform des Schädels, besonders die Vorwölbung des pränasalen Schnauzenteils, die weit rückwärtige Lage der Nasen und die weite Vorstreckung der Squamosa-Ecke ist diese Form im Rahmen der *Phytosauridae* so deutlich gekennzeichnet, dass ich für sie daraufhin einen neuen Gattungstypus vorschlagen, und ihm den Namen *Metarhinus* geben möchte."

It is probably well to refer this form tentatively to the genus *Lophoprosopus* till further discoveries settle the point.

² Op. cit., p. 94.

8. Mesorhinus Jaekel

Mesorhinus fraasi Jaekel

9. Parasuchus Lydekker

P. hislopi Lydekker

Doubtful genera and species:

Rylea platyodon E. von Huene gen., Riley and Stutchbury sp.

These few imperfect remains, consisting of incomplete limb bones, teeth, caudal vertebrae, etc., are in all probability phytosaurian, but the material seems to be too meager to receive a generic or even a specific name.

Episcoposaurus E. D. Cope

E. horridus E. D. Cope

E. haplocerus E. D. Cope

Little is known of either of these two forms and their reference to the phytosaurs is not entirely warranted.

The genus *Palaeochtinus*^T Cope, under which were described *P. appalachianus*, *P. orthodon*,² and *P. dumblainus*,³ was based on a few teeth that Cope took to be those of a large dinosaur. These resemble closely some of the teeth figured with *Angistorhinus* and other phytosaurs and may well be phytosaurian remains. Incertae sedis:

Steganolepis robertsoni T. H. Huxley

While the fragmentary remains that represent this form may indicate their phytosaurian affinity, the relationship is not at all clear. In view of our meager knowledge of this form and also *Mesorhinus*, it hardly seems advisable at this time to remove the latter form from the *Phytosauridae* and place it with *Steganolepis* in the family Steganolepidae as F. von Huene has suggested.⁴ Probably undue stress has been placed on the presence of a parietal foramen in *Mesorhinus*. Only a single incomplète and poorly preserved skull has as yet been found. This fact being considered, it would seem that the presence of the parietal foramen is in nowise definitely established.

¹ Proceedings Amer. Philos. Soc., 1877, p. 182.

² "A Preliminary Report of the Vertebrate Paleontology of the Llano Estacado," Geol. Survey of Texas, Fourth Ann. Rept., 1892, p. 15, Pl. 2, Fig. 1.

³ Ibid., p. 16, Pl. 2, Figs. 4–6. ⁴ Op. cit., p. 50.

164

The writer wishes to take this opportunity to express his appreciation for the privilege of studying the material in the University of Chicago collections and also to thank Dr. S. W. Williston for his generous aid.

BIBLIOGRAPHY

A list of the important contributions to the literature of the phytosauria up to the year 1906 is given by McGregor in his important work "The Phytosauria, with Especial Reference to *Mystriosuchus* and *Rhytidodon*" (*Memoirs Amer. Mus. Nat. Hist.*, IX, Part II).

ADDITIONAL BIBLIOGRAPHY

HUENE, FR. VON.

- 1911. "Beiträge zur Kenntnis und Beurteilung der Parasuchier," Geologische und palaeontologische Abhandlungen, Neue Folge, Band X, Heft I.
- 1913. "A New Phytosaur from the Palisades near New York," Bull. Amer. Mus. Nat. Hist., XXXII, Art. XV.

JAEKEL, OTTO.

1910. "Über einen neuen Belodonten aus dem Buntsandstein von Bernburg," Sitzungsberichten der Gesellschaft naturforschender Freunde, No. V.

LEES, J. H.

1907. "The Skull of Palaeorhinus," Jour. Geol., XV.

Mehl, M. G.

1913. "Angistorhinus, A New Genus of Phytosauria from the Trias of Wyoming," Jour. Geol., XXI, No. 2.