

THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

August, 1965

Paper 2

A NEW WYOMING PHYTOSAUR

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ABSTRACT

The skull of a new species of *Angistorhinus*, family Phytosauridae, is described from the Popo Agie Member of the Chugwater Formation, Upper Triassic, Fremont County, Wyoming. It is large but not maximum for the genus, rostrum slender and slightly concave in dorsal outline, septomaxillaries slender, antorbital fenestrae long and spindle-shaped, skull roof of medium height and broadly curved. The skull, including palate, is complete except for part of the roof.

INTRODUCTION

The phytosaurs are a suborder, Parasuchia, of large semiaquatic thecodont reptiles known from the Triassic of Europe and North America. All except one, *Paleorhinus* (formerly *Mesorhinus*) *fraasi* of Germany, are found in Upper Triassic beds. They comprise a homogeneous family, Phytosauridae, of which the most distinctive features are their structural analogies with the Crocodylia, which replaced them ecologically in the Jurassic and later periods. Unlike crocodiles, the phytosaurs had a rostrum composed of the premaxillary bones, and the external nares were located dorsally, at or behind the mid-point of the skull. The food was probably large fishes and the larger stereospondyl amphibians which occur commonly in the same beds.

The specimen described here is a skull, without lower jaw, of a new species of *Angistorhinus*, found in the Popo Agie Member of the Chugwater Formation, Upper Triassic, in Fremont County, Wyoming, by a field party from the University of Kansas Museum of Natural History in

the summer of 1960. The skull (KU 11659) is unusually well preserved in all parts except the uppermost 2 or 3 inches of the cranium, from the nasal crest posteriorly, which had been exposed to stream erosion before it was found. As is commonly observed, the teeth had been lost from their alveoli before the specimen was buried. A few fragments of the missing parts of the skull, but no postcranial bones, were found.

ACKNOWLEDGMENTS

Here I wish to acknowledge assistance in the field by RICHARD C. FOX and ROBERT D. PLATZ, and subsequent careful work of preparation in the laboratory by the latter and by RUSSELL R. CAMP, who finished preparing the skull for exhibit in the Museum of Natural History at the University of Kansas. To GEORGE F. CARINI, then a graduate student at the University of Missouri, I owe useful information concerning the locality, and stratigraphy of the exposures. Dr. WILLIAM A. CLEMENS and CLYDE T. WILLIAMS on a later trip to the area gave further help, especially with stratigraphic measurements. Miss KATHRYN REINHARDT drew the illustrations, except for a part added by MERTON C. BOWMAN, who also painted the background for the museum exhibit.

LOCALITY AND STRATIGRAPHIC RELATIONSHIPS

Along the northeast-facing flank of the Wind River Range the Mesozoic and late Paleozoic sedimentary beds of the Wind River Basin are tilted upward and truncated, the more resistant rocks forming several parallel ridges at an eleva-

tion between 6,500 and 7,500 feet, the lower beds being closest to the main slope of the range. Among these the red beds of the Triassic Chugwater Formation make a nearly continuous belt of exposures having a width of one to three

miles. They form an uneven trough bounded laterally by the overlying buff-colored Nugget Sandstone of the Jurassic. Minor ridges occur in the Chugwater as the result of a few beds of limestone or hard sandstone. The Alcova Limestone Member is the most prominent of these, with a thickness of about 5 feet near the locality where the skull was found. Below the Alcova stratigraphically (toward the mountains) is the Red Peak Member, and above it the Popo Agie Member (pronounced "po-pózhic"). The latter has received particular attention because of the reptiles, stereospondyl amphibians, and fragments of fishes in its upper levels.

The locality for the specimen here described is the southeast corner of section 14, Township 1 North, Range 3 West, Fremont County, Wyoming. It is reached by following U.S. highway 287 northwest 23 miles from Lander, then turning west on the Sage Creek road to a point 11 miles from the highway. The Popo Agie is then on both sides of the road, and the bone bed lies 0.25 to 0.5 mile to the left (southeast) below an escarpment of the Nugget Sandstone. This is evidently the Sage Creek Locality, no. 6, of MEHL (1928) from which *Borborophagus (Eupelor) wyomingensis* and *Paleorhinus parvus* were collected, but in MEHL's map (*loc. cit.*, p. 170) the circle containing no. 6, to designate this locality, is not quite accurately placed in relation to the south fork of

Sage Creek, and it should be in T. 1 N. instead of T. 2 N. This is confirmed by a letter from GEORGE F. CARINI, saying, "Dr. MEHL informed me that his Sage Creek locality is approximately three miles south of the South Fork of Sage Creek, just off the St. Lawrence Ranger Station road."

The dip of the Popo Agie beds here is between 10° and 15°, in a direction 20° east of magnetic north. In the low wash at the foot of the bluff capped by Nugget Sandstone is a coarse limestone 2 to 3 feet thick, which can be followed up a gentle slope to the southwest about 200 yards, to where the new skull was found in a tributary dry wash, embedded in the same layer. From a detached boulder of this bed in the lower wash was taken a part of the interorbital skull roof of another phytosaur (KU 11660), probably also *Angistorhinus*, described at the end of this paper. The soft reddish sandstone and gray shale above the limestone contain teeth of fishes, labyrinthodonts, and phytosaurs, scraps of labyrinthodont (*Eupelor*) and phytosaur bones, and fish scales. Presumably these beds represent the top of the Popo Agie at this locality. The Alcova Limestone forms another escarpment facing the mountains about 0.5 mile southwest. The thickness of the Popo Agie here is about 220 feet, and the limestone containing the skull is about 50 feet from the top.

SYSTEMATIC DESCRIPTIONS

In his recent study of the genera of phytosaurs GREGORY (1962) recognized only 5 genera in one family and thus greatly simplified the classification of this group. The genera known from the Popo Agie are *Paleorhinus* and *Angistorhinus*, both primitive in having the posterior temporal arches at the level of the top of the skull. *Paleorhinus* is the most primitive, with the external nares anterior to the antorbital fenestrae, whereas in *Angistorhinus* and all others they are between those fenestrae. A European species named *Mesorhinus fraasi*, placed by GREGORY in *Paleorhinus*, is the only phytosaur known to retain a parietal foramen; this and its much greater age (Buntsandstein of the Lower Triassic) may justify retention of the original genus. The remaining genera, *Phytosaurus*, *Rutiodon*, and *Myrstriosuchus*, are specialized in having the posterior tem-

poral arches depressed to form a shelf, underlying the insertion of the most dorsal muscles of the neck.

Four species were referred to *Angistorhinus* by GREGORY. Three of them, *A. grandis* MEHL (1913), *A. gracilis* MEHL (1915), and *A. maximus* MEHL (1928), are from the Popo Agie in Wyoming, and one, *A. alticephalus* STOVALL & WHARTON (1936), from the Dockum Group in Howard County, Texas. To these should be added the species described by CASE (1929) as *Brachysuchus megalodon*, also from the Dockum of Texas, for GREGORY has recently reported (at annual meeting of Society of Vertebrate Paleontology, 1964) that the posterior temporal arches had been displaced by crushing from a position at the level of the top of the skull, and that they show the widening posteriorly that is characteristic of *Angistorhinus*.

FIG. 1 [Explanation.]—A. Ventral view of skull, $\times 0.17$.—B. Dorsal view of skull showing surfaces (oblique interrupted lines) where bone was broken away by stream erosion, $\times 0.17$.—C. Left lateral view of skull, parts above heavy line restored (broken lines), $\times 0.17$.

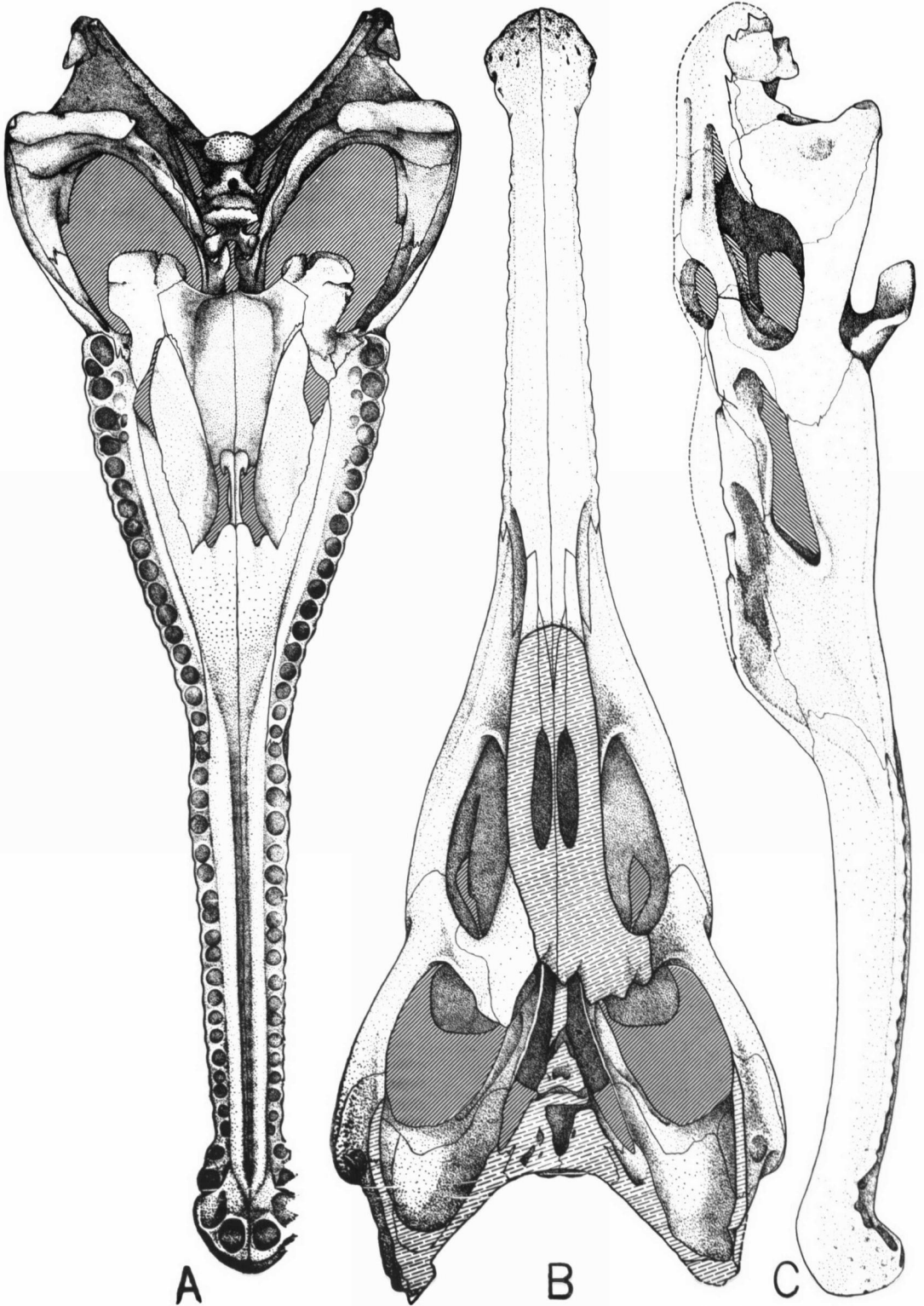


FIG. 1. *Angistorhinus aequalis* EATON, n. sp., Upper Triassic, Wyoming (see explanation on facing page).

Thus it is no longer necessary to separate *Brachysuchus* from *Angistorhinus*, although the rostrum is relatively short.

The new skull described below differs from each of those listed about as much as they differ from one another, and the nature of the differences seems inconsistent with ordinary individual variation. Within the genus the most available and significant characters are those of the skull. It would be necessary to obtain a much larger series of skulls before the possibility of either horizontal or vertical intergradation could be considered.

Order THECODONTIA Owen, 1860

Suborder PARASUCHIA Huxley, 1875

Family PHYTOSAURIDAE Lydekker, 1888

Genus ANGISTORHINUS Mehl, 1913

ANGISTORHINUS AEOLAMNIS Eaton, n. sp.

Figures 1, 2

Name derived from Gr. *Aiolus*, god of the winds, and Lat. *amnis*, stream.

Holotype. KU 11659, skull lacking lower jaw.

Diagnosis. Size large but not maximum for genus; rostrum slender (at point halfway in its length, width goes into length 6.5 times), upper surface gently concave; end of rostrum expanding gradually instead of abruptly; first 2 pairs of alveoli much enlarged, not in transverse line; third and fourth alveoli on widening base of expanded tip; prenarial length of skull approximately equals postnarial length; external nares between antorbital fenestrae; septomaxillaries long, slender, partly separated by premaxillaries; antorbital fenestrae long, spindle-shaped; curvature of skull roof gradual, without abrupt angle at sides; orbits facing as much up as laterally; lower temporal opening extending farther forward than orbits; quadratojugal concealing most but not all of quadrate in lateral view; lower margin of jugal nearly straight line; pterygoids meeting to form complete vault posterior to internal nares.

Discussion. In lateral view (Fig. 1C) the skull of *Angistorhinus aeolamnis* is of moderately slender proportions, less massive than that of *A. megalodon* (CASE, 1929) but somewhat heavier than *A. gracilis* (MEHL, 1915). The maximum length of the skull is 1,164 mm.; in the mid-line, to the tip of the condyle, it is 1,043 mm. The maximum width, across quadratojugals, is 415 mm. These dimensions suggest that the total length of the animal was between 7 and 8 meters.

In Figure 1C the heavy line from the front of the nasal crest to the orbit, across the suborbital bar, and behind the lower temporal opening designates the upper edge of the skull as it was preserved; parts above that line are restored. The broken surface is also shown in Figure 1B, by areas of oblique interrupted lines. The restoration (outlined by broken lines in Figs 1B, 1C, 2A, and 2B) includes the contour of the dorsal surface, the shape of the temporal arches (postorbital-squamosal and parietal-squamosal) and the shape and position of the external nares, as well as the pattern of the roof. Normal outlines of these parts were adjusted to the preserved edges of the skull.

Most features of *Angistorhinus aeolamnis* are closely comparable to those of *A. megalodon*. The snout of *A. aeolamnis* is longer and narrower; at a point halfway back the width goes into length 6.5 times, but in *A. megalodon* it goes 4.5. In lateral view the high part of the nasal crest is attained much farther forward in *A. aeolamnis*, some 80 mm. anterior to the antorbital fenestra, but in *A. megalodon* the crest slopes upward more gradually and does not reach its upper level until it is over the antorbital fenestra. CASE (*loc. cit.*, p. 23) mentions, and shows in his Fig. 3, a slight convexity near the mid-point of the upper surface of the premaxillary in *A. megalodon*, which as he says characterizes most phytosaurs; in *A. aeolamnis* this surface is entirely concave, as in *Rutiodon carolinensis*.

The first 2 pairs of alveoli in the premaxillary are much larger than others, about 23 mm. in diameter, the third 17 mm., and the fourth 12 mm. The third and fourth are in the narrowest base of the expanded tip of the snout. The fifth alveolus has a diameter of 7.5 mm., and those following increase irregularly until, at the posterior end of the premaxillary, they are again large (16 to 18 mm.). Twenty-three teeth emerge from the premaxillary on each side, but the 23rd, which apparently starts from the maxillary under a thin overlap of the premaxillary, is smaller and is comparable with the succeeding maxillary teeth (19 on the left and 18 on the right in this specimen). They increase unevenly, the largest maxillary alveolus being the most posterior. The edges of the alveoli are nearly circular and they are separated, but in *A. megalodon*, which has nearly the same number and variation in size, most alveoli are crowded, so that the walls between them are incomplete and do not come to the surface of the bone. The teeth may have grown at a rate incongruent with that of the bones carrying them.

In ventral view (Fig. 1A) differences between *Angistorhinus aeolamnis* and *A. megalodon* are

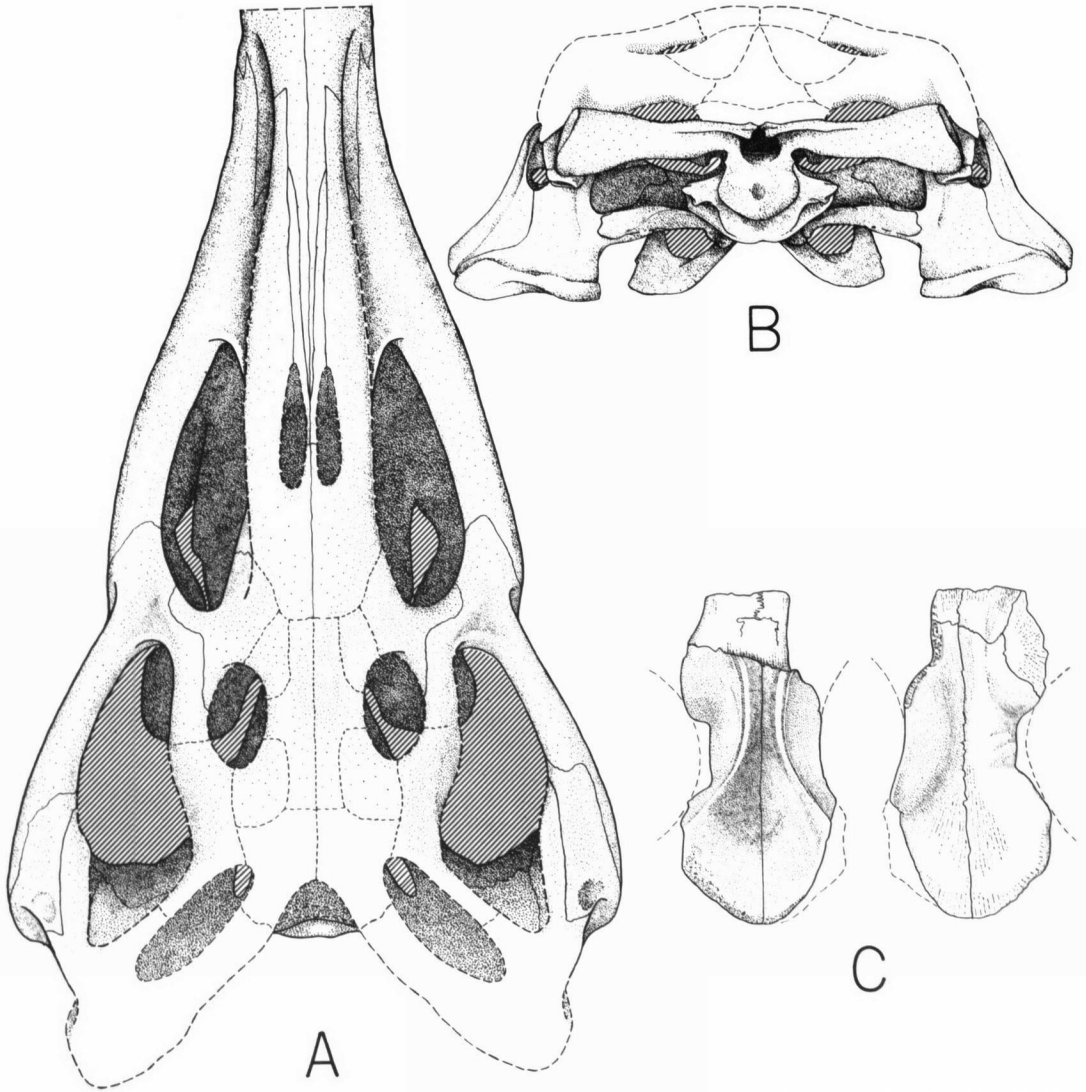


FIG. 2. *Angistorhinus aeolamnis* EATON, n. sp., and *A. sp.*, both Upper Triassic, Wyoming.—A, B. *A. aeolamnis*, dorsal and occipital views of skull with missing parts restored (broken lines), $\times 0.19$.—C. *A. sp.*, part of interorbital roof of specimen (KU 11660) showing position of orbits (broken lines), ventral surface on left and dorsal on right, $\times 0.39$.

readily observed. The premaxillary in *A. aeolamnis* sends back a long process between the palatine and maxillary on each side as far as a small palatine fenestra; this is not shown in *A. megalodon* or in other phytosaurs that I have seen figured. On the medial side of the posterior maxillary alveoli there are 4 shallow pits in a series parallel to the row of alveoli; these pits evidently received the ends of the teeth of the lower jaw that were long enough to reach the bone at that point. The internal nares of *A. aeolamnis* flare anterolaterally between premaxillary and palatine,

but those of *A. megalodon* do not. The length of the basioccipital anterior to its condyle is equal to the width of the condyle in *A. aeolamnis*, but in *A. megalodon* the condyle is much closer to the anterior end of the bone.

From *Angistorhinus alticephalus* STOVALL & WHARTON (1936) the new species differs in several ways. The skull of *A. alticephalus* is unusually high and steep-sided, with the external nares at the angle between the ascending edge of the nasal crest and the roof. The septomaxillaries are short and broad as in *A. gracilis* and perhaps *A.*

grandis, but unlike *A. aeolamnis* and *A. megalodon*. The teeth of *A. alticephalus* are pictured as small and rather widely spaced. The quadratojugal covers the quadrate as seen from the side, but in *A. aeolamnis* the upper end of the quadrate is exposed and in *A. megalodon* the whole posterior edge of it can be seen. The lower temporal opening of *A. alticephalus* is rhomboidal.

The most distinctive feature of the incomplete skull named *Angistorhinus maximus* by MEHL (1928) is the deep, narrow notch between the two posterior temporal arcades, which in the other species (including probably *A. aeolamnis*) was open at an angle of about 90 degrees. *A. maximus* also shows a strong downward-pointing angle in the lower margin of the jugal, which the others do not. In MEHL's figures (1913, 1915) of *A. grandis* the teeth are restored as nearly uniform in size and shape except for the most anterior; the alveoli should be re-examined, I think, because in most phytosaurs, including this genus, there is a conspicuous lack of uniformity in the series. *A. grandis* is also described as having only 2 pairs of greatly enlarged anterior teeth in a nearly transverse row on the deflected tip of the rostrum.

Concerning mobility of the components of the phytosaur skull, it is clear that there was freedom between the basiptyergoid processes and the facets of the pterygoids into which they fitted. Therefore, one would expect some movement of the braincase relative to the palate, pterygoids, quadrates, and other elements to which the latter were firmly attached. In *Angistorhinus aeolamnis* (Fig. 4) the basioccipital, exoccipitals, and opisthotics form a transverse bar, the ends of which rest against the posterior end of the squamosal and upper end of the quadrate on each side, in what

seems to be a relatively free sliding joint. In *A. megalodon*, according to CASE (1929), the quadrate and opisthotic are closely united and move as a unit against the squamosal, into which a rounded dorsal head of the quadrate fits. CASE also noted (*loc. cit.*, p. 18) "a distinct separation between the parietal and the supraoccipital, permitting anterior posterior movement of the supraoccipital-opisthotic-quadrate mass. The type specimen of *Leptosuchus crosbyensis* [of the Dockum, placed in *Ruitiodon* by GREGORY, 1962] shows that the whole brain case was loosely attached to the roof of the skull by cartilage." He added that the parietal is not firmly attached to the supraoccipital in any of the specimens in the University of Michigan collection. This may be assumed true in *A. aeolamnis*, although the relevant part of the skull is missing.

ANGISTORHINUS sp.

Figure 2C

A piece of the interorbital skull roof of a phytosaur (KU 11660) (Fig. 2C) was found by ROBERT D. PLATZ in a boulder of the same bed of coarse limestone as the skull, but about 200 yards to the north in the lower wash. On the ventral surface of the frontals is a smooth concavity, probably covering the anterior part of the cerebrum. From this concavity a shallow groove that runs anteriorly presumably covered the long, slender olfactory lobes (compare CAMP, 1930, figs. 25, 46, 47 of *Machaeroprotopus*). The sutures on the dorsal surface between the nasals, prefrontal, and frontals are consistent with those of *Angistorhinus* but are not adequate for determining the species.

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