

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3116, 26 pp., 10 figures, 1 table
December 28, 1994

The Late Cretaceous Alligatoroid *Brachychampsa Montana* (Crocodylia): New Material and Putative Relationships

MARK A. NORELL,¹ JAMES M. CLARK,²
AND J. HOWARD HUTCHISON³

ABSTRACT

The Late Cretaceous alligatoroid *Brachychampsa montana* was one of the first Mesozoic taxa to be recognized as an eusuchian crocodylian referable to a modern group. A spectacular new specimen from the Hell Creek Formation of North Dakota permits a critical examination of the morphology and relationships of this species. The skull of the new specimen is described in reference to the holotype cranium. To place this species within a taxonomy reflecting phylogenetic relationships,

we define the taxa Alligatoroidae and Alligatoridae to be the descent community and crown group, respectively, of extant alligatorids (*Alligator*, *Caiman*, *Melanosuchus*, and *Paleosuchus*). Preliminary comparisons suggest that *Brachychampsa* and its sister taxon *Albertochampsa langstoni* form a natural group with all alligatoroids except *Diplocynodon hantoniensis*. We find no evidence placing *Brachychampsa* within the Alligatoridae (i.e., the crown group).

INTRODUCTION

During paleontological reconnaissance of the Late Cretaceous Hell Creek Formation in western North Dakota in 1986, J. H. Hutch-

ison and L. Bryant collected a remarkable specimen of the poorly known crocodylian *Brachychampsa montana* Gilmore, 1911.

¹ Associate Curator, Department of Vertebrate Paleontology, American Museum of Natural History.

² Frick Postdoctoral Fellow, Department of Vertebrate Paleontology, American Museum of Natural History; current address: Department of Biological Sciences, George Washington University, Washington, DC 20052.

³ Curator Emeritus, Museum of Paleontology, University of California, Berkeley CA 94720.

This specimen comprises an extremely well-preserved, nearly entire skeleton and constitutes one of the most complete examples of a Cretaceous eusuchian yet collected. It therefore provides a firm basis for assessing the relationships of this and related taxa, and for revising their taxonomy to reflect these relationships.

The holotype of *Brachychampsa montana*, AMNH-DVP 5032 (fig. 1), was collected from the Hell Creek Formation in eastern Montana (fig. 2) by Barnum Brown in 1909. This specimen consists mainly of a rostrum broken across the orbits, with some associated cranial fragments, probably representing a juvenile or subadult. Nevertheless, prominent similarities with alligators and caimans are preserved, which led Gilmore (1911) to consider it a "true though primitive member of the Alligatoridae" (p. 297). Among the most obvious of these features are the broad, short rostrum, the occlusion pit for the fourth mandibular tooth medial to the lateral edge of the rostrum, and thick, bulbous teeth. Unfortunately, Gilmore did not provide a diagnosis for this species, nor did he discuss its specific relationships with alligatorids.

The new specimen of *Brachychampsa montana* permits detailed comparison of this species with alligatorids and a preliminary assessment of its phylogenetic relationships to the Alligatoridae. Until recently, phylogenetic relationships among alligatorid taxa have been unclear. Densmore (1983) and Densmore and Owen (1989) made some progress in deciphering patterns of relationship within the family using biochemical techniques. However, since their analysis was not based on morphological features, fossils cannot be readily incorporated into their branching diagram.

Norell (1990) provided a morphological analysis of alligatorid taxa that was largely congruent with the branching pattern preferred by Densmore (1983). In particular, a basal dichotomy into a clade including the two extant species of *Alligator* and another including the extant caimans—*Caiman*, *Melanosuchus*, and *Paleosuchus*—is common to both hypotheses. Norell included some of the better known fossils purported to be alligatorids into his analysis. Surprisingly, most of these taxa are within the crown group of the

family, and thus bear close relationship to one of the two extant clades of alligatorids. Because many of the fossils were not studied firsthand by Norell (1990), his conclusions about affinities of these extinct taxa were only preliminary.

As phylogenetic relationships among extant crocodylians become better known, their taxonomy must be modified to more accurately reflect these relationships. Throughout the text we use a revised taxonomy based upon the principles of the crown group and stem group (Ax, 1985; DeQueiroz and Gauthier, 1990, 1992) (fig. 3). We use Alligatoridae to signify the group including all species belonging to the crown group of the extant taxa *Caiman*, *Paleosuchus*, *Melanosuchus*, and *Alligator*, i.e., those taxa that we infer to have descended from the most recent common ancestor of these genera (fig. 3). We use the superfamilial name Alligatoroidea to refer to the group comprising Alligatoridae and stem members of this clade extending back to the most recent common ancestor of Alligatoridae and its closest extant relative, the Crocodylidae (Norell, 1989). This clade thus comprises Alligatoridae and all descendants of its closest common ancestor with Crocodylidae. Stem alligatoroids, therefore, include fossil taxa such as *Diplocynodon hantoniensis* (Wood, 1844) that possess synapomorphies allying them with the alligatorid crown group, but which are not closely related to a particular lineage of Alligatoridae. Although the relationships of crocodylids are not the subject of this paper, we recommend that for consistency Crocodylidae be used for the crown group and Crocodyloidea for the stem group plus crown group in crocodyloids.

We provisionally follow a taxonomy based on the relationships indicated by morphological features (Norell, 1989) as opposed to those indicated by molecular analyses (Densmore, 1983; Densmore and Owen, 1989). In particular, we consider the extant sister group of Alligatoridae to be Crocodylidae rather than Gavialidae or Crocodylidae + Gavialidae. Furthermore, we consider *Tomistoma* to be more closely related to *Crocodylus* than to *Gavialis*, and we therefore place it within Crocodylidae.

In this paper we describe the cranial and mandibular morphology of the new *Brachy-*



Fig. 1. Holotype of *Brachychampsia montana* (AMNH-DVP 5032); rostrum. Light area is reconstructed. (A) Dorsal view. (B) Ventral view.

champsia montana specimen. Unless otherwise noted, the holotype is identical to UCMP 133901 in those elements preserved. We restrict our description to the cranium and mandible because most characters used in previous phylogenetic studies of crocodylians are in these regions. We also provide a diagnosis of this taxon based on synapomorphies evident from a preliminary phylogenetic analysis of primitive alligatoroids.

ABBREVIATIONS

- AMNH-DHI American Museum of Natural History, Department of Herpetology and Ichthyology
 AMNH-DVP American Museum of Natural History, Department of Vertebrate Paleontology

BMNH British Museum of Natural History
 DMNH Denver Museum of Natural History
 MAN Mark A. Norell (now housed at AMNH-DHI)

PM Yale Peabody Museum
 SMM Science Museum of Minnesota
 UCMP University of California Museum of Paleontology
 UF University of Florida, Florida State Museum

SYSTEMATIC PALEONTOLOGY

REPTILIA LAURENTI, 1768

CROCODYLOMORPHA HAY, 1930

CROCODYLIA GMELIN, 1788

ALLIGATOROIDEA GRAY, 1844

DEFINITION: Alligatoroidea is defined here as the descent community of extant Alligatoridae, including the crown group alligator-

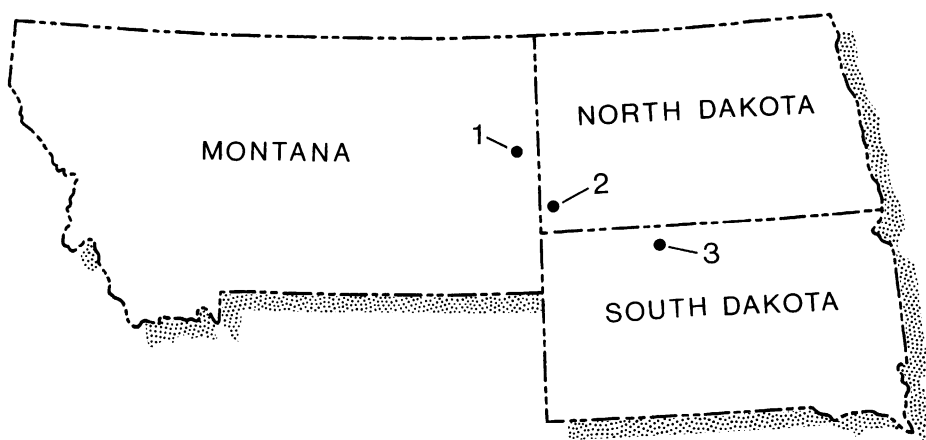


Fig. 2. Map of northern plains states. 1. Locality of *Brachychampsia montana* holotype (AMNH 5032). 2. Locality of UCMP 133901. 3. Locality of "*Bottosaurus perrugosus*" holotype (AMNH 1110).

ids (*Caiman*, *Melanosuchus*, *Paleosuchus*, and *Alligator*) and their stem group.

DIAGNOSIS: We provisionally diagnose this group by the following derived features: pit in the rostrum for occlusion of the fourth mandibular tooth, quadratojugal spine on the posterior margin of the lateral temporal fenestra very small or absent, foramen aërum on the dorsal surface of the articular, displaced laterad to medial edge of retroarticular process, atlas intercentrum longer than broad.

DISCUSSION: Following the principle of coordination of the International Code of Zoological Nomenclature, the author of the family-group name (in this case Gray) is considered to be the author of any other groups within the family group. We consider this taxon to include the stem group and the crown group of Alligatoridae, regardless of what particular taxon is hypothesized to be their closest extant relative. As discussed in the Introduction, we consider the closest relative to the Alligatoroidea to be the Crocodylidae, including *Tomistoma*; the Alligatoridae, thus, comprises all descendants of the most recent common ancestor of Alligatoridae and Crocodylidae that are more closely related to Alligatoridae than to Crocodylidae. Modifying the content of the Crocodylidae (the outgroup) to include *Tomistoma schlegelii* (Müller, 1838) in a monophyletic clade with *Gavialis gangeticus* (Gmelin, 1789) as the sister group to the traditional Crocodyli-

dae (as proposed by Densmore, 1983) or the sister group of the Alligatoroidea (Densmore and Owen, 1989) on the basis of molecular information has no effect on the polarity of diagnostic characters used here.

Brachychampsia montana Gilmore, 1911

DIAGNOSIS: Anterior end of rostrum very broad and blunt, narial aperture more than half as wide as rostrum, incisive foramen nearly half as wide as rostrum, suborbital fenestra smaller than in other alligatoroids, divided choana large, nearly excluding pterygoids from the ventral midline. Infratemporal fenestra large, nearly as large as orbit. Fifth maxillary tooth largest in the tooth row (reversal to the primitive condition for Crocodylia).

HOLOTYPE: AMNH-DVP 5032 (fig. 1), a rostrum and fragments of the left pterygoid and temporal region.

TYPE LOCALITY: "Twenty-five miles southeast of Lismas, Dawson County, Montana" (Gilmore, 1911: 298) (fig. 2). The specimen is said to be from the "upper sandstone" of the Hell Creek Formation, but it is unclear to what unit this refers.

REFERRED SPECIMENS: UCMP 133901, the subject of this paper, comprises a skull with articulated mandible; the hyoid skeleton; the vertebral column from atlas to sacrum but posterior part of the series poorly preserved;

dorsal osteoderms of neck, trunk and proximal part of tail; ventral armor of throat (there appears to have been no belly armor); most of forelegs lacking only the distal ulnae and parts of the right manus; proximal parts of scapula and coracoid; interclavicle; right femur; left femur lacking distal end; proximal fibula; partial right ilium.

DMNH 471, a left dentary from the Hell Creek Formation of South Dakota, shares with UCMP 133901 the unique "angle of the symphysis to the tooth row" (Carpenter and Lindsay, 1980: 1214). We interpret this as referring to the acute angle of the anterior ramus lateral to the symphyseal region, reflecting the characteristic squared off, blunt end to the rostrum. This character alone is sufficient for assigning this specimen to *Brachychampsa*. Carpenter and Lindsay (1980) cited other reasons for assigning this specimen to *Brachychampsa montana*, including tooth morphology (short crowns and heavy wrinkling) and the robust construction of the dentary. Both short tooth crowns and heavy wrinkling of the tooth enamel have an extensive distribution outside the taxon *Brachychampsa montana* (e.g., *Allognathosuchus mooki* Simpson, 1930, many taxa of North American Eocene "*Crocodylus*" including "*Crocodylus*" *affinis* Marsh, 1871), and are therefore insufficient basis for referring a specimen to *Brachychampsa*.

PREVIOUSLY REFERRED MATERIAL: In his description of *Brachychampsa montana*, Gilmore placed *Bottosaurus perrugosus* Cope, 1874, within *Brachychampsa*, modifying the name to *Brachychampsa perrugosa* [sic]. The *Bottosaurus perrugosus* holotype (Cope, 1875: p. 6) includes a dentary, a posterior mandibular fragment, two vertebral fragments, and associated bone fragments from the Lance Formation of eastern Colorado. Some of these associated bone fragments appear to belong to ceratopsian dinosaurs. In his type description of this species, Cope (1874) provisionally assigned it to *Bottosaurus* Agassiz, 1849, a common but poorly known genus supposedly of alligatoroid affinity from the Late Cretaceous Greensand of New Jersey (Steel, 1973).

Williston (1906) suggested that *Bottosaurus perrugosus* might be synonymous with "*Crocodylus*" *humilis* Leidy, 1856, a taxon

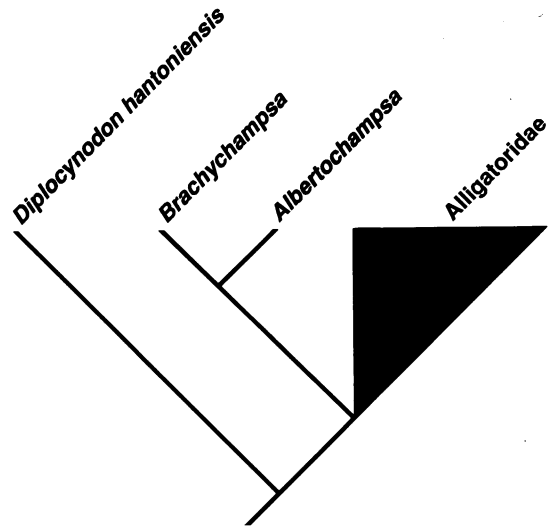


Fig. 3. Phylogenetic relationships of *Brachychampsa montana* suggested in this paper. The crown group Alligatoridae is composed of the descendants of the last common ancestor of the living taxa *Alligator mississippiensis*, *Alligator sinensis* Fauvel 1879, *Paleosuchus trigonatus* (Schneider 1801), *Paleosuchus palpebrosus*, *Melanosuchus niger*, *Caiman latirostris* (Daudin, 1802), and *Caiman crocodilus*. The Alligatoroidea is the closed descent community of the Alligatoridae and is indicated by the group composed of all of the taxa in this diagram including their ancestral stem species. The unnamed clade composed of *Albertochampsa langstoni* and *Brachychampsa montana* may be a member of the Alligatoridae, but, because this *Albertochampsa langstoni* + *Brachychampsa montana* clade cannot be related preferentially with a subclade of Alligatoridae, it cannot be ascribed to this group.

based on isolated teeth from the Late Cretaceous Judith River Formation of Montana, but the validity of the latter taxon is questionable. In his revision of Mesozoic crocodylians of North America, Mook (1925) did not mention "*Crocodylus*" *humilis*, considered *Bottosaurus perrugosus* to be valid "provisionally," and considered *Brachychampsa montana* to be valid beyond doubt; curiously, he failed to consider the possibility that the latter two species and genera may be synonymous.

Although Gilmore could not locate the *Bottosaurus perrugosus* holotype, it has since been found and is cataloged as AMNH-DVP

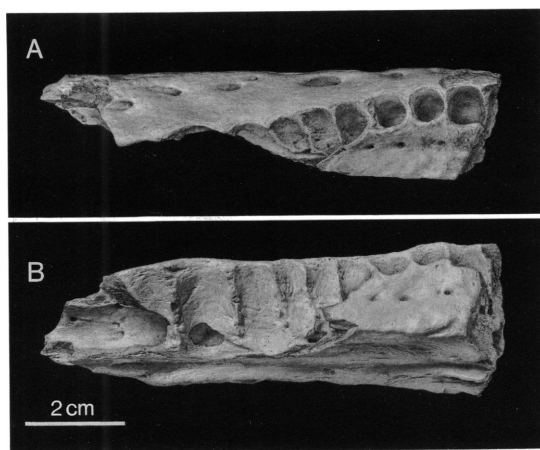


Fig. 4. The "*Bottosaurus perrugosus*" holotype (AMNH-DVP 1110), fragment of left dentary, a species ascribed by Gilmore, 1911 to *Brachychampsia* but considered here to be a nomen dubium. (A) Dorsal view. (B) Medial view.

1110 in the collection of the American Museum of Natural History. Gilmore's decision to synonymize these taxa was based on their occurrence in correlative formations and on Cope's statement that there is a slight difference in the sizes of the alveoli of the mandible. Examination of the holotype mandible (fig. 4) indicates that, although it may be referable to the Alligatoroidea, it cannot be allocated with certainty to *Brachychampsia* or differentiated from several other alligatoroid species. Derived features suggestive of alligatoroid affinity include the broad dorsal surface of the bone medial to the anterior teeth and the convex, highly vascularized dorsal surface of the dentary lateral to the more posterior alveoli. The holotype of *Bottosaurus perrugosus* may represent either the same species as *Brachychampsia montana* or an alligatoroid taxon distinct from all others yet named; we consider it a nomen dubium because the holotype material cannot be distinguished from several named species of alligatoroids, including the extant taxon *Alligator mississippiensis* (Daudin, 1801).

Isolated teeth from the Hell Creek Formation of Montana and the correlative Lance Formation of Colorado and Wyoming have been referred to *Brachychampsia montana* (e.g., Estes, 1964; Bryant, 1989), and isolated

teeth from the approximately correlative Kirtland Formation of New Mexico have been referred to this genus (Gilmore, 1916). Isolated crocodylomorph teeth are undiagnostic, however, due to their great intraspecific variability and extensive homoplastic similarity among taxa (Langston, 1965: 13). At this time we consider the allocation of isolated crocodylian teeth to species- and genus-level taxa to be impossible because patterns of dental variation within single taxa have not been adequately surveyed. Although teeth from the Late Cretaceous of western North America may resemble those of *Brachychampsia montana* in being bulbous and having a crenulate surface, they cannot be referred with certainty to this species because they are virtually identical to the teeth found in some ontogenetic stages of virtually all brevirostrine Crocodylia.

LOCALITY AND HORIZON OF UCMP 133901. UCMP locality V86049, sec. 14, T. 134 N., R. 106 W., Slope County, North Dakota. Specimen found in lag pocket in the basal part of a sandstone and mudstone filled channel complex of the upper Hell Creek Formation 23.3 m below its contact with the Ludlow Formation.

DESCRIPTION

GENERAL FEATURES OF THE CRANIUM: The cranium (fig. 5) is short and broad. It is dorsoventrally flattened, but this is partly due to crushing. The overall rectangular shape of the skull in dorsal view, especially anteriorly where the rostrum is squared off, is unusual among Crocodylia. Sculpturing is widespread and in places (e.g., the jugal) very deep. The undivided nares are extremely large, nearly circular, and face dorsally. The lateral temporal fenestra is larger than in other alligatoroids due to the narrowness and ventral position of the lower temporal arch. The orbit is smaller and more circular than in other alligatoroids, approximately comparable in size to the lateral temporal fenestra. The supratemporal fenestra is large, and, as in crocodylids and gavialids, lacks a roof over the posterior part of the fossa. The parietal table is heavily sculptured and flat.

The suborbital fenestra is short with an anterolaterally directed long axis. Its medial

TABLE 1

Selected Measurements of *Brachychampsia montana* for UCMP 133901 and AMNH-DVP 5032, in mm
Maximum dimensions unless otherwise indicated

	UCMP 133901	AMNH-DVP 5032
Skull		
Midline length (premaxilla to end of parietal table)	392.0	
Skull width at maxilla-premaxilla suture	162.0	95.1
Width of rostrum at 8th maxillary tooth	191.5	118.3
Minimum interorbital width across frontals	36.7	25.8
Width of skull at postorbital bar	261.0	165.0
Skull width (across quadrates)	278.0	—
Skull table width across squamosal horns	166.0	—
Supratemporal fenestra width	36.7	—
Supratemporal fenestra length	39.1	—
Interfenestral width across parietal	15.1	—
Orbit length	66.6	—
Depth of frontal (including crista cranii)	19.0	13.8
Nares length	80.4	—
Nares width	65.7	41.4
Lateral temporal fenestra length	62.5	—
Maximum width of incisive foramen	52.9	32.7
Quadrate articular condyle width	61.7	—
Width across distal pterygoid flanges	208.0	—
Choana length (some distortion)	32.0	—
Choana width (some distortion)	35.0	—
Suborbital fenestra length	68.3	—
Suborbital fenestra width	28.0	—
Minimum interfenestral width across palatines	61.9	—
Anteroposterior diameter of 1st pmx alveolus	13.4	7.3
Anteroposterior diameter of 5th maxillary alveolus	21.7	8.9
Mandible		
Symphyseal length	60.7	—
Retroarticular process length	62.0	—
Retroarticular process width	56.3	—
Mandibular fenestra height	39.6	—
Mandibular fenestra length (some distortion)	84.0	—

edge is strongly concave. The choana is large (although not as large as in *Sebecus*), almost filling the space between the palatine-ptyergoid suture and the posterior margin of the pterygoid, and nearly reaching the palatine anteriorly. The choana is wider than long, and its posterior edge is rimmed by a single labium choanalis. The choana is circular in ventral view and is completely divided by a delicate median septum as in extant alligatoroid species. The foramen magnum is obscured by elements of the axis and atlas that have not been separated from the occiput.

The mandible is articulated to the skull, and both sides are damaged posteriorly. Most of the upper and lower teeth are in tight oc-

clusion, and the posterior teeth, especially those of the dentary, are not completely exposed. The size and shape of the mandibular fenestra are distorted by postmortem compression, but the opening was apparently large. Cranial measurements of UCMP 133901 and the holotype (AMNH 5032) are provided in table 1.

CRANIAL BONES: The nasal ramus of the premaxilla is very long. It tapers posteriorly between the nasal and the maxilla, extending nearly half the length of the rostrum. Anteriorly the premaxilla is broad, and the rostrum does not narrow anteriorly until the anterior end. Rather, the plan of the skull bends sharply mesad at the fourth premaxillary



Fig. 5. *Brachychampsops montana* UCMP 133901. (A) Dorsal view. (B) Ventral view. (C) Occipital view. (D, E) Left lateral view. In B and D, a photograph of the posterior third of the left ramus is integrated with a photograph of the main block. Abbreviations: a angular, ar articular, ba basihyal, bo basioccipital, ch ceratohyal, d dentary, ec ectopterygoid, eo exoccipital, f frontal, j jugal, l lacrimal, ls laterosphenoid, m maxilla, n nasal, na₁ first neural arch, p parietal, pl palatine, pm premaxilla, po postorbital, pr proatlas, prf prefrontal, pt pterygoid, q quadrate, qj quadratojuagal, s splenial, sa surangular, so supraoccipital, sq squamosal, vc vertebral centrum. A muscle scar "A", C choana, IF incisive foramen, LTF lateral temporal fenestra, ME middle eustachian tube, SOF suborbital fenestra, STF supratemporal fenestra, V trigeminal foramen.

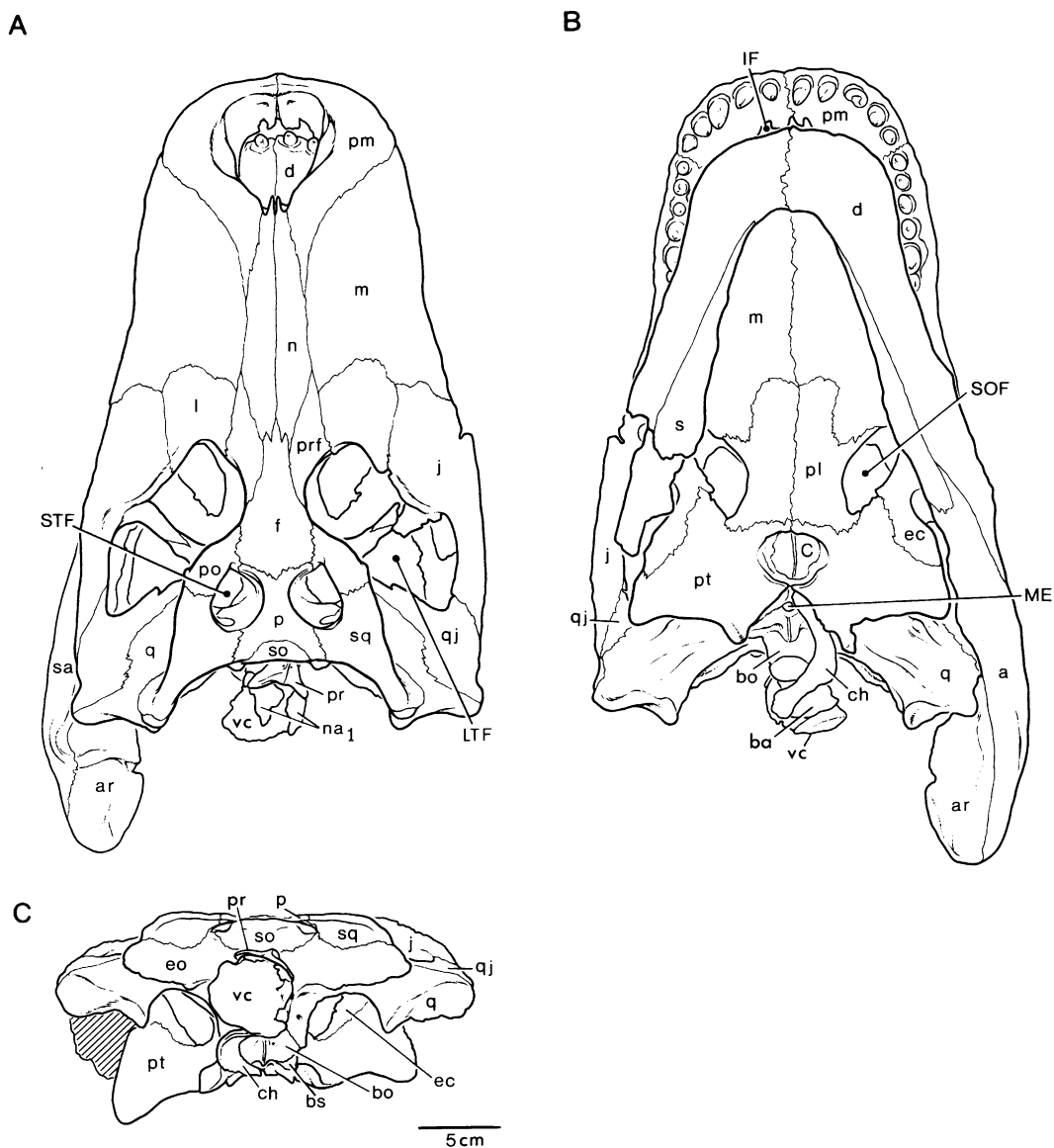


Fig. 5. Continued.

tooth, giving the skull an almost rectangular appearance. An internarial bar is absent, but there is a small protuberance on the dorsal midline of each premaxilla at the anterior end of the nares. Broad processes of the premaxillae meet to form a thick wall anterior to the narial opening. Within the narial chamber this wall is slightly concave. The premaxillae are widely separated posteriorly by the nasals. The premaxilla forms a flat, smooth,

dorsomedially oriented surface along the lateral edge of the nares. Posteriorly, this rim is elevated. Within the naris the premaxilla forms a longitudinal ridge beneath this flat surface, similar to a ridge in the nares of *Alligator* but larger and more horizontally oriented. A similar ridge is also present on the holotype.

The incisive foramen is gigantic, larger than in any other known crocodylian except *Al-*

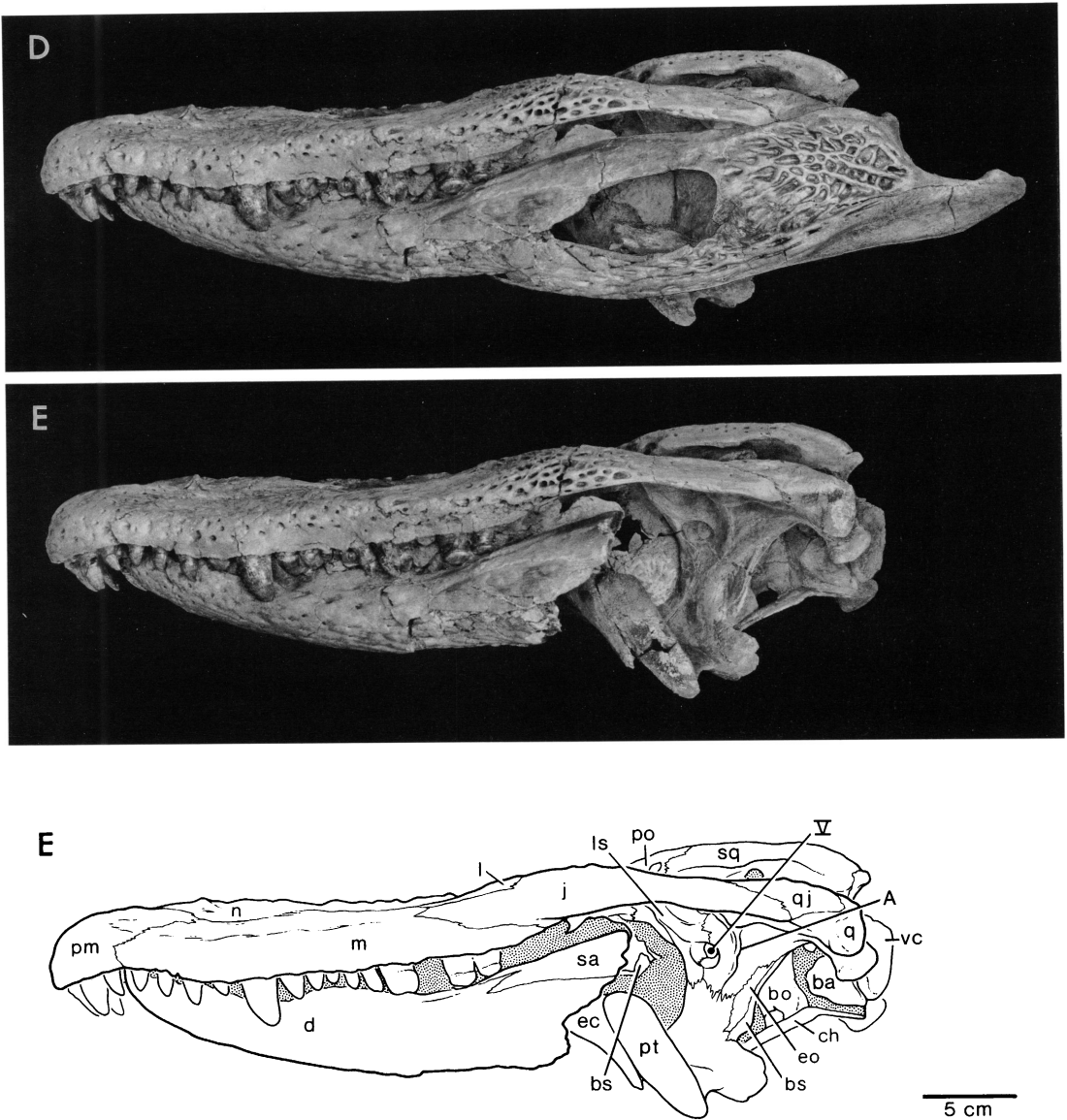


Fig. 5. Continued.

bertochampsia langstoni Erickson, 1972. It is about half the width of the snout and extends from the third maxillary tooth forward. The premaxillae meet broadly anterior to the foramen but are widely separated behind it, so that the maxillae form the posterior border of the opening. Shallow occlusion pits are present posterior to the first through third

teeth. The pits for the anteriormost dentary teeth have perforated the palatal lamina of the premaxilla anterior to the incisive foramen. These holes are broken posteriorly, so that they appear as notches emanating from the anterior arc of the premaxilla, however, in the holotype they are disconnected from the incisive foramen. A pit for reception of

the fourth dentary tooth lies at the premaxilla-maxilla contact, as in all extant alligatoroids. In the holotype a foramen opens ventrally at the posterior edge of the pit for the fourth mandibular tooth and leads into the premaxillary sinus. Because the lower jaws are in occlusion, this condition is unknown in UCMP 133901. No diastema separates the maxillary and premaxillary teeth. The sutural contact of the premaxilla with the maxilla on the palate is unusual among Crocodylia in being posteriorly convex, a feature that may be correlated with the large size of the incisive foramen. Many tiny "nutrient foramina" are present on the outer surface of the premaxilla, and the surface is sculptured on its posterior dorsal surface. A large foramen is present in the anterior wall of the nares near the midline.

The maxilla is very broad and flat. Its medial contact with the nasal is short, and it has a broad contact with the premaxilla anteriorly. Canthi rostrali are absent, and the maxilla is not expanded dorsally above the 4th to 5th maxillary teeth. Posteriorly the lateral edge of the maxilla is downturned and faces ventrolaterally, overhanging the posterior tooth row as in *Albertochampsia langstoni*. On the palate, the maxillary-palatine suture is squared off, with a transverse contact near the midline and parasagittal lateral contacts, similar to those in *Alligator*.

Posterolaterally, a shelf of maxilla is present between the very small suborbital fenestra and the maxillary tooth row (figs. 1, 6), as in Alligatoridae. The maxilla does not form any part of the medial edge of the suborbital fenestra. The lateral edge of the maxilla is slightly festooned, about the same as in *Alligator*. Sculpturing is very light on the dorsal surface, but vascularization canals are deep and numerous in places. The lateral edge of the maxilla contains many 'nutrient' foramina and passages for branches of the facial nerves. In the holotype, the posterior four maxillary teeth lie in a groove unseparated by bony septae; this area is not exposed on UCMP 133901.

The vomer is poorly exposed. A fragment visible between the posterior ends of the maxillae on UCMP 133901, where the maxillae were separated during diagenesis, may be part of the anterior end of the vomer.

Therefore there was no vomer exposure on the palatal surface as in *Melanosuchus niger*.

The nasal extends from the nares to oppose the anterior end of the orbits. Together the nasals formed a spine that entered the nares, but did not form a complete internarial bar. The spines are not in contact along the midline, possibly owing to crushing or preburial desiccation of the specimen. A small depression lies immediately lateral to the spine, between the nasal spine and the premaxilla.

The nasal is broader than in crocodylids. Its sides are almost parallel, although they broaden slightly posteriorly and reach their widest point at the anterior tip of the prefrontals. Posteriorly, the nasals are divided by an anterior process of the frontal along the midline. The dorsal surface of the nasal is flat, with very little sculpturing.

The prefrontal extends anteriorly beyond the lacrimal to exclude it from contact with the nasals. The lacrimal also does not contact the nasal in *Alligator*, but this is due to its unusually long prefrontal, whereas in *Brachychampsia montana* it is due to its short lacrimal. The prefrontals are separated by the frontal and do not meet along the midline. The prefrontal extends posteriorly about $\frac{2}{3}$ the length of the orbit. Its orbital margin is flat, hence no supraciliary rims are present. No palpebral bones are preserved. The medial descending process of the prefrontal (the prefrontal pillar) is unusually wide. Ventrally, at its contact with the palatine, it is transversely oriented, and it twists gradually upward, coming to face more laterally toward its dorsal end. A single small foramen occurs in the orbital surface of the prefrontal just dorsal to the prefrontal pillar. The dorsal surface of the prefrontal is heavily sculptured except at its anterior end. A transverse ridge on the dorsal surface of the prefrontal and frontal, as is found in many caimans and some other crocodylian taxa, is absent.

The lacrimal is broad and has a nearly square outline in dorsal view. Its lateral edge is slightly longer than its medial edge and its posterior margin is concave. The large lacrimal duct is in the usual alligatoroid position near the anterior corner of the orbit. The anterior contact between the lacrimal and the maxilla is sinusoidal, with two waves. The

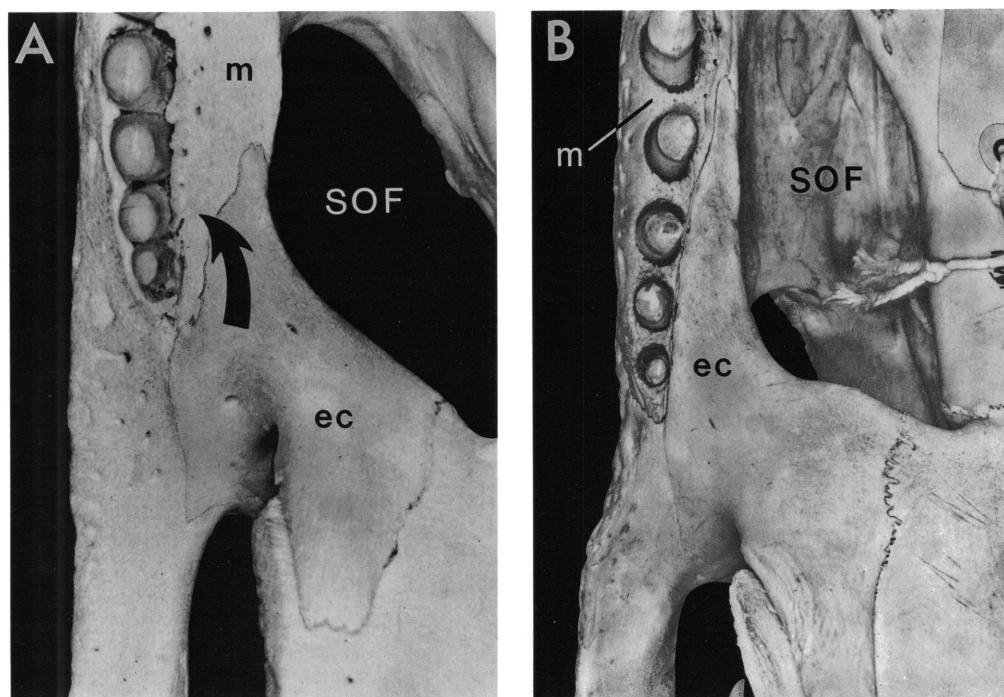


Fig. 6. (A) The alligatorid palate (shown in *Melanosuchus niger* UF 62641) where a process of the maxilla (indicated by arrow) separates the ectopterygoid from contacting the posterior tooth row. (B) The primitive condition (in *Crocodylus niloticus* YPM 10081) where the ectopterygoid contacts the posterior tooth row.

dorsal surface of the bone is flat and heavily sculpted. Posteriorly, together with the jugal, it forms a suborbital rim having a horizontal edge.

The jugal forms only the posterior half of the ventral margin of the orbit. As in caimans, the postorbital bar is not deeply inset, although it is not as superficial as in Gavialidae. The lateral margin of the jugal is not raised above the base of the postorbital bar to form a deep continuous trough as in *Crocodylus*. Anteriorly, the jugal forms a strongly sculptured ventrolaterally facing surface that overhangs the posterior tooth row and is confluent with the overhanging edge of the maxilla. Posteriorly, behind the tooth row, the heavily sculpted surface tapers to form the lateral boundary of a concave ventromedially directed fossa. Foramina anterior and posterior to the postorbital bar on the jugal's medial surface are tiny. The quadratojugal ramus of the jugal is thin beneath the lateral

temporal fenestra, and articulates posterolaterally with the quadratojugal well anterior to the articular condyle.

The quadratojugal has a very broad body that nearly reaches the squamosal medially. An anterior process extends along the medial surface of the jugal halfway along the length of the lateral temporal fenestra. The quadratojugal extends dorsally along the anterior edge of the quadrate to reach the postorbital, forming the entire posterior margin of the lateral temporal fenestra. An ascending process of the quadratojugal on the postorbital bar is lacking.

A small, anterodorsally projecting spine is present halfway up the quadratojugal in the lateral temporal fenestra. It is larger than in any other adult alligatorid but smaller than in most crocodylids and gavialids. Posteriorly, the lateral edge of the quadratojugal overhangs the quadrate, forming a distinct laterally open excavation. On the concave

ventral surface of the quadratojugal a small foramen lies near the posteroventral apex of the bone adjacent to its juncture with the quadrate and jugal. The quadratojugal does not take part in the mandibular articulation. Sculpturing is confined to a well-defined area on the posterolateral surface, and a distinct groove forms the posterior edge of the sculptured area.

The quadrate is a large bone forming the lateral wall of the braincase and the mandibular articulation. The mandibular articulating surface is constricted in the middle, so that in posterior view the lateral and medial portions are vertically expanded. The medial surface is flat and does not form a condyle, the lateral surface is larger and forms a convex condyle. A small foramen ærum, similar in size to that of caimans and unlike the large foramen ærum found in *Alligator*, is present on the dorsal surface just anterior to the external auditory opening. The external auditory opening is large and subtriangular. A dorsal process of the quadrate meets the squamosal lateral to the cranioquadrate passage. The surface on the quadrate to which the tympanum attached is marked by a distinct rim. Posterior to the tympanic rim a robust process projects dorsally from the quadrate.

The ventral surface of the quadrate is distinguished by a large, longitudinally oriented boss. This boss lies near the base of tendon scar A (Iordansky, 1964) but is not connected with it. A similar boss occurs in the primitive eusuchian *Hylaeochampsia vectiana* Owen, 1874 (Clark and Norell, 1992). Tendon scar A is very well developed, but other muscle scars are weak or absent. Posterior to tendon scar A the quadrate faces posteriorly, but it is separated from the occipital surface by a ridge formed by the exoccipital. The ventral contact with the pterygoid and the anterior contact with the laterosphenoid are as in other eusuchians.

The dorsal surface of the single frontal is flat, lacking a raised orbital rim. It is heavily sculpted, and lacks a midline ridge. The participation by the frontal in the orbital margin is very short due to the great posterior length of the prefrontal. The frontal is slightly broader than usual in alligatoroids, although it is much narrower than in *Gavialis*. It does

not extend posteriorly into the borders of the supratemporal fenestrae, but, posterolaterally the frontal is depressed forming a low shelf anterior to the supratemporal fenestra. Crista cranii on its ventral surface are very low and rounded. The sutural connection of the frontal with the parietal is broadly V-shaped with the frontal extending posteriorly to a point even with the anterior ¼ of the supratemporal fenestrae. This is unlike the condition seen in most Crocodylia where the frontal-parietal suture is transverse and lies anterior to the supratemporal fenestrae.

The single parietal has a concave lateral edge bordering the supratemporal fenestra. The interfenestral surface is narrow due to the large fenestrae. Medially the parietal overhangs the supratemporal fenestra slightly; however, no overhang is present laterally near the contact with the squamosal. The medial overhang is like that in *Alligator*, and unlike the roofing of the supratemporal fenestra in caimans where the parietal extends out over the supratemporal fenestra. The parietal forms the roof of the posttemporal fenestra, but it is just visible in posterior view, forming only a negligible part of the occipital surface. The dorsal surface of the bone is heavily sculptured. Posteriorly, the parietal roof contains a pair of large, anteromedially oriented depressions.

The postorbital is unusual, and corresponds to the condition in *Albertochampsia* (Wu, personal commun.), in having a rounded anterolateral corner, giving the skull table a somewhat triangular outline. The postorbital surface on the skull table is deeply sculptured dorsally. A single large foramen is present on the lateral surface of the postorbital at the top of the postorbital bar. A low tubercle lies on the dorsal posterolateral surface of the postorbital bar. It corresponds to the postorbital spine of *Gavialis* but is more posterior, as in *Melanosuchus*. The postorbital bar is compressed transversely and laterally concave, as in caimans. The postorbital meets the ectopterygoid along a straight suture that is uninterrupted by the jugal. A small descending process of the postorbital at the posterodorsal angle of the lateral temporal fenestra may be present; however, damage to this area makes this feature difficult to determine. It was evidently not as extensive as

in caimans. A postorbital process is typical of alligatoroids and lacking in crocodylids and gavialids, but it "appears to be present" in the Early Cretaceous neosuchian *Bernissartia fagesii* Dollo, 1883 (Norell and Clark, 1990: 118).

The pterygoids are separate anterior to the choana. Posterior to the choana the pterygoids may be fused, as in all other Eusuchia, but a crack has separated and displaced the pterygoids along the midline. Each pterygoid forms the medial half of the posterolateral margin of the suborbital fenestra. This contribution is relatively greater than in any other alligatoroids observed. The pterygoid is much shorter at the midline than in other Crocodylia, but the flange is of more typical proportions. Large pterygoid wings are present posterior to the choana and medial to the median eustachian opening. The pterygoid plate is depressed and has a broad posterior surface ventral to the median eustachian opening. The posterior edge of the pterygoid plate is gently concave. The pterygoid does not form part of the border of the trigeminal foramen on the lateral surface of the braincase because the quadrate contacts the laterosphenoid ventral to this opening. The lateral pterygoid flange is roughly rectangular (box-shaped) in outline and does not narrow anteriorly as in crocodylids. The choanal sinus as seen in *Alligator* cannot be examined in UCMP 133901 because matrix fills the lumen inside the palatines. Pterygoid bullae are absent. The pterygoid extends anteriorly above the palatine to meet the prefrontal pillar. The prefrontal ramus of the pterygoid extends dorsomedial to the prefrontal process of the palatine.

The palatine is very wide and has a flat ventral surface. It extends a short distance posteriorly to form the posterior angle of the suborbital fenestra. The posterior contact with the pterygoid is generally straight transversally, but bends anteriorly at the posterolateral corner. The palatine has a strong anterolateral process. A posterior palatine shelf (where a flat dorsal surface of the palatines lies just anterior to the contact with the pterygoid) as in caimans, is lacking. An anterodorsal-facing cuplike excavation is present at the base of the prefrontal pillar. The lateral edge of this cup rises posteriorly to form the

ascending ramus of the prefrontal pillar. The prefrontal pillar ascends medial to the middle of the suborbital fenestra. As in other alligatoroids, a large foramen is present on the dorsal surface of the palatine bone anterior to the postorbital bar. Whether this is an opening to the palatine sinus, as in caimans, or simply a hollow pocket (the palatine caecum of Wegner, 1958) cannot be determined. Palatine bullae are absent.

The ectopterygoid contacts the pterygoid along two-thirds of the lateral edge of the pterygoid flange. A posterior ectopterygoid process is present, but the condition is not like that in caimans. It is more similar to the configuration in *Alligator* where a process of the jugal separates the posterior part of the ectopterygoid from the posterior part of the postorbital at the base of the postorbital bar's medial surface. The ectopterygoid forms the anterior two-thirds of the lateral edge of the suborbital fenestra, but it does not reach to the anterior end of the fenestra. The separation of the ectopterygoid from the posterior tooth row is not visible on UCMP 133901 because of the occlusion of the dentaries, but this feature is present on the holotype.

The squamosal forms nearly all of the lateral edge of the skull table. The anteriormost part of its lateral edge forms a slight elevation where it overlaps the postorbital. The posterior edge is gently concave in dorsal view and overhangs the occiput posteriorly. The medial margin slightly overhangs the lateral surface of the supratemporal fenestra. A pronounced muscle scar occurs on the medial part of the occipital surface, just beneath the skull table. A distinct groove for the ear-flap muscles is lacking on the lateral edge. The sculptured dorsal surface grades into the posterolateral "horn." Its lateral edge is highly vascularized but not sculptured.

The basisphenoid is exposed along the midline posterior to the pterygoid. It is also broadly exposed along the ventrolateral surface of the exoccipital. The fragmentary basisphenoid rostrum is exposed between orbits. It is convex anteriorly.

The prootic is exposed within the trigeminal foramen, but it does not appear on the lateral surface of the braincase.

The basioccipital bears a well-developed sagittal ridge on its posterior surface. Tubera

are lacking but bilateral muscle scars are present along the entire ventral surface of the bone and surround the sagittal ridge.

The exoccipital and opisthotic are fused into a single otoccipital element. The posterior carotid foramen is widely separated from the basioccipital, unlike that in caimans. Two hypoglossal foramina are present. A very small part of the otoccipital enters into the occipital condyle. The paroccipital process has a concave posterior surface but its distal end turns anteriorly. It broadly overhangs the cranioquadrate passage posteriorly. Its ventrolateral edge is a high, thin ridge. The dorsal contact between the paroccipital process and the squamosal is concave.

The supraoccipital is much broader than high. Its occipital surface is flat, devoid of either a sagittal ridge or parasagittal excavations. The postoccipital process, beneath the posttemporal fenestra, has a flat dorsal surface and projects posteriorly above the occiput. The supraoccipital has a large trapezoidal sculptured surface on the parietal table that widens posteriorly. Its appearance is very similar to the condition seen in some caimans. Historically, there has been some confusion as to whether this bone is part of the endochondral supraoccipital or is a new element of dermal origin (the dermosupraoccipital of Mook, 1921) that fuses to the supraoccipital during ontogeny. This is impossible to assess without detailed embryological investigation. However, examination of near and posthatchling *Caiman crocodilus* (Schneider, 1901) (MAN 61, 112) shows no evidence of a suture between occipital and parietal table components of the supraoccipital, suggesting, contrary to Mook, that this element ossifies as a single unit.

The laterosphenoid forms the anterolateral wall of the braincase. A single laterosphenoid bridge (in life covering the anterior ramus of the trigeminal nerve), formed by a descending process of the laterosphenoid, is present anterior to the trigeminal opening. A cotylar crest is well developed. A distinct ridge rises dorsally from the bridge. The laterosphenoids meet along the midline ventral to the olfactory foramen. The capitate process is lodged in an excavation on the ventral surface of the postorbital.

MANDIBLE: The retroarticular process is

short, broad, and roughly horizontal in orientation. It is composed of the surangular and articular. The ridge into which the foramen aërum passes is displaced laterally away from the medial edge of the retroarticular process on the articular, as in other alligatoroids. The foramen aërum is closed, as in some adult crocodylians. The medial edge of the articular is convex and not depressed as in crocodylids. A notch is present anteriorly on the medial edge just posterior to the glenoid fossa. Posteriorly, the dorsal surface of the broad retroarticular process of the articular is divided into two fossae by a longitudinal ridge. Anterior to the articulating surface, the articular has a concave dorsal surface (the subarticular fossa). The medial surface of the articular faces dorsomedially.

The angular extends to the posterior end of the retroarticular process. The area on its lateral surface for the insertion of the M. pterygoideus is smooth and extends over the entire lateral surface of the bone posteriorly. Sculpturing is very deep over the remainder of the lateral surface. The exposure of the angular is shorter than that of the surangular on the lateral surface of the mandible. The bones surrounding the large mandibular fenestra are poorly preserved, obviating any meaningful discussion concerning their positional relationships. The angular forms the posterior and ventral edges of the caudal intermandibular foramen on the lingual side of the mandible, but the foramen is very poorly preserved.

The surangular forms part of the mandibular articulation surface. Its lateral surface is heavily sculptured posterior to the mandibular fenestra, but it is very smooth above the fenestra. The dorsal surface of the surangular is straight. Anteriorly the surangular is forked and a deep foramen pierces the notch.

The splenial extends anteriorly to within 1 cm of the mandibular symphysis but does not take part in it. It is broadly exposed on the ventral surface of the mandible, where it is slightly sculptured. The right splenial shows a ventrally directed cup-shaped pathological lesion anteromedially. Both splenials are poorly preserved posteriorly and they are too fragmented to determine whether a splenial foramen is present.

The dentarys form a broad, flat symphysis,

with a blunt, nearly straight anterior end. The dorsolateral edge of the dentary is festooned to the same extent as the opposing maxilla. The lateral surface of the dentary is densely vascularized but only lightly sculptured. An occlusion pit is present on the left dentary opposite the 5th maxillary tooth but is lacking on the right element.

DENTITION: All of the teeth appear to be preserved, but some are concealed within matrix between the occluded jaws. Five premaxillary teeth and 14 maxillary teeth are present on each side. Only 11 dentary teeth (8 on the right and 3 on the left) are exposed in the specimen. Anterior teeth are generally subconical, whereas posterior teeth become gradually more bulbous and constricted at their bases. All exposed teeth have longitudinal striations.

The premaxillary teeth are nearly equal in size, but the 3rd is slightly larger and the 5th slightly smaller than the others. They are labiolingually compressed, with weak carinae. Some, at least (e.g., the first right tooth) are slightly curved inward and the 5th is curved posteriorly. Extensive wear facets are present on some teeth (e.g., the 2nd and the 3rd teeth on the left side). The premaxillary alveoli are separated by septa.

Unlike that in other alligatoroids, the 5th maxillary tooth is the largest tooth in the upper jaw. The anterior three maxillary teeth are compressed labiolingually; the following four teeth are neither compressed nor bulbous. The posterior teeth are longer than wide and have expanded bulbous crowns. Inter-alveolar septa are present anteriorly but cannot be observed posteriorly due to articulation of the mandibles. Inter-alveolar septa are, however, very weak (as in *Alligator mississippiensis*) in the last four teeth of the maxillary tooth row of the type specimen.

The anteriormost dentary tooth is slightly procumbent and curves posteriorly. Other dentary teeth cannot be examined in detail because they are hidden inside the upper tooth row.

HYOBRANCHIAL SKELETON: The hyobranchial skeleton of UCMP 133901 is represented by a single ceratobranchial (cornu branchiale I of Schumacher, 1973) preserved beneath the right side of the basioccipital (fig. 5B). The ceratobranchial is flattened, as in

extant alligatorids but unlike the rodlike ceratobranchial of other crocodyliforms. It is curved, so that the medial surface is gently concave and the lateral surface has a sharp bend slightly distal to the middle. The distal end expands slightly, but not to the same degree as in extant alligatorids. The proximal end tapers slightly.

DISCUSSION

Many issues remain to be resolved in alligatoroid systematics, especially in regard to the monophyly and relationships among several genera of early Tertiary alligatoroids. A detailed phylogenetic analysis of alligatoroid relationships is beyond the scope of this paper. Nevertheless, synapomorphies suggesting the relationship of *Brachychampsa montana* were identified. One taxon that is critical as a basal alligatoroid is *Diplocynodon*. Only cast material (AMNH-DVP 27632) of a single species, *Diplocynodon hantoniensis* Wood, 1846 (BMNH 30392 and 30396), was available for this study. Extensive literature on *Diplocynodon* exists (Berg, 1966; Steel, 1973), and this genus may be monophyletic, diagnosable by the two enlarged mandibular teeth sharing a common alveolus with a greatly elevated rim (W. Langston, personal commun.). Unfortunately, most morphological features discussed here are not adequately described or illustrated in *Diplocynodon*; hence our comparisons with *Diplocynodon* are restricted to *Diplocynodon hantoniensis*.

Brachychampsa montana shares with other alligatoroids (including *Diplocynodon hantoniensis*) the following derived characters:

1. The fourth mandibular tooth occludes into a pit in the rostrum rather than passing into a lateral notch at the premaxillo-maxillary suture.
2. The quadratojugal spine on the posterior edge of the lateral temporal fenestra is small or absent.
3. The foramen aërum on the articular lies lateral to, rather than near, the medial edge of the retroarticular process.

The signature feature of the alligatoroid clade is that the fourth mandibular tooth occludes into a pit in the rostrum that is bounded laterally by union of the premaxilla with

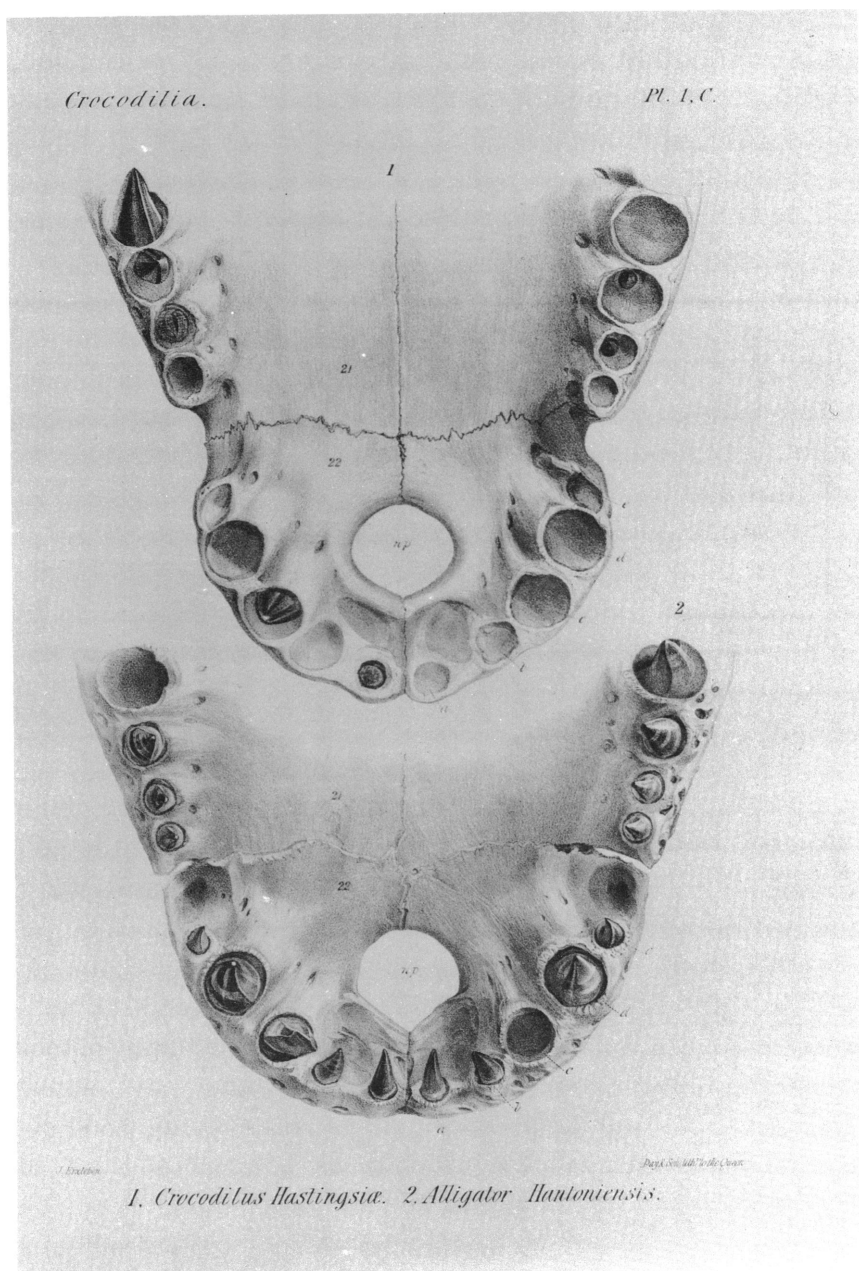


Fig. 7. Figures from Owen (1849–84) (*Crocodilia*, pl. 1C) showing the variable condition of occlusion of the fourth mandibular tooth with the rostrum in *Diplocynodon hantoniensis*. Because of this difference, Owen considered these to be different taxa, *Crocodilus* (sic) *hastingsiae* and *Alligator hantoniensis*. However, elsewhere Owen (1848) and others (Huxley, 1859) suggested that these were varieties of the same species. Citing numerous examples of such variation in large collections of these taxa, Woodward (1885) also accepted this synonymy.

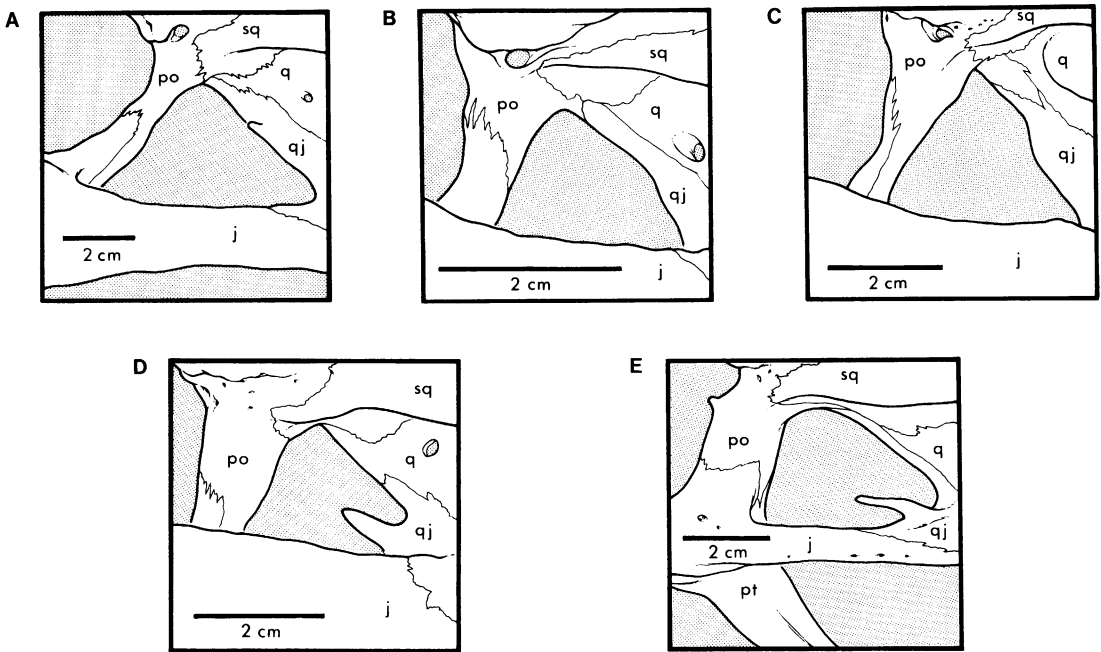


Fig. 8. Lateral temporal region of (A) *Brachychampsia montana* (UCMP 133901), (B) *Melanosuchus niger* (UF 62641), (C) *Alligator mississippiensis* (AMNH-DHI 46842), (D) *Crocodylus niloticus* (AMNH-DHI 7136), and (E) *Gavialis gangeticus* (AMNH-DHI 110145).

the maxilla (Duméril, 1806). This character is one of the features that was classically used to separate the alligatoroids from other Crocodylia, as can be determined from Duméril's figure (Norell, 1989: fig. 4). Among crown group Crocodylia, this pit occurs only in alligatoroids; though, it also occurs in the neosuchian mesoeucrocodylian *Shamosuchus djadochtaensis* Mook, 1924. However, this feature is variable within the taxon *Diplocynodon hantoniensis* (fig. 7). In some *Caiman crocodilus* it disappears during ontogeny, when the fourth mandibular tooth pierces the rostrum and the lateral wall of the pit is ultimately lost on one or both sides of the rostrum (Kälin, 1933). The resulting notch is, however, less regular and is generally smaller than the analogous feature in crocodylids. In outgroup taxa the fourth mandibular tooth occludes with the rostrum in a notch that is open laterally.

Primitively, crocodylians have a large, anteriorly directed quadratojugal spine on the posterior margin of the lateral temporal fenestra (Norell, 1989: figs. 2A, C and fig. 8).

When present, this spine forms part of the origin of the *M. adductor mandibularis externus pars superficialis*. As discussed by Norell (1989), the quadratojugal spine was incorrectly considered a derived character at the level of Crocodylia by Buffetaut (1985). The quadratojugal spine is reduced or lost in all alligatoroids. Although in some taxa (i.e., *Caiman crocodilus* and *Brachychampsia montana*) and in juveniles of most alligatoroid taxa (Norell, 1989: fig. 2C) vestiges of a spine may be present and a tiny spine is present in the primitive alligatoroid *Diplocynodon hantoniensis*, it is never as large as in outgroup taxa. Much of the variation found in crocodylids is related to absolute size; smaller taxa (e.g., *Osteolaemus tetraspis* Cope, 1860) have smaller quadratojugal spines than larger taxa (e.g., *Crocodylus niloticus* Laurenti, 1768). Only in alligatoroids do large taxa have reduced or absent quadratojugal spines.

The extensive siphonial cavity in the quadrate of crocodylians communicates with a cavity within the articular via the siphonium through the foramen aërum (Brühl, 1862).

This foramen is relatively largest in small taxa and in juvenile individuals of large taxa. In large adults it is often closed, but its position is always obvious because a narrow crest of bone develops around it. Primitively, this foramen lies on the articular near the medial edge of the retroarticular process (Norell and Clark, 1990). In the derived condition found in alligatoroids, the foramen aërum is displaced laterally away from the medial edge of the retroarticular process (fig. 9).

Two other features may be alligatoroid synapomorphies. In all extant Alligatoridae and in *Brachychampsa montana* the atlas intercentrum is longitudinally elongate, so that it is longer than it is broad rather than broader than long (fig. 5B). Also, in all extant Alligatoridae and in *Brachychampsa montana*, the ceratobranchial is flattened (fig. 5B) rather than being rodlike. The conditions in *Diplocynodon hantoniensis* are not known and, until known, it will not be clear if these are alligatoroid synapomorphies of *Brachychampsa montana* and Alligatoridae.

Two derived features indicate that *Brachychampsa montana* is a member of a clade containing all members of the Alligatoroidea except *Diplocynodon hantoniensis*. Both of these features concern the size and topographic relationships among palatal elements:

1. A posterior process of the maxilla excludes the ectopterygoid from any contact with the posterior tooth row.
2. The palatines have a wide, hour-glass shape in ventral view, and the suborbital fenestrae are small.

In other Eusuchia, the ectopterygoid abuts the alveoli of the posterior maxillary tooth row (fig. 6). In the derived condition found in alligatoroids except *Diplocynodon hantoniensis*, a medial shelf of the maxilla separates the ectopterygoid and the posterior tooth row lateral to the suborbital fenestra. As noted by Langston (personal commun.), some individual variation is occasionally encountered in non-alligatoroids, in which a thin sliver of maxilla lies between the ectopterygoid and the maxilla. However, in all such representatives that we have encountered this condition is easily differentiated from the alligatoroid (excluding *Diplocynodon hanton-*

iensis) synapomorphy where the ectopterygoid and maxilla contact along a strongly sinusoidal suture as opposed to the nearly straight suture of nonalligatoroids.

Several characters are present on the palatine that diagnose monophyletic groups of alligatoroids. Of interest here is the shape of the paired palatines relative to the suborbital fenestrae. In crocodylids and non-eusuchian crocodyliforms (with the possible exception of the Late Cretaceous *Shamosuchus djadochtaensis*) the palatines are generally narrow and parallel-sided in ventral view, meeting the pterygoids anterior to the posterior margin of the suborbital fenestrae (see Kålin, 1933: fig. 9).

Among alligatorids, except *Diplocynodon hantoniensis*, palatines are hourglass shaped, very broad, and meet the pterygoids at the posterior margin of the suborbital fenestrae. In some large examples of *Alligator mississippiensis*, *Alligator sinensis*, and *Brachychampsa montana* the transformation continues and the hourglass shape is modified during ontogeny into a thick, wide palatine bar (W. Langston, personal commun.).

Typically in Crocodylia, a broad anterior process of the palatine extends between the maxillae along the midline of the palate and terminates along a bluntly arched or bilobed transverse suture line. In the primitive condition, the palatines are not broadly exposed between the maxillae and end in an acuminate suture. Correspondingly, in alligatoroids (except for *Diplocynodon hantoniensis*) the suborbital fenestra is much smaller than in other Crocodylia. With more study, variation in these features may be found to support additional monophyletic levels within alligatoroids (e.g., the condition in some caimans where the palatines exclude the pterygoid from participation in the suborbital fenestrae); nevertheless, palatine shape and suborbital size in alligatoroids (except *Diplocynodon hantoniensis*) are unique among Crocodylia.

An unusual feature of *Brachychampsa montana* concerns the pattern of tooth size within the maxillary dentition. Primitively the fifth tooth is the largest in the maxillary tooth row in Crocodylia. All alligatoroids that we have studied except *Brachychampsa montana* show the derived feature of the fourth

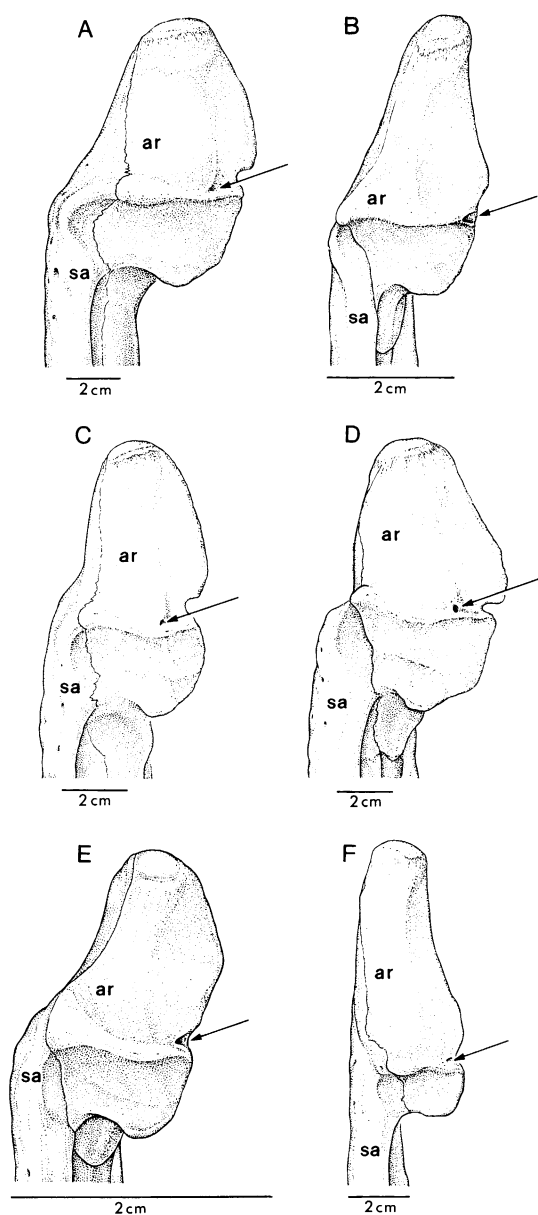


Fig. 9. Articular and retroarticular region of (A) *Brachychampsa montana* (UCMP 133901), (B) *Crocodylus porosus* (AMNH-DVP 2204), (C) *Melanosuchus niger* (UF 62641), (D) *Alligator mississippiensis* (AMNH-DHI 46842), (E) *Osteolaemus tetraspis* (MAN 503), and (F) *Gavialis gangeticus* (AMNH-DHI 110145). The foramen aërum (arrows) in alligatoroids is lateral to the medial edge of the retroarticular process.

tooth being largest. However, in both UCMP 133901 and the holotype, the fifth maxillary tooth is the largest in the entire tooth row. Patterns of heterodonty within crocodylians have not been adequately explored beyond simple tooth counts (Iordansky, 1973) and the plotting of diastema width against tooth number for a subset of taxa (Langston, 1965; Clark and Norell, 1992) and the changes in relative sizes of teeth probably need more attention. However, the most parsimonious explanation of maxillary tooth size is that the condition in *Brachychampsa montana* represents a reversal to the primitive crocodyloid condition.

The characters discussed above tentatively suggest the following relationships. First, alligatoroids are a monophyletic clade comprising Alligatoridae, *Brachychampsa montana*, and *Diplocynodon hantoniensis* as well as such taxa as *Allognathosuchus* and *Ceratosuchus*. Second, within this clade, *Brachychampsa montana* forms a monophyletic clade with Alligatoridae, to the exclusion of *Diplocynodon hantoniensis*.

Within this unnamed clade, *Brachychampsa montana* and *Albertochampsa langstoni* share the following derived characters:

1. The incisive foramen is very large.
2. The nares are very large.
3. The choana is extremely large and in the middle of the pterygoid plate.
4. The anterolateral corner of the postorbital is rounded.
5. Posteriorly the lateral edge of the maxilla is downturned and faces ventrolaterally, overhanging the posterior tooth row (Wu, personal commun.).

Alligatoroids, like other Crocodylia, undergo an extensive amount of ontogenetic change. Among the many features that are modified during growth are the sizes and relative proportions of many of the cranial elements. Consequently, unless growth series are available, many characters used to diagnose fossil taxa may be size-related features whose similarity or difference reflects nothing more than the growth stage of the specimen. This is particularly relevant to characters uniting and diagnosing extremely closely related taxa like *Albertochampsa langstoni* and *Brachychampsa montana*. In comparisons

between the two closely related taxa discussed here, differences in size must be noted. The two specimens of *Brachychampsa montana* differ in size by about 35% (table 1), with the type specimen (AMNH-DVP 5032) being the smaller. The holotype of *Albertochampsa langstoni* (SMM P67.15.3) is slightly smaller than the holotype of *Brachychampsa montana*. This discussion is particularly relevant to the case of characters 1, 2, and 3 above, all of which are also used in the diagnosis of *Brachychampsa montana*. In each case, and as discussed below, the general condition is found in both taxa; however, specific states of each character can be clearly differentiated between taxa and their presence in different size classes of *Brachychampsa montana* confirms this result.

The incisive foramen of crocodylians is a large aperture in the premaxilla piercing the floor of the external narial chamber. In life, the aperture is covered ventrally by the palatal epidermis. In *Albertochampsa langstoni* and *Brachychampsa montana* the incisive foramen is circular and larger than in any other Crocodylia. In all Crocodylia except *Melanosuchus*, *Brachychampsa montana*, and possibly *Albertochampsa langstoni*, the premaxillae meet posterior to the incisive foramen on the secondary palate. In *Melanosuchus niger* (Spix, 1825) the large, exposed vomer in the palate partly separates the premaxillae. In *Albertochampsa langstoni* the posterior palatal processes of the premaxillae are poorly preserved, but the published restoration (Erickson, 1972: fig. 4) shows the premaxillae in contact posteriorly. Following examination of the holotype specimen (Science Museum of Minnesota P67.15.13), it appears likely that, as in *Brachychampsa montana*, the posterior border of the incisive foramen was formed by the maxillae; however the specimen is too badly damaged in this region to determine this condition conclusively. Additionally, in the Oligocene alligatoroid "*Alligator*" *mcgrewi* (AMNH-DVP 8700; Schmidt, 1941: fig. 11), the incisive foramen divides the premaxillae posteriorly at the premaxillary-maxillary suture (Wu, personal commun.). However, although the anterior palatal elements of AMNH-DVP 8700 are distorted, it can be determined that the shape of the incisive foramen in "*Alligator*" *mc-*

grewi differs in being smaller and more elliptical than the condition in *Brachychampsa montana* and *Albertochampsa langstoni*. Also, failure of the premaxillae to contact posteriorly is characteristic of immature individuals of many crocodylian species, and it is likely that AMNH-DVP 8700 represents a less than full grown individual.

The external narial opening of eusuchians is a simple, dorsally or anterodorsally directed opening bounded by the premaxilla and sometimes to a limited extent by the nasals. In *Brachychampsa montana* and *Albertochampsa langstoni* the narial opening is larger than in other Eusuchia. Both of these taxa also display an eversion of the lateral rim of the narial chamber, but this feature appears to vary continuously among other alligatoroid taxa.

In many alligatoroids (e.g., *Ceratosuchus burdoshi* Schmidt, 1938, and *Allognathosuchus*), the anterior margin of the narial chamber is low; hence the nares are oriented anteriorly and the narial chamber lacks an anterior rim. Erickson (1972: 2) suggested that the anterior margin of the external narial opening in *Albertochampsa langstoni* was "thin and low as indicated by the preserved and undistorted lateral borders of the openings as well as the floor of the narial chamber." In *Brachychampsa montana* the anterior border of the nares is relatively high with a posterior tectum that partly roofs the narial chamber anteriorly. This is characteristic of extant crocodylians and unlike the condition in the primitive eusuchian *Leidyosuchus formidabilis* Erickson, 1976, and the eusuchian sister taxon *Bernissartia* (Norell and Clark, 1990) where the nares are oriented anteriorly because of a low anterior narial rim. In *Albertochampsa langstoni* the anterior part of the skull is damaged across the nares in an area corresponding to the low flat areas lateral to the nares, so it is unclear whether the anterior margin is low or high.

The extremely large size and anterior position of the choana in these two taxa is anomalous within Crocodylia. In each of them the choana is large and circular, surrounded by a slight labium choanalis, and located near the middle of the pterygoid plate. Apparently the choana is larger in *Albertochampsa langstoni* than in *Brachychampsa montana*; how-

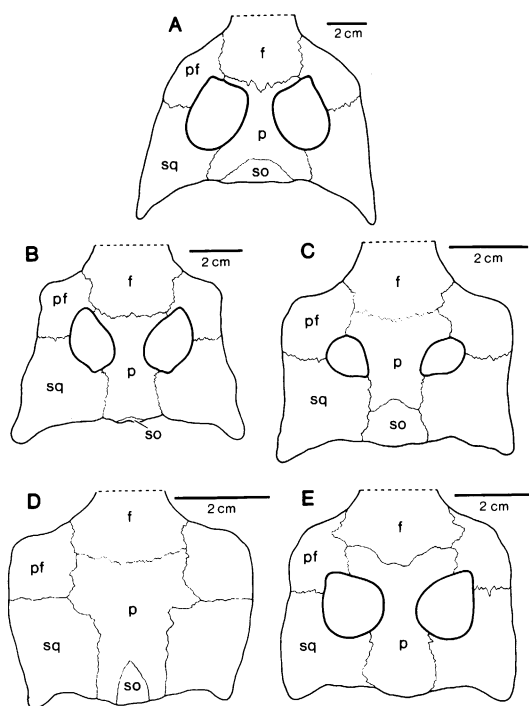


Fig. 10. The posterior skull table in (A) *Brachychampsa montana* (UCMP 133901), (B) *Alligator mississippiensis* (AMNH-DVP 1106), (C) *Caiman latirostris* (UF 62649), (D) *Paleosuchus palpebrosus* (UF 62509), and (E) *Crocodylus porosus* (AMNH-DVP 2204), showing the enlarged supraoccipital (so) in caimans and *Brachychampsa montana*.

ever, this may be influenced by crushing of the posterior pterygoid in the holotype specimen of *Albertochampsa langstoni*.

In both *Brachychampsa montana* and *Albertochampsa langstoni* the anterolateral corner of the postorbital on the dorsal surface of the skull table is rounded, almost to the point of giving the skull table a subtriangular shape (fig. 10). In other Crocodylia the anterolateral corner of the postorbital is rather angular giving the skull table a rectangular or square shape.

The posterolateral edge of the maxilla in these taxa overhangs the posterior tooth row (Wu, personal commun.). The overhanging rim is nearly dorsally oriented, giving the tooth row a recessed appearance. This differs from the condition seen in other alligatoroids

where the posterior tooth row is nearly confluent with the lateral margin of the maxilla, or slightly medial to it. In the latter case the overhanging edge of maxilla is convex, lacking the ventrally oriented shelf seen in *Brachychampsa montana* or *Albertochampsa langstoni*.

Perhaps the most apparent feature distinguishing these taxa is the relatively larger size of the infratemporal fenestra in *Brachychampsa montana*. Usually in crocodylians the lateral temporal fenestra is smaller than the orbits, and this typical condition is seen in *Albertochampsa langstoni*. In *Brachychampsa montana* the infratemporal fenestra is very large, approximately equivalent in size to the orbits. The enlargement is caused by a thinning of the part of the jugal forming the ventral infratemporal bar.

Variation in the pattern of heterodonty between *Albertochampsa langstoni* and *Brachychampsa montana* is not restricted to the maxillary teeth. In *Brachychampsa montana* the premaxillary teeth are nearly homodont except that the fifth tooth is markedly smaller than the others. In his description of *Albertochampsa langstoni*, Erickson indicated that the premaxillary teeth are of disparate size. As with the maxillary dentition, no comprehensive survey of variation patterns in tooth size among crocodylians has been completed for the premaxillary dentition. Preliminary observations suggest that patterns are not extremely different between taxa.

Erickson (1972) noted the similarity between *Albertochampsa langstoni* and *Brachychampsa montana*. His comparisons, however, were limited by the incompleteness of the *Brachychampsa montana* holotype (AMNH-DVP 5032). Erickson suggested (pp. 10-11) that *Albertochampsa langstoni* differs from *Brachychampsa montana* in the following features: 1) the nares are larger, 2) the anterior rim of the nares is depressed and not "massive and high," 3) the premaxillary teeth are not uniform in size, 4) the largest maxillary tooth is the fourth rather than fifth, 5) the posterior maxillary teeth share a common alveolar groove, 6) the rostrum is longer, 7) the frontal is narrower between the orbits, 8) there are 15 rather than 14 teeth, 9) prominent pits for the reception of mandibular teeth lie medial to the maxillary teeth, and 10) the

palatines are longer and have a convex anterior border.

Our examination of the *Albertochampsa langstoni* holotype indicates that the nares are no larger in *Albertochampsa langstoni* than in *Brachychampsa montana*, and that the palatines are similar in both species. The premaxillary teeth of *Brachychampsa montana* are not homodont, but they are, indeed, less heterodont than in *Albertochampsa langstoni*. We interpret the alveolar groove housing the posterior maxillary teeth to be a juvenile feature, since this condition is typical of subadult crocodylians, and the *Albertochampsa langstoni* holotype is approximately two-thirds the size of the *Brachychampsa montana* holotype and less than half the size of UCMP 133901. Erickson reported the relative width of the frontal in the holotype of *Brachychampsa montana* to be greater than in *Albertochampsa langstoni*, and this observation is borne out in UCMP 133901 (table 1). The number of maxillary teeth is, indeed, different, but this may not be significant because Iordansky (1973) showed that variation within many extant alligatoroid species includes either 14 or 15 teeth.

All but two of the features (size of the fifth maxillary tooth and the morphology of the palatine bar) in which *Albertochampsa langstoni* differs from *Brachychampsa montana* are either plesiomorphic for Alligatoroidea or are difficult to polarize. In all extant alligatoroids the fourth maxillary tooth is the largest, whereas the fifth is the largest in all other extant crocodylians. Thus, contrary to our hypothesis, the presence of this derived feature in *Albertochampsa langstoni* and not in *Brachychampsa montana* may indicate that *Albertochampsa langstoni* is more closely related to Alligatoridae than is *Brachychampsa montana*.

As noted above, the palatine bar separating the suborbital fenestrae in *Brachychampsa montana* is much wider than in *Albertochampsa langstoni*. In *Alligator mississippiensis* the shape of the palatine bar changes drastically during ontogeny. In young individuals the bar is very similar to the condition in *Albertochampsa langstoni*, transforming during growth into the *Brachychampsa montana* condition, seen only in large adult examples. The significance of this feature in

the fossil taxa is, therefore, difficult to test when complete growth series are lacking. Nevertheless, available evidence allows us to tentatively posit that this feature distinguishes between these taxa, although the polarity is difficult to assess.

Because of the derived characters shared by *Brachychampsa montana* and *Albertochampsa langstoni*, we propose that they form a natural group exclusive of other Crocodylia. But this is only a preliminary conclusion until a more detailed analysis of alligatoroid phylogeny is completed. However, in spite of the tight genealogic connection between these two taxa, a number of differences between *Brachychampsa montana* and *Albertochampsa langstoni* are apparent.

Other characters that *Brachychampsa montana* shares with other alligatoroid taxa may suggest diagnostic groups. The distribution of these features has not been extensively surveyed and they are difficult to polarize using outgroup analysis.

One such character, shared by *Brachychampsa montana* and *Alligator*, is the relative length of the prefrontal. In these taxa the prefrontal extends so far anteriorly that it prevents the lacrimal from contacting the nasals. This feature is present in some other eusuchians (including alligatoroid stem taxa, such as *Allognathosuchus polyodon* (Cope, 1873) [AMNH-DVP 27444] and closely related non-eusuchian mesoeucrocodylians like *Bernissartia* [Buscalioni and Sanz, 1990]). Lacrimal-nasal contact occurs in all other eusuchians. There are several elements involved in this character, not least of which is the short and boxlike lacrimal in *Caiman* and *Alligator* and the long and attenuate lacrimal in *Gavialis* and *Leidyosuchus*. Before ascribing any phylogenetic significance to this feature, variation in the jugal, nasals, and prefrontals in all taxa needs to be adequately surveyed.

Brachychampsa montana also displays a number of unusual features with disjunct distributions among other eusuchians. One such feature is the exposure of the supraoccipital on the parietal table. In hatchlings, the braincase of crocodylians is bulbous and the skull lacks the flat parietal table characteristic of the Crocodyliformes. This vaulting of the braincase includes a supraoccipital compo-

nent dorsal to the occiput. During formation of the parietal table the configuration of the bones surrounding the braincase transforms and in some crocodylians (i.e., *Alligator*) the supraoccipital completely disappears from the parietal table. Primitively, only a small portion of the supraoccipital is exposed as a small wedge of bone on the parietal table. In caimans, however, the exposure is large, and in some (*Melanosuchus* and *Caiman*), the bone is so large that it contacts the squamosals laterally, completely separating the parietal from the posterior skull table (fig. 10). The condition in *Brachychampsa montana* is similar to that in *Paleosuchus*, where the supraoccipital is exposed on the parietal table but does not contact the squamosal laterally. Erickson (1972) pointed out that only a small portion of the supraoccipital is exposed on the parietal table in *Albertochampsa langstoni*.

CONCLUSIONS

Brachychampsa montana is an important taxon in understanding the relationships among, and early history of, the alligatoroids. Because of its relatively early discovery it has been mentioned often in reviews of alligatoroid morphology. For the most part it was considered to be a specialized offshoot of the main "alligatorid" branch of evolution (Sill, 1968), although, some authors considered it to be ancestral to all later alligators (Kälin, 1955). From a phylogenetic perspective, *Brachychampsa montana* can now be considered a member of a specialized clade of North American Late Cretaceous alligatoroids, sharing only a remote ancestry with more typical (i.e., extant) forms. Important comparisons, however, remain to be made. For instance, a detailed comparative review of the Paleocene taxon *Wannaganosuchus brachymanus* Erickson, 1982, and an undescribed form from the Late Cretaceous of Baja California (W. Langston, personal commun.) should prove illuminating in regard to the diversity and relationships of Late Cretaceous and early Tertiary alligatoroids. The monophyly and cladistic relationships among the several species of *Allognathosuchus* and *Diplocynodon* are also yet to be explored, and their phylogenetic placement is crucial to

sorting out higher-level relationships among alligatoroids.

ACKNOWLEDGMENTS

We thank Darrel Frost (AMNH), John Bolt (Field Museum), Bruce Erickson (SMM), John Ostrom (Yale Peabody Museum), and Robert Emry and Robert Purdy (USNM) for allowing us access to collections in their care. Angela Milner kindly provided a cast of *Diplocynodon hantoniensis*. Chester Tarka, Lorraine Meeker, Mick Ellison, and Ed Heck skillfully executed the illustrations. Joan Davis aided in production of the manuscript. This project was supported by the Frick Laboratory Endowment Fund at the American Museum, the AMNH Department of Vertebrate Paleontology, and the Annie M. Alexander Endowment to the University of California Museum of Paleontology. Laurie Bryant and Mike Luten provided valuable field assistance and Kyoko Kishi skillfully prepared the new specimen. Wann Langston and Xiao-chun Wu are thanked for careful reviews of the manuscript.

REFERENCES

- Ax, P.
1985. Stem species and the stem lineage concept. *Cladistics* 1(3): 279–286.
- Berg, D. E.
1966. Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*?, aus dem Eozän von Messel bei Darmstadt/Hessen. *Abh. hess. L.-AMT Bodenforsch.*, 52: 1–105.
- Brühl, C. B.
1862. Das Skelet der Krokodilinen. Vienna: Wilhelm Braumüller.
- Bryant, L.
1989. Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana. *Univ. California Publ. Geol. Sci.* 134: 1–107.
- Buffetaut, E.
1985. The place of *Gavialis* and *Tomistoma* in eusuchian evolution: a reconciliation of paleontological and biochemical data. *Neues Jahrb. Geol. und Paläontol. Monatsh.* 12: 707–716.
- Carpenter, K., and D. Lindsay
1980. The dentary of *Brachychampsa montana* Gilmore (Alligatorinae; Crocodyliidae), a Late Cretaceous turtle-eating alligator. *J. Paleontol.* 54(6): 1213–1217.

- Clark, J. M., and M. A. Norell
1992. The Early Cretaceous Crocodylomorph *Hylaeochampsia vectiana* from the Wealden of the Isle of Wight. *Am. Mus. Novitates* 3032: 1–19.
- Cope, E. D.
1874. Review of the Vertebrata of the Cretaceous Period found west of the Mississippi River. *Bull. of the U. S. Geol. Surv. of the Territories* 2: 5–51.
1875. The Vertebrata of the Cretaceous formations of the West. Washington, D.C.: U. S. Geol. Surv., 302 pp.
- Densmore, L. D. III
1983. Biochemical and immunological systematics of the order Crocodilia. *In* M. K. Hecht, B. Wallace, and G. T. Prance (eds.), *Evolutionary Biology* 16: 397–466. New York: Plenum Press.
- Densmore, L. D. III, and R. D. Owen
1989. Molecular systematics of the order Crocodilia. *Am. Zool.* 29: 831–841.
- DeQueiroz, K., and J. A. Gauthier
1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Syst. Zool.* 39(4): 307–322.
1992. Phylogenetic taxonomy. *Annu. Rev. Ecol. Syst.* 23: 449–480.
- Duméril, A. M. C.
1806. *Zoologie analytique, ou méthode naturelle de classification des animaux*. Paris: Allais.
- Erickson, B. R.
1972. *Albertochampsia langstoni*, gen. et sp. nov., a new alligator from the Cretaceous of Alberta. *Sci. Publ. Sci. Mus. Minnesota n. ser.* 2(1): 1–13.
- Estes, R.
1964. Fossil vertebrates from the Late Cretaceous Lance Formation eastern Wyoming. *Univ. California Publ. Geol. Sci.* 49: 1–187.
- Gilmore, C. W.
1911. A new fossil alligator from the Hell Creek beds of Montana. *Proc. U. S. Nat. Mus.* 41: 297–302.
1916. Contributions to the geology and paleontology of San Juan County, New Mexico. 2. Vertebrate faunas of the Ojo Alamo, Kirtland and Fruitland Formations. *U. S. Geol. Sur. Professional Paper* 98Q: 279–302.
- Huxley, T. H.
1859. On the dermal armor of *Crocodylus hastingiae*. *Q. J. Geol. Soc. London* 15: 440–460.
- Iordansky, N. N.
1964. The jaw muscles of the crocodiles and some relating structures of the crocodilian skull. *Anat. Anz.* 115: 256–280.
1973. The skull of the Crocodylia. *In* C. Gans (ed.), *Biology of the Reptilia*: 201–262. New York: Academic Press.
- Kälin, J. A.
1933. Beiträge zur vergleichenden Osteologie des Crocodilidenschädels. *Zool. Jahrb. Abt. Anat.* 57(4): 53–714.
1955. Crocodilia. *In* J. Piveteau (ed.), *Traité de paléontologie*, 5: 695–784. Paris: Masson.
- Langston, W.
1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *Univ. California Publ. Geol. Sci.* 52: 1–152.
- Mook, C. C.
1921. *Allognathosuchus*, a new genus of Eocene crocodilians. *Bull. Am. Mus. Nat. Hist.* 44(10): 105–110.
1925. A revision of the Mesozoic crocodilians of North America. *Bull. Am. Mus. Nat. Hist.* 51(9): 319–432.
- Norell, M. A.
1989. The higher level relationships of the extant Crocodylia. *J. Herpetol.* 23(4): 325–334.
1990. Cladistic approaches to evolution and paleobiology as applied to the phylogeny of alligatorids. *Diss. Abstr. Int.* 50(11): 4938B.
- Norell, M. A., and J. M. Clark
1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bull. Inst. R. Sci. Nat. Belgique (Sci. Terre)* 60: 115–128.
- Owen, R.
1848. On the fossils obtained by the Marchioness of Hastings from the freshwater Eocene beds of the Hordle Cliffs. *Rep. Br. Assoc. Adv. Sci.* 17(2): 65–66.
1849–84. *A history of British fossil reptiles Vol. 2*. London: Casell & Company Limited.
- Schmidt, K. P.
1941. A new fossil alligator from Nebraska. *Field Mus. of Nat. Hist. Geol. Ser.* 8(4): 27–32.
- Schumacher, G.-H.
1973. Head muscles and hyolaryngeal skeleton of turtles and crocodylians. *In* C. Gans and T. Parsons (eds.), *Biology of the Reptilia* 4: 101–199. New York: Academic Press.
- Sill, W. D.
1968. The zoogeography of the Crocodilia. *Copeia* 1968(1): 76–88.

Steel, R.

1973. Crocodylia. Encyclopedia of paleoherpetology, Part 16. Portland, Oregon: Gustav Fischer Verlag. 116 pp.

Wegner, R. N.

1958. Die Nebenhöhlen der Nase bei den Krokodilen (Studien über Nebenhöhlen des schädels Z. teil). Wiss. Z. Ernst Moritz Arndt-Univ. Greifswald, Jahrgang VII, 1957/58-Eingereicht am 8.7.1957-

Mathematisch naturwiss. Reihe 7(1-2): 1-39.

Williston, S. W.

1906. American amphicoelian crocodiles. J. Geol. 14(1): 1-17.

Woodward, A. S.

1885. On the literature and nomenclature of British fossil Crocodilia. Geol. Mag. (3) II: 496-510.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates*, *Bulletin*, and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org