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FIELDIANA
Geology

Published by Field Museum of Natural History

Volume 33, No. 16 December 19, 1975

This volume is dedicated to Dr. Rainer Zangerl

Ziphodont Crocodiles:[1]
Pristichampsus vorax (Troxell), New Combination, From the Eocene of North America

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INTRODUCTION

In 1956 I speculated on the possibility that certain so-called dinosaur-toothed crocodilians, the Order Sebecosuchia, had a world-wide distribution during the Tertiary Period. It has now been shown that whereas a true sebecosuchian, *Bergisuchus* Kuhn, existed in Europe during the Eocene, most of the specimens to which I referred probably belong to a eusuchian (Order Eusuchia), which is best represented by a genus variously termed *Pristichampsus* or *Weigeltisuchus* in Europe. Specimens displaying dental characters reminiscent of *Pristichampsus* are also known from Eocene strata in North America. My suspicion, long held, that these North American taxa were closely related to *Pristichampsus* has been reinforced recently by the discovery of a magnificently preserved skull from Washakie beds in Wyoming and now in Field Museum of Natural History. This volume honoring Rainer Zangerl seems a fitting place to offer a description of this specimen, for it was Dr. Zangerl who first called it to my attention and then generously placed it at my disposal.

[1] Ziphodont is the vernacular derived from the taxon *ziphodon (nomen nudum)* proposed by O. C. Marsh for a species of dinosaur-toothed crocodilians from Wyoming. The term is descriptive of the principal distinguishing character state of this group of crocodilians and is less clumsy and more precise than the term "dinosaur-toothed" previously employed.

Library of Congress Catalog Card Number: 75-38177

Publication 1222

During the course of this study other specimens of what I shall term ziphodont crocodiles were located in other museums in the United States. Space does not permit detailed consideration of this additional material, but it is listed and some specimens are mentioned when they supplement data available from the Field Museum skull.

ABBREVIATIONS

AMNH – American Museum of Natural History

FMNH – Field Museum of Natural History

ME – Museum für Erdgeschichte-Geiseltalsammlung, Halle

MNHN – Muséum National d'Histoire Naturelle, Paris

USNM – United States National Museum

YPM – Peabody Museum of Natural History

TAXONOMIC NOTES ON ZIPHODONT CROCODILES

Study of the Field Museum specimen has led to a review of the taxonomy of the ziphodont crocodiles which is confused by typological problems and clouded by a number of possibly synonomous taxa in both North American and European literature. A brief summary of these problems will be helpful before considering the Field Museum specimen in detail.

The first report of ziphodont crocodiles in North America dates back more than a hundred years. O. C. Marsh (1871), in one of his many "Notices of some new fossil reptiles, etc.," gave a brief description of a new Eocene crocodilian from the Bridger Basin of southwestern Wyoming. Marsh was impressed by its sharp, laterally-compressed, curved, and doubly-serrated teeth, and he named the species *Crocodylus ziphodon.* Marsh also included a description of an unusual quadrate bone "found with one series of the remains" assigned to this species, and indicated the existence of cranial bones and osteoscutes. No holotype was designated, no illustrations were provided, and catalogue numbers were not mentioned. Later Marsh (1872) noted "new" but unspecified material belonging to the species, which he transferred to a new genus, *Limnosaurus.*[1] Characteristically, a promised "full descrip-

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[1] The name *Limnosaurus* makes three unrelated appearances (homonyms) in the literature: Marsh, 1872 (*L. ziphodon,* the crocodile); Nopsca, 1899 (= the hadrosaurian dinosaur *Orthomerus*); Aldrich & Jones, 1930 (Paleozoic ichnites).

tion" of this material was not forthcoming, and except for brief mention by Leidy (1872) and a few others, *L. ziphodon* remained in taxonomic limbo for almost 50 years. Then in 1925, as part of a review of the Bridger crocodiles, Troxell listed as "holotype" of *C. ziphodon* YPM 1347, which he believed to be the material of Marsh's original description. It appears that this procedure is inadmissible, for not only was there no assurance that the specimens concerned were actually those referred to by Marsh, but bones representing two distinct crocodilian taxa and at least three individuals are included under No. 1347 in the Yale collection. If, therefore, *Limnosaurus ziphodon* is to be retained, the typological questions still must be resolved, but, as will appear, I believe this is impossible.

An examination of records in the Peabody Museum reveals that the material described by Marsh in 1871 was obtained by the Yale party of 1870 at Grizzly Buttes, in the Bridger Basin. Specimens numbered YPM 1347 comprise: the distal end of a right quadrate subsequently assigned number YPM 5890 but believed by Troxell to be the bone described by Marsh, a second right quadrate of similar form but of smaller size, a pair of articulars, parts of a right angular and surangular, some fragments of dermal roofing bones, four teeth, a posterior cervical vertebra, parts of two rib heads, a few incomplete osteoscutes, and some small fragments. Other specimens bearing the same number, including a quadrate of *Crocodylus* form noted by Troxell, are clearly different. In addition, the Yale collection contains two teeth numbered YPM 1348, and two others found in 1966 in trays containing fragments numbered 1347, but which are unnumbered. They may have been included originally with one or the other of the two assemblages referred to by Marsh.

Most of the specimens numbered YPM 1347 bear accession number 249+. The latter number appears twice on the same page of the Peabody Museum register, once for an anaspid fish from Scotland and again for "limbs and two teeth" of a crocodilian numbered 1343 (not 1347), which, according to the catalogue, was collected by Marsh at Grizzly Buttes in 1871, not 1870. Specimen YPM 1347, designated in the catalogue as the holotype of *C. ziphodon,* if it is in fact the material originally described by Marsh, should belong to accession 136, which is the appropriate number for the Peabody Museum Bridger collection of 1870. No ziphodont crocodilian specimens bearing this accession number have been found in the collection despite careful search by several individuals.

One of the unnumbered teeth has the same crown length and anteroposterior diameter as the tooth measured by Marsh in his original description. But the transverse diameter of the base given by Marsh as 2.6 lines, that is, about 5.5 mm., is .4 mm. greater than in this specimen. The thin sides of the tooth are broken away near the base, and if restored might yield a measurement close to the figure given by Marsh. It could be argued therefore that this is in fact the original tooth, and that part of its side has been chipped off since the published measurements were made. But this cannot be substantiated.

There is, therefore, no substantive evidence that any of the original materials on which *C. ziphodon* was based have been seen in the collection since 1871, and they may be presumed to be either unrecognizable or lost. In this situation a lectotype cannot be designated. Nor is assignment of a neotype appropriate because no known specimens that might be sufficiently characteristic of *C. ziphodon* have come from the same provenance as the original sample and thus cannot be shown to be from the same geological horizon [ICZN Rules, art. 75(c) (6)]. Taxonomic stability will best be served by regarding *C. ziphodon* Marsh 1871 and *Limnosaurus* Marsh 1872 as *nomina nuda.*

The earliest available name that can be applied to a North American ziphodont crocodile is *Crocodylus vorax* Troxell (1925). Holotype of this species is a crushed and incomplete skull (YPM 249) which, like Marsh's material, was collected in the Bridger Basin, probably from the Bridger A horizon ("Greensand formation") of older authors (Wheeler, 1961). This specimen and the material numbered YPM 1347 and 1348 are at hand. The ziphodont teeth are essentially similar, and it is curious that Troxell failed to notice this when he discussed the supposed Marsh specimens only a few pages prior to his description of *C. vorax.* (To my own embarrassment, it must also be recorded that owing to mistaken identification, I reported erroneously in 1956 that the teeth of *C. vorax* "are round . . . rather like those of other crocodiles.")

Neither Marsh nor Troxell seem to have been aware of ziphodont teeth from Europe, long before attributed by Cuvier (1824) to *les Crocodiles des marnières d'Argenton.* Much additional material, including complete skeletons (most recently reviewed by Berg, 1966) has come to light, but the taxonomy of the European ziphodonts is hardly less complicated than that of their American relatives. Syntypes were established when Gray (1831) based the new species *Crocodylus rollinati* Gray on two of Cuvier's specimens (MNHM AG 3 and AG 4).[1] Berg accepts *Pristichampsus* Gervais (1853) as the valid generic name, and while expressing slight reservations, he equates *P. rollinati* (Gray) with *Weigeltisuchus geiseltalensis* Kuhn 1938, a conclusion not fully accepted by Kuhn (1968). To my knowledge, no lectotype for *P. rollinati* has been selected, and it is not at all certain that either of the "syntypes" is sufficiently diagnostic to furnish the basis for more than a monotypic taxon. It may well be that the earliest taxon of diagnostic value will prove to be *Weigeltisuchus geiseltalensis,* but pending solution of this problem, I shall follow Berg in using *P. rollinati* for the European ziphodont.

DESCRIPTION

The Field Museum skull, FMNH PR 399, was collected in 1958 by a party led by Dr. W. D. Turnbull, from a "Sandstone rim just below Dobytown Rim, Sweetwater County, Wyoming, about 7 miles NE of Kinney Ranch." The horizon lies within Roehler's beds 614-618 (see Roehler, 1973) and is thus high in the Washakie A of older usage (e.g., Granger, 1909). Admirably preserved, the specimen has suffered only slight dorsoventral crushing and loss of parts of the right quadrate and left pterygoid, and most of the teeth. It was imbedded in a green sandy pebble conglomerate which has not been removed from the orbits and the temporal spaces.

A lengthy description is unnecessary as the general features of the specimen are clearly shown in the accompanying illustrations. A number of details are, however, worthy of emphasis. The skull is 452 mm. long (snout-quadrate) and 223 mm. wide (transquadrate). In general, it conforms to the eusuchian pattern, although its proportions differ from those of all existing crocodilians (table 1). Dental occlusion appears to have been intermediate between the alligatoroid "overbite" and the crocodyloid "interbite" as occlusal pits occur in the palatal surface medial to several maxillary teeth. There is nevertheless a crocodyloid notch in the upper jaw margin between the premaxilla and maxilla. Lateral festooning of the snout

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[1] Catalogue numbers for Cuvier's figured specimens (Cuvier, 1824, pl. 10) in the Muséum National d'Histoire Naturelle, Paris, have never been published. They are: AG 1, tooth (fig. 16); AG 2, tooth (fig. 15); AG 3, tooth (fig. 14); AG 4, vertebra (fig. 24); AG 5, radius (fig. 21); AG 6, ulna (fig. 22); AG 7, ?lacrimal (fig. 18); AG 8, dentary (fig. 17); AG 9, vertebra (fig. 23), AG 10, femur (fig. 19); AG 11, femur (fig. 20).

TABLE 1. Selected cranial indices (Kälindexes) of *Pristichampsus* compared with some existing crocodiles of similar basal length.

	KÄLININDEX		*Pristichampsus vorax* FMNH PR 399	*Crocodylus niloticus**	*Crocodylus porosus**	*Crocodylus acutus*	*Crocodylus cataphractus***	*Crocodylus siamensis***
	Basal skull length (mm.)		410.0	420.0	408.0	415.0	406.50	422.00
I.	$\frac{\text{Transquadrate diameter}}{\text{Basal length}}$	X 100	54.4	55.9	49.0	49.0	45.70	46.90
II.	$\frac{\text{Width of snout at anterior end of orbits}}{\text{Snout length from anterior end of orbit}}$	X 100	48.1	63.0	54.0	53.0	35.25	50.55
III.	$\frac{\text{Snout length from anterior end of orbit}}{\text{Skull length from posterior edge of skull table}}$	X 100	64.6	64.3	67.1	68.0	71.26	70.25
IV.	$\frac{\text{Least width of interorbital space}}{\text{Length of orbit}}$	X 100	72.1	70.0	63.1	75.0	58.50	79.15
V.	$\frac{\text{Midsaggital length of skull roof}}{\text{Width of skull table, posteriorly}}$	X 100	51.6	64.8	49.1	54.0	60.50	64.45
VI.	$\frac{\text{Length of orbit}}{\text{Skull length from posterior edge of skull table}}$	X 100	14.9	14.3	13.9	13.0	13.42	14.07
VII.	$\frac{\text{Width of orbit}}{\text{Length of orbit}}$	X 100	67.2	61.7	66.7	73.6	64.20	67.90
VIII.	$\frac{\text{Transverse diameter of nares}}{\text{Length of nares}}$	X 100	91.1	28.0	23.9	89.5	70.72	83.33

* Data from Iordansky, 1973. ** Data from Kälin, 1933.

is not marked in dorsal aspect, but from the side the rostrum appears moderately festooned. The lateral outline of the cheek region makes an angle with the rostrum below the middle of the orbits (fig. 1A, B). The palatal surface is unusually vaulted, reflecting elevation of the maxillary and anterior palatine roof and the festooning of the jaw margins opposite the big maxillary teeth. Of special interest is the relative height of the rostrum (fig. 1C, D), particularly in its posterior half where the sides of the skull are steeply inclined, and a strong angular relationship exists between lateral and dorsal roofing bones. The postorbital bars are depressed and ovate in transverse section. Posteriorly a thickened, deeply emarginated transverse occipital crest overhangs the occiput.

Those sutures that can be seen are indicated in the drawings. The incomplete but persistent median division between opposite frontal and parietal elements is notable. The lacrimal makes a long contact with the nasal; the prefrontals are separated by a narrow anterior process of the frontals; nasals end posteriorly in a transverse suture with frontals and prefrontals some distance anterior to the orbits. Frontals do not enter the supratemporal fenestrae but are excluded from them by sculptured surfaces of the parietal and postorbitals. The supraoccipital appears to reach the skull roof as a narrow median wedge lying in a deep triangular notch at the posterior edge of the skull table. Premaxillae are separated posterodorsally by a narrow continuation of the nasals into the nares.

Osteodermal scuplture comprises mainly shallow pits and grooves over most of the surface, but heavy pitting occurs on the skull table and between the orbits. Edges bounding the orbits and below the lateral temporal fenestra are thickened, as are the lateral edges of the skull table; the superior orbital rims are slightly elevated. A few deep longitudinal sulci appear on the jugals; one, shorter and lateral to the other, parallels the ventral edges of the orbit and the lateral temporal fenestra. A short but deep sulcus, coaxial with the lateral temporal fenestra, is seen on the dorsolateral surface of the quadratojugal. Except for some transverse depression of the interorbital and parietal skull roof, the superior surface of the skull table is virtually flat, but a median ridge lying between the anterior half of the orbits lends a wrinkled appearance to this area. The facial ridges that are believed to provide strength against deformational stresses in many crocodilian skulls (Iordansky, 1973; Langston, 1973) are expressed as thickened

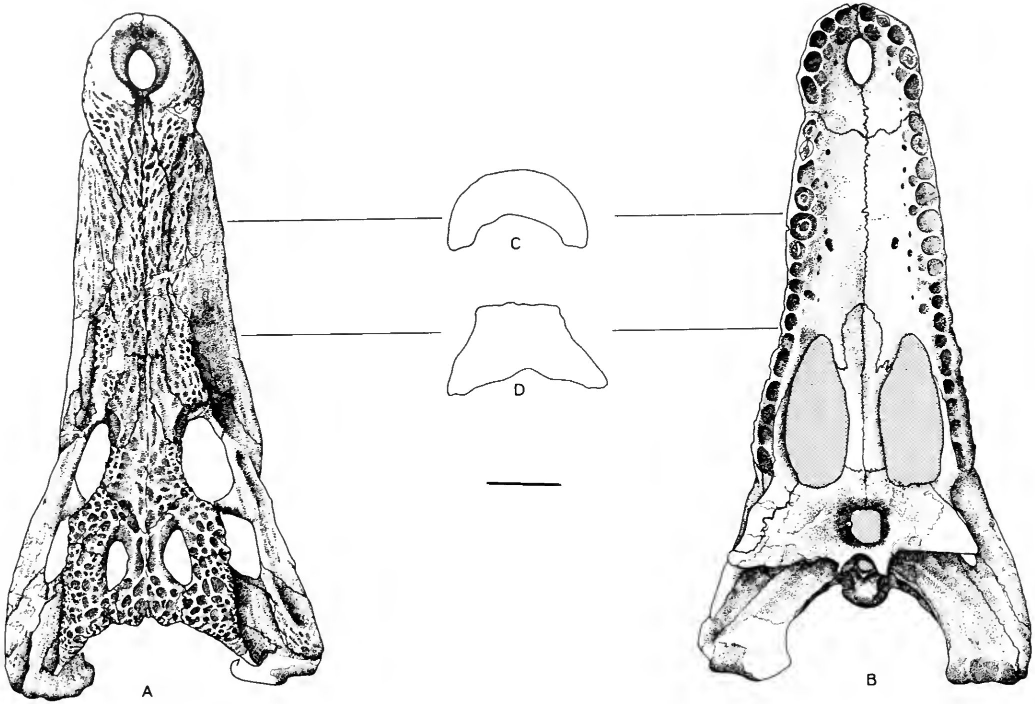


FIG. 1. *Pristichampsus vorax* (Troxell). FMNH PR 399. Skull: **A,** dorsal; **B,** ventral aspect; **C, D,** cross-section through snout at indicated levels. Scale = 5 cm.

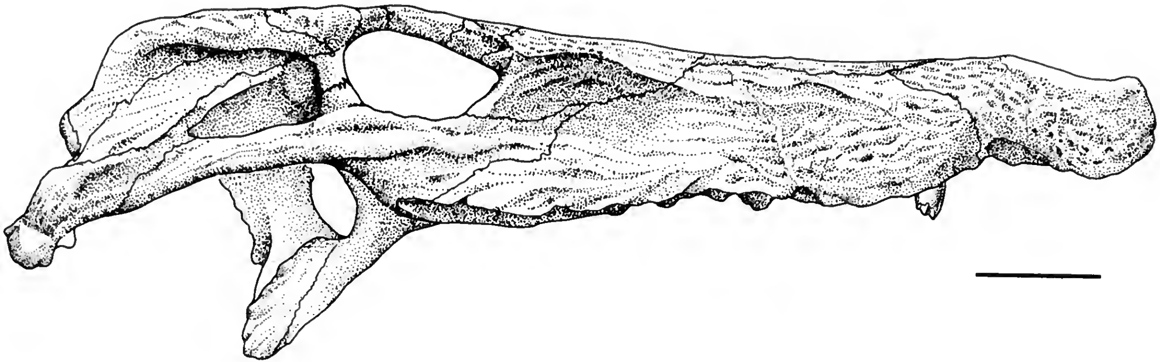


FIG. 2. *Pristichampsus vorax* (Troxell). FMNH PR 399. Skull: lateral aspect. Scale = 5 cm.

crests extending from the anterosuperior corners of the orbits anteriorly across the lacrimal and onto the maxilla. Ventrolateral to these ridges the side of the face is broadly depressed, but the surface within the depressed area is sculptured, and, except along the lacrimal crest, its margins are not sharply defined. A few tiny foramina emerge from within the depression, largely toward the anterior tip of the jugal.

A long, faceted, and roughened surface at the anterosuperior edge of the orbits, involving both prefrontal and lacrimal, is probably evidence of the former presence of heavy palpebral bones.

The nares seem large for a skull of these proportions and are subround; the vestibule opens upward and a little forward, giving the end of the rostrum a slightly downturned, mesosuchian appearance when seen from the side. In primitive fashion, the narial rims are not raised above the level of the adjacent skull bones, nor does the usual eusuchian paranasal roofing by premaxillae occur. The nares were probably partly divided posteriorly by a projection of the nasal bones, now broken off. The incisive foramen seems exceptionally large for a narrow-snouted crocodilian. The orbits look mostly to the side; if, as supposed, palpebral bones were present, vision would have been largely restricted to the lateral field. The lateral temporal fenestra is completely bounded posterodorsally by a slender process of the quadratojugal; there was no quadratojugal spine. Almond-shaped superior temporal fenestrae seem small considering the length of the jaws. The undivided choanae are large for the size of the pterygoid plate, are situated well back in the plate, and boundaries are only weakly elevated at the sides. A septum 7.5 mm. thick separates the choanae from the median eustachian foramen, which is relatively large (almost one-sixth the size of the choanae). Small lateral eustachian exits are placed higher than usual in eusuchians, on the edges of the lateral basioccipital crest. Posttemporal fenestrae are so tiny as to appear occluded. The subtemporal fossae are long, reflecting the attenuation of the ventral temporal arcade. Palatal fenestrae are unusual in having an exceptionally wide pterygoid border posteriorly.

Pterygoids and ectopterygoids seem small for the size of the skull, which thus appears relatively depressed in lateral view. Viewed from behind (fig. 3), the occipital region appears deep for its width. The paroccipital processes are exceptionally broad and extend far out onto the quadrates, which as a consequence appear

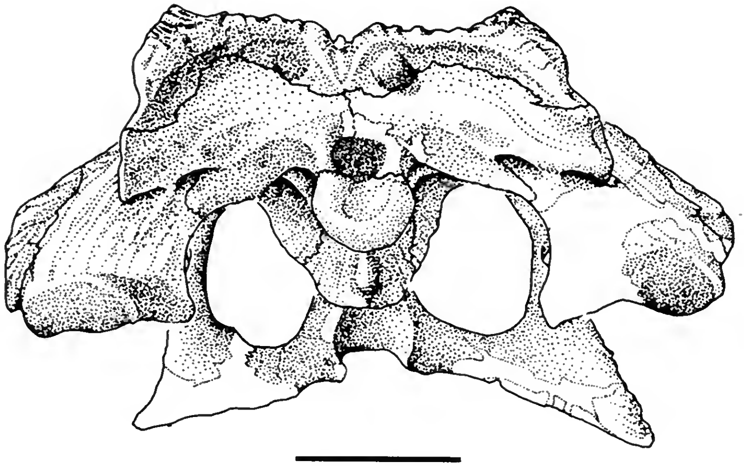


FIG. 3. *Pristichampsus vorax* (Troxell). FMNH PR 399. Skull: occipital aspect. Scale = 5 cm.

short and thick. The basioccipital plate is triangular and bears a well-developed saggital crest. The occipital condyle is relatively a little wider and less convex than in *Crocodylus* skulls of comparable size, and the articular surface curves onto the posteroventral side somewhat more than usual so that the major area of articulation with the atlas slants downward and forward at an angle of about 39°.

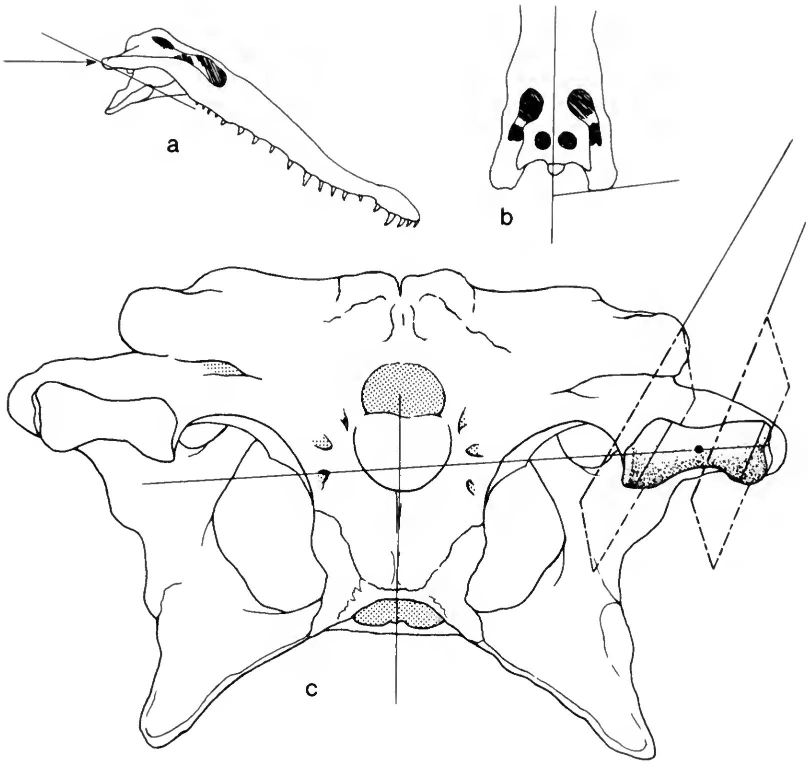
The jaw joint was peculiar; the axis of breadth across the jaw articulation is approximately transverse, but the trochlear surfaces are slightly inclined so that the lateral quadrate condyle reaches a lower plane than the medial one (see fig. 3, left side). Viewed from above or below, the quadrates have an inwardly-hooked appearance distally so that their medial edges are widest apart at midlength. This condition is reflected in the horizontal arching of the suspensorium (fig. 1A, B).

Owing perhaps to a rather complicated geometry, crocodilian jaw articulations are rarely described in detail, and occasional statements of authors that there is nothing unusual about a particular quadrate may be misleading because certain aspects of quadrate architecture are often distinctive. The shape of the trochlear surface in *Pristichampsus* is peculiar and may best be understood by comparison with the trochlea of other more "conventional" crocodilians (fig. 4). A brief description of the trochlea and associated features in *Crocodylus acutus* will be useful here.

Viewed perpendicular to the hinge surface (fig. 4a), the outline of the distal end of a medium-sized *C. acutus* quadrate appears irregularly rhomboidal and about twice as wide as it is long (fig. 4D). The long superior and inferior sides are concave, in conformity with a broad, saddle-shaped intercondylar fossa that separates the two almost equal but differently-shaped condyles. The joint surface is continuous across the fossa. The trochlea is helicoid, with its twist passing from ventromedial to dorsolateral (the torsion can be visualized by holding a strip of paper in both hands and twisting the ends in opposite directions between 35° and 45°). The axis of breadth for the jaw joint is inclined to the horizontal and vertical planes (fig. 4b, c). Planes bisecting the greatest arc of each condyle differ in position, that of the medial condyle slanting more strongly outward above than the other (fig. 4c). Thus lines drawn along the greatest arcs of the condyles pass from in front and below, backward, upward, and outward at different angles, and if projected will intersect at a point beyond the lateral tangential plane of the skull. A line similarly drawn about the deepest part of the intercondylar fossa will approximately bisect the angle formed by intersection of the other two lines. Except in very young individuals, the lateral condyle tends to be hemispherical, with joint surfaces extending from below, upward across the posterior end of the bone and, narrowly, onto the superior surface. The joint also extends over a small, roughly-triangular area on the side of the

FIG. 4. Crocodilian quadrate architecture. Trochlear outlines are drawn perpendicular to the hinge surface, i.e., with longitudinal axis of skull inclined about 65° as in **(a)**. The axis of breadth of the jaw joint is inclined both to the horizontal **(b)** and the vertical **(c)**. Planes bisecting the greatest arcs of the condyles as described in the text are shown in (c) where the black dot is in the line of sight indicated by the arrow in (a).

Trochlear surfaces of various crocodilian right quadrates are figured below (all figures drawn from photographs; lateral edge to right, superior edge at top). **A,** *Pristichampsus vorax,* YPM 5890; **B,** *P. vorax,* AMNH 2090; **C,** *P. rollinati,* AMNH 2406 (left quadrate reversed); **D,** *Crocodylus acutus* (medium-sized individual); **E,** *C. acutus* (small individual); **F,** *C. niloticus* (medium sized); **G.** *C. porosus* (small); **H,** *Alligator mississippiensis* (large); **I,** *A. mississippiensis* (medium size). All figures drawn to same transverse diameter. Scale = 1 cm.


a
b
c

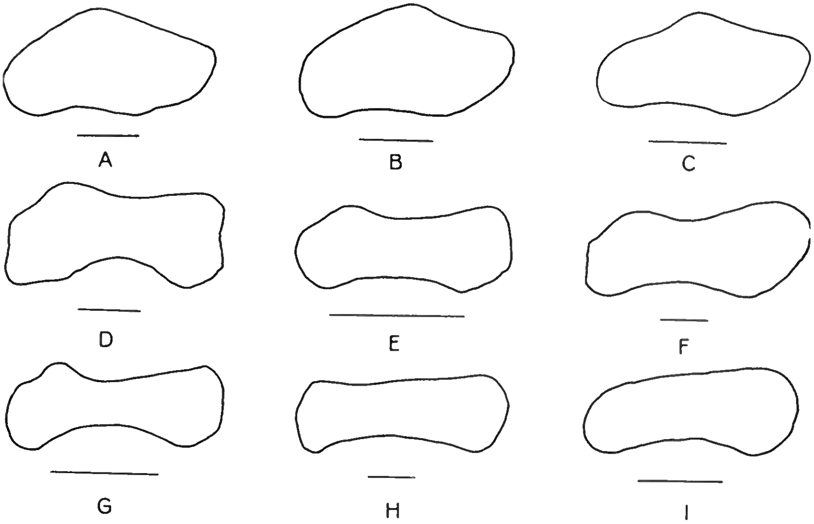

A
B
C
D
E
F
G
H
I

PLATE 1. *Pristichampsus vorax* (Troxell), YPM 249. Crushed holotype skull of *Crocodylus vorax*. Vertebrae at upper left are those of a mammal. Approximately one-fourth natural size.

quadrate below the posterior tip of the quadratojugal. The medial condyle appears less tumid, its ventral surface extends farther forward than the lateral condyle, and its flattened joint surface does not pass so far onto the superior surface of the quadrate. Thus the working surface is but slightly visible from above. Much of the joint surface of the medial condyle can, however, be seen in lateral view; it ends abruptly along the sharp medial edge of the quadrate.

In existing crocodiles, the shape of the trochlear surface varies somewhat among individuals of similar size within one species, and considerable differences may exist between individuals of different species of one genus (compare figs. 4D and F; E and G). Generic differences are pronounced (fig. 4D and I; F and H). Changes mainly affecting the relative size and convexity of the medial condyle, expecially in various species of *Crocodylus,* occur ontogenetically (fig. 4D, E).

Trochlea of FMNH PR 399 are damaged, but their essential qualities can be discerned. They clearly resemble the articular end of a right quadrate YPM 5890 (which may have been the bone

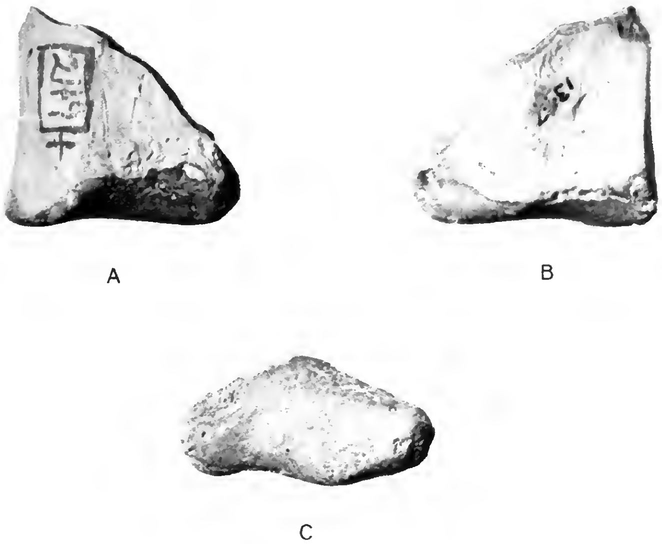


PLATE 2. *Pristichampsus vorax* (Troxell), YPM 5890. Distal end of right quadrate formerly included with YPM 1347. **A,** superior; **B,** inferior; **C,** trochlear aspects. Natural size.

referred to by Marsh in 1871). This specimen (pl. 2) is excellently preserved and, though smaller than PR 339, furnishes a better idea of the structure than can be obtained from the Field Museum specimen. It differs greatly from the quadrate of *C. acutus.* The posterior outline of the distal end (fig. 4A) is much less rhomboidal, the joint surface is relatively flat with a wide and shallow intercondylar fossa. Anteriorly, where the fossa is deepest in *C. acutus,* the bridge between the condyles is only a little excavated in the fossil. Nevertheless, the medial condyle projects forward beyond the lateral one, which is relatively undeveloped and virtually without any of the hemispherical expansion that is characteristic of other eusuchian quadrates. Instead of the small triangular joint surface that appears on the side of the quadrate below the quadratojugal in *C. acutus,* the lateral condyle comes to an obtuse point just beyond the end of the quadratojugal. What is probably the homologue of the lateral joint area occurs as a larger, smoothly-rounded surface of triangular outline at the anteroventral corner of the trochlea. It would hardly be visible from the side.

The helix of the joint of YPM 5890 is more pronounced than in *C. acutus,* and the condylar planes are less inclined. They are also more nearly parallel and hence lend a more regular appearance to

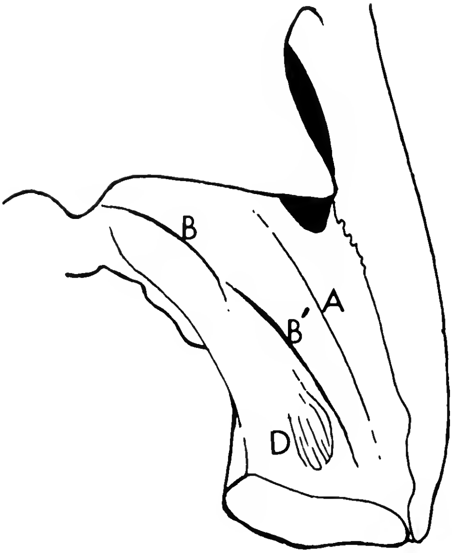


FIG. 5. *Pristichampsus vorax.* Tendon crests on ventral side of left quadrate, based on FMNH PR 399.

the screw-shaped hinge. The strong edge of the medial condyle is a little thickened and relatively longer than in the *C. acutus* quadrate. It ends above the center of the trochlea at the thickest part of the joint. Just lateral to the edge and immediately in front of the joint surface, on the superior face of the bone, there is a small but distinct tubercle. This does not occur in any living crocodilian known to me – instead, the corresponding area is distinctly excavated parallel to the dorsal edge of the trochlear surface. (Troxell's statement that the dorsal surface of YPM 5890 is divided by a dominating ridge is puzzling, as a transverse section of the quadrate about 2 cm. above the trochlea has only a slightly convex upper outline.) Ventrally, about 1.5 cm. above the joint, there is a sculptured area which is better seen in PR 399 where it comprises a small ovate elevation. This corresponds to tendon crest D of Iordansky (1964; 1973). Other tendon crests (A, B, B^1) are sharply defined in PR 399 (fig. 5), but crests A^1 and C are apparently undeveloped. These crests, related to the *M. adductor mandibulae posterior* group, exhibit some variation, but are believed to be distinctive in the different species of existing crocodilians (Iordansky, 1964).

The transverse diameter of the distal end of the quadrate is 33.2 mm., and the vertical diameter at the middle of the trochlea is

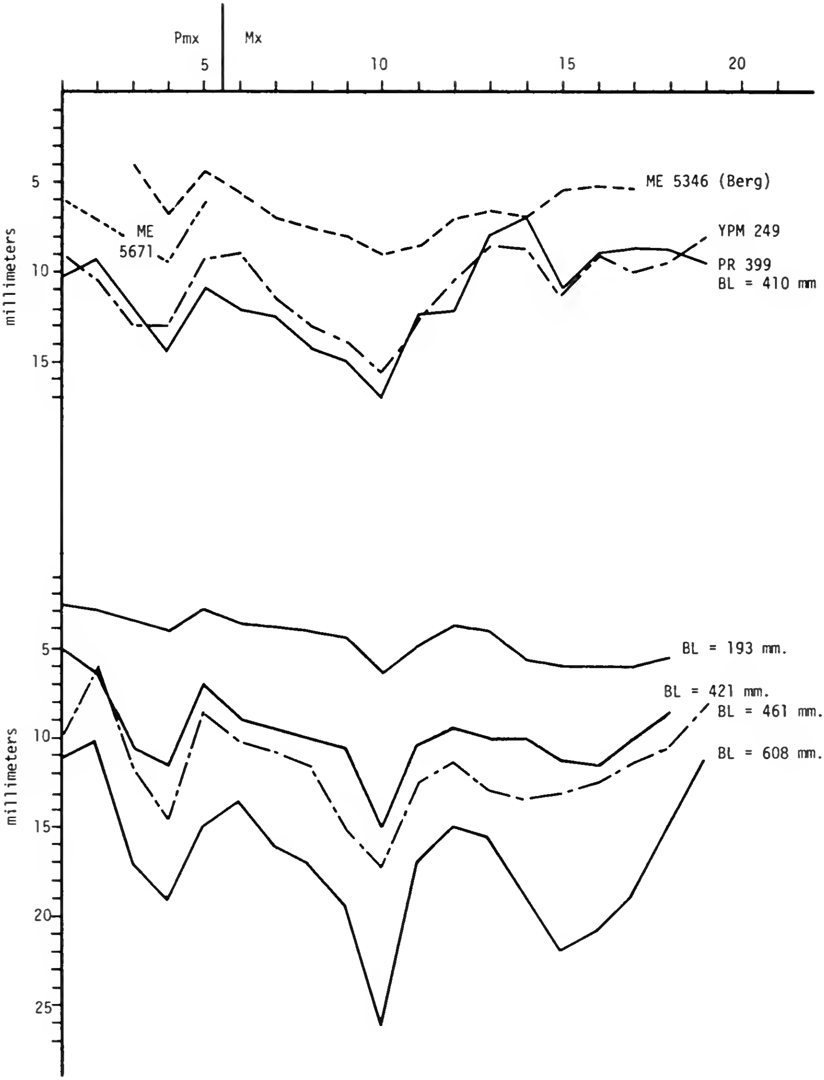


FIG. 6. Tooth size based on fore-and-aft diameters of cranial alveoli in various crocodiles. Upper graph, *Pristichampsus rollinati* ME 5346 and 5671 compared with *P. vorax* FMNH PR 399 and YPM 249; lower graph, *C. acutus* continuous line and *C. porosus,* broken line. BL = basal length of skull.

16.9 mm. in YPM 5890; corresponding dimensions in FMNH PR 399 are 48.5 and 22.5 mm., respectively.

A quadrate belonging to AMNH 2090 is a little smaller than YPM 5890 but is otherwise similar to it (fig. 4B). The tapering part of the lateral condyle is a little shorter, the tubercle on the superior surface above the middle of the trochlea is larger, and tendon crest D is a depression instead of an elevation. To judge from the variability observed in quadrates of existing crocodilians, such differences which may reflect individual variation in muscle architecture, may have little taxonomic significance.

There are apparently 22 alveoli on the left side of the Field Museum skull, but only 21 are present on the right. The dental pattern as determined from alveolar measurements is distinctive (fig. 6) and seems closer to that of existing crocodiles than to alligators or caimans. Of the four teeth remaining in the skull, only left pmx 2 and right mx 2 are represented by more than truncated roots, and only the maxillary tooth retains any serrations. This tooth by itself would be indistinguishable from several teeth in the Yale collection including those of the holotype of *C. vorax* Troxell (YPM 249) or from some that may have been among the "*Crocodylus ziphodon*" material of Marsh. There are about six serrations per millimeter on the leading edge of the crown (the posterior edge is not preserved). This tooth has a fore-and-aft diameter of 10.1 mm. at the base of the crown, where it is 7.0 mm. wide. It appears distinctly inclined posterodorsally, a feature characteristic of *Pristichampsus,* which is somewhat accentuated by the fact that the leading edge of each tooth is longer than the trailing edge. The second premaxillary tooth was less blade-like but nevertheless has principal diameters of 6.0 and 8.25 mm. In section its edge-to-edge diameter is oriented about 45 degrees of the midsaggital plane, whereas that of the second maxillary tooth deviates by about 20 degrees, its trailing edge being laterad of the leading edge. Left pmx 4, represented by the base of the crown, has principal diameters of 11 and 6 mm.

SYSTEMATIC POSITION AND RELATIONSHIPS OF ZIPHODONT CROCODILES

A comparison of the holotype of *C. vorax* and the Field Museum skull shows them to be of nearly the same size, YPM 249 being slightly the smaller. Otherwise they seem very similar. The only differences to be noted are in the alveolar patterns (fig. 6) and what seems to be slightly coarser sculpture on the side of the maxilla in the Yale skull. Also in that specimen the jaw edge is a little more deeply festooned. These differences are best attributed to individual variation, if we may be guided by conditions in existing crocodilians.

Excellent photographs of some of the referred *Pristichampsus rollinati* specimens are available to me through the courtesy of Dr. Berg. Also at hand is a cast of the quadrate of a Geiseltal skull at Halle (ME D.-5894) which was generously provided through Dr. Berg by Prof. Dr. H. W. Matthes, Director of the Museum für Erdgeschichte-Geiseltalsammlung. A posterior part of a skull, probably of *P. rollinati* (AMNH 2406, Poissier Collection), stated to be from the "Eocene of France" has also been available for comparison with the North American material.

Agreement between European and North American specimens appears close, but some differences involving cranial proportions and the dentition patterns are significant. The snout of the Field Museum specimen is neither so long nor as slender as indicated in a reconstructed Geiseltal skull (Berg, 1966, fig. 7), and the premaxillary rostrum is distinctly shorter in the American skull. The external nares are less, the supratemporal fenestrae more, elongate than in the Geiseltal skull. Berg concluded that a snout of *P. rollinati* described by Weitzel contained 13 maxillary teeth whereas 16 to 17 were clearly present in PR 399 and probably also in YPM 249. The alveoli of *P. rollinati* are shown more oval and are more widely spaced than in PR 399 (Berg, 1966, fig. 6a), and the occlusal pits in the palate are indicated as more regularly arranged medial to the tooth row. The dental pattern as reflected by alveolar diameters differs mainly in the posterior third of the series (fig. 6), but this is the region where alveolar partitions are least well formed and measurements tend to vary more here than farther forward in all crocodilian species. The main differences in the patterns have to do with the relative size of the larger teeth which are known to increase disproportionately with growth of the individual in *C. acutus* and other living species. The larger *P. vorax* specimens might therefore be expected to display greater variation in the teeth than *P. rollinati.*

The Field Museum skull of *P. vorax* confirms the eusuchian palatal construction of ziphodont crocodiles previously suggested by Berg's study of Geiseltal specimens. Combining a eusuchian palate and procoelous vertebrae, *Pristichampsus* is by definition elimi-

TABLE 2.

Character	Sebecosuchia	*Pristichampsus*	Eusuchia
Secondary palate	"Mesosuchian," shorter	As in Eusuchia	Eusuchian, longer
Choanae	Very large	Moderate in size, closer to eusuchian proportions	Smaller
Rostrum	Very high, narrow, with median crest formed by nasal bones	Intermediate in height and width, without median crest	Low, primitively broad, flat to saddle-shapped on top, no median crest
Direction of orbits	Lateral	Lateral	Dorsolateral
Quadrate articulation	Axis transverse, condyles not well differentiated	Resembles sebecosuchians	Axis transverse, condyles well differentiated
Teeth	Ziphodont, serrated margins; numbers reduced	Ziphodont, serrated margins, numbers slightly reduced	Conical to blunt, margins not serrated, greater numbers
Vertebral centrum	Feebly amphicoelous	As in eusuchians	Procoelous

nated as a possible sebecosuchian. Nevertheless the question may be asked whether the eusuchian palate and eusuchian vertebrae may not have been acquired by sebecosuchians in the course of their evolutionary history (Langston, 1973). In this event, it might be possible to regard *Pristichampsus* as an advanced sebecosuchian of "eusuchian grade." The best counter to such a proposal is a comparison of *Pristichampsus* with the character states that define the Sebecosuchia and Eusuchia, respectively (table 2). This reveals that the principal areas of agreement between *Pristichampsus* and the sebecosuchians are related to the feeding mechanism. It seems easier to view the tooth design (apparently the most efficient shearing mechanism possible for large carnivorous reptiles and mammals) and the elevation of the face, and similar jaw joints as evolving by convergence in a primitive eusuchian in the direction of the sebecosuchian condition than to suppose the opposite. Indeed, the overall appearance of the *Pristichampsus* skull is so much that of an eusuchian crocodile that there is no alternative at present to following Kuhn (1968) and Steel (1974) in assigning the taxon to the Crocodylidae, as that family is currently drawn by these authors.

The North American ziphodont crocodiles as presently known may be summarized as follows:

Order Crocodylia
Suborder Eusuchia Huxley, 1875
Crocodylidae Cuvier, 1807 (*sensu* Kälin, 1933)

Pristichampsus Gervais, 1853 (*sensu* Berg, 1966)
P. vorax (Troxell, 1925) new combination
Crocodylus ziphodon Marsh, 1871, p. 453
Limnosaurus ziphodon Marsh, 1872, p. 309
Crocodylus vorax Troxell, 1925, p. 42

Type. — YPM 249, an incomplete crushed skull and mandible with associated postcranial elements.

Locality. — "... near Red Dog Butte" (Troxell, 1925, p. 42).

Horizon. — "... Greensand formation", "Bridger (Eocene)" (*ibid.*)

Referred specimens. — A skull, FMNH PR 399, from within Roehler's beds 614-618, close to common corner of sections 17, 19, and 20, T.16N, R.97W, Sweetwater Co., Wyoming; a crushed skull and associated skeletal scraps, FMNH PR 479, from Granger's bed 1 (i.e., near base of Washakie A), from within the sequence of

Roehler's beds 571-580, from within area limited by SE ¼, Sec. 22, and NE ¼, Sec. 27, T. 16N, R. 95W, Sweetwater Co., Wyoming; an incomplete right quadrate, YPM 5890, from the Bridger Basin, at Grizzly Buttes, probably in Sec. 28, T.14N, R.113W, Uinta Co., Wyoming (Bridger B), and various teeth and bone fragments numbered YPM 1343 and 1347 from the same general area; a fragmentary skeleton, AMNH 2090, from the upper White Layer (Bridger D) at Henry's Fork Hill (= Cedar Mountain), presumably in sections 25-30, T.13N, R.112W (Wheeler, *in litt.*); a more complete skeleton, USNM 12957, from "Bridger D horizon," 2 miles N of Lone Tree P. O., Bridger Basin, Uinta Co., Wyoming.

Amended diagnosis. — Larger than *P. rollinati,* with slightly wider and shorter snout, and a greater number of teeth in the maxilla (16 *vs.* 13).

Distribution. — Eocene of the Bridger and Washakie Basins, Wyoming.

ACKNOWLEDGMENTS

I am indebted first of all to Rainer Zangerl for generously offering the Field Museum skull to me for study. Drs. J. H. Ostrom and J. S. McIntosh have been indispensable in reconstructing the history of the Marsh specimens at Yale; stratigraphic and locality data on North American Eocene localities has been furnished by Drs. W. A. Wheeler, P. O. McGrew, and W. D. Turnbull. The counsel and assistance of Drs. E. H. Colbert, D. E. Berg, D. E. Russell, and Mme. F. de Broin are gratefully acknowledged. Drawings are by Mrs. Doris Tischler (Figure 4 by Edwina Traverso).

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