

**Article V.—SKULL CHARACTERS AND AFFINITIES OF THE
EXTINCT FLORIDA GAVIAL *GAVIALOSUCHUS*
AMERICANA (Sellards)¹**

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PLATES V TO IX

Excavations for rock phosphate in the Miocene of Florida in the last few years have brought to light a considerable number of specimens of fossil crocodiles. Some of the specimens thus obtained by the Amalgamated Phosphate Company have been presented, through the good offices of its superintendent, Mr. Anton Schneider, by the company to The American Museum of Natural History. Others have been presented to the Florida Geological Survey, the United States National Museum, and the Museum of Comparative Zoology.

In 1915 Dr. E. H. Sellards² described the anterior portion of the snout of one of these crocodiles under the name *Tomistoma americana*. In 1916 he published further descriptions, chiefly of the mandibles.³ The American Museum collections include one nearly complete skull of this species (Amer. Mus. No. 5663) and the anterior portions of the skull and jaws of another specimen (Amer. Mus. No. 5662). This material is much more complete than the material described by Sellards and forms a better basis of comparison with other tomistomoid species.

In the general form of the skull and the arrangement of the sutures on the superior surface of the snout, this species bears considerable resemblance to the living *Tomistoma schlegelii* and to several known fossil species of *Tomistoma*. After careful examination of the type specimen (U. S. Nat. Mus. No. 8816) and the well-preserved skull in the American Museum (Amer. Mus. No. 5663) and comparison with specimens of *T. schlegelii* and with specimens and figures of fossil species of *Tomistoma*, it appears that these resemblances may be more or less superficial, and tend to distract the attention of the observer from differences which are perhaps more important. In the following description these resemblances and differences are analyzed, and an attempt is made to evaluate them correctly. The species is here referred to *Gavialosuchus* Toula and Kail.

¹Contributions to the Osteology, Affinities, and Distribution of the Crocodilia. No. 2.

²E. H. Sellards, 1915. A New Gavial from the Late Tertiary of Florida. Amer. Journ. Sci., (4) XL, pp. 135-138, 2 figs.

³E. H. Sellards, 1916. A New Tortoise and a Supplementary Note on the Gavial, *Tomistoma americana*. Amer. Journ. Sci., (4) XLII, pp. 235-240, 3 figs.

GENERAL FORM

As in *Tomistoma schlegelii*, the skull of *Gavialosuchus americana* is long and slender; it resembles the skull of the living *Crocodylus cataphractus* in many respects; it is much less slender than the skulls of *T. schlegelii*, *T. gavialoides* Andrews from the Eocene of Egypt, and the living gavial, *Garialis gangeticus*; it resembles more closely in this respect *T. calaritanus* Capellini from the Italian Tertiary and *Gavialosuchus eggenburgense* Toulia and Kail from the Miocene of Austria. It is decidedly broader than the skull of *T. schlegelii*, but is not so deep vertically, nor does the external surface of the snout roll under as in the latter species; crushing of the fossil specimens has probably had little or nothing to do with this character. The expansion of the snout posterior to the narial aperture is not gradual, as in typical species of *Tomistoma*, but irregular, the snout expanding and then contracting slightly, somewhat as in the typical crocodiles. The snout expands abruptly immediately posterior to the notches which received the fifth premaxillary teeth; posterior to this the sides remain parallel to the fourth maxillary teeth, where the snout expands abruptly again; the transverse diameter of the snout across the fifth maxillary teeth is much greater than across the fourth. Posterior to the fifth maxillary teeth the snout contracts gradually as far back as the space between the seventh and eighth maxillary teeth; then it expands suddenly and continues to expand steadily from the eighth maxillary teeth to the fourteenth, or last; posterior to the last maxillary teeth is a slight constriction, and then a steady expansion behind the orbits; the quadrate region is not preserved.

The cranial table is considerably broader than long, and is almost rectangular in form. It is relatively large in size, considerably surpassing, in this respect, other tomistomoid species except *G. eggenburgense*.

The breadth of the skull is great in proportion to its vertical height.

CAVITIES OF THE SKULL

SUPRATEMPORAL FENESTRÆ.—The supratemporal fenestræ in this species are very large; they are oval in outline and are broader than long, also close together. In their form these fenestræ differ from the fenestræ of the various species of *Tomistoma*; they resemble those of *Gavialosuchus eggenburgense*. In size they resemble the fenestræ of *T. gavialoides* Andrews and *T. africanum* Andrews, and differ from the existing *Tomistoma* and from *T. calaritanus* Capellini. Each fenestra is larger than the narial opening and is about the same size as the orbit.

ORBITS.—The orbits are widely separated. They are rather large in size, and their axes of greatest length converge anteriorly; their diameters from the antero-internal to the postero-external ends are considerably greater than from the antero-external to the postero-internal sides.

NASAL ORIFICE.—The nasal orifice is large; it has a straight transverse anterior border; its lateral borders are curved and converge slightly in the posterior direction; the narrow posterior border is smoothly rounded.

PREMAXILLARY FORAMEN.—This opening is small, but not so small as in *Tomistoma schlegelii*; it is irregularly elongate in outline, resembling that of *T. calaritanus*.

PALATINE FENESTRÆ.—The borders of the palatine fenestræ are incompletely preserved. They extend as far forward as the anterior edges of the eleventh maxillary teeth.

THE BONES IN DETAIL

PREMAXILLARIES.—The premaxillaries do not extend as far back on the surface of the skull as in the recent *Tomistoma*. They extend as far back as the level of the third maxillary teeth on the superior surface and slightly farther back on the palate. They are longer in proportion to the length of the maxillaries than in *T. schlegelii* when measured along the sides of the snout; their posterior processes are shorter than in the latter species. Along the median line the two premaxillaries have a contact with each other, which is proportionally less than one-half the length of the same contact in the living *Tomistoma*. The premaxillo-nasal suture is nearly four times as long as in *T. schlegelii*.

Each premaxillary contains five teeth, differing in this respect from *T. schlegelii* and *T. gavioloides* and agreeing with *T. africanum*, *T. calaritanus*, and probably *G. eggenburgense*. None of these teeth are especially weak, though the second is the smallest, the first and fifth next in size, and the third and fourth largest. The full development of the second premaxillary tooth is a primitive character. All of these teeth are much larger than the premaxillary teeth of the existing species, and they are spaced somewhat differently. The first and second are rather far apart, and there is no prominent excavation posterior to the first for reception of the first mandibular tooth as in the modern species. (In one of the specimens in the collection of the Florida Geological Survey, Fla. Geol. Surv. No. 6158, there is a somewhat more prominent excavation,

according to Sellards¹); the second is close to the third, which is the homologue of the second of *T. schlegelii*; the third is widely spaced from the fourth, corresponding to the wide spacing of the second and third of the modern *Tomistoma*; the fourth and fifth are relatively close together, contrasting with the wide spacing between the third and fourth teeth in the existing species of *Tomistoma*.

The suture of the premaxillaries with the maxillaries on the palate is shaped quite differently from the same suture in *T. schlegelii* and resembles more that of *T. gavioloides* and *G. eggenburgense*. In the living *Tomistoma* the suture is W-shaped, with the central point of the W directed forward; in *T. calaritanus* it is irregularly W-shaped in the reverse direction; in *T. gavioloides* it is a simple acute V, directed backward; in *G. eggenburgense* it is a modified W, with the center of the W directed backward, complicated by a slight indentation at the median line, and with the internal bars of the W much greater than the external, so that the suture is nearly V-shaped. In the Florida species the suture extends slightly inward from the lateral border of the skull, then almost directly backward to a point opposite the space between the first and second maxillary teeth, then more nearly inward a very short distance, then almost directly backward but very slightly inward to the median line at a point slightly anterior to the third maxillary teeth, and thence in reverse direction to the external border of the skull on the opposite side.

MAXILLARIES.—The maxillary bones are of about the same length as in *T. schlegelii*. The maxillo-nasal sutures are similar in shape to those of the latter species, but are much longer proportionally. The form of the maxillo-lacrymal suture is not discernible at the contact with the nasals; the lower part of the suture is not characteristic in form; the same is true of the maxillo-jugal suture.

On the palate the maxillaries are very short along the median line; this is due to the considerable posterior extension of the premaxillaries and the anterior extension of the palatines. The sutures of the palatines extend forward in a sharp V, which reaches the median line slightly posterior to the level of the eighth maxillary teeth. The sutures with the ectopterygoids are situated at the level of the thirteenth maxillary teeth on the borders of the palatine fenestræ, then turn sharply backward to points slightly posterior to the fourteenth maxillary teeth, then turn outward and backward to the external border of the skull.

¹E. H. Sellards, 1915. A New Gavial from the Late Tertiary of Florida. Amer. Journ. Sci., (4) XL, pp. 135-138, 2 figs.

The teeth of the maxillaries, like those of the premaxillaries, are very large; they are much larger than the teeth of any species of *Tomistoma*, except perhaps *T. kerunense* Andrews, and resemble the teeth of *G. eggenburgense*. The first three teeth are about uniform in size and the fourth is smaller; the fifth is very large and the sixth is only slightly smaller than the fifth; the teeth posterior to the sixth are all large. So far as they are preserved, all of these teeth appear to be relatively short vertically, circular or elliptical in outline at the base, keeled very slightly on their edges in some cases; on a few teeth there are faint striations. They are not so sharp as the teeth of the modern species.

NASALS.—The nasals in this species are much longer than in the living *Tomistoma*; they extend to within a comparatively short distance from the narial aperture, as in *T. calaritanus* and *G. eggenburgense*. They resemble the nasals of the latter species and differ from those of *T. calaritanus* in that they do not extend as far forward as the premaxillo-maxillary sutures at the lateral borders of the skull; the anterior tips are slightly anterior in position to the level of the first maxillary teeth. The anterior portions of the nasals, between the premaxillaries, widen rapidly in the posterior direction; the larger portions, between the maxillaries, widen very gradually, much more so than in *T. schlegelii*. The greatest breadth of the nasals is at the level of the eleventh maxillary teeth; the breadth is about the same as in the recent form. The sutures with the lacrymals and maxillaries are evidently longer than in the modern *Tomistoma*. The naso-lacrymal sutures are not wholly preserved; from the parts which are preserved they do not appear to be characteristic in outline. The sutures with the prefrontals are shorter and much simpler than in the recent *Tomistoma*, consisting of obliquely placed straight lines. The contact with the frontal is also very short; the processes of the nasals, which wedge in between the prefrontals and frontal, are short and broad.

PREFRONTALS.—The prefrontals are relatively small in size; they have no anterior processes wedging in between posterior processes of the nasals as in the living *Tomistoma*.

LACRYMALS.—The complete outlines of the lacrymal bones are not fully determinable, owing to incomplete preservation. It is clear, however, that they are relatively large and that they are broader than in the modern species.

JUGALS.—The jugals are only partly preserved, the posterior portions being missing. They are rather broad and are short antero-posteriorly. The sutures with the lacrymals are only one-half as long as in *T. schlegelii*.

FRONTAL.—The frontal bone is characteristic in outline. Its anterior process is about as long as in the modern form but is much broader and more blunt, wedging the nasals farther apart at their posterior ends. The interorbital and cranial portions of the frontal are also broad. The frontal bone resembles that of *G. eggenburgense* in form.

POSTORBITALS.—These bones are large in size. Their longitudinal and transverse diameters, also their vertical thicknesses, are considerably greater than in *T. schlegelii*. Their inferior processes are also very stout, but this may be partly due to a slight flattening of the skull.

SQUAMOSALS.—The squamosal bones are characterized by their relatively small size. They are about equal in surface area to the postorbitals; in most crocodilians, including the modern *Tomistoma*, the squamosals are larger than the postorbitals.

PARIETAL.—This bone is broader than in *T. schlegelii* but occupies a smaller area of the skull-top because of the large size of the supratemporal fenestræ. The entire posterior border of the superior surface of the skull between the squamosals, which is greater than in the recent *Tomistoma*, is composed entirely of the parietal, the supraoccipital being entirely excluded. There is no median posterior notch such as that which characterizes *T. schlegelii*.

SUPRAOCCIPITAL.—The supraoccipital bone is broad and is deep vertically; it evidently extended downward nearly to the foramen magnum. It is entirely confined to the posterior surface of the skull.

PALATINES.—The anterior processes of the palatines only are preserved. They differ from the palatines of the modern *Tomistoma* in extending forward as in the true crocodiles, instead of ending abruptly at or near the anterior end of the palatine fenestræ.

ECTOPTYERYGOIDS.—The right ectopterygoid is nearly complete in No. 5663; its chief characteristic is a great thickness of the neck of the vertical process.

MANDIBLE

The mandible is known from a considerable amount of material in the collection of the Florida Geological Survey. In the American Museum collections No. 5662 contains the anterior portion of the mandible of a large individual. In this specimen the teeth are large and distant from each other, as in the maxillary and premaxillary. The first mandibular teeth are large and spaced a considerable distance from each other; the second teeth are large and are distant from the first; the first and second teeth are bent out sharply from the borders of the jaw; this is

correlated with the absence of deeply excavated pits in the premaxillaries to receive the first mandibular teeth. The third teeth are relatively small and are moderately distant from the second in one direction and the fourth in the other; the fourth teeth (as judged from the alveoli) are large. The teeth from the fifth to the ninth, inclusive, are all large and far apart. From the tenth back they are all large and close together. The number of teeth in the mandible cannot be determined from this specimen; the latter has the sixteenth tooth preserved on the right side, with the alveolus of another posterior to it; the number of mandibular teeth must therefore have been at least seventeen. Sellards estimates the number to be seventeen or eighteen, basing the determination not on a single complete specimen but by comparison of a number of incomplete ones.

The symphysis extends to the twelfth teeth, contrasting with the condition in *T. schlegelii*, in which it extends to the fifteenth, and with *T. africanus*, in which it extends equally as far. The mandible is slender, with nearly parallel sides as far back as the tenth teeth; from this point it expands rapidly to the posterior end of the specimen. The splenial bones extend into the symphysis as far forward as the space between the seventh and eighth teeth; they occupy a little over one-third of the length of the symphysis.

REMARKS

This species resembles other tomistomoid species in many respects and differs in others. The greatest resemblance is with the species from the Miocene beds of Austria, described by Toulou and Kail under the name of *Gavialosuchus eggenburgense* and later referred by Lydekker to *Tomistoma*. In some characters, however, the Florida species differs from the latter and resembles typical species of *Tomistoma* more closely. The resemblances and differences between the Florida species and the other species are indicated in the accompanying table.

Whether or not the Florida species is to be referred to *Tomistoma* is a difficult problem. Analysis of the table and comparison of the characters lead to the conclusion that the species should be referred to *Gavialosuchus* Toulou and Kail, which genus is closely related to *Tomistoma* but is not identical with it. *Gavialosuchus* presents characters which are in some respects intermediate between *Tomistoma* and *Crocodylus*; in the totality of characters, of course, the resemblance to *Tomistoma* is the greater. *Gavialosuchus* may be considered as a more primitive genus than *Tomistoma*.

The skull of the genus *Gavialosuchus* differs from that of *Tomistoma* in being more robust throughout; it is broader in proportion to its length; the teeth are fewer in number and more widely spaced; the premaxillo-maxillary suture on the palate is more or less V-shaped, instead of W-shaped as in most species of *Tomistoma*; the maxillo-palatine suture is more elongate; the cranial table is larger, especially broader; the supratemporal fenestræ are larger, more oblique in position, and closer together; the vertical depth of the skull is not so great; the expansion of the snout is relatively more abrupt; the number of premaxillary teeth is five, instead of the four which is typical of *Tomistoma*; the premaxilla is excavated much less for the reception of the first mandibular teeth; the teeth are not set in cylinder-like processes of the jaws, with deep depressions between them. Some species of *Tomistoma* approach a few of these characters very closely.

The species *Gavialosuchus americana* (Sellards) differs from *G. eggenburgense* Toula and Kail, in the following characters: the snout expands abruptly at the fifth maxillary teeth; the postorbital bones are unusually large; the cranial table is very broad; the sides of the cranial table are parallel; the premaxillo-maxillary suture on the palate extends back to the level of the third maxillary teeth; the maxillo-palatine suture is decidedly elongate; the fifth maxillary teeth are considerably larger than the fourth. Of the two species, *G. americana* is evidently the more primitive.

MEASUREMENTS

Amer. Mus. No. 5663

Length of Skull, Extremities of Squamosals to Tip of Snout	90.0 cm.
Length of Skull, Median Line	86.0
Breadth Across Extremities of Squamosals	22.0
Breadth of Cranial Table	21.3
Length of Cranial Table	14.0
Breadth Across the Supratemporal Fenestræ	15.5
Breadth Between Supratemporal Fenestræ	1.5
Breadth Across Jugals, Estimated	33.3
Breadth Across Orbits	20.5
Breadth Between Orbits	5.2
Length of Posterior Border of Skull to Anterior End of Anterior Process of Frontal, Along Median Line	24.7
Total Length of Nasal Bone	46.2
Total Length of Premaxillaries, Superior Surface of Skull	29.8
Median Length of Premaxillaries, Superior Surface of Skull	10.8
Breadth of Snout Across Narial Opening	10.0

Breadth of Snout Across Notch at Premaxillo-maxillary Suture on Lateral Surfaces	7.8cm.
Breadth of Snout Across First Maxillary Teeth	10.5
Breadth of Snout Across Fifth Maxillary Teeth	13.6
Breadth of Snout Across Ninth Maxillary Teeth	17.0
Breadth of Snout Across Fourteenth Maxillary Teeth	25.0
Length of Dental Series of Maxillary, Right Side	47.3
Vertical Height of Skull, Lower Ends of Ectopterygoids to Cranial Table	17.2
Length of Premaxillaries on Palate	30.0
Length of Maxillaries Along Median Line on Palate	21.5
Diameter of Alveolus of Fifth Maxillary Tooth	3.2
Amer. Mus. No. 5662	
Length of Portion of Skull Preserved (About to Last Maxillary Teeth)	72.0
Breadth of Snout Opposite Narial Opening	11.6
Breadth of Snout Across Fifth Maxillary Teeth	14.2
Length of Portion of Mandibles Preserved (to Alveolus of Seventeenth tooth)	71.3
Length of Symphysis	51.2
Splénial Portion of Symphysis	17.5
Breadth of Mandibles at Ninth Teeth	10.1

PLATE V

Skull of *Gavialosuchus americana* (Sellards)

Amer. Mus. No. 5663

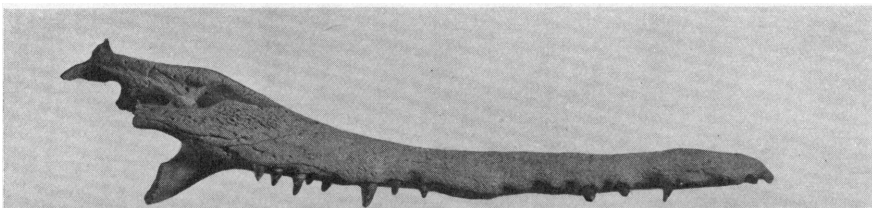
One-tenth natural size

A. Lateral view, left side

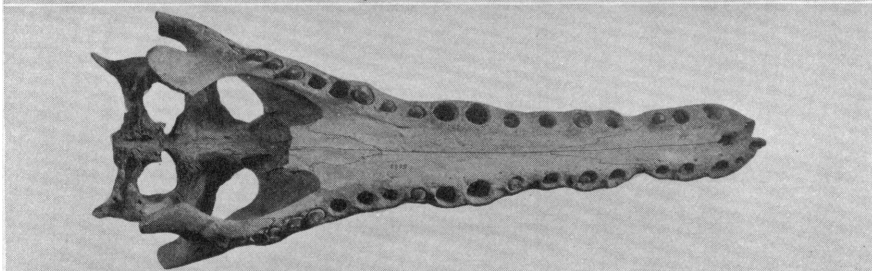
B. Inferior view

C. Superior view

A



B



C



PLATE VI

Skull and Jaws of *Gavialosuchus americana* (Sellards)

Amer. Mus. No. 5662

One-fourth natural size

Superior view

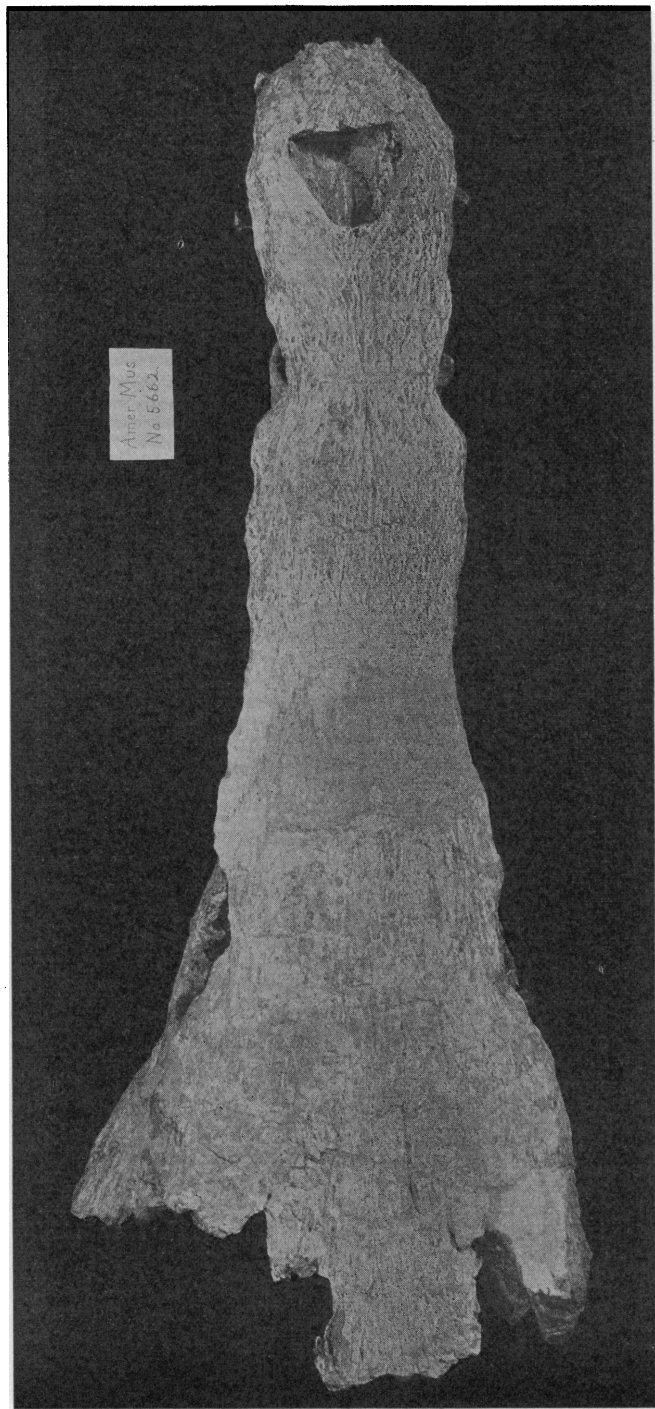


PLATE VII

Skull of *Gavialosuchus americana* (Sellards)

Amer. Mus. No. 5662

One-fourth natural size

Inferior view

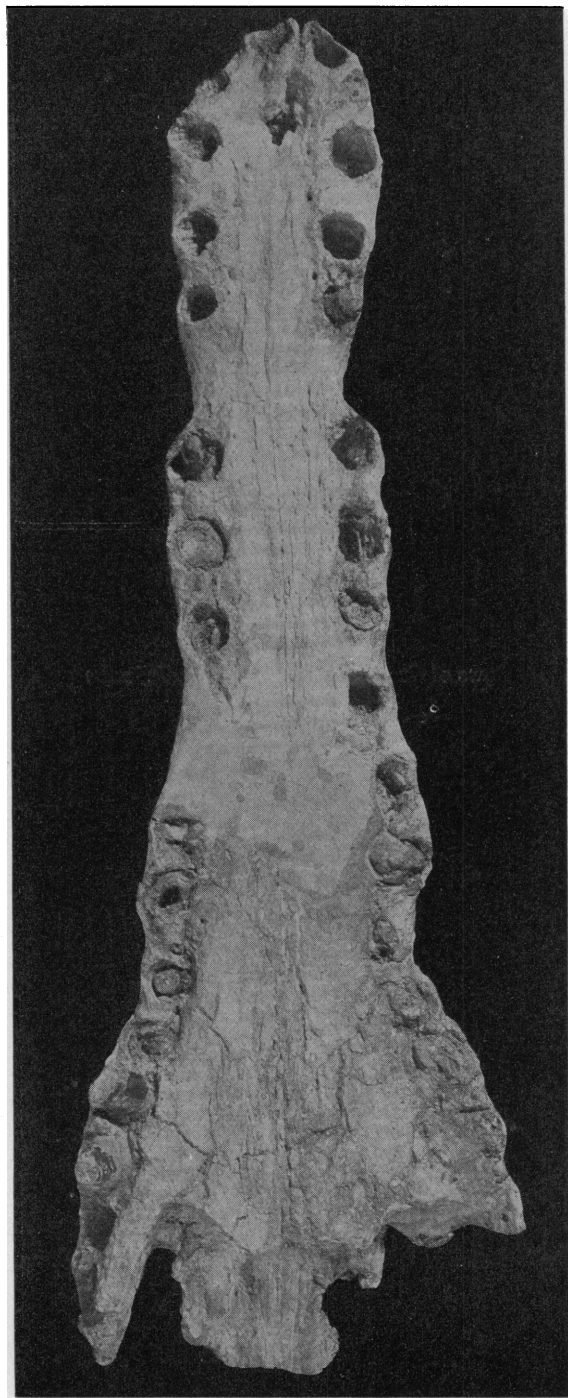


PLATE VIII

Jaws of *Gavialosuchus americana* (Sellards)

Amer. Mus. No. 5662

One-fourth natural size

Superior view

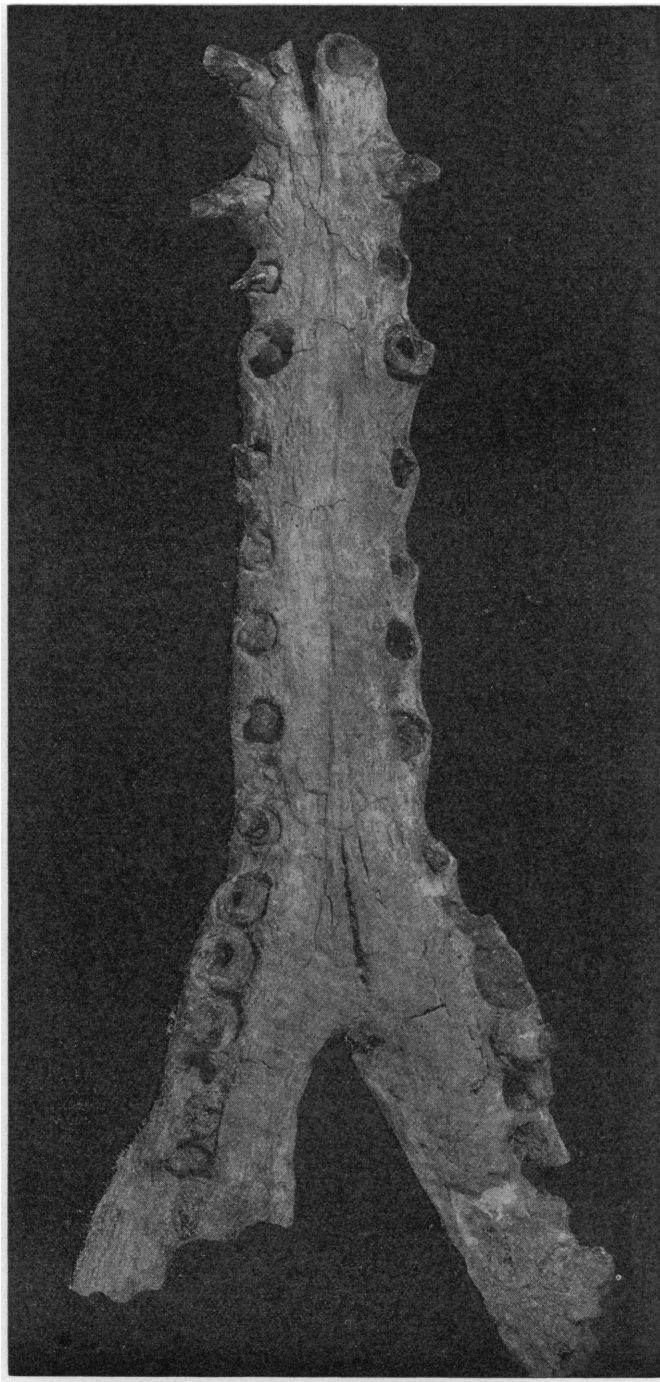


PLATE IX

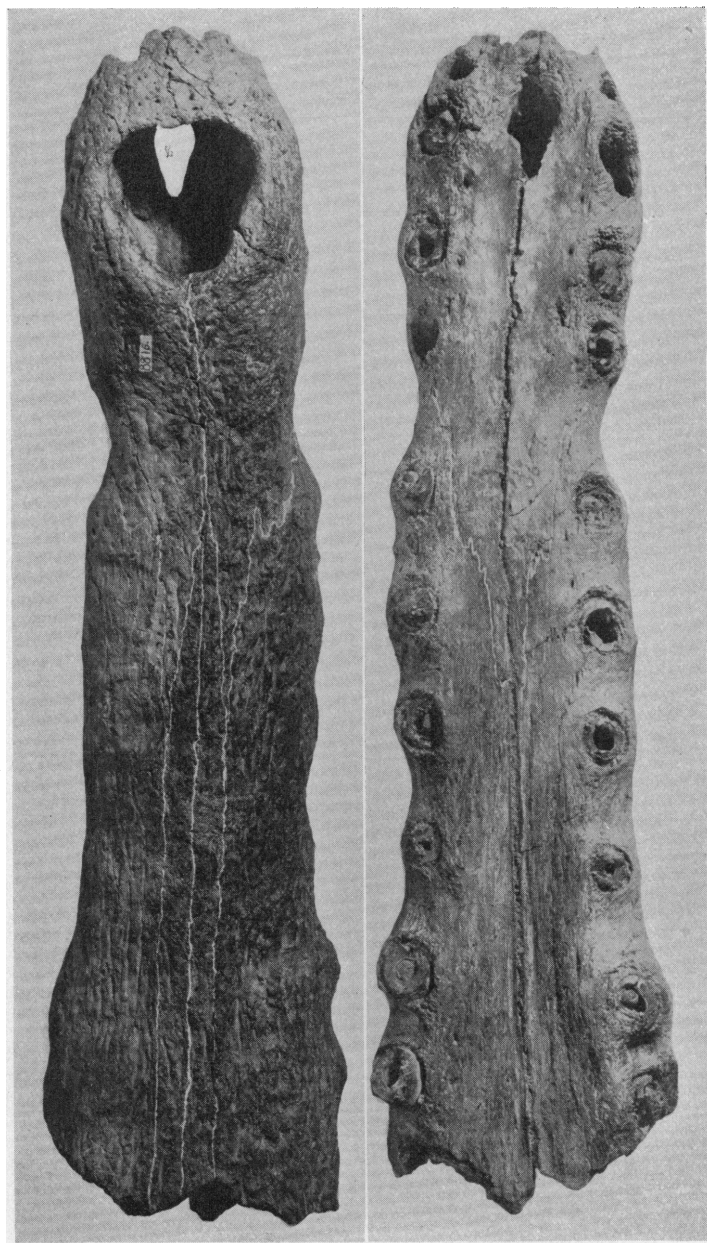
Snout of *Gavialosuchus americana* (Sellards)

U. S. Nat. Mus. No. 8816, type specimen

One-third natural size

A. Superior view

B. Inferior view



A

B

Florida Specimen	<i>Gavialosuchus eggenburgense</i>	<i>Tomistoma calaritanus</i>	<i>Tomistoma gavaloides</i>	<i>Tomistoma kerunense</i>	<i>Tomistoma schlegelii</i>
1. Skull relatively broad and flat.	Skull relatively broad and flat.	Skull of medium breadth and depth.	Skull long and narrow.	Skull long and narrow, of medium depth.
2. Snout very slightly expanded at end.	Snout very slightly expanded at end.	Snout very slightly expanded at end.	Snout expanded as in the gavial.	Snout very slightly expanded at the end.
3. Abrupt expansion of snout at first maxillary teeth.	Abrupt expansion at first maxillary teeth.	Very slight expansion at first maxillary teeth.	No abrupt expansion at first maxillary teeth.	No abrupt expansion at first maxillary teeth.
4. Snout has abrupt expansions farther back than first maxillary teeth.	None.	None.	None.	None.	None.
5. Nasals do not extend as far forward as the premaxillo-maxillary sutures on the sides of the snout.	The same.	Nasals extend farther forward.	Nasals do not extend as far forward.	Nasals come far short of forward extensions of premaxillo-maxillary sutures.
6. Nasals swell abruptly near their posterior ends.	The same.	Nasals expand regularly.	No lateral swelling of nasals.	Nasals swell considerably near posterior ends.
7. Anterior process of frontal broad.	The same.	Anterior process of frontal narrow.	Anterior process broad.	Anterior process narrow.
8. Orbits converge so that axes cross over anterior processes of frontals.	The same.	The same.	The same.	Orbits not so oblique: axes cross anterior to anterior processes of frontals.
9. Orbits elongate.	The same.	Orbits slightly elongate.	Orbits slightly elongate.	Orbits elongate.
10. Anterior process of frontal extends farther forward than the prefrontals.	The same.	The same.	The same.	Anterior process of frontal does not extend as far forward as prefrontals.
11. Supratemporal fenestræ very close together.	The same.	Supratemporal fenestræ rather close together.	Supratemporal fenestræ rather far apart.	Supratemporal fenestræ rather far apart.
12. Supratemporal fenestræ large, elongate, and oblique.	The same.	Supratemporal fenestræ small and round.	Supratemporal small and round.	Supratemporal fenestræ of medium size and nearly round.
13. Supraoccipital does not occupy space on skull-top.	Apparently the same.	Apparently the same.	Supraoccipital occupies a considerable space on skull-top.	Supraoccipital occupies a small area on skull-top.
14. Postorbitals very large, surface area exceeding that of squamosals.	Postorbitals not quite so large.	Postorbitals small.	Postorbitals evidently small.	Postorbital small.
15. Cranial table very broad.	Cranial table of medium size.	Cranial table small.	Cranial table broad.	Cranial table narrow.
16. Cranial table has parallel sides and angular anterior borders.	Cranial table has angular borders but sides converge anteriorly.	Sides and anterior border rounded.	Sides converge; anterior border angular.	Sides converge slightly, anterior border semi-angular.
17. Cranial table concave.	The same.	Cranial table flat.	Cranial table flat.	Cranial table slightly concave.
18. Premaxillo-maxillary suture on palate pointed, extends back to third maxillary teeth.	Premaxillo-maxillary suture W-shaped, extends back to point between first and second maxillary teeth.	Suture in form of a modified W, extends back to point between second and third maxillary teeth.	Suture pointed, extends back to point between second and third maxillary teeth.	Suture W-shaped, extends back to second maxillary teeth.
19. Five premaxillary teeth.	?	Five premaxillary teeth.	Four premaxillary teeth.	Four premaxillary teeth.
20. Fourteen maxillary teeth.	Fifteen maxillary teeth.	?	Fifteen maxillary teeth.	Sixteen maxillary teeth.
21. Teeth not on ridges with intervening depressions.	The same.	Teeth on elevations, with alternating depressions.	Teeth on elevation with alternating depressions.	Teeth on elevations with alternating depressions.
22. Teeth large.	Teeth large.	Teeth of medium size; curved.	Teeth small.	Teeth small.
23. Fifth maxillary teeth much larger than fourth.	Fifth maxillary teeth equal fourth in size.	Fifth maxillary teeth equal fourth in size.	Fifth maxillary teeth equal fourth in size.	Fifth maxillary teeth much larger than fourth.
24. Expansion of skull begins at fifth maxillary teeth.	At eighth maxillary teeth.	Near eighth maxillary teeth.	At fourteenth maxillary teeth.	At tenth maxillary teeth.
25. Maxillo-palatine suture elongate, extends forward to eighth maxillary teeth.	Elongate, extends forward to ninth maxillary teeth.	?	Apparently pointed and extending far forward.	Abruptly pointed, extends only a short distance forward.
26. Little or no excavation of premaxillary for reception of first mandibular teeth.	Apparently no excavation.	Slight excavation.	Deep excavation.	Deep excavation.
27. Probably 17 or 18 teeth in mandible.	?	15 plus.	19-20.	20.
28. Teeth of mandible large, widely spaced.	?	Teeth of medium size and rather widely spaced.	Teeth small and close together.	Teeth small and close together.
29. Symphysis extends back to twelfth teeth.	?	To about twelfth teeth.	To sixteenth teeth.	To fifteenth teeth.
30. Anterior end of splenial opposite eighth maxillary teeth.	?	Opposite eighth or ninth teeth.	Opposite sixteenth teeth.	To fifteenth teeth.

