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THE SKULL CHARACTERS OF *CROCODILUS MEGARHINUS* ANDREWS¹

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INTRODUCTORY REMARKS

The species *Crocodylus megarhinus* was based by Andrews, in 1905, upon an incomplete rostrum (Brit. Mus. No. R.3327).² This specimen, though incomplete, exhibits distinctive characters. The length of the expanded rostrum, anterior to the normal crocodylian constriction, is considerable in proportion to its breadth. Its breadth, however, is great, making this anterior process of relatively large size. The large external narial aperture is located entirely within this process of the rostrum, and does not extend backward beyond the level of the constriction as in *C. niloticus* and other species of the same general proportions. Andrews described this material more fully, and figured it in 1906.³ Recently more complete material has been described by L. Müller.⁴

In the American Museum Fayûm Collection of 1907 is a well-preserved skull, which is clearly referable to *Crocodylus megarhinus*. This skull (Amer. Mus. No. 5061) from the lower beds of the Fluvio-marine formation, of upper Eocene age, near Birket-el-Qurun, Fayûm, Egypt, is nearly perfect, and permits the description of many characters of the species which were not preserved in the type. The following description is based upon this skull and upon a large mandible which is probably referable to this species (Amer. Mus. 5095).

GENERAL FORM

In its general form the skull is relatively short, broad, and stoutly constricted, resembling somewhat the skull of *C. niloticus*. The proportion of the length of the snout anterior to the orbits, to its breadth at the level of the anterior ends of the orbits, is exactly the same as in *C. niloticus*. The snout occupies a somewhat greater proportion of the total length of the skull in the present species, however, than in *C. niloticus*, the preorbital region being shorter.

¹Contributions to the Osteology, Affinities, and Distribution of the Crocodylia, No. 18.

²Andrews, C. W., 1905, 'Notes on some New Crocodylia from the Eocene of Egypt,' Geol. Mag., N.S., II, Dec. 5, pp. 481-484 (482).

³Andrews, C. W., 1906, 'A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt,' Brit. Mus. Nat. Hist., pp. 264-266, text-fig. 85.

⁴Müller, Lorenz, 1927, 'Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens, V. Tertiäre Wirbeltiere, I. Beiträge zur Kenntnis der Krokodilier des ägyptischen Tertiärs,' Abhandl. d. Bayerischen Akad. d. Wissensch. Matem.-naturw. Abt., XXXI, 2 Abh. pp. 1-96, 3 pls. (pp. 59-66, 81, p. 2, figs. 5a, 5b, 5c, 5d).

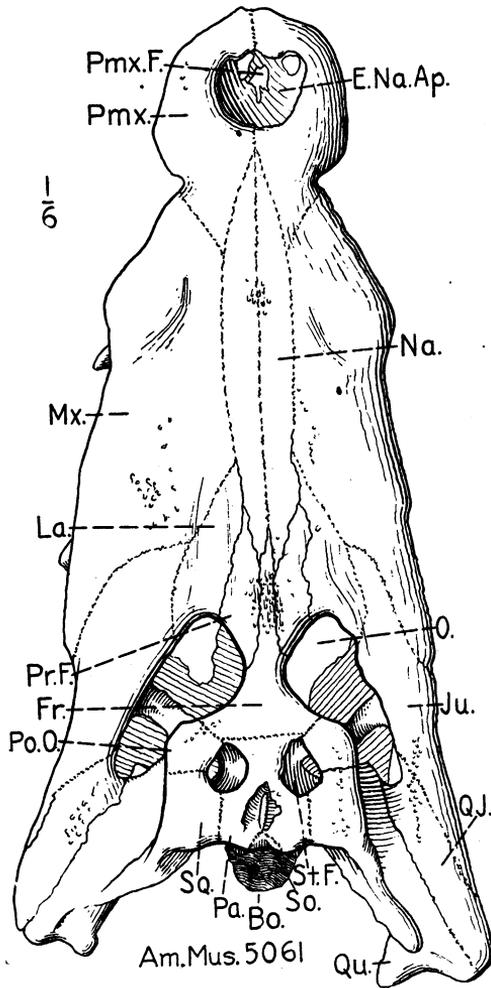


Fig. 1. *Crocodilus megarhinus* Andrews. Skull (Amer. Mus. 5061). Fluvio-marine Beds of Upper Eocene age, near Birket-el-Qurun, Fayûm, Egypt. One-sixth natural size.

Superior view. Bo., basioccipital; E. Na. Ap., external narial aperture; Fr., frontal; Ju., jugal; La., lacrymal; Mx., maxillary; Na., nasal; O., orbit; Pa., parietal; Pmx., premaxillary; Pmx. F., premaxillary foramen; Po. O., Postorbital; Pr. E., prefrontal; QJ., quadratojugal; Qu., quadrate; So., supraoccipital; Sq., squamosal; St. F., supratemporal fenestra.

The cranial table is small. A comparison of its measurements in any direction shows it to be considerably smaller in proportion to other dimensions of the skull than in *C. niloticus*. The lateral borders converge more sharply forward than do those in the latter species.

The festooning of the lateral border of the skull, viewed from the side, is considerable, but its extent cannot be determined accurately, owing to a certain amount of distortion in the specimen.

The constriction at the premaxillo-maxillary suture is not great; the snout expands very rapidly back to the level of the fifth maxillary teeth; there is a slight constriction at the level of the seventh maxillary teeth, followed by an expansion to the level of the ninth maxillary teeth, back of which the borders remain parallel.

THE CAVITIES OF THE SKULL

EXTERNAL NARIAL APERTURE.—The position of this opening has already been noted. In outline it is quite distinct from either *C. americanus*, *C. niloticus*, or *C. porosus*. It is broadest at its anterior end. The gently rounded anterior border is interrupted by processes of the premaxillaries which extend backward at the median line. The lateral borders are nearly straight. They converge sharply backward. The posterior border is broadly rounded.

ORBITS.—These cavities are relatively large, especially in the lateral dimension. Their external borders are nearly straight; their posterior, anterior, and internal borders form continuous curves. The general outlines of the orbits correspond rather closely with those of *C. niloticus*. The internal borders are not upturned, as in *C. porosus*. The space between the orbits is flat, and is relatively narrow; it is not deeply pitted in comparison with the rest of the skull.

SUPRATEMPORAL FENESTRÆ.—These fenestræ are rather small and are irregular in shape. Their axes of maximum length converge sharply forward. The median area of the cranial table separating the two fenestræ is narrow.

INFRATEMPORAL FENESTRÆ.—These cavities are not distinctive, and require no special description.

PREMAXILLARY FORAMEN.—The premaxillary foramen is characteristic in outline. Its form is that of an isosceles triangle in which the parallel sides are approximately twice the length of the base. A small posterior extension of the foramen is due to splitting of the specimen along the palatal median premaxillary suture before mineralization of the specimen.

PALATINE FENESTRÆ.—These cavities are irregular in shape. They resemble the corresponding fenestræ of *C. niloticus* more closely than those of any other living species of *Crocodylus*, but differ from them in details. They extend as far forward as the level of the anterior borders of the ninth maxillary teeth. Their external borders are slightly irregular, but in a broad way converge slightly backward. At a point about three-fourths of the total length backward they converge more sharply backward, as far as the junction of the ectopterygoid-pterygoid suture with the fenestral border. Posterior to this point the border again turns more nearly directly backward to the end of the fenestra.

The internal borders curve with only slight irregularities as far back as the junctures of the palatine-pterygoid sutures with the fenestral borders. From these points they extend almost directly backward to the posterior ends of the fenestræ. This portion of the skull shows the effects of crushing, consequently the two sides are not exactly alike.

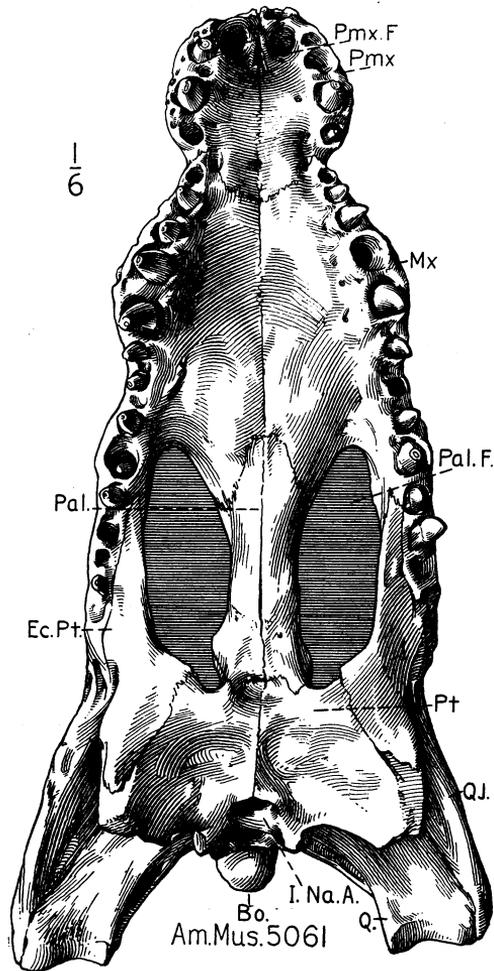


Fig. 2. *Crocodilus megarhinus* Andrews. Skull (Amer. Mus. 5061). Fluvio-marine Beds of Upper Eocene age; near Birket-el-Qurun, Fayûm, Egypt. One-sixth natural size. Inferior view.

B., basioccipital; Ec. Pt., ectopterygoid; I. Na. A., internal narial aperture; Mx., maxillary; Pal., palatine; Pal. F., palatine fenestra; Pmx., premaxillary; Pmx. F., premaxillary foramen; Pt., pterygoid; Q., quadrate; QJ., quadratojugal.

The anterior and posterior ends are abruptly rounded.

The length of the fenestræ in proportion to the length of the skull from premaxillaries to condyle is greater than in any living crocodilian, but resembles various other early Tertiary forms and the Pleistocene *C. robustus* Vaillant and Grandidier, from Madagascar.

INTERNAL NARIAL APERTURE.—This cavity is not especially distinctive. It faces obliquely downward and backward, as in most living crocodiles. It is rounded triangular in outline, and its antero-posterior diameter is about seven tenths of its transverse diameter.

THE BONES OF THE SKULL

PREMAXILLARY.—The premaxillary bones are short and broad. Their anterior portions, between the nares and the anterior border, is moderately broad. It is not so broad, relatively, as in *C. americanus* or *C. niloticus*, but is much broader than in long-snouted crocodiles such as *C. cataphratus*. Perforations which lodged mandibular teeth are present in the floor of the nasal aperture anterior to the premaxillary foramen. The maximum breadth of the snout across the two premaxillaries is at the level of the posterior border of the aperture, not opposite its centre as in most crocodiles. The posterior processes of the premaxillaries which wedge between the nasals and maxillaries, are short and blunt.

On the palatal surface the premaxillaries each contain alveoli for five teeth. The first alveoli, of moderate size, are close together. On each side the first is widely separated from the second, which is small. The second is close to the third, which is large. A moderate space separates the third from the very large fourth. The small fifth is placed rather distant from the fourth, but not as distant as the first is from the second. The constriction at the side of the snout which received the fourth mandibular teeth is pronounced.

On the palate the premaxillo-maxillary suture extends forward and inward, on each side, for about twenty-two millimeters, then curves backward and inward to meet its fellow at the median line at about the level of the second maxillary teeth. The curve on each side roughly approximates a quarter circle.

The palatal length of the premaxillaries is slightly greater than their breadth.

MAXILLARIES.—These bones are relatively broad, even for a short-snouted crocodile. They occupy fully seventy-five per cent of the total breadth of the snout. The maxillo-nasal suture is unusually short.

On the palate the boundary with the premaxillaries has been described. The length along the median line is only about eighty per cent of its maximum breadth. Each maxillary occupies slightly less than one-third of the external border. The suture with the palatines extends obliquely forward and inward from the inner border of the palatine fenestra to a point on a level with the space between the eighth and ninth maxillary teeth, and about nine millimeters from the median line, thence transversely across the median line to a corresponding point on the opposite side, and obliquely backward and outward to the opposite palatine fenestra.

Each maxillary contains alveoli for thirteen teeth, many of which are preserved. The fifth teeth are, of course, the largest, but the fourth nearly equal them in size. Throughout the whole dental series the teeth are stout. Only the extreme posterior teeth are small, and they are only moderately so. All of the teeth, even at the posterior

end of the series, are lodged in distinct alveoli. The teeth are all spaced from each other, although somewhat irregularly; none of the teeth are closely appressed, as in some crocodylians.

NASALS.—The exact outlines of the nasal bones are somewhat uncertain, although enough of the sutures can be distinguished to make the main outlines reasonably certain.

The nasals do not enter the narial aperture at the surface, although it is possible that they may do so in depth. They expand regularly to the level of their maximum breadth, which is only slightly posterior to the inner ends of the premaxillo-maxillary sutures. They retain this breadth for some distance, and are only slightly narrower at their contacts with the jugals. From this point backward they narrow irregularly to the level of the eleventh maxillary teeth, where they are wedged apart by the anterior process of the frontal. At their maximum breadth they occupy about one-fourth of the total breadth of the skull.

The contacts of the nasals with the jugals and lacrymals are about equal in length, and are very short. The sutures with the prefrontals are slightly longer, and are very irregular.

LACRYMALS.—The lacrymals are long and slender. Their longest contacts are with the jugals, but the contacts with the prefrontals are nearly as long. The nasal border is short, and the orbital border is even shorter on one side.

PREFRONTALS.—These are irregularly wedge-shaped bones. Their longest contacts are those with the lacrymals. The borders with the frontal are also long, while the nasal and orbital borders are of moderate length. The prefrontals are narrow at their anterior ends, where they wedge between the nasals and lacrymals, and are broad at their posterior ends, where they form part of the orbital borders.

FRONTAL.—The frontal is of moderate size only. Its posterior portion, or inter-orbital plate, is flat and not excavated or elevated as in many crocodylians. This may be partly due to crushing of the specimen. This posterior plate of the bone is considerably shorter than the narrow anterior wedge which separates the opposite prefrontals and nasals.

POSTORBITALS.—These bones are, relatively, considerably smaller than the squamosals, occupying about one-half the area of the latter. Their orbital borders are very small, but their external edges constitute fully one-third on the lateral border of the cranial table. In shape they are very irregular.

SQUAMOSALS.—The squamosal bones are relatively large. They are nearly rectangular in outline at the surface. They occupy about two-thirds of the lateral borders of the cranial table, and about half of its posterior border.

PARIETAL.—This is moderately large, slightly exceeding in its dimensions the parietal of a skull of *C. porosus* of similar size. It occupies about one-third of the posterior border of the cranial table.

On the posterior portion of the superior surface, immediately anterior to the dorsal plate of the supraoccipital, is a small depression that is crossed longitudinally by a low ridge. This is a modification of the sculptured pitting of the rough bone surface, but is quite distinct from anything seen in other crocodylians.

SUPRAOCCIPITAL.—This bone is large. It occupies about three-fourths of the distance from the posterior border of the cranial table to the foramen magnum on the posterior surface of the skull, and about one-sixth of the posterior border of the cranial table. The dorsal plate of the bone, which is part of the cranial table, is moderately

large, and is distinctly triangular in outline. The expansion of the bone on the posterior surface of the skull is considerable, the supraoccipital at this point being about three-fifths as wide as the cranial table.

JUGALS.—The jugal bones are somewhat distorted by crushing, and their characters are somewhat obscured. It is clear, however, that they were unusually slender, especially at their posterior ends.

QUADRATOJUGALS.—These bones are not especially distinctive, except that they occupy somewhat less than the usual proportion of the posterior border of the infratemporal fenestra. The sharp process, extending forward into the fenestra, which is characteristic of *Crocodylus* and *Tomistoma*, is missing on both sides of this specimen. The edge of the bone is broken at this point on both sides, however, and the process may have been present originally.

QUADRATES.—The quadrates are not especially characteristic except in the fact that they occupy somewhat more of the border of the infratemporal fenestra than is usual.

PALATINES.—The suture of the palatines with the maxillaries has already been described. The two palatines expand somewhat near their posterior ends. They are excluded from the posterior portions of the internal borders of the palatine fenestræ by narrow processes of the pterygoid, which overlap them at these points.

PTERYGOIDS.—The pterygoids occupy appreciable portions of the borders of the palatine fenestræ, external and internal, as well as posterior. The sutures with the ectopterygoids converge sharply forward.

ECTOPTYRGOIDS.—The anterior bar of each ectopterygoid extends forward to the level of the tenth maxillary teeth. The posterior bar extends quite far backward over the pterygoid.

THE MANDIBLE

The characters of the mandible are taken from another specimen (Amer. Mus. No. 5095). This jaw was not found in association with a skull, but its proportions render its reference to *C. megarhinus* practically certain.

The mandible is moderately short and broad. Its maximum breadth is between fifty and fifty-one per cent of its length. The degree of festooning of the border is relatively slight.

The symphysis is moderately long. It extends back to the level of the anterior edges of the seventh teeth. In this character it resembles the symphysis of *C. articeps* Andrews, from the same beds. The relation of the splenial bones to the symphysis is not quite clear, but apparently they did not quite meet each other at the symphysis.

The vertical diameter of the jaw is small, especially in the anterior portion. Both the external and the internal mandibular foramina are small.

The usual number of fifteen alveoli are present in the right ramus. The left ramus is incomplete; thirteen alveoli are visible in it, and probably it originally contained two more. The fourth alveoli are decidedly the largest, the tenth alveoli are second in size, and the first alveoli are third in size. The first alveoli face obliquely forward and upward. The third, fourth, and fifth alveoli are close together; the eighth and ninth are far apart; the remainder are more or less evenly spaced.

A few of the actual teeth are preserved. These are all stout and strong, with moderately sharp anterior and posterior edges. The points of the crowns tend to turn

slightly inward. The posterior teeth are as large as most of those in the anterior part of the jaw. The length of the right ramus posterior to the last alveolus is 93 per cent of the length of the alveolar series. The degree of relative shortness of the dental series does not reach the extreme condition observed in *C. porosus*. (Amer. Mus. No. 15179) in which the alveolar border is actually shorter than the postalveolar portion of the jaw.

MEASUREMENTS

Length of skull, occipital condyle to premaxillaries	688 mm.
Breadth across quadrato-jugals	340
“ “ anterior ends of orbits	286
“ “ fifth maxillary teeth	237
“ “ constriction	108
“ “ premaxillaries	152
Length, snout	495
Length external narial aperture	56
Breadth, external narial aperture	66
Length, right orbit	90
Breadth, right orbit	56
Length, right supratemporal fenestra	60
Breadth, right supratemporal fenestra	57
Breadth, interorbital plate	35
Breadth, interfenestral plate	17
Length of cranial table along right border	114
Breadth across anterior end of cranial table	142
Breadth across pterygoids	262
Median length of mandible	800
Length of right ramus of mandible	818
Breadth across condyles	345
Breadth, maximum	401
Breadth, symphysis	150
Length, symphysis	162
Length, tooth-row, right	425

REMARKS

In its proportions and its dental characters the skull of *Crocodylus megarhinus* resembles that of *C. niloticus*. It is not so short or massive as the living *C. palustris* or *C. porosus* of India, and it is shorter than long-snouted species such as *C. americanus*. In some characters it resembles *Osteolemus tetraspis* of Africa, but in these same characters it resembles some of the Eocene crocodylians of North America and Europe. It is slightly shorter in the snout than in *C. niloticus*, but in most characters it agrees very closely with that species. This is true to such a degree that ancestral relationship appears probable. It is very probable that *C. megarhinus* is a direct ancestor of *C. niloticus*.