SEBECUS, REPRESENTATIVE OF A PECULIAR SUBORDER OF FOSSIL CROCODILIA FROM PATAGONIA

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INTRODUCTION

In 1937 Dr. George Gaylord Simpson described very briefly a remarkable crocodilian from the Eocene of Patagonia, which he named *Sebecus icaeorhinus*. The original description by Simpson, which was published without illustrations, was based upon a disarticulated skull and mandible that had been found by himself and Mr. Coleman S. Williams in Patagonia during the course of the First Scarritt Expedition of the American Museum of Natural History. The specimen, together with some supplementary materials from the same horizon, constitutes one of the principal discoveries of the Scarritt Expeditions, made possible by the generosity of Mr. Horace S. Scarritt.

The bones of the skull and mandible were prepared by Mr. Albert Thomson, formerly chief preparator in the Paleontological Laboratory at the American Museum of Natural History. From the disarticulated bones, Mr. Thomson reconstructed the skull and mandible; this reconstruction was cast in plaster by Mr. Otto Falkenbach, also of the American Museum Paleontological Laboratory, and the plaster cast was then tinted, to show the areas represented by fossil bone as well as those reconstructed. A dorsal view of this cast was published by Brown and Schlaikjer in 1940 (pl. 4) and to date this is the only illustration of *Sebecus* in the literature.

It had been Dr. Simpson's intention to prepare a detailed monograph of this most important form, and indeed some preliminary pages of this monograph were written. Owing to the pressure of other matters, however, he was unable to proceed with the study, and consequently at the time of his entry into the Army of the United States he turned over his notes to me, with the request that I prepare the manuscript for publication. This I have done, but not without considerable delay, occasioned by an increase of curatorial duties and prior interests in certain other research problems. Recently, however, it has been possible to take up the study and to carry it through to completion.

Mr. John C. Germann of the Department of Geology and Paleontology at the American Museum of Natural History had prepared a series of drawings under Dr. Simpson's direction to illustrate the separate bones of the skull and jaw in *Sebecus*. These, together with additional drawings by Mr. Germann, constitute the figures published in this paper.

I wish at this place to express my great appreciation to Dr. Simpson for his generosity in turning over to me this study and for his kind permission to make free use of his notes, illustrations, and preliminary pages of manuscript in the preparation of this paper.

THE OCCURRENCE OF *SEBECUS ICAEORHINUS*

DR. SIMPSON HAS PREPARED the following statement with regard to the occurrence of the materials under consideration in the present paper:

"All the known specimens are from the Casamayor formation, probably of Lower Eocene age, of the Territory of Chubut (central Patagonia) in the Argentine Republic. The principal specimen, A.M.N.H. No. 3160, was found in Cañadón Hondo, which is a roughly circular drainage basin, without permanent water, tributary to the southeast or right side of the Río Chico del Chubut immediately above the crossing usually called Paso Niemann. The exact locality is not far from the middle of the southeast rim of the basin, the part farthest from the Río Chico, on the floor of the very irregular depression but near its highest part. Here the channel of a small intermittent stream had, at the time of our work, cut a nearly vertical bank about 5 feet high in a series of very pure, clear green bentonites interbedded with nearly white layers of more ashy bentonite. This small exposure, which might well be obliterated by a swing in the erosion channel, was discovered by Ingeniero A. Piatnitzky, of the Argentine Federal Petroleum Administration (Yacimientos Petrolíferos Fiscales), and indicated to us by his colleague Dr. Egidio Feruglio.

"In the green bentonites there were numerous bones of some medium-sized flying bird,[1] also the type material of the meiolaniid turtle *Crossochelys corniger* (see Simpson, 1937a, 1938), fragments of other unidentifiable turtles, a new amphibian resembling *Ceratophrys*, and a single mammal jaw, type of *Coöna pattersoni*. The type of *Sebecus icaeorhinus* was scattered through the matrix with these other highly varied remains.

"All the identifiable specimens from this small fossil pocket represent hitherto unknown forms and with the exception of *Sebecus* itself, as noted below, none of the associated species has ever been found at any other locality. The internal evidence as to age is extremely vague. The faunule on its own evidence might belong almost anywhere in the later Mesozoic or the Tertiary. In Cañadón Hondo, however, were found mammals of the *Notostylops* fauna, characteristic of the Casamayor formation, at horizons apparently both above and below that of *Sebecus*. The exact succession of strata is here very confused, since the exposures are discontinuous and are folded and faulted, but it seems highly probable that this green bentonite is a peculiar local facies of the Casamayor formation. This is confirmed by the occurrence of *Sebecus* at other surely Casamayor localities.

"The principal referred specimen of *Sebecus*, A.M.N.H. No. 3159, was found in Cañadón Vaca, as is Cañadón Hondo, tributary to the Río Chico and also just above Paso Niemann, but on the other, the northwest, side of the Río Chico Valley. The exact locality is in an embayment known locally and in our field notes as the Oficina del Diablo, on the northeast wall of Cañadón Vaca, which here is a scarp bounding the Pampa Pelada, near the upper end of the Cañadón. The specimen was entirely weathered out, but the conditions of erosion were such that it could only have come from beds in which a rich, unified, and typical *Notostylops* fauna occurs. It is hence certainly of Casamayor age.

"Several isolated teeth almost surely of *Sebecus* have been found, and always in sure or probable association with Casamayor guide fossils. At least one tooth in the Ameghino Collection (No. 10872 in the Museo Nacional de Historia Natural of Buenos Aires) appears to belong to *Sebecus*. It is recorded as from *Notostylops* (i.e., Casamayor) beds west of the Río Chico, probably in the vicinity of Cañadón Vaca. We also have a single tooth, probably of this genus, A.M.N.H. No. 3162, found in place in the Casamayor of Cañadón Vaca."

[1] These are now in the hands of Dr. Alexander Wetmore for description.

TAXONOMY

Order CROCODILIA

Suborder SEBECOSUCHIA Simpson, 1937

Diagnosis: Basically crocodilian in cranial structure and with secondary palate. Internal nares very wide. Whole skull, and expecially the facial part, relatively much narrower and deeper than in other Crocodilia; snout very deep and with median crest above. Orbits directed laterally. Teeth reduced in number and generally strongly compressed laterally, with serrated edges, the larger teeth with crowns almost indistinguishable from those of some carnivorous dinosaurs. Vertebrae feebly amphicoelous.

Family SEBECIDAE Simpson, 1937

Type: *Sebecus.*

Distribution: As for the genus.

Diagnosis: Skull compressed and deep, especially in the facial region. Internal nares anteriorly placed, the front border being formed by the palatines, the back border by the pterygoids; palatine tube incipient. Well-developed quadratojugal-surangular articulation; quadrate inclined. Supratemporal fenestra rather small, broader than long. Four teeth in the premaxilla, 10 in the maxilla, and 13 in the dentary, none of which are greatly differentiated as to size. The premaxillary and anterior dentary teeth are rounded in cross section, while the other teeth are laterally compressed, with well-developed serrations on the anterior and posterior cutting edges. There is a shallow notch along the premaxillary-maxillary suture for the reception of the fourth dentary tooth.

Genus SEBECUS[1] Simpson, 1937

Type: *Sebecus icaeorhinus.*

Distribution: Casamayor formation, Eocene, Patagonia.

Diagnosis: Sole known genus of Sebecidae. Therefore at the present time generic and specific diagnoses cannot be distinguished from the family diagnosis.

Sebecus icaeorhinus[2] Simpson, 1937

Type: A.M.N.H. No. 3160, most of the bones of the skull and jaw, as listed below. Collected by Coleman S. Williams and G. G. Simpson, March 7, 1931, in Cañadón Hondo, Chubut.

Principal Referred Specimen: A.M.N.H. No. 3159, numerous skull and skeletal fragments, as listed below. Collected by G. G. Simpson, January 3, 1931, in Cañadón Vaca, Chubut.

A.M.N.H. Nos. 3160 and 3159 differ in size and in various minor details, and it cannot be absolutely established that the referred specimen is of the same species as the type, but this is very probable and there is no proper basis for specific separation.

Horizon: Casamayor formation, Eocene.

Localities: Cañadón Hondo and Cañadón Vaca, tributaries to the Río Chico del Chubut, Chubut, Patagonia, Argentina.

Diagnosis: Sole known species of *Sebecus.*

Family BAURUSUCHIDAE Price, 1945[3]

Type: *Baurusuchus.*

Distribution: As for the genus.

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[1] Egyptian *sbk*, or *sebek*, the crocodile god, arbitrarily Latinized. The usual hieroglyphic writing of the Egyptian word for crocodile appears to have been *mswk* or *emsuh*, according to one of several arbitrary methods of making the vowelless hieroglyphs pronounceable. The use here of the word *sebek*, for the crocodile god, is introduced to vary the general practice of using the word Champsa in the nomenclature of fossil reptiles of crocodilian relationships or crocodilian appearance. Χάμψαι is not a Greek word but was given by Herodotus ("History," Book II) as the Egyptian word for the crocodile. According to the same authority, κροκόδειλος, whence comes the word for crocodile in most modern languages, properly meant lizard. The crocodile was called ὁ κροκόδειλος ὁ ποτάμιος, "river lizard," and eventually the qualifier "river" was dropped. It is an interesting parallelism in languages that the word "alligator" also originally meant only "the lizard," *el lagarto.*

[2] Εἰκαῖος, random, not according to plan, and ῥινός, snout, in allusion to the remarkable departure of this animal's snout from the crocodilian plan.

[3] After the manuscript of the present paper had been completed and was ready for press, the author received from Mr. L. I. Price of the Divisão de Geologia e Mineralogia, Ministério da Agricultura, Rio de Janeiro, Brazil, a paper describing a new and remarkable crocodilian obviously related to *Sebecus.* This new crocodilian, considered as representative of a separate family of the Sebecosuchia, is inserted here and is discussed briefly on a subsequent page of the present contribution. How-

DIAGNOSIS: Skull compressed and deep, especially in the facial region. Internal nares posteriorly placed, bounded in front and in back by the pterygoids and laterally by the expanded ectopterygoids. Well-developed palatine tube. Quadrate vertical. Supratemporal fenestra large and longer than it is broad. Teeth greatly reduced as to number, very strongly differentiated as to size, and laterally compressed. Three teeth in the premaxilla, and in the anterior part of the maxilla two large "caniniform" teeth. A "caniniform" tooth in the dentary for the reception of which there is a very deep notch in the anterior part of the maxilla.

ever, it was considered inadvisable to attempt detailed comparisons between the new genus described by Price and *Sebecus*, especially since Price's paper is a preliminary note in which many of the anatomical details of the new form are omitted. We will look forward with pleasure to the appearance of Mr. Price's larger study, which is promised at some future date.

GENUS **BAURUSUCHUS** PRICE, 1945

TYPE: *Baurusuchus pachecoi.*

DISTRIBUTION: Baurú formation, Cretaceous, São Paulo, Brazil.

DIAGNOSIS: Sole known genus of Baurusuchidae. Therefore at the present time generic and specific diagnoses cannot be distinguished from the family diagnosis.

Baurusuchus pachecoi Price, 1945

TYPE: D.G.M. [Divisão de Geologia e Mineralogia] No. 299 R. A skull and mandible with the left side partially destroyed by erosion.

HORIZON: Baurú formation, Upper Cretaceous.

LOCALITY: "Twelve leagues (approximately 72 km) Southwest of Vila de Veadinho, municipia of Paulo de Faria, State of Sao Paulo." Brazil.

DIAGNOSIS: Sole known species of *Baurusuchus.*

MORPHOLOGY

MATERIAL

ASIDE FROM ISOLATED TEETH, adding no morphological data, the material of *Sebecus* available consists of the two specimens already mentioned. In more detail, these include the following parts:

A.M.N.H. No. 3160: Left premaxilla, right and left maxillae, right and left nasals, right and left frontals, right and left parietals, right and left lacrimals, right and left prefrontals, left jugal, left squamosal, left quadratojugal, right and left palatines, right and left ectopterygoids, left quadrate, left exoccipital, left postoptic, basisphenoid, right and left palpebrals, right and left dentaries, left angular, left surangular, and right articular. Some of these are incomplete (see figures) but they are for the most part well preserved.

A.M.N.H. No. 3159: Left maxilla, left nasal, left frontal, right and left prefrontals, right and left jugals, left ectopterygoid, right and left quadrates, left quadratojugal, left squamosal, right surangular—all of these are incomplete and most of them are mere fragments but so characteristic that they leave no doubt that the genus and probably the species are the same as the type. The following parts present in this specimen are not entirely duplicated in the type: parts of both sides probably of fused pterygoids; the lower part of the occiput with the basioccipital, essentially complete; part of the supraoccipital; one vertebral centrum; most of the right femur; distal end of the right fibula. In addition, there are various fragments, too incomplete for identification.

The material included under No. 3159 was all weathered out and scattered over a small area, with a small amount of extraneous washed material. It is thus not certain that this is a single individual or even that it all belongs to the same species, but it is highly probable. The material considered extraneous is obviously so. There is no material probably of another crocodilian, or reptile. The various fragments duplicated in No. 3160 are all clearly of the same genus as the latter and are all from a somewhat smaller individual. All the fragments are of such size and character as to belong to one animal, and there is no duplication. No. 3160 was also disarticulated and scattered, although *in situ*, but certainly represents a single animal, from the perfect articulation and harmony of the various parts.

The skull is thus almost completely known. The only elements that were present in the living animal but that are not known in the fossils are the postorbital, prevomer, and prootic. From imperfections of the preserved bones the exact configuration of the external nares and of the pterygoid region remains doubtful. In the lower jaw the coronoid and splenial are lacking, leaving doubts as to part of the region near the internal mandibular foramen, but otherwise the mandible, too, is well known. Very little is yet known of the postcranial skeleton, but that little is of some value, especially revealing the nature of a typical vertebra and the essentially crocodilian modification of the hind limb.

Nothing definitely recognizable as a postcranial dermal scute was found with either specimen. In view, however, of the scarcity of postcranial material in general, this negative fact has little value for inference.

These cranial and mandibular elements were mostly disarticulated as found, and the disarticulation has been completed and retained except for the most posterior elements, occiput, squamosal, and quadrate. The separate bones are thus remarkably adapted for study. In order to have a representation of the skull as a whole, each separate part of No. 3160 was cast in plaster, as mentioned above, and a set of these casts was incorporated in a plaster reconstruction of the articulated skull and of the mandible. The bones are little crushed, especially when the fragile nature of some of them and the usually destructive effect of a bentonite matrix are considered, but there is some slight distortion that has demanded correction and compromise in the reconstruction so that it doubtless differs in certain small details from a fresh skull of the species. However, the differences cannot be great except, perhaps, for the external nares and pterygoids.

THE SKULL

General Remarks

One is impressed when first viewing the skull of *Sebecus* by its lack of similarity to the typical crocodilian skull, for this skull, narrow and deep, with strongly compressed teeth, appears in a superficial view to have little in common with the flattened skull so characteristic of the Crocodilia. Yet a careful examination of the skull in *Sebecus* will show that it is crocodilian through and through, and although there are many important anatomical differences that separate it from the skulls of any other known crocodilians, much of its strange appearance is due to the differences in proportions between it and other crocodilian skulls.

In discussing the skull and mandible of this genus, I propose to take up each element separately, and after all of the known bones have been described and compared in this manner, to treat the skull and jaw as a whole. Thus the details will be presented first, after which a synthesis of the whole will be attempted, and comparisons of the structure in its entirety will be made with other forms.

Bones of the Skull

Sculpturing of Bony Surfaces: In *Sebecus*, as in most of the other members of the Crocodilia, the bones on the surface of the skull are heavily sculptured. This character, common to the order, is to be expected, even in an animal seemingly so aberrant as *Sebecus*, and needs no particular comment at this place. Mention might be made, however, of the form of the bony rugosities in *Sebecus*, for in this genus the surfaces of the bones are irregularly broken up by the sculpturing, as is the case in the more primitive crocodilians such as the mesosuchians. There is in *Sebecus* none of the rather regular reticulated pattern of ridges and pits that is seen particularly on the skull roof but frequently over the entire surface in the eusuchian skull. In this respect *Sebecus* retains a primitive character.

Premaxilla: The premaxilla is a rather short bone that carries the alveoli for four teeth. Of these, the two middle teeth would appear to have been somewhat larger than the anteriormost or the posterior tooth. In palatal aspect, there are to be seen two pits in the premaxilla, one placed internally to the front edge of the alveolus for the enlarged third tooth, the other just inside the alveolus for the fourth tooth. These pits were for the reception of the points of the second and third dentary teeth. A groove extending from the inner side of the premaxilla, between the alveoli of the first and second teeth and around onto the external surface of the bone indicates that the first dentary tooth bit upward between the first and second premaxillary teeth. Evidently the two first premaxillary teeth were very close to each other.

The premaxillary aperture, or foramen incisivum, was a narrow, elongated opening, extending from just behind the first premaxillary tooth to a point opposite the middle of the third tooth.

Immediately behind the last premaxillary tooth and in front of the suture between this bone and the maxilla there is a vertical groove or notch for the accommodation of the enlarged fourth dentary tooth during the closure of the jaws, a character whereby this genus resembles the Crocodilidae among the Eusuchia. Unfortunately the upper portion of the premaxilla is not present in the materials at hand, but it would seem that the external nares were rather large, probably with their rims raised or flared to some extent. Only a small portion of the edge of the left naris is preserved. Whether or not the basal bones extended forward to form a median bridge dividing the nares is a point that cannot be settled upon the basis of the evidence at hand.

Maxilla: The maxilla in *Sebecus* is noteworthy, above all, by reason of its great depth. Here we see a character whereby this bone shows great contrast to the maxilla of other crocodilians, and gives to the skull of *Sebecus* much of its distinctive appearance. The outer surface of the maxilla in this crocodilian is essentially vertical, and because of its height the top of the muzzle, in its posterior region, is virtually on a level with the frontal region, a condition contrasting with that in the typical crocodilians, in which the external surface of the maxilla is largely horizontal and there is a decided drop in level from the frontal and interorbital region to the muzzle. In its posterior portion the maxilla in *Sebecus* is about twice the depth that it is anteriorly, and this naturally causes the muzzle to slope down from the preorbital to the nasal region. As a result of the deep muzzle in *Sebecus* the narial passage is very deep and narrow, whereas in the Eusuchia, for instance, it is broad and shallow.

There are some interesting points to be brought out in connection with the alveolar border in the maxilla of *Sebecus* whereby this crocodilian may again be contrasted with other members of the order. In the first place there are but 10 teeth in the maxilla of this genus, a low number as compared with most other crocodilians, either fossil or recent. Moreover, of these teeth, as shown by such teeth as are preserved (particularly in the left maxilla) and by the alveoli, the last six are of almost the same size. Subequal maxillary teeth are common in the long-snouted crocodilians of the suborders Mesosuchia and Eusuchia, but in those genera where no elongation of the tooth carrying elements has taken place, there is a tendency for a strong differentiation in size among the maxillary and dentary teeth. Of the first four maxillary teeth in *Sebecus*, the first two are definitely smaller than the more posterior teeth, while the third and fourth teeth in the series are noticeably larger than the teeth behind them. However, the difference between these enlarged teeth and the teeth that follow them is not particularly great, as it is in many eusuchians.

Except for the first two teeth, all of the maxillary teeth are large, with correspondingly large alveoli. Indeed, the enlargement of the last five or six teeth has resulted in swellings of the maxilla on its internal surface for the accommodation of the tooth bases. These swellings occur above the horizontal palatine plate of the maxilla. Naturally, the alveoli are elongated and rather narrow, to accommodate the unique, laterally compressed teeth that characterize this crocodilian genus.

Because of the subequal size of the maxillary teeth, the alveolar border in *Sebecus* is comparatively even, showing little of the sinuosity so typical of this border in many eusuchian crocodiles; in fact this border is essentially straight from the third maxillary tooth to the end of the series. But in front of the third maxillary tooth (the first of the large maxillary teeth) the alveolar border makes a sharp bend upward, to meet the ventral border of the premaxilla.

Between the last seven alveoli and close to their inner edges are well-developed pits in the maxilla for the reception of the points of the lower teeth. This is a character frequently seen in modern crocodilians. Also, placed medially to the alveoli there is on

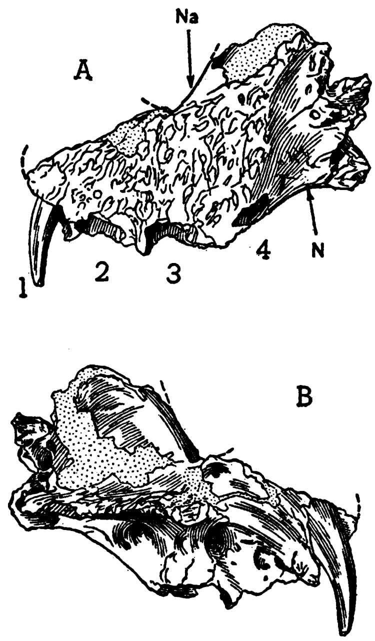


FIG. 1. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left premaxilla, $\times\frac{1}{2}$. A, External lateral view; B, internal view. Na, Border of external narial opening; N, notch in premaxilla, just in front of suture, for reception of the fourth dentary tooth; 1, 2, 3, 4, numbers of premaxillary teeth and alveoli.

either side a row of small, but quite distinct vascular canals or foramina, developed in the palatal plate of the maxilla. In the modern crocodilians these canals communicate with the alveolar sinus, which is located in the outer portion of the maxilla above the tooth row and separated from the nasal passage by a vertical bony wall. In the persisting Eusuchia this alveolar sinus is very large and well developed, extending for a greater portion of the length of the maxilla and occupying a considerable width within the muzzle. It would appear that the alveolar sinus must have been much constricted in *Sebecus*, being hardly more than a narrow canal running the length of the maxilla immediately internal to the alveolar borders and superior to the vascular canals upon the palatal surface. Moreover it would appear that there was no enclosed space for a diverticulum of the nasal sac between the alveolar sinus and the nasal passage, as is so characteristic of the modern crocodilians.

One other point with regard to the maxilla should be brought out at this place. This is the fact that although there is some reduction in the number of maxillary teeth in *Sebecus*, there has not been much reduction in the length of the alveolar region. This means that *pari passu* with the reduction in the number of the teeth, there was a general increase in the size of these teeth, with the result that the tooth row occupies almost the same amount of space, in relation to the total length of the skull, that it does in many other crocodilians in which the teeth are more numerous but comparatively smaller than they are in *Sebecus*.

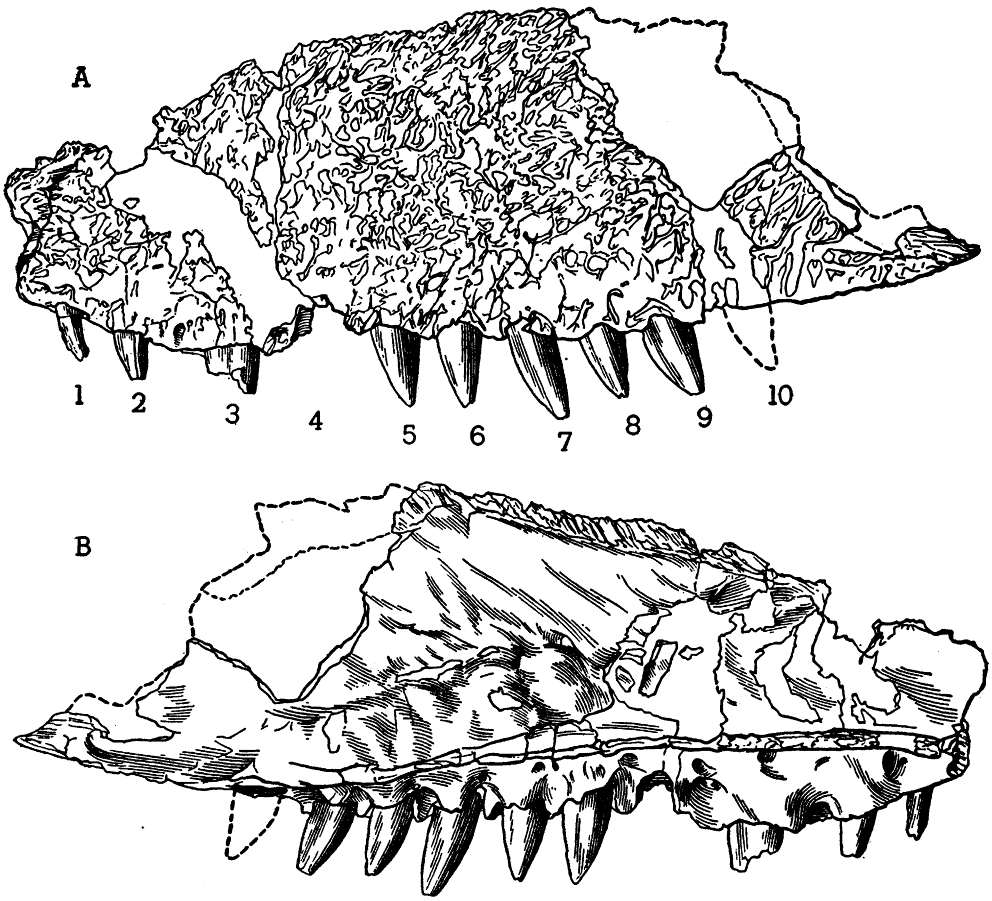


FIG. 2. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left maxilla, ×½. A, External lateral view; B, internal view. 1–10, Numbers of maxillary teeth and alveoli.

The materials at hand show that the maxilla was in contact suturally with the nasal, lacrimal, and jugal—in other words, that there was no preorbital foramen in this genus. This is of course a typical crocodilian feature, to be expected even in an aberrant form such as *Sebecus*.

NASAL: Like the maxilla, the nasal in *Sebecus* is distinguished from the same element in other crocodilians in that its surface is for the most part approximately vertical rather than horizontal. The two nasals meet along a greater portion of their length to form a narrow crest to the muzzle in this crocodilian. The anterior portions of both nasals are missing in the materials at hand, but it seems probable from the configuration

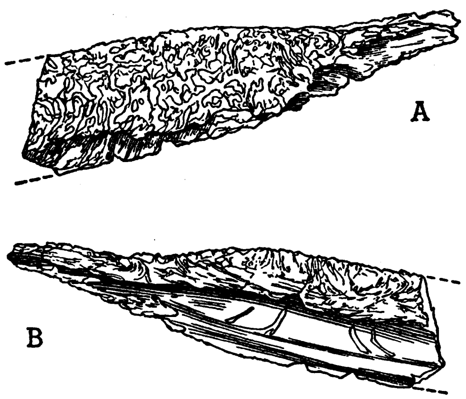


FIG. 3. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left nasal bone, anterior portion missing, ×½. A, External lateral view; B, internal view.

of the premaxilla and maxilla that the nasals were somewhat expanded anteriorly and separated the premaxillae from each other just behind the external narial openings. Posteriorly these bones are broadened, and each shows two distinct external surfaces—a vertical surface and a horizontal surface almost at right angles to the vertical surface. The vertical part of the nasal joins the lacrimal, behind the maxillary suture, while the horizontal surface terminates in a sutural junction with the prefrontal and frontal.

LACRIMAL: The lacrimal bone in *Sebecus* has been deepened, correlative with the deepening of all of the bones forming the side of the skull in this genus, and its external surface is vertical, rather than horizontal as in the typical crocodilians. It has an anterior extension in the form of a point, bounded above by the nasal and below by the maxilla. Behind the nasal, this bone articulates with the prefrontal. Posteroventrally the lacrimal is again pointed, and in this case the upper edge of the point forms a part of the orbital border, while below it is suturally joined with the jugal.

There is a well-defined lacrimal duct within the bone, the posterior exit of which is at the anterior upper corner of the orbit near the juncture of the lacrimal and prefrontal, while its anterior opening is on the inner surface of the bone near its upper border. This duct in *Sebecus* is not very long, nor is its expansion within the bone so great as it is in the modern crocodiles.

PREFRONTAL: This bone in *Sebecus* shows the usual crocodilian relationships since it forms the anterodorsal section of the orbital rim, while it is joined on either side by the maxilla and frontal, respectively, and anteriorly by the nasal. However, the prefrontal in this fossil differs from the same bone in many of the modern crocodilians in that it is not produced anteriorly into a long point, running far forward between the nasal, maxilla, and lacrimal.

On the other hand, the prefrontal in *Sebecus* extends farther back over the orbit than it does in any of the other crocodilians with the possible exception of certain metriorhynchids. Along much of their length the two prefrontals are separated from each other by a narrow anterior tongue of the frontal.

Curving down from the posteroventral sur-

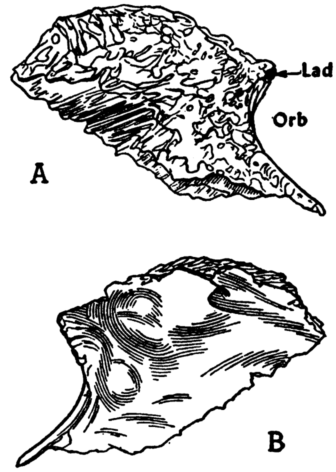


FIG. 4. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left lacrimal, ×½. A, External lateral view; B, internal view. Orb, Position of orbit; Lad, lacrimal duct.

face of each prefrontal in *Sebecus* is a bony lamina which terminates at a comparatively short distance below the cranial roof in an irregularly broken edge. This is the bony extension homologous with a similar downward process which in the Eusuchia extends down to meet the palatine and pterygoid bones. The question is, Was there a bridge of bone in *Sebecus* similar to that connecting the top and the bottom of the skull in the modern crocodilians? Probably, but it must have been considerably different from the same structure seen in the Eusuchia. In the first place, the distance between the upper surface of the palatines and the lower surface of the prefrontals is relatively small in the modern forms, whereas it is considerable in the deep-skulled *Sebecus*. Therefore the bony pillar must have been rather long in the extinct genus. However, the dorsally directed laminae on the palatines are so thin, it would seem probable that the connection between the roof and the palate must have been constituted either of very thin bone or in part of cartilage. In the modern crocodilians this bony connection serves in part to separate the nasal sacs from the orbital region, and in part (where the two plates join each other ventrally along the median line) to form a support for the free ends of the olfactory bulbs. It is probable that the same functions were performed by the homologous partitions in *Sebecus*, whether they were wholly bony or in part cartilaginous.

PALPEBRAL: Attached to the orbital rim as formed by the prefrontal there is on each side a large palpebral bone in *Sebecus*. The bones are roughly triangular in shape, and of the two the one on the left side is considerably larger than the one on the right side.

FRONTAL: This bone is flat and very broad in its posterior region, where it is bounded behind by the parietal and on each side by the postorbital. It forms a small part of the upper rim of the orbit on each side, and in this region it is perfectly flat and rather thin —not thickened and raised into a prominent rim as in the modern crocodilians. Evidently the eye did not protrude above the skull roof in *Sebecus* as it does in the eusuchians, but rather it occupied a more normal position and was directed laterally. Anteriorly the frontal is constricted into a long tongue or process, forming somewhat more than half the length of the bone, and bounded on either side by the large prefrontals.

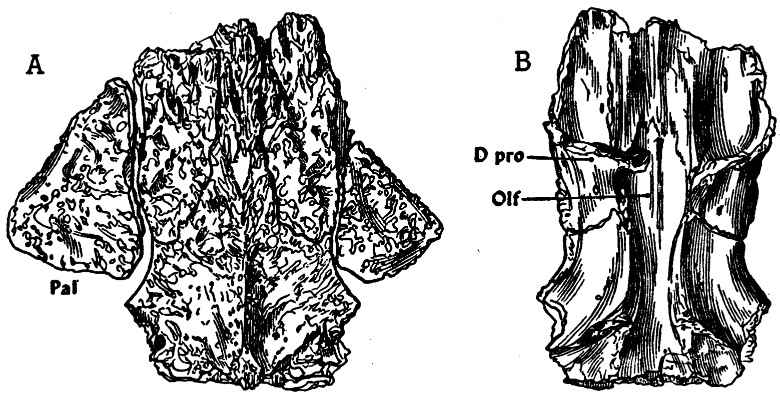


FIG. 5. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, frontal, prefrontals, and palpebrals, ×½. A, Dorsal view; B, ventral view. Pal, Palpebral bone; D pro, descending process of prefrontal; Olf, impression of olfactory bulbs on the under surface of the frontal.

It might be said here that the interorbital portion of the frontal is relatively broad. Perhaps this is owing in no small part to the lack of the raised orbital rim which characterizes the modern Eusuchia, and of which so many have the dorsal rims of the orbits very close to each other. There is a well-defined median ridge on the back part of the frontal, and the bone terminates posteriorly in a very strong transverse suture for articulation with the parietal.

Ventrally the frontal shows in its posterior portion a concave surface for the cerebral portion of the brain, bounded on either side by the strong articulations for the postoptics.

The endocranial surface takes the form of a broad groove, which is continued forward with but little diminution for the accommodation of the olfactory stalks. Anteriorly, where this groove enters the region of the prefrontals, it is broadened again, to give room for the enlarged olfactory bulbs.

PARIETAL: The parietal, articulating with the frontal by a very heavy sutural union, is a relatively short bone, much constricted in its middle region by the development of the supratemporal fenestrae. The upper surface of the parietal, which is heavily rugose, is bounded on either side by a strong ridge that serves to separate the upper surface of the bone from the supratemporal fenestra, and it is to be presumed that this ridge marked the upper limits of attachment for the strong temporal muscles. The two ridges, closely appressed to each other anteriorly by the encroaching temporal fenestrae, diverge sharply from front to back at an angle of about 75 degrees.

The upper surface of this bone rises sharply from front to back, so that in a lateral view there is a strong upswing of the cranial roof behind the frontal-parietal junction. This may be contrasted with the more typical crocodilian condition in which the back portion of the upper frontal and the parietal surfaces are on the same horizontal plane. Because of this upward growth of the parietal bone, the occipital crest, that is the posterior transverse boundary of the skull roof formed by the parietal and the squamosals on either side, is raised high above the rest of the skull, and this feature serves, together with many other characters, to distinguish the skull of *Sebecus* very strongly from any other crocodilian skulls. The reason for this particular development in the skull of *Sebecus* is a matter for conjecture; perhaps it is a corollary of the general growth trend in this genus, whereby vertical forces were very strong as compared with horizontal forces of growth. It did give an expanded area for the origin of some of the temporal muscles, which will be described below, and perhaps it may be correlated with the development of strong adductor muscles in this region.

At the back the parietal is very deep, and shows sinus cavities which occupied a position above the back portion of the brain. There is an extensive sutural union for the articulation of the supraoccipital, which latter bone excluded the parietal from the back margin of the skull. Ventrally the parietal shows on either side, as does the frontal anterior to it, a strong articulation for the postoptic.

POSTORBITAL: This bone is not represented in the materials of *Sebecus* so far known, but there is good reason to think that it was not greatly dissimilar from the same element in the eusuchian crocodiles. Thus, it undoubtedly formed a part of the border of the upper

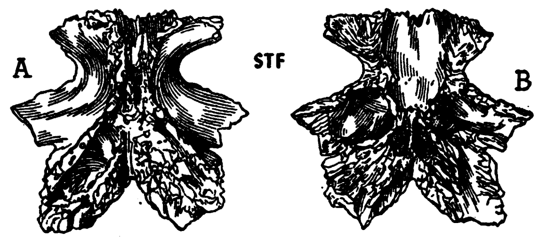


FIG. 6. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, parietal, $\times \frac{1}{2}$. A, Dorsal view; B, ventral view, STF, Position of supratemporal fenestra.

temporal fenestra, as well as the back portion of the orbital border. As seen from above it was probably an L-shaped bone, with the angle of the L directed anterolaterally. From its under surface there was undoubtedly a subdermal postorbital bar which was directed ventrally to meet a similar bar reaching up from the jugal.

JUGAL: The jugal in *Sebecus* is a long, compressed bone, which, except for its proportions, is generally similar to the same element in other crocodilians. The front part of the bone is rather deep, and the postorbital bar arises at a point somewhat in front of the middle of the bone, a condition contrasting with that in many Eusuchia, in which the postorbital bar is closer to the back end of the jugal bone than to the front border. Anteriorly the jugal forms the lower border of the orbit and posteriorly the lower border of the lateral temporal fenestra. It might be said here that in *Sebecus* both of these openings are directed laterally, whereas in the eusuchians the two openings are pointed in an upward direction. In its anterior region the jugal shows an extensive squamous sutural overlap over the back border of the maxilla, while posteriorly there is a long junction with the quadratojugal.

As mentioned above in connection with the remarks concerning the postorbital, the postorbital bar in *Sebecus* is subdermal, a character whereby this genus resembles the eusuchians.

QUADRATOJUGAL: In *Sebecus* the quadratojugal is an elongated bone, which shows the usual eusuchian relationships of being bounded along its entire length by the jugal below and the quadrate above. Anteriorly this bone is notched by the back corner of the lateral temporal fenestra.

The quadratojugal is unusual in *Sebecus* in that its posterior portion takes part in the articulation between the skull and the lower jaw. Consequently, instead of terminating posteriorly in a point near the posterior extremity of the quadrate, as is characteristic of many other crocodilians, the quadratojugal in this genus is expanded posteriorly into a small condyle. This expanded condyle is continuous with the quadrate articulating surface, and it forms the external part of the transverse condylar joint upon which the glenoid in the articular bone of the mandible rotates.

QUADRATE: In its general aspects and rela-

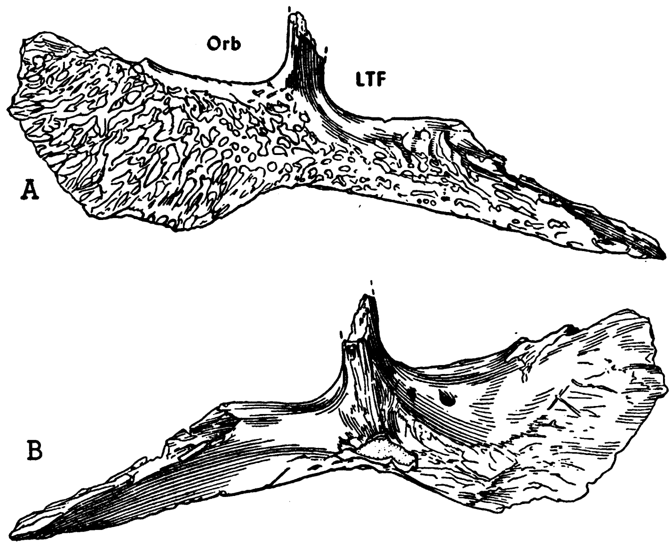


FIG. 7. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left jugal, ×½. A, External lateral view; B, internal view. Orb, Position of orbit; LTF, position of lateral tempora fenestra.

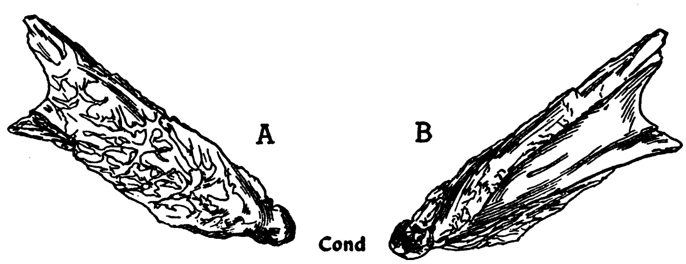


FIG. 8. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left quadratojugal, ×½. A, External lateral view; B, internal view. Cond, Condyle forming outer portion of quadrate-quadratojugal articulation with the lower jaw.

tionships the quadrate bone in *Sebecus* shows strong similarities to the same bone in the eusuchian crocodiles. This is to say that it is an exceedingly complicated bone, not only as to its shape but also as to its relationships with the various other bones that join it.

Generally speaking, this is an elongated bone directed posterolaterally, terminating at its free end in the transverse condylar surface for articulation with the lower jaw, bounded below by the quadratojugal, and at its anterior end firmly wedged in between the postorbital, parietal, exoccipital, postoptic, squamosal, basisphenoid, and pterygoid. Of these several bones, the exoccipital and squamosal overlap the quadrate extensively, thereby hiding a considerable portion of it from view externally.

Along its back surface there is a longitudinal ridge, running from the posterior junction of the exoccipital and squamosal with the quadrate to the articulating surface. This ridge is placed about medially upon the bone, and it serves to divide the upper surface of the quadrate very distinctly into a medial and an external portion. The ridge terminates distally at the articular surface of the quadrate, where its development has caused the articulation to assume a shape quite different from the same surface in the modern Eusuchia. In these latter, for instance, the articulation takes the form of a rather elongated hourglass, as seen in a posteroventral view, expanded at each lateral end and constricted in the middle. In *Sebecus*, however, the articulation is much broader in the middle than it is at either end, because of the expansion of the posterodorsal ridge on the back of the quadrate. In outline the lower border of the articular surface is essentially straight, while the upper border is produced posterodorsally into a prominent point in its middle region. The comparison will be made clear by figure 9.

On the inner side of the upper or back surface of the quadrate there may be seen a canal, the opening of which is shortly above the articulation, running along the length of the bone toward the tympanic cavity. The lower course of this canal has been exposed by a breakage of the bone which originally roofed it in. According to Miall, "Stannius first pointed out that by means of this canal [in recent crocodilians] a pneumatic communication subsists between the tympanic cavity and the articular piece of the mandible" (Miall, 1878, p. 23).

There is also a canal on the ventral side of the quadrate, seemingly running from the tympanic region to a point about 40 mm. from the articulation, where there is a posteriorly directed opening or exit.

In a lateral view two prominent openings are seen, namely, a very large external auditory meatus, in which the tympanic membrane was lodged, bounded below by the quadrate and above by the squamosal, and an enlarged foramen in front of the meatus, leading into the tympanic cavity.

In a posterior view of the quadrate there may be seen the opening between this bone and the exoccipital which served as an exit for the facial nerve.

SQUAMOSAL: The squamosal bone in *Sebecus*, as in the eusuchians, forms the postero-external corner of the skull and broadly overhangs the ear region, forming a sort of protective roof for the latter. From the similarities between the squamosal in *Sebecus* and in the Eusuchia, it would seem probable that in the extinct genus, as in the existing crocodilians, there was an epidermal flap attached to the outer edge of the squamosal, which served to close the ear during submergence of the animal. In the modern crocodilians this flap, attached at its upper edge to the squamosal, is movable. It can be lowered when the animal submerges, so that it effectively seals the eardrum from contact with the water. When the animal raises the head above the water this flap is raised, so that the crocodilian can readily hear airborne vibrations.

The squamosal, as seen from above, is essentially a three-cornered bone, the dorsal surface of which is roughly pitted and sculptured. Anteriorly this bone forms the posterior boundary of the supratemporal fenestra, and, as in recent eusuchians, the bone is smooth below the upper rim of the fossa. Unfortunately the squamosal is broken in the region where it would normally articulate with the parietal; there is reason to think, however, that in this genus, as in recent eusuchians, there was a foramen for the entrance of the temporal artery into the skull at the junction of the two bones.

As in the Eusuchia, the squamosal in *Sebecus* is characterized by a vertical descending plate beneath its posteriorly directed process. On its anterior side this plate articulates with the quadrate behind the external auditory meatus, and, as it rises anteromedially to meet the lower surface of the horizontal plate of the squamosal, it is developed as a free edge that forms the upper border of the meatus. Posteriorly this vertical plate is overlapped by the upper edge of the large exoccipital.

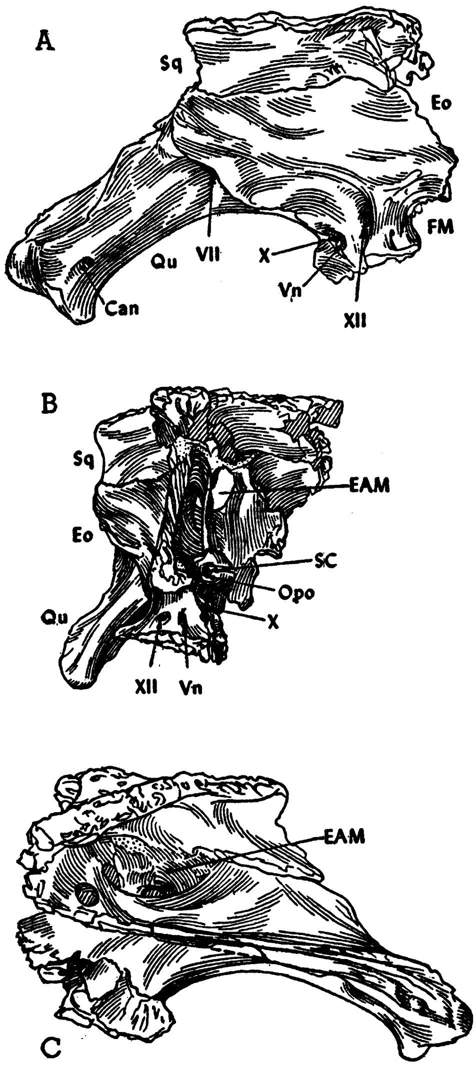


FIG. 9. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left quadrate, squamosal, and exoccipital, ×½. A, Occipital view; B, internal view; C, external lateral view. EAM, External auditory meatus; FM, foramen magnum; SC, semicircular canal; Eo, exoccipital; Can, exit of canal in quadrate communicating with tympanic cavity; Opo, opisthotic; Qu, quadrate; Sq, squamosal; Vn, passage for small vein from tympanic cavity; VII, X, XII, foramina for the seventh, tenth, and twelfth cranial nerves, respectively.

EXOCCIPITAL: As seen in posterior view, the occiput of *Sebecus* is dominated by the large exoccipitals, so characteristic of the crocodilians. The paired exoccipitals extend from the foramen magnum, of which they form all but the ventral border, laterally to a point on either side just beneath the posterior edge of the squamosal. Thus each exoccipital is a broad bone, and in addition is an element of considerable depth, since its lower border is depressed on either side to a level below the occipital condyle, while its upper border extends well up on the occipital surface. This bone overlaps rather extensively the quadrate, thereby hiding a considerable portion of the latter bone, as seen in posterior or occipital view.

Five foramina are visible in the posterior view of the exoccipital, as is commonly the case in the modern Eusuchia. Immediately lateral to the foramen magnum is the large hypoglossal foramen for the passage of the twelfth cranial nerve, while lateral to the hypoglossal foramen at a distance of about 15 mm. are two foramina, located very close to each other and contained in a common depression on the surface of the bone. Of these the inner one is small and served for the passage of a small vein from the tympanic cavity, while the outer one is a large foramen—the exit for the vagus nerve. Below these foramina is the exit for the internal carotid artery, which latter traversed the exoccipital vertically from its lower exit, passing from this bone into the tympanic cavity. Finally, near the lateral extremity of the exoccipital, between the juncture of this bone with the quadrate, is a large, vertically elongated foramen which is directed toward the articular surface of the quadrate. This foramen served for the exit of the seventh or facial nerve, as well as for a branch of the jugular vein and an artery. A long canal traversing the exoccipital-quadrate suture led from this foramen into the tympanic cavity and served for the passage of the nerve and blood vessels.

The exoccipital of *Sebecus* resembles the same element in the Eusuchia in that it has a very broad, ventrally directed sutural surface for articulation with the basioccipital, and a broken edge of bone shows that there was also a ventrally directed process, as in the Eusuchia, also for articulation with the basioccipital. Between these two articulations there is seen in *Sebecus* a large cavity within the bone, located immediately lateral and slightly ventral to the posterior part of the brain case. This is the rhomboidal sinus of the lateral Eustachian passage, to be discussed below.

As seen from a medial viewpoint, the exoccipital of *Sebecus* shows the inner wall of the foramen magnum, which formed the lateral enclosure for the medulla oblongata. This strongly concave surface is pierced by three foramina, as in the Eusuchia. These are the large hypoglossal foramen at the back, through which the twelfth nerve passed, a small foramen for a vein, which joined the vein from the tympanic cavity, mentioned above, and an elongated slit-like opening at the front. This last opening is actually located at the junction of the exoccipital with the opisthotic, which latter bone in the adult crocodilians generally is firmly fused with the exoccipital. The slit, inclined at an angle of about 45 degrees to the floor of the brain base, is the opening through which passed the vagus nerve. The opisthotic, in front of the slit, is rather well preserved and will be described below.

In this median view of the exoccipital-quadrate-squamosal complex the tympanic cavity, which is exposed, is seen to be large and even more expanded than it is in the recent crocodilians.

In this region of the skull there is a difference in structure whereby *Sebecus* may be contrasted with the modern forms with which it has been compared. In *Crocodilus*, for instance, the bone of the exoccipital behind the tympanic cavity is thickened so that its anteroposterior diameter is as great as the same dimension of the cavity in front of it. Internally the bone shows a certain amount of excavation by small sinus cavities, but these are not extensive. In *Sebecus*, on the other hand, the back wall of the exoccipital is more posteriorly placed and its thickness behind the tympanic cavity is much less than in the eusuchians, so that there is a large, hollow space or pocket in this region almost as large as the tympanic cavity itself. Moreover, there is only a partial bony wall between the two cavities, and consequently the cavities are open to each other over much of their extent. In effect the tympanic cavity has been greatly enlarged; as a matter of fact, it has almost doubled in size.

It is difficult to speculate as to the reason for this development in *Sebecus*. It is to be noted, however, that the external auditory meatus, and by inference the tympanic membrane, is much larger than in recent crocodilians. Perhaps the enlargement of the tympanic cavity in *Sebecus* is correlated with the large meatus, and together they may indicate an unusualy acute sense of hearing in the extinct genus.

In *Sebecus* the exoccipital is very firmly fused to the quadrate by means of a strong and extensive suture. This afforded an almost inseparable union between the two bones.

OPISTHOTIC: The opisthotic is firmly fused to the exoccipital in the Crocodilia, and generally this bone is with difficulty distinguished as a distinct element. In the *Sebecus* skull, however, the opisthotic is plainly seen. Its lateral portion is a squamous plate, attached firmly to that thin wall of the exoccipital which partially separates the tympanic cavity proper from the enlarged posterior cavity described above. Medially, the opisthotic is thickened and pierced by those portions of the semicircular canals traversing this bone.

SUPRAOCCIPITAL: Although the supraoccipital is missing in the *Sebecus* materials so far known, the sutures on the exoccipital, squamosal, and parietal give an adequate idea as to the extent and shape of this particular element. This bone extended up from the two exoccipitals (which meet each other above the foramen magnum) flaring from bottom to top so that the upper edge of the bone was something more than twice the lateral width of its lower edge. The supraoccipital evidently met the squamosal on either side, whence its upper border extended forward on the roof of the skull in a wedge-shaped process that met the parietal.

Thus the parietal was excluded from the back border of the skull in *Sebecus* by the forward growth of the superior part of the supraoccipital, a relationship that sometimes is seen in certain eusuchians.

BASIOCCIPITAL: Our knowledge of the basioccipital in *Sebecus* must be gained from a specimen supplementary to the skull and jaw upon which the bulk of this description is based. This bone is partially preserved in A.M.N.H. No. 3159. Here again, as is so frequently the case in *Sebecus*, the resemblances of the basioccipital are with the same element in the Eusuchia.

At its upper margin the basioccipital carries the rounded occipital condyle, and it extends inward from the condyle to form the floor of the foramen magnum and the brain case. Below the condyle the bone extends downward, its edges being embraced on either side by the large exoccipitals. As is common in the crocodilians, there are on the outer edges of this bone near its ventral termination large expansions in the form of elongated tubercles which are for the attachment of certain neck muscles. Between these basilar tubercles, in the base of the basioccipital, is the vertically directed single opening of the median Eustachian canal, located between the basioccipital and the basisphenoid. The development of the complicated system of Eustachian tubes in *Sebecus* and in other crocodilians, of which this median canal is one element, will be described in detail below. On the outside of the bone, directly behind the vertically directed Eustachian canal, is a sharp and well-defined vertical ridge.

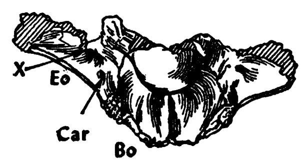


FIG. 10. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3159, basioccipital and exoccipitals, ×½. Occipital view. Bo, Basioccipital; Car, exit of internal carotid artery; Eo, exoccipital; X, foramen for tenth cranial nerve.

On either side of the median Eustachian canal, and again in the sutural surface between the basioccipital and the basisphenoid, are the lateral Eustachian canals, running upward parallel to the median canal. These also will be described below.

BASISPHENOID: The basisphenoid is only partially preserved in *Sebecus*, but such of this bone as is present shows the characters of the element very well. It is quite apparent that the basisphenoid of *Sebecus*, like so many of the other skull bones, shows very close resemblances to the same bone in the Eusuchia. On its upper surface is the elongated, transversely concave floor upon which the medulla oblongata rested. On either side this floor is pierced by a small foramen which afforded an exit for the sixth cranial nerve.

At the anterior termination of this cranial floor is a large fossa, directed backward and down, so that it is beneath the medullar portion of the brain. This opening is the sella turcica that housed the pituitary body of the brain which in *Sebecus*, as in large modern crocodilians, was a lobe of considerable size. In this connection it might be said that a part of the function of the pituitary is the secretion of the growth hormones, and it is an interesting fact, as has been shown by Edinger, that the large and giant reptiles are characterized by large pituitaries. At the bottom of the sella turcica are two foraminal exits, directly laterally. These are for the passage of the carotid arteries, which leave the basisphenoid dorsolaterally and enter the tympanic region in the prootic bone. In the development of these openings within the

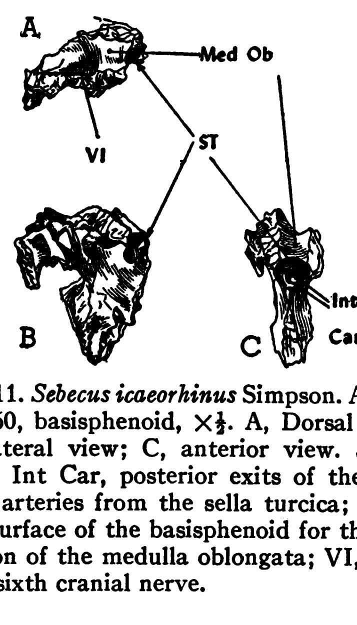


FIG. 11. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, basisphenoid, ×½. A, Dorsal view; B, right lateral view; C, anterior view. ST, Sella turcica; Int Car, posterior exits of the internal carotid arteries from the sella turcica; Med Ob, dorsal surface of the basisphenoid for the accommodation of the medulla oblongata; VI, foramen for the sixth cranial nerve.

basisphenoid there is almost complete identity between *Sebecus* and the Eusuchia.

Ventrally, beneath the sella turcica the basisphenoid is constricted, and along its anterior edge it shows a narrow articular surface, probably for a juncture with the pterygoids.

PALATINE: Both palatines are preserved in the *Sebecus* skull, and these show a rather primitive stage of development that differentiates this Eocene crocodilian sharply from the Eusuchia. At the same time, the development of the palatines, together with

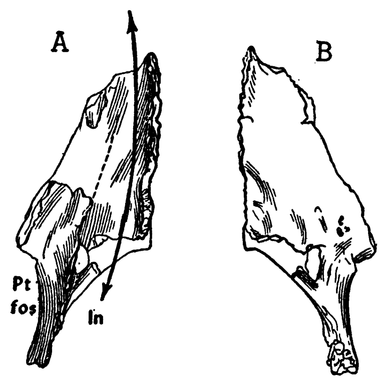


FIG. 12. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, palatine ×½. A, Dorsal view; B, ventral view. In, Position of the internal nares; Pt fos, position of the pterygoid fossa. The arrow shows the course of the nasal passage across the dorsal surface of the bone.

the conjoined pterygoids, is markedly different from what is seen in the Mesosuchia, a fact that emphasizes once again the distinct position of *Sebecus* in the phylogenetic history of the Crocodilia.

Each palatine is shaped something like an arrowhead, the front portion being pointed, the back portion drawn out into a slender ramus or projection. The two palatines meet along their midline, and laterally each of them is bounded in front by the palatine extensions of the maxilla. At the back the palatine articulates with the pterygoid, and this articulation is carried up on a lateral vertical plate of the palatine that serves to enclose, in part, the nasal passage. From the manner in which this vertical plate thins to a very delicate edge it would seem apparent that the upper part of the nasal passage, enclosed within the muzzle of the animal, was bounded by cartilaginous walls. Posteriorly between the two vertical plates of the conjoined palatines, these bones together form a semicircular free edge which constitutes the front border of the internal nares. This anterior placement of the narial border is a character whereby *Sebecus* resembles the mesosuchians. However, the development of the pterygoids, as mentioned above, indicates most clearly the fact that, in spite of certain resemblances, there are at the same time strong differences between *Sebecus* and the mesosuchians.

On each side, lateral to the large semicircular boundary of the anterior nares, the smooth surface of the palatine formed by the rounded angle between the horizontal and the vertical plates makes up a part of the inner border of the large palatal foramen. The inner boundary for the foramen is continued posteriorly by the pterygoid, while its external boundary is formed by the maxilla, and its posterior border by the ectopterygoid.

ECTOPTERYGOID: The ectopterygoids are long slender bones, each of which articulates proximally with the maxilla and the jugal by a broad, sutural surface. The bone then extends ventroposteriorly to form the front border of the large ectopterygoid-pterygoid flange, or wing. That portion of the ectopterygoid articulating with the pterygoid is therefore attenuated as a slender, curved point, of which the concave surface is in contact with the pterygoid behind it.

As is the case with so many of the other bones in the skull and mandible of *Sebecus*, the extraordinary downward extension of the ectopterygoids and pterygoids in this crocodile are an expression of the dominance of vertical growth factors over horizontal growth factors during the development of the skull. Yet in spite of the differences in shape and proportions, the ectopterygoid of *Sebecus* shows identically the same relationships to the bones with which it articulates, namely, the maxilla, jugal, and pterygoid, as are to be seen in the modern Eusuchia. Therefore Miall's statement concerning this bone in the Eusuchia may be applied with equal validity to the same element in *Sebecus*. "The transpalatine [ectopterygoid] has two expanded smooth surfaces, an outer and an inner; the first is covered by the mucous membrane of the mouth; the other is in contact with the mandibular muscles which fill the pterygoid fossa" (Miall, 1878, p. 27).

PTERYGOID: Two fragments of A.M.N.H. No. 3159 have been identified as portions of the right and left pterygoids, which bones in life were very probably joined to form a single extensive element. The larger fragment contains the median dorsally directed process, which extended up to meet the basioccipital, and a lateral flange which extended out to join the right ectopterygoid. The other fragment is a part of the lateral wing of the left pterygoid. The dorsal process shows no sign of a sutural division along the midline, and similarly the recent eusuchians show no sutural division between the pterygoids where they join behind the internal nares.

The dorsal surface of the lateral pterygoid wing is smooth, and it was across this smooth surface that the anterior pterygoid muscles moved as they were extended or flexed. The ventral surface of the bone is interesting, in that it bears a low ridge, running from the median part of the bone laterally and anteriorly. In front of this ridge the bone is excavated into a sort of pocket.

Thus it is clear that while the internal nares of *Sebecus* were mesosuchian-like in that they were wide, with the anterior border formed by the palatines, they were eusuchian-like in that there was also a posterior border formed by the pterygoids. All of the evidence points to the fact that the nares were very large in *Sebecus*. There evidently was a roof above the nares, formed by a forward extension of the pterygoids over at least a part of the narial opening, but it is quite possible that this roof was in part cartilaginous, since the vertical flanges of the palatines with which it would have joined are very thin. Indeed, it is quite possible that the roofing of the internal nares was not complete, just as the enclosing of the nasal passage dorsally might not have been complete. It is evident that the nasal tube, so characteristic of the eusuchians, was in *Sebecus* only incipient.

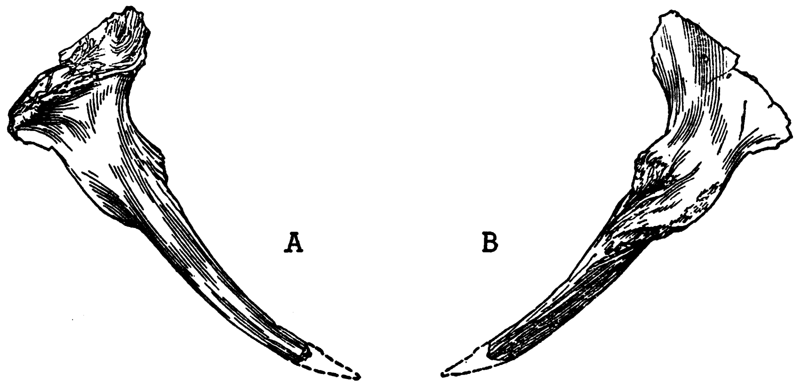


FIG. 13. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left ectopterygoid, ×½. A, External lateral view; B, internal view.

The pterygoid in *Sebecus* must have been a large extensive bone laterally. It articulated in front with the palatine and in the back with the quadrate, postoptic, and basisphenoid. The long, downward sweep of the ectopterygoid shows that the pterygoid wing was very large indeed, suggesting the development of strong pterygoid muscles between the skull and the lower jaw.

At this place it may be well to discuss the development of the internal nares and the bones associated with their formation in *Sebecus* as compared to the development of the nares and associated bones in the mesosuchians and the eusuchians. As already stated, the nares of *Sebecus* show some points of resemblance to those in the mesosuchians, and some to those in the eusuchians. In the mesosuchians, the internal nares are completely open behind, while their anterior border is formed by the palatines. The pterygoids are of medium size, with rather small flanges or wings projecting back behind the ectopterygoids. Medially the pterygoids extend far back on either side of the basicranium, while between them is a large ventral exposure of the basisphenoid bone. In *Sebecus* the anterior border of the nares is still formed by the palatines, but there is now a broad posterior border, formed by the pterygoid bones. The pterygoids have increased greatly in size, in a large part by the development of very large, posteroventrally directed flanges

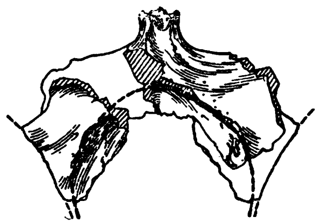


FIG. 14. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3159, portion of the conjoined pterygoids, ×½. Dorsal view. The heavy dotted line shows the course of the low ridge that enclosed posteriorly the internal nares.

or wings, and, moreover, the ectopterygoids have been carried back to form the outer borders of these large wings. It would seem, moreover, that because of the enlargement of the pterygoids the basisphenoid has been greatly constricted in its ventral exposure, so that very little of this bone is now to be seen on the under surface of the skull. The eusuchians differ from *Sebecus* in that the internal nares are much smaller and now are contained entirely within the pterygoids. There is a strong resemblance, however, in the large size of the pterygoids in *Sebecus* and the eusuchians, in the large pterygoid wings, the outer edges of which are formed by backward extensions of the ectopterygoids, and in the small ventral exposure of the basisphenoid. With regard to this part of the skull, a progressing line might be made up of mesosuchian, *Sebecus*, and eusuchian, in that order. By a closing together of the pterygoids beneath the basisphenoid and by an enlargement of the pterygoid wings, the condition seen in *Sebecus* might have been derived from some basic mesosuchian stock. The eusuchian represents an advance beyond *Sebecus* mainly by reason of the reduction in size of the nares and their posterior migration to a position entirely within the pterygoids. Actually, it would seem probable that the Sebecosuchia and the Eusuchia developed parallel with one another, rather than that one was successive to the other. Perhaps the accompanying diagram (fig. 15) will make clear the comparison of bones and structures in this part of the skull in the three suborders of the Crocodilia.

POSTOPTIC: This bone, commonly known in the literature as the "alisphenoid," is well developed in *Sebecus*. Along its anterior and dorsal edges it shows strong articulations for the frontal, postorbital, and parietal bones.

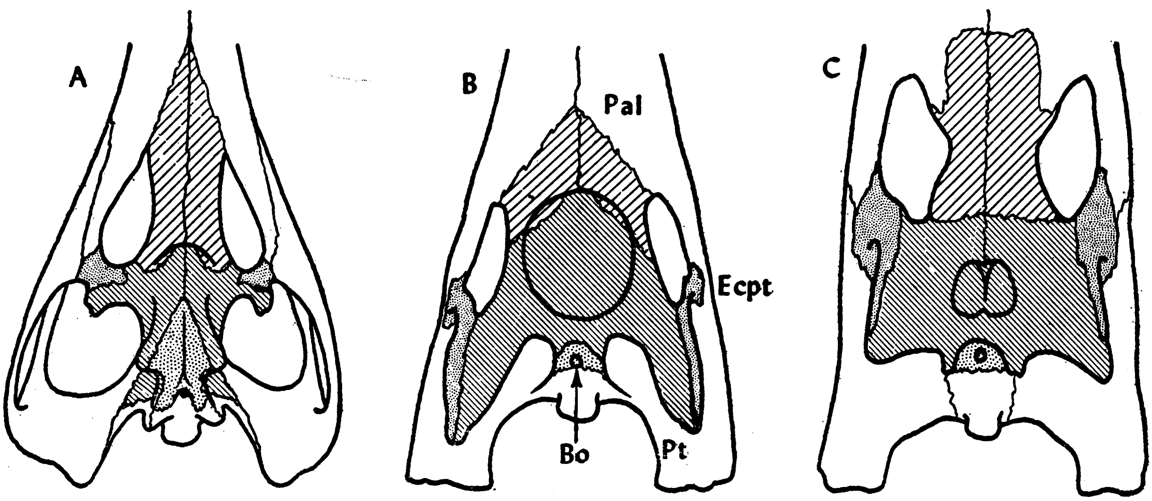


FIG. 15. A comparison of the region of the internal nares in: A, *Steneosaurus* (Mesosuchia); B, *Sebecus* (Sebecosuchia); C, *Alligator* (Eusuchia). Bo, Basioccipital; Ecpt, ectopterygoid; Pal, palatine; Pt, pterygoid. Compare the intermediate condition of the internal nares in *Sebecus* between the mesosuchian on the one hand and the eusuchian on the other.

Posteriorly there is a broad articulation for the quadrate, and presumably to some degree for the prootic, while posteroventrally is an articular surface that probably was in contact with the pterygoid. Between these latter two articulations is a smooth surface that marks a part of the anterior border of the foramen ovale for the passage of the fifth cranial nerve. It is not possible to be com-

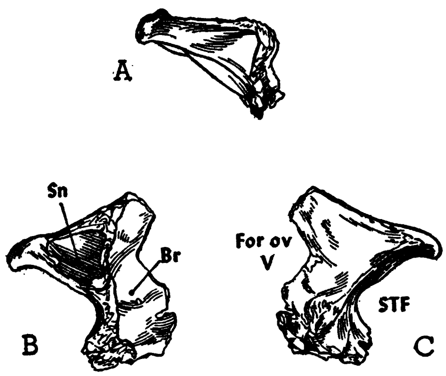


FIG. 16. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left postoptic, ×½. A, Left lateral view; B, dorsal (internal) view; C, ventral view. STF, Position of supratemporal fenestra; Br, surface for the accommodation of the left cerebral hemisphere of the brain; For ov V, foramen ovale for the passage of the fifth cranial nerve; Sn, sinus cavity.

pletely definite about these last articulations, because of the absence of the pterygoid and the prootic from the preserved materials of *Sebecus* and because of some destruction of the proximal portion of the quadrate. However, there is every reason to think that the relationships were essentially the same as those seen in the modern eusuchians.

Medially the postoptic thins to a very attenuated edge, which in the specimen unfortunately has been broken, so that none of the original edge is preserved. It is this edge which forms a median fissure just above and anterior to the sella turcica, a fissure which in the recent crocodilians is bridged by cartilage and through which passes the optic nerves. Just below the median fissure for the optic nerves there is on either side another fissure, the upper edge of which is formed by the postoptic, and through which passes the third cranial nerve, the orbital artery, and the sixth nerve. On the posterior edge of the bone, between the upper and lower articular surfaces, serving for articulation with the quadrate, prootic complex, and the pterygoid, respectively, is a smooth surface mentioned above, which formed the front border of the foramen ovale.

The ventral and lateral surfaces of the postoptic are smooth, the former looking down into the orbital region, the latter forming a portion of the front edge of the supratemporal fenestra. In this respect it should be pointed out that the postoptic of *Sebecus* is more horizontally placed than is the same bone in the modern eusuchians, with the result that its ventral surface has a much lower angle than the same surface in the recent crocodilians. The inner surface of the postoptic is deeply excavated to form the anterolateral wall for the braincase, enclosing the cerebral hemispheres.

THE MANDIBLE

Bones of the Mandible

DENTARY: The dentary in *Sebecus* is relatively deep, as would be expected in an animal in which factors of vertical growth have been strong as is the case in this crocodilian. Correlative with this, the dentary in *Sebecus* is also very thin and compressed, as compared with the same bone in other crocodilians.

Along the upper edge of the bone are 13 elongated and laterally compressed alveoli for the lower teeth, which resemble the upper teeth in every respect. These 13 lower teeth are opposed to the 14 teeth in the skull.

It will be remembered that the maxillary teeth of *Sebecus* are arranged in a comparatively straight series, that is, the alveolar border does not show the undulations so typical of other crocodilian genera. Similarly, most of the dentary teeth, specifically those from the fifth tooth back, are contained in an almost straight alveolar border, to match the opposing border of the upper jaw. The

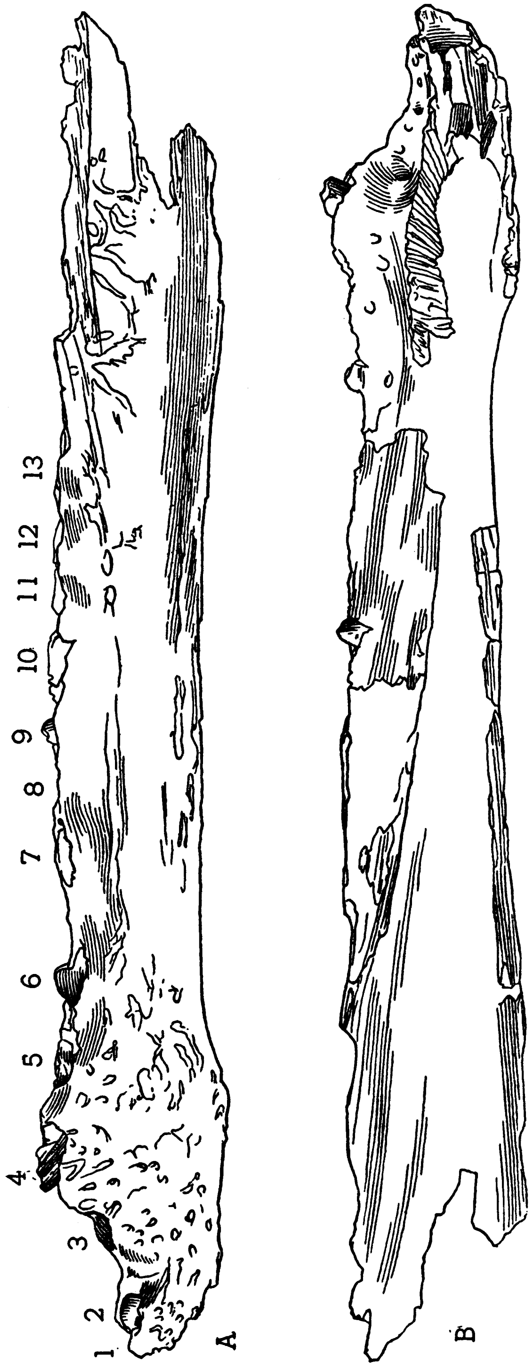


FIG. 17. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left dentary, ×½. A, External lateral view; B, internal view; 1–13, numbers of dentary teeth and alveoli.

fourth dentary tooth, however, is raised by the upgrowth of its alveolus above the level of the other teeth, so that it forms in effect a "canine," biting into the notch between the last premaxillary and the first maxillary tooth. From the raised alveolus for the fourth dentary tooth the alveolar border drops abruptly, so that the first three dentary teeth are much lower than teeth behind them, while the jaw is correspondingly shallow in this region. The first alveolus in the dentary is directed forward on either side, so that the first dentary tooth is partially procumbent. It might be said at this place that the first three dentary teeth, to judge by the alveoli, were rounded in cross section, as are the premaxillary teeth with which they occluded.

In this region of the lower jaw the external surface of the dentary is strongly rugose, in contrast to its more posterior regions where it becomes externally comparatively smooth. The symphysis, which is rather long, extends back to a point between the sixth and the seventh dentary teeth. At its posterior end the dentary is very thin, and it is notched where it forms a part of the anterior border of the external mandibular foramen.

SPLENIAL: Unfortunately the splenials are not preserved in the *Sebecus* material so far obtained from Patagonia, but it is possible from the extent of the sutural surfaces on the dentaries to get a pretty fair idea as to the extent and the shape of these elements in the genus under consideration. In the first place, it may be said that the splenial in *Sebecus* extends forward to participate in the symphysis, as it does in some of the Eusuchia. Behind the symphysis the splenial was very deep and thin, covering the inner surface of the mandibular ramus from the alveolar border (or, in the anterior portion, a short distance below the alveolar border) to the lower edge of the jaw.

CORONOID: The coronoids, like the splenials, are missing from the materials at hand. It is very probable that the coronoid in *Sebecus* was a comparatively small element at the posterior end of the splenial, as it is in the modern Eusuchia.

ANGULAR: The angular in *Sebecus* is a long bone extending from a point approximately under the last dentary tooth to the back of the lower jaw. It shows in most of its features relationships that are similar to those seen in the eusuchian angular, but there are certain important differences, which will be described below. Unfortunately only a part of one angular is preserved in the materials now available for study, but this fragment, together with sutures on other bones which articulated with the angular, gives us fairly accurate information as to the shape and the relationships of this bone.

The angular forms the lower border of the mandibular ramus for about half of its length. This relatively great extent of the angular is

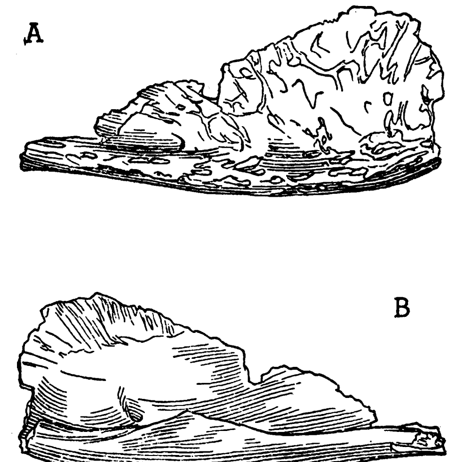
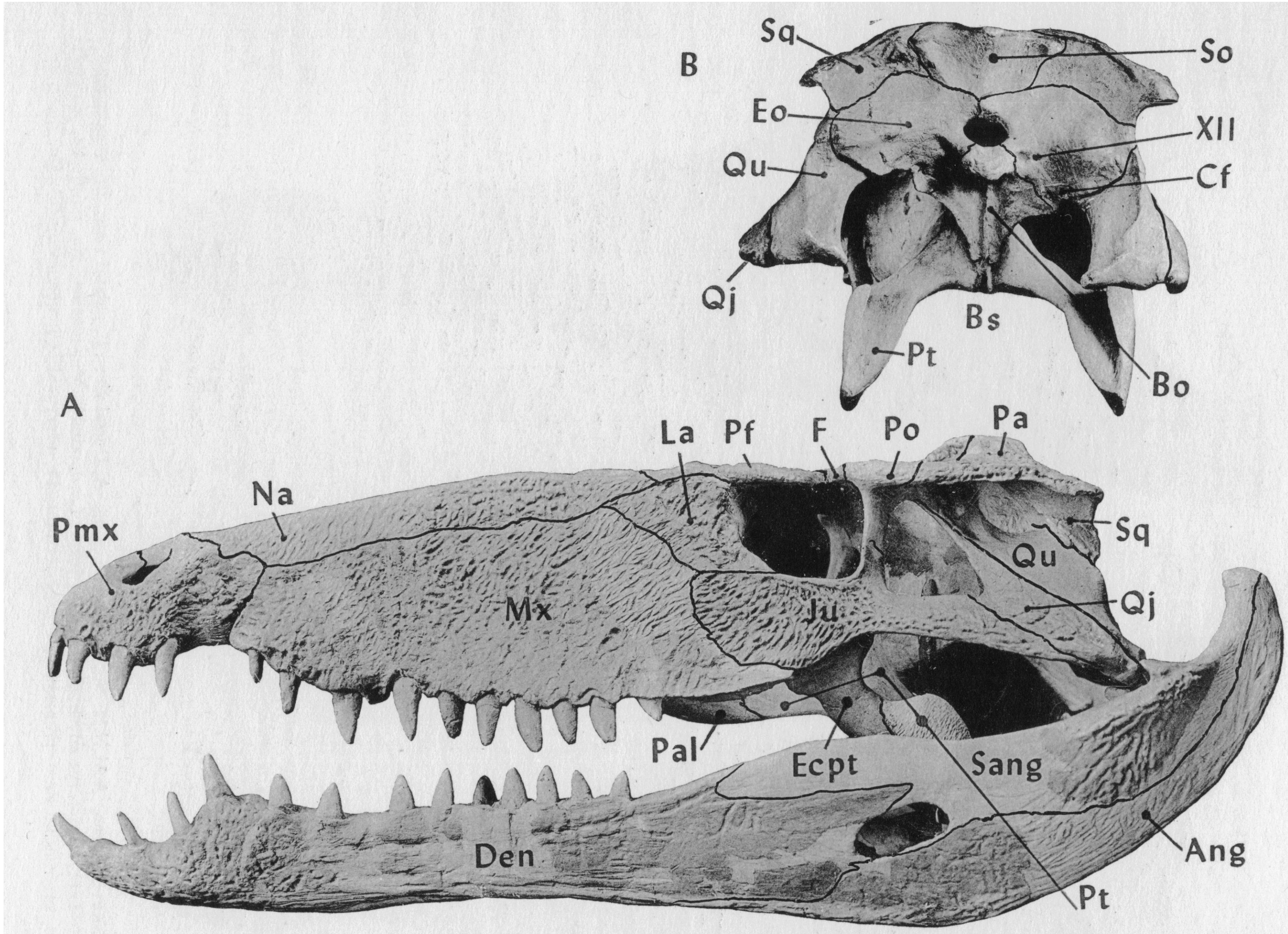


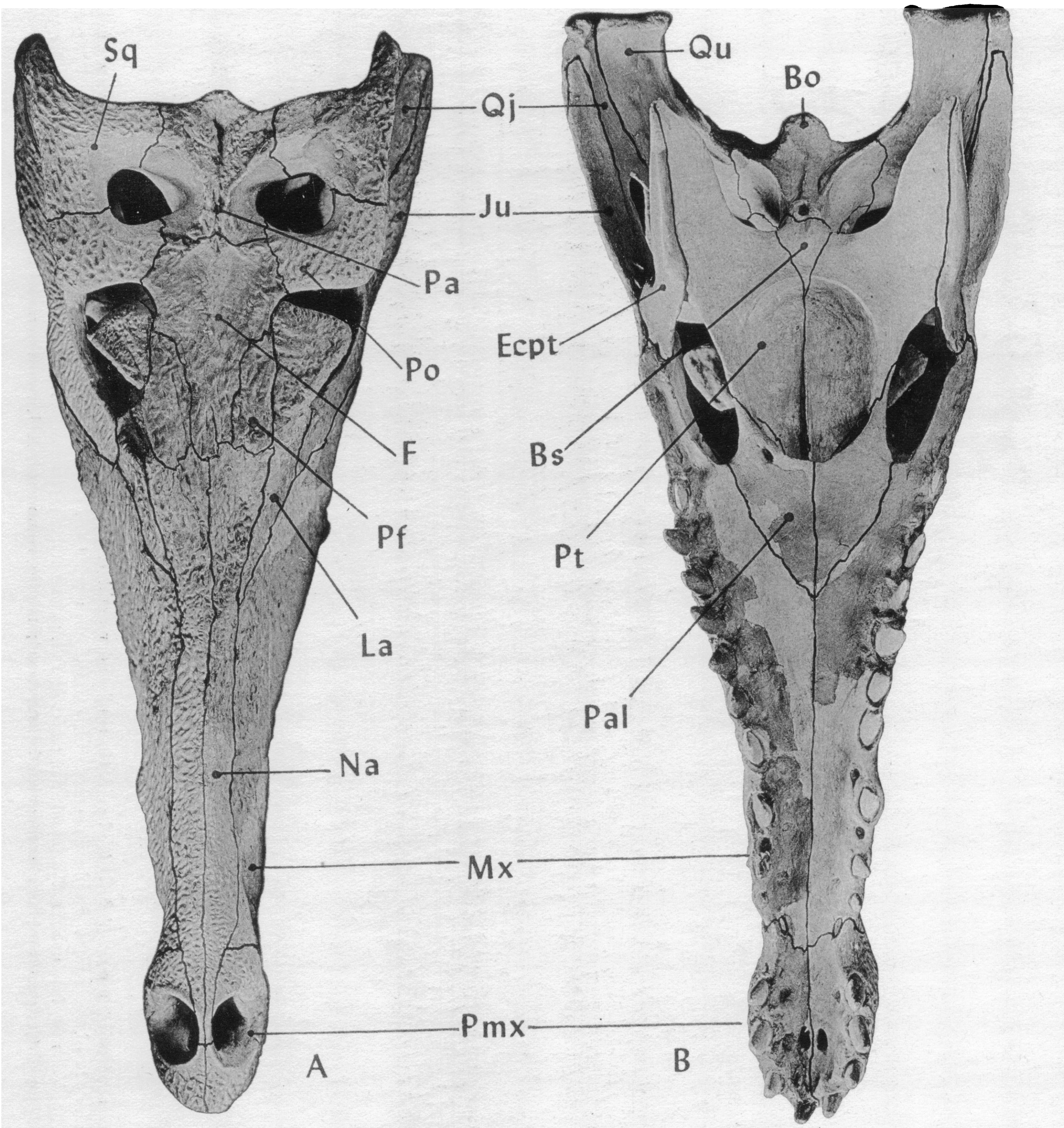
FIG. 18. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left angular, $\times\frac{1}{2}$. A, External lateral view; B, internal view.

owing to a long anterior process of the bone, extending forward beneath the dentary to a point below the last dentary tooth. Behind this process the external surface of the angular, which incidentally is rugose, rises to form a part of the lower border of the external mandibular foramen, while behind this opening the bone still continues to rise, to lap far up on the external surface of the ramus. The back portion of the angular is unknown, but from the articular it may be seen that the angular extended back beneath the surangular and articular to form the ventral surface of the postarticular process.

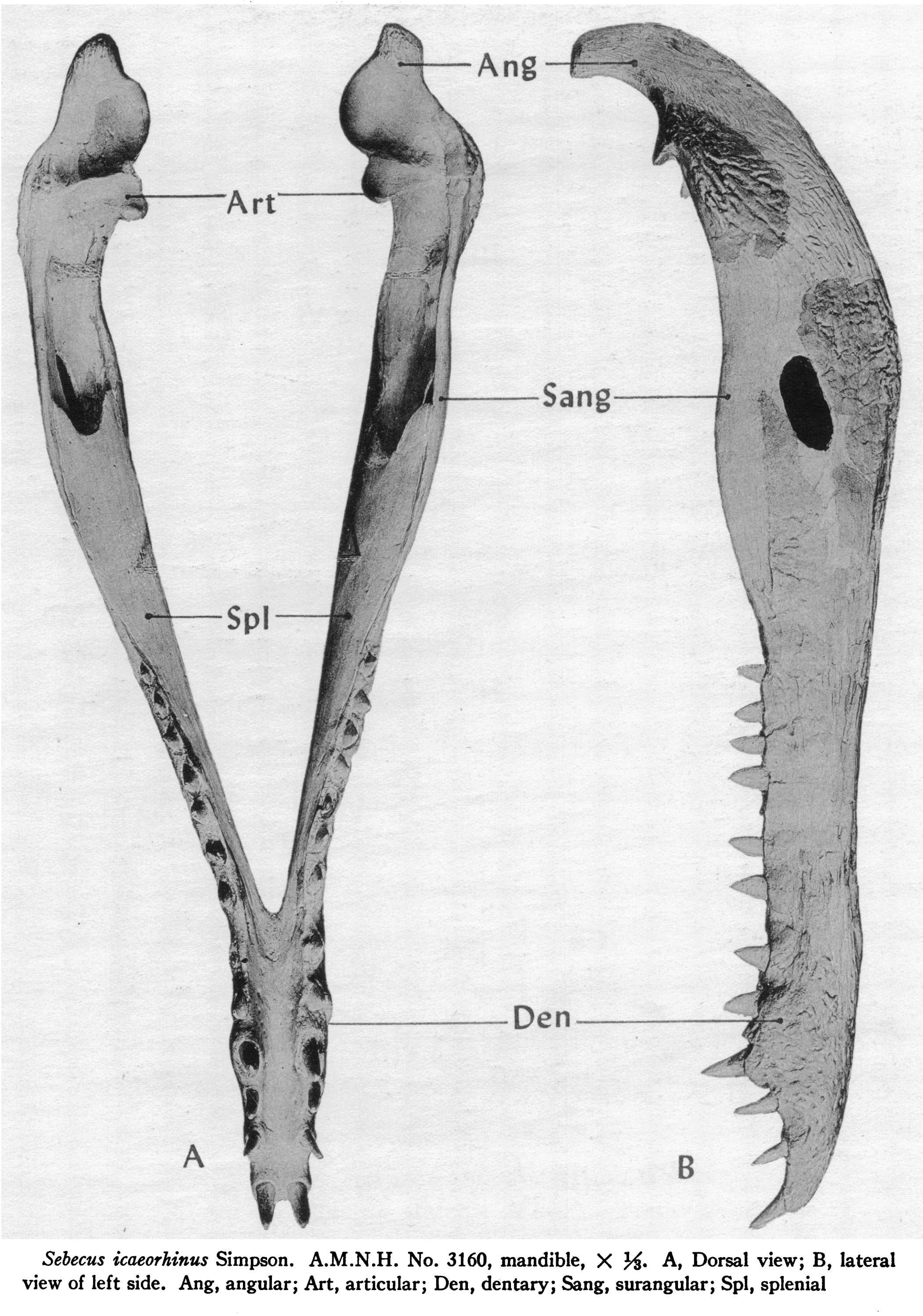
On its internal surface the angular shows certain important differences from the same element in many of the Eusuchia. On its



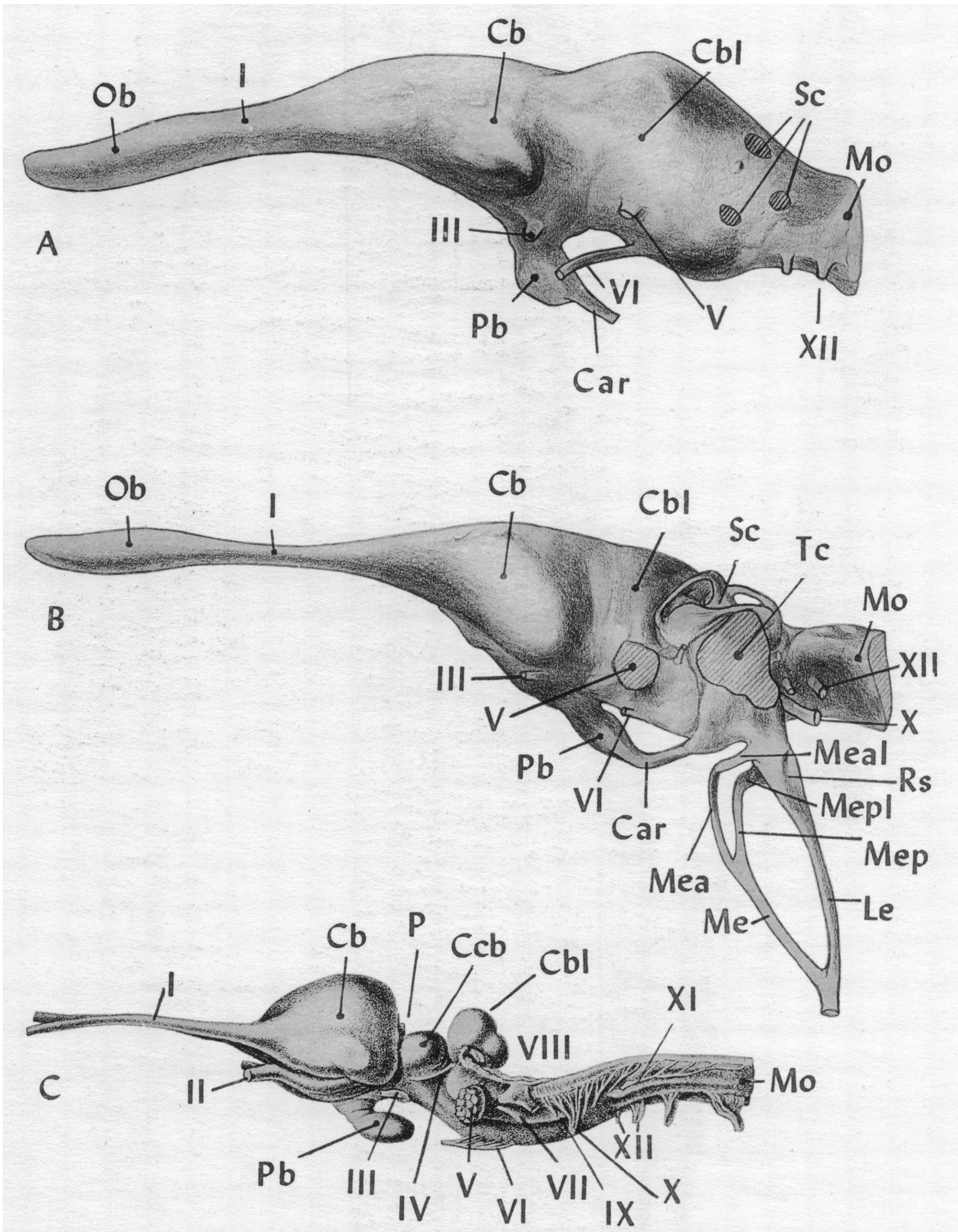
Sebecus icaeorhinus Simpson. A.M.N.H. No. 3160, skull and mandible, × ⅓. A, Lateral view of left side; B, occipital view of skull. Ang, angular; Bo, basioccipital; Bs, basisphenoid; Cf, carotid foramen; Den, dentary; Ecpt, ectopterygoid; Eo, exoccipital; F, frontal; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Pa, parietal; Pal, palatine; Pf, prefrontal; Pmx, premaxilla; Po, postorbital; Pt, pterygoid; Qj, quadratojugal; Qu, quadrate; Sang, surangular; So, supraoccipital; Sq, squamosal; XII, twelfth cranial nerve



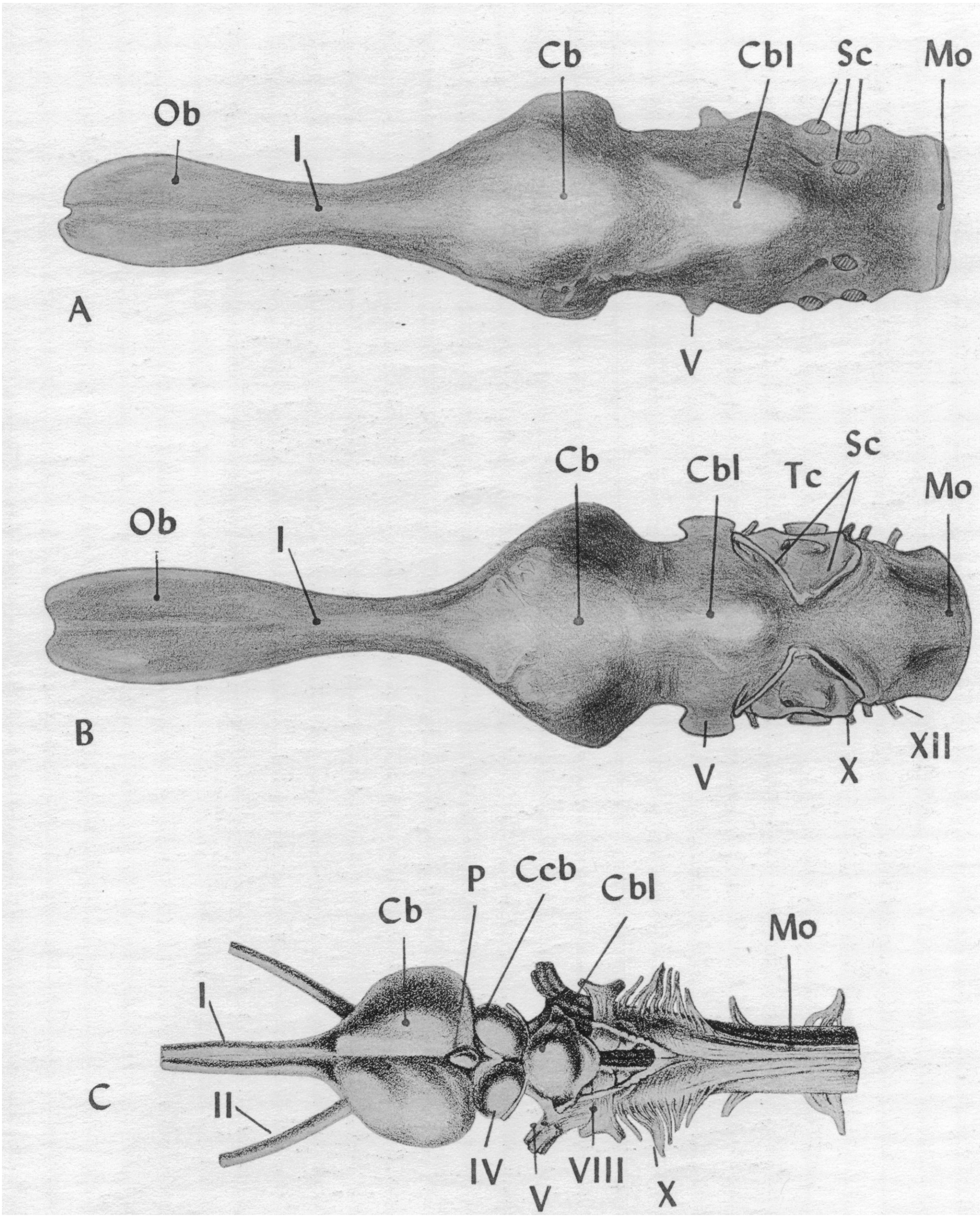
Sebecus icaeorhinus Simpson. A.M.N.H. No. 3160, skull, × ⅛. A, Dorsal view; B, palatal view. Bo, basioccipital; Bs, basisphenoid; Ecpt, ectopterygoid; F, frontal; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Pa, parietal; Pal, palatine; Pf, prefrontal; Pmx, premaxilla; Po, postorbital; Pt, pterygoid; Qj, quadratojugal; Qu, quadrate; Sq, squamosal



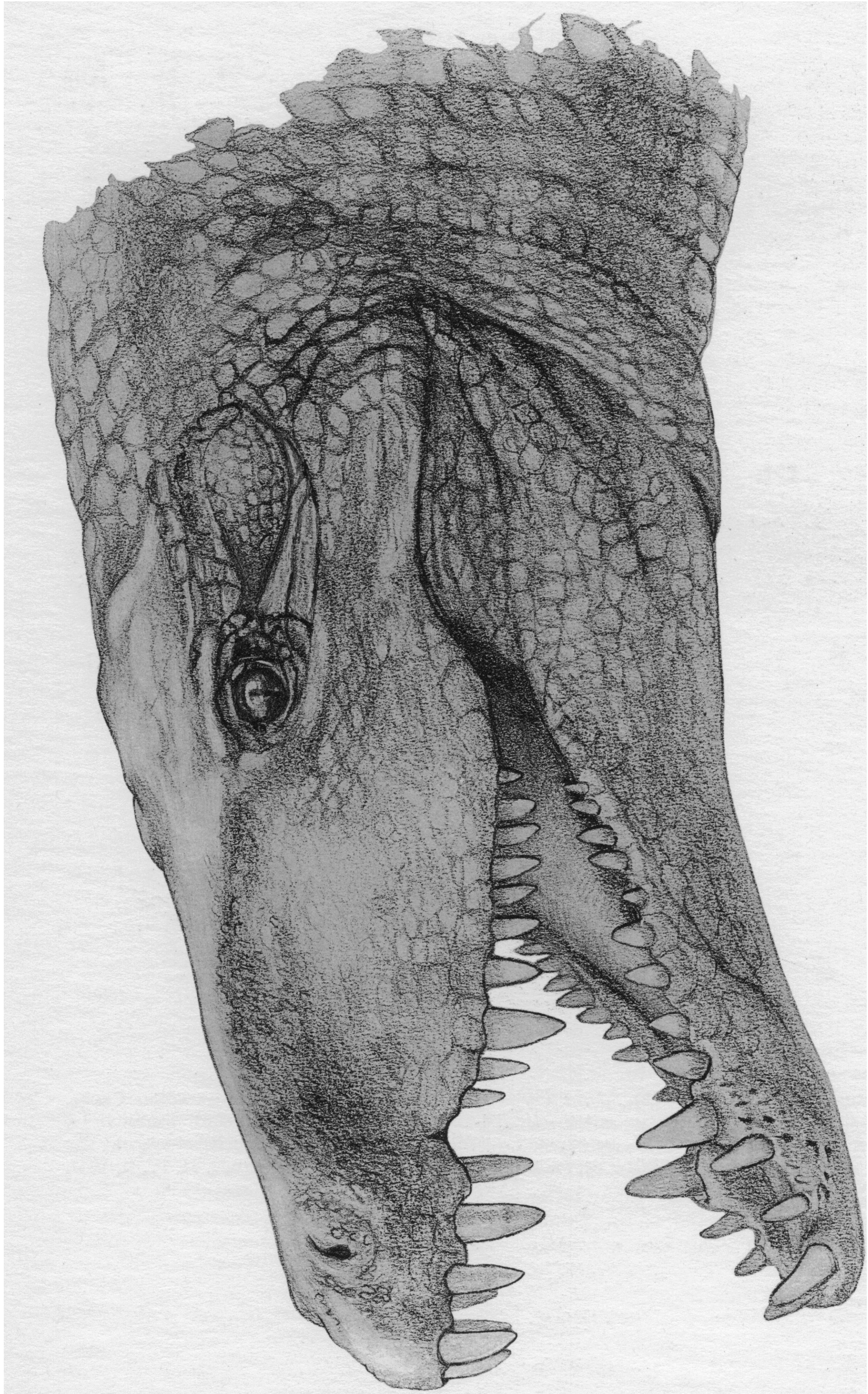
Sebecus icaeorhinus Simpson. A.M.N.H. No. 3160, mandible, × 1/3. A, Dorsal view; B, lateral view of left side. Ang, angular; Art, articular; Den, dentary; Sang, surangular; Spl, splenial



Endocranial casts of (A) *Sebecus icaeorhinus* Simpson and (B) *Crocodylus acutus* Cuvier, and the brain (C) of *Alligator mississipiensis* Daudin (from Hoffmann *in* Bronn). Left lateral views, × 1. Car, internal carotid artery; Cb, cerebrum; Cbl, cerebellum; Ccb, corpora bigemina; Le, lateral Eustachian tube; Me, median Eustachian tube; Mea, anterior branch of median Eustachian tube; Meal, left lateral branch of anterior median Eustachian tube; Mep, posterior branch of median Eustachian tube; Mepl, left lateral branch of posterior median Eustachian tube; Mo, medulla oblongata; Ob, olfactory bulb; P, pineal body; Pb, pituitary body; Rs, rhomboidal sinus; Sc, semicircular canals; Tc, tympanic cavity; I–XII, cranial nerves



Endocranial casts of (A) *Sebecus icaeorhinus* Simpson and (B) *Crocodylus acutus* Cuvier, and the brain (C) of *Alligator mississipiensis* Daudin (from Hoffmann *in* Bronn). Dorsal views, × 1. Cb, cerebrum; Cbl, cerebellum; Ccb, corpora bigemina; Mo, medulla oblongata; Ob, olfactory bulb; P, pineal body; Sc, semicircular canals; Tc, tympanic cavity; I, II, IV, V, VIII, X, XII, cranial nerves



Restoration by John C. Germann of the head of *Sebecus icaeorhinus* Simpson inner edge the angular curls around, in front of the articular, to form a low, free edge that runs far forward on the inner side of the jaw. At the very front end of the preserved part of this inner edge (its anteriormost extremity is missing) a surface can be seen that served for the articulation of either the splenial or the coronoid. Whichever bone may have extended down onto the angular at this point, it is quite evident that the inner wall of the ramus, formed by the conjoined splenial and coronoid, did not extend back relatively so far as is the case in the Eusuchia. For instance, in the eusuchian jaw the posterior border of the inner wall of the ramus, formed for the most part by the coronoid, extends back to such a degree that it is opposite about the middle part of the external mandibular foramen. Correlative with this backward extension of the inner wall of the ramus, a small internal mandibular foramen is commonly present, opposite the front of the external foramen, and bounded by the angular behind and the splenial in front. In *Sebecus*, however, the posterior border of the inner wall of the ramus is so far forward that it lies considerably in front of the external mandibular foramen. With the inner side of the ramus completely open opposite this foramen, there was no occasion for an internal foramen to be formed as in the Eusuchia.

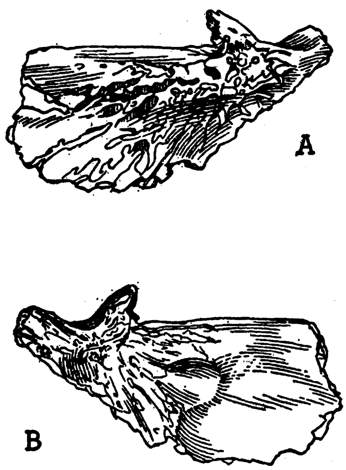


FIG. 19. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, left surangular, ×½. A, External lateral view; B, internal view.

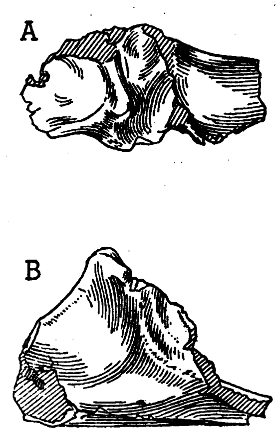


FIG. 20. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, right articular, ×½. A, Dorsal view; B, internal lateral view.

SURANGULAR: This bone, like the angular, is preserved in the *Sebecus* materials by a fragment, but again the fragment, plus supplementary information afforded by sutures on other bones, gives a fairly comprehensive picture as to the relationships of the whole element.

The surangular occupies a position above the angular, while anteriorly it laps over on the upper edge of the dentary. Although there is no definite evidence at hand, there cannot be much doubt that the surangular formed a part of the back border of the external mandibular foramen, as it does in the Eusuchia. In the glenoid region the surangular is laterally expanded to form the outer portion of the glenoid itself, while externally the surface is very strongly rugose. Internally it has a very strong articular surface for its junction with the articular. Behind the glenoid it would appear that the surangular extended back for some distance, finally coming to a point where it was compressed between the angular below and the articular above.

ARTICULAR: So far as may be determined from the rather broken fragment at hand, the articular in *Sebecus* is essentially similar to the same bone in the Eusuchia. Thus it was occupied by a transverse glenoid surface for articulation with the condyle on the quadrate. The glenoid is expanded backward in its medial-lateral portion, where the articular and angular join, correlative with a similar expansion in the articular surface of the quadrate. On its external edge the glenoid surface of the articular terminates abruptly, since the external portion of the glenoid is carried by the surangular. Naturally, there is a strong, expanded, sutural surface on the external surface of the articular, for junction with the surangular.

In front of the glenoid the articular is produced forward as a point, which joins the angular and surangular, while behind the glenoid the bone is produced back to form the upper surface of the strong postarticular process, for the attachment of the depressor mandibulae muscles.

THE DENTITION

The dental formula for *Sebecus* has already been discussed in the description of the premaxillary, maxillary, and dentary bones. However, it might be well to repeat here that *Sebecus* is characterized by the comparatively low number of teeth, for along with the specialization of the dentition in this crocodile there evidently was a loss of teeth in the posterior portions of the maxilla and the dentary. Consequently *Sebecus* has a smaller number of teeth than is to be seen in any of the recent eusuchians, and in most other crocodilians, for that matter. In this respect it approaches some of the mesosuchians, particularly the Notosuchidae, of which the type genus, *Notosuchus*, occurs in the Cretaceous of Patagonia. In this regard, an extreme of reduction in the dentition is reached by the notosuchian *Libycosuchus*, from the Cretaceous of Egypt, for this genus attained an almost edentulous condition.

Some comparisons of *Sebecus* with other crocodilians, with regard to the number of teeth, may be made as follows:

	Premaxilla	Maxilla	Upper	Dentary
Sebecosuchia				
Sebecus	4	10	14	13
Mesosuchia				
Notosuchus	4	7	11	10
Teleosaurus gladius	5	53–55	58–60	58–60
Eusuchia				
Osteolaemus	4	13	17	14–15
Gavialis	5	22–24	27–29	25–26

Of course one of the remarkable characters distinguishing *Sebecus* from other crocodilians (except *Baurusuchus*) is the strong lateral compression of the maxillary and of all but the first three dentary teeth. The premaxillary and the three anteriormost dentary teeth do not show this compression, but rather are rounded in cross section, as is the case in other crocodilians.

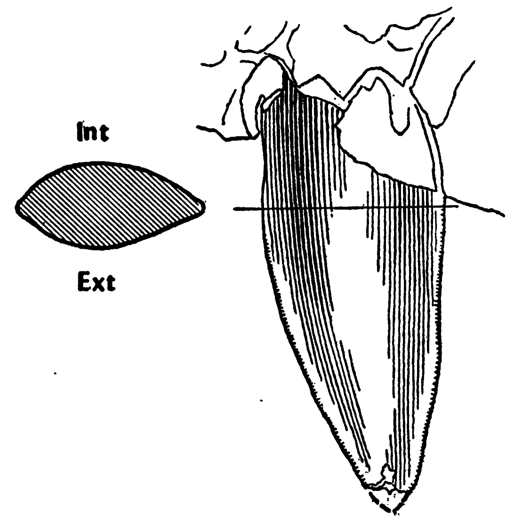


FIG. 21. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3160, seventh left maxillary tooth, ×2. A, Cross section of tooth near base; B, external lateral view. Note the serrations on the anterior and posterior edges of the tooth.

However, the teeth of *Sebecus*, and similarly those of *Baurusuchus*, are further distinguished from the teeth in other crocodilians by the fact that they have ridged, serrated edges. In the Eusuchia, for instance, there is a sharp ridge on the anterior and the posterior surfaces of each tooth (laterally placed in the front teeth) but these ridges are smooth, not serrated. In *Sebecus*, on the other hand, the serrations are invariably

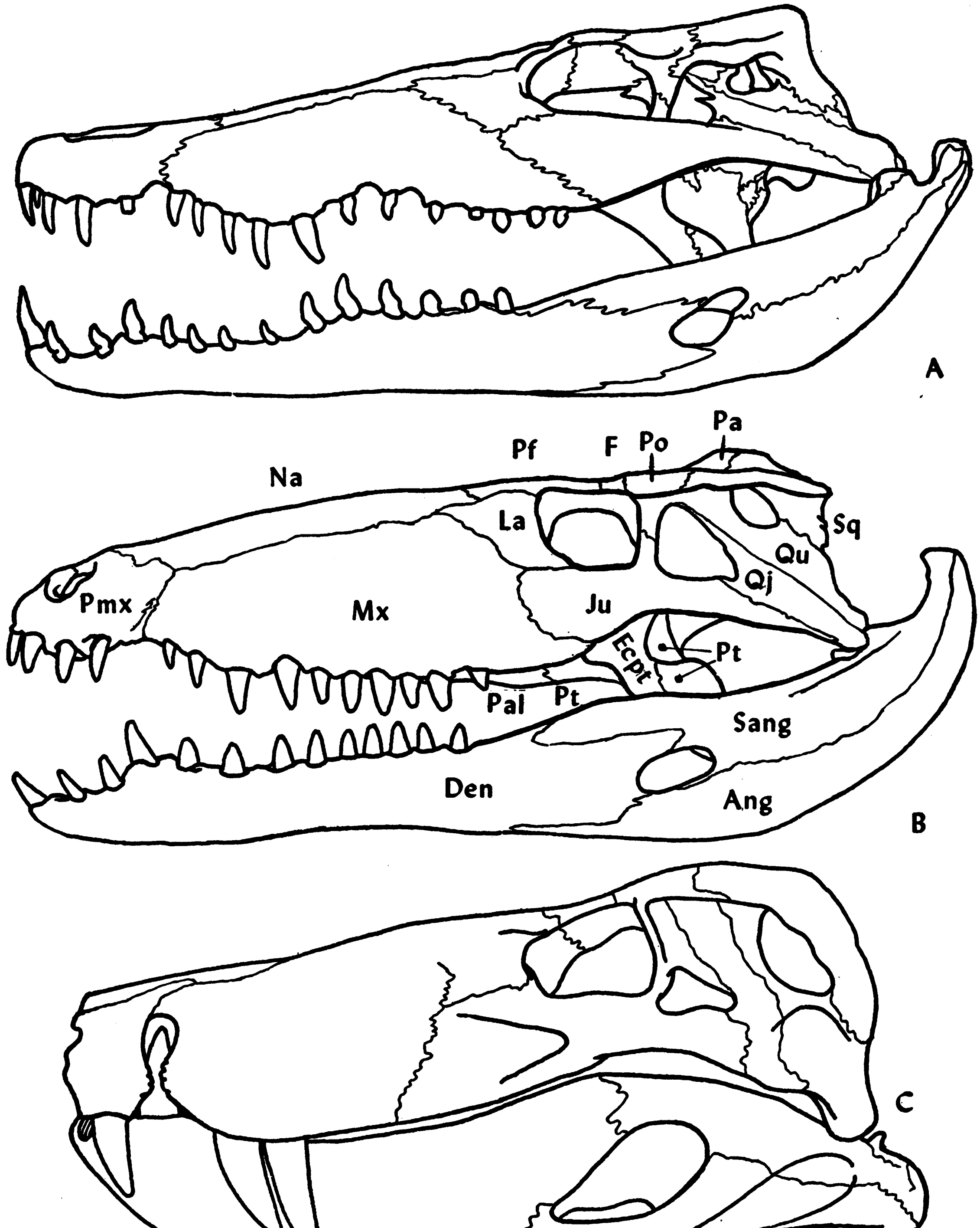


FIG. 22. Comparison of the skull and jaw in: A, *Crocodylus rhombifer* Cuvier (Eusuchia) modified from Mook; B, *Sebecus icaeorhinus* Simpson (Sebecosuchia); C, *Baurusuchus pachecoi* Price (Sebecosuchia) modified from Price. Left lateral views, not to scale. Ang, Angular; Den, dentary; Ecpt, ectopterygoid; F, frontal; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Pa, parietal; Pal, palatine; Pf, prefrontal; Pmx, premaxilla; Po, postorbital; Pt, pterygoid; Qj, quadratojugal; Qu, quadrate; Sang, surangular; Sq, squamosal.

present, even on the rounded premaxillary teeth in which the ridges are very faint. It was the discovery of these compressed teeth with serrated edges that led von Huene to express the opinion that in Patagonia the theropod dinosaurs had persisted into the Eocene period. Of course, without the evidence of the skull, his mistake was a natural one, for the teeth of *Sebecus*, by themselves, look for all the world like the teeth of a theropod dinosaur. This problem will be considered in more detail on another page.

The teeth of *Sebecus* are so arranged that those in the upper and lower jaws for the most part alternate, while the upper teeth naturally bite over the lower teeth. As has been noted above, the fourth dentary tooth bites up into a notch formed in the skull at the junctures of the premaxilla and maxilla, while the first dentary tooth, which is partially procumbent, bites between the first and second premaxillary teeth.

This arrangement of the teeth in *Sebecus* provides a strongly secant dentition, since the edges of the teeth sheared past each other rather closely. The shear in *Sebecus* is not to be compared in perfection of its development with the shear attained in the carnassial teeth of the carnivorous mammals, but it is none the less significantly evolved in this fossil genus. Moreover, opposing shearing edges are repeated many times over along the length of the jaws in *Sebecus*, which must have increased the scissors-like effect of the bite in this animal. Finally, the development of the articular surfaces between the quadrate and articular bones and the great downward extension of the pterygoid-ectopterygoid wings provided a strictly orthal motion to the jaws, as is the case in the persisting *Eusuchia*.

The shape and the development of the teeth in *Sebecus* described above indicate that the eating habits of this extinct crocodilian may have been somewhat different from what they are in the modern members of the order. Recent crocodilians are very aggressive, predatory carnivores. For a majority of them, the bulk of the diet consists of fishes, but all crocodilians will seize and devour any prey that they are able to capture. Consequently mammals and birds, especially the former, constitute no small portion of the crocodilian diet, and in the larger species the adult animals are a real menace to any but the very largest mammals that may venture into crocodilian-infested waters. The modern crocodilians generally seize their prey and gulp it down whole, but if a crocodilian manages to catch a large animal, the reptile will twist over and over rapidly, thereby tearing off a limb or a part of the body of the unfortunate victim. Often two crocodilians will get a hold on the same animal and twist in opposite directions, and by this method of cooperation they are able to reduce an animal of some size to pieces that they can crush and swallow.

Sebecus must have been predaceous, but it was probably a predator of a kind different from the modern crocodilians. The front teeth in this extinct reptile probably were for grasping, but most of the teeth—the compressed teeth of the maxillaries and the dentaries—were obviously cutting teeth. Therefore it would seem probable that *Sebecus*, after having seized its prey, was able to cut off large pieces of meat, or limbs, by a scissors-like action of the upper and lower jaws. In this respect, *Sebecus* may have had eating habits similar to those of the theropod dinosaurs, which it so closely paralleled, in so far as the development of the teeth is concerned.

THE POSTCRANIAL SKELETON

Of the postcranial elements discovered, all belong to A.M.N.H. No. 3159, and since this was a weathered specimen, the bones are rather poorly preserved. Unfortunately only a few postcranial bones were found; these will be described below.

VERTEBRA

One centrum of a cervical, or perhaps an anterior dorsal vertebra, was discovered, which is fortunate, for this bone shows the nature of the articular surfaces, an important feature in the classification of the Crocodilia, and of the Reptilia in general.

This vertebra is surprisingly small when compared with the skull, A.M.N.H. No. 3160. The evidence would seem to indicate, however, that No. 3159 is definitely smaller than No. 3160, perhaps on the order of 15 or 20 per cent in linear dimensions, and when this vertebral centrum is compared with the occiput of No. 3159, of which the complete condyle is preserved, there can be no doubt that there is an agreement in size between them. Consequently it is logical to assume that this vertebra belongs to the second specimen of *Sebecus* and is not an intruded part of another skeleton.

As mentioned above in the diagnosis, the vertebra is characterized particularly by the fact that both articular surfaces are amphicoelous. They are not strongly so; in fact they approach a condition that is almost amphiplatyan. Thus a primitive condition persists in the vertebrae whereby *Sebecus* shows definite relationships with the Mesosuchia.

Ventrally the centrum is compressed, with a median ventral ridge, which in its anterior portion is extended down to form a distinct hypapophysis. The presence of a hypapophysis on the cervical vertebrae is characteristic of the Crocodilia.

On the lateral surface of the centrum there is, on either side, a facet for the articulation of the capitulum of the rib, while dorsally there may be seen the sutures for the articulation of the neural arch upon the centrum.

Limb Bones

Femur: A broken right femur is preserved among the materials numbered A.M.N.H. No. 3159, and in addition there is a part of the distal end of another femur.

The femur of *Sebecus* is on the whole characteristically crocodilian. It is an elongated and rather slender bone, with the head of the femur set at somewhat of an angle to the shaft. On the ventral surface of the bone in its proximal region there is a faint trochanteric ridge, not nearly so pronounced as the trochanter in the modern Eusuchia. Proximally and in its mid-region the shaft of the femur is laterally compressed, so that in cross section its greater dimension is vertical, its lesser dimension horizontal. Distally the bone expands, and terminates in two distinct condyles, separated from each other by a well-defined fossa.

Fibula: In addition to the fragments of femora preserved, there is a small single fragment that has been identified as the distal end of the fibula. The small section of shaft preserved is approximately triangular in cross section, with one flat surface directed medially towards the tibia, and the other two surfaces facing anteriorly and posteriorly, respectively. At its termination the bone is expanded with an articular surface for the calcaneum or fibulare. The bone appears to be less expanded, with the shaft more angular and less rounded than is the same bone in the modern eusuchians.

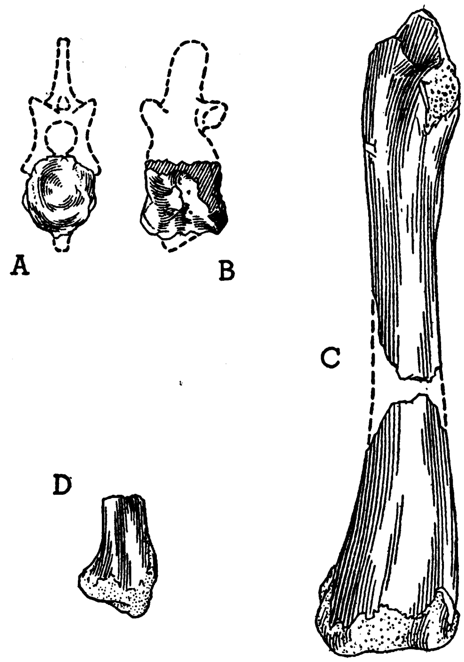


Fig. 23. *Sebecus icaeorhinus* Simpson. A.M.N.H. No. 3159, vertebra and limb bones, $\times\frac{1}{2}$. A, Centrum of cervical vertebra, anterior view; B, the same, left lateral view; C, right femur, anterior view; D, distal end of fibula, external lateral view.

THE BRAIN

Descriptions and comparisons of the known osteological elements in *Sebecus* having been presented, it may be of some value to consider so far as possible and as determined from an interpretation of the skull bones some points regarding the soft anatomy in this extinct crocodilian. It is possible to discuss to a limited extent the brain of

Sebecus (as interpreted from an endocranial cast), the Eustachian tubes, and the myology of the head. These subjects will be considered below.

With the prefrontals and frontal, the parietal, one postoptic, one exoccipital, and a partially preserved basisphenoid, it has been possible to obtain a partial endocranial cast of *Sebecus*, a difficult task most skilfully carried out by Mr. Otto Falkenbach of the American Museum Paleontological Laboratory. This endocranial cast of *Sebecus*, used in conjunction with a very fine endocranial cast of a recent *Crocodylus* (also made by Mr. Falkenbach), affords some opportunity for making an interpretation of the brain in the extinct genus and for comparing it with the brain in recent crocodilians.

The brain in *Sebecus* is, generally speaking, very similar to the brain in *Crocodylus*. There is a slight difference in the flexure of the brain in the two genera, because of the relatively lower position of the medulla oblongata in *Sebecus*, as compared with *Crocodylus*, which is in turn a reflection of the relatively deep skull in the extinct genus.

It would appear that the brain of *Sebecus* shows some difference from that of *Crocodylus* in the rather high position of the upper surface of the cerebellar region, again a reflection of the deep skull in the fossil form. An exact comparison is not possible in this respect, however, because of the lack of the supraoccipital bone in *Sebecus*.

In *Sebecus*, as in *Crocodylus*, there is a long olfactory tract running forward from the cerebral hemispheres and terminating anteriorly in the well-developed olfactory bulbs. In this regard it might be said that the shape of the olfactory bulbs is more clearly defined on the under surface of the frontal bones in *Sebecus* than is the case in *Crocodylus*.

In the recent crocodilians the cerebral hemispheres are marked by their shortness and breadth, the two of them being greater in combined breadth than they are in length. In *Sebecus* the cerebral hemispheres are perhaps somewhat narrower and longer than they are in *Crocodylus* or *Alligator*, and they taper more gradually into the olfactory stalk than they do in the recent crocodilians. Moreover, the expansion of the temporal lobe of the cerebrum in the extinct genus is less than in modern crocodilians, and all in all one gets the impression that the forebrain was enlarged to a lesser degree in *Sebecus* than it is in *Crocodylus* or *Alligator*. Naturally, this is what would be expected in a comparison of an Eocene crocodilian with a recent form, although it must be pointed out that the difference is not great, since these animals are representative of a phylogenetic line in which evolutionary change was comparatively slow.

At the base of the cerebral portion of the brain is the large and well-developed pituitary body, projecting posteroventrally beneath the mid-brain. This part of the brain is housed within the sella turcica in the basisphenoid bone, and its form in the Crocodilia is quite distinct. In *Sebecus*, it is somewhat elongated, and it tapers posteriorly from its rounded and rather thick anterior region.

As may be seen in the basisphenoid bone, the internal carotid arteries traversed the sella turcica in *Sebecus*, as they do in the eusuchians. A dissection of a recent crocodilian will show that on either side the artery, emerging from the tympanic cavity, enters the sella turcica from behind by a foramen, and leaves the sella turcica anteriorly by its enlarged anterior opening.

Behind that portion of the endocranial cast representing the cerebrum there is a drop in the upper profile and a lateral constriction, and this represents the region of the corpora bigemina or optic lobes. Evidently this part of the brain in *Sebecus* was very similar in development to the same region in the modern crocodilian brain.

Behind the optic lobes the upper profile of the endocranial cast of *Sebecus* rises again, as mentioned above, possibly an indication of an enlarged cerebellum in this genus. This part of the cast then descends very steeply to the medulla oblongata. In the anterior part of the medullar region is the large stalk of the complex trigeminus nerve, which passed from the brain to various parts of the head by way of the foramen ovale. The other nerves shown in the endocranial cast of *Sebecus* are the third or oculomotor, beneath the posterior part of the cerebrum, the sixth or abducens, projecting forward from the base of the brain on either side of the pituitary body, and the large hypoglossal, at the posterior end of the medulla.

The endocranial cast of *Sebecus*, as compared with that of *Crocodylus*, is shown in plates 14 and 15.

THE EUSTACHIAN TUBES

The recent Crocodilia are characterized, among other things, by an unusual complexity in the development of their Eustachian tubes. In fact, the development of the tubes is advanced over anything seen in any other vertebrate.

The exoccipital and quadrate bones, the basisphenoid, and the basioccipital of the supplementary specimen of *Sebecus* all indicate that there was a development in this extinct genus similar to that in the recent crocodilians. Since the specialization of the Eustachian tubes in the recent crocodiles is of very great interest and generally not well known, it will be described briefly at this place. This description will serve to show in an approximate manner the degree to which the Eustachian tubes were specialized in *Sebecus*.

In the Crocodilia there is a ventrally directed medial opening in the skull, between the occipital condyle and the posterior nares and at the junction of the basioccipital and basisphenoid bones. This was first shown by Owen in 1850 to be the exit for a medial Eustachian tube. On either side of this foramen there is a very small foramen, also between the basioccipital and the basisphenoid, for the lateral Eustachian tubes—seemingly the homologues of the Eustachian tubes in other tetrapods.

The two lateral tubes join the median tube at a point just below the median foramen, and there is a single common opening into the throat behind the posterior nares.

The median Eustachian tube passes upward through the basioccipital bone, and at some distance up from the foramen it divides into an anterior and a posterior branch. The anterior branch of the median tube continues forward into the basisphenoid bone, and in turn divides into two lateral branches, and each of these branches enters an enlargement of the lateral Eustachian tube which Owen designated as the rhomboidal sinus. From the rhomboidal sinus a single passage connects to the tympanic cavity. In a like manner, the posterior median branch divides into lateral branches, each of which enters the rhomboidal sinus on either side.

This complex system of Eustachian tubes is shown by plate 14.

In the material of *Sebecus* at hand a portion of the median Eustachian tube can be seen in the basioccipital bone, and in addition the ventral openings for the lateral tubes. Also, in the exoccipital is the cavity in which the rhomboidal sinus was located. From these evidences of structure in the extinct form, and in addition from the large size of the tympanic cavity, it is reasonable to suppose that the development of the complex system of Eustachian tubes was essentially the same in *Sebecus* as it is in the recent crocodilians, as described above.

It is not in the least surprising to find the Eustachian tubes complicated in *Sebecus* as they are in the modern crocodilians, because the evidence indicates that this unusual specialization was established very early in the history of the order. Thus the system of median and lateral Eustachian tubes, presumably with intercommunicating tubes joining them, is to be seen in the Jurassic teleosaurs and thalattosuchians as described by Andrews. Whether this specialization of the Eustachian system had already taken place in the Triassic ancestral Protosuchia is not determinable in the present stage of preparation of the unique specimen of *Protosuchus*. Be that as it may, the fact is that the complex Eustachian system is certainly an ordinal character for all of the post-Triassic crocodilians, and its presence in *Sebecus* is one more character in the long list of anatomical features that mark this genus as thoroughly crocodilian, in spite of its aberrant proportions and appearance.

MYOLOGY OF THE HEAD OF *SEBECUS*

General Remarks

The restoration of the muscles in extinct vertebrates is at best a difficult task, fraught with many chances for error. We know that in modern vertebrates the origins and insertions of muscles are variously adapted, so that even in closely related genera the relationships of the same muscle may differ considerably. Moreover, the adaptations that cause these differences in the relationships of muscles to bones may not be apparent in the bony structure, so that frequently the osteology of an animal is not entirely a safe guide as to its myology. Therefore, when we deal with extinct forms, especially those forms that are unlike any persisting related forms, the difficulties of interpreting the muscular relationships are thereby greatly augmented.

Sebecus is a crocodilian which, despite its clear crocodilian affinities, is quite different from any persisting member of the order. This fact points to the difficulties to be encountered in restoring the musculature of this extinct animal. On the other hand, in their development the individual skull bones, despite differences in proportions, show so many resemblances to the same bones in the persisting Eusuchia that it is not unreasonable to expect the muscles in the living forms to be fairly accurate guides as to the development of the same muscles in the extinct genus. Upon this premise an attempt has been made to restore the musculature of the head in *Sebecus* as described and figured below.

In a discussion of the muscles of the Crocodilia, or of any other reptiles for that matter, the problem of nomenclature looms large. Various names have been applied by different authors to the jaw muscles in the reptiles, with the result that there is considerable confusion and no very great uniformity to be found among the several works that bear upon this subject. The earlier authors used names that had been applied to mammalian muscles; subsequently there was a tendency to apply new names to the muscles in the lower vertebrates—names that would express functions rather than any assumed homologies with like muscles in the mammals. Thus, in 1919 Adams, in his review of the phylogeny of the jaw muscles and following precedents set by other authors, used the term adductor mandibulae for the muscles closing the jaws in the fishes and innervated by the third branch of the fifth cranial nerve. In the amphibians, reptiles, and birds these muscles were termed the capiti-mandibularis and pterygoideus muscles, which in the mammals became the masseter, temporalis, pterygoideus, and certain other small muscles.

In 1926 Lakjer, in a very thorough review of the jaw musculature of the Sauropsida, proposed a system of nomenclature based upon functions, and more or less uniform throughout the group. This system was followed by Anderson in 1936, in his comparison of the jaw musculature of the extinct phytosaur, *Machaeroprosopus*, with certain modern reptiles, particularly the alligator and *Sphenodon*.

In the present work both Lakjer's and Adams' terms are used in discussing the jaw

NOMENCLATURE OF JAW MUSCLES IN THE CROCODILIA

Edgeworth, 1907	Adams, 1919		Lakjer, 1926; Anderson, 1936	
Innervated by the fifth cranial nerve				
Temporal	Capiti-mandibularis	superficialis medius profundus	Adductor mandibulae externus	superficialis medialis profundus
			Adductor mandibulae posterior	
	Capiti-mandibularis (in part)		Adductor mandibulae internus	Pseudotemporalis Pterygoideus dorsalis Pterygoideus ventralis Intramandibularis
Pterygoid	Pterygoideus	anterior posterior		
Innervated by the seventh cranial nerve				
	Depressor mandibulae		[Depressor mandibulae]	

muscles of *Sebecus* as compared with the same muscles in modern crocodiles. It is felt that by doing this there will be less chance for confusion than if either system were used alone, with no attempt at correlation with the other system of nomenclature. To make the names of the jaw muscles readily understandable, perhaps it may be well to include a table at this place which shows the synonymies of muscle names in the Crocodilia, as applied by several authors.

The Jaw Muscles

Adductor mandibulae externus Lakjer
Capiti-mandibularis superficialis and *medius* Adams
Adductor mandibulae externus superficialis

Alligator: This outer slip of the temporal muscle mass arises along the outer edge of the quadrate between the jaw articulation and the postorbital and, descending as a thin sheet, inserts on the dorsal face of the surangular.

Sebecus: There is every reason to think that the relationships and the development of this muscle in *Sebecus* were essentially the same as in *Alligator*. In *Sebecus*, however, this muscle was proportionately longer than the same muscle in the alligator, because of the deep skull and jaw of the extinct genus.

Adductor mandibulae externus medialis

Alligator: According to Lakjer (1926) and to Anderson (1936) the medial portion of the temporal muscle mass has two heads, an anterior one arising from the dorsal portion of the medioventral face of the postorbital and a posterior head arising from the anterior part of the rostral face of the quadrate, deep to the superficial slip, described above. These two heads join to form a thin plate of muscle which is inserted upon the dorsal face of the surangular, underneath the superficial slip of the muscle.

Sebecus: It would seem probable that this muscle slip had the same relationships in *Sebecus* as in the alligator. Again, however, this muscle must have been long, by reason of the deep skull of the extinct crocodilian.

Adductor mandibulae externus profundus

Alligator: Anderson has described this muscle in detail, showing how in the alligator it consists of four portions, located deep to the medialis slip. There is a rostral slip, the origin of which is on the postoptic behind the eye, and the fibers of this muscle are directed ventrally to insert on the intermuscular tendon of what Lakjer had termed the intramandibularis muscle. Of more importance in the alligator are the middle slips of this muscle, which originate upon the quadrate, squamosal, and parietal within the supratemporal fossa and are inserted in part upon the intermuscular tendon of the intramandibularis muscle and in part upon the medial face of the surangular. Finally there is a caudal slip originating upon the quadrate, deep to the medialis slip, and inserting upon the medial face of the angular and surangular, in front of the articular.

Sebecus: In *Sebecus* the bones on the posterior and internal border of the supratemporal fossa rise abruptly from the level of the frontal, as already described. Specifically these are the parietal and squamosal bones, elevated into a sort of crest at the back of the skull. Moreover, there is a strong crest or edge formed along the back and inner side of the fossa, where it is bounded by the parietal and squamosal bones, and there cannot be much doubt that this raised rim afforded a particularly strong and expanded origin for the profundus muscles. In addition, the supratemporal fossa in *Sebecus* is relatively larger than it is in *Alligator* and many other recent eusuchians. These correlated developments point to the presence of a rather large and strong profundus muscle mass in *Sebecus*. In this connection it may be recalled that the inner wall of the mandibular ramus, formed by the splenial and the coronoid, extends back to a much lesser degree in *Sebecus* than it does in the modern eusuchians. Thus, the profundus group of muscles, inserting in the suprameckelian fossa, would have more room in which to bulge in *Sebecus* than is the case in the modern crocodilians, and this again is an indication that these muscles in *Sebecus* may have been stronger than the same muscles in the Eusuchia.

Adductor mandibulae posterior Lakjer
Capiti-mandibularis profundus Adams

ALLIGATOR: This is an independent muscle in the Crocodilia, located entirely behind the mandibular ramus of the trigeminal nerve. The origin is on the deep portion of the quadrate behind the foramen ovale, and the insertion is on the lower surface of the angular along the posterior part of the lateral mandibular fenestra and on the inner wall of the angular, medial to this fenestra. The muscle is split in its lower portion by the insertion of the pseudotemporalis.

SEBECUS: The origin and insertion of this muscle in *Sebecus* must have been essentially the same as in the modern crocodiles. Here again, however, the muscle was elongated in the fossil form, and its direction must have been more nearly vertical than it is in *Alligator*. In this latter genus the muscle is inclined at an angle of about 45 degrees, whereas in *Sebecus* the angle was more on the order of 60 degrees.

Adductor mandibulae internus Lakjer
Pseudotemporalis
Capiti-mandibularis (in part) Adams

ALLIGATOR: The pseudotemporalis has its origin on the postoptic, just in front of the foramen ovale, and it is inserted between the two layers of the adductor mandibulae posterior, described above. According to Anderson the functions of these two muscles are closely related.

SEBECUS: One can only assume that the same muscle was present in *Sebecus*.

Pterygoideus

Modern crocodilians are characterized by the very great development of the pterygoid muscles, the anterior slips of which extend far forward into the skull, while the posterior slips are so greatly enlarged as to form swellings on the back of the lower jaws. As Anderson has shown, this muscle is separable into four heads in the alligator, one of which is anterior in position, and three posterior.

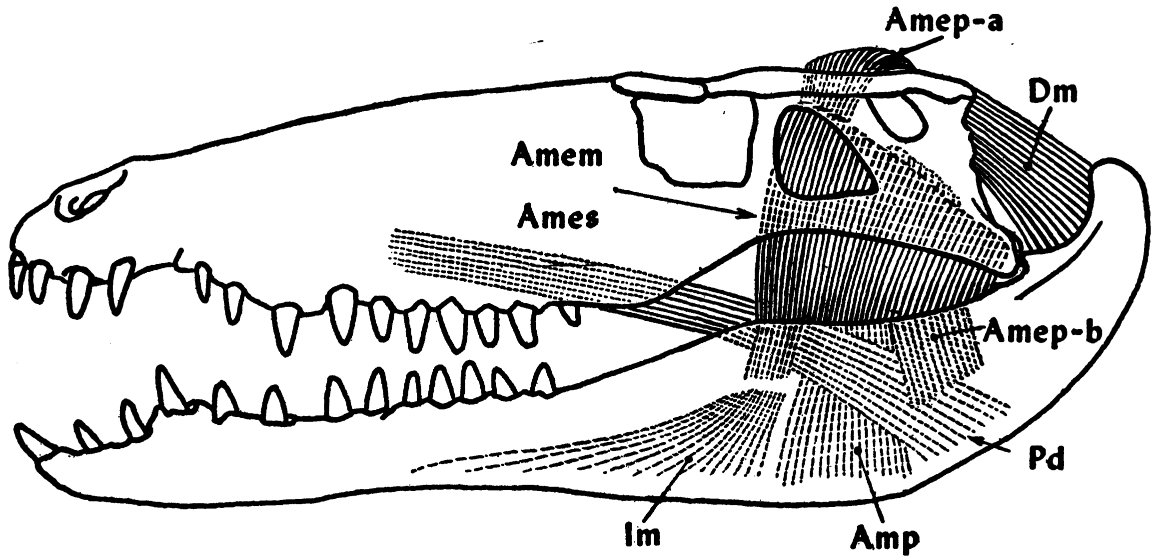


FIG. 24. Diagrammatic reconstruction of the jaw muscles in *Sebecus icaeorhinus*. Amem, Adductor mandibulae externus medialis; Amep-a, adductor mandibulae externus profundus, rostral and middle slips; Amep-b, adductor mandibulae externus profundus, caudal slip; Ames, adductor mandibulae externus superficialis; Amp, adductor mandibulae posterior; Dm, depressor mandibulae; Im, intramandibularis; Pd, pterygoideus dorsalis.

Pterygoideus dorsalis Lakjer
Pterygoideus anterior Adams

ALLIGATOR: The crocodilians are characterized by the forward extension of the anterior slip of the pterygoid complex, so that it is carried far forward within the muzzle of the skull. In the alligator this muscle arises beneath and in front of the orbit, as far forward as the posterior wall of the olfactory capsule, and it is attached over a broad area to the dorsal surface of the palatal plate of the maxilla, to the edge of the palatine and to the upper surface of the pterygoid above the nasal passage. It is inserted on the medial surface of the angular below and in front of the articulation. There is also a tendon extending to the intermuscular tendon of the intramandibularis.

SEBECUS: The evidence would seem to indicate that the relationships of the anterior pterygoid muscle in *Sebecus* were essentially similar to those existing in the modern crocodilians. The internal surface of the maxilla in this extinct form shows that the cartilaginous posterior wall of the olfactory capsule met the inner surface of the maxilla along a line above the space between the fourth and fifth maxillary teeth. This then determines the forward limits of the origin for this muscle.

Pterygoideus ventralis Lakjer
Pterygoideus posterior Adams

ALLIGATOR: There are three parts to this division of the pterygoid group in the alligator, and these have been designated by Anderson as "A," "B," and "C." Portion A, arising by a tendon from the ventral tip of the ectopterygoid, wraps around the posterior end of the lower jaw to insert on the lateral faces of the angular and surangular on the postarticular process. In its posterior extensions this muscle becomes very fleshy and forms a large bulge on the posteroventral portion of the lower jaw. The second part of the posterior pterygoid, "B" of Anderson, originates along the posterior margin of the pterygoid bone and is inserted on the ventromedial faces of the angular and articular. The third portion of this muscle group arises from the medial posterior edge of the pterygoid bone and from the basisphenoid and is inserted upon the posterior portion of the postarticular process.

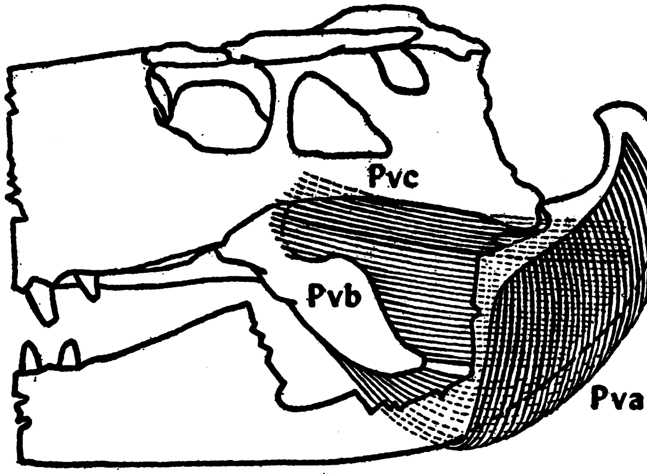


FIG. 25. Diagrammatic reconstruction of the jaw muscles in *Sebecus icaeorhinus*. Pva, Pterygoideus ventralis, portion "A"; Pvb, Pvc, pterygoideus ventralis, portions "B" and "C."

SEBECUS: Here again the relationships of the muscles in *Sebecus* were probably very similar to what they are in the modern alligator. Consequently, so far as may be determined, the above description for the alligator may be taken as indicating essentially the conditions that probably held for *Sebecus*.

Intramandibularis

This muscle, described by Anderson as a separate entity, was not differentiated from the capiti-mandibularis by Adams (1915). It is distinguished as a separate muscle by Lakjer because it lies medial to the mandibular ramus of the trigeminal nerve. Anderson makes the following remarks concerning the intramandibularis muscle:

"This muscle may be regarded as an adaptation of the adductors of the mandible to the elongation of the lower jaw. With elongation of the jaw mechanical advantage must be gained by increasing the distance between the application of the force (muscle insertion) and the fulcrum (jaw articulation). Hence we find the muscle insertions within the primordial canal of the mandible migrating forward. As such insertions proceed anteriorly to underlie the dentigrous part of the jaw, a tendinous area must develop within the muscle to ride over the coronoid at the anterior end of the aditus of the primordial canal. Thus the muscle within the jaw becomes a separate muscle arising from this tendon. The insertion upon this tendon of muscles of the internal and external adductor groups permits both to take advantage of the anterior insertion gained by the m. intramandibularis" (Anderson, 1936, p. 565).

ALLIGATOR: This muscle arises from the tendon that receives the insertions of the rostral and middle slips of the adductor mandibulae externus profundus, as well as a slip from the anterior pterygoid. The tendon rides over the coronoid, and the muscle inserts in the meckelian fossa of the mandible, extending forward beneath the lower teeth.

SEBECUS: It is probable that much the same relationships held for *Sebecus* that are seen in the modern alligator. Because of the anterior position of the coronoid in the fossil form, the tendinous connection between the intramandibular muscle and the temporal muscles above it may have been placed somewhat farther forward than it is in *Alligator*.

Depressor mandibulae

This single muscle opposes all of the muscles previously described. It is the great disparity of strength between the powerful adductor muscles of the jaws and the single depressor that accounts for the fact that in the crocodilians the power to open the jaws is relatively slight, even though their closing power is tremendous.

ALLIGATOR: The depressor mandibulae arises for the most part on the occipital portion of the squamosal and is inserted upon the postarticular process of the mandible.

SEBECUS: Similarly, in *Sebecus* the depressor mandibulae muscle ran from that part of the squamosal on the back of the skull to the postarticular process of the mandible. It is interesting to see that even though the postarticular process in *Sebecus* is directed strongly upward so that it extends high above the glenoid (in comparison with the almost horizontal process in the alligator), the direction of the muscle in the two genera is approximately the same. This is owing to the fact that the skull in *Sebecus* is so deep that the origin of the muscle is comparatively much higher than it is in *Alligator*. In other words, both the origin and the insertion of the muscle have been raised in the fossil form, with the net result that the direction and action of the muscle must have been about the same as they are in the persisting Eusuchia.

THE NECK MUSCLES

It is to be assumed that the neck muscles of *Sebecus* were essentially similar in their origins and insertions, relationships and functions to the muscles of modern crocodilians. Unfortunately, since no cervical vertebrae are completely preserved, it probably is not feasible to attempt restorations of the muscles connecting the occiput with the anterior vertebrae. However, some attempt to restore the areas of insertions for the muscles leading to the occiput may be in order, and this will be described below.

In the modern crocodilians the occiput is low and wide, and the spines of the cervical vertebrae are correspondingly low. Therefore, one is led to conclude that in *Sebecus*, with a rather high occiput, the spines of the cervical vertebrae may have been somewhat elongated. This in turn leads to the supposition that there were relatively increased areas for the origins and insertions of the neck muscles in the extinct genus, as compared with modern eusuchians, and therefore relatively strong muscles in the fossil form. Indeed, one character whereby *Sebecus* may be compared with modern crocodilians is the comparatively expanded occiput to be seen in the extinct genus.

For instance, as seen in occipital view, the occiput of *Sebecus* (the area included by the occipital surfaces of the supraoccipital, squamosal, exoccipital, and basioccipital bones) has an area that is approximately 30 per cent greater than the same area in an alligator with a corresponding occipital width. The figures are as follows:

	Area of Occiput
Sebecus	126 sq. cm.
Alligator	98 sq. cm.

The comparison is shown also by figure 26.

A few remarks as to the probable insertions of muscles on the occiput of *Sebecus* follow. The occipital muscles of the modern alligator,

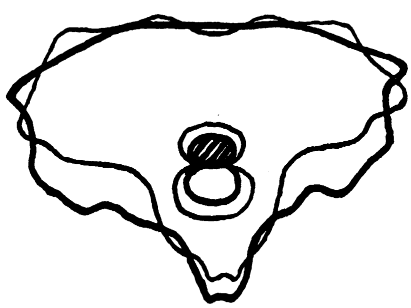


FIG. 26. Comparison of the relative areas of the occiput in *Sebecus* (heavy line) and *Alligator* (light line).

as described by Anderson, are used as a guide to the restoration of the insertions in *Sebecus*, although Anderson's terminology is not used in this connection.

Depressor mandibulae

This, the muscle for closing the jaws, has already been described. In *Alligator* the origin for the muscle is on the occipital surface of the squamosal, whence it stretches to the postarticular process of the mandible. The same relationships undoubtedly held in *Sebecus*. Consequently the muscle in *Sebecus* may have had a broad, low origin, although it is quite possible that in the fossil it was confined to the inner part of the squamosal, since the external portion of this bone runs almost parallel to the course of the muscle.

Rectus capitis posterior

It is possible that there were two insertions of this muscle on the occiput of *Sebecus*, a superficialis part on the supraoccipital bone, medial to the depressor mandibulae, and a profundus part on the exoccipital, below the depressor mandibulae. In *Alligator* this is a broad muscle inserting on both the exoccipital and the supraoccipital, below and somewhat median to the depressor mandibulae.

Obliquus capitis magnus

In *Sebecus* this muscle probably was inserted for the most part on the exoccipital, as it is in *Alligator*, in part deep, and in part lateral to the rectus capitis muscle.

Longissimus capitis

It is probable that there were two insertions on the occiput in *Sebecus*, a transversalis capitis part, to the external tip of the exoccipital, lateral to the rectus capitis posterior and the obliquus capitis, and a more ventral transversalis cervicis portion, to the lower border of the exoccipital and possibly in part to the basioccipital. Muscles showing these relationships are to be seen in the alligator.

Rectus capitis anterior

This muscle, to judge by the alligator, was inserted in *Sebecus* by a tendon to the expanded tubercles at the suture between the basioccipital and basisphenoid bones.

Of the above neck muscles inserting upon the skull, the rectus capitis posterior group served for extension of the head, the rectus capitis anterior and the longissimus capitis pars transversalis cervicis for flexion of the head, and the obliquus capitis magnus and longissimus capitis pars transversalis capitis for rotation and abduction of the head.

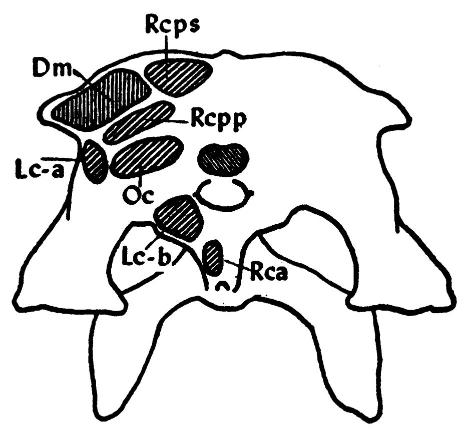


FIG. 27. Diagrammatic reconstruction of the areas of insertion of the neck muscles and one jaw muscle on the occiput of *Sebecus*. Dm, Depressor mandibulae; Lc-a, longissimus capitis, transversalis capitis portion; Lc-b, longissimus capitis, transversalis cervicis portion; Oc, obliquus capitis magnus; Rca, rectus capitis anterior; Rcpp, rectus capitis posterior, profundus portion; Rcps, rectus capitis posterior, superficialis portion.

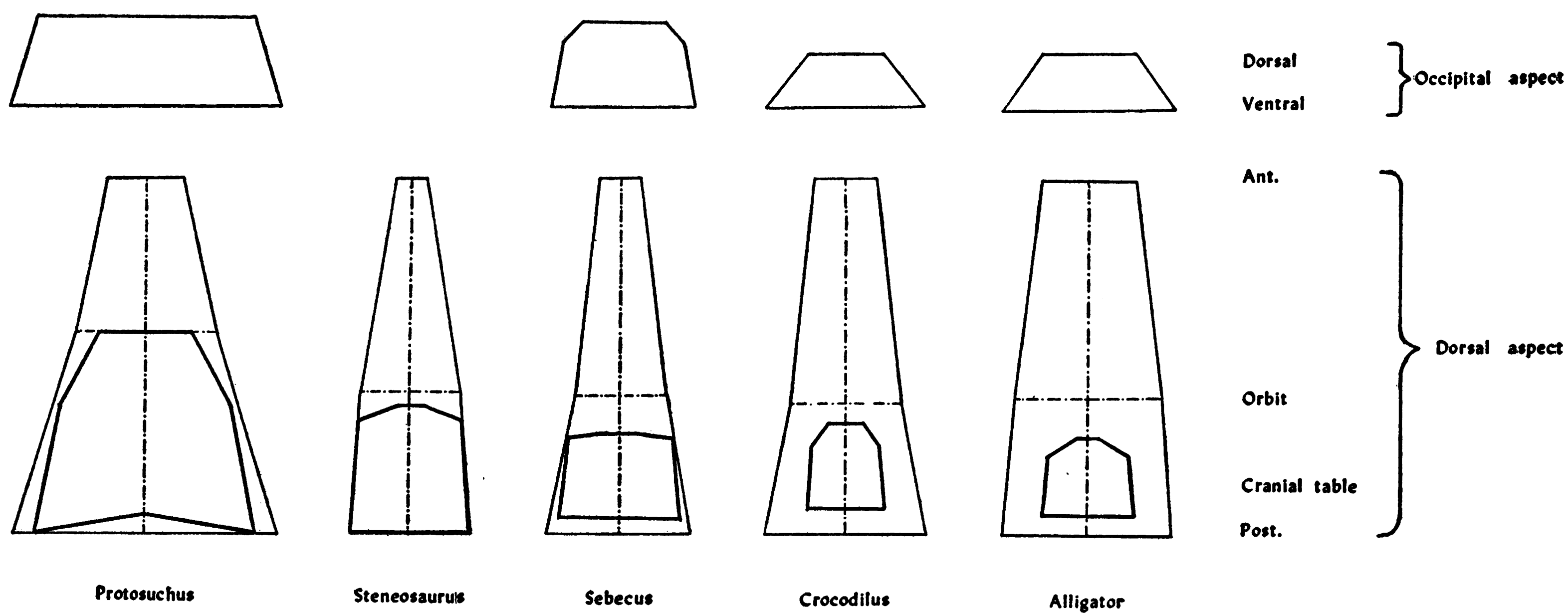


FIG. 28. Diagrammatic comparison of the general shapes of the skulls of several crocodilians, in occipital and dorsal aspects. Length of skulls reduced to unity, and other measurements in proportion. This figure gives a comparative diagrammatic impression of the depth of the skull as related to its width in the occipital region, the position of the orbit and the shape of the cranial table, when the length of the skull is reduced to unity. *Protosuchus* (Protosuchia), *Steneosaurus* (Mesosuchia), *Sebecus* (Sebecosuchia), *Crocodylus*, and *Alligator* (Eusuchia).

SKULL PROPORTIONS OF *SEBECUS* AND OF OTHER CROCODILIANS

GENERAL REMARKS

Sebecus HAS ALREADY BEEN COMPARED morphologically with other crocodilians, and this comparison has covered the bones of the skull and jaw, the teeth, the postcranial elements, so far as they are known, and certain soft structures as interpreted by the osteology. It has already been emphasized that *Sebecus* is distinct from all other crocodilians except *Baurusuchus* because of its high, narrow skull and jaw, and its laterally compressed maxillary and posterior dentary teeth. These peculiarities of proportion at once distinguish *Sebecus*, *Baurusuchus*, and by inference the Sebecosuchia, from all of the Protosuchia (known from the single genus *Protosuchus*), Mesosuchia, Thalattosuchia, and Eusuchia. The proportional differences between the skull and jaws in *Sebecus* and in other crocodilians are brought out in the accompanying tables of measurements and ratios and indices (tables 1 and 2), and they may be still further emphasized by some simple diagrams.

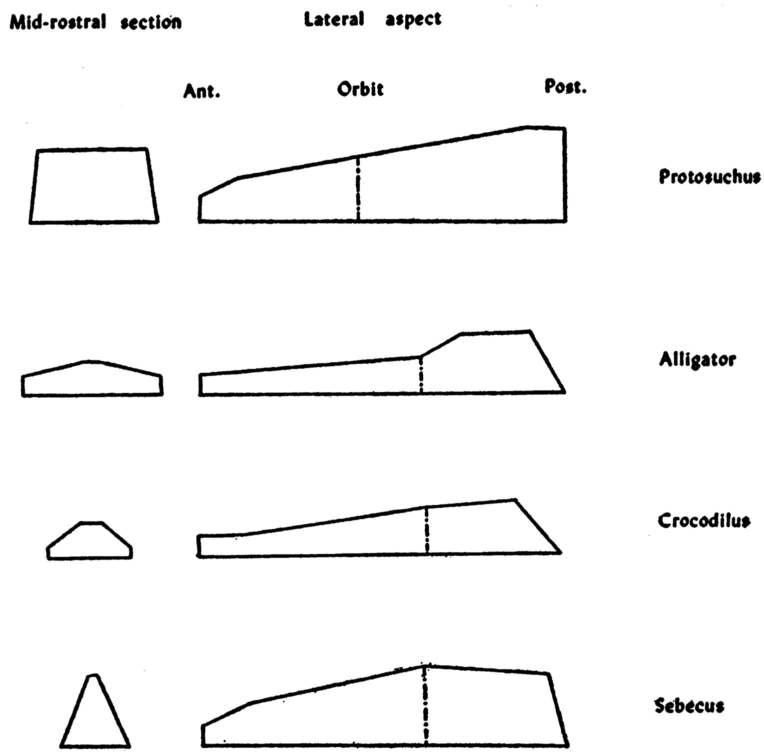


FIG. 29. Diagrammatic comparison of the general shapes of the skulls of several crocodilians, in mid-rostral sections and lateral aspects. Length of skulls reduced to unity, and other measurements in proportion. This figure gives a comparative diagrammatic impression of the depth of the skull as related to its width in the mid-rostral region, of the depth of the skull anteriorly, posteriorly, and at the orbit, and the position of the orbit, when the length of the skull is reduced to unity. *Protosuchus* (Protosuchia), *Sebecus* (Sebecosuchia), *Crocodylus*, and *Alligator* (Eusuchia).

This is done by reducing the outlines of the skull in various crocodilians, as seen in the dorsal, lateral, and occipital views, to simple lines. In this way minor structures that tend to confuse the general picture of skull proportions are eliminated and thereby a broad comparison of the skulls is facilitated.

long, narrow, and deep preorbital part of the skull that makes *Sebecus* so distinctive.

Sebecus is noteworthy also because of its comparatively large cranial table, extending almost the full width of the skull. *Protosuchus*, interestingly enough, has a very large, broad

TABLE 1

COMPARATIVE MEASUREMENTS (IN MILLIMETERS)

Measurements	*Sebecus icaeorhinus* A.M.N.H. No. 3160	*Crocodylus niloticus* A.M.N.H. No. 23466	*Alligator mississipiensis* A.M.N.H. No. 7141	*Steneosaurus obtusidens* (From Andrews)	*Protosuchus richardsoni* A.M.N.H. No. 3024
A. Length of skull: premaxilla to quadrates	476	414	342	1206	115
B. Length of snout: premaxilla to anterior rim of orbits	291	260	209	720	49
C. Breadth of skull: across quadratojugal	190	185	159	402	80
D. Breadth of snout: in plane of anterior orbital rims	125	130	139	204	36
E. Breadth of snout: midway between tip and occiput	87	94	129	112	40
F. Breadth of snout: maximum on premaxilla	54	72	89	102	26
G. Breadth of cranial table: maximum (posterior)	160	89	90	—	71
H. Breadth of cranial table: minimum (anterior)	140	80	80	—	56
I. Interorbital breadth: minimum	47	40	20	84	30
J. Anteroposterior length of orbit	60	51	57	84	21
K. Height of orbit (or width)	65	35	45	—	—
L. Height of snout: vertically from alveolus of last tooth	104	53	36	—	24 (e)
M. Height of snout: vertically from alveolus of last premaxillary tooth	55	25	21	—	16
N. Height of snout: vertically midway between tip and occiput	101	44	32	—	23
O. Total length of tooth row	274	272	214	720	—
P. Length of mandible: maximum	526	451	377	1308	109
Q. Length of mandible: to articulation	464	401	337	1170	109
R. Depth of ramus: vertically from lower border to articular	97	65	56	—	15
S. Length of tooth row	252	246	188	—	—

Dorsally, the skull of *Sebecus* is noteworthy, of course, because of its lateral compression. For instance, the skull in this genus is noticeably narrower than is the skull in *Crocodylus*—a narrow-skulled eusuchian. On the other hand, the skull of *Steneosaurus*, a mesosuchian, is proportionately narrower than the skull of *Sebecus*. But in *Steneosaurus* the orbit is placed relatively far forward, and the skull is generally low. It is the combination of the cranial table, but in the eusuchians the cranial table is generally much reduced in relative size. In many mesosuchians, such as the one chosen for comparison, the upper temporal openings are so large that a cranial table is difficult to define.

In an occipital view, the skull of *Sebecus* is distinguished again by its depth and by its straight sides. Depth of the skull is also a distinctive character in a lateral view of the

Sebecus skull. As may be seen, the depth extends from the back well forward on the muzzle, and is greatest at the front of the orbit. This may be contrasted with the general crocodilian condition, in which the muzzle is shallow, and the postorbital part of the skull is the region of greatest depth.

TABLE 2

COMPARATIVE RATIOS AND INDICES

	Sebecus	*Crocodylus*	*Alligator*	*Steneosaurus*	*Protosuchus*
$\frac{\text{Skull width}}{\text{Skull length}}$ $\frac{100\ C}{A}$	40	45	47	33	70
$\frac{\text{Snout length}}{\text{Skull length}}$ $\frac{100\ B}{A}$	61	63	61	60	43
$\frac{\text{Snout breadth}}{\text{Snout length}}$ $\frac{100\ D}{B}$	43	50	67	28	73
$\frac{\text{Snout height}}{\text{Snout width}}$ $\frac{100\ L}{D}$	83	41	26	—	67
$\frac{\text{Snout height (anterior)}}{\text{Snout height (posterior)}}$ $\frac{100\ M}{L}$	53	47	58	—	67
$\frac{\text{Interorbital breadth}}{\text{Skull breadth}}$ $\frac{100\ I}{C}$	25	22	13	21	37
$\frac{\text{Tooth row}}{\text{Skull length}}$ $\frac{100\ O}{A}$	58	66	63	60	—
$\frac{\text{Tooth row}}{\text{Jaw length}}$ $\frac{100\ S}{Q}$	54	61	56	—	—
$\frac{\text{Skull height}}{\text{Skull length}}$ $\frac{100\ L}{A}$	22	13	10	—	21
$\frac{\text{Skull cranial table}}{\text{Skull width}}$ $\frac{100\ G}{C}$	84	48	57	—	89

SEBECUS AND OTHER FOSSIL CROCODILES FROM PATAGONIA

Of the crocodilians contemporaneous with *Sebecus*, there is a single described form, *Eocaiman cavernensis* Simpson, which like *Sebecus* is found in the Casamayor formation. This is the common crocodilian in the Casamayor, and, as Simpson has shown, it seems to stand near the ancestry of the South American eusuchians, *Caiman* and *Jacare*. In general, the skull bones and the teeth of this short-faced alligatoroid are hardly to be confused with the laterally compressed bones and teeth of *Sebecus*. Indeed, all of the differences that have been cited above that distinguish *Sebecus* from *Alligator* also separate it from *Eocaiman*.

Simpson has also described a somewhat earlier form, *Necrosuchus ionensis*, from Patagonian sediments of probable Paleocene age. This is an eusuchian belonging to the Crocodilidae and as such is readily distinguishable from *Sebecus*. Two still older genera are the mesosuchians *Notosuchus* and *Cynodontosuchus*, first described by Smith Woodward in 1896. *Notosuchus*, a short-faced and almost edentulous mesosuchian, cannot be mistaken for *Sebecus*, although there is some possibility that the crocodilian bones and the single tooth figured by Ameghino in 1906 as belonging to *Notosuchus terrestris* actually are referable to *Sebecus*. *Cynodontosuchus* is based upon imperfect evidence, but it certainly is distinct from *Sebecus*.

Other Patagonian crocodiles are *Symptosuchus contortidens*, described by Ameghino upon the basis of insufficient material and therefore virtually indefinable, and certain rather indeterminate fragments, described by Kuhn in 1933.

THE PHYLOGENETIC POSITION OF *SEBECUS*

Sebecus AND THE RECENTLY DESCRIBED Brazilian genus *Baurusuchus* are crocodilians quite distinct from all the other members of the Order Crocodilia, and for this reason they are placed in a separate suborder, the Sebecosuchia. Consequently the Order Crocodilia is here regarded as being composed of five suborders, as follows:

Order Crocodilia
- Suborder Protosuchia
- Suborder Mesosuchia
- Suborder Thalattosuchia
- Suborder Sebecosuchia
- Suborder Eusuchia

The Protosuchia, typified by the single genus *Protosuchus*, which is in turn known from a unique, but nevertheless well-preserved skeleton, already show numerous definite crocodilian characters, in spite of the early and general position of this group within the phylogeny of the Crocodilia. For instance, the skull in *Protosuchus* is on the whole primitive and not particularly crocodilian in appearance, yet it shows a reduction of the superior temporal fenestrae and a development of a cranial table, formed by the postorbital, squamosal, supraoccipital, parietal, and frontal bones, that is remarkable because of its similarity to the cranial table in the highly specialized eusuchians. In other respects, too, *Protosuchus* shows its crocodilian relationships, particularly in the elongation of the carpal bones and the virtual exclusion of the pubis from the acetabulum.

On the basis of our present knowledge, *Protosuchus* must serve as the structural ancestor for all of the Crocodilia, and it is probable that this genus approaches rather closely the actual ancestry of the order. Unfortunately a detailed and comprehensive study of *Protosuchus* has not been as yet made, and our final judgment as to the position this genus occupies in the phylogenetic history of the Crocodilia must of necessity wait until such a study has been published. However, it seems evident upon the knowledge furnished by *Protosuchus* that the Crocodilia, having originated from thecodont ancestors, had become established as a separate group of ordinal rank by late Triassic or early Jurassic times.

From the Protosuchia the later Mesozoic Crocodilia originated. It would seem probable that the derivation of more specialized forms from this ancestral group showed an early Jurassic division into what might be termed the "central" line of the Mesosuchia and the more "lateral" line of the highly specialized Thalattosuchia. Both of these groups were marked by a specialization in the skull whereby the internal nares were carried far back, with a sort of secondary palate formed by the maxillae and palatines separating the nasal passage from the buccal cavity. On the other hand, the two suborders may be contrasted by the great variety in adaptive radiation among the Mesosuchia as compared with the rather straight, "orthogenetic" trend among the Thalattosuchia for life in marine waters.

The Mesosuchia show long-snouted and short-snouted forms, with consequent multiplications and reductions in the dentition; in some the supratemporal fenestrae are very large while in others they are much reduced; some are large and others quite small. Yet in spite of the great variety shown by the development of the skull, the dentition, and the size of body in the Mesosuchia, there is a comparatively uniform trend in the habitus of the group. These were all shallow-water crocodilians, adapted to life along the banks of inland streams or the shores of larger bodies of water. Although thoroughly aquatic the mesosuchians must have spent a great deal of time on dry land—but ever in close proximity to the water—as do the modern crocodiles.

As compared with this mode of life, the Thalattosuchia show an early and a very strong trend to adaptations for open, marine waters. In these crocodilians the armor and claws so characteristic of other crocodilians have been lost, while the bones of the skull are secondarily smooth, in contrast to the typically pitted external surfaces in the skull bones of other crocodilians. The thalattosuchians also show the development of sclerotic plates (a common adaptation in marine reptiles), a transformation of the feet into paddles, and a downturning of the caudal vertebrae to form a reversed heterocercal tail.

It is probable that while the mesosuchians and thalattosuchians were following their separate trends of evolutionary specializations through the Jurassic period, the sebecosuchians were at the same time evolving from a protosuchian stem. Thus the specializations of the Mesosuchia, the Sebecosuchia, and the Thalattosuchia in the Jurassic period may be regarded as the first broad adaptive radiation of the Crocodilia.

What may be regarded as a second period of adaptive radiation among the Crocodilia seemingly took place during Cretaceous and early Cenozoic times. In this period there was a continuation of the mesosuchians from the preceding Jurassic period. Here there appear for the first time the Sebecosuchia, probably as a continuation from Jurassic ancestors. In addition to these established crocodilian groups a new line arose, that of the Eusuchia. This line was destined to flourish during Cretaceous and early Cenozoic times and to continue into the latest stages of earth history, whereas all other lines of crocodilian evolution were to vanish.

It is known that the Eusuchia were derived during Cretaceous times from the Mesosuchia through transformations, the characters of which are plainly apparent in the latter suborder. Thus, there was a further retreat of the internal nares so that in the Eusuchia they came to be located far back and completely enclosed by the pterygoid bones. Furthermore, the Eusuchia show a complete withdrawal of the postorbital bar to a subdermal position, again a development already under way within the Mesosuchia. Finally, the Eusuchia are marked by the appearance of procoelous vertebrae. From this, and in addition from much other evidence which might be cited, it is plain that the Mesosuchia evolved gradually into the Eusuchia, and that although there were specializations in morphology from the one to the other, the trend in habitus was carried on virtually without interruption. The Eusuchia, like the Mesosuchia before them, were shallow-water crocodiles, living in streams and rivers, or along the shores of lakes and the sea.

From the morphological characters of *Sebecus* and *Baurusuchus* it would seem evident that these crocodiles, and by inference the suborder to which they belonged, were derived from a basic mesosuchian ancestry. Both *Sebecus* and *Baurusuchus* show large internal nares bounded anteriorly by the palatines as in the Mesosuchia, but extending back into the pterygoids and bounded posteriorly by these bones. In *Baurusuchus* the expanded ectopterygoids form in part the lateral borders of the internal nares. The vertebrae in *Sebecus* are platycoelous. In many ways *Sebecus* shows close resemblances to the Eusuchia in the basic structure of the skull and jaws; the reason why this genus is so different from the eusuchians is, aside from the structure of the internal nares and of the teeth, mainly a matter of proportions. It is therefore evident that the Sebecosuchia, although independently derived from a mesosuchian stem, have paralleled the Eusuchia in many respects. The Sebecosuchia, like the Eusuchia, must have been shallow-water crocodiles, living, so far as our present evidence indicates, along the banks of rivers and streams. Like the Eusuchia, the Sebecosuchia must have spent a part of their life in the water and a part of it on dry land, near the water. But unlike the Eusuchia or the Mesosuchia, the Sebecosuchia were deep-skulled crocodilians, and in this respect they show either a retention of primitive characters or a reversal in evolutionary trends whereby they approximate to some degree the thecodont reptiles that were the ancestors to all of the Crocodilia.

Thus the strong divergence of the Sebecosuchia from all other crocodiles affords an interesting contrast to the strong divergence of the Thalattosuchia from the Mesosuchia. For in the specialization of the Thalattosuchia there was a divergence not only in morphology, but in habitat as well; the adaptations of the two suborders Thalattosuchia and Mesosuchia were for two entirely different modes of life. As contrasted with this, the divergence of the Sebecosuchia from other crocodilians, although marked by differences in structure and by very great differences in proportions, seemingly was not marked by a particular divergence in habits. It appears that both the Sebecosuchia and the Eusuchia followed essentially the same types of patterns in habits and ecology, and it is very probable that they may have been for a time competitors in the struggle for

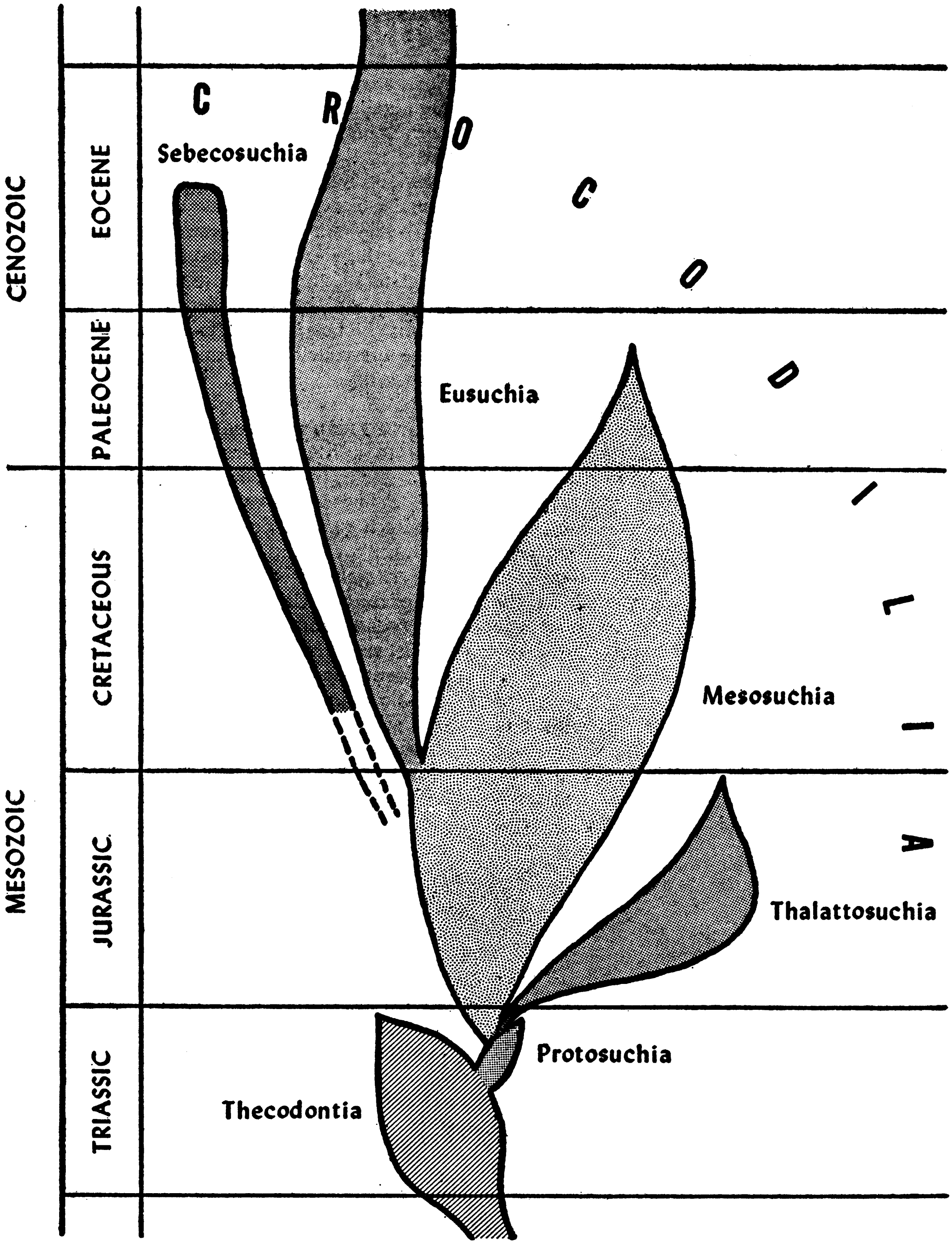


FIG. 30. A phylogeny of the suborders of Crocodilia.

existence. If this is so, then it would seem that the Sebecosuchia were the less well adapted for continuation.

The presence of *Baurusuchus* in the Cretaceous and *Sebecus* in the Eocene of South America leads to some interesting speculations. Why should these crocodilians, so different from all other members of the order, have evolved? In the case of the thalattosuchians we can correlate the specializations in the skull and body with a very definite change in habitat; they were marine crocodiles and were widely spread over large geographical areas. The sebecosuchians on the other hand show adaptations that, while divergent from those seen in other crocodilians, are not to be correlated with any recognizable divergence in habitat. It is possible, as suggested on a preceding page of this work, that *Sebecus* may have had habits of hunting and eating somewhat different from those of the modern crocodilians. But granting that such differences did exist—a supposition at best—it is still difficult to account for the extreme divergence in the form of the skull, jaws, and teeth of the sebecosuchians from other members of the order.

One is led to wonder if the presence of *Sebecus* in the Eocene of Patagonia, and similarly of *Baurusuchus* in the Cretaceous of Brazil, may not represent the genetic isolation of phylogenetic lines in restricted localities. Simpson (1944, pp. 68–69) has suggested that mutations might be more effectively utilized and changes brought about more quickly in small, isolated populations than is the case in large, widely spread populations. Since the sebecosuchians have been found only as rare and isolated fossils, there is the possibility that they represent elements in a phylogenetic line that had become isolated and was developing within relatively small successive populations. Of course the present geographic and geologic restriction of these crocodilians may be due entirely to accidents of collecting, but in view of relatively large numbers of eusuchians and some mesosuchians found in other parts of the world, one is led to think that the restriction of *Sebecus* to Patagonia and *Baurusuchus* to Brazil may represent a real condition that held to a large degree for this crocodilian suborder in Cretaceous and Eocene times. If the Sebecosuchia were restricted to the southern part of South America throughout their history, and if they were at all times rather sparsely distributed animals within their range, then the key to their wide divergence from other crocodilians may be in these very facts. Perhaps we see here a phylogenetic line that has resulted from genetic isolation and the consequent cumulative piling up of successive mutations. If so, there is no particular necessity in trying to correlate the structure of the skull of *Sebecus* too closely with possible eating or hunting habits.

SEBECUS AND THE MOOTED CASAMAYOR DINOSAURS

IN 1932 SIMPSON DISCUSSED IN SOME DETAIL the long-argued question as to whether or not dinosaurs occur in the Casamayor and whether, if so, this indicates that the Casamayor is Cretaceous, or that dinosaurs survived into the Tertiary. The conclusion was that dinosaurs are not known from the Casamayor and that this formation is of Tertiary age. This conclusion is not altered but is indeed strengthened by the discovery of *Sebecus*. Moreover this discovery permits what may be the last word on this subject, at least as far as previous discoveries and claims are concerned.

Without again going into full detail, the evidence for association of dinosaurs with mammals of Tertiary aspect in Patagonia consisted of a series of early discoveries by various hands, unskilled for the most part, and another series of somewhat later discoveries by Carlos Ameghino. As regards the first discoveries, it has been conclusively shown that they are not worthy of credence, either because the field data were quite unreliable or because the interpretation placed on those data was a *non sequitur*. As regards the work of Carlos Ameghino, although his field data were questioned by others, Simpson found no reason to doubt their essential accuracy, but he refused to accept the identification of Ameghino's specimens as dinosaurs. Some of the Ameghino specimens disappeared without being figured or exactly described, but those remaining as evidence appear to be sufficiently typical of all.

These specimens are teeth of two sorts. One sort is indubitably crocodilian. F. Ameghino himself identified as crocodilian certain teeth practically indistinguishable from these, so that his failure to correct the earlier identification as dinosaurian can be imputed to an oversight. However, there remain teeth that are very like those of carnivorous dinosaurs and quite unlike those of any previously known crocodilians, typified by No. 10872 in the Ameghino Collection of the Buenos Aires Museum. One of the best authorities on dinosaurs, von Huene (1929), agreed with Ameghino that these are dinosaur teeth, but doubted the horizon record. Simpson confirmed the horizon record by subsequent repetition of the discovery, but suggested that the teeth were not, or at least were not proved to be, dinosaurian because (1) they did not agree exactly with dinosaur teeth despite the close but inconclusive resemblance, (2) the histology is not characteristically dinosaurian, and (3) dinosaur bones are invariably more abundant than teeth in dinosaur beds, and yet no such bones have been found at the localities or horizons from which these teeth came. As shown by Simpson in 1937, this negative conclusion is confirmed beyond reasonable doubt by the discovery of *Sebecus*, in the same horizon. In every way, the tooth in the Buenos Aires Museum (M.N.H.N. No. 10872), described by Ameghino and refigured and discussed by Simpson (1932), corresponds with the flattened teeth of *Sebecus*. It is like the teeth of *Sebecus* in size, in shape, especially in the curved anterior edge and the relatively straight posterior edge, in cross section, and in the development of serrated cutting edges. It thus appears that the mystery of the "Eocene dinosaurs" of South America is at last really solved.

In his paper of 1932 Simpson described a flattened caniniform tooth, which he considered as possibly similar to the tooth described by Ameghino (M.N.H.N. No. 10872), and which he regarded as mammalian because of its probable but uncertain association with mammalian cheek teeth. Whether the tooth that was associated with the mammal *Florentinoameghinia mystica*, described by Simpson, should be identified with this species is a question that cannot be decided upon the basis of present evidence. What is clear is the fact that the tooth earlier described by Ameghino as of dinosaurian relationships and now shown to be a tooth of *Sebecus* is not the same as the flat, cutting tooth that Simpson provisionally identified as belonging to *Florentinoameghinia*.

The tooth associated with *Florentinoameghinia*, and figured by Simpson (1932, fig. 6), is considerably larger than the largest teeth in *Sebecus*. Moreover it is differently shaped, for both front and back edges are curved, whereas in *Sebecus* the back edge is rather straight. In addition, the tooth figured by Simpson, though crushed, evidently has a much thinner cross section than any of the flattened teeth of *Sebecus*. Finally, and this is a most important point, this tooth under a microscope shows no trace of serrations along its edges, whereas every tooth in *Sebecus* has distinctly serrated edges. For these reasons it is concluded there that there is no identity between the flattened tooth associated with the type of *Florentinoameghinia* and the teeth of *Sebecus*.

To summarize the foregoing paragraphs:

1. Flat, dinosaur-like teeth have been found associated with mammals in South America.

2. These teeth and the associated mammals are indubitably of Eocene age.

3. These teeth are without much doubt the teeth of *Sebecus*.

4. The flat tooth found associated with the type of *Florentinoameghinia* is different from the teeth of *Sebecus*. Its relationships must be considered questionable at the present time.

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