

THE SEBECOSUCHIA: COSMOPOLITAN CROCODILIANS ?

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ABSTRACT. It has hitherto been supposed that the extinct *Sebecosuchia*, or "dinosaur-toothed" crocodiles, were confined to South America. Discovery of compressed recurved crocodilian teeth with serrated secant edges fore and aft in North America (Eocene), Europe (Eocene), Africa (Miocene), and Asia (Jurassic) raises the question: Were the *Sebecosuchia* cosmopolitan crocodilians? What evidence there is, both direct and circumstantial, seems to support the affirmative. Definite evidence favoring the alternative supposition, that carnosaur-like teeth evolved in other crocodilian suborders independently, cannot be adduced from published accounts of known fossil material.

Careful comparison of sebecid teeth with those of carnivorous dinosaurs reveal useful criteria for distinguishing between them.

INTRODUCTION

The *Sebecosuchia* are a suborder of extinct crocodiles hitherto recognized only in Cretaceous and Tertiary deposits of South America. They are characterized by a deep and narrow snout, laterally placed orbits, and an arrangement of the choanae structurally intermediate between mesosuchian and eusuchian conditions. The only known vertebra is amphicoelous. Most peculiar is the dentition: in presently recorded sebecosuchians the teeth have elongate laterally compressed crowns with serrated secant edges fore and aft. These teeth are so unlike other crocodilians' generally that their true affinities have sometimes gone unsuspected. On the other hand so similar are they to teeth of some carnivorous dinosaurs that they have occasionally been mistaken for these. In fact such teeth seemed for years to support the contention of Florentino Ameghino that dinosaurs persisted into the Tertiary period in South America.¹

In South America the group was first recognized as crocodilian on the basis of a fragmentary skeleton, the type of *Sebecus icaeorhinus* Simpson (1937), from the Eocene Casamayor formation of Argentina. A second sebecosuchian, *Baurusuchus pachecoi* Price (1945) represents another family. It is from the Upper Cretaceous Bauru formation of Brazil. *Sebecus* is now known to have lived in Colombia as recently as the late Miocene (Savage, 1951).² Other records of the genus are cited from the Eocene of Brazil (de Paula Couto, 1948) and what, to judge from the illustration, may have been a *Sebecus* from the Oligocene of Argentina was referred to *Ilchunaia parca* by Rusconi (1946).

Until now it has been supposed (Colbert, 1946, and others) that the *Sebecosuchia* were confined to South America where they evolved in pre-Cretaceous times, experienced a modest radiation in the Cretaceous and early Tertiary, and became extinct before the beginning of the Pliocene epoch. There are, however, enough references to "dinosaur-like" teeth of Tertiary origin in paleontological literature to suggest that the *Sebecosuchia* had a

¹ For an account of the "Tertiary dinosaur" controversy see Simpson (1932).

² References to *Sebecus* from Colombia in this paper are based on specimens in the Museum of Paleontology at the University of California (Berkeley). These include numerous teeth of Eocene to Miocene age and a mandible of a large undescribed Upper Miocene species.

wider distribution. Teeth seemingly of the characteristic sort have been reported from North America, Europe, Africa, and Asia. The records of these teeth and the associated skeletal remains are reviewed below.

THE RECORDS

North America.—*Crocodylus ziphodon* Marsh (1871, p. 453) was founded on small flattened recurved teeth with secant serrated edges, a peculiar quadrate bone, and associated deeply sculptured suturally united plaques, from Eocene rocks near Grizzly Buttes, Uinta County, Wyoming. The quadrate may have resembled *Sebecus* which differs from other crocodylian quadrates in several ways. Following discovery of "additional material" Marsh (1872) transferred the species to his new genus *Limnosaurus*.³ Leidy (1872) thought the animal was not a crocodylian, and Troxell (1925) believed the quadrate at least was not *Crocodylus*. Most authors have for convenience retained the species in that genus. The animal has apparently not been encountered since 1872, and the whereabouts of the original material is unknown. In describing *Crocodylus vorax* Troxell (1925) said that the teeth ". . . are entirely smooth, except for the anterior and posterior edges which are serrated, cutting edges; the crowns are recurved, pointed and much compressed." However, Dr. J. T. Gregory has examined the Yale type of *C. vorax* at my request and writes, "The teeth are normal, nearly round, blunt pointed, rather like those of other crocodiles. I see no real differences from other Bridger crocodiles such as *C. affinis*." Troxell did not mention teeth of *Limnosaurus* in his review of the Bridger crocodiles, but his description of *C. vorax* teeth recalls the words of Marsh with reference to *C. ziphodon*. Perhaps the two were confused in the Troxell paper.

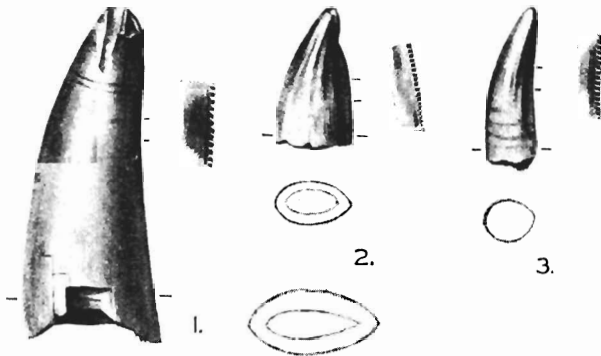
Europe.—Cuvier in 1824 recognized (or guessed) the crocodylian nature of some *Sebecus*-like teeth collected from the Eocene *Lophiodon* marls near Argenton, France. These teeth, said to occur abundantly, were associated with eusuchian postcranial elements. Cuvier called the animal "Crocodyle des manières d'Argenton" and assigned to it a fragmentary maxilla with vertical sides. He concluded (p. 167) that the snout was ". . . étroit et élevé verticalement." The illustration (pl. 10, fig. 17) shows ovate alveoli of sebecosuchian pattern. Postcranial elements assigned to the same form may not belong with the teeth.

The Crocodile of Argenton was named "*Croc. Rollinatti*" by J. E. Gray (1831) who implicitly designated as syntypes a tooth and caudal vertebra (probably not from one individual, and likely from different species) figured by Cuvier (pl. 10, figs. 14 and 24 respectively). Gervais (1853a) in assigning other teeth from the Beauchamp sandstone to this species proposed a new generic name, *Pristichampus* (spelled "*Pristichampsa*" and considered a subgenus of *Crocodylus* in 1853b). But in 1859 he returned the species to *Crocodylus*. Lydekker (1888) figured a tooth of "*Pristichampsa rollinatti*" from Argenton in the British Museum collection which is practically identical with a tooth of a late Miocene *Sebecus* from Colombia.

Three teeth of *Pristichampus rollinatti* from the *Lophiodon* marls of Argenton are preserved in the University of California Museum of Paleontol-

³ Not to be confused with *Limnosaurus* Nopcsa (1899), an iguanodont dinosaur.

PLATE 1



Sebecosuchian teeth. Fig. 1, *Sebecus* sp. from the Miocene of Colombia, Univ. Calif. Mus. Pal. no. 40220. Fig. 2 and 3, *Pristichampsus rollinatti* (Gray) from the Eocene of Argenton, France, Univ. Calif. Mus. Pal. no. 43921. Teeth drawn natural size, serrations from middle of posterior edge enlarged $\times 4$. Sections drawn at base of crowns.

ogy (no. 43921). One (pl. 1, fig. 3) superficially resembles *Gavialis*, *Tomistoma*, or other slender-toothed crocodiles in its length, slenderness, and slightly bent crown. It is subround in basal cross section, and not much flattened from side to side. The crown is broadly but shallowly fluted from tip to base, but there are distinct fore and aft carinae bearing fine and regular serrations. The rounded section of this tooth recalls that premaxillary and anterior mandibular teeth of *Sebecus icaeorhinus* were apparently little compressed. The other teeth (fig. 2) show the characteristic "megalosaur aspect." The numbers of serrations on these teeth are compared with some *Sebecus* teeth in table 1. There it will be noted that in general the size of the serrations decreases towards the base of the crown, and that this decrease is most marked on the trailing edge of the tooth, especially in *Pristichampsus*. Serrations vary in size from place to place where division of the cutting edge skips a space occasionally. This variation is less common in *Sebecus* teeth from the Eocene, Oligocene, and Miocene of Colombia, and seems not to occur in *S. icaeorhinus*. The surfaces of the crowns are vertically fluted like the rounded tooth described above, but the grooves are much broader and shallower than there. Fluting of some sort is a fairly uniform feature of crocodilian teeth generally, but teeth of *Sebecus* from Colombia are perfectly smooth, and fluting is but slightly developed if at all in *S. icaeorhinus*. It has not been reported in *Baurusuchus*. Among other crocodiles fluting is lacking in *Alligator* and some caimans so variation can be expected in sebecosuchians. One *Sebecus* tooth, A.N.N.H. no. 3162, even has a slightly wrinkled surface like an *Alligator*.

Barnes (1926) referred some *Sebecus*-like teeth, from the mid-Eocene Braunkohl of Geiseltal, to *Diplocynodon rollinatti*, presumably because plaques associated with them resembled those of *Diplocynodon*. However, this common early Tertiary European genus is generally conceded to be a highly variable alligatoroid: it has in all its species blunt peg-like teeth, and there is little

Comparative Measurements of *Sebecus* and *Pristichampsus* Teeth

TABLE 1

Number*	Height of crown	Transverse diameter at base of crown	Fore and aft diameter at base of crown	Serrations in one millimeter	
				Leading edge	Trailing edge
U.C.M.P.					
	42.8 mm	<i>Sebecus</i> sp. (Colombia-Eocene, Oligocene, Miocene forms)	17.6 mm	6.4-2.2**	6.5**
40220	40.0	8.6 mm	17.2	7.4-5	5.3-5
44564	—	8.6	16.3	3-3.5	—
44563	—	7.9	12.8	—4	4-3.3
44565	—	7.0	14.2	5.5—	4.5—
41308	34.8	6.8	14.6	7-6	7-6
37877	22.5 +	—	—	6.5-6	5.5-5
44562					
A.M.N.H.					
	20.1	<i>Sebecus icacorhinus</i> (Argentina—Eocene)	8.2	8—	—
3160 (Pmx 1)	23.7	6.9	12.6	6—	5—
3160 (Mx 7)	11.5	4.7	9.5	5—	5—
3160					
U.C.M.P.					
	16.4	<i>Pristichampsus rollinatti</i> (France—Eocene)	6.6	8-7	8-5.5
43921 (Pmx?)	18.4	5.0	9.9	8.4-7	8-6.5
43921	12.5	5.4	7.6	7-7.5	8-7
43921		4.9			

* Numbers from Museum of Paleontology, University of California (Berkeley) and American Museum of Natural History.

** First figure near base of crown, second near top.

reason to believe Barnes' flattened teeth pertain to it. On the other hand a "dinosaur-toothed" crocodile *Weigeltisuchus* occurs in the same deposit (see below).

Weitzel (1938) assigned a rostrum from the mid-Eocene of the Messel region of Germany to *P. rollinatti* because of its compressed and serrated teeth. The specimen is said to resemble a slender, vertical-sided rostrum from Eocene deposits at Naves (about 60 km east of Toulouse, France) earlier referred to this species by Caraven-Cachin (1880). The snout of the Messel crocodile appears depressed when seen from the side, but its vertical walls and narrow rostrum recall Cuvier's remark about the Crocodile of Argenton. The nasals form a flat roof lying at a sharp angle to the sides of the snout. The outline of the rostrum from above resembles *Sebecus* more than other crocodiles, but there is a wider and deeper notch on the side for the large fourth mandibular tooth. (Caraven-Cachin notes perforations in the premaxillae of his specimen through which projected the first mandibular teeth). The dental margin is more broadly festooned vertically in Weitzel's specimen than in *Sebecus icaeorhinus*, and the teeth appear to be slightly more numerous and perhaps less uniform in shape than there. Weitzel notes no peculiarities of palatal construction, but these may be obscured by imperfect preservation. The illustration suggests, however, that the internal nares lay farther forward than in eusuchians, and there appears to be a mid-palatal ridge which might represent a sort of narial septum exposed by partial destruction of the secondary palate. The mandible has not been freed from the cranial rostrum, and its alveolar margin is hidden except around the base of the fourth tooth where the dorsal outline of the dentary is elevated apparently as in *Sebecus*. The splenial contributes 20 percent of the mandibular symphysis exactly as in a large Miocene *Sebecus* jaw from Colombia; as there the symphysis probably extends to about the posterior vertical of the sixth tooth. The teeth seem heavier and perhaps less flattened than those of *Sebecus icaeorhinus*, but resemble somewhat two large *Sebecus* or related teeth from Colombia. Caraven-Cachin implies that only the posterior edges of the teeth were serrated in his specimen, and states that the teeth were conical though flatter than in any known crocodile. The animal from Messel was a little more than half as large as the type of *S. icaeorhinus*. Weitzel's animal may qualify as a sebecosuchian even if it is not correctly referred to *P. rollinatti*. The same may be said for the specimen described by Caraven-Cachin, though perhaps it is less likely to belong to that species.

Pristichampsus may belong in the same family as *Sebecus*, although it is practically certain that the genera are distinct. Some dental characters that can be used to distinguish between them are:

1. *Pristichampsus* teeth are fluted at least in some cases; the surfaces of *Sebecus* teeth from Colombia are perfectly smooth, and only one tooth of *S. icaeorhinus* shows the slightest suggestion of vertical ridging.

2. Serrations in *Pristichampsus* teeth are of smaller relative size than are serrations of *Sebecus* teeth of comparable proportions.

3. Serrations are less regular in *Pristichampsus*. If the animal from Messel is *Pristichampsus*, its depressed and strongly festooned rostrum and robust teeth are additional distinguishing features.

The mid-Eocene Braunkohl of Geiseltal has yielded several almost complete but disappointingly preserved skeletons of *Weigeltisuchus geiseltensis* Kuhn (1938). This animal resembles *Sebecus* in its compressed serrated teeth, slender skull with a broad trench on the side of the elevated rostrum for the fourth mandibular tooth, and a long mandibular symphysis. So far as can be determined from crushed specimens the orbits were laterally placed. The relationship between length of snout and cranium is also similar to *Sebecus*, but the rostrum is relatively a little shorter in *Weigeltisuchus*. Vertical festooning of the upper jaw is more pronounced than in *Sebecus*, and the undivided nasal opening is completely unlike the South American genus but agrees with the Cretaceous sebecosuchian *Baurusuchus*. Palatal structure is not mentioned in Kuhn's account, and other cranial features are not significant in the present connection.

This species, if sebecosuchian, is of particular interest because much of the postcranial skeleton is preserved. Among unusual features noted is what may be the most complete armor of any crocodylian showing suturally united dorsal scutes (cf. *Limnosaurus* Marsh), plaques on the limbs as far down as the metapodials, and in primitive fashion, a complete armored tube enclosed the tail. The animal also possessed hoof-like terminal phalanges, a unique feature among crocodylians. Kuhn interprets an "opisthocoealous" vertebra as the second sacral; it would be interesting to know if any of the vertebrae are biconcave as supposed in *Sebecus*.

Africa.—In discussing some early Miocene vertebrates from near Lake Victoria Andrews (1914, p. 185) mentions a serrated tooth that ". . . is extraordinarily like those of some Carnivorous Dinosaurs, . . . but is most probably crocodylian. . . . It indicates the survival in Africa of a similar type of crocodile to *Pristichampsus* until the Miocene Period." The tooth is very small and seems to have a few broad rounded ridges on the crown. The illustration does not resemble *Sebecus* or *Pristichampsus* in detail, but the description at least suggests a sebecosuchian.

Asia.—Young and Chow (1953) have described *Hsisosuchus chungkingensis* from a head and some plaques said to have come from Upper Jurassic rocks in Szechuan. This unusual crocodylian resembles *Sebecus* in dental characters, and its authors note several osteological similarities but maintain that the animal represents a distinct suborder but distantly related to the Sebecosuchia. Still it seems not improbable to me that the animal is really an ancestral sebecosuchian; some palatal features are difficult to explain, but on the whole the descriptions and figures could be interpreted as favoring a sebecosuchian relationship as easily as the converse.

DISCUSSION

In preceding paragraphs I have relied heavily on similarities of tooth construction. Tooth structure is not usually very reliable in crocodylian systematics, and it may seem that I have laid too much emphasis on the carnosaur-like qualities of the teeth herein considered. But it is precisely these qualities

that have led me through the literature; such teeth have always been regarded as unusual and their resemblances to dinosaur teeth have been universally noted. Furthermore little else of use is available for comparison with the "typical" sebecosuchians from South America. Even the vertical-sided elevated maxillae preserved in several specimens are to be correlated with long flattened teeth and are themselves without much systematic importance unless the teeth are significant.

The evidence presented allows two interpretations: some or all the animals cited are sebecosuchians, or none of them is. In the first case the Sebecosuchia must have been cosmopolitan; in the second carnosaur-like teeth must have evolved independently in more than one crocodylian suborder. In either case the scarcity of fossils reflects similar and unusual habits of the animals concerned.

So far as known these animals exhibit no features that certainly bar them from the Sebecosuchia as defined from the South American genera; I believe most if not all belong in that group. The alternate view might seem to have support from the fluting of the *Pristichampsus* teeth and the opisthocoelous vertebra of *Weigeltisuchus*. But the fluting of crocodylian teeth is almost an ordinal character whose presence in some form is to be expected, and the *Pristichampsus* (and perhaps *Sebecus icaeorhinus*) fluting is not exactly like the fluting of any other crocodylian known to me. The vertebra of *Weigeltisuchus* is the second sacral which might appear opisthocoelous even in an otherwise amphicoelous column. The palates of these supposed sebecosuchians should provide helpful information on relationships, but no useful points favoring either argument can be adduced from the inadequate descriptions of the imperfectly preserved specimens. Finally, the procoelous caudal vertebra chosen by Gray as a syntype of *C. rollinatti* probably belonged to some eusuchian whose remains were associated with *Pristichampsus* teeth at Argenton.

If the Sebecosuchia were cosmopolitan they may have evolved in Jurassic or earlier times, possibly from a pre-protosuchian ancestor (details of armor, teeth, and palatal structure of *Hsisosuchus* may suggest this in the absence of any knowledge of the palate of *Protosuchus*). Before the end of the Mesozoic representatives reached South America, presumably from Asia via North America (where no Mesozoic records are known). The South American stock experienced a modest adaptive radiation in the late Cretaceous. Some sebecosuchians remained outside South America or emigrated from there, giving rise to Eocene species in North America and Europe. The group survived into the late Miocene in South America and left its last Old World record in Miocene rocks of Africa. Further speculation into phylogeny of the group seems pointless until more complete material comes to light, and the known specimens have been re-examined with the possibility of sebecosuchian affinities in mind.

DISTINGUISHING FEATURES OF SEBECOCUCHIAN TEETH

Although the crocodylian nature of sebecosuchians is now established, correct identification of their teeth may still present a problem when these are

found in deposits where carnivorous dinosaurs can be expected. Isolated finds from undated rocks may also prove difficult. Simpson (1932, p. 16) noted that teeth of *Sebecus* (then not recognized as a crocodile) “. . . are not exactly like those of *Genyodectes serus* (a true carnivorous saurischian) or any other known dinosaur. . . . In thin section the enamel structure of the teeth was not exactly matched in any dinosaur examined.” Careful comparison of additional *Sebecus* and *Pristichampsus* teeth with teeth of several carnosaurs reveals numerous though individually fallible differences:

1. Sebecid (I assume *Sebecus* and *Pristichampsus* belong to one family) teeth are generally more compressed laterally and do not show the tendency of most carnosaur teeth to become quadrangular in basal section.
2. Sebecid teeth—excepting the most anterior ones—have much shorter roots in relation to the height of the crown than most functional carnosaur teeth where the mature root often exceeds the crown in length. The root in carnosaurs is essentially straight, that of a sebecid is usually curved if the crown is curved.
3. Sebecid teeth never have the vertical groove on the root and lower crown which often appears in large carnosaurs, both externally and medially.
4. Serrations on sebecid teeth are smaller on the average than in carnosaurs of comparable size.
5. The leading edge of a carnosaur tooth crown is longer than the trailing edge. This accentuates the curvature of the tooth when viewed laterally and gives a certain plumpness of outline to the crown. Though the sebecid teeth may be strongly curved, the disparity in length between leading and trailing edges is never great enough to give the same degree of plumpness to the lateral outline.
6. The anterior serrate carina in carnosaur teeth generally ends some distance above the base of the crown and at a higher level than the posterior one. The difference in length of fore and aft carinae is less in sebecids.
7. The positions of the carinae change in a given series of carnosaur maxillary teeth so that from front to back the areas of the labial and lingual surfaces become subequal. In more anterior teeth the carinae may lie largely on the lingual surface of the crown. Carinae of sebecid maxillary and most dentary teeth more nearly coincide with the geometric fore and aft edges of the crown (as they come to do only in the more posterior teeth of carnosaurs), and the anterior teeth of most sebecids (the Miocene species from Colombia is an exception) have a rounded cross section with carinae oriented to the sides.
8. Sebecid maxillary and dentary teeth have the fore and aft edges about equally trenchant, and in cross section the crowns are uniformly lenticular. Cross sections of carnosaur teeth mostly have a broader outline, considerably thicker in the anterior half than behind.
9. *Pristichampsus* and to a slight degree some *Sebecus icaeorhinus* teeth have longitudinal fluting unlike anything seen in carnosaurs,⁴ and resembling various eusuchian crocodylians.

⁴ Small flattened serrated teeth with vertical ridging occur in certain Upper Cretaceous rocks of North America and are usually assumed to be from carnivorous dinosaurs (for

I have had no chance to compare sebecosuchian and dinosaur teeth microscopically, for none of the University of California specimens lends itself to sectioning. It may be that *Sebecus* enamel is thinner than usual in carnosaurs, but the difference is not great.

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example, see Russell, 1935, pl. 2, fig. 8). These teeth are much flatter on one side than the other. They are further distinguishable from sebecid teeth by the irregularity and sharpness of the vertical ridges, their heavy posterior and almost invisible anterior serrations.

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