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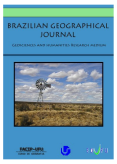

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A new reconstruction of the skull of *Sebecus icaeorhinus* (Crocodyliformes: Sebecosuchia) from the Eocene of Argentina

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ABSTRACT

A new reconstruction of the skull of *Sebecus icaeorhinus* was made following a re-examination of the holotype material. The previous reconstruction of the skull of *Sebecus icaeorhinus* is too long, because the left maxilla was incorrect restored. The maxilla bore nine, not ten, teeth. The quadrate was more vertical in its orientation and the articular condyle for the mandible was nearly horizontal. The snout of *S. icaeorhinus* has inclined, nearly straight lateral sides, and is apparently relatively lower and longer than in *Barinasuchus*, *Bergisuchus*, *Bretesuchus* and *Zulmasuchus*.

RESUMO – UMA NOVA RECONSTRUÇÃO DO CRÂNIO DE *SEBECUS ICAEORHINUS* (CROCODYLIFORMES: SEBECOSUCHIA) A PARTIR DO EOCENO DA ARGENTINA. Uma nova reconstrução do crânio de *Sebecus icaeorhinus* foi realizado na sequência de um re-exame do holótipo. A reconstrução anterior do crânio de *Sebecus icaeorhinus* demonstra que este é muito alongado, pois a maxila esquerda foi de forma erronea restaurada. O número de dentes da maxila antes correspondiam a nove, agora consideramos com a presença de dez dentes. O quadrado era mais vertical na sua orientação e do côndilo articular da mandíbula encontra-se em posição quase horizontal. O focinho de *S. icaeorhinus* tem uma inclinação, quase reta

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lateralmente, e é aparentemente relativamente menor e do que em *Barinasuchus*, *Bergisuchus*, *Bretesuchus* e *Zulmasuchus*.

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1. Introduction

Sebecus icaeorhinus Simpson (1937) is the name-bearer for prominent clades of ziphodont crocodyliforms, sebecids and sebecosuchians. Although not the first discovered such crocodyliform (LANGSTON, 1975), *Sebecus* was the first that attracted wide attention, due to the monograph of Colbert (1946). Ziphodont crocodyliforms are often characterized by a deep, narrow, laterally compressed snout, and laterally placed orbits. The term ziphodont refers to the teeth, that are serrate, and often laterally flattened (LANGSTON, 1975; PRASAD; DE BROIN, 2002). At least five clades of derived (post-sphenosuchian) crocodylomorphs, *Hsisosuchus* (PENG; SHU, 2004), Metriorhynchids (ANDRADE; YOUNG; DESOJO,; BRUSATTE, 2010), sebecosuchians and *Doratodon* (COMPANY; PEREDA SUBERBIOLA; RUIZ-OMEÑACA,; BUSCALIONI, 2005), pristichampsines (LANGSTON, 1975) and quinkans (WILLIS, 1997), developed laterally compressed, serrate teeth independently. Sebecosuchians are known chiefly from South America, where they were apparently most diverse in the Late Cretaceous (Table 1). However, they did not form a uniquely South American clade, as the phylogenetic analysis of Turner and Calvo (2005) shows, and were also found in Africa, India and Europe. They were the most widely distributed ziphodont clade, pristichampsines having occurred in Eurasia and North America, *Hsisosuchus* in China, doratodonts in Europe, and quinkans in Australia; metriorhynchids were marine, and thus not closely comparable.

Table 1. The tetrapod fauna found at Cañadon Hondo

Clade	Species	Citation	Other occurrences
Lissamphibia, Anura	*Eophractus casamayorensis*	SCHAEFFER, 1949	none
Testudines, Cryptodira	*Niolamia argentina*	SIMPSON, 1937	from unknown locality
Lepidosauria, Serpentes	*Waincophis australis*	ALBINO, 1987	none
Crocodylomorpha, Sebecosuchia	*Sebecus icaeorhinus*	SIMPSON, 1937	Cañadon Vaca
Aves, Phoenicopteriformes	*Telmabates antiquus*	HOWARD, 1955	none
Aves, Phoenicopteriformes	*Telmabates howardae*	CRACRAFT, 1970	none
Aves, Opisthocomiformes	*Onychopteryx simpsoni*	CRACRAFT, 1971	none
Mammalia, Marsupialia	*Coona pattersoni*	SIMPSON, 1938	none
Mammalia, Marsupialia	*Microbiotherium gutierrezi*	D. CORRO, 1977	none
Mammalia, Notoungulata	*Thomashuxleya externa*	CIFELLI, 1985	Cañadon Vaca, Rio Chico oeste & Rio Chico este
Mammalia, Notoungulata	*Pleurostylodon similis* ?	CIFELLI, 1985	Cañadon Vaca

Until recently, the genus *Sebecus* was represented by three species, *S. icaeorhinus*, *S. huilensis* (LANGSTON, 1965) and *S. querejazus* (BUFFETAUT; MARSHALL, 1991). Two of these have now been reassigned as *Zulmasuchus querejazus* and *Langstonia huilensis* (PAOLILLO; LINARES, 2007). The holotype of *Sebecus icaeorhinus* was discovered in a small pocket of green bentonite at Cañadon Hondo, Chubut, Argentina (SIMPSON, 1937). Although it was disarticulated, none of the elements were duplicated nor were they scattered over a large area. They are thus assumed to belong to one individual. The referred specimen (AMNH 3159) was discovered in Cañadon Vaca, about 30 km from Cañadon Hondo (CIFELLI, 1985, Fig. 1), after having been entirely weathered out. A third specimen (MMP 235) was also found at Cañadon Vaca.

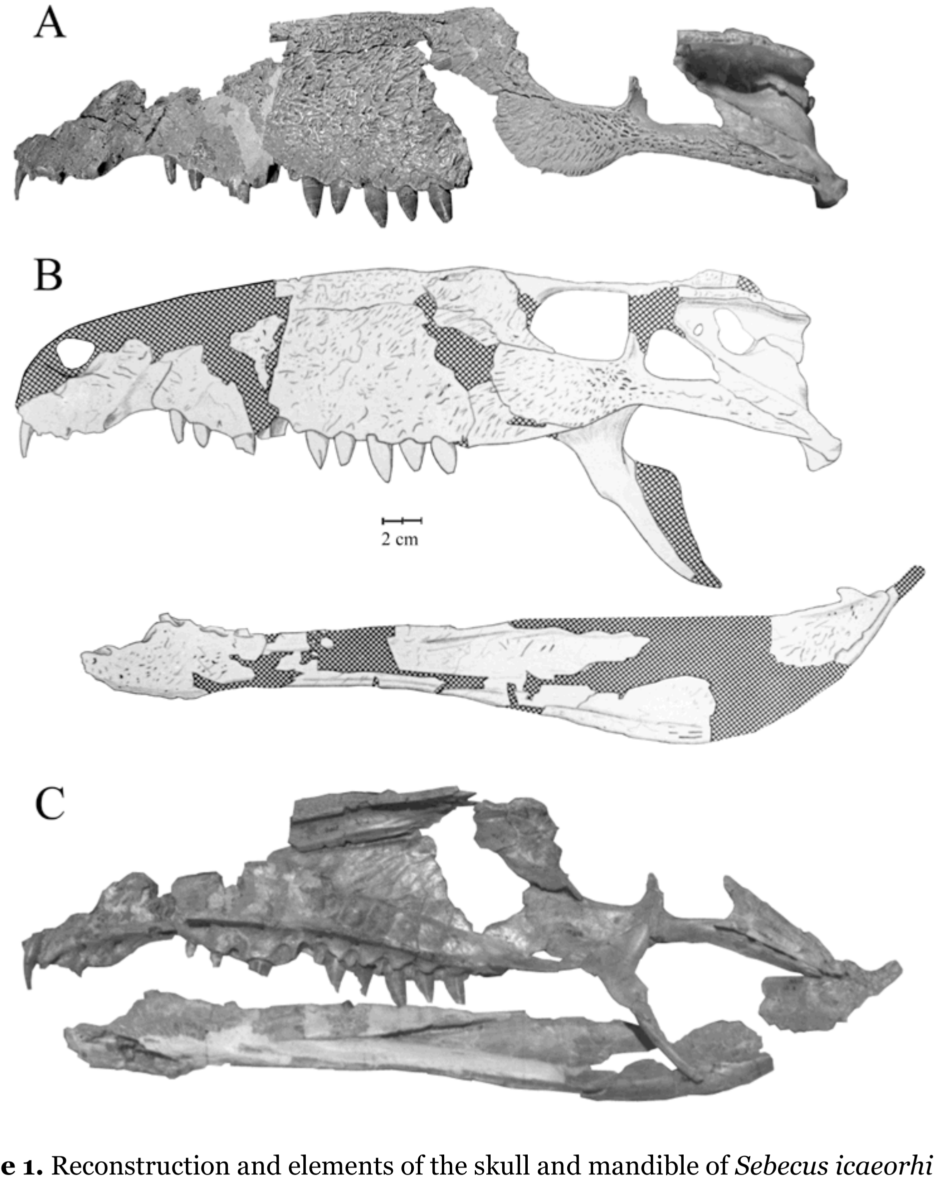

Figure 1. Reconstruction and elements of the skull and mandible of *Sebecus icaeorhinus* (based on AMNH 3160) in left lateral view. A. Preserved cranial bones of *S. icaeorhinus*, AMNH 3160, in left lateral view. B. Reconstruction of the skull and mandible, hatched areas represent missing material. C. Preserved left cranial bones of AMNH 3160 in medial view, reversed. Scale 2 cm.

The small bentonite pocket yielding the holotype did not contain a characteristic *Notostylops* fauna, as is often found in rocks of the Casamayor (now Sarmiento) Formation (SIMPSON, 1937), but yielded mostly avian material (HOWARD, 1955), and so was described by Simpson in his field notes as the “bird clay” (SCHAEFFER, 1949). This fauna is given in Table 1. All taxa are distinctive at the generic level (cf. SIMPSON, 1938), except

Crossochelys corniger (now recognized as a juvenile *Niolamia argentina*, GAFFNEY, 1996) and the mammals *Microbiotherium gutierrezi*, *Pleurostylodon similis* (if properly identified) and *Thomashuxleya externa*. Only *N. argentina* and *T. externa* (and *P. similis* if actually present at Cañadon Hondo) are found elsewhere (CIFELLI, 1985), and the locality of the other *N. argentina* material is uncertain. An alternative interpretation, that this facies samples a component of the characteristic fauna not represented at other localities is also possible. The sediments were apparently laid down in a shallow lake or pond (SCHAEFFER, 1949; HOWARD, 1955). The exact stratigraphic position of the pocket was regarded as uncertain by Simpson (1937), and seems still to be so. Andreis (1977) discussed the geology of the Cañadon Hondo region, but did not mention *Sebecus*. He concluded that his Cañadon Hondo Formation, that would presumably include the pocket yielding *Sebecus*, formed the lower part of his Sarmiento Group. The Sarmiento Formation (or Group) is now considered to be Late Eocene in age (e.g., MADDEN; CARLINI; VUCETICH; KAY, 2010).

The fauna at Cañadon Vaca, although considered by Simpson (1937) to be a “characteristic Casamayor mammalian fauna”, is sufficiently different from the other Casamayoran faunae for Cifelli (1985) to propose its own (Vacan) subage, older than the better-known Barrancan fauna. So *S. icaeorhinus* may not have lived among the better-known Argentinian late Eocene mammals. Isolated ziphodont crocodyliform teeth were long taken to indicate the presence of *S. icaeorhinus* elsewhere (e.g. SIMPSON, in COLBERT, 1946) when it was the only ziphodont crocodyliform known from that time. However, with the discovery of several other ziphodont crocodyliform taxa in the Argentinean Eocene (Table 2), this identification can no longer be assumed.

Few papers have been devoted to *S. icaeorhinus*. The initial description of Simpson (1938) was short and not illustrated. The descriptive monograph, commenced by Simpson, was completed by Colbert (1946), based on Simpson’s manuscript (so it is unclear which features of the final work were due to which of these workers). Gasparini (1972) described the third specimen. The reconstruction presented here is an updated version of part of a thesis submitted as part of the requirements for the degree of Master of Arts at the University of Texas, Austin, in 1969.

Collection abbreviations: AMNH: American Museum of Natural History, New York City, U.S.A.; MMP: Museo Municipal de Mar del Plata, Mar del Plata, Argentina.

Table 2. Occurrence of sebecosuchian crocodyliforms in South America

	Argentina	**Brasil**	**Peru**	**Bolivia**	**Colombia**	**Venezuela**
Miocene			***Barinasuchus arveloi***		***Langstonia huilensis***	*Barinasuchus arveloi*
Oligocene	Sebecid					
Eocene	*Ayllusuchus fernandezi*, *Barinasuchus* sp., *Ilchunaia parca*, *Sebecus icaeorhinus*				***Sebecus sp.***	
Palaeocene	***Bretesuchus bonapartei***	undescribed		***Zulmasuchus querejazus***		
Late Cretaceous	*Cynodontosuchus rothi*, *Pehuenchesuchus enderi*, *Wargosuchus australis*	*Baurusuchus pachecoi*, *B. salgadoi*, *B. albertoi*, *Stratiotosuchus maxhechti*		Baurusuchid		

Note: Material not assigned to genus is included only where it is the sole indication of sebecosuchians at that time and place, and finds of isolated teeth are omitted. References: GASPARINI, 1981; GASPARINI, 1984; BUFFETAUT; HOFFSTETTER, 1977; BUFFETAUT; MARSHALL, 1991; GASPARINI; FERNANDEZ; POWELL, 1993; TURNER, CALVO, 2005; PAOLILLO; LINARES, 2007; MARTINELLI; PAIS, 2008; CARVALHO; CAMPOS; NOBRE, 2005, NASCIMENTO; ZAHER, 2010.

2. Materials and Methods

Sebecus icaeorhinus is known from three specimens, the holotype, AMNH 3160, and two referred specimens, AMNH 3159 (COLBERT, 1946) and MMP 235 (GASPARINI, 1972), of which the holotype remains the most complete. This study involves the holotype specimen only.

The new reconstruction was carried out by inspection, and by fitting together the isolated bones of the skull. Although broken into pieces, AMNH 3160 shows no evidence of post-mortem crushing, plastic deformation or other distortion.

Comparison of the ventral margins of the maxillae was carried out using the 'background eraser' tool in Adobe 'Photoshop' 5.5 for Mac to produce an image that could be superimposed over other digital images. For *Sebecus* and *Bretesuchus*, the images were superimposed matching the distance between the premaxillary-maxillary notch and the highest point of the arch, the inflection point, of the ventral margin of the jugal. Because of the incompleteness of the other specimens compared, those images were superimposed by inspection, by closely matching the form of the ventral margins.

The general form of the skull

The new reconstruction of the skull of *Sebecus icaeorhinus* in lateral view is presented in Figure 1, it does not substantially alter the form of the skull in dorsal aspect from that previously figured (COLBERT, 1946). This reconstruction differs from the previous in two features. The 1946 reconstruction of the skull is slightly too long. The left maxilla of AMNH 3160, is preserved in three pieces, one representing the anteroventral, one the central, and one the posteroventral region of the bone. In attaching the posteroventral piece to the central piece, a plaster-filled gap of 14 mm was left between them (Fig. 2). In this space an alveolus is restored. Upon articulation of the central piece of the left maxilla with the left nasal, lachrymal, and jugal, I found that the posteroventral piece of the left maxilla would fit between the jugal and the central piece of the maxilla without need for the plaster-filled gap and reconstructed alveolus (Fig. 1B). Furthermore, the right maxilla of this specimen, which is unbroken in this region, does not show this alveolus (Fig. 2). The length of the right maxilla from the sixth alveolus is shorter (by the distance of this plaster-filled gap) than that of the left maxilla as it had been restored. Hence, in the present reconstruction, the gap has been removed. This change does not much affect the general appearance of the skull, but does indicate that the maxilla bore nine, not ten, alveoli.

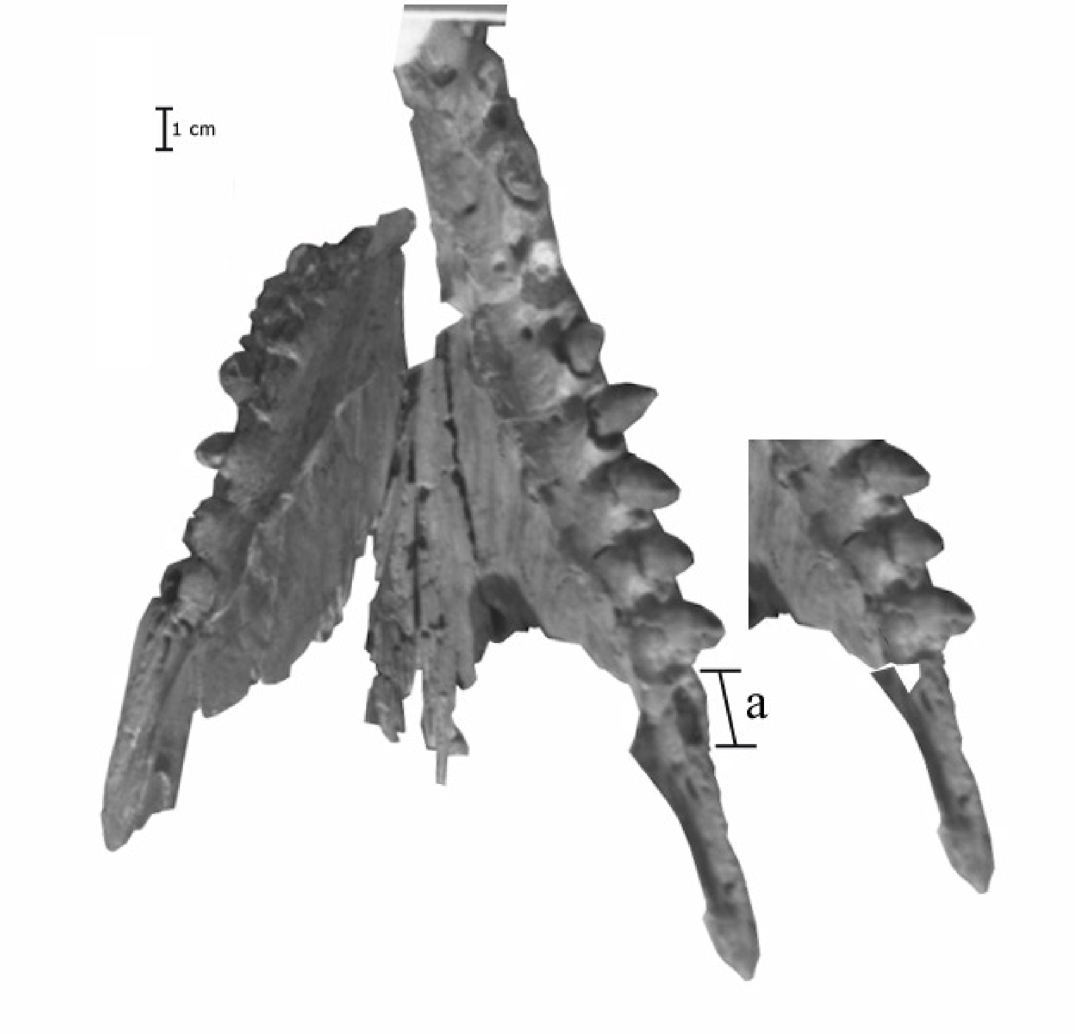

Figure 2. Maxillae and nasals of *Sebecus icaeorhinus* (AMNH 3160) articulated and seen in ventral view. The region marked 'a' is reconstructed in plaster. The inset indicates the appearance of this part of the left maxilla, with the plaster removed. The bar at the anterior end of the left maxilla is a support for the maxilla. Scale 1 cm.

The articulation of the left quadrate, squamosal, and part of the exoccipital as preserved were previously accepted as normal. A close examination of the piece comprising these three elements indicates that this is not the case (Fig. 3). When viewed from the anterior, it may be seen that the part of the internal surface of the supratemporal fenestra formed by the squamosal overlaps that part formed by the quadrate. The overlap is at least 8 mm. Furthermore, it appears that the quadrate has been rotated about a longitudinal axis by approximately 30 degrees, thus raising the external (lateral) edge of the quadrate relative to its position in life, and depressing the internal (medial) edge. It is this rotation, raising the squamosal, that has caused the overlap.

When the whole fragment is viewed from behind, it may be seen that the portion of the quadrate articulating with the squamosal and the exoccipital has been forced posteriorly away from the squamosal leaving a gap of 4 mm. An examination of the external (lateral) face of the fragment reveals that the quadrate has been displaced dorsally and thrust under the ventral edge of the squamosal by about 2 mm. Therefore the articular condyle of the quadrate is not preserved in its in vivo position relative to the squamosal and exoccipital; in life the transverse axis of the articular surface of the quadrate was approximately horizontal. Thus the lateral end was not elevated and the medial end depressed as previously restored (COLBERT, 1946, fig. 9A, C). Furthermore, the posterior part of the quadrate has been displaced more dorsally than the anterior part so that in life the bone was slightly more vertical in its orientation than appears in the specimen.

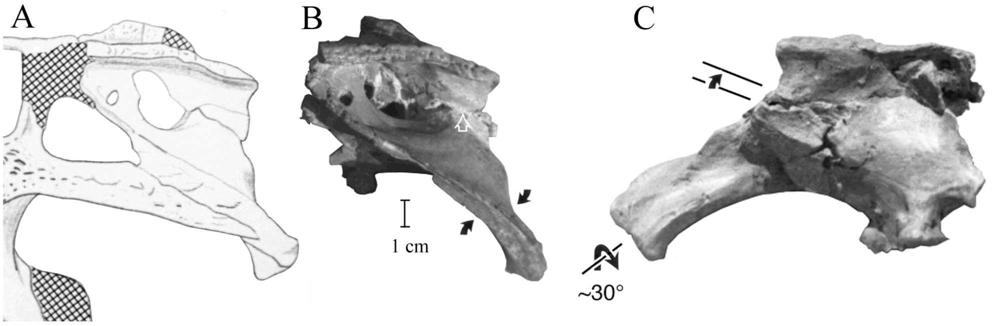

Figure 3. The temporal complex of *Sebecus icaeorhinus* (AMNH 3160) indicating the displacement of the quadrate. A. Reconstruction of the temporal-quadrate region in lateral view. B. The temporal complex as preserved in lateral view, black arrows indicate the rotation of the quadrate, and the white arrow indicates the displacement of the quadrate from the squamosal. C. The temporal complex as preserved in caudal view, indicating the rotation of the quadrate and its displacement from the squamosal. Scale 1 cm.

The smoothly curved part of the broken posterodorsal edge of the left maxilla could conceivably be regarded as the margin of an antorbital fenestra. It is not; unlike *Bergisuchus dietrichbergi* (BERG, 1966, Abb. 9), *S. icaeorhinus* shows no sign of an antorbital fenestra. This portion of the edge, although at about the same position on the maxilla as the small fenestra in *B. dietrichbergi*, is seen, upon close inspection, to be the result of a break.

I have changed the form of the snout slightly from that given by Colbert (1946) because of evidence provided by more recent discoveries of other sebecosuchians, particularly *Barinasuchus arveloi* (BUFFETAUT; HOFFSTETTER, 1977) and *Langstonia huilensis* (LANGSTON; GASPARINI, 1997). In both specimens a process rises nearly vertically from the anterior extremity of the premaxilla and, in *Barinasuchus* (and presumably also in *Langstonia*) arches posteriorly to contact the nasals. The nares of mesoeucrocodylians tend to open anterodorsally, as opposed to those of the eusuchians which open dorsally. In *Barinasuchus*, *Bretesuchus* and *Langstonia* the nares are more laterally directed, and this was probably also true of *Sebecus*.

As *Sebecus* is one of the few sebecosuchians with a reasonably complete and undistorted snout, it is appropriate to present cross sections of the snout. Figure 4 presents two cross-sections at the level of the fifth maxillary tooth and at the level of the ninth maxillary tooth. These sections differ from that of *Barinasuchus arveloi* (BUFFETAUT; HOFFSTETTER, 1977, Fig. 1D) in that the lateral faces of snout are inclined to the vertical and approximately straight. In *B. arveloi*, the lateral faces are nearly vertical dorsally and ventrally, but inclined at about 60 degrees to the vertical between these vertical portions. In *Zulmasuchus querejazus* the dorsal portions of the lateral faces of the maxillae are described as subvertical (BUFFETAUT; MARSHALL, 1991).

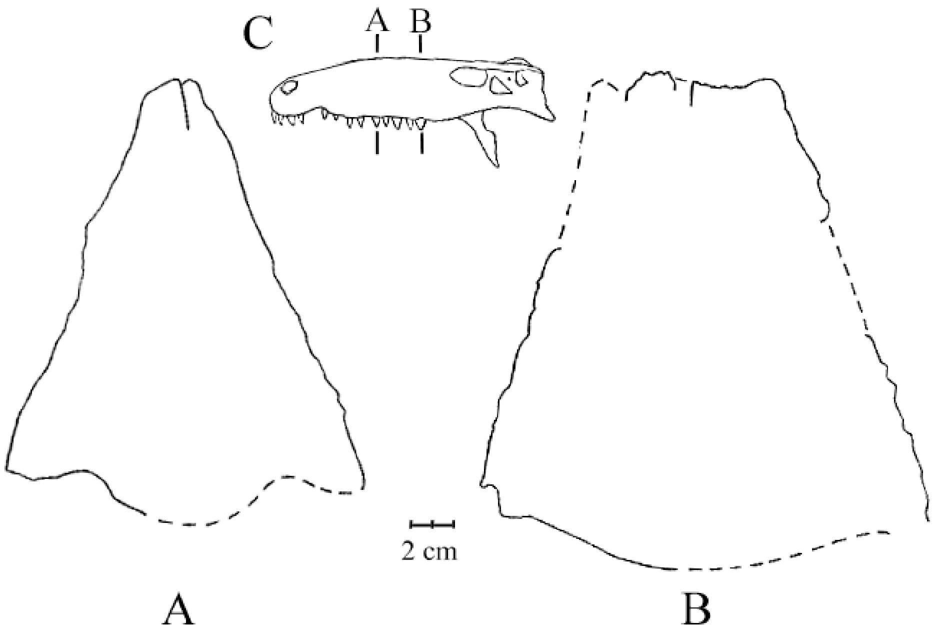

Figure 4. Cross sections of the snout of *Sebecus icaeorhinus* (AMNH 3160). A. Section at the level of the fifth maxillary tooth. B. Section at the level of the ninth maxillary tooth. C. Outline of reconstructed skull, showing positions of the cross sections. Dotted lines indicate missing material. Scale 2 cm.

The general form of the mandible

In the 1969 thesis I had reconstructed the mandible as deeper than in the 1946 study for two reasons. In all modern crocodilians known to me, when the jaw is closed, the ectopterygoid barely, if at all, projects below the ventral margin of the lower jaw. Second, the skull form of *Sebecus* is similar to that of the eusuchian *Pristichampsus ziphodon* (MARSH, 1871) in which the posterior part of the jaw is deeper than in the previous restoration of *Sebecus*. However, the mandible of MMP 235 clearly demonstrates that the post-dentary portion of that mandible was shallow (GASPARINI, 1972, lam. 1B), shallower than both my 1969 reconstruction and the 1946 reconstruction. The reconstruction of the depth of the postdentary region in AMNH 3160 is constrained by the articulation of the dentary with the angular. This indicates that the postdentary region of AMNH 3160 was substantially deeper than that of MMP 235 (Fig. 5). MMP 235 also differs somewhat in the form of the angular. MMP 235 derives from an individual about 67% as large as that of

AMNH 3160. Because MMP 235 is not obviously deformed, these differences may result from variation in growth or individual or sexual variation.

A mandibular fenestra was restored in *Sebecus*, contacting the preserved elements only at one small region of the dentary (1946, pl. 11). On close examination, this region of the dentary does not differ from that which articulates with the angular, and thus does not provide evidence for the placement of a fenestra. However, the mandible of MMP 235 shows that a fenestra existed near the region where it was reconstructed in the 1946 study (Fig. 5).

Of the retroarticular process of *Sebecus* only the basal section of the retroarticular region of the surangular is preserved. This resembles that of *Alligator* more closely than that of *Crocodylus*. Since the preserved portion of the retroarticular process of the surangular of *Sebecus* does not curve upward as strongly as that of a *Crocodylus* of the same size, it has here been restored as being more nearly horizontal. The only other sebecosuchians from which the retroarticular process is known are *Baurusuchus* and *Bretesuchus*. The process in *B. pachecoi* does not extend dorsally, but strongly medially, with little posterior development (PRICE, 1945), as does that of *Baurusuchus salgadoi* (CARVALHO; CAMPOS; NOBRE, 2005). The surangular of the holotype of *Sebecus icaeorhinus* also has a medially directed retroarticular portion. The process is more posteriorly elongate in *Baurusuchus albertoi*, but still not projecting much dorsally (NASCIMENTO; ZAHER, 2010). In *Bretesuchus bonapartei* the retroarticular process projects posteriorly and slightly dorsally (GASPARINI; FERNANDEZ; POWELL, 1993). Thus the retroarticular process of *Sebecus* has been restored in that form (Fig. 1B).

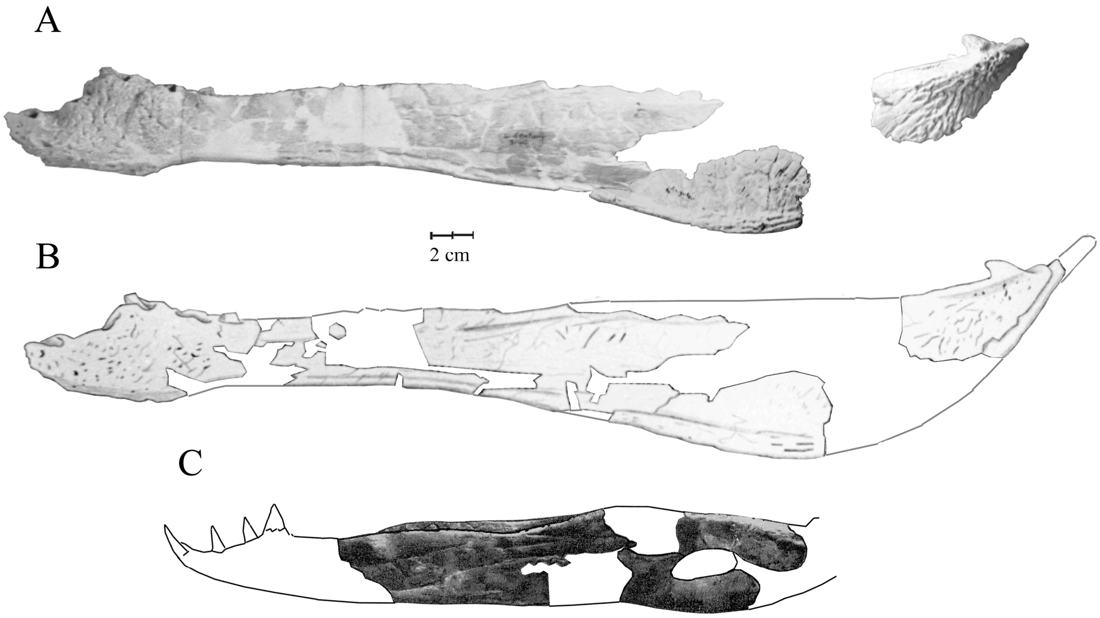

Figure 5. The mandible of *Sebecus icaeorhinus*. A. Left mandibular elements of AMNH 3160 in lateral view. B. reconstruction of that mandible. C. Mandibular elements of *Sebecus icaeorhinus* (MMP 235) in left lateral view, approximately to scale with mandible of AMNH 3160.

3. Comparison

Since the latest work on *Sebecus icaeorhinus*, in 1969, several more Palaeogene sebecosuchians have been described (GASPARINI, 1984; GASPARINI; FERNANDEZ; POWELL, 1993; BUFFETAUT; HOFFSTETTER, 1977; BUFFETAUT; MARSHALL, 1991; PAOLILLO; LINARES, 2007). Most of these, *Bretesuchus bonapartei*, *Barinasuchus arveloi*, *Zulmasuchus querejazus* and *Bergisuchus dietrichbergi* appear to have deeper snouts relative to the orbito-narial length in lateral view, than *Sebecus icaeorhinus* (Fig. 6). *Ayllusuchus* has a substantially shallower snout (GASPARINI, 1984). *Barinasuchus* and *Zulmasuchus* have a more pronouncedly convex ventral maxillary margin, while that of *Bretesuchus* is very like that of *S. icaeorhinus* in form, but with a ventrally ‘hooked’ premaxilla. *Barinasuchus* is substantially larger than *Sebecus*, so this stronger development of the marginal convexity may be an allometric effect of increased size (although obviously not in *Zulmasuchus*). This margin in *Ayllusuchus* is flatter than in

S. icaeorhinus. All, in which the region is preserved, show a pronounced notch in the ventral margin of the upper jaw for the lower caniniform tooth (number 4). *S. icaeorhinus* has a lower, relatively longer snout than *Barinasuchus* and *Zulmasuchus*. The snout of *Bretesuchus* is sufficiently close in proportions in lateral view to that of *Sebecus* to suggest that the difference may be due to individual variation or post-mortem deformation.

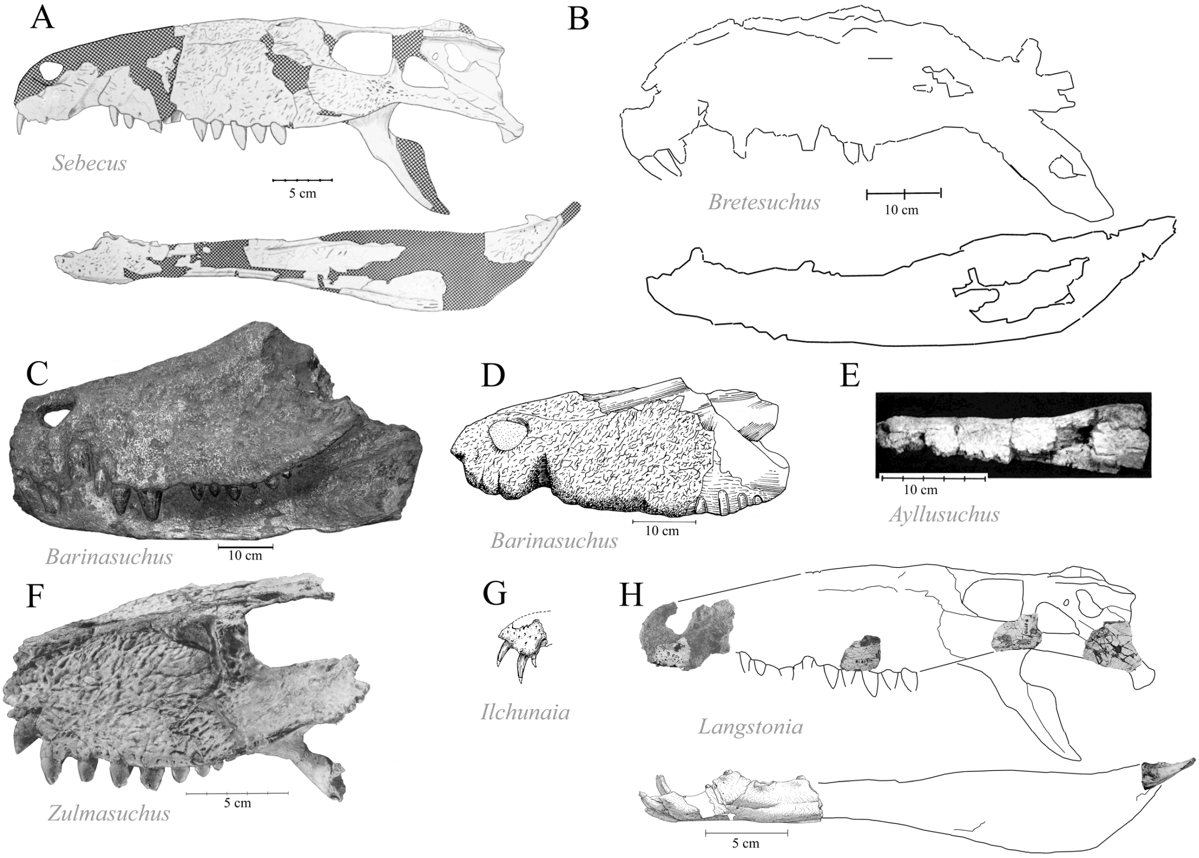

Figure 6. Crania of Cenozoic South American sebecosuchian crocodyliforms compared. Images are shown with approximately the same orbito-narial distance. A. *Sebecus icaeorhinus*. B. *Bretesuchus bonapartei* (the back of the skull has been crushed (Gasparini, pers. comm., 2010). C. *Barinasuchus arveloi*, holotype. D. *Barinasuchus arveloi* from Peru (reversed). E. *Ayllusuchus fernandezi*. F. *Zulmasuchus querejazus*. G. *Ilchunaia parca*. H. *Langstonia huilenesis*. *L. huilensis* image comprising several specimens, scaled to reconstruction of *S. icaeorhinus* skull, scale bar for holotype mandibular piece. *I. parca* included here (and in Table 2) although it is not certainly known to be a sebecosuchian. (After BUFFETAUT; HOFFSTETTER, 1977; PAOLILLO; LINARES, 2007; BUFFETAUT; MARSHALL, 1991; GASPARINI; FERNANDEZ; POWELL, 1993, GASPARINI, 1972; LANGSTON 1965; BUSBEY, 1986, LANGSTON; GASPARINI, 1997; GASPARINI, 1984.)

4. Conclusions

A new reconstruction of the skull of *Sebecus icaeorhinus* differs from that of Colbert (1946). The previous reconstruction of the skull is slightly too long, due to a lengthened reconstruction of the left maxilla. As in Gasparini's (1972) maxilla, the maxilla bore nine, not ten, teeth. The quadrate was slightly more vertical in its orientation and the transverse axis of the mandibular articular condyle was nearly horizontal. In cross section, the snout of *S. icaeorhinus* has inclined, nearly straight lateral sides, unlike that of *Barinasuchus*. The difference in depth of the post-dentary portion of the mandible between AMNH 3061 and MMP 235 may be due to ontogenetic or other variation.

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