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A NEW SEBECOSUCHIAN CROCODYLIFORM FROM THE LATE CRETACEOUS OF PATAGONIA

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ABSTRACT—A well-preserved dentary from the Late Cretaceous of Neuquén Province, Argentina, represents a new taxon of sebecosuchian crocodyliform, *Pehuenchesuchus enderi*. The specimen retains a number of diagnostic characters and is referable to Sebecosuchia on the basis of two derived features (a longitudinal groove on the lateral surface of the dentary and a sigmoidal tooth row in dorsal view). The new taxon differs from all other sebecosuchians by possessing laterally compressed teeth that lack serrated carinae. A phylogenetic analysis of 30 crocodyliform taxa and two character-taxon matrices, which include many putative sebecosuchians, supports a monophyletic Sebecosuchia. In both analyses, *Pehuenchesuchus enderi* was resolved as the sister taxon to all other sebecosuchians. A clear division of Sebecosuchia into Sebecidae and Baurusuchidae was not supported.

INTRODUCTION

Sebecosuchia is an extinct clade of deep-snouted crocodyliforms with laterally compressed teeth known from the Late Cretaceous through the Miocene. A paucity of complete remains has contributed to a poor understanding of the clade's systematics and biogeography. Sebecosuchians are best known and most abundant from terrestrial deposits of South America. However, putative sebecosuchians are known from the Late Cretaceous of Pakistan, the Eocene of Algeria, and the Eocene and Miocene of France, Germany, and Portugal (Antunes, 1975; Buffetaut, 1989; Ortega et al., 1996; Wilson et al., 2001), lending support to the notion that Sebecosuchia was a diverse clade with a complex evolutionary history.

South America, and Argentina in particular, has a diverse fossil crocodyliform fauna. Most of the fossil vertebrates recorded from the continental Cretaceous of the Neuquén basin (Patagonia, Argentina) come from the center of Neuquén Province. A number of small-bodied crocodyliforms such as *Araripesuchus*, *Notosuchus*, and *Comahuesuchus* are also known from the province (Bonaparte, 1991; Martinelli, 2000; Martinelli, in press; Ortega et al., 2000; Woodward, 1896). However, from 1996 to 2000, many Cretaceous vertebrates were collected from the region of Rincón de los Sauces, northern Neuquén province. The subject of this paper is a well-preserved sebecosuchian jaw from this locality. The specimen was recovered during the 1997 field season through ongoing fieldwork by the Museo de Geología y Paleontología, Universidad Nacional de Comahue at Cañadon Rio Seco quarry, two kilometers north of Rincón de los Sauces (Fig. 1).

The material comes from a reddish sandstone within the Neuquén basin. The stratigraphy of the basin was subdivided by Groeber (1946) based on three supercycles. The last supercycle (Lower Cretaceous to Paleocene) is divided into the Neuquenian cycle and Malalhueyan cycle corresponding to the Neuquén Group (Albian to lower Campanian) and the Malargue Group (Maastrichtian to Paleocene), respectively. The Neuquén group is a series of continental red beds comprised of conglomerates, reddish sandstones and claystones corresponding to fluvial, alluvial, eolian, and playa-lake environments (Cazau and Uliana, 1973; Digregorio, 1972). It was laid down during the late Albian through the early Campanian. The Neuquén group is divided in three subgroups, Rio Limay, Rio Neuquén, and Rio Colorado (Leanza, 1999). The fossil described here was found in the Rio Neuquén subgroup, placing its age as Turonian-Coniacian.

The Cañadon Rio Seco locality has been notable for its extraordinarily abundant and diverse titanosaurid sauropod fossils. These fossils include numerous articulated and disarticulated specimens (Calvo et al., 1997; Calvo and González Riga, 1999; Coria and Salgado, 1998; González Riga and Calvo, 2001) as well as a newly described titanosaurid species (Calvo and González Riga, in press). The discovery of a sebecosuchian jaw and a number of isolated ziphodont teeth belonging to an undetermined crocodyliform mark the first records of crocodyliform material from the north of Neuquén province.

Many questions remain regarding the break-up of Gondwana during the Cretaceous, crocodyliform dispersal during the Tertiary, and the census of taxa affected by the K-T extinction. Given its Gondwanan distribution during the Cretaceous, its South American and putative Euro-African distribution during the Tertiary, and its evident survivorship across the Cretaceous-Tertiary boundary, Sebecosuchia is a clade well suited to address these questions. A well-tested phylogenetic hypothesis for the group is, therefore, invaluable towards answering many of these persisting questions.

BACKGROUND

Sebecosuchian History

Laterally compressed, serrated teeth have long been held as a characteristic of sebecosuchians. However, this dental condition, termed 'ziphodont', is known to occur in a number of other crocodyliform clades such as the pristichampsines and mekosuchines. This tooth morphology and associated dorsoventral deeping of the snout has been noted as an effective means for minimizing snout torque in terrestrial predators during feeding (Auffenberg, 1978; Busbey, 1986; Busbey, 1995), and its multiple independent derivations within crocodyliforms seem consistent with this. Indeed, early taxonomic work was confounded by this fact and most ziphodont crocodyliforms found were grouped within Sebecosuchia based on the presence of this character (Langston, 1956; Berg, 1966; Hecht and Archer, 1977).

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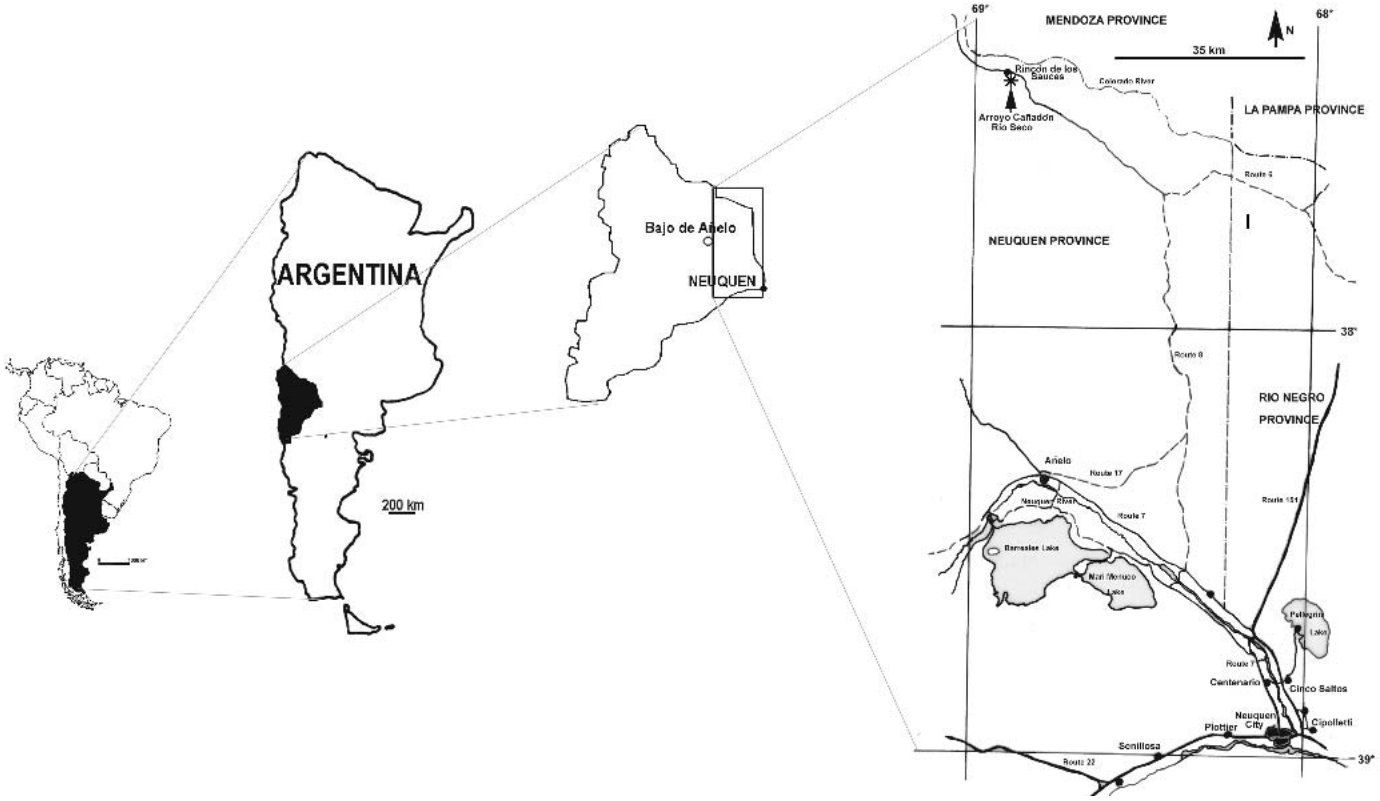

FIGURE 1. Map of Neuquén Province, Patagonia, Argentina. The arrow and asterisk on the far right map marks the location of Cañadón Rio Seco quarry, 2 km north of Rincón de los Sauces.

The taxon Sebecosuchia was erected in 1946 by Colbert for a peculiar fossil crocodyliform with a deep snout and laterally compressed serrated teeth from the Eocene of Argentina, *Sebecus icaeorhinus* Simpson (1937). Price (1945) described *Baurusuchus*, another deep-snouted South American form, and placed it within the new taxon Baurusuchidae. Colbert (1946) included this, with Sebecidae, in Sebecosuchia. The exact membership of Baurusuchidae is currently unclear but would appear to at least include *Baurusuchus pachecoi* and *Stratiotosuchus maxhechti* from the Late Cretaceous of Brazil (Campos et al., 2001) as well as *Pabwehshi pakistanensis* from the Late Cretaceous of Pakistan (Wilson et al., 2001). A number of other South American taxa have been referred to Sebecosuchia, including *Ayllusuchus fernandezi* from the lower Eocene of Argentina (Gasparini, 1984), *Ilchunaia parca* from the late Eocene of Argentina (Rusconi, 1946; Langston, 1956; Gasparini, 1972), the Paleocene Itaborai Crocodile from Brazil (*sensu* Buffetaut, 1982), *Bretesuchus bonapartei* from the late Paleocene of Argentina (Gasparini et al., 1993) and two other species referred to *Sebecus*—the early Paleocene *S. querejazus* from Bolivia (Buffetaut and Marshall, 1991) and the mid-Miocene *S. huilensis* from Colombia (Langston, 1965).

The first non-South American ziphodont 'mesosuchian' to be included within the Sebecosuchia was *Bergisuchus dietrichbergi* (Berg, 1966; Kuhn, 1968), though Buffetaut (1988) later removed *Bergisuchus* from Sebecosuchia and assigned it to Trematochampsidae. In 1975, Antunes described the crocodyliform *Iberosuchus macrodon* from the Eocene of Portugal and assigned it to Sebecosuchia, and later Buffetaut (1989) described *Eremosuchus elkoholicus*, a small ziphodont crocodyliform from the Eocene of Algeria, and referred this taxon to Trematochampsidae as well. 'Trematochampsids', however, remain enigmatic and the group is of questionable composition and validity (Buckley and Brochu, 1999; Rasmusson, 2002). Moreover, the referral was not a strong one, based primarily on the participation of the surangular in the craniomandibular articulation, the general shape of the teeth, and a broad concave symphysis. Laterally compressed teeth and a broad concave symphysis are not limited to 'trematochampsids', being characters that are also shared with *Sebecus* and *Baurusuchus*. Additionally, a surangular that forms part of the craniomandibular articulation is not uncommon among primitive mesoeucrocodylians. This trait is found in *Libycosuchus*, *Sebecus*, *Trematochampsa*, and dyrosaurids and therefore not sufficient grounds for referral to one particular group (Stromer, 1914; Rasmusson, 2002; AHT pers. obs.). Ortega et al. (1996) departed from Buffetaut's classification and included *Eremosuchus* within Sebecosuchia based on phylogenetic analysis. Interestingly, it is with *Eremosuchus* that the new taxon shares the most similarity, with both forms lacking the strongly procumbent anterior dental margin seen in other sebecosuchians.

In general, we agree with Ortega et al.'s (1996) assessment of *Eremosuchus* and have included it along with many other putative sebecosuchians and closely related crocodyliforms in attempts to avoid any preconception of membership or diagnostic characters in our present analysis.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **GSP-UM**, Geological Survey of Pakistan-University of Michigan collection, Quetta; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MAU**, Museo Municipal Argentino Urquiza, Neuquén, Argentina; **MNN**, Musée National du Niger, Niamey, Niger Republic; **MUC**, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Benton and Clark, 1988
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
SEBECOSUCHIA Colbert, 1946
PEHUENCHESUCHUS ENDERI, gen. et sp. nov.
(Figs. 2, 3)

Holotype—MAU-PV-CRS-440, an isolated right dentary.

Etymology—Pehuenche, after the name for the region, in the Mapuche language, where the specimen was found; souchus, Greek name for the Egyptian crocodile-headed god. Specific name after the fictional character Ender Wiggin.

Diagnosis—A crocodyliform with a narrow and deep lower jaw (plesiomorphic). Sixteen teeth in the dentary, the first and the fourth larger than the remaining ones with the first slightly procumbent. Tooth row sigmoidal in dorsal view with lateral surface of dentary bearing a longitudinal depression anterior to the external mandibular fenestra (plesiomorphic). Differs from all other sebecosuchians by having laterally compressed teeth with carinae lacking serrations (autapomorphic).

Horizon, Locality, and Age—Río Neuquén Formation (Neuquén Group), Late Cretaceous, late Turonian-Coniacian according to Leanza and Hugo (2001). The fossils come from Cañadón Río Seco site, 2 km North of Rincón de los Sauces, Neuquén province, Patagonia, Argentina (Fig. 1). Material was recovered by JOC and his team from the Museo de Geología y Paleontología, Universidad Nacional de Comahue.

DESCRIPTION

Dentary—The specimen consists of a nearly complete right dentary (Figs. 2 and 3). The jaw is very narrow with very little medial curvature of the symphysis. As a result the mandible is very narrow and acute in dorsal view. The posteriormost portion of the dentary is missing and the posteriormost portion of the symphysial region is slightly damaged. The dentary comprises most of the symphysis, extending to the fifth alveolus. The splenials are not preserved, but, based on the suture scar, at least the anteriormost portion of the splenial participated in the symphysis. There are 16 alveoli, all oval in outline, with the first and fourth containing enlarged teeth. The first tooth is slightly recurved and very slightly procumbent. The fourth alveolus is elevated above the level of the other alveoli (a condition shared by most crocodyliforms) and is laterally shifted along with the third and fifth alveoli. The seventh and eighth tooth appear to be the smallest of the preserved teeth. Posterior to the eighth alveolus, the alveoli remain nearly constant in size and interalveolar distance, with only the last two alveoli showing any significant reduction in size. The dentary is similar to that of *Sebecus icaeorhinus*; however, in *S. icaeorhinus* the first three teeth are strongly procumbent and positioned ventrally to the other teeth (Colbert, 1946). The dentary shares an even more striking resemblance with that of *Eremosuchus*. However, the oval alveoli and lack of serrations on the teeth distinguish *Pehuenchesuchus* from *Eremosuchus*.

FIGURE 2. Right dentary of *Pehuenchesuchus enderi,* MAU-PV-CRS-440. **A**, lateral view. **B**, medial view. **C**, dorsal view. Scale bar equals 25 mm.

The lateral surface is heavily sculpted with deep grooves. In lateral view, the anteriormost portion of the dentary from the fifth alveolus forward gradually slopes ventromedially forming a dish-shaped anterior region, another feature common to sebecosuchians. Also seen in lateral view is a slightly festooned alveolar margin. The seventh, eighth, and ninth aveoli are located in the swale between the anterior and posterior portions of the dentary. Posterior to the symphysis, the dentary is nearly vertically oriented. As one moves posteriorly the dentary expands slightly dorsoventrally with the dorsal margin extending upwards very slightly. The posterior portion of the dentary, although in poor condition, does preserve the anterior border of the external mandibular fenestra.

Medially, a portion of the dentary surrounding alveoli 6–12 is missing. A deep groove similar to that in *S. icaeorhinus* is present just posterior to the symphysis, while a very smooth surface is present posteriorly (the Meckelian fossa) for the insertion of the pars internus of the M. adductor mandibulae internus (Iordansky, 1973).

In dorsal view, two aspects of the mandiblar ramus are noteworthy. The first is the shallow trough-shaped anterior portion of the mandible. The second is the sigmoid pattern of the alveoli with the anterior six alveoli laterally shifted, 7–9 centered and 10–16 lingually displaced. These two features, along with the laterally compressed teeth, are diagnostic of sebecosuchians and are strong indicators that this new taxon is related to the group.

Dentition—Of the seven teeth preserved, most are worn and in places superficially covered with matrix. All are laterally compressed with anterior and posterior carinae. The first and fourth teeth are more triangular in outline while the others (2, 3, 5, 6, and 7) have a more rounded apex. Because of the preservational quality of the teeth, the presence of enamel texture on the carinae of the teeth cannot be determined for all. However, the fourth and fifth tooth lack serrations but the enamel is wrinkled on the anterior margin (Fig. 4). This is similar to the lower teeth of *Sebecus icaeorhinus*, but more closely resembles the teeth of *Sebecus querejazus* in having rounded apices. This is a fairly common tooth morphology, however, having arisen multiple times in different crocodyliform clades. Among 'mesosuchian' crocodyliforms it is seen in *Sebecus*, *Mahajangasuchus*, *Araripesuchus wegeneri*, 'trematochampsids' and peirosaurids (Colbert, 1946; Gasparini et al., 1991; Buckley and Brochu, 1999). In crown-group crocodylians this morphology evolved at least twice, once in pristochampsines and again in mekosuchines.

PHYLOGENETIC ANALYSIS

Data Sets and Character Coding

In order to explore sebecosuchian relationships in general, and the informativeness of jaw and dental characters in particular, two morphological data matrices were analyzed and their resulting phylogenetic hypotheses compared. The first data set is adapted from Buckley et al. (2000), which was in turn based

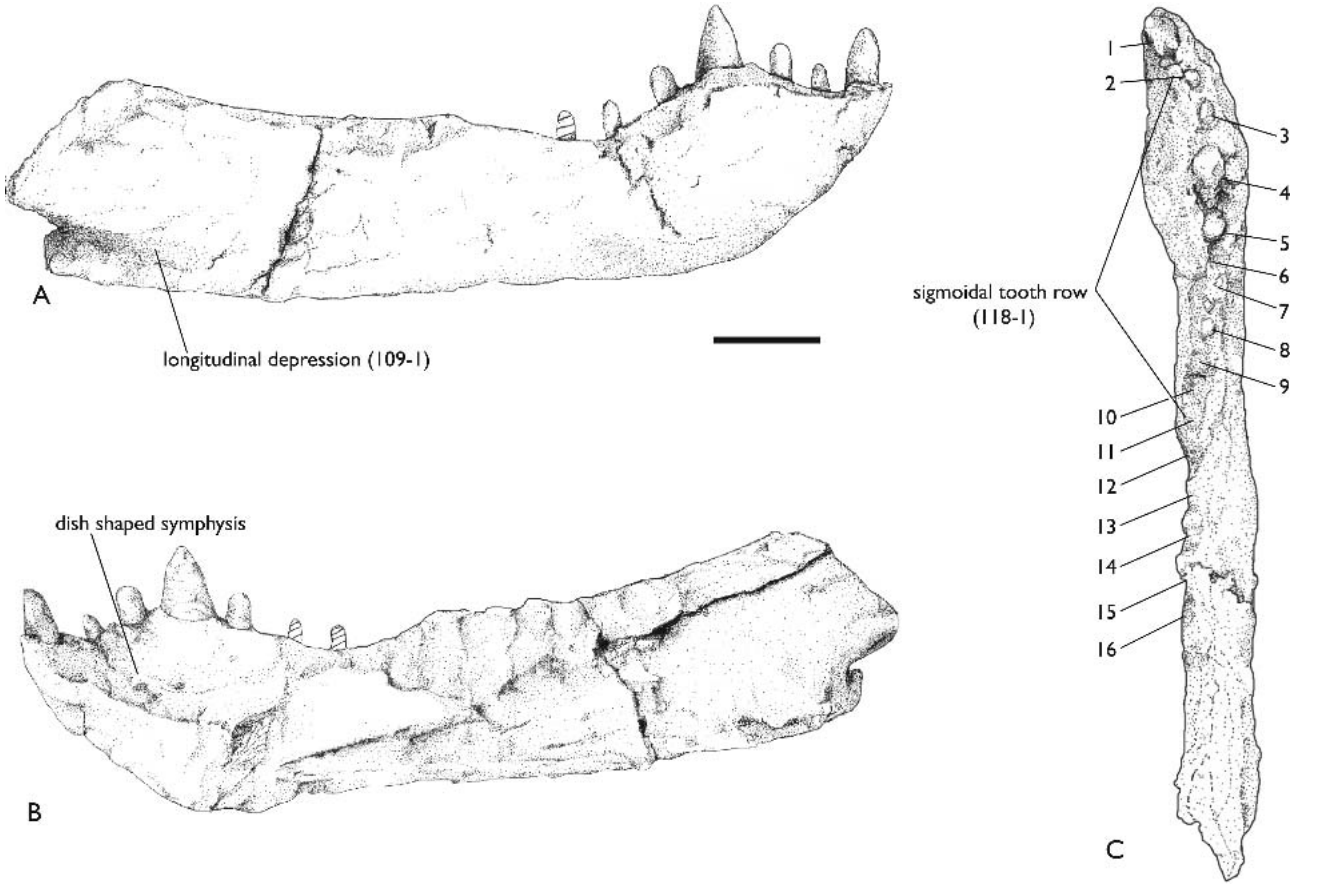

FIGURE 3. Stippled drawing of right dentary of *Pehuenchesuchus enderi*, MAU-PV-CRS-440. **A**, lateral view showing one of two sebecosuchian synapomorphies (character 109–1). **B**, medial view. **C**, dorsal view showing second sebecosuchian synapomorphy (character 118–1). Scale bar equals 25 mm.

largely upon the matrix by Clark (1994). The second data set is derived from Ortega et al. (1996). This character matrix is a much smaller subset of the first being composed almost entirely of jaw or dental characters (16 of the17 characters used).

The data matrix used in Analysis 1 is expanded from the version published by Buckley et al. (2000) through the inclusion of ten additional characters and eight taxa. The characters added are: 118—Tooth row of dentary in dorsal view straight or gently curved (0) or sigmoidal (1) (modified from character 15 of Ortega et al., 1996); 119—Palatines running parasagittally along midline with their entire length participating in ventral surface of nasopharyngeal passage (0) or palatines diverging laterally becoming rod-like caudally (1); 120—Quadratojugal not forming part of mandibular condyle of quadrate (0) or forming part of lateral hemicondyle (1); 121—Mandibular condyle of quadrate positioned ventral to occipital condyle (0) or on level with occipital condyle (1) (modified from character 124 of Wu et al., 1997); 122—Anteriorly, palatines transversely flat and not sharply separating maxillae (0) or narrow and 'arrow'-shaped, sharply separating maxillae (1); 123—Foramen intramandibularis oralis small or absent (0) or large and slot-like (1) (modified from Ortega et al., 1996); 124—Median diastemata (upper, lower) absent (0) or present (1) (modified from character 74 of Sereno et al., 2003); 125—Position of anterior portion of upper tooth row adjacent to (0) or offset labially and ventrally from (1) dentary tooth row (modified from character 75 of Sereno et al., 2003); 126—Surface of choanal septum smooth (0) or marked by groove (1); 127—Second maxillary tooth same size or only slightly larger than other maxillary teeth (0) or hypertrophied and much larger than other maxillary teeth (1).

The eight taxa added to the data set are *Bretesuchus bonepartei, Iberosuchus macrodon, Anatosuchus minor, Pabwehshi pakistanensis*, *Pehuenchesuchus enderi, Eremosuchus elkoholicus*, an undescribed malagasy crocodyliform, and Buckley et al.'s (2000) *Araripesuchus,* which was split into *Araripesuchus gomesii* and *Araripesuchus patagonicus*. With the exception of the added characters and taxa, codings follow Buckley et al. (2000) with the following modifications: *Comahuesuchus*—21(1), 42(1), 111(1), 114(1), 115(1), and *Notosuchus*—115(1). Modified codings and added taxa are based on fossils examined by AHT including *Anatosuchus* (MNN GDF 603), *Araripesuchus gomesii* (AMNH 24450), *Araripesuchus patagonicus* (MUCPV 267, 268, 269), *Notosuchus* (MACN 1027, 1037, 1044, and MUCPV 287), and new material of *Comahuesuchus* (Martinelli, 2000; Martinelli, in press). *Pabwehshi* was coded from a cast of GSP-UM 2000, while *Bretesuchus*, *Eremosuchus*, and *Iberosuchus* were coded from the literature (Antunes, 1975; Buffetaut, 1989; Gasparini et al., 1993; Ortega et al., 1996).

Analysis 2 differed from that of Ortega et al. (1996) by the addition of two new characters and four taxa: *Comahuesuchus*, *Araripesuchus*, *Hsisosuchus*, and *Pehuenchesuchus enderi.* Codings were taken from Ortega et al. (1996, 2000) with one modification: in our analysis *Sebecus* is coded as possessing a sigmoidal tooth row in dorsal view—15(1). This recoding is based on the authors' reexamination of the holotype of *Sebecus icaeorhinus* (AMNH 3160), which shows a clearly sigmoidal tooth row in

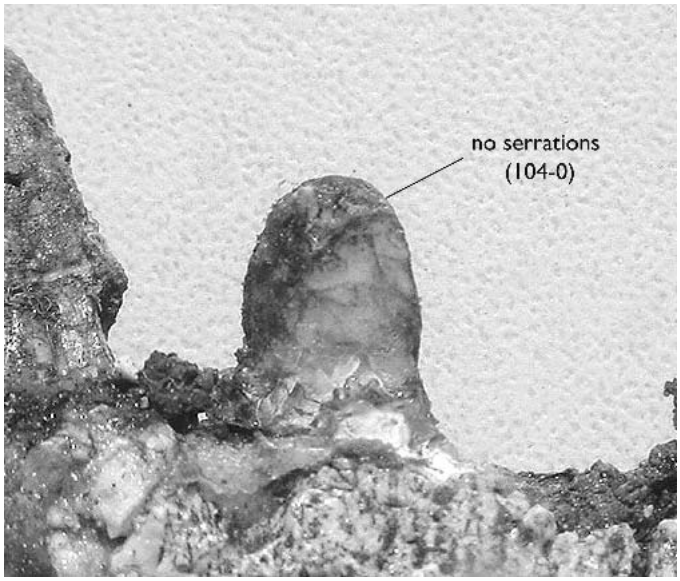

FIGURE 4. Detail of fifth dentary tooth illustrating the lack on serrations on the carina (character 104–0).

dorsal view. *Comahuesuchus* and *Araripesuchus* were coded from specimens examined by AHT and *Hsisosuchus* was coded from the literature (Li et al., 1994; Wu et al., 1994). This data set differs from that of Analysis 1 by consisting of 17 characters, which code mainly the morphology of the lower jaw and dentition. Additionally, *Pabwehshi* could not be coded for the most of these characters and was thus excluded from the analysis.

Parsimony Analysis

Analysis 1 used 127 discrete characters, 30 ingroup taxa and three outgroup taxa (*Orthosuchus*, *Protosuchus*, and *Hemiprotosuchus*). Analysis 2 used 17 discrete characters, 12 ingroup taxa and one outgroup taxon (*Hsisosuchus*). In both analyses characters were equally weighted and treated as unordered. Matrices were subjected to maximum parsimony analysis using PAUP* (Swofford, 2001).

The results of both analyses (Fig. 5) show general correspondence with each other. An Adams consensus of each analysis recovered a notosuchian clade, a sebecosuchian clade, and *Trematochampsa*, peirosaurids, and *Araripesuchus* were found to be successive sister taxa to Neosuchia. Beyond this, the relative positions of taxa within these clades varied slightly between the two data sets, specifically in regards to the sister taxon of Neosuchia and the unresolved position of *Notosuchus* + *Comahuesuchus* in Analysis 2. Nevertheless, in both analyses, *Pehuenchesuchus enderi* was the basal-most member of a clade consisting of *Sebecus*, *Bretesuchus, Iberosuchus*, *Baurusuchus,* and *Eremosuchus* (Analysis 1 places *Pabwehshi* in this clade as well).

These results indicate that a sufficient number of synapomorpies is present in the jaw and dental characters used by Ortega et al. (1996) and Analysis 2 (Fig. 5B) of this paper to recover a phylogenetic hypothesis consistent with that recovered from a matrix composed of more numerous characters spread throughout the skeleton. Approximately 18% of the characters from this large matrix are jaw or dental characters. It was thought that perhaps a jaw/dental signal was driving the pattern in the larger matrix, thereby resulting in general agreement between Analysis 1 and 2. To test this, an analysis using the large data set was run excluding all jaw and dental characters. The resulting tree was not dramatically different, with most major clades from Analysis 1 recovered, including a sebecosuchian clade. Although resolution decreased with the removal of the jaw and dental characters, topological differences were not significant enough to indicate the presence of an overriding jaw/dental signal. Such performance from a small character matrix is generally not anticipated, and in this case most likely results from much of the known sebecosuchian material being cranial and possessing apomorphic characters.

Given the better sampling of taxa and characters in the larger data set (Analysis 1), the phylogenetic hypothesis recovered from that analysis is preferred (Fig. 5A). According to this analysis, *Pehuenchesuchus* is the basal-most taxon in a monophyletic Sebecosuchia. This clade consists of a number of Cretaceous and Tertiary crocodyliforms that have before been considered as sebecosuchian (e.g. *Iberosuchus*, *Bretesuchus*, *Baurusuchus*, *Sebecus*, *Pabwehshi*, *Eremosuchus*). The sebecosuchian clade is the sister group of a monophyletic clade of small-bodied notosuchian taxa (e.g. *Notosuchus*, *Anatosuchus*, *Comahuesuchus*, *Malawisuchus*, *Uruguaysuchus*, *Simosuchus*). This large, more inclusive group of crocodyliforms is similar in composition (but not topology) to the Ziphosuchia/Notosuchia clade (Ortega et al., 2000 and Sereno et al., 2001 respectively) recovered in several phylogenetic analyses (Ortega et al., 2000; Sereno et al., 2001; Pol, 2003). *Libycosuchus brevirostris*, considered closely related to *Baurusuchus* by some authors (Clark, 1986; Clark, 1994; Ortega et al., 2000), was found to be very labile in the present study. Its position within Mesoeucrocodylia was unresolved in the Adams consensus (Fig. 5A), but was not found within the sebecosuchian clade in any of the most parsimonious trees.

Character support of Sebecosuchia consists of two unequivocal synapomorphies: lateral surface of the dentary with longitudinal groove (109–1) and a sigmoidal tooth row in dorsal view (118–1; see Fig. 3C). A sigmoidal tooth row refers to the 'S' shape the position of the dentary teeth describe in dorsal view as one moves antero-posteriorly along the lower jaw. However, this morphology is not unique to sebecosuchians, and the most parsimonious distribution of characters renders this character homoplastic in the present analysis. A sigmoidal tooth row is also present in some peirosaurids and *Trematochampsa oblita* (Rasmusson, 2002), though *Trematochampsa taqueti* lacks this trait (Buffetaut, 1976; Ortega et al., 1996).

The basal position of *Pehuenchesuchus* is supported by the lack of serrations on the carinae of its teeth (104–0; Fig. 4)—all other sebecosuchians possess serrations (104–1). *Iberosuchus*, *Baurusuchus*, *Bretesuchus,* and *Pabwehshi* form a clade within Sebecosuchia supported by three unequivocal synapomorpies. These characters are: external surfaces of cranial and mandibular bones heavily ornamented, with deep grooves and pits (1–2); premaxilla and maxilla with broad contact on face and laterally open notch between them (9–1); and large and slot-like foramen intramandibularis oralis (123–1).

In all of the most-parsimonious trees, *Sebecus* is the sister taxon to the *Iberosuchus* + *Bretesuchus* + *Baurusuchus* + *Pabwehshi* clade, though *Eremosuchus* is resolved to this node in the Adams consensus due to its unstable position among these more derived taxa. Lastly, *Baurusuchus* and *Pabwehshi* are resolved as sister taxa with unequivocal support from two synapomorphies: posterior two premaxillary teeth much longer than anterior teeth (78–1) and anterior dentary teeth opposite premaxilla-maxilla contact more than twice the length of other dentary teeth (80–1). Wilson et al. (2001) referred *Pabwehshi* to Baurusuchidae based on its affinities with *Baurusuchus.* The present analysis corroborates this referral and places *Pabwehshi* in a larger phylogenetic context.

SEBECOSUCHIAN MONOPHYLY

Under early definitions (Colbert, 1946; Gasparini, 1972), the monophyly of Sebecosuchia was implicit. Clark (1986) was first

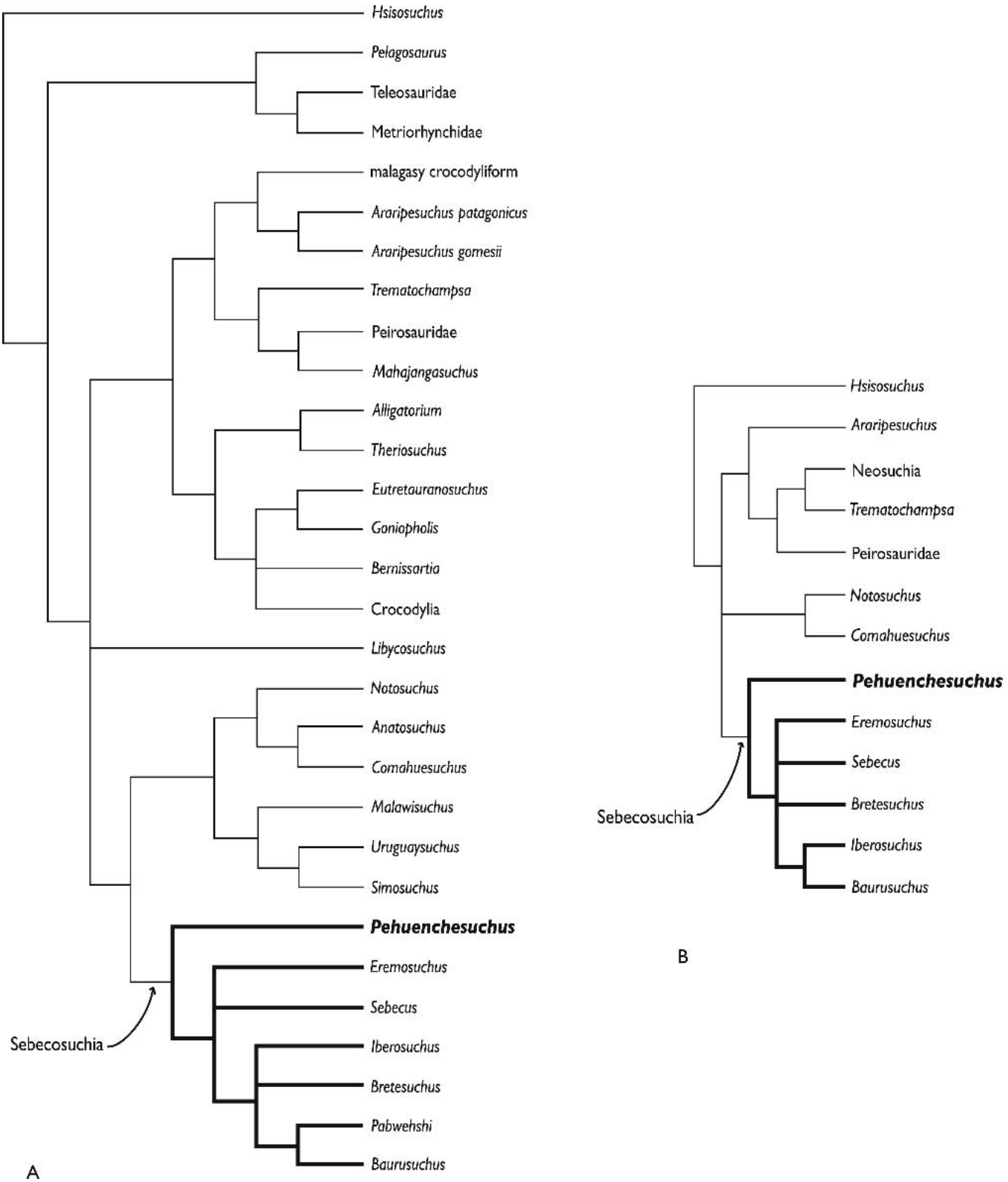

FIGURE 5. **A**, Analysis 1—Adams consensus of 95 most-parsimonious trees (MTPs) for seven sebecosuchians and other mesoeucrocodylians. Tree length is 311 with a CI of .4319 (after excluding uninformative characters) and a RI of .6600. See Appendix 1 for a list of characters used in analysis and Appendix 2 for codings. **B**, Analysis 2—Adams consensus of 63 most-parsimonious trees for six sebecosuchians and closely related basal mesoeucrocodylians. Tree length is 23 with a CI of .7000 (after excluding uninformative characters) and a RI of .8182. Matrix is based on Ortega et al. (1996).

to test this notion and this work first explicitly supported a monophyletic Sebecosuchia. Later work (Benton and Clark, 1988; Clark, 1994) contradicted this and found the clade paraphyletic. Since then, the monophyly of Sebecosuchia has been supported in most phylogenetic analyses (Gasparini, 1972; Gasparini et al., 1993; Ortega et al., 1996; Buckley and Brochu, 1999; Buckley et al., 2000; Ortega et al., 2000; Sereno et al., 2001; Pol, 2003). A recent reanalysis by Sues and Larsson (2002) of *Hamadasuchus* found *Sebecus* to be more closely related to a clade containing peirosaurids and *Araripesuchus* than to notosuchians. That Sebecosuchia is a poorly understood group is evident from the many questions of membership and even validity of the clade. This uncertainity results, in part, from the poor quality or incompleteness of many of the referred specimens. Such material makes rigorous and comprehensive phylogenetic analyses difficult by limiting the potential to uncover synapomorphy and as a result leads to poorly resolved topologies. Additionally, most analyses that have included sebecosuchians often include only *Sebecus* and *Baurusuchus* (Gasparini et al., 1991; Buckley and Brochu, 1999; Buckley et al., 2000; Larsson and Gado, 2000). Only Ortega et al. (1996) and Ortega et al. (2000) have included a larger number of potential Sebecosuchians in their analyses. As is usually the case, more taxa and more characters will ultimately help clarify the phylogenetic signal of the clade.

In this paper, we have attempted a similar approach by including a broad sample of potential sebecosuchians and closely related crocodyliforms. Although the present analysis could not resolve two nodes within the Sebecosuchia clade, our data support a monophyletic Sebecosuchia with moderate character support for two successively less inclusive sebecosuchian clades. Support for Colbert's division of Sebecosuchia into the Sebecidae and Baurusuchidae is inconclusive in this analysis. Phylogenetic analysis provides weak character support for a Baurusuchidae clade, interpreted here to include *Baurusuchus*, *Pabwehshi*, and *Bretesuchus* (hypertrophied maxillary tooth [127–1], nearly tubular rostrum [3–1], quadratojugal extending dorsally as broad sheet contacting most of postorbital portion of postorbital bar [19–1], reduced premaxillary tooth formula). *Cynodontosuchus* and *Stratiotosuchus* may belong to this clade as well, though Gasparini (1972, 1981) considers *Cyndontosuchus* likely synonymous with *Baurusuchus* and the affinities of *Stratiotosuchus* remain untested in a phylogenetic context. Character support for Sebecidae is essentially non-existent and a monophyletic Sebecidae has not been recovered in any cladistic study to date (Ortega et al., 1996; Ortega et al., 2000); membership of Sebecidae remains uncertain. Indeed, the inclusion of taxa such as *Ilchunaia* and *Ayllusuchus* may alter conclusions of this study. Nevertheless, presently 'sebecids' appear to represent a paraphyletic assemblage of sebecosuchian crocodyliforms basal to baurusuchids.

CONCLUSION

A phylogenetic analysis with one of the largest samplings of putative sebecosuchian crocodyliforms supports the monophyly of the group. The new taxon *Pehuencheusuchus enderi* is found to be the basal-most member of the clade. Topological resolution within Sebecosuchia, however, remains unclear and questions of the validity of Baurusuchidae and Sebecidae persist. Continued fieldwork in South America, Africa, and Europe will assist future systematic and phylogenetic work in clarifying these issues. We feel that it should be noted that as we move away from a topological system of taxonomy to a phylogenetic one (de Queiroz and Gauthier, 1994; Cantino and de Queiroz, 2000) supraspecific taxon names such as Sebecosuchia, Baurusuchidae, and Sebecidae will need to be redefined. These definitions will be based on common ancestry as opposed to taxonomic content or possession of particular characters. At the present time we would like to stress the need for prudent reservation from assigning phylogenetic definitions to Sebecosuchia (or to most 'mesosuchian' clades for that matter) due to present phylogenetic uncertainty of most groups.

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APPENDIX 1

List of characters used in Analysis 1. Characters 1–101 are from Clark (1994). Character 1 is modified according to Pol (2003), while characters 2–101 are unmodified. Characters 102–106 are from Buckley and Brochu (1999). Characters 107–110 and 118 are modified from Ortega et al. (1996). Characters 111–114 are modified from Gomani (1997). Characters 115–117 are unmodified from Buckley et al. (2000). Character 121 is modified from Wu et al. (1997). Characters 124–125 are modified from Sereno et al. (2003). Characters 119, 120, 122, 123, 126, and 127 are new.

1. External surfaces of cranial and mandibular bones smooth (0), slightly grooved (1), or heavily ornamented, with deep grooves and pits (2) [Pol, 2003, character 1]
2. Rostrum narrow anterior to orbits, broadening abruptly at orbits (0) or broad throughout (1)
3. Rostrum higher than wide (0) or nearly tubular (1) or wider than high (2)
4. Premaxilla forming at least ventral half of internarial bar (0) or forming little, if any, of internarial bar (1)
5. Premaxilla narrow anterior to nares (0) or broad, similar in breadth to part lateral to nares (1)
6. Dorsal part of premaxilla vertical, nares laterally oriented (0), or dorsal part of premaxilla nearly horizontal, nares dorsolaterally or dorsally oriented (1)
7. Palatal parts of premaxillae not meeting posterior to incisive foramen (0) or meeting posteriorly along contact with maxillae (1)
8. Premaxilla loosely overlying maxilla on face (0), or premaxilla and maxilla sutured together along butt joint (1)
9. Premaxilla and maxilla with broad contact on face, rostrum not narrowing at contact (0), or broad, laterally open notch between maxilla and premaxilla (1), or rostrum constricted at contact with premaxilla and maxilla, forming narrow slit (2), or rostrum constricted at contact with premaxilla and maxilla, forming broad, laterally directed concavity (3)
10. Posterior ends of maxillae not meeting on palate anterior to palatines (0), or ends meeting (1)
11. Nasals contacting lacrimal (0) or not (1)
12. Lacrimal contacting nasal along medial edge only (0) or on medial and anterior edges (1)
13. Nasal taking part in narial border (0) or not (1)
14. Nasal contacting premaxilla (0) or not (1)
15. Descending process of prefrontal not contacting palate (0), or contacting palate (1), or contacting palate in robust suture (2)
16. Postorbital anterior to jugal on postorbital bar (0), postorbital medial to jugal (1), or postorbital lateral to jugal (2)
17. Anterior part of jugal as broad as posterior part (0) or about twice as broad as posterior part (1)
18. Jugal transversely flattened beneath lateral temporal fenestra (0) or rod-shaped beneath fenestra (1)
19. Quadratojugal narrowing dorsally, contacting only a small part of postorbital (0), or quadratojugal extending dorsally as broad sheet contacting most of postorbital portion of postorbital bar (1)
20. Frontals narrow between orbits (similar in breadth to nasals) (0) or broad, about twice nasal breadth (1)
21. Frontals paired (0) or fused (1)
22. Dorsal surface of frontal and parietal flat (0) or with narrow midline ridge (1)
23. Frontal extending well into supratemporal fossa (0) or extending only slightly or not at all (1)
24. Supratemporal roof with complex dorsal surface (0), or dorsally flat "skull table" developed, with squamosal and postorbital with flat shelves extending laterally beyond quadrate contacts (1)
25. Postorbital bar weak, lateral surface sculpted (if skull sculpted) (0), or postorbital bar robust, unsculpted (1)
26. Postorbital bar transversely flattened, unsupported by ectopterygoid (0), or postorbital bar columnar, supported by ectopterygoid (1)
27. Vascular opening on lateral edge of dorsal part of postorbital bar absent (0) or present (1)
28. Postorbital without anterolateral process (0) or with anterolateral process (1)
29. Dorsal part of postorbital with anterior and lateral edges only (0) or with anterolaterally facing edges (1)
30. Dorsal end of postorbital bar broadened dorsally, continuous with dorsal part of postorbital (0), or dorsal part of postorbital bar constricted, distinct from dorsal part of postorbital (1)
31. Bar between orbit and supratemporal fossa broad and solid, with broadly sculpted dorsal surface (0), or bar narrow, with sculpturing on anterior part only (1)
32. Parietal without broad occipital portion (0) or with broad occipital portion (1)
33. Parietal with broad, sculpted region separating fossae (0) or with sagittal crest between supratemporal fossae (1)
34. Postparietal (dermosupraoccipital) as distinct element (0) or not distinct (fused with parietal?) (1)
35. Posterodorsal corner of squamosal squared off, lacking extra "lobe" (0) or with unsculpted "lobe" (1)
36. Posterior edge of squamosal nearly flat (0), or posterolateral edge of squamosal extending posteriorly as long process (1)
37. Palatines not meeting on palate below narial passage (0), or forming palatal shelves and not meeting (1), or meeting ventral to narial passage, forming part of secondary palate (2)
38. Pterygoid restricted to palate and suspensorium, joints with quadrate and basisphenoid overlapping (0), or pterygoid extending dorsally to contact laterosphenoid and forming ventrolateral edge of trigeminal foramen, strongly sutured to quadrate and laterosphenoid (1)
39. Choana opening ventrally from palate (0) or opening posteriorly into midline depression (1)
40. Palatal surface of pterygoid smooth (0) or sculpted (1)
41. Pterygoids separate posterior to choanae (0) or fused (1)
42. Choana moderate in size, less than one-fourth skull breadth (0), or choana extremely large, nearly half skull breadth (1)
43. Pterygoids not enclosing choanae (0) or enclosing choanae (1)
44. Choanae situated near anterior edge of pterygoids (or anteriorly) (0) or in middle of pterygoids (1)
45. Quadrate without fenestrae (0), or with single fenestra (1), or with three or more fenestrae on dorsal and posteromedial surfaces (2)
46. Posterior edge of quadrate broad medial to tympanum, gently concave (0), or posterior edge narrow dorsal to otoccipital contact, strongly concave (1)
47. Dorsal, primary head of quadrate articulating with squamosal, otoccipital, and prootic (0) or with prootic and laterosphenoid (1)
48. Ventrolateral contact of otoccipital with quadrate very narrow (0) or broad (1)
49. Quadrate, squamosal, and otoccipital not meeting to enclose cranioquadrate passage (0), enclosing passage near lateral edge of skull (1), or meeting broadly lateral to passage (2)
50. Pterygoid ramus of quadrate with flat ventral edge (0) or with deep groove along ventral edge (1)
51. Ventromedial part of quadrate not contacting otoccipital (0) or contacting otoccipital to enclose carotid artery and form passage for cranial nerves IX-XI (1)
52. Eustachian tubes not enclosed between basioccipital and basisphenoid (0) or entirely enclosed (1)
53. Basisphenoid rostrum (cultriform process) slender (0) or dorsoventrally expanded (1)
54. Basipterygoid process prominent, forming movable joint with pterygoid (0), or basipterygoid process small or absent, with basipterygoid joint closed suturally (1)
55. Basisphenoid similar in length to basioccipital, with flat or concave ventral surface (0), or basisphenoid shorter than basioccipital (1)
56. Basisphenoid exposed on ventral surface of braincase (0) or virtually excluded from ventral surface by pterygoid and basioccipital (1)
57. Basioccipital without well-developed bilateral tuberosities (0) or with large, pendulous tubera (1)
58. Otoccipital without laterally concave descending flange ventral to subcapsular process (0) or with flange (1)

59. Cranial nerves IX-XI passing through common large foramen vagi in otoccipital (0), or cranial nerve IX passing medial to nerves X and XI in separate passage (1)
60. Otoccipital without large ventrolateral part ventral to paroccipital process (0) or with large ventrolateral part (1)
61. Crista interfenestralis between fenestrae pseudorotunda and ovalis nearly vertical (0) or horizontal (1)
62. Supraoccipital forming dorsal edge of foramen magnum (0), or otoccipitals broadly meeting dorsal to foramen magnum, separating supraoccipital from foramen (1)
63. Mastoid antrum not extending into supraoccipital (0) or extending through transverse canal in supraoccipital to connect middle ear regions (1)
64. Posterior surface of supraoccipital nearly flat (0) or with bilateral posterior prominences (1)
65. One small palpebral present in orbit (0), or two large palpebrals present (1), or one large palpebral present (2)
66. External nares divided (0) or confluent (1)
67. Antorbital fenestra as large as orbit (0), or about half diameter of orbit (1), or much smaller than orbit (2), or absent (3)
68. Supratemporal fenestrae much longer than orbits (0) or equal in length to or shorter than orbits (1)
69. Choanae confluent (0) or divided by septum (1)
70. Dentary extending posteriorly beneath mandibular fenestra (0) or not extending beneath fenestra (1)
71. Retroarticular process very short and robust (0), or absent (1), or short, robust, and ventrally situated (2) or posterodorsally curving and elongate (3), or posteroventrally projecting and paddle-shaped (4), or posteriorly projecting from ventral part of mandible and attenuating (5) [modified from Clark, 1994]
72. Prearticular present (0) or absent (1)
73. Articular without medial process articulating with otoccipital and basisphenoid (0) or with process (1)
74. Dorsal edge of surangular flat (0) or arched dorsally (1)
75. Mandibular fenestra present (0) or absent (1)
76. Insertion area for M. pterygoideus posterior not extending onto lateral surface of angular (0) or extending onto lateral surface of angular (1)
77. Splenial not involved in symphysis (0), or involved slightly in symphysis (1), or involved extensively in symphysis (2)
78. Posterior two premaxillary teeth similar in size to anterior teeth (0) or much longer (1)
79. Maxillary teeth homodont, with lateral edge of maxilla straight (0), or teeth enlarged in middle of tooth row, with edge of maxilla extending outward at these loci (1), or teeth enlarged and edge of maxilla curved in two waves ("festooned") (2)
80. Anterior dentary teeth opposite premaxilla-maxilla contact no more than twice length of other dentary teeth (0) or more than twice length (1)
81. Dentary teeth posterior to tooth opposite premaxilla-maxilla contact homodont (0) or enlarged opposite smaller teeth in maxillary tooth row (1)
82. Anterior and posterior scapular edges symmetrical in lateral view (0), or anterior edge more strongly concave than posterior edge (1)
83. Coracoid no more than half length of scapula (0) or about equal in length to scapula (1)
84. Anterior process of ilium similar in length to posterior process (0) or one-quarter or less length of posterior process (1)
85. Pubis rod-like, without expanded distal end (0) or with expanded distal end (1)
86. Pubis forming anterior half of ventral edge of acetabulum (0), or pubis at least partially excluded from acetabulum by anterior process of ischium (1)
87. Distal end for femur with large lateral facet for fibula (0) or with very small facet (1)
88. Fifth pedal digit with (0) or without (1) phalanges.
89. Atlas intercentrum broader than long (0) or as long as broad (1)
90. Neural spines on posterior cervical vertebrae as broad as those on anterior cervical vertebrae (0) or anteroposteriorly narrow, rodlike (1)
91. Cervical vertebrae without well-developed hypapophyses (0) or with well-developed hypapophyses (1)
92. Cervical vertebrae amphicoelous or amphiplatyan (0) or procoelous (1)
93. Trunk vertebrae amphicoelous or amphiplatyan (0) or procoelous (1)
94. All caudal vertebrae amphicoelous or amphiplatyan (0), or first caudal vertebra biconvex, with other caudal vertebrate procoelous (1), or all caudal vertebrae procoelous (2)
95. Dorsal osteoderms rounded, ovate (0), or rectangular, broader than long (1), or square (2)
96. Dorsal osteoderms with straight anterior edge (0) or with anterior process laterally on anterior edge (1)
97. Dorsal osteoderms in two parallel, longitudinal rows (0) or in more than two longitudinal rows (1)
98. Some or all osteoderms imbricated (0), or osteoderms sutured to one another (1)
99. Tail with dorsal osteoderms only (0) or completely surrounded by osteoderms (1)
100. Osteoderms absent from ventral part of trunk (0) or present (1)
101. Osteoderms with longitudinal keels on dorsal surface (0) or without keels (1)
102. Surangular forming only lateral wall of glenoid fossa (0), or surangular forming approximately one-third of glenoid fossa (1) [Buckley and Brochu, 1999:character 102]
103. Anterior margin of femur linear (0), or anterior margin of femur bearing flange for coccygeofemoralis musculature (1) [Buckley and Brochu, 1999:character 103]
104. Teeth without carinae, or with smooth carinae (0) or teeth serrated (1) [Buckley and Brochu, 1999:character 104]
105. Dentary smooth lateral to seventh alveolus (0), or dentary with large occlusion pit lateral to seventh alveolus (1) [Buckley and Brochu, 1999:character 105]
106. Scapular blade no more than twice length of the scapulocoracoid articulation (0), or scapular blade very broad and greater than twice length of scapulocoracoid articulation (1) [Buckley and Brochu, 1999:character 106]
107. Dorsal edge of dentary straight (0), or dorsal edge of dentary sinusoidal, with two concave waves (1) [modified from Ortega et al., 1996:character 1]
108. Compressed dentary (0), or transversely expanded dentary, almost as wide as high (1) [modified from Ortega et al., 1996:character 2]
109. Lateral surface of dentary continuous, without longitudinal groove (0), or lateral surface of dentary with longitudinal groove (1) [modified from Ortega et al., 1996:character 5]
110. Splenial thin posterior to symphysis (0), or splenial robust posterodorsal to symphysis (1) [modified from Ortega et al., 1996:character 7]
111. Prefrontals broad (0), or narrow and short (1), or narrow and long (2) [Gomani, 1997:character 4]
112. Snout long (0), or relatively broad and shorter than remainder of skull (1), or narrow and shorter than remainder of skull (2) [Gomani, 1997:character 6]
113. Posterior cheek teeth not multicusped (0), multicusped with cusps in single row (1), or multicusped with cusps in more than one row (2) [modified from Gomani, 1997:character 46]
114. Occipital condyle in posterior position (0) or posteroventral position (1) [modified from Gomani, 1997:character 32]
115. Vomer exposed (0) or not exposed (1) on palate [Buckley et al., 2000:character 115]
116. Posterior cheek teeth conical (0), or laterally compressed (1), or strongly spatulate (2) [Buckley et al., 2000:character 116]
117. Cheek teeth not constricted at base of crown (0) or constricted (1) [Buckley et al., 2000:character 117]
118. Tooth row in dorsal view straight or gently curved (0) or sigmoidal (1) [modified from Ortega et al., 1996:character 15].
119. Palatines running parasagittally along midline with entire length participating in ventral surface of nasopharyngeal passage (0) or palatines diverging laterally, becoming rodlike caudally (1). [new]
120. Quadratojugal not forming part of quadrate condyle (0) or forming part of quadrate condyle (1) [new]
121. Mandibular condyle of quadrate positioned ventral to occipital condyle (0) or on level with occipital condyle (1) [Wu et al., 1997:character 124]
122. Anteriorly, palatines transversely flat and not sharply dividing maxillae (0) or narrow and "arrow"-shaped, sharply dividing maxillae (1) [new]
123. Foramen intramandibularis oralis small or absent (0) or large and slot-like (1) [modified from Ortega et al., 1996:character 8].

124. Median diastemata (upper, lower) absent (0) or present (1) [Sereno et al., 2003:character 74]
125. Position of anterior portion of upper tooth row adjacent to (0) or offset labially and ventrally from (1) dentary tooth row [Sereno et al., 2003:character 75]
126. Surface of choanal septum smooth (0) or marked by groove (1) [new]
127. Second maxillary tooth same size or only slightly larger than other maxillary teeth (0) or hypertrophied and much larger than other maxillary teeth (1) [new]

APPENDIX 2

Character matrix used in Analysis 1.

Notosuchus
10210211010100111010111110?0110000002?10110020112011?1000?10?110?1111?5?010?110?0101?????0000??????0?0??000000010111001000000100

Baurusuchus
10000011111??00?110101??110?0110??????2?1011??1111201 1?1000??0?11??03?015?01011101 0?????????0??????????0?1??001101???101000?100?1

Sebecus
2000?01101000?1100011?111?0?10001012110110 0?1112011110 00??0?1??1031005100011 0000????????0?00????????0010?001?0100110101010 00?0

undescribed Malagasy crocodyliform
212101?1211?00211010101111001100010121?0100011112?11?1000??0?11010211061000110101111111?001000???????0100111000111011000000000

Araripesuchus patagonicus
212??????100???111101011110011100101 2??0100011?1??11?1000??0?1?01?211151000???1??1?11?1????10???000?0001001?1000101?11?000000001?

Araripesuchus gomesii
212001?12100002111101011110011100101 2??0100011 1?2011?1000??011?010?11?5100011010?11111?1?0100?1?0000001001110001011 1?0010000010

Alligatorium
212101?03?0000?10000101111?00?100?10???0??00??11??1??1000???????10?1??4?00101?10110111110 0????1?0010000000110001 0????00010?00?0

Theriosuchus
212101?131010011000011011110011001102110100 01?11?0111100 0?????1?10210?4?0010101011011111??0011?1100100000001100000010000 0?0000?0

Pelagosaurus
211?0111010011020101000000000000001012110100000011011110010 01?1000120 0?3000012000011011 1?0000001100011000000100000010 0??000000??

Teleosauridae
011?0111010011010100100000000000011002110100 0?0011011110010 11?1?0012 00?3?0001200000101111?0000?1100010000000100000 0?00??00??00??

Metriorhynchidae
011?0111010011?2010110000000000001100211 0?000?0011011110010 11?1?0012 00?3000112000001 01?11?0000??????0?0000001 00?000100??00??00??

Eutretauranosuchus
212??1110100102110001001 11?00?0001001110?000?1112011?1010??0?1?0?121104?0000101011 1???1??0??0?1??????0000011000000100??01??00??

Goniopholis
212?11?131?010?1100010111 1?0010001002?101000?1112011?1010?10?1?011311?4?001?101011?1??1??0?00?1100?1100000110000001000001000?0

Bernissartia
212?111131??00?1100010?111?001000?002?????0001112?11?10100?0?1???131??4?0010?01011?1?11??0000210101100000011000000100001 1000?0

Crocodylia
212011131000021100010011110010001002110101101120111010010111001310031000110101111111101111110101110000011000000100000100 0?0

Protosuchus
000000001000 00?0001000110000010011?0010100002011011111100101011010 11?120110011010100011100000?1100110000000000?0200?0000100000?0

Hemiprotosuchus
?00??0?1???????10010?0??00?0010011????01??0020?00?11?1100101??1?1?11??2?11????01?????????0????1?00?1?0000000?0200?0?000?00???0

Orthosuchus
200?0001101?000100100011000001000100 0?0000000011001111100??1?1?01011?0?000?0010001000111000 00?1100100000000?2000000000?00???0

Mahajangasuchus
2???151010????011?1111?0110000010???111111001??0??000????0???0

Peirosauridae
212?1111211?002?10?0100111?0110001012110110 01?1120111000?00?1?0??2010????0?1?1?????????????????????????????11?1?????10(0&1)0(0&1)(0&1)000000

Hsisosuchus
200??????11?00?0001010011?0011000101211010001 01?1111?1000?0??1?02?10011?000?1?10010?01?????????1?001100?00000??2000?000000000?0

Trematochampsa
212?0011?100??211??0100111?0110001 01????????11112?11????0000?1?0??10??5?0????1?????????????10002 0?0???1111?1100???0?000?11??????

Uruguaysuchus
111?0??10???00??10?11??????01?1??1?12?1??00011?????????????????????111?????0??0000??1?1?????????????????11??0????011?21000?000000

Malawisuchus
110?00?1010100?1111011111?011?0001012??0100020?11??????00????????1?211041?00?111?0?????????100???????1??0??0???1121?11?000000000

Comahuesuchus
11??02?1011?00?????0111????????001002????1??1??1?????????????1????1?1?0????0?10100?????????????????????00??00?1101110010000011?0

Anatosuchus
2121?2?1011?00211?10101110000?1100???2110110011112011?1100?10?1?0?12111510000?1010?????????????????????0?00???001101?10?100001100

Simosuchus
1120101100l?00?000101101l0?0110001011?10110001?11001???00011?1?0102111410l0?00000???????01000?2010?100?10?000011110210000000000

Pehuenchesuchus enderi
2???0????0?1??00?????????????????????????00?001???0??101????0???

Bretesuchus
1010001111??00?????????????????????????????101000?????????????????????????03?0?5??10?10200?????????????????????????10?1011?10?10010??1?00?1

Iberosuchus
1000?011110?00211?001??1???0??????0?????1?001???2?????0???1??1???0?11??10?0?1?00011????????0????0???00?1??00?1?1?1?10000??100??

Pabwehshi
1?1010111???00???0??????????21?1?????????????????????????1????????0?010??????????1

Libycosuchus
?10?001101??00?1101010?110?011000?002?????00?1112011?1010??0???0?0?1??5?0001?0000????????00?0???????????1??00???10????0010?0????