Alcheringa: An Australasian Journal of Palaeontology

Revision of Sulcusuchus erraini (Sauropterygia, Polycotylidae) from the Upper Cretaceous of Patagonia, Argentina

José P. O'gorman & Zulma Gasparini

Revision of *Sulcusuchus erraini* (Sauropterygia, Polycotylidae) from the Upper Cretaceous of Patagonia, Argentina

JOSÉ P. O'GORMAN and ZULMA GASPARINI

Sulcusuchus erraini, from the upper Campanian–lower Maastrichtian of Patagonia, Argentina, is the only polycotylid from the Southern Hemisphere for which the skull and mandible are known. The diagnosis of the species and genus is emended based on new observations. *Sulcusuchus* is characterized by the following autapomorphies: (1) deep and broad rostral and mandibular grooves and (2) a wide notch on the posterior margin of the pterygoids that are combined with a part of the body of the basioccipital, forming a wide plate. Several hypotheses about the identity of the structures that could have been housed in the rostral and mandibular grooves are evaluated. Only two of several hypotheses were not discarded. The first is that the grooves may have accommodated oral glands (supralabial and sublabial), but the biological role of such glands could not be inferred. The second hypothesis is the presence of special structures of an electrosensitive and/or mechanosensitive nature, which might allow the detection of infaunal or semi-infaunal food in soft substrates, as is represented in modern analogues, such as dolphins.

José P. O'Gorman [joseogorman@fcnym.unlp.edu.ar] and Zulma Gasparini [zgaspari@fcnym.unlp.edu.ar], División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n., B1900FWA La Plata, Argentina. Also affiliated with Consejo Nacional de Investigaciones Científicas y Técnicas, Av. Rivadavia 1917 (C1033AAJ), Ciudad Autónoma de Buenos Aires, Argentina and CONICET: Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina. Received 5.6.2012; revised 31.7.2012; accepted 4.9.2012.

POLYCOTYLIDS are a group of longirostrine Plesiosauroidea (*sensu* O'Keefe 2001) whose stratigraphic range extends from the Aptian to the Maastrichtian. They have been recorded on every continent including Antarctica (Williston 1903, 1906, 1908, Persson 1963, Carpenter 1996, Wiffen & Moisley 1986, Gasparini & de La Fuente 2000, Sato & Storrs 2000, Druckenmiller 2002, Bardet *et al*. 2003, Kear 2003, 2006, Buchy *et al*. 2005, Salgado *et al*. 2007, D'Angelo *et al*. 2008, O'Keefe 2004a, 2008).

The Polycotylidae, like other plesiosaurs, had both forelimbs and hindlimbs modified to participate in lift-based appendicular locomotion (Storrs 1993). Polycotylidae are usually considered to have been rapid swimmers and highly maneuverable—valuable characters for the pursuit of prey (O'Keefe 2004a,b)

Traditionally, polycotylids were included in the Superfamily Pliosauroidea based on their elongate rostrum and short neck (Welles 1962, Brown 1981). However, these characters have been regarded as homoplasic in recent phylogenetic analyses and most authors agree on their assignment to a clade of Plesiosauroidea (Carpenter 1996, O'Keefe 2001, 2004b, Ketchum & Benson 2011). A few authors retain the Polycotylidae within the Pliosauroidea (Druckenmiller

& Russell 2008a). The systematics of polycotylids have been modified in recent years by the discovery of new specimens, by the revision of established taxa and by the application of new phylogenetic techniques (O'Keefe 2001, 2004a, 2008, Druckenmiller 2002, Bardet *et al*. 2003, Buchy *et al*. 2005, Albright *et al*. 2007, Schumacher 2007, Druckenmiller & Russell 2008a). However, there is little consensus about the polycotylid affinities of some taxa, such as the Albian *Nichollssaura borealis* (Druckenmiller & Russell 2008b, Ketchum & Benson 2011).

Most records of polycotylids are from the Northern Hemisphere and are based on cranial and postcranial materials (Williston 1903, 1906, Carpenter 1996, Sato & Storrs 2000, Bardet *et al*. 2003, Albright *et al*. 2007). In the Southern Hemisphere, although there are records of polycotylids from Australia, New Zealand, Patagonia and Antarctica (Wiffen & Moisley 1986, Kear 2003, Salgado *et al*. 2007, D'Angelo *et al*. 2008), only one valid species has been established based on cranial material: *Sulcusuchus erraini* Gasparini & Spalletti, 1990. Consequently, the recent assessments of the osteology of Polycotylidae incorporating skull morphology have not been corroborated by specimens from the Southern Hemisphere.

The record of polycotylids from South America is particularly scarce, and is restricted to the upper Campa-

nian–lower Maastrichtian of northern and central Patagonia (Argentina). They have only been found in south and central Río Negro Province and in northeastern Chubut Province (Fig. 1). The holotype of *Sulcusuchus erraini* was found near Laguna Cari-Laufquén Grande, Río Negro Province (Fig. 1B), in the Los Alamitos Formation (see locality and stratigraphic details). In northeastern Chubut Province, Cerro Bosta locality (Fig. 1C), part of a skull and mandible referred to *S. erraini* was found in the middle levels of the La Colonia Formation (Gasparini & de La Fuente 2000). The sections of the Allen, Los Alamitos and La Colonia formations, from which the polycotylids were recovered, are late Campanian–early Maastrichtian in age (Ballent 1980, Getino 1995, Papú & Sepúlveda 1995, Page *et al.* 1999, Dingus *et al.* 2000). Polycotylid postcranial remains are known from the Allen Formation, in the area of the Salitral de Santa Rosa, Rio Negro province (Salgado *et al.* 2007, O'Gorman *et al.* 2011).

The anatomical evaluation of *Sulcusuchus erraini* specimens allows the revision of the osteological description of the holotype and the addition of many anatomical characters to those reported by Gasparini & de La Fuente (2000). The identity of the special soft structures housed in the rostral and mandibular grooves are also analysed.

Institutional abbreviations. MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MLP, Museo de La Plata, La Plata, Argentina.

Anatomical abbreviations. al, alveolus; ang, angular; ar, articular; bo, basioccipital; bot, basioccipital tuber; bs, basisphenoid; c, coronoid; de, dentary; dr, dentary ridge; ept, epipterygoid; exf, exoccipital facet; fs, foramina set; ft, functional tooth; fr, frontal; gr, groove; ju, jugal; mca, Meckelian canal; mg, mandibular groove; mx, maxilla; nad, nasal duct; oc, occipital condyle; pa, parietal; pal, palatine; pif, pineal foramen; pipv, posterior interpterygoid vacuity; pmr, posterior maxillar ridge; pmx, premaxilla; pop, paraoccipital process; prq, pterygoid process of the quadrate; ps, parasphenoid; psk, parasphenoid keel; pt, pterygoid; q, quadrate; rg, rostral groove; rap, retroarticular process; rt, replacement tooth; sa, secondary alveolus; su, surangular; sp, splenial; sq, squamosal; suo, supraorbital; to, tooth; v, vomer.

Systematic palaeontology
SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943 (*sensu* O'Keefe 2001)
POLYCOTYLIDAE Cope, 1869

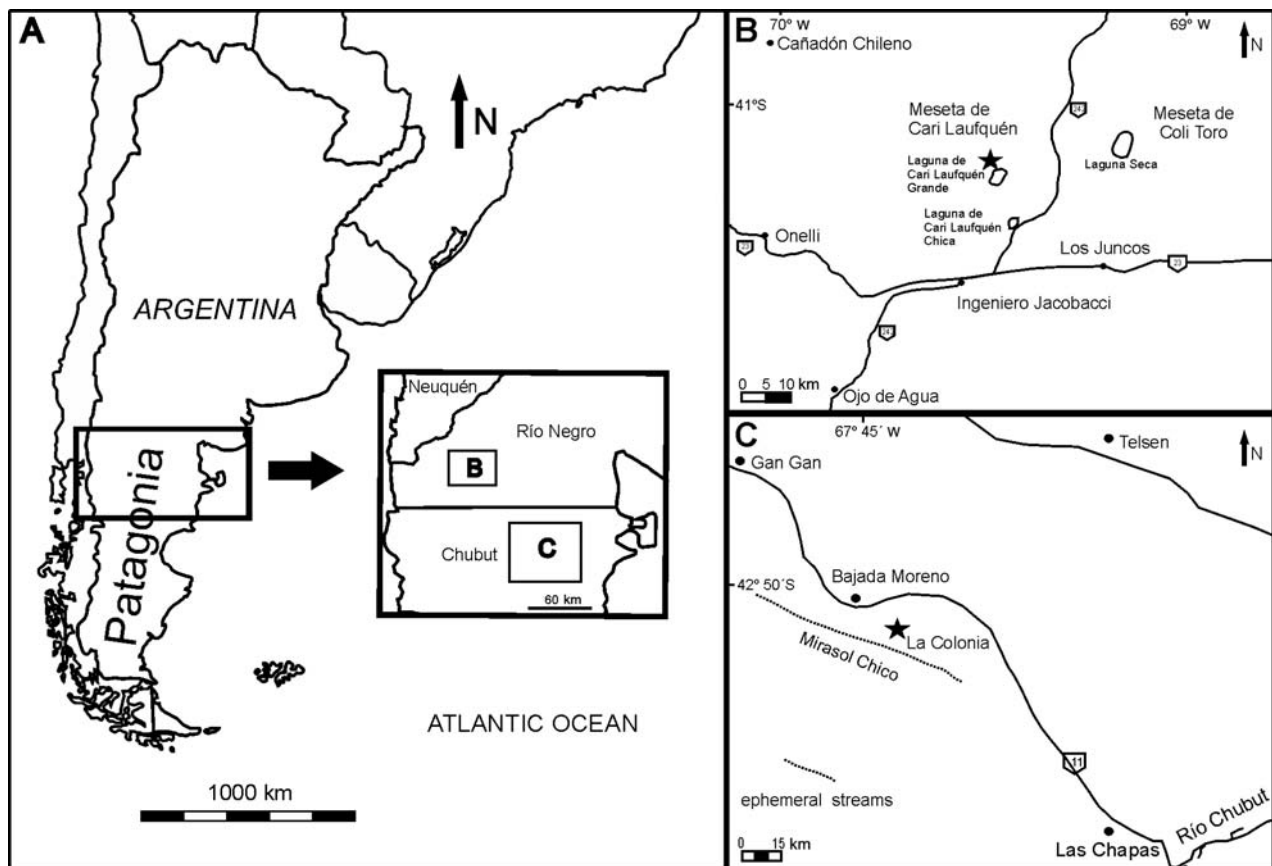*Fig. 1.* Locality maps. **A**, Map of Argentina showing sampling areas where *Sulcusuchus erraini* was found. **B**, MLP 88-IV-10-1, holotype locality (Star), Río Negro Province; **C**, Source of MPEF 650, referred material (star), Chubut Province.

Sulcusuchus Gasparini & Spalletti, 1990

Type species. Sulcusuchus erraini Gasparini & Spalletti 1990.

Revised diagnosis. Polycotylid with comparatively narrow rostrum formed by the premaxillary and maxillary, characterized by the following autapomorphies: (1) deep and broad rostral and mandibular grooves and (2) a wide notch on the posterior margin of the pterygoids that is combined with a part of the body of the basioccipital, forming a flat plate together with the posteromedial processes of the pterygoids.

Sulcusuchus erraini Gasparini & Spalletti, 1990 (Figs 2–8)

Holotype. MLP 88-IV-10-1, fragment of mandibular symphysis (Figs 2D, E, 6A–D; Gasparini & Spalletti 1990, pl, 1).

Type locality, stratum and age. Northeastern margin of Laguna Cari-Laufquén Grande, 25 km north of

Ingeniero Jacobacci (41°01′50″S, 69°27′78″W), Río Negro Province, Argentina (Fig. 1B); Los Alamitos Formation (basal levels of the 'Coli Toro' Formation *sensu* Gasparini & Spalletti 1990); upper Campanian–lower Maastrichtian (Getino 1995, Papú & Sepúlveda 1995).

Referred material. MPEF 650, part of the rostrum, fragment of left maxillary, fragment of right maxillary, fragment of the frontoparietal bridge, incomplete basicranium associated with fragments of the pterygoids, squamosal and left quadrate, fragment of mandibular symphysis, posterior part of the left mandibular ramus and fragment of the right mandibular ramus (Figs 2–5, 7 and 8).

Locality, host stratum and age. Cerro Bosta (43°00′21″S; 67°37′13″W), northeastern Chubut Province, Argentina (Fig. 1C); middle levels of the La Colonia Formation, upper Campanian–lower Maastrichtian (Page *et al.* 1999).

Emended diagnosis. Relatively small polycotylid plesiosaur with keeled parasphenoid, occipital

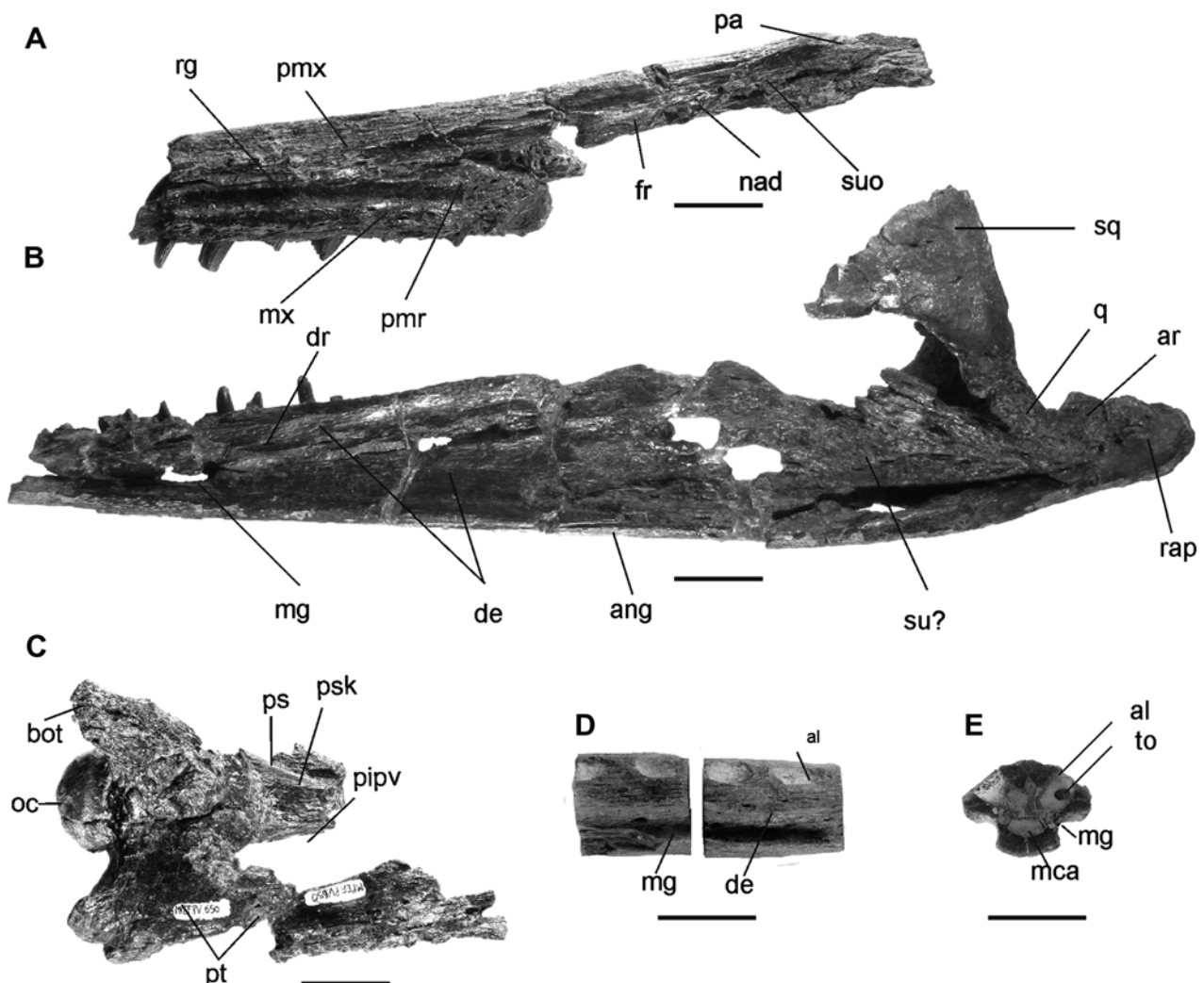*Fig. 2. Sulcusuchus erraini* (MPEF 650). **A**, Rostrum and skull roof in left lateral view; **B**, left mandibular ramus, quadrate and squamosal in lateral view; **C**, basicranium and posterior part of palate in ventral view; **D**, **E**, mandibular symphysis of *Sulcusuchus erraini* (holotype: MLP 88-IV-10-1). **D**, Right lateral view and **E**, cross-sections in posterior view. Scale bars = 20 mm.
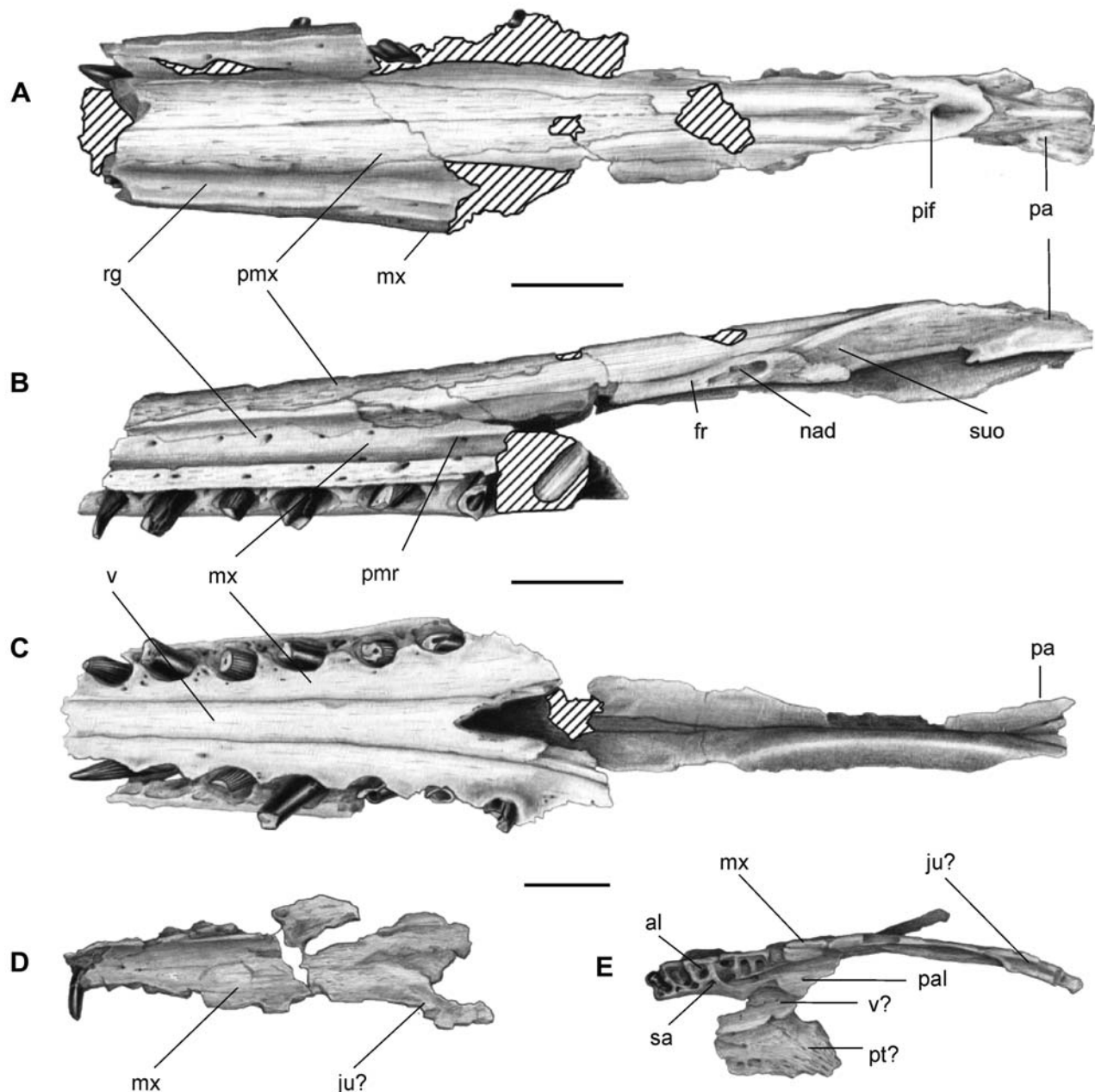
Fig. 3. Sulcusuchus erraini (MPEF 650). Interpretative drawings. **A–C**, Rostrum and skull roof in **A**, dorsal; **B**, left lateral and **C**, ventral views. **D**, **E**, Maxillary fragment in **D**, lateral and **E**, ventral views. Scale bars = 20 mm.

condyle with well-defined neck, long and postero-directed basioccipital tubercle, premaxilla with strong longitudinal striations, relatively short angular that is not visible in ventral view at least ten alveoli behind the symplysis. Posterior maxillary ridge, striated teeth with almost smooth anterior surface present.

Results
General remarks on holotype. The holotype of *Sulcusuchus erraini* (MLP 88-IV-10-1) was originally described as a mandibular fragment of a new crocodyliform cf. Dyrosauridae (Gasparini & Spalletti 1990). Later,

Gasparini & de La Fuente (2000) determined it was a rostral fragment and they reassigned it to the Polycotylidae, within the Plesiosauria. However, after new preparations and several comparisons drawn with the MPEF 650, the holotype is here identified as a fragment of the mandibular symphysis.

Rostrum. The most complete specimen of *Sulcusuchus erraini* is MPEF 650, in which the middle and posterior portions of the rostrum have been preserved (Figs 2A, 3A, B). The rostrum consists of both the premaxilla and maxilla (Fig 2A, 3A, C) as is typical of polycotylids, but differs from *Edgarosaurus*, which has a much shorter rostrum and the maxilla forms only the
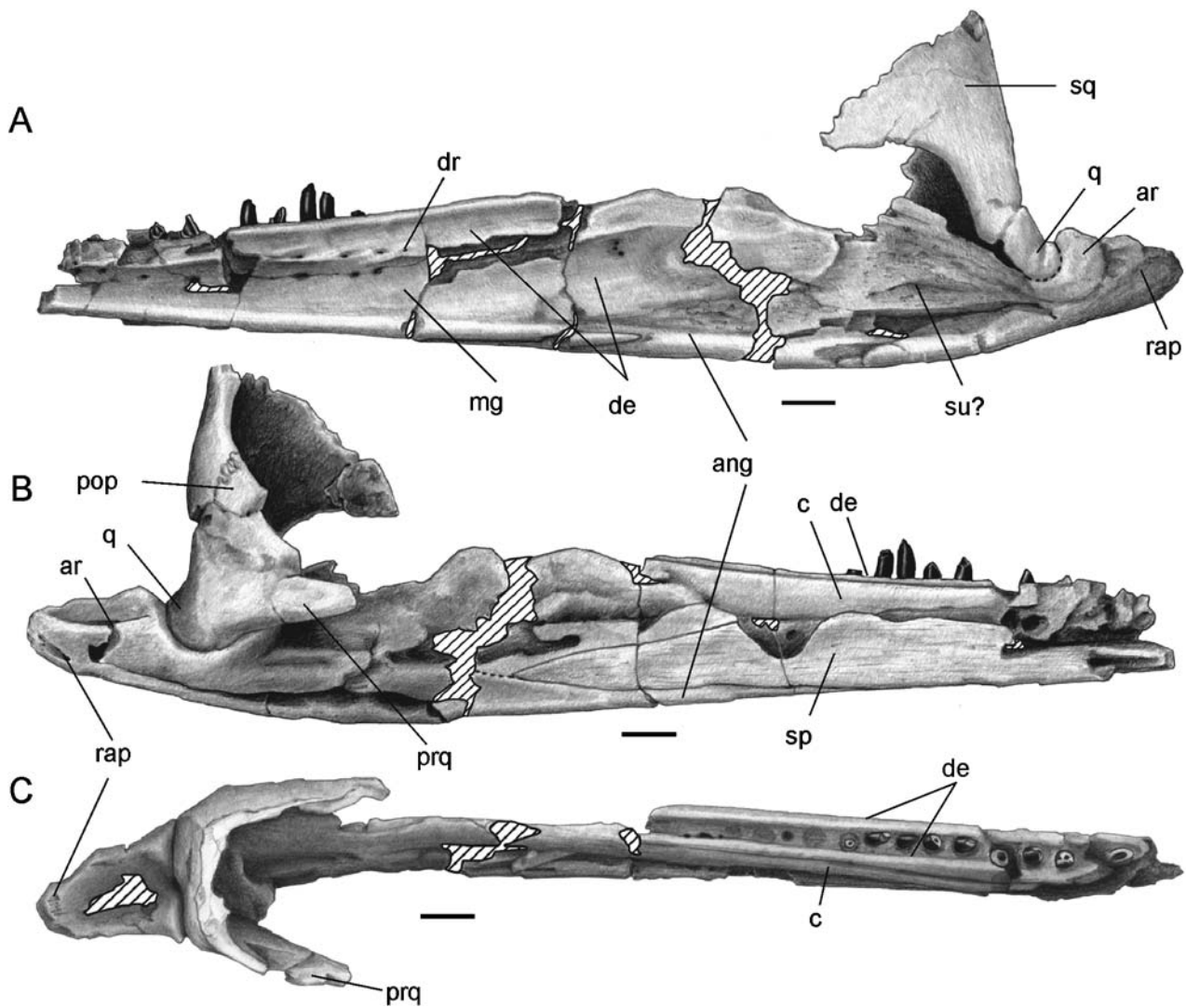
Fig. 4. Sulcusuchus erraini (MPEF 650). Interpretative drawings. Left mandibular ramus, quadrate and squamosal in **A**, lateral; **B**, medial and **C**, dorsal views. Scale bars = 20 mm.

posteriormost portion of it (Carpenter 1996, Druckenmiller 2002, Bardet *et al*. 2003, Buchy *et al*. 2005).

Each premaxilla extends posteriorly forming a medial dome and joining along the dorsum of the rostrum through a clear sagittal suture (Fig 2A, 3A). This strong dorsal convexity is less marked posteriorly where it divides into two narrower and lower domes. The suture between the premaxillaries and the frontal is strongly jagged (Fig. 3A). The whole surface of the premaxilla is covered by slight longitudinal striae (Fig. 3A, B) that are similar to and in the same position as those evident in *Dolichorhynchops osborni* (O'Keefe 2004a).

In lateral view, the maxilla forms a broad and deep rostral groove (Fig 2A, 3A, B). The dorsal limit of the rostral groove is ventral to the maxilla–premaxilla suture, hence the groove is excavated exclusively on the maxilla (Fig. 3B). The ventral limit of the rostral groove is dorsal to the labial margin of the maxilla, which expands laterally (Figs 2A, 3A, B). The surface of the rostral groove is smooth and has slightly

anteroposteriorly elongated foramina, of which the largest are located in the deepest part of the groove. The surface between the ventral margin of the rostral groove and the labial margin of the maxilla is covered by foramina (Fig. 3B). Towards the posterior end of the rostral groove, a weak horizontal ridge, here designated the posterior maxillary ridge, divides the rostral groove into dorsal and ventral sectors (Fig. 3B).

Eight alveoli have been preserved on the right maxilla and seven on the left maxilla (Figs 2A, 3B, C). The alveoli are slightly anteroposteriorly elongated (see Dentition section for detailed description of the teeth). Two additional isolated rostral fragments have been preserved with the referred specimen. The most complete fragment is the posteriormost section of the left maxilla, which contains the last six alveoli (Fig. 3D, E). The three anteriormost alveoli foramina are for replacement teeth (Fig. 3 E). Such foramina are not evident on the anterior section of the rostrum and mandible of MPEF 650, likely because the maxilla is narrower and the
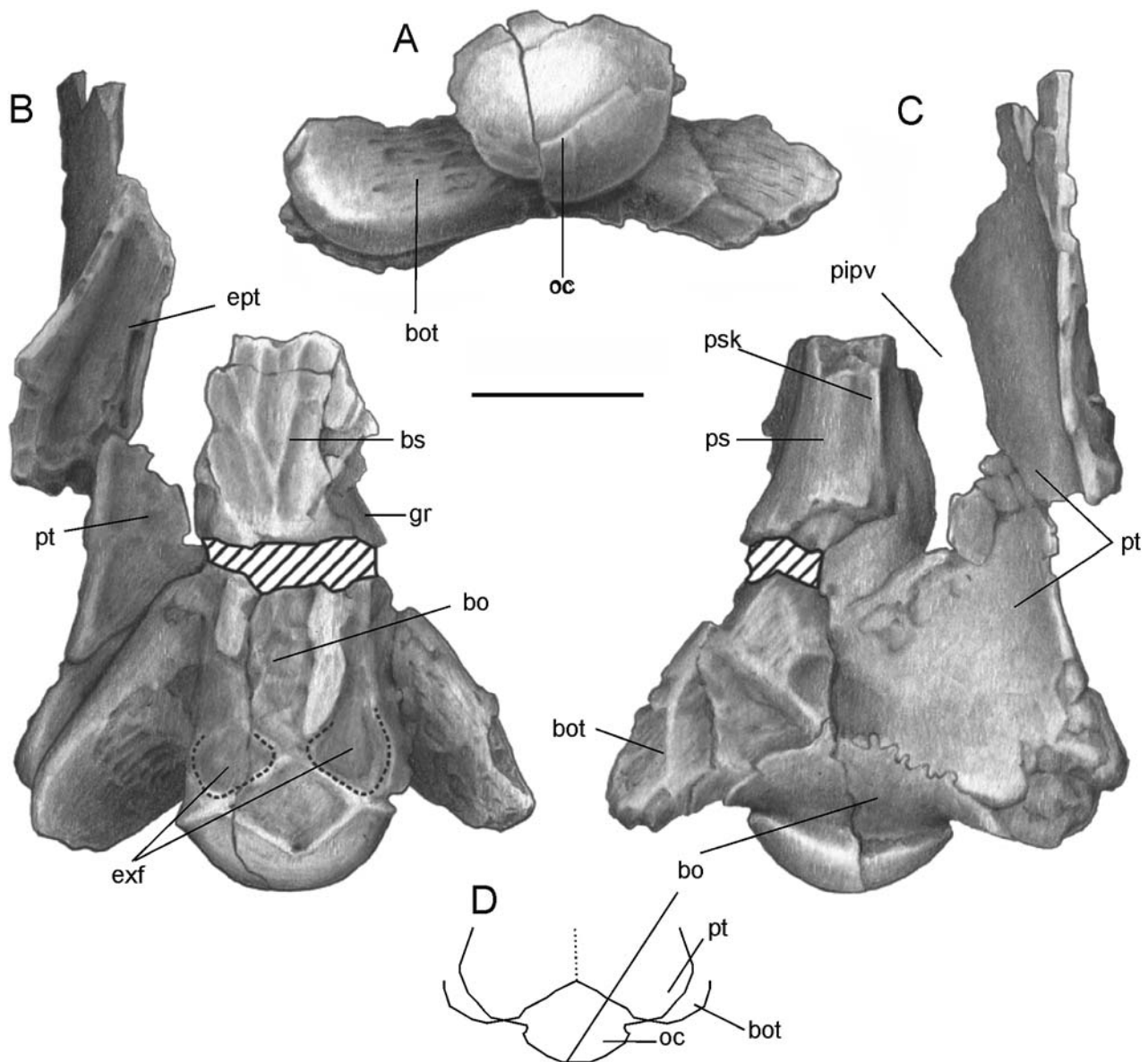
Fig. 5. Sulcusuchus erraini (MPEF 650). Interpretative drawings. Basicranium and posterior part of palate in **A**, posterior; **B**, dorsal and **C,** ventral views; **D**, schematic drawing showing the posterior notch in the pterygoid symphysis. Scale bar = 20 mm for all illustrations.

alveoli for replacement teeth are placed below the functional teeth. Articulating with this maxillary fragment are three additional fragments that are interpreted to be part of the palatine, pterygoid and vomer (Fig. 3 E).

Skull roof. Originally, Gasparini & de La Fuente (2000) stated that the pineal foramen is absent in *Sulcusuchus erraini*. However, behind the premaxilla–parietal suture there is a depression with a small foramen, which is here interpreted to be the pineal foramen (Fig. 3A). This is not unexpected because the presence of the pineal foramen has been recorded for other polycotylids (O'Keefe 2001). Ventral to the posterior portion of the premaxilla, there is a small expansion that corresponds to a fragment of the frontal (Figs 2A, 3A, B). Atop the frontal, there is a duct, of which only the dorsal margin has been preserved. This is probably the nasal duct as it

is also evident in other plesiosaurs such as *Edgarosaurus muddi*, *Libonectes morgani* and *Nicollssaura borealis* (Carpenter 1997, Druckenmiller 2002, Druckenmiller & Russell 2008b).

Concave elements form the dorsomedial walls of the orbits. These elements seem to be independent from the frontal but, because of poor preservation, this can not be confirmed. A similarly positioned bone was first described by Williston (1903) and named the supraorbital. Carpenter (1996) identified the element in *Dolichorhynchops osborni*, and O'Keefe (2008) discussed its identity and determined its presence in *Dolichorhynchops osborni*, *D. bonneri* and *Trinacromerum bentonianum*, and its absence in the basal genus *Edgarosaurus muddi* (O'Keefe 2008). However, the poor preservation of this element in MPEF 650 does not permit secure identification of the element as a supraorbital.
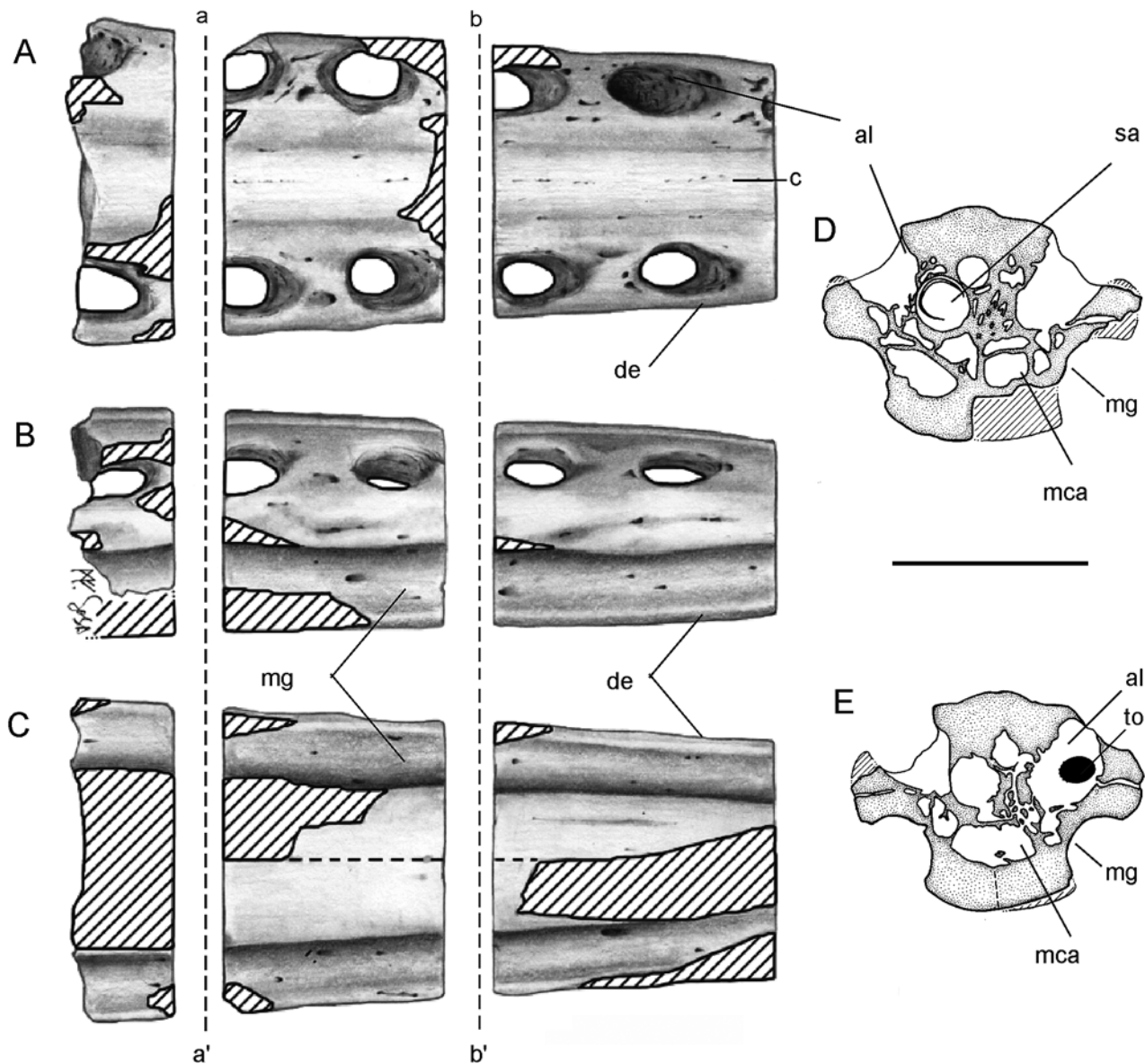
Fig. 6. Sulcusuchus erraini (MLP 88-IV-10-1, holotype). Interpretative drawings. Mandibular symphysis in **A**, dorsal; **B**, right lateral and **C**, ventral views. **D**, **E**, Cross-sections in posterior view. **D**, aa′; **E**, bb′. Scale bar = 20 mm for all illustrations.

In MPEF 650, most of the left squamosal and quadrate are preserved attached to the corresponding mandible (Figs 2B, 4A, B, C). The squamosal contacts ventrally with the quadrate through a lateral (Figs 2B, 4A) and medial (Fig. 4B) descending processes. The medial process is shorter than the lateral process, as in other polycotylids (O'Keefe 2001). In lateral view, the squamosal surface has smooth striae dorsoventrally oriented. The posterior margin of the squamosal (suspensorium) is almost straight and vertical (Figs 2B, 4A) as in *Dolichorhynchops* and differs from *Trinacromerum*, in which the suspensorium is inclined posteriorly (Carpenter 1996). In medial view, there is a fragment of bone interpreted to be the distal part of the paraoccipital process (Fig. 4B). Whether the paraoccipital process articulates only in a notch of the squamosal or with the squamosal and the quadrate can not be determined because of the poor preservation of this area.

Nevertheless, the distal articulation of the paraoccipital process differs from that of other polycotylids (with the possible exception of *Edgarosaurus*), in which the paraoccipital process articulates only with the quadrate (O'Keefe 2001, Druckenmiller 2002).

The quadrate, which is still fitted in the glenoid fossa formed by the articular, has two condyles that contact with the articular. The medial condyle is anterior to and slightly larger than the lateral one. The quadrate preserves part of the pterygoid process below the articulation with the squamosal. The pterygoid process projects anteriorly and medially (Fig. 4B, C).

Braincase and palate. The occipital condyle is entirely formed by the basioccipital; it is hemispherical and has a well-defined neck (Fig. 5A–C) as in other polycotylids (O'Keefe 2001). In posterior view, the condyle is subcircular in outline, except for the dorsal section,
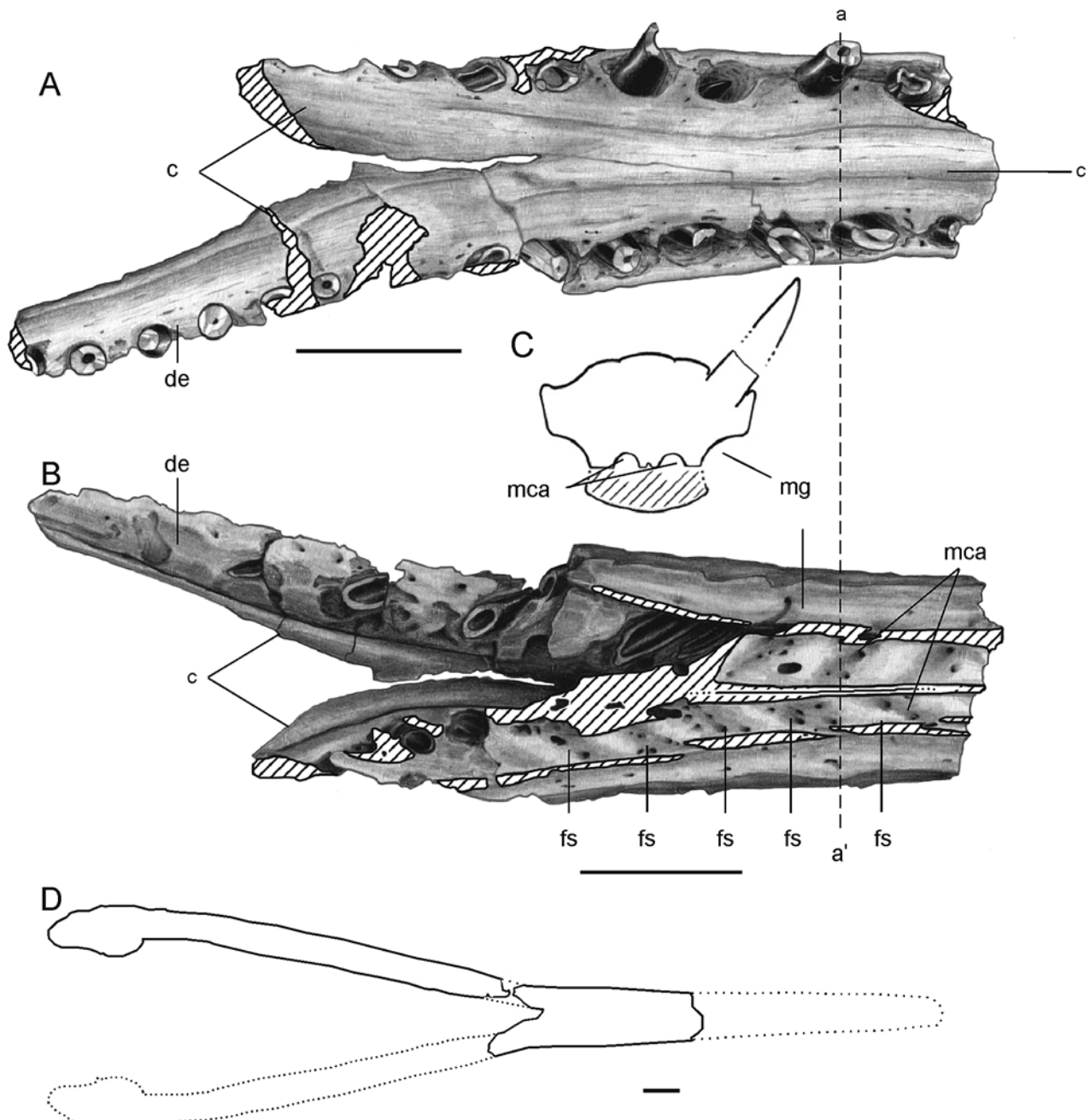
Fig. 7. Sulcusuchus erraini (MPEF 650). Interpretative drawings. Mandibular symphysis in **A**, dorsal and **B**, ventral views; **C**, reconstructed cross-section aa´; **D**, schematic reconstruction of mandible showing the position of the preserved left mandibular ramus and proximal part of the symphysis. Scale bars = 20 mm.

which forms the ventral margin of the foramen magnum (Fig. 5A). In ventral view, the posterior and medial margins of the pterygoids form a wide notch, in which part of the body of the basioccipital is located, forming a large and flat palatal plate (Figs 2C, 5C, D). This is a unique characteristic among polycotylids. In others polycotylids the pterygoids cover the ventral surface of the basioccipital body and a notch in the posterior part of the pterygoid is lacking (O'Keefe 2001). The basioccipital forms the basioccipital tubercles, which project laterally and posteriorly, reaching almost as far back as the level of the posterior end of the occipital condyle

(Fig. 5B, C). The dorsal surface of each basioccipital tubercle bends posteromedially (Fig. 5B). The articular facets of the exoccipitals are developed on the dorsal surface of the basioccipital, and they form anteroposteriorly elongated depressions that do not contact at the mid-line (Fig. 5B).

There are two superposed elements in front of the basioccipital. The dorsal one is the basisphenoid (Fig. 5B) and the ventral element is the parasphenoid (Figs 2C, 5C). There is a groove on each side that denotes the contact between them. A similar groove has been observed in the basicranium of *Dolichorhynchops* sp.
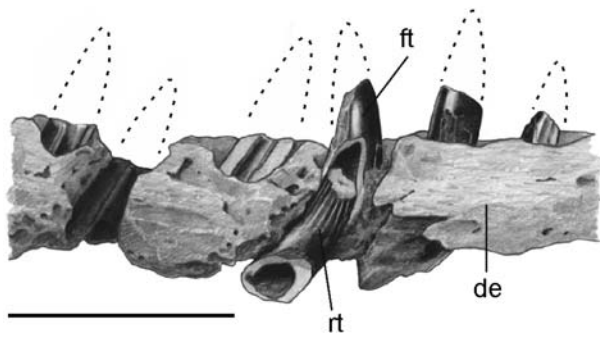
Fig. 8. *Sulcusuchus erraini* (MPEF 650). Interpretative drawing. Right mandibular ramus in lateral view with tooth replacement details. Scale bar = 20 mm.

(Sato *et al*. 2011). There is a marked depression on both sides of the posterolateral end of the dorsal surface of the basisphenoid (Fig. 5B). This depression has been interpreted as the articulation point of an anterior projection of the prootic that forms the ventromedial margin of the fenestra ovalis (Sato *et al*. 2011). The dorsal surface of the basisphenoid is almost flat with a smooth keel that separates two depressions on the posterior portion. This keel expands anteriorly and splits into two parts that limit a slight medial cavity (Fig. 5B).

In ventral view, the vomers project between both maxilla forming most of the palatal surface of the rostrum (Fig. 3C). Besides the fused vomers, the other preserved elements of the palate are the posterior portion of the parasphenoid and pterygoids (Fig. 5C).

The parasphenoid is subtriangular in cross-section. A keel is evident along its ventral surface. This keel is sharper in the anterior part of the preserved fragment (Figs 2C, 5C). The lateral margins of the parasphenoid form part of the posterior interpterygoid vacuity.

The pterygoids form a broad plate where they join along the posteromedial processes. A wide notch is developed on the posterior margin of the pterygoid, which makes the body of the basioccipital visible in ventral view, and forms a plate within the pterygoid. The lateral margin of the pterygoid is surrounded by a well-defined rim, which generates a dish-shaped central plate (Figs 2C, 5C). This structure is similar to that described by O'Keefe (2001, 2004a) in the genera *Dolichorhynchops* and *Trinacromerum*. One badly preserved element located dorsal to the pterygoid is identified as the epipterygoid (Fig. 5B). The epipterygoid is similar in morphology to that of other polycotylids (Sato *et al*. 2011).

Mandible. As in other polycotylids, the mandible is gracile with a long symphysis. The mandible is represented by four pieces: two fragments of the symphysis (the holotype and MPEF 650) and two fragments of the mandibular ramus (MPEF 650).

Dorsally, the symphysis has a slight anteroposterior elevation not limited by sutures. This elevation coincides with the fusion line of both anterior processes of

coronoids (Fig. 6A, D, E). The dentaries expand laterally below the alveoli line forming a roof that protects the dorsal side of the conspicuous and deep mandibular groove (Figs 6B–E, 7B). This groove is lateroventral and has a smooth surface with numerous foramina. Ventrally, the mandibular symphysis is slightly convex (Fig. 6D, E). Six pairs of alveoli are preserved and they are subcircular, with the anteroposterior diameter larger than the transverse (Figs 6A, 7A). The alveoli have a strong posteroventral inclination (Figs 6A, 7A). There are no external alveoli for replacement teeth. On the interalveolar spaces there are small circular pores (Figs 6A, 7A). In the holotype, the right ramus and left series of alveoli are displaced so that each alveolus of the right mandibular ramus is slightly displaced ahead of the corresponding alveolus of the left mandibular ramus (Fig. 6A). This feature is also present in the holotype and indicates that it is probably not a taphonomical feature (Fig. 7A).

The anterior process of the coronoid is included into the symphysis. Ventral to the coronoid, in the area of the mandibular symphysis, an elongate space is present that was likely occupied by the splenials (Fig. 7B). Consequently, the splenials likely form part of the symphysis of *S. erraini* as in others polycotylids (O'Keefe 2008).

Because the ventral side of the mandibular symphysis of MPEF 650 is not preserved, the internal structure can be observed (Fig. 7B). In this view, the Meckelian canals are almost parallel to the mandibular grooves. In this entire sector, the cross-section of the Meckelian canal is constant. The dorsal and lateral external surfaces of the Meckelian canal are smooth and have two sets of foramina. According to their location, two types of foramina sets can be distinguished. One of them is on the roof of the Meckelian canal and the other on its lateral external surface (Fig. 7B). The foramina located on the roof of the Meckelian canal are grouped in elongated sets with their long axis posteromedially (Fig. 7B). Each set is separated from the adjacent by a slightly convex zone that varies in anterioposterior length between 10 mm in the anterior zone to 7 mm in the posterior zone. These convex zones coincide approximately in number, position and size with the alveoli for functional teeth. The foramina that puncture the lateral external wall of the Meckelian canal are posteromedially directed, connecting the Meckelian canal with the mandibular groove (Fig. 7B). Two of these foramina have been preserved in each mandibular ramus and such foramina are rare (15 mm apart: left mandibular ramus; and 20 mm apart: right mandibular ramus). Hence, they do not coincide with the number of alveoli for functional teeth (Fig. 7B).

Part of the left mandibular ramus has been preserved in MPEF 650, from the retroarticular process to the posterior 14 alveoli (Fig. 4). This sector of the mandible is strongly compressed laterally and its height increases up

to the coronoid process. Its ventral margin, posterior to the symphysis, is straight, similar to *Trinacromerum* and *Manemergus*, and unlike *Dolichorhynchops*, *Thililua* and *Edgarosaurus*, in which the ventral margin is convex (Carpenter 1996, Druckenmiller 2002, Bardet *et al*. 2003, Buchy *et al*. 2005, Sato 2005).

In lateral view, the posterior portion of the mandibular groove is shallower than in the anterior portion and expands dorsoventrally forming a strong edge on the ventral margin (Figs 2B, 4A). On the lateral mandibular surface there are several foramina aligned at the level of the seventh to ninth alveoli counting from the last posterior alveolus. These foramina are arranged in two anteroposterior rows separated by a weak horizontal dentary ridge (Fig. 4A). In dorsal view, the left mandibular ramus preserves 12 alveoli, but some smooth depressions at the posterior end of the series suggest that there were at least two more. Unlike the alveoli of the mandibular symphysis, the alveoli of the posterior part of the mandible are placed in a groove (Fig. 4C).

The splenial is a thin and planar bone that in medial view (Fig. 4B) contacts the angular and dentary ventrally, and the coronoid dorsally (Fig. 4B). The entire surface of the splenial has horizontal striae (Fig. 4B).

The coronoid process is present, although not complete. Besides this process, the coronoid has an anterior process that extends along the dorsal margin of the medial surface of the mandible participating in the mandibular symphysis and forming part of its dorsal surface (Figs. 4B, 7A).

The angular projects anteriorly between the splenial and the dentary, reaching approximately the 11th alveolus, counting from the posterior-most alveolus. The angular is not visible in medial view until the 10th alveoli behind the mandibular symphysis (Figs. 4B, 7D), so it is short compared with almost every polycotylid (O'Keefe 2001, 2008).

The surangular is anteroposteriorly elongated in lateral view, contacting the coronoid dorsally and the angular ventrally (Figs 2B, 4A). The prearticular is badly preserved. However, its suture with the posterodorsal area of the splenial is visible (Fig. 4B). In the medial mandibular surface, the prearticular forms a slight shelf in front of the articular (Fig. 4B, C). This shelf is located in the same position as described by O'Keefe (2001) for other polycotylids.

The retroarticular process is short, laterally compressed, with a subtriangular section and with a concave dorsal surface (Figs 2B, 4A–C). The ventral margin of the retroarticular process is slightly dorsally directed.

Only one fragment of the middle part of the right mandibular ramus has been preserved. This fragment has a dentary ridge similar to that described for the left mandibular ramus. This indicates that the dentary ridge is not a taphonomical artefact.

The holotype of *S. erraini* was sectioned by three transverse cuts. In cross-sections a-a′ and b-b′ of the holotype (Fig. 6D, E), several internal cavities of different size and distribution are present. The large lateral cavities are alveoli for functional teeth (Fig. 6D, E). On the left dentary (Fig. 6D), a fragment of a replacement tooth occurs mesially to the alveolus for the functional teeth. Neither of the cuts show a pair of alveoli intersected at the same level, this is due to the displacement between the right alveoli with respect to the left ones (Fig. 6A, D). Another conspicuous element in these cross-sections is the large ventral cavity (Fig. 6D, E). In the posterior cross-section (Fig. 6D), two major ventral cavities are evident, whereas in the most anterior cross-section (Fig. 6E) there is a single ventral cavity. These cavities are interpreted to be arms of the Meckelian canal that merge toward the anterior part of the symphysis.

Dentition. On the maxilla of MPEF 650 (Fig. 3B, C), the crowns of the teeth are strongly recurved forming an anterior convex surface and a posterior concave one. Many of the left maxillary teeth have marked striations on their labial, lingual and posterior sides, but the anterior side is smooth. Some of the teeth have no striations but this is likely due to the loss of enamel (Fig. 3C). Scanning electron microscopy reveals the striations have an irregular pattern; some striations disappear far from the apex and others disappear near the apex. Although most of them begin as a single striation from the base of the crown, others arise in pairs and immediately fuse into a single striation. The anterior face of each crown is smooth. An alternating pattern of teeth with striate crowns and smooth teeth or teeth with reduced striae is evident on the rostrum of MPEF 650 (Fig. 3C).

The morphology of the mandibular teeth is similar to that of the maxillary teeth. There is also an alternate pattern of striate and non-striate crowns and, as observed in the rostrum, the striated teeth are the smallest. The right dentary has a strongly striated replacement tooth associated with a functional tooth lacking striae (Fig. 8). The left mandible fragment (Fig. 7A) has a tooth in the replacement stage, with the apex of the replacement tooth visible in the postero-medial border of the alveolus. In the same mandibular ramus, one tooth has a smooth crown and another represents a replacement that has not reached its ultimate position.

Discussion

Relationships

The morphology of the dish-shaped central plate of the pterygoids, the presence of a long and narrow rostrum formed by the premaxilla and maxilla, a mandibular symphysis with gracile teeth, and the incorporation of the anterior process of the coronoid in the symphysis clearly confirm the polycotylid affinities of *S. erraini*. These affinities are compatible with the definition of Polycotylidae *sensu* Ketchum and Benson (2011) or *sensu* Druckenmiller & Russell (2008a). This species has two autapomorphies: (1) deep and broad rostral and

mandibular grooves (Figs 3A, (6B) and (2) a wide notch on the posterior margin of the pterygoids that are combined with a part of the body of the basioccipital, forming a flat plate together with the posteromedial processes of the pterygoids (Fig. 5C, D).

Several features of *S. erraini* differ from those of other polycotylids. The parasphenoid of *S. erraini* is keeled, which differs from that recorded in *Manemergus* and *Edgarosaurus* (Druckenmiller 2002, Buchy *et al.* 2005, O'Keefe 2008). The presence of a keel in the parasphenoid and the difficulty of scoring this character were discussed by Sato *et al.* (2011). Unfortunately, only the posterior part of the parasphenoid is preserved in MPEF 650 and no information can be obtained about the morphology of the anterior part (e.g., the shape of the parasphenoid in cross-section Sato *et al.* 2011). Another characteristic of the parasphenoid of *S. erraini* is that in its posterior part, it is as wide as the occipital condyle, a character shared with *Dolichorhynchops osborni* and *D. herschelensis*, but different from *Edgarosaurus*, in which the parasphenoid is (in ventral view) narrower than the condyle (Druckenmiller 2002, O'Keefe 2008, Sato *et al.* 2011).

A mandibular groove (called the 'longitudinal mandibular groove') was recorded in *Nicollssaura borealis* (Druckenmiller & Russell 2008b). The mandibular groove of *N. borealis* shares some features with that recorded in *Sulcusuchus erraini*, such as its inner surface being covered by foramina and its division into two zones by a longitudinal ridge (Druckenmiller & Russell 2008b). However, there are some remarkable differences between these structures. In *Nicollssaura borealis*, this structure is not associated with a long mandibular symphysis or a broad rostral groove, features present in *S. erraini*. In addition, the ventral zone of the mandibular groove in *S. erraini* is longer than the dorsal zone and, therefore, it differs from that observed in *Nicollssaura borealis*, where the ventral zone is restricted to the anterior part of the mandible. The systematic relationships of *Nicollssaura borealis* are disputed, since two large-scale analyses have resolved *Nicollssaura borealis* nesting either with the Polycotylidae (Druckenmiller & Russell 2008b) or with the Leptocleididae (Ketchum & Benson 2011). This lack of consensus has made it difficult to determine whether the mandibular groove evolved independently. It is interesting to note that the second autapomophy of *S. erraini*, regarding the plate formed by the basioccipital and pterygoid, seems similar to features recorded in *Nicollssaura borealis*, although in the holotype of the latter the palatal zone of contact between the pterygoids and basioccipital is not flat as in *S. erraini* and the relation between the basioccipital and the pterygoids is difficult to determine. These similarities between *S. erraini* and *Nicollssaura borealis* could indicate a phylogenetic affinity; however other features such as the structure of the rostrum and mandibular symphysis detract from a close relationship.

Sulcusuchus erraini has a short angular, which is not visible in medial view until the tenth alveoli behind the mandibular symphysis, unlike some polycotylids, in which the angular either reaches the posterior part of the symphysis in medial and ventral view (*Eopolycotylus* and *Dolichorhynchops osborni*), or actually enters into it as in *Edgarosaurus muddi*, *Thililua longicollis*, *Trinacromerum bentonianum* and *Manemergus anguirostris* (Carpenter 1996, Adams 1997, O'Keefe 2001, 2008, Druckenmiller 2002, Bardet *et al.* 2003, Buchy *et al.* 2005, Albright *et al.* 2007).

In *S. erraini*, the anterior extension of the coronoid extends along the dorsal limit of the medial surface of the mandibular ramus, and it is separated from the medial edge of the dentary by a deep suture. Furthermore, in the symphysis fragment (Fig. 7A, B) these projections are attached to the dentary, entering into the mandibular symphysis. O'Keefe (2008) recorded the anterior process of the coronoid in all genera represented by well-preserved material and argued that the presence of an anterior process of the united coronoids, visible in the dorsal view of the mandible symphysis, is a synapomorphy of Polycotylidae. In *Sulcusuchus erraini*, the coronoids meet and form an anterior process that is visible on the dorsal surface of the symphysis, supporting O'Keefe's hypothesis.

The strong vascularization associated with the alveoli has been observed in at least one other polycotylid, but associated with the rostral dentition (Buchy *et al.* 2005). MPEF 650 shows that this strong vascularization is also present in the mandible.

The presence of an asymmetric displacement of the alveoli in the mandibular symphysis in both specimens may have taxonomic value in *S. erraini*. However, this is likely a very variable character in long-rostrum species with a large number of homodont teeth as in the extant dolphin *Pontoporia blainvillei*, in which these kind of displacements have also been observed (J.P.O'Gorman *pers. obs.*). Therefore, more specimens of *S. erraini* are needed to evaluate the systematic value of this character.

Alternating teeth, with and without striae, in the mandible and the rostrum may be due to the state of wear or to some taphonomic process. Interestingly, the teeth in MPEF 650 'without striae' completely lack even residual striae, unlike the condition expected if the loss of striae were due to gradual wear.

Palaeobiology

The presence of a smooth interior surface in the rostral and mandibular grooves that differs from the bone surface outside the grooves suggests that these grooves housed a soft structure that differed from tissues associated with the surrounding surface. Moreover, the surface of the rostral and mandibular grooves is covered by foramina that indicate the presence of vascularization and/or innervation and suggests the presence of a soft structure housed in the grooves.

Among the soft structures potentially housed in such grooves are salt glands. In the polycotylid *Pahasapasaurus haasi*, from the Cenomanian of South Dakota (Schumacher 2007), a pair of rostral globose structures are preserved that were interpreted to be salt glands by Martin and Fernández (2009). However, the structures evident in *P. haasi* are very different from the long, deep and broad grooves of *Sulcusuchus* and salt glands have never been detected in the mandible of an amniote (Peaker and Linzell 1975).

Another option is that the grooves housed the germinative epithelium of a corneal beak. However, the grooves are broader and deeper than required for this. Besides, tetrapods that generate a corneal beak commonly either lack teeth or these are reduced in the area of the beak, e.g., as evident in some dinosaurs, turtles, birds and monotremes (Davit-Béal *et al.* 2009). In the case of *S. erraini*, well-developed teeth make this hypothesis quite improbable.

Another possibility is that the rostral and mandibular grooves housed vessels and nerves that run along the rostrum and mandible. Weak grooves on the mandible in crocodyliforms have been interpreted to represent the bony correlate of different ramifications of the mandibular ramus of the trigeminus nerve (Schumacher 1973). A weak groove is also evident in the rostrum and mandible of some ichthyosaurs (McGowan and Motani 2003) but its correlation with soft tissues is unknown. Rostral and mandibular grooves are present in the dolphin *Pontoporia blainvillei*. They house nerves and vessels of the anterior part of the rostrum and mandible (Barnes 1985). However, the grooves of *P. bainvillei* are narrow and deep, whereas those of *S. erraini* are too broad to act only as protection. In addition, there is a foramen at the proximal end of the grooves for the passage of nerves and vessels in *P. blainvillei* (J.P. O'Gorman pers. obs. of six specimens of *P. blainvillei*). The mandibular groove of *S. erraini* lacks a single foramen at its proximal end and it does not end sharply towards the posterior as in *P. blainvilei*. On the contrary, it vanishes towards the posterior part of the mandible.

A fourth possibility is that the mandibular and rostral grooves housed glands similar to the infralabial and supralabial glands of some extant ophidians (de Oliveira *et al.* 2007). However, the rostral and mandibular grooves recorded in *S. erraini* are larger than those expected for a gland. Moreover, the presence of supralabial and infralabial glands is related to venom or mucous secretion (Underwood 1997), which makes this option quite improbable because we do not have any other evidence of poison production (such as the modification of tooth surface related to poison inoculation), and lubrication is not a problem in the aquatic environment. However, this hypothesis can not be discarded.

The fifth option is that the rostral and mandibular grooves housed sensory organs. In modern vertebrates, special sensory organs (mechanosensory or electrosensory)

have been found associated with the rostrum and the mandible. Modern crocodylians have special structures named dome pressure receptors (DPRs) in the rostrum and/or mandible (Soares 2002). The DPRs in crocodylians are located in small depressions (not in a groove) and are innervated by the trigeminus nerve (Soares 2002). The trigeminus also innervates specialized sensory structures in the anterior area of the skull in other amniotes, including infrared receptors in ophidians (Newman & Hartline 1982), and the electrosensory and mechanosensory organs in the platypus *Ornithorhynchus* (Pettigrew 1999). It is noteworthy that in *Sulcusuchus erraini*, the grooves follow the usual trajectory of the V_2 (maxillary) and V_3 (mandibular) rami of the trigeminus.

The position of the rostral and mandibular grooves in the anterior area of the skull and their conspicuous vascularization and/or innervation is consistent with the presence of some associated special sensory structure. In extant cetaceans, areas with high skin sensitivity can be detected through concentrated vascularization. This technique was employed to infer the sensory function of rostral follicles in the dolphin *Sotalia guianensis* (Mauck *et al.* 2000). Recently, electrosensitivity has been detected in follicles of the rostrum of *Sotalia guianensis*, which are probably used to detect fish buried in the sand (Wilkens & Hofmann 2008). A similar feeding behaviour has been observed in the dolphin *Tursiops truncatus*, although in this species electroreception has not been yet recorded (Rossbach & Herzing 1997). Although the presence of electroreceptors and mechanoreceptors in *Sulcusuchus erraini* is difficult to confirm, the analogy with dolphins can not be discarded. A system of high sensitivity could have been related to the capacity to detect prey hidden in soft substrates. The targeting of infaunal or semi-infaunal prey by plesiosaurs has been previously recorded based on invertebrates preserved as stomach contents of elasmosaurids (McHenry *et al.* 2005). Andrews (1910) also found sand and gravel in the stomach contents of pliosaurs. In addition, traces found in Liesberg, Switzerland (Middle Jurassic), were interpreted to be the result of plesiosaur or pliosaur feeding in soft substrates (Geister 1998). This evidence indicates that the targeting of infaunal or semi-infaunal prey developed in the Plesiosauria clade before the Late Cretaceous.

Conclusions

Sulcusuchus erraini is the only South American polycotylid plesiosaur represented by skull remains, which were found in two localities in central Patagonia. This revision of *Sulcusuchus erraini* reinterprets the holotype to be a mandibular fragment.

Sulcusuchus erraini is a polycotylid characterized by the following autapomorphies: (1) deep and broad rostral and mandibular grooves and (2) a wide notch on the posterior margin of the pterygoids that is combined

with a part of the body of the basioccipital to form a plate together with the posteromedial processes of the pterygoids.

The hypothesis of the existence of glands housed in the rostral and mandibular grooves can not be discarded. Several lines of evidence favour the presence of some special sensory (either electrosensory or mechanosensory) structure in the grooves that increased the ability of the animal to locate infaunal or semi-infaunal biota in soft substrates.

Acknowledgements

References

ADAMS, D.A., 1997. *Trinacromerum bonneri*, new species. Last and fastest pliosaur of the Western Interior Seaway. *Texas Journal of Science 49*, 179–198.

ALBRIGHT, B.A., GILLETTE, D.D. & TITUS, A., 2007. Plesiosaurs from the Upper Cretaceous (Cenomanian–Turonian) Tropic Shale of southern Utah, part 2, Polycotylidae. *Journal of Vertebrate Paleontology 27*, 41–58.

ANDREWS, C.W., 1910. *A descriptive catalogue of the marine reptiles of the Oxford Clay*. Part I. British Museum (Natural History), London, England, 273 pp.

BALLENT, S.C., 1980. Ostrácodos de ambiente salobre de la Formación Allen (Cretácico Superior) en la Provincia de Río Negro (República Argentina). *Ameghiniana 17*, 67–82.

BARDET, N., SUBERBIOLA, X.P. & JALIL, N.-E., 2003. A new polycotylid plesiosaur from the Late Cretaceous (Turonian) of Morocco. *Comptes Rendus Palevol 2*, 307–315.

BARNES, L.G., 1985. Fossil pontoporiid dolphins (Mammalia, Cetacea) from the Pacific Coast of North America. *Contributions in Science Natural History Museum of Los Angeles County 363*, 1–34.

BROWN, D.S., 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauroidea. *Bulletin of the British Museum of Natural History (Geology) 35*, 253–347.

BUCHY, M.-C., METAYER, F. & FREY, E., 2005. Osteology of Manemergus anguirostris n. gen. et sp., a new plesiosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Morocco. *Palaeontographica A 272*, 97–120.

CARPENTER, K., 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. *Neues Jahrbuch für Geologie und Palaontologie Abhandlungen 201*, 259–287.

CARPENTER, K., 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs. In *Ancient Marine Reptiles*. CALLAWAY, J.M. & EICHOLLS, E.L., eds, Academic Press, San Diego, 191–216.

COPE, E.D., 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society (new series) 14*, 1–252.

D'ANGELO, J.S., NOVAS, F.E., LIRIO, J.M. & ISASI, M.P., 2008. Primer registro de Polycotylidae (Sauropterygia, Plesiosauroidea) del Cretácico Superior de Antártida. *III Congreso Latinoamericano de Paleontología de Vertebrados, Resúmenes 1*. Neuquén, Argentina, 72.

DAVIT-BÉAL, T., TUCKER, A.S. & SIRE, J.-Y., 2009. Loss of teeth and enamel in tetrapods: fossil record, genetic data and morphological adaptations. *Journal of Anatomy 214*, 477–501.

DE BLAINVILLE, H.D., 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'Erpetologie et d'Amphibiologiem. *Nouvelles Annales du Muséum (National) d'Histoire Naturelle 4*, 233–296.

DE OLIVEIRA, L., JAREDA, C., DA COSTA PRUDENTE, A.L., ZAHER, H. & ANTONIAZZI, M.M., 2007. Oral glands in dipsadine 'goo-eater' snakes: Morphology and histochemistry of the infralabial glands in Atractus reticulatus, Dipsas indica, and Sibynomorphus mikanii. *Toxicon 51*, 898–913.

DINGUS, L., CLARKE, J., SCOTT, G.R., SWISHER, C., CHIAPPE, L.M. & CORIA, R.A., 2000. Stratigraphy and magnetostratigraphic/faunal constraints for the age of sauropod embryo–bearing rocks in the Neuquén Group (Late Cretaceous, Neuquén Province, Argentina). *American Museum Novitates 3290*, 1–11.

DRUCKENMILLER, P.S., 2002. Osteology of a new plesiosaur from the Lower Cretaceous (Albian) Thermopolis Shale of Montana. *Journal of Vertebrate Paleontology 22*, 29–42.

DRUCKENMILLER, P.S. & RUSSELL, A.P., 2008. A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. *Zootaxa 1863*, 1–120.

DRUCKENMILLER, P.S. & RUSSELL, A.P., 2008. Skeletal anatomy of an exceptionally complete specimen of a new genus of plesiosaur from the Early Cretaceous (Early Albian) of northeastern Alberta, Canada. *Palaeontographica A 283*, 1–33.

GASPARINI, Z. & DE LA FUENTE, M., 2000. Tortugas y plesiosaurios de la Formación La Colonia (Cretácico superior) de Patagonia, Argentina. *Revista Española de Paleontología 15*, 23–35.

GASPARINI, Z. & SPALLETTI, L.A., 1990. Un nuevo crocodilo en los depósitos mareales maastrichtianos de la Patagonia noroccidental. *Ameghiniana 27*, 141–150.

GEISTER, J., 1998. Lebensspuren von Meeressauriern und ihren Beutetieren im mittleren Jura (Callovien) von Liesberg. Schweiz. *Facies 30*, 105–124.

GETINO, P.R., 1995. Estratigrafía del sector suroccidental de la meseta Colitoro, provincia de Río Negro. *Revista de la Asociación Geológica Argentina 50*, 243–256.

KEAR, B.P., 2003. Cretaceous marine reptiles of Australia, a review of taxonomy and distribution. *Cretaceous Research 24*, 277–303.

KEAR, B.P., 2006. Marine reptiles from the Lower Cretaceous of South Australia, elements of a high-latitude cold-water assemblage. *Palaeontology 49*, 837–856.

KETCHUM, H.F. & BENSON, R.B.J., 2011. A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early–Middle Jurassic pliosaurids. *Special Papers in Palaeontology 86*, 109–129.

MARTIN, J. & FERNÁNDEZ, M., 2009. Salt gland identified in a Late Cretaceous polycotylid plesiosaur. *Journal of Vertebrate Paleontology 29* (3, Supplement), 143A.

MAUCK, B., EYSEL, U. & DEHNHARDT, G., 2000. Selective heating of vibrissal follicles in seals (*Phoca vitulina*) and dolphins (*Sotalia fluviatilis guianensis*). *Journal of Experimental Biology 203*, 2125–2131.

MCGOWAN, C. & MOTANI, R., 2003.*Handbook of Paleoherpetology, Pt. 8, Ichthyopterygia.* PFEIL, Dr. Friedrich, ed., 175 pp.

MCHENRY, C.R., COOK, A.G. & WROE, S., 2005. Bottom-feeding plesiosaurs. *Science 310*, 75.

NEWMAN, E.A. & HARTLINE, P.H., 1982. The infrared vision of snakes. *Scientific American 246*, 116–127.

O'GORMAN, J.P., SALGADO, L. & GASPARINI, Z., 2011. Plesiosaurios de la Formación Allen (Campaniano–Maastrichtiano) en el área del Salitral de Santa Rosa (Provincia de Río Negro, Argentina). *Ameghiniana 48*, 129–135.

O'KEEFE, F.R., 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia, Sauropterygia). *Acta Zoologica Fennica 213*, 1–63.

O'KEEFE, F.R., 2004a. On the cranial anatomy of the polycotylid plesiosaurs, including new material of *Polycotylus latipinnis* Cope, from Alabama. *Journal of Vertebrate Paleontology 24*, 326–340.

O'KEEFE, F.R., 2004b. Preliminary description and phylogenetic position of a new plesiosaur (Reptilia, Sauropterygia) from the Toarcian of Holzmaden, Germany. *Journal of Paleontology 78*, 973–988.

O'KEEFE, F.R., 2008. Cranial anatomy and taxonomy of *Dolichorhynchops bonneri* new combination, a polycotylid (Sauropterygia, Plesiosauria) from the Pierre Shale of Wyoming and South Dakota. *Journal of Vertebrate Paleontology 28*, 664–676.

OWEN, R., 1860. On the orders of fossil and recent Reptilia, and their distribution through time. *Report of the British Association for the Advancement of Science 29*, 153–166.

PAGE, R., ARDOLINO, A., DE BARRIO, R.E., FRANCHI, M., LIZUAIN, A., PAGE, S. & SILVA NIETO, A., 1999.*Geología Argentina.* CAMINOS, R., ed., Servicio Geológico Minero Argentino. Anales 29, Buenos Aires, 460–488.

PAPÚ, O. & SEPÚLVEDA, E., 1995. Datos palinológicos de la Formación Los Alamitos en la localidad de Montoniló, Departamento 25 de Mayo, Río Negro, Argentina. Sus relaciones con unidades colindantes coetáneas. *6° Congreso Argentino de Paleontología y Bioestratigrafía. Actas 1*, 195–200.

PEAKER, M. & LINZELL, J.L., 1975. *Salt Glands in Birds and Reptiles.* Cambridge University Press, Cambridge, 307 pp.

PERSSON, P.O., 1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. *Lunds Universitets årsskrift 59*, 1–60.

PETTIGREW, J.D., 1999. Electroreception in monotremes. *Journal of Experimental Biology 202*, 1447–1454.

ROSSBACH, K.A. & HERZING, D.L., 1997. Underwater observations of feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. *Marine Mammal Science 13*, 498–503.

SALGADO, L., PARRAS, A. & GASPARINI, Z., 2007. Un plesiosaurio de cuello corto (Plesiosauroidea, Polycotylidae) del Cretácico Superior del norte de Patagonia. *Ameghiniana 4*, 349–358.

SATO, T., 2005. A new polycotylid plesiosaur (Reptilia: Sauropterygia) from the Upper Cretaceous Bearpaw Formation of Saskatchewan, Canada. *Journal of Palaeontology 79*, 969–980.

SATO, T. & STORRS, G.W., 2000. An early polycoylid plesiosaur (Reptilia, Sauropterygia) from the Cretaceous of Hokkaido, Japan. *Journal of Paleontology 74*, 907–914.

SATO, T., WU, X.-C., TIRABASSO, A. & BLOSKIE, P., 2011. Braincase of a polycotylid plesiosaur (Reptilia: Sauropterygia) from the Upper Cretaceous of Manitoba, Canada. *Journal of Vertebrate Paleontology 31*, 313–329.

SCHUMACHER, B., 2007. A new polycotylid plesiosaur (Reptilia; Sauropterygia) from the Greenhorn Limestone (Upper Cretaceous; lower upper Cenomanian), Black Hills, South Dakota. *Geological Society of America Special Paper 427*, 133–146.

SCHUMACHER, G.H., 1973. The head muscles and hyolaryngeal skeleton of turtles and crocodilians. In *Biology of the Reptilia Vol. 4*. GANS, C. & PARSONS, T.S., eds, Academic Press, New York, 101–199.

SOARES, D., 2002. An ancient sensory organ in crocodilians. *Nature 417*, 241–242.

STORRS, G.W., 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. *American Journal of Science 293A*, 63–90.

UNDERWOOD, G., 1997. An overview of venomous snake evolution. In *Venomous Snakes: ecology, evolution and snakebite.* THORPE, R.S., WÜSTER, W. & MALHOTRA, A., eds, The Zoological Society of London. Clarendon Press, Oxford, 1–13.

WELLES, S.P., 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. *Memoirs of the University of California 13*, 125–254.

WELLES, S.P., 1962. A new species of elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. *University of California Publications in Geological Sciences 44*, 1–96.

WIFFEN, J. & MOISLEY, W.L., 1986. Late Cretaceous reptiles (families Elasmosauridae and Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand. *New Zealand Journal of Geology and Geophysics 29*, 205–252.

WILKENS, L.A. & HOFMANN, M.H., 2008. Electroreception. In *Sensory Evolution on the Threshold. Adaptations in Secondarily Aquatic Vertebrates.* THEWISSEN, J.G.M. & NUMMELA, S., eds, University of California Press, Berkeley, California, 318–325.

WILLISTON, S.W., 1903. North American plesiosaurs, Part 1. *Field Columbian Museum Publication (Geology) 73*, 1–77.

WILLISTON, S.W., 1906. North American plesiosaurs, *Elasmosaurus*, *Cimoliasaurus* and *Polycotylus*. *American Journal of Science, Fourth Series 21*, 221–236.

WILLISTON, S.W., 1908. North American plesiosaurs: *Trinacromerum*. *Journal of Geology 16*, 715–736.