

The braincase of a specimen of *Proterochampsia* Reig (Archosauriformes: Proterochampsidae) from the Late Triassic of Argentina

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Abstract The proterochampsids are a Triassic group of superficially crocodile-like forms belonging to the Archosauriformes. In the present contribution, we present new information regarding the braincase of the proterochampsid *Proterochampsia* Reig 1959, from the Ischigualasto Formation (Carnian) of Argentina, and discuss its phylogenetic considerations. Some unique neurocranial features of *Proterochampsia* are described, including: the prominence and thickness of the V-shaped ridge that surrounds the basisphenoidal fossa; the medially concave lateral arms of the same ridge; and the semilunar depression on the parabasisphenoid ventrolaterally exposed. Other features are only shared with likely unrelated archosauriforms, including: the great lateral development of the basiptyergoid processes and caudal development of its distal end; an eight-shaped metotic foramen; laterally directed basiptyergoid processes; and rostral boundary of the basisphenoidal recess V-shaped. *Proterochampsia* differs in many other aspects from the archosauriform *Chanaresuchus*, including: a proportionally shorter basioccipital basal

tubera; cultriform process ovoid in cross-section; longitudinal sulcus dorsal to the basiptyergoid process; deep basisphenoidal recess; and the absence of a prominent intertuberal plate. In many braincase features, *Proterochampsia* is more similar to archosaurs than to *Euparkeria*, erythrosuchids and *Proterosuchus*. They include a reduced semilunar depression. A ventral border of the basioccipital forming a wide convexity and a dorsoventrally thin paroccipital process likely represents a feature shared with *Chanaresuchus*, but not with *Doswellia* and other basal archosauriforms.

Keywords Anatomy · Braincase · Archosauriformes · Proterochampsids · Ischigualasto formation · Northwestern Argentina

Kurzfassung Die Proterochampsiden stellen eine triassische Gruppe dar, die oberflächlich betrachtet krokodilähnliche Formen aufweist, und den Archosauriformen angehört. Im gegenwärtigen Beitrag präsentieren wir neue Informationen bezüglich des Hirnschädels des Proterochampsiden *Proterochampsia* REIG 1959, von der Ischigualasto-Formation (Carnium) Argentiniens, und besprechen einige phylogenetische Ansätze. Die wesentlichen Neurocranial-Eigenschaften von *Proterochampsia* werden beschrieben. Dazu gehören die Bedeutung und Dicke des V-förmigen Kamms, der die Basisphenoid-Grube (basisphenoidal fossa), die mittleren konkaven seitlichen Arme desselben Kamms, und die halbmondförmige Vertiefung, die den ventrolateralen Parabasisphenoid umgibt. Andere weisen wahrscheinlich unabhängig von Archosauriformis die gleiche Funktion auf, wie die laterale Endwicklung des Basisptyergoid-Prozesses und die Schwanzentwicklung seines Distal-Endes. Des 8-förmigen metotic Foramen, des seitlich (lateral)

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gelegenden Basisperygoid Prozesse und der an der rostral Grenze des Basisphenoidal V-förmige Vertiefung. *Proterochampsa* unterscheidet sich in vielen anderen Aspekten mit der Archosauriform *Chanaresuchus*, einschließlich durch ein proportional kürzeres basioccipital basalen Tubera, ein im Querschnitt einförmiges cultriform Prozess, Längs-Sulcus dorsal der basipterygoid Prozess, tiefe basisphenoidal Ausnehmung und das Fehlen eines prominenten intertuberal Platte. In vielen Hirnschädel-Eigenschaften(Funktionen) weist *Proterochampsa* eine höhere Ähnlichkeit mit dem archosaurus (Archosauriern) als mit *Euparkeria*, Erythrosuchiden und *Proterosuchus* auf. Dazu gehört eine reduzierte halbmondförmige Vertiefung. Ein ventraler Rand des Basioccipital bildet ein breites Konvexität und ein dorsoventral dünnen paroccipital Prozess, dass wahrscheinlich ein Merkmal darstellt, was ebenfalls in *Chanaresuchus* zu finden ist, nicht aber in *Doswellia* und anderen basalen Archosariformen.

Schlüsselwörter Anatomie · Hirnschädel · Archosauriformes · Proterochampsids · Ischigualasto-Formation · Nordwestliches Argentinien

Introduction

The proterochampsids represent a group of superficially crocodile-like forms belonging to the Archosauriformes, a diverse natural group that also includes the Proterosuchidae, the Erythrosuchidae, *Euparkeria capensis* Broom 1913, and the Archosauria (Gauthier 1986; Gauthier et al. 1989; Sereno 1991; Parrish 1993; Brochu 2001). In the 1960s and 1970s, proterochampsids were alternatively assigned to different clades, and some taxa were considered as related to the earliest crocodiles (Reig 1959, 1970; Sill 1967) or phytosaurs (Walker 1968). The discovery of the proterochampsids *Chanaresuchus bonapartei* Romer 1971 and *Gualosuchus reigi* Romer 1971, in the Los Chañares Formation (northwestern Argentina), led Romer (1971) and Bonaparte (1971) to rule out these hypotheses of relationships. Both Romer (1971) and Bonaparte (1971) considered *Proterochampsa* to be closely related to the mentioned Los Chañares taxa and to the Brazilian taxon *Cerritosaurus binsfeldi* Price 1946. Romer (1971) included all these taxa within the Proterochampsidae, and this was accepted in later systematic studies (Benton and Clark 1988; Sereno 1991). Sereno and Arcucci (1990) and Sereno (1991), in explicit phylogenetic analyses, proposed that proterochampsids were the sister group of the Archosauria. This hypothesis has been supported by later phylogenetic analyses (e.g., Parrish 1993; Juul 1994; Brusatte et al. 2008; Dilkes and Sues 2009) (Fig. 1). In a recent contribution, Dilkes and Sues (2009) recovered *Younghesuchus sangbiensis* Wu et al. 2001 and

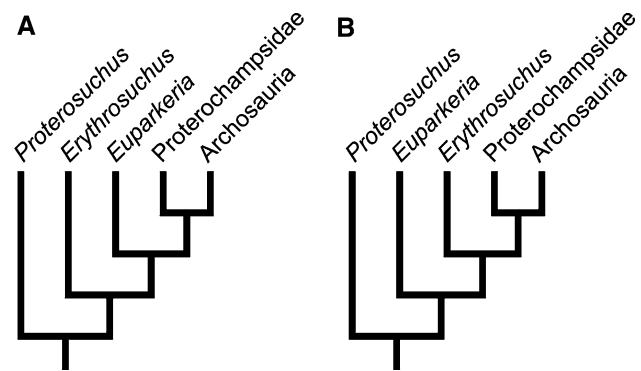


Fig. 1 Current phylogenetic hypotheses of proterochampsid relationships with other archosauriforms. **a** According to Sereno and Arcucci (1990), Sereno (1991), Parrish (1993), and Juul (1994). **b** According to Dilkes and Sues (2009)

Turfanosuchus dabanensis Young 1973 as the only archosauriforms more closely related to Archosauria than the Proterochampsidae. A phylogenetic analysis of Proterochampsidae has never been done including *Proterochampsa* and *Chanaresuchus*. Therefore, the close relationship of these two taxa has been hypothesized, but never explicitly tested. In relation to this fact, this contribution attempts to provide anatomical information useful in a future phylogenetic analysis, where information on *Proterochampsa* and *Chanaresuchus* will be included.

Even though relevant phylogenetic studies based on archosauriform braincase characters have been published, especially for basal archosauriforms (Gower and Sennikov 1996) and pseudosuchians (Gower 2002), none of these included data from proterochampsids. This seems to be a consequence of the fact that previous accounts of proterochampsid osteology only included brief descriptions of neurocranial material, mostly based on occipital and ventral surfaces (e.g., Sill 1967; Romer 1971). Furthermore, in the case of *Proterochampsa*, some inaccurate interpretations were made. Thus, the aim of this contribution is to increase the available information regarding the braincase anatomy of proterochampsids and to point out some comparisons derived from the observed characters that may be useful for future phylogenetic analyses. This study is a first step in this direction, which will hopefully be followed by descriptions of more unpublished proterochampsid neurocrania. Here we describe the braincase anatomy of a new specimen of *Proterochampsa* Reig 1959 (PVSJ 77) from the Ischigualasto Formation. In this specimen, the neurocranial elements are disarticulated from the other cranial bones, thus providing valuable morphological evidence.

Systematic paleontology

Diapsida Osborn 1903
Archosauromorpha von Huene 1946

Archosauriformes Gauthier et al. 1989
Proterochampsidae Sill 1967
Proterochampsia Reig 1959

Holotype of the type species PVL 2063 skull and jaw, holotype of *Proterochampsia barrionuevoi*, Reig 1959.

Referred material MCZ 3408, complete skull and 13 articulated vertebrae and ribs; MACN-PV 18165, partial skull; PVL 2058, partial skull and jaw; PVL 2057 partial skull; and PVSJ 77 complete skull and both jaws.

We refer the specimen PVSJ 77 to the genus *Proterochampsia* on the basis of the following characters noted by Bonaparte (1978): very marked nodular cranial and mandibular ornamentation, very low temporal region of the skull, dorsal exposition of the infratemporal fenestrae, dorsal position of the orbits, and dorsal exposition of the antorbital fossae. PVSJ 77 resembles the species *Proterochampsia barrionuevoi* in the following characters: numerous nodular crests and trapezoidal infratemporal fenestrae in the lateral view. However, PVSJ 77 shares with *Proterochampsia nodosa* the following characters noted by Barberena (1982): a very developed circumorbital crest of liriform shape and jugal excluded from the sub-orbital fenestrae. Because of this we cannot unequivocally refer this specimen to any of the currently recognized species of the genus *Proterochampsia*. The differences between these two species will be revised in a future study.

Horizon and locality Lower part of the Ischigualasto Formation (Upper Triassic, Late Carnian; Rogers et al. 1993; Furin et al. 2006), Cancha de Bochas Member (Currie et al. 2009) San Juan Province, northwestern Argentina.

Materials and methods

The specimen described here includes an isolated skull (PVSJ 77). The braincase of PVSJ 77 presents a considerably complete occipital region and basicranium. The studied material consists of some entire bones, such as the exoccipital, basioccipital, and laterosphenoid, as well as nearly complete bones such as the parabasisphenoid and opisthotic. The supraoccipital and especially the prootic are poorly preserved.

The braincase was preserved in seven different pieces: one including the basioccipital, ventral half of the left exoccipital-opisthotic, right exoccipital-opisthotic and right part of the supraoccipital, a second one including the dorsal part of the left exoccipital-opisthotic and left part of the supraoccipital, a third one including the main part of the parabasisphenoid, and perhaps the ventral parts of the

prootics, two including both distal ends of the basiptyergoid processes, and the two laterosphenoids, which are naturally attached to the frontal. The preservation is regular; although the bones are not deformed, many surface details are poorly preserved. The borders of the articular surfaces, as in the dorsal surface of the occipital condyle, are poorly preserved, and many foramina are difficult to discern. The basioccipital and parabasisphenoid are not articulated, and it is not easy to determine their exact articular position because the caudal surface of the parabasisphenoid is not completely well preserved. The exoccipital opisthotics are slightly disarticulated from the basioccipital, sliding laterally along the articular contact.

We present the material used for comparison in Table 1. Collection numbers in the table indicate specimens studied first hand, and bibliographic quotations imply both published observations and figures of other authors. The anatomical nomenclature follows that of Gower (2002), except for the pneumatic fossae, which follows that of Gower and Sennikov (1996), and follow conventions regarding directions and planes indicated in Weishampel et al. (2004) for dinosaurs.

The family Proterochampsidae was coined by Sill (1967) to include *Proterochampsia* and its potentially closest relatives, but the taxon has not been phylogenetically defined yet. In the present contribution, we consider the genera *Cerritosaurus*, *Proterochampsia*, *Chanaresuchus*, *Gualosuchus*, and *Tropidosuchus* to be proterochampsids, following pre-cladistic hypotheses of relationships by Romer (1971) and Arcucci (1990).

Institutional abbreviations AMNH: American Museum of Natural History, New York; BMNH: Natural History Museum, London; BPI: Bernard Price Institute for Palaeontology, Johannesburg; BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, Munich; GMB: Geological Institute, Beijing; HMN: Humboldt Museum für Naturkunde, Berlin; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MACN: Museo Argentino de Ciencias Naturales, Buenos Aires; MCP: Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCT: Museu de Ciências da Terra, Rio de Janeiro; MSM: Mesa Southwest Museum, Mesa; PIN: Paleontological Institute of the Russian Academy of Science, Moscow; PVL: Instituto Miguel Lillo, Tucumán; PVSJ: Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan; SAM: South African Museum, Cape Town; SMNS: Staatliches Museum für Naturkunde, Stuttgart; UCMP: University of California Museum of Paleontology, Berkeley; ULR: Museo de Ciencias Naturales de la Universidad Nacional de La Rioja, La Rioja; UMCZ: University Museum of Zoology, Cambridge;

Table 1 Sources of information for taxa cited in the text

<i>Adeopapposaurus magnai</i> , PVSJ 610; Martínez (2009); personal observation
<i>Arizonasaurus babbitti</i> , MSM P4590, MSM P4647; Gower and Nesbitt (2006)
<i>Batrachotomus kupferzellensis</i> , SMNS 80260; Gower (2002)
<i>Caiman latirostris</i> , personal collection; personal observation
<i>Cerritosaurus binsfeldi</i> , MCP 1694 PV; Price (1946)
<i>Chanaresuchus bonapartei</i> , ULR 07; Romer 1971; personal observation
<i>Ctenosaura pectinata</i> ; Oelrich (1956)
<i>Doswellia kaltenbachi</i> , USNM 214823; Weems (1980); Dilkes and Sues (2009)
<i>Erythrosuchus africanus</i> , BMNH R3592, UMCZ T700, SAM 3612, BPI 3893; Gower (1997)
<i>Euparkeria capensis</i> , SAM 5867; SAM 7696; UMZC T692; Ewer (1965); Gower and Weber (1998)
<i>Fugusuchus hejiapensis</i> , GMB V 313, Gower and Sennikov (1996)
<i>Garjainia prima</i> , PIN 951-60; Gower and Sennikov (1996)
<i>Herrerasaurus ischigualastensis</i> , PVSJ 407; Sereno and Novas (1994); personal observation
<i>Hypsilophodon foxii</i> , BMNH R2477; Galton (1974)
<i>Leptosuchus gregorii</i> , UCMP A272/27200; Camp (1930)
<i>Massospondylus carinatus</i> , BPI 1-5231; Gow (1990).
<i>Pantyraco caducus</i> , BMNH P24; Yates (2003)
<i>Plateosaurus engelhardti</i> , AMNH 6810, HMN A58; Galton (1985)
<i>Proterochampsa nodosa</i> , MCP 1694 PV; Barberena (1982)
<i>Proterosuchus fergusi</i> , BPI 3993, BSPG 1934-VIII-514; Broili and Schroeder (1934); Gow (1975)
<i>Pteranodon</i> sp., YPM 2707; Bennett (2001)
<i>Saurosuchus galilei</i> , PVSJ 32; Alcober (2000); personal observation
<i>Shansisuchus shansisuchus</i> , IVPP V 2511; Gower and Sennikov (1996)
<i>Silesaurus opolensis</i> , ZPAL Ab III/364, ZPAL Ab III/362, ZPAL Ab III/361; Dzik (2003)
<i>Sphenosuchus acutus</i> , SAM 3014; Walker (1990)
<i>Tapejara wellnhoferi</i> , MCT 1500-R; Kellner (1996)
<i>Tropidosuchus romeri</i> , PVL 4601; Arcucci (1990)
<i>Xilousuchus sapingensis</i> , IVPP 6026; Gower and Sennikov (1996)
Basal sauropodomorph specimen YPM 2192; Benton et al. (2000); Galton (2007)

USNM: National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington; **YPM:** Peabody Museum of Natural History, Yale University, New Haven; **ZPAL:** Institute of Paleobiology of the Polish Academy of Sciences, Warsaw.

Anatomical abbreviations **bbpt** rostral border of basiptyergoid process; **bo** basioccipital; **bpt** basiptyergoid process; **bsr** basisphenoidal recess; **btbo** basioccipital basal tuber; **btbs** parabasisphenoidal basal tuber; **cl** caudal lobe; **cp** capitate process; **cr** chochlear recess; **crbt** ridge on caudal surface of basal tubera; **cseo** condylar articular surface on exoccipital, **cu** cultriform process; **eo** exoccipital; **es** endocranial surface (median fossa); **fbf** basioccipital-basisphenoidal fossa; **fls** fossa on lateral surface of the laterosphenoid, **fm** foramen magnum **fs** fossa for supraoccipital on parietal; **gr** groove; **lr** lateral ridge, **ls** laterosphenoid; **mf** metotic foramen; **mff** metotic foramen floor; **mr** medial ridge; **mvf** medioventral flange; **mwie** medial wall of inner ear; **mf?** probable nutrient foramen; **oc** occipital condyle; **ocf** occipital condyle fossa; **op**

opisthotic; **p** parietal; **pf** pituitary fossa (fossa hypophys-eos); **popr** paroccipital process; **pps** sulcus on paroccipital process; **pr?** possible prootic; **pras** articular surface for prootic; **prp** prootic caudolateral process; **pt** pterygoid; **roa** sulcus of occipital ramus of ophthalmic artery; **robp** ridge between the ventral ramus of opisthotic and basioccipital basal tubera; **S XII** sulcus for the XII nerve; **sbpt** sulcus dorsal to the basiptyergoid process base; **sfbb** sulcus leading to the basioccipital-basisphenoidal fossa; **sfo** sulcus leading to the fenestra ovalis; **sl** ridge delimiting semilunar depression; **smf** sulcus leading to the metotic foramen; **so** supraoccipital; **“V”** V-shaped ridge; **vr** vestibular recess; **vrop** ventral process of the opisthotic; **wpf** caudal wall of pituitary fossa; **XII** XII nerve foramina; **?** unrecognized bony fragment.

Description

The braincase is rostrocaudally short (Fig. 2), being 1.43 times longer (from the rostral end of the base of the

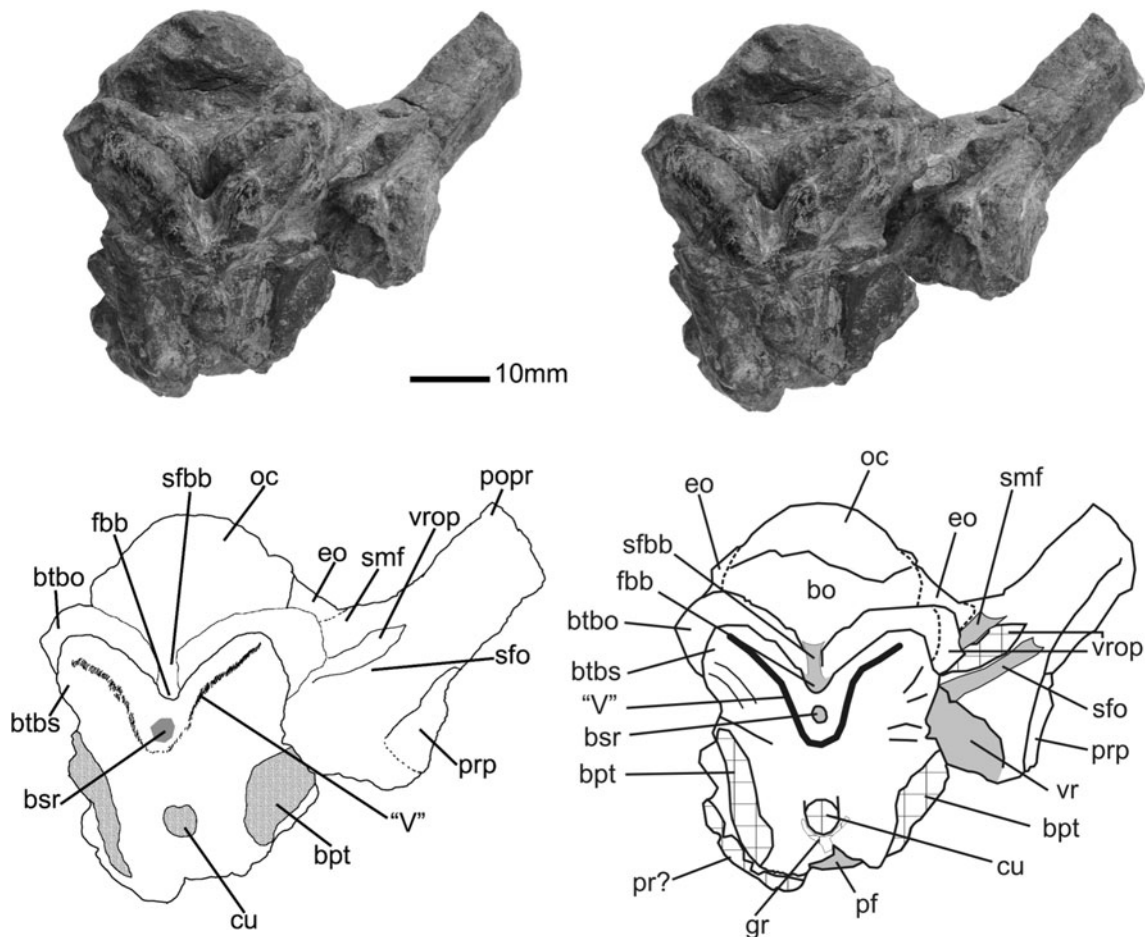


Fig. 2 Stereopair of the ventral aspect of most of the basicranium of *Proterochampsia* spp. (PVSJ 77)

basipterygoid processes to the caudalmost part of the occipital condyle) than its width between the lateral parts of the basal tubera. The relative shortness of the braincase is reminiscent of that of other basal archosauriforms (e.g., *Erythrosuchus africanus* Broom 1905—BMNH R3592; UMCZ T700; *Fugusuchus hejiapanensis* Cheng 1980—GMB V313; *Shansisuchus shansisuchus* Young 1964—IVPP V 2511×).

Basioccipital

The basioccipital is complete and forms most of the occipital condyle. The occipital condyle is flattened, wider than tall, and sub-equal in size to the foramen magnum (Fig. 3), resembling the condition in *Tropidosuchus romeri* Arcucci 1990 (PVL 4601). Centered on its articular surface, the condyle presents a median fossa (Fig. 3), resembling other archosauriforms (e.g., *Doswellia kaltenbachi* Weems 1980). There is no longitudinal groove on the caudal part of the dorsal surface of the basioccipital (Figs. 3, 7b), contrasting with the condition figured in the specimens studied by Sill (1967; Fig. 3). The main body of

the basioccipital, caudal to the basal tubera, is proportionately wider at the condyle, relative to its length, than in *Chanaresuchus* (URL 07) and *Tropidosuchus* (PVL 4601). The condylar stalk is not differentiated (Fig. 2). Rostrally, the main body of the basioccipital forms the caudal part of the medial half of the eight-shaped metotic foramen (Fig. 4). This medial (and ventral) half of this foramen seems to have been misinterpreted as the foramen of the internal carotid artery by Sill (1967). We do not agree with Sill's (1967) assignment, because in his interpretation the internal carotid foramen would be confluent with the metotic foramen, a very unlikely arrangement. There is no ridge on the lateral part of the basioccipital (Fig. 4), contrasting with the condition present in the specimen SMNS 80260 of *Batrachotomus kupferzellensis* Gower 1999.

The basioccipital basal tubera are proximodistally short (Fig. 3), contrasting with the elongated ones of *Chanaresuchus* (ULR 07), and ventrolaterally projected. The medial border of the basioccipital basal tubera is short and not as convex in the caudal view as it is in *Chanaresuchus* (ULR 07) (Fig. 3). In the caudal view, the ventral border of each basioccipital tuber is convex (Fig. 3). Both ventral

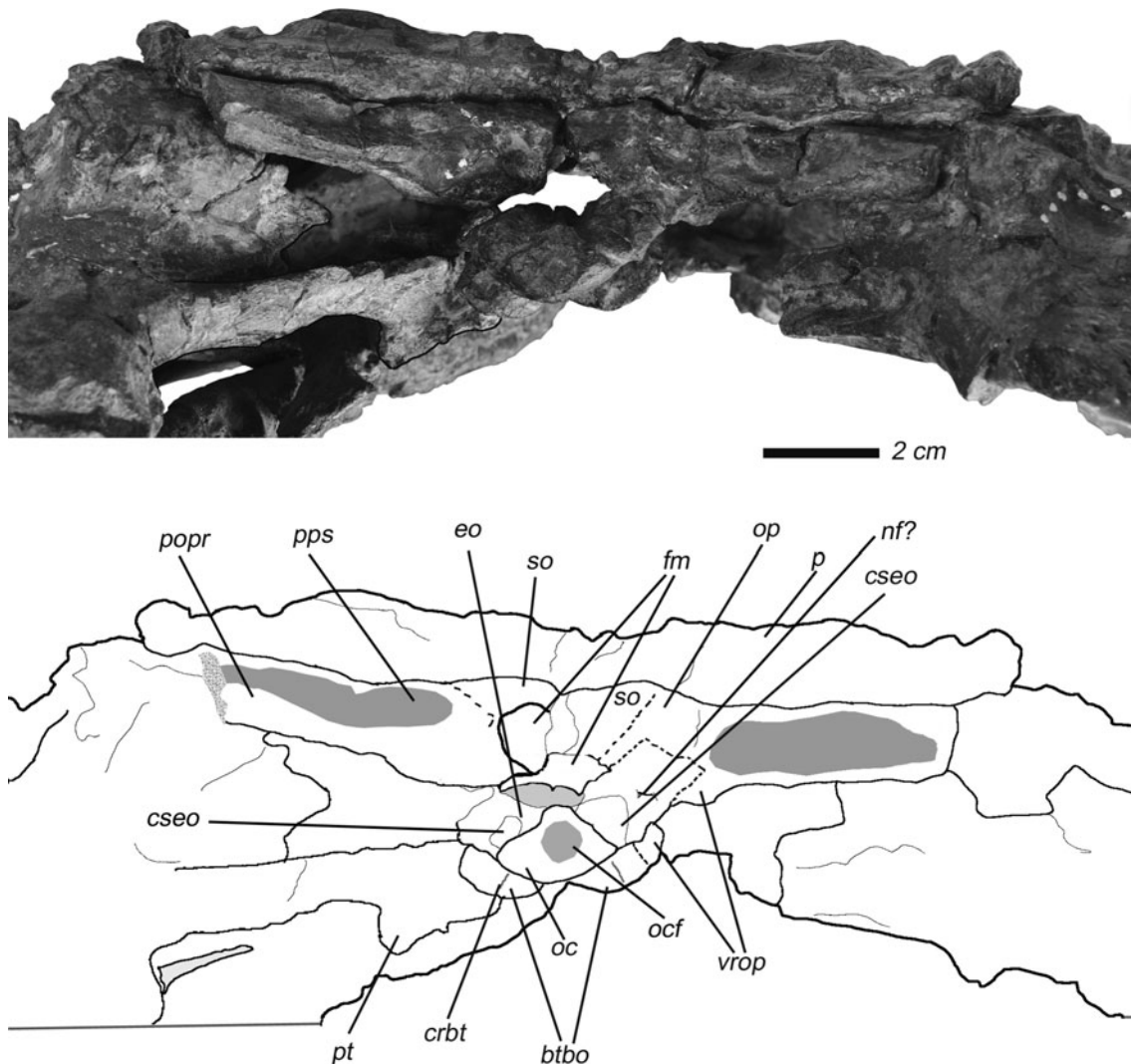


Fig. 3 Caudal view of the skull of *Proterochampsa* spp. (PVSJ 77)

borders form an angle much larger than 90° between themselves (Fig. 3), contrasting with *Batrachotomus* and *Arizonasaurus babbitti* Welles 1947, in which the purportedly homologous borders are ventrolaterally oriented. On the caudal aspect of each tuber, there is a prominent and ventrolaterally directed buttress, which separates a caudolateral and a caudomedial surface, respectively (Fig. 3). On their dorsolateral part, the basal tubera form, at least, the ventromedial border of the metotic foramen (Fig. 4). Rostrolaterally to this point, the basioccipital tubera seem to have fused to the ventral ramus of the opisthotic (Figs. 3, 4, 5). In the caudal view, the lateral contour of the ventral process of the opisthotic and the ventral contour of the basioccipital basal tubera are smoothly continuous and form a convexity (Fig. 3), contrasting with the condition present in some basal archosauriforms (e.g., *Garjainia prima* Ochev 1958, *Fugusuchus*).

The separation between both basioccipital tubera is represented by a small, transversely narrow, and rounded notch in the caudal view (Fig. 3). This notch continues rostrally as a shallow median sulcus, which is exposed in both ventral and rostral views (Figs. 2, 5). This sulcus forms the caudal wall of the small, deep, and rounded median basioccipital-basisphenoid fossa (Fig. 5), which is rostrally limited by the parabasisphenoid (Fig. 2).

The rostroventral surface of the basioccipital tubera has a convex and pitted texture (Figs. 2, 5), which may have supported a cartilaginous coverage, which in turn likely contacted with the parabasisphenoidal basal tubera. This pitted surface seems to continue on the ventral ramus of the opisthotic (Figs. 4, 5). The cartilaginous coverage would be homologous with the cartilage that covers the gap between the basal tubera of the basioccipital and parabasisphenoid in other basal archosauriforms (pseudolagenar

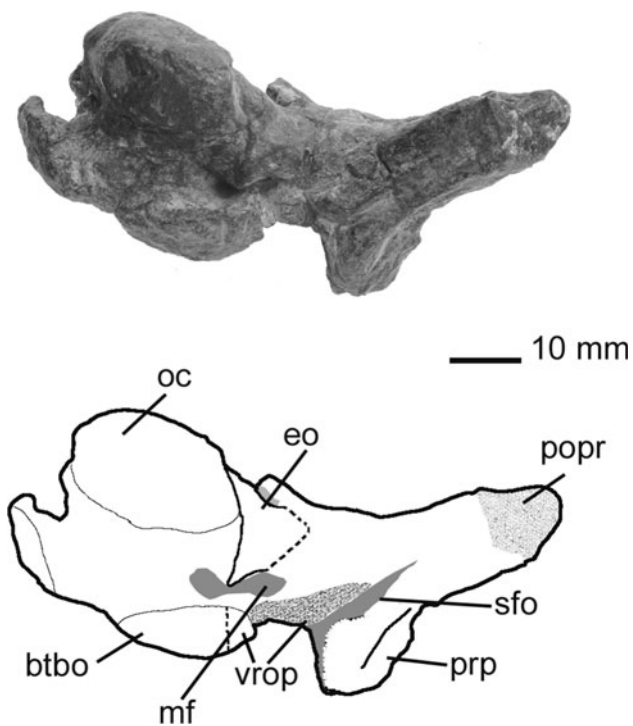


Fig. 4 Oblique caudoventrolateral view of a braincase fragment including the basioccipital, exoccipitals, right opisthotic, right caudolateral fragment of the supraoccipital, and right caudolateral process of the prootic of *Proterochampsia* spp. (PVSJ 77)

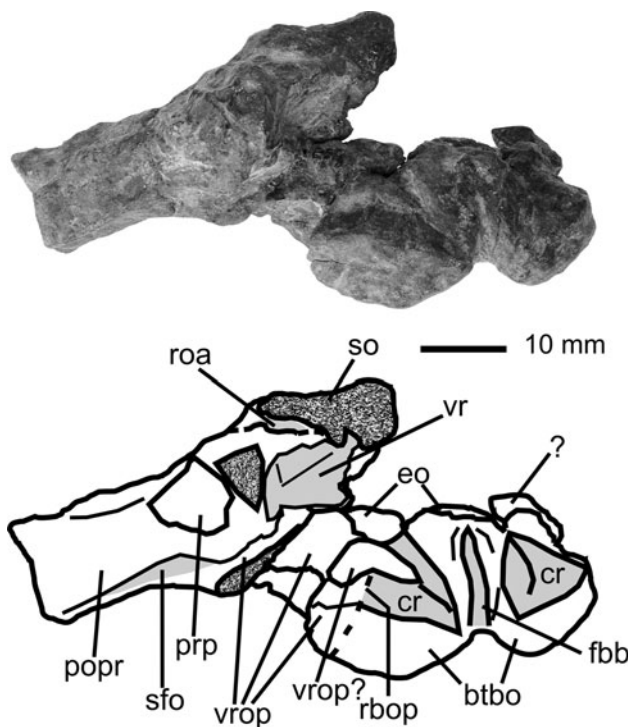


Fig. 5 Rostral view of a braincase fragment including the basioccipital, exoccipitals, right opisthotic, right caudolateral fragment of the supraoccipital, and right caudolateral process of the prootic of *Proterochampsia* spp. (PVSJ 77)

recess sensu Gower and Sennikov 1996). However, although the fit between the basioccipital and parabasisphenoid is not perfect, there is no evidence of a large unossified gap between both basal tubera contributions (Fig. 2), unlike most basal archosauriforms (Gower and Sennikov 1996) and most basal pseudosuchians (Gower 2002). On the medial part of the rostral surface of each tuber, a nearly vertical sulcus is present, which bows laterally and almost reaches the ventral border of the tuber (Fig. 5). This sulcus may correspond to the cochlear recess (char. 9 in Gower 2002). The ventral part of the sulcus directs ventromedially and tapers towards the ventromedial corner of each basioccipital tuber. This sulcus is separated from a more dorsolaterally located surface by an oblique ridge (Fig. 5). Due to its position adjacent to the cochlear recess, this ridge may represent part of the rim to which the membrane of the fenestra ovalis attached. The ridge may also represent the suture between the opisthotic and basioccipital, thus its interpretation is currently uncertain. The structure hypothesized in this contribution to correspond to the cochlear recess of *Proterochampsia* would be longer than the cochlear recess of *Leptosuchus gregorii* (Camp 1930), according to the published figures of its inner ear endocast. The structure of *Proterochampsia* would approach more the more elongated condition shown in the published figures of endocasts of dinosaurs such as *Plateosaurus engelhardti* Meyer 1837.

The dorsal surface of the basioccipital bears at least two longitudinal ridges, and most likely three, at least at its rostral region (the caudal end of the bone is overlapped by the partially articulated exoccipitals) (Fig. 6). A median ridge extends along the midline of the bone and seems to be the medial limit of both exoccipital articular facets. The other ridge, located in the left side, directs caudolaterally and represents the lateral-most extent of the exoccipital articular facet. A similar ridge on the right side would be covered by the right exoccipital. These ridges delimit grooves in which the rostral end of the ventral part of the exoccipitals fits. At least on the left side, lateral to these ridges, there is an oblique groove, which corresponds to the floor of a tunnel caudolaterally leading to the external opening of the metotic foramen (Fig. 6). This groove is rostrolaterally surrounded by the ventral ramus of the opisthotic.

Exoccipital

The exoccipitals are complete (Figs. 3, 4). The sutures that separate the exoccipitals and opisthotics are not entirely marked, as in many other basal archosauriforms (Gower and Sennikov 1996). Some indication of the suture with the opisthotic is present on the caudal surface (Fig. 3), but this suture appears to be indicated by a ridge on the medial

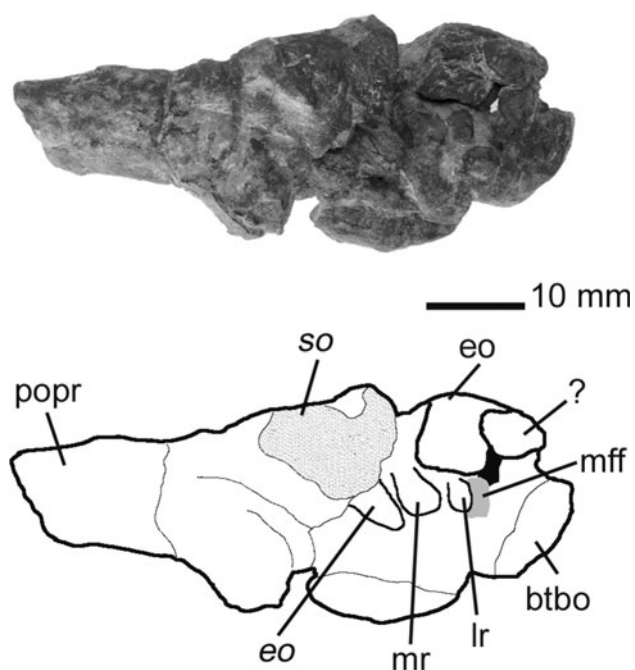


Fig. 6 Rostrodorsal view of braincase fragment including the basioccipital, exoccipitals, right opisthotic, right caudolateral fragment of the supraoccipital, and right caudolateral process of the prootic of *Proterochampsia* spp. (PVSJ 77)

surface (Fig. 7a). Accepting that the suture is well identified, the exoccipital does not form part of the dorsal border of the foramen magnum, which is formed by the opisthotic and supraoccipital (Fig. 3), as in the basal sauropodomorph dinosaur *Adeopapposaurus magnai* Martínez 2009 (PVSJ 610). This condition contrasts with that present in the phytosaur *Leptosuchus* (UCMP A272/27200). On the caudal surface of the dorsal part of the exoccipital, there seems to be a natural foramen, probably of nutrient function (Fig. 3), similar to that found in other archosaurs, e.g., *Arizonasaurus*, *Pantyraco caducus* Yates 2003.

The caudal surface of the base of each exoccipital contributes to the condylar articular surface (Fig. 3), as in other archosauriforms. Both exoccipitals approached each other very closely in the floor of the endocranial cavity (Fig. 7b). Whether or not they contacted at the midline, as in *Erythrosuchus*, is uncertain because they are disarticulated. The ventral surface of the exoccipital, which abuts with the basioccipital, is rostrocaudally longer than wide, as in most basal archosauriforms (e.g., Gower and Sennikov 1996), and tapers rostrally (Fig. 6). The rostral half of the exoccipital ventral surface is more medially directed than the caudal half. The former structure contacts with the side of the median ridge in the rostral half of the basioccipital dorsal surface. The tapering rostral part of the base of the exoccipital forms the caudoventral border of the dorsal portion of the metotic foramen (Fig. 7a).

The ventral half of the ventrolateral surface of the exoccipital is strongly convex in its caudal region (Fig. 4). The rostralateral surface of the base of the exoccipital is laterally overlapped by the ventral process of the opisthotic so that the hypoglossal nerve foramina are not exposed in the lateral view (Fig. 8). This overlapped region represents the caudomedial wall of a canal that forms the metotic foramen. A slight, oblique, and rostroventrally directed crest separates the lateral surface from the rostralateral one, which is rostrocaudally concave. There are two foramina for the hypoglossal nerve (XII) on the medial surface of the exoccipital (Fig. 7b). The first foramen is small and close to the ventral border, located on the rostral third of the base of the bone. The other foramen is larger, more dorsal and caudal, and located close to the mid-length of the bone. The path of the caudal hypoglossal channel is exposed in the broken left exoccipital, and it is mostly laterally directed (Fig. 7b), as in *Erythrosuchus* (SAM 3612).

Supraoccipital

The supraoccipital is very incomplete, preserving its caudolateral regions, and lacking its rostradorsal and medial regions (Fig. 3, 5). The supraoccipital is not fused with the parietal in PVSJ 77 (Figs. 3, 9a), contrasting with fused condition of the holotype of *Proterochampsia nodosa* (MCP 1694 PV). The supraoccipital seems to have been rostradorsally oriented and would have formed the caudal part of the ceiling of the endocranial cavity (Fig. 7a). There seems to be no trace of a differentiated epiotic. The supraoccipital does not articulate with the exoccipital (Fig. 3), as occurs in some archosaurs (e.g., the sauropodomorph *Adeopapposaurus*-PVSJ 610-), but unlike the phytosaur *Leptosuchus* (UCMP A272/27200) where it contacts a small part of the exoccipital. The suture with the opisthotic is poorly discernable, but seems to be represented by two continuous ridges on the caudal (Fig. 3) and medial (Fig. 7a) surfaces. The ridge on the caudal surface is dorsolaterally directed, whereas the ridge on the medial surface is almost horizontal. These ridges seem to meet at the dorsal border of the foramen magnum, so the supraoccipital would have formed part of the foramen magnum (Fig. 3), similar to the condition of *Tropidosuchus* (PVL 4601), but contrasting with the condition described by Sill (1967), Fig. 3 for *Proterochampsia* (MCZ 3408). The external surface of the preserved regions of the supraoccipital is smooth (Fig. 3). The available caudolateral region does not seem to have included part of the vestibular recess, and there is no evidence of foramina representing the crus commune or the vertical semicircular canals (Figs. 5, 7a). The articulation with the prootic seems not to be preserved (Fig. 5). Thus, it cannot be assessed if part of the floccular fossa reached the supraoccipital.

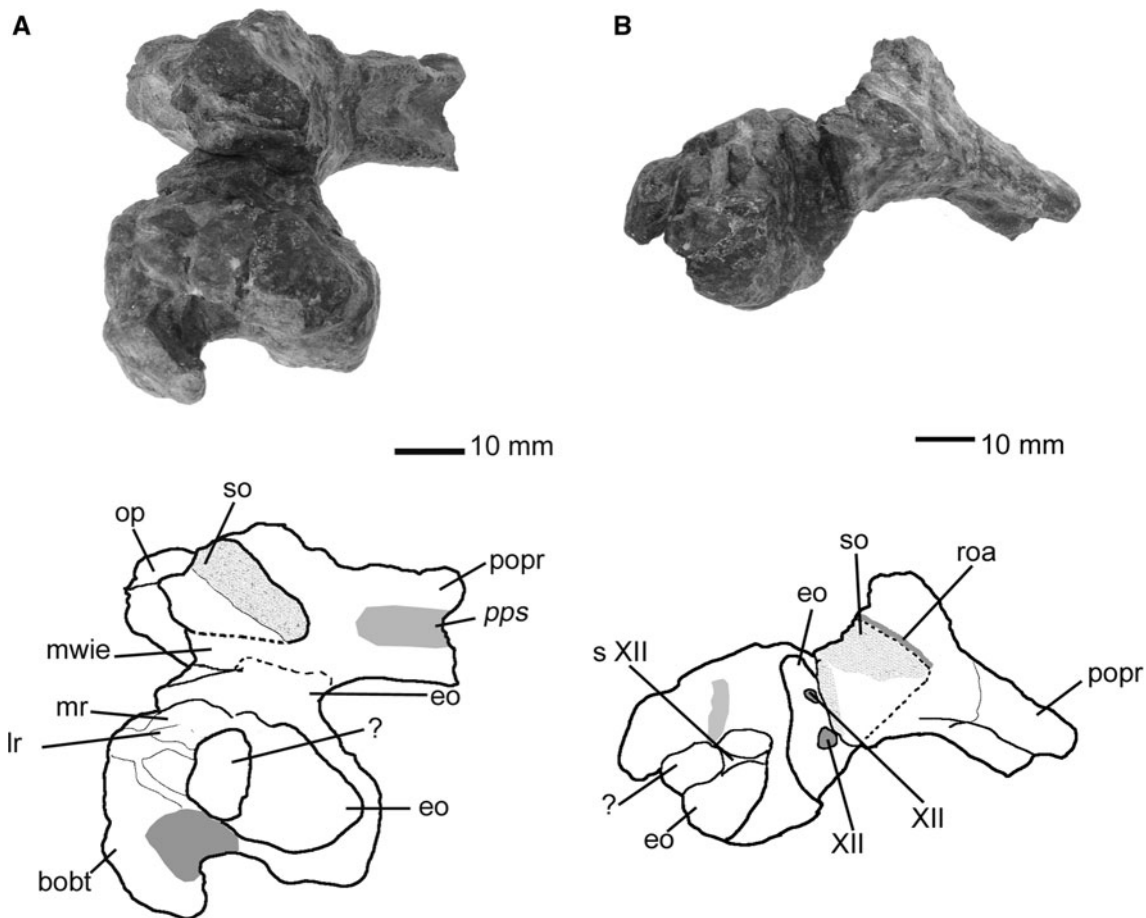


Fig. 7 Views showing the endocranial surface of the braincase fragment including the basioccipital, exoccipitals, right opisthotic, right caudolateral fragment of the supraoccipital, and right

caudolateral process of the prootic of *Proterochampsia* spp. (PVSJ 77). **a** Medial view. **b** Oblique dorsomedial view

The posttemporal fenestra would be very small, surrounded ventrally by the braincase and dorsally by the parietal (Fig. 3) (Serenó and Novas 1994, char. 14). On the dorsal surface of the braincase, there is a groove that is rostro-medially directed from the posttemporal fenestra (Fig. 7b). This groove seems to represent the ventral part of the canal for the occipital branch of the external ophthalmic artery (following avian nomenclature, Baumel 1993), and likely coincides with the union between the supraoccipital and opisthotic. A large and median boomerang-shaped fossa is present on the ventral surface of the parietal (Fig. 9a) and appears to represent a fossa for the reception of the supraoccipital. The latter suggests a triangular-shaped supraoccipital (Fig. 9a), as indicated by Sill (1967).

Opisthotic

The opisthotic is almost completely preserved, with the exception of the ventrolateral portion of the ventral ramus and the distal tip of the paroccipital processes (Figs. 3, 5).

Accepting the exoccipital-opisthotic suture inferred previously, the opisthotic forms the dorsolateral part of the border of the foramen magnum and most of the paroccipital processes (Fig. 3). The paroccipital processes are elongate, straight, and dorsoventrally narrow in caudal view (Fig. 3), as illustrated by Sill (1967). Except for the distal ends, the dorsal and ventral contours of the processes are straight and parallel in this view. In these features of the process, the specimen resembles *Chanaresuchus* (specimen URL 07) more closely than other archosauriforms (e.g., *Erythrosuchus*, *Euparkeria*, *Doswellia*, *Arizonasaurus*). The distal ends are dorsoventrally narrower than the rest of the process, contrasting with the condition of most other archosauriforms, in which they are dorsoventrally expanded (e.g., *Doswellia*, *Erythrosuchus*). The caudal surface of the processes forms a conspicuous sulcus that encompasses most of the length of the process, as in *Chanaresuchus* (URL 07), and is only lacking at the tip (Fig. 3). This sulcus is dorsally and ventrally bounded by two prominent ridges, which separate the caudal surface from the dorsal and ventral surfaces of the process. The ventral ridge

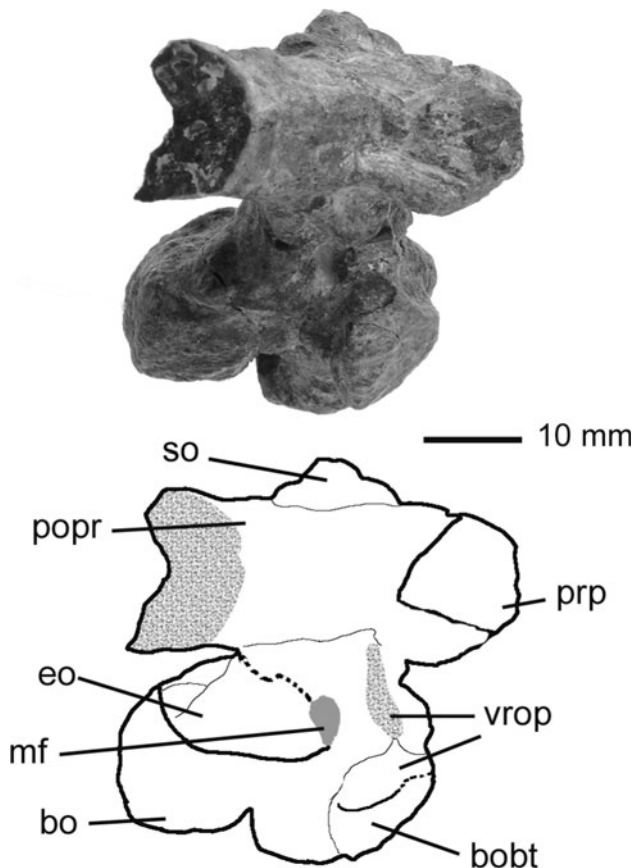


Fig. 8 Lateral view of braincase fragment including the basioccipital, exoccipitals, right opisthotic, right caudolateral fragment of the supraoccipital, and right caudolateral process of the prootic of *Proterochampsia* spp. (PVSJ 77)

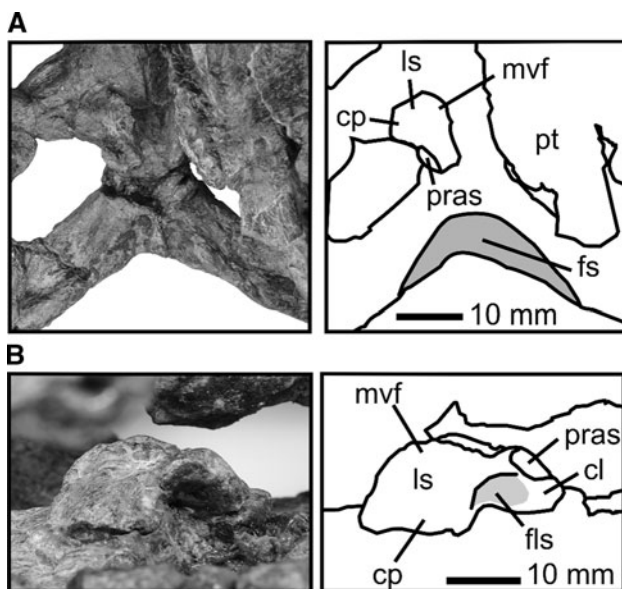


Fig. 9 Laterosphenoid and parietal of *Proterochampsia* spp. (PVSJ 77); **a** Ventral view of the laterosphenoid and parietal. **b** Right laterosphenoid in lateral view. In **b**, ventral is to the top

curves dorsally on the distal tip of the process, so that the ventral surface “twists” to face caudoventrally at its distal end. Except at the base, the processes are nearly as thick dorsoventrally (Fig. 3) as they are rostrocaudally (Fig. 2), unlike most other archosauriforms (e.g., *Fugusuchus*, *Xilousuchus sapingensis* Wu 1981 -IVPP 6026-, *Euparkeria*, *Arizonasaurus*, *Saurosuchus galilei* Reig 1959). The processes have an almost constant rostrocaudal width along most of their length, as observed in ventral view (Fig. 2). They are caudolaterally directed and together form an oblique angle in the dorsal view. The rostrolateral surface of the proximal half of the process is flat, as is most of the ventral surface (i.e., in the region lateral to the ventral ramus and proximal to the constricted tip) (Fig. 8). The dorsolateral surface is rostrolaterally convex (Fig. 8), with only its dorsalmost portion articulating with the parietal. The level of the ventral surface of the paroccipital processes is dorsal to that of the ventral border of the foramen magnum (Fig. 3). The ventral surface of the proximal end of the process bears two canals of caudolateral direction that lead to the dorsal part of the metotic foramen and fenestra ovalis, respectively (Fig. 2). The dorsal end of the ventral ramus of the opisthotic is located between these canals (Fig. 2). The ventral ramus is prominent and exposed in the lateral (Fig. 8), ventral (Fig. 2), and caudal (Fig. 3) views of the braincase. It is a thick and almost transverse lamina that separates the fenestra ovalis from metotic foramen. It directs ventrally and fuses with the laterodorsal part of the basioccipital basal tubera (Fig. 5). As most of the ventral ramus is poorly preserved, there is no evidence of a contribution of the opisthotic to the formation of a cochlear eminence. Besides, unequivocal remains of the perilymphatic foramen cannot be distinguished in the ventral ramus. The caudal part of the vestibular recess locates medial to the dorsal end of the ventral ramus (Fig. 5). The roof of the vestibular recess is dorsal to the level of the ventral surface of the paroccipital process (Fig. 5). It tapers caudolaterally into what seems to be the caudal ampulla. The caudal part of the medial wall of the recess is preserved (Fig. 7a).

Prootic

Most of the prootics are lacking, preserving only the tips of the caudolateral processes (Figs. 5, 8), and probably portions adjacent to the parabasisphenoid (Fig. 10a–e). The caudolateral process is pointed and articulated with the base of the paroccipital process. It overlaps rostrolaterally less than half of the length of the paroccipital process. Some fragments found on the dorsal surface of the parabasisphenoid seem to correspond to the prootic. These regions and their homologies will be considered in the description of the parabasisphenoid.

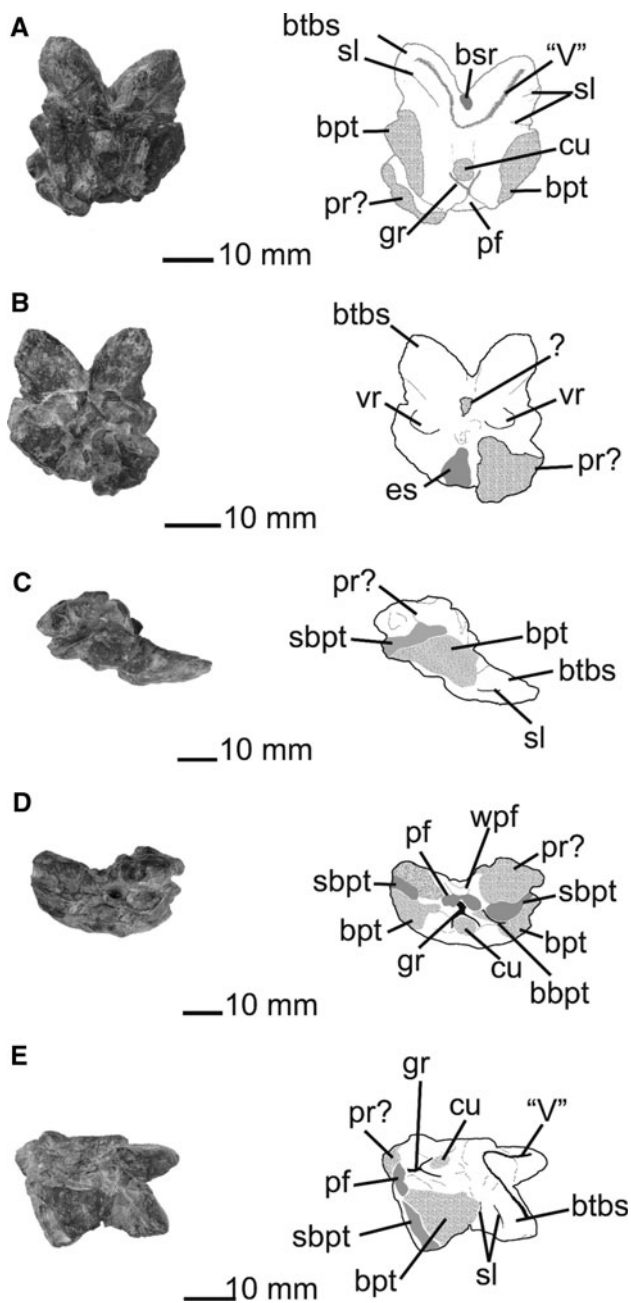


Fig. 10 Fragment including most of the parabisphenoid and probably part of the prootic of *Proterochampsia* spp. (PVSJ 77). **a** Ventral view. **b** Dorsal view. **c** Left lateral view. **d** Rostral view. **e** Right ventrolateral view

Parabisphenoid

Most of the parabisphenoid is preserved, excluding the cultriform process (Fig. 10a). The orientation of the parabisphenoid relative to the rest of the skull is difficult to assess, i.e., whether it was held mainly vertical, horizontal, or oblique. We will describe the parabisphenoid considering that the parabisphenoid basal tubera are caudoventrally directed. The parabisphenoid is proportionally

wide (Figs. 2, 10a), with a ratio between its length, from the rostralmost point of the base of the basiptyergoid processes to the caudal tip of the basal tubera, and a width comprised by the basal tubera of 1.02. The parabisphenoidal basal tubera are almost as long as transversely wide (Figs. 2, 10a, b). The distal end of the tubera is slightly pointed in the ventral view. Their caudodorsal surfaces are concave (Fig. 10b) for articulation with the basioccipital basal tubera, likely forming the rostral wall of what was identified as the cochlear recess. A small and rostromedially directed ridge is present on the ventrolateral surface of the tubera (Fig. 10a, c, e). On the right side, this ridge is bowed and forms the prominent rostral and caudal borders of a fossa (Fig. 10e). The rostral border is adjacent to the caudal part of the base of the basiptyergoid process. On the left side, the rostral end of the ridge is ventral to the caudal part of the base of the basiptyergoid processes (Fig. 10c). This ridge appears to be homologous with the ridge that ventrally limits the semilunar depression in other basal archosauriforms (e.g., *Erythrosuchus*, *Fugusuchus*, *Chanaresuchus*). However, in these taxa, the fossa is exposed mostly laterally, contrasting with the mainly ventrolateral exposure of its purported homologue in *Proterochampsia*. In the lateral view, the parabisphenoidal tubera are very slender and pointed (Fig. 10c), unlike most other archosauriforms (e.g., *Erythrosuchus*, *Arizonasaurus*, *Chanaresuchus*). This suggests that the parabisphenoidal basal tubera in *Proterochampsia* seem to be rotated along their proximodistal axis, in comparison with those of other basal archosauriforms. So, the surface that in other basal archosauriforms faced laterally faces ventrolaterally in *Proterochampsia*. This would explain the location of the semilunar depression on the ventrolateral surface of the bone, which instead faces laterally, as in most basal archosauriforms (Gower and Sennikov 1996). Furthermore, such rotation would also explain the slenderness of the parabisphenoidal tubera in the lateral view in *Proterochampsia*, but in the ventral view in *Chanaresuchus*. As in *Doswellia*, there is no prominent intertuberal plate between the parabisphenoidal basal tubera (Figs. 2, 10a, e) (Dilkes and Sues 2009). The parabisphenoidal caudal border is V-shaped in the ventral view (Fig. 2, 10a), with each arm of the “V” corresponding to the convex caudo-medial border of each tuber. Rostral to the median part of the caudal border, there is a deep and caudoventrally facing pit filled by matrix, which likely corresponds to the basisphenoidal recess (Fig. 2, 10a). The basisphenoidal recess is rostrally delimited by a very prominent and thick ridge, which is V-shaped and oriented as the caudal border (Figs. 2, 10a, e). The arms of this ridge are medially convex and reach the distal tip of the parabisphenoidal basal tubera. The external foramina of the canal for the internal carotid arteries were not positively identified on the ventral

or lateral surfaces of the bone. We tentatively hypothesize the foramina for the internal carotids would be located within the basisphenoidal recess, because the recess presents a position comparable to the region in which the carotid entrances locate in material of *Doswellia* (USNM 214823) and *Erythrosuchus* (BMNH R3592), and because of the lack of foramina in other regions of the parabasisphenoid. However, a problem with this interpretation is that a location of the carotid openings within the basisphenoidal recess is something not seen in other archosauriforms (e.g., *Proterosuchus fergusi* Broom 1903, *Fugusuchus*, *Erythrosuchus*, *Euparkeria*, *Chanaresuchus*, *Arizonasaurus*, and *Herrerasaurus ischigualastensis* Reig 1963).

The basiptyergoid processes are mostly laterally directed, as in *Fugusuchus*, but contrasting with most archosauriforms, in which they are more ventrally directed (e.g., *Erythrosuchus*, *Shansisuchus*, *Chanaresuchus*, *Euparkeria*, and *Arizonasaurus*). The basiptyergoid processes are much larger than the parabasisphenoidal basal tubera, in both lateral and ventral aspects, and the width comprised between them largely surpasses that comprised between the parabasisphenoidal tubera. The basiptyergoid processes present an acute rostral border (Fig. 10d), and their bases are rostrocaudally expanded (Fig. 10c). Their ventral surfaces are not connected by a buttress (Figs. 2, 10a), contrasting with some archosaurs such as *Saurosuchus* (PVSJ 32) and *Herrerasaurus*. The rostralmost part of the base of the processes rostrally surpasses the base of the cultriform process (Fig. 10a), unlike most archosaurs (e.g., Gower and Sennikov 1996). The distal ends present a conspicuous caudal development (Fig. 11a). The articulation with the pterygoid covers the lateral and ventral surfaces of the basiptyergoid processes (Fig. 11b), contrasting with *Tropidosuchus* (PVL 4601), which presents only a laterally facing articular surface on the basiptyergoid processes. The articular surface, hidden because of being preserved in natural articulation with the pterygoid, seems to be very convex in order to fit into the apparently deep fossa formed by the articular surface in the pterygoid (Fig. 11b). On the lateral surface of the parabasisphenoid, just dorsal to the base of each basiptyergoid process, a wide horizontal groove formed between the dorsal surface of the basiptyergoid process and a laterally directed part of the lateral wall of the braincase is present (Fig. 10c–e). Such a groove, dorsal to the base of the basiptyergoid process, resembles the condition of the basal dinosauriform *Silesaurus opolensis* Dzik 2003. However, the sulcus reaches the rostral border of the processes, unlike *Silesaurus*. Most of the cultriform process is lacking, but its base is preserved (Fig. 10a). It is ovoid in the preserved section, and not laminar (Fig. 10d), contrasting with *Chanaresuchus*. The base of

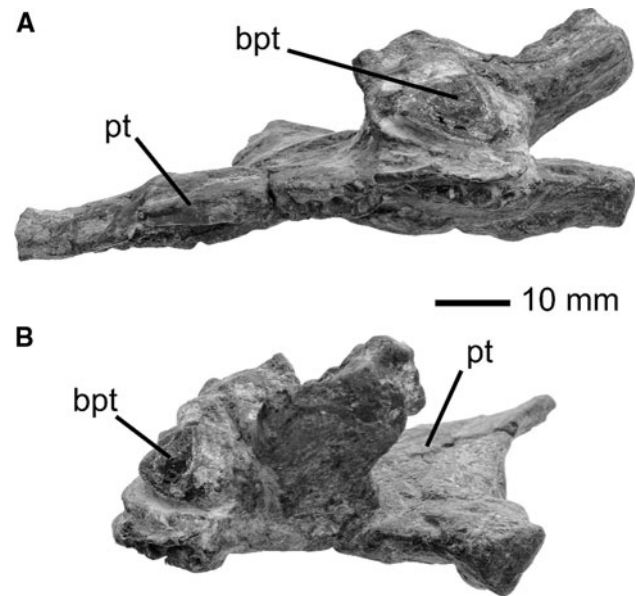


Fig. 11 Fragment including the articulated right basiptyergoid process and pterygoid of *Proterochampsia* spp. (PVSJ 77). **a** Medial view. **b** Caudal view

the cultriform process does not present a longitudinal sulcus on its dorsal surface.

The homologies of all the bony regions dorsal to the basiptyergoid processes, parabasisphenoidal basal tubera, and cultriform process are doubtful: they may correspond either to the prootic or the parabasisphenoid. On the caudal surface, rostral and dorsal to the basal tubera, there are two rounded fossae (Fig. 10b), which resemble those described as the rostroventral part of the vestibular recesses in *Batrachotomus*. This region is part of the prootic in *Batrachotomus* and *Caiman latirostris* Daudin 1801, suggesting that this region in *Proterochampsia* also corresponds to a prootic fused to the parabasisphenoid. A median depression is present on the dorsal surface of the parabasisphenoid, being much deeper at its center (Fig. 10b). We tentatively consider it as the region of the endocranial fossa immediately caudodorsal to the hypophyseal fossa. Lateral and caudal to this depression, there are rugose areas. Rostral and ventral to the median depression, and rostral and dorsal to the base of the cultriform process, there is a pair of rostrally facing fossae (Fig. 10d). It is here hypothesized that this pair of fossae represents a single pituitary fossa that was more rostroventrally expanded, but whose rostralateral walls have been artificially broken and collapsed caudomedially. The rostroventral walls of these fossae are separated by a median groove, which caudoventrally bifurcates at a point rostradorsal to the proximal end of the cultriform process (Fig. 10a, d). These grooves are here hypothesized to represent broken structures produced when the hypophyseal fossa collapsed. If not produced by

distortion, the homology of these grooves is difficult to interpret.

The possibility that the depression surrounded by rugosities represents the pituitary fossa is disregarded here. In that scenario, the dorsum sellae would be abnormally low, accepting that the prootic is preserved and fused to the parabasisphenoid. Alternatively, this would require to hypothesize that the prootic is detached from the parabasisphenoid, and thus that the rostroventral part of the vestibular recess, or a novel recess, is located on the parabasisphenoid. It also needs to accept that the lateral walls of the pituitary fossa were thick, unlike most archosaurs (e.g., *Arizonasaurus*, *Silesaurus*). A further problem is that the dorsal surface of the parabasisphenoid, caudal to the pituitary fossa, would be rostrocaudally much shorter than the exposition of the pituitary fossa in dorsal view, contrasting with the condition present in other diapsids (e.g., *Ctenosaura pectinata* Wiegmann 1834), including archosauriforms (e.g., *Arizonasaurus*, *Caiman*, and *Massospondylus* Owen 1854). Besides, the pair of fossae rostral to the median dorsal depression would have to represent the place where the caudal end of the trabecular cartilages fitted, which is unlikely, because the size of the trabeculae would be unusually large, and these fossae would have to be unrelated to the dorsal surface of the base of the cultriform process. The latter morphology clearly contrasts with the condition known in other archosauriforms (e.g., *Silesaurus*) and other diapsids (e.g., *Ctenosaura*). Although the hypophyseal fossa in some archosaurs (e.g., *Silesaurus*) is located between the bases of the basipterygoid processes, as is the median depression of *Proterochampsa*, the region immediately caudal to the hypophyseal fossa is located between the bases of the basipterygoid processes in other diapsids (e.g., *Ctenosaura*), including archosauriforms (e.g., *Caiman*). Thus, the hypothesis considered here that the median fossa represents the region of the endocranial fossa immediately caudodorsal to the hypophyseal fossa is less contradicted by our observations.

Laterosphenoid

The laterosphenoid is almost completely preserved, especially on the right side (Fig. 9a, b). It is a very thick bone, quite different from the more laminar condition in pseudosuchians (Gower and Sennikov 1996; pers. obs.) and at least some dinosaurs (e.g., *Hypsilophodon foxii* Huxley 1869). Its dorsal contact with the frontal is bilobate, and not trilobate as in *Erythrosuchus* (Gower and Sennikov 1996). The rostral and capitate processes are indistinct, and the caudal process is the only distinct lobe. The rostral process is poorly developed and not pointed, whereas the capitate process is well developed. No sulcus is present on the rostromedial surface of the bone between the rostral and

capitate process, contrasting with *Erythrosuchus* (BMNH R3592). A ridge is present on the lateral surface, which is mostly caudoventrally oriented and extends from the base of the capitate process to the articular surface for the prootic. This ridge forms the ventral limit of a fossa extended between the caudodorsal part of the laterosphenoid and the frontal (Fig. 9b). This fossa separates laterally the caudal lobe of the dorsal surface of the laterosphenoid from the rostral lobe, including the rostral and capitate processes. A similar fossa that is ventrally delimited by a ridge is observed on the left side of the laterosphenoid of *Shansisuchus*, but is absent on the right (Gower and Sennikov 1996; Fig. 6f). The process for the prootic is short and located on the caudal portion of the bone, and is caudally, laterally, and ventrally directed (Fig. 9a). The articular surface for the prootic faces caudoventrolaterally (Fig. 9b). This articular surface is lateral to the base of the basipterygoid processes. The latter suggests that the region of the lateral wall of the braincase formed by the prootic had to direct dorsolaterally for its dorsal region, which bears the articular surfaces for the laterosphenoid, to lie slightly laterally to the corresponding articular surface in the laterosphenoid. There is a short medioventrally directed flange on the rostral two-thirds of the bone (Fig. 9a, b). This flange would partially separate the olfactory tracts from cranial nerves II-IV. Rostrodorsal to the process for the prootic, the medial surface of the laterosphenoid forms a rostrocaudally directed canal.

Discussion

In this section, the significance of some characters from the braincase anatomy of *Proterochampsa*, based on comparison with those of other archosauriforms, is assessed in order to help future systematic studies on proterochampsids and basal archosauriforms in general.

1. The presence of the ridge that ventrally delimits the semilunar depression (Gower and Sennikov, char. 11, modified) is shared by *Proterochampsa* and non archosaurian archosauriforms (e.g., *Proterosuchus*, *Fugosuchus*, *Garjainia*, *Xilousuchus*, *Erythrosuchus*, *Euparkeria*, and *Chanaresuchus*), but is lacking in archosaurs, including the Ornithodira (e.g., *Silesaurus*, the basal sauropodomorph YPM 2192) and the Pseudosuchia (Gower 2002). However, the reduction of the semilunar depression here hypothesized forms an intermediate state between the prominence of this feature in many basal archosauriforms (e.g., *Proterosuchus*, *Erythrosuchus*, and *Euparkeria*) and its absence in Archosauria (Gower and Sennikov 1996).
2. The lack of a clear concavity between the lateral contour of the ventral process of the opisthotic and the

ventral border of the basioccipital basal tubera in caudal view is shared with *Chanaresuchus*, *Doswellia*, and many basal archosaurs (e.g., *Batrachotomus*, *Silesaurus*), but not with some basal archosauriforms (e. g., *Fugusuchus*, *Garjainia*), with the notable exception of the erythrosuchids *Erythrosuchus* and *Shansisuchus*, where the ventral process of the opisthotic is reduced (Gower and Sennikov 1996).

3. The tapered cochlear recess (Gower 2002, char. 9, in part) is a feature *Proterochampsa* shares with non-archosaurian archosauriforms and phytosaurs, but not with pseudosuchians more derived than phytosaurs, according to Gower (2002), or dinosaurs such as *Plateosaurus*, according to published figures of its inner ear endocast.
4. The presence of an elongated cochlear recess (Gower 2002, char. 9, in part) hypothesized in this contribution would indicate a similarity between *Proterochampsa* and many archosaurs, and a difference with *Euparkeria* and other basal archosauriforms (Gower 2002), including some archosaurs close to the base of the Pseudosuchia, such as *Leptosuchus*.
5. The absence of an intertuberal plate (Parrish 1992, char. 10; Gower and Sennikov 1996, char. 2) resembles the condition in *Doswellia*, *Euparkeria*, and the Archosauria, but differs from the condition of *Chanaresuchus* and most other basal archosauriforms, including *Proterosuchus* and *Erythrosuchus* (Gower and Sennikov 1996).
6. A small posttemporal fenestra (Gower and Sennikov 1996, char. 31) is a feature of *Proterochampsa* shared with purported close relatives, such as *Chanaresuchus* (Sereno and Novas 1994), *Cerritosaurus*, and *Doswellia*, as well as dinosaurs (Sereno and Novas 1994), crocodyliforms (Sereno and Novas 1994), and erythrosuchids (Gower and Sennikov 1996), but the size of this fenestra is larger in many other archosauriforms (e.g., *Proterosuchus*, *Leptosuchus*, *Saurosuchus*, and certain pterosaurs, as *Tapejara wellnhoferi* Kellner 1989 and *Pteranodon* Marsh 1876).

Proterochampsids are currently considered as non-archosaurian archosauriforms more closely related to archosaurs than *Euparkeria*, erythrosuchids, and *Proterosuchus* (e.g., Sereno 1991; Brusatte et al. 2008; Dilkes and Sues 2009). Some neurocranial features observed are consistent with that phylogenetic placement. These features include a similarity with non-archosaurian archosauriforms not present in archosaurs (trait 1), similarities with archosaurs and some archosauriforms closely related to *Proterochampsa*, which are lacking in most non-archosaurian archosauriforms (reduction of the semilunar depression and

trait 2), and a similarity with both non-archosaurian archosauriforms and basal pseudosuchians (trait 3). Feature 4, shared by *Proterochampsa* and subgroups of the Archosauria, as well as trait 5, in which purportedly related proterochampsids differ, and feature 6, which is shared with many likely unrelated taxa, must be explained as homoplasies under the mentioned phylogenetic hypothesis (i.e., Sereno 1991; Brusatte et al. 2008; Dilkes and Sues 2009).

Some features are exclusive to *Proterochampsa*. These include the prominence and thickness of V-shaped ridge that rostrolaterally surrounds the basisphenoidal fossa, the medial convexity of the lateral arms of the same ridge, and a ventrolaterally exposed semilunar depression on the parabasisphenoid. The presence of dorsoventrally low distal ends of the paroccipital processes is only observed in *Proterochampsa*, but the condition in *Chanaresuchus* is currently unknown. Some other features are shared with likely unrelated archosauriforms, including: the strong development of the basiptyergoid processes when compared with the parabasisphenoidal basal tubera and caudal development of the distal end of the basiptyergoid processes (also present in some basal crocodylomorphs such as *Sphenosuchus acutus* Haughton 1915); the partially subdivided (eight-shaped) metotic foramen (Fig. 3) (also found in some in dinosaurs; e.g., *Plateosaurus*); the mostly laterally directed basiptyergoid processes, and the rostral limit of the basisphenoidal recess V-shaped (elsewhere known in the proterosuchid *Fugusuchus*).

Some features observed in *Proterochampsa* are shared with *Chanaresuchus*. One of these features is the dorsoventrally thin paroccipital process (this feature is not shared by *Cerritosaurus*, for which the processes have been illustrated as thick in caudal view). The strongly developed caudal sulcus on the paroccipital process represents another character shared by *Proterochampsa* and *Chanaresuchus* (Fig. 3). The widely convex ventral border of the basioccipital basal tubera is a further similarity between *Proterochampsa* and *Chanaresuchus* not found in many other archosauriforms (e. g., *Euparkeria*, *Doswellia*, *Silesaurus*, *Garjainia*, *Fugusuchus*, *Arizonasaurus*, *Saurosuchus*). According to Gower and Weber (1998), the basal tubera are completed with cartilage in many basal archosauriform specimens, so it can be argued that the convexity may just imply further ossification of previously cartilaginous areas because of reaching a late ontogenetic age. However, Yates (2004) has provided evidence that the presence of unossified gaps between the parabasisphenoid and basioccipital (which partially locate between opisthotic and basioccipital) does not represent a juvenile character in dinosaurs.

A currently prevailing, although never tested, hypothesis of relationships of *Proterochampsa* is that *Chanaresuchus*,

Tropidosuchus, and *Cerritosaurus* are more closely related to *Proterochampsa* (Romer 1971) than those basal archosauriforms for which the neurocranium has been described or illustrated in depth (e.g., *Proterosuchus*, *Fugusuchus*, *Erythrosuchus*, *Euparkeria*, *Doswellia*, *Arizonasaurus*, *Silesaurus*). In this regard, *Proterochampsa* differs in many aspects from *Chanaresuchus* (which is the other proterochampsid taxon for which the braincase is well preserved or prepared), aside from the previously discussed unique features of *Proterochampsa*. These features include: the basioccipital basal tubera shorter relative to their thickness in caudal view; the caudal border of the parabasisphenoid V-shaped in ventral view (contrasting with the U-shaped caudal border of *Chanaresuchus* and *Tropidosuchus*); the absence of a prominent intertuberal plate; the presence of a pit representing the basioccipital-basisphenoidal fossa (which is not distinct in *Chanaresuchus*); the cultriform process not laminar (differing from the laminar, much transversely compressed process of *Chanaresuchus*); the notch between the basioccipital basal tubera transversely thinner than each basal tuber (contrasting with a notch much wider than each tuber in *Chanaresuchus*); the presence of a longitudinal sulcus dorsal to the basipterygoid process; and the presence of a deep basisphenoidal recess.

Knowledge of these braincase features may be very important for future phylogenetic analysis directed to elucidating the relationships between proterochampsids.

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