

## THE BRAINCASE OF *CHANARESUCHUS ISCHIGUALASTENSIS* (ARCHOSAURIFORMES) FROM THE LATE TRIASSIC OF ARGENTINA

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**ABSTRACT**—Here, we present information regarding the braincase anatomy of *Chanaresuchus ischigualastensis*, from the Ischigualasto Formation (Carnian) of Argentina. The braincase is very similar to that previously described for *Chanaresuchus bonapartei*, but bears some differences: rostral contour of the basal tubera nearly transversely oriented in ventral view; basal tubera with rounded distal tips in ventral view; paroccipital processes with a slight distal widening in caudal view; sulcus on the caudal surface of each paroccipital process restricted to the proximal two-thirds of the latter; and parabasisphenoidal ventral surface transversely concave. A phylogenetic analysis was performed using exclusively neurocranial characters, including a few new characters, to investigate phylogenetic hypotheses suggested by the neurocranial evidence. The neurocranial data support a sister-group relationship between *Chanaresuchus ischigualastensis* and *C. bonapartei*, on the basis of the presence of an intertuberal plate with a concave border. Our analysis also suggests the monophyly of a group formed by both species of *Chanaresuchus* and *Proterochampsia*. This group was supported by one apomorphy: the paroccipital processes are elongated relative to their height, which did not show homoplasy in our results. Our results show that *Doswellia* is the sister group of the clade formed by these proterochampsids, supporting inclusion of the former within the Proterochampsia, and this clade is recovered as more closely related to archosaurs than to *Euparkeria*.

### INTRODUCTION

The proterochampsids are a group of superficially crocodile-like forms belonging to the Archosauriformes, a diverse group that also includes the Proterosuchidae, Erythrosuchidae, *Euparkeria capensis* Broom, 1913, and the Archosauria, among other taxa (Gauthier, 1986; Gauthier et al., 1989; Sereno, 1991; Parrish, 1993; Brochu, 2001; Ezcurra et al., 2010; Nesbitt, 2011). Numerous hypotheses have been proposed for the relationships of proterochampsids (e.g., Romer, 1956, 1971; Reig, 1959; Walker, 1968). The proterochampsid *Cerritosaurus binsfeldi* Price, 1946, was originally considered to be of uncertain relationships (Price, 1946) and an ornithosuchid by Romer (1956). *Proterochampsia barrionuevoi* Reig, 1959, was first interpreted as an early crocodile (Reig, 1959, 1970; Sill, 1967). An important study by Walker (1968) argued against a relationship with crocodiles, and instead proposed that proterochampsids were related to phytosaurs. Later, Bonaparte (1971) and Romer (1971) gave evidence of a closer relationship between these two species, and gathered them in a group in to which they also placed new material found in the Los Chañares Formation (northwestern Argentina), for which the taxa *Chanaresuchus bonapartei* Romer, 1971, and *Gualosuchus reigi* Romer, 1971, were erected. This group was named Proterochampsia by Bonaparte (1971) and Proterochampsidae by Romer (1971). Of these, only the former name was given a phylogenetic definition (Kischlat, 2000; Nesbitt, 2011). Romer (1971) argued that the features shown by the members of this group indicated a primitive ‘grade,’ which ruled out specific relationships with both crocodiles

and phytosaurs. Ever since, *Cerritosaurus*, *Proterochampsia*, *Chanaresuchus*, and *Gualosuchus* were included within the Proterochampsidae by most scientists (Romer, 1971; Benton and Clark, 1988; Arcucci, 1990; Sereno, 1991). Sereno and Arcucci (1990) and Sereno (1991) found in explicit phylogenetic analyses that the proterochampsids were non-archosaurian archosauriforms, more closely related to the Archosauria than either is to erythrosuchids, *Euparkeria*, or proterosuchids (Fig. 1A). This hypothesis has been supported by other phylogenetic analyses that incorporate more characters and taxa (e.g., Brusatte et al., 2008; Dilkes and Sues, 2009; Ezcurra et al., 2010) (Fig. 1B, C). However, in a recent phylogenetic analysis based on a larger data set, Nesbitt (2011) recovered the Proterochampsidae as less related to the Archosauria than to *Euparkeria*. Dilkes and Sues (2009) recovered *Yonghesuchus sangbiensis* Wu, Liu, and Li, 2001, and *Turfanosuchus dabanensis* Young, 1973, as the only archosauriforms more closely related to Archosauria than the Proterochampsidae, although in more recent phylogenetic studies, Ezcurra et al. (2010) and Nesbitt (2011) recovered *Turfanosuchus* Young, 1973, as a crurotarsan archosaur. The relationships of proterochampsids with *Doswellia kaltenbachi* Weems, 1980, are also uncertain. *Doswellia* was considered to be a close relative of the Proterochampsidae by Benton and Clark (1988) and Dilkes and Sues (2009) (Fig. 1B), but Ezcurra et al. (2010) found *Doswellia* to be more closely related to archosaurs than to proterochampsids (Fig. 1C). The phylogenetic relationships within the Proterochampsidae, including as an independent operational taxonomic unit (OTU) the well-known material of *Proterochampsia* (Sereno, 1991; Dilkes and Sues, 2009; Nesbitt et al., 2009; Ezcurra et al., 2010), have never been explicitly tested by a phylogenetic analysis.

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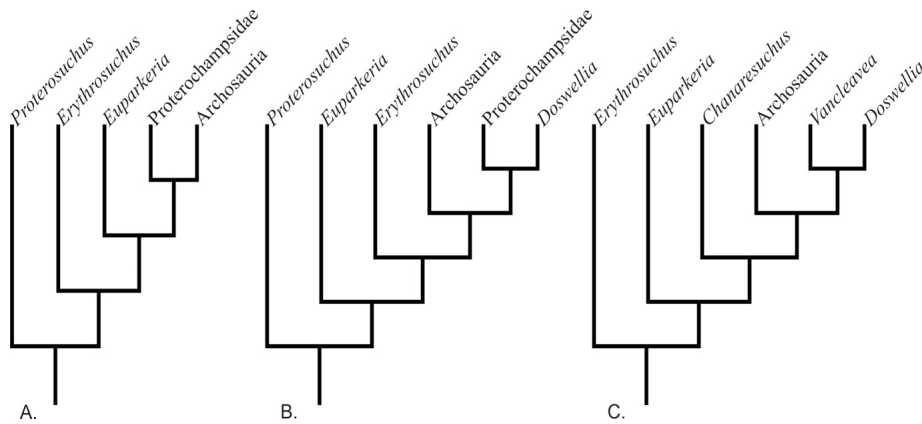


FIGURE 1. Recent phylogenetic hypotheses of proterochampsid relationships with other archosauriforms: **A**, Sereno (1991); **B**, Dilkes and Sues (2009); **C**, Ezcurra et al. (2010).

The remains of a nearly complete proterochampsid skeleton were found in 1994 during exploration of the Ischigualasto Formation by staff from the Instituto y Museo de Ciencias Naturales de the Universidad Nacional de San Juan (Sill et al., 1994). This skeleton was established as the holotype of a new species, *Chanaresuchus ischigualastensis* Trotteyn, Martínez, and Alcober, 2012. This new species was referred to the genus *Chanaresuchus* due to many similarities with *Chanaresuchus bonapartei* (Trotteyn et al., 2012), and because a phylogenetic analysis incorporating characters from the entire skeleton supported a sister-group relationship between *Chanaresuchus ischigualastensis* and *C. bonapartei* (Trotteyn, 2011). Interestingly, this skeleton includes a relatively well-exposed braincase. Literature on proterochampsid braincases is scarce (i.e., Sill, 1967; Romer, 1971; Arcucci, 1990) because the neurocranium is usually found articulated with the rest of the skull and surrounded by the dermatocranium except for the occipital and ventral surfaces (e.g., Sill, 1967; Romer, 1971; Barberena, 1982; Arcucci, 1990). Recently, a disarticulated braincase referable to *Proterochampsia* provided a detailed description of its anatomy and comparison with other archosauriforms, including other proterochampsids where the braincase is only partially exposed (Trotteyn and Haro, 2011). That study was largely descriptive and comparative, and did not include a phylogenetic analysis.

Phylogenetic studies based specifically on archosauriform braincase characters have been produced, especially for basal archosauriforms (Gower and Sennikov, 1996) and pseudosuchians (Gower, 2002), but none of these have included data from proterochampsids. This has been partially rectified with the recent appearance of a phylogenetic study that analyzed a wealth of braincase data from a few proterochampsids in the context of a much more complete sample of both taxa and characters (Nesbitt, 2011). Nevertheless, as the braincase only yields a small number of the characters currently used to infer archosauriform relationships (Nesbitt, 2011), the use of braincase-only data sets is of much lower reliance in determining phylogenetic relationships. Although braincase features were once considered as less prone to convergence than other skeletal characters (e.g., Gow, 1975; Parrish, 1993; Coria and Currie, 2002), it has been shown that this is not true (Gower and Sennikov, 1996; Rauhut, 2007), so that a privileged status for braincase features compared with other skeletal characters is unwarranted.

The main aim of this contribution is to describe the braincase of *Chanaresuchus ischigualastensis* in order to further our knowledge of neurocranial anatomy and variation in the Proterochampsidae and to provide characters for a future phylogenetic analysis of archosauriforms that includes additional anatomical information from *Proterochampsia*, *C. bonapartei*, and *C. ischigualastensis*. A secondary aim of this work is explore

the phylogenetic implications of the braincase data, by way of a braincase character-only phylogenetic study. Our intention in using a braincase-only phylogenetic analysis is not to provide a definitive phylogeny, but to evaluate which phylogenetic relationships are supported by braincase evidence alone.

## MATERIALS AND METHODS

The holotype of *Chanaresuchus ischigualastensis* (PVSJ 567) is a nearly complete skeleton that includes a skull (Fig. 2A, B). The braincase of this specimen exposes the following bones: exoccipital, basioccipital, opisthotic, prootic, parabasisphenoid, and basioccipital. Only the supraoccipital is lacking, and the laterosphenoid is not exposed (Fig. 2A). The braincase is better exposed than in other proterochampsid material because its dorsal part has been preserved largely caudal to the dermatocranium, and not hidden by the supraoccipital (Fig. 2A). Individual bones are not severely deformed; however, many surface details are poorly preserved and some expected neurocranial foramina were impossible to identify. The preserved braincase elements are articulated with the exception of the right braincase wall, which is slightly displaced caudolaterally relative to the base of the braincase (Fig. 2B). The occipital condyle is caudally covered by an unidentified fragment of bone (Figs. 3–5), which likely does not correspond to part of the condyle. Most of the lateral surface of the parabasisphenoid is hidden by matrix and the quadrate and pterygoid. The cultriform process is completely hidden by the dermal skull roof dorsally and the pterygoids ventrally (Fig. 2A, B), and laterally by the artificial contact between skull roof and pterygoids produced by post-mortem flattening of the skull.

The material used for comparison and data matrix scorings is listed in Appendix 1. Anatomical nomenclature follows usage by Gower (2002), except that for the pneumatic fossae, which follows usage by Gower and Sennikov (1996). Conventions regarding directions and planes are those described in Weishampel et al. (2004). The orientation of the braincase relative to the rest of the skull is difficult to assess due to disarticulation in the dorsal region, as the paroccipital processes are disarticulated from the parietals. Recently, it was indicated that the parabasisphenoid is verticalized in *Tropidosuchus romeri* Arcucci, 1990, and *Chanaresuchus* (Nesbitt, 2011). Judging from the alignment of and tight contact between the parabasisphenoid and basioccipital in the holotype of *C. bonapartei* (UNLR 07), this would suggest that the entire ventral part of the braincase was verticalized. Thus, it may be hypothesized that the same orientation was present in *Chanaresuchus ischigualastensis*. However, in the interest of simplicity, the orientation of the longest axis of the basis cranii is assumed to be horizontal. Here,

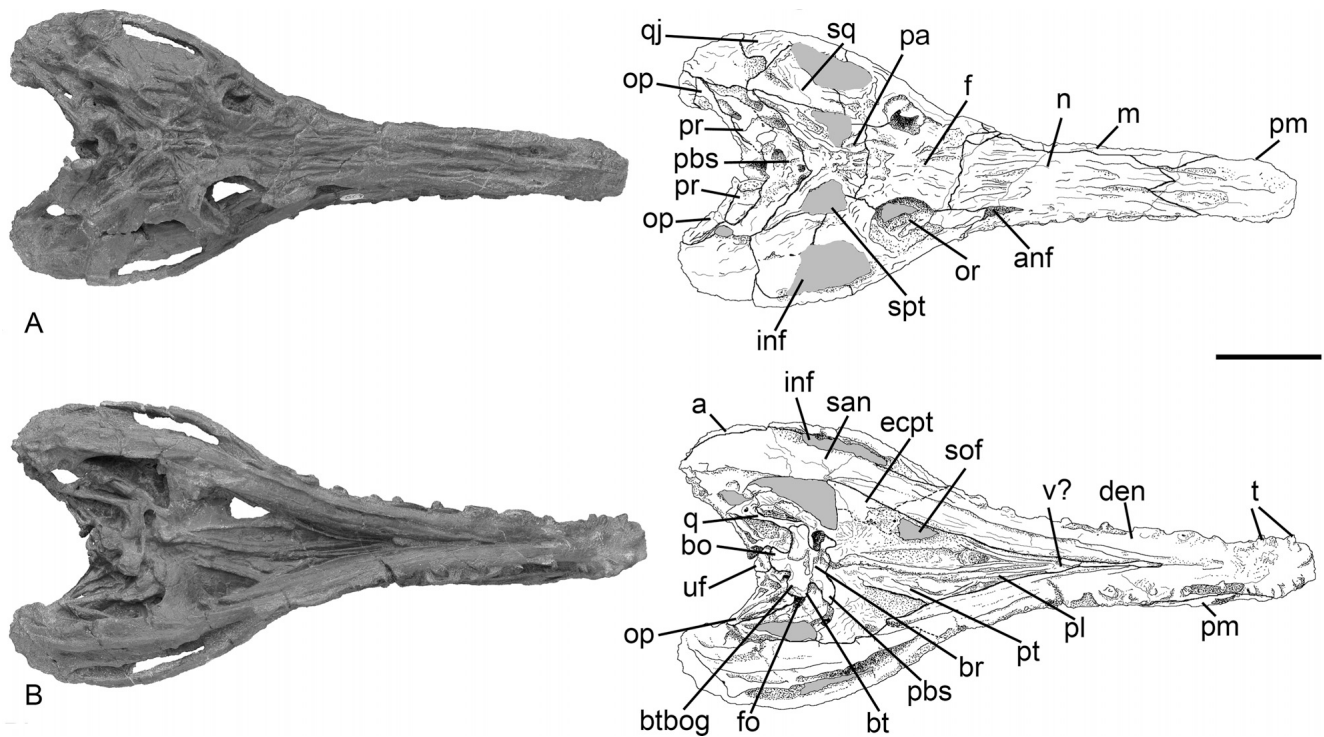


FIGURE 2. Skull of *Chanaresuchus ischigualastensis* (holotype: PVSJ 567): **A**, dorsal view; **B**, ventral view. Photographs to the left, schematic drawings to the right. Gray areas in the schematic drawings represent holes and/or fenestrae. Scale bar equals 5 cm.

we consider *Proterochampsia*, *C. ischigualastensis*, *C. bonapartei*, *Cerritosaurus*, and *Tropidosuchus* to be proterochampsids, following pre-cladistic hypotheses of relationships by Bonaparte (1971), Romer (1971), and Arcucci (1990). We still use the taxon Proterochampsidae in this work in addition to Proterochampsia, because even when not phylogenetically defined, Proterochampsidae permits us to refer to proterochampsians to the exclusion of *Doswellia* (and taxa more closely related to *Doswellia* than to *Proterochampsia*), following usage in previous works (e.g., Benton and Clark, 1988; Dilkes and Sues, 2009). The phylogenetic analysis was performed using TNT, version 1.1 (Goloboff et al., 2008a, 2008b). Searches were accomplished using the ‘traditional search’ option, with 1000 random addition sequences, and TBR (tree bisection-reconnection) as the branch-swapping algorithm.

**Institutional Abbreviations**—**BPI**, Bernard Price Institute for Palaeontological Research, Johannesburg; **CAMZM**, University Museum of Zoology, Cambridge, U.K.; **CPEZ**, Coleção Municipal, São Pedro do Sul; **GMB**, Geological Institute, Beijing; **ISI**, Geology Museum, Indian Statistical Institute, Calcutta; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **MCP**, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **MCZD**, University of Aberdeen Zoology Department, Aberdeen; **MSM**, Mesa Southwest Museum, Mesa; **NHMUK**, Natural History Museum, London; **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; **QG**, Queen Victoria Museum, Salisbury; **SAM**, Iziko South African Museum, Cape Town; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart; **TTUP**, Texas Tech University Paleontology Collections, Lubbock; **UCMP**, University of California Museum of Paleontology, Berkeley; **UNLR**, Museo

de Ciencias Naturales de la Universidad Nacional de La Rioja, La Rioja; **USNM**, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C.; **ZPAL**, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw.

**Anatomical Abbreviations**—**a**, angular; **anf**, antorbital fenestra; **ap**, alar process; **bbf**, basioccipital-basisphenoid fossa; **bo**, basioccipital; **bof**, caudolateral fossa on the basioccipital; **bpt**, basiptyergoid process; **br**, basisphenoidal recess; **bt**, basal tuber; **btbo**, basioccipital part of the basal tuber; **btbog**, groove between basioccipital parts of the basal tubera; **btbs**, parabasisphenoidal part of the basal tuber; **cbps**, caudal border of the parabasisphenoid; **cint**, crista interfenestralis; **clp**, clinoid process; **clpr**, caudolateral process of the prootic; **cpr**, crista prootica; **cspr**, caudal sulcus on the paroccipital process; **cu**, cultriform process; **cvr**, caudal and ventral ridges on the paroccipital process located between sulci on the caudal and ventral surfaces of the processes; **de**, dorsal prominence; **den**, dentary; **ds**, dorsum sellae; **ecpt**, ectopterygoid; **eo**, exoccipital; **f**, frontal; **fdfo**, fossa dorsal to fenestra ovalis; **fm**, foramen magnum; **fo**, fenestra ovalis; **inf**, infratemporal fenestra; **lw**, lateral wall of the pituitary fossa; **m**, maxilla; **mab**, border of muscular attachment area on prootic; **mf**, metotic foramen; **n**, nasal; **oc**, occipital condyle; **op**, opisthotic; **or**, orbit; **pa**, parietal; **pbs**, parabasisphenoid; **pif**, pituitary fossa; **pl**, palatine; **pm**, premaxilla; **popr**, paroccipital process; **pr**, prootic; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **rs**, rostral surface of the paroccipital processes; **san**, surangular; **seb**, suture between exoccipital and basioccipital; **sof**, suborbital fenestra; **spt**, supratemporal fenestra; **sq**, squamosal; **stgr**, stapedial groove; **t**, teeth; **uf**, indeterminate fragment; **v**, vomer; **Vn**, trigeminal nerve notch; **vpf**, ventral paired foramina on parabasisphenoid, probably for the cerebral internal carotid artery; **vsbt**, ventral sulcus on basal tuber; **vsbo**, ventral sulcus on paroccipital process leading to the metotic foramen.

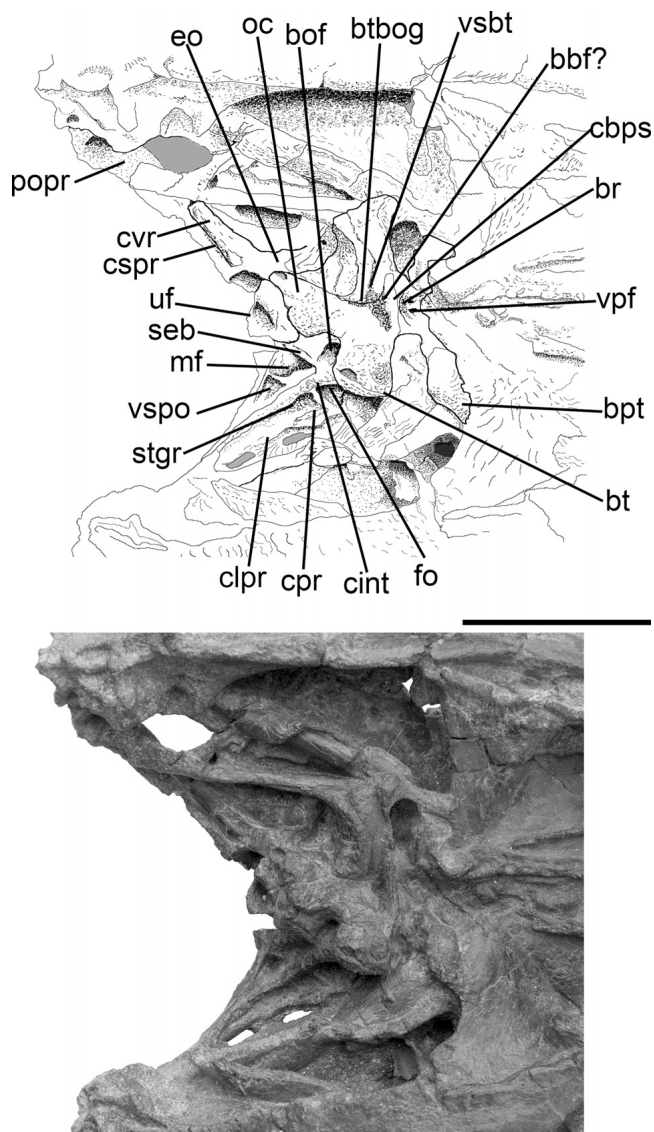


FIGURE 3. Ventral view of the braincase of *Chanaresuchus ischigualastensis* (holotype: PVSJ 567). Photograph above, schematic drawing below. Gray areas in the schematic drawing represent holes and/or fenestrae. Scale bar equals 3 cm.

### DESCRIPTION

The braincase is relatively short (Fig. 3), being 1.1 times wider across the basal tubera than it is long from the base of the basiptyergoid processes to the occipital condyle tip. The relative shortness of the braincase regarding this measurement differs from the lower ratio in *Chanaresuchus bonapartei* (0.91), and the even lower ratio of *Proterochampsa* (0.7; Trotteyn and Haro, 2011). The braincase lateral walls apparently faced slightly ventrally (Fig. 3) in addition to laterally, although this might represent post-mortem deformation. There is no evidence of pneumatization.

### Basioccipital

The basioccipital is complete and forms most of the occipital condyle. The condyle is located rostral to the craniomandibular articulation (Dilkes and Sues, 2009:character 27) (Fig. 2A, B).

The condyle is caudally capped by an unidentified bony structure with many cavities (Figs. 2B, 3). The occipital condyle seems to be wider than high, as in *Proterochampsa* (Sill, 1967:fig. 3; Trotteyn and Haro, 2011) and the *C. bonapartei* holotype (UNLR 07). The basioccipital caudal to the basal tubera is slightly shorter than the transverse width of the occipital condyle (Fig. 3), as in *C. bonapartei* (Fig. 6; Romer, 1971:fig. 3; UNLR 07) and *Tropidosuchus* (Arcucci, 1990:fig. 3), and proportionally more elongated than in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011:fig. 2) or *Archeopelta arborensis* Desojo, Ezcurra, and Schultz, 2011 (Desojo et al., 2011:fig. 5). The occipital condyle and basal tubera are laterally separated by a very deep, conical fossa (Figs. 3–5). We cannot identify any connection between this fossa and the portion of the metotic foramen surrounded by the exoccipital and ventral process of the opisthotic (Figs. 3, 4), contrasting with the condition in *Proterochampsa*, in which a similarly placed feature represents the ventral lobe of the eight-shaped metotic foramen (Trotteyn and Haro, 2011). The fossa is dorsally bordered by a raised ridge that might represent the suture between the basioccipital and exoccipital-opisthotic, if the latter is not just the product of breakage (Figs. 3, 4); this ridge is more prominent than in *C. bonapartei* (UNLR 07). We cannot discern the basioccipital-parabasisphenoid suture at the distal end of each basal tuber (Fig. 3), contrasting with the condition in *C. bonapartei* (Fig. 6; pers. observ.). The basioccipital contribution to each basal tuber does not seem to be blade-like (Nesbitt, 2011:character 106). The shape of the ventrolateral contour of the basioccipital contribution to the tubera cannot be determined because the parabasisphenoid-basioccipital suture cannot be discerned at the tubera tips. A slight convexity is present on the distal extremity of the left tuber, but not the right one, indicating that at least one of the tubera was deformed (Fig. 5). The tubera are longer than wide at midlength in caudal view (Fig. 5), resembling the condition in *C. bonapartei* (UNLR 07), but differing from the proportionally wider tubera of *Proterochampsa* (PVSJ 77). The caudally prominent border on the distal ends of the basal tubera in *Proterochampsa* (PVSJ 77) is absent in PVSJ 567 and *C. bonapartei* (UNLR 07). The basal tubera are ventrally and laterally directed (Fig. 5), as in *C. bonapartei* (UNLR 07). The basioccipital contribution to the basal tubera in PVSJ 567 seems to differ from that in *Erythrosuchus* Broom, 1905, and *Euparkeria*, in which they are relatively more ventrally orientated in caudal view (Gower, 1997:figs. 2B, D, 11A; Gower and Weber, 1998:fig. 4). In ventral view, the tubera are rounded and do not taper laterally (Fig. 3), contrasting with the triangular tubera of the Chanarean proterochampsids *C. bonapartei* (Fig. 6; UNLR 07) and *Tropidosuchus* (Arcucci, 1990:fig. 3), and the basal dinosauriforms *Marasuchus lilloensis* (Romer, 1972a) (Bonaparte, 1975:fig. 3; Sereno and Arcucci, 1994:fig. 2) and *Lewisuchus admixtus* Romer, 1972b (UNLR 01). A mediolaterally directed sulcus on the basal tubera ventral surface (Fig. 3) seems to represent the original contact with the caudal border of the parabasisphenoid, suggesting that the border was displaced by distortion. The rostral parts of the basal tubera are separated by a ventrally facing, deep, and wide ‘basioccipital-basisphenoid fossa’ (sensu Gower and Sennikov, 1996) (Fig. 3). In the *C. bonapartei* holotype, this fossa is also wide, but much shallower (Fig. 6; UNLR 07). The greater depth of the fossa in *Chanaresuchus ischigualastensis* is probably due to the ventral deflection of the parabasisphenoid caudal border. No pseudolagenar recess (sensu Gower and Sennikov, 1996) is present on the basal tubera (Fig. 3), or between the tubera and the opisthotic (Gower and Sennikov, 1996:character 14), as in *C. bonapartei* (Fig. 6; UNLR 07) and some basal dinosauriforms including *Marasuchus* Sereno and Arcucci, 1994, *Lewisuchus*, and *Silesaurus opolensis* Dzik, 2003 (Romer, 1972a; Bonaparte, 1975:fig. 3; Sereno and Arcucci, 1994:fig. 2; Dzik, 2003:fig 7D; UNLR 01), and differing from many other archosauriform braincases (e.g., *Euparkeria*

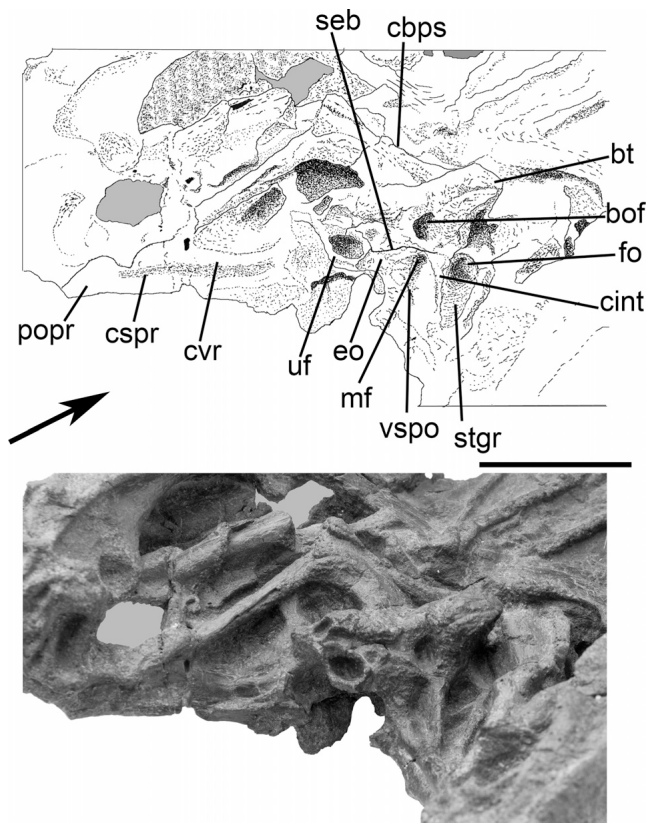


FIGURE 4. Left caudoventrolateral view of the braincase of *Chanaresuchus ischigualastensis* (holotype: PVSJ 567). Photograph above, schematic drawing below. Gray areas in the schematic drawing represent holes and/or fenestrae. Scale bar equals 3 cm.

and *Arizonasaurus* Welles, 1947; Gower and Sennikov, 1996; Gower and Nesbitt, 2006). The lack of this recess may be related to the non-bilobate shape of the tubera in ventral view (not caudal view, differing from the character noted for *Xilousuchus sapingensis* Wu, 1981, by Gower and Sennikov, 1996) (Fig. 3), as in *Tropidosuchus* (Arcucci, 1990:fig. 3) and the above-mentioned taxa that lack pseudolagenar recesses.

In caudal view, the basal tubera are separated by a wide ‘V’-shaped notch (Fig. 5), as in *C. bonapartei* (UNLR 07), which differs from the narrow rounded notch of *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011) and the wider ‘U’-shaped notch of *Archeopelta* (Desojo et al., 2011:fig. 4A–D). This notch is as deep as in *C. bonapartei* (UNLR 07) and deeper than in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011). The notch depth seems to correlate with tubera length in caudal view among these proterochampsids. A sagittally oriented groove separates both tubera along the ventral surface, extending from the basioccipital-basisphenoid fossa to the level of the caudal contour of the tubera—this groove should not be confused with a breakage line that continues caudally (Fig. 3). The sulcus extension is shared with *C. bonapartei* (UNLR 07; Fig. 6), but not with *Proterochampsa* (PVSJ 77), in which the sulcus does not reach the caudal border of the tubera in ventral view (Trotteyn and Haro, 2011:fig. 2), in relation to the prominence of the caudoventral border of the tubera. No basioccipital recess is found on the ventral surface of the basioccipital between the tubera, as in other basal archosauriforms, but unlike crocodylomorphs (Nesbitt, 2011:character 107).

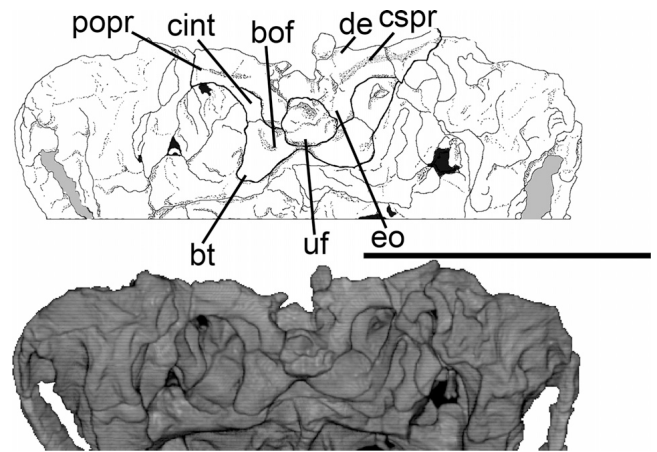


FIGURE 5. Caudal view of the braincase of *Chanaresuchus ischigualastensis* (holotype: PVSJ 567). Computerized tomographic scan picture above, schematic drawing below. Gray areas in the schematic drawing represent holes and/or fenestrae. Scale bar equals 5 cm.

### Exoccipital

The exoccipitals are complete (Figs. 3–5). The exoccipital-occipital sutures are not clearly marked (Figs. 4, 5), as also occurs in many other basal archosauriforms (Gower and Sennikov, 1996; Dilkes and Sues, 2009:character 22). The exoccipitals form a part of the occipital condyle, although the proportion cannot be determined. The exoccipitals are strut-like in caudal view ventral to the paroccipital process and dorsal to the occipital condyle, and form the lateral borders of the foramen magnum (Fig. 5). This resembles the condition in *Chanaresuchus bonapartei* (UNLR 07) and *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011:fig. 3), but differs from the latter in the gracility of the strut (Trotteyn and Haro, 2011:fig. 3). The exoccipital strut widens transversely and rostrocaudally towards its articulation with the basioccipital (Fig. 5), unlike in *Proterochampsa* (PVSJ 77), in which only the rostrocaudal widening is present (Trotteyn and Haro, 2011:fig. 3). The basioccipital articular surface is rostrocaudally longer than wide, as in most basal archosauriforms (e.g., Gower and Sennikov, 1996), and tapers rostrally. On the endocranial surface, the left exoccipital-basioccipital suture reaches a more medial position rostrally. Thus, the exoccipitals did not exclude the basioccipital from the ventral border of the foramen magnum, but they may have met rostrally (Gower and Sennikov, 1996:character 17). However, this is difficult to ascertain as the ventral surface of the endocranial cavity is poorly preserved. The exoccipital forms the caudoventral border of the metotic foramen (Fig. 4). The exoccipital lateral surface is not as convex as in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011). We were unable to discover foramina for the exit of the cranial nerve XII in the external surface (Figs. 4–5); they might have been very small and/or badly preserved. The same condition occurs in *C. bonapartei* (Romer, 1971). A large subvertical ridge on the lateral side of the exoccipital, as seen in some pseudosuchians (e.g., *Batrachotomus kupferzellensis* and *Stagonolepis robinsoni* Agassiz, 1844; Gower, 2002; Gower and Walker, 2002:fig. 6), is absent (Gower, 2002:character 2), as in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011:fig. 8) and *C. bonapartei* (UNLR 07). A slight change in slope of the lateral surface of the bone, of the kind observed in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011) cannot be ascertained in either *C. ischigualastensis* or *C. bonapartei* (UNLR 07).

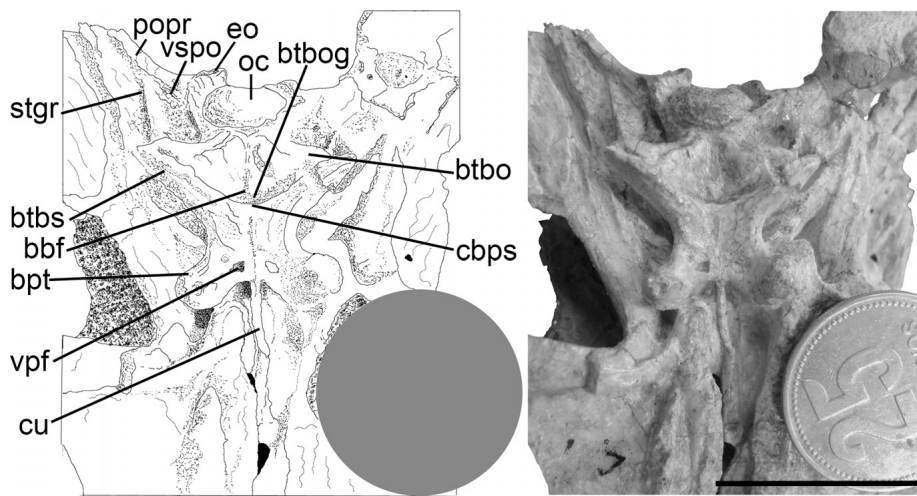


FIGURE 6. Ventral view of the braincase of the holotype of *C. bonapartei* (UNLR 07). Photograph to the right, schematic drawing to the left. Gray areas in the schematic drawing represent holes and/or fenestrae. Scale bar equals 2.4 cm.

### Opisthotic

The opisthotics are complete, but not fully exposed. It is likely that they did not exclude the supraoccipital from the foramen magnum (Fig. 5). The paroccipital processes appear to be laterally directed, but this is difficult to assess due to disarticulation. The processes are elongate and dorsoventrally narrow (Figs. 5, 7), as in *Chanaresuchus bonapartei* (UNLR 07) and *Proterochampsa* (Sill, 1967:fig. 3; PVSJ 77), and dorsoventrally narrower than in non-proterochampsids (e.g., *Euparkeria*, *Doswellia*; Ewer, 1965:fig. 2B; Dilkes and Sues, 2009:fig. 1C) and *Cerritosaurus* (Price, 1946:fig. 3). The processes are slightly expanded dorsoventrally distally, as in another *Chanaresuchus* specimen (PVL 4575), but differing from the condition in most proterochampsids (e.g., the *Chanaresuchus bonapartei* holotype, *Proterochampsa* [PVSJ 77], *Tropidosuchus*, and *Cerritosaurus*; Price, 1946:fig. 3; Arcucci, 1990; Trotteyn and Haro, 2011; UNLR 07). The expansion is less than in some rauisuchids (e.g., *Postosuchus kirkpatricki* Chatterjee, 1985; Nesbitt, 2011:character 108). The paroccipital processes gradually taper at the tip in the horizontal plane. The vertical expansion coupled with horizontal narrowing results in a laminar distal end, unlike the process in *Proterochampsa* (PVSJ 77), which has a rostrocaudally thicker distal end. In dorsal view, the paroccipital processes are caudally and laterally directed and together form an angle of approximately 90°. This angle can be inferred despite disarticulation of the paroccipital processes due to the angle formed along the caudal border of the parietals (Fig. 2A). The 90° angle between the processes is shared with *C. bonapartei* (UNLR 07) and *Tropidosuchus* (Arcucci, 1990:fig. 2), but not with *Cerritosaurus*, *Proterochampsa* (PVSJ 77), and *Doswellia*, which all exhibit a wider angle (Price, 1946:fig. 2; Dilkes and Sues, 2009:fig. 1B; pers. observ.). Near the base of the right paroccipital process, a dorsally placed pointed eminence seems to indicate the lateral extent of the supraoccipital articulation (Fig. 5), but the dorsomedial surface of the bone is not well preserved (Figs. 7, 8).

The paroccipital processes are approximately triangular in cross-section near to their bases, differing from the approximately irregular hexagonal cross-sections found in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011:fig. 8). The rostral surface of the paroccipital processes, which is partially exposed also dorsally and laterally, is flat at the distal end of the process, and slightly convex dorsoventrally at the proximal end (Fig. 9). This unique surface differs from the condition in *Proterochampsa* (PVSJ 77), in which a flat surface facing dorsally and laterally is separated by an edge from another flat surface that faces ros-

trally and laterally (Trotteyn and Haro, 2011:fig. 8). The caudal surface of the process has a sulcus that extends along its proximal two-thirds (Fig. 5), which is shorter than that in *C. bonapartei* (UNLR 07) and *Proterochampsa* (Sill, 1967:fig. 3; Trotteyn and Haro, 2011). This sulcus is not present in *Doswellia* (Weems, 1980: pl. 2A; Dilkes and Sues, 2009:fig. 1C) or *Euparkeria* (SAM PK-K5867 and SAM PK-K7696). The sulcus is bounded by two low rounded ridges, of which the ventral one separates the caudal and ventral surfaces of the process (Figs. 3, 4). The ridge ventrally limiting the sulcus is straight and vanishes distally, contrasting with the condition in *Proterochampsa*, in which it is longer and twists dorsally at the distal end (Sill, 1967:fig. 3; Trotteyn and Haro, 2011). The ventral contour of the proximal part of the paroccipital processes is located dorsal to the ventral border of the foramen magnum (Fig. 5), as in *Chanaresuchus bonapartei* (UNLR 07) and the *Proterochampsa* specimen PVSJ 77 (Trotteyn and Haro, 2011); this contrasts with the ventral contour of the processes lower than the foramen magnum in *Erythrosuchus* (Gower, 1997:fig. 1B), and probably in another *Proterochampsa* specimen, MCZ 3408 (contra Sill, 1967:fig. 3; D. Dilkes, pers. comm.), and *Doswellia* (Weems, 1980:pl. 2A; Dilkes and Sues, 2009:fig. 1C; D. Dilkes, pers. comm.). The contact between the paroccipital process and the parietals immediately lateral to the supraoccipital cannot be ascertained due to disarticulation (Fig. 2A). On the ventral surface of the paroccipital process, two sulci extend along the process long axis, separated by a ridge (Fig. 3), as in *C. bonapartei* (Fig. 6; UNLR 07) and *Proterochampsa* (PVSJ 77). The length of the caudal sulcus is much shorter than the rostral one (Fig. 3), as in *C. bonapartei* (Fig. 6; UNLR 07), and differing from the relatively longer sulcus present in *Proterochampsa* (PVSJ 77). No separate opening or sulcus immediately dorsal to the metotic foramen was preserved, thereby differing from *Batrachotomus* (Gower, 2002). The ridge that separates the sulci continues medially as the crista interfenestralis, a well-developed laminar structure that is disposed obliquely between the sagittal and transverse planes (Figs. 3, 4). The crista interfenestralis can be observed in caudal view (Figs. 4, 5), as in most basal archosauriforms (Gower and Sennikov, 1996:character 5), but differing from *Erythrosuchus*, in which the crista is much smaller and hidden in caudal view by the exoccipital (Gower and Sennikov, 1996). It can be also seen in ventral view (Fig. 3). The crista interfenestralis reaches the base of the basal tubera, separating the metotic foramen from the fenestra ovalis (Figs. 3, 4). We cannot discern sutures between the ventral ramus of the opisthotic and the basioccipital or parabasisphenoid, nor can we determine if it articulated with



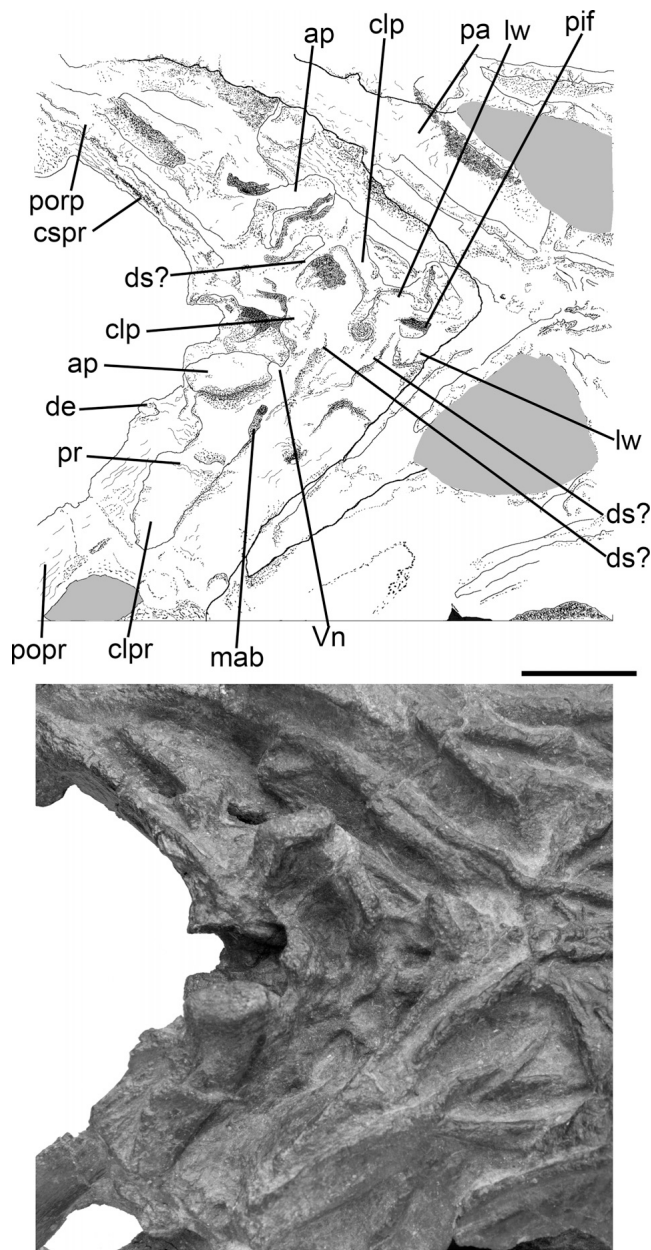


FIGURE 7. Dorsal view of the braincase of *Chanaresuchus ischigualastensis* (holotype: PVSJ 567). Photograph above, schematic drawing below. Gray areas in the schematic drawing represent depressions. Scale bar equals 1.5 cm.

the prootic as in crocodylomorphs (Gower, 2002). A distinctive thickening of the ventral end of the opisthotic, of the kind seen in *Erythrosuchus* (Gower, 1997:fig. 3), is probably absent (Fig. 3). The opisthotic does not contribute to a cochlear prominence (Figs. 3, 4). There is no unequivocal evidence for the perilymphatic foramen (Figs. 3, 4) (Gower, 2002:character 21). The metotic foramen is obliquely elongate, in both caudal and dorsal directions, and is very thin (Figs. 3, 4). The rostral groove on the ventral surface of the paroccipital process, the stapedia groove, is rostrally limited by the crista prootica. Medially this groove leads to the fenestra ovalis (Figs. 3, 4). The dorsal border of the fenestra is strongly laterally projected (Figs. 3, 4). It is possible that the raised border is an artefact related to a similarly

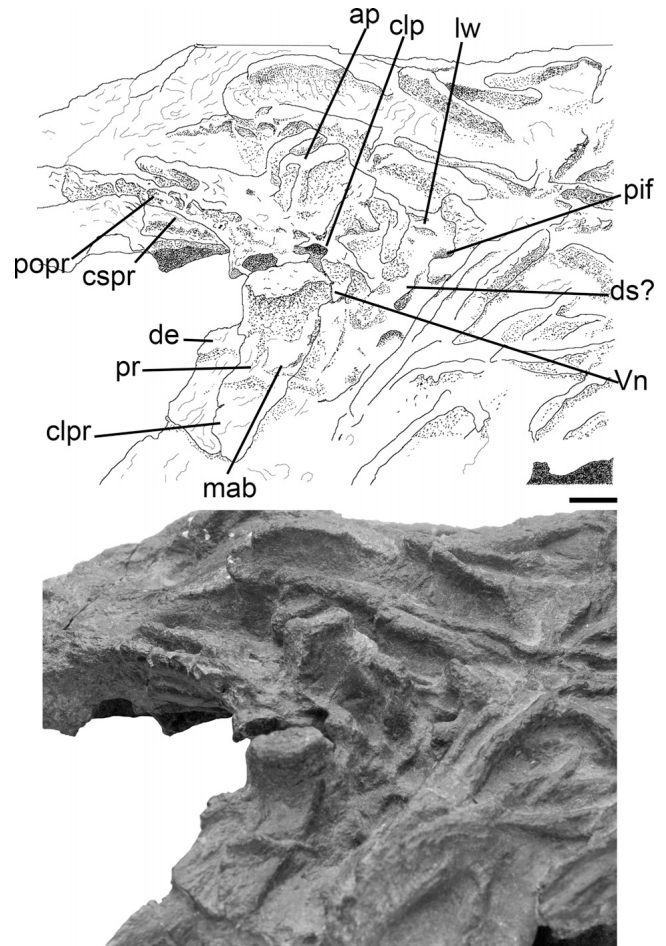


FIGURE 8. Right dorsolateral view of the braincase of *Chanaresuchus ischigualastensis* (holotype: PVSJ 567). Photograph above, schematic drawing below. Gray areas in the schematic drawing represent holes and/or fenestrae. Scale bar equals 1.5 cm.

oriented breakage line that subdivides the ventral sulcus of the paroccipital process leading to the metotic foramen. The inner ear cavity, and its medial wall, cannot be discerned (Figs. 7, 8).

### Prootic

Most of the prootic is preserved (Figs. 7, 8). In lateral view, the dorsal border of the prootic (contacting the supraoccipital in its rostral part) is concave (Figs. 7, 8), as in many basal archosauriforms (e.g., *Fugosuchus* Cheng, 1980, and *Erythrosuchus*; Gower, 1997:fig. 3; Gower and Sennikov, 1996:figs. 4C, 6B). The prootic bears a somewhat laminar caudolateral process above the fenestra ovalis that overlaps the paroccipital process of the opisthotic (Figs. 7, 8). It thins distally, but the distal end is either blunt or broken (Figs. 7, 8), and its ventral border likely forms the crista prootica (Fig. 3). It overlaps less than one-half the length of the paroccipital process, as in *Proterochampsia* (PVSJ 77; Trotteyn and Haro, 2011). Although its articulation with the opisthotic is slightly displaced, it seems to have contacted the opisthotic broadly, in comparison with the condition in *Sphenosuchus acutus* Haughton, 1915 (Nesbitt, 2011:fig. 23A). Ventral to this process, the prootic forms the rostral border of the fenestra ovalis, which is located at the level of the midpoint of the rostrocaudal extension of the basal tubera (Figs. 3, 4). A suture between the prootic and the bones of the basis cranii appears to

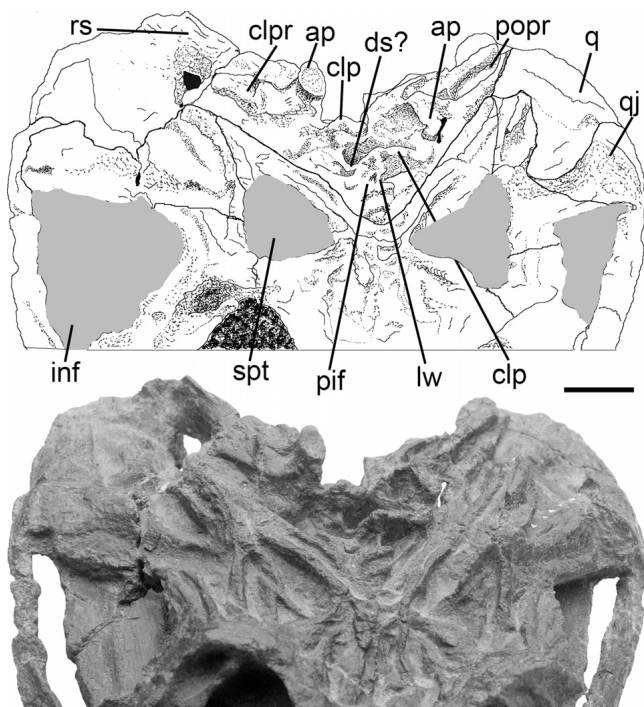


FIGURE 9. Rostrodorsal view of the braincase of *Chanaresuchus ichigualastensis* (holotype: PVSJ 567). Photograph above, schematic drawing below. Gray areas in the schematic drawing represent holes and/or fenestrae. Scale bar equals 2 cm.

extend rostrally from a point slightly ventral to the fenestra. The path of the crista prootica cannot be ascertained because it is not sufficiently exposed. In lateral view, the prootic forms a large part of the braincase wall (Figs. 7, 8). Rostrally, the prootic has a notch for the exit of the trigeminal nerve (V) and probably the middle cerebral vein (Figs. 7, 8). The notch is undivided, except for a small convexity near the dorsal extremity of its border, which may be due to suboptimal preservation. Dorsal to the notch, the lateral wall of the endocranial cavity is formed by a transversely thick alar process (sensu Oelrich, 1956; Figs. 7, 8). This process is quadrangular in lateral view (Fig. 8). The process possesses an elliptical surface that abutted the laterosphenoid (Fig. 7). This well-developed articular facet is a strong argument for inferring the presence of a laterosphenoid. The lateral surface of the prootic caudal and dorsal to the trigeminal nerve notch, which encompasses both the caudolateral process and the caudal part of the prootic contribution to the lateral wall of the endocranial cavity, is concave and separated from the rest of the prootic lateral surface by a dorsally concave ridge (Fig. 8). This fossa seems to be homologous to a proportionally smaller depression in *Archeopelta* (Desojo et al., 2011:fig. 7A, B). The ridge ventrally limiting the fossa extends from the ventral border of the caudolateral process to the dorsal part of the notch of the trigeminal nerve (Fig. 8). This ridge is also present in *Euparkeria* (SAM PK-K7696), the dinosaur *Coelophysis rhodesiensis* (Raath, 1969) (Raath, 1985:fig. 1A), and in non-archosauriform diapsids (e.g., *Ctenosaura pectinata* Wiegmann, 1834; Oelrich, 1956). In *Ctenosaura*, the concave area ventral to the ridge represents the origin of the *M. adductor mandibulae externus profundus* (Oelrich, 1956). Ventral to the trigeminal notch, the clinoid processes are laminar and much thinner than the alar processes (Figs. 7–9). The lamina of the clinoid process is located on a plane perpendicular to the alar processes, as seen in rostradorsal

view (Fig. 9). A ridge for the *M. protractor pterygoideus* is absent from the external surface of the clinoid process (Fig. 9), as also occurs in many archosaurs (e.g., *Silesaurus* and *Arizonasaurus*; Dzik, 2003:fig. 7A, E; Gower and Nesbitt, 2006; Gower and Sennikov, 1996) and contrasting with the condition present in some basal archosauriforms (e.g., *Garjainia* Ochev, 1958, and *Fugusuchus*; Gower and Sennikov, 1996:character 6). The exit for the facial nerve (VII) is not exposed or preserved on the lateral surface of the prootic, but a foramen on the medial surface of the left prootic, slightly caudal and ventral to the trigeminal nerve notch, probably represents the nerve exit. We cannot recognize the abducens nerve (VI) foramen nor the retractor bulbi musculature attachment fossa on the rostral surface of ventral part of the either prootic (Fig. 9); similarly, we cannot determine the presence or absence of a midline contact between the prootics (Fig. 7). The medial surface of the dorsal portion of the prootic endocranial wall appears to lack an auricular (flocular) recess (Fig. 8), which suggests it was either located entirely on the supraoccipital, thereby differing from the condition present in many other archosauriforms (e.g., *Erythrosuchus* and *Arizonasaurus*; Gower, 1997; Gower and Nesbitt, 2006:fig. 5), or that the flocular fossa was not clearly marked, as in Recent crocodylians (Gower, 2002). A small aperture near the dorsal border of the left prootic resembles a similar foramen in the medial side of the prootic of *Erythrosuchus*, which was labeled as the rostral semicircular canal by Gower (1997:figs. 8, 10). In *C. ichigualastensis*, the inner ear cavity seems to be collapsed on the right side of the braincase and it is not exposed on the left. The medial surface of the alar process has a rostroventrally directed short and shallow sulcus that reaches the trigeminal nerve notch and probably accommodated the middle cerebral vein.

### Parabasisphenoid

The parabasisphenoid appears to be complete, but only its ventral surface caudal to the cultriform process and part of the dorsal surface closed to the hypophyseal fossa are exposed (Figs. 2A, B, 3, 7). The parabasisphenoid long axis is aligned with that of the basioccipital. The parabasisphenoid is proportionally wide, with a ratio between its rostrocaudal length measured from the rostral-most point of the base of the basipterygoid processes to the caudal tip of the basal tubera and width across the basal tubera of 0.35. In ventral view (Fig. 3), the parabasisphenoid is relatively more gracile than in *Proterochampsia* (PVSJ 77; Trotteyn and Haro, 2011:fig. 2), and resembles in robustness its homologue in *C. bonapartei* (Romer, 1971:fig. 3; UNLR 07; Fig. 6); this is due, at least in part, to the thinner basipterygoid processes, and the likely more vertical orientation of the plane of each parabasisphenoid contribution to the basal tubera (see below) (Trotteyn and Haro, 2011). The parabasisphenoid is constricted between the basipterygoid processes and its caudal border (Fig. 3). The length of the parabasisphenoid main body (excluding the cultriform process, basipterygoid processes, and basal tubera contributions), relative to its transverse width (at the constriction between the basipterygoid processes and basal tubera), is proportionally much shorter than in the *C. bonapartei* holotype (Figs. 3, 6) (Romer, 1971:fig. 3; UNLR 07). We hypothesize this to be produced by the ventral deflection of the caudal border of the parabasisphenoid in PVSJ 567. Even accounting for the lack of a clear separation between the parabasisphenoid and basioccipital within at the basal tubera, the extent of the contribution of the parabasisphenoid to the basal tubera (cristae ventrolaterales sensu Dilkes and Sues, 2009) can be approximately inferred. The caudal border of the parabasisphenoid, distinguishable medial to the tubera, contacts only the rostral-most region of the tubera in ventral view, and thus it appears that the parabasisphenoid only formed a thin, laminar rostral part of the tubera (Fig. 3), contrasting with the condition in *C. bonapartei*, *Proterochampsia*, and *Doswellia*, in



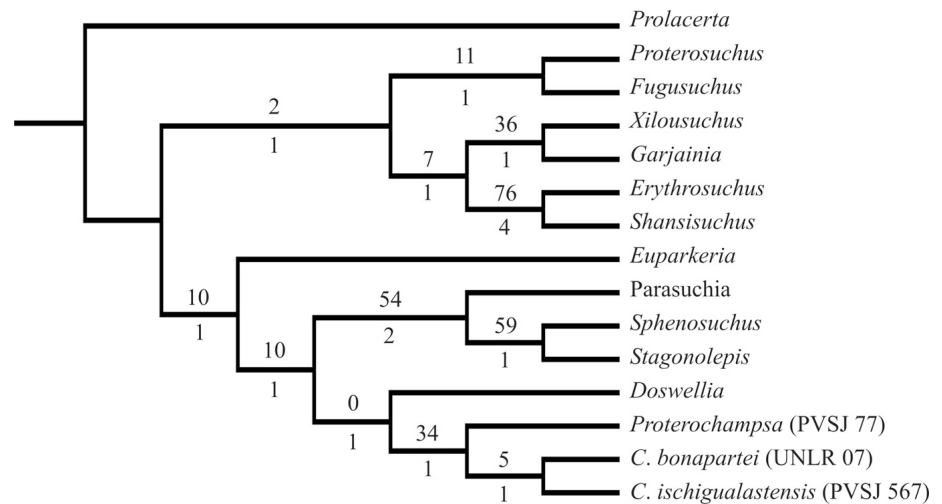


FIGURE 10. Results of the phylogenetic analysis using braincase data supported in the present study. Consensus of 63 most parsimonious trees (MPTs) with *Tropidosuchus* and *Cerritosaurus* removed from the tree, but not excluded from the analysis. Tree length (TL) = 46 steps, consistency index (CI) = 0.609, and retention index (RI) = 0.731. Jackknife absolute frequencies provided above the branch representing the base of the group, decay index (Bremer support) values below the same branches.

which the parabasisphenoid forms a larger share of the ventral surface of the basal tubera (Fig. 6) (Weems, 1980:pl. 2B; Dilkes and Sues, 2009:fig. 1B; Trotteyn and Haro, 2011:fig. 2; UNLR 07). We consider the condition in *Chanaresuchus ischigualastensis* to result from the ventral deflection of the caudal border. The parabasisphenoidal contribution to the basal tubera is more extended transversely than rostrocaudally (Fig. 3), differing from the more caudally and laterally directed contributions to the basal tubera present in *C. bonapartei* (Fig. 6), *Tropidosuchus*, *Proterochampsa*, and *Doswellia* (Romer, 1971:fig. 3; Weems, 1980:pl. 2B; Arcucci, 1990:fig. 3; Dilkes and Sues, 2009:fig. 1B; Trotteyn and Haro, 2011:fig. 2). Accordingly, the rostral contour of the tubera in *Chanaresuchus ischigualastensis* is closer to the transverse axis than to the longitudinal axis in ventral view (Fig. 3), contrasting with the more obliquely angled contour of the tubera in other proterochampsids (e.g., *Tropidosuchus*, *Proterochampsa*, and *C. bonapartei*; Arcucci, 1990:fig. 3; Trotteyn and Haro, 2011:fig. 2; UNLR 07; Fig. 6), and most other archosauriform taxa (e.g., *Doswellia*, *Turfanosuchus*, and *Lewisuchus*; Wu and Russell, 2001:fig. 5; Dilkes and Sues, 2009:fig. 1B; UNLR 01). The parabasisphenoid contribution to the basal tubera is ventrally and laterally directed. As the lateral surface of the parabasisphenoid is poorly exposed, the presence of the semilunar depression and the rostral tympanic recess cannot be confirmed. The parabasisphenoidal basal tubera are relatively dorsoventrally expanded, as in *C. bonapartei* (UNLR 07), contrasting with the dorsoventrally lower condition present in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011:fig. 10C). From this we can infer that, if their shape was relatively planar as in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011), the plane of each parabasisphenoid contribution to a basal tuber was less horizontal than in the latter. The caudal and medial part of the parabasisphenoid forms a lamina that is ventrally deflected (Fig. 3), and seems to form what Gower and Sennikov (1996) and Gower and Weber (1998) termed the 'intertuberal plate,' and that Parrish (1992) and Nesbitt (2011) termed the 'basisphenoid plate.' This plate is much less ventrally deflected in *C. bonapartei* (UNLR 07; Fig. 6), and this probably explains many differences between the basicrania of both specimens. The parabasisphenoidal caudal border is only slightly concave in ventral view (Fig. 3), contrasting with the more conspicuously concave contour of the border in *C. bonapartei* (UNLR 07; Fig. 6) and *Tropidosuchus* (Arcucci, 1990:fig. 3), and the 'V'-shaped contour in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011) and *Doswellia* (Dilkes and Sues, 2009:fig. 1B). However, the ventral border of the deflected plate

is more ventrally concave than in *C. bonapartei* (UNLR 07). So, accounting for the deflection inferred, the border would be very similar to that of UNLR 07, and both may reflect the concave state of the 'basisphenoidal plate' as coded by Nesbitt (2011:character 96, state 1). In ventral view, asymmetry is present in the caudal border of the parabasisphenoid, which is more concave on the left side (Fig. 3). This suggests that deformation was present at the caudal border of the parabasisphenoid, which in turn supports the possibility that the ventral deflection observed is due to post-mortem distortion. The parabasisphenoid ventral surface has a concavity surrounded by its caudal border, the basiptyergoid processes, and the lateroventral borders of the bone (Fig. 3). This fossa is exposed ventrally and somewhat rostrally, and may be homologous with the similar positioned depression in *Proterochampsa* (PVSJ 77) that was identified as the basisphenoidal recess (Trotteyn and Haro, 2011). The ventral deflection of the caudal border seemingly exaggerated the depth of the fossa and enhanced the rostral component of its exposure. Nonetheless, the presence of a deeply concave fossa differs from the condition present in *C. bonapartei*, which lacks a fossa on the ventral surface (UNLR 07; Fig. 6). *C. ischigualastensis* lacks prominent ridges on the parabasisphenoid ventral surface (Fig. 3), similar to *C. bonapartei* (UNLR 07) (Fig. 6) and *Archeopelta* (Desojo et al., 2011:fig. 5C, D), but unlike material referred to *Proterochampsa* (Trotteyn and Haro, 2011). A pair of foramina is present medial to the bases of the basiptyergoid process on the ventral surface (Fig. 3) and is probably homologous to similar though slightly more rostrally positioned foramina in *C. bonapartei* (Fig. 6). These foramina have been considered to represent the entries of the cerebral internal carotid arteries into the pituitary fossa (Romer, 1971:fig. 3). Similar foramina are found slightly more caudally in the region between the basiptyergoid processes in *Tropidosuchus* (Arcucci, 1990:fig. 3). This condition contrasts with that observed in some *Proterochampsa* material (PVSJ 77), where the foramina cannot be discerned (Trotteyn and Haro, 2011), and from *Doswellia*, in which the foramina are located well caudal to the basiptyergoid processes (Dilkes and Sues, 2009:fig. 1B). The basiptyergoid processes are directed obliquely, both ventrally and laterally, as in *C. bonapartei* (UNLR 07), in a condition that is intermediate between the mostly vertically directed processes of *Archeopelta* (Desojo et al., 2011), and the mainly laterally directed processes of *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011). The basiptyergoid processes are approximately as large as the basal tubera in ventral view, and their joint breadth is not greater than that of the basal tubera (Fig. 3).

The relative rostrocaudal thickness of the base of the processes is also much less than in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011:fig. 10A), and is probably more similar to the condition in *Chanaresuchus bonapartei* (UNLR 07; Fig. 6). The basiptyergoid processes size is proportionally much smaller than in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011; Nesbitt, 2011:character 124). The ventral surfaces of the processes are not connected by a transverse buttress (Fig. 3), which is also absent in *Proterochampsa* (PVSJ 77) and *C. bonapartei* (Trotteyn and Haro, 2011; UNLR 07; Fig. 6), contrasting with the condition in some archosaurs (e.g., *Saurosuchus galilei* Reig, 1959, and *Herrerasaurus ischigualastensis* Reig, 1963; Sereno and Novas, 1994:figs. 7D, 8D; Alcober, 2000:fig. 9B; PVSJ 32, PVSJ 407). The distal ends of the basiptyergoid processes lack a caudal prominence (Fig. 3), as in *Chanaresuchus bonapartei* (UNLR 07; Fig. 6) and *Tropidosuchus* (Arcucci, 1990:fig. 3), but differing from the prominent caudal projection present in *Proterochampsa* (PVSJ 77; Trotteyn and Haro, 2011). The articulated pterygoid likely covers only a portion of the ventral surface of the basiptyergoid process in ventral view (Fig. 3). On the dorsal surface, sutures with the other bones cannot be discerned (Figs. 7, 8), and a deep pituitary fossa is exposed (Fig. 7). The fossa is approximately triangular in this view, and its sides caudally diverge (Fig. 7), as in several archosauriforms (e.g., *Osmolskina czatkowicensis* Borsuk-Białynicka and Evans, 2003, *Silesaurus*, and *Arizonasaurus*; Dzik, 2003:fig. 7E; Gower and Nesbitt, 2006:fig. 1B; Borsuk-Białynicka and Evans, 2009:fig. 20C<sub>2</sub>). The lateral walls of the pituitary fossa are relatively thin (Fig. 7), as in several archosauriforms (e.g., *Osmolskina*, *Silesaurus*, and *Arizonasaurus*; Dzik, 2003:fig. 7E; Gower and Nesbitt, 2006:fig. 1B; Borsuk-Białynicka and Evans, 2009:fig. 20C<sub>2</sub>). The dorsal borders of the lateral walls of the fossa hypophyseos are concave (Fig. 8), as in *Osmolskina* (Borsuk-Białynicka and Evans, 2009:fig. 20C<sub>2</sub>). This concavity probably represents the ventral part of the pituitary vein foramen. The caudal wall of the fossa, the dorsum sellae, is damaged as a result of the detachment and displacement of the right side wall of the braincase from the basicranium, but portions of it seem to contact the medial borders of the clinoid processes (Fig. 7). In relation to this, we cannot discern the foramen of the abducens nerve (VI) on the possible remnants of the dorsum sellae.

## RESULTS AND DISCUSSION

### General Similarities and Distinctions

*Chanaresuchus ischigualastensis* possesses one unique neurocranial feature when compared with other proterochampsids, namely the nearly transversely oriented rostral contour of the basal tubera in ventral view. A more oblique, caudally and laterally oriented contour is observed in other proterochampsid and non-proterochampsid basal archosauriforms: consequently, this feature of *Chanaresuchus ischigualastensis* seems to represent an autapomorphy. *Chanaresuchus ischigualastensis* differs from most other proterochampsids, except for the *C. bonapartei* specimen PVL 4575, in the presence of distally expanded paroccipital processes, but not from other archosauriforms.

*Chanaresuchus ischigualastensis* shares a large number of similarities with the holotype of *C. bonapartei* that are lacking in the *Proterochampsa* specimen PVSJ 77. These include (1) the relatively longer (compared with its width) main basioccipital body caudal to the basal tubera; (2) greater proximodistal length than width at midlength of the basal tubera in caudal view, with widely separated distal tips; (3) the lack of a prominent caudal border on the basioccipital basal tubera; (4) the caudal sulcus on the ventral surface of the paroccipital process is much shorter than the rostral one; (5) the bases of the basiptyergoid processes are not as strongly expanded rostrocaudally; (6) the parabasisphenoidal component of the basal tubera sheaths the basioccipital component mostly rostromedially rather than

ventrally; (7) the caudal border of the parabasisphenoid is evenly concave; (8) a prominent 'V'-shaped ridge on the ventral surface of the parabasisphenoid is absent; (9) a caudal projection of the basiptyergoid processes is absent; (10) a pair of well-exposed foramina, probably for the cerebral internal carotid arteries, is present on the ventral surface of the parabasisphenoid between the bases of the basiptyergoid processes; (11) the strut of the exoccipital, ventral to the paroccipital processes and dorsal to the occipital condyle, is relatively transversely gracile, as can be observed in caudal view; (12) the angle between the paroccipital processes is not larger than 90° in dorsal view; (13) the basicranium is shorter from the rostral-most point of the basiptyergoid processes to the caudal extremity of the occipital condyle relative to the width comprised by the basal tubera; and (14) the possession of ventrally and laterally directed basiptyergoid processes. However, the last of these features is not systematically useful for distinguishing *Chanaresuchus ischigualastensis* from *Proterochampsa* because the basiptyergoid processes in at least one *Proterochampsa* specimen (MCZ 3408) also project ventrally and laterally, in addition to slightly caudally (D. Dilkes, pers. comm.). *Chanaresuchus ischigualastensis* shares at least one similarity with *Proterochampsa* (PVSJ 77) that is not found in *C. bonapartei*, namely the transverse concavity in the caudal portion of the ventral surface of the main body of the parabasisphenoid. A second possible similarity between *C. ischigualastensis* and *Proterochampsa* that is lacking in *C. bonapartei* might be the presence of the prominent ridge-like structure at the exoccipital-basioccipital suture on the lateral surface of the braincase wall.

In addition to those previously mentioned in this section, the differences observed between *Chanaresuchus ischigualastensis* and the holotype of *C. bonapartei* are two, namely: (1) the rounded, instead of pointed, distal extremity of the basal tubera; and (2) the basis cranii caudal to the cultriform process shorter relative to the width constituted by the basal tubera.

The number of differences with the *Proterochampsa* specimen PVSJ 77 is larger. In addition to those previously mentioned in this section, they include the following five differences: (1) the lateral surface of the exoccipitals not as convex rostrocaudally; (2) the cross-section of the paroccipital processes approximately triangular near the base, instead of approximately irregular hexagonal (related to the presence of a continuously convex rostromedial surface instead of distinct dorsal and rostral flat surfaces connected at a ridge); (3) the distal end of the paroccipital processes with a laminar shape; (4) the sulcus located on the caudal surface of the paroccipital process extending only along the proximal two-thirds of the process; and (5) the ridge ventrally limiting the sulcus on the caudal surface of each paroccipital process distally vanishing and not twisted dorsalwards.

Comparisons with other proterochampsids are less fruitful because less information has been published. *Chanaresuchus ischigualastensis* resembles *Tropidosuchus* in a number of features in which it also resembles the holotype of *C. bonapartei*, namely: (1) the relatively elongated occipital condyle in ventral view; (2) the presence of a pair of well-exposed foramina on the ventral surface of the parabasisphenoid almost directly medial to the bases of the basiptyergoid processes; (3) the concave caudal border of the parabasisphenoid; and (4) the lack of a caudal prominence in the distal extremity of the basiptyergoid process. *Chanaresuchus ischigualastensis* differs from *Tropidosuchus* in the rounded, instead of pointed, distal extremities of the basal tubera, as well as the distally widening paroccipital processes, and the nearly transversely oriented rostral contour of the basal tubera in ventral view. There are three differences between *Chanaresuchus ischigualastensis* and the paroccipital processes of *Cerritosaurus*, the only part of the braincase shared with the specimen PVSJ 567 (Price, 1946:fig. 3). The gradual distal divergence of the dorsal and ventral borders in caudal view of the specimen

PVSJ 567 is not observed in *Cerritosaurus* (Price, 1946:fig. 3). In addition, the processes seem to be dorsoventrally thinner than in *Cerritosaurus* (Price, 1946:fig. 3) and form a near 90° angle in dorsal view, contrasting with the larger angle found in *Cerritosaurus* (Price, 1946:fig. 2). Thus, the data support the conclusion that PVSJ 567 is a different taxon sharing greater similarities with *C. bonapartei* and *Tropidosuchus* among known proterochampsids.

Some similarities previously observed between *Proterochampsia* (PVSJ 77) and *C. bonapartei* (Trotteyn and Haro, 2011) are also shared by *Chanaresuchus ischigualastensis*. One of these is the dorsoventrally thin paroccipital process, which, as mentioned, is apparently thicker in *Cerritosaurus*. The strongly developed caudal sulcus on the paroccipital process represents the other.

In addition, we notice a unique feature that is not shared with other archosauriforms, except crocodylians: the lack of indication of a floccular recess on the alar process of the prootic. Indeed, Gower (2002) indicated that this character varied between being located entirely on the prootic, which is common in basal archosauriforms, to being shared between the prootic and supraoccipital, which is present in archosaurs. If we consider the absence of the floccular recess in the prootic as an indication of complete absence of the recess from the neurocranium, then the feature would represent, on the basis of currently supported phylogenies, a convergence with crocodylians. If, however, it represents a shift of the recess into the supraoccipital, we may see it as a trait more related to the archosaurian character state than to that of basal archosauriforms, because the state of archosaurs would actually be intermediate between the proposed one for *Chanaresuchus ischigualastensis* and that of more basal archosauriforms. In either case, the condition present would be more similar to that in archosaurs than to that in non-archosaurian archosauriforms. If the recess was completely lacking, the similarity with crocodylians may be related with similar life habits, given that amphibious habits have been suggested for proterochampsids by both Bonaparte (1971) and Romer (1971).

Some of the differences between *Chanaresuchus ischigualastensis* and *Proterochampsia* appear to be associated in part with the greater robustness of the skull in the latter, which may in turn be related to its larger size. This might account for the proportionally thicker basal tubera, the position of the basioccipital main body caudal to the tubera, differences in the robustness of the exoccipital struts, and basipterygoid processes, as well as for the presence of rostrocaudally thicker paroccipital processes in the latter taxon. This consideration may also explain some of the differences between *C. bonapartei* and *Tropidosuchus*, on one side, and *Proterochampsia*, on the other. Other differences between the *Chanaresuchus* species and *Proterochampsia*, such as the proportionally proximodistally longer basal tubera and more ventrally oriented basipterygoid process (in *Chanaresuchus*), seem to be at least partially related to the less dorsoventrally compressed skull, which was previously noted by Bonaparte (1971) and Romer (1971) in the case of *Chanaresuchus bonapartei*. We think caution is required regarding the independence of these features in future phylogenetic analyses.

### Phylogenetic Analysis

Our phylogenetic analysis is based primarily on the data matrix of Gower and Sennikov (1996), which included only neurocranial characters. To this matrix were added several proterochampsids: *Chanaresuchus ischigualastensis*, *C. bonapartei* (scored on the basis of the holotype), *Proterochampsia* (scored on the basis of PVSJ 77), *Tropidosuchus* (scored from Arcucci, 1990), and *Cerritosaurus* (scored from Price, 1946), as well as the purported proterochampsid relative *Doswellia* (scored from Weems, 1980, and Dilkes and Sues, 2009), comprising a total of 17 taxa. We added three braincase characters from the analysis in Dilkes and Sues

(2009:characters 20, 22, and 31) and four new braincase characters, proposed in this study, providing a total of 24 characters. In addition, some characters in Gower and Sennikov (1996) were modified. The details of the character list used can be found in Appendix 2 and the data matrix in Appendix 3. Codifications for *Xilousuchus* were modified from Gower and Sennikov (1996), using new data provided by Nesbitt et al. (2011). The details of the search are given in the Materials and Methods section. The analysis yielded 63 most parsimonious trees (MPTs) with tree length (TL) of 46 steps, consistency index (CI) of 0.609, and retention index (RI) of 0.731. The consensus tree was nearly completely unresolved, except for a group formed by *Parasuchia*, *Stagonolepis*, and *Sphenosuchus*, which is fully resolved (also present in Gower and Sennikov, 1996). This led us to use the pruning option in TNT, which identifies those OTUs that fall in the greatest number of alternative positions in the trees and removes them from the consensus tree without excluding the data from these OTUs from the analysis. In this way, the results are based in all the data available. Pruning revealed that resolution of seven additional nodes could be gained by excluding *Cerritosaurus* from the consensus, and another three can be gained by excluding *Tropidosuchus*. When both *Cerritosaurus* and *Tropidosuchus* are excluded, 10 nodes are gained in the consensus, and the consensus tree becomes completely resolved (Fig. 10). Bremer support and probabilistic support values were generally low (see Fig. 10). Our analysis supported the monophyly of the Proterochampsidae (when *Tropidosuchus* and *Cerritosaurus* were not considered). This group was supported by only one apomorphy, the paroccipital processes elongated relative to their height (character 21, state 1). This character is non-homoplastic, but the condition was not scored for many taxa. Within the Proterochampsidae, *Chanaresuchus ischigualastensis* was recovered as the sister taxon of *C. bonapartei*, on the basis of a single character, the acquisition of a parabasisphenoidal intertuberal plate with a concave border (character 2, state 1). This feature is homoplastic, however, because it appears independently in *Euparkeria*. This sister-group relationship implies that the phylogenetic hypothesis suggested by the braincase data supports inclusion of *Chanaresuchus ischigualastensis* within *Chanaresuchus* (only when taxa of ambiguous relationships are excluded from consideration). This sister-group relationship is also recovered by a phylogenetic analysis encompassing a larger data matrix that includes characters from other parts of the skeleton (Trotteyn, 2011). Our data agree with the analyses of Benton and Clark (1988) and Dilkes and Sues (2009), and contrast with the results of Ezcurra et al. (2010) and Desojo et al. (2011), in recovering *Doswellia* as a proterochampsian, more closely related to *Proterochampsia* and *Chanaresuchus* than to archosaurs. The only one apomorphy supporting the Proterochampsia is the presence of a parietal-paroccipital process contact immediately lateral to the supraoccipital (character 20, state 1), which is, however, unknown in the members of the genus *Chanaresuchus* scored, and homoplastic, as it is present in many archosauriforms less related to the Archosauria than proterochampsians. Archosauria was recovered as the sister taxon to the Proterochampsia, and these two groups share the following three apomorphies: absence of the ridge on the clinoid process of the prootic (character 6, state 1), absence of a pseudolagenar recess between the basal tuber and ventral ramus of the opisthotic (character 14, state 1), and parabasisphenoidal contribution to the basal tubera not wider than the basioccipital contribution to the basal tubera (character 24, state 1). The two first features are homoplastic: notably, they also appear apomorphically in the *Shansisuchus* Young, 1964 + *Erythrosuchus* clade. The final feature of these three is not homoplastic, but we were unable to score it for members of the *Shansisuchus* + *Erythrosuchus* clade. *Euparkeria* is the sister taxon to the Proterochampsia + Archosauria group, and the clade formed by all these is diagnosed by the following character states: the position of the abducens

foramina on the ventral surface of the dorsum sellae (character 4, state 1; although scoring for this character is lacking for proterochampsians and most archosaurs), and the convex ventrolateral contour of the basioccipital part of the basal tubera in caudal view (character 23, states 1–2). Character 4 is homoplastic in this study, appearing independently in the group formed by *Erythrosuchus* + *Shansisuchus*. Character 23 is homoplastically acquired by at least one specimen of *Erythrosuchus* (BPI 3893; Gower, 1997:fig. 2D), but not all (NHMUK R3592; Gower, 1997:fig. 2B). Our results resemble those of Gower and Sennikov (1996), Ezcurra et al. (2010), and Nesbitt (2011), but differ from those of Dilkes and Sues (2009), in showing a closer relationship between *Euparkeria* and archosaurs than either of these taxa has with *Erythrosuchus*. The large amount of homoplasies observed between the *Erythrosuchus* + *Shansisuchus* clade and some subsets of members of the sister group to *Euparkeria* previously mentioned suggests widespread convergent evolution. Our results agree with the results of Gower and Sennikov (1996) in suggesting a monophyletic Proterosuchia, with *Erythrosuchus* most closely related to *Proterosuchus* Broom, 1903, than to Archosauria, but disagree with the results obtained from the more comprehensive data sets of Sereno (1991), Dilkes and Sues (2009), Ezcurra et al. (2010), and Nesbitt (2011). Our results also agree with Gower and Sennikov's (1996) hypothesis that *Xilousuchus* is an erythrosuchid, although this was falsified by more recent analyses based on larger data sets, which recover it as an archosaur (Nesbitt, 2011; Nesbitt et al., 2011). These relationships seem to result from the proportionally greater reliance on data from the Gower and Sennikov (1996) study than from the other works mentioned, and the phylogenetic hypothesis presented herein should not be preferred over more complete phylogenies generated on the basis of more evidence. Our results show lower values for both the CI and RI than those obtained by Gower and Sennikov (1996) (compare our CI of 0.609 with their value of 692, and our RI of 0.731 with their value of 0.81). This is expected because our data matrix incorporates a larger number of taxa and characters than that offered by Gower and Sennikov (1996), and matrices with more taxa and characters generally show more homoplasy, or less consistency, as measured by the consistency index (Sander and Donoghue, 1989; Hauser and Boyajian, 1997). In relation with this, our results further support the suggestion of Gower and Sennikov (1996) and Gower (2002) that homoplasy is potentially common in the braincases of basal archosauriforms, a result echoed by work on neotheropods by Rauhert (2007).

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#### APPENDIX 1. Sources of information for taxa used in comparisons and character scorings.

- Archeopelta arborensis*, CPEZ-239a; Desojo et al. (2011).
- Arizonasaurus babbitti*, MSM P4590, MSM P4647; Gower and Nesbitt (2006); Nesbitt (2011).
- Batrachotomus kupferzellensis*, SMNS 80260; Gower (2002); Nesbitt (2011).
- Cerritosaurus binsfeldi*, MCP 1694 PV; Price (1946).
- Chanaresuchus bonapartei*, PVL 4575, PVL 4647, UNLR 07; Romer (1971); Nesbitt (2011); personal observation.
- Coelophysis rhodesiensis*, QG 193, QG 194, QG 196; Raath (1985).
- Ctenosaura pectinata*; Oelrich (1956).
- Doswellia kaltenbachi*, USNM 214823; Weems (1980); Dilkes and Sues (2009).
- Erythrosuchus africanus*, NHMUK R3592, BPI 3893, CAMZM T700; Gower and Sennikov (1996); Gower (1997).
- Euparkeria capensis*, SAM PK- K5867, SAM PK- K7696, CAMZM T692; Ewer (1965); Gower and Sennikov (1996); Gower and Weber (1998); personal observation from photographs.
- Fugusuchus hejiapanensis*, GMB V 313; Gower and Sennikov (1996).
- Garjainia prima*, PIN 951-60; Gower and Sennikov (1996).
- Herrerasaurus ischigualastensis*, PVSJ 407; Sereno and Novas (1994); personal observation.
- Lewisuchus admixtus*, UNLR 01; Romer (1972b).
- Marasuchus lilloensis*, PVL 3872; Bonaparte (1975); Sereno and Arcucci (1994).
- Osmolskina czatkowiczensis*, ZPAL RV /412; Borsuk-Białynicka and Evans (2009).
- Parasuchia*, ISI R 42, ISI R 44, ISI R 45, ISI R 47, ISI R 160, UCMP A272/27200; Camp (1930); Chatterjee (1978); Gower and Sennikov (1996).
- Postosuchus kirkpatricki*, TTUP 9000; Chatterjee (1985); Long and Murry (1995).
- Prolacerta broomi*, BPI 2675, CAMZM 2003.40, UCMP 37151; Gow (1975); Evans (1986).
- Proterochampsia* sp., MCZ 3408, PVSJ 77; Sill (1967); Trotteyn and Haro (2011); personal observation.
- Proterosuchus fergusi*, BPI 3993; Gow (1975).
- Saurosuchus galilei*, PVSJ 32; Alcober (2000); personal obser-vation.
- Shansisuchus shansisuchus*, IVPP V 2511; Gower and Sen-nikov (1996).

- Silesaurus opolensis*, ZPAL Ab III/361, ZPAL Ab III/362, ZPAL Ab III/364; Dzik (2003).
- Sphenosuchus acutus*, SAM PK-K3014; Walker (1990); Gower (2002); Gower and Walker (2002); Nesbitt (2011).
- Stagonolepis robinsoni*, MCZD 2-4, MCZD 2-5; Gower and Walker (2002).
- Tropidosuchus romeri*, PVL 4601, PVL 4606; Arcucci (1990).
- Turfanosuchus dabanensis*, IVPP V3237; Wu and Russell (2001).
- Xilousuchus sapingensis*, IVPP V6026; Wu (1981); Gower and Sennikov (1996); Nesbitt et al. (2011).

#### APPENDIX 2. Characters used in the phylogenetic analysis.

- (1) Position on parabasisphenoid of foramina for the cerebral branches of the internal carotid arteries leading to the pituitary fossa: caudal (0); caudolateral (1); or rostrrolateral (2) (additive) (Gower, 2002:character 1).
- (2) Parabasisphenoid intertuberal plate: present (0); absent (1) (Parrish, 1992:character 10).
- (3) Elements enclosing abducens foramen: parabasisphenoid and prootic (0); prootic only (1) (Gower and Sennikov, 1996:character 3).
- (4) Position of external abducens foramina: on ventral (0); or rostral (1) surface (Gower, 2002; modified from Gower and Sennikov, 1996:character 4).
- (5) Ventral ramus of the opisthotic: prominent (0); recessed (1) (Gower and Sennikov, 1996:character 5).
- (6) Ridge on lateral surface of clinoid process: present (0); absent (1) (Gower and Sennikov, 1996:character 6).
- (7) Parabasisphenoid orientation: horizontally (0); or more vertically (1) oriented (Gower and Sennikov, 1996:character 7).
- (8) Crista prootica outline: simply curved (0); sinusoidal (1) (Gower and Sennikov, 1996:character 8).
- (9) Prootic midline contact on endocranial cavity floor: absent (0); present (1) (Gower and Sennikov, 1996:character 9).
- (10) Parabasisphenoid midline exposure on endocranial cavity floor: present (0); absent (1) (Gower and Sennikov, 1996:character 10).
- (11) Semilunar depression: present (0); absent (1) (Gower and Sennikov, 1996:character 11).
- (12) Laterosphenoid rostrrodorsal channel: absent (0); present (1) (Gower and Sennikov, 1996:character 12).
- (13) Parasphenoid cultriform process: simple (0); dorsoventrally constricted towards the base (1) (Gower and Sennikov, 1996:character 13).
- (14) 'Pseudolagenar recess' between ventral surface of the ventral ramus of the opisthotic and the basal tubera: present (0); absent (1) (Gower and Sennikov, 1996:character 14).
- (15) Base of cultriform process of parabasisphenoid: relatively short dorsoventrally (0); tall, with the dorsal edge extending dorsally between clinoid processes and ventral part of cristae prootica (1) (Gower and Sennikov, 1996:character 15).
- (16) Number of hypoglossal foramina: two (0); one (1) (Gower and Sennikov, 1996:character 16).
- (17) Medial margin of exoccipitals: do not make contact (0); meet rostrally, but diverge caudally (1); make contact for majority of their length (2) (additive) (modified from character 17 in Gower and Sennikov, 1996).
- (18) Orientation of basiptyergoid processes: rostrrolateral (0); lateral (1) (Dilkes, 1998:character 43).
- (19) Exoccipitals and opisthotics: discrete (0); fused (1) (Juul, 1994).
- (20) Association between paroccipital process and parietal: no contact (0); contact present immediately lateral to supraoccipital (1) (Dilkes and Sues, 2009:character 31).



- (21) Proximodistal length of the paroccipital processes relative to their dorsoventral thickness as measured by a ratio between length and height: ratio lower than 2.5 (0); ratio higher than 2.5 (1).
- (22) Caudal surface of the paroccipital process: convex, flat, or with a sulcus on its medial section (0); or with a strongly developed caudal sulcus (1).
- (23) Ventrolateral contour of the basioccipital basal tubera in caudal view: not convex (0); slightly convex (1); strongly convex (2) (additive).
- (24) Relative transverse extent of the basal tubera components: parabasisphenoidal element more laterally prominent (0); basioccipital element more prominent or as laterally prominent as the parabasisphenoidal (1).

APPENDIX 3. Data matrix employed in this work.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Prolacerta</i>	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0
<i>Proterosuchus</i>	0	0	0	0	0	0	0	?	?	?	?	0	1	0	0	?	?	1	0	1	?	0	0	0
<i>Fugusuchus</i>	0	0	?	0	0	0	0	0	?	?	?	?	1	0	0	1	1	1	1	1	?	?	?	0
<i>Xilousuchus</i>	0	0	1	0	0	?	1	1	1	?	0	?	0	0	0	0	1	1	1	?	?	?	0	0
<i>Garjainia</i>	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	1	1	1	1	1	?	?	0	0
<i>Erythrosuchus</i>	0	0	1	1	1	1	1	0	1	1	0	1	0	1	1	1	2	1	1	1	?	?	[01]	?
<i>Shansisuchus</i>	0	?	1	1	1	1	1	0	1	?	0	1	0	1	1	1	2	1	1	1	?	?	?	?
<i>Euparkeria</i>	0	1	0	1	0	0	1	?	?	?	0	?	1	0	0	0	0	1	1	0	0	0	2	0
<i>Sphenosuchus</i>	2	2	0	1	0	1	1	0	0	1	0	0	0	1	1	0	0	1	1	?	?	0	2	1
<i>Parasuchia</i>	1	2	0	?	0	1	?	0	1	0	1	?	1	1	0	?	2	1	1	0	?	0	[12]	?
<i>Stagonolepis</i>	2	2	?	?	0	1	?	?	?	?	?	?	?	1	1	0	?	0	1	0	0	?	[12]	?
<i>C. ischigualastensis</i> (PVSJ 567)	0	1	?	?	0	1	?	?	?	?	?	?	?	1	?	?	?	?	1	?	1	1	?	?
<i>C. bonapartei</i> (UNRL 07)	0	1	?	?	0	?	?	?	?	?	0	?	?	1	?	?	?	?	1	?	1	1	1	?
<i>Proterochampsa</i> (PVSJ 77)	?	2	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	1	1	1	1	1	1
<i>Doswellia</i>	0	2	?	?	0	1	0	?	?	?	?	?	?	?	?	1	0	?	1	1	0	?	?	1
<i>Tropidosuchus</i>	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cerritosaurus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Saurosuchus</i>	2	2	?	1	0	1	1	0	?	?	?	?	0	0	0	1	2	1	?	?	?	?	?	?
<i>Arizonasaurus</i>	0	0	1	1	0	1	1	?	1	1	1	?	0	0	?	0	2	?	1	?	0	?	0	?