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A NEW PEIROSAURID (CROCODYLIFORMES, MESOEUCROCODYLIA) FROM THE UPPER CRETACEOUS OF PATAGONIA, ARGENTINA

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Abstract. Peirosaurids are a group of Cretaceous continental crocodyliforms from Gondwana. Two species are known from the Neuquén Group in Argentina: *Lomasuchus palpebrosus* (Portezuelo Formation, late Turonian–early Coniacian) and *Gasparinisuchus peirosauroides* (Bajo de la Carpa and Anacleto formations, Santonian and early Campanian, respectively). Here, we describe the first peirosaurid from the Cerro Lisandro Formation, *Bayomesasuchus hernandezi* gen. et sp. nov. The material corresponds to a fragmentary skull and mandible. Although fragmentary, this is the most complete crocodyliform specimen recorded for the Cerro Lisandro Formation. In a phylogenetic analysis *Bayomesasuchus* is depicted in a polytomy together with South American peirosaurids and the African form *Hamadasuchus rebouli*.

Key words. *Bayomesasuchus*. Peirosauridae. Cerro Lisandro Formation. Cretaceous.

Resumen. UN NUEVO PEIROSÁURIDO (CROCODYLIFORMES, MESOEUCROCODYLIA) DEL CRETÁCICO SUPERIOR DE PATAGONIA, ARGENTINA. Los peirosáuridos constituyen un grupo de crocodiliformes continentales del Cretácico de Gondwana. Para el Grupo Neuquén, Argentina, se conocen dos especies: *Lomasuchus palpebrosus* (Formación Portezuelo, Turoniano tardío–Coniaciano temprano) y *Gasparinisuchus peirosauroides* (Formaciones Bajo de la Carpa y Anacleto, Santoniano y Campaniano temprano, respectivamente). Aquí, describimos el primer peirosáurido identificado para la Formación Cerro Lisandro, *Bayomesasuchus hernandezi* gen. et sp. nov. El material corresponde a cráneo y mandíbula fragmentarios. Aunque fragmentario, este es el espécimen de crocodiliforme más completo registrado para la Formación Cerro Lisandro. En un análisis filogenético, *Bayomesasuchus* es agrupado en una politomía junto con los peirosáuridos sudamericanos y la forma africana *Hamadasuchus rebouli*.

Palabras clave. *Bayomesasuchus*. Peirosauridae. Formación Cerro Lisandro. Cretácico.

LATE Cretaceous Crocodyliformes of Argentina occur mainly in the Neuquén Basin, specifically in the Neuquén Group units (Leanza *et al*., 2004; Candeiro and Martinelli, 2006; Pol and Gasparini, 2007). Among mesoeucrocodylian notosuchians (Pol *et al*., 2012), Peirosauridae are a group of Gondwanan Cretaceous continental crocodyliforms (Carvalho *et al*., 2010) known from South America (Gasparini, 1982; Gasparini *et al*., 1991; Carvalho *et al*., 2004, 2007; Leardi and Pol, 2009; Martinelli *et al*., 2012) and Africa (Buffetaut, 1994; Larsson and Sues, 2007; Sertich and O'Connor, 2014).

The species currently recognized in the Neuquén Group are *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández, 1991, and *Gasparinisuchus peirosauroides* (Martinelli, Sertich, Garrido and Pradeiro, 2012) from the Portezuelo (late Turonian–early Coniacian), Bajo de la Carpa (Santonian) and Anacleto (early Campanian) formations (Garrido, 2010). Fragmentary remains from the Portezuelo Formation were in turn assigned to Peirosauridae (Lio *et al*., 2014; Barrios and Bona, 2015). Here we present a new peirosaurid species from the Cerro Lisandro Formation (mid–late Turonian), which is also the oldest representative of the family in the Neuquén Group (Fig. 1). The new taxon, *Bayomesasuchus hernandezi* gen. et sp. nov., is represented by a fragmentary skull and mandibular elements, which allowed us to test its phylogenetic affinities.

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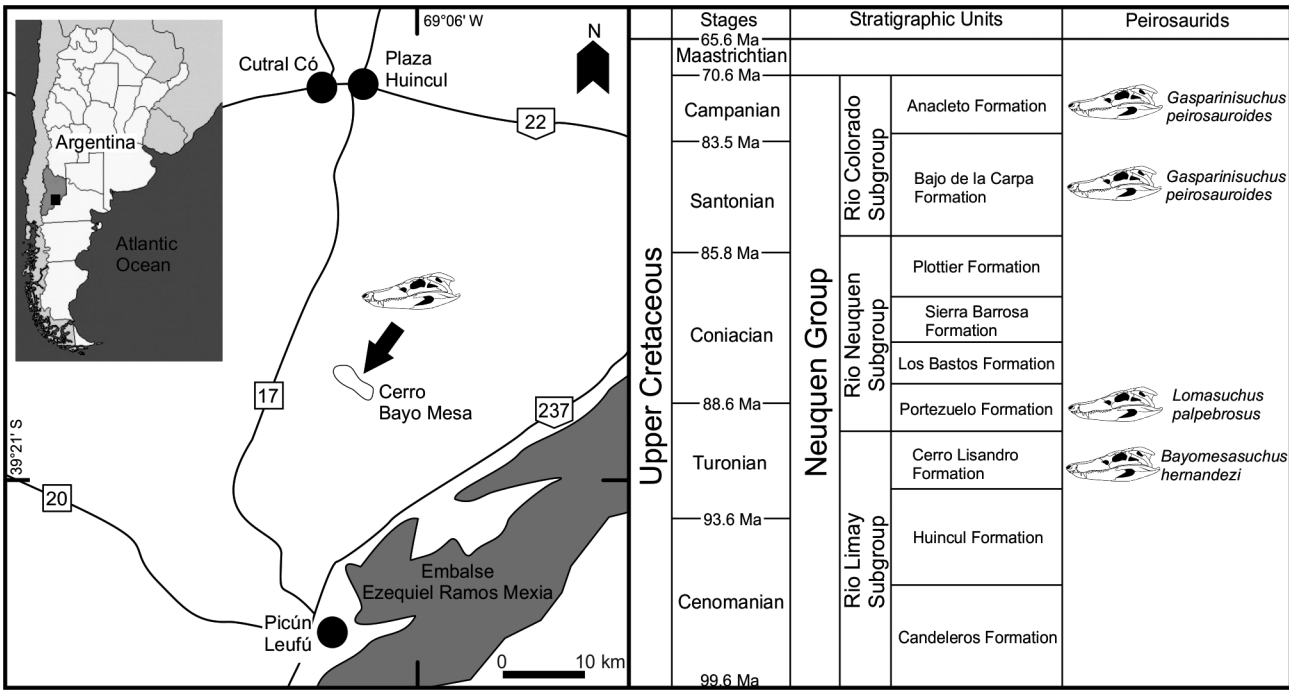

Figure 1. Location map of ***Bayomesasuchus hernandezi*** gen. et sp. nov. (**MCF PVPH**-822) with stratigraphic section showing the provenance of Neuquén Group peirosaurids.

Institutional Abbreviations. **CPP,** Centro de Pesquisas Paleontológicas L. I. Price, Peirópolis, Brazil; **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MCF,** Museo Municipal Carmen Funes, Plaza Huincul, Neuquén, Argentina; **MLP,** Museo de La Plata, La Plata, Buenos Aires, Argentina; **MOZ,** Museo Provincial Profesor Dr. J. A. Olsacher, Zapala, Neuquén, Argentina; **PVL,** Paleontología de Vertebrados Lillo, Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina; **ZSM,** Zoologische Staatssammlung, München, Germany.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Hay, 1930 (*sensu* Walker, 1970)
CROCODYLIFORMES Hay, 1930 (*sensu* Clark, 1986)
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NOTOSUCHIA Gasparini, 1971 (*sensu* Pol *et al.*, 2012)
PEIROSAURIDAE Gasparini, 1982

Bayomesasuchus gen. nov.
Bayomesasuchus hernandezi sp. nov.
Figures 2–4

Derivation of name. *Bayomesasuchus* refers to the Cerro Bayo Mesa locality, Neuquén Province, Argentina; the specific epithet *hernandezi* was dedicated to the former technician Mr. Daniel Hernández (Museo Carmen Funes, Municipalidad de Plaza Huincul), a resourceful assistant in the fieldwork.

Type material. MCF PVPH-822, fragmentary mandibular symphysis, right fragmentary maxilla, right fragmentary ectopterygoid, left fragmentary postorbital, left fragmentary squamosal, right articular, right fragmentary surangular, left fragmentary palatine and other indeterminate fragments (Figs. 2–4).

Geographic and stratigraphic occurrence. Cerro Bayo Mesa (39° 15′ 02.3″ S; 69° 12′ 59.2″ W), 35 km south from Plaza Huincul, Neuquén, Argentina; Cerro Lisandro Formation (mid–late Turonian) (Garrido, 2000, 2010).

Diagnosis. *Bayomesasuchus hernandezi* gen. et sp. nov. is characterized by the following combination of characters (*autapomorphies): ziphodont and pseudoheterodont (different sizes and morphologies) dentition; dentary with festooned margins, ornamented with pits and grooves; elongated mandibular symphysis extending posteriorly up

to the 10th alveolus (shared with *Montealtosuchus arrudacamposi* Carvalho, Vasconcellos and Tavares, 2007), whereas in *Hamadasuchus rebouli* Buffetaut, 1994, it exceeds that level and in *Gasparinisuchus* (Martinelli, Sertich, Garrido and Pradeiro, 2012) the mandibular symphysis reaches the 8th alveolus; symphyseal region flattened dorsoventrally and narrow mediolaterally (shared with *Montealtosuchus* Carvalho, Vasconcellos and Tavares, 2007 and *Hamadasuchus* Buffetaut, 1994); dorsal and ventral exposure of splenial triangular in shape (shared with other peirosaurids, although the strong wedge-shape is present in longirostrine crocodyliforms such as thalattosuchians, dyrosaurids, pholidosaurids, gavialoids); postorbital with posteroventral process anterior to otic recess and with facet for palpebral bone; squamosal with ornamented and elongate posterolateral process forming an angle of 30° with dorsal plane (shared with South American peirosaurids and uruguaysuchids); maxillary tooth-row extending caudally beyond anterior margin of suborbital fenestra; maxillary palate with occlusal depressions; surangular with prominent posterolateral ridge; surangular forming part of the mandibular joint (shared with *Montealtosuchus* but absent in *Uberabasuchus terrificus* Carvalho, Ribeiro and Ávila, 2004); dentary with diastema between 4th–5th alveoli*; 5th–6th dentary alveoli confluent*; sub-vertical rostrum (shared with other notosuchians).

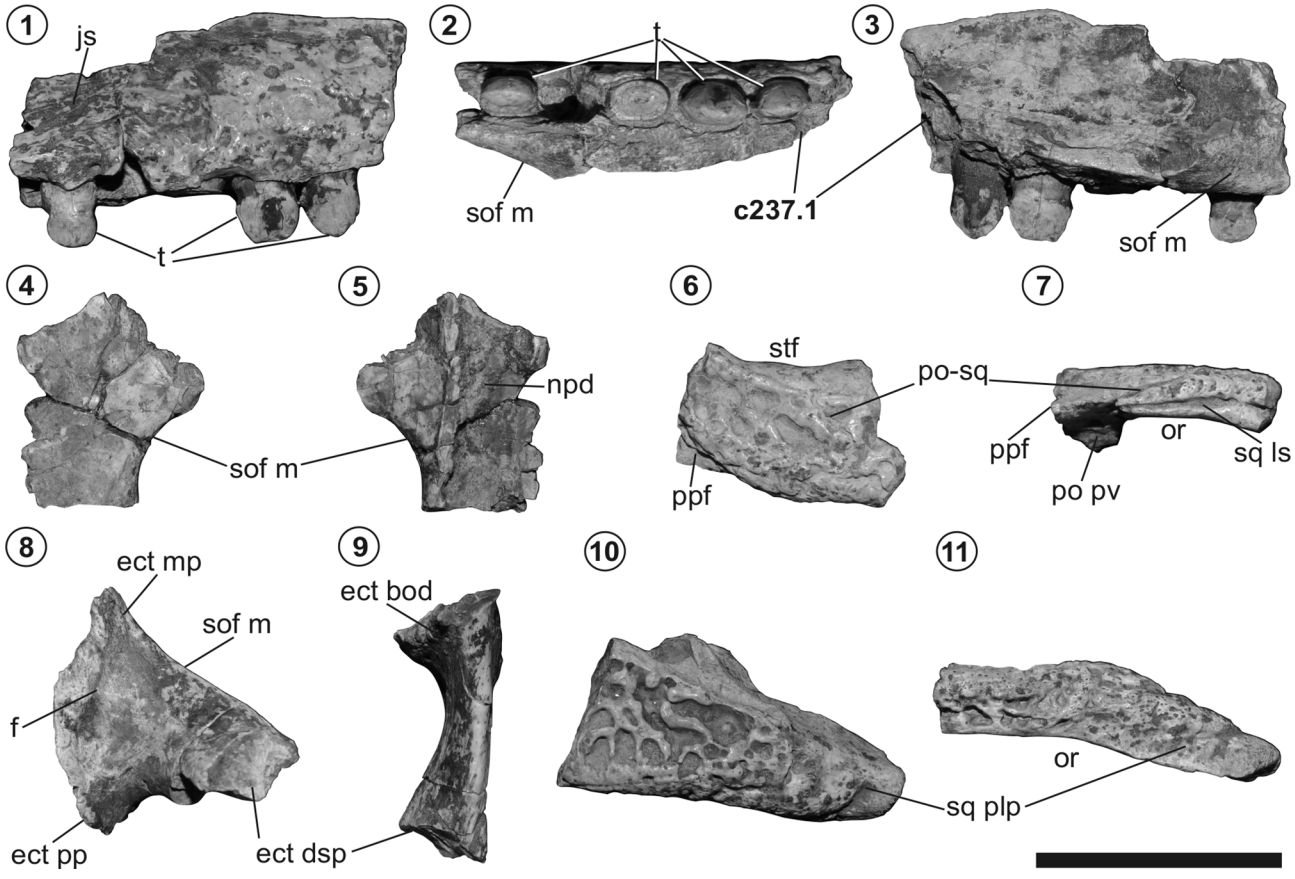

Figure 2. ***Bayomesasuchus hernandezi*** gen. et sp. nov., **MCF PVPH**-822; **1–3,** right fragmentary maxilla in **1,** lateral, **2,** palatal and **3,** medial views; **4–5,** left fragmentary palatine in **4,** palatal and **5,** dorsal views; **6–7,** left postorbital-squamosal fragment in **6,** dorsal and **7,** lateral views; **8–9,** right fragmentary ectopterygoid in **8,** ventral and **9,** anterior views; **10–11,** left fragmentary squamosal in **10,** dorsal and **11,** lateral views. Abbreviations: **ect bod,** ectopterygoid body; **ect dsp,** ectopterygoid descending process; **ect mp,** ectopterygoid maxillary process; **ect pp,** ectopterygoid posterior process; **f,** foramen; **js,** jugal suture; **npd,** nasopharyngeal duct; **or,** otic recess; **po pv,** postorbital posteroventral process; **po-sq,** post-orbital-squamosal suture; **ppf,** posterior palpebral facet; **sof m,** suborbital fenestra margin; **sq ls,** squamosal lateral suture; **sq plp,** squamosal posterolateral process; **stf,** supratemporal fossa; **t,** tooth; **c237.1,** synapomorphy of Peirosauridae. Scale bar= 2.5 cm.

DESCRIPTION AND COMPARISONS

Skull

Maxilla. A fragment of the posterior region of right maxilla is preserved (Fig. 2.1–3). This is subvertical, as a convex ornamented lateral wall preserving the surface of contact with the jugal posteriorly (Fig. 2.1). Medially, the maxilla is flat anteriorly and slightly concave posteriorly. Ventrally, there are five complete alveoli and one partially preserved, which would correspond to the 7th–12th maxillary teeth, all of them aligned within the alveolar groove (Fig. 2.2). Medially to the first three preserved alveoli there are three depressions that correspond to the occlusal pits for the mandibular teeth. This character also represents a synapomorphy of Peirosauridae (Turner and Sertich, 2010; Sertich and O'Connor, 2014). Posteromedially, part of the anterolateral margin of the right suborbital fenestra is preserved on the palatal shelves of the maxillae. The extension of the maxillary participation in the suborbital fenestra is variable among peirosaurids. In *Hamadasuchus* the maxilla barely enters into the lateral margin of the suborbital fenestra before being excluded by the palatine anteriorly and ectopterygoid posteriorly (Larsson and Sues, 2007), whereas in *Bayomesasuchus*, *Montealtosuchus*, *Lomasuchus* Gasparini, Chiappe and Fernández, 1991, *Gasparinisuchus* and *Pepesuchus deiseae* Campos, Oliveira, Figueiredo, Riff, Azevedo, Carvalho and Kellner, 2011, the maxillary participation in the suborbital fenestra is wide. The tooth-row extends caudally beyond the anterior margin of these fenestrae as in all peirosaurids, contrarily to the condition in advanced notosuchians and baurusuchids (Montefeltro *et al.*, 2011; Pol *et al.*, 2014).

Postorbital and squamosal. The preserved fragment of the articulated postorbital and squamosal corresponds to a section of the anterolateral margins of the left supratemporal fenestra and fossa (Fig. 2.6–7). The postorbital fragment corresponds to the anterolateral corner of the skull table. In dorsal view (Fig. 2.6), the postorbital has a flat and ornamented surface with a convex anterolateral margin, suggesting that the anterolateral corner of the skull table is blunt as in most notosuchians. It also has a descending process that forms the anterior limit of the otic recess, which is partially exposed in lateral view (Fig. 2.7) as in all notosuchians (Pol *et al.*, 2014). In the anterolateral corner (Fig. 2.6–7), the postorbital forms a small portion of the rugose anterior process for the articulation with the posterior palpebral. Within the supratemporal fossa the postorbital is smooth and sutured to the squamosal posteriorly. In dorsal view (Fig. 2.6), the anterolateral exposure of the supratemporal fossa is narrow as in *Lomasuchus* and the African peirosaurids *Hamadasuchus* and *Rukwasuchus yajabalijekundu* Sertich and O'Connor, 2014 (Larsson and Sues, 2007: figs.1, 7; Sertich and O'Connor, 2014: fig. 2) but differing from *Montealtosuchus* (Carvalho *et al.*, 2007: pl. 1) and *Uberabasuchus* Carvalho, Ribeiro and Ávila, 2004. The postorbital dorsally overlaps the squamosal along an interdigitated suture (Fig. 2.6–7).

The left squamosal is preserved in two fragments (Fig. 2.10–11). The anterior fragment has a flat ornamented dorsal surface that forms the lateral margin of the supratemporal fossa and fenestra (Fig. 2.6). Within the supratemporal fossa the descending lamina is smooth. It forms the roof of the otic recess ventrally (Fig. 2.7, 11). In dorsal view, the posterior fragment has an anteriorly flat ornamented surface with a straight lateral border (Fig. 2.10–11). It is caudolaterally projected forming a prominent posterolateral process (also ornamented) as in most notosuchians (Pol *et al.*, 2014). The posterolateral process of the squamosal has a marked ventral inclination (Fig. 2.11), forming an angle of 30° with the dorsal plane, a condition similar to that present in all South American peirosaurids (*Lomasuchus*, *Montealtosuchus* and *Uberabasuchus*). This angle is lower than 30° in African peirosaurids (*Hamadasuchus* and *Rukwasuchus* Sertich and O'Connor, 2014). The posterolateral process is anteroposteriorly elongated and bears a wide ventral sulcus, which is roofing the otic recess (Fig. 2.11). The lateral edge of the squamosal has a narrow longitudinal sulcus at the level of the postorbital suture, presumably for the attachment of the muscles associated with an external ear flap, as in extinct and extant crocodyliforms (Shute and Bellairs, 1955; Larsson and Sues, 2007). In occipital view the squamosal preserves part of the surface contacting with the paroccipital process and with the quadrate more anteriorly.

Palatine. A fragment of the left palatine is preserved, in which some characters can be observed (Fig. 2.4–5). Its anterior and posterior ends are missing but it is broader anteriorly. The anterior end of the palatine extends between palatal branches of the maxilla, as in most notosuchians

except baurusuchids (Montefeltro *et al*., 2011). The posterolateral border is curved and corresponds to the anteromedial corner of the suborbital fenestra. The suture with the maxillary palatal process is incomplete and part of the contact with its counterpart is broken. The suture with the maxilla is posterolaterally inclined. Dorsomedially, the palatine has a longitudinal arcuate crest that corresponds to the wall of the nasopharyngeal duct.

Ectopterygoid. The right ectopterygoid is T-shaped and the descending process articulating with the pterygoid flanges is missing (Fig. 2.8–9). The anterior process is short and has two articular facets, one for the maxilla and another one for the jugal (Fig. 2.8). The contact surface with the maxilla is flat, short and anteromedially oriented, whereas the surface of contact with the jugal is larger and anteroposteriorly oriented. The body of the ectopterygoid and the base of the descending process have a lateral torsion and are oval in section, with a flat medial surface (Fig. 2.9). A small foramen pierces the ventral surface where it turns laterally to abut the jugal (Fig. 2.8). The ectopterygoid forms the posterolateral margin of the suborbital fenestra as in many other crocodyliforms.

Mandible

Dentary. The most complete mandibular fragment corresponds to the symphyseal region, which is eroded at its anterior end (Fig. 3.1–3). The fragment is 54.4 mm long, 44.5 mm wide and 15.5 mm thick. The dentary is ornamented ventrally (Fig. 3.2). Anteriorly, both dentaries join along an elongated mandibular symphysis, which extends back to the level of the 10th alveolus (Fig. 3.1) as in *Montealtosuchus*. In *Hamadasuchus* the symphysis extends back to the level of the 11th alveolus (Larsson and Sues, 2007), while in *Gasparinisuchus* (MOZ Pv-1750) it extends to the level of the 8th alveolus. In the narrow-snout peirosaurids *Itasuchus jesuinoi* Price, 1955, and *Pepesuchus* Campos, Oliveira,

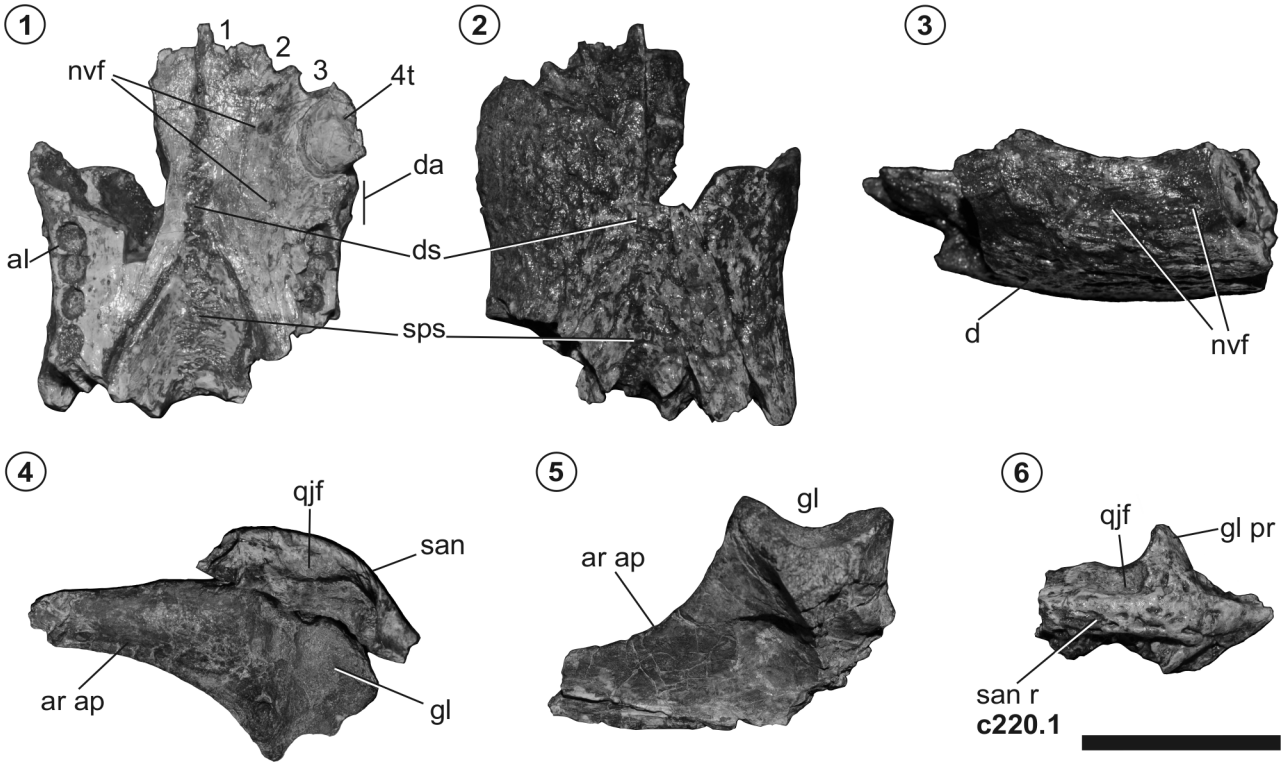

Figure 3. ***Bayomesasuchus hernandezi*** gen. et sp. nov., **MCF PVPH**-822, mandible fragmentary. **1–3,** symphyseal region in **1,** dorsal, **2,** ventral and **3,** lateral views; **4–6,** right articular-surangular in **4,** dorsal, **5,** medial and, **6,** lateral (mirrored image) views. Abbreviations: **al,** alveolus; **ar ap,** articular anterior process; **d,** dentary; **da,** diastema; **ds,** dentary symphysis; **gl,** glenoid fossa; **gl pr,** glenoid posterior ridge; **nvf,** neurovascular foramina; **qjf,** quadratojugal fossa; **san,** surangular; **san r,** surangular ridge; **sps,** splenial symphysis; **4t,** 4th tooth; **1–4** position teeth; **c.220.1,** synapomorphy of Peirosauridae. Scale bar= 2.5 cm.

Figueiredo, Riff, Azevedo, Carvalho and Kellner, 2011, the symphysis extends back beyond the level of the 10th alveolus. The symphyseal region in *Bayomesasuchus* is flattened as in specimens referred to *Hamadasuchus* (Larsson and Sues, 2007: fig. 6), whereas in *Gasparinisuchus* it is concave. In *Uberabasuchus* (CPP 630) and *Gasparinisuchus* the symphyseal region is thicker than in other peirosaurids (*e.g.*, *Bayomesasuchus* and *Montealtosuchus*), whereas in *Hamadasuchus* it is narrower. In the right dentary the 1st–3rd alveoli are anteriorly damaged, the 4th–5th alveoli are complete and the 6th–7th alveoli are partially preserved (Fig. 3.1). The dentary bulges laterally at the level of the 4th dentary tooth, which is the largest of the series. Alveoli preserved in the left dentary are 1st and 4th (partially preserved), 5th to 8th (complete) and 9th (preserved only anteriorly). The mandibular symphysis has an interdigitate suture, particularly along its posterior region (Fig. 3.1). Lingual and lateral to the alveolar row there are small neurovascular foramina (Fig. 3.1, 3).

The alveolar margin of the dentary is festooned in dorsal and lateral views (Fig. 3.1, 3). In dorsal view, the fragment is anteriorly wide and spatula-shaped, being its maximum width coincident with the 4th alveolus. Posteriorly, it slightly narrows up to the level of the 6th and 7th alveoli (Fig. 3.1). In lateral view, the alveolar margin is deeply concave at the level of the 4th dentary tooth (Fig. 3.3). Posteriorly and ventrally to that level, there is a smooth dorsolateral depression for the maxillary teeth during occlusion.

Splenial. The splenial forms part of the mandibular symphysis (Fig. 3.1–2), as in basal crocodyliforms, notosuchians, and many long-snouted neosuchians (Clark, 1994). In dorsal and ventral views, the dentary-splenial suture is oriented anteromedially, as in other peirosaurids and long-snout neosuchians (Carvalho *et al.*, 2007; Larsson and Sues, 2007; Leardi and Pol, 2009; *e.g.*, *Gavialis gangeticus* [MLP 602] pers. obs.). The ventral exposure of both splenials along the symphyseal region is broad, contrasting with derived notosuchians (Pol *et al.*, 2014). Dorsally, the splenial is transversely expanded and slightly concave (Fig. 3.1). The splenial symphysis is wedge-shaped, unlike other notosuchians such as *Notosuchus terrestris* Woodward, 1896 (MCF PVPH-710), and it extends anteriorly to the level of the 6th alveolus as in *Gasparinisuchus* and *Montealtosuchus* (Carvalho *et al.*, 2007). In *Hamadasuchus* the splenial symphysis is more acute and extends to the 7th alveolus (Larsson and Sues, 2007). The splenial expands dorsally behind the mandibular symphysis. The ventral surface of this bone is ornamented (Fig. 3.2), as in *Uberabasuchus* and possibly *Hamadasuchus* and *Montealtosuchus*. The inter-splenial suture is markedly interdigitated (Fig. 3.1–2). In the preserved fragment, the posterior end of the splenial does not reach the alveolar row (Fig. 3.1). Immediately behind the posterior end of the symphyseal facet, part of anterior margin of the *foramen intermandibularis oralis* is preserved, as observed in uruguaysuchids, baurusuchids and others peirosaurids such as *Hamadasuchus* (Larsson and Sues, 2007; Montefeltro *et al.*, 2011; Pol *et al.*, 2014).

Articular. The articular is triangular and partially preserved, missing the retroarticular process and a small portion of the prearticular process (Fig. 3.4–5). The prearticular process has a dorsal surface that is markedly concave anteroposteriorly. A well-defined, curved, and anteroventrally oriented crest separates the dorsal and medial surfaces. The medial surface is wider and also concave. The glenoid fossa has an anteromedially triangular projection that is continuous with the previously mentioned crest (Fig. 3.4). The medial and lateral concavities for the quadrate condyles are separated by an oblique ridge. Ventrally, a section of the surface of contact for the angular is preserved. The retroarticular process is damaged but the fracture plane suggests that it was posteroventrally oriented (Fig. 3.5).

Surangular. Only the portion of the surangular adjacent the glenoid fossa is preserved (Fig. 3.4, 6). It contacts the articular laterally, forming the lateral wall of this fossa. Laterally, the surangular forms an elevated posterior buttress for the lateral condyle of the quadrate (Fig. 3.6), a feature shared by several notosuchians such as peirosaurids, sebecids and baurusuchids, but absent in uruguaysuchids and derived notosuchians (Pol *et al.*, 2014). Posterior to this projection, there is a smooth concave surface that corresponds to the lateral portion of the base of the retroarticular process. Part of the surface of contact for the angular is preserved at the posteroventral end. Laterally, the surangular is ornamented and bears a longitudinal prominent ridge (Fig. 3.6) also observed in *Montealtosuchus* and *Uberabasuchus*. This ridge forms the dorsal limit of an ornamented depression. On this ridge and lateral to the glenoid fossa (Fig. 3.4, 6) there is an oval concavity for the articula-

tion with the quadratojugal condyle, indicating the double mandibular articulation (quadrate-articular/surangular and quadratojugal-surangular). This double mandibular joint is a feature shared with *Montealtosuchus*, *Mahajangasuchus insignis* Buckley and Brochu, 1999 and *Lomasuchus* (MCF PVPH-160), as well as many basal mesoeucrocodylians (*e.g., Sebecus icaeorhinus* Simpson, 1937), but is absent in *Uberabasuchus* (Carvalho *et al*., 2007). The glenoid fossa and this concavity are separated by a sharp ridge (Fig. 3.4).

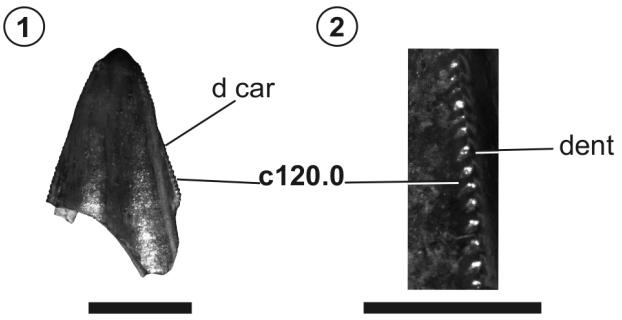

Figure 4. ***Bayomesasuchus hernandezi*** gen. et sp. nov., **MCF PVPH**-822; **1–2,** isolated left 4th dentary tooth in **1,** labial view; **2,** close-up denticle morphology. Abbreviations: **dent,** denticle; **d car,** denticulated carinae; **c120.0,** synapomorphy of Peirosauridae. Scale bars= 5 mm (**1**) and 2.5 mm (**2**).

Ornamentation

The ornamentation of the mandibular fragment is characterized by a smooth dorsolateral depression with neurovascular foramina, and rugose ventral and lateral surfaces characterized by the presence of pits and vermiform grooves (Fig. 3.2–3). This contrasts with some mesoeucrocodylians (*e.g.,* modern crocodylians) that are ornamented with subcircular pits. The surangular fragment has subcircular pits on the lateral prominent ridge, but within the depression these pits are larger. This ornamentation disappears towards the glenoid fossa area (Fig. 3.6). The ornamentation of the maxillary fragment is formed by isolated longitudinal shallow grooves, crests, and circular pits (Fig. 3.1). In the preserved skull table (Fig. 3.6–7, 10–11), the ornamentation consists on deep pits with irregular shapes and crests, which are more evident in the squamosal than in the postorbital. The posterolateral process of the squamosal presents a marked ornamented ledge formed by small pits except at the distal end. The ornamentation of the skull and lower jaw elements of *Bayomesasuchus* is similar to that of basal notosuchians such as uruguaysuchids and peirosaurids, as well as that of neosuchians.

Dentition

The preserved teeth show pseudoheterodonty (*sensu* Iordansky, 1973), and two morphologies are distinguished: large teeth with conical crown (caniniform) and small teeth with globose crown (post-caniniform) (Figs. 2.1–3, 4.1). The 4th dentary tooth is the largest of the preserved tooth-row (Figs. 3.1, 4.1) and is a caniniform with a posteriorly curved apex and cylindrical cross-section. The preserved maxillary teeth have slightly compressed globose crowns (Fig. 2.1–3). The isolated left caniniform tooth corresponds to the 4th dentary tooth and preserves the apical portion of the enamel showing convex labial and lingual surfaces (although the latter is slightly flattened). This tooth is ziphodont, a condition present in most notosuchians (*e.g.*, sebecids, baurusuchids) and some eusuchians (Brochu, 2013). The mesial and distal keels are fully denticulated and each keel bears three or four denticles per millimeter (Fig. 4.2), although the denticle density is greater at the apex (Fig. 4.1). The denticle density is lower than that of the peirosaurid *Barcinosuchus gradilis* Leardi and Pol, 2009 in which there are 11–12 denticles per millimeter. The maxillary post-caniniform teeth have crowns with subequal labial and lingual surfaces separated by a mesiodistal keel. The crown in these teeth is separated from the root by a marked constriction or neck (Fig. 2.1, 3). The preserved anterior maxillary tooth has a triangular crown, whereas in the smaller posterior tooth the crown is low, blunt and spatulate (Fig. 2.1–3). Although poorly preserved, the enamel of these teeth presents denticles on the distal keel. The posteriormost tooth has no preserved denticles.

As in *Montealtosuchus*, *Gasparinisuchus* and *Hamadasuchus*, the anterior dentary alveoli are subcircular, whereas the posterior ones are oval in cross-section (Fig. 3.1, 5). The 1st–4th teeth are implanted in discrete equidistant alveoli, the 5th and 6th alveoli are confluent, and the 7th alveolus is clearly separated but close to the 6th alveolus. The separation between the 7th and 8th alveoli is clear, whereas the 8th and 9th alveoli are confluent because the septum is incomplete. The interalveolar space between the 4th and 5th alveoli is wide (diastema), similar in anteroposterior length

to the 5th alveolus. The preserved maxillary tooth-row is located along an almost straight alveolar groove (Fig. 2.2). The maxillary alveoli are smaller posteriorly, although the 2nd alveolus is slightly larger. All maxillary teeth are equidistant and close to each other. In the dentary, the 4th alveolus is the largest, the 1st–3rd alveoli are smaller and subequal and are followed in size by the 5th and 6th alveoli (which are equal in size). The 7th and 8th alveoli are slightly smaller than the anterior ones but subequal in size, and finally the 8th alveolus is slightly larger (Fig. 2.1). In *Montealtosuchus*, *Gasparinisuchus* and *Hamadasuchus* the dentary diastema between the 4th and 5th alveoli is absent, and the 5th alveolus is not confluent with the 6th alveolus in these peirosaurids, contrary to the condition observed in *Bayomesasuchus* (Larsson and Sues, 2007: fig. 6D; Pol *et al.*, 2014: fig. 40C) (Fig. 5).

DISCUSSION

***Peirosaurid characters in* Bayomesasuchus.** Most peirosaurids studies were based on skull remains (*e.g.*, Gasparini *et al.*, 1991; Carvalho *et al.*, 2004, 2007; Larsson and Sues, 2007; Martinelli *et al.*, 2012; Sertich and O'Connor, 2014). The taxa *Lomasuchus* and *Rukwasuchus* have no comparable mandibular elements, and *Barcinosuchus* Leardi and Pol, 2009 is very fragmentary compared to *Bayomesasuchus*. This new taxon (a reconstructed image of the skull of *Bayomesasuchus* is shown in Figure 7) shares with peirosaurids the following combination of characters (*synapomorphies of Peirosauridae): ziphodont (except in *Gasparinisuchus*) and pseudoheterodont dentition*, festooned dental margins, ornamentation with pits and grooves, elongated dentary and splenial symphysis, symphyseal region flattened and laterally narrow, splenial dorsal and ventral exposure triangular, postorbital with process descending to anterior otic recess and facet to palpebral bone, squamosal with elongate ornamented posterolateral process*, maxillary tooth-row reaching caudally beyond the anterior margin of the suborbital fenestra, maxillary palate with occlusal depressions*, subvertical rostrum, surangular with prominent posterolateral ridge forming part of the mandibular joint (except in *Uberabasuchus*).

The autapomorphies that justify *Bayomesasuchus hernandezi* as a new taxon are: diastema between 4th–5th dentary alveoli, and confluence of 5th and 6th alveoli. As mentioned in the description, in *Montealtosuchus*, *Gasparinisuchus* and *Hamadasuchus* there is no diastema between the 4th–5th alveoli, and the 5th alveolus is not confluent with the 6th alveolus (Fig. 5). In the narrow snouted peirosaurids *Itasuchus* Price, 1955 and *Pepesuchus*, the 6th and 7th alveoli are very close to each other but not confluent, with a complete interalveolar septum between them. The same occurs with the next alveolar pair, the 8th and 9th. The 4th–5th, 5th–6th, 7th–8th, and 9th–10th alveoli are separated by a diastema, differing in this from *Bayomesasuchus*. In living crocodilians (F. Barrios, pers. obs.), when a diastema occurs (*e.g.*, *Caiman crocodilus*, ZSM 87/1937,

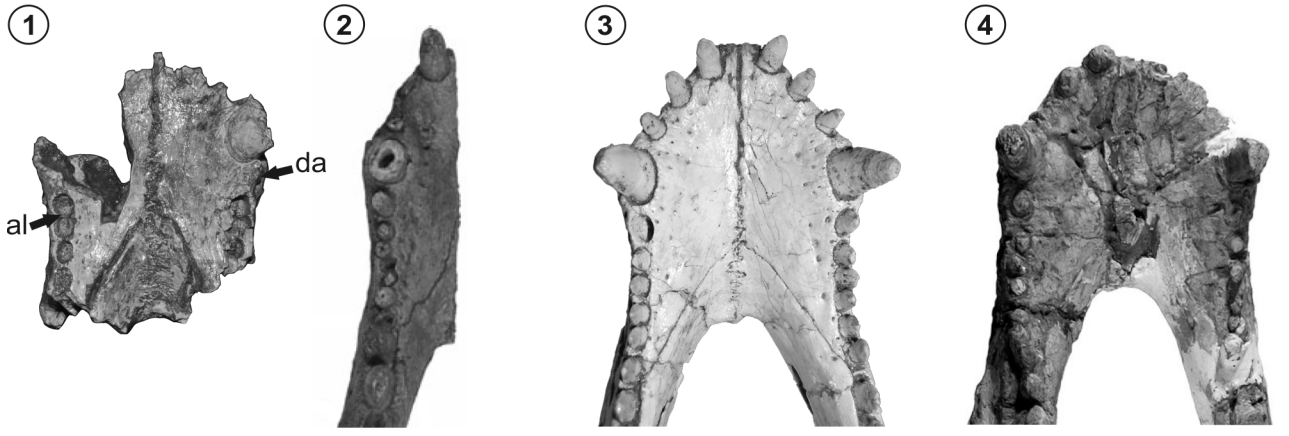

Figure 5. 1, ***Bayomesasuchus hernandezi*** gen. et sp. nov. autapomorphies (*i.e.,* **da,** diastema between 4th–5th; **al,** confluent alveoli) compared with **2,** *Hamadasuchus rebouli*; **3,** *Montealtosuchus arrudacamposi*, and **4,** *Gasparinisuchus peirosauroides*.

ZSM 206/1925; *Caiman yacare*, MACN 8268, MACN 30536, MACN 30555, MLP R 5041, ZSM 163/1929, ZSM 163/1933, ZSM 164/1933, ZSM 167/1933, ZSM 168/1629, ZSM 170/1937; *Melanosuchus niger*, ZSM 67/1911) and confluence of alveoli (*Crocodylus niloticus*, PVL 6524; *C. crocodilus*, ZSM 101/1911; *C. yacare*, MACN 8262, ZSM 167/1929), they are symmetrically disposed on both mandibular rami, as in *Bayomesasuchus*, *Pepesuchus*, and *Itasuchus*. Therefore, we consider as valid the two autapomorphies listed for *Bayomesasuchus hernandezi*, as they are features not seen in other peirosaurids.

Phylogenetic analysis. A phylogenetic analysis was undertaken to test the position of *Bayomesasuchus* within Crocodyliformes. The matrix published by Pol *et al.* (2014) was modified to include the specimen described here (character scorings in Appendix 1). The resulting matrix, with 412 morphological characters and 110 terminal taxa, was analyzed under maximum parsimony criteria using the software TNT version 1.1 (Goloboff *et al.*, 2008a, b). A heuristic tree search strategy of 10,000 replicates of Wagner trees (random addition sequences) was conducted followed by tree branched reconnection (**TBR**) branch swapping (holding 10 trees per replicates). The cladistic analysis resulted in 20,380 most parsimonious trees (**MPTs**) of 1558 steps, with a consistency index (**CI**) of 0.317 and a retention index (**RI**) of 0.739. The analysis supports Peirosauridae as a monophyletic group within Notosuchia and the clade formed by South American peirosaurids + *Hamadasuchus* as the sister group of the other African notosuchians and Uruguaysuchidae, as proposed by Pol *et al.* (2012, 2014) and Sertich and O'Connor (2014).

The consensus tree placed *Bayomesasuchus* within Peirosauridae (Fig. 6), forming a polytomy with *Hamadasuchus*, *Gasparinisuchus*, *Lomasuchus*, *Montealtosuchus* and *Uberabasuchus*, contrasting the analysis by Sertich and O'Connor (2014), in which *Hamadasuchus* is deeply nested among other peirosaurids. In previous phylogenetic analyses *Hamadasuchus* is shown either as the sister group of the South American peirosaurids (Larsson and Sues, 2007; Pol *et al.*, 2014) or forming a polytomy with the South American relatives (Turner and Sertich, 2010; Pol *et al.*, 2012). On the other hand, *Mahajangasuchus* Buckley and Brochu, 1999 + *Kaprosuchus* Sereno and Larsson, 2009 and *Stolokrosuchus* Larsson and Gado, 2000 are depicted as successive sister groups of peirosaurids, as in Pol *et al.* (2014) and partially in Sertich and O'Connor (2014), where *Stolokrosuchus* has a terminal position.

The present analysis reveals five unambiguous synapomorphies diagnosing Peirosauridae: tooth with denticulate carinae (character 120.0) (absent in the holotype of *Gasparinisuchus*); nasal-maxilla suture nearly parallel (character 128.0); supraoccipital not exposed in skull roof (character 171.0); foramen present in perinarial depression of premaxilla (character 237.1); maxilla-palatine suture with palatine anterior end slightly invaginate (character 243.2); prominent depression on the maxillary palate at the level of the sixth or seventh alveolus (character 396.1) (see Pol *et al.*, 2014). In some MPTs two other character states provide unambiguous synapomorphies of peirosaurids: choanal groove partially septate (character 69.1) and longitudinal ridge along the dorsolateral surface of surangular (character 220.1). Of all these synapomorphies, only three can be recognized in the holotype of *Bayomesasuchus hernandezi* gen. et sp. nov.: ziphodont tooth, depression on the maxillary palate at the level of the sixth or seventh alveolus, and longitudinal ridge dorsolateral to surangular.

The fragmentary nature of the cranial remains of *Bayomesasuchus* and the lack of postcranial remains precludes the resolution of the polytomy obtained for the studied peirosaurids. Phylogenetic relationships of other mesoeu-

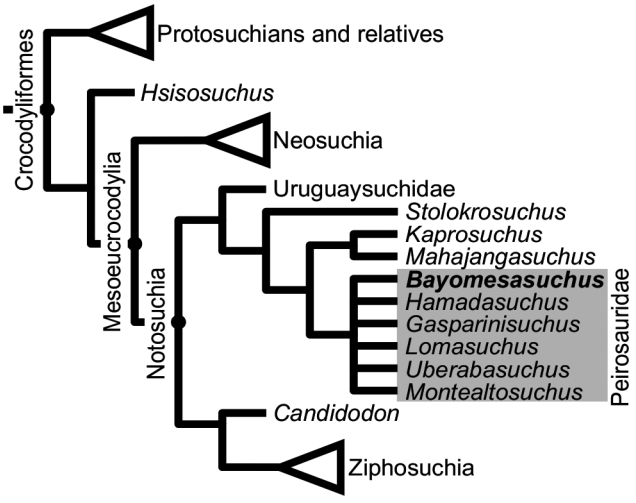

Figure 6. Strict consensus tree, in gray the node including ***Bayomesasuchus hernandezi*** gen. et sp. nov. **CI**= 0.308; **RI**= 0.745.

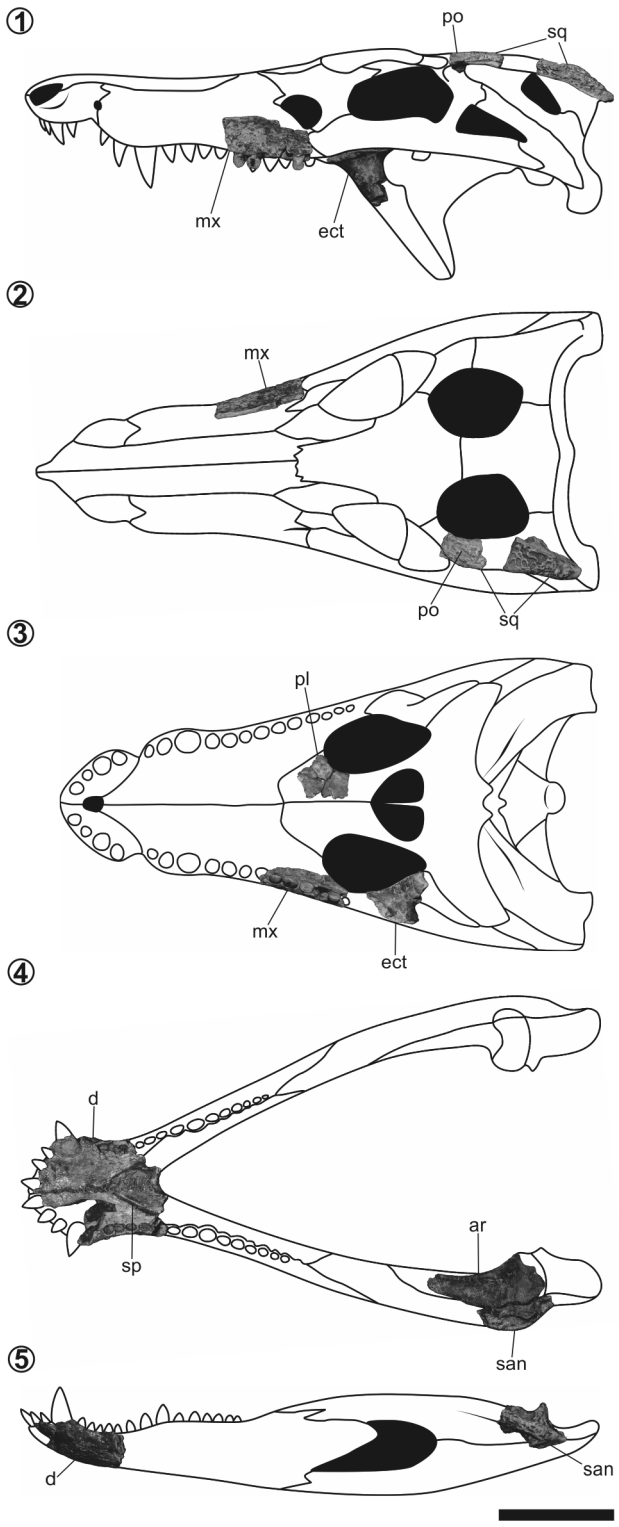

Figure 7. ***Bayomesasuchus hernandezi*** gen. et sp. nov. schematic skull reconstruction; **1–3,** skull in **1,** left lateral (maxilla mirrored), **2,** dorsal, and **3,** palatal views; **4–5,** mandible in **4,** dorsal (articular and surangular mirrored), and **5,** left lateral views (surangular mirrored). Abbreviations: **ar,** articular; **d,** dentary; **ect,** ectopterygoid; **mx,** maxilla; **pl,** palatine; **po,** postorbital; **san,** surangular; **sp,** splenial; **sq,** squamosal. Scale bar= 5 cm.

crocodylians with peirosaurid affinities (*e.g.*, *Mahajangasuchus*, *Stolokrosuchus*, *Kaprosuchus*, and *Trematochampsa* Buffetaut, 1974) is controversial (Buckley and Brochu, 1999; Larsson and Gado, 2000; Larsson and Sues, 2007; Sereno and Larsson, 2009; Turner and Sertich, 2010; Pol *et al.*, 2012; Sertich and O'Connor, 2014) and further studies including other peirosaurids (*e.g., Barcinosuchus*) and probable peirosaurids (*e.g., Pepesuchus*, and *Itasuchus*) need to be carried out in order to better understand a more comprehensive phylogenetic context of Peirosauridae relationships.

Stratigraphic precedence and implications. Peirosaurids are currently known from South America and Africa, indicating a Gondwanan distribution for the group. Peirosauridae is known from the Cretaceous of South America (Argentina and Brazil), and Africa (Morocco, Niger and Tanzania) (Gasparini, 1982; Gasparin *et al.*, 1991; Larsson and Gado, 2000; Larsson and Sues, 2007; Sertich and O'Connor, 2014). The oldest records of the family are from the Aptian of Africa: *Rukwasuchus yajabalijekundu* (Galula Formation, Aptian–Cenomanian), *Hamadasuchus rebouli* (Kem Kem beds, Albian–Cenomanian), and Patagonia: *Barcinosuchus gradilis* (Cerro Barcino Formation, Aptian–Albian) (Larsson and Sues, 2007; Leardi and Pol, 2009; Sertich and O'Connor, 2014).

The two named peirosaurids from the Neuquén Group (*Lomasuchus palpebrosus* and *Gasparinisuchus peirosauroides*) are from Late Cretaceous units, the Portezuelo, Bajo de la Carpa, and Anacleto formations (late Turonian–Campanian), which form the Río Neuquén and Río Colorado subgroups. Until now, peirosaurid materials from the Cerro Lisandro Formation (mid–upper Turonian) from the underlying Río Limay Subgroup (Cenomanian–Turonian; Garrido, 2010) were restricted to isolated teeth, plates/scutes, and other poorly informative fragments from the Cerro Bayo Mesa locality (Coria *et al.*, 1996; Garrido, 2000). *Bayomesasuchus hernandezi* is the first peirosaurid species identified not only from the Cerro Lisandro Formation, but also from the Río Limay Subgroup, representing the oldest record (mid Turonian; Garrido, 2010) of Peirosauridae in the Neuquén Basin and increasing the crocodyliform diversity of the Neuquén Group.

The resultant polytomy between African and South American peirosaurids (Fig. 6), however, reinforces a Gondwana distribution of the Peirosauridae clade, and does not

support the hypothesis of a South American endemic peirosaurid clade (Carvalho *et al*., 2007). The obtained topology provides a clear faunal link between these two landmasses during the Cretaceous. New discoveries are needed to improve our understanding of the paleobiogeographic history of Peirosauridae in Gondwana during this period.

CONCLUSIONS

The presence of the new small-size peirosaurid *Bayomesasuchus hernandezi* improves the systematic understanding of this group in South America, while increasing the diversity of Patagonian crocodyliforms. The new taxon is also important as it is the first peirosaurid identified from the Río Limay Subgroup, being the oldest record of Peirosauridae from the Neuquén Basin. Although the specimen is fragmentary, the preserved material allowed a phylogenetic analysis that shows *Bayomesasuchus* closely related to the African (*e.g., Hamadasuchus*) and the South American peirosaurids (*Uberabasuchus*, *Montealtosuchus*, *Lomasuchus* and *Gasparinisuchus*), reinforcing the Gondwanan distribution of Peirosauridae.

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