

Redescription and reevaluation of the taxonomical status of *Microsuchus schilleri* (Crocodyliformes: Mesoeucrocodylia) from the Upper Cretaceous of Neuquén, Argentina



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ABSTRACT

Fragmentary remains of *Microsuchus schilleri* (Crocodyliformes: Mesoeucrocodylia) from the Bajo de La Carpa Formation (Santonian, Late Cretaceous) of northern Patagonia, Argentina, are described and reevaluated taxonomically. The type specimen is an articulated individual with hindlimb and axial remains. *Microsuchus* has several traits that allow to recognize it as a valid taxon (the presence of bulge lateral to the prezygapophyses of the second sacral vertebra; elongated posterior zeugopodia; proximal caudal centra with triangular cross section). *Microsuchus* was originally assigned as a goniopholidid based on the platycely of its vertebral centra, a character that is widely distributed among fossil crocodyliforms. A phylogenetical analysis using an expanded data matrix focusing on postcranial data was performed in which *Microsuchus* and another long-limbed crocodyliform from the same location, *Neuquensuchus*, were included. *Microsuchus* is depicted in a polytomy as a basal mesoeucrocodylian, with its position as a neosuchian or notosuchian supported by a single synapomorphy on the different most parsimonious trees. Additionally, *Neuquensuchus* is well nested among notosuchians, in contrast to previous hypothesis. These findings further increase the crocodyliform diversity of the Bajo de la Carpa Formation and emphasize the relevance of its fauna in studies of the diversification of mesoeucrocodylians and notosuchians. Furthermore, the occurrence of both *Microsuchus* and *Neuquensuchus* gives evidence of a basal stock of mesoeucrocodylians with elongated limbs that was not previously reported for northern Patagonia.

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1. Introduction

During the Late Cretaceous, Patagonia and the rest of Gondwana was dominated by an astonishing fauna of dinosaurs (de la Fuente et al., 2007; Gasparini et al., 2007). Nevertheless, the fossil crocodyliforms possess an equally important fossil record in Gondwana, becoming abundant and even dominating in particular paleoenvironments with a great diversity during the Cretaceous (Candeiro and Martinelli, 2006; Pol and Gasparini, 2007). In Argentina the findings of Mesozoic crocodyliforms are mostly centered on the Upper Cretaceous of the northern part of Patagonia.

Most of the Argentinean crocodyliform diversity is represented by two groups of notosuchians that also dominated in other Gondwana areas: 1) a basal group formed by Peirosauridae and Uruquaysuchidae; and 2) the ziphosuchians (Pol and Gasparini, 2007). After numerous studies in the last thirty years, a more complete picture of phylogenetic relationships and evolutionary patterns within fossil crocodyliforms was obtained, resulting in important conclusions on their biodiversity, distribution, paleobiology and paleoecology (Clark, 1986; Buckley & Brochu, 1999; Turner, 2004; Candeiro and Martinelli, 2006; Pol and Gasparini, 2007; Sereno and Larson, 2009; Turner and Sertich, 2010; Pol et al., 2012). In total, thirteen different taxa were identified in the northern region of Patagonia: two from the Candeleros Formation (*Araripesuchus buitreaensis* Pol and Apesteguía, 2005; *Araripesuchus patagonicus* Ortega, Gasparini, Buscalioni and Calvo, 2000); one from the Anacleto Formation (*Pehuenschuchus enderi* Turner and Calvo, 2005); one from the Portezuelo Formation (*Lomasuchus palpebrosus*

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Gasparini, Chiappe and Fernández, 1991); one from the Plottier Formation (a putative new peirosaurid [Arcucci et al., 2011]); and eight taxa from the Bajo de La Carpa Formation (*Notosuchus terrestris* Woodward, 1896; *Cynodontosuchus rothi* Woodward, 1896 [see Pol and Gasparini, 2007]; *Comahuesuchus brachybuccalis* Bonaparte, 1991; *Wargosuchus australis* Martinelli and Pais, 2008; *Neuquensuchus universitas* Fiorelli and Calvo, 2007; *Gasparinisuchus peirosauroides* Martinelli, Sertich, Garrido and Pradeiro, 2012; *Microsuchus schilleri* Dolgopol de Sáez, 1928; and a purported new peirosaurid [Fiorelli, 2010]). The Bajo de La Carpa Formation is the most prolific unit in Patagonia in terms of the notosuchian record. Many of the taxa from that formation were discovered in the last twenty five years, while others (*Notosuchus*) were known since the 19th century but have been recently redescribed (Pol, 2005; Fiorelli and Calvo, 2007). However, there is one taxon that has been almost ignored in recent studies – *Microsuchus schilleri*.

In the early twentieth century, field trips were performed to the areas surrounding the city of Neuquén by Santiago Roth and Walter Schiller, following the initiative of Smith Woodward. During one of these trips, in 1921, the articulated remains of *Microsuchus schilleri* were found. Afterwards, Dolgopol de Sáez (1928) described this new crocodyliform for first time and pointed out that the remains of *Microsuchus schilleri* came from the “layers with dinosaurs” approximately 5 km north from the Neuquén and Limay rivers confluence. Nowadays, this is the area of the Campus of the National University of Comahue (NUC), in the city of Neuquén (area formerly called “Boca del Sapo”), where sediments of the Bajo de la Carpa and Anacleto formations crop out (Garrido, 2000; Heredia and Calvo, 2002; Fernández et al., 2013). The original description of the remains was very precarious mainly because of the poor knowledge at that time of the diversity and anatomy of the group (Dolgopol de Sáez, 1928). Due to the very small size of this crocodyliform, Dolgopol de Sáez proposed the name *Microsuchus* and described it as a new goniopholidid, mainly based on its vertebral and osteoderm anatomy. This idea was also consistent with the ideas of F. von Huene, whose technician prepared the specimen. Thus, very little is known about *Microsuchus* besides that is a very tiny and fragmentary, represented only from postcranial remains.

In this paper, the anatomy of *Microsuchus schilleri* is redescribed in detail based on the holotype. Deep technical preparations on the original material were performed in order to study the postcranial remains. The objective of this redescription is to clarify the taxonomical status of *Microsuchus* and its phylogenetic relationships. In addition, *Microsuchus* shares with *Neuquensuchus*, an enigmatic taxon recovered from the same locality (Fiorelli and Calvo, 2007), a very elongated hindlimb with the tibia being longer than the femur. This is a very unusual character for any crocodyliform, potentially indicating the presence of a poorly sampled group of long-legged basal mesoeucrocodylians in the Neuquén basin.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, U.S.A.; FMNH PR, Field Museum of Natural History, Chicago, U.S.A.; GPIT, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCF, Museo Carmen Funes, Plaza Huinca, Argentina; MCZ, Museum of Comparative Zoology, Massachusetts, USA; MLP, Museo de La Plata, La Plata, Argentina; MNK-PAL, Museo de Historia Natural Noel Kempf Mercado, Santa Cruz de la Sierra, Bolivia; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MUC-PV, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; MZSP, Museu Zoologia, Universidade de São Paulo, São Paulo, Brazil; SAM, Iziko-South African Museum, Cape Town, South Africa;

UA, University of Antananarivo, Madagascar; ZPAL, Instytut Paleobiologii PAN, Warszawa, Poland.

2. Systematic paleontology

Crocodyliformes Hay 1930 (sensu Clark, 1986)
 Mesoeucrocodylia Whetstone and Whybrow, 1983
Microsuchus schilleri Dolgopol de Sáez, 1928
 Figs. 2–7

Holotype: MLP-PV 26-IV-30-1. Partially articulated specimen including four posterior dorsal, two sacral and three postsacral vertebrae; right and left illia with partial remains of the ischium; left articulated hindlimb which includes the femur, tibia, proximal and distal ends of the fibula, tarsus, proximal ends of the metatarsals; and, isolated ventral osteoderms (Fig. 2).

Type Locality: The outcrops located North of the Neuquén City in the classic locality of “Boca del Sapo”, now the campus (and surrounding areas) of the NUC, Neuquén Province, Argentina (Fig. 1).

Stratigraphic horizon: Deposits of the Bajo de la Carpa and Anacleto formations, Río Colorado Subgroup, Neuquén Group (middle to upper Santonian *sensu* Leanza et al., 2004). The sedimentary matrix surrounding the fossil was coarse-grained pink sandstone, similar to other fossil examples from the Bajo de la Carpa Formation (Bonaparte, 1991; Fiorelli and Calvo, 2007, 2008; Martinelli and Pais, 2008). The sediments of the Bajo de la Carpa Formation from the area of the NUC campus were deposited in fluvial and aeolian systems (Sánchez et al., 2006). For sedimentary and taphonomic characteristics of the campus area and its fossils, see Fiorelli (2010) and Fernández et al. (2013).

Emended Diagnosis: Mesoeucrocodylian crocodyliform characterized by the following diagnostic postcranial characters (autapomorphies marked with an asterisk): prezygapophyses continue posteriorly as sharp laminae (prezygapophyseal laminae)*; lateral bulge present laterally to the prezygapophyses of the second sacral vertebra*; parallelogram-shaped second sacral centrum, with the anterior articular surface being lateromedially wider than the posterior one*; proximal caudal centra with triangular cross section, bearing a well developed ventral crest and deep lateral depressions*; moderately deep acetabulum; anteroposteriorly short postacetabular process; sacral rib scars separated by a non-articular surfaces; second sacral rib scar does not extend on the posteroventral edge of medial surface of postacetabular process; poorly marked fourth trochanter on the femur; tibia longer than the femur; distal medial hook on the fibula; the anterior hollow of the astragalus is a continuous depression and bears a distinct pit correlated with the astragal-tarsale ligament; rectangular ventral osteoderms*.

3. Materials and methods

The postcranial remains were described following the osteological nomenclature proposed by Mook (1921), Romer (1956), and Hoffstetter and Gasc (1969). In contrast to the semi-erect postures of extant crocodylians, basal crocodyliforms have been inferred to possess erect postures (Parrish, 1986, 1987; Pol, 2005). Thus we follow the limb bone orientation of Pol (2005), where they are oriented as if they were held in vertical position.

The comparisons were made using the following taxa and specimens: *Anatosuchus minor* (Serenó and Larsson, 2009); *Araripesuchus gomesii* (AMNH 2450); *Araripesuchus tsangatsangana* (Turner, 2006);

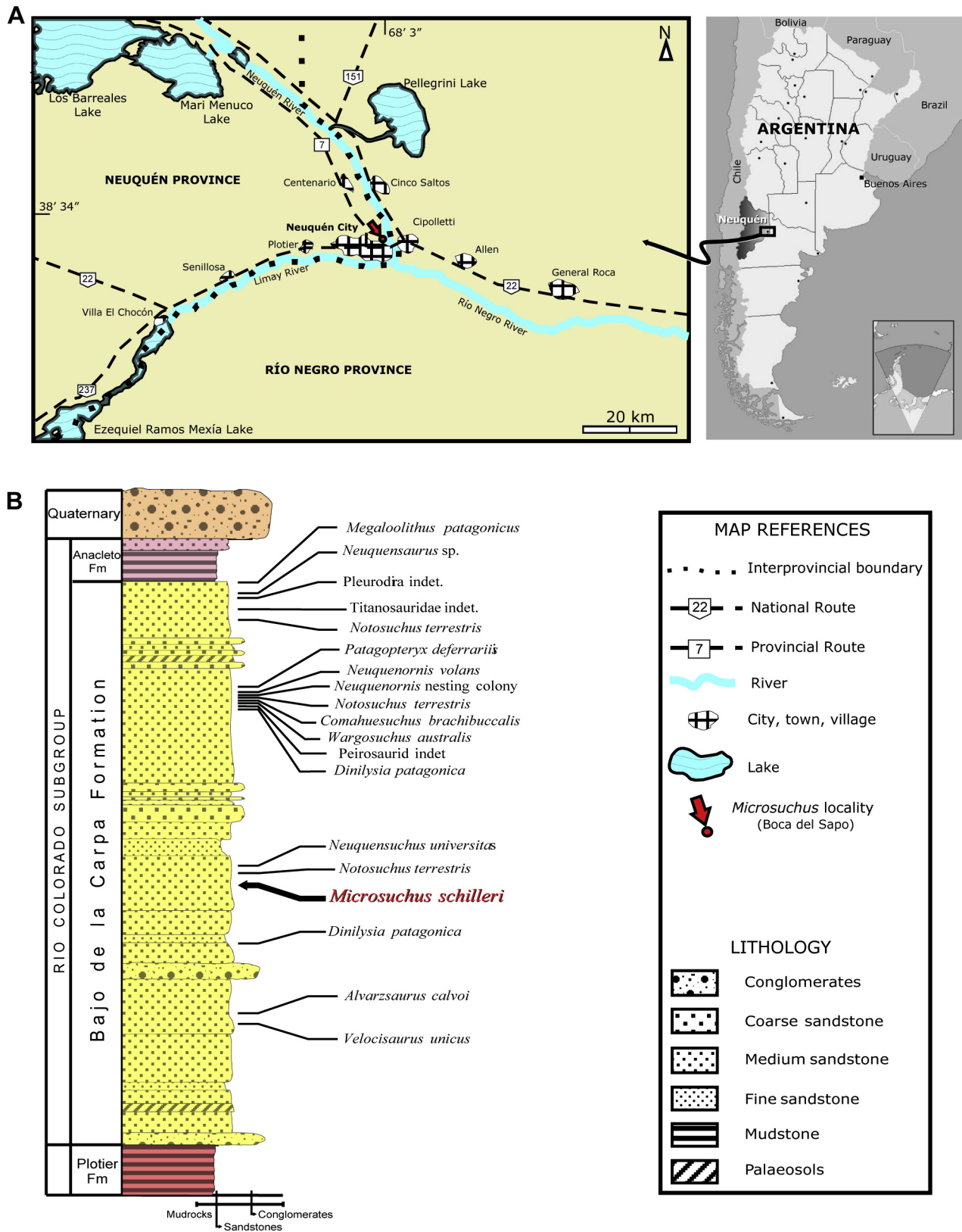


Fig. 1. Geographical map and stratigraphic section of the Neuquén University Campus (NUC). **A.** Location of the study area (left) on the territory of Argentina (right). **B.** Detail of the NUC area. **B.** Stratigraphical section measured at the studied area with the provenance of *Microsuchus schilleri* and the diverse biota spread through the Bajo de la Carpa Formation in the horizons of the NUC.

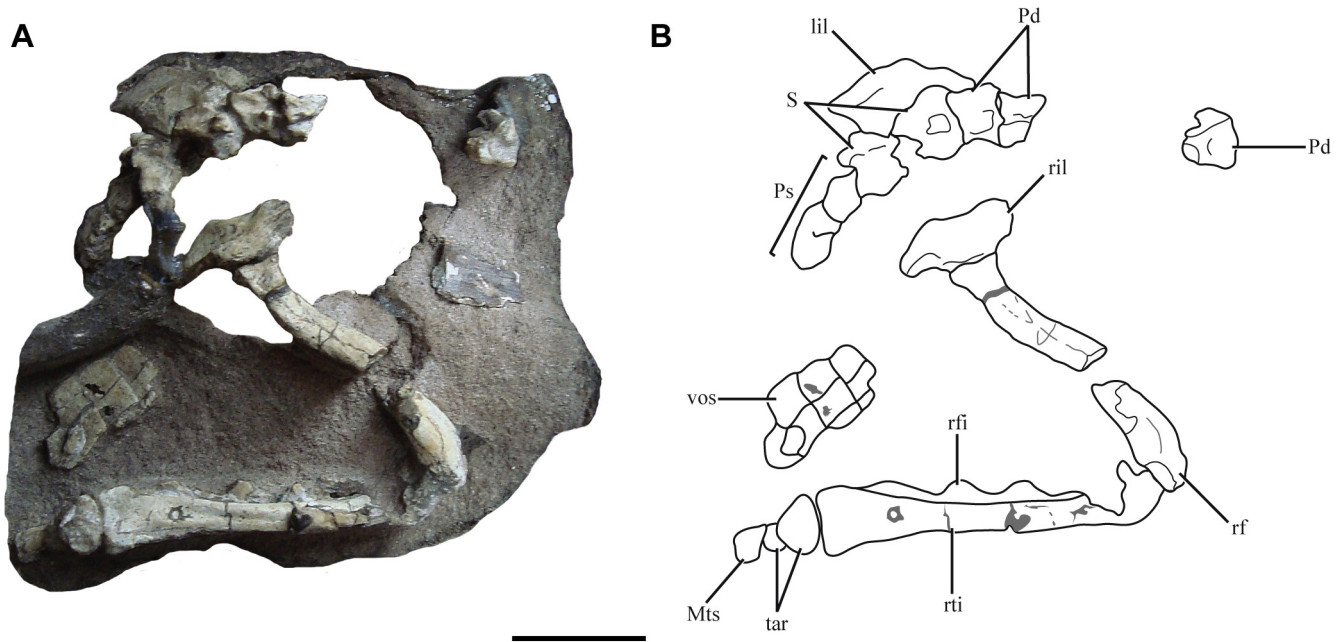


Fig. 2. **A**, General view of the type specimen of *Microsuchus schilleri* (MLP-PV 26-IV-30-1) before the mechanical preparation was performed. **B**, Line drawing of the same specimen. References: **lil**, left ilium; **Mts**, metatarsals; **Pd**, posterior dorsal vertebrae; **Ps**, postsacral vertebrae; **rf**, right femur; **rfi**, right fibula; **ril**, right ilium; **rti**, right tibia; **S**, sacral vertebrae; and **tar**, proximal tarsals; **vos**, ventral osteoderms; Scale bar equals 2 cm.

Baurusuchus albertoi (Nascimento, 2008; Nascimento and Zaher, 2010); *Caiman latirostris* (MPEF-AC 205); *Chimaerasuchus paradoxus* (IVPP V 8274; Wu and Sues, 1996); *Lomasuchus palpebrosus* (MCF-PVPH 160); *Mahajangasuchus insignis* (UA 8654); *Mariliasuchus amarali* (MZSP-PV 50; Nobre and Carvalho, 2013); *Neuquensuchus universitas* (MUC-PV 47; Fiorelli and Calvo, 2007); *Notosuchus terrestris* (MACN-PV RN 1037; MACN-PV RN 1042; MACN-PV RN S/N; MUC-PV 900; Pol, 2005; Fiorelli and Calvo, 2008); *Orthosuchus stormbergi* (SAM-PK 409); *Protosuchus richardsoni* (AMNH 3024; MCZ 6727); *Sebecus icaeorhinus* (AMNH 3159; MPEF-PV 1776; MPEF-PV 3971; MPEF-PV 3972; Pol et al., 2012); *Simosuchus clarki* (UA 8679; FMNH PR 2596; FMNH PR 2597; FMNH PR 2598; Georgi and Krause, 2010; Sertich and Groenke, 2010); *Stenosaurus bollensis* (GPIT 1909 s.264); *Stratiosuchus maxhechti* (Riff, 2007; Riff and Kellner, 2011); *Uruguaysuchus aznarezi* (Rusconi, 1933); *Yacarerani boliviensis* (MNK-PAL5064A-E; Leardi, Pol, Novas, and Suárez Riglos, unpublished data).

4. Description

4.1. Axial skeleton

The axial skeleton of *Microsuchus schilleri* includes six vertebrae, mostly represented by their centra, and four partial vertebral centra. These elements were preserved partially articulated with the rest of the specimen and disarticulated posteriorly, allowing us to be certain that these vertebrae are posterior dorsals, sacrals and proximal caudals (Fig. 2). The only exception to this are two vertebrae (anterior half of a centrum; and, a complete centrum and very fragmentary remains of the neural arch) that were found slightly apart from the rest of the skeleton, and are here identified also as posterior dorsal vertebrae.

When the neural arches are preserved, they are firmly sutured with the centra, allowing us to infer that the specimen of *Microsuchus* is an adult (Brochu, 1992). All the vertebrae are platycoelous to weakly amphicoelous. The presence of flat vertebral articular surfaces was used by Dolgopol de Sáez (1928) to assign *Microsuchus*

as a member of Goniopholididae. Platycoelous dorsal vertebrae have been recognized in other mesoeucrocodylians such as *Araripesuchus tsangatsangana* and *Anatosuchus*, thus the platycoelous of the dorsal vertebrae is not a definitive character that supports the assignment of *Microsuchus* to Goniopholididae.

4.1.1. Posterior dorsals

Four posterior dorsal vertebrae are recognized in the holotype specimen of *Microsuchus*, although two of them are represented only by half of the centrum and by partial remains of the neural arch. These fragmentary vertebrae bear no valuable information.

All the completely preserved centra are elongated, being always anteroposteriorly longer than dorsoventrally high. This condition is more developed on the anteriormost vertebrae preserved. Besides this elongation, this vertebra is somewhat constricted lateromedially, having lateral depressions on its lateral surfaces and bearing a slight median crest. The neural arch is very fragmentary, only having fragments of the neural arch pedicles and a fragment of the rib.

The most complete posterior dorsal preserved is the posterior-most, as it is in articulation with the first sacral vertebra (Fig. 3 A–C). As it was mentioned above, the centrum of this vertebra is elongated but is anteroposteriorly shorter than the other dorsal vertebra. Also contrasting with the other posterior dorsal, and more alike the sacral ones, this posterior most dorsal is dorsoventrally lower. The centrum is wide in ventral view and lacks a median crest, although elongated depressions are present on its lateral surface (Fig. 3C). The pedicles of the neural arch are short and do not occupy the whole anteroposterior length of the dorsolateral surface of the centrum. The transverse process seems to be complete on the right side of the vertebra and has a short lateromedial development (Fig. 3A). The prezygapophysis is also preserved on the right side, is poorly marked and has the articular surface facing dorsomedially at an angle of 45°. The prezygapophyses continues posteriorly as a sharp crest that is not connected with the neural spine. This crest seems to go through the entire dorsal surface of the neural arch (Fig. 3B). The neural spine is only preserved at its base,

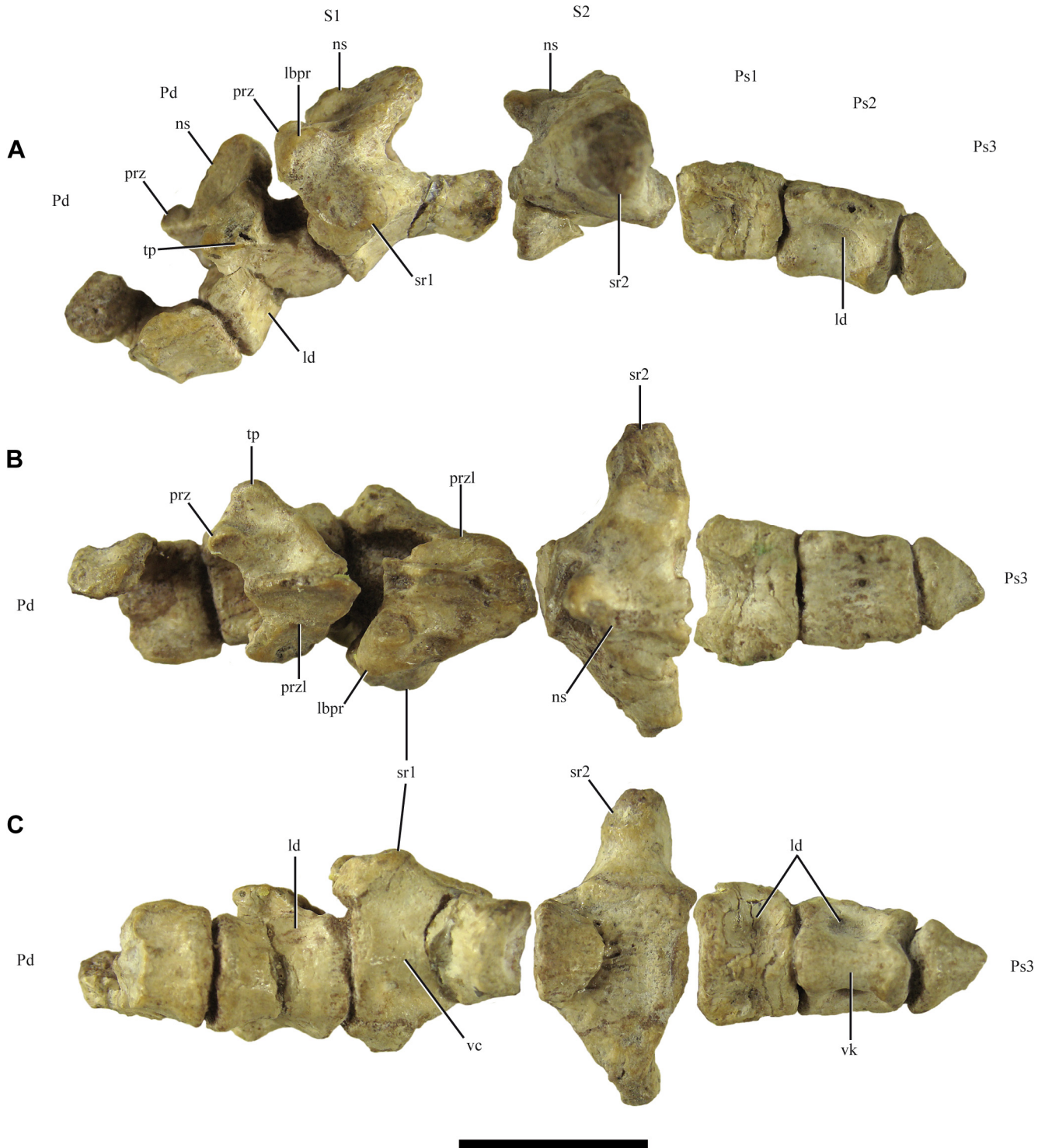


Fig. 3. Axial skeleton of *Microsuchus schilleri* (MLP-PV 26-IV-30-1) in **A**, lateral; **B**, dorsal; and **C**, ventral views. References: lbpr, lateral bulge of the prezygapophyses; ld, lateral depression; ns, neural spine; prz, prezygapophyses; przl, prezygapophyseal lamina; sr1, sacral rib 1; sr2, sacral rib 2; tp, transverse processes; vc, ventral crest; vk, ventral keel; see previous figures for other references. Scale bar equals 1 cm.

and occupies the whole dorsal surface of the neural arch. A small triangular depression is present on the posterior surface of the neural spine.

4.1.2. Sacral vertebrae

At least two sacral vertebrae were identified (see below). The presence of an additional sacral, common in notosuchians

(*A. gomesii*, *Notosuchus*, *Mariliasuchus*, *B. albertoi*, *Stratiotosuchus* with the exception of *A. tsangatsangana* and *Neuquensuchus*) is not evidenced in the specimen described. The presence of two scars for the sacral ribs is suggestive of the presence of two sacral vertebrae. Although as it was noted by Pol et al. (2012), inferring the number of sacrals based on the number of scars in the medial surface of the ilium might be misleading as some taxa have the sacral ribs fused

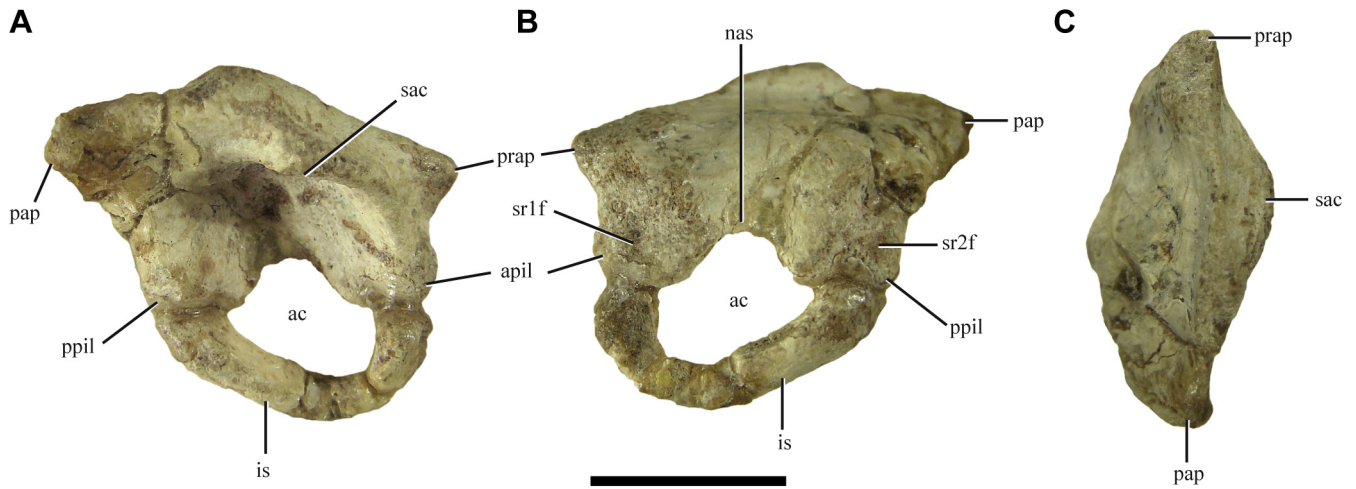


Fig. 4. Right ilium of *Microsuchus schilleri* (MLP-PV 26-IV-30-1) in **A**, lateral; **B**, medial; and **C**, dorsal view. References: **ac**, acetabulum; **apil**, anterior process of the ilium; **is**, ischium; **nas**, non-articular surface; **pap**, postacetabular process; **prap**, preacetabular process; **sac**, supraacetabular crest; **sr1f**, facet for sacral rib 1; **sr2f**, facet for sacral rib 2. Scale bar equals 5 mm.

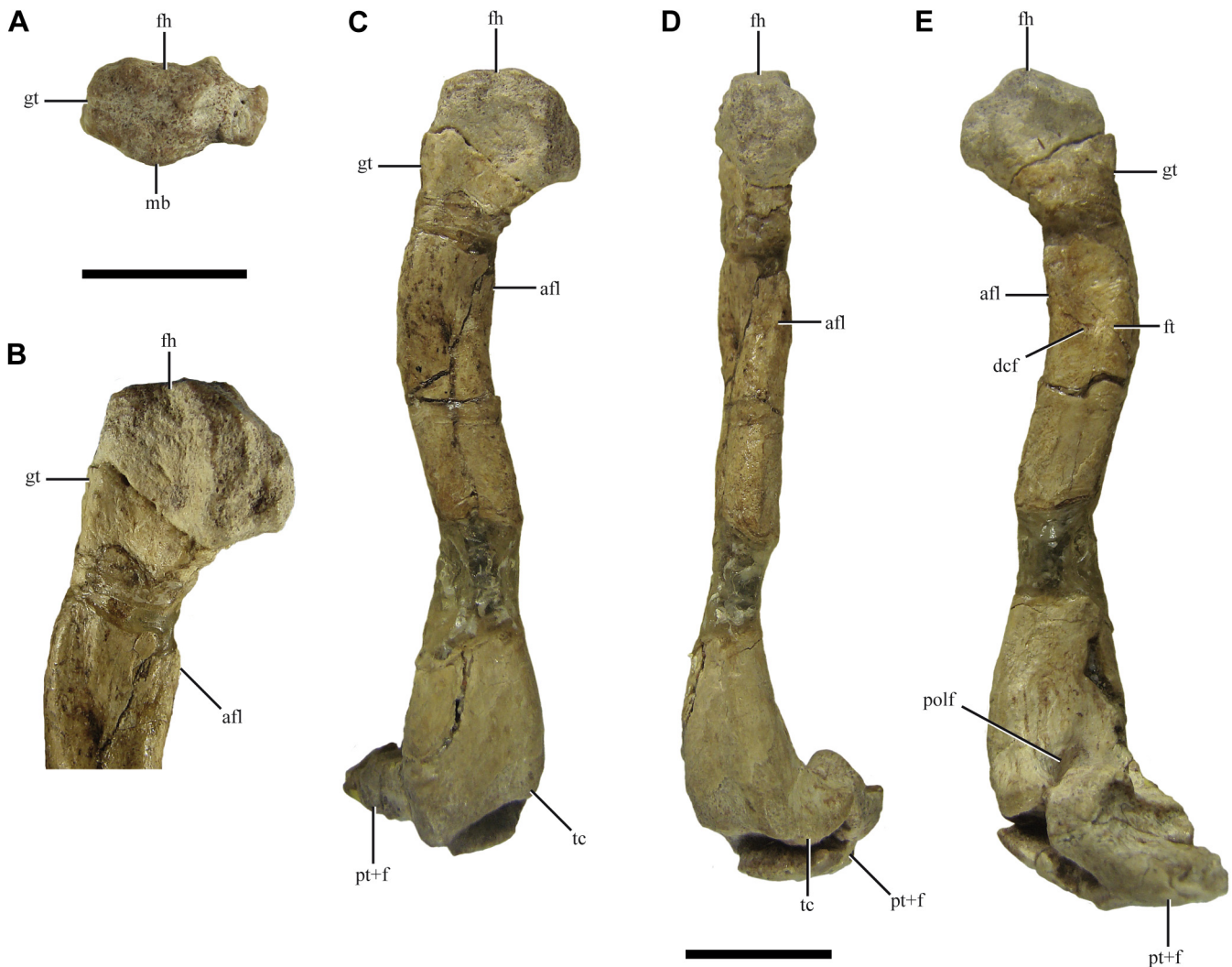


Fig. 5. Femur of *Microsuchus schilleri* (MLP-PV 26-IV-30-1). **A**, Proximal end of the left femur in proximal view. Right femur **B**, detail of the proximal end in anterolateral view; **C**, anterior view; **D**, medial view; and **E**, posterior view. References: **afl**, anterior flange of the femur; **dcf**, depression for the caudofemoral musculature; **fh**, femoral head; **ft**, fourth trochanter; **gt**, greater trochanter; **mb**, medial bulge; **polf**, polipetal fossa; **pt + f**, proximal end of the tibia and the fibula; **tc**, tibial condyle. Scale bar equals 1 cm.

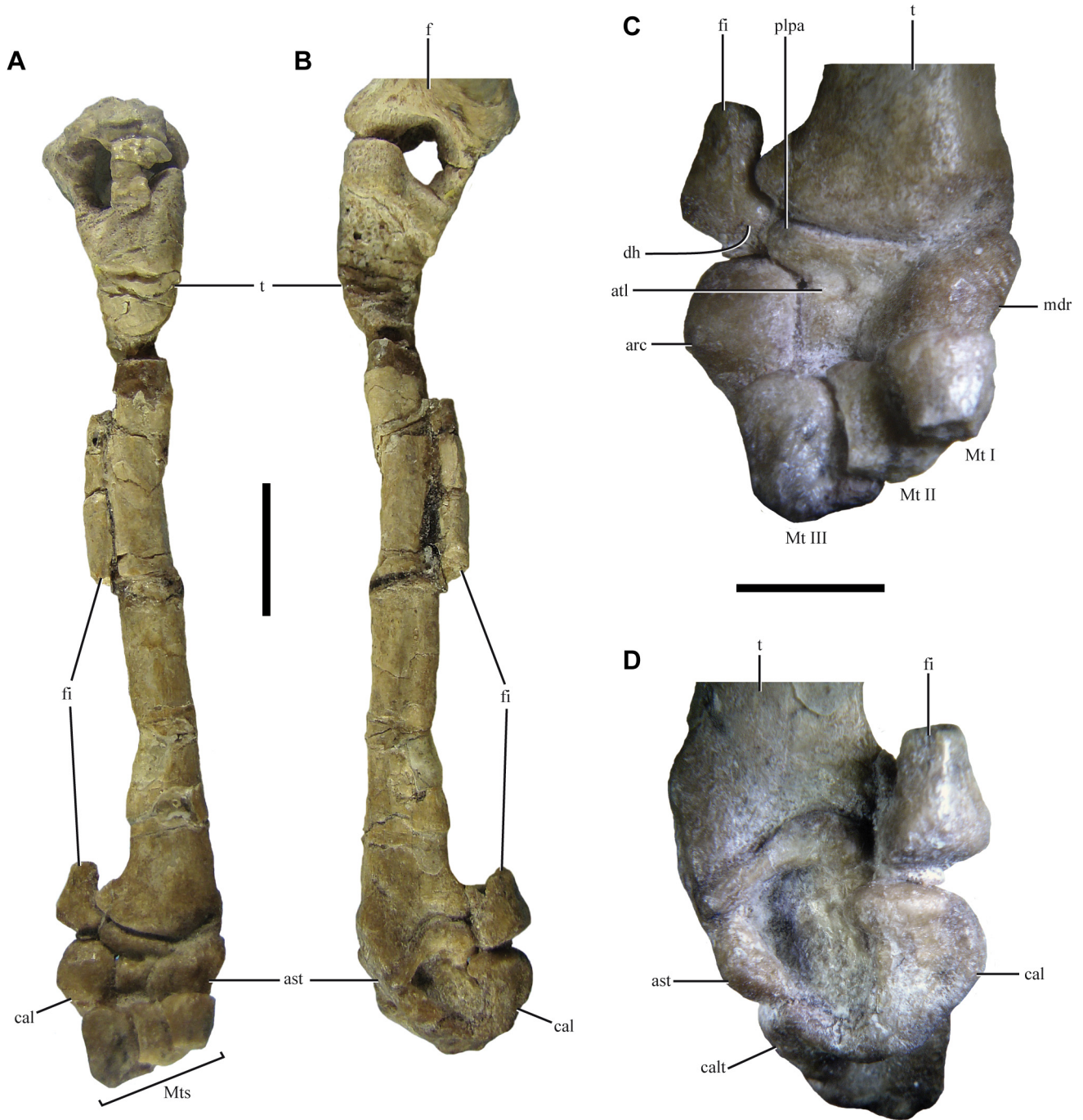


Fig. 6. Right zeugopodium and partial autopodium of *Microsuchus schilleri* (MLP-PV 26-IV-30-1) in **A**, anterior; and **B**, posterior views. Detail of the autopodium in **C**, anterior; and **D**, posterior view. References: **atl**, depression for the astragalar tarsale ligament; **arc**, anterior roller of the calcaneum; **ast**, astragalus; **cal**, calcaneum; **calt**, calcaneal tuber; **dh**, distal hook of the fibula; **f**, femur; **fi**, fibula; **mdr**, medial distal roller of the astragalus; **t**, tibia; **plpa**, proximalateral process of the astragalus; see previous figures for other references. Scale bars equal 1 cm (**A** and **B**) and 5 mm (**C** and **D**).

(e.g., *Notosuchus*). These vertebrae were originally found articulated with the posteriormost dorsal vertebrae and the proximal caudal/s, but were disarticulated during the mechanical preparation of the specimen. Both sacral preserve at least partial remains of their centra, neural arch and sacral rib (Fig. 3A–C).

The centrum of the first sacral vertebra is almost completely preserved and is notable because its very low dorsoventral development. The centrum is rectangular to trapezoidal in ventral view, as its anterior end is much more lateromedially expanded than the posterior one (Fig. 3C). Unlike the posterior dorsals, the ventral

surface bears lateral concavities separated by a very slight central crest. The pedicles of the neural arch fuse with the centrum on the anterior half or third, leaving a posterior region free of any attachment to the neural arch (Fig. 3A). A posterior region of the centrum free of any attachment with the neural arch is also observed in modern eusuchians (*Caiman yacare*), although is much more extended in *Microsuchus*.

The sacral rib is only preserved at its base and is borne at the junction of the neural arch and the centrum (Fig. 3A). Only the right prezygapophysis is preserved. This process is very small and has the

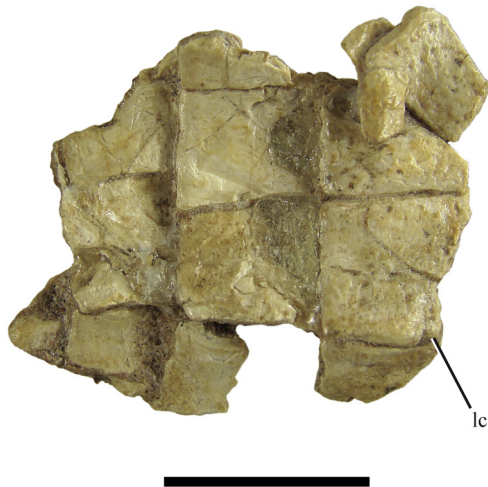


Fig. 7. Ventral osteoderms of *Microsuchus schilleri* (MLP-PV 26-IV-30-1) in dorsal view. References: **lc**, lateral crest. Scale bar equals 1 cm.

articular surface facing dorsomedially at an angle of approximately 45° to the horizontal plane, as in the posterior dorsals (Fig. 3B). This condition contrasts with the much lower angle present in the anterior sacral vertebrae of extant crocodylians (e.g., *Caiman latirostris*). Laterally to the prezygapophysis a distinct bulge is present (Fig. 3A). This bulge is anteroposteriorly longer than the prezygapophysis and is separated from it by a shallow groove. Also as in the posterior dorsals, a crest posterior to the prezygapophyses crosses the whole dorsal surface of the neural arch. The neural spine is incomplete, being only preserved at its base. The neural spine of the first sacral vertebra is anteroposteriorly very long, occupying almost entirely the dorsal surface of the neural arch only leaving a very small prespinal fossa anteriorly.

The second sacral vertebra is less complete than the first, but unlike the first it preserves partial remains of the sacral rib (Fig. 3A–C). The vertebral centrum is damaged on most of its length, but its anterior end is almost complete. Unlike the centrum of the first sacral vertebra it is dorsoventrally tall on anterior view. This condition contrasts with that observed in non-sebecosuchian taxa (*A. gomesii*, *A. tsangatsangana* and *Mariliasuchus*), while dorsoventrally high second sacral centra are present in *Mahajangasuchus* and *B. albertoi*.

The neural arch pedicles fuse with the centrum along almost its entire length (Fig. 3A). This observation is consistent with the condition seen in the second sacral vertebrae of other notosuchians where the second sacral is exposed in lateral view (*Mahajangasuchus*, *B. albertoi*), but contrasts with the condition of extant crocodylians where neural arch pedicles of the second sacral does not reach the posterior most end of the dorsal surface of the centrum. The sacral rib attaches to the entire lateral surface of the neural arch and to the dorsal region of the lateral surface of the centrum. The sacral rib is very stout and is directed slightly ventrolaterally. The distal ends of the sacral rib were not preserved. The neural spine is incomplete and occupies the whole dorsal surface of the arch (Fig. 3B). Posteriorly a narrow triangular depression is present.

4.1.3. Postsacral vertebrae

Three postsacral vertebrae were preserved in the type specimen of *Microsuchus*, although the last one is only represented by the anterior end of the centra precluding the observation of any relevant characters (Fig. 3A–C). All the preserved elements lack remains of the neural arches.

The two anterior centra are triangular in section. This particular shape in section is given by the development of a wide saggital crest on ventral view and by deep lateral depressions to it, on the lateral surface of the centra (Fig. 3C). The second vertebra is longer than the first one and neither of them bears ventral surfaces for the articulation with the chevrons. The anteriormost caudal vertebrae of extant crocodylians lack chevrons (Larson, 1994). In notosuchians where fully articulated anterior caudals are known (*Mariliasuchus* and *B. albertoi*), the hemapophyses are present in the second caudal vertebra. This also seems to occur in *Simosuchus* (Georgi and Krause, 2010) and *Neuquensuchus*. Thus, the anteriormost vertebrae preserved in *Microsuchus* might represent the posteriormost sacral. The general proportions of the centrum are not common for a sacral vertebra as it has pretty high dorsoventral development, unlike the more posteriorly elongated third caudal centra present in most notosuchians. However, a dorsoventrally high third sacral centrum is observed in *B. albertoi*.

4.2. Pelvic girdle

The pelvic girdle in is represented partially in the type specimen, as remains of both ilia and ischia are present. The only informative materials are the ilia, as the only fragments preserved of the ischia are their proximal end. The ischia limit the acetabulum anteriorly, excluding the pubis from its margins, as in most mesoeucrocodylians (Fig. 4A–B).

4.2.1. Ilium

The right ilium is the better preserved than the left one, being the main source of the current anatomical description. The ilium is anteroposteriorly short in lateral view; unlike the anteroposteriorly long ilia of other basal mesoeucrocodylians such as *A. tsangatsangana*, *A. gomesii*, *Uruguaysuchus*, *Mahajangasuchus*, *Notosuchus*, *Mariliasuchus*, *B. albertoi*, *S. icaeorhinus* and extant crocodylians. This difference is mainly attributed to the length of the postacetabular process, as in *Microsuchus* the postacetabular process is the 25% of the total length of the ilium (Fig. 4A), unlike other notosuchians and extant crocodylians where this ratio is higher than 34% (Pol et al., 2012). A long postacetabular process is also present in *Neuquensuchus*, although its relative length compared with the total length of the ilium can not be evaluated, as it is incompletely preserved. The postacetabular process of *Microsuchus* has its ventral margin dorsoventrally aligned and tappers posteriorly ending in a pointed tip as in extant crocodylians (e.g., *Caiman latirostris*) and basal crocodyliiforms (e.g., *Protosuchus richardsoni* and *Orthosuchus*) (Pol et al., 2012). This morphology contrasts with that observed in *Neuquensuchus* and notosuchians which have a horizontal or concave ventral margin of the postacetabular process with a dorsoventrally high posterior end. Also unlike the condition present in notosuchians (Pol et al., 2012), the ventral border of the postacetabular process is located at the same level of the acetabular roof. As in most mesoeucrocodylians, the preacetabular process of the ilium has a very small anterior projection.

The acetabulum is moderately deep in lateral view, with its dorsal border being limited by a sharp and laterally projected supraacetabular crest, leaving a laterodorsally exposed area just dorsally to the supraacetabular crest (Fig. 4A). This condition is shared with basal crocodyliiforms (e.g., *Protosuchus richardsoni* and *Orthosuchus*) and other basal mesoeucrocodylians, such as uruguaysuchids (*A. tsangatsangana*, *A. gomesii* and *Anatosuchus*), *Mahajangasuchus* and peirosaurids (*Montealtosuchus* and *Uberabasuchus*). On the other hand, the mentioned condition contrasts with shallow acetabula with slightly laterally deflected supraacetabular crest of neosuchians (e.g., *Stenosaurus*, *Caiman yacare*);

and with the deep acetabula with strongly laterally deflected supraacetabular crests of *Notosuchus*, *B. albertoi*, *Stratiotosuchus* and *S. icaeorhinus*. The supraacetabular crest is developed in the anterior half of the ilium, giving this bone a sigmoid lateral surface in dorsal view. Some rugosities are present on the apex of the supraacetabular crest which correspond topologically with the origins of the Mm. iliobtibialis 1 and 2 (Romer, 1923; Carrano and Hutchinson, 2002). As in all crocodyliiforms, the iliac blade has very small dorsoventral development dorsally to the supraacetabular crest (Fig. 4A). The medial margin of the acetabulum is damaged in both ilia, precluding the observation of a notch on the ventral margin of the acetabulum. The posteroventral margin of the acetabulum of the left ilium has slight rugosities, although the bad preservation of the external surface of the bone makes the interpretation of those as an antitrochanter dubious. The pubic and ischial peduncles have a similar ventral projection (Fig. 4A), as in *S. icaeorhinus* but contrasting to the more dorsally placed pubic peduncle of most crocodyliiforms (e.g., *Caiman yacare*, *Mahajangasuchus*, *Uruguaysuchus*, *Protosuchus richarsoni*).

In medial view, the ilium is convex and has a well developed dorsal crest dividing its lateral surface from the medial one. Two scars for the sacral ribs can be observed on the ventral region of the ilium (Fig. 4B). The articular surface for the first sacral rib subquadrangular, being almost as high as wide, and is located on the anterior border of the ilium. The articular surface for the second sacral rib is dorsoventrally higher and is slightly more anteroposteriorly developed than the articular surface for the first sacral rib. This condition is present in notosuchians where the medial surface of the ilium is exposed (*A. tsangatsangana* and *S. icaeorhinus*), contrasting with the anteroposteriorly shorter scar of the second sacral rib present in eusuchians (*C. yacare*). In *Microsuchus*, the scar for the second sacral rib is separated from the scar of the first sacral rib by a non-articular surface and it does not reach the posteroventral edge of postacetabular process in medial view (Fig. 4B). This condition is shared with *S. icaeorhinus* and *Chimaerasuchus*, unlike other basal mesoeucrocodylians (*A. tsangatsangana*, *Lomasuchus* and *Mahajangasuchus*) which have a scar for the second sacral rib that extends onto the postacetabular process, occupying its posteroventral edge in medial view, and that contacts the scar for the first sacral rib. Extant crocodylians (e.g., *C. yacare*) have a mixed condition of these characters, as the scar for the second sacral rib does not reach the posteroventral edge postacetabular process in medial view but contacts the scar for the first sacral rib.

4.3. Hindlimb

The type specimen of *Microsuchus schilleri* preserves an articulated right hindlimb lacking most part of the fibula and the pes, which is represented by the astragalus, calcaneum, and the proximal ends of metatarsals I–III (Fig. 2). The holotype also includes a proximal end of the left femur. In general, these elements are very badly preserved.

4.3.1. Femur

Although the femur is broken on the distal third of the shaft, the articulated nature of the material and the access to it allowed us to estimate the relative length of the femur. *Microsuchus* has the particular condition among crocodyliiforms of having a femur proximodistally shorter than the tibia (Fig. 2). This condition is also shared with other basal crocodyliiforms (*Shantungosuchus chuhsienensis* [Wu et al., 1994] and is inferred in *Edentosuchus* [Pol et al., 2004]), *Neuquensuchus* and some non crocodyliiform crocodylomorphs (*Terrestrisuchus* [Crush, 1984], *Macelognathus* [Göhlich et al., 2005]). In other crocodyliiforms where both

elements are known from the same specimen, the femur is always proximodistally longer than the tibia. Thus, the length of the femur compared with the length of the tibia seems to be a highly homoplastic character among basal crocodylomorphs and crocodyliiforms.

The proximal end of the femur is not markedly rotated with respect to the distal end, and it does not bear a distinct neck (Fig. 5B–E) as in non crocodyliiform crocodylomorphs (Parrish, 1986). The femoral head is mediolaterally elongated in proximal view and has a bulge on the midpoint of its medial surface (Fig. 5A) as in most crocodyliiforms (*Caiman latirostris*, *Yacarerani*, *Mahajangasuchus*) except for *Simosuchus*. On the anterior surface of the proximal end, just distally to the articular surface of the femoral head, a slight proximal fold is present. As in most crocodyliiforms, the proximal fold originates on the medial surface and crosses obliquely the anterior surface of the proximal end to reach the lateral surface. The posterior surface of the proximal end bears a well developed major trochanter, which is limited by sharp lateral and medial ridges. The surface for the insertion of the M. puboischiofemoralis externus is flat and it extends distally approximately to the level of the fourth trochanter, as in most crocodyliiforms.

The fourth trochanter is located on the medial surface of the femur, at one third of the total length of the femur. As in *Yacarerani* and *S. icaeorhinus*, the fourth trochanter is reduced to a very low structure. A rounded depression which can be correlated with the insertion of the M. caudofemoralis longus (Fig. 5E) is observed on this region. An anteriorly projected flange is present just anteriorly to this depression (Fig. 5B–E), as in most notosuchians (*Mahajangasuchus*, *A. tsangatsangana*, *A. gomesii*, *Uruguaysuchus*, *Simosuchus*, *Mariliasuchus*, *Notosuchus*, *B. albertoi*, *Stratiotosuchus*) with the exception of *Yacarerani*, *S. icaeorhinus* and *Neuquensuchus*. However, this flange has a low anterior development in *Microsuchus*, a condition shared in *Mariliasuchus*, contrasting with the great development of this flange in other notosuchians. This anteromedial flange corresponds topologically with the insertion of the M. puboischiofemoralis internus (Turner, 2006).

The femoral shaft is elongated anteroposteriorly in cross section. The femur is broken on the distal third and as a consequence the distal end of the femur is separated from the rest of the bone, precluding us to evaluate the degree of rotation of the distal end with respect to the proximal one. The distal end of the femur is damaged on the lateral surface, thus the articular surface for the fibula on the fibular condyle is missing (Fig. 5C). The anterior surface of the distal end is almost flat and bears a well developed medial supracondylar ridge. The lateral side of the distal end is damaged. The posterior surface of the distal end bears a deep polipetal fossa (Fig. 5E).

4.3.2. Tibia

As it was mentioned before, and was already noted by Dolgopod de Sáez (1928), the tibia of *Microsuchus* is very slender and long. This condition contrasts strongly with the one seen in most crocodyliiforms, where the tibia is a stout element and is proximodistally shorter than the femur.

The proximal end of the tibia is lateromedially narrow, being slightly narrower than the distal end (Fig. 6A–B). The proximal end is badly preserved, as its lateral surface and posterior surface are almost missing. Only the rough triangular outline of the proximal end can be observed. The shaft is anteroposteriorly flattened, unlike the more circular shafts in cross sections of most crocodyliiforms. The distal end of the tibia is more expanded laterally than medially, giving the anterior surface an asymmetrical profile in anterior view (Fig. 6C). In this view, the distal end is rather straight as in *Simosuchus*, *Mahajangasuchus*, *Notosuchus* and *Mariliasuchus*,

contrasting with the strongly oblique distal end of the tibia in anterior view of *A. tsangatsangana*, *Yacarerani*, *Stratiotosuchus*, *S. icaeorhinus* and extant crocodylians. The lateral margin of the distal end of the tibia is markedly projected, forming a lateral flange that covers the medial border of the distal end of the fibula. In posterior view, the distal end of the tibia bears a fossa bounded by an oblique crest that is located just on the limit with the articular surface of the distal end.

4.3.3. Fibula

Only fragments of the fibula, still articulated with the tibia, are preserved. These fragments include parts of the proximal end, part of the shaft around the midlength of the bone, and the distal end. Most of them, specially the proximal end, are badly damaged precluding the observation of the main structures. Only the distal end of the fibula preserved some anatomical detail, where a distal medial hook is present (Fig. 6C) as in extant crocodylians, but unlike most notosuchians (Leardi, Pol, Novas, and Suárez Riglos, unpublished data).

4.3.4. Astragalus

The astragalus is articulated with the rest of the pes and the distal ends of the tibia and fibula (Fig. 6A). Thus it is only exposed on its anterior, medial and posterior surfaces, although the posterior and medial ones are badly preserved. The astragalus is wide anteriorly, bearing a well developed distal roller and a lateromedially narrow proximolateral process (Fig. 6C).

The anterior hollow of the astragalus is moderately deep and is limited dorsally by a strong crest that runs along the limit of the anterior surface of the astragalus and the proximal articular surface for the tibia (Fig. 6C). This crest is continuous along the dorsal edge of the anterior surface, not having a notch at the junction with the distal roller as in *A. gomesii*, *Lomasuchus*, *B. albertoi*, *Stratiotosuchus* and *S. icaeorhinus*. The ventral, medial and lateral margins of the anterior hollow are not limited by marked crest. On the medial region of the anterior hollow, just between the proximolateral process and the astragalar peg, a circular depression is present (Fig. 6C). This depression corresponds topologically with the astragalar-tarsale ligament (Brinkman, 1980) and is also present in all known notosuchians, but contrasting with most extant crocodylians where this depression is generally absent (Leardi, Pol, Novas, and Suárez Riglos, unpublished data). Unlike non sebecosuchian notosuchians, the depression for the astragalar-tarsale ligament is not separated from the dorsal region of the anterior hollow by a well developed crest.

The medial distal roller is rounded anteriorly, and almost flat in medial view. The posterior surface of the astragalus is badly preserved (Fig. 6D), precluding the observation of significant details on its anatomy.

4.3.5. Calcaneum

The calcaneum is preserved inclined posteriorly, so that the ventral surface of the distal roller is oriented anteroventrally. The calcaneum is incomplete, as most of distal end of the calcaneal tuber is not preserved. Given this preservation few relevant details can be given about this element.

The distal roller is anteroposteriorly short but dorsoventrally high (Fig. 6C). The dorsal edge of the distal roller has a well developed rim, while the anterior and the rest of the dorsal surface is convex and the ventral surface is flat. The calcaneal tuber is preserved partially and does not allow inferring the orientation of the main axis of the tuber (Fig. 6D).

4.3.6. Distal tarsals and metatarsals

Differing with the observations of Dolgopol de Sáez (1928), no distal tarsals could be recognized. We assume that part of the calcaneal tuber was misidentified as a distal tarsal (3 and 4 fused), although it is clearly continuous with the distal roller of the calcaneum (Fig. 6D).

Only the proximal ends of the medialmost three metatarsals (I–III) were preserved (Fig. 6C–D). The metatarsals I and II are strongly compressed dorsoventrally, and are almost laminar in section. Metatarsal III, on the contrary, is elliptical in section. The metatarsals are imbricated, with the first being overlapped by metatarsal II and the metatarsal II by the III. This conditions contrast with the one in most mesoeucrocodylians (*Araripesuchus gomesii*, *Araripesuchus wegneri*, *Simosuchus*, *Yacarerani*), where the medial metatarsals overlap the lateral ones. Metatarsal I is the stoutest and the metatarsal III is the most gracile one.

4.4. Osteoderms

The osteoderms were recovered slightly displaced from their original position (Fig. 2). Four rows of articulated osteoderms are preserved, a lateral row and three paramedian rows. These are interpreted as ventral osteoderms. The osteoderms are rectangular in ventral view (Fig. 7). The paramedian osteoderms lack a dorsal crest. The ventral surface is badly preserved, but the imbrication of the osteoderms can be observed in lateral view. The lateral most osteoderms have a raised lateral edge that forms a lateral crest.

5. Phylogenetic relationships

In order to evaluate the phylogenetic position of *Microsuchus schilleri*, we incorporated this taxon on the phylogenetic data set of Leardi, Pol, Novas, and Suárez Riglos (unpublished data), which is a modified of previous analyses (Turner and Sertich, 2010; Pol et al., 2012, 2014; among others). This data set incorporated new information on postcranial anatomy, which is expected to be relevant for this study as *Microsuchus* completely lacks any cranial remains. Two new characters were incorporated to the matrix, describing the variation on the second sacral rib scar and the length of the tibia with respect to the femur (chars. 438 and 439). Additionally, the taxon *Neuquensuchus universitas* was incorporated, as it was recovered from the same locality than *Microsuchus* and shares with it a particularly elongated posterior zeugopodium. The resulting data matrix consists of 439 characters and 111 taxa (see Supplementary Information).

The data matrix was analyzed using TNT ver. 1.1 (Goloboff et al., 2008a; 2008b) under equally weighted parsimony. An heuristic search was performed using 1000 random addition sequences followed by a TBR branch-swapping and zero-length branches were collapsed under the strictest criterion (rule 1 of Coddington and Scharff, 1994). The resulting most parsimonious trees (MPTs) were subjected to a final round of TBR. As a result, 58320 MPTs were obtained ($L = 1687$; $CI = 0.311$; $RI = 0.740$). Some very incomplete taxa have an unstable position (*Coringasuchus*, *Pabhweshi*, *Cynodontosuchus*; and the two newly included taxa, *Microsuchus* and *Neuquensuchus*), thus causing the great amount of MPTs recovered.

The topology obtained in the strict consensus of this study is similar to the one recovered in previous analyses (Pol et al., 2014; Leardi, Pol, Novas, and Suárez Riglos, unpublished data), as two main clades of mesoeucrocodylians are identified: Notosuchia and Neosuchia (Fig. 8). Although, a politomy is observed at the base of Mesoeucrocodylia, which is caused by the unstable position of one of the new taxa added (see below). Also large politomy is observed among sebecosuchians and advanced notosuchians, which is solved when the alternative positions of *Coringasuchus*, *Pabhweshi* and

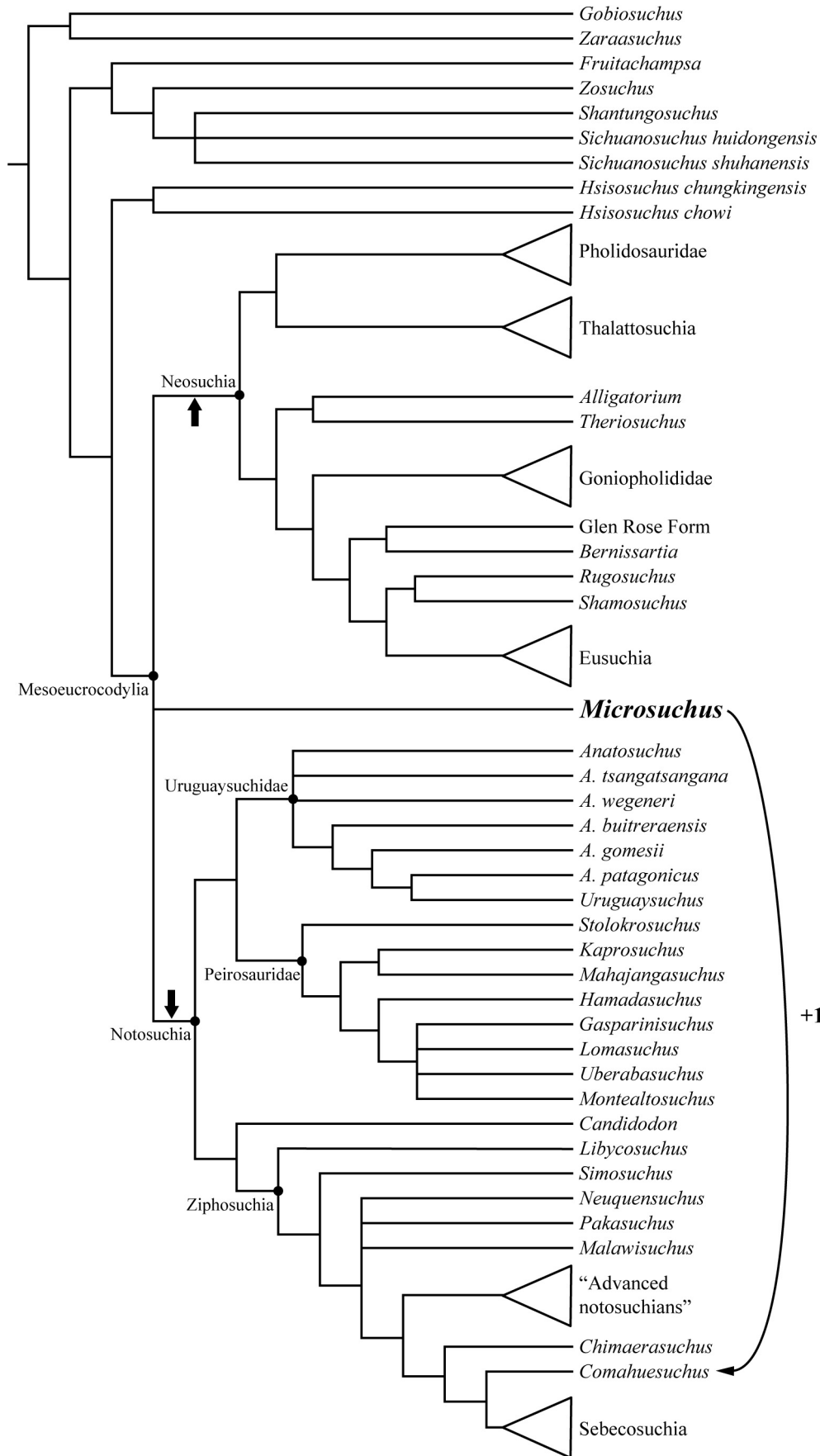


Fig. 8. Strict consensus of 58320 trees retrieved of the parsimony analysis. Block arrows indicate the alternative positions of *Microsuchus* in the different MTPs and the long arrow indicates how many extra steps are implied when the scorings of *Microsuchus* and *Comahuesuchus* are fused.

Pehuenchesuchus are ignored in the strict consensus. *Microsuchus* is depicted at a polytomy on the base of Meseocrocodylia on the strict consensus (Fig. 8), as its phylogenetical position varies between the base of Notosuchia or Neosuchia on different MTPs. These phylogenetical positions of *Microsuchus* are supported by a single synapomorphy each: the presence of a distal medial hook on the fibula (char. 425.1; Leardi, Pol, Novas, and Suárez Riglos, unpublished data) supports *Microsuchus* as a neosuchian, while the presence of an anteroproximal flange on the femur for the insertion of the PIFI 1 and CFL (char. 157.1; Buckley and Brochu, 1999) support its placement as a notosuchian.

Another result of the phylogenetic analysis is the position of *Neuquensuchus* (Fig. 8). Unlike the results of Fiorelli and Calvo (2007), this taxon was found nested within Notosuchia, as a member of Ziphosuchia. *Neuquensuchus* is depicted as more derived than *Simosuchus*, forming a polytomy with *Pakasuchus*, *Malawisuchus* and the 'advanced notosuchians' + *Sebecosuchia* and its related forms. *Neuquensuchus* is depicted either as basal to the mentioned taxa or as the sister group of any of them in the different MTPs. The notosuchian affinities of *Neuquensuchus* are supported by the presence of several postcranial characters that were recently identified as synapomorphies of that clade (Pol et al., 2012; Leardi, Pol, Novas, and Suárez Riglos, unpublished data), such as: at least the neural spines of the posterior cervical vertebrae are rodlike (char. 90.1; Clark, 1994); a distinct rounded depression on the dorsal surface of the anterior dorsal neural arches, located between the neural spine and the postzygapophyseal process (char. 302.1- Pol et al., 2012); a dorsoventrally high postacetabular process with its posterior border vertically oriented and its ventral margin horizontally or ventrally deflected (chars. 326.1 and 327.1; Pol et al., 2012); a wide scapular blade (char. 305.1; Buckley and Brochu, 1999); scapular portion of the glenoid proximally exposed and limited anteriorly by a bulge (chars. 414.1 and 415.1; Leardi, Pol, Novas, and Suárez Riglos, in review). However, many of the mentioned characters are not depicted as notosuchian synapomorphies on the strict consensus. This is caused by the alternative position of *Microsuchus* as a basal notosuchian, as it lacks many of the mentioned characters producing an ambiguous optimization of them on the base of Notosuchia. Finally, a more derived position than *Simosuchus* is supported by the absence of a sharply delimited pit on the proximoposterior surface of the humerus, usually related to the common insertion of the *Mm. teres major* and *latissimus dorsi* (char. 315.1; Pol et al., 2012).

6. Discussion

6.1. Taxonomical status of *Microsuchus schilleri*

As it was mentioned in the description, *Microsuchus* is only represented by postcranial remains. Thus, when the affinities of *Microsuchus* were analyzed, we came with a problem: is *Microsuchus* a valid taxon? Fortunately, many taxa recovered from the Bajo de la Carpa Formation have well preserved postcranial remains, allowing a direct comparison between them. Unlike these taxa, *Microsuchus* has several traits that are unique to it, particularly the combination of its iliac and femoral morphology (see Diagnosis). Even *Neuquensuchus*, that comes from the same locality and also has a very elongated hindlimb, has clear anatomical differences with *Microsuchus* such as the posteriorly elongated postacetabular process and the absence of an anterior flange on the femur anteriorly to the fourth trochanter. Furthermore, significant differences in size can be observed between these taxa (the femur of *Neuquensuchus* is 77% longer than the one of *Microsuchus*), and ontogenetic differences can be ruled out to explain those differences as both taxa have the neurocentral sutures on their vertebrae well sutured with the vertebral centrum. Thus, *Microsuchus* has a unique

combination of postcranial characters that support its status as a valid and independent taxon.

Despite the particular postcranial anatomy of *Microsuchus*, there is still a problem towards resolving its taxonomical position due to the lack of any cranial remains on the type specimen (MLP 26-IV-30-1). Although many taxa recovered from Bajo La de la Carpa preserve at least some postcranial bones, there are still other taxa for which their postcranial anatomy is completely unknown such as *Comahuesuchus*, *Cynodontosuchus* and *Wargosuchus*. Among these taxa *Comahuesuchus* is of relevance as the skull of this taxon is approximately on the size range of *Microsuchus*, based on the general body proportions of the latter. Moreover, if both taxa are fused on the data matrix (with the command Merge Taxa of Mesquite v. 2.75) treating them as a single taxonomical entity, the phylogenetical position of this new "artificial" taxon is the same that the one we obtain using only the data of the skull of *Comahuesuchus*. This alternative phylogenetical position requires only one extra step ($L = 1688$). Thus, considering the evidence available at hand, *Microsuchus* could represent the postcranial skeleton of *Comahuesuchus*. This would imply that *Comahuesuchus* would not be a valid taxon anymore, resulting in being a junior synonym of *Microsuchus*. Although this solution seems to have at least some support, we disregard it, as the specimens of *Microsuchus* and *Comahuesuchus* lack any overlapping material that justifies the synonymy.

In summary, we consider that *Microsuchus* has enough unique characters to be a valid taxon. However, the scenario in which the type specimen of *Microsuchus* represents the postcranial skeleton of *Comahuesuchus* is not unlikely. Future findings of new specimens of *Comahuesuchus* and *Microsuchus* that include cranial and postcranial remains might shed new light on this problem.

6.2. New phylogenetic results

Besides the position of *Microsuchus* in our phylogenetical hypothesis we recover new information on the phylogenetical position of *Neuquensuchus*. Unlike the original study where *Neuquensuchus* was found as a closely related with *Shantungosuchus* and other non-meseocrocodylian crocodyliforms (Fiorelli and Calvo, 2007), we found it as a ziphosuchian notosuchian. Our results make the presence of non-meseocrocodylian crocodyliforms on the northern region of Patagonia for the Late Cretaceous equivocal, as *Neuquensuchus* was the only representative of that clade (Fiorelli and Calvo, 2007).

When the phylogenetical position of *Microsuchus* is also considered, new evidence comes to light on evolutionary history of basal meseocrocodylians in Patagonia. Both *Microsuchus* and *Neuquensuchus* share a very elongated hindlimb, a rare condition in basal meseocrocodylians. Some basal uruguayasuchids exhibit a very gracile hindlimb (*A. tsangatsangana* or *A. wegneri*), but none of them have their zeugopodium proximodistally longer than their stylopodium. A similar condition to the one observed in these Patagonian taxa can be observed in the shartegosuchids (*Fruitachampsia* [Clark, 2011]) and other related forms (*Shantungosuchus chuhsienensis* [Wu et al., 1994]). *Microsuchus* and *Neuquensuchus* might represent a basal group of basal meseocrocodylians with particular cursorial adaptations that was not reported yet. Also, the occurrence of this particular group in the Upper Cretaceous of the Neuquén Basin further highlights the relevance of the study of this area and its relevance to understand the evolution of basal meseocrocodylians and notosuchians.

7. Conclusions

The poorly known crocodyliform taxon *Microsuchus schilleri* is redescribed. A detailed examination of the only available specimen

of *Microsuchus* and the comparison with other taxa of the same unit where it was recovered allowed us to recognize it as a valid taxon. However, the possibility that the type specimen of *Microsuchus* might represent the postcranial skeleton of *Comahuesuchus* can not be completely disregarded, as both taxa have approximately the same size range. The lack of any comparable material between both taxa precludes the analysis of the synonymy. Using the available data, *Microsuchus* along with another long limbed crocodyliform from the same locality (*Neuquensuchus*) were included in a phylogenetical analysis. *Microsuchus* is recovered as a basal mesoeucrocodylian, but conflicting characters present on its hindlimb (an anterior flange just anteriorly to the fourth trochanter of the femur and a distal hook on the fibula) do not allow a stable placement within Mesoeucrocodylia. On the other hand, *Neuquensuchus* is recovered as a basal ziphosuchian based on several postcranial synapomorphies.

Finally, these findings further increase the diversity of basal mesoeucrocodylians and notosuchians in the Bajo de la Carpá Formation. The occurrence of both *Microsuchus* and *Neuquensuchus* give evidence of a basal stack of basal mesoeucrocodylians with elongated limbs that were not previously reported for northern Patagonia.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2014.09.007>.