

REDESCRIPTION OF THE EOCENE CATFISH *BACHMANNIA CHUBUTENSIS* (TELEOSTEI: BACHMANNIIDAE) OF SOUTHERN SOUTH AMERICA

MARÍA DE LAS MERCEDES AZPELICUETA^{*1} and ALBERTO LUIS CIONE²

¹División Zoología Vertebrados, Museo de La Plata, 1900 La Plata, Argentina azpeli@ciudad.com.ar;

²División Paleontología Vertebrados, Museo de La Plata, 1900 La Plata, Argentina, acione@museo.fcnym.unlp.edu.ar

ABSTRACT—The Siluriformes constitutes an important monophyletic ostariophysan group of mainly freshwater fishes that occurs in almost all continents. They are extremely abundant and diverse in South America, where the oldest ostariophysans and siluriforms occur. We restudied two putative catfish species from the early Eocene lacustrine Tufolitas Laguna del Hunco of northwestern Patagonia, Argentina, concluding that *Arius argentinus* Dolgopol, 1941, is a junior synonym of *Bachmannia chubutensis* Dolgopol, 1941. Phylogenetic analyses were performed to show the relationships of *B. chubutensis*, which appears as the sister group of *Diplomystes*. *Bachmannia chubutensis* is one of the most primitive catfishes known and we based on it a new family. The family is clearly diagnosed by the presence of a anterior ventrolateral expansion of cleithrum, short maxilla with two rows of teeth, double-headed autopalatine, accessory tooth plates, very huge teeth, supraoccipital process long and acute, first and fifth vertebrae not joined to complex vertebra, neural arch of fifth and sixth vertebrae very well developed, enlarged supraneural 5, suture between ceratohyal and epiphyal without interdigitations, suture between contralateral cleithra and coracoids without interdigitations, six hypurals. Individuals of *B. chubutensis* inhabited lakes and were preserved into fine-grained, laminated fall-out and reworked pyroclastic debris inside a caldera.

INTRODUCTION

Siluriformes (catfishes) constitutes one of the most diverse vertebrate groups both morphologically and taxonomically (35 families with almost 3500 species; Eschmeyer, 2010). South America is the only continent where catfishes are relatively common in Cretaceous rocks (Arratia and Cione, 1996; Gayet and Meunier, 2003). The early evolution of the catfishes is very poorly known; however, the oldest remains present typical autapomorphies of the group. Most authors consider that the primitive catfishes are the Campanian to Recent South American diplomystids. For this, any record in the Cretaceous or early Paleogene is relevant for a better understanding of the evolution of the group.

Dolgopol (1941) described the new genus *Bachmannia* and two species, *B. chubutensis* and *Arius argentinus*. In this paper, we redescribe *B. chubutensis*, synonymize *A. argentinus*, recognize a new catfish family, and discuss its relationships with the most primitive siluriform taxa.

MATERIALS AND METHODS

Methods

The studied fossil fishes are always distorted and there is no complete specimen. Fish are mostly preserved as negative impressions with scarce bone preserved. Bony material was etched from specimens by immersing it in a bath of 50% technical grade HCl and 50% water for several hours. From these preparations, latex peels were made in order to obtain specimens with positive relief.

The phylogenetic parsimony analysis was accomplished with TNT software (Goloboff et al., 2007). Searches were done under equal weighting, implied weighting, and self-weighted optimization (Goloboff, 1993, 1997). Searches were done from 1000

random addition sequences, followed by TBR and a round of parsimony ratchet (Nixon, 1999), tree drifting, tree fusing, and sectorial searches (Goloboff, 1999). Implied weighting and self-weighted optimization searches were done under broad ranges of values of K (1 to 64 under both analyses). Analyses were rooted in a functional outgroup constructed from the generalized states in non-siluriform Ostariophysii; because the new taxon was a priori considered to be a relatively basal siluriform, such functional root became necessary to adequately test the possibility of *Bachmannia* to be the sister group of remaining Siluriformes.

The matrix was taken from Rodilez-Hernández et al. (2009). The characters of *Bachmannia* used here are in the Appendix 1; the remaining 81 characters did not apply to *Bachmannia* and were coded as missing.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **ANSP**, Academy of Natural Sciences, Philadelphia; **CAS**, California Academy of Sciences, San Francisco; **CENPAT**, Centro Nacional Patagónico, Puerto Madryn; **FMNH**, Field Museum of Natural History, Chicago; **PVL**, Instituto Miguel Lillo, San Miguel de Tucumán; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Sección Paleontología Vertebrados, Buenos Aires; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **MLP**, Museo de La Plata, División Paleontología de Vertebrados, La Plata; **CIC**, Museo Naturalístico, Antropológico e Histórico “Jorge Gerhold,” Ingeniero Jacobacci, Río Negro; **MPBAR**, Museo Paleontológico de la Asociación Paleontológica Bariloche, San Carlos de Bariloche; **MPEF-PV**, Museo Paleontológico Egidio Feruglio, Trelew; **UMMZ**, Museum of Zoology, University of Michigan, Ann Arbor; **NMNH (USNM)**, National Museum of Natural History, Washington, D.C.

Anatomical Abbreviations—**aar**, angular + articular + retroarticular; **afr**, anal fin rays; **app**, anterior pelvic process; **boc**, basioccipital; **br**, branchiostegal rays; **c**, ceratohyal; **cl**, cleithrum; **clap**, crest for attachment of levator arcus palatini muscle

*Corresponding author.

(broken); **cor**, scapulocoracoid; **cv**, complex centrum of Weberian apparatus; **d**, dentary; **dfr**, dorsal fin rays; **ds 1**, dorsal spine 1; **ds 2**, dorsal spine 2; **eh**, epihyal; **ep**, epural; **epi**, epiotic; **exes**, extrascapula; **exo**, exoccipital; **f**, frontal; **fv**, first vertebra; **h 1–6**, hypurals 1–6; **hs**, hemal spines; **hy**, hyomandibula; **ip**, indetermined pterygoid; **iop**, interopercle; **laar**, left angular + articular + retroarticular; **lcl**, left cleithrum; **ld**, left dentary; **let**, lateral ethmoid; **lptscl**, left posttemporal + supracleithrum; **m**, maxilla; **mes**, mesethmoid; **met**, metapterygoid; **na 5**, neural arch of vertebra 5; **np 1**, anterior nuchal plate; **np 2**, medial or posterior nuchal plate; **ns**, neural spine of vertebra 5; **op**, opercle; **orb**, orbitosphenoid; **pal**, autopalatine; **pas**, parasphenoid; **pcf**, posterior cranial fontanelle; **pfr**, pectoral fin rays; **ph**, parhypural; **pm**, premaxilla; **pop**, preopercle; **pro**, prootic; **ps**, pectoral spine; **pt**, pterotic; **pter**, pterosphenoid; **ptg**, pterygiophores; **ptg 1–7**, pterygiophores 1–7; **ptscl**, posttemporal + supracleithrum; **pvr**, pelvic fin rays; **pvs**, pelvic splint; **q**, quadrate; **t**, tooth; **tp**, tooth plate; **tpcv**, transverse process of complex centrum; **tr**, tripus; **sn**, supraneural 5; **soc**, supraoccipital; **sp**, sphenotic; **spop**, suprapreopercle; **un**, uroneural; **v**, vomer; **vle**, ventrolateral extension of cleithrum; **v5–6**, vertebrae 5–6.

SYSTEMATIC PALEONTOLOGY

Order SILURIFORMES sensu Grande 1987
 Family BACHMANNIIDAE, new family

Type and Only Known Genus—*Bachmannia* Dolgopoi, 1941.

Known Distribution—As for *B. chubutensis*.

Family Diagnosis—Bachmanniidae differs from all the other Siluriformes by the following combination of characters: Small size (<125 mm); body deep; an anterior lateroventral expansion in cleithrum; pterosphenoid not sutured to parasphenoid; both cleithra and scapulacoracoids sutured at midline without interdigitations; ceratohyal and epihyal without interdigitations; 1st and 5th vertebrae have normal intervertebral joints with complex vertebra; neural arches of 5th and 6th vertebrae well developed; supraneural 5 anteroposteriorly expanded, deep, and long; toothed maxilla with articular process relatively long; two articular fosses and lateral process short, bearing two rows of teeth; very large teeth on premaxilla, maxilla, dentary, vomer, and ac-

cessory tooth plates; autopalatine anteriorly broad, with two anterior articular processes and posterior half slender; anteriorly narrow mesethmoid with short cornua; levator arcus palatini crest horizontal and large; posterior surface of neurocranium and cleithrum strongly ornamented; two cranial fontanelles opened; posterior cranial fontanelle large and reaching base of supraoccipital spine; supraoccipital spine long and acute; second dorsal spine stout and laterally striated with an anterior ridge; pectoral spines stout, laterally striated, anteriorly smooth but with rather strong posterior dentations; six hypurals.

Genus *BACHMANNIA*

Arius partim Dolgopoi, 1941.

Type Species—*Bachmannia chubutensis* Dolgopoi, 1941.

Known Distribution—As for *B. chubutensis*.

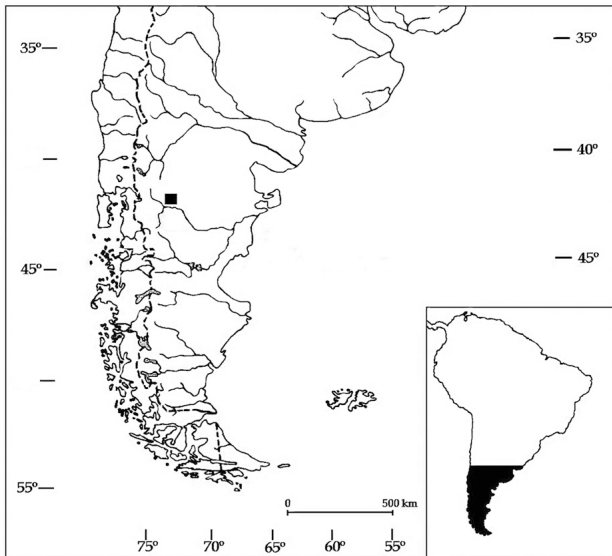
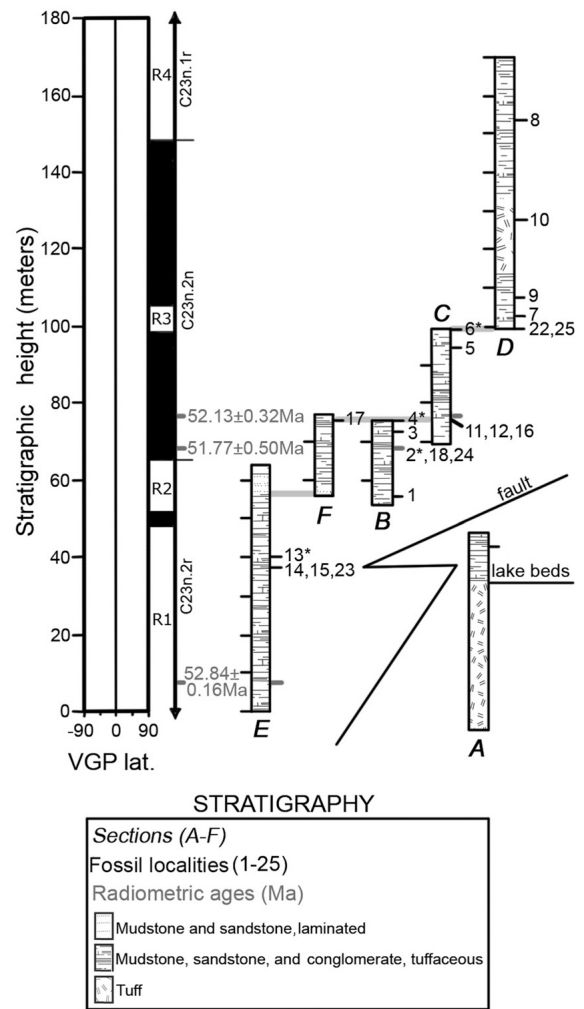


FIGURE 1. Map of location. Square indicates the fish locality.

FIGURE 2. Stratigraphic section of the Tufolitas Laguna del Hunco, aggregate thickness 170 m, showing principal lithologies; six local sections; correlations along marker beds for the five continuous sections (B to F); fossil localities; radiometrically dated samples, with 95% confidence intervals; virtual geomagnetic pole latitudes (VGP lat.); intervals of reversed and normal polarity (R1, N1, etc.), assignments to magnetic polarity subchrons. The base of the Tufolitas LH was found only in section A, which could not be traced accurately across a fault to continuous sections B to F; these sections were measured on outcrops extending 1.3 km along a single drainage and were correlated by bed tracing (modified from Wilf et al., 2003).

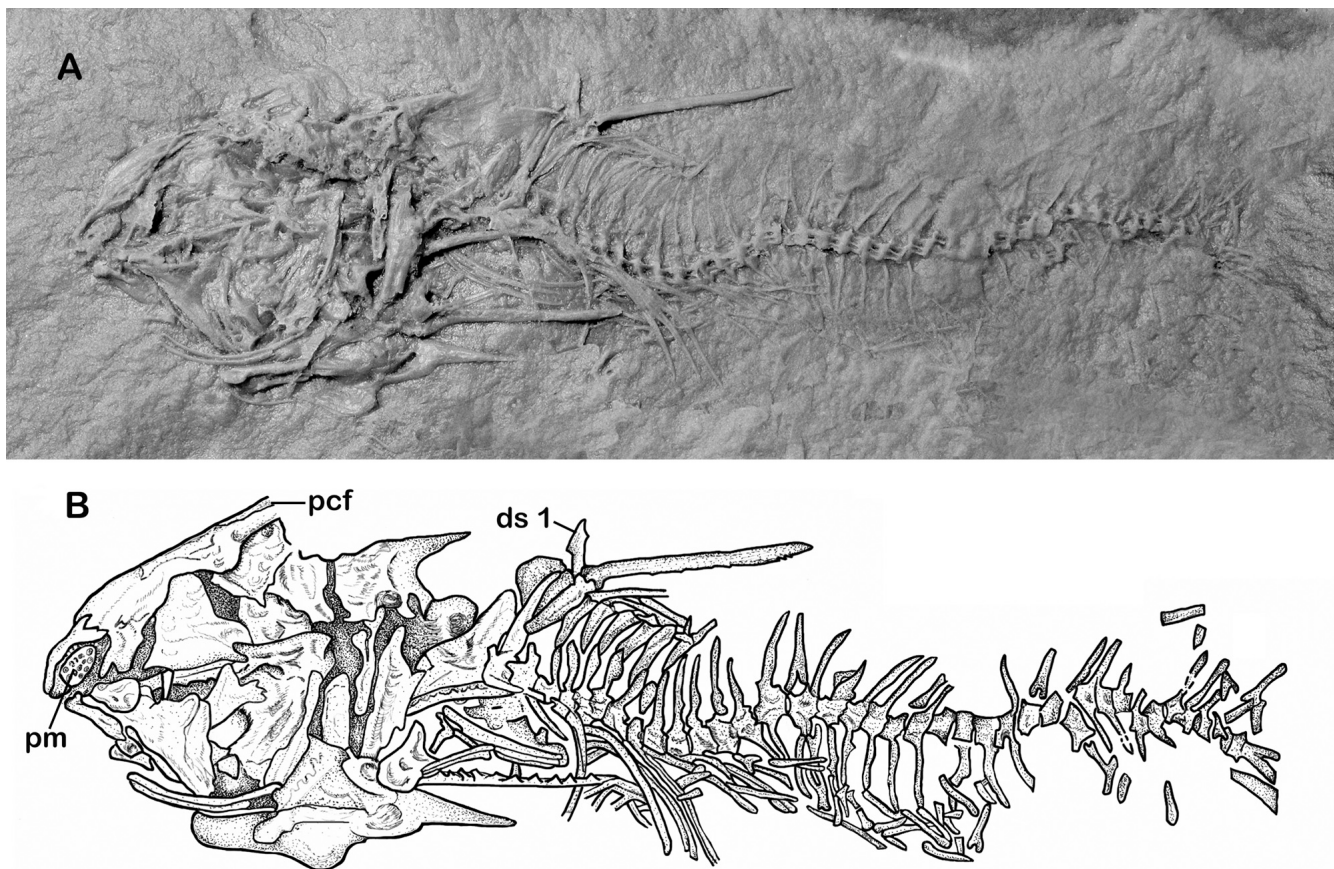


FIGURE 3. *Bachmannia chubutensis*, MLP 40-V-17-1, holotype, about 80 mm from tip of snout to hypural joint. **A**, photograph; **B**, line drawing.

Generic Diagnosis—As for the family.

Etymology—From Ernesto Bachmann (Dolgopol, 1941).

BACHMANNIA CHUBUTENSIS Dolgopol, 1941
(Figs. 3–13)

Bachmannia chubutensis Dolgopol, 1941.
Arius argentinus Dolgopol, 1941.

Holotype—MLP 40-V-17-1. A nearly complete impression of a fish about 80 mm (Fig. 3).

Referred Specimens—We examined 107 specimens. CIC: 75/1, 75/3–8, 75/10–14, 75/16–18. MACN PV: 19785–19806. MLP 35-X-4–8, MLP 40-V-17–3 (holotype of *Arius argentinus*), MLP: 40-V-17–4/6/7/9/11/14/15/17/19/21/23/24, 40-V-20–1, 77-VI-6–1/2/3/4. PVL: 4305–4307, 4309–4316, 4318–4331, 4365–4367, 4369–4370. MPBAR: 1091–1044. MPEF-PV: 1514/1516/1519, 1524a–b, 1525a–b, 1526–1527, 1537/1545/1549/1551, 1555a–b, 1900a–b, 1901a–b, 1902–1905.

Horizon and Locality—The material comes from the early Eocene Tufolitas Laguna del Hunco, outcropping near the Laguna del Hunco, Chubut, Argentina (42°20'S, 70°W; Fig. 1). The Laguna del Hunco biota was deposited in tuffaceous mudstones and sandstones. The sedimentation was accompanied by synchronous felsic volcanic events mainly in an intracaldera setting, resulting in foliated domes and lavas, silts, hyaloclastites, small and pumiceous ignimbrites, and rhyolitic dykes (Aragón and Mazzoni, 1997).

Age—Three ⁴⁰Ar/³⁹Ar analyses from tuffs, coupled with six paleomagnetic reversals, calibrated the fossiliferous strata to ages

near 52 Ma (Ypresian) and near the base of magnetic polarity Chron 23 (Wilf et al., 2003, 2005; Fig. 2).

Environment—*Bachmannia chubutensis* lived during the time of the early Eocene climatic optimum, when tropical plant taxa and warm, equable climates reached middle latitudes of both hemispheres (Wilf et al., 2005). At this moment, the Laguna del Hunco area was located near the southern limit of Neotropical floral influence, certainly a frost-free humid biome (Romero, 1986). As no significant uplift of the Southern Central Andes occurred before the Miocene (Marshall and Salinas, 1990), the Eocene Laguna del Hunco area lay at a low elevation, and a significant maritime influence moderated its climate. As sedimentation was accompanied by synchronous volcanic events mainly in the intracaldera setting (Aragón and Mazzoni, 1997) gases in water could have occasionally provoke massive fish kills. Specimens are relatively twisted.

Diagnosis—As for the family.

Etymology—Derived from Chubut, Argentina.

DESCRIPTION

General Morphology—*Bachmannia chubutensis* is a small species, the largest specimen is 125 mm SL. The body of *B. chubutensis* is relatively short; the head and the anterior part of the body are deep (Fig. 3). The dorsal profile of the head is convex (Fig. 3). The profile of the head resembles that of some callichthyids such as *Corydoras*. The skull appears to have not been wide because almost all the specimens were not preserved in dorsal or ventral positions such as is common in other fossil

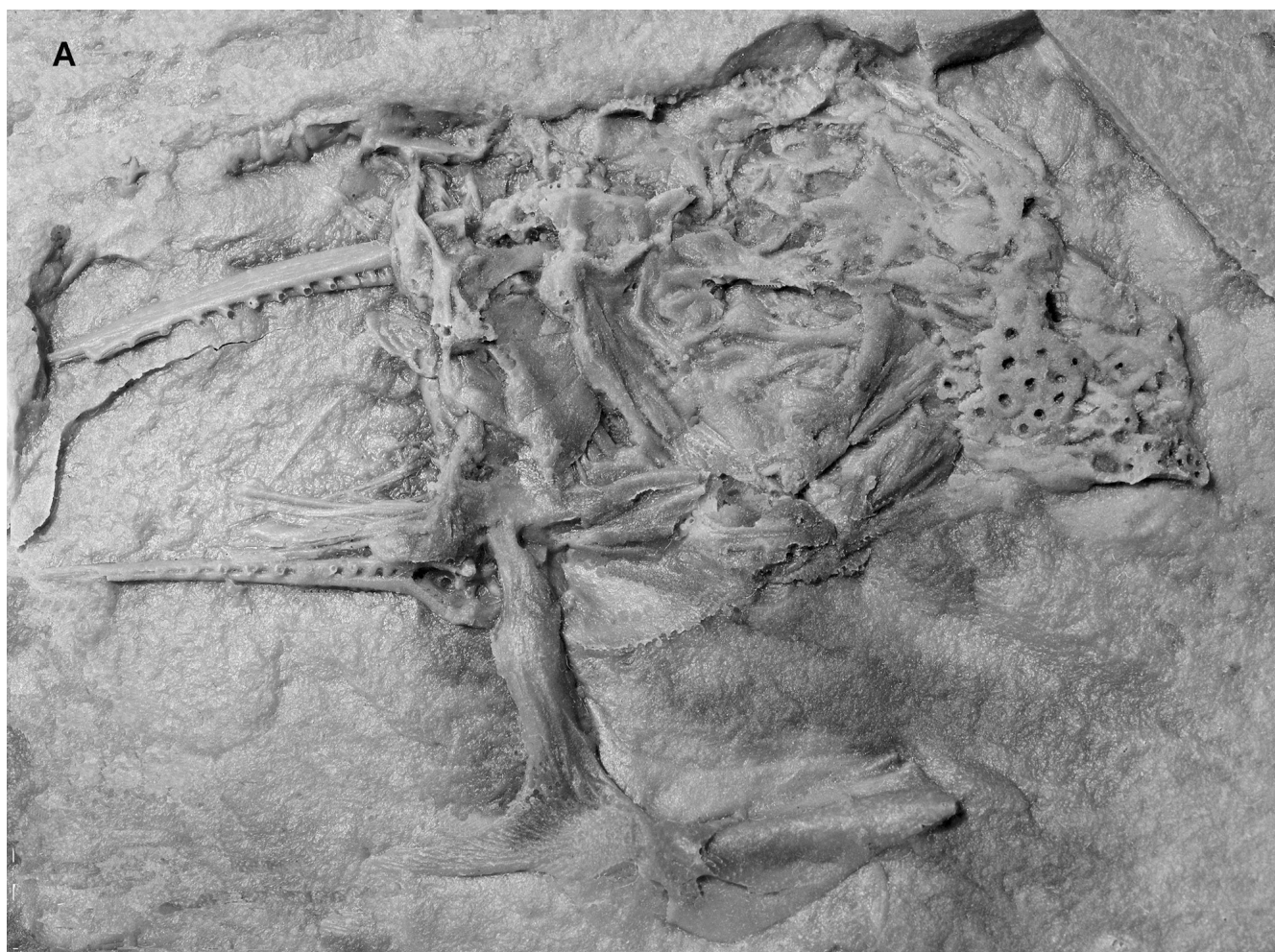


FIGURE 4. **A**, *Bachmannia chubutensis*, MLP 40-V-17-3, holotype of *Arius argentinus*. **B**, *Bachmannia chubutensis*, line drawing; scale bar equals 1 cm; **C**, cleithrum of *B. chubutensis*, with ventrolateral expansion; **D**, cleithrum of *Diplomystes viedmensis*. (Continued on next page.)

siluriforms preserved in slabs. This preservation is mainly referred to the head because the body is usually twisted to a lateral position (see *Hypsidoris farsonensis*: Grande, 1987).

Neurocranium—It is heavily ossified. Due to the state of preservation of the material, many bones are incompletely known. The dorsal surface of pterotic, supraoccipital, epioccipital, sphenotic, and posterior part of frontals appears strongly sculptured with pits and ridges although the mesethmoid and the anterior part of the frontals are almost smooth. The mesethmoid (**mes**, Figs. 3, 4, 5) is narrow, short, with slender small cornua; its anterior cleft is deep; the mesial lamina is deep and broad. The contact with frontal is weakly interdigitated. Neither nasal nor infraorbitals were observed. The posterior part of the mesethmoid is not well preserved but the anterior fontanelle appears to begin in it. The lateral ethmoid (**let**, Figs. 3–6) is large and stout; it has posterior projections sutured with orbitosphenoid. In dorsal view, it is almost completely overlapped by frontal. Ventrally, it has a broad contact with parasphenoid. The frontal is relatively long, wider posteriorly than anteriorly; it lacks crests for muscle attachment on the dorsal surface. The orbital margin is slightly curved and smooth. Sutures with supraoccipital and pterotic are weakly interdigitated; suture with sphenotic is smooth. The epiphysial bar is broad, located at about the middle part of frontals. Both cranial fontanelles are always opened. The posterior fontanelle reaches the base of the supraoccipital spine

(Fig. 6). The supraoccipital (**soc**, Figs. 3–6) is very large, with a long and slender supraoccipital spine. The posterior tip of the spine is not bifid. Supraoccipital is close but not in contact with supraneural 5 (Fig. 10). Other supraneurals were not observed. The supraoccipital has a small transversal crest that seems to be continued with another most conspicuous on the extrascapula. The epioccipital (**epi**, Fig. 6) forms the posterior dorsal surface of neurocranium, although we cannot describe its shape and sutures. The basioccipital is short (**boc**, Fig. 5B). The exoccipital is large (**exo**, Figs. 3, 5). The short sphenotic (**sp**, Figs. 3, 4, 5B, 6) does not have an anterior sphenotic spine. The contact with frontal is not interdigitated. In the pterotic (**pt**, Figs. 4, 6), we only observed two short posterior processes. The large prootic (**pro**, Figs. 3, 5) sutures with sphenotic, pterotic, exoccipital, and parasphenoid. The extrascapula (**exes**, Fig. 6) is short, thin, and wide; a crest crosses its surface. It lies among pterotic, epiotic, and supraoccipital. Because it is missing in most specimens, it was probably not strongly attached to the other bones. The posterior part of vomer (**v**, Figs. 4, 8) is short and somewhat triangular; its dorsal lamina is deep. The sole vomerine tooth plate has the anterior margin rounded. It has the largest teeth, covering completely the anterior portion. Teeth are conic, short, very stout, and unordered (Figs. 5, 7, 8). In the vomer, as in the other tooth-bearing bones of *Bachmannia*, teeth are disarticulated (Figs. 4, 8). However, well-preserved tooth sockets in the tooth bearing bones give a

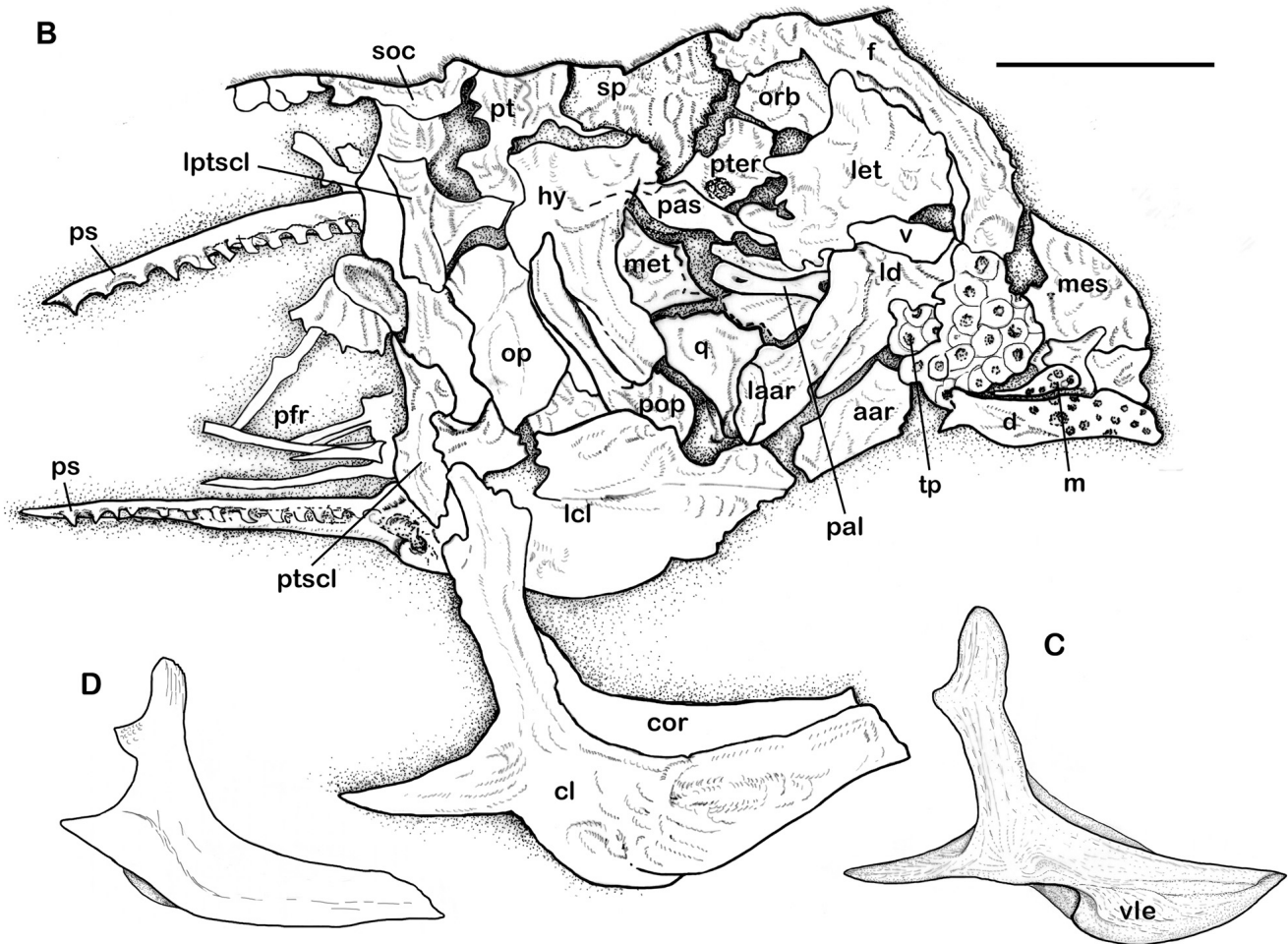


FIGURE 4. Continued.

good idea of the extent and number of tooth coverage. Accessory tooth plates, with smaller teeth, are present at sides of the vomer (Fig. 8). The orbitosphenoid (**orb**, Figs. 4, 5) is large, quadrangular, and very deep. The pterosphenoid (**pter**, Figs. 4–6) is rather large, quadrangular; it sutures with orbitosphenoid leaving two openings. It is located far from parasphenoid. The parasphenoid (**pas**, Figs. 3–5) was observed only from lateral views. It is long, with deep lateral wings; a keel seems to be developed ventrally.

Upper Jaw—We only observed ventral views of the premaxilla (**pm**, Fig. 3). It is short, quadrangular, and scarcely tapers distally. Premaxilla bears three tooth rows close to the symphysis. The external row includes the largest teeth. The toothed maxilla (**m**, Figs. 4, 6–8) has an articular process relatively long; the posterior laminar process is short, expanded distally, bearing two rows of large teeth. The maxilla has a double-headed articulation for autopalatine (Fig. 6C). There are some longitudinal striae on the posterior process and some pits in the anterior part.

Lower Jaw—The lower jaw is short and stout, with striae on the external surface and it has a high coronoid process (Figs. 3, 4, 6, 7). The dentary (**d**) has conical, long, pointed end, and robust teeth. There are four rows near the symphysis. Teeth cover nearly entirely the dorsal margin of the dentary. We did not observe sutures between the angular + articular + retroarticular bones (**aar**, Figs. 3, 4, 6, 7) nor the presence of coronomeckelian bone. The articular fossa for quadrate is large and slightly concave.

Opercular Apparatus—The opercle (**op**, Figs. 3, 4, 6) is ornamented with small pits and very low ridges. The interopercle (**iop**, Fig. 9A) is almost rectangular with a well-developed oblique external ridge; in some specimens, it also has very small pits (Fig. 10). The elongate preopercle (**pop**, Fig. 3, 4, 6) is wider ventrally than dorsally. The opening for the truncus hyomandibularis branch pierces the bone near the suture with the hyomandibula (Fig. 6). There is one suprapreopercle.

Suspensorium—The hyomandibula (**hy**, Figs. 3–6) has a well-developed anterior dorsal process for articulation with the sphenotic. The posterodorsal articular surface connects it with sphenotic, pterotic, and probably prootic. There is a large, horizontal levator arcus palatini crest. We could not recognize foramina in the external surface. The condyle for articulation with opercle is very prominent. The metaapterygoid (**met**, Figs. 4, 6) is subrectangular in outline. The suture with the hyomandibula is wide. A small dorsal process is present. There is a well-marked anterior interdigitated suture with another undetermined pterygoid bone. The quadrate (**q**, Figs. 4, 6) is triangular, relatively large, with a small ventroanterior process. Its suture with metaapterygoid is weakly interdigitated. The autopalatine (**pal**, Figs. 4, 5B) has an anterior portion flattened and expanded, whereas the posterior portion is slender. Both portions have similar length. The anterior portion has two anterior articular processes for articulation with the maxilla. It also has a median articular surface for lateral ethmoid.

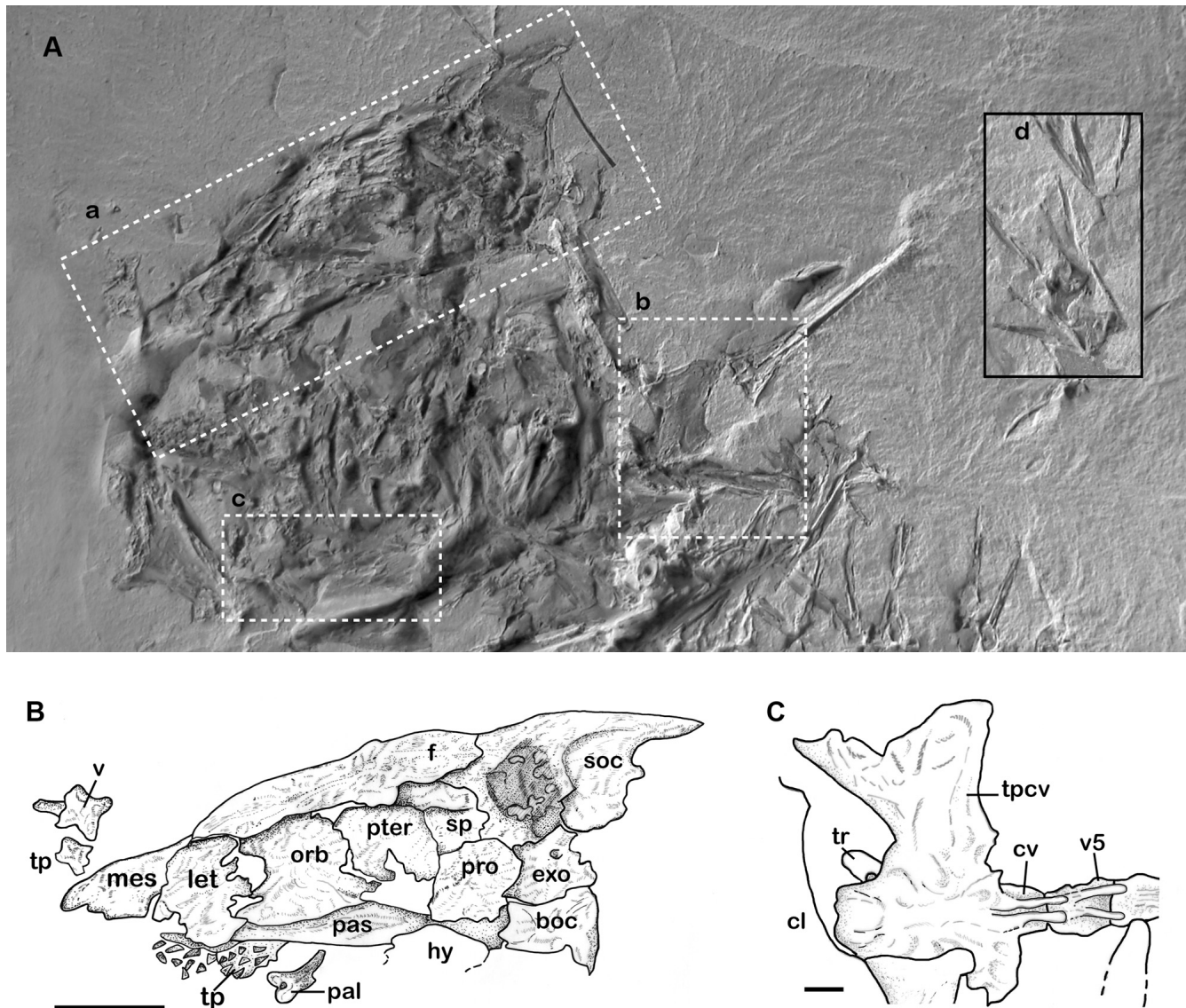


FIGURE 5. *Bachmannia chubutensis*, MPEF-PV 1525. **A**, photograph of (a) neurocranium in lateral view, with disarticulated autopalatine and vomer, (b) Weberian apparatus in dorsal view, (c) parurohyal (line drawing in Fig. 9C of present paper), and (d) basiptyergium (line drawing in Fig. 13C of present paper); **B**, line drawing of neurocranium (a), scale bar equals 1 cm; **C**, detail of Weberian apparatus in dorsal view (b), scale bar equals 1 mm.

Hyoid Elements—Hypohyals were not preserved. Suture between ceratohyal and epihyal is smooth, not interdigitated (Fig. 9B). The parurohyal is anteriorly wide (Fig. 9C). We counted five branchiostegal rays. The first one is broad, especially in the distal half.

Vertebral Column and Weberian Apparatus—Weberian apparatus of most of specimens is laterally preserved and the transverse process is broken. The first vertebra is free (**fv**, Fig. 10). The complex centrum is short and formed by 2nd, 3rd, and 4th vertebrae (**cv**, Figs. 5C, 10). We did not find neither supraneural 3 or 4 nor ventral lamina of 5th centrum. The body of 5th vertebra is longer than posterior ones. The neural arch (**na**, Figs. 3, 10) of vertebrae 5th and 6th are deep; the first one is almost as long as neural arch of complex centrum and the neural arch of 6th vertebra is shorter than the 5th one (Fig. 10). The transverse process of the complex

vertebra is well developed, and by with lateral and posterior margins straight (Figs. 5, 6). The tripus is anteriorly acute (Figs. 5C, 6B). The scaphium is well preserved only in CIC 16-XII-75/12, although it was not figured; its dorsal process is slender and the horizontal one is wide. We counted 35–37 vertebrae + four of Weberian apparatus.

Ribs—We counted 10 pairs of ribs. We did not observe a rib on 5th vertebra.

Dorsal Fin—The dorsal fin (Fig. 10) is located at the level of 5th and 13th vertebrae. Dorsal fin is formed by a short and small first spine (spinelet), a large second spine, and seven rays. The spinelet is triangular, very stout, and ornamented with pits at both sides. The dorsal spine 2 is longitudinally striated, more slender than pectoral spine. The anterior edge is smooth with a blunt medial longitudinal ridge. The posterior face of the spine includes

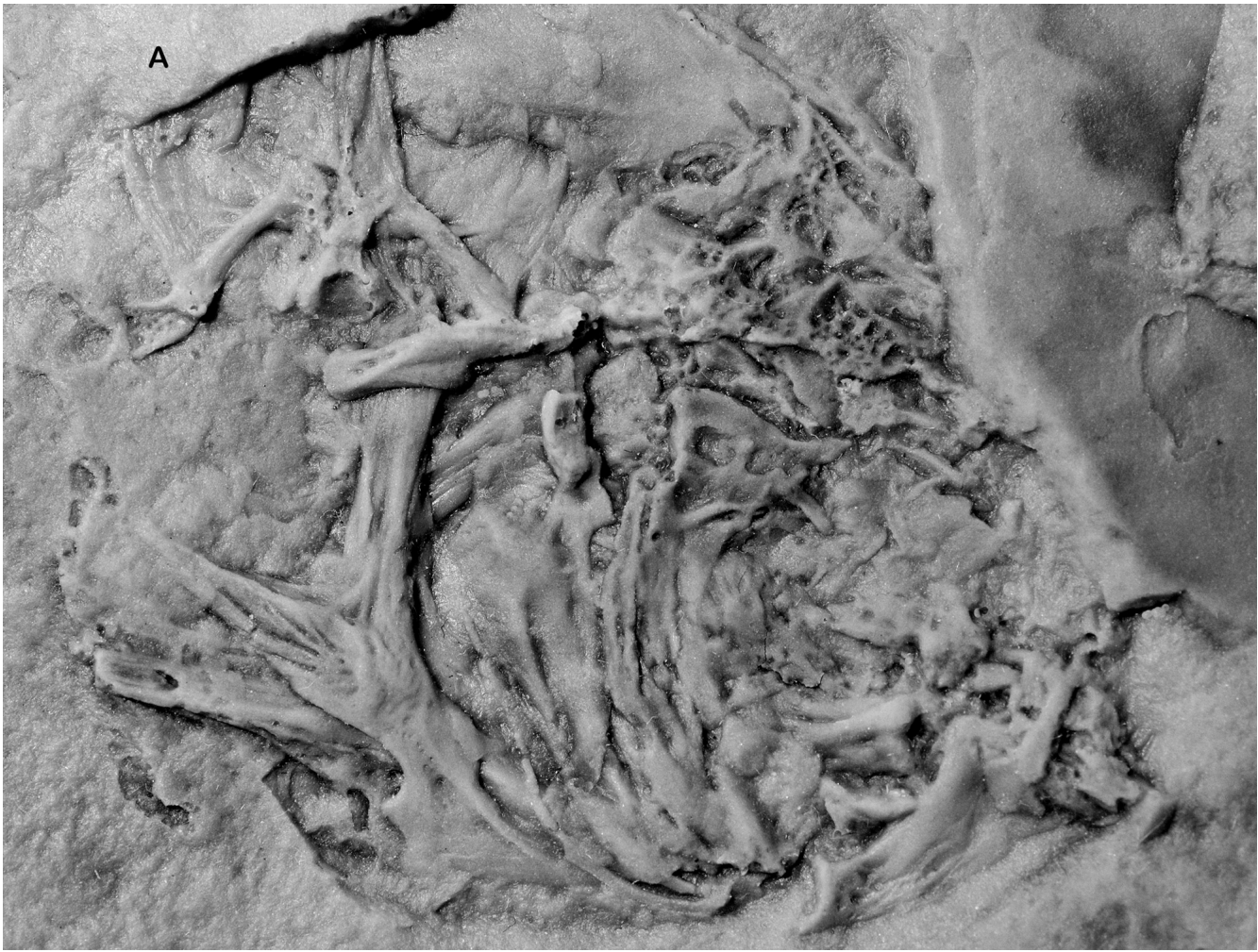


FIGURE 6. *Bachmannia chubutensis*, CIC 16-XII-75/12, suspensorium and anterior region of cranium with maxilla, partial posterior region of neurocranium in dorsal view, complex centrum of Weberian apparatus in dorsal view. **A**, photograph; **B**, line drawing, scale bar equals 1 cm; **C**, detail of maxilla with an incomplete series of teeth, scale bar equals 1 mm. (Continued on next page.)

some small distal tubercles. The supraneural 5 (**sn**, Figs. 3, 10) is triangular, laminar, and very expanded; it is located between neural spines of Weberian apparatus and 5th vertebra. Although the two nuchal plates (**np**, Fig. 10) are not very well preserved, pits are seen on them. We counted seven pterygiophores (**ptg**, Fig. 10).

Anal Fin—The anal fin is badly preserved; we counted 10 rays.

Caudal Fin—The caudal skeleton (Fig. 11) was reconstructed from different specimens. It consists of parhypural (**ph**), six hypurals (**h**), uroneural (**un**), epural (**ep**), centra, and badly preserved lepidotrichia. The parhypural is laminar and hypurals 1 and 2 are separated. Hypural 2 has broken hypurapophysis. The dorsal portion of the complex centrum is not preserved. The hemal spine of preural centrum 2 is wide.

Pectoral Fin and Girdle—The fin is composed by one spine and at least nine soft rays (Fig. 12). The spine (**ps**, Figs. 3, 4, 6) is long, large, and stout, and dorsoventrally compressed. There are 12–13 posterior dentations inside a longitudinal groove; dentations are more closely arranged basally than distally. Proximal and medial dentations are gently curved basad but those distal ones are almost straight. Shaft spine is ornamented by deep longitudinal, non-anatomosed striae. The anterior edge does not present a ridge and is smooth excepting for some tubercles on the distal

portion. The posttemporal + supracleithrum (**ptscl**, Figs. 3, 4, 6) is stout, long, and heavily sculptured. Its ventral limb is long, broad, and it is not bifid. The scapulocoracoid (**cor**, Figs. 4, 6, 12) is usually seen in dorsal view. In the sole specimen preserved in ventral view (Fig. 12), a portion of mesocoracoid is observed. The mesial margin of scapulocoracoid is straight. The cleithrum (**cl**, Figs. 4, 6) is heavily sculptured and stout. Its long ascending process is slender but strong. The dorsal tip is acute and single. The ornamentation on ascending process is less marked than in the rest of the bone, especially formed by dorsoventrally oriented grooves. The posterior cleitral process is very long, more than half of ascending process length; it is relatively slender and sharply pointed. Its ornamentation is strong, formed by pits and grooves (Figs. 4, 6). The suture between left and right cleithra is smooth, without interdigitations. In lateral view, the anterior half of the cleithrum is very deep because its ventral margin abruptly slants downward forming a lamina. Notwithstanding that the cleithrum of *Bachmannia* conforms to the generalized siluriform shape, the anterior lateroventral expansion is not seen in any other species of catfishes (see Figs. 4, 6).

Pelvic Fin and Girdle—The fin is located about the 14th and 15th vertebrae. The pelvic bone usually has two long and slender anterior processes (**app**, Fig. 13A) but in one specimen there are

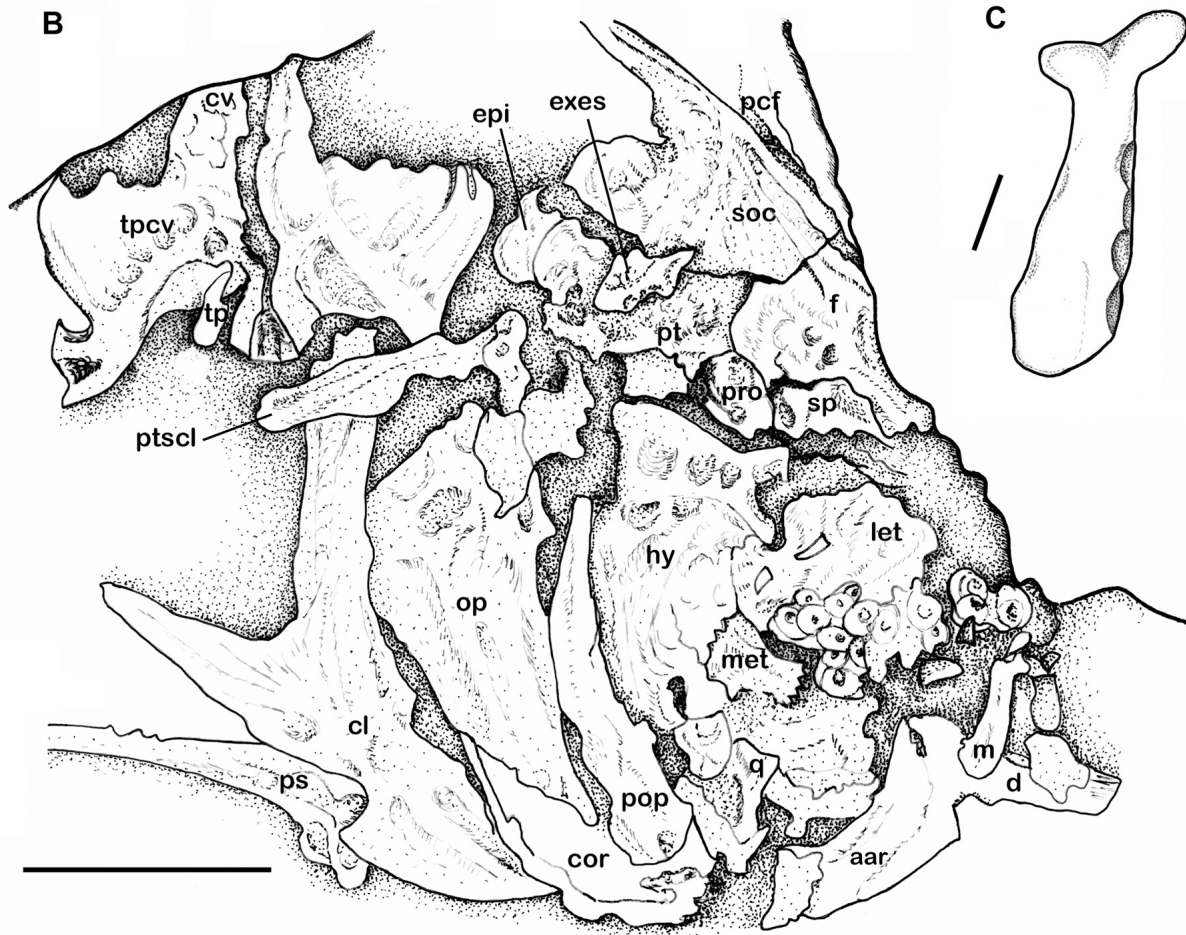


FIGURE 6. Continued.

three (Fig. 13C). Posterior and lateral processes of pelvic bone are medium sized. There are a pelvic splint (**pvs**, Fig. 13B) and six rays.

DISCUSSION

How Many Genera and Species are in Laguna del Hunco?—The species *A. argentinus* Dolgop, 1941, was based on a sole and fragmentary specimen. However, the material does not correspond to the family Ariidae. Bone morphology of the holotype of *A. argentinus* is actually identical to that of holotype and additional material of *B. chubutensis* and we consider the first as a junior synonym of the second.

Phylogeny—Catfishes are known since the Campanian of Argentina (Cione and Báez, 2007). They also occur in the Cretaceous of North America, India, and possibly Africa (Cione and Prasad, 2002). In the Paleocene they also were present in Europe and in the Eocene of North America and Antarctica (Grande, 1987; Grande and Pinna, 1998). Only two fossil catfish families were recognized: Hypsidoridae in the Eocene of North America (Grande, 1987) and Andinichthyidae in the

Late Cretaceous and Paleocene of Bolivia (Gayet and Meunier, 2003).

Grande (1987) proposed a catfish phylogeny. In his hypothesis, Diplomystidae (Diplomystoidei) is the sister group of all remaining catfishes (Siluroidei). Besides, the monotypic new family Hypsidoridae (Hypsidoroidea) was considered the sister group of all the other catfish families (Siluroidea).

Other subsequent morphological analyses agree in considering Diplomystidae as the most basal catfish group (Mo, 1991; Grande and de Pinna, 1998; de Pinna, 1998; Hardman, 2005; Diogo, 2006; Rodiles-Hernández et al., 2009). Rodiles-Hernández et al. (2009) proposed that the sister group of Diplomystidae was a polytomy including Hypsidoridae, Cetopsidae, and the many other taxa. Sullivan et al. (2006), in a molecular analysis, proposed a radically different phylogeny where Loricarioidei is the sister group of Diplomystidae + the other catfishes.

Grande (1987) diagnosed Siluroidei by the following characters: (1) 17 or fewer principal caudal rays (vs. 18 in *Diplomystes* and other primitive teleosts such as most characiformes); (2) an extension of lamellar bone below the ventral surface of 5th centrum; (3) 5th centrum joined closely to complex centrum by two ventral ridges of superficial ossification. Arratia (1992) added

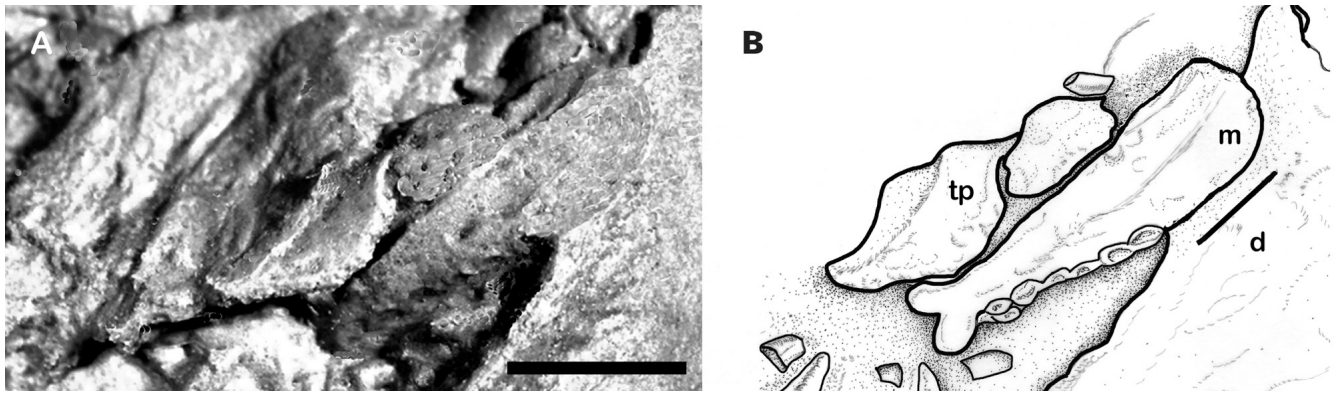


FIGURE 7. *Bachmannia chubutensis*, MACN PV 1980, ventrolateral view of maxilla with two anterior processes. **A**, photograph; **B**, line drawing. Scale bars equal 1 mm in A; scale bar equals 0.8 mm in B.

several characters for Siluroidei: (E) dorsal and ventral hypohyal of different sizes; (F) maxilla with two rudimentary processes bearing small facets for articulation with autopalatine. In *Bachmannia* we could not observe characters 1 and E; according to all preserved evidence, the other ones are not present, indicating that it is a very primitive catfish.

Notwithstanding that many data are missing in a fossil fish such as *Bachmannia*, we reanalyzed siluriform relationships considering the data matrix used by Rodilez-Hernández et al. (2009; we observed 47.5% of the characters included in the matrix). The most parsimonious tree resulted among 4096 trees of 701 steps under equal weighting criterion. A strict consensus tree (CI = 0.43; RI = 0.74) is presented in Figure 14.

Bachmanniidae appears as the sister group of Diplomystidae, formerly the sister group of all the other catfishes. Excepting for this new clade, the topology of the tree agrees with that of previous authors excepting the last molecular one (Sullivan et al., 2006). The presence of a double anterior palatine head (character 98) constitutes the unique, uncontradicted synapomorphy,

supporting the close relationship between Bachmanniidae and Diplomystidae. This character is also the only synapomorphy supporting the clade in the analyses under implied weighting and self-weighted optimization, in the entire range of explored values of K. Those analyses do not modify the position of Bachmanniidae and Diplomystidae.

Comparison of *B. chubutensis* with the Sister Group Diplomystes—*Bachmannia* shares some characters with *Diplomystes* such as the anteriorly narrow mesethmoid with short cornua, anterior and posterior fontanelles very large, a supraoccipital spine not bifid, lateral ethmoid almost completely covered by frontal, lateral ethmoid deep with an extended suture with orbitosphenoid, orbitosphenoid very deep, pterosphenoid far from parasphenoid, thin extrascapula tightly sutured on skull roof, toothed maxilla, vomerine tooth plate, 'palatal' accessory tooth plates, palatine with a double articulation for maxilla, a remarkable development of levator arcus palatini crest on hyomandibula, ceratohyal and epihyal with straight suture, first vertebra unfused and short, 5th vertebra joined to Weberian complex centrum, seven dorsal soft rays, six caudal hypurals, suture between cleithrum and coracoid without interdigitations, and some specimens with three anterior processes in the basiptyergium.

However, *Bachmannia* differs from *Diplomystes* in having cleithrum with an anterior ventrolateral expansion (Fig. 4C, D), ornamented skull roof, frontal wider posteriorly than anteriorly, sphenotic without anterior spine, very long supraoccipital spine, very large supraoccipital, posterior cranial fontanelle penetrating supraoccipital spine deeply, absence of well-developed crests on the dorsal surface of skull (on frontal and supraoccipital) suggesting that there is no muscular invasion on it, shorter maxilla, absence of spatulate teeth (Arratia, 1987:figs. 14–15; Azpelicueta, 1994:fig. 10a), quadrate with an anteroventral process, ornamented interopercle, second dorsal spine with anterior ridge, pectoral spine with posterior sulcus and smaller serrae.

Comments on Some Characters of Bachmanniidae—The cleithrum has the typical morphology of catfishes including a strong ornamentation. However, the horizontal lamina has an anterior ventrolateral expansion not seen in other siluriforms representing a unique character of the family (Figs. 4, 6).

The teeth of Bachmanniidae are remarkably large in contrast to those very small present in most Siluriformes. Teeth are conical, stout, and with broad bases; some of them show blunt tips; vomerine teeth are the largest. Large teeth are also present in Diplomystidae, some Cetopsidae, Plotosidae, some species of

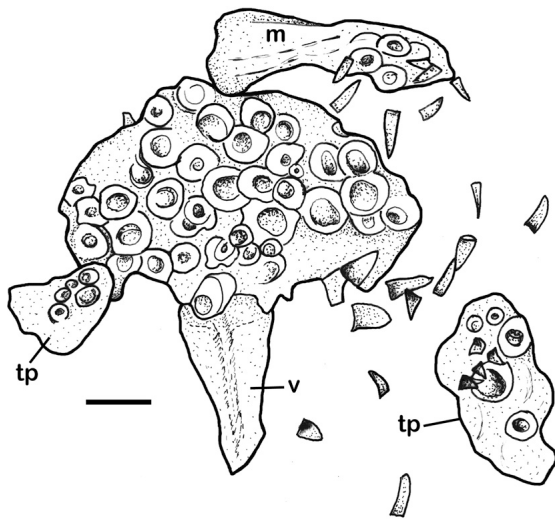


FIGURE 8. *Bachmannia chubutensis*, MACN PV 19792, line drawing of maxilla, vomer and tooth plates. Scale bar equals 1 mm.

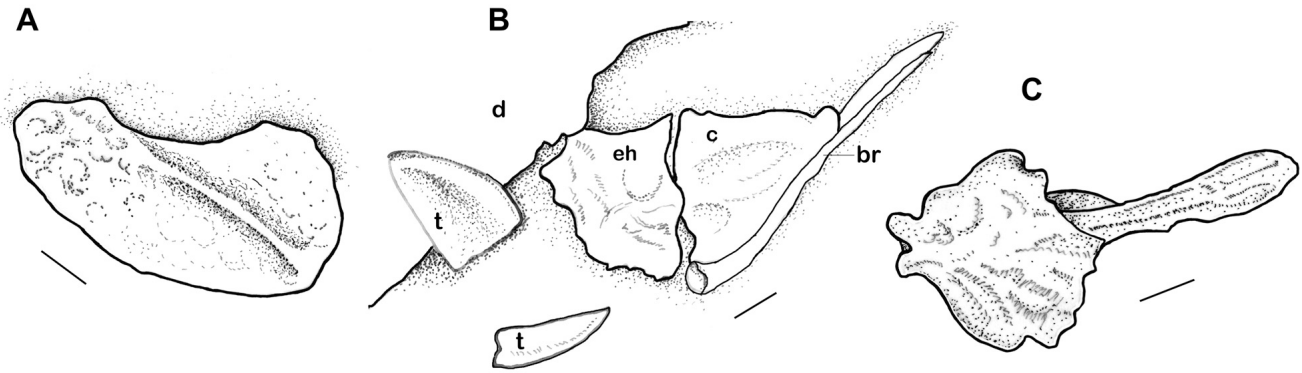


FIGURE 9. *Bachmannia chubutensis*. **A**, MPBAR 1091-44, interopercle; **B**, MACN PV 19800, ceratohyal and epihyal; **C**, MPEF-PV 1525, parurohyal. Scale bars equal 1 mm.

Ariidae (e.g., *Cathorops spixii*), and some Pimelodidae (e.g., *Exallodontus aguanai*). The occurrence of these large teeth seems to be homoplasies.

Bachmanniidae has a toothed maxilla, a primitive catfish character only known otherwise in Diplomystidae and Hysidoridae. A maxilla with one anterior process bearing two articulations for autopalatine and completely separating premaxilla and autopalatine is present in adult diplomystids. Arratia (1992) considered that condition unique in Diplomystidae. Although Bachmanniidae has the same shape of articular processes and autopalatine, because both maxilla and autopalatine are always disarticulated, we could not confirm that condition.

Diplomystidae, Hysidoridae, and Bachmanniidae are the only three known families with toothed maxilla, but the shape differs in them. Diplomystidae has the longest and, comparatively, the most distally expanded maxilla (Arratia, 1987:fig. 26). In Hysidoridae, it is shorter and slightly expanded (Grande, 1987:fig. 4); Bachmanniidae has the shortest maxilla, also slightly expanded distally (Figs. 6, 7).

The maxilla of Bachmanniidae includes only two rows of teeth (Fig. 6), whereas in Diplomystidae the number of rows is variable (*D. viedmensis* has until five rows [Azpelicueta, 1994:fig. 16b-f]; *D. nahuelbutaensis* has only two [Arratia, 1987:fig. 7]; and Hysidoridae has teeth anteriorly placed [Grande, 1987:fig. 6; Grande and de Pinna, 1998:fig. 7; personal observation, MMA]). The presence of accessory tooth plates is variable in catfishes. Some species of *Diplomystes* (Arratia, 1987; Azpelicueta, 1994:fig. 16a), the two species of *Hysidoris* (Grande, 1987:fig. 5; Grande and de Pinna, 1988:fig. 7) and *Bachmannia* (Fig. 8) have these plates. This character is considered a derived one (Fink and Fink, 1981).

Bachmannia has a depressed, anteriorly broad autopalatine with two anterior condyles for maxilla. Those characters are shared with Diplomystidae and Hysidoridae. However, the autopalatine of *Bachmannia* (Fig. 5) has an anterior notch also present in most species of *Diplomystes* (Arratia, 1987:fig. 24) but absent in *Hysidoris* (Grande, 1987:fig. 4).

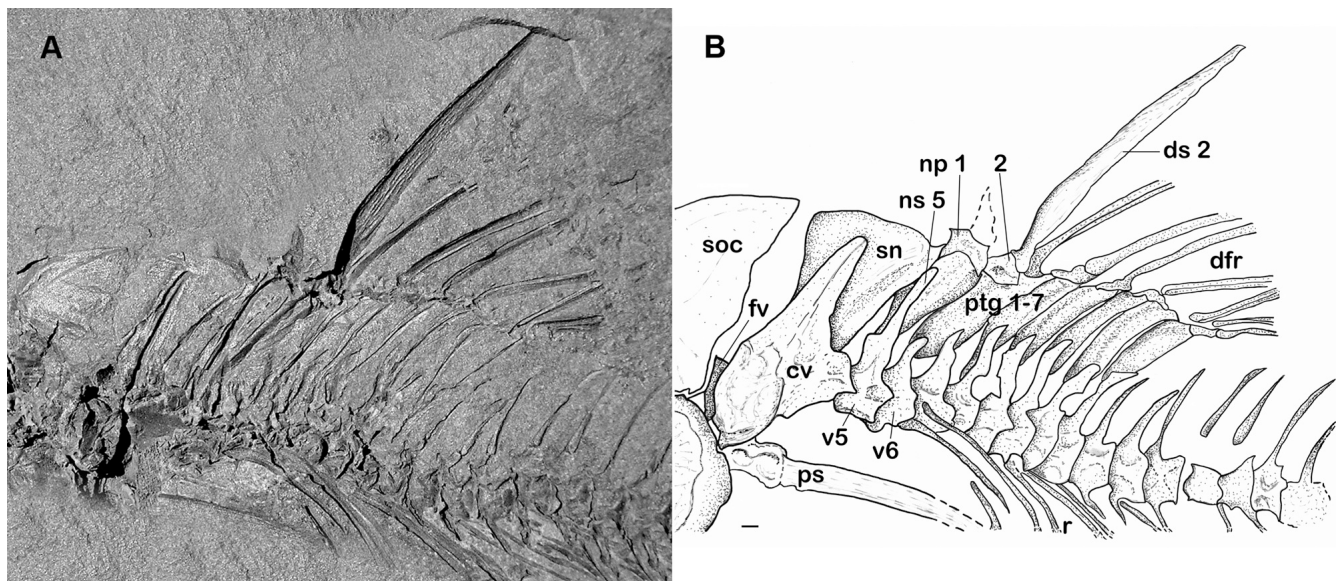


FIGURE 10. *Bachmannia chubutensis*, MLP 77-VI-6-2, dorsal fin. **A**, photograph; **B**, line drawing. Scale bar equals 1 mm.

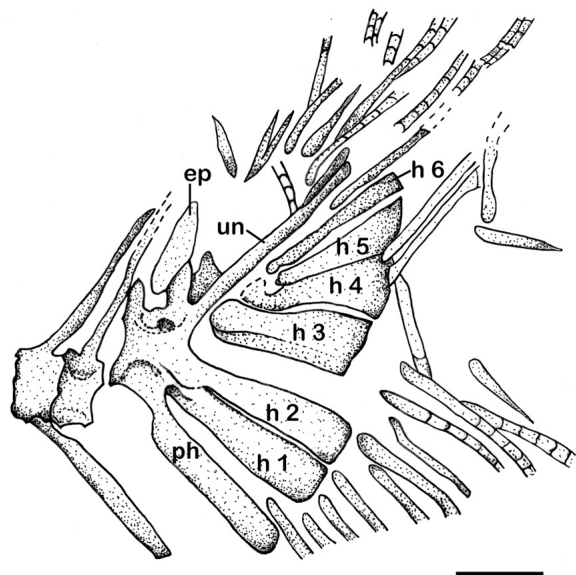


FIGURE 11. *Bachmannia chubutensis*, caudal skeleton from MLP 40-V-17-7. Scale bar equals 1 mm.

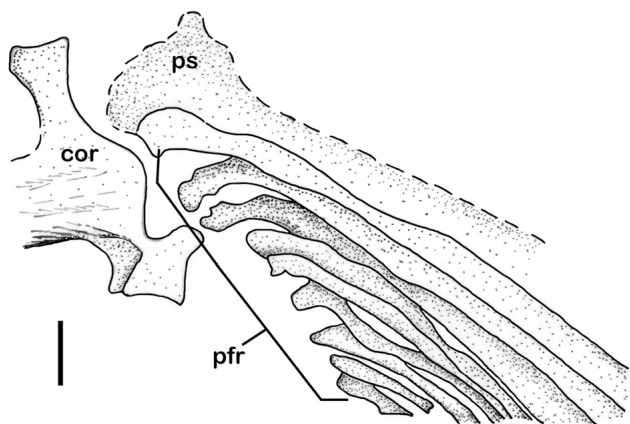


FIGURE 12. *Bachmannia chubutensis*, MACN PV 19804, pectoral fin rays and broken coracoid. Scale bar equals 1 mm.

The 5th vertebra is shorter than the following ones, its arch and neural spine are well developed; the neural spine is almost as deep as that of the complex centrum or deeper. Within the Siluriformes, this last character is only present in Diplomystidae (Arratia, 1987:fig. 4) and Bachmanniidae (Fig. 10).

The deep neurocranium of *Bachmannia* makes that mesial bone as orbitosphenoid and pterosphenoid reach a large development in its dorsoventral axis (Fig. 5). The common condition in Siluriformes is a suture between pterosphenoid and parasphenoid, a character that is not present in *Bachmannia* and *Diplomystes* (Arratia, 1987:figs. 5B, 23).

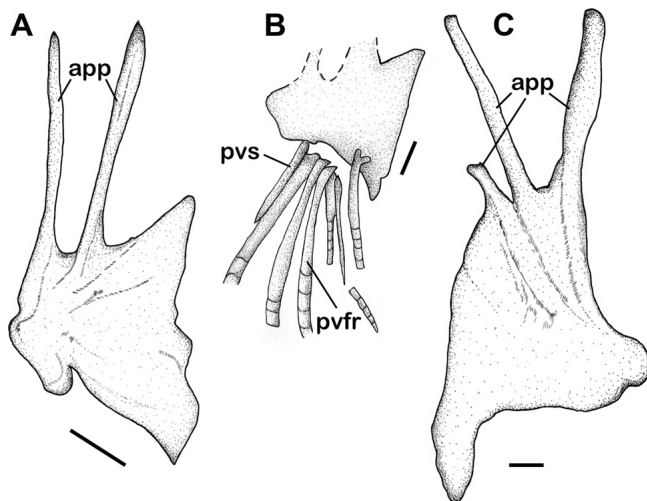


FIGURE 13. *Bachmannia chubutensis*, **A**, CIC 16-XII-75-14, basiptyergium with two anterior processes; **B**, MPBAR 1091-44, basiptyergium and fin rays; **C**, MPEF-PV 1525, basiptyergium with three anterior processes. Scale bars equal 1 mm.

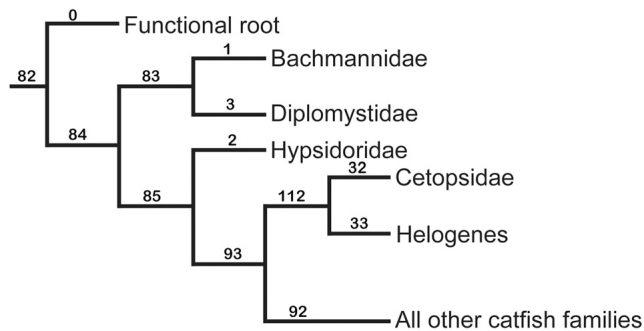


FIGURE 14. Cladogram showing the position of *Bachmannia chubutensis*. Single strict consensus tree obtained under equal weighting among 4096 trees of 701 steps (CI = 0.43; RI = 0.74).

ACKNOWLEDGMENTS

We thank the Agencia Nacional de Promoción Científica y Tecnológica, Consejo Nacional de Investigaciones Científicas y Técnicas, National Science Foundation (DEB-0345750, 2004-2008), and Universidad Nacional de La Plata for financial support; M. Mirande for help in the phylogenetic analysis; A. Martínez for composition of the figures; Ø. Bratland and F. Goin for the photographs; A. M. Báez, N. Brugni, the late R. Casamiquela, N. Cúneo, C. Ferraris Jr., J. Fiori, L. Grande, J. Lundberg, J. Powell, E. Romero, E. Ruigómez, M. Sabaj, R. Vari, and P. Wilf for loan of material under their care; and P. Puerta, K. Johnson, and P. Wilf for help in the field work. Detailed comments and suggestions provided by two anonymous reviewers greatly improved the manuscript.

LITERATURE CITED

Aragón, E., and M. Mazzoni. 1997. Geología y estratigrafía del complejo volcánico y piroclástico del río Chubut medio (Eoceno),

- Chubut, Argentina. *Revista de la Asociación Geológica Argentina* 52:243–256.
- Arratia, G. 1987. Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications. *Bonner Zoologische Monographien* 24:1–120.
- Arratia, G. 1992. Development and variation of the suspensorium of primitive catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships. *Bonner Zoologische Monographien* 32:1–148.
- Arratia, G., and A. L. Cione. 1996. The fossil fish record of Southern South America; pp. 9–72 in G. Arratia (ed.), *Contributions of Southern South America to Vertebrate Paleontology*. Münchener Geowissenschaftliche Abhandlungen 30, Munich.
- Azpélicueta, M. M. 1994. Three East-Andean species of *Diplomystes* (Siluriformes: Diplomystidae). *Ichthyological Exploration of Freshwaters* 5:223–240.
- Cione, A. L., and A. M. Báez. 2007. Peces y anuros cenozoicos de Argentina: los últimos cincuenta años. *Publicación Especial de la Asociación Paleontológica Argentina* 11:195–220.
- Cione, A. L., and G. V. Prasad. 2002. The oldest known catfish (Teleostei: Siluriformes) from Asia (India, Late Cretaceous). *Journal of Paleontology* 76:190–193.
- de Pinna, M. C. C. 1998. Phylogenetic relationships of Neotropical Siluriformes (Teleostei: Ostariophysi): historical overview and synthesis of hypotheses; pp. 279–330 in Z. M. Lucena, R. E. Reis, R. P. Vari, and C. A. Lucena (eds.), *Phylogeny and Classification of Neotropical Fishes*. EDIPUCRS, Porto Alegre, Brazil.
- Diogo, R. 2006. Cordelia's dilemma, historical bias, and general evolutionary trends: catfishes as a case study for general discussions on phylogeny and macroevolution. *International Journal of Morphology* 24:607–618.
- Dolgopol, M. D. 1941. Noticias sobre peces fósiles argentinos. *Siluroideos terciarios de Chubut*. *Notas del Museo de La Plata* 35:451–457.
- Eschmeyer, W. 2010. Online Catalog of Fishes. Available at <http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp>. Accessed July 2010.
- Fink, W. L., and S. V. Fink. 1981. Interrelationships of the Ostariophysan Fishes (Teleostei). *Zoological Journal of the Linnean Society of London* 72:297–353.
- Gayet, M., and F. Meunier. 2003. Palaeontology and palaeobiogeography of catfishes; pp. 491–522 in G. Arratia, A. S. Kapoor, M. Chardon, and R. Diogo (eds.), *Catfishes 2*. Science Publishers, Plymouth.
- Grande, L. 1987. Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships. *Journal of Vertebrate Paleontology* 7:24–54.
- Grande, L., and M. C. C. de Pinna. 1998. Descriptions of a second species of the catfish *Hypsidoris* and a reevaluation of the genus and the Family Hypsidoridae. *Journal of Vertebrate Paleontology* 18:451–474.
- Goloboff, P. A. 1993. Estimating character weights during tree search. *Cladistics* 9:83–91.
- Goloboff, P. A. 1997. Selfweighted optimization: tree searches and character state reconstructions under implied transformation costs. *Cladistics* 13:225–245.
- Goloboff, P. A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics* 15:415–428.
- Goloboff, P. A., J. S. Farris and K. Nixon. 2007. TNT: Tree Analysis Using New Technology. Version 1.1, February 2007. Available at www.zmuc.dk/public/phylogeny. Accessed September 2010.
- Hardman, M. 2005. The phylogenetic relationships among non-diplomystid catfishes as inferred from mitochondrial cytochrome *b* sequences; the search for the ictalurid sister taxon (Otophysi: Siluriformes). *Molecular Phylogeny and Evolution* 37:700–720.
- Marshall, L., and P. Salinas. 1990. Stratigraphy of the río Frías Formation (Miocene), along the Alto Río Cisnes, Aisén, Chile. *Revista Geológica de Chile* 17:57–87.
- Mo, T. 1991. *Anatomy, Relationships, and Systematics of the Bagridae*. Koeltz Scientific Books, Koenigstein, 216 pp.
- Nixon K. C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15:407–414.
- Rodílez-Hernández, R., D. A. Hendrickson, J. Lundberg, and J. Humphries. 2009. An unpublished first cladistic analysis of the Chiapas catfish (*Lacantunia enigmatica*) among all catfishes and two anonymous reviews. Available at <https://catfishbone.ansp.org/Lacantuniidae/Lacantunia/enigmatica/pdfs/PhylogenyandReviews.pdf>. Accessed September 2010.
- Romero, E. J. 1986. Fossil evidence regarding the evolution of *Nothofagus* Blume. *Annals of the Missouri Botanical Garden* 73:276–283.
- Sullivan, J. P., J. G. Lundberg, and M. Hardman. 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag1* and *rag2* nuclear gene sequences. *Molecular Phylogenetics and Evolution* 41:636–662.
- Wiley, E. O. 2008. Homology, identity and transformation; pp. 9–21 in G. Arratia, H.-P. Schultze, and M. V. H. Wilson (eds.), *Mesozoic Fishes 4—Homology and Phylogeny*. Verlag Dr. Friedrich Pfeil, Munich.
- Wilf, P., N. R. Cúneo, K. Johnson, J. Hicks, S. Wing, and J. D. Obradovich. 2003. High plant diversity in Eocene South America: evidence from Patagonia. *Science* 300:122–125.
- Wilf, P., K. R. Johnson, N. R. Cúneo, M. Elliot Smith, B. S. Singer, and M. A. Gandolfo. 2005. Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. *American Naturalist* 6:634–650.

Submitted September 24, 2009; accepted October 26, 2010.

Handling editor: Terry Grande.

APPENDIX 1. Characters of *Bachmannia* used in this study.

1 = 0; 3 = 0; 7 = 0; 10 = 0; 11 = 0; 12 = 0; 13 = 0; 14 = 0; 16 = 0; 17 = 0; 18 = 0; 20 = 0; 21 = 0; 22 = 0; 24 = 0; 25 = 0; 26 = 0; 27 = 0; 28 = 0; 29 = 0; 31 = 0; 32 = 1; 33 = 0; 34 = 1; 36 = 0; 37 = 1; 40 = 0; 41 = 0; 42 = 0; 43 = 0; 45 = 0; 46 = 0; 55 = 0; 56 = 0; 57 = 0; 58 = 0; 60 = 0; 62 = 0; 63 = 0; 65 = 0; 66 = 0; 67 = 0; 69 = 1; 70 = 0; 71 = 0; 72 = 0; 73 = 0; 74 = 0; 75 = 0; 76 = 0; 77 = 0; 78 = 0; 79 = 0; 80 = 0; 82 = 0; 88 = 0; 92 = 0; 93 = 0; 94 = 0; 96 = 0; 97 = 0; 98 = 1; 99 = 0; 100 = 1; 102 = 0; 104 = 0; 107 = 0; 108 = 0; 109 = 0; 111 = 0; 112 = 0; 113 = 0; 121 = 0; 122 = 0; 123 = 0; 124 = 0; 125 = 0; 126 = 0; 129 = 0; 130 = 0; 132 = 0; 133 = 0; 138 = 0; 139 = 0; 213 = 0; 216 = 0; 217 = 0; 218 = 0; 219 = 0; 222 = 0; 223 = 0; 225 = 0; 226 = 0; 227 = 0; 228 = 0; 229 = 0; 230 = 0; 232 = 0; 233 = 0; 234 = 0; 235 = 0; 236 = 0; 237 = 0; 239 = 0; 240 = 0; 242 = 0; 243 = 0; 244 = 1; 245 = 0; 246 = 0; 248 = 0; 249 = 0; 250 = 0; 253 = 0; 254 = 0; 255 = 0; 256 = 0; 257 = 0; 258 = 0; 260 = 0; 261 = 0; 262 = 0; 263 = 0; 265 = 0; 266 = 0; 268 = 0; 270 = 0; 271 = 0; 272 = 0; 273 = 0; 276 = 0; 278 = 0; 282 = 0; 283 = 0; 284 = 0; 285 = 0; 286 = 0; 287 = 0; 288 = 0.

APPENDIX 2. Comparative material examined.

Diplomystes camposensis: ANSP 177915, 1 ex. *Diplomystes chilensis*: ANSP 84194, 1 ex.; MCZ 8290, 3 ex.; NMNH 259097. *Diplomystes cuyanus*: MLP 286, holotype; FMNH 58003, 1 ex. *Diplomystes mesembrinus*: MLP 948, holotype; MLP 8966, 1 ex. C&S. *Diplomystes nahuelbutaensis*: ANSP 177914, 2 ex.; CAS 55425, 1 ex.; UMMZ 215443, 1 ex. C&S. *Diplomystes viedmensis*: MLP 214, holotype; MLP 8966, paratype; CAS 67698, 1 ex. *Hypsidoris farsonensis*: cast of FMNH 10641; AMNH 6888, 1 ex., peel. We also examined many other recent and fossil catfishes in different institutions.