Kooiichthys jono n. gen. n. sp., a primitive catfish (Teleostei, Siluriformes) from the marine Miocene of southern South America

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Abstract.—A specimen of a remarkable new catfish genus and species was collected in middle/late Miocene marine beds of the Puerto Madryn Formation at the base of the marine cliff of the sea lion colony area near Puerto Pirámide, southern coast of Península Valdés, northeastern Patagonia, Argentina. Siluriforms (catfishes) constitute a most important monophyletic ostariophysan group of mainly freshwater fishes that occurs in almost all continents but it is especially diverse in South America. Catfishes are presently distributed in tropical to temperate areas and a small number of species are marine or amphibiotic. The new catfish shows many primitive features for catfishes in the maxilla, autopalatine, hyal elements, and Weberian apparatus. The genus is clearly distinguished by four autapomorphies: sand clock–shaped autopalatine, posterior limb of autopalatine widening strongly, post-articular arm of autopalatine longer, and a metapterygoid longer than broad. One tree was obtained both under equal and implied weighting with the following topology: a basal polytomy in the Siluriformes formed by Diplomystidae, Bachmanniidae, *Kooiichthys* and the Siluroidei. The new species appears to have been a marine or amphibiotic taxon: it was collected in beds considered to represent the Maximum Flooding Horizon of the transgression that deposited the Puerto Madryn Formation. The coast at this moment was at approximately 90 km to the west. According to faunistic evidence, the sea was warm temperate.

Introduction

Siluriformes (catfishes) comprise one of the most diverse vertebrate groups both morphologically and taxonomically (Fink and Fink, 1996; Nelson, 2006). Presently, there are approximately 37 families with almost 3,400 species in all continents except Antarctica (Ambruster, 2011). However, they inhabited Antarctica at least during the Eocene, when radically climatic conditions prevailed in the world (Grande and Eastman, 1986). Only a small number of catfishes (most of the ariids and many of the plotosids) are marine and some species of other families can enter brackish waters (Nelson, 2006).

The most plesiomorphic catfishes in a morphological sense are the living Diplomystidae of Patagonia and central Chile (Arratia, 1987; Azpelicueta, 1994) and the Eocene Bachmanniidae of Patagonia (Azpelicueta and Cione, 2011). The oldest fossils assignable to Siluriformes occur in the Campanian (late Cretaceous) of southern South America (Cione and Laffite, 1980; Cione, 1987). Moreover, South America is the only continent where catfishes are relatively common in Cretaceous rocks (Argentina: Cione and Lafitte, 1980; Cione et al., 1985; Arratia and Cione, 1996. Bolivia: Gayet and Meunier, 2003. Brazil: Bertini et al., 1993). The only extra–South American Cretaceous records are otoliths in North America

(Nolf and Stringer, 1996) and one spine from India (Cione and Prasad, 2002).

South America is the continent where siluriforms are most diverse and where the most primitive catfishes occur (Azpelicueta and Cione, 2011). Since the Cretaceous, lineage-splitting should have been coupled with many independent evolutionary experiments and ecological specializations. They are relatively common in Cenozoic rocks in the continent (Arratia and Cione, 1996; Azpelicueta and Cione, 2011). The discovery of the present catfish in Miocene beds of Patagonia deserves special attention; unfortunately, only the anterior part of the neurocranium, great part of visceral skeleton, anterior vertebrae, and great part of pectoral girdle were preserved. No other material was collected despite repeated collecting visits to the area.

In this paper, we describe the new genus and species and discuss its relationships based on morphological features with the most primitive siluriform taxa and the rest of catfishes.

Stratigraphy

The fossil-bearing bed is formed of muddy sandstones included in the Puerto Madryn Formation (Fig. 1). These beds were deposited during the late part of the extensive marine encroachment that lasted from the late Oligocene until the late

Miocene ("Mid Tertiary Transgressive Onlap Sequence"), paralleling the early Neogene trend of the global eustatic rise (Uliana and Biddle, 1988; del Río, 1991; del Río et al., 2001). The Puerto Madryn Formation consists of a sequence of coquinas, cross-bedded sandstones, shales with heterolithic lamination, and massive shales totally bioturbated or laminated. According to Scasso and del Río (1987), the sequence belongs to a transgressive-regressive cycle within an overall regressive sequence. These sediments were deposited on a shallow shelf with storm influence, changing upward into a tide-dominated estuarine environment.
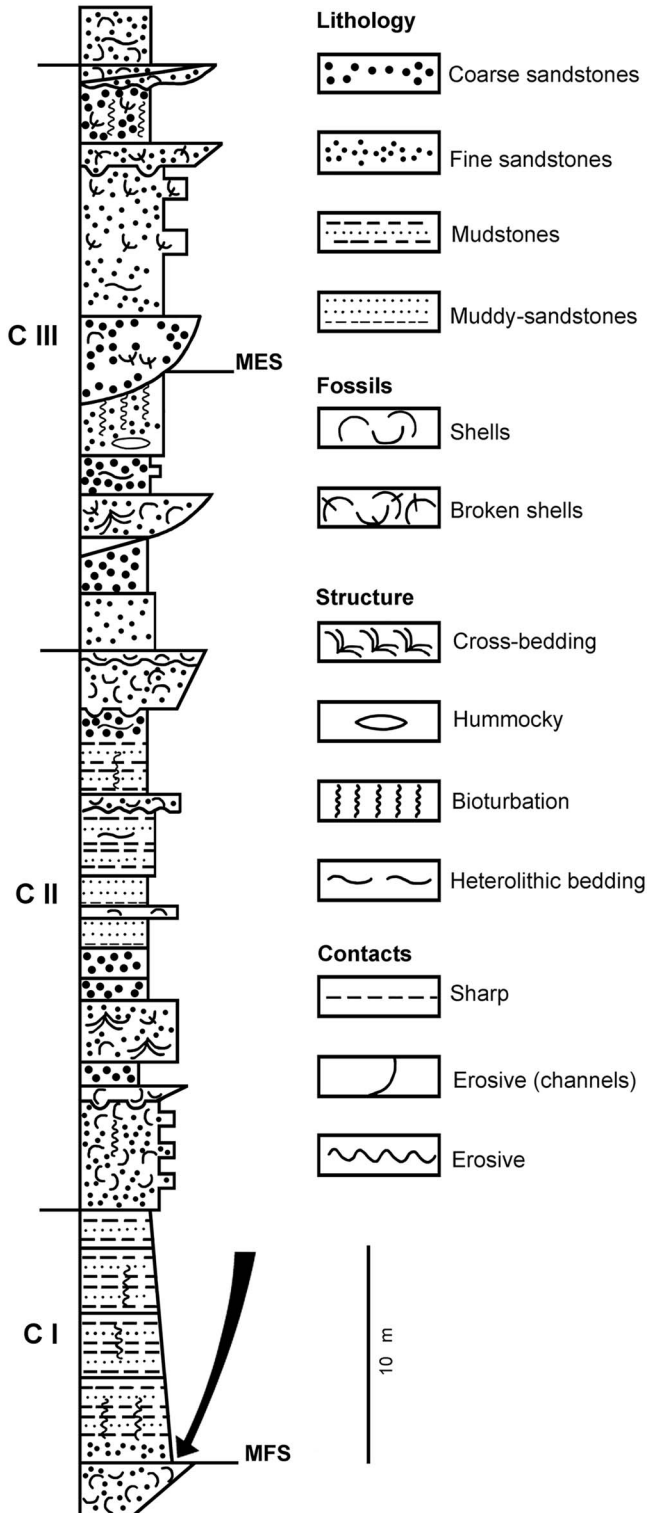
Age.—The age of the Puerto Madryn Formation has been widely discussed. In recent years, it has been referred to the middle Miocene (biostratigraphic evidence; del Río 1988) and more recently to the early late Miocene (strontium dates; del Río et al., 2001; Scasso et al., 2001). However, according to cetacean evidence, the deposition appears to have started during the middle Miocene and continued until the Tortonian (Cione et al., 2005).

Environment.—The bearing bank corresponds to the Oyster (AOA) Assemblage of del Río et al. (2001). This level corresponds to the Maximum Highstand phase. In the Maximum Highstand Phase, the sea extended approximately 25 km westward of the city of Puerto Madryn and approximately 90 km westward from Puerto Pirámide (Fig. 2). The sea temperature was warm-temperate according to faunistic evidence (Cione et al., 2011).

Material and methods

Methods.—Few vertebrate fossils were found in the Puerto Madryn Formation compared to other Cenozoic marine unit in the area. However, the few skeletons found are very well preserved, many in three dimensions (e.g., jaws of *Squatina*; Cabrera et al., 2012). The skeleton (MPEF-PV 1613) was prepared mechanically. A radiograph was used for examining the complex vertebra for possible fusion of vertebrae. The comparative material is presented in Appendix 1.

The phylogenetic parsimony analysis was accomplished with TNT software (Goloboff et al., 2008). Searches were done under both equal and implied weighting (Goloboff, 1993).
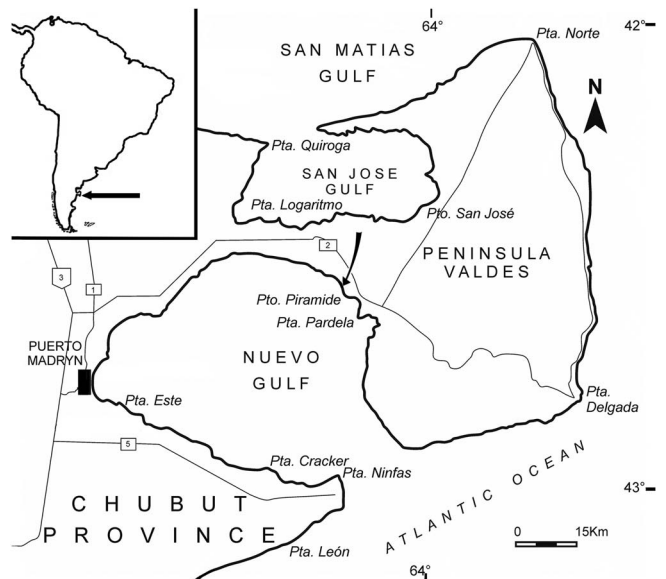

Figure 1. Profile at the Lobería de Puerto Pirámide. The arrow indicates the bearing bed.

Figure 2. Map of location. The arrow indicates de collection site.

Searches were performed from random addition sequences, followed by TBR and rounds of parsimony ratchet (Nixon, 1999), tree drifting, tree fusing, and sectorial searches (Goloboff, 1999) hitting five times the optimal scores. Implied weighting was done under K-values ranging from 3 to 100 (Goloboff, 1993). Node reliability was estimated through symmetric resampling (Goloboff et al., 2003) and relative Bremer support (Bremer, 1994; Goloboff and Farris, 2001).

The matrix was taken from morphological analysis of Rodiles-Hernández et al. (2005). This is the unique matrix with morphological characters for all siluriform families. Although it was criticized in a revision, most modifications include species or genera of Siluroidei that were not treated in this paper. Diogo (2005, 2006) published morphological (303 characters) and myological phylogenies (91 characters), without the inclusion of all families.

To the matrix of Rodiles-Hernandez et al. (2005), characters of *Bachmannia chubutensis* (Azpelicueta and Cione, 2011), *Kooiichthys jono*, the characiform *Brycon orbignyanus*, and the gymnotiform *Eigenmannia trilineata* were added. All characters used here are in the Appendix 2. Some character were coded as missing (?), and the characters 81, 100, 101, 102, and 111 do not apply (−) for *Kooiichthys*. Modifications of five characters were done to include *Kooiichthys jono*. The modified character states are: character 99, autopalatine size and shape: large, sand clock–shaped (state 2); character 107, posterior limb of autopalatine: widening strongly (state 2); character 108, relative lengths of both autopalatine arms: post-articular arm of autopalatine longer (state 2); character 132, metapterygoid: longer than broad (state 2). Analyses were rooted in Gymnotiformes and Characiformes, with equal results. The matrix is included in Appendix 3.

Institutional Abbreviations.—AMNH, American Museum of Natural History, New York, U.S.A.; ANSP, Academy of Natural Sciences, Philadelphia, U.S.A.; CAS, California Academy of Sciences, San Francisco, U.S.A.; CI-FML, Fundación e Instituto Miguel Lillo, Tucumán, Argentina. FMNH, Field Museum of Natural History, Chicago, U.S.A.; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.; MLP, Museo de La Plata, División Paleontología de Vertebrados, La Plata, Argentina; MPEF-PV, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; UMMZ, Museum of Zoology, University of Michigan, Ann Arbor, U.S.A.; USNM, United States National Museum, Washington, U.S.A.

Systematic paleontology

Order Siluriformes sensu Regan, 1911
Family indeterminate
Genus *Kooiichthys* new genus

Type species.—*Kooiichthys jono* new species.

Included species.—Type species only.

Diagnosis.—*Kooiichthys* is clearly distinguished by several unique characters: autopalatine very strong, with anterior and posterior portions depressed, expanded and equally wide,

middle part narrow, posterior end gently convex, and post-articular portion longer than anterior one; metapterygoid longer than broad; and body of the Weberian complex extremely short. *Kooiichthys* also differs from all the other Siluriformes in the following combination of characters: large size; premaxillary dorsolateral process claw-shaped; toothed maxilla with a long arm and five or six rows of teeth; maxillary bone head with autopalatine condyle paired; anteriorly narrow mesethmoid with short neck and long cornua; lateral ethmoid wing absent; vomer anteriorly rhomboidal with two tooth plates; acccesory tooth patches under autopalatine present; at least two laminar infra-orbitals; large anterior metapterygoid process on which contact the autopalatine; anterior and posterior ceratohyal without interdigitations; both coracoids sutured at midline without interdigitations; both cranial fontanelles widely open; first and fifth vertebrae with normal intervertebral joint; stout pectoral fin spines striated and anteriorly smooth but with rather irregular posterior dentations.

Occurrence.—As for *Kooiichthys jono*, the only known species.

Etymology.—*Kooi*, fish in the language of the Tehuelches (aborigines that inhabited the Patagonia before the invasion of the Araucanos from Chile in the XVII century) plus *ichthys*, fish in Greek.

Kooiichthys jono new species
Figures 3–10

Holotype.—MPEF-PV 1613: Anterior part of neurocranium, suspensorium, basicranium, part of pectoral skeleton and fin, and anterior part of vertebral column.

Diagnosis.—As for genus.

Occurrence.—Type locality is the top of the lower bank in the marine cliffs of the Lobería (sealions reserve) of Puerto Pirámides, northwest of Puerto Pirámide, southern Península Valdés, Provincia del Chubut, Argentina (42° 35' 05" S 64° 18' 11"W; Figs. 1, 2). Middle part of Puerto Madryn Formation, Chubut, Argentina, middle-late Miocene.

Etymology.—*jono*, ocean in the language of the Tehuelches, a substantive in apposition.

Description

General morphology.—The material is preserved in three dimensions, bones do not show deformation, and there is little dorsoventral flattening of the articulated elements (Figs. 3–6). The head appears to have been wide and relatively flat, differing from other primitive catfishes such as Diplomystidae and Bachmannidae. For this, the head preservation is in life position, as is frequent in other fossil catfishes such as *Hypsidoris farsonensis* and *Astephus antiquus* (Grande and Lundberg, 1988; Grande and Pinna, 1998). The preserved skeleton is greatly made up of trabecular bone, with relatively thin laminar bone. *Kooiichthys jono* n. gen. n. sp. is a medium-sized species. The minimum length from the snout tip to the end of
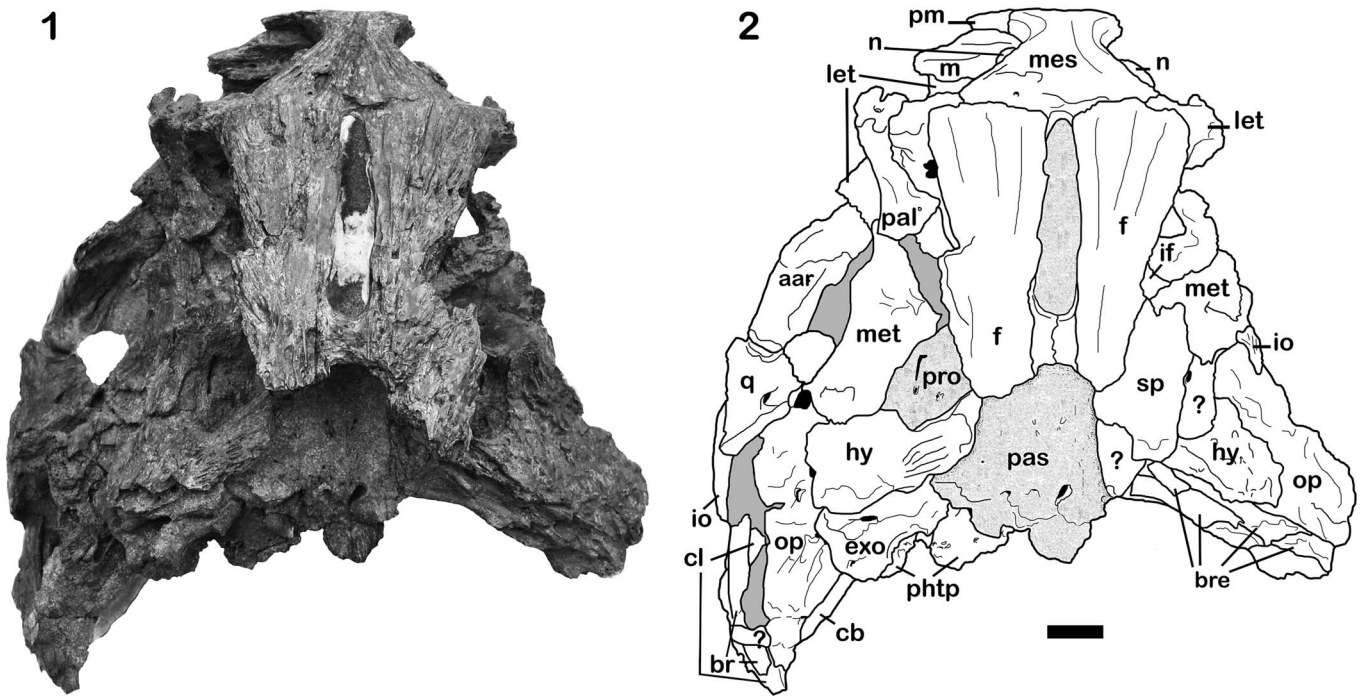
Figure 3. *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613), dorsal view of the skull. (**1**) Photograph, (**2**) line drawing. Abbreviations: *aar* = angular + articular + retroarticular; *br* = branchiostegal rays; *bre* = branchial elements; *cb* = ceratobranchial; *cl* = cleithrum; *exo* = exoccipital; *f* = frontal; *hy* = hyomandibula; *if* = infraorbital; *io* = interopercle; *let* = lateral ethmoid; *m* = maxilla; *mes* = mesethmoid; *met* = metapterygoid; *n* = nasal; *op* = opercle; *pal* = autopalatine; *pas* = parasphenoid; *phtp* = pharyngobranquial tooth plate; *pm* = premaxilla; *pro* = prootic; *q* = quadrate; *sp* = sphenotic. Scale bar = 1 cm.
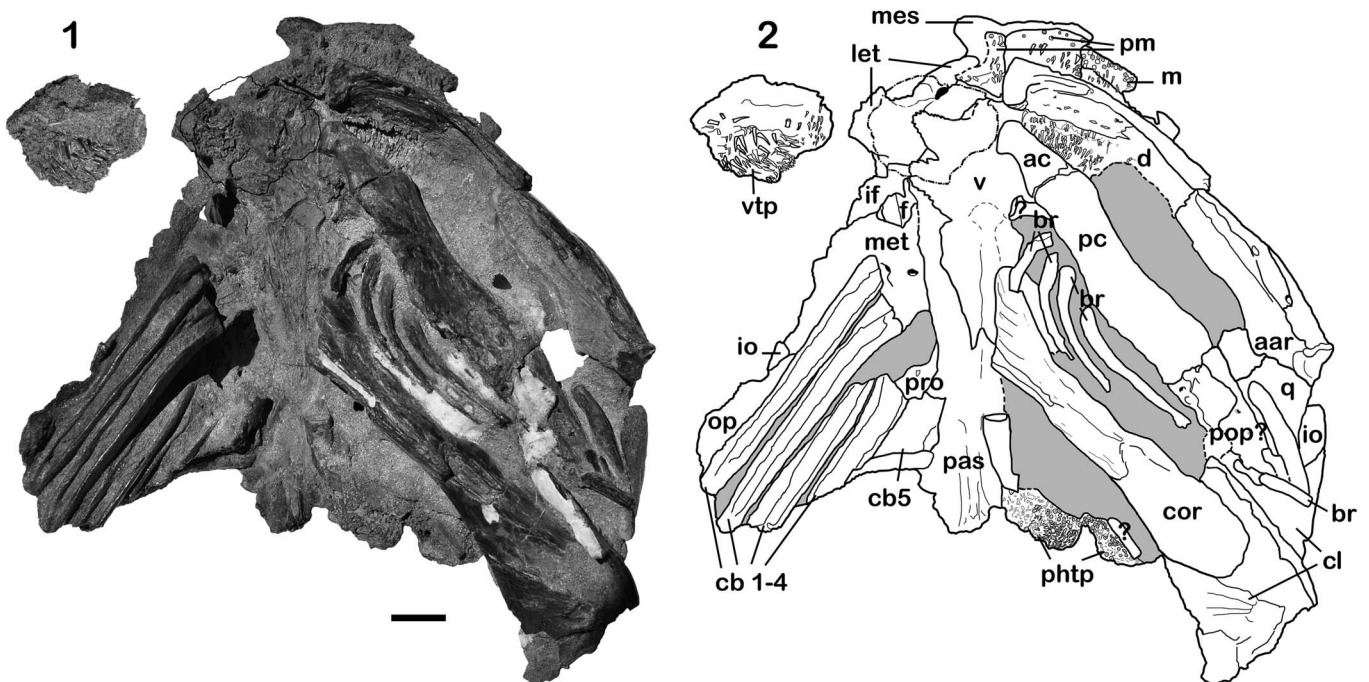

Figure 4. *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613), ventral view of the skull. (**1**) Photograph, (**2**) line drawing. Abbreviations: *ac* = anterior ceratohyal; *cb1-4* = ceratobranchial 1-4; *cb5* = ceratobranchial 5; *cor* = coracoid; *d* = dentary; *pc* = posterior ceratohyal; *pm* = premaxilla; *v* = vomer; *vtp* = vomerine tooth plate. Other abbreviations as in Figure 3. Scale bar = 1 cm.

basioccipital is about 15 cm. The length from snout tip to anterior margin of epiphyseal bar is 7 cm.

Neurocranium.—The neurocranium is rather heavily ossified (Figs. 3, 4). The anterior half of the neurocranium is well preserved. The dorsal surface of mesethmoid and frontals is sculptured by low wide ribs that are more conspicuous posteriorly (Fig. 3). On the other hand, a small fragment of preserved sphenotic is smooth. The posterior half of the neurocranium is missing, excepting the basioccipital
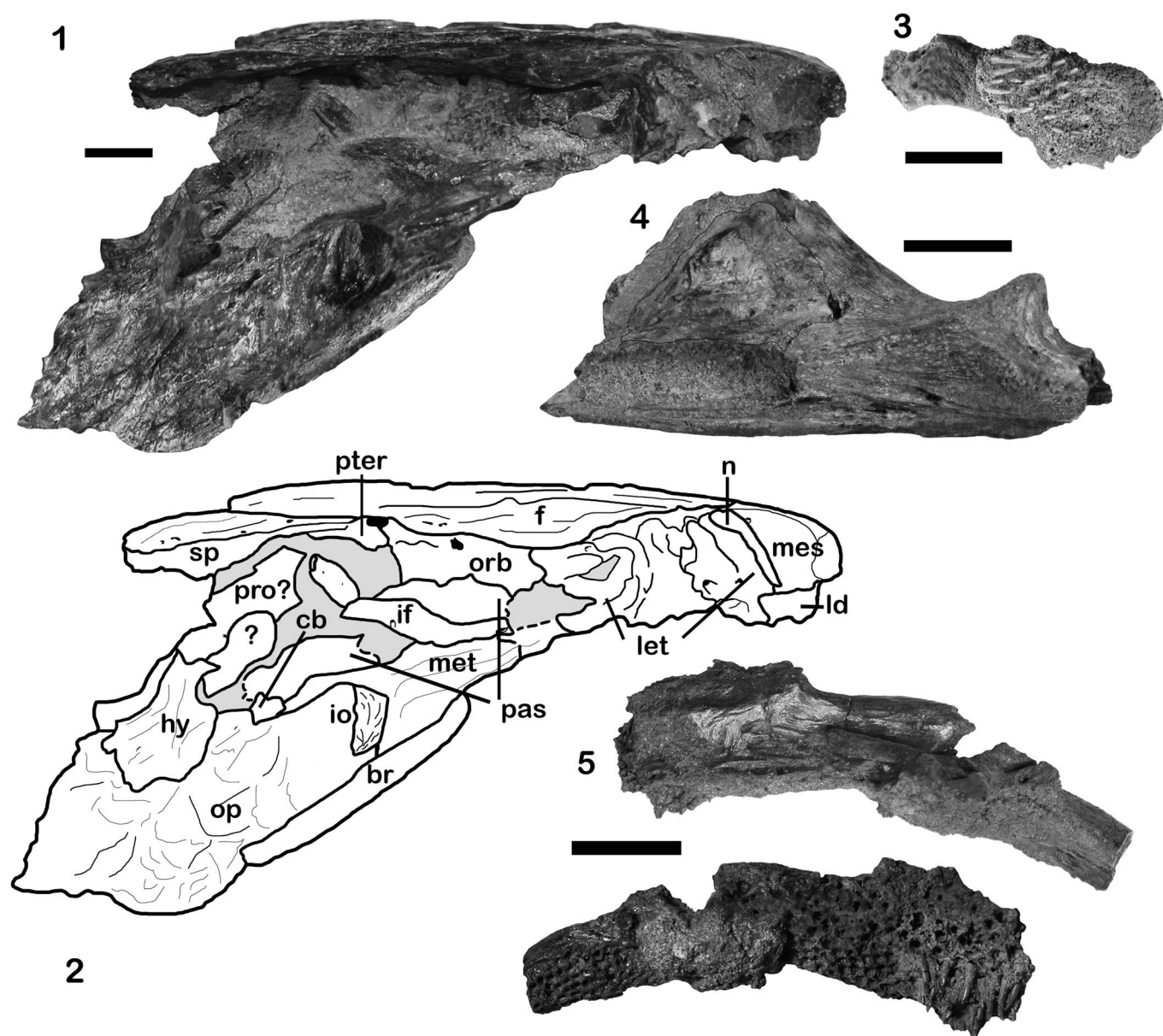
Figure 5. *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613). (**1**) Photograph of right lateral view, (**2**) line drawing, (**3**) right autopalatine and palatine tooth plate, (**4**) internal view of right angular + articular + retroarticular with coronomeckelian bone, (**5**) dorsal and ventral view of right premaxilla and maxilla. Abbreviations: *ld* = left dentary; *orb* = orbitosphenoid; *pter* = pterosphenoid. Other abbreviations as in Figure 3. Scale bar = 1 cm.

and the two prootics. The mesethmoid is short, and presents a short and broad neck. The cornua are stout, well developed, and with a very shallow anterior cleft (Figs. 3, 4). The mesial lamina is deep and flat. The contact with frontal is straight. The mesethmoid reaches the anterior part of anterior cranial fontanelle. A complete right and a fragment of left nasals are preserved. The bone is relatively short and broad (Fig. 5, 6). The lateral ethmoid is relatively deep and stout. Posteriorly it articulates with the orbitosphenoid. In dorsal view, it is almost covered by the frontal; only the anterior margin is exposed (Fig. 3). The exit for the olfactory nerve opens in the middle of the anterior surface. Ventrally it has a contact with parasphenoid. The preserved portion of the frontal is stout and flat. The anterior lateral portion is very thick (Figs. 5, 6). The suture with the mesethmoid is curved and smooth. The orbital

margin is broken. The anterior fontanelle is large and the epiphyseal bar is long. The anterior edge of the posterior fontanelle suggests that it was also large (Fig. 3). The right sphenotic is fragmentary but an anterior spine is clearly seen forming the dorsal flat surface of neurocranium. There is no evidence of origin of muscles on skull roof. The suture with the frontal is straight. The anterior part of the vomer is rhomboidal; the posterior shaft is very short. There are two separated vomerine toothed patches joined in the middle by means of a straight suture (Fig. 4.1, 4.2). The teeth are villiform, long and narrow, slightly curved, pointed, with a distal enameloid cap (Fig. 5.3). The orbitosphenoid is somewhat rectangular and anteroposteriorly elongate (Figs. 5, 6). It is not as deep as in Diplomystidae or Bachmannidae. It sutures dorsally and posteriorly with the frontal, anteriorly with lateral ethmoid, ventrally with
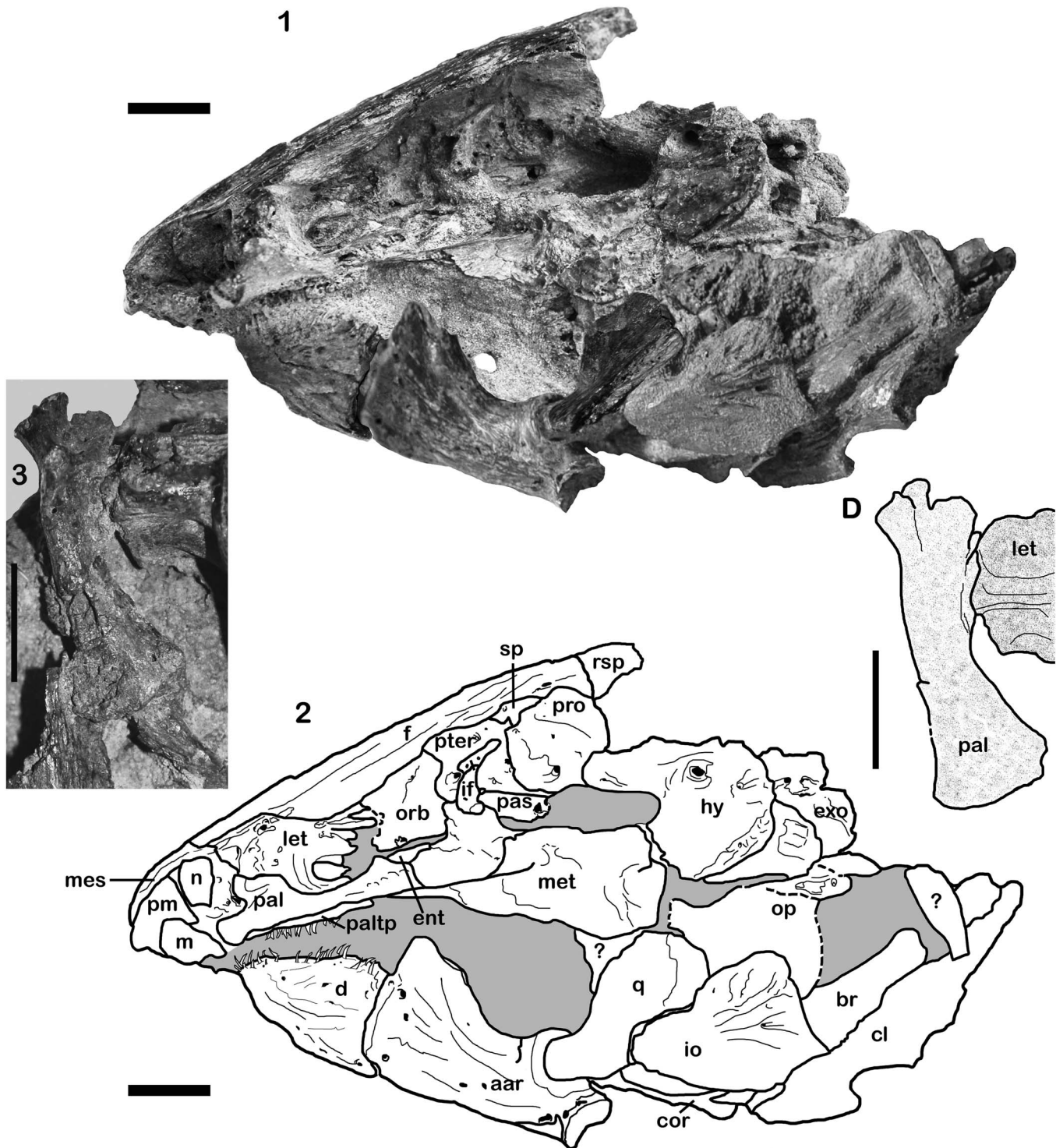
Figure 6. *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613). (**1**) Photograph of left lateral view, (**2**) line drawing, (**3**) photograph of the left autopalatine, (**4**) line drawing of the autopalatine. Abbreviations: *ent* = entopterygoid; *paltp* = autopalatine tooth plate; *rsp* = right sphenotic. Other abbreviations as in Figures 3–5. Scale bars = 1 cm.

parasphenoid, and posteriorly with the pterosphenoid. The anteriormost part of parasphenoid is flat, but the medial section appears to have a low keel. The posterior part is fragmentary excepting for a small portion articulating with basioccipital. The prootic is quadrangular, externally flat, and smooth. The

basioccipital is short and its base is concave in lateral view. The articular condyle is wider (20 mm) than deeper (16 mm).

Infraorbitals.—Against the orbitosphenoid, two bones are interpreted as infraorbitals on each side (Figs. 5.2, 6.2). One is
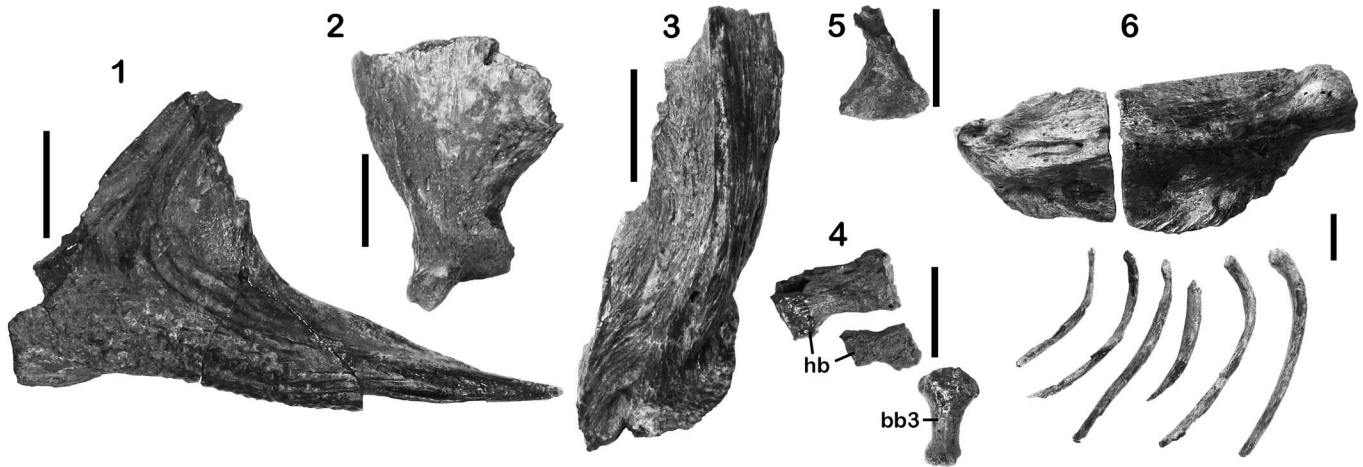
Figure 7. *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613). (**1**) Right cleithrum, (**2**) right quadrate, (**3**) left preopercle, (**4**) right hypobranchials and basibranchial 3, (**5**) right interhyal, (**6**) anterior ceratohyal, posterior ceratohyal, and branchiostegal rays. Abbreviations: *hb* = hypobranchial; *bb3* = basibranchial 3. Scale bars = 1 cm.
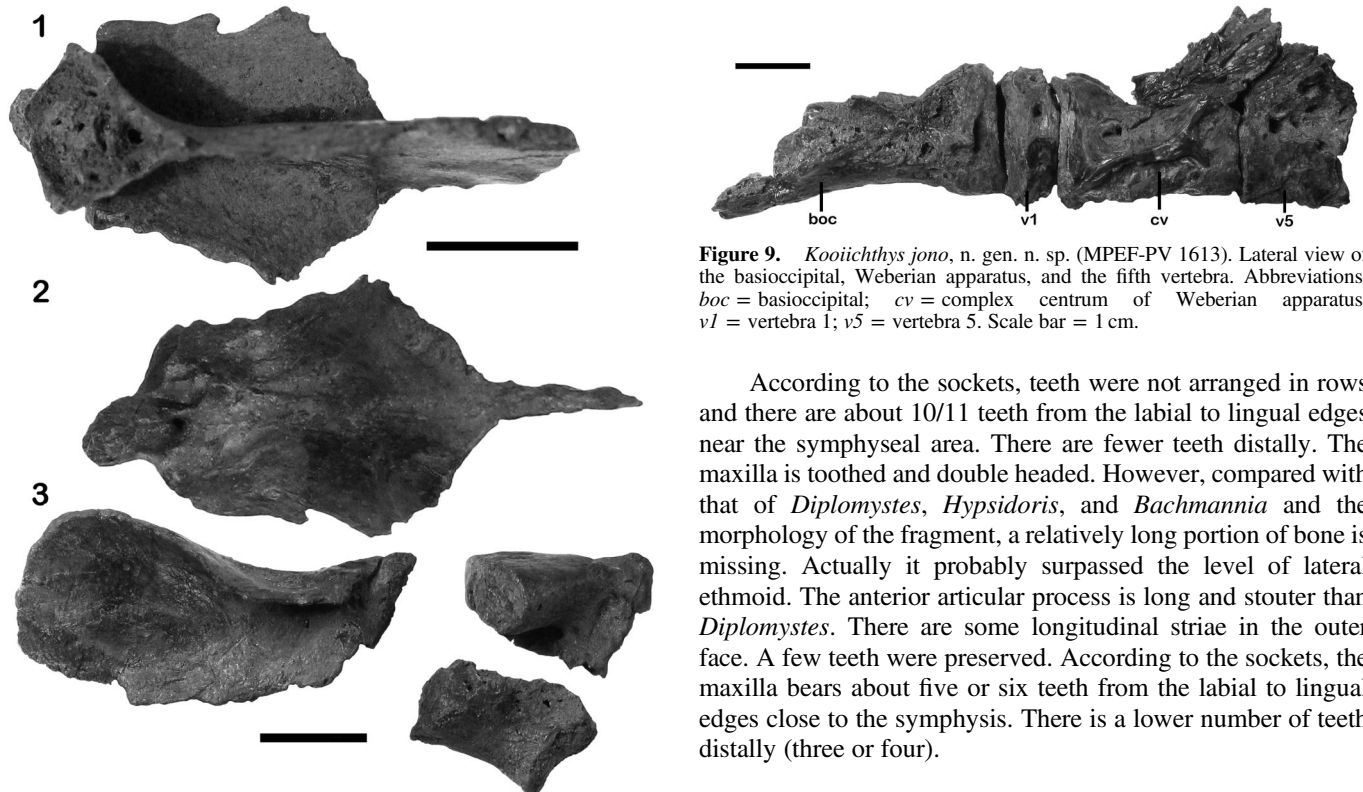

Figure 8. *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613). (**1**) Dorsal view of parurohyal, (**2**) ventral view of parurohyal, (**3**) lateral view of parurohyal and dorsal and ventral hypohyals. Scale bars = 1 cm.

tubular in shape and the other is crescent-like and laminar; this latter bears the sensory canal close to the upper edge.

Upper Jaw.—The premaxilla is rectangular (Figs. 4.2, 5.5). It is slightly wider by the symphysis. The dorsal surface is slightly concave. It connects posteriorly with the maxilla. Most teeth are not preserved in position. Teeth are conic and elongated (longest: 5.2 mm).
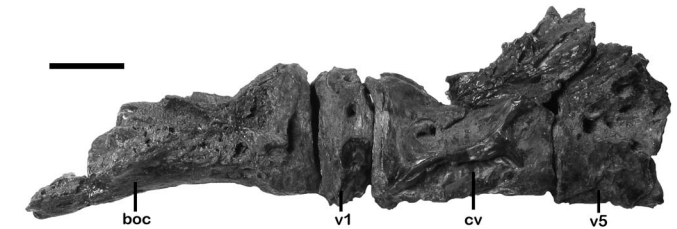

Figure 9. *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613). Lateral view of the basioccipital, Weberian apparatus, and the fifth vertebra. Abbreviations: *boc* = basioccipital; *cv* = complex centrum of Weberian apparatus; *v1* = vertebra 1; *v5* = vertebra 5. Scale bar = 1 cm.

According to the sockets, teeth were not arranged in rows and there are about 10/11 teeth from the labial to lingual edges near the symphyseal area. There are fewer teeth distally. The maxilla is toothed and double headed. However, compared with that of *Diplomystes*, *Hypsidoris*, and *Bachmannia* and the morphology of the fragment, a relatively long portion of bone is missing. Actually it probably surpassed the level of lateral ethmoid. The anterior articular process is long and stouter than *Diplomystes*. There are some longitudinal striae in the outer face. A few teeth were preserved. According to the sockets, the maxilla bears about five or six teeth from the labial to lingual edges close to the symphysis. There is a lower number of teeth distally (three or four).

Lower jaw.—The lower jaw is relatively long and stout (Figs. 5.4, 6). The coronoid process is slightly posterior to the middle of the jaw. The dentary is long and relatively deep. The oclusal face is flat and wide. The ventral part of the bone is compressed. There are three elongated pores of the sensory canal near the lower edge. Teeth are not arranged in rows and there are about nine/ten teeth from the labial to lingual edges near the symphyseal area. The angular + articular + retroarticular complex is long. The coronoid process appears to have been relatively low (perhaps 1:3 in total jaw length). The complex is externally ornamented with anteroposteriorly directed ridges. The articular surface for the quadrate is oval and transversally wide. The retroarticular is triangular and part of the upper suture

Figure 10. *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613). (**1**) Ventral view of left pectoral spine, (**2**) detail of the articular portion, (**3**) detail of the posterior face. Scale bars = 1 cm.
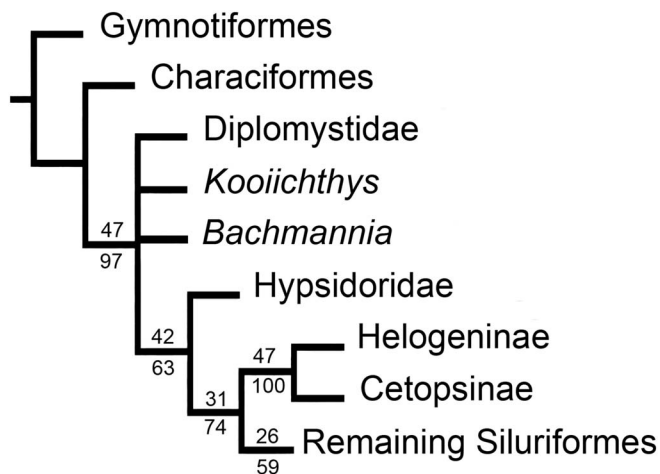

Figure 11. Phylogenetic relationships of *Kooiichthys jono*, n. gen. n. sp. (MPEF-PV 1613), obtained both under equal and implied weighting. Values over branches are absolute frequencies obtained after Symmetric Resampling and values under branches are Relative Bremer Supports, both calculated under implied weighting with K = 10.

with the articular is still visible. The retroarticular process is long. The coronomeckelian bone is laminar and trapezoidal and occupies a great portion of the lingual part of the angular + articular + retroarticular complex.

Opercular apparatus and suspensorium.—The opercle is preserved but it is so smashed that it can not be described. The interopercle is almost triangular, is thicker in the anterior part, and shows well developed anteroposterior radiating and anastomosing ridges (Figs. 1, 2, 5, 6). A part of preopercle is missing but it can be seen that the exposed surface of the bone is narrow (Fig. 7.3). The hyomandibula is very poorly preserved (Figs. 5, 6). The metapterygoid is subrectangular in outline with a dorsolateral process (Figs. 5, 6). The suture with the hyomandibula is wide. There is a large anterior process that is contacted by the autopalatine. The entopterygoid is bar-like and contacts anteriorly with the autopalatine which is long and stout. The autopalatine has two anterior well-separated processes, both ending in concave surfaces for articulation with the maxilla. A strong process articulates with the lateral ethmoid in the anterior third of the bone. The posterior half is as broad and flat as the anterior portion (Figs. 5.3, 6.3D). The quadrate is thick and trapezoidal, similar to that of *Diplomystes*. The suture with the hyomandibula is straight and occupies the two posterior thirds of dorsal margin.

Hyoid and branchial elements.—The shape of parurohyal is vaguely hexagonal in basal view with a short posterior process (Fig. 8). There is a deep, rectangular dorsal lamina occupying the entire length of the posterior process. The robust anterior medial process carries the exit for vessels. The dorsal and ventral hypohyals are robust and triangular. The dorsal one is larger and carries the process for articulation with paurohyal. The suture is straight and smooth. The exit of the hypohyal artery is bounded by both hypohyal bones. Anterior and posterior ceratohyals sutures are smooth. Both are huge and thick along the mid external surface. The posterior ceratohyal has a small exit for the artery. The interhyal is triangular with a slender dorsal process (Fig. 7.5, 7.6). The ceratobranchials 1–4 are long and hollow. The ceratobranchial 5 is fragmentary. We did not observe either tooth patches or gill rakers. A putative basibranchial 3 is anteriorly expanded. Only two rectangular hypobranchials were preserved (Fig. 7.4). The pharygobranchial tooth plate is broken but appears to have been oval in shape (Fig. 4). We counted seven branchiostegals. Six are very slender but the first is laminar.

Vertebral column and Weberian apparatus.—All the vertebrae of Weberian apparatus were preserved. No ossicles were found. The first vertebra is very short, wide, and completely free. The complex centrum is remarkably short. Putatively it is formed by second, third, and fourth vertebrae. The transverse process of the fourth vertebrae is broken. The body of the fifth vertebrae is short, completely free, without even a ventral lamina such as that of *Diplomystes* (Fig. 9). Only the base of both halves of the vertebra 4 neural arch is preserved.

Pectoral fin and girdle.—An almost complete left fin spine and a portion of the proximal right fin spine were preserved. The pectoral fin spine is long and stout. The head for articulation is radially striated distally. The shaft is covered dorsally and ventrally by longitudinal ridges. Proximally they are subparallel and distally they anastomose. There is a posterior sulcus with 19 irregular serrae. Some of them are bifid or trifid. Proximal and distal serrae are small but proximal are more robust than distal ones. Proximal serrae are oriented distally and distal ones are oriented posteriorly (Fig. 10). Neither soft rays nor radials are preserved. Only the horizontal lamina of both coracoids is present (Fig. 4). The suture between coracoids is smooth. The right cleithrum is much better preserved than the left one. It can be seen that the posterior cleithral process is short. The ornamentation on the postcleithral process is strong, with anteroposteriorly directed ridges, some of them anastomosed, and tubercles (Fig. 7.1).

Discussion

Phylogeny.—Catfishes are known since the Upper Cretaceous but especially during the Cenozoic when they became widespread mostly in freshwater. Only two extinct catfish families are recognized: Hypsidoridae in the Eocene of North America (Grande, 1987) and Bachmanniidae in the Eocene of South America (Azpelicueta and Cione, 2011). Another putative extinct family from South America, Andinichthyidae, based on three genera of the Upper Cretaceous and Paleocene of Bolivia is not supported by enough evidence (Arratia and Gayet, 1995). Grande (1987) proposed the first cladistic relationships of catfishes. In his hypothesis, Diplomystidae was the sister group of all remaining catfishes (Siluroidei). Other subsequent morphological analyses agree in considering that family as the most basal catfish group (for a synthesis of the literature see Rodiles-Hernández et al., 2009 and Azpelicueta and Cione, 2011). Sullivan et al. (2006), in a molecular analysis, proposed a radically different phylogeny where Loricarioidei was the sister group of Diplomystidae + the other catfishes. Recently, we suggested that the family Bachmanniidae was the sister group of Diplomystidae and both the sister group of all other Siluriforms based on a phylogenetic morphological analysis (Azpelicueta and Cione, 2011). Grande (1987) and Arratia (1992) diagnosed Siluroidei by the following characters: 17 or fewer principal caudal rays (vs. 18 in *Diplomystes* and other teleosts such as most characiformes); an extension of lamellar bone below the ventral surface of fifth centrum; fifth centrum joined closely to complex centrum by two ventral ridges of superficial ossification; dorsal and ventral hypohyal of different sizes; maxilla with two rudimentary processes bearing small facets for articulation with autopalatine. According to these characters, the new genus *Kooiichthys* is not a Siluroidei. In this paper, we reanalyze siluriform relationships considering the data matrix used by Rodiles-Hernández et al. (2005) and our modifications (due to the fragmentary preservation of the fossil, we only observed 30% of the characters included in their matrix). The analysis under equal weights produce 1312 equally most parsimonious trees of 737 steps (CI = 42.9; RI = 73.3), whereas the analyses under implied weighting with concavity values (K) from 3 to 100 produced different most parsimonious tree topologies ranging from 754 (CI = 41.9; RI = 72.2) to 737 steps (CI = 42.9; RI = 73.3) All these trees are congruent in a basal polytomy in the Siluriformes composed of the Diplomystidae, Bachmanniidae, *Kooiichthys*, and the Siluroidei (Fig. 11). This polytomy is not resolved because the lack of information about synapomorphies relating some pair of these taxa, rather than for conflict of information. The new genus *Kooiichthys* is supported by four exclusive autapomorphies; sand clock-shaped autopalatine, posterior limb of autopalatine widening strongly, postarticular arm of autopalatine longer than prearticular arm, and a metapterygoid longer than broad.

We suggest that, although the morphology of the new species *Kooiichthys jono* is very different from the other fossil and recent taxa, it is not worthwhile to erect a new family based on it until finding more complete material.

Comparison of K. jono with Diplomystidae and Bachmanniidae.—*Kooiichthys jono* n. gen. n. sp. shares a synapomorphy (double anterior autopalatine head) and other characters with these two taxa such as the anteriorly narrow mesethmoid, mesethmoid-frontal suture convex and not interdigitated, anterior and posterior fontanelles very large, lateral ethmoid almost completely covered by frontal, lateral ethmoid deep with an extended suture with orbitosphenoid, orbitosphenoid deep, toothed maxilla, maxilla bone head with autopalatine condyles paired; vomerine tooth plate, "palatal" accesory tooth plates, autopalatine with a double articulation for maxilla and a large articulation with lateral ethmoid, anterior and posterior ceratohyals with straight suture, first vertebra unfused and short, fifth vertebra not joined to Weberian complex centrum, suture between coracoids without interdigitations. *Kooiichthys jono* shares with Diplomystidae the rhomboidal shape of vomer but this state is unknown in Bachmanniidae. This character was considered to be a synapomorphy of Diplomystidae (Arratia, 1987, 1992). *Kooiichthys jono* differs from Diplomystidae and Bachmanniidae in having very large size, robust mesethmoid with large cornua, very wide posteriorly mesethmoid, large anterior metapterygoid process on which contact the autopalatine, a much longer maxilla, shorter Weberian complex, and pectoral spine serrae smaller. *Kooiichthys jono* differs from Diplomystidae in having ornamented skull roof, absence of spatulate teeth, and pectoral spine with posterior sulcus. *Kooiichthys jono* differs from Bachmanniidae in having much smaller and slender teeth, a quadrate without an anteroventral process, and a different shaped parurohyal.

Comparison of Kooiichthys with the other marine catfishes.—There are two marine or amphibiotic catfish families: Plotosidae and Ariidae. Both are Siluroidei. Besides, *Kooiichthys jono* n. gen. n. sp. clearly differs from ariids because they present the external posterior branch of lateral ethmoid columnar, lateral ethmoid and frontal bones connected mesially and laterally delimiting a fontanel, and otic capsule enlarged (Marceniuk et al., 2012). *Kooiichthys jono* clearly differs from plotosids because the absence of a specialized buccal and pharyngeal dentition among other cranial characters.

Comments on some characters of Kooiichthys.—The most striking feature of *Kooiichthys* n. gen. is the very strong autopalatine, with anterior and posterior portions depressed, expanded and equally wide. The middle portion of the bone is narrow and the posterior end gently convex. The postarticular portion is longer than the anterior one. The posterior end contacts the long anterior metapterygoid process. The metapterygoid is notably longer than broad, an uncommon shape in siluriforms. Bachmanniidae, Diplomystidae, and Hypsidoridae have a depressed, anteriorly broad autopalatine with two anterior condyles for maxilla. *Kooiichthys* has an anterior notch also present in *Bachmannia* and in most species of *Diplomystes* (Arratia, 1987) but absent in *Hypsidoris* (Grande, 1987). *Kooiichthys* has a toothed maxilla, a primitive catfish character only known otherwise in Diplomystidae, Hypsidoridae, and Bachmanniidae but the shape differs in them. *Kooiichthys* has the longest maxilla with the higher number of tooth rows. The maxilla of Diplomystidae is longer than that of Hypsidoridae which is longer than that of Bachmanniidae. 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. We found the same character in *Kooiichthys*.

The maxilla of *Kooiichthys* includes more rows of teeth (five-six) than the other catfish with toothed maxilla. Bachmanniidae has only two rows of teeth (Fig. 6), whereas in Diplomystidae the number of rows is variable (*D. viedmensis* has up to five rows [Azpelicueta, 1994, fig. 16 b-f]; *D. nahuelbutaensis* has only two [Arratia, 1987, fig. 7], and Hypsidoridae has teeth anteriorly placed [Grande, 1987, fig. 6; Grande and de Pinna, 1998, fig. 7; personal observation M.M.A.]). The Weberian complex of *Kooiichthys* has a very short body length (approximately three times the length of the first vertebra); in Diplomystidae it is about five times the length of the first vertebra. The neurocranium of *Kooiichthys* is relatively deep, although not so deep as that of Bachmanniidae and Diplomystidae. The common condition in Siluriformes is a suture between pterosphenoid and parasphenoid, a character that is not present in Bachmanniidae, Diplomystidae, and *Kooiichthys* (Arratia, 1987, figs. 5B, 23).

Acknowledgments

References

Ambruster, J.W., 2011, Global catfish biodiversity: American Fisheries Society Symposium, v. 77, p. 15–37.

Arratia, G., 1987, Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications: Bonner Zoologische Monographies, v. 24, p. 1–120.

Arratia, G., 1992, Development and variation of the suspensorium of primitive catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships: Bonner Zoologische Monographies, v. 32, p. 1–148.

Arratia, G., and Cione, A.L., 1996, The fossil fish record of Southern South America, *in* Arratia, G., ed., Contributions of Southern South America to Vertebrate Paleontology: München, Germany, Münchener Geowissenschaftliche Abhandlungen, v. 30, p. 9–72.

Arratia, G., and Gayet, M., 1995, Sensory canals and related bones of Tertiary Siluriform crania from Bolivia and North America and comparison with recent forms: Journal of Vertebrate Paleontology, v. 15, p. 482–505.

Azpelicueta, M.M., 1994, Three East-Andean species of *Diplomystes* (Siluriformes: Diplomystidae): Ichthyological Exploration of Freshwaters, v. 5, p. 223–240.

Azpelicueta, M.M., and Cione, A.L., 2011, Redescription of the Eocene catfish *Bachmannia chubutensis* (Teleostei: Bachmanniidae) of southern South America: Journal of Vertebrate Paleontology, v. 31, p. 258–269.

Bertini, R., Marshall, L.G., Gayet, M., and Brito, P., 1993, Vertebrate fauna from the Adamantina and Marilia formations (Bauru Group, Late Cretaceous, Brazil) in their stratigraphic and paleobiogeographic context: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 188, p. 71–101.

Cabrera, D., Cione, A.L., and Cozzuol, M., 2012, Three dimensioned angel shark jaw elements (Elasmobranchii, Squatinidae) from the Upper Miocene of southern Argentina: Ameghiniana, v. 49, p. 126–131.

Cione, A.L., 1987, The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina, the fishes, Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Paleontología, v. 3, p. 111–120.

Cione, A.L., and Laffite, G., 1980, El primer siluriforme (Osteichthyes, Ostariophysi) del Cretácico de Patagonia, consideraciones sobre el área de diferenciación de los siluriformes, aspectos biogeográficos: Actas del II Congreso Argentino de Paleontologia y Biostratigrafia y I Congreso Latinoamericano de Paleontología, v. 2, p. 35–46.

Cione, A.L., Pereira, S.M., Alonso, R., and Arias, J., 1985, Los bagres (Osteichthyes, Siluriformes) de la Formación Yacoraite (Cretácico tardío): Consideraciones biogeográficas y bioestratigráficas. Ameghiniana, v. 21, p. 294–304.

Cione, A.L., and Prasad, G.V., 2002, The oldest known catfish (Teleostei, p. Siluriformes) from Asia (India, Late Cretaceous): Journal of Paleontology, v. 76, p. 190–193.

Cione, A.L, Azpelicueta, M.M., Casciotta, J.R., and Dozo, M.T., 2005, Tropical freshwater teleosts from Miocene beds of eastern Patagonia, southern Argentina: Geobios, v. 38, p. 29–42.

Cione, A.L., Cozzuol, M.A., Dozo, M.T., and Acosta Hospitaleche, C., 2011, Marine vertebrate assemblages in the Southwest Atlantic during the Miocene: Biological Journal of the Linnean Society, v. 103, p. 423–440.

del Río, C., 1991, Revisión sistemática de los bivalvos de la Formación Paraná (Mioceno medio), provincia de Entre Ríos, Argentina: Monografías de la Academia Nacional de Ciencias Exactas, Físicas y Naturales, v. 7, p. 11–90.

del Río, C., 2001, Malacofauna de las formaciones Paraná y Puerto Madryn (Mioceno marino, Argentina): su origen, composición y significado bioestratigráfico: Serie Correlación Geológica, v. 14, p. 77–102.

del Río, C.J., 1988, Bioestratigrafía y cronoestratigrafía de la Formación Puerto Madryn (Mioceno medio), Provincia del Chubut, Argentina: Anales de la Academia Nacional de Ciencias Exactas, Físicas y Naturales, v. 40, p. 231–254.

del Río, C.J., Martínez, S., Scasso, R., 2001, Nature and origin of spectacular marine Miocene shell beds of northeastern Patagonia (Argentina): Paleoecological and bathymetric significance. Palaios, v. 16, p. 3–25.

Diogo, R., 2005, Morphological Evolution, Aptations, Homoplasies, Constraints and Evolutionary Trends, Catfishes as Case Study on General Phylogeny and Macroevolution: Plymouth, Massachusetts, Science Publishers, Inc., 491 p.

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, v. 24, p. 607–618.

Fink, S.V., and Fink, W.L., 1996, Interrelationships of ostariophysan fishes (Teleostei), *in* Stiassny, M.L.J., Parenti, L.R., and Johnson, G.D., eds., Interrelationships of Fishes: San Diego, California, Academic Press, p. 209–249.

Gayet, M., and Meunier, F., 2003, Palaeontology and palaeobiogeography of catfishes, *in* Arratia, G., Kapoor, A.S., Chardon, M., and Diogo, R., eds., Catfishes 2: Plymouth Massachusetts, Science Publishers, Inc., p. 491–522.

Grande, L., 1987, Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships: Journal of Vertebrate Paleontology, v. 7, p. 24–54.

Grande, L., and Eastman, J.T., 1986, A review of Antarctic ichthyofaunas in the light of new fossil discoveries: Palaeontology, v. 20, p. 113–137.

Grande, L., and Lundberg, J.G., 1988, Revision and redescription of the genus *Astephus* (Siluriformes: Ictaluridae) with a discussion of its phylogenetic relationships: Journal of Vertebrate Paleontology, v. 8, p. 139–171.

Grande, L., and de Pinna, M.C.C., 1998, Descriptions of a second species of the catfish *Hypsidoris* and a reevaluation of the genus and the Family Hypsidoridae: Journal of Vertebrate Paleontology, v. 18, p. 451–474.

Goloboff, P.A., 1993, Estimating character weights during tree search: Cladistics, v. 9, p. 83–91.

Goloboff, P.A., 1999, Analyzing large data sets in reasonable times: solutions for composite optima: Cladistics, v. 15, p. 415–428.

Goloboff, P.A., and Farris, J.S., 2001, Methods for quick consensus estimation: Cladistics, v. 13, p. 225–245.

Goloboff, P.A., Farris, J.S., and Nixon, K., 2008, TNT: a free program for phylogenetic analysis: Cladistics, v. 24, p. 774–786.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J., and Szumik, C.A., 2003, Improvements to resampling measures of group support: Cladistics, v. 19, p. 324–332.

Marceniuk, A.P., Menezes, N.A., and Britto, M.R., 2012, Phylogenetic analysis of the family Ariidae (Ostariophysi: Siluriformes), with a hypothesis on the monophyly and relationships of the genera: Zoological Journal of the Linnean Society, v. 165, p. 534–669.

Nelson, J.S., 2006, Fishes of the World: Hokoken, New Jersey, John Wiley & Son, 601 p.

Nixon, K.C., 1999, The parsimony ratchet, a new method for rapad parsimony análisis: Cladistics, v. 15, p. 407–414.

Nolf, D., and Stringer, G.L., 1996, Cretaceous fish otoliths - a synthesis of the North American record, *in* Arratia, G., and Viohl, G., eds., Mesozoic Fishes - Systematics and Paleoecology: München, Germany, Verlag Dr. Friedrich Pfeil, p. 433–459.

Regan, C.T., 1911, The classification of the Teleostean fishes of the order Ostariophysi. 2. Siluroidea: Annals and Magazine of Natural History (series 8), v. 8, p. 553–577.

Rodiles-Hernández, R., Hendrickson, D.A., Lundberg, J., and Humphries, J., 2005, An unpublished first cladistic analysis of the Chiapas catfish (*Lacantunia enigmatica*) among all catfishes and two anonymous reviews. Available at http://catfishbone.ansp.org/Lacantuniidae/Lacantunia/enigmatica/pdfs/PhylogenyandReviews.pdf. Accessed October 30, 2015.

Scasso, R.A., and del Río, C., 1987, Ambientes de sedimentación, bioestratigrafía y proveniencia de la secuencia marina del Terciario superior de la región de Península Valdés, Chubut: Revista de la Asociación Geológica Argentina, v. 42, p. 291–321.

Scasso, R.A., McArthur, J.M., del Río, M.C., Martínez, S., and Thirlwall, M.F., 2001, 87Sr/86Sr Late Miocene age of fossil molluscs in the "Entrerriense" of the Valdés Peninsula (Chubut, Argentina): Journal of South American Earth Sciences, v. 14, p. 319–329.

Sullivan, J. P., Lundberg, J.G., and Hardman, M., 2006, A phylogenetic analysis of the major groups of catfishes (Teleostei, p. Siluriformes) using *rag1* and *rag2* nuclear gene sequences: Molecular Phylogenetics and Evolution, v. 41, p. 636–662.

Uliana, M.A., and Biddle, K.T., 1988, Mesozoic-Cenozoic paleogeographic and geodynamic evolution of southern South America: Revista Brasileira de Geociências, v. 18, p. 172–190.

Appendix 1. Comparative Material Examined

Bachmannia chubutensis: MLP 40-V-17-1 (holotype); CIC 75/1, CIC 75/3-8, CIC 75/10-14, CIC 75/16-18; MACN PV: 19785-19806; MLP 35-X-4-8, MLP 40-V-17-3, MLP 40-V-17-4/6/7/9/11/14/15/17/19/21/23/24, MLP 40-V-20-1, MLP 77-VI-6-1/2/3/4; PVL 4305-7, PVL 4309-4316, PVL 4318-4331, PVL 4365-67, PVL 4369-70; MPBAR 1091-44; MPEF-PV 1514/1516/15-19, MPEF-PV 1524a-b, MPEF-PV 1525a-b, MPEF-PV 1526-27, MPEF-PV 1537/1545/ 1549/1551, MPEF-PV 1555a-b, MPEF-PV 1900a-b, MPEF-PV 1901a-b, MPEF-PV 1902-05; 107 ex.; early Eocene Tufolitas Laguna del Hunco, outcropping near the Laguna del Hunco, Chubut, Argentina.

Brycon orbignyanus: CI-FML 3874, 1 ex., rio Guayquiraró, Corrientes, Argentina.

Diplomystes camposensis: ANSP 177915, 1 ex., Lago Piuihue, Chile.

Diplomystes chilensis: MCZ 36195, 1 ex., Santiago, Chile; USNM 259097, 1 ex., rio Nuble, Chile.

Diplomystes cuyanus: MLP 286, holotype; FMNH 58003, 1 ex.; both San Juan, Argentina.

Diplomystes mesembrinus: MLP 948, holotype; MLP 8966, 1 ex. C&S; Río Senguer, Chubut, Argentina.

Diplomystes nahuelbutaensis: CAS 55425, 1 ex., rio Cautin, Chile; UMMZ 212177, 1 ex. C&S; Río Bio-Bio, Chile.

Diplomystes viedmensis: MLP 214, holotype; MLP 8966, para type, both Río Negro, Río Negro, Argentina.

Eigenmannia trilineata: CI-FML 6162, 2 ej. C&S, Riacho Mbiguá, Estancia El Bagual, Formosa, Argentina.

Hypsidoris farsonensis: cast of FMNH 10641; AMNH 6888, 1 ex., peel. We also examined many other recent and fossil catfishes in different institutions.