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Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

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Gymnogeophagus Eocenicus, n. sp. (Perciformes: Cichlidae), an Eocene Cichlid from the Luján Formation in Argentina

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Online publication date: 24 March 2010

To cite this Article Malabarba, Maria C. , Malabarba, Luiz R. and Papa, Cecilia Del (2010) '*Gymnogeophagus Eocenicus*, n. sp. (Perciformes: Cichlidae), an Eocene Cichlid from the Luján Formation in Argentina', *Journal of Vertebrate Paleontology*, 30: 2, 341 – 350

To link to this Article: DOI: 10.1080/02724631003618348

URL: <http://dx.doi.org/10.1080/02724631003618348>

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GYMNOGEOPHAGUS EOCENICUS, N. SP. (PERCIFORMES: CICHLIDAE), AN EOCENE CICHLID FROM THE LUMBRERA FORMATION IN ARGENTINA

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ABSTRACT—A new cichlid referable to the extant genus *Gymnogeophagus* is described from the Eocene Lumbrera Formation of the Salta Group, northwestern Argentina. †*Gymnogeophagus eocenicus*, n. sp., presents the synapomorphies that support the genus: absence of supraneurals and a presence of a forward spine in the first dorsal pterygiophore. The existence of an early to middle Eocene-aged species presenting the synapomorphies and the appearance of a modern genus requires the acceptance of an extensive differentiation from the basal cichlid lineages. Extant *Gymnogeophagus* species are restricted to the La Plata drainage and a few coastal drainages of southern Brazil and Uruguay. The occurrence of an Eocene fossil in the geographical area corresponding to the present distribution of the genus suggests the patterns of distribution and endemism of the Neotropical fish fauna have a very old history in the continent.

INTRODUCTION

Cichlids are teleost fishes found chiefly in fresh waters. They are one of the major vertebrate families with more than 1500 species (Eschmeyer and Fong, 2008), being one of the most speciose families of percoid fishes. Due to this speciosity besides the ecological and evolutionary features, cichlids are among the most widely studied fish. Contrasting with this effervescence of the recent forms is the scarce fossil record. Even with the recent reports (Murray, 2000, 2001; Carnevale et al., 2003; Malabarba et al., 2006), the cichlid fossil record is still meager if it is compared to such diversity of the recent forms.

Fossil cichlids are known from Africa, Europe, Central and South America, and the Near East. In South America, cichlids are recorded for Oligocene–Miocene of Brazil and Miocene and Eocene of Argentina (Arratia and Cione, 1996; Malabarba et al., 2006). The first cichlid records in the Argentinean sediments, †*Aequidens saltensis* and †*Acaronia longirostrum*, were reported by Bardack (1961) from the exposures in the Salta Province, northwestern Argentina. Casciotta and Arratia (1993a) described Miocene cichlid fossils from northern Argentina and proposed a phylogenetic hypothesis of relationships for Recent and fossil American cichlids. The only fossil fish remains reported for the Lumbrera Formation, northwestern Argentina, were detached dental plates assigned to *Lepidosiren paradoxa* (Fernandez et al., 1973), until the description of the cichlid fish, †*Proterocara argentina* Malabarba, Zuleta, and del Papa, 2006, from this formation and from the same fossil level as the material reported here.

Currently, the genus *Gymnogeophagus* Miranda Ribeiro, 1918, includes 10 species occurring in the southern South America drainages. *Gymnogeophagus* is a geophagine genus whose monophyly is supported by the absence of supraneurals and the presence of a forward spine in the first dorsal pterygiophore in the analyses of Reis and Malabarba (1988) and Casciotta and Arratia (1993a). It has been also diagnosed by the presence of

three infraorbitals posterior to the lachrymal, in a complete series from the lachrymal to the sphenotic; by the lachrymal extensively overlapping for up to half the length of the first infraorbital; by the vertebral hypapophyses long, co-ossified distally; by the first hemal arch positioned on the antepenultimate or up to fourth from last abdominal vertebra; and by the pointed pelvic fin shape, with the inner branch of the first soft ray longest according to Kullander (1998).

The genus has a wide distribution in the South American subtropical drainages, occurring in the Paraná, Paraguay, and Uruguay basins and along small coastal drainages of southern Brazil. In this paper, a new *Gymnogeophagus* species, †*Gymnogeophagus eocenicus*, coming from Lumbrera Formation, northwestern Argentina, is described. The sediments of this formation were deposited in a lake during the early to middle Eocene (Pascual et al., 1981; Babot et al., 2002). Along with †*P. argentina*, the new fossil constitutes the oldest cichlid records for South America.

Institutional Abbreviations—CNS, Universidad Nacional de Salta, Salta; MCP, Museu de Ciências e Tecnologia, Porto Alegre; MLP, Museo de La Plata, La Plata; UFRGS, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre.

GEOLOGICAL SETTING

The Paleogene record in northwestern Argentina is composed of continental deposits mainly of lacustrine origin. The characteristic of these lakes varies in their geographical extension and style from saline, saline-alkaline, to freshwater, the climate being the main factor controlling them (del Papa, 1999).

The Lumbrera Formation constituted a complex continental Eocene lithostratigraphic unit divided by an unconformity surface in two informal members: lower Lumbrera and upper Lumbrera (Gómez Omil et al., 1989; del Papa, 2006). The specimen described here comes from uppermost section of the lower

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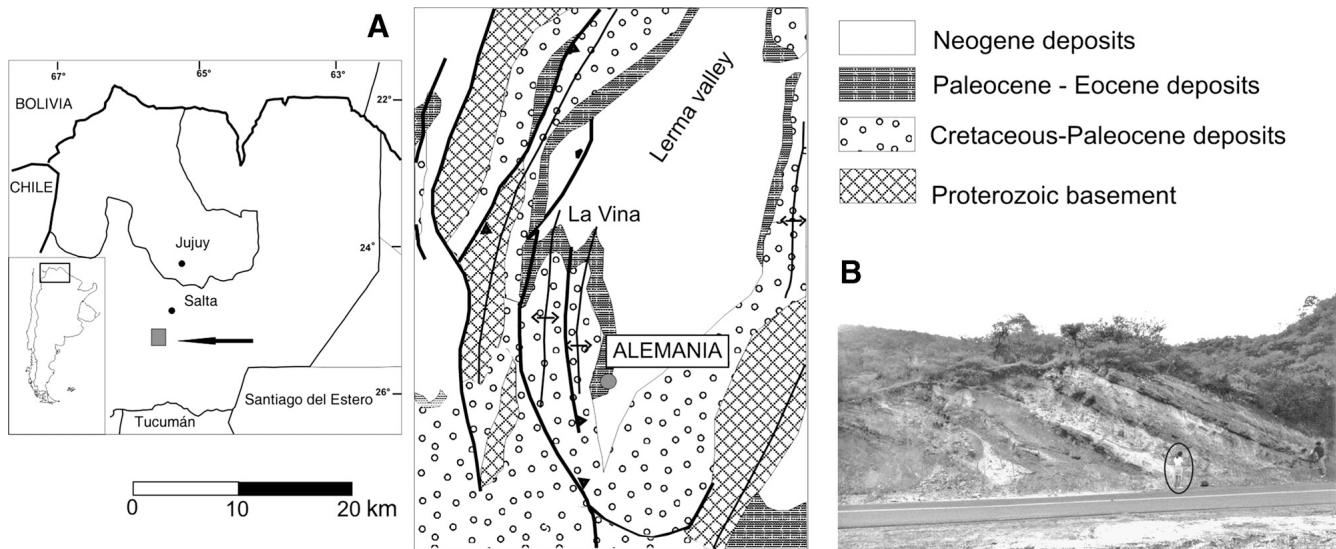


FIGURE 1. Study area. **A**, location and geological maps; **B**, outcrop view of fine-grained lacustrine deposits of Faja Verde at Alemania (person for scale).

Lumbrera known as “Faja Verde” because its lacustrine origin, at the Alemania locality (Fig. 1).

The age of this unit is based on magnetostratigraphic studies (Sempere et al., 1997) and the vertebrate paleontological record assigned as Lower to Middle Eocene (Pascual et al., 1981; Babot et al., 2002; among others).

PALEOENVIRONMENTAL SETTING

Gymnogeophagus has been identified in the Paraná, Paraguay, and Uruguay, large fluvial systems that constitute stationary rivers with extensive and vegetated floodplains (Menni, 2004). The highly variable dynamics (including suspended load and volume of water) of these fluvial systems provoke a complex floodplains evolution where backswamps, pools, small lakes, and secondary streams developed (Neiff, 1990). Specifically, *Gymnogeophagus* is known to occur in fluvial-lakes (Bonetto et al., 1969) related to the alluvial plains and to the abandoned meanders (oxbow lakes). In the Northwest of Argentina, *Gymnogeophagus* has been reported in the tropical Bermejo River (Monasterio de Gonzo, 2003) and in the Juramento River. In the latter, it has been noted that *Gymnogeophagus* lives in marginal areas protected from the high-energy streams of the main channels. Hence the environmental conditions of these modern rivers seem to be quite like the conditions of the Faja Verde lake. Based on sedimentary and palynological studies, del Papa et al. (2002) interpreted the Faja Verde lake as a perennial freshwater system with fixed coastline.

In the littoral areas, Gilbertean-type deltaic systems developed. The thickness of this system’s stacked sandy clinofolds does not exceed 3 m, suggesting progradation in shallow water (Overeem et al., 2001). However, in the inner lake, the water column should be deep enough to sporadically provoke stratification and bottom anoxia (del Papa et al., 2002), favoring a good preservation of fish fossils.

In both littoral and inner lake settings, sedimentary facies are dominated by medium- to fine-grained sediments rich in organic matter and irregular distributed algal stromatolites (Fig. 2). The algae, *Botryococcus* and *Pediastrum*, and the preserved organic matter (bacterially reworked biomass of algae and plankton) suggest a lake with moderate to high primary organic pro-

ductivity under temperate climatic conditions (Quattrocchio and Volkheimer, 2000; del Papa, 2006). Moreover, in littoral areas, the abundance of translucent phytoclasts derived from terrestrial vascular plants (wood and leaves), with both anaerobic and aerobic degradation in dark muddy sediments, suggests temporally flooded areas like interdistributary bays and swamps (del Papa et al., 2002). The recognition of terrestrial insects, such as Carabidae, Tricoptera, and Orthoptera, reinforces the interpretation of highly vegetated littoral areas and wet humus-rich soils (Naón, 1998).

All these data from the Faja Verde section support the interpretation of a lake of low-energy, of freshwater chemistry, and surrounded by low-relief vegetated areas sporadically flooded (Fig. 2). Therefore, this scenario is quite similar to present-day described occurrence for *Gymnogeophagus* in the region.

MATERIAL AND METHODS

Specimen and Preparation

The fossil material is made up of a single articulated specimen (Fig. 3), preserved as impression and deposited in the Universidad Nacional de Salta, Salta, Argentina (CNS-V10024). It was collected in the Lumbrera formation (early to middle Eocene) in Northwest Argentina. The material was prepared using standard paleontological tools under a microscope. Anatomical illustrations were prepared from sketches of structures as viewed through a camera lucida mounted on a Zeiss SV-6 microscope. Photographs were taken using a digital Nikon camera. Species listed as *Gymnogeophagus* sp. A, sp. B, sp. D, and sp. E in the text and comparative material correspond to the extant undescribed species listed using the same terminology as Wimberger et al. (1998).

The morphometric data (Table 1) were taken following Reis and Malabarba (1988) for the general head and body measurements, except for the caudal peduncle length, which here is from the end of anal-fin base to the last vertebra-hypural junction, and preorbital length is taken from the anterior margin of the premaxilla to the orbital rim. Jaw measurements and nomenclature follow Casciotta and Arratia (1993b). The coulter area term employed in the description refers to the lower jaw area formed by

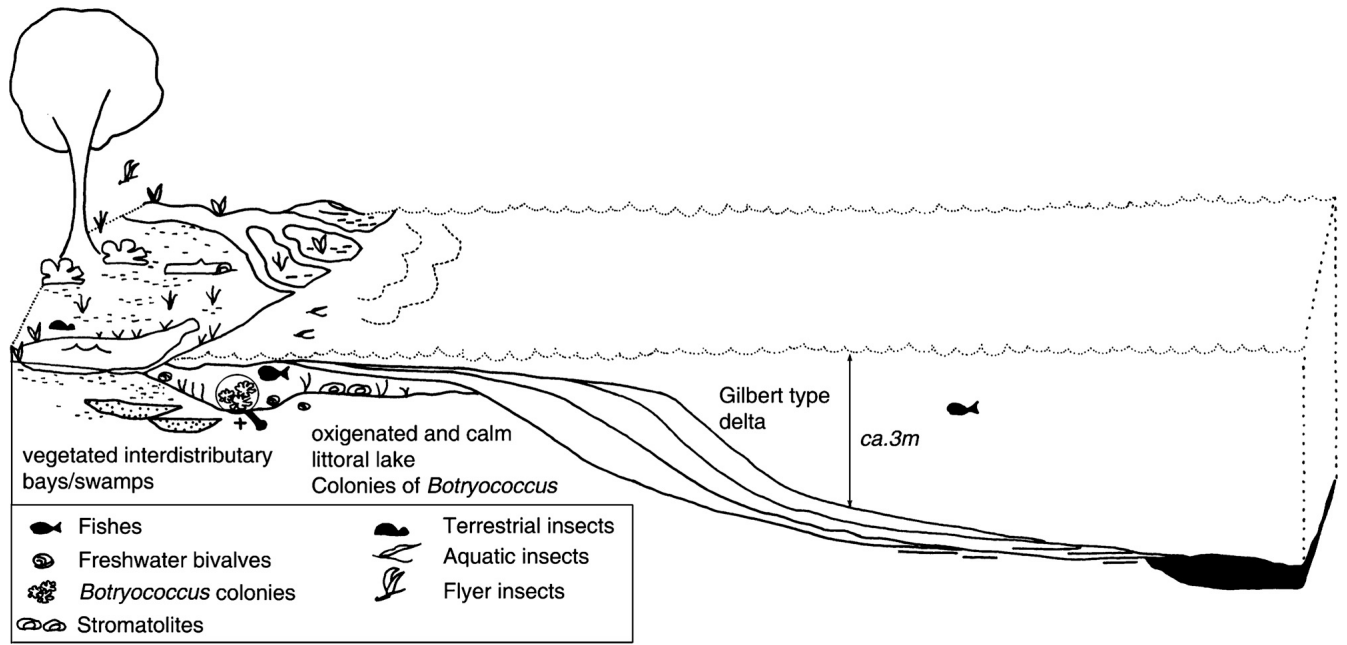


FIGURE 2. Cartoon illustrating the paleoenvironment interpreted for the Eocene Faja Verde lake, showing low-energy littoral areas and intense vegetated margins.

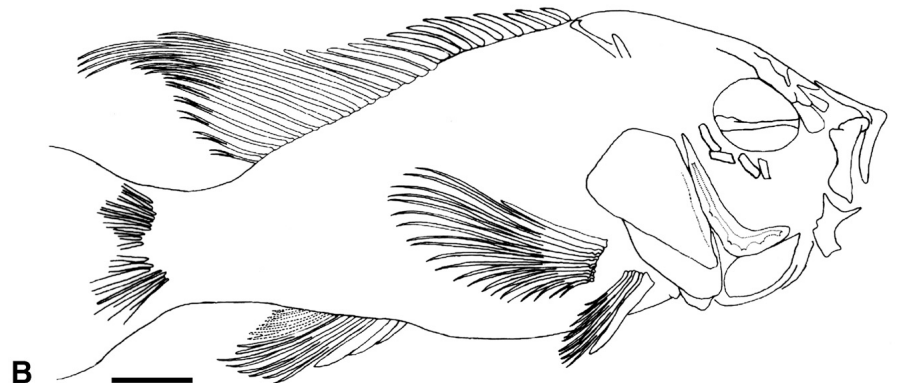
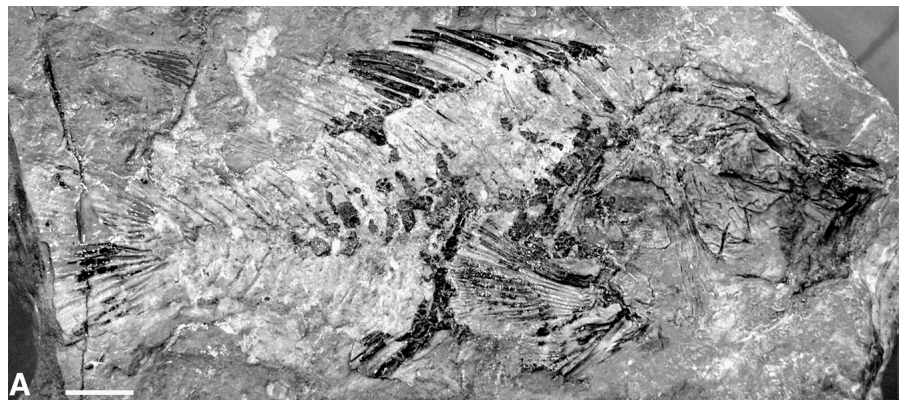


FIGURE 3. †*Gymnogeophagus eocenicus* n. sp., CNS-V10024, holotype. **A**, photograph of CNS-V10024; **B**, restoration of general outline and fins. Scale bar equals 7 mm.

TABLE 1. Morphometrics of *Gymnogeophagus eocenicus*, n. sp., holotype (CNS V10024).

Character	holotype
Standard length (mm)	56.84
Percentages of standard length	
Head length	41.39
Greatest body depth	38.52
Head depth	37.15
Snout to anal-fin origin	65.05
Snout to pelvic-fin origin	47.36
Anal-fin base length	17.11
Dorsal-fin base length	57.7
Caudal peduncle length	14.21
Caudal peduncle depth	15.28
Pelvic-fin length	—
Pectoral-fin length	25.66
Percentages of head length	
Snout length	33.86
Eye diameter	21.94
Upper jaw length	36.2
Postorbital length	48.40
Preorbital length	36.40
Ascending arm of premaxilla	35.38
Dentigerous arm of premaxilla	22.76
Countings	
Dorsal-fin spines	14
Dorsal-fin soft rays	11–12
Anal-fin spines	3
Anal-fin soft rays	—
Pectoral-fin rays	13
Abdominal vertebrae	12–13
Caudal vertebrae	15

Standard length is expressed in mm; other measurements are percentages.

the retroarticular and by the canal-bearing ventral portion of the anguloarticular. In the counts of fin rays, uppercase roman numerals indicate spines, and Arabian numerals indicate branched rays.

Comparative Material—All specimens cleared and stained. *G. balzanii*, MCP 22845; *G. che*, MLP 8748; *G. setequedas*, MCP 11903, MCP 14705, MCP 14637; *G. meridionalis*, MCP 14767, MCP 16120, MCP 10002; *G. rhabdotus*, MCP 9203, MCP 18118, MCP 16121, MCP 14827; *G. gymnogenys*, MCP 17236; *G. lacustris*, MCP 13925 (2); *G. labiatus*, MCP 27763 (2); *G. sp. A*, MCP 11251; *G. sp. B*, MCP 18362; *G. sp. D*, MCP 12725 (3); *G. sp. E*, MCP 12958 (2).

SYSTEMATIC PALEONTOLOGY

Order PERCIFORMES Bleeker, 1859

Suborder LABROIDEA Bleeker, 1859

Family CICHLIDAE Bonaparte, 1840

GYMNOGEOPHAGUS EOCENICUS, n. sp.

(Figs. 3–7)

Holotype—CNS-V10024, an articulated specimen preserved as impression in right lateral view.

Diagnosis—The lack of supraneurals and the presence of a forward-directed spine at the distal tip of the first pterygiophore diagnoses †*G. eocenicus* from other cichlids, except from the *Gymnogeophagus* species. The caudal peduncle longer than deep and the number of caudal vertebrae (15) diagnoses †*G. eocenicus* from the species of *Gymnogeophagus* bearing a caudal peduncle shorter than or as long as deep and 13 or 14 caudal vertebrae (*G. balzanii*, *G. rhabdotus*, *G. meridionalis*, *G. setequedas*, and *G. che*). The lack of a reduced frontoparietal crest diagnoses †*G. eocenicus* from *G. australis*, *G. labiatus*, *G. gymnogenys*, and *G. lacustris*.

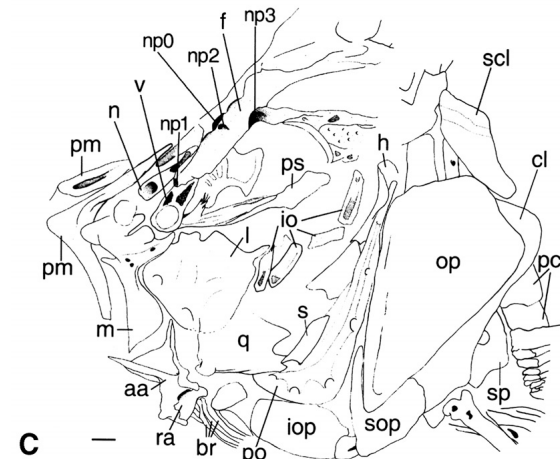
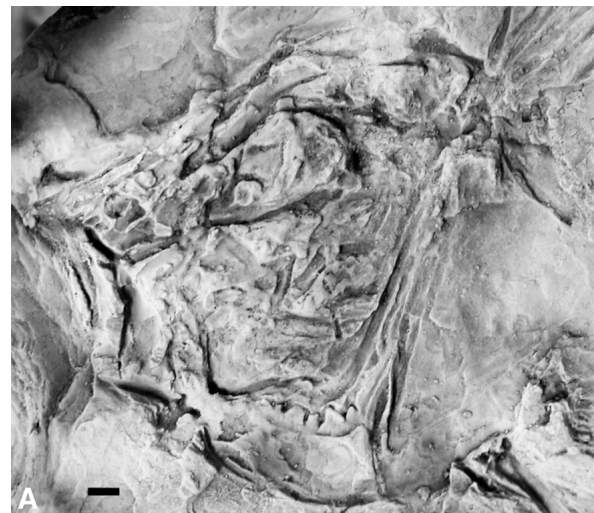


FIGURE 4. †*Gymnogeophagus eocenicus*, n. sp., skull in lateral view: **A**, CNS-V10024, original fossil impression sprinkled with ammonium chloride; **B**, cast in latex of the holotype (reversed) sprinkled with ammonium chloride; **C**, interpretative drawing. **Abbreviations:** **aa**, anguloarticular; **br**, branchiostegal rays; **cl**, cleithrum; **f**, frontal; **h**, hyomandibular; **io**, infraorbitals; **iop**, interopercle; **l**, lachrymal; **m**, maxilla; **n**, nasal; **np0–3**, neurocranial lateral line pores 0–3; **op**, opercle; **pm**, premaxilla; **q**, quadrate; **pc**, postcleithrum; **po**, preopercle; **ps**, parasphenoid; **ra**, retroarticular; **s**, symplectic; **sp**, scapula; **scl**, supracleithrum; **sop**, subopercle; **v**, vomer. Scale bar equals 2 mm.

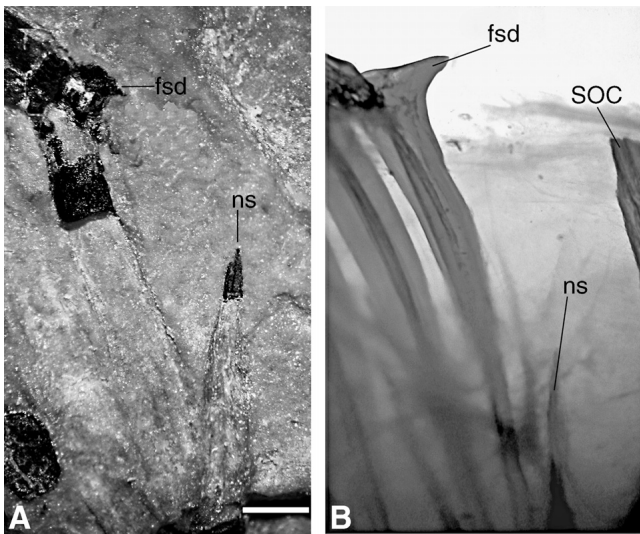


FIGURE 5. Predorsal region in the fossil †*Gymnogeophagus eocenicus*, n. sp. (A), and in *G. setequedas* (B). **Abbreviations:** fsd, forward spine in the first dorsal pterygiophore; ns, first neural spine; soc, supraoccipital crest. Scale bar equals 1 mm.

Age—Eocene.

Horizon and Locality—Lumbrera Formation, Faja Verde II level, at the Alemania locality (Fig. 1), northwestern Argentina.

Description

Body Shape—Morphometric data of CNS-V10024 are in Table 1. CNS-V10024 is a moderately deep-bodied cichlid (Fig. 3) that reaches 56.8 mm of standard length (SL). The greatest body depth is at about the third spine of dorsal fin. The head is slightly longer than deep; its length is about 43% of the SL. The dorsal contour of head is straight from snout to supraoccipital crest; the dorsal body contour is slightly convex from dorsal-fin origin to caudal peduncle. The ventral contour of the body is gently convex from lower jaw tip to the anal-fin origin; the anal-fin base is posterodorsally slanted. The caudal peduncle is longer than deep.

Skull—The skull (Fig. 4) is roughly triangular in lateral view, a little longer (24.4 mm) than deep (21.1 mm), with a terminal mouth. Some identified bones are crushed and dislocated from the original position making it difficult to determine their anatomic details and contacts.

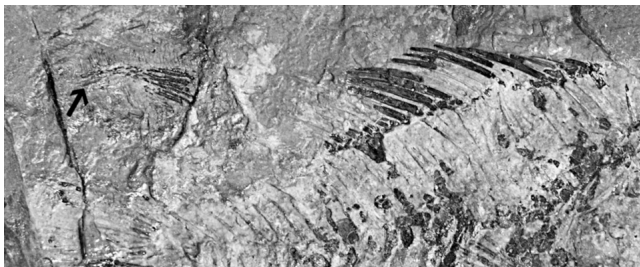


FIGURE 6. Dorsal fin of †*Gymnogeophagus eocenicus*, n. sp., showing the elongation of the anterior soft rays (arrow).

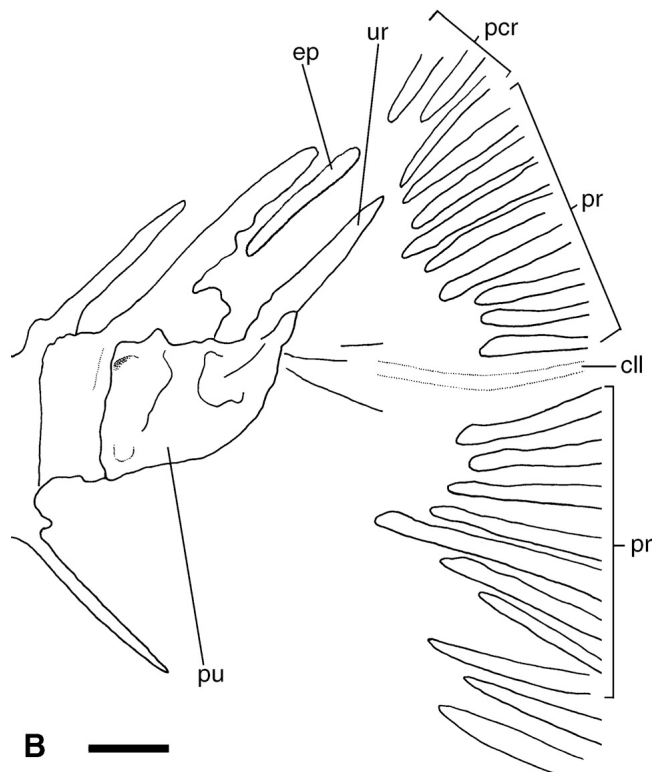


FIGURE 7. †*Gymnogeophagus eocenicus*, n. sp., caudal fin skeleton. **A**, cast in latex sprinkled with ammonium chloride; **B**, interpretative drawing. **Abbreviations:** cll, caudal-fin segment of the lateral line; ep, epural; pu, last vertebral centrum; pcr, procurrent rays; pr, principal rays; ur, uroneural. Scale bar equals 1 mm.

Neurocranium—The skull roof region is in part smashed and collapsed with the orbit. Only one of the frontals is entirely preserved; it is smooth and crossed longitudinally by the sensory lateral canal. The lateralis canal foramina (NLF) 1–3 were preserved; NLF2 is a single opening. The collapsed frontal crest exhibits the coronalis lateralis foramen (NLF0 of Stiassny, 1991) as a single pore at the end of canal. The orientation of the sphenotic-pterotic canal is sharply angled. The supraoccipital is hexagonal with a moderately developed crest, but its relation to the adjacent bones is concealed by the scale impressions. A very low parietal crest begins near NLF3 in the frontal, directed posteriorly through parietal and epioccipital bones.

Anterior to the frontals, parts of the mesethmoid, nasal and vomer, were preserved. The tubular ventral end of the nasal, bearing the supraorbital canal, is placed lateral to the ascending arm of the premaxilla. The most anteroventral part of the vomer with a roundish spongious surface is visible just above the maxilla. Remains of an interdigitating suture between the vomer and the lateral ethmoid is preserved; the suture with the parasphenoid cannot be distinguished. The lateral ethmoid presents a trabecular surface and forms the anteroventral contour of the orbit. The parasphenoid is seen crossing the lower third of the orbit.

A square lachrymal is followed by four canal-bearing elements, probably corresponding to the infraorbitals 2–5. The infraorbitals are displaced from the orbital contour, but judging from the extension of the lachrymal posterodorsal corner, it should overlap part of the first infraorbital.

Jaws and Suspensorium—The mouth is terminal (Fig. 4). The robust premaxilla is preserved as an impression in lateral view, showing the ascending arm longer (8.5 mm) than the dentigerous arm (5.5 mm). The ascending arm is straight and slender (1.2 mm thick); however, anatomical details, including foramina and articulatory facets and ridges, cannot be accurately distinguished. The angle formed by the confluence of the ascending and dentigerous arms is 84° and not projected rostrad. The dentigerous arm is slightly convex, with impressions of a few alveoli in its ventral margin, probably representing the outer tooth series. The maxilla has a well-developed head; posteriorly it extends beyond the end of the dentigerous arm of the premaxilla.

Of the lower jaw only the anguloarticular, retroarticular, and suspensorium were preserved. The anguloarticular is nearly so long (6.5 mm) as deep (6.8 mm), with a high and slightly anteriorly directed primordial process. The coulter area is nearly rectangular in shape, deeper (3.4 mm) than wide (2.7 mm) and just slightly rostrad directed ($\gamma = 95^\circ$, $\alpha = 107^\circ$), almost straight. In lateral view, the retroarticular is approximately triangular, forming the posterodorsal corner of the coulter area. The mandibular canal on the anguloarticular seems to be short and almost straight, with a very wide posterior opening.

In lateral view, the quadrate is triangular, with a conspicuous roundish head for articulating with the anguloarticular. The symplectic is short, rectangular and fits along the quadrate lateroventral edge. The dorsal portion of the hyomandibula is visible, but poorly preserved.

Opercular Apparatus—All opercular elements are preserved in CNS-V10024 (Fig. 4): preopercle, opercle, subopercle, and interopercle. They have smooth surfaces and margins. The L-shaped preopercle has a rounded posterior corner and a vertical arm much longer than the horizontal one. The lateralis canal in the preopercle has two terminal and four medial pores for a total of six pores. The opercular bone is short, almost triangular, with a straight dorsal border. The subopercle is aligned to the opercle ventral margin and has an anterior ascending process projecting between opercle and preopercle. The interopercle is nearly oval and recovered by scales. Rows of cycloid scales were preserved as impressions on the opercle, subopercle, and interopercle, whereas the preopercle is scaleless (see Squamation).

Vertebrae and Supraneurals—The vertebral column is nearly straight, with the greatest body depth at the origin of the dorsal fin. The vertebrae are badly preserved and the numbers presented here are based on the impressions of centra, neural spines, and pterygiophores. It is estimated a total of 27–28 vertebrae, including 12–13 precaudal and 15 caudal vertebrae. The first neural spine is shorter than the others and placed anterior of the first dorsal pterygiophore.

There is no supraneural bone present in CNS-V10024 (Fig. 5). This feature constitutes one of the synapomorphies of the genus *Gymnogeophagus*.

Pectoral Fin and Girdle—The pectoral girdle and fin are poorly preserved in CNS-V10024 (Fig. 4). All that is preserved of the cleithrum is the notched region above the pectoral-fin insertion, with the lamella forming a projection curved caudally. Impressions of scapula and both proximal and distal postcleithra can be seen below this lamella. The supracleithrum is completely preserved, overlying the dorsal part of the cleithrum. It is oval and elongate; anteroposteriorly crossed by the lateralis canal along its dorsal border.

The pectoral fin is elongated (12.5 mm length of the longest ray), extending further posteriorly than the pelvic fin and reaching the anal-fin origin. There are 13 rays in the pectoral fin. The first ray seems to be shorter than the second one, suggesting a rounded shape for the pectoral fin; however, the preservation does not allow a definitive shape determination.

Pelvic Fin—Little of the pelvic fin was preserved. It is inserted very anteriorly, at the side of the subopercle; just the posterior portion of the basipterygium articulating with a strong fin spine is present. There are at least four soft rays preserved.

Dorsal and Anal Fins—As the dorsal fin is only partly preserved, the dorsal-fin total ray count is estimated. There are 14 spines that increase in length up to the sixth; the remaining spines are about the same size. The spiny portion is immediately followed (no gap) by 11–12 segmented rays longer than the spines. The second to fourth soft rays are very extended in their length (25.55 mm = 48.46% SL), reaching the middle of the caudal fin length (Fig. 6), which represents a sexually dimorphic character of the males of most extant species of *Gymnogeophagus*. The posterior end of the dorsal fin base (85.3 mm) is opposite to the estimated final third of the anal fin. The ventral ends of the first two dorsal pterygiophores are placed between the first and second neural arches. The distal end of the first pterygiophore has a forward-directed spine that represents one of the synapomorphies of the genus *Gymnogeophagus*.

The anal fin is poorly preserved. Only the proximal part of the seven most anterior elements are visible, comprising three strong spines (1.1 mm width) followed by at least four segmented rays. The pterygiophores cannot be counted either.

Caudal Fin—Neither caudal-fin skeleton or shape were entirely preserved. The anterior epural is elongated and parallel to the neural spine of the antepenultimate vertebra. The urostile is short, curve, and associated to the uroneural. There were 16 principal rays, 8 ventral and 8 dorsal. Three to four procurrent rays were preserved in the dorsal lobe of the caudal fin (Fig. 7).

Lateral Line—The lateral line is preserved well enough and its entire route can be determined. Two scales bearing tubes of the sensory canal were preserved behind the posterior border of the supracleithrum, marking the very beginning of the lateral line in the flank. It extends from there caudally directed and describing a gentle curve laterally along the body, and nearly parallel to the dorsal body outline. At the level of the insertion of the most posterior soft dorsal-fin rays, the line bends towards the vertebral column, reducing the gap between the two sections to one or two scales. The most anterior indication of the lower lateral line section is on the 25th vertebra extending very close to the ventral border of the vertebral column onto the caudal fin base.

Apparently, this lower segment enters in the caudal-fin base between the dorsal and ventral lobes with no bifurcation.

Squamation—There are scale impressions scattered over the body. On the opercular apparatus, medium-sized scales are aligned on the ventral border of the opercle and scarcely on its surface, but the number of rows cannot be precisely determined. A row of large cycloid scales covers the subopercle; and smaller scales are on the interopercle. On the caudal-fin base, over the hypural there are some fragments of cycloid scales preserved, suggesting that the base of this fin was scaled.

DISCUSSION

Cichlid Systematics

Studies on cichlid systematics have been based on phylogenetic analyses produced by morphological (e.g., Cichocki, 1976; Stiassny, 1991; Casciotta and Arratia, 1993a; Kullander, 1998), molecular (Farias et al., 1999; Sparks and Smith, 2004; López-Fernández et al., 2005b), and combined (“total evidence”; Farias et al., 2000; López-Fernández et al., 2005a; Smith et al., 2008) data. Although there are differences among the resulting classifications, all these studies have managed to recover a monophyletic clade for geophagines. Kullander (1998) proposed seven synapomorphies to support the monophyly of the subfamily Geophaginae, which included 16 genera distributed into three tribes. More recent phylogenetic analyses, based on molecular (Farias et al., 1999; López-Fernández et al., 2005a) and combined (Farias et al., 2000; López-Fernández et al., 2005b; Smith et al., 2008) data, added the genera *Crenicichla* and *Teleocichla* to the Geophaginae, expanding the subfamily to 18 genera. In the analyses based on combined data, Farias et al. (2000, including the morphological data set of Kullander, 1998) found *Gymnogeophagus* forms a clade with *Geophagus*, *Mikrogeophagus*, and *Biotodoma*; Smith et al. (2008, also including the morphological data set of Kullander, 1998) found *Gymnogeophagus* forms a clade with *Geophagus* and *Biotodoma*; and López-Fernández et al. (2005b, using morphological data taken from extensive literature and resulting from their own study) found *Gymnogeophagus* forms a clade with *Geophagus* and *Mikrogeophagus* within geophagines.

Reis and Malabarba (1988) defined *Gymnogeophagus* as monophyletic based on two synapomorphies: a forward directed spine on the first dorsal pterygiophore (character 1) and the loss of supraneurals (character 2), further supported by Casciotta and Arratia (1993a). Both synapomorphies are present in the fossil.

According to the analysis of Kullander (1998), *Gymnogeophagus* is characterized by three infraorbitals in a complete series (character 41:2), with the first one extensively overlapped by the lachrymal (character 44:2). †*Gymnogeophagus eocenicus* is here reported to have four infraorbitals, but because they are displaced, we cannot unquestionably determine about the number and the overlapping. However, the lachrymal outline suggests that this bone could have overlapped the first infraorbital by some extension. The other characters found by Kullander for *Gymnogeophagus* (character 77:2; 70:0; 86:2) were not preserved in the fossil. Based on the presence of a minute cartilage, Kullander (1998) coded one supraneural (character 66:1) for *Gymnogeophagus*, because it is typical for geophagines. Regardless of Kullander's treatment of this character, the absence of an ossified supraneural is constant and unique to this genus, and is here considered as a valid synapomorphy occurring in all *Gymnogeophagus* species, including the fossil.

We further tested the relationships of the fossil species using the matrix of morphological data presented by López-Fernández et al. (2005b) for geophagines. Only 48 of 136 characters (35.3%) were observable in the fossil and included in the matrix. We have obtained a similar topology presented in fig. 1A of López-Fernández et al. (2005b), with the addition of †*G. eocenicus* in the clade formed by the two *Gymnogeophagus* species included

in the analysis (Fig. 8). Again the lack of supraneurals (character 127:2) and the presence of a forward-directed spine on anterodorsal margin of the first dorsal pterygiophore (character 128:1) support the inclusion of the fossil in *Gymnogeophagus*, along with the single opening of the NLF2 (character 53:1) and NLF4 (character 54:1), and the orientation of the sphenotic-pterotic canal sharply angled (character 85:1). The remaining characters which group *G. balzanii*, *G. rhabdotus*, and †*G. eocenicus* were coded as missing in the fossil (character 3, 69, 98, 103).

Reis and Malabarba (1988) proposed a hypothesis of relationship among the seven species known at that time: *G. rhabdotus* (Hensel, 1870), *G. labiatus* (Hensel, 1870), *G. gymnogenys* (Hensel, 1870), *G. balzanii* (Perugia, 1891), *G. australis* (Eigenmann, 1907), *G. lacustris* Reis and Malabarba, 1988, and *G. meridionalis* Reis and Malabarba, 1988. Fifteen derived characters were used to support this hypothesis, but only six (characters 3, 4, 6, 11, 12, and 17) could be verified in CNS-V10024, with all of them occurring in the primitive state in the fossil. †*Gymnogeophagus eocenicus* lacks the elevated dorsal contour (character 3), the high number of dorsal soft rays (character 4), and the rostrocaudal shortening of the supraoccipital crest (character 6) considered autapomorphic to *G. balzanii*. It lacks a conspicuously high supraoccipital crest (character 11; according to Reis et al., 1992:271, the phylogenetic value of this character must be reevaluated) considered synapomorphic to *G. meridionalis* and *G. rhabdotus*. It lacks a reduced frontoparietal crest (character 12; although this state was tentatively assumed as derived by Reis and Malabarba, 1988:286) considered synapomorphic to *G. australis*, *G. labiatus*, *G. gymnogenys*, and *G. lacustris*. Finally, it lacks a narrow supraclithrum (character 17) considered autapomorphic to *G. lacustris*. The lack of these characters does not support the recognition of †*Gymnogeophagus eocenicus* as belonging to any of the three main branches of the cladogram of Reis and Malabarba (1988:301, fig. 25).

Wimberger et al. (1998) proposed a *Gymnogeophagus* phylogeny based on mitochondrial DNA and tRNA sequences. This hypothesis is mostly coincident with that of Reis and Malabarba (1988), except in removing *G. balzanii* from a basal position in the genus and placing the species among “*gymnogenys*-like” species. Gene sequences, however, are not available for †*Gymnogeophagus eocenicus* for comparison.

There are four *Gymnogeophagus* species described after the review of Reis and Malabarba: *G. setequedas* Reis, Malabarba, and Pavanelli, 1992; *G. che* Casciotta, Gomez, and Toresanni, 2000; *G. caaguazuensis* Staeck, 2007; and *G. tiraparae* González-Bergonzoni, Loureiro, and Oviedo, 2009. *Gymnogeophagus setequedas* is related to the clade formed by *G. meridionalis* and *G. rhabdotus* and it is distinguished from them and from the other *Gymnogeophagus* species by the color pattern and number of scales. *Gymnogeophagus che* was also considered related to *G. setequedas* and *G. rhabdotus* and differed from them by the reduction of spots on the fins and for the presence of a wide and distinct symphyseal articular facet (not present in the fossil specimen). *Gymnogeophagus caaguazuensis* was distinguished from the other species by having a lyreate caudal fin. Additionally, *G. caaguazuensis* is diagnosed as having a short caudal peduncle (15.92% SL), but it is still longer than in the fossil (14.21% SL). *Gymnogeophagus tiraparae* was described for the lower rio Uruguay basin and diagnosed by a unique color pattern in the dorsal fin, being considered related to the *G. gymnogenys* group based on molecular data (González-Bergonzoni et al., 2009).

We found two characters not considered previously and potentially useful in assessing †*Gymnogeophagus eocenicus* relationships among extant groups of species. The fossil possesses 15 caudal vertebrae, as well as a very long soft dorsal fin (Fig. 6), characteristic of mature males of some extant species. Mapping those characters in the phylogeny of Wimberger et al. (1998) for *Gymnogeophagus*, we find all the species of the *G. gymnogenys*

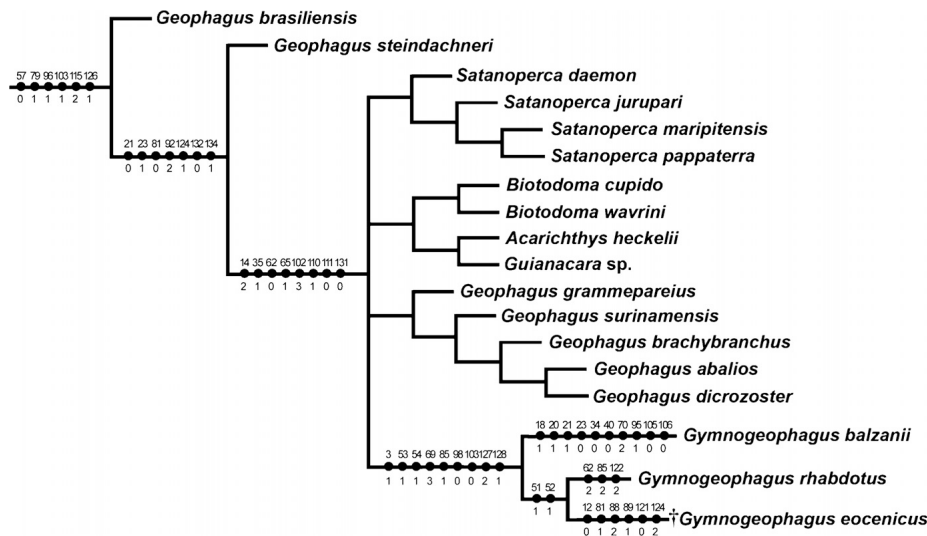


FIGURE 8. Hypothesis of relationships of †*Gymnogeophagus eocenicus*, n. sp., to other Geophaginae based on the matrix and list of morphological characters presented by López-Fernández et al. (2005b). The tree figures only the Clade containing *Gymnogeophagus*. The topology of the remaining tree is identical to that presented by López-Fernández et al. (2005b:fig. 1A). Only 48 of 136 characters were observable in the fossil, and coded as follows (character:state): 1:1; 2:0; 4:0; 5:2; 6:0; 8:0; 11:0; 12:0; 46:0; 47:0; 48:0; 50:1; 51:1; 52:1; 53:1; 54:1; 55:1; 57:1; 58:0; 60:0; 61:4; 62:0; 76:0; 77:0; 79:1; 80:1; 81:1; 85:1; 86:0; 87:0; 88:2; 89:1; 95:0; 115:2; 116:1; 117:1; 118:0; 119:1; 120:1; 121:0; 122:1; 123:0; 124:2; 125:1; 127:2; 128:1; 129:1; 130:0. Characters not listed were coded as missing (?).

clade share the very long soft dorsal fin in mature males and the presence of 15–16 caudal vertebrae (with the exception of *G. balzanii*, with 14 caudal vertebrae, $n = 3$): *G. gymnogenys* (16, $n = 1$), *G. lacustris* (15, $n = 1$), *G. labiatus* (15–16, $n = 2$), *G. sp. A* (15–16, $n = 3$), *G. sp. B* (15–16, $n = 3$), *G. sp. D* (15–16, $n = 3$), and *G. sp. E* (14–15, $n = 2$). Besides, all species of the *G. rhabdotus* clade possess only 13–14 caudal vertebrae (*G. che*, 14, $n = 1$; *G. meridionalis*, 13–14, $n = 3$; *G. rhabdotus*, 13–14, $n = 2$; and *G. setequedas*, 12–13, $n = 2$, and lack the very long soft dorsal fin. This supports †*G. eocenicus* as more related to the *G. gymnogenys* clade than to *G. rhabdotus* clade (Fig. 9A, B).

The *G. gymnogenys* clade contains all mouth breeder species of the genus, whereas *G. rhabdotus*, *G. meridionalis*, and *G. setequedas* are all substrate breeder species. So far, available evidences supports †*G. eocenicus* as a stem branch of the *G. gymnogenys* clade (Fig. 9C), but not allowing us to predict unambiguously the presence of a mouth breeder habit in that species.

Biogeographic Considerations

The new systematic studies, mainly based on molecular data (see above), produced alternative phylogenies that triggered off a discussion on cichlid biogeography. Dispersion and vicariance events have been used to support the biogeographic hypotheses proposed to explain the Gondwanan distribution pattern of cichlids. In the last years, cichlid fossil species have been registered for Eocene freshwater sediments in Argentina (Malabarba et al., 2006), Brazil (Malabarba and Malabarba, 2008), and Africa (Murray, 2001). †*Gymnogeophagus eocenicus*, as †*Proterocara argentina* Malabarba, Zuleta, and del Papa, 2006, comes from freshwater lacustrine sediments (Lumbrera Formation) that have been dated as lower to middle Eocene (del Papa, 2006). Recently, a new absolute age obtained from levels above the fish-bearing level support the Bartonian age (Bosio et al., 2009), suggesting a lower-middle Eocene age for the fossiliferous strata (~49 Ma). Although these species are not old enough to definitely corroborate the drift hypothesis (as a Cretaceous cichlid would be), they provide some evidence that can contribute to this discussion. All

these fossil species have modern aspect and are phylogenetically nested within the South American or African clades. Smith et al. (2008) have recovered †*P. argentina* in an apical position within Geophagini, supporting the hypothesis that cichlids are considerably older than previously suggested. The existence of a pre-Bartonian species presenting not only the synapomorphies, but the appearance of a modern genus (in the case of †*G. eocenicus*, also a dimorphic sexual character), would require an extensive differentiation from the basal cichlid lineages and a morphological conservatism since at least the Eocene (~50 Ma). This differentiation must have taken time, evidencing that the origin of the group long predates the minimum age provided by the fossils (as noted by Stiassny, 1991, and Sparks, 2004), which could be in the Cretaceous. As already pointed out by Sparks (2004), even considering the known rapid diversification, these records represent examples of morphologically conserved forms persisting since Eocene (~50 Ma). An additional example is given by the catfish †*Corydoras revelatus* Cockerell, 1925, registered for the upper Paleocene (~57 Ma) Maíz Gordo Formation (underlying the Lumbrera Formation) of the northern Argentina. Based on the presence of derived characters, Reis (1998) confirmed the assignment of the fossil to the modern genus *Corydoras*, which is in a derived position in the callichthyid phylogenetic framework. Fossils of the Callichthyidae are scarce and †*C. revelatus* is the earliest record of the family, already in a modern morphology, also indicating a substantial differentiation from the basal stock.

All the species currently assigned to the genus *Gymnogeophagus* have their distribution restricted to the southern part of South America, including the La Plata drainage (Paraná, Paraguay, and Uruguay rivers) and some coastal river systems in southern Brazil and Uruguay. The only exception is *G. balzanii*, also found in the Guaporé River, Amazon basin that possesses a natural headwater connection with the Jauru River, a tributary of the Paraguay River (Reis and Malabarba, 1988; Lowe-McConnell, 1975). According to geological data, events related to the uplift of the Central Andes, occurring during the Middle Eocene–early Oligocene, moved the boundary between Amazonas and Paraná

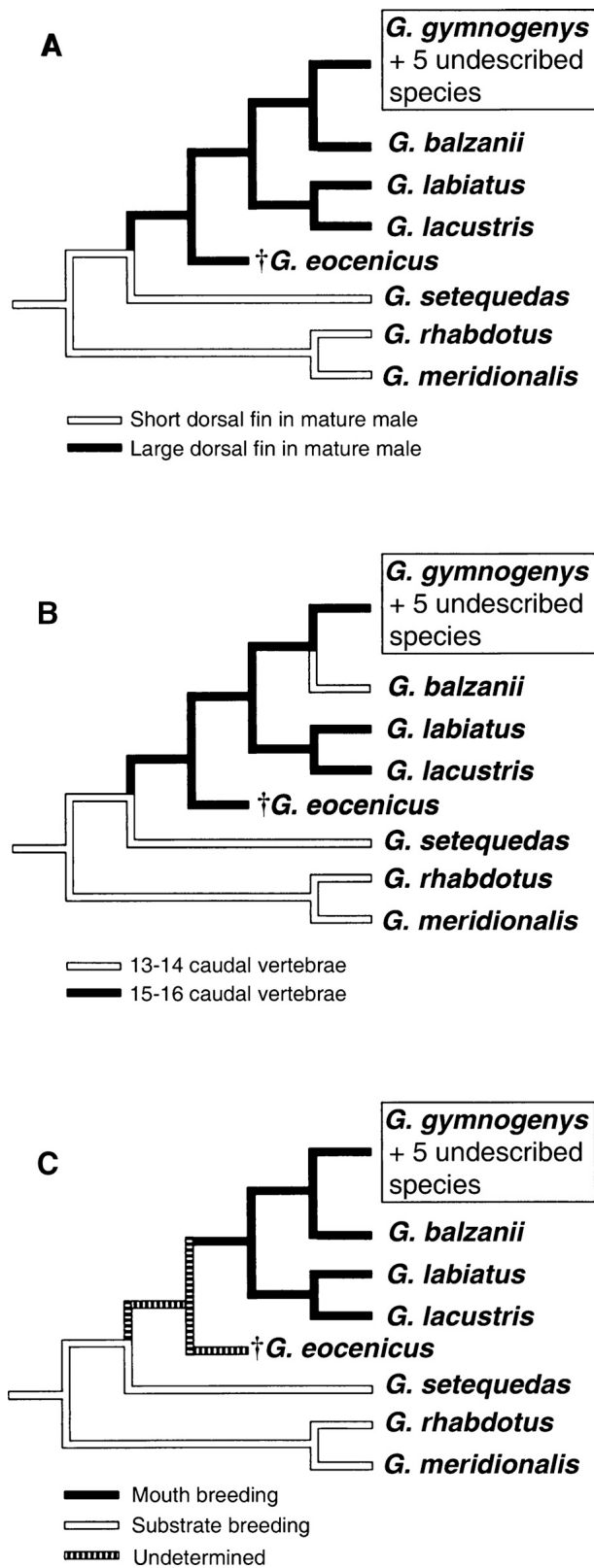


FIGURE 9. Cladograms mapping (A) dorsal fin elongation, (B) number of vertebrae, and (C) breeding strategy for *Gymnogeophagus* species in the phylogeny of Wimberger et al. (1998). The five undescribed species correspond to *Gymnogeophagus* sp. A, *G.* sp. B, *G.* sp. C, *G.* sp. D, and *G.* sp. E, referred by Wimberger et al. (1998) and discussed in the text.

northward, with the Paraná capturing the headwaters of the paleo-Amazonas-Orinoco system (Lundberg et al., 1998). Endemism of extant *Gymnogeophagus* species in the southern portion of the continent and the occurrence of this *Gymnogeophagus* fossil species in the sediments of a lake formed during the early to middle Eocene in northwestern Argentina, constituting along with †*P. argentina* the oldest cichlid records for South America, support the hypothesis that current patterns of distribution of Neotropical freshwater fish lineages have a very old history in the continent.

ACKNOWLEDGMENTS

We thank G. M. de Gonzo for useful comments on the distribution of *Gymnogeophagus* in Salta rivers. Also thanks are extended to O. Zuleta for field assistance and the collection of the material presented here. This work was partially funded by AN-PCyT PICT 2006-381, Conicet PIP 5255 (CdP), and CNPq (MCM and LRM) grants.

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Submitted January 15, 2009; accepted June 10, 2009.