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ABSTRACT
Teleostean evolution produced enormous variation in tooth morphology. This variation is related to the exploration and exploitation of very diverse dietary niches. Among extant fishes, several taxa of the order Tetraodontiformes (e.g. pufferfishes, porcupinefishes and ocean sunfishes) have evolved highly specialized beak-like tooth structures. Here we provide the first description of tetraodontiform crushing beaks from Argentina. A single complete premaxillary beak recovered from the early Miocene Gaiman Formation in Chubut Province is assigned to Molidae based on its premaxillaries being completely fused to one another along the midline, general morphology, and size. Moreover, due to
Key Words
Beaked-dentition, Paraná Formation, Gaiman Formation, Southern Hemisphere.

Introduction
Bony-fish dentition shows a remarkable variability in morphology (e.g., Berkovitz & Shells 2017). Also, the development of teeth occurs in several different ways (Huysseune & Sire 1992; Trapani 2001; Sire et al. 2002; Berkovitz & Shells 2017). Bony-fish dentition has a first generation of tooth germs originating directly from the oral epithelium (e.g., Sire et al. 2002). In some osteichthyans taxa, the origin of teeth has been related to the resorption cavities in the cartilage (Huysseune & Sire 1992). The origin of the replacement tooth generations varies and might be extraosseous – in the soft tissue outside the bone to which posteriorly attach – or intraosseous – in sockets within the bone (Trapani 2001; Berkovitz & Shells 2017).

Crushing dentitions appeared early in the fossil record of Osteichthyes (Moya-Smith & Campbell 1987; Smith 1988; Kriwet 2005; Poyato-Ariza 2005; Johanson & Smith 2005; Wu et al. 2013). Hiherto, one of the most specialized crushing type dentitions appears in living Tetraodontiformes – a group which includes the porcupinefishes (Diodontidae Bonaparte, 1838), pufferfishes (Tetraodontidae Bonaparte, 1832), ocean sunfishes (Molidae Ranzani, 1837), filefishes (Monacanthidae Nardo, 1842), boxfishes (Ostraciidae Rafinesque, 1810), tigerfishes (Balistidae Rafinesque, 1810), and several other taxa (Tyler 1980; Santini & Tyler 2003; Close et al. 2016; Bannikov et al. 2017). The beak-like dentition of several tetraodontids (i.e., porcupinefishes, pufferfishes, ocean, and sunfishes) is a complex of bony and dental tissues with teeth that form intraosseously (Trapani 2001). Replacement teeth in tetraodontids develop beneath the functional teeth and, when resorption occurs, they move into the newly opened area, thus completing their growth (Fraser et al. 2012).

Tetraodontiformes has a long-known fossil record dating back to the Late Cretaceous, and are best-known in the Eocene and Miocene (Tyler & Santini 2002; Santini & Tyler 2003; Aguilera et al. 2017 and references therein). Late Cretaceous Tetraodontiformes have no evident teeth in their jaws (Tyler & Sorbini 1996; Santini & Tyler 2003).
However, Tetraodontoidei or Gymnodontes (i.e., Triodontidae Bleeker, 1859, Tetraodontidae, Molidae, Diodontidae, and Avitoplectidae Bemis, Tyler, Bemis, Kumar, Rana & Smith, 2017) have beak-dentitions originating by the fusion of teeth and their jaw bones (Tyler 1980: Andreucci & Britski 1982). The fossil record of Tetraodontoidei goes back to the Eocene (Tyler 1980; Tyler & Bannikov 1992; Tyler & Santini 2002; Santini & Tyler 2003).

In South America, fossil Tetraodontoidei have been reported from the Miocene-Pliocene of Perú (Muizon & Devries 1985), and the Miocene of Argentina, Brazil, Colombia, and Venezuela (Woodward 1901; Cione et al. 2011; Aguilera et al. 2017). An isolated dental plate has been reported in the Late Cretaceous of Brazil (Gallo et al. 2009). However, the age of that finding remains doubtful (see discussion in Dornburg et al. 2014 and Bannikov et al. 2017).

Considering the Argentinian specimens, Woodward (1901: 576) assigned with doubts a “portion of typical jaw” to the genus Mola Koelreuter, 1776 (Orthogoriscus Bloch & Schneider, 1801). Woodward mentioned that the material comes from the Patagonian Formation which crops out in Chubut Province. The rocks exposed in that area are formally known as Gaiman and Chenque formations and are considered early Miocene in age (Bertels 1970, see also Parras & Cuitiño 2021). That and other material, reported later (Cione 1988; Cione & Azpelicueta 2002; Cione et al. 2011) was never formally described.

Here we provide a qualitative study of beaked-dentitions found in the early Miocene Gaiman Formation (Chubut Province, Patagonia Argentina) and the late Miocene of Paraná Formation (Entre Ríos Province, North Eastern Argentina). We compare these records with those of other parts of the globe.

MATERIAL AND METHODS

The material studied herein consists of one upper beak (MLP 86-II-22-1) recovered in the Gaiman Formation and several partially preserved upper beaks (CICYTTP-Pv-P-1-323, CICYTTP-Pv-P-1-426, CICYTTP-Pv-P-1-543, CICYTTP-Pv-P-1-569, CICYTTP-Pv-P-1-631, CICYTTP-Pv-P-1-724) recovered in several independent expeditions made by one of the authors (ALC) to the fossiliferous units of the Paraná Formation (Entre Ríos Province, North Eastern Argentina). We compare these records with those of other parts of the globe.

GEOLOGICAL SETTING

The Gaiman and Paraná formations were deposited during the Miocene as consequence of a marine transgression from the Atlantic that covered most of the eastern regions of South America, especially Argentina, Uruguay, Brazil, and Bolivia. As a consequence of this event, the so-called *Entreriense* or *Paranense* seas develops.

**PARANÁ FORMATION**

The Paraná Formation represents a widespread marine deposits of the Atlantic Ocean in South America, being part of the so called *Entreriense* or *Paranense* Sea. During the middle and late Miocene, this sea covered most of the Chaco-Paraná Basin and eastern Patagonia to the northern portion of the Sierras Subandinas and the northwestern Sierras Pampeanas in Argentina, reaching as far north and east as Bolivia, Paraguay, western Uruguay, and southern Brazil (Hernández et al. 2005; Vélez-Juarbe et al. 2012 and references therein). The age of the Paraná Formation has been largely debated on contrast image of the examined surface. Backscattered electrons (BE) detectors of two sectors BSED were employed in order to observe variations in the atomic number (Z) of the elements detected on surface. Heterogeneity of the sample is expressed in the image through different gray tonalities depending on the atomic number.

Descriptive terminology (Fig. 2) follows Tyler (1980), Weems (1985) and Aguilera et al. (2017). Also, an extensive review of the literature was made in order to compare the specimens. Material from extant species housed at Sección de Zoología Vertebrados, Museo de La Plata (MLP) and Cátedra de Ictiología, Facultad de Ciencias Naturales y Museo (FCNyM) was used for comparison. Meristics follows Weems (1985).

ESEM images were obtained using a JEOL 840A equipped with electron source from a tungsten filament with 200 V-30 kV accelerating voltage. The samples were analyzed under Low Vacuum mode (LoVac) with a precision of 0.1 to 1 Torr, without metalizing. Secondary electron detectors, were used looking for a high topographic
the basis mainly of different biostratigraphic interpretations regarding its included invertebrate fauna, ranging from middle (e.g. Acenolaza 2000; del Río 2000; Acenolaza & Acenolaza 2000) to late Miocene (e.g. Frenguelli 1920; Camacho 1967; Acenolaza 1976; Zabert 1978; Cione et al. 2000). However, recent studies supported by new paleontological evidence and radioisotope dating tend to assign at least the outcropping beds to the late Miocene (Pérez 2013; del Río et al. 2018).

**GAIMAN FORMATION**

The Gaiman Formation was deposited during the marine Patagoniense transgression. To date no isotopic data are available for Gaiman Formation and an early Miocene age is supported by correlations with other dated basins and formations, fossils, and palinomorphs (Palazzesi et al. 2006; Cione et al. 2011; Parras et al. 2012; Parras & Cuitiño 2021).

**SYSTEMATIC PALEONTOLOGY**

Class ACTINOPTERYGII Cope, 1887  
Infra-class TELEOSTEI Müller, 1844  
Order TETRAODONTIFORMES Regan, 1929  
Family MOLIDAE Ranzani, 1839  
Genus Ranzania Nardo, 1840  

* cf. Ranzania sp.

*Ranzania* sp. – Nardo 1840: 111.  
Molid indet. – Cione 1988: 447. — Cione & Azpelicueta 2002: 370.  
molid teleost – Cione et al. 2011: 429.

**FAMILIAL STRATIGRAPHIC RANGE.** — Upper Eocene to Recent (Tyler & Bannikov 1992).  

**MATERIAL REFERRED.** — MLP 86-II-22-1, a beak formed by fused premaxillaries.  

**GENERIC DIAGNOSIS.** — Modified from Weems (1985). Endoskeleton mainly cartilaginous. Body covered by dermal polygonal plates. Beak formed by the fusion of both premaxillaries in the upper jaw and both dentaries in the lower jaw. Upper beak posteriorly containing rows or patches of teeth fused against a thick mass of bone overlying roof of mouth.

**GEOLOGY AND STRATIGRAPHY.** — The material was recovered at the Gaiman Formation, lower Miocene, Chubut Province, Patagonia Argentina (Parras & Cuitiño 2021; Fig. 2).

**DESCRIPTION**

The preserved upper jaw is thick and wide (Fig. 3) and has two portions: a well-developed and sharp beaked portion and a bony palate. In lateral view the beak and the bony palate form an obtuse angle. The preserved total length of the upper jaw is *c.* 40 mm, the total wide is *c.* 50 mm, and the beak length is *c.* 12 mm. The external and lingual surfaces of the beaked portion have a shiny tissue that we interpret as enamel (Fig. 3D). The bony external surface of the upper jaw is striated (grooved or creased). Some sections of the upper jaw show its internal core which has a structure composed of “tubules” that might be vascular canals of osteodentine (Fig. 3). This tubular structure is also evidenced on the surface of the specimen studied herein due to post-mortem wear (Fig. 3A, C). In lingual view, the beak portion is slightly concave and has almost the same width along the biting margin (Fig. 3B). The bony palate is not very well preserved and is triangular. Caudal, some conical structures are recognized; we interpret those structures as poorly preserved teeth (Fig. 3B). Some of these teeth might have enamel. Thus, the caudal region has at least three irregular rows and is clearly differentiated from the biting portion (Fig. 3B).

**TAXONOMIC REMARKS**

Members of the family Molidae are known as ocean sunfishes. Molds have an extreme complex jaw formed by the fusion of bone and dental tissues (Tyler 1980). Premaxillaries and dentaries are indistinguishably fused in the midline (Tyler 1980). Recent molds are represented by three genera and five species *Mola mola* Linnaeus, 1758; *M. alexandrini* (Ranzani, 1839); *M. tecta* Nyegaard, Sawai, Gemmell, Gillum, Loneragan, Yamanoue & Stewart, 2017, *Masturus lanceolatus* (Liénard, 1840); and *Ranzania leavis* Pennant, 1776.

The fossil record of moids is patchy since their endoskeletons are largely cartilaginous and their pelagic habitat is not conducive to fossilization. Thus, the family is mainly represented by beaked dentitions and dermal scale plates (Tyler & Santini 2002). To date, fossil moids are represented by four genera: *Eomola* Tyler & Bannikov, 1992; *Austromola* Gregorova, Schultz, Harzhauser, Kroh & Coriç, 2009; *Ranzania* Nardo, 1840; and *Mola* Koelreuter, 1776.

The beak described herein was previously reported as an indeterminate Molidae (Cione 1988; Cione & Azpelicueta 2002; Cione et al. 2011) but it was not formally described. It is assigned to Molidae because of the presence of completely fused premaxillaries, general morphology, and size. Moreover, based on the putative presence of rows of teeth fused to the thick and massive bone structure, the specimen might belong to the genus *Ranzania*. However, more specimens are needed to provide a precise taxonomic assignment.

Molid fishes occur in tropical and temperate waters around the world, being solitary and pelagic. In South America, the southernmost record of extant moids corresponds to *Mola mola* Linnaeus, 1758 recovered in Solano Bay 40 km north of Comodoro Rivadavia city in Chubut Province (Aramburu 1957) and the southernmost extant record of *Ranzania laevis* Pennant, 1776 is New Zealand (Smith et al. 2010). Fossil specimens of the genus *Ranzania* have been recovered from the lower Miocene of North Carolina (Weems 1985), middle Miocene of Italy, (Carnevale 2005), Japan (Uyeno & Saka-moto 1994), and late Miocene (Messinian) of northwestern of Argelia (Carnevale & Santini 2007).

Family TETRAODONTIDAE Bonaparte, 1832  

**FAMILIAL STRATIGRAPHIC RANGE.** — Middle Eocene to Recent (Tyler & Santini 2002).
Miocene tetraodontiforms from Argentina

MATERIAL REFERRED. — CICYTTP-Pv-P-1-323, right almost complete premaxilla, CICYTTP-Pv-P-1-426, incomplete right premaxilla represented by the biting portion, CICYTTP-Pv-P-1-543, fragmentary biting portion; CICYTTP-Pv-P-1-631, fragmentary left premaxilla with biting portion; CICYTTP-Pv-P-1-724, two fragments of biting portion with rod-like dental units and a fragmentary left premaxilla biting portion.

GEOLOGY AND STRATIGRAPHY. — Uppermost levels of the Paraná Formation, upper Miocene (Tortonian-Messinian), Entre Ríos Province, Argentina (del Río et al. 2018; Fig. 2). Most of the specimens were collected at La Juanita locality (level 1) and CICYTTP-Pv-P-1-323 was recovered at Toma Vieja locality (level 3).

DESCRIPTION. — Massive crushing plates formed by the articulation of premaxillaries. In medial or symphyseal view, the articulation between both premaxillary is composed of four to six well-developed projections of each premaxillary bone (Figs 4; 5C). The projections at the middle section of the symphysis seem to be transversally longer than those of *Lagocephalus* Swainson, 1839 (see Tyler 1980: 269). In occlusal view, the premaxillary has an internal cavity containing the pulp cavity of the long, rod-like teeth. The teeth lie parallel to the anterior edge of the premaxillary bone. There are four to twelve replacement teeth (Fig. 4C) and only two (possibly
three) of them are visible at the premaxillary biting edge. On the ventral surface, three more or less blunt, elongated, and sigmoidal teeth lie in shallow sockets arranged in a longitudinal row just lateral to the medial edge (Figs 4B, D; 5E). The anterior tooth is at least half of the length of remaining teeth (Figs 4B, D; 5A, C, F); it is more or less triangular with a tall anterior vertex close to symphysis. The teeth are ornamented with faint lines.

In lingual view, the beak is formed by parallel dental units (Fig. 4B, D). These units are arranged in two groups: long (nine to ten) and short (three or four). The dental units are shorter near the symphysis and considerably longer caudad (Fig. 4B, D). CICYTTP-PV.P.1. 569 in labial view shows long dental units intercalated by small units (Fig. 4D). CICYTTP-PV.P.1. 426 in labial view shows the notches of articulation among premaxillae (Fig. 4E).

Since there are only three well-preserved beaks and the histology of beaks in Tetraodontidae is not fully understood, we preferred not performing histological sections. However, because some of the material from the Paraná Formation show different degrees of wear, we briefly describe it. Wear has its maximum development in the dental units near the symphysis, which decreases backward. In the beaks CICYTTP-PV-P-1-323 and CICYTTP-PV-P-1-426 the biting portions have the maximum degree of wear (Fig. 5A-D). However, replacement dental units in CICYTTP-PV-P-1-323 do not show wear but in CICYTTP-PV-P-1-426 the same units have well-developed wear. In CICYTTP-PV-P-1-569 the

Fig. 3. — MLP 86-II-22-1, cf. Ranzania Nardo, 1840 beak dentition: A, dorsal view; B, lingual view; C, left view; D, right view. Abbreviations: en, enamel; os.t, osteodentine tubules; t, teeth. Scale bars: 1 cm.
beak does not show wear and the dental units forming the cutting edge are antero-posteriorly compressed (Fig. 5E, F). Since CICYTTP-PV-P.1-569 is the smallest specimen, we hypothesize that it is a young adult and that wear is caused by biting hard organisms like coral or gastropods as in many extant tetraodontiforms.

**TAXONOMIC REMARKS**
Within the Tetraodontiformes, we assign the Paraná Formation specimens to the tetraodontoids or gymnodontids because they have crushing beaks composed of upper and lower jaw bones fused with teeth which characterizes this beak-toothed group. Within the Tetraodontoidei, the material belongs in...
FIG. 5.—Tetraodontidae indet. premaxillary dentitions under SEM: A, B, CICYTTP.PV.P.1.323 lingual view of a portion of the beak and bone of an adult specimen: A, dental units and bone; B, close up to show the wear in the anterior dental units; C, D, CICYTTP.PV.P.1.426: C, backscattered image showing a general view of the dental units; D, backscattered image showing a close up to show the wear over life in the anterior dental unit; E, F, CICYTTP.PV.P.1.569, young adult specimen: E, general view of the dental units, note the non-wearing enamel; F, close up of the anterior dental unit of E, note the sharp edge of the anterior dental unit. Scale bars: A, C, 1 mm; B, D, F, 200 μm; E, 500 μm.
the family Tetraodontidae *sensu* Tyler (1980) based on the presence of long, slender, rod-like, and parallel dental units (Fig. 4); premaxillae not fused in the midline but articulated by interlocking emarginations; few small and one large trituration dental units present (CICYTTP-Pv-P-1-323; Fig. 4). According with Tyler (1980) the subfamily Tetraodontinae is the only one with trituration dental units.

We compare the Miocene material from Argentina with those of the family Tetraodontidae in which premaxillae were described in detail (see Tyler 1980) and also with recent material from the ichthyological collection of the La Plata Museum. Since the Argentinian material has crushing dental units which are characteristic of Tetraodontinae it is possible that the specimens belong to this family. However, a more detailed study is needed.

The Argentinian material differs from *Lagocephalus* in having more replacement dental units (12) vs five to ten and interlocking emarginations between premaxillae four to five vs twelve. It presents also three trituration dental units vs two to six; however, we cannot be certain of this feature since we only have one specimen with trituration dental units (i.e., CICYTTP-Pv-P-1-323; Fig. 4A, B). The Argentinian specimens differ from *Canthigaster* Swainson, 1839 by having trituration dental units. Also, *Canthigaster* has more replacement teeth (15 to 20) and more interlocking emarginations (15 to 20). Argentinian specimens differs form those reported from the Miocene of Angola (Antunes 1978; Antunes *et al.* 1981) because African specimens have more parallel long dental units (c. 20).

**DISCUSSION**

Tetraodontiformes is a primarily marine actinopterygian group that shows a widespread distribution with a remarkable body plan variety, including the porcupinefishes (*Diodonidae*), pufferfishes (*Diodonidae*), ocean sunfishes (*Molidae*), boxfishes (*Ostraciidae*), and tigerfishes (*Balistidae*). The Tetraodontiformes fossil record dates back to the Late Cretaceous (Tyler & Sorbini 1996; Tyler & Santini 2002; Arcila *et al.* 2015; Close *et al.* 2016; Arcila & Tyler 2017; Bannikov *et al.* 2017). All Tetraodontiformes have a specialized diet and most of them feed on molluscs (i.e., bivalves and gastropods). However, molid fishes are highly specialized to feed on jellyfishes, although they also can feed on squids and small actinopterygians (Berkovitz & Shellis 2017).

Cenozoic marine outcrops are exposed at the southwestern Atlantic coasts of southeastern Brazil to southern Argentina (del Río *et al.* 2018). The *Patagoniense* Sea (late Oligocene to early Miocene), which was located at the eastern of Patagonia in southern South America, represents the oldest major flooding event by the Atlantic Ocean. The outcrops include four formations known as Monte León, Carmen Silva, Chenque, and Gaiman (Cuitiño *et al.* 2017). The youngest Atlantic Ocean flooding is known as the *Paranense* or Entrerriense Sea, which occurred mainly during the late Miocene and comprises units in Uruguay (i.e., Camacho Formation) and Argentina (i.e., Paraná Formation) in Entre Ríos Province, “Entrerriense Beds” in Buenos Aires Province, Balneario La Lobería facies of the Río Negro Formation in Río Negro Province and Puerto Madryn Formation in Chubut Province (see del Río *et al.* 2018 and the references therein).

The *Paranense* units are known by an extremely diverse molluscan fauna (del Río 1991; del Río *et al.* 2018) and other hard invertebrates (i.e., foraminifers, bryozoans, brachiopods, arthropods, and echinoderms) (Pérez *et al.* 2013). At Gaiman and Paraná formations, the ichthyoфаuna is characterized by the presence of several chondrichthyans and also a few teleosteans (Cione *in Scasso & Castro* 1999; Cione & Azpelicueta 2002; Cione *et al.* 2011, 2013). This proportion is certainly due to taphonomic reasons (Cione *et al.* 2013).

The specimens described herein represent the first formal description of fossil Tetraodontiformes from Argentina. The new descriptions presented herein are relevant in terms of the distribution of Tetraodontiformes during the Miocene in the Southern Hemisphere, being the southernmost record of fossil Tetraodontiformes worldwide. The specimens recovered at Paraná Formation are assigned to Tetraodontidae; other Southern Hemisphere records are isolated and fragmentary dentitions from the Miocene of Angola (Antunes 1978; Antunes *et al.* 1981). Considering the available source of food – mainly molluscan and gastropods – but also annelids, echinoderms, and brachiopods (Pérez *et al.* 2013), we consider that tetraodontid actinopterygians lived and fed in the shallow temperate warm waters near the coastline of the present Entre Ríos Province (e.g. Cione *et al.* 2013). This is also in agreement with previous hypotheses about global and local temperatures during the Miocene (see Zachos *et al.* 2001; Cione *et al.* 2013).

The molid records of the Gaiman Formation (Chubut Province) could be random findings. Recent molid records in Patagonia are extremely rare and those actinopterygians are captured accidentally in trawler fishing (e.g. di Giacomo *et al.* 2015). However, since mollids are usually pelagic solitary (e.g. Pope *et al.* 2010), the latitudinal temperature gradients of the Atlantic Ocean were not as strong as today, and the waters were warmer (Zachos *et al.* 2001; Bellwood & Wainwright 2002; Bellwood *et al.* 2012), the fish could have inhabited the area during the Miocene.

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REFERENCES

ACÉNOLAZA F. G. 1976. — Consideraciones bioestratigráficas sobre el Terciario marino de Paraná y alrededores. Acta Geológica Lilloana 13: 91-107.

ACÉNOLAZA F. G. 2000. — La Formación Paraná (Mioceno medio): estratigrafía, distribución regional y unidades equivalentes, in ACÉNOLAZA F. G. & HERBST R. (eds), El Neógeno de Argentina. Instituto Superior de Correlación Geológica, Serie de Correlación Geológica 14: 9-27.

ACÉNOLAZA F. G. & ACÉNOLAZA G. 2000. — Trazas fósiles del Terciario marino de Entre Ríos (Formación Paraná, Mioceno medio), República Argentina. Boletín de la Academia Nacional de Ciencias 64: 209-233.

AGUILERA O., SILVA G. O. A., LOPES R. T., MACHADO A. S., DOS SANTOS T. M., MARQUES G., BERTUCCI T., AGUIAR T., CARRILLO-BRICESCO J., RODRÍGUEZ F. & JARAMILLO C. 2017. — Neogene Proto-Caribbean porcupinefishes (Diodontidae). PLoS ONE 12: e0181670. https://doi.org/10.1371/journal.pone.0181670

ANDREUCCI R. D. & BRITSKI H. A. 1982. — Structure and evolution of Tetraodontoid Teeth: An autoradiographic study (Pisces, Tetraodontiformes). Journal of Morphology 292: 283-292. https://doi.org/10.1002/jmor.1051710304

ANTUNES M. T. 1978. — Faunes ichtyologiques du Néogène supérieur d’Angola, leur âge, remarques sur le Pliocène marin en Afrique Australe. Ciências da Terra 4: 59-90.

ANTUNES M. T., JONET S. & NASCIMENTO A. 1981. — Vertébrés (crocdiliens, poissons) du Miocène marin d’Algarve occidentale. Ciências da Terra 6: 9-38.

ARAMBURU A. S. 1957. — Una nueva cita de Mola mola (Linné) para el Atlántico Sur (Piscis: Plactognathi). Notas del Museo de La Plata 19: 92-99.

ARCILA D. & TYLER J. C. 2017. — Mass extinction in tetraodontiform fishes linked to the Paleocene-Eocene thermal maximum. Proceedings of the Royal Society B - Biological Sciences 284: 1-8. https://doi.org/10.1098/rspb.2017.1777

ARCILA D., PYRON A., TYLER J. C., ORTÍ I. & BETANCUR R. C. 2015. — An evaluation of fossil tip-dating versus node-age calibrations in tetraodontiform fishes (Teleostei: Perciformes). Molecular Phylogenetics and Evolution 82: 131-145. https://doi.org/10.1016/j.ympev.2014.10.011

BANNIKOV A. F., TYLER J. C., ARCILA D. & CARNEVALE G. 2017. — A new family of gymnotid fish (Tetraodontiformes) from the earliest Eocene of the Peri-Tethys (Kabardino-Balkaria, northern Caucasus, Russia). Journal of Systematic Palaeontology 15: 129-146. https://doi.org/10.1080/14772019.2016.1149115

BELLWOOD D., WAINWRIGHT P. C. 2002. — The history and biogeography of fishes on coral reefs, in Sale P. (ed.), Coral Reef Fisheries. Academic Press, Ontario, Canada: 5-32.

BELLWOOD D. R., RENEMA W. & ROSEN B. R. 2012. — Biodiversity hotspots, evolution and coral reef biogeography: a review, in GROWER D. J., JOHNSON K., RICHARDSON J., ROSEN B., RUBER L. & WILLIAMS S. (eds), Biotic evolution and environmental change in Southeast Asia. Cambridge University Press, Cambridge: 216-245.

BERKOVITZ B. & SHELLIS P. 2017. — The Teeth of Non-Mammalian Vertebrates. 1st edition. Elsevier Academic Press, Amsterdam, 343 p.

BERTELS A. 1970. — Sobre el “Piso Patagónico” y la representación de la época del Oligoceno en Patagonia austral, República Argentina. Revista de la Asociación Geológica Argentina 25: 495-501.

CAMACHO H. 1967. — Las transgresiones del Cretácico Superior y del Terciario de la Argentina. Revista de la Asociación Geológica Argentina 12: 253-280.

CARNEVALE G. 2005. — Fossil fishes from the Serravallian (Middle Miocene) of Torricella Péligna, Italy. Palaeontographia Italica 91: 1-67.

CARNEVALE G. & SANTINI F. 2007. — Record of the slender mola, genus Ranzania (Teleosteoi, Tetraodontiformes), in the Miocene of the Chelif Basin, Algeria. Comptes Rendus Palevol 6: 321-326. https://doi.org/10.1016/j.crpb.2007.04.001

CIONE A. L. 1988. — Los peces de las formaciones marinas del Cenozoico de Patagonia. PhD thesis, unpublished, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata: 580.

CIONE A. L. & AZPELICUETA M. M. 2002. — An Oligo-Miocene beak (Osteichthyes: Perciformes) from the Early Miocene of Patagonia. Expiration of several vertebrates from the southern Atlantic Ocean. Geobios 35: 367-373. https://doi.org/10.1016/S0016-6995(02)00032-3

CIONE A. L., AZPELICUETA M. M., BOND M., CARLINI A. A., CASCIO TTA J. R., COZZUOL M. A., DE LA FUENTE M., GASPARINI Z., TONNI E. P., VERZI D. & VICETICH M. G. 2000. — Miocene vertebrates from Entre Ríos Province, eastern Argentina, in ACÉNOLAZA F. G. & HERBST R. (eds), El Neógeno de Argentina. Instituto Superior de Correlación Geológica, Serie de Correlación Geológica 14: 191-237.

CIONE A. L., COZZUOL M., DOZO M. T. & ACOSTA HOSPITALECHE C. 2011. — Marine vertebrate assemblages in the southwest Atlantic during the Miocene. Biological Journal of the Linnean Society 103: 423-440. https://doi.org/10.1111/j.1095-8312.2011.01685.x

CIONE A. L., CABRERA D. A., AZPELICUETA M. M., CASCIO TTA J. R. & BARLA M. J. 2013. — Peces del Mioceno marino y continental en Entre Ríos, oriente central de Argentina, in BRANDONI D. & NORIEGA J. I. (eds), El Neógeno de la Mesopotamia argentina. Asociación Paleontológica Argentina, Publicación Especial, Ciudad autónoma de Buenos Aires, 14: 71-83.

CLOSE A. R., JOHNSON Z., TYLER J. C., HARRINGTON R. C. & FRIEDMAN M. 2016. — Mosaicism in a new Eocene pufferfish highlights rapid morphological innovation near the origin of crown tetraodontiforms. Palaeontology 59: 499-514. https://doi.org/10.1111/pal.12245

CUITINO J. L., DOZO M. T., DEL RÍ O C., BUENO M. R., PALAZZI L., FUENTES S. & SCASSO R. 2017. — Miocene Marine Transgressions: Paleoenvironments and Paleobiodiversity, in BOUZA P. & BILMES (eds), Late Cenozoic of Peninsula Valdés, Patagonia, Argentina. An interdisciplinary approach. Springer: 47-84. https://doi.org/10.1007/978-3-319-48508-9

DEL RÍ O C. 1991. — Revisión sistemática de los bivalvos de la Formación Paraná (Provincia de Entre Ríos, Mioceno medio) de la Argentina. Academia Nacional de Ciencias Exactas, Físicas y Naturales 7: 11-93.

DEL RÍ O C. J. 2000. — Malacoofauna de las Formaciones Paraná y Puerto Madryn (Mioceno marino, Argentina): su origen, composición y significado bioestratigráfico, in ACÉNOLAZA F. G. & HERBST R. (eds), El Neógeno de Argentina. Instituto Superior de Correlación Geológica, Serie Correlación Geológica 14: 77-101.

DEL RÍ O C., MARTÍNEZ S., MACTHUR M., THIRWALL M. & PÉREZ L. M. 2018. — Dating late Miocene marine incursions across Argentina and Uruguay with Sr-isotope stratigraphy. Journal of South American Earth Sciences 85: 312-324. https://doi.org/10.1016/j.jsames.2018.05.016

DI GIACOMO E. E., ELIAS I., ALEGRE B., GOSTONYI A. E. & PERIER M. R. 2015. — Peces marinos patagónicos, in ZAIXSO, J. I. (eds), El Neógeno de la Mesopotamia argentina. Academia Nacional de Ciencias Exactas, Físicas y Naturales 12: 253-280.

GOUIRIC-CAVALLI S. 2017. — Mammalian vertebrates from the Miocene of southern Patagonia, Argentina: a new dental record of the long-footed bat Hypsignathus monstrosus (Chiroptera, Rhinolophidae). Journal of Systematic Palaeontology 15: 147-159. https://doi.org/10.1080/14772019.2016.1149115
possible occurrence of Diodontidae (Teleostei, Tetraodontiformes) in the Upper Cretaceous of the Parába Basin, northeastern Brazil. Cretaceous Research 30: 599-604. https://doi.org/10.1016/j.cretres.2008.12.001

Hernández R. M., Jordan T. E., Daleen Farjat A., Echavarria L., Ideaman B. D. & Reynolds J. H. 2005. – Age, distribution, tectonics, and eustatic controls of the Paranane and Caribbean marine transgressions in southern Bolivia and Argentina. Journal of South American Earth Sciences 19: 495-512. https://doi.org/10.1016/j.jseaes.2004.06.007

Huysseune A. & Sire J.-Y. 1992. – Bone and cartilage re-sorption in relation to tooth development in the anterior part of the mappable in chichlid fish: a LighT a TEM study. The Anatomical Record 234: 1-14. https://doi.org/10.1002/ar.1092340102

Johnson Z. & Smith M. M. 2005. – Origin and evolution of gnathostome dentitions: a question of teeth, denticles and tooth plates for the fishes of the Order Plectognathi (Teleostei, Tetraodontiformes). Copeia 2005: 35-51. https://doi.org/10.1643/0045-8511(2005)008<0035:OEOBDT>2.0.CO;2

Kemp A. 1997. – Four Species of Metaceratodus (Osteichthyes: Dipnoi, Family Ceratodontidae) from Australian Mesozoic and Cenozoic Deposits. Journal of Vertebrate Paleontology 17: 26-33. https://doi.org/10.1080/02724634.1997.10010949

Kriwet J. 2005. – A comprehensive study of the skull and dentition of pygmy sunfishes. Zitteliana An International Journal of Palaeontology and Geobiology Series A/Reihe A Mitteilungen der Bayerischen Staatsammlung für Paläontologie und Geologie 45: 135-188.

Moya-Smith M. & Campbell K. S. W. 1987. – Comparative morphology, histology, and growth of the dental plates of the Devonian dipnoan Chirodipterus. Philosophical Transactions of the Royal Society B 317: 329-363. https://doi.org/10.1098/rspb.1987.0060

Muizon B., C. D. E. & Devries T. J. 1985. – Geology and palaeontology of late Cenozoic marine deposits in the Sacaco area (Peru). Geologische Rundschau 74: 547-563. https://doi.org/10.1007/BF01821211

Nardo G. 1840. – Considerazioni sulla famiglia dei pesci Mola, e sui caratteri che li distinguono. Annali delle Scienze del Regno Lombardo-Veneto, Padova 10: 105-112.

Palazzesi L., Barreda V. D. & Scasso R. A. 2006. – Early Miocene spore and pollen record of the Gaiman Formation (Eastern Patagonia, Argentina): correlations and palaeoenvironmental implications. 4th Latin American Congress on Sedimentology and 11th Argentinean Meeting of Sedimentology, Bariloche 2006: 161.

Parras A. & Cuttino J. I. 2021. – Revised chrono and lithostratigraphy for the Oligneocene-Miocene Patagonian marine deposits in Patagonia: Implications for stratigraphic cycles, paleogeography, and major drivers. Journal of South American Earth Sciences 110: 103327. https://doi.org/10.1016/j.jseaes.2021.103327

Parras A., DiG R. & Griffin M. 2012. – Sr-isotope chronosestratigraphy of Paleogene/Neogene marine deposits: Austral Basin, southern Patagonia (Argentina). Journal of South American Earth Sciences 37: 122-135.

Pérez L. M. 2013. – Nuevo aporte al conocimiento de la edad de la formación Paranal, Mioceno de la Provincia de Entre Ríos, Argentina, to Brandoni, D. & Nobrega, J. I. (eds), El Neógeno de la Mesopotamia argentina. Asociación Paleontológica Argentina, vol. 14. Publicación Especial, Ciudad autónoma de Buenos Aires: 56-70.

Pérez L. M., Griffin M. & Mancenido M. 2013. – Los macro-invertebrados de la Formación Paraná: Historia y diversidad de la fauna bentónica del mioceno marino de Entre Ríos, Argentina, to Brandoni D. & Nobrega, J. I. (eds), El Neógeno de la Mesopotamia Argentina. Asociación Paleontológica Argentina, Ciudad autónoma de Buenos Aires: 56-70.

Pope E., Hays G. C., Thys T. M., Doyle T. K., Sims D. W., Queiroz N., Hobson V. J., Kurecek L. & Houghton J. D. R. 2010. – The biology and ecology of the ocean sunfish Mola mola: a review of current knowledge and future research perspectives. Reviews in Fish Biology and Fisheries 20: 471-487. https://doi.org/10.1007/s11160-009-9155-9

Poyato-Ariza F. J. 2005. – Pycnodont fishes: morphologic variation, ecomorphologic plasticity, and a new interpretation of their evolutionary history. Bulletin of the Kitakyushu Museum of Natural History and Human History Series A Natural History, Series A: 169-184. https://www.jsstage.jst.go.jp/article/kkmh/3/0/3_169/_pdf

Ranzani C. 1839. – Dispositio familiaris Molarum in generet in species. Novi Commentarii Academiae Scientiarum Institutii Bononiensis 3: 63-82, Pl. 6 + foldout table. https://doi.org/10.5962/bhl.title.61542

Ryan W. B. F., Carbotti S. M., Coplan J. O., O'Hara S., Melkonian A., Arko R., Weisell R. A., Ferrini V., Goodwillie A., Nitsche F., Bonscekowski J. & Zemsky R. 2009. – Global Multi-Resolution Topography synthesis. Geochimica et Geophysical Geosystems 10: Q03014. https://doi.org/10.1029/2008GC002332.

Santini F. & Tyler J. C. 2003. – A phylogeny of the families of fossil and extant tetraodontiform fishes (Actinopterygii, Tetraodontiformes), Upper Cretaceous to Recent. Zoological Journal of the Linnean Society 139: 565-617. https://doi.org/10.1111/j.1096-3642.2003.00088.x

Scasso R. A. & Castro L. N. 1999. – Cenozoic phosphatic deposits in North Patagonia, Argentina: Phosphogenesis, sequence-stratigraphy and paleoceanography. Journal of South American Earth Sciences 12: 471-487. https://doi.org/10.1016/S0959-9811(99)00035-8

Sire J.-Y., Dayt-Beal T., Delgado S., Van Der Heyden C. & Huysseune A. 2002. – First-generation teeth in nonmammalian lineages: Evidence for a conserved ancestral character? Microscopy Research & Technique 59: 408-434. https://doi.org/10.1002/jemt.10220

Smith M. M. 1988. – The dentition of Palaeoniscidae (bands; a consideration of the significance of teeth, denticles and tooth plates for dipnoan phylogeny. Mémoires du Muséum national d’Histoire naturelle de Paris C 53: 177-193.

Smith K. A., Hammond M., Close P. G. 2010. – Aggregation and stranding of elongate sunfish (Ranzania laevis) (Pisces: Molidae) on the southern coas of Western Australia. Journal of the Royal Society of Western Australia 93: 181-188. https://www.biodiversitylibrary.org/page/58034604

Trapani J. 2001. – Position of Developing Replacement Teeth in Teleosts. Copeia 2001: 35-51. https://doi.org/dgs9d

Tyler J. C. 1980. – Osteology, phylogeny, and higher classification of the fishes of the Order Plectognathi (Tetraodontiformes). National Oceanic and Atmospheric Administration, Seattle: 422. https://doi.org/10.5962/bhl.title.63022

Tyler J. C. & Bannikov A. F. 1992. – New genus of primitive ocean sunfish with separate premaxillae from the Eocene of Southwest Russia (Molidae, Tetraodontiformes). Copeia 4: 1014-1023. https://doi.org/10.2307/11466631

Tyler J. C. & Santini F. 2002. – Review and reconstructions of the tetraodontiform fishes from the Eocene of Monte Bolca, Italy, with comments on related Tertiary taxa. Studi e Ricerche sui Giacimenti Ternari di Bolca, Museo Civico di Storia Naturale di Verona 9: 47-119.
TYLER J. C. & SORBINI L. 1996. — New superfamily and three new families of Tetraodontiform fishes from the Upper Cretaceous: The earliest and most morphologically primitive Plectognaths. Smithsonian Contributions to Paleobiology 82: 1-59. https://doi.org/10.5479/si.00810266.82.1

UYENO T. & SAKAMOTO K. 1994. — Ranzania ogaii, a New Miocene Slender Mola from Saitama, Japan (Pisces: Tetraodontiformes). Bulletin of the National Science Museum 20: 109-117.

VELEZ-JUARBE J., NORIEGA J. & FERRERO B. 2012. — Fossil Dugongidae (Mammalia, Sirenian) from the Parana Formation (Late Miocene) of Entre Rios Province, Argentina. Ameghiniana 49: 585-593. https://doi.org/10.5710/AMGH.27.6.2012.568

WEEBS R. E. 1985. — Miocene and Pliocene Molidae (Ranzania, Mola) from Maryland, Virginia, and North Carolina (Pisces: Tetraodontiformes). Proceedings of the Biological Society of Washington 98: 422-438. https://www.biodiversitylibrary.org/page/34648701

WOODWARD A. S. 1901. — Catalogue of the fossil fishes in the British Museum (Natural History) Volume IV: Actinopterygian teleostomi of the suborders Isospondyli (in part), Ostariophysi, Apodes, Percomorpha, Hemibranchii, Acanthopterygii, and Anactinini. Longman & Co. and the British Museum (Natural History), London: 636 p., 19 pls.

WU F., CHANG M., SUN Y. & XU G. 2013. — A new saurichthyiform (Actinopterygii) with a crushing feeding mechanism from the Middle Triassic of Guizhou (China). PLoS ONE 8: e81010. https://doi.org/10.1371/journal.pone.0081010

ZABERT L. L. 1978. — Micropaleontología de la Formación Paraná (Mioceno superior) en el subsuelo de la provincia de SantaFé, República Argentina. Facena 2: 101-165.

ZACHOS J. C., PAGANI M., SLOAN L., THOMAS E. & BILLUPS K. 2001. — Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686-693. https://doi.org/10.1126/science.1059412

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