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New pycnodontiform fishes (Actinopterygii, Neopterygii) from the Early Cretaceous of the Argentinian Patagonia

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Abstract

Here we describe new pycnodontiform fish material recovered from the marine Agrio Formation (lower Valanginian–lower Hauterivian) of the Neuquén Province in the south-western of Patagonia, Argentina. The new material include an incomplete skull and an incomplete prearticular dentition. The incomplete skull consists of some dermal and endochondral elements as well as dental remains and represents a new large-sized gyrodonid that is referred to a new species, *Gyrodus huiliches*. *Gyrodus huiliches* sp. nov. is characterized by a unique combination of tooth crown ornamentations and tooth shape separating it easily from all known *Gyrodus* species. The incomplete prearticular dentition shows a tooth arrangement and sculpture that resembles that of “*Macromesodon*” *agrioensis*—the previously only known pycnodontiform in the area. This allows revising this species, which was based on an isolated vomerine dentition and which we refer to a new genus, *Tranawuen*. The new Patagonian fishes reported here expand the knowledge of South American pycnodontiforms. We hypothesize that meanwhile the new Patagonian genus—*Tranawuen*—diverged from *Gyrodus* after it migrated into the eastern Pacific through the Hispanic Corridor during the Late Jurassic, the new species—*Gyrodus huiliches*—most likely diverged from a Central or South American species of *Gyrodus*. Both represent the youngest gyrodonid records and simultaneously the southernmost Early Cretaceous occurrences of pycnodontiform fishes.

Keywords

Gyrodus huiliches nov. sp.; *Tranawuen* nov. gen.; Agrio formation; Argentina; Palaeogeography; Evolution

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1 Introduction

The order Pycnodontiformes is a morphologically and ecologically very distinctive actinopterygian clade (Marramá et al., 2016), which has been recognized as a taxonomic entity since the descriptions of Agassiz (1843–44). They first appeared in the Late Triassic and became extinct in the Eocene (Kriwet, 2005; Cawley and Kriwet, 2018).

Pycnodontiforms inhabited mostly coastal and also pelagic marine waters as well as brackish, freshwater-influenced and freshwater environments (Nursall, 1996a; Poyato-Ariza et al., 1998; Poyato-Ariza, 2005; Martín-Abad and Poyato-Ariza, 2013). Although most taxa only are known by their isolated dentitions or even teeth (e.g., Poyato-Ariza and Wenz, 2002; Kriwet, 2008; Stumpf et al., 2017), complete and well-preserved specimens occur in Mesozoic and Early Cenozoic *Konservat-Lagerstätten* deposits of the Tethys area (Lambers, 1991; Forey et al., 2003; Kriwet, 2005; Kriwet and Schmitz, 2005; Poyato-Ariza and Wenz, 2005; Ebert, 2013, 2018; Vullo et al., 2017). Moreover, some taxa previously assumed to be invalid such as the large pycnodontiform *Cosmodus*, which is based on isolated dentitions recently was redescribed and recognized as a valid distinct genus (Vullo et al., 2018).

The value of dental characters for phylogenetic purposes has been discussed controversially in the last decades (Poyato-Ariza, 2003; Kriwet, 2005), the common conclusion of those studies is that “dentitional characters and their variation are still inadequately understood, and it is, of course, possible to identified species and genera based on isolated dentitions” (Kriwet, 2005: 160). Subsequently, Poyato-Ariza and Bermúdez-Rochas (2009), for instance, established a new Early Cretaceous pycnodontiform genus based on isolated dental remains. The phylogenetic importance of dental characters, however, remains ambiguous.

The dentition of pycnodontiform fishes is composed of molariform teeth on the paired prearticular and unpaired vomer bones, while incisiform or grasping teeth with variable morphologies are located on the premaxilla and dentosplenial (Cawley and Kriwet, 2018). Most pycnodontiforms having crushing dentitions were characterized as being predominantly durophagous (Nursall, 1996a,b; Kriwet, 2001a,b). However, herbivorous, grazing and cutting-type forms were also reported (Kriwet, 2001a,b; Vullo et al., 2017).

Early pycnodontiform fishes from the Late Triassic to Early Jurassic are exclusively known from Europe, but latest in the Late Jurassic they attained a global distribution. Southern South American pycnodontiforms have been described so far from marine sediments of Late Jurassic (Oxfordian) age of Chile (Martill et al., 1998; Kriwet, 2000) and from Early and Late Cretaceous strata of Argentina (Benedetto and Sánchez, 1971, 1972; Bocchino, 1977; Cione and Pereira, 1990; Arratia and Cione, 1996; Cónsole Gonella et al., 2012). In this study, we report new pycnodontiform material, which was recovered from Lower Cretaceous fossil-bearing levels of the Pilmatué Member (lower Valanginian – lower Hauterivian) of the Agrio Formation in the Neuquén Province, Patagonia (southwestern) Argentina. Based on this new material, a new species of *Gyrodus* is erected representing a large and the most complete pycnodontiform recovered in the Early Cretaceous of southern South America up to now. Also, this new taxon is the first record of the genus *Gyrodus* from Argentina. Additionally, a single new prearticular with partially preserved dentition allows revising the

only Early Cretaceous pycnodontiform fish from Argentina known to date, *Macromesodon agrioensis* Bocchino, 1977 and referring it to a new genus.

2 Material and methods

The material comprises an incomplete skull with remains of the right lower jaw and an additional incomplete right lower jaw assigned to two different pycnodontiform fishes.

2.1 Preparation techniques, preservation, and study methodology

Both pycnodontiforms (MOZ-Pv 1316 and MOZ-Pv 1327) described herein were mechanically prepared using pneumatic tools by the technician, L. Acosta Burllaile at the División Paleontología Vertebrados of the Museo de La Plata except for the holotype of *Macromesodon agrioensis* (MLP 75-V-18-1), which did not require additional preparations. The specimens are preserved three dimensionally and were studied under a binocular microscope (Zeiss Stemi 2000-C) with different magnifications. Digital photographs were obtained using a digital compact camera Canon PowerShot G10 attached to a microscope and a Canon Rebel T2i with a compact macro lens Canon EF 50 mm f/2.5. Additionally, we used UV light (short and long wave) to highlight some morphological characters.

2.2 Measurements

Measurements were obtained with a Digital Caliper and using Fiji on high-resolution photograph as Fig. 1 indicates.

2.3 Morphologically terminology

The morphological terminology follows Nursall (1996a, 1999) and Poyato-Ariza and Wenz (2002). Consequently, we use the term ‘coronoid process’ here, although this structure cannot be considered homologous to the coronoid process in non-pycnodontiform neopterygians, where it is formed by the dentary, the surangular, and/or the angular. The systematic arrangement is adapted from Poyato-Ariza and Wenz (2002). In this study, the nomenclature used for describing dermal skull bones follows homology criteria (see Westoll, 1943; Schultze, 1993, 2008). However, to avoid confusion in the specimen descriptions and figure captions, the traditional terminology –which is not based on homology criteria– is given in square brackets. Additionally, we use ‘lateral’ for labial tooth rows and ‘medial’ for the lingual tooth row.

2.4 Anatomical abbreviations

Anatomical abbreviations are giving in figure captions.

2.5 Institutional abbreviations

MLP, Museo de La Plata, Buenos Aires, Argentina; MOZ, Museo Prof. Dr. Juan Olsacher, Zapala, Neuquén, Argentina.

2.6 Geological methods

Fieldwork included systematic sampling of the sections with the purpose of making textural and mineralogical distinctions between the lithological types recognized in the field (by MR). To characterize and define sedimentary textures and lithological types, standard thin sections (30 μm) were studied. Samples rich in organic matter were polished at 25 μm . Also, some samples were studied by X-ray diffraction. For this study, the rocks were grounded in a mortar and subsequently, analyses were carried out with a diffractometer PANalytical X'Pert PRO (Centro de Investigaciones Geológicas, La Plata, Argentina) using Cu radiation ($K\alpha = 1.5405 \text{ \AA}$) and Ni filter configured at 40 kV and 40 mA. The proportion of minerals in the total rock was obtained from the intensity of the main peak of each mineral in the diffractogram (Schultz, 1964; modified with second author –MR– patterns; Moore and Reynolds, 1997). Determination of minerals components is of semiquantitative character, because this method has a methodological error of 10% according to Richiano et al. (2015).

3 Geological and stratigraphic setting

The fossils described herein were recovered from marine offshore deposits of the Early Cretaceous Agrio Formation (Weaver, 1931). This unit, with a thickness up to 1600 m, is composed of three members: Pilmatué, Avilé and Agua de la Mula (Leanza et al., 2001). The Pilmatué and Agua de la Mula members are composed of basinal shales, offshore mudstones and subordinated shallow-marine siliciclastic and mixed sandstones, and sandy limestones (Spalletti et al., 2011). Non-marine sandstones interpreted as a lowstand wedge produced by a suddenly relative sea-level drop, conversely, characterize the middle Avilé Member (Legarreta and Gulisano, 1989). The levels from where the pycnodontiform remains were discovered correspond mainly to marine deposits of mixed composition deposited below the level of storm waves (Sagasti, 2002; Spalletti et al., 2011; Schwarz et al., 2016), allowing to accumulate fine-grained deposits and thus a quite good fossil preservation.

The deposits of the Pilmatué Member accumulated in a mixed clastic-carbonate low-gradient marine ramp, partially connected to the Proto-Pacific (=Panthalassic) Ocean, and dominated by the action of fair weather and storm waves (Spalletti et al., 2011). According to detailed ammonoid and nannofossil associations and absolute age dating, the Pilmatué Member ranges from the early Valanginian to the early Hauterivian (Aguirre-Urreta et al., 2017 and cites therein, Schwarz et al., 2016).

The studied sections of the Pilmatué Member are located in a South-North transect in the North-Central sector of the Neuquén Basin (Fig. 2). The fossils were collected from offshore deposits at Puerta Curaco and Pampa de Tril localities (Fig. 2). At Puerta Curaco locality the section is *ca.* 600 m thick and shows a complete record of the Pilmatué Member dominated by marls and mudstones in the lower interval, and claystones and siltstones towards its upper part. At Pampa de Tril locality, only a 217 m thick section of the lower interval is exposed.

Specimen MOZ-Pv 1327 (an incomplete skull) was recovered from the lower interval of the Pampa de Tril section, where mudstones and marlstones are predominant. Specimen MOZ-

Pv 1316 (an incomplete right prearticular bone) was collected from the upper, fine-grained siliciclastic rich interval of the Puerta Curaco section (Fig. 3).

4 Systematic palaeontology

Superclass Actinopterygii Cope, 1887

Subclass Neopterygii Regan, 1923

Order Pycnodontiformes Berg, 1937

Family Gyrodontidae Berg, 1940

Genus *Gyrodus* Agassiz, 1833

Type species: *Stromateus hexagonus* (Blainville, 1818) from the lower Tithonian of the “*Solnhofener Plattenkalke*”, Bavaria, Germany.

Gyrodus huiliches sp. nov.

Figs. 4–5 A,B.

Holotype. MOZ-Pv 1327, incomplete skull with articulated right lower jaw with dentition.

Locality and Horizon. Puerta de Curaco section, Pampa de Tril locality, Pilmatué Member of the Agrio Formation, Neuquén Province (Fig. 3). lower Valanginian–lower Hauterivian, Lower Cretaceous.

Etymology. *Huiliches*, meaning 'south people' for the Mapuche population that inhabit the Patagonian region of Southwestern South America, which is a Mapudungun dialect of the aboriginal Mapuche, in allusion to the fossil site from where the new species was recovered.

Diagnosis. Large-sized gyrodontid fish with the following character combination: prearticular bone elongated and pointed showing a long and narrow mandibular symphysis, with a stout and high ‘coronoid process’, teeth subcircular, oval, and kidney-shaped in occlusal view. Teeth on prearticular dentition arranged in four well-defined rows, two rows composed of large and low oval teeth plus two rows with small subcircular to subrectangular teeth. Alternating rows with large and small teeth. No intercalating teeth are present. Main tooth row with more than 10 teeth (11 preserved teeth in the holotype including one missing). Main tooth row flanked by two lateral (=labial) rows and a single medial (=lingual) one. Long axes of medial (=lingual) teeth very obliquely oriented in relation to teeth of main row, teeth of second –outermost– lateral (=labial) row only slightly obliquely oriented. Tooth crowns with two wrinkled walls surrounding an apical furrow with a small lump, posterior teeth of the two lateral rows ornamented with coarse wrinkles and tubercles with a deep furrow which delimit an internal lump. Lateral crown faces of main and outer lateral (=labial) teeth also ornamented with wrinkles. First lateral (=labial) row with large teeth increasing in size posteriorly. Second lateral (=labial) row with teeth markedly increasing posteriorly. Medial (=lingual) teeth row occupies more than two-third of the

dentition, the teeth of the medial (=lingual) row are subcircular and slightly decrease in size anteriorly.

Description

General features. The new species of *Gyrodus* is represented by a complete, well-preserved right prearticular bone with teeth, angular and articular bones, several cranial endochondral and dermal elements, and some scales. Identification of individual bones, however, is rendered difficult due to the mode of preservation.

Dermal bones. The dermal cover consists mainly of unidentifiable bones but all elements covering the cheek region and those below the orbit are seemingly present. Traces of sensory canals are present in some elements directly above the prearticular dentition indicating the presence of infraorbital bones (Fig. 4B). Additional dermal tesseræ are present (Fig. 4A), which represents a typical feature of gyrodonitids according to Nursall (1996a). Their exact outline and arrangement, nevertheless, can't be established (Fig. 4A). A large, almost sub-triangular bone is present posterior to the prearticular that might represent the preopercle bone (Fig. 4A). Posterior to it, a large bone directed ventrally extending below the base of the prearticular bone most likely represents remains of the cleithrum. All dermal elements seemingly lack any superficial ganoin layer, which represents a synapomorphy of Gyrodontidae according to Nursall (1996a).

On the medial surface, a bony fragment is present at the dorsal margin of the specimen, which represents a portion of the parietal [= frontal] bone (Fig. 4A). This bone is ornamented with small tubercles and faint ridges that radiate from the ossification centre.

The entopterygoid is large and rectangular with its long axis oriented vertically (Fig. 4A). Ventrally, an elongated but short and smooth bony structure is preserved that might represent remains of the ectopterygoid (Fig. 4A).

Endochondral bones. Endochondral bones are also difficult to identify. The suspensorium is more or less completely preserved and almost vertically oriented similar to the condition in other pycnodontiforms (Fig. 4A). The hyomandibular bone is disarticulated, incomplete, and located at the posterior margin of the preserved skull (Fig. 4A). It is elongated with an extended, but very incomplete and crushed head. No distinct anterior condylar process can be identified, because the anterior portion is overlain by the entopterygoid, but a reduced (vestigial) posterior opercular process on the hyomandibular bone is present (Fig. 4A). A reduced (or vestigial) opercular process represents a synapomorphy for *Gyrodus* according to Poyato-Ariza & Wenz (2002) (compare also Nursall, 1996a). The most dorsal portion of the hyomandibula seems to be cartilaginous, nerve foramina are not observed.

Dorsal to the hyomandibular bone, some bony fragments are preserved that are characterized by a very smooth, slightly concave surface. These bones most likely represent remains of the bones that form the articular facet for the head of the hyomandibular bone (Fig. 4A). Consequently, the anterior element would correspond to the sphenotic, the posterior element to the prootic bone.

Anterior and ventrally to the hyomandibula, the elements of the palatoquadrate arch are preserved, which display the typical arrangement and orientation for *Gyrodus* (compare Lambers, 1991: fig. 12; Kriwet, 2005: fig. 16). The preserved metapterygoid is large and covers the dorsal portion of the ventrally placed entopterygoid (Fig. 4A).

Both quadrate and symplectic forming part of the characteristic pycnodontiform double lower jaw articulation are preserved and are arranged in close contact dorso-ventrally (Fig. 4A). The quadrate is large, its outline, however is difficult to ascertain because of its incompleteness and fractured nature. Anteriorly, it articulates with the angular bone of the lower jaw. The symplectic bone is rather large and positioned at the antero-ventral border of a large bony element that seems to be the preopercle in medial view. It articulates with the massive articular bone of the lower jaw.

Anterior portions of the endocranium include remains that we interpret as the endochondral median mesethmoid, which is enlarged and forms the snout (Fig. 4A). The posterior extend of this element remains ambiguous.

Hyoid arch. Ventrally to the symplectic, two bony elements are recognizable that most likely represent the ceratohyal (anterior?) and basihyal (Fig. 4A). These elements belong to the hyoid arch. The posterior ceratohyal and interhyal are either not preserved or not identifiable.

Lower jaw and dentition. The lower jaw comprises prearticular, angular, and articular bones. The prearticular is a massive, large making up most of the lower jaw, and well-ossified bone. It measures 90 mm in total length and 58 mm in height, measured from the tip of the 'coronoid process' perpendicular to the ventral margin of the dentition. The angle between the 'coronoid process' and the long axis of the prearticular is *ca.* 130°. The symphysis is narrow and elongated showing a rugose pattern indicating the presence of limited kind of connective tissue which is allow some lateral movements (see also Kriwet, 2005). The medioventral lamina is reduced in size and concave in cross-sectional view.

The 'coronoid process' is high and club-shaped with an anterior slope and a straight the dorsal margin (Fig. 4). It extends posterolaterally to form the 'coronoid ridge' of Nursall (1996a). Faint ridges are present over the surface of the 'coronoid process'.

The angular bone is roughly triangular in outline and restricted to the postero-lateral region of the lower jaw (Fig. 4). The posterior margin is thickened forming the articulation facet for the quadrate. Ventrally, the massive articular bone forms the postero-ventral margin of the lower jaw and the articulation facet with the symplectic. Other bones (e.g., retroarticular) are not identifiable.

The dentition of the prearticular (Fig. 4) consists in total of 54 preserved molariform teeth that are closely arranged in four well-defined rows (two laterals –inner and outer–, a main and an internal or medial row). The main row is composed of 11 teeth, which are sub-circular anteriorly but oval posteriorly with a faintly concave anterior margin in occlusal view. The first lateral (inner) row comprises 19 sub-circular teeth, which are significantly smaller and arranged in trough-like groove that runs antero-posteriorly. The long-axes of the

teeth are oriented antero-posteriorly. The outer lateral has 15 rhomboidal teeth with the long-axes being oriented perpendicular to the axis of the prearticular bone. Laterally, the teeth display a low and blunt apex. The inner-most (medial) tooth row comprises nine teeth that are restricted to the anterior half of the prearticular bone, whereas all other rows extend posteriorly to the level of the anterior margin of the “coronoid process”. The long-axes of the inner-most teeth are oriented obliquely to the long-axis of the prearticular. Nor intercalary teeth neither an additional tooth row at the base of the ‘coronoid process’ are present. In occlusal view the most posterior teeth still preserve their original ornamentation, whereas the anterior show signs of wear that occurred in life (see below).

The teeth increase in size posteriorly. The lateral inner and internal rows bear the smallest teeth of the dentition, while the main row displays the largest teeth. Larger teeth measure 8,2 mm in height and 6,7 mm in mesio-lateral width. The posterior teeth have an almost perpendicular main axis in relation with the long axis of the bone but the anterior teeth, which are the most abraded ones, have an oblique main axis in relation to the prearticular bone (Fig. 4). In occlusal view the anterior teeth are oval and the posterior ones are kidney-shaped. The posterior-most depression observed on the main prearticular tooth row housed a very large more oval tooth that is, however, not preserved. Similarly, two posterior-most depressions are observed in the medial (=lingual) tooth row that housed two medium-sized teeth.

Tooth ornamentation, Wear, and Ontogeny. Most teeth are heavily worn (see below) so that the tooth ornamentation is best preserved only on the posterior-most teeth (Fig. 5A, B). These teeth display a short coronal indent that either is directed mesio-distally (outer lateral and main rows) or more or less antero-posteriorly (inner lateral and medial rows). The indent is surrounded by a ring of coarse granules that vanishes quickly during wear forming a broad and smooth margin (Fig. 5A, B). A second, marginal ring of coarse granules delimiting a shallow, outer groove that follows the tooth outline is present. Anteriorly, the groove seems to be broader than posteriorly. The lateral edge of the outer lateral teeth is tapering forming a low and blunt, displaced apex (Fig. 5A, B). Centrally, a small irregular central papilla with a granular surface is developed in smaller teeth of the inner lateral and medial tooth rows, which sometimes are broader than deep and irregular. Conversely, the surface of the apical indent is very granular in larger teeth of the main and outer lateral rows.

Tooth replacement in pycnodonts still is not well established and contradicting hypotheses occur. For instance, Woodward (1893), Thurmond (1974), and Longbottom (1984) assume that teeth are added successively from anterior to posterior. Nevertheless, potential of replacing lost or damaged teeth might be possible (Longbottom, 1984; Poyato-Ariza, 2005). The presence of very strong abrasion on anterior teeth diminishing posteriorly supports the hypothesis that oldest teeth are found anteriorly and new teeth are added successively posteriorly. Thus, wear is qualitatively indicative of age. Still, abrasion and polishing of tooth surfaces can be caused by the pH of the surrounding water, sand, and rocks that are consumed with food (see Kemp and Berrel, 2013). Thus, the ornamentation of teeth has a minor taxonomic value because the teeth within a jaw show different degrees of wear of the occlusal surface of teeth resulting in smooth tooth surfaces in heavily used teeth and

increasing age of the individual (Kriwet, 2005). However, wear patterns are helpful to reconstruct dental functions and to help to understand the mode of life of these fishes.

The single specimen of the new species studied here shows a high degree of wear in almost all teeth. Wear is particularly strong on the anterior and middle portion of the dentition (Fig. 5A). The highest degree of wear occurs in the lateral outer row where the oral surface is vertical (Fig. 5A).

According to the wear pattern and the degree of abrasion of teeth we assume that wear appeared first in the anterior teeth where abrasion is strongest and subsequently continued posteriorly, most likely with age, to the larger posterior teeth. Additionally, wear patterns occur laterally first on those teeth where the occlusal surface is oblique or vertical (compare Kriwet, 2005; Fig. 5A, B). Most pycnodontiforms are considered durophagous fishes eating either soft or hard-shelled invertebrates (e.g., Nursall, 1996a,b; Poyato-Ariza and Wenz, 2002; Kriwet, 2005). The teeth of the upper dentated jaw (vomer, not preserved in the present specimen) and the prearticulars form a mortar and pestle-like structure for crushing prey (see Maisey, 1991: 129). This crushing action alters and changes the form of the occlusal surface of the teeth and commonly this eventually results in a smooth tooth surface. If wear is severe the tooth surface might even get a cupped morphology (Fig. 5).

According to the lack of ornamentation in anterior teeth and the abrasion pattern of almost all other teeth but the posterior-most ones, we suggest an adult ontogenetic stage for specimen MOZ-Pv 1327. Also, we assume a large overall size for this specimen based on the large size of the prearticular bone (for comparison see sizes of dentitions depicted in Kriwet, 2005; Poyato-Ariza and Wenz, 2005). A comparison with complete specimens of *Gyrodus hexagonus* and *G. circularis* from the Late Jurassic Solnhofen limestones housed in various institutional collections (JK unpublished data) enables us to provide a tentative relation equation between standard length (SL) and prearticular length (prl), which is *ca.* 65 mm (SL)/10 mm (prl). The prearticular length of the new species described here measures 90 mm and the corresponding SL thus would be *ca.* 580 mm. This size falls well within the range seen in large adult Late Jurassic *Gyrodus* species.

Comparison

The number of tooth rows and arrangement of teeth is considered to be of taxonomic value for identifying different genera, if not species (e.g., Kriwet, 2005; Kriwet and Schmitz, 2005). Also, almost all teeth have a smooth occlusal surface most likely resulting from abrasion. Some teeth, especially in the posterior portion of the dentition, nevertheless still display the characteristic sculpture for teeth of *Gyrodus* consisting of two crimped and continuous rims surrounding an inner indent with a central papilla and an outer groove (Fig. 5A–C).

The character combination displayed by the prearticular dentition comprising four distinct longitudinal tooth rows without intercalating teeth, teeth with two apical crenulated rims or walls that surround an inner and an outer indent, presence of a tubercle in the apical indent (at least in smaller teeth) and a blunt lateral apex in at least some teeth of the outer lateral tooth row are very characteristic for dentitions of *Gyrodus* and support the assignment of the

prearticular to this genus. The central papilla in the apical indent is considered an autapomorphic character of *Gyrodus* (Poyato-Ariza and Wenz, 2002; Kriwet and Schmitz, 2005; Vullo et al., 2017). The lack of ganoine on the dermal skull bones in addition with tesserae covering the dermal cheek region and the distinct hyomandibular bone with a vestigial opercular process represent additional characters reinforcing its assignment to *Gyrodus* (Nursall, 1996a; Kriwet, 2005).

Gyrodus is a very common pycnodontiform fish in the Jurassic with more than 30 species described from the Late Jurassic based on skeletal remains or isolated dentitions and teeth up to now (e.g., Wagner, 1851; Woodward, 1895; Lambers, 1991). Lambers (1991), however, synonymized most of these species with *Gyrodus hexagonus* and only two species, which are based on articulated specimens are currently considered valid, *G. hexagonus* and *G. circularis* (Kriwet and Schmitz, 2005). The status of other Jurassic species from Europe remains ambiguous momentarily pending further detailed studies. Here, we restrict our observations mainly to these two species since the Argentinian species is represented by more than isolated dentitions but also compare it to other relevant pycnodontiforms from Central and South America.

Gyrodus circularis is easily distinguishable from the Argentinian specimen in the presence of more strongly sculptured prearticular teeth with a less developed central indent. Additionally, the posterior-most main prearticular teeth in *G. circularis* lack any central indent but display instead a broad and blunt, irregularly wrinkled and folded occlusal surface (compare Kriwet and Schmitz, 2005: fig. 2F). The prearticular dentition of the Argentinian species differs from *G. hexagonus* in having more main prearticular teeth (8–9 in *G. hexagonus* and *G. circularis*; Poyato-Ariza & Wenz, 2002; Kriwet & Schmitz, 2005) and additionally sculptured crown faces of at least the main and outer lateral teeth.

In the Early Cretaceous, *Gyrodus* is known from isolated prearticular dentitions from, for instance, northern Germany and France (e.g., Kriwet and Schmitz, 2005; Vullo et al., 2018). These specimens differ from the new Patagonian gyrodontid in the distinct occlusal sculpture (well pronounced inner crimped wall and low, partially incomplete or very reduced outer wall) and the smooth lateral crown faces.

Only few fossil remains assigned to species of *Gyrodus* have been reported from Central and South America up to now. Gregory (1923) described some remains including vomerine, prearticular, and skeletal remains from the Oxfordian Jagua Formation of Cuba that he identified as a variation of *Gyrodus macrophthalmus* and subsequently named *G. macrophthalmus cubensis*, mainly because of its spatial separation from the European species. The teeth, when well preserved, display the typical ornamentation *Gyrodus* and resemble closely those of *Gyrodus hexagonus* (*G. macrophthalmus* is considered a junior synonym of *G. hexagonus* by Lambers, 1991) and differ thus from the new species described here (compare Gregory, 1923: fig. 1B, C).

A right prearticular with preserved dentition identified as *Gyrodus* sp. cf. *G. macrophthalmus* was also reported from the Kimmeridgian (Tamán Formation) of Mexico by Dunkle and Maldonado-Koerdell, 1953. This specimen differs significantly from *G.*

huiliches in the presence of circular rather than oval main teeth and mesio-laterally shorter outer lateral teeth. Additionally, the ornamentation of prearticular teeth in the Mexican specimen differs significantly from those of the Patagonian species (compare Dunkle and Maldonado-Koerdell, 1953: fig 1B).

The only South American record of *Gyrodus* that has been described so far comes from the Oxfordian of Chile and was identified as a new species of *Mesturus*, *M. cordillera*, by Martill et al. (1998). Kriwet (2000) subsequently revised this specimen and assigned it to *Gyrodus* because of the very characteristic tooth morphology. This species also differs from the new species presented here in the ornamentation and general morphology of teeth although no complete, well-preserved dentition has been recovered up to now.

The Early Cretaceous pycnodontiform *Cosmodus* from the Cenomanian of western Europe, which resembles *Gyrodus* superficially in prearticular and vomerine tooth ornamentation differs nevertheless in the absence of defined crimped ridges surrounding a central indent with papilla and an outer groove, and the presence of only three prearticular and vomerine tooth rows (compare Vullo et al., 2018: fig. 3F, 4).

Although the cranial skeleton is not well preserved and bony margins are difficult to identify, some bones nevertheless also support that *Gyrodus huiliches* sp. nov. represents a different species from *G. hexagonus* and *G. circularis*. The ‘coronoid process’ of *G. huiliches* sp. nov., for instance, is very club-shaped with an elongated, slightly concave dorsal, a rather low and vertical anterior and an almost sigmoidal posterior margin. In this, the ‘coronoid process’ of the Patagonian species resembles that of various pycnodontiforms such as, e.g., *Macromesodon*, *Turbomesodon*, *Micropycnodon*, *Neoproscinetes*, and *Tepeixichthys* (Poyato-Ariza and Wenz, 2002; Poyato-Ariza and Wenz, 2004; Ebert, 2013) but differs from that of both *Gyrodus hexagonus* and *G. circularis* (compare Kriwet, 2005: figs 16B, 30A). In *Gyrodus hexagonus*, the ‘coronoid process’ is low and antero-posteriorly broad with an almost straight dorsal margin and a vertical, anteriorly inclined posterior margin, where as it is higher, antero-posteriorly narrower and has an almost horizontal dorsal margin in *G. circularis*.

Additionally, the form of the hyomandibular head and the position of the vestigial opercular process differ in the Patagonian species from that of both *Gyrodus hexagonus* and *G. circularis* as far as can be ascertained (compare Lambers, 1991: fig. 12; Kriwet, 2005: fig. 16).

Order Pycnodontiformes Berg, 1937

Family Gyrodontidae Berg, 1940

Genus *Tranawuen* gen. nov.

Fig. 6

Type species. Macromesodon agrioensis Bocchino, 1977

Etymology. The generic name is derived from the native Mapudungun dialect of the Mapuche aboriginal population for which *trana*, means ‘mortar’ and *wün* (= *wuen*) means “mouth” in allusion to the function of tooth rows.

Diagnosis. A pycnodontiform fish characterized by the following combination of characters: vomer rather stout with five irregular longitudinal rows of closely arranged teeth; uneven number and unequal size of teeth in corresponding lateral tooth rows; intercalated teeth between tooth rows occasionally present; oral surface of dentigerous part almost horizontal; teeth of central –main– row are the largest, they are circular anteriorly but oval posteriorly; teeth with two, broad and granular occlusal rims surrounding an inner indent with slightly displaced, central stout papilla with irregular apex, and an outer narrow, circular groove. Prearticular seemingly massive and stout; with four longitudinal tooth rows comprising a main, two lateral, and a medial tooth row; intercalated teeth between main and first lateral tooth rows; additional irregular teeth may occur medially to the medial tooth row; teeth of main row are the largest; teeth of outermost lateral row smaller than those of first (inner) lateral row; tooth size in occlusal view increases in first lateral row posteriorly up to the middle of the row and then decreases again in size.

Stratigraphic and geographic distribution. Lower Cretaceous, Neuquén Province, Argentina.

Tranawuen agrioensis (Bocchino, 1977).

1977 *Macromesodon agrioensis* – Bocchino, p. 176, pl. 1.

Holotype. MLP-75-V-18-1, vomerine dentition, Fig. 6A.

Additional material. MOZ-Pv 1316, incomplete right prearticular with remains of dentition, Fig. 6B, C.

Diagnosis. Same as for genus by monotypy.

Occurrences. *Vomer.* Bajada del Agrio, Agrio Formation, Neuquén Province; lower Valanginian – lower Hauterivian, Lower Cretaceous. *Prearticular.* Puerta de Curaco section, Puerta de Curaco locality (15 km to the South from where *Gyrodus huiliches* sp. nov. was found), upper section of the Pilmatué Member of the Agrio Formation, Neuquén Province (Fig. 3); lower Hauterivian, Lower Cretaceous.

Description

Vomer. The unpaired vomer that represents the holotype –MLP-75-V-18-1– of the single species of the new genus and which was originally described by Bocchino (1977), is characterized by five, somewhat irregular tooth rows of closely spaced teeth with additional erratically intercalated teeth between main and first lateral row and also medially to medial (inner) tooth row. The teeth are more irregularly arranged in the anterior portion of the dentition becoming more regular posteriorly. Almost all teeth exhibit a smooth occlusal surface that most likely is the result of wear (Fig. 6A). However, some small lateral teeth on the posterior right side of the main row (in occlusal view) are not worn and still display the original ornamentation consisting of two irregular rims that surround an apical indent, in

which a small central papilla is located, and an outer furrow (Figs. 5D, 6A). The apex of the central papilla is somewhat irregular and not acute (Figs. 5D, 6A).

The main row consists of six preserved teeth and two additional bases of broken-off teeth. The teeth are significantly larger than the lateral ones and increase rostrad to caudad. Additionally, the teeth are circular anteriorly becoming oval in shape posteriorly in occlusal view (Fig. 6A).

The first lateral row on the left side (in occlusal view) consists of seven, completely smooth teeth that are alternating with the main teeth (Fig. 6A). They are larger than those on the right side and less in numbers (six versus eleven-twelve). They also increase in size posteriorly and change their shape in occlusal view from circular to sub-oval posteriorly (Fig. 6A).

The second left lateral row is very incompletely preserved. It preserves only two, sub-circular teeth that are arranged in an alternating pattern with the teeth of the first left lateral row (Fig. 6A). These teeth are oval and have a faint ornamentation consisting of an irregular rim surrounding a central depression (Fig. 6A).

The first lateral tooth row on the right side of the main row comprises comparably small teeth that are arranged somewhat irregular and not alternating with the main teeth as in the lateral row on the other side (Fig. 6A). The teeth are sub-circular to sub-triangular anteriorly becoming more oval posteriorly. At least four additional, small teeth are intercalated between the main and first right lateral row (in occlusal view).

In total, 13 teeth display remains of the original ornamentation, of which the posterior-most three teeth in the first right lateral row and the posterior-most of the intercalated teeth display almost no wear patterns. This is probably the result of these teeth are quite small having occlusal surfaces that are positioned below the grinding surface of the jaws and thus escaped abrasion (Fig. 6A). The ornamentation in these teeth consists of two rather broad and crimped ridges surrounding a central indent in which a slightly displaced papilla is located, and an outer furrow surrounding the tooth crown. Additional nine teeth display an apical indent, which is surrounded by a more or less wrinkled, broad ridge. Reduction from two to a single, broad occlusal ridge resulted from wear.

Prearticular. MOZ-Pv 1316 is a partially preserved and massive right prearticular bone that is almost as long as wide. The total width of the prearticular bone is about 40 mm, the angle between the ‘coronoid process’ and the prearticular is *ca.* 163°. However, it is not clear how much anteriorly is missing. There are at least 19 preserved teeth and 12 additional tooth bases on the dentigerous surface of the prearticular bone (Fig. 6B). The teeth are arranged in four closely arranged tooth rows with at least two additional intercalated teeth between the main and first lateral tooth rows and one medially to the innermost (medial) tooth row. The ‘coronoid process’ is seemingly low also it seems to be slightly abraded (Fig. 6B).

Almost all teeth have a more or less horizontal and completely smooth occlusal surface indicating strong wear, which is conspicuous and comparable over all preserved teeth (Fig. 6B). However, the second anterior tooth of the outermost lateral tooth row displays remnants

of an apical, very narrow and mesio-distally short irregular indent indicating the originally presence of a crimped rim surrounding the rim (Fig. 6B).

All teeth are of sub-circular to rectangular shape in occlusal view. Four teeth of the main row, which are more or less of similar size and shape, are preserved with several teeth obviously lacking as indicated by a gap in the row and a tooth base at its posterior end (Fig. 6B). The anterior-most tooth of the main row either displays heavy wear or is pathological altered (Fig. 6B).

The first lateral row comprises seven complete and one incomplete teeth as well as two tooth bases anteriorly and posteriorly, respectively. They are arranged slightly irregular giving is an undulating appearance (Fig. 6B). In occlusal view, the teeth increase posteriorly up to the middle of the tooth row and then decrease again in size posteriorly. The occlusal surface of these teeth is saddle-like abraded due to continuous wear.

The outer-most lateral tooth row is short and placed at the base of the low ‘coronoid process’. It comprises five teeth and an additional posterior tooth base. They are conspicuously smaller than those in the middle portion of the first (inner) lateral row but almost equal in size to those in the anterior and posterior portion of this row (Fig. 6B).

Teeth of the medial row are not preserved but are represented by their respective tooth bases (Fig. 6B). The tooth bases imply that this row is the only in which teeth have a more horizontally oriented oral surface, which is due to the trough-like cross-section of the prearticular bone. The occlusal surface of teeth in the main and lateral tooth rows, conversely, is very vertically oriented.

The medio-ventral lamina of the prearticular bone is well-developed being flat and wider than in, for instance, the new species of *Gyrodus* described here (Figs. 5 and 6). According to the wear pattern observed in the teeth of MOZ-Pv 1316, the specimen is considered an adult; its size, however, cannot be established due to the incomplete nature of the single specimen.

Comparisons

The two specimens assigned to the new taxon were recovered from lower Valanginian to lower Hauterivian and lower Hauterivian sediments of two closely situated localities in the Neuquén Basin. We consider both the vomerine MLP-75-V-18-1 and prearticular MOZ-Pv 1316 dentitions to belong to the same species even though they do not come from the same locality based on the following characters: The arrangement of teeth in slightly irregular tooth rows with randomly intercalated teeth in both dental elements, the general morphology (irregularly rounded shape) of teeth, the ornamentation pattern (where preserved), and the correspondence of the dentated portions when occluded forming an effective crushing device. We therefore also exclude the possibility that the rather irregular tooth arrangement represent pathological patterns. However, more material might provide more information about the dentition of this pycnodontiform fish in the future.

The character combination consisting of five longitudinal tooth rows with uneven number and unequal size of teeth, the lateral vomerine tooth row with intercalated teeth, four prearticular tooth rows with also intercalated teeth between and outside tooth rows and small lateral-most teeth associated with an ornamentation pattern that remind that of the teeth of, e.g., *Gyrodus*, easily distinguishes the new taxon from all other known pycnodontiform fishes.

Bocchino (1977) originally assigned the vomer to *Macromesodon* based on the presence of five, irregular tooth rows and presented a list of characters supporting her interpretation (see Bocchino, 1977: 183), even so her also recognized similarities to *Micropycnodon*. Numerous isolated vomers having five longitudinal tooth rows were assigned to *Macromesodon* (= *Mesodon* Wagner, 1851) by Blake (1905). Woodward (1895), for instance, listed 14 species of *Mesodon*. Unfortunately, the vomerine dentition is not accessible in the holotype of the type-species of *Macromesodon*, *M. macropterus* (BSPM AS VII 345). Another species, *M. surgens* (Poyato-Ariza and Wenz, 2002) displays five longitudinal tooth rows and teeth with occasional crenulations. Additionally, several specimens identified as *M. macropterus* by Woodward (1895: 199–200) were assigned to a different genus *Turbomesodon* by Poyato-Ariza and Wenz (2004). *Turbomesodon* is characterised by three longitudinal vomerine tooth rows. Most pycnodontiform fishes, however, have five longitudinal tooth rows in their vomerine dentition (e.g., *Brembodus*, *Coelodus sensu stricto*, *Gyrodus*, *Iemanja*, *Micropycnodon*, *Mesturus*, *Oelodus*, *Pycnodus*, *Tepexichthys*). The new taxon, nevertheless, differs significantly from all other pycnodontiform fishes with five longitudinal vomerine tooth rows in the very irregular number and size of teeth in corresponding lateral tooth rows combined with the presence of intercalated teeth and the *Gyrodus*-like crown ornamentation. Additionally, all vomerine teeth in *Macromesodon*, as far as they are known, are sub-circular in outline and completely devoid of any ornamentation (Poyato-Ariza and Wenz, 2004).

The arrangement of prearticular teeth into four rows in the dentigerous part of the prearticular is also very peculiar. Most pycnodontiform fishes have three tooth rows, but some only have two prearticular tooth rows (e.g., *Coccodus*), while others have more than four tooth rows (e.g., *Anomoeodus*, *Brembodus*, *Coelodus sensu stricto*, *Mesturus*). *Hensodon* from the Cenomanian of Lebanon might have even only a single prearticular tooth row (Capasso et al., 2010). Therefore, the new taxon described here is easily distinguishable from these pycnodonts.

Four longitudinal prearticular tooth rows are present in *Gyrodus* (Middle Jurassic – early Early Cretaceous), *Proscinetes* (Middle Jurassic – late Early Cretaceous?), *Texasensis* (= *Callodus*) (late Early Cretaceous), and *Micropycnodon* (Late Cretaceous). We follow Poyato-Ariza and Wenz (2002) and consider *Hadrodus* (which also have four longitudinal tooth rows in the lower jaw) most likely not be a pycnodontiform fish at all.

Tranawuen agrioensis is easily to separate from the other pycnodontiform fish also occurring in the Neuquén Basin, *Gyrodus huiliches*, nov. sp. but also from other *Gyrodus* species in the presence of intercalated teeth and outermost lateral teeth that are smaller than those in

the middle portion of the first (inner) lateral row (in *Gyrodus*, lateral-most teeth are significantly larger than those of the first lateral row; see also above).

It should be noted that the prearticular teeth of *Tranawuen* nov. gen. display more variable tooth outlines ranging from circular to oval and even sub-rectangular conversely to the condition seen in *Macromesodon* in which prearticular teeth are predominantly oval as far as can be ascertained.

Poyato-Ariza and Wenz (2002) coded the number of prearticular tooth rows in *Proscinetes* as being three obviously interpreting one of the rows comprising small teeth adjacent to the main row to represent intercalated teeth, an interpretation we do not follow here. The new taxon, however, is easily distinguishable from *Proscinetes* in lacking the very regular tooth arrangement into rows, distinctly mesio-distally elongated main teeth, and lateral-most teeth that are significantly broader than those of the first lateral row. Additionally, the teeth of the medial tooth row extend far more anteriorly in the new pycnodontiform than in *Proscinetes*.

Another pycnodontiform fish that has four prearticular tooth rows but which was not yet reported from South America is *Texasensis coronatus* from the Albian of Texas (Thurmond, 1974). This taxon differs, however, significantly from the Patagonian genus in having three well-defined lateral tooth rows and no medial one. Additionally, the main teeth are broader.

Mircopycnodon differs in that teeth on the prearticulars are more irregularly arranged without any clear arrangement into four rows. Posteriorly, even five rows may be developed while anteriorly the tooth rows merge to four. Additionally, the main teeth are much broader while the teeth of the first lateral row are distinctly smaller than those of the outermost row.

An incomplete left prearticular dentition from the Early Cretaceous of Colombia assigned to *Macromesodon couloni* by Porta (1970) differs clearly from *Tranawuen* nov. gen. in having three tooth rows (with additional intercalated teeth) and much broader and almost rectangular main teeth. The assignment of the Colombian specimen to *Macromesodon* remains ambiguous.

Another Early Cretaceous pycnodont fish, *Paramicrodon* that also occurs in South America (Chile) differs in having only three longitudinal vomerine and prearticular tooth rows, respectively (Schultze, 1981). The prearticular also comprises an additional reduced row of teeth medial to the main row.

5 Discussion and conclusions

Pycnodontiform fishes are a highly diverse group with major diversity peaks in the Late Jurassic and Late Cretaceous with most records coming from Europe and the middle East (e.g., Kriwet, 2001a,b; Martín-Abad and Poyato-Ariza, 2013). Long ghost-lineages imply that the fossil record of Early Cretaceous pycnodonts is very incomplete (compare Martín-Abad & Poyato-Ariza, 2013). In the Early Cretaceous of Central and South America, the highly incomplete fossil record of pycnodontiform may certainly represents a collecting bias. Thus, additional fieldwork –with focus on fishes– will provide more material which may fill gaps in the stratigraphic distribution of pycnodontiform fishes and help shorten

ghost-lineages. Yet, in South America, Early Cretaceous pycnodontiforms have been reported from the Santana Formation (Aptian – Albian) of Brazil i.e., *Iemanja palma*, *Neoproscinetes penalvai*, *Mercediella riachuelensis*; all known from skeletal remains (Wenz, 1989; Figueiredo and Silva Santos, 1991; Maisey, 1991), the Rosablanca Formation (Barremian – Aptian) of Colombia i.e., *Macromesodon couloni* (Porta, 1970), the Lo Valdés Formation (Aptian) of Chile i.e., *Paramicrodon volcanensis* (Bocchino, 1977; Schultze, 1981; Arratia and Cione, 1996), and the Agrio Formation (upper Valanginian – upper Hauterivian) of Argentina i.e., *Tranawuen agrioensis* (Bocchino, 1977).

The new Patagonian records increase the diversity of Early Cretaceous pycnodontiform fishes of the Neuquén Basin in Argentina. Additionally, both taxa are the southernmost occurrences of pycnodontiforms to date.

Both new Patagonian taxa described here display discrete dental characters that separate these pycnodontiforms readily from all other known pycnodontiforms but also support their close relationships with *Gyrodus*, either being a new species of this genus or a closely related genus. *Gyrodus* is considered a Bajocian – Tithonian genus that inhabited the Western Tethys and Peritethyan regions with its greatest taxonomic diversity and palaeobiogeographical distribution during the Late Jurassic (Kriwet, 2000; Kriwet and Schmitz, 2005; Martín-Abad and Poyato-Ariza, 2013). Early Cretaceous records of *Gyrodus* are very rare and according with Kriwet and Schmitz (2005), questionable. Martín-Abad and Poyato-Ariza (2013) presented a dispersal scenario of pycnodontiform fishes explaining the dispersal of pycnodontiforms from the Tethys Sea, which is assumed to represent their centre of radiation and their final refuge. These authors assume that seven genera dispersed to the Americas including North and Central America. During the Late Jurassic, basal pycnodontiforms might have been dispersed through the Hispanic Corridor to South America (Kriwet, 2000; Kriwet and Schmitz, 2005; Martín-Abad and Poyato-Ariza, 2013; Poyato-Ariza and Martín-Abad, 2013). Thus, *Gyrodus*, a basal pycnodontiform fish, might have lived and proliferate in the warm ocean waters of southern South America at least during the Early Cretaceous being a relict taxon. The new species –*Gyrodus huiliches*– most likely diverged from a Central or South American species of *Gyrodus* while the new Patagonian gyrodontid genus –*Tranawuen*– described here seemingly diverged from *Gyrodus* (we assume both taxa described here to be closely related), which invaded the eastern Pacific coast line through the Hispanic Corridor latest in the Oxfordian (Kriwet, 2000).

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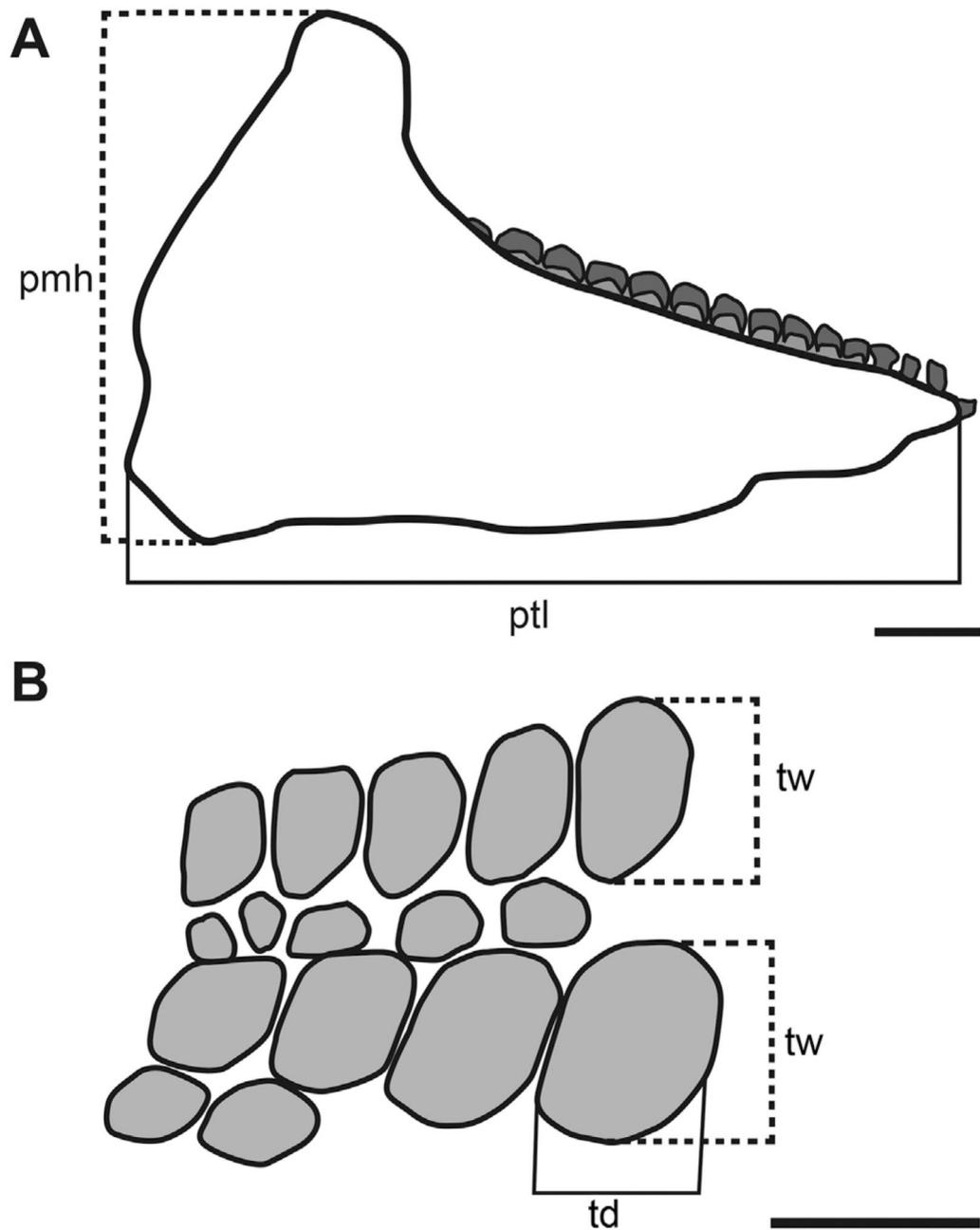


Fig. 1. Measurements taken over the studied specimens. Abbreviations: pmh, prearticular maximum height; ptl, prearticular total length; tw, tooth width; td, tooth depth. Scale bar: 10 mm.

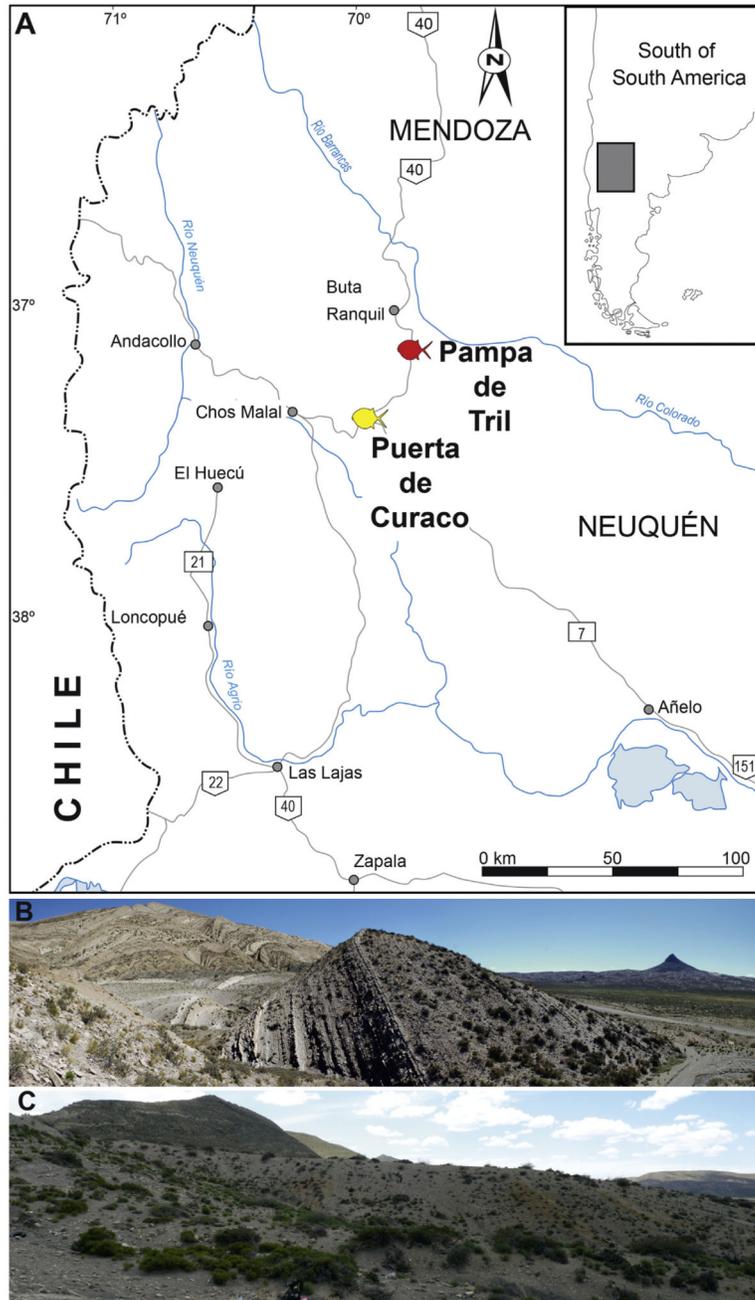


Fig. 2. **A**, Location map showing the pycnodontiform localities. Pampa de Tril locality ($37^{\circ} 15' 05''$ S, $69^{\circ} 48' 21''$ W) and Puerta de Curaco locality ($37^{\circ} 22' 47''$ S, $69^{\circ} 55' 45''$ W); **B**, general view of lower section of the Pampa de Tril locality; **C**, General view of the upper section of Puerta de Curaco locality.

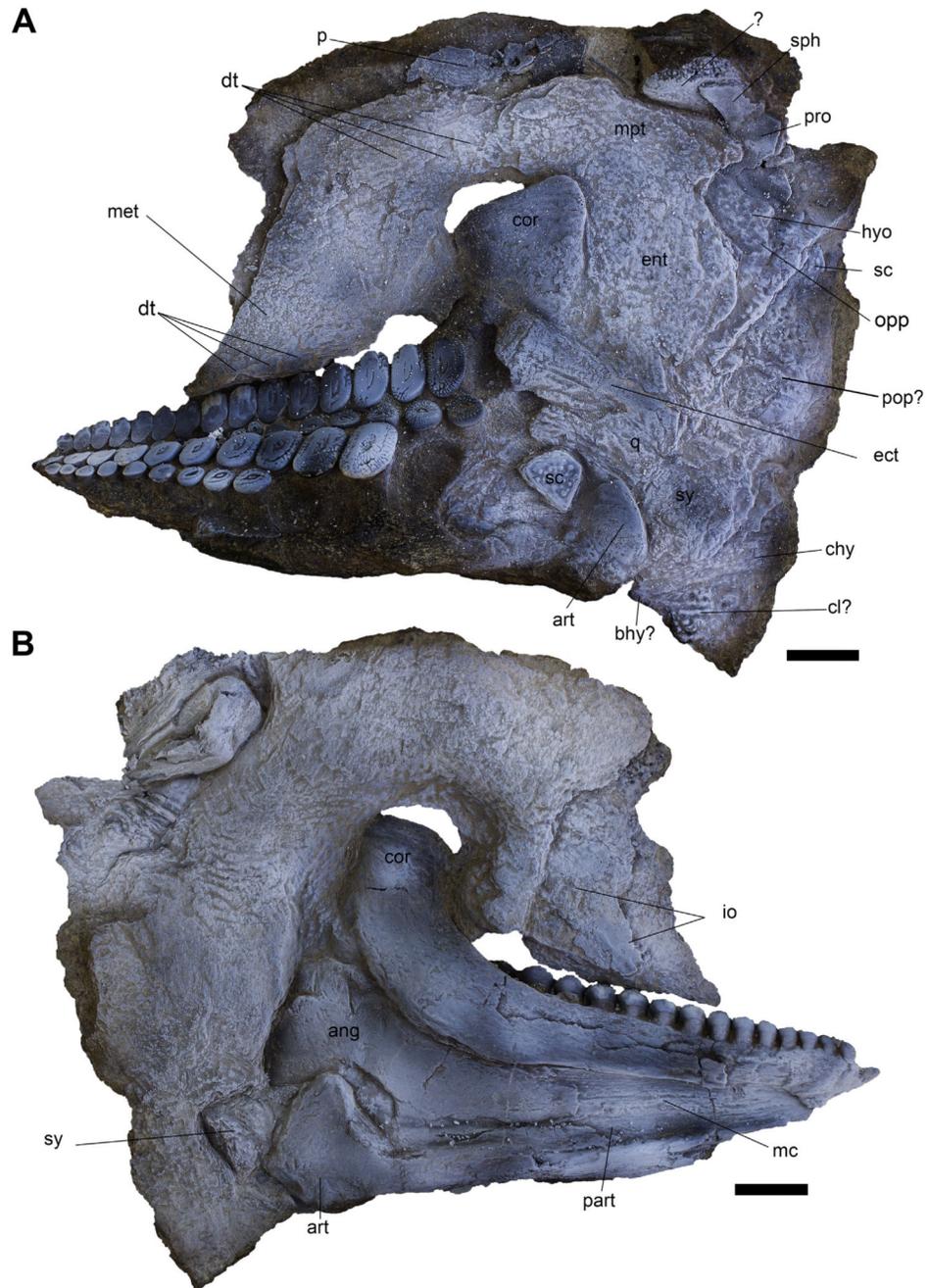


Fig. 4. *Gyrodus huiliches* sp. nov., MOZ-Pv 1327, **A**, holotype in medial view and **B**, labial view. Anatomical abbreviations: ang, angular; art, articular; bhy, basihyal; chy, ceratohyal; cl, cleithrum; cor, 'coronoid process'; dt, dermal tesserae ect, ectopterygoid; ent, entopterygoid; io, infraorbital; p, parietal [= frontal]; hyo, hyomandibula; mc, Meckel's canal; met, mesethmoid; mpt, metapterygoid; opp, opercular process; pop, preopercle; preart, prearticular; pro, prootic; q, quadrate; sc, scale; sph, sphenotic; sy, symplectic. Scale bar: 10 mm.

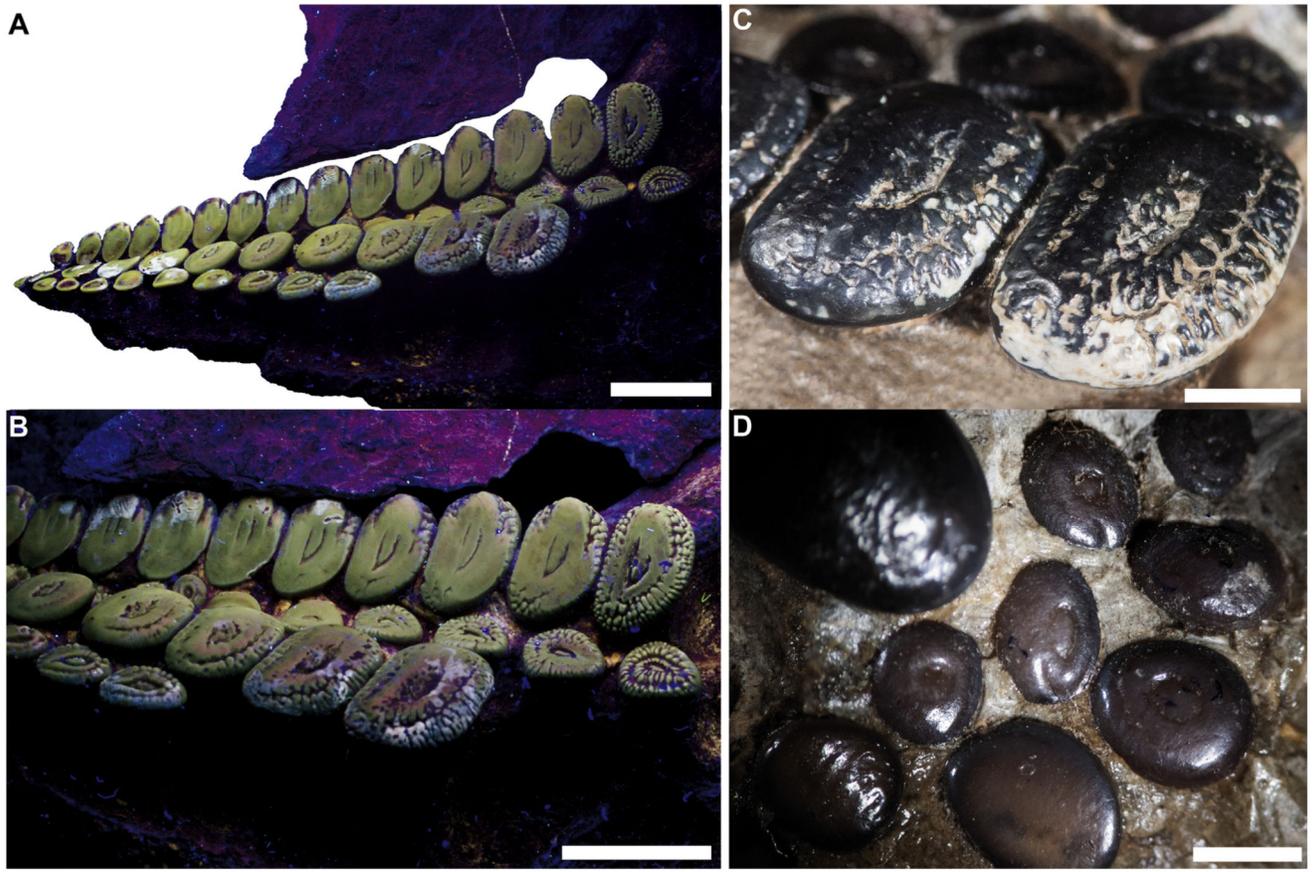


Fig. 5. Dentitions A–C, holotype of *Gyrodus huiliches* sp. nov. MOZ-Pv 1327, prearticular dentition under Uv light; **C**, detail of tooth ornamentation; **D**, holotype of *Tranawuen agrioensis* gen. nov. MLP- 75-V-18-1, detail of the ornamented teeth of the vomerine dentition. Scale bar: A–B, 10 mm; C–D, 3 mm.

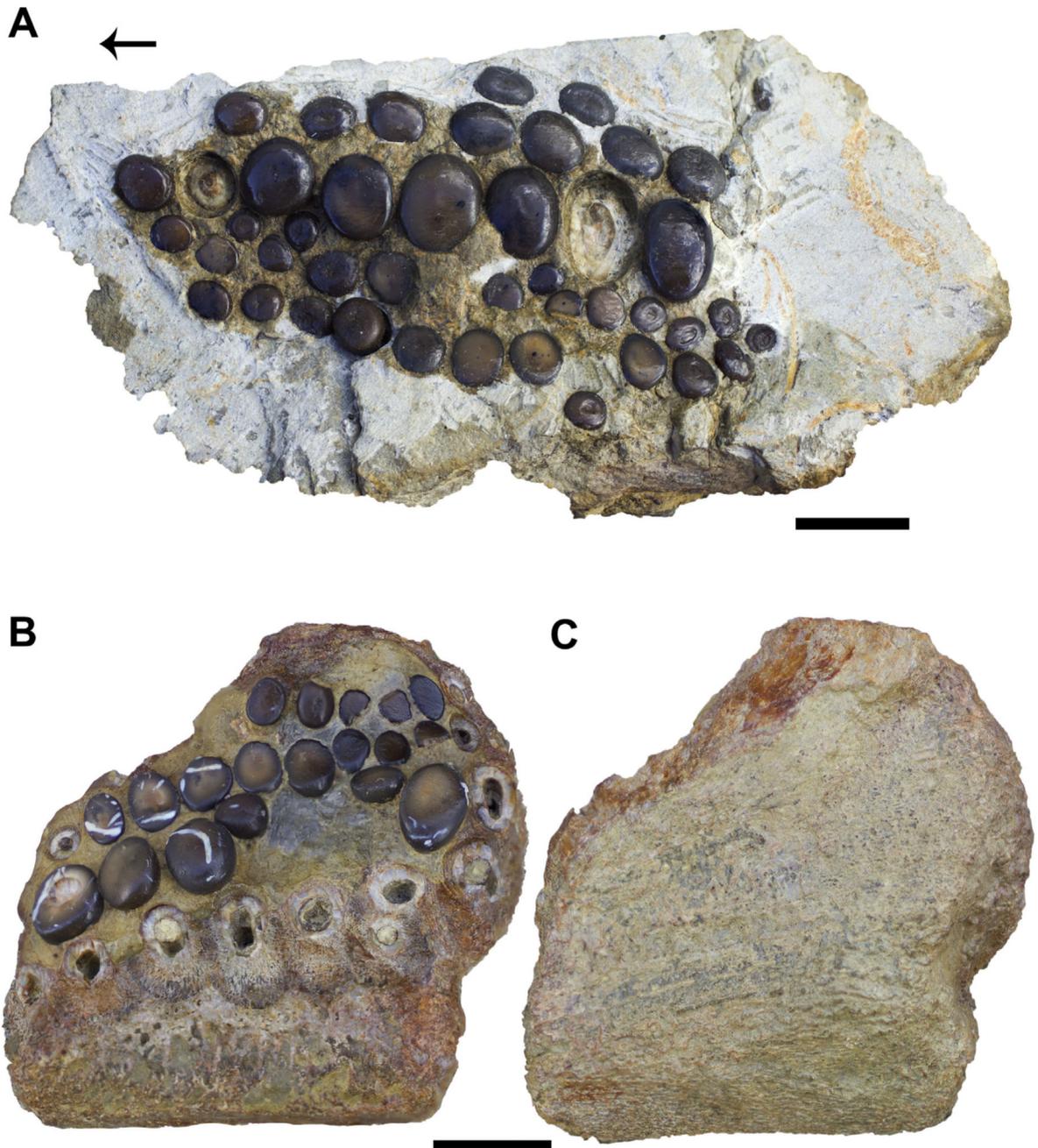


Fig. 6. *Tranawuen agrioensis* gen. nov. (Bocchino, 1977), **A**, holotype MLP 75-V-18-1 vomerine dentition; **B**, MOZ-Pv 1316 prearticular dentition in lingual view; **C**, MOZ-Pv 1316 prearticular dentition in labial view. The arrow indicates rostrally direction. Scale bar: 10 mm.