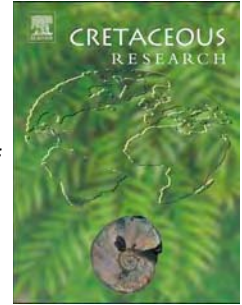


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New pycnodontiform fishes (Actinopterygii, Neopterygii) from the Early Cretaceous of the Argentinian Patagonia

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

3

4

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25 **ABSTRACT**

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

46 **Keywords:** *Gyrodus huiliches* nov. sp., *Tranawün* nov. gen., Agrio Formation,
47 Argentina, palaeogeography, evolution

48

49 **1. Introduction**

50

51 The order Pycnodontiformes is a morphologically and ecologically very
52 distinctive actinopterygian clade, which has been recognized as a taxonomic entity
53 since the descriptions of Agassiz (1843-44). They first appeared in the Late
54 Triassic and became extinct in the Eocene (Kriwet, 2005; Cawley et al., 2018).
55 Pycnodontiforms inhabited mostly coastal but also pelagic marine waters as well
56 as brackish, freshwater-influenced and freshwater environments (Nursall, 1996a;
57 Poyato-Ariza et al., 1998; Poyato-Ariza, 2005; Martín-Abad and Poyato-Ariza,
58 2013). Although most taxa only are known by their isolated dentitions or even teeth
59 (e.g., Poyato-Ariza and Wenz, 2002; Kriwet, 2008; Stumpf et al., 2017), complete
60 and well-preserved specimens occur in Mesozoic and Early Cenozoic *Konservat-*
61 *Lagerstätten* deposits of the Tethys area (Lambers, 1991; Forey et al., 2003;
62 Kriwet, 2005; Kriwet and Schmitz, 2005; Poyato-Ariza and Wenz, 2005; Ebert,
63 2013, 2018; Vullo et al., 2017). Moreover, some taxa previously assumed to be
64 invalid such as the large pycnodontiform *Cosmodus*, which is based on isolated
65 dentitions recently was redescribed and recognized as a valid distinct genus (Vullo
66 et al., 2018).

67 The value of dental characters for phylogenetic purposes has been discussed
68 controversially in the last decades (Poyato-Ariza, 2003; Kriwet, 2005), the common
69 conclusion of those studies is that “dentitional characters and their variation are still
70 inadequately understood, and it is, of course, possible to identified species and
71 genera based on isolated dentitions” (Kriwet, 2005: 160). Subsequently, Poyato-

72 Ariza and Bermúdez-Rochas (2009), for instance, established a new Early
73 Cretaceous pycnodontiform genus based on isolated dental remains. The
74 phylogenetic importance of dental characters, however, remains ambiguous.

75 The dentition of pycnodontiform fishes is composed of molariform teeth on the
76 paired prearticular and unpaired vomer bones, while incisiform or grasping teeth
77 with variable morphologies are located on the premaxilla and dentosplenia
78 (Cawley and Kriwet, 2018). Most pycnodontiforms having crushing dentitions were
79 characterized as being predominantly durophagous (Nursall, 1996a, 1996b; Kriwet,
80 2001). However, herbivorous, grazing and cutting-type forms were also reported
81 (Kriwet, 2001; Vullo et al., 2017).

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

96 prearticular with partially preserved dentition allows revising the only Early
97 Cretaceous pycnodontiform fish from Argentina known to date, *Macromesodon*
98 *agriensis* Bocchino, 1977 and referring it to a new genus.

99

100

101 **2. Materials and Methods**

102

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

106

107 *2.1. Preparation techniques, preservation, and study methodology*

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

119

120 *2.2. Measurements*

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

123

124 *2.3. Morphologically terminology*

125 The morphological terminology follows Nursall (1996a, 1999) and Poyato-Ariza
126 and Wenz (2002). Consequently, we use the term ‘coronoid process’ here,
127 although this structure cannot be considered homologous to the coronoid process
128 in non-pycnodontiform neopterygians, where it is formed by the dentary, the
129 surangular, and/or the angular. The systematic arrangement is adapted from
130 Poyato-Ariza and Wenz (2002). In this study, the nomenclature used for describing
131 dermal skull bones follows homology criteria (see Westoll, 1943; Schultze 1993,
132 2008). However, to avoid confusion in the specimen descriptions and figure
133 captions, the traditional terminology –which is not based on homology criteria– is
134 given in square brackets. Additionally, we use ‘lateral’ for labial tooth rows and
135 ‘medial’ for the lingual tooth row, we add the terminology in brackets in the
136 specimen descriptions.

137

138 *2.4. Anatomical abbreviations*

139 Anatomical abbreviations are giving in figure captions.

140

141 *2.5. Institutional abbreviations* MLP, Museo de La Plata, Buenos Aires,
142 Argentina; MOZ, Museo Prof. Dr. Juan Olsacher, Zapala, Neuquén, Argentina.

143

144 2.6. Geological methods

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

159

160 3. Geological and stratigraphic setting

161

162 The fossils described herein were recovered from marine offshore deposits of
163 the Early Cretaceous Agrio Formation (Weaver, 1931). This unit, with a thickness
164 up to 1600 m, is composed of three members: Pilmatué, Avilé and Agua de la Mula
165 (Leanza *et al.*, 2001). The Pilmatué and Agua de la Mula members are composed
166 of basinal shales, offshore mudstones and subordinated shallow-marine siliciclastic
167 and mixed sandstones, and sandy limestones (Spalletti *et al.*, 2011). Non-marine

168 sandstones interpreted as a low-stand wedge produced by a suddenly relative sea-
169 level drop, conversely, characterize the middle Avilé Member (Legarreta and
170 Gulisano, 1989). The levels from where the pycnodontiform remains were
171 discovered correspond mainly to marine deposits of mixed composition deposited
172 below the level of storm waves (Sagasti, 2002; Spalletti *et al.*, 2001; Schwarz *et al.*,
173 2017), allowing to accumulate fine-grained deposits and thus a quite good fossil
174 preservation.

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

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

189 Specimen MOZ-Pv 1327 (an incomplete skull) was recovered from the lower
190 interval of the Pampa de Tril section, where mudstones and marlstones are
191 predominant. Specimen MOZ-Pv 1316 (an incomplete right prearticular bone) was

192 collected from the upper, fine-grained siliciclastic rich interval of the Puerta Curaco
193 section (Fig. 3).

194

195

196 **4. Systematic Palaeontology**

197

198 Superclass Actinopterygii Cope, 1887 □

199 Subclass Neopterygii Regan, 1923 □

200 Order Pycnodontiformes Berg, 1937

201 Family Gyrodontidae Berg, 1940

202

203 Genus **Gyrodus** Agassiz, 1833

204

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

207

208

209 ***Gyrodus huiliches***, sp. nov.

210 Fig. 4–5 A,B

211

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

214

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

218

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

223

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

239 (=labial) row with large teeth increasing in size posteriorly. Second lateral (=labial)
240 row with teeth markedly increasing posteriorly. Medial (=lingual) teeth row occupies
241 more than two-third of the dentition, the teeth of the ~~middle~~ medial (=lingual) row
242 are subcircular and slightly decrease in size anteriorly.

243

244 **Description**

245

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

250

251 *Dermal bones.* The dermal cover consists mainly of unidentifiable bones but all
252 elements covering the cheek region and those below the orbit are seemingly
253 present. Traces of sensory canals are present in some elements directly above the
254 prearticular dentition indicating the presence of infraorbital bones (Fig. 4B).

255 Additional dermal tesserae are present (Fig. 4A), which represents a typical feature
256 of gyrodontids according Nursall (1996a). Their exact outline and arrangement,
257 nevertheless, can't be established (Fig. 4A). A large, almost sub-triangular bone is
258 present posterior to the prearticular that might represent the preopercle bone (Fig.
259 4A). Posterior to it, a large bone directed ventrally extending below the base of the
260 prearticular bone most likely represents remains of the cleithrum. All dermal
261 elements seemingly lack any superficial ganoin layer, which represents a
262 synapomorphy of Gyrodontidae according to Nursall (1996a).

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

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

270

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

283 Dorsal to the hyomandibular bone, some bony fragments are preserved that
284 are characterized by a very smooth, slightly concave surface. These bones most
285 likely represent remains of the bones that form the articular facet for the head of

286 the hyomandibular bone (Fig. 4A). Consequently, the anterior element would
287 correspond to the sphenotic, the posterior element to the prootic bone.

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

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

301 Anterior portions of the endocranium include remains that we interpret as the
302 endochondral median mesethmoid, which is enlarged and forms the snout (Fig.
303 4A). The posterior extend of this element remains ambiguous.

304

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

309

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

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

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

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

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

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

356

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

371 Tooth replacement in pycnodonts still is not well established and contradicting
372 hypotheses occur. For instance, Woodward (1893), Thurmond (1974), and
373 Longbottom (1984) assume that teeth are added successively from anterior to
374 posterior. Nevertheless, potential of replacing lost or damaged teeth might be
375 possible (Longbottom, 1984; Poyato-Ariza, 2005). The presence of very strong
376 abrasion on anterior teeth diminishing posteriorly supports the hypothesis that
377 oldest teeth are found anteriorly and new teeth are added successively posteriorly.
378 Thus, wear is qualitatively indicative of age. Still, abrasion and polishing of tooth
379 surfaces can be caused by the pH of the surrounding water, sand, and rocks that
380 are consumed with food (see Kemp, 2013). Thus, the ornamentation of teeth has a

381 minor taxonomic value because the teeth within a jaw show different degrees of
382 wear of the occlusal surface of teeth resulting in smooth tooth surfaces in heavily
383 used teeth and increasing age of the individual (Kriwet, 2005). However, wear
384 patterns are helpful to reconstruct dental functions and to help to understand the
385 mode of life of these fishes.

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

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

403 According to the lack of ornamentation in anterior teeth and the abrasion
404 pattern of almost all other teeth but the posterior-most ones, we suggest an adult

405 ontogenetic stage for specimen MOZ-Pv 1327. Also, we assume a large overall
406 size for this specimen based on the large size of the prearticular bone (for
407 comparison see sizes of dentitions depicted in Kriwet, 2005; Poyato-Ariza and
408 Wenz, 2005). A comparison with complete specimens of *Gyrodus hexagonus* and
409 *G. circularis* from the Late Jurassic Solnhofen limestones housed in various
410 institutional collections (JK unpublished data) enables us to provide a tentative
411 relation equation between standard length (SL) and prearticular length (prl), which
412 is ca. 65 mm (SL) / 10 mm (prl). The prearticular length of the new species
413 described here measures 90 mm and the corresponding SL thus would be ca. 580
414 mm. This size falls well within the range seen in large adult Late Jurassic *Gyrodus*
415 species.

416

417 **Comparison**

418

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

426 The character combination displayed by the prearticular dentition comprising
427 four distinct longitudinal tooth rows without intercalating teeth, teeth with two apical
428 crenulated rims or walls that surround an inner and an outer indent, presence of a

429 tubercle in the apical indent (at least in smaller teeth) and a blunt lateral apex in at
430 least some teeth of the outer lateral tooth row are very characteristic for dentitions
431 of *Gyrodus* and support the assignment of the prearticular to this genus. The
432 central papilla in the apical indent is considered an autapomorphic character of
433 *Gyrodus* (Poyato-Ariza and Wenz, 2002; Kriwet and Schmitz, 2005, and Vullo et
434 al., 2017). The lack of ganoine on the dermal skull bones in addition with tesserae
435 covering the dermal check region and the distinct hyomandibular bone with a
436 vestigial opercular process represent additional characters reinforcing its
437 assignment to *Gyrodus* (Nursall, 1996a; Kriwet, 2005, 2010).

438 *Gyrodus* is a very common pycnodontiform fish in the Jurassic with more than
439 30 species described from the Late Jurassic based on skeletal remains or isolated
440 dentitions and teeth up to now (e.g., Wagner, 1851; Woodward, 1895; Lambers,
441 1991). Lambers (1991), however, synonymized most of these species with
442 *Gyrodus hexagonus* and only two species, which are based on articulated
443 specimens are currently considered valid, *G. hexagonus* and *G. circularis* (Kriwet
444 and Schmitz, 2005). The status of other Jurassic species from Europe remains
445 ambiguous momentarily pending further detailed studies. Here, we restrict our
446 observations mainly on these two species since the Argentinian species is
447 represented by more than isolated dentitions but also compare it to other relevant
448 pycnodontiforms from Central and South America.

449 *Gyrodus circularis* is easily distinguishable from the Argentinian specimen in
450 the presence of more strongly sculptured prearticular teeth with a less developed
451 central indent. Additionally, the posterior-most main prearticular teeth in *G.*
452 *circularis* lack any central indent but display instead a broad and blunt, irregularly

453 wrinkled and folded occlusal surface (compare Kriwet and Schmitz, 2005: fig. 2F).
454 The prearticular dentition of the Argentinian species differs from *G. hexagonus* in
455 having more main prearticular teeth (8–9 in *G. hexagonus* and *G. circularis*;
456 Poyato-Ariza & Wenz, 2002; Kriwet & Schmitz, 2005) and additionally sculptured
457 crown faces of at least the main and outer lateral teeth.

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

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

473 A right prearticular with preserved dentition identified as *Gyrodus* sp. cf. *G.*
474 *macrophthalmus* was also reported from the Kimmeridgian (Tamán Formation) of
475 Mexico by Dunkle and Maldano-Koerdell (1953). This specimen differs significantly
476 from *G. huiliches* in the presence of circular rather than oval main teeth and mesio-

477 laterally shorter outer lateral teeth. Additionally, the ornamentation of prearticular
478 teeth in the Mexican specimen differs significantly from those of the Patagonian
479 species (compare Dunkle and Maldano-Koerdell 1953: fig 1B).

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

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

493 Although the cranial skeleton is not well preserved and bony margins are
494 difficult to identify, some bones nevertheless also support that *Gyrodus huiliches*
495 sp. nov. represents a different species from *G. hexagonus* and *G. circularis*. The
496 'coronoid process' of *G. huiliches* sp. nov., for instance, is very club-shaped with an
497 elongated, slightly concave dorsal, a rather low and vertical anterior and an almost
498 sigmoidal posterior margin. In this, the 'coronoid process' of the Patagonian
499 species resembles that of various pycnodontiforms such as, e.g., *Macromesodon*,
500 *Turbomesodon*, *Micropycnodon*, *Neoprosclinetes*, and *Tepeixichthys* (Poyato-Ariza

501 and Wenz, 2002; Poyato-Ariza and Wenz, 2004; Ebert, 2013) but differs from that
502 of both *Gyrodus hexagonus* and *G. circularis* (compare Kriwet 2005: figs 16B,
503 30A). In *Gyrodus hexagonus*, the ‘coronoid process’ is low and antero-posteriorly
504 broad with an almost straight dorsal margin and a vertical, anteriorly inclined
505 posterior margin, where as it is higher, antero-posteriorly narrower and has an
506 almost horizontal dorsal margin in *G. circularis*.

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

511

512

513 Order Pycnodontiformes Berg, 1937

514 Family Gyrodontidae Berg, 1940

515 Genus ***Tranawün*** gen. nov.

516 Fig. 6

517

518 *Type species. Macromesodon agrioensis* Bocchino, 1977

519

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

523

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

538

539 *Stratigraphic and geographic distribution.* Lower Cretaceous, Neuquén Province,
540 Argentina.

541

542 ***Tranawün agrioensis*** (Bocchino, 1977)

543 1977 *Macromesodon agrioensis* – Bocchino, p. 176, pl. 1

544

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

546

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

549

550 *Diagnosis.* Same as for genus by monotypy.

551

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

557

558

559 **Description**

560

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

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

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

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

582 The second left lateral row is very incompletely preserved. It preserves only
583 two, sub-circular teeth that are arranged in an alternating pattern with the teeth of
584 the first left lateral row (Fig. 6A). These teeth are oval and have a faint
585 ornamentation consisting of an irregular rim surrounding a central depression (Fig.
586 6A).

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

593 In total, 13 teeth display remains of the original ornamentation, of which the
594 posterior-most three teeth in the first right lateral row and the posterior-most of the

595 intercalated teeth display almost no wear patterns. This is probably the result of
596 these teeth are quite small having occlusal surfaces that are positioned below the
597 grinding surface of the jaws and thus escaped abrasion (Fig. 6A). The
598 ornamentation in these teeth consists of two rather broad and crimped ridges
599 surrounding a central indent in which a slightly displaced papilla is located, and an
600 outer furrow surrounding the tooth crown. Additional nine teeth display an apical
601 indent, which is surrounded by more or less wrinkled, broad ridge. Reduction from
602 two to a single, broad occlusal ridge resulted from wear.

603

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

614 Almost all teeth have a more or less horizontal and completely smooth occlusal
615 surface indicating strong wear, which is conspicuous and comparable over all
616 preserved teeth (Fig. 6B). However, the second anterior tooth of the outermost
617 lateral tooth row displays remnants of an apical, very narrow and mesio-distally

618 short irregular indent indicating the originally presence of a crimped rim
619 surrounding the rim (Fig. 6B).

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

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

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

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

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

646

647 **Comparisons**

648

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

662 The character combination consisting of five longitudinal tooth rows with
663 uneven number and unequal size of teeth, the lateral vomerine tooth row with
664 intercalated teeth, four prearticular tooth rows with also intercalated teeth between

665 and outside tooth rows and small lateral-most teeth associated with an
666 ornamentation pattern that remind that of the teeth of, e.g., *Gyrodus*, easily
667 distinguishes the new taxon from all other known pycnodontiform fishes.

668 Bocchino (1977) originally assigned the vomer to *Macromesodon* based on the
669 presence of five, irregular tooth rows and presented a list of characters supporting
670 her interpretation (see Bocchino, 1977: 183), even so her also recognized
671 similarities to *Micropycnodon*. Numerous isolated vomers having five longitudinal
672 tooth rows were assigned to *Macromesodon* (= *Mesodon* Wagner, 1851) by Blake
673 (1905). Woodward (1895), for instance, listed 14 species of *Mesodon*.
674 Unfortunately, the vomerine dentition is not accessible in the holotype of the type-
675 species of *Macromesodon*, *M. macropterus* (BSPM AS VII 345). Another species,
676 *M. surgens* (Poyato-Ariza and Wenz, 2002) displays five longitudinal tooth rows
677 and teeth with occasional crenulations. Additionally, several specimens identified
678 as *M. macropterus* by Woodward (1895: 199-200) were assigned to a different
679 genus *Turbomesodon* by Poyato-Ariza and Wenz (2004). *Turbomesodon* is
680 characterised by three longitudinal vomerine tooth rows. Most pycnodontiform
681 fishes, however, have five longitudinal tooth rows in their vomerine dentition (e.g.,
682 *Brembodus*, *Coelodus sensu stricto*, *Gyrodus*, *Iemanja*, *Micropycnodon*, *Mesturus*,
683 *Oeloedus*, *Pycnodus*, *Tepexichthys*). The new taxon, nevertheless, differs
684 significantly from all other pycnodontiform fishes with five longitudinal vomerine
685 tooth rows in the very irregular number and size of teeth in corresponding lateral
686 tooth rows combined with the presence of intercalated teeth and the *Gyrodus*-like
687 crown ornamentation. Additionally, all vomerine teeth in *Macromesodon*, as far as

688 they are known, are sub-circular in outline and completely devoid of any
689 ornamentation (Poyato-Ariza and Wenz, 2004).

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

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

703 *Tranawün agrioensis* is easily to separate from the other pycnodontiform fish
704 also occurring in the Neuquén Basin, *Gyrodus huiliches*, nov. sp. but also from
705 other *Gyrodus* species in the presence of intercalated teeth and outermost lateral
706 teeth that are smaller than those in the middle portion of the first (inner) lateral row
707 (in *Gyrodus*, lateral-most teeth are significantly larger than those of the first lateral
708 row; see also above).

709 It should be noted that the prearticular teeth of *Tranawün* nov. gen. display
710 more variable tooth outlines ranging from circular to oval and even sub-rectangular

711 conversely to the condition seen in *Macromesodon* in which prearticular teeth are
712 predominantly oval as far as can be ascertained.

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

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

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

731 An incomplete left prearticular dentition from the Early Cretaceous of Colombia
732 assigned to *Macromesodon couloni* by Porta (1970) differs clearly from *Tranawün*
733 nov. gen. in having three tooth rows (with additional intercalated teeth) and much

734 broader and almost rectangular main teeth. The assignment of the Colombian
735 specimen to *Macromesodon* remains ambiguous.

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

740

741

742 **5. Discussion and conclusions**

743

744 Pycnodontiform fishes are a highly diverse group with major diversity peaks in
745 the Late Jurassic and Late Cretaceous with most records coming from Europe and
746 the middle East (e.g., Kriwet 2001, Martín-Abad and Poyato-Ariza, 2013). Long
747 ghost-lineages imply that the fossil record of Early Cretaceous pycnodonts is very
748 incomplete (compare Martín-Abad & Poyato-Ariza, 2013). In the Early Cretaceous
749 of Central and South America, the highly incomplete fossil record of
750 pycnodontiform may certainly represents a collecting bias. Thus, additional
751 fieldwork –with focus on fishes– will provide more material which may fill gaps in
752 the stratigraphic distribution of pycnodontiform fishes and help shorten ghost-
753 lineages. Yet, in South America, Early Cretaceous pycnodontiforms have been
754 reported from the Santana Formation (Aptian – Albian) of Brazil i.e., *Iemanjá*
755 *palma*, *Neoproscinetes penalvai*, *Mercediella riachuelensis*; all known from skeletal
756 remains (Wenz, 1989; Figueiredo and Silva Santos, 1991; Maisey, 1991), the
757 Rosablanca Formation (Barremian – Aptian) of Colombia i.e., *Macromesodon*

758 *couloni* (Porta, 1970), the Lo Valdés Formation (Aptian) of Chile i.e., *Paramicrodon*
759 *volcanensis* (Bocchino, 1977; Schultze, 1981; Arratia and Cione, 1996), and the
760 Agrio Formation (upper Valanginian – upper Hauterivian) of Argentina i.e.,
761 *Tranawün agrioensis* (Bocchino, 1977).

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

766 Both new Patagonian taxa described here display discrete dental characters
767 that separate these pycnodontiforms readily from all other known pycnodontiforms
768 but also support their close relationships with *Gyrodus*, either being a new species
769 of this genus or a closely related genus. *Gyrodus* is considered a Bajocian –
770 Tithonian genus that inhabited the Western Tethys and Peritethyan regions with its
771 greatest taxonomic diversity and palaeobiogeographical distribution during the Late
772 Jurassic (Kriwet, 2000; Kriwet and Schmitz, 2005; Martín-Abad and Poyato-Ariza,
773 2013). Early Cretaceous records of *Gyrodus* are very rare and according with
774 Kriwet and Schmitz (2005), questionable. Martín-Abad and Poyato-Ariza (2013)
775 presented a dispersal scenario of pycnodontiform fishes explaining the dispersal of
776 pycnodontiforms from the Tethys Sea, which is assumed to represent their centre
777 of radiation and their final refuge. These authors assume that seven genera
778 dispersed to the Americas including North and Central America. During the Late
779 Jurassic, basal pycnodontiforms might have been dispersed through the Hispanic
780 Corridor to South America (Kriwet, 2000; Kriwet and Schmitz, 2005; Martín-Abad
781 and Poyato-Ariza, 2013). Thus, *Gyrodus*, a basal pycnodontiform fish, might have

782 lived and proliferate in the warm ocean waters of southern South America at least
783 during the Early Cretaceous being a relict taxon. The new species –*Gyrodus*
784 *huiliches*– most likely diverged from a Central or South American species of
785 *Gyrodus* while the new Patagonian gyrodontid genus –*Tranawün*– described here
786 seemingly diverged from *Gyrodus* (we assume both taxa described here to be
787 closely related), which invaded the eastern Pacific coast line through the Hispanic
788 Corridor latest in the Oxfordian (Kriwet, 2000).

789

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791

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806 **7. References**

807

- 808 1. Agassiz, L. 1833–44. Recherches Sur Les Poissons Fossiles. Neuchâtel et
809 Soleure, Petitpierre, 1420 pp.
- 810 2. Aguirre-Urreta, M.B., Schmitz, M., Lescano, M., Tunik, M., Rawson, P.,
811 Concheyro, A., Buhler M., Ramos. V.A., 2017. A high-precision U-Pb
812 radioisotopic age for the Agrio Formation, Neuquén Basin, Argentina:
813 Implications for the chronology of the Hauterivian Stage. Cretaceous
814 Research 75, 193-204.
- 815 3. Arratia, G., Cione, A.L., 1996. The record of fossil fishes of Southern South
816 America. Müncher Geowissenschaftliche Abhandlugen 30 A, 9–72.
- 817 4. Benedetto, J.L., Sánchez, T., 1971. El hallazgo de peces Pycnodontiformes
818 (Holostei) en la Formación Yacoraite (Cretácico Superior) de la Provincia
819 de Salta, Argentina, y su importancia paleobiológica. Acta Geológica
820 Lilloana 11, 151–176.
- 821 5. Benedetto, J.L., Sanchez, T., 1972. *Coelodus toncoensis* nov. sp. (pisces,
822 Holostei, Pycnodontiformes) de la Formación Yacoraite (Cretácico
823 Superior) de la Provincia de Salta. Ameghiniana 14, 59–71.
- 824 6. Bengston, P., 1988. Open Nomenclature. Palaeontology 31, 223–227.
- 825 7. Berg, L.S., 1937. A classification of fish-like vertebrates. Bulletin de
826 l'Académie Des Sciences de l'URSS 4.
- 827 8. Berg, L.S., 1940. Classification of fishes both recent and fossil [in Russian].
828 Travaux de l'Institut Zoologique de l'Académie Des Sciences de l'URSS 5
829 1277–1280.

- 830 9. Blainville, H.D. de., 1818. Poissons fossiles. Nouvelle Dictionnaire d'Histoire
831 Naturelle. Nouvelle Édition 27, 334–361.
- 832 10. Blake J.F., 1905. A monograph of the fauna of the Cornbrash.
833 Palaeontographical Society.
- 834 11. Bocchino, A., 1977. Un nuevo Gyrodontidae (Pisces, Holostei,
835 Pycnodontiformes) de la Formación Agrio (Cretácico Inferior) de la
836 Provincia de Neuquén, Argentina. *Ameghiniana* 14:175–185.
- 837 12. Capasso L.L., Taverne L., Nohra A.R. 2010. A re-description of , a
838 remarkable coccodontid fish (Actinopterygii, †Pycnodontiformes) from the
839 Cenomanian (Late Cretaceous) of Haqel, Lebanon. *Bulletin de l'Institut*
840 *Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 80, 145–
841 162.
- 842 13. Cawley, J., Kriwet J., 2018. A new pycnodont fish, *Scalacurvichthys naishi*
843 gen. et sp. nov., from the Late Cretaceous of Israel. *Journal of Systematic*
844 *Palaeontology* 16:659–673.
- 845 14. Cione, A.L., Pereira S.M., 1990. Los peces del Jurásico posterior a los
846 movimientos intermálmicos y del Cretácico inferior de Argentina In W.
847 Volkheimer and E.A. Musacchio (Eds.), *Bioestratigrafía de los Sistemas*
848 *Regionales del Jurásico y Cretácico en América del Sur. Vol. 1: Jurásico*
849 *anterior a los movimientos intermálmicos. Comité Sudamericano del*
850 *Jurásico y Cretácico. Editorial Inca., Mendoza, 385–395.*
- 851 15. Cónsole Gonella, C.A., Griffin, M., Cione, A.L., Gouiric-Cavalli, S.,
852 Aceñolaza F., 2012. Paleontología de la Formación Yacoraite
853 (Maastrichtiano-Daniano) en el ámbito de la Subcuenca de Tres Cruces,

- 854 Cordillera Oriental de la provincia de Jujuy, Argentina. XIII Reunión
855 Argentina de Sedimentología, Relatorio, 45–56.
- 856 16. Cope, E.D., 1887. Zittel's Manual of Paleontology. American Naturalist 17,
857 1014–1019.
- 858 17. Dunkle, D. H., Maldonado-Koerdell, M., 1953, Notes on some Mesozoic
859 fossil fish remains from Mexico: Journal of Washington Academic Science
860 43, 311–317.
- 861 18. Ebert, M., 2013. The Pycnodontidae (Actinopterygii) in the late Jurassic:
862 The genus *Proscinetes* Gistel, 1848 in the Solnhofen Archipelago
863 (Germany) and Cerin (France). Archaeopteryx 31, 22–43.
- 864 19. Ebert, M., 2018. *Cerinichthys koelblae*, gen. et sp. nov., from the Upper
865 Jurassic of Cerin, France, and its phylogenetic setting, leading to a
866 reassessment of the phylogenetic relationships of Halecomorphi
867 (Actinopterygii). Journal of Vertebrate Paleontology
868 doi.org/10.1080/02724634.2017.1420071.
- 869 20. Figueiredo, F.J., Silva Santos, R., 1991. Pycnodontes da Formação
870 Riachuelo, Membro Taquari, Estado de Sergipe, Nordeste do Brasil. Anais
871 Da Academia Brasileira de Ciências 64, 369–379.
- 872 21. Forey, P.L., Lu, Y., Patterson, C., Davies, C.E. 2003. Fossil fishes from the
873 Cenomanian (Upper Cretaceous) of Namoura, Lebanon. Journal of
874 Systematic Palaeontology 1, 227–330.
- 875 22. Gale, A.S., 2000. The Cretaceous world. In: S. J. Culver, P. F. Rawson,
876 (Eds.), Biotic Response to Global Change. The Last 145 Million Years.
877 Cambridge University Press, Cambridge, 1–19.

- 878 23. Gregory, W. 1923. A Jurassic fish fauna from western Cuba: with an
879 arrangement of the families of holostean ganoid fishes. Bulletin of the
880 American Museum of Natural History 48, 223–242.
- 881 24. Hennig, E. 1906. *Gyrodus* und die organisation der Pycnodonten.
882 Palaeontographica 53, 137–208.
- 883 25. Howell, J.A., Schwarz, E., Spalletti, L.A., Veiga, G.D., 2005. The Neuquen
884 Basin: an overview In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E.
885 (Eds.), The Neuquen Basin, Argentina: a Case Study in Sequence
886 Stratigraphy and Basin Dynamics. Geological Society, London, Special
887 Publications, vol. 252, 1–14.
- 888 26. Kemp, A. Berrel, R.W., 2013. Lungfish as environmental indicators. In: G.
889 Arratia, H.-P. Schultze, M. V. H. Wilson (Eds.), Mesozoic Fishes-Global
890 Diversity and Evolution. Verlag Dr. Friedrich Pfeil, München, 499–508.
- 891 27. Kriwet, J., 2000. Revision of *Mesturus cordillera* Martill et al., 1998
892 (Actinopterygii, Pycnodontiformes) from the Oxfordian (Upper Jurassic) of
893 Northern Chile. Journal of Vertebrate Paleontology 20, 450–455.
- 894 28. Kriwet, J., 2001a. Feeding mechanisms and ecology of pycnodont fishes
895 (Neopterygii, Pycnodontiformes). Mitt. Mus. Nat.kd. Berl., Geowiss. Reihe
896 4:139–165.
- 897 29. Kriwet, J. 2001b. Palaeobiogeography of pycnodontiform fishes
898 (Actinopterygii, Neopterygii). Seminario de Paleontología de Zaragoza 5.1:
899 121-130.
- 900 30. Kriwet, J., 2005. A comprehensive study of the skull and dentition of
901 pycnodont fishes. Zitteliana Reihe A: Mitteilungen Der Bayerischen

- 902 Staatssammlung Fur Palaontologie Und Geologie 45, 135–188.
- 903 31. Kriwet, J., 2008. The dentition of the enigmatic pycnodont fish, *Athrodon*
904 *wittei* (Fricke, 1876) (Neopterygii, Pycnodontiformes; Late Jurassic; NW
905 Germany). Fossil Record 11, 61–66.
- 906 32. Kriwet, J., Schmitz, L., 2005. New insight into the distribution and
907 palaeobiology of the pycnodont fish *Gyrodus*. Acta Palaeontologica
908 Polonica 50, 49–56.
- 909 33. Lambers, P.H., 1991. The Upper Jurassic actinopterygian fish *Gyrodus*
910 *dichactinius* Winkler 1862 (*Gyrodus hexagonus* [Blainville 1818]) from
911 Solnhofen, Bavaria and anatomy of the genus *Gyrodus* Agassiz.
912 Proceedings Koninklijke Akademie van Wetenschappen 94, 489–544.
- 913 34. Leanza, H.A., Hugo, C.A., Repol, D., 2001. Hoja geológica 3969-I, Zapala,
914 provincia de Neuquén. Servicio Geológico Minero Argentino, Boletín 275,
915 128 pp.
- 916 35. Legarreta, L., Gulisano C.A., 1989. Análisis estratigráfico secuencial de la
917 Cuenca Neuquina (Triásico superior-Terciario inferior). In: G. Chebli and L.
918 A. Spalletti (Eds.), Cuencas Sedimentarias Argentinas. Serie Correlación
919 Geológica 6, INSUGEO, San Miguel de Tucumán, Argentina, 221–243.
- 920 36. Longbottom, A.E. 1984. New Tertiary pycnodonts from the Tilemsi valley,
921 Republic of Mali. Bulletin of the British Museum (Natural History), Geology
922 38, 1–26.
- 923 37. Maisey, J.G., 1991. Santana Fossils Illustrated Atlas.pdf. T.F.H.
924 Publications, Inc., United States, 459 pp.
- 925 38. Martill, D. M., Chong, G., Pardo G., 1998. A new pycnodont (Pisces,

- 926 Actinopterygii) from the Jurassic of Chile. *Neues Jahrbuch Für Geologie*
927 *Und Paläontologie – Monatshefte*, 485–493.
- 928 39. Martín-Abad, H., Poyato-Ariza, F. J., 2013. Historical patterns of distribution
929 in Pycnodontiform and Amiiform fishes in the context of moving plates.
930 *Geologica Belgica* 16, 217–226.
- 931 40. Marramá, G., Villier, B., Dalla Vecchia, F.M., Carnevale, G., 2016. A new
932 species of *Gladiopycnodus* (Coccodontoidea, Pycnodontomorpha) from the
933 Cretaceous of Lebanon provides new insights about the morphological
934 diversification of pycnodont fishes through time. *Cretaceous Research* 61,
935 34–43.
- 936 41. Moore, D.M., Reynolds Jr., R.C., 1997. X-Ray Diffraction and the
937 Identification and Analysis of Clay Minerals, 2nd ed. Oxford, New York:
938 Oxford University Press, 378 pp.
- 939 42. Nursall, J.R., 1996a. The phylogeny of pycnodont fishes. In G. Arratia and
940 G. Viohl (Eds.), *Mesozoic Fishes-Systematics and Paleoecology*. Verlag Dr.
941 Friedrich Pfeil, München, 125–152.
- 942 43. Nursall, J.R., 1996b. Distribution and ecology of pycnodont fishes. In: G.
943 Arratia and G. Viohl (Eds.), *Mesozoic Fishes-Systematics and*
944 *Paleoecology*. Verlag Dr. Friedrich Pfeil, München, 115–124.
- 945 44. Nursall, J.R., 1999. The pycnodontiform bauplan: the morphology of a
946 successful taxon. In: G. Arratia and H.-P. Schultze (Eds.), *Mesozoic Fishes*
947 *2—Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil, Munich, 189–
948 214.
- 949 45. Porta, J., 1970. Presencia de Pycnodontiformes en el Cretáceo inferior de

- 950 Colombia. Geología Colombiana 7, 99–103.
- 951 46. Poyato-Ariza, F.J., 2003. Dental characters and phylogeny of
952 pycnodontiform fishes. Journal of Vertebrate Paleontology 23, 937–940.
- 953 47. Poyato-Ariza, F.J., 2005. Pycnodont fishes: morphologic variation,
954 ecomorphologic plasticity, and a new interpretation of their evolutionary
955 history. Bulletin of the Kitakyushu Museum of Natural History and Human
956 History A, 169–184.
- 957 48. Poyato-Ariza, F.J., Martín-Abad, H., 2013. History of two lineages:
958 Comparative analysis of the fossil record in Amiiformes and
959 Pycnodontiformes (Osteichthyes, Actinopterygii). Spanish Journal of
960 Palaeontology 28, 79–90.
- 961 49. Poyato-Ariza, F.J., Bermúdez-Rochas, D.D. 2009. New pycnodont fish
962 (*Arcodonichthys pasiegae* gen. et sp. nov.) from the Early Cretaceous of
963 the Basque-Cantabrian Basin, Northern Spain. Journal of vertebrate
964 Paleontology 29, 271–275.
- 965 50. Poyato-Ariza, F.J., Wenz S., 2002. A new insight into pycnodontiform
966 fishes. Geodiversitas 24:139–248.
- 967 51. Poyato-Ariza, F. J., Wenz, S., 2004. The new pycnodontid fish genus
968 *Turbomesodon*, and a revision of *Macromesodon* based on new material
969 from the Lower Cretaceous of Las Hoyas, Cuenca, Spain. In: G. Arratia and
970 A. Tintori (Eds.), Mesozoic Fishes 3—Systematics, Paleoenvironments and
971 Biodiversity. Verlag Dr. Friedrich Pfeil, Munich, 341–378.
- 972 52. Poyato-Ariza, F.J., Wenz S., 2005. *Akromystax tilmachiton* gen. et sp. nov
973 ., a new pycnodontid fish from the lebanese Late Cretaceous of Haqel and

- 974 En Nammoura. *Journal of Vertebrate Paleontology* 25, 27–45.
- 975 53. Poyato-Ariza, F.J., Talbot, M.R., Fregenal-Matínez, M.A., Meléndez, N.,
976 Wenz, S., 1998. First isotopic and multidisciplinary evidence for nonmarine
977 coelacanths and pycnodontiform fishes: palaeoenvironmental implications.
978 *Palaeogeography, Palaeoclimatology, Palaeoecology* 144, 65–84.
- 979 54. Regan, C.T., 1923. The skeleton of *Lepidosteus*, with remarks on the origin
980 and evolution of the lower neopterygian fishes. *Proceedings of the*
981 *Zoological Society of London* 1923, 445–461.
- 982 55. Richiano, S., Varela, A.N., Gómez Peral, L.E., Cereceda, A., Poiré, D.G.,
983 2015. Composition of the Lower Cretaceous source rock from the Austral
984 Basin (Río Mayer Formation, Patagonia, Argentina): Regional implication
985 for unconventional reservoirs in the Southern Andes. *Marine and Petroleum*
986 *Geology* 66, 764–790.
- 987 56. Schultz, L.G., 1964. Quantitative interpretation of mineralogical composition
988 from X-ray and chemical data for Pierra Shale. *United States Geological*
989 *Survey Professional Paper* 391, 1–31.
- 990 57. Schultze, H.-P., 1981. A pycnodont dentition (*Paramicrodon volcanensis* n.
991 sp.; Pisces, Actinopterygii) from the Lower Cretaceous of El Volcán Región,
992 South East Santiago, Chile. *Revista Geológica de Chile* 12, 87–93.
- 993 58. Schultze, H. P. 1993. The head skeleton of fishes. In: J. Hanken and B.K.
994 Hall (Eds.), *The skull*. Volume 2. The University of Chicago Press, Chicago,
995 189–254.
- 996 59. Schultze, H.-P., 2008. Nomenclature and homologization of cranial bones
997 in actinopterygians. In: G. Arratia, H-P. Schultze and M.V.H Wilson (Eds.),

- 998 Mesozoic Fishes 4—Homology and Phylogeny. Verlag Dr. Friedrich Pfeil,
999 Munich, 23–48.
- 1000 60. Schwarz, E., Spalletti, L.A., Veiga, G.D., Fanning M., 2016. First U-Pb
1001 SHRIMP Age for the Pilmatué Member (Agrio Formation) of the Neuquén
1002 Basin, Argentina: Implications for the Hauterivian Lower Boundary.
1003 Cretaceous Research 58, 223–233.
- 1004 61. Spalletti, L.A., Veiga, G.D., Schwarz E., 2011. La Formación Agrio en la
1005 Cuenca Neuquina. In H. Leanza, C. Arregui, O. Carbone, J. C. Danieli and
1006 J. Vallés (Eds.), Relatorio del XVIII Congreso Geológico Argentino.
1007 Asociación Geológica Argentina, Neuquén, Argentina, 145-160.
- 1008 62. Stumpf, S., Ansorge, J., Pfaff, C., Kriwet J., 2017. Early Jurassic
1009 diversification of pycnodontiform fishes (Actinopterygii, Neopterygii) after
1010 the end-Triassic extinction event: evidence from a new genus and species,
1011 *Grimmenodon aureum*. Journal of Vertebrate Paleontology, DOI:
1012 10.1080/02724634.2017.1344679.
- 1013 63. Thurmond, J.T., 1974. Lower vertebrates faunas of the Trinity Division in
1014 North-Central Texas. Geoscience and man 8, 103–129.
- 1015 64. Vullo, R., Cavin, L., Khalloufi, B., Amaghazaz, M., Bardet, N., Jalil, N.E.,
1016 Jourani, E., Khaldoune, F., Gheerbrant, E., 2017. A unique Cretaceous-
1017 Paleogene lineage of piranha-jawed pycnodont fishes. Scientific Reports 7,
1018 1–9.
- 1019 65. Vullo, R., Archambeau, J.-P., Bailly, G., Bénéfice P., 2018. Reassessment
1020 of *Cosmodus* Sauvage, 1879, a poorly known genus of large pycnodont fish
1021 (Actinopterygii, Pycnodontiformes) from the Cenomanian (Upper

- 1022 Cretaceous) of Western Europe. *Cretaceous Research* 91, 217–228.
- 1023 66. Wagner, A. 1851. Beiträge zur Kenntnis der in den lithographischen
1024 Schiefen abgelagerten urweltlichen Fische. *Abhandlungen der königlich
1025 bayerischen Akademie der Wissenschaften* 6, 80 pp.
- 1026 67. Weaver, C.E., 1931. *Paleontology of the Jurassic and Cretaceous of West
1027 Central Argentina*. University of Washington, Memoir 1, 469 pp.
- 1028 68. Wenz, S. 1989. *Iemanja palma* n. g., n. sp., Gyrodontidae nouveau (Pisces,
1029 Actinopterygii) du Crétacé inférieur de la Chapada do Araripe (N-E du
1030 Brésil). *Comptes Rendus des Séances de l'Académie des Sciences de
1031 Paris sér. 2a*, 308, 975–980.
- 1032 69. Westoll, T.S., 1943. The origin of the tetrapods. *Biological Review* 18, 78–
1033 98.
- 1034 70. Woodward, A.S., 1893. Some Cretaceous pycnodont fishes. *Geological
1035 Magazine, Decade 3*, 10, 433–436, 487–493.
- 1036 71. Woodward, A.S. 1985. *Catalogue of the fossil fishes in the British Museum
1037 (Natural History)*. Part III; Containing the Actinopterygian Teleostomi of the
1038 Orders Chondrostei (concluded), Protospondyli, Aethospondyli, and
1039 Isospondyli (in part). Trustees of the British Museum (Natural History),
1040 London, 544 p.
- 1041

1042 **Figure captions**

1043

1044 **Figure 1.** Measurements taken over the studied specimens. Abbreviations: pmh,
 1045 prearticular maximum height; ptl, prearticular total length; tw, tooth width; td, tooth
 1046 depth. Scale bar: 10 mm.

1047 **Figure 2. A,** Location map showing the pycnodontiform localities. Pampa de Tril
 1048 locality (37° 15' 05''S, 69° 48' 21''W) and Puerta de Curaco locality (37° 22'
 1049 47''S, 69° 55' 45'' W); **B,** general view of lower section of the Pampa de Tril
 1050 locality; **C,** General view of the upper section of Puerta de Curaco locality.

1051 **Figure 3.** Stratigraphic log of the Agrio Formation at Puerta de Curaco and Pampa
 1052 de Tril localities.

1053 **Figura 4.** *Gyrodus huiliches* sp. nov., MOZ-Pv 1327, **A,** holotype in medial view
 1054 and **B,** labial view. Anatomical abbreviations: ang, angular; art, articular; bhy,
 1055 basihyal; chy, ceratohyal; cl, cleithrum; cor, 'coronoid process'; dt, dermal tesserae
 1056 ect, ectopterygoid; ent, entopterygoid; io; infraorbital; p, parietal [= frontal]; hyo,
 1057 hyomandibula; mc, Meckel's canal; met, mesethmoid; mpt, metapterygoid; opp,
 1058 opercular process; pop, preopercle; preart, prearticular; pro, prootic; q, quadrate;
 1059 sc, scale; sph, sphenotic; sy, symplectic. Scale bar: 10 mm.

1060 **Figure 5.** Dentitions **A–C,** holotype of *Gyrodus huiliches* sp. nov. MOZ-Pv 1327,
 1061 prearticular dentition under Uv light; **C,** detail of tooth ornamentation; **D,** holotype of
 1062 *Tranawün agrioensis* gen. nov. MLP- 75-V-18-1, detail of the ornamented teeth of
 1063 the vomerine dentition. Scale bar: A–B, 10 mm; C–D, 3 mm.

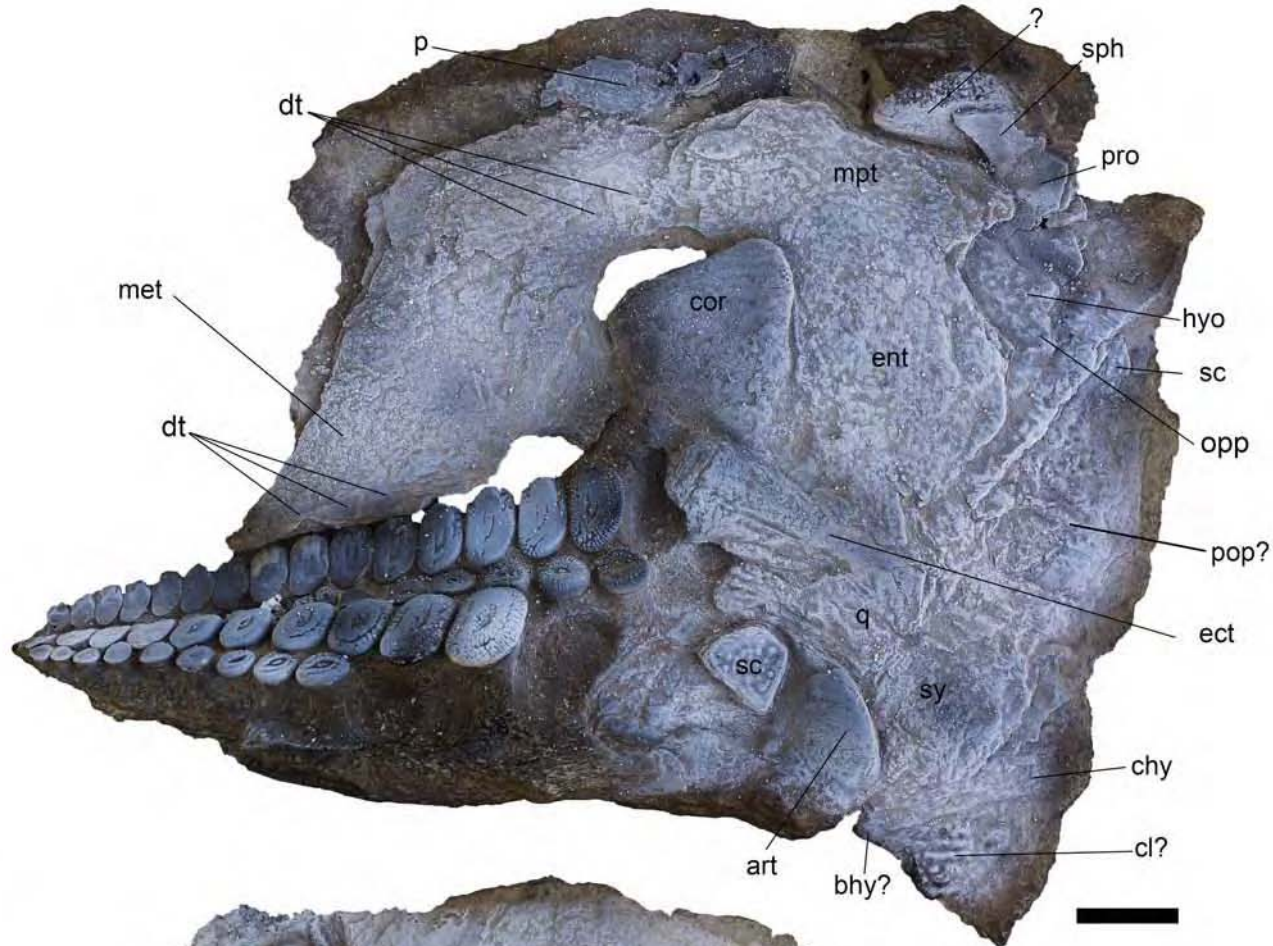
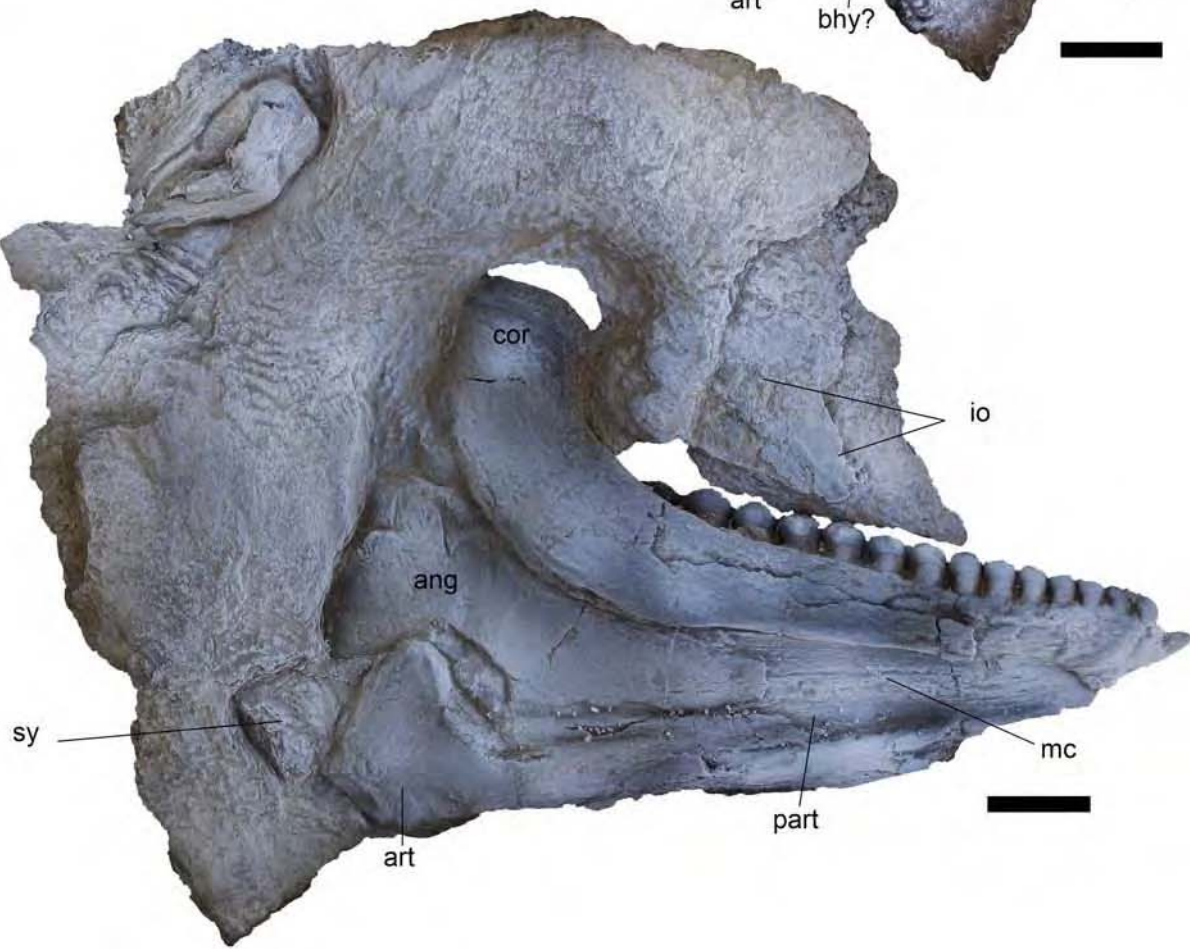
1064 **Figure 6.** *Tranawün agrioensis* gen. nov. (Bocchino, 1977), **A,** holotype MLP 75-V-
 1065 18-1 vomerine dentition; **B,** MOZ-Pv 1316 prearticular dentition in lingual view; **C,**

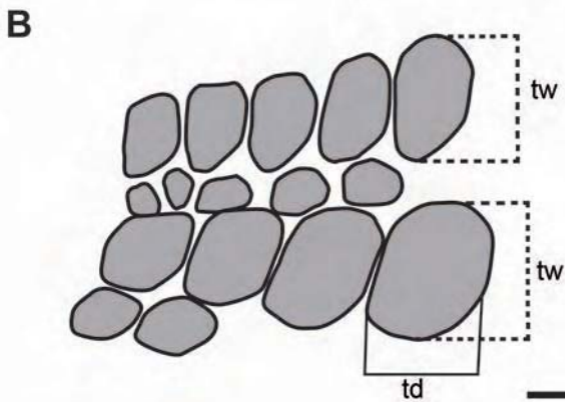
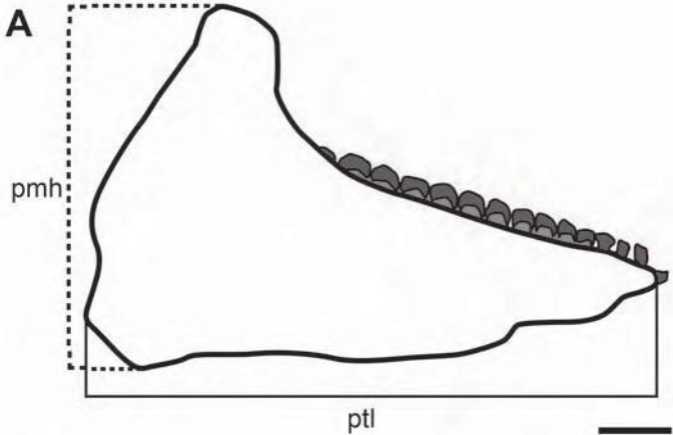
1066 MOZ-Pv 1316 prearticular dentition in labial view. The arrow indicates rostrally

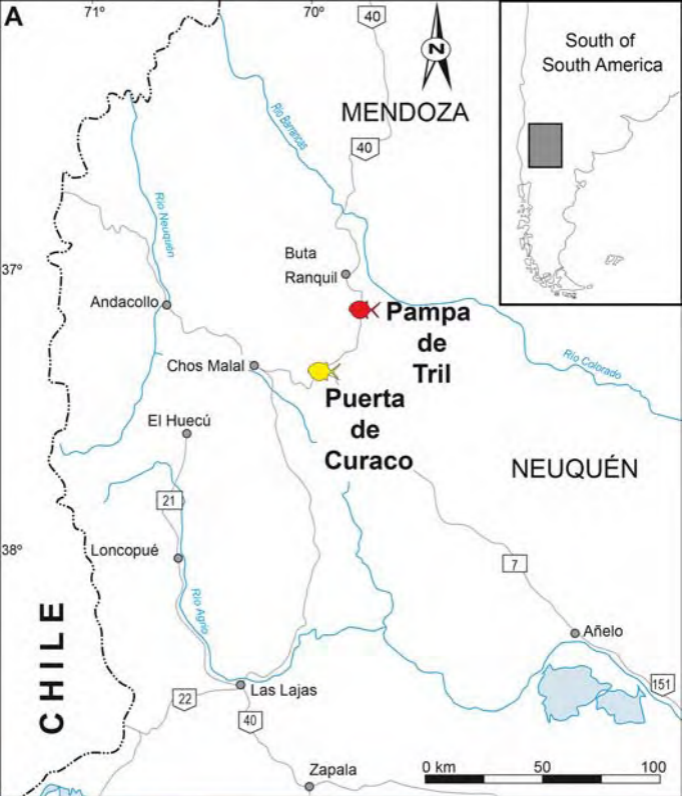
1067 direction. Scale bar: 10 mm.

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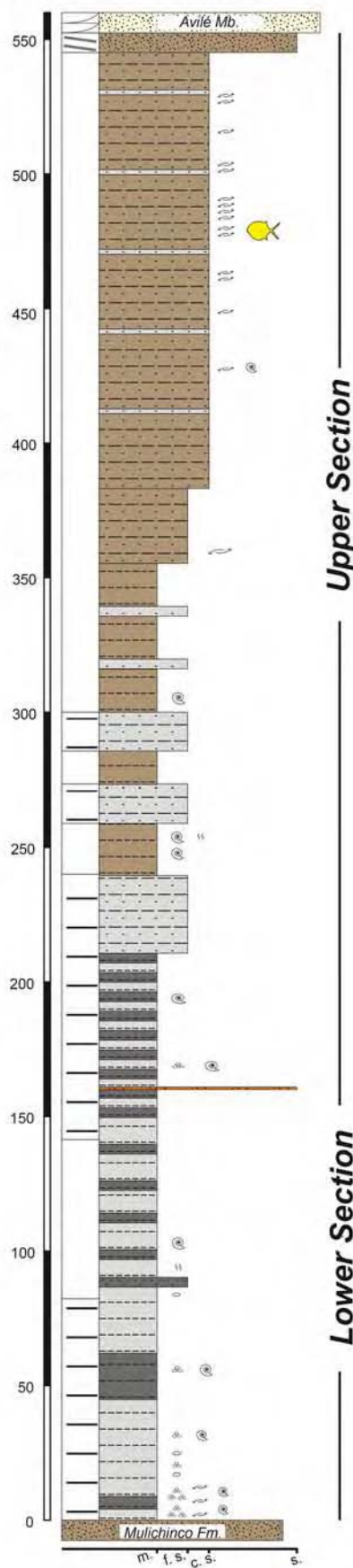
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A**B**





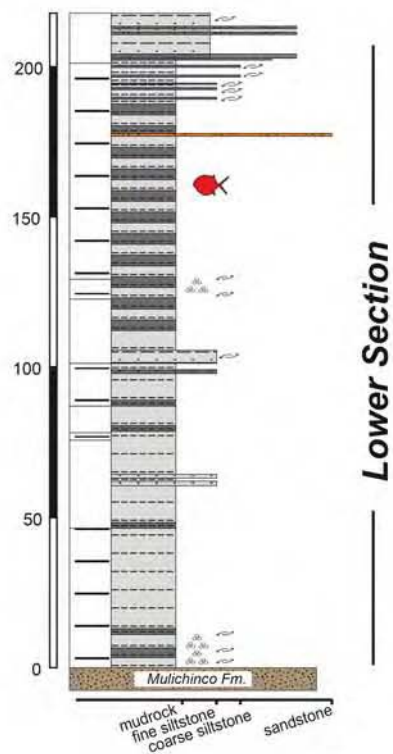
Puerta de Curaco section



Upper Section

Lower Section

Pampa de Tril section



Lower Section

- | Lithology | | Fossils | |
|-------------------|--------------------|----------------------------|--|
| Mudrocks | Claystones | Disarticulated bivalves | |
| | Maristones | Ammonoids | |
| | Mudstones | Foraminifers | |
| Fine siltstones | Siliciclastic-rich | <i>Gyrodus hueche</i> | |
| | Carbonate-poor | <i>Tranawün agrioensis</i> | |
| | Carbonate-rich | | |
| Coarse siltstones | Siliciclastic-rich | | |
| | Carbonate-poor | | |
| | Carbonate-rich | | |
| Sandstones | Siliciclastic-rich | | |
| | Carbonate-rich | | |
| | Tuff layer | | |
| | | Structures | |
| | | Lamination | |
| | | Massive | |



