A quantitative approach to determine the taxonomic identity and ontogeny of the pycnodontiform fish *Pycnodus* (Neopterygii, Actinopterygii) from the Eocene of Bolca Lagerstätte, Italy

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Background. The pycnodontiform fish *Pycnodus* is one of the representatives of the highly diverse actinopterygian fish fauna from the early Eocene Bolca Lagerstätte, representing one of the youngest and thus last occurrences of the extinct neopterygian clade Pycnodontiformes. This genus has historically been used as a wastebasket taxon in regards to poorly known pycnodontiform fossils and authors have argued over the specific status of the Bolca Lagerstätte *Pycnodus* in terms of how many species are contained within the genus with some arguing for multiple species and others suggesting lumping all Bolca specimens together into one species.

Methods. Here, we use a quantitative approach performing biometric and geometric morphometric analyses on 39 specimens of *Pycnodus* in order to determine if the morphological variability within the sample might be related to inter- or intraspecific variation.

Results. The analyses revealed that the variations of body shape, morphometric and meristic characters are continuous and cannot be used to distinguish different morphotypes. On the contrary, our results show a remarkable link between shape and size, related to ontogeny.

Discussion. Differences in body shape of small (juvenile) and large (adult) individuals is probably related to different microhabitats occupation on the Bolca reef with juveniles sheltering within crevices on the reef and adults being more powerful swimmers that swim above the coral. There is no evidence of nocturnal feeding in this pycnodont as previously hypothesized. Taxonomically, we suggest that the Bolca *Pycnodus* should be referred to strictly as *Pycnodus apodus* as this was the name given to the holotype. Additionally, an overview of species assigned to *Pycnodus* is given.

1 **A quantitative approach to determine the taxonomic identity**
2 **and ontogeny of the pycnodontiform fish Pycnodus**
3 **(Neopterygii, Actinopterygii) from the Eocene of Bolca**
4 **Lagerstätte, Italy**

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31 **ABSTRACT**

33 **Background.** The pycnodontiform fish *Pycnodus* is one of the representatives of the highly

34 diverse actinopterygian fish fauna from the early Eocene Bolca Lagerstätte, representing one of

35 the youngest and thus last occurrences of the extinct neopterygian clade Pycnodontiformes. This

36 genus has historically been used as a wastebasket taxon in regards to poorly known

37 pycnodontiform fossils and authors have argued over the specific status of the Bolca Lagerstätte

38 *Pycnodus* in terms of how many species are contained within the genus with some arguing for

39 multiple species and others suggesting lumping all Bolca specimens together into one species.

40 **Methods.** Here, we use a quantitative approach performing biometric and geometric

41 morphometric analyses on 39 specimens of *Pycnodus* in order to determine if the morphological

42 variability within the sample might be related to inter- or intraspecific variation.

43 **Results.** The analyses revealed that the variations of body shape, morphometric and meristic

44 characters are continuous and cannot be used to distinguish different morphotypes. On the

45 contrary, our results show a remarkable link between shape and size, related to ontogeny.

46 **Discussion.** Differences in body shape of small (juvenile) and large (adult) individuals is

47 probably related to different microhabitats occupation on the Bolca reef with juveniles sheltering

48 within crevices on the reef and adults being more powerful swimmers that swim above the coral.

49 There is no evidence of nocturnal feeding in this pycnodont as previously hypothesized.

50 Taxonomically, we suggest that the Bolca *Pycnodus* should be referred to strictly as *Pycnodus*

51 *apodus* as this was the name given to the holotype. Additionally, an overview of species assigned

52 to *Pycnodus* is given.

INTRODUCTION

Pycnodontiform fishes were a highly successful group of neopterygian fishes that colonized shallow marine, brackish, and freshwater habitats from the Norian to the middle Eocene and were a very successful group of bony fishes for ca. 170 Ma (e.g., Tintori, 1981; Longbottom, 1984; Poyato-Ariza et al., 1998; Kriwet 2005). They were particularly diverse during the Late Cretaceous when they showed the highest degree of morphological diversity (Marramà et al., 2016a; Cawley & Kriwet, 2017). Pycnodonts underwent a severe drop in their diversity and disparity at end of the Cretaceous, and the last representatives survived in restricted biotopes until the Middle Eocene (Poyato-Ariza, 2005; Marramà et al., 2016a). One of the last Palaeogene representatives is *Pycnodus apodus* (Volta 1796), represented by several complete and articulated skeletons from the early Eocene (late Ypresian, c. 49 Ma) (Papazzoni et al., 2014; Marramà et al., 2016b) Bolca Koservat-Lagerstätte. This deposit yielded a huge amount of exquisitely preserved fishes, which are housed today in several museums and research institutions around the world, and that are represented by more than 230 bony and cartilaginous fish species (see e.g. Blot, 1987; Blot & Tyler, 1990; Bannikov, 2004, 2006, 2008; Bannikov & Carnevale, 2009, 2010, 2016; Carnevale & Pietsch, 2009, 2010, 2011, 2012; Carnevale et al., 2014, 2017; Marramà & Carnevale, 2015a, b, 2016, 2017; Marramà et al., 2017a, b).

Pycnodus apodus has had a long and complex taxonomic history (see e.g., Blot, 1987; Poyato-Ariza & Wenz, 2002). Volta (1796) originally designated it as *Coryphaena apoda*. Blainville (1818) subsequently redescribed the same specimens without illustrations, and erected for them the taxon *Zeus platessus*. Finally, Agassiz (1833, 1839) created the genus *Pycnodus* for these specimens but keeping the specific name of Blainville (1818). Heckel (1856) erected using the same material (but probably also including other specimens) from Bolca a second species of *Pycnodus*, *P. gibbus*, due to differential characters such as the relative length of the first caudal vertebral apophyses and the body depth being one and a half times that of the body length in contrast to *P. platessus* having a body depth twice that of the length. Agassiz (1844), however, regarded this species as a juvenile *Pycnodus platessus*. More recently, Blot (1987) examined specimens that were labelled *P. platessus* in various institutional collections and compared their anatomy to that of specimens, labelled *P. gibbus* and concluded that *P. gibbus* is synonymous with *P. platessus* and variations recorded among specimens were due to intraspecific differences. However, this hypothesis has never been tested employing a robust quantitative approach.

85 Traditional and geometric morphometrics (Zelditch et al., 2004) have been successfully used to

86 interpret the patterns of morphospace occupation, quantifying the morphological diversification,

87 solve taxonomic debates, as well as to test if morphological variations are due to intra- or

88 interspecific variability (Wretman, Blom & Kear, 2016; Marramà & Carnevale, 2017; Marramà

89 et al., 2017c).

90   In this perspective, this paper aims to analyse if the morphological variation among

91 *Pycnodus* species of Bolca, can be related to interspecific or intraspecific (ontogenetic)

92 variability as hypothesized by Blot (1987). For this, we examined abundant *Pycnodus* specimens

93 from various museum collections which were labelled as either *P. apodus*, *P. platessus*, *P.*

94 *gibbus* or *Pycnodus* sp. to establish whether these species separate substantially from each other

95 in the morphospace and if morphometric and meristic data can be useful to detect significant

96 differences between morphotypes and thus taxa. Since the studied sample had a range of

97 specimens of different sizes, we investigated whether different shapes can be related to possible

98 ontogentic differences of *Pycnodus* representing different growth stages from juvenile to adult.

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100

MATERIAL AND METHODS

Specimen sampling

103 We studied a selection of *Pycnodus* specimens from various museum collections, which were

104 labelled either *P. apodus*, *P. platessus*, *P. gibbus* or *Pycnodus* sp. A total of 39 *Pycnodus*

105 specimens from nine museum collections were finally used because they provided sufficient

106 morphological information for the aim of this study (BM; Museo dei Fossili di Bolca; BMNH,

107 Natural History Museum of London; BSPG, Bayerische Staatssammlung für Paläontologie und

108 Geologie, München, Germany; CM, Carnegie Museum, Pittsburgh, Pennsylvania; FMNH, Field

109 Museum of Natural History, Chicago; MGP-PD; Museo di Geologia e Paleontologia

110 dell'Università di Padova; MNHN, Muséum National d'Histoire Naturelle, Paris; MCSNV,

111 Museo Civico di Storia Naturale di Verona; NHMW; Naturhistorisches Museum Wien) (see

112 Supplementary material). The sample includes 17 specimens identified originally as *Pycnodus*

113 sp., 14 specimens as *P. platessus*, six specimens as *P. gibbus*, and two specimens as *P. apodus*.

114

Geometric morphometric protocol

116   A total of 18 landmarks and 14 semi landmarks were digitized on photos taken from the studied

117   specimens in the corresponding collections using the software TPSdig (Rohlf, 2005). Landmarks

118   indicating homologous points and were selected on the basis of their possible ecological or

119   functional role following the scheme applied in some studies about shape variation in modern or

120   extinct fishes (Figure 1). The landmark coordinates were translated, rotated and scaled at unit

121   centroid size by applying a Generalized Procrustes Analysis (GPA) to minimize the variation

122   caused by size, orientation, location and rotation (Rohlf & Slice, 1990; Zelditch et al., 2004). The

123   GPA was performed using the TPSrelw software package (Rohlf, 2003) and a principal

124   component analysis (PCA) was performed on Procrustes coordinates to obtain the Relative Warp

125   (RW). Shape changes were shown along the axes using deformation grid plots.

126   Two non-parametric tests were performed to analyse the quantitative morphospace

127   occupation of our *Pycnodus* specimens. In order to assess the degree of overlap between

128   morphospaces, an analysis of similarities (ANOSIM, Clarke, 1993) was performed on the entire

129   dataset of standardised morphometric and meristic parameters. PERMANOVA (Anderson, 2001)

130   was used to test similarities of in-group centroid position between the different groups

131   representing a species of *Pycnodus*. Euclidean distances are the distance measure chosen for both

132   tests. All statistical analyses were performed in PAST 3.18 (Hammer, Harper & Ryan, 2001).

133   Since the studied specimens vary greatly in size (smallest being 4.0 cm and largest being

134   30.6 cm) we also investigated whether size could be correlated with shape change in *Pycnodus*

135   and enable us to see whether and how body shape changes throughout ontogeny. To analyse the

136   relationship between size and shape, we performed a Partial Least Square analysis (PLS) using

137   the software TPSpls (Rohlf & Corti, 2000). Alpha (level of significance) was set to 0.05.

138

139   **Biometric analyses**

140   We used nine meristic counts and 19 measurements in order to capture morphological variability,

141   to test the homogeneity of the sample, and confirming its assignment to a single species.

142   Histograms were used to illustrate the continuous variation of morphometric and meristic data in

143   order to ascertain if more than one species of *Pycnodus* could be identified. Least squares

144   regression was used to obtain the relationship between standard length (SL) and all other

145   morphometric variables. Specimens of possible additional taxa were indicated by the presence of

146   statistical outliers from the regression line (Simon et al., 2010) and will require additional

147 scrutiny in order to truly differentiate the outlier from all other specimens. The linear regression

148 results were shown using scatterplots. Log-tranformed data were used to perform the least

149 squares regression in order to determine the degree of correlation between the standard length

150 (SL) and all other morphometric variables.

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152

153 **RESULTS**

154 **Geometric morphometrics**

155 The relative warp analysis produced 38 RWs with the first three axes together explaining about

156 72% of the total variation. Figures 2 and 3 show that there is significant overlap between the

157 morphospaces of the *Pycnodus* taxonomic groups and the thin plate splines show the changes in

158 shape along the axes. Negative values on RW1 (56.1% explained) are related to *Pycnodus*

159 specimens with large orbits and deep bodies while positive scores identify *Pycnodus* with

160 reduced orbits and elongated bodies. Negative values of RW2 (10.4% explained) show

161 specimens having the pectoral fin with a wide base moved higher up the body alongside a long

162 caudal peduncle (Figure 2). Conversely, on positive scores of RW2 lie specimens with pectoral

163 fin with a narrower base located more ventrally on the body alongside a small caudal peduncle.

164 The negative values of RW3 (6% explained) show the skull becoming deeper and more

165 elongated with the dermosupraoccipital in particular reaching far back (Figure 3). Body becomes

166 shallower near the caudal peduncle with the cloaca shifting posteriorly, as well as the dorsal

167 apex. Positive scores of RW3 are related to a shorter and shallower skull with the body becoming

168 deeper close to the caudal peduncle and the anterior shift in the cloaca with the body becoming

169 deeper just anterior to the cloaca. The dorsal apex shifts forward in position.

170   ANOSIM performed on the first three axes suggests that there is strong overlap between

171 groups, showing they are barely distinguishable from each other (p > 0.05; see Table 1), except

172 for a single pairwise comparison between *Pycnodus* sp. and *P. platessus* (p < 0.05). The

173 PERMANOVA suggests the same trend, showing that group centroids are not significantly

174 different on each pairwise comparison (p > 0.05), except between *Pycnodus* sp. and *P. platessus*

175 (p < 0.05). Significant differences detected between *Pycnodus* sp. and *P. platessus* can be

176 explained with the fact that the indeterminate *Pycnodus* specimens show a wide range of

177 morphologies, with the extreme shapes ranging from negative to positive values of all the first

178 three axes.

179   The PLS performed on the entire sample (Figure 4) revealed a strong and significant

180 correlations between size and shape (r = 0.88; p < 0.05), therefore suggesting that different

181 shapes of the individuals are related to changes in shape of different ontogenetic stages. In fact,

182 small-sized individuals are associated with larger orbits, deeper skull and body shape, long skull,

183 higher position of pectoral fin and a wide, indistinct caudal peduncle that is in distant proximity

184 to both medial fins. Larger individuals, on the other hand, have a reduced orbit, shallower skull

185 and body depth, shorter skull, lower position of pectoral fin and narrow caudal peduncle in close

186 proximity to both medial fins. The PLS analysis therefore suggests that the morphological

187 variations of the orbit, body depth and caudal peduncle are strongly related to ontogeny.

188

189 **Biometric analyses**

190 Morphometrics and meristic counts for all the studied specimens are given in Table 2 and mean

191 biometric parameters are given in Table 3. Most of the histograms based on meristic counts

192 (Figure 5) show a normal (Gaussian) distribution with intermediate states dominating and

193 extreme states being rare. The linear regression performed on morphometric characters (Figure

194 6) shows that all specimens fit within the cloud of points near the regression line and that no

195 particular specimens of *Pycnodus* deviates from this line. This is confirmed by the high values of

196 the coefficient of determination (r^2) ranging from 0.76-0.99 (Table 4) indicating a high degree of

197 positive correlation between standard length and each morphometric character. Linear regression

198 analysis also revealed the highly significant relationship between the standard length and all

199 morphometric characters (p < 0.001). Neither morphometric nor meristic characters are therefore

200 useful in determining two or more different morphologically identifiable morphotypes within

201 *Pycnodus*, corroborating definitively Blot's (1987) hypothesis that only one species (*P. apodus*;

202 see also below) is present in the Bolca Lagerstätte.

203

204

205 **DISCUSSION**

206 **Intraspecific variation of *Pycnodus apodus***

207   The results demonstrate that all *Pycnodus* species cannot be separated in a quantitative approach,

208   confirming the intraspecific variation hypothesis of Blot (1987). The hypothesis by Agassiz

209   (1844) that *Pycnodus gibbus* is specifically the juvenile of *P. platessus* can be rejected as a

210   specimen referred to as *P. platessus* (MGP-PD 6880Z) is smaller than most of the specimens

211   assigned to *P. gibbus*, including all of them in our sample (see Supplementary Material). As

212   suggested by Grande and Young (2004), ontogenetic variation of morphological characters

213   actually represents a primary source of intraspecific variation; this is confirmed by our analysis,

214   specifically by the morphological changes mostly occurring along RW1 in the morphospace that

215   are related to ontogeny and the very significant results deriving from the PLS analysis. The

216   unimodal (Gaussian) distribution of most of the meristic data, displayed by the frequency

217   histograms, reveals a clear domination of intermediate values and comparably rare extremes,

218   which is typical of a homogenous population. Data show that any morphological variation is

219   continuous and the recognition of high frequency of intermediate states and low frequency of

220   extreme values makes separation of the *Pycnodus* sample into discrete groups impossible. This

221   suggests that all specimens studied belong to a single or taxonomic entity (see Dagys, Bucher &

222   Weitschat, 1999; Dagys, 2001; Weitschat, 2008; Marramà & Carnevale, 2015a; Sferco, López-

223   Arbarello & Báez, 2015). Furthermore, the linear regression showed a significant dependence

224   between standard length and all morphometric variables, therefore suggesting that morphometric

225   characters are not useful to distinguish different morphotypes.

226   Figure 7 shows some notable differences between the juvenile and larger specimens

227   including the degree of ossification, particularly in the skull and caudal fin, being smaller in

228   juvenile in comparison to adults and the notochord not being surrounded by arcocentra in

229   juveniles whereas it is completely enclosed in adults. Differences in meristic counts (Table 5) are

230   suggestive of intraspecific variation as seen in other fossil actinopterygians (Stensiö, 1935;

231   Lehman, 1952; Patterson, 1973; Su, 1973; Zhang & Zhang, 1980; Olsen, 1984; Tintori, 1990;

232   Bürgin, 1992; Dietze, 1999, 2000; Thies & Hauff, 2011; Xu, Shen & Zhao, 2014; Tintori et al.,

233   2015; Wretman, Blom & Kear, 2016; Marramà et al., 2017c). The analysis of the morphological

234   variability of *Pycnodus*, one of the last representatives of a basal neopterygian lineage that has

235   been around since at least the Late Triassic (Tintori, 1981; Kriwet 2001a; Poyato-Ariza, 2015;),

236   indicates that pycnodontiforms also produce substantial intraspecific variation similar to living

237   representatives of other ancient actinopterygian lineages such as amiids (Jain, 1985) and

238   acipenserids (Hilton & Bemis, 1999). Therefore, the identification of different Bolca *Pycnodus*

239   species such as *P. gibbus* (Heckel, 1856), may be the result of species over-splitting and can be

240   on the contrary explained by intraspecific variation.

241

242   **Habitat use during ontogeny**

243   Our morphometric results show that the morphology of the smaller individuals differ

244   significantly from that of the adults and that *Pycnodus*, like extant actinopterygians, would go

245   through morphological changes throughout ontogeny. Large eye size found in the smaller

246   *Pycnodus* specimens is usually a sign of the specimen being in a juvenile stage as can be seen in

247   many extant teleosts (Pankhurst & Montgomery, 1990). This rejects the interpretation of

248   Goatley, Bellwood & Bellwood (2010), who interpreted *Pycnodus* in the Monte Bolca

249   assemblage to be a nocturnal feeder based on the orbit size in relation to standard length.

250   Seemingly, these authors only used juveniles in their analysis. The deep body shape of the

251   smaller *Pycnodus* specimens can be interpreted as a sign that the juveniles live within the

252   branches of corals and as they get bigger they start to occupy the water column above the reef.

253   This change to a benthopelagic lifestyle also is supported by the more fusiform body and the

254   narrower caudal peduncle (Webb, 1982) seen in larger specimens. Ecologically similar extant

255   analogues to *Pycnodus*, the sparid species *Diplodus sargus* and *D. puntazzo* also spend their time

256   as juveniles in crevices in the rocks in shallow water 0-2 m deep and move to rocky bottoms and

257   sea grass beds when adult (Macpherson, 1998). Ontogenetically–related habitat changes also

258   occur in other coral fishes, such as labrids, in which the pectoral fins increase their aspect ratio as

259   these fishes grow in size, enabling them to increase their use of the water column while juveniles

260   stay closer to the bottom (Fulton, Bellwood & Wainwright, 2002). Since both juveniles and

261   adults of *Pycnodus* are found in the Bolca Lagerstatte, we hypothesize that unlike many modern

262   coral reef fishes, which significantly change the habitat during ontogeny (Nagelkerken et al.,

263   2002; Dorenbosch et al., 2005a, b; Adams et al., 2006; Nagelkerken, 2007; Nakamura et al.,

264   2008; Shibuno et al., 2008; Kimirei et al., 2011), there is a shift instead in microhabitat use

265   within the reef, in this case juveniles living within coral crevices to adults roaming over the coral

266   reefs.

267

268   **The taxonomic history of *Pycnodus***

269

270   *Pycnodus* has long been used as wastebasket taxon in the study of pycnodontiforms, being used

271   as a default name for many taxa even in the Mesozoic until later revisions revealed the taxa to

272   have significant morphological differences with *Pycnodus* as to be renamed as separate taxa.

273   Species of pycnodontiforms previously referred to as *Pycnodus* include *Anomoeodus subclavatus*

274   from the Maastrichtian of the Netherlands (Agassiz, 1833; Davis, 1890; Forir, 1887); other

275   species of *Anomoeodus* referred to as *Pycnodus* include *A. angustus*, *A. muensteri*, *A. phaseolus*,

276   *A. sculptus* (Agassiz, 1844) and *A. distans* (Coquand, 1860; Sauvage, 1880). *Pycnodus liassicus*

277   Egerton, 1855 from the Early Jurassic, of Barrow-on-Soar of Leicestershire, United Kingdom

278   was assigned to the genus *Eomesodon* by Woodward (1918) and *Stemmatodus rhombus*

279   (Agassiz, 1839) from the Early Cretaceous of Capo d'Orlando, close to Naples, Italy was

280   originally named *Pycnodus rhombus* (see Heckel, 1854). *Pycnodus flabellatum* Cope, 1866 from

281   the Cenomanian-Coniacian of Brazil was assigned to *Nursallia flabellatum* by Blot (1987). The

282   pycnodonts *Pycnodus achillis* Costa 1853, *Pycnodus grandis* Costa 1853 and *Pycnodus*

283   *rotundatus* Costa 1864 are all synonymous with *Ocloedus costae* (d'Erasmo, 1914, Poyato-Ariza

284   & Wenz, 2002). Poyato-Ariza (2013) revised *"Pycnodus" laveirensis* Veiga Ferreira 1961 from

285   the Cenomanian of Lavieras, Portugal and found that due to morphological differences in

286   characters such as absence of dermocranial fenestra, number of premaxillary teeth, contact type

287   of arcocentra and median fin morphology, it represents a member of a different genus and

288   consequently erected the new genus *Sylvienodus* as a replacement. An articulated specimen of

289   '*Pycnodus*' was found in the Campanian-Maastrichtian of Nardo, Italy, which certainly

290   represents a different pycnodont (Taverne, 1997). An extremely fragmentary specimen referred

291   to as "*Pycnodus" nardoensis* from Apulia (Nardo), Italy is comprised of the anterior part of the

292   body along with some posterior elements of the skull (Taverne, 1997). However, in a later study

293   Taverne (2003) studied new material of this taxon, which revealed that this species does not

294   belong to *Pycnodus* due to as the possession of a narrower cleithrum and peculiar morphology of

295   the contour scales. This new data led to *Pseudopycnodus* being erected as a new genus for the

296   Nardo material.

297   All other Mesozoic species of *Pycnodus* are based on isolated dentitions or teeth. The

298   earliest records of *Pycnodus* are dentitions found in the limestones from the Upper Jurassic

299   (Kimmeridgian) of Orbagnoux, France (Sauvage, 1893). Isolated teeth and an isolated vomerine

300   dentition were referred to cf. *Pycnodus* sp. (Goodwin et al., 1999) from the Mugher Mudstone

301   formation of the Tithonian. However, its identity is doubted due to the stratigraphic position and

302   could be attributed to *Macromesodon* (Kriwet, 2001b). Pictet, Campiche & Tribolet (1858-60)

303   described remains of the Early Cretaceous fish assemblages from Switzerland where three

304   species of *Macromesodon* (*M. couloni* from the Hauterivian and Barremian, *M. cylindricus* from

305   the Valanginian, Barremian, and Aptian and *M. obliqus* from the Albian) were all originally

306   referred to as *Pycnodus*. Isolated dentitions belonging to '*Pycnodus*' *heterotypus* and '*Pycnodus*'

307   *quadratifer* were reported from the Hauterivian of the Paris basin (Cornuel, 1883, 1886). Several

308   isolated teeth derived from the Cenomanian strata of the Chalk Group of southern England were

309   attributed to *Pycnodus scrobiculatus* Reuss 1845 whose systematic affinity is still uncertain.

310   Other teeth belonging to *P. scrobiculatus* were reported from the Turonian of northern Germany.

311   Roemer (1841) described isolated remains belonging to *Pycnodus harlebeni* from the Late

312   Cretaceous of Hilsconglomerat of Ostenvald, Germany. Another possible Portuguese

313   representative of *Pycnodus* is reported from the Turonian of Bacarena, '*Pycnodus*' sp. aff. '*P.*'

314   *gigas* Jonet 1964. However, the identification of the Portuguese specimens as *Pycnodus* are

315   uncertain and the material most likely pertains to a differentpycnodont taxon (Kriwet, 2001b).

316   Isolated dentitions of what were claimed to be *Pycnodus scrobiculatus*, *P. rostratus* and *P.*

317   *semilunaris* from the Turonian of Czechoslovakia (Reuss, 1845) should be regarded as

318   indeterminable pycnodontids due to the lack of characters useful to determine their affinities

319   (Kriwet, 2001b). Isolated teeth attributed to "*Pycnodus*" *lametae* were reported from the

320   Maastrichtian Lameta Formation of Dongargaon, India (Woodward, 1908).

321   *Pycnodus* is the most dominant taxon of the Palaeogene pycnodont faunas being widely

322   distributed in shallow water contexts worldwide. The earliest record of *Pycnodus* in the

323   Palaeogene is represented by *Pycnodus praecursor* from the Danian of Angola (Dartevelle &

324   Casier, 1949) and *P.* sp. cf. *P. praecursor* from the Thanetian of Niger (Cappetta, 1972).

325   *Pycnodus toliapicus* was reported from the Thanetian of Togo, Thanetian of Nigeria and the

326   upper Palaeocene of Niger (White, 1934; Kogbe & Wozny, 1979; Longbottom, 1984). Several

327   remains of isolated dentitions and teeth from the Eocene have been attributed to *Pycnodus*. These

328   include *Pycnodus bicresta* from the northwestern Himalayan region, India (Prasad & Singh,

329   1991); *Pycnodus bowerbanki* from the Ypresian, England, middle Eocene of Mali and Ypresian

330   of Algeria (Longbottom, 1984; Savornin, 1915); *Pycnodus* sp. cf. *P. toliapicus* from the Eocene

331   of Katar at the Persian Gulf (Casier, 1971); *Pycnodus toliapicus* from the Ypresian and Lutetian

332   of England and Lutetian of the Paris basin and Belgium (Savornin, 1915; Casier, 1950; Taverne

333   & Nolf, 1978); *Pycnodus mokattamensis* from the Lutetian of Egypt (Priem, 1897); *P.*

334   *mokattamensis* occurs alongside *Pycnodus legrandi*, *Pycnodus lemellefensis*, *Pycnodus*

335   *thamallulensis*, *Pycnodus vasseuri* and *Pycnodus pellei* from the Ypresian of Algeria (Savornin,

336   1915); *Pycnodus pachyrhinus* Grey-Egerton 1877 from the Ypresian of Kent, England; *Pycnodus*

337   *funkianus* Geinitz 1883 from the Ypresian of Brunswick, Germany; *Pycnodus munieri* Priem

338   1902 and *Pycnodus savini* Priem 1902 from the Ypresian, France and a rather diverse

339   assemblage from the middle Eocene of Mali which includes *Pycnodus jonesae*, *P. maliensis*, *P.*

340   *munieri*, *P. variablis* and *P. zeaformis* (Longbottom, 1984).

341   A nearly complete specimen of *P. lametae* with crushed skull and missing caudal fins

342   was reported from the freshwater Maastrichtian of Bhatali, India close to the Dongargaon area

343   (Mohabey & Udhoji, 1996). However, the assignment of the name *Pycnodus* to this fish is

344   dubious, since it has an operculum and lacks the post-parietal process typical of the

345   Pycnodontidae (pers. obs.). A more complete specimen of *Pycnodus* was found from the

346   Palaeocene rocks of Palenque, Mexico (Alvarado-Ortega et al., 2015), its only difference with

347   the Eocene specimens from Bolca being a greater number of ventral and post-cloacal ridge

348   scales, less dorsal- and anal-fin pterygiophores and a large or regular-sized posteriormost neural

349   spine. However, due to the inadequacy of the available sample, it is not possible to determine the

350   actual differences between the Palaeocene material from Mexico and that from the Eocene of

351   Bolca, and for this reason this taxon is referred to as *Pycnodus* sp.

352   In this perspective, most species referred to *Pycnodus* are not valid (all Jurassic and

353   Cretaceous *Pycnodus* specimens being other taxa) and with the majority of Palaeogene *Pycnodus*

354   being represented by isolated dentitions and teeth it seems that the only definitive articulated

355   skeletal remains attributed to the genus *Pycnodus* are the Bolca specimens and *Pycnodus* sp.

356   from south-eastern Mexico (Alvarado-Ortega et al., 2015).

357

358

359   **CONCLUSIONS**

360   The quantitative approach here performed confirms the findings of Blot (1987) that the various

361   *Pycnodus* species (*P. apodus*, *P. platessus*, *P. gibbus*) from the Eocene Bolca Konservat-

362 Lagerstätte actually belong to a single species. Due to the holotype of *Pycnodus* being given the
363 specific name of *apoda*, all known specimens of *Pycnodus* from Bolca should be referred to as
364 *Pycnodus apodus*. Most of the morphological variation can be explained by the close association
365 between morphology and ontogeny with juveniles and adults occupying different parts of the
366 morphospace. The morphological differences between juveniles and adults may be due to
367 occupation of different habitats with juveniles sheltering within nooks and crannies on the reef
368 and adults being better adapted to a benthopelagic lifestyle of swimming over the reef and going
369 to the benthos to feed. Future studies should look at other problematic pycnodontiform taxa such
370 as the widely distributed *Gyrodus* from the Middle Jurassic to the Early Cretaceous (Kriwet &
371 Schmitz, 2005) to investigate if the intraspecific variation might explain the supposed diversity
372 of species this genus contains.

373

374

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829 **Figure captions**

830

831 Figure 1: Landmarks represented by black circles, which were used on *Pycnodus* for the

832 geometric morphometric analysis. These are 1) tip of premaxilla; 2) ventralmost margin of orbit;

833 3) posteriormost margin of orbit; 4) anteriormost margin of orbit; 5) dorsalmost margin of orbit;

834 6) first dorsal pterygiophore; 7) last dorsal pterygiophore; 8) tip of dorsal lobe of caudal fin; 9)

835 medial convex margin of caudal fin; 10) tip of ventral lobe of caudal fin; 11) final anal

836 pterygiophore; 12) first anal pterygiophore; 13) posterior cloacal scale; 14) anterior cloacal scale;

837 15) joint between quadrate and prearticular; 16) ventral most concave margin of cleithrum

838 accommodating pectoral fin; 17) dorsal most concave margin of cleithrum accommodating

839 pectoral fin; 18) Point of contact between neurocranium and vertebral column. The

840 semilandmarks are reperesented by small white circles and are split into two sets; the first set

841 consists of seven semilandmarks between the tip of the dermosupraoccipital and the base of the

842 first principal caudal fin ray; the second set has an additional seven semilandmarks between the

843 base of the ventral most principal caudal fin ray and the antero-ventral corner of the cleithrum.

844 Illustration of *Pycnodus* is modified from Blot (1987).

845

846 Figure 2: Morphospace of *Pycnodus* on the first two RW axes together accounting for about 66%

847 of the overall shape variation. Deformation grids illustrate the shapes lying at extreme values

848 along each axis.

849

850   Figure 3: Morphospace of *Pycnodus* showing RW 1 on the x-axis and RW 3 on y-axis the latter
851   accounting for 6% of the overall shape variation. Deformation grids illustrate the shapes lying at
852   extreme values along each axis.

853

854   Figure 4: PLS analysis showing a correlation of morphology with ontogeny. Smallest, medium
855   sized and largest specimens are used to represent the juvenile, small adult and large adult stages
856   respectively. Significance of this correlation is shown by the r and p-values. Smallest specimen
857   is 4.02 cm,medium sized specimen is 10.6 cm, largest specimen is 30.6 cm.

858

859   Figure 5: Histograms showing the distributions of meristic characters of *Pycnodus*. The x-axis
860   represents the number of elements and the y-axis the relative frequency. Anatomical
861   abbreviations: Anal-fin pterygiophores AFP, Anal-fin rays AFR, Caudal-fin rays CFR, Dorsal-
862   fin pterygiophores DFP, Dorsal-fin rays DFR, Pectoral-fin rays PEC, Pelvic-fin rays PEL, Rib
863   pairs RIB, Scale bars SCL, Vertebrae VER.

864

865   Figure 6: Scatterplots and regression lines with 95% confidence bands of the relationships
866   between each morphometric character and the standard length of *Pycnodus*. Anatomical
867   abbreviations: Anal-fin base AFB, Caudal peduncle depth CPD, Caudal peduncle length CPL,
868   Caudal-fin span CFS, Dorsal-fin base DFB, Head depth HD, Head length HL, Lower jaw length
869   JL, Maximum body depth MBD, Orbit diameter OD, Pectoral-fin base PFB, Postorbital length
870   POSTO, Preanal distance PANA, Predorsal distance PDOR, Preorbital length PREO, Prepectoral
871   distance PPEC, Prepelvic distance PPEL.

872

873   Figure 7: Ontogenetic series of *Pycnodus*. (a) juvenile 4.02 cm (MCSNV T.309). (b) small adult
874   13.25 cm (BSPG AS I 1208). (c) large adult 30.61 cm (BSPG AS I 1209). Scale bar for (a) and
875   (b) equals 1 cm and is 10 cm for (c).

876

877   **Table captions**

878

879   Table 1: ANOSIM and PERMANOVA results.

880

881   Table 2: Measurements as percentage of SL (mean values in parentheses) for *Pycnodus*. Range

882   of measurements are represented by the 25th and 75th percentile in order to exclude outliers.

883

884   Table 3: Mean morphometric and meristic data for the examined specimens of *Pycnodus*.

885

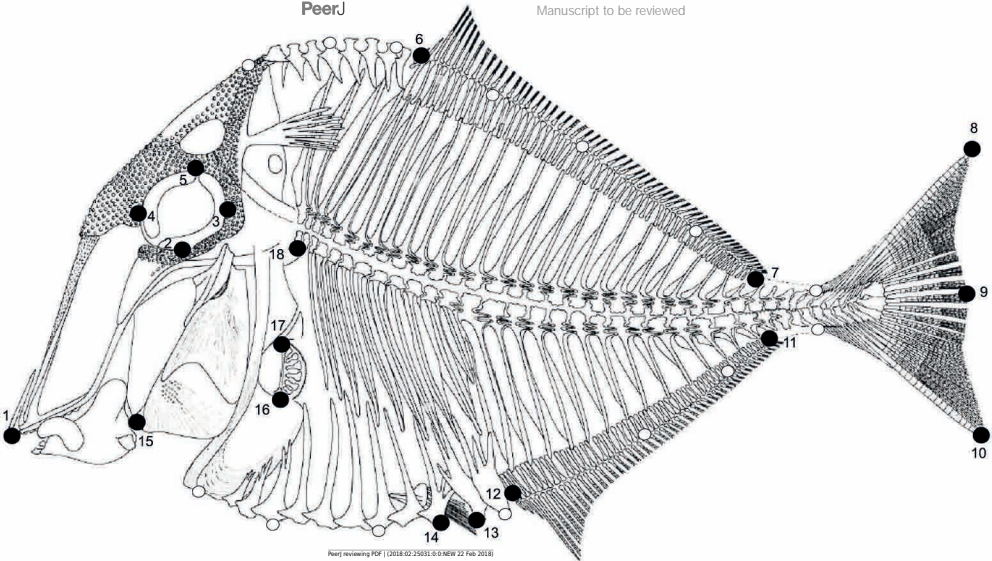
886   Table 4: Relationships between morphometric characters and standard length using least squares

887   regression for *Pycnodus*.

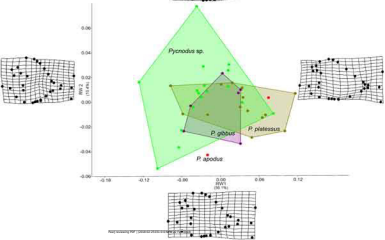
888

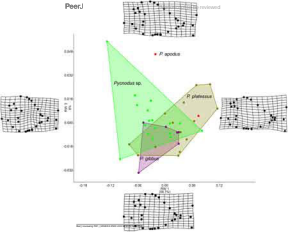
889   Table 5: Meristic counts of *Pycnodus*.

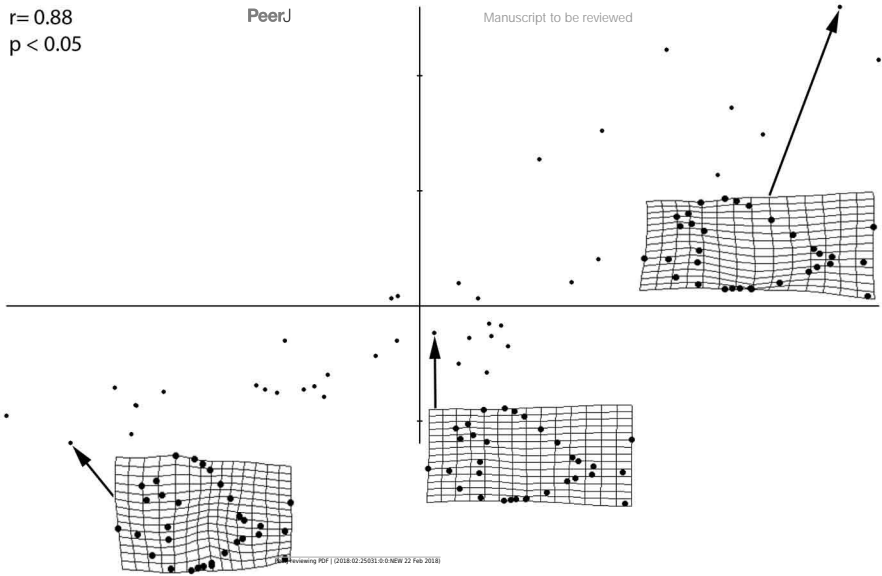
Landmarks represented by black circles, which were used on *Pycnodus* for the geometric morphometric analysis.

These are 1) tip of premaxilla; 2) ventralmost margin of orbit; 3) posteriormost margin of orbit; 4) anteriormost margin of orbit; 5) dorsalmost margin of orbit; 6) first dorsal pterygiophore; 7) last dorsal pterygiophore; 8) tip of dorsal lobe of caudal fin; 9) medial convex margin of caudal fin; 10) tip of ventral lobe of caudal fin; 11) final anal pterygiophore; 12) first anal pterygiophore; 13) posterior cloacal scale; 14) anterior cloacal scale; 15) joint between quadrate and prearticular; 16) ventral most concave margin of cleithrum accommodating pectoral fin; 17) dorsal most concave margin of cleithrum accommodating pectoral fin; 18) Point of contact between neurocranium and vertebral column. The semilandmarks are represented by small white circles and are split into two sets; the first set consists of seven semilandmarks between the tip of the dermosupraoccipital and the base of the first principal caudal fin ray; the second set has an additional seven semilandmarks between the base of the ventral most principal caudal fin ray and the antero-ventral corner of the cleithrum. Illustration of *Pycnodus* is modified from Blot (1987).

Morphospace of *Pycnodus* on the first two RW axes.

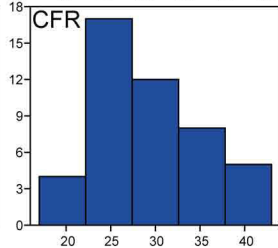
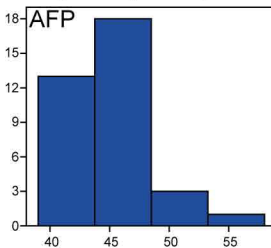
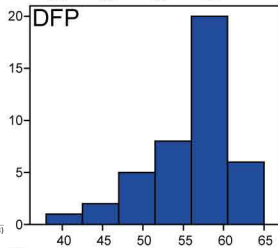
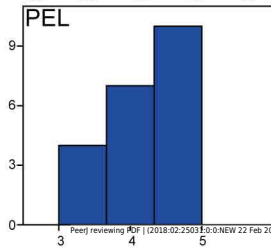
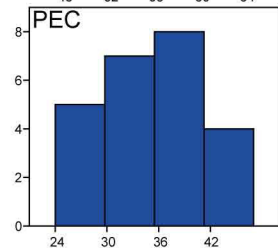
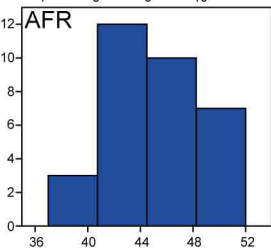
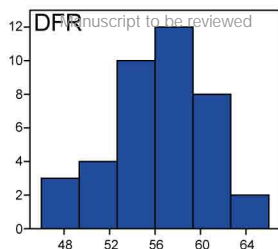
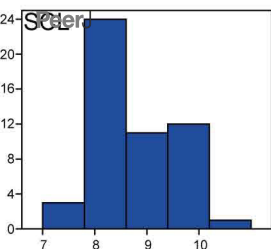
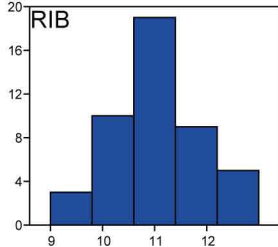
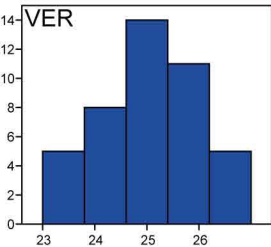
The first two RW axes together accounting for about 66% of the overall shape variation.

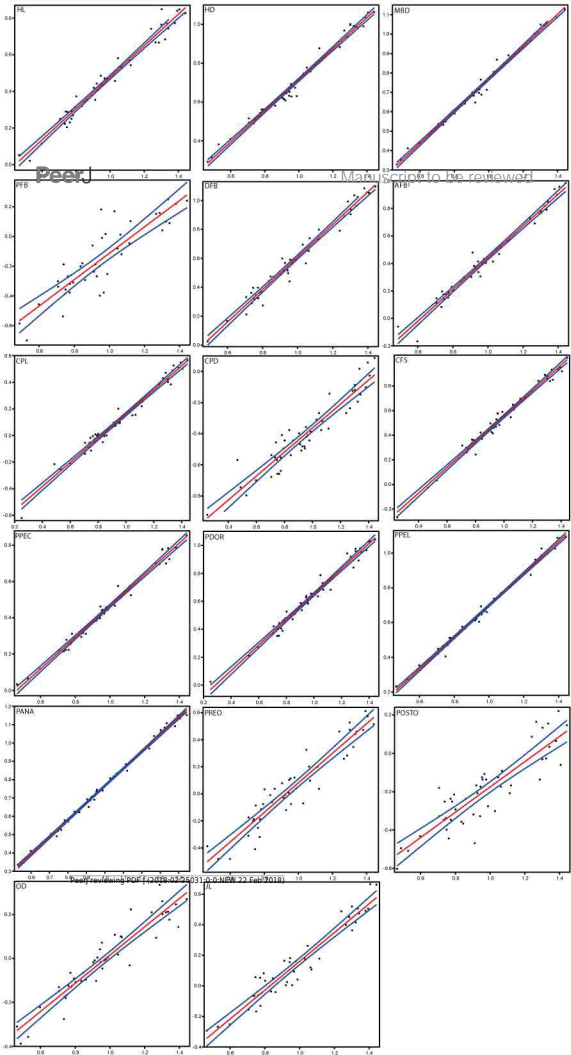
Deformation grids illustrate the shapes lying at extreme values along each axis.

Morphospace of *Pycnodus* showing RW 1 on the x-axis and RW 3 on y-axis.

RW3 accounts for 6% of the overall shape variation. Deformation grids illustrate the shapes lying at extreme values along each axis.

PLS analysis showing a correlation of morphology with ontogeny.

Smallest, medium sized and largest specimens are used to represent the juvenile, small adult and large adult stages respectively. Significance of this correlation is shown by the r and p-values. Smallest specimen is 4.02 cm,medium sized specimen is 10.6 cm, largest specimen is 30.6 cm.

r= 0.88
p < 0.05

Histograms showing the distributions of meristic characters of *Pycnodus*.

The x-axis represents the number of elements and the y-axis the relative frequency. Anatomical abbreviations: Anal fin pterygiophores AFP, Anal fin rays AFR, Caudal fin rays CFR, Dorsal fin pterygiophores DFP, Dorsal fin rays DFR, Pectoral fin rays PEC, Pelvic fin rays PEL, Rib pairs RIB, Scale bars SCL, Vertebrae VER.

Scatterplots and regression lines with 95% confidence bands of the relationships between each morphometric character and the standard length of *Pycnodus*.

Anatomical abbreviations: Anal fin base AFB, Caudal peduncle depth CPD, Caudal peduncle length CPL, Caudal fin span CFS, Dorsal fin base DFB, Head depth HD, Head length HL, Lower jaw length JL, Maximum body depth MBD, Orbit diameter OD, Pectoral fin base PFB, Postorbital length POSTO, Preanal distance PANA, Predorsal distance PDOR, Preorbital length PREO, Prepectoral distance PPEC, Prepelvic distance PPEL.

Ontogenetic series of *Pycnodus*.

(a) Juvenile 4.02 cm (MCSNV T.309). (b) small adult 13.25 cm (BSPG AS I 1208). (c) large adult 30.61 cm (BSPG AS I 1209). Scale bar for (a) and (b) equals 1 cm and is 10 cm for (c).

ANOSIM and PERMANOVA results.

2

PERMANOVA	*P. apodus*	*P. gibbus*	*P. platessus*	*Pycnodus* sp.
P. apodus	0	0.3228	0.5671	0.1586
P. gibbus	0.3228	0	0.2538	0.2876
P. platessus	0.5671	0.2538	0	0.0048
Pycnodus sp.	0.1586	0.2876	0.0048	0

F-value	2.83
P-value	0.03

ANOSIM	*P. apodus*	*P. gibbus*	*P. platessus*	*Pycnodus* sp.
P. apodus	0	0.3583	0.7879	0.1717
P. gibbus	0.3583	0	0.3411	0.4755
P. platessus	0.7879	0.3411	0	0.0389
Pycnodus sp.	0.1717	0.4755	0.0389	0

R-value	0.10
P-value	0.06

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Measurements as percentage of SL (mean values in parentheses) for *Pycnodus*.

Range of measurements are represented by the 25th and 75th percentile in order to exclude outliers.

2

Meristic Character	Measurements as % of SL)
Vertebrae	24-26 (25)
Rib pairs	10-12 (11)
Scale bars	8-10 (9)
Dorsal fin rays	54-60 (56)
Anal fin rays	42-47,75 (45)
Pectoral fin rays	30,25-39,75 (35)
Dorsal fin pterygiophores	52,75-60 (56)
Anal fin pterygiophores	41-47 (45)
Caudal fin rays	25-33,5 (30)

Mean morphometric and meristic data for the examined specimens of *Pycnodus*.

Morphometric/meristic data	Min	Max	Mean	Median	Variance	Standard deviation
Standard length	1.8	27.7	10.9	8.8	47.6	6.9
Head length	1.1	7.1	3.3	2.8	2.9	1.7
Head depth	2.0	11.6	5.6	4.4	7.7	2.8
Maximum body depth	2.1	13.4	5.8	4.9	8.4	2.9
Pectoral fin base	0.2	1.8	0.8	0.7	0.2	0.4
Dorsal fin base	1.1	12.5	4.9	3.7	10.5	3.2
Anal fin base	0.7	9.6	3.4	2.5	5.6	2.4
Caudal peduncle depth	0.1	1.2	0.5	0.4	0.1	0.3
Caudal peduncle length	0.2	3.7	1.6	1.3	0.8	0.9
Caudal fin span	0.5	10.7	4.1	3.0	6.9	2.6
Prepectoral distance	1.1	7.2	3.1	2.8	2.5	1.6
Predorsal distance	1.1	11.0	5.0	4.2	7.6	2.8
Prepelvic distance	1.7	12.4	5.3	4.3	8.9	3.0
Preanal distance	2.2	14.2	6.6	5.4	12.8	3.6
Preorbital distance	0.3	4.1	1.4	1.1	1.0	1.0
Postorbital length	0.3	1.7	0.7	0.6	0.1	0.3
Orbit diameter	0.4	2.2	1.1	1.0	0.2	0.4
Lower Jaw	0.5	4.6	1.7	1.3	1.1	1.0
Vertebrae	23	27	25.1	25	1.4	1.2
Rib pairs	9	13	11.1	11	1.1	1.1
Scale bars	7	11	8.7	8	0.9	1.0
Dorsal fin rays	46	66	56.4	56.0	18.2	4.3
Anal fin rays	37	52	45.0	45.0	14.5	3.8
Pectoral fin rays	24	47	35.2	35.5	43.9	6.6
Pelvic fin rays	3	5	4.3	4.0	0.6	0.8
Dorsal fin pterygiophores	38	65	55.8	57.0	30.5	5.5
Anal fin pterygiophores	39	58	44.8	45.0	16.3	4.0
Caudal fin rays	17	43	29.2	28.5	38.4	6.2

Relationships between morphometric characters and standard length using least squares regression for *Pycnodus*.

Variable character log (y)	Slope (a)	Intercept (b)	Coefficient of determination (r²)	95% CI on a		95% CI on b	
Head length	0.86	-0.38	0.97	0.80	0.90	-0.42	-0.33
Head depth	0.80	-0.09	0.98	0.77	0.83	-0.11	-0.06
Maximum body depth	0.83	-0.06	0.99	0.81	0.85	-0.08	-0.04
Pectoral fin base	0.89	-1.00	0.76	0.77	0.99	-1.11	-0.88
Dorsal fin base	1.12	-0.51	0.97	1.07	1.17	-0.56	-0.46
Anal fin base	1.16	-0.71	0.97	1.09	1.22	-0.78	-0.64
Caudal peduncle depth	0.77	-1.13	0.89	0.68	0.87	-1.23	-1.05
Caudal peduncle length	0.91	-0.75	0.97	0.85	0.97	-0.81	-0.69
Caudal fin span	1.04	-0.49	0.98	1.00	1.09	-0.54	-0.45
Prepectoral distance	0.87	-0.40	0.98	0.83	0.90	-0.43	-0.36
Predorsal distance	0.91	-0.26	0.98	0.86	0.95	-0.30	-0.21
Prepelvic distance	0.92	-0.22	0.99	0.89	0.94	-0.24	-0.19
Preanal distance	0.93	-0.17	0.99	0.91	0.95	-0.19	-0.14
Preorbital distance	1.09	-1.01	0.89	0.99	1.20	-1.12	-0.90
Postorbital length	0.66	-0.83	0.78	0.56	0.76	-0.93	-0.74
Orbit diameter	0.64	-0.63	0.89	0.57	0.71	-0.69	-0.56
Lower jaw	0.94	-0.78	0.92	0.87	1.02	-0.86	-0.70
All P < 0.001							

Meristic counts of *Pycnodus*.

Species	Specimen number	No. of vertebrae	Rib pairs	No. of scale bars	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Dorsal fin pterygiophores	Anal fin pterygiophores	Caudal fin rays
Pycnodus sp.	Coll Baja Pesciara 4 (T.998)	26	13	8	56	44	17?		56	43	30
Pycnodus sp.	Coll Baja Pesciara 5 (T.999)	24?		9	55	43	16?		58	41	24
Pycnodus sp.	I.G.23695	20	6?		17	7?		?	?	?	15
Pycnodus sp.	I.G.135608	26	9	8	58	46?		4	59	58	31
Pycnodus sp.	I.G.135609	25	10	10	59	44	24	5	59	41?	
Pycnodus sp.	I.G.135664	26	12	8	49	37	7?		46	37	30
Pycnodus sp.	II D 167	27	11	8	51	47	33?		52	46	25
Pycnodus sp.	II D 168	30?		9	54	44?		?	55	40	25
Pycnodus sp.	II D 170	28?		7	59	51?		?	60	47	28
Pycnodus sp.	II D 171	27	11	8	56	42?		?	53	39	24
Pycnodus sp.	II D 180	30	11	9	60	49	18	4	62	50	33
Pycnodus sp.	T.309	27	11	8?	?	?		?	29	?	34
Pycnodus sp.	sp 1 (I.G.23???)	23	11	9	54	43?		4	55	42	23
Pycnodus sp.	sp 2 (I.G.186666)	22	10	10	46	39?		?	50	42	23
Pycnodus sp.	sp 3 (I.G.186667)	22	11	10?	?	?		?	43	33	27
Pycnodus sp.	sp 4 (I.G.24497)	27	11	11?	?	?		?	38	26	18
Pycnodus sp.	sp 5	24	10	8	54	41?		?	51	40	30
Pycnodus sp.	sp 6 (I.G.135680)	?	9	11?	?		22?	?	?	?	?
Pycnodus sp.	sp 7 (I.G.37581)	28	12?		?	?		?	44?		23
Pycnodus sp.	12058	25	13	8	60?		39	3	57	39	32
Pycnodus sp.	12059	25?		9	52?		29?		53?		29
Pycnodus sp.	12808	24	12	8?		?	29?		50	40	26
Pycnodus sp.	12809	26	14	8	56	42	23	2	56	44	30
Pycnodus sp.	26968?		12	8?		43	29	16?		40?	
Pycnodus sp.	26969	26	11	10	55	46	27?		58	44	30
Pycnodus platessus	BSPG AS I 1208	23	9	8	53	42	37	4	56	44	42
Pycnodus platessus	BSPG AS I 1209	24	12	8	60	47?		?	58	48	22
Pycnodus platessus	BMNH P.1633	28	11	9	59	47	31	5	62	45	29
Pycnodus platessus	BMNH 38000	31	10	8	66?		?	5	65	48	24
Pycnodus platessus	BMNH P.7459	25	10	8	63	45	36	5	59	51	34
Pycnodus platessus	1853.XXVII.i.a/b	23	10	9	61	46	47	5?		47?	
Pycnodus platessus	1855.VI.75	27	10	8	54	42	38	3	54	40	24
Pycnodus platessus	A.III.a.S.48	26	11	8	56	45?		?	59	46	28
Pycnodus platessus	CM 4479	?	12	8?		?	?	5?		?		?
Pycnodus platessus	CM 4479a	26	12	8?		?	?		?	52	41?	
Pycnodus platessus	6880Z	27	13	10?		?	24?		48	30	22
Pycnodus platessus	8867C	25	11	8	56?		?	?	57	46	23
Pycnodus platessus	8868C	23	13	6	54	49	18?		60	46	25
Pycnodus gibbus	BMNH P.1632/P.3760	29	11	11	49?		14	3	53	32	31
Pycnodus gibbus	BMNH P.11992	27	11	10	55?		?	3	60	46	26
Pycnodus gibbus	BMNH P.17025	26	10	12	52	41	30?		49	39	27
Pycnodus gibbus	BMNH P.44519	30	12	8	61	50	35	3	63	44	36
Pycnodus gibbus	BMNH P.44520	27	10	9	62	39?		?	60	37	37
Pycnodus gibbus	BMNH P.4386	?	12	10?		?	46	5	32?		43
Pycnodus gibbus	CM 4480	25?		8	60	49	45	4	61	50	34
Pycnodus gibbus	CM 4480.1	29	11	7	59	48?		?	60	48	39
Pycnodus gibbus	CM 4481	25	11	8	59	46	35	4	58	46	40
Pycnodus gibbus	PF 3234	24	13	10	54?		38	5	56?		25
Pycnodus gibbus	7433C	25	11	9?		?	?	4	52	37	25
Pycnodus apodus	Bol 94/95	27	11	8	62	52	22?		59	45	43
Pycnodus apodus	Bol 126/127	26	11	10	52?		40	5?		?	33
Pycnodus apodus	Bol 130/131	29	10	9?		?	?		?	?		?
Pycnodus apodus	Bol 134/135	25	11	10	59	52?		7	61	48	37