

A quantitative approach to determine the taxonomic identity and ontogeny of the pycnodontiform fish *Pycnodus* (Neopterygii, Actinopterygii) from the Eocene of Bolca Lagerstätte, Italy (#25031)

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

John Joseph Cawley^{Corresp., 1}, Giuseppe Marrama¹, Giorgio Carnevale², Jürgen Kriwet¹

¹ Department of Paleontology, University of Vienna, Vienna, Austria

² Dipartimento di Scienze della Terra, Università degli Studi di Torino, Turin, Italy

Corresponding Author: John Joseph Cawley
Email address: john.cawley@univie.ac.at

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.

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JOHN JOSEPH CAWLEY^{1*}, GIUSEPPE MARRAMÀ¹, GIORGIO CARNEVALE² & JÜRGEN KRIWET¹

¹ Department of Paleontology, University of Vienna, Geozentrum, Althanstrasse 14, Vienna, Austria.

² Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso, Turin, Italy

Corresponding Author:

John Joseph Cawley

Althanstr. 14, Vienna, 1090, Austria

Email address: john.cawley@univie.ac.at

ABSTRACT

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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 Konservat-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.

Traditional and geometric morphometrics (Zelditch et al., 2004) have been successfully used to interpret the patterns of morphospace occupation, quantifying the morphological diversification, solve taxonomic debates, as well as to test if morphological variations are due to intra- or interspecific variability (Wretman, Blom & Kear, 2016; Marramà & Carnevale, 2017; Marramà et al., 2017c).

In this perspective, this paper aims to analyse if the morphological variation among *Pycnodus* species of Bolca, can be related to interspecific or intraspecific (ontogenetic) variability as hypothesized by Blot (1987). For this, we examined abundant *Pycnodus* specimens from various museum collections which were labelled as either *P. apodus*, *P. platessus*, *P. gibbus* or *Pycnodus* sp. to establish whether these species separate substantially from each other in the morphospace and if morphometric and meristic data can be useful to detect significant differences between morphotypes and thus taxa. Since the studied sample had a range of specimens of different sizes, we investigated whether different shapes can be related to possible ontogenetic differences of *Pycnodus* representing different growth stages from juvenile to adult.

MATERIAL AND METHODS

Specimen sampling

We studied a selection of *Pycnodus* specimens from various museum collections, which were labelled either *P. apodus*, *P. platessus*, *P. gibbus* or *Pycnodus* sp. A total of 39 *Pycnodus* specimens from nine museum collections were finally used because they provided sufficient morphological information for the aim of this study (BM; Museo dei Fossili di Bolca; BMNH; Natural History Museum of London; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; CM, Carnegie Museum, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago; MGP-PD; Museo di Geologia e Paleontologia dell'Università di Padova; MNHN, Muséum National d'Histoire Naturelle, Paris; MCSNV, Museo Civico di Storia Naturale di Verona; NHMW; Naturhistorisches Museum Wien) (see Supplementary material). The sample includes 17 specimens identified originally as *Pycnodus* sp., 14 specimens as *P. platessus*, six specimens as *P. gibbus*, and two specimens as *P. apodus*.

Geometric morphometric protocol

A total of 18 landmarks and 14 semi landmarks were digitized on photos taken from the studied specimens in the corresponding collections using the software TPSdig (Rohlf, 2005). Landmarks indicating homologous points and were selected on the basis of their possible ecological or functional role following the scheme applied in some studies about shape variation in modern or extinct fishes (Figure 1). The landmark coordinates were translated, rotated and scaled at unit centroid size by applying a Generalized Procrustes Analysis (GPA) to minimize the variation caused by size, orientation, location and rotation (Rohlf & Slice, 1990; Zelditch et al., 2004). The GPA was performed using the TPSrelw software package (Rohlf, 2003) and a principal component analysis (PCA) was performed on Procrustes coordinates to obtain the Relative Warp (RW). Shape changes were shown along the axes using deformation grid plots.

Two non-parametric tests were performed to analyse the quantitative morphospace occupation of our *Pycnodus* specimens. In order to assess the degree of overlap between morphospaces, an analysis of similarities (ANOSIM, Clarke, 1993) was performed on the entire dataset of standardised morphometric and meristic parameters. PERMANOVA (Anderson, 2001) was used to test similarities of in-group centroid position between the different groups representing a species of *Pycnodus*. Euclidean distances are the distance measure chosen for both tests. All statistical analyses were performed in PAST 3.18 (Hammer, Harper & Ryan, 2001).

Since the studied specimens vary greatly in size (smallest being 4.0 cm and largest being 30.6 cm) we also investigated whether size could be correlated with shape change in *Pycnodus* and enable us to see whether and how body shape changes throughout ontogeny. To analyse the relationship between size and shape, we performed a Partial Least Square analysis (PLS) using the software TPSpls (Rohlf & Corti, 2000). Alpha (level of significance) was set to 0.05.

Biometric analyses

We used nine meristic counts and 19 measurements in order to capture morphological variability, to test the homogeneity of the sample, and confirming its assignment to a single species. Histograms were used to illustrate the continuous variation of morphometric and meristic data in order to ascertain if more than one species of *Pycnodus* could be identified. Least squares regression was used to obtain the relationship between standard length (SL) and all other morphometric variables. Specimens of possible additional taxa were indicated by the presence of statistical outliers from the regression line (Simon et al., 2010) and will require additional

scrutiny in order to truly differentiate the outlier from all other specimens. The linear regression results were shown using scatterplots. Log-transformed data were used to perform the least squares regression in order to determine the degree of correlation between the standard length (SL) and all other morphometric variables.

RESULTS

Geometric morphometrics

The relative warp analysis produced 38 RWs with the first three axes together explaining about 72% of the total variation. Figures 2 and 3 show that there is significant overlap between the morphospaces of the *Pycnodus* taxonomic groups and the thin plate splines show the changes in shape along the axes. Negative values on RW1 (56.1% explained) are related to *Pycnodus* specimens with large orbits and deep bodies while positive scores identify *Pycnodus* with reduced orbits and elongated bodies. Negative values of RW2 (10.4% explained) show specimens having the pectoral fin with a wide base moved higher up the body alongside a long caudal peduncle (Figure 2). Conversely, on positive scores of RW2 lie specimens with pectoral fin with a narrower base located more ventrally on the body alongside a small caudal peduncle. The negative values of RW3 (6% explained) show the skull becoming deeper and more elongated with the dermosupraoccipital in particular reaching far back (Figure 3). Body becomes shallower near the caudal peduncle with the cloaca shifting posteriorly, as well as the dorsal apex. Positive scores of RW3 are related to a shorter and shallower skull with the body becoming deeper close to the caudal peduncle and the anterior shift in the cloaca with the body becoming deeper just anterior to the cloaca. The dorsal apex shifts forward in position.

ANOSIM performed on the first three axes suggests that there is strong overlap between groups, showing they are barely distinguishable from each other ($p > 0.05$; see Table 1), except for a single pairwise comparison between *Pycnodus* sp. and *P. platessus* ($p < 0.05$). The PERMANOVA suggests the same trend, showing that group centroids are not significantly different on each pairwise comparison ($p > 0.05$), except between *Pycnodus* sp. and *P. platessus* ($p < 0.05$). Significant differences detected between *Pycnodus* sp. and *P. platessus* can be explained with the fact that the indeterminate *Pycnodus* specimens show a wide range of

morphologies, with the extreme shapes ranging from negative to positive values of all the first three axes.

The PLS performed on the entire sample (Figure 4) revealed a strong and significant correlations between size and shape ($r = 0.88$; $p < 0.05$), therefore suggesting that different shapes of the individuals are related to changes in shape of different ontogenetic stages. In fact, small-sized individuals are associated with larger orbits, deeper skull and body shape, long skull, higher position of pectoral fin and a wide, indistinct caudal peduncle that is in distant proximity to both medial fins. Larger individuals, on the other hand, have a reduced orbit, shallower skull and body depth, shorter skull, lower position of pectoral fin and narrow caudal peduncle in close proximity to both medial fins. The PLS analysis therefore suggests that the morphological variations of the orbit, body depth and caudal peduncle are strongly related to ontogeny.

Biometric analyses

Morphometrics and meristic counts for all the studied specimens are given in Table 2 and mean biometric parameters are given in Table 3. Most of the histograms based on meristic counts (Figure 5) show a normal (Gaussian) distribution with intermediate states dominating and extreme states being rare. The linear regression performed on morphometric characters (Figure 6) shows that all specimens fit within the cloud of points near the regression line and that no particular specimens of *Pycnodus* deviates from this line. This is confirmed by the high values of the coefficient of determination (r^2) ranging from 0.76-0.99 (Table 4) indicating a high degree of positive correlation between standard length and each morphometric character. Linear regression analysis also revealed the highly significant relationship between the standard length and all morphometric characters ($p < 0.001$). Neither morphometric nor meristic characters are therefore useful in determining two or more different morphologically identifiable morphotypes within *Pycnodus*, corroborating definitively Blot's (1987) hypothesis that only one species (*P. apodus*; see also below) is present in the Bolca Lagerstätte.

DISCUSSION

Intraspecific variation of *Pycnodus apodus*

The results demonstrate that all *Pycnodus* species cannot be separated in a quantitative approach, confirming the intraspecific variation hypothesis of Blot (1987). The hypothesis by Agassiz (1844) that *Pycnodus gibbus* is specifically the juvenile of *P. platessus* can be rejected as a specimen referred to as *P. platessus* (MGP-PD 6880Z) is smaller than most of the specimens assigned to *P. gibbus*, including all of them in our sample (see Supplementary Material). As suggested by Grande and Young (2004), ontogenetic variation of morphological characters actually represents a primary source of intraspecific variation; this is confirmed by our analysis, specifically by the morphological changes mostly occurring along RW1 in the morphospace that are related to ontogeny and the very significant results deriving from the PLS analysis. The unimodal (Gaussian) distribution of most of the meristic data, displayed by the frequency histograms, reveals a clear domination of intermediate values and comparably rare extremes, which is typical of a homogenous population. Data show that any morphological variation is continuous and the recognition of high frequency of intermediate states and low frequency of extreme values makes separation of the *Pycnodus* sample into discrete groups impossible. This suggests that all specimens studied belong to a single or taxonomic entity (see Dagys, Bucher & Weitschat, 1999; Dagys, 2001; Weitschat, 2008; Marramà & Carnevale, 2015a; Sferco, López-Arbarello & Báez, 2015). Furthermore, the linear regression showed a significant dependence between standard length and all morphometric variables, therefore suggesting that morphometric characters are not useful to distinguish different morphotypes.

Figure 7 shows some notable differences between the juvenile and larger specimens including the degree of ossification, particularly in the skull and caudal fin, being smaller in juvenile in comparison to adults and the notochord not being surrounded by arcocentra in juveniles whereas it is completely enclosed in adults. Differences in meristic counts (Table 5) are suggestive of intraspecific variation as seen in other fossil actinopterygians (Stensiö, 1935; Lehman, 1952; Patterson, 1973; Su, 1973; Zhang & Zhang, 1980; Olsen, 1984; Tintori, 1990; Bürgin, 1992; Dietze, 1999, 2000; Thies & Hauff, 2011; Xu, Shen & Zhao, 2014; Tintori et al., 2015; Wretman, Blom & Kear, 2016; Marramà et al., 2017c). The analysis of the morphological variability of *Pycnodus*, one of the last representatives of a basal neopterygian lineage that has been around since at least the Late Triassic (Tintori, 1981; Kriwet 2001a; Poyato-Ariza, 2015;), indicates that pycnodontiforms also produce substantial intraspecific variation similar to living representatives of other ancient actinopterygian lineages such as amiids (Jain, 1985) and

acipenserids (Hilton & Bemis, 1999). Therefore, the identification of different Bolca *Pycnodus* species such as *P. gibbus* (Heckel, 1856), may be the result of species over-splitting and can be on the contrary explained by intraspecific variation.

Habitat use during ontogeny

Our morphometric results show that the morphology of the smaller individuals differ significantly from that of the adults and that *Pycnodus*, like extant actinopterygians, would go through morphological changes throughout ontogeny. Large eye size found in the smaller *Pycnodus* specimens is usually a sign of the specimen being in a juvenile stage as can be seen in many extant teleosts (Pankhurst & Montgomery, 1990). This rejects the interpretation of Goatley, Bellwood & Bellwood (2010), who interpreted *Pycnodus* in the Monte Bolca assemblage to be a nocturnal feeder based on the orbit size in relation to standard length. Seemingly, these authors only used juveniles in their analysis. The deep body shape of the smaller *Pycnodus* specimens can be interpreted as a sign that the juveniles live within the branches of corals and as they get bigger they start to occupy the water column above the reef. This change to a benthopelagic lifestyle also is supported by the more fusiform body and the narrower caudal peduncle (Webb, 1982) seen in larger specimens. Ecologically similar extant analogues to *Pycnodus*, the sparid species *Diplodus sargus* and *D. puntazzo* also spend their time as juveniles in crevices in the rocks in shallow water 0-2 m deep and move to rocky bottoms and sea grass beds when adult (Macpherson, 1998). Ontogenetically-related habitat changes also occur in other coral fishes, such as labrids, in which the pectoral fins increase their aspect ratio as these fishes grow in size, enabling them to increase their use of the water column while juveniles stay closer to the bottom (Fulton, Bellwood & Wainwright, 2002). Since both juveniles and adults of *Pycnodus* are found in the Bolca Lagerstätte, we hypothesize that unlike many modern coral reef fishes, which significantly change the habitat during ontogeny (Nagelkerken et al., 2002; Dorenbosch et al., 2005a, b; Adams et al., 2006; Nagelkerken, 2007; Nakamura et al., 2008; Shibuno et al., 2008; Kimirei et al., 2011), there is a shift instead in microhabitat use within the reef, in this case juveniles living within coral crevices to adults roaming over the coral reefs.

The taxonomic history of *Pycnodus*

Pycnodus has long been used as wastebasket taxon in the study of pycnodontiforms, being used as a default name for many taxa even in the Mesozoic until later revisions revealed the taxa to have significant morphological differences with *Pycnodus* as to be renamed as separate taxa. Species of pycnodontiforms previously referred to as *Pycnodus* include *Anomoeodus subclavatus* from the Maastrichtian of the Netherlands (Agassiz, 1833; Davis, 1890; Forir, 1887); other species of *Anomoeodus* referred to as *Pycnodus* include *A. angustus*, *A. muensteri*, *A. phaseolus*, *A. sculptus* (Agassiz, 1844) and *A. distans* (Coquand, 1860; Sauvage, 1880). *Pycnodus liassicus* Egerton, 1855 from the Early Jurassic, of Barrow-on-Soar of Leicestershire, United Kingdom was assigned to the genus *Eomesodon* by Woodward (1918) and *Stemmatodus rhombus* (Agassiz, 1839) from the Early Cretaceous of Capo d'Orlando, close to Naples, Italy was originally named *Pycnodus rhombus* (see Heckel, 1854). *Pycnodus flabellatum* Cope, 1866 from the Cenomanian-Coniacian of Brazil was assigned to *Nursallia flabellatum* by Blot (1987). The pycnodonts *Pycnodus achillis* Costa 1853, *Pycnodus grandis* Costa 1853 and *Pycnodus rotundatus* Costa 1864 are all synonymous with *Ocloedus costae* (d'Erasmus, 1914, Poyato-Ariza & Wenz, 2002). Poyato-Ariza (2013) revised "*Pycnodus*" *laveirensis* Veiga Ferreira 1961 from the Cenomanian of Lavieras, Portugal and found that due to morphological differences in characters such as absence of dermocranial fenestra, number of premaxillary teeth, contact type of arcocentra and median fin morphology, it represents a member of a different genus and consequently erected the new genus *Sylvienodus* as a replacement. An articulated specimen of '*Pycnodus*' was found in the Campanian-Maastrichtian of Nardo, Italy, which certainly represents a different pycnodont (Taverne, 1997). An extremely fragmentary specimen referred to as "*Pycnodus*" *nardoensis* from Apulia (Nardo), Italy is comprised of the anterior part of the body along with some posterior elements of the skull (Taverne, 1997). However, in a later study Taverne (2003) studied new material of this taxon, which revealed that this species does not belong to *Pycnodus* due to as the possession of a narrower cleithrum and peculiar morphology of the contour scales. This new data led to *Pseudopycnodus* being erected as a new genus for the Nardo material.

All other Mesozoic species of *Pycnodus* are based on isolated dentitions or teeth. The earliest records of *Pycnodus* are dentitions found in the limestones from the Upper Jurassic (Kimmeridgian) of Orbagnoux, France (Sauvage, 1893). Isolated teeth and an isolated vomerine

dentition were referred to cf. *Pycnodus* sp. (Goodwin et al., 1999) from the Mugher Mudstone formation of the Tithonian. However, its identity is doubted due to the stratigraphic position and could be attributed to *Macromesodon* (Kriwet, 2001b). Pictet, Campiche & Tribolet (1858-60) described remains of the Early Cretaceous fish assemblages from Switzerland where three species of *Macromesodon* (*M. couloni* from the Hauterivian and Barremian, *M. cylindricus* from the Valanginian, Barremian, and Aptian and *M. obliquus* from the Albian) were all originally referred to as *Pycnodus*. Isolated dentitions belonging to '*Pycnodus*' *heterotypus* and '*Pycnodus*' *quadratifera* were reported from the Hauterivian of the Paris basin (Cornuel, 1883, 1886). Several isolated teeth derived from the Cenomanian strata of the Chalk Group of southern England were attributed to *Pycnodus scrobiculatus* Reuss 1845 whose systematic affinity is still uncertain. Other teeth belonging to *P. scrobiculatus* were reported from the Turonian of northern Germany. Roemer (1841) described isolated remains belonging to *Pycnodus harlebeni* from the Late Cretaceous of Hilsconglomerat of Ostervald, Germany. Another possible Portuguese representative of *Pycnodus* is reported from the Turonian of Bacarena, '*Pycnodus*' sp. aff. '*P. gigas* Jonet 1964. However, the identification of the Portuguese specimens as *Pycnodus* are uncertain and the material most likely pertains to a different pycnodont taxon (Kriwet, 2001b). Isolated dentitions of what were claimed to be *Pycnodus scrobiculatus*, *P. rostratus* and *P. semilunaris* from the Turonian of Czechoslovakia (Reuss, 1845) should be regarded as indeterminable pycnodontids due to the lack of characters useful to determine their affinities (Kriwet, 2001b). Isolated teeth attributed to "*Pycnodus*" *lametae* were reported from the Maastrichtian Lameta Formation of Dongargaon, India (Woodward, 1908).

Pycnodus is the most dominant taxon of the Palaeogene pycnodont faunas being widely distributed in shallow water contexts worldwide. The earliest record of *Pycnodus* in the Palaeogene is represented by *Pycnodus praecursor* from the Danian of Angola (Darteville & Casier, 1949) and *P. sp. cf. P. praecursor* from the Thanetian of Niger (Cappetta, 1972). *Pycnodus toliapicus* was reported from the Thanetian of Togo, Thanetian of Nigeria and the upper Palaeocene of Niger (White, 1934; Kogbe & Wozny, 1979; Longbottom, 1984). Several remains of isolated dentitions and teeth from the Eocene have been attributed to *Pycnodus*. These include *Pycnodus bicresta* from the northwestern Himalayan region, India (Prasad & Singh, 1991); *Pycnodus bowerbanki* from the Ypresian, England, middle Eocene of Mali and Ypresian of Algeria (Longbottom, 1984; Savornin, 1915); *Pycnodus* sp. cf. *P. toliapicus* from the Eocene

of Katar at the Persian Gulf (Casier, 1971); *Pycnodus toliapicus* from the Ypresian and Lutetian of England and Lutetian of the Paris basin and Belgium (Savornin, 1915; Casier, 1950; Taverne & Nolf, 1978); *Pycnodus mokattamensis* from the Lutetian of Egypt (Priem, 1897); *P. mokattamensis* occurs alongside *Pycnodus legrandi*, *Pycnodus lemellefensis*, *Pycnodus thamallulensis*, *Pycnodus vasseuri* and *Pycnodus pellei* from the Ypresian of Algeria (Savornin, 1915); *Pycnodus pachyrhinus* Grey-Egerton 1877 from the Ypresian of Kent, England; *Pycnodus funkianus* Geinitz 1883 from the Ypresian of Brunswick, Germany; *Pycnodus munieri* Priem 1902 and *Pycnodus savini* Priem 1902 from the Ypresian, France and a rather diverse assemblage from the middle Eocene of Mali which includes *Pycnodus jonesae*, *P. maliensis*, *P. munieri*, *P. variabilis* and *P. zeaformis* (Longbottom, 1984).

A nearly complete specimen of *P. lametae* with crushed skull and missing caudal fins was reported from the freshwater Maastrichtian of Bhatali, India close to the Dongargaon area (Mohabey & Udhoji, 1996). However, the assignment of the name *Pycnodus* to this fish is dubious, since it has an operculum and lacks the post-parietal process typical of the Pycnodontidae (pers. obs.). A more complete specimen of *Pycnodus* was found from the Palaeocene rocks of Palenque, Mexico (Alvarado-Ortega et al., 2015), its only difference with the Eocene specimens from Bolca being a greater number of ventral and post-cloacal ridge scales, less dorsal- and anal-fin pterygiophores and a large or regular-sized posteriormost neural spine. However, due to the inadequacy of the available sample, it is not possible to determine the actual differences between the Palaeocene material from Mexico and that from the Eocene of Bolca, and for this reason this taxon is referred to as *Pycnodus* sp.

In this perspective, most species referred to *Pycnodus* are not valid (all Jurassic and Cretaceous *Pycnodus* specimens being other taxa) and with the majority of Palaeogene *Pycnodus* being represented by isolated dentitions and teeth it seems that the only definitive articulated skeletal remains attributed to the genus *Pycnodus* are the Bolca specimens and *Pycnodus* sp. from south-eastern Mexico (Alvarado-Ortega et al., 2015).

CONCLUSIONS

The quantitative approach here performed confirms the findings of Blot (1987) that the various *Pycnodus* species (*P. apodus*, *P. platessus*, *P. gibbus*) from the Eocene Bolca Konservat-

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

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Figure captions

Figure 1: 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).

Figure 2: Morphospace of *Pycnodus* on 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.

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

Figure 4: 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.

Figure 5: 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.

Figure 6: 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.

Figure 7: 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).

Table captions

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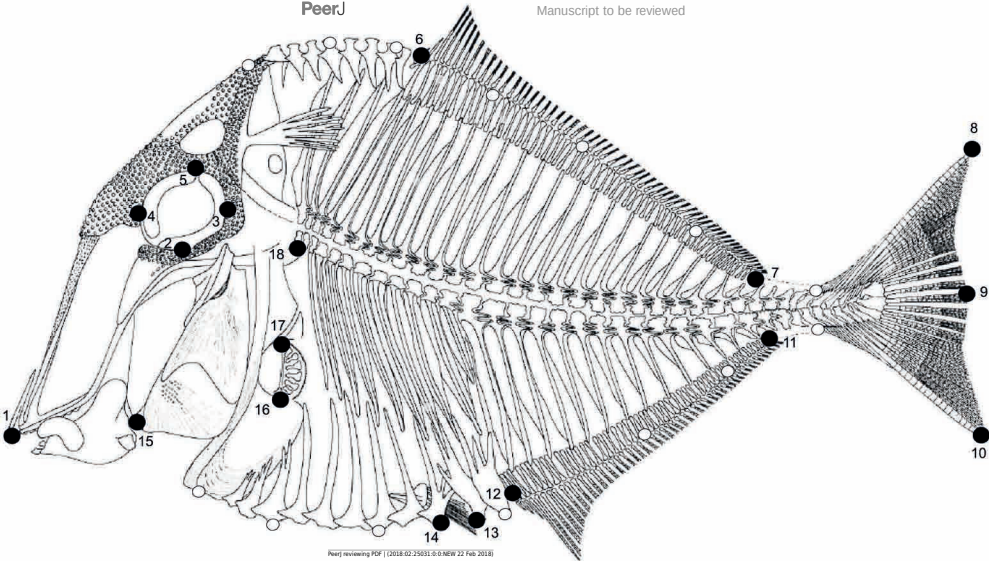


Figure 2 (on next page)

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.

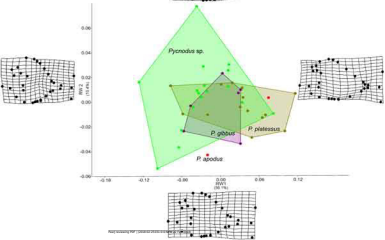


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Morphospace of *Pycnodus* showing RW 1 on the x-axis and RW 3 on y-axis.

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

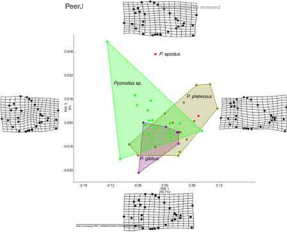


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PLS analysis showing a correlation of morphology with ontogeny.

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.

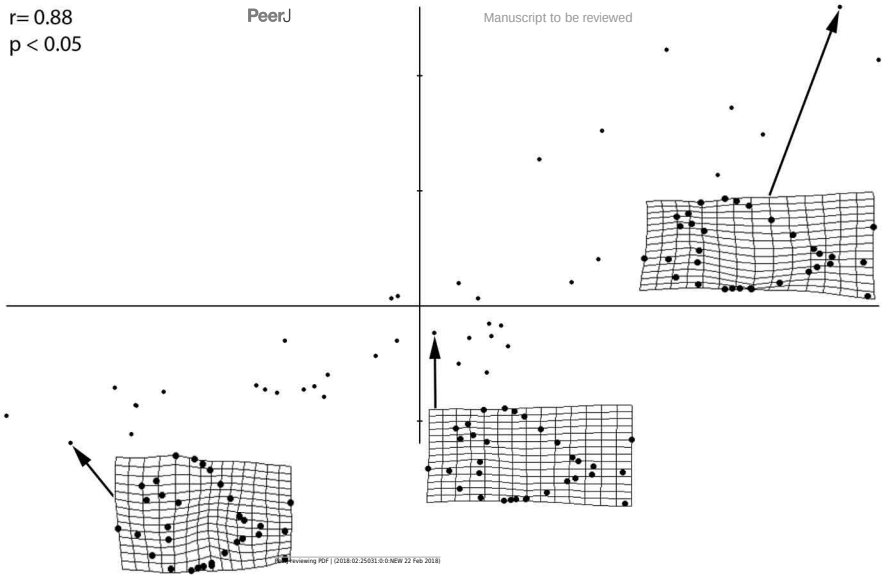


Figure 5 (on next page)

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.

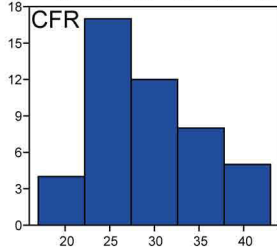
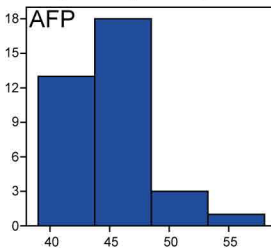
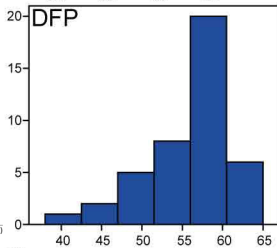
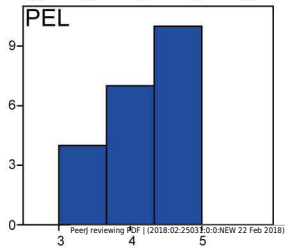
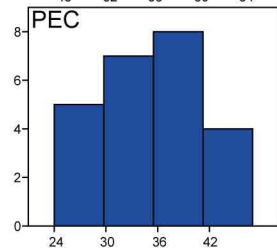
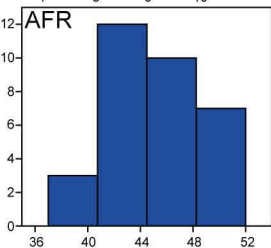
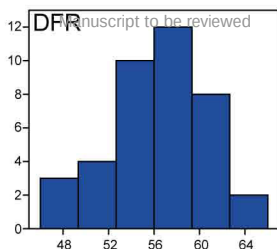
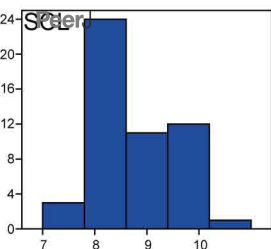
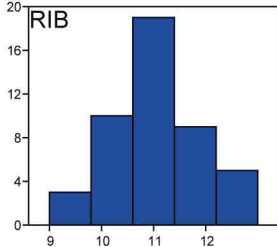
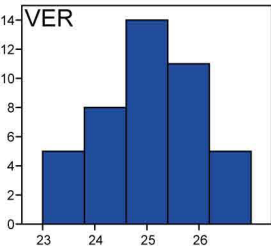


Figure 6(on next page)

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.

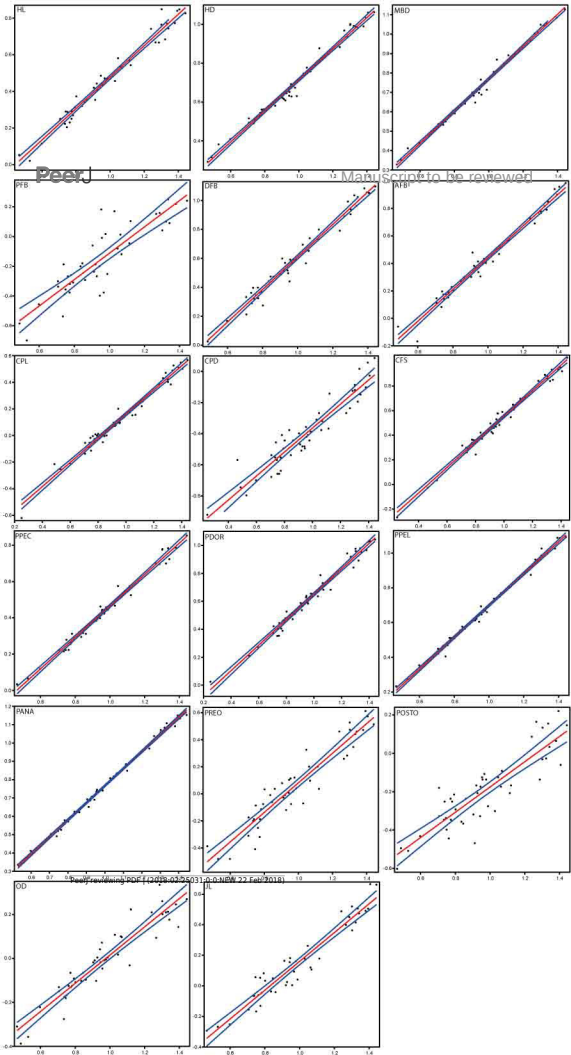


Figure 7(on next page)

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).



Table 1 (on next page)

ANOSIM and PERMANOVA results.

PERMANOVA	<i>P. apodus</i>	<i>P. gibbus</i>	<i>P. platessus</i>	<i>Pycnodus</i> sp.
<i>P. apodus</i>	0	0.3228	0.5671	0.1586
<i>P. gibbus</i>	0.3228	0	0.2538	0.2876
<i>P. platessus</i>	0.5671	0.2538	0	0.0048
<i>Pycnodus</i> sp.	0.1586	0.2876	0.0048	0
F-value	2.83			
P-value	0.03			

ANOSIM	<i>P. apodus</i>	<i>P. gibbus</i>	<i>P. platessus</i>	<i>Pycnodus</i> sp.
<i>P. apodus</i>	0	0.3583	0.7879	0.1717
<i>P. gibbus</i>	0.3583	0	0.3411	0.4755
<i>P. platessus</i>	0.7879	0.3411	0	0.0389
<i>Pycnodus</i> sp.	0.1717	0.4755	0.0389	0
R-value	0.10			
P-value	0.06			

Table 2 (on next page)

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.

1
2
3

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)

Table 3(on next page)

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

1

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

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Table 4(on next page)

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

1

Variable character log (y)	Slope (a)	Intercept (b)	Coef ficient of determination (r ²)	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 fn base	0.89	-1.00	0.76	0.77	0.99	-1.11	-0.88
Dorsal fn base	1.12	-0.51	0.97	1.07	1.17	-0.56	-0.46
Anal fn 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 fn 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							

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Table 5(on next page)

Meristic counts of *Pycnodus*.

1

Species	Specimen number	No. of vertebrae	Rib pairs	No. of scale bars	Dorsal f h rays	Anal f h rays	Pectoral f h rays	Pelvic f h rays	Dorsal f h pterygiophores	Anal f h pterygiophores	Caudal f h rays
<i>Pycnodus</i> sp.	Coll Baja Pesciara 4 (T.998)	26	13	8	56	44	17?		56	43	30
<i>Pycnodus</i> sp.	Coll Baja Pesciara 5 (T.999)	24?		9	55	43	16?		58	41	24
<i>Pycnodus</i> sp.	I.G.23695	20	6?		17	7?		?	?		15
<i>Pycnodus</i> sp.	I.G.135608	26	9	8	58	46?		4	59	58	31
<i>Pycnodus</i> sp.	I.G.135609	25	10	10	59	44	24	5	59	41?	
<i>Pycnodus</i> sp.	I.G.135664	26	12	8	49	37	7?		46	37	30
<i>Pycnodus</i> sp.	II D 167	27	11	8	51	47	33?		52	46	25
<i>Pycnodus</i> sp.	II D 168	30?		9	54	44?	?		55	40	25
<i>Pycnodus</i> sp.	II D 170	28?		7	59	51?	?		60	47	28
<i>Pycnodus</i> sp.	II D 171	27	11	8	56	42?	?		53	39	24
<i>Pycnodus</i> sp.	II D 180	30	11	9	60	49	18	4	62	50	33
<i>Pycnodus</i> sp.	T.309	27	11	8?		?	?	?	29?		34
<i>Pycnodus</i> sp.	sp 1 (I.G.23???)	23	11	9	54	43?		4	55	42	23
<i>Pycnodus</i> sp.	sp 2 (I.G.186666)	22	10	10	46	39?	?		50	42	23
<i>Pycnodus</i> sp.	sp 3 (I.G.186667)	22	11	10?		?	?		43	33	27
<i>Pycnodus</i> sp.	sp 4 (I.G.24497)	27	11	11?		?	?	?	38	26	18
<i>Pycnodus</i> sp.	sp 5	24	10	8	54	41?		?	51	40	30
<i>Pycnodus</i> sp.	sp 6 (I.G.135680)	?	9	11?		?	22?	?	?		?
<i>Pycnodus</i> sp.	sp 7 (I.G.37581)		28	12?		?	?	?	44?		23
<i>Pycnodus</i> sp.	12058	25	13	8	60?		39	3	57	39	32
<i>Pycnodus</i> sp.	12059	25?		9	52?		29?		53?		29
<i>Pycnodus</i> sp.	12808	24	12	8?		?	29?		50	40	26
<i>Pycnodus</i> sp.	12809	26	14	8	56	42	23	2	56	44	30
<i>Pycnodus</i> sp.	26968?		12	8?		43	29	16?		40?	
<i>Pycnodus</i> sp.	26969	26	11	10	55	46	27?		58	44	30
<i>Pycnodus platessus</i>	BSPG AS I 1208	23	9	8	53	42	37	4	56	44	42
<i>Pycnodus platessus</i>	BSPG AS I 1209	24	12	8	60	47?		?	58	48	22
<i>Pycnodus platessus</i>	BMNH P.1633	28	11	9	59	47	31	5	62	45	29
<i>Pycnodus platessus</i>	BMNH 38000	31	10	8	66?		?		65	48	24
<i>Pycnodus platessus</i>	BMNH P.7459	25	10	8	63	45	36	5	59	51	34
<i>Pycnodus platessus</i>	1853.XXVII.i.a/b	23	10	9	61	46	47	5?		47?	
<i>Pycnodus platessus</i>	1855.VI.75	27	10	8	54	42	38	3	54	40	24
<i>Pycnodus platessus</i>	A.III.a.S. 48	26	11	8	56	45?		?	59	46	28
<i>Pycnodus platessus</i>	CM 4479	?	12	8?		?		5?	?		?
<i>Pycnodus platessus</i>	CM 4479a	26	12	8?		?		?	52	41?	
<i>Pycnodus platessus</i>	6880Z	27	13	10?		?	24?		48	30	22
<i>Pycnodus platessus</i>	8867C	25	11	8	56?		?		57	46	23
<i>Pycnodus platessus</i>	8868C	23	13	6	54	49	18?		60	46	25
<i>Pycnodus gibbus</i>	BMNH P.1632/P.3760	29	11	11	49?		14	3	53	32	31
<i>Pycnodus gibbus</i>	BMNH P.11992	27	11	10	55?		?	3	60	46	26
<i>Pycnodus gibbus</i>	BMNH P.17025	26	10	12	52	41	30?		49	39	27
<i>Pycnodus gibbus</i>	BMNH P.44519	30	12	8	61	50	35	3	63	44	36
<i>Pycnodus gibbus</i>	BMNH P.44520	27	10	9	62	39?		?	60	37	37
<i>Pycnodus gibbus</i>	BMNH P.4386	?	12	10?		?	46	5	32?		43
<i>Pycnodus gibbus</i>	CM 4480	25?		8	60	49	45	4	61	50	34
<i>Pycnodus gibbus</i>	CM 4480.1	29	11	7	59	48?		?	60	48	39
<i>Pycnodus gibbus</i>	CM 4481	25	11	8	59	46	35	4	58	46	40
<i>Pycnodus gibbus</i>	PF 3234	24	13	10	54?		38	5	56?		25
<i>Pycnodus gibbus</i>	7433C	25	11	9?		?		4	52	37	25
<i>Pycnodus apodus</i>	Bol 94/95	27	11	8	62	52	22?		59	45	43
<i>Pycnodus apodus</i>	Bol 126/i27	26	11	10	52?		40	5?			33
<i>Pycnodus apodus</i>	Bol 130/i31	29	10	9?		?		?			?
<i>Pycnodus apodus</i>	Bol 134/135	25	11	10	59	52?		7	61	48	37

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