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STUDIES ON PYCNODONT FISHES (II): REVISION OF THE SUBFAMILY PYCNODONTINAE, WITH SPECIAL REFERENCE TO ITALIAN FORMS

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Abstract: The diagnosis, composition, and phylogenetic relationships of the European subfamily Pycnodontinae are revised; its record is pushed back from the Cenozoic into the Mesozoic. The Pycnodontinae is confirmed as a monophyletic group. It is diagnosed by: thin, laminar supraoccipital exposed all along the posterior border of the skull roof; cleithrum with two posterior expansions framing the notch for the pectoral fin; reduction in the ossification of the flank scales (clathrate pattern); reduction of the preopercular into a very low bone, never higher than the exposed, ornamented portion of the dermohyomandibular; and presence of a bifid cloacal scale. The subfamily includes the tribe Pycnodontini (*Pycnodus* + *Oropycnodus*), *Polazzodus*, *Sylvienodus*, and *Tergestinia*. The former "*Coelodus*" *gridellii* is moved to *Polazzodus gridellii* n. comb. The Italian genera, *Pycnodus*, *Polazzodus*, and *Tergestinia*, form a monophyletic group together with the French *Oropycnodus*. The present analysis shows that *Polazzodus*, *Sylvienodus*, and *Tergestinia* are pycnodontin fishes, but *Haqelpycnodus*, *Libanopycnodus, Scalacurvichthys*, and *Sigmapycnodus* do not belong to the Pycnodontinae. "*Pseudopycnodus*" and "*P. nardoensis*" are considered *nomina dubia*. This revision has revealed new aspects of the last known diversification in the evolutionary history of the Pycnodontiformes, showing that the group was still thriving in the Western Tethys during the Late Cretaceous. For the present analysis, additional arguments involving ontogenetic restrictions are provided to favour ordering multistate characters in pycnodonts.

INTRODUCTION

The evolutionary history of the Pycnodontiformes has been subject of re-evaluation in recent years. They are regarded as a plastic, versatile group rather than an excessively specialized group slowly declining to leave room to teleosteans. They were very successful for a long time and kept increasing their diversity in the places where they remained present (Poyato-Ariza 2005a; Martín-Abad & Poyato-Ariza 2013; Poyato-Ariza & Martín-Abad 2013). In this context, the subfamily Pycnodontinae shows a special evolutionary interest, since they are among the youngest and most derived pycnodonts (e.g., Poyato-Ariza & Wenz 2002). Martín-Abad & Poyato-Ariza (2013) documented up to five radiation events in the history of the Pycnodontiformes. They tentatively proposed additional diversification of the most derived pycnodonts in the Western Tethys during the Late Cretaceous. Thus, the objective of the present paper is twofold: to update the taxonomy and phylogeny of this subfamily and similar forms, and to test such diversification hypothesis.

The subfamily Pycnodontinae was first formally used by Poyato-Ariza & Wenz (2002) to include *Pycnodus*, the type genus, plus *Oropycnodus*. The former represents part the last fossil record of the Pycnodontiformes, from the Eocene of Italy, and the latter is from the Paleocene of France. The presence of pycnodonts after the Eocene is unconfirmed (Poyato-Ariza 2005a). Among the numerous pycnodont taxa described in the last decade, six

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new monospecific genera were also associated to this subfamily: *Haqelpycnodus* (Taverne & Capasso 2018a), *Libanopycnodus* (Taverne & Capasso 2018b), *Polazzodus* (Poyato-Ariza 2010), *Scalacurvichthys* (Cawley & Kriwet 2018), *Sigmapycnodus* (Taverne & Capasso 2018b) and *Sylvienodus* (Poyato-Ariza 2013), all from the Late Cretaceous. *Polazzodus* was pointed to show similarities with "*Coelodus*" *gridellii* d'Erasmo, 1952 and *Tergestinia* Capasso, 2000, but the assessment of all these forms to the Pycnodontinae remained untested, pending revision of the group. In turn, all phylogenies of the Pycnodontinae by Taverne & Capasso (2012, 2018a,b) are ad-hoc, hand-made trees based on a preassigned distribution of a selected choice of characters. There is no cladistics analysis, therefore they are not necessarily the most parsimonious hypotheses of relationships of those genera and the family Pycnodontidae.

The present paper presents the first cladistic analysis of the genera assessed to or related with the Pycnodontinae. With this purpose, all well-known genera of the family Pycnodontidae are included in the analysis; some of them have been re-evaluated because of their possible relationship with the subfamily Pycnodontinae. These taxa, in alphabetical order, are:

"*Coelodus*" *gridellii* d'Erasmo, 1952 (Fig. 1). Originally described from three specimens of small size, about 12 cm of total length, from an outcrop near Polazzo, Carso Isontino, northeastern Italy. The outcrop was destroyed during World War I, so the precise provenance is unknown. Similar outcrops in the nearby area are considered early Santonian (Late Cretaceous). Amidst the three original type specimens, one of the paratypes ("Esemplare N. 3" in d'Erasmo 1952) seems to be currently lost. The other paratype (MCSNT 12361, "Esemplare N. 2" in d'Erasmo 1952) was reassessed to *Polazzodus coronatus* by Poyato-Ariza (2010), together with an additional specimen in the same collection (MCSNT 12447). The holotype, MCSNT-12366, was explicitly designated as "tipo" by d'Erasmo (1952: 84, "Esemplare N. 1"). It is, therefore, the only currently known specimen of this species (Fig. 1). For further details, see Poyato-Ariza (2010: 650-651, 662).

Fig. 1 - *Polazzodus gridellii* n. comb. (formerly "*Coelodus*" *gridellii*). Holotype and only specimen, MCSNT-12366. Late Cretaceous, probably early Santonian, near Polazzo, Italy (see text for details). Photo A. Colla, archives MCSNT. The total length of the preserved part of the specimen is around 11 cm.

Haqelpycnodus Taverne & Capasso 2018a. Erected for two complete, apparently well preserved specimens from late Cenomanian (Late Cretaceous) deposits of Haqel, Lebanon. Considered to present some, but not all, characters of the Pycnodontinae, hence "immediate plesiomorphic (sic) sister-taxon of Pycnodontinae" and their "direct plesiomorphic sister-lineage (sic)" by Taverne & Capasso (2018a: 117, 131; no cladistic analysis). Both specimens in a private collection, therefore coded from the information in the original publication.

Libanopycnodus Taverne & Capasso, 2018b. Based on a single nearly complete, imperfect specimen from the late Cenomanian (Late Cretaceous) of En Namoura, Lebanon. Considered as "the most basal member of the Pycnodontinae" by Taverne & Capasso (2018b: 27; no cladistic analysis). Specimen in a private collection, therefore coded from the information in the original publication.

Oropycnodus Poyato-Ariza & Wenz, 2002 (Fig. 2). Known from several specimens of small size, about 14 cm of total length, from the Montian (Paleocene) of Mont Aimé in Chalons-sur-Marne, northeastern France. The type and only species is *Oropycnodus ponsorti* (Heckel, 1854). Although the original spelling of the specific name was *ponsortii*, it was changed to *ponsorti* following ICZN Article 33.3.1 for prevailing usage. For further details see Poyato-Ariza & Wenz (2002: 150).

Polazzodus Poyato-Ariza, 2010 (Fig. 3). Initially described from abundant, well preserved, mostly complete specimens from the early Santonian (Late Cretaceous) near Polazzo, Carso Isontino, northwestern Italy. An isolated vomerine dentition was subsequently cited as cf. *Polazzodus* sp. by Križnar

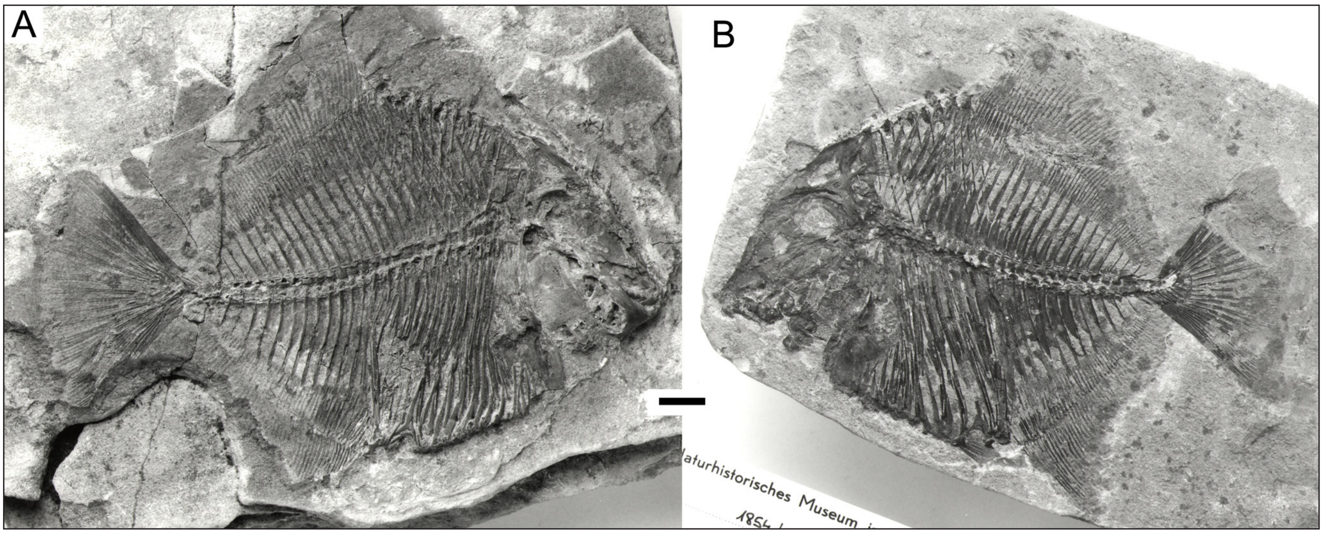

Fig. 2 - *Oropycnodus ponsorti*. A) Lectotype, NMW 1854/XXXIX/38; B) paralectotype NMW 1854/XXXIX/40. Photos Schumacher, courtesy O. Schultz (modified from Poyato-Ariza & Wenz 2002). Scale bar equals 1 cm for both specimens.

(2014) from the Albian-Cenomanian of Mrzlek near Solkan, Slovenia.

Pseudopycnodus Taverne, 2003. Replacement genus created for its type and only species, *Pycnodus nardoensis* Taverne, 1997, after revision with some new material (Taverne 2003) from the Campanian-Maastricthian (Late Cretaceous) of Nardò, Apulia, southeastern Italy. Initially known from scarce, fragmentary, partially disarticulated, very incomplete specimens of medium size. The longest one was part of a body without head, the preserved portion some 22 cm long. Later on, it was re-described by Taverne & Capasso (2012) on the basis of additional specimens in the private collection of the latter.

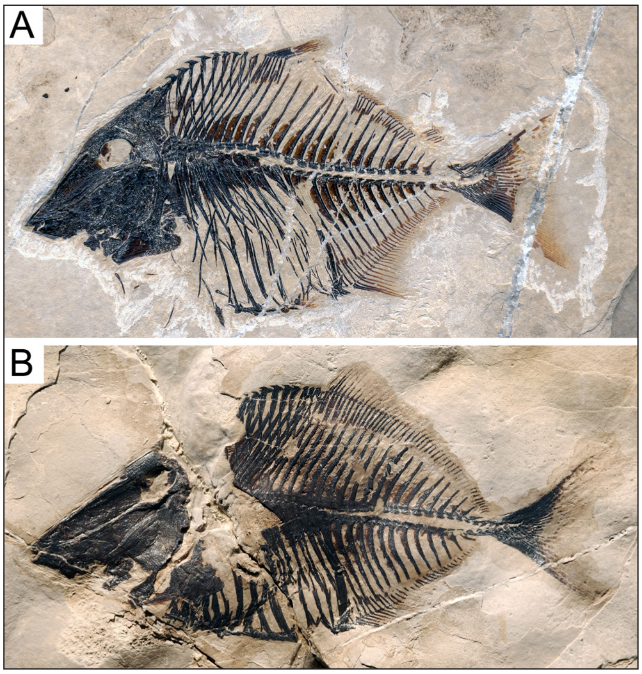

Fig. 3 - *Polazzodus coronatus*. A) Holotype, MPCM-13464, standard length 7,6 cm; B) paratype MPCM 12214, standard length 6,6 cm. Photos M. Tentor, MPCM (modified from Poyato-Ariza 2010; see p.650-651 in this reference for comments on the apparent differences of body shape among specimens of this taxon due to preservational artifacts).

Pycnodus Agassiz, 1833. Type genus (Fig. 4). Abundant specimens, including ontogenetic series; adults of medium size, up to some 26 cm. Comes from the early-middle Eocene of Bolca, Verona, and Vicenza Provinces, northern Italy, where it represents the last reliable fossil record of the Pycnodontiformes. It is part of a diversified fauna that also includes *Nursallia veronae* and *Palaeobalistum* in strict sense (Poyato-Ariza & Wenz 2002; Poyato-Ariza 2005a). The type species, *Pycnodus apodus* (Volta, 1809) is currently regarded as the sole species of this genus known from articulated remains (Poyato-Ariza 2013). For further details on the nomenclatural history of this taxon, see Blot (1987: 11-15) and Poyato-Ariza & Wenz (2002: 152).

Scalacurvichthys Cawley & Kriwet, 2018. A single species, *S. naishi*, based on an incomplete, imperfectly preserved, partially disarticulated specimen from the early-mid Cenomanian, Late Cretaceous, of 'Ein Yabrud in Israel. A member of the subfamily Pycnodontinae according to Cawley & Kriwet (2018).

Sigmapycnodus Taverne & Capasso, 2018b. Based on a single incomplete, imperfect specimen, artificially restored, from the late Cenomanian (Late

Cretaceous) of Haqel, Lebanon. Specimen in a private collection, therefore coded from the information in the original publication.

Sylvienodus Poyato-Ariza, 2013 (Fig. 5). Abundant specimens of very small size, up to about 6 cm, from the upper Cenomanian of Laveiras, near Lisbon, west central Portugal. It only contains the species *Sylvienodus laveirensis* (Veiga Ferreira, 1961), initially assessed to *Pycnodus*. It was noted to show part of the diagnostic characters of the Pycnodontinae but not all, very much like *Polazzodus* and *Tergestinia*, thus triggering the present revision of the subfamily (Poyato-Ariza 2013: 98-99).

Tergestinia Capasso, 2000 (Fig. 6). Abundant specimens of very small size, up to 4-5 cm, from the early Paleocene of Trebiciano, near Trieste, northeastern Italy. Originally assessed to a "family Tergestiniidae" created ad hoc by Capasso (2000). It was noted to show significant similitudes with *Pycnodus* and *Polazzodus* by Poyato-Ariza (2010), and included in the Pycnodontinae by Taverne & Capasso (2012) and Taverne et al. (2019) without the benefit of a phylogenetic analysis.

Fig. 4 - *Pycnodus apodus*, syntype of the type species, MNHN-BOL-0095 (the only syntype currently available; counterpart is labelled 0094 in the same collection). Photo D. Serrette, courtesy S. Wenz. The standard length of the specimen is 21,5 cm, total length 24 cm.

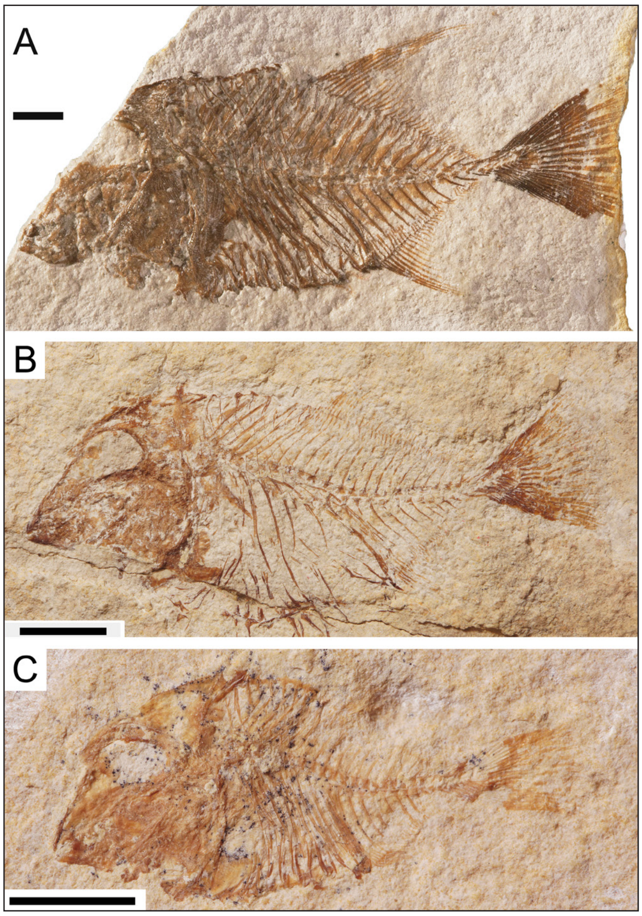

Fig. 5 - *Sylvienodus laveirensis*. A) Lectotype, LNEG-MG 6659. Modified from Poyato-Ariza (2103); B) subadult specimen IST-MDT 592-6; C) juvenile specimen IST-MDT 592-1. B, C, photos M. F. Costa-Pereira (IST-MDT). Line bars equal 5 mm.

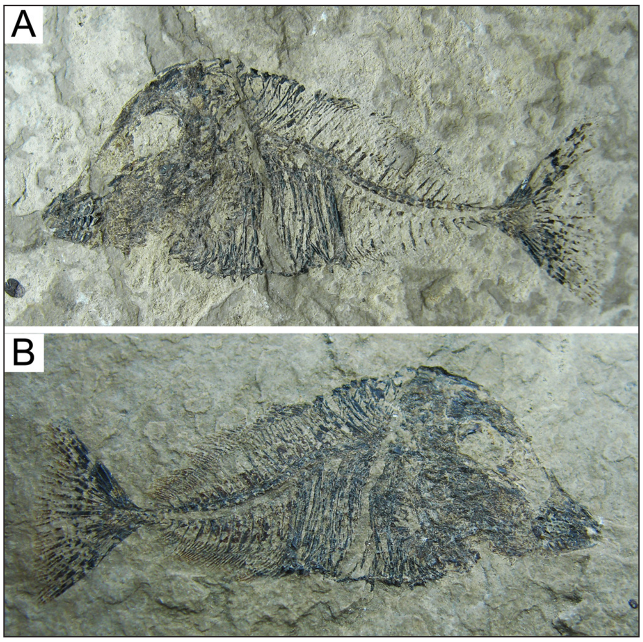

Fig. 6 - *Tergestinia sorbinii*, holotype. A) Part, MCSNT-T.203; B) counterpart, MCSNT T-204. The total length of the individual is 43,3 mm. Photos A. Colla, archives MCSNT.

MATERIAL AND METHODS

The revision attempted in this paper is based on articulated, complete, well preserved specimens. Isolated dentitions are purposefully excluded from this revision in order to avoid the numerous parataxonomical problems involved, and also because dental characters alone are not useful to clarify the interrelationships of the Pycnodontidae (Poyato-Ariza 2003).

All specimens were studied in their corresponding institutions and/or from the literature, with one exception. It was not possible to study the type specimen of "*Pycnodus*" *nardoensis* (Taverne 1997) or any subsequently assessed material (Taverne 2003) directly. Photographs were not made available for study either because of problems with the allocation of the fishes from Nardò (Zorzin pers. comm.: 2015). In turn, the specimens described by Taverne & Capasso (2013) belong to the private collection of the latter. Therefore, this fish was studied only from the descriptions and illustrations by Taverne (1997, 2003) and Taverne & Capasso (2012). Unfortunately, all illustrations showing anatomic detail are idealised restorations. Photographs only show general views without detail, and camera lucida drawings are altogether absent. In addition, detailed comparisons of the illustrations reveal relevant discordant features among the different specimens. For instance, the last arcocentra before the caudal endoskeleton articulate with each other and show crenulated medial borders in the restoration by Taverne (2003: fig. 8), but are largely separated from each other and show smooth borders in the restorations by Taverne & Capasso (2012: figs. 10 and 11, quite different in the morphology of the epichordal elements of the caudal endoskeleton). Vomerine teeth are largely separated from each other and those on the main row are elongated in lateral sense in Taverne (2003: fig. 2), but they are tightly packed and elongated in meso-distal sense in Taverne & Capasso (2013: fig.7). All specimens are considered to be from the same locality of Nardò, but the type specimen comes from Portoselvaggio, whereas most of the other material comes from the apparently different sites of Canale and Alessano del Capo (Taverne 2003: 15; Taverne & Capasso 2012: 31-33; no further explanations provided). In this confusing situation, there is no point on trying to code such heterogeneous material into the data matrix for the present analysis. This problematic taxon will remain in need of revision until the taxonomic status of all particular specimens is solved (see Discussion below).

Institutional abbreviations

IST-MDT, Instituto Superior Técnico, Museu Décio Thadeu, Lisbon, Portugal; LNEG-MG, Laboratorio Nacional de Energia e Geologia, Museu de Geologia, Lisbon, Portugal; MCSNT, Museo Civico di Storia Naturale di Trieste, Italy; MCSNV, Museo Civico di Storia Naturale di Verona, Italy; MNHN, Muséum national d'Histoire naturelle de Paris, France; MPCM, Museo Paleontologico Cittadino di Monfalcone, Italy; NHMUK, Natural History Museum, London, UK; NMW, Naturhistorisches Museum in Wien, Vienna, Austria.

Material

"*Coelodus*" *gridellii*: MCSNT-12366, holotype and only specimen. Transferred to the genus *Polazzodus* in the present paper.

Oropycnodus ponsorti: NMW 1854/XXXIX/38 (lectotype), 1854/XXXIX/39 and 1854/XXXIX/40 (paralectotypes); MNHN MTA 3-7, 9-13, 15-17 and 38-49 ; NHMUK 30035-30040, 30042-30047, P1638.

Polazzodus coronatus: MPCM-13464 (holotype), 2536, 9724, 10856, 10879, 10880, 11333, 11360, 11849, 11897, 12035, 12045, 12046, 12050, 12174, 12214, 12215, 12264, 12268 (paratypes), 2531, 2532, 9655a/b, 9687, 9729, 11796a, 11949a/b, 12042, 13539; MCSNT-12361 (paratype, specimen "number 2" in D'Erasmo, 1952) and 12447 (paratype).

Pycnodus apodus: MNHN-BOL-0094 and 0095 (syntype, part and counterpart), 0124-0127, 0130-31, and 0134-35; MCSNV B1, II.D.167-68, 170-71, 180, T.998-999, I.G.135608-09, 135664; NHMUK P.1634, P.44520.

Sylvienodus laveirensis: LNEG-MG 6659 (lectotype), 4716 (paralectotype), 6658 (paralectotype); IST-MDT 527 (paralectotype), 580, 583.1-6, 589, 591, 592 (paralectotype), 617.

Tergestinia sorbinii: MCSNT T.203-204 (holotype, part and counterpart); T.11, T.17, T.19, T.66, T.201-202, T.206-207, T. 211-212 (all paratypes).

Nomenclature

In this paper "pycnodont" is used to refer to any taxon of the order Pycnodontiformes and "pycnodonts" is used to refer to all taxa or the order Pycnodontiformes.

The superordinal rank of the pycnodonts as proposed by Nursall (2010) is not kept in the present paper following Poyato-Ariza (2015).

The length of the teeth is referred to the relative orientation of the teeth in the jaw, not as the major measure regardless of orientation. That is, "length" is always the meso-distal measure, not necessarily the longest measure in absolute value.

List of characters

The characters used in the present analysis are based on the characters by Poyato-Ariza & Wenz (2002) as revised and re-polarised for the Pycnodontoidei by Poyato-Ariza & Wenz (2004, 2005). Some of those characters have been deleted because they do not show variation within the ingroup genera of the present analysis (i.e., they are present only in Coccodontoidea, which are not included herein). In turn, other characters are added for the present analysis in order to account for the variation observed in the revised genera. The new character list below includes the former number of each character in parenthesis (as in Poyato-Ariza & Wenz 2005), so that they can be traced back to previous analyses. Other than this, and in order to avoid confusion, all references to character numbers in the present paper refer exclusively to their current number in the list below.

Small modifications on a few characters have been made by eliminating the character states that are not present in the ingroup genera included in the present analysis (in characters 5, 38, 51, 54, 56, 59, 62-64, 66, and 70-84). The variation observed among the genera revised for this analysis has resulted on the addition of new derived states in characters 13 (also reworded), 15, 19 (with rewording of previous states), 22, 23, 26, 51, and 61. Finally, there are changes for a better explanation of anatomical variation in characters 3, 6, 8, 15, 46, 71, 72, 78, and 79. A typing mistake from previous analyses has been corrected in character 45. New states in previously existing characters are commented correspondingly in each particular character. Characters 14, 27, and 67 are new, in order to account for new features observed in the material revised herein (mostly *Polazzodus* and *Sylvienodus*).

The taxa included in the present analysis are all based on articulated specimens; they include those in Poyato-Ariza & Wenz (2005). *Anomoeodus* has been added for the present analysis by revising its characters from Poyato-Ariza & Wenz (2002). *Flagellipinna* is coded with the information from Cawley & Kriwet (2019); *Haqelpycnodus, Libanopycnodus,* and *Sigmapycnodus* from Taverne & Capasso (2018a,b); *Potiguara* as in Machado & Brito (2006); *Scalacurvichthys* according to Cawley & Kriwet (2018); *Thiollierepycnodus* as in Ebert (2019); and *Turboscinetes* as in Ebert (2016) Unclear or disagreeing interpretations are discussed in the corresponding characters below. "*Coelodus*" *gridellii*, *Polazzodus*, *Sylvienodus*, and *Tergestinia* are coded into the pycnodontid data matrix for the first time. Therefore, particular comments in the list below refer mostly to these taxa. For character coding of the other genera included in the analysis, see Poyato-Ariza & Wenz (2004, 2005). The complete data matrix used in the present analysis is presented in Table 1.

1. Body shape (as measured by ratio maximum body height/standard length): discoid, 70–100% (0); intermediate, 40–70% (1); fusiform, less than 40% (2); deep, more than 100% (3). See Fig. 7A-F for comparative outlines of the body in the genera revised herein. The state in *Flagellipinna* is coded as in the adult specimen (Cawley & Kriwet 2019: Table 1; state 0).

2. Relative position of dorsal apex: between the skull and the point of insertion of dorsal fin (0); apex absent (1); in point of insertion of dorsal fin (2); in skull (3). Many characters involving the body contour of *Sigmapycnodus* are coded as ? because it is not preserved in the only specimen known. The lectotype of *Sylvienodus laveirensis*, among other specimens, shows that, although the contour scales are often preserved slightly disarticulated, there really is no distinct dorsal apex because the dorsal border of the body is sub-horizontal between the skull and the dorsal fin (state 1; Figs. 5, 7E). Correct orientation of the holotype of *Thiollierepycnodus* (Ebert 2019: fig. 2) and *Turboscinetes* (Ebert 2016: Fig. 3, specimens should be shifted clockwise to make caudal fin completely vertical) indicates that the dorsal apex is placed in the point of insertion of the dorsal fin in the former (coded as 2) and between the skull and the dorsal fin in the latter (coded as 0). Character state 3, previously unknown in pycnodonts, is added in the present analysis because it was found to be present in *Tergestinia*, resulting on a specially truncated overall shape (Figs. 6, 7F).

3. Dorsal prominence: absent (0); present, curved, dorsally oriented (1).

4. Relative position of ventral apex: apex absent (0); before point of insertion of anal fin (1); in point of insertion of anal fin (2).

5. Mouth gape: horizontal or subhorizontal (0); inclined (1). The mouth gape in *Turboscinetes* as shown by Ebert (2016: Fig. 5) is subhorizontal rather than inclined (coded as 0).

6. Prognathism: absent (i.e., anterior part of mouth gape not distinctively projected, although the whole ethmoid region is hypertrophied) (0); present by elongation of mesethmoid, vomer and prearticular in the horizontal plane, marking a concavity in the anterior border of the head (1); present by expansion of premaxilla and dentary (2). *Flagellipinna* is not considered to be prognathous (unlike Crawley & Kriwet 2019) because neither the vomer or the prearticular are elongated, the mesethmoid is hypertrophied as in other pycnodonts, and there is no concavity in the anterior border of the head (coded as 0).

7. Caudal pedicle: not differentiated (0); differentiated (1).

8. Morphology of frontal bones: narrow above the orbit (0); broad, expanded all throughout their length, nearly hemispheric in overall shape (1).

9. Prefrontal bones: absent (0); present (1). A paired prefrontal bone is present in *Flagellipinna* according to Cawley & Kriwet (2019: text, figs. 3, 4) and in *Haqelpycnodus* and *Libanopycnodus* according to Taverne & Capasso (2018a: 123, Fig. 9; 2018b: 6, Fig. 4). However, whenever a prefrontal bone is present, it is clearly distinct from, and observed in addition to, the superficial, ornamented portion of the mesethmoid, which is T-shaped in section

(e.g., Poyato-Ariza & Wenz 2005: Figs. 3, 5; see Nursall 1996: 129, figs. 5, 6 and 1999: 193, fig. 3, for the structure of the pycnodont mesethmoid). Such portion of the mesethmoid is restored absent in these three genera, which strongly indicates that their supposed prefrontal corresponds in fact to the shallow portion of the mesethmoid present in all pycnodonts (coded as 0). Most characters of the incomplete, very poorly preserved skull of *Sigmapycnodus* are coded as ? because the restoration and description by Taverne & Capasso (2008b: 17-23, fig. 17) appear unreliable when compared with the photos (op. cit.: figs. 15-16).

10(11). Dermocranial fenestra: absent (0); present (1). Personal observations confirm that the dermocranial fenestra is absent in *Tergestinia* (coded as 0 for this genus).

11(13). Parietal process: absent (0); present (1). This character is not observable in all taxa included in the analysis; when it is, the pectinated parietal process is always present. The character has been kept because it is a very particular, traditionally remarked feature of many pycnodonts.

12(16). Extrascapular(s) fused to parietal: no (0); yes (1).

13(17). Endocranium (supraoccipital bone): completely covered by dermal skull in lateral view (0); exposed posteriorly (1); largely exposed posteriorly (2). The type specimen of *"C." gridellii* (Figs. 1, 7A) shows that the endocranium is very largely exposed posteriorly, comparatively more than in other pycnodonts (state 2). This is due partly to a posterior expansion of the endocranium and partly to the presence of a remarkable concavity in the posterior border of the dermal skull. The result is that the exposed portion of the endocranium is about as wide as it is deep (Fig. 7A). In other pycnodonts such as *Polazzodus* and *Pycnodus* the exposed portion is at least twice as high as it is wide (Fig. 7C, D; Poyato-Ariza 2010: fig. 3). The small ossifications identified as basioccipital and exoccipital, even intercalar, in *Haqelpycnodus* and *Libanopycnodus* (Taverne & Capasso 2018a: Fig. 9; 2018b: Fig.4) do not correspond to the supraoccipital as exposed all throughout the posterior border of the parietal in *Pycnodus* or *Polazzodus* (e.g, Poyato-Ariza 2010: Fig. 3; coded as 0 for *Haqelpycnodus* and *Libanopycnodus*). *Scalacurvichthys* is reported to have a posteriorly exposed endocranium (Cawley & Kriwet 2018). However, the assessment of this character is not clear. In the only specimen, this region is not well preserved and partially covered by matrix; the zone pointed as endocranium (Cawley & Kriwet op. cit.: figs. 2A, 3) looks hemispheric and massive, like an arcocentrum or an exoccipital rather than the thin, laminar supraoccipital of other genera such as *Pycnodus* or *Polazzodus*. *Scalacurvichthys* was therefore conservatively coded as (?) for the present analysis; the homologies of the bones exposed in this region need confirmation in further, better preserved material.

14 (new). Postcephalic lacuna in endocranium (supraoccipital): supraoccipital not visible in lateral view (0); lacuna absent (1); lacuna present (2). This character is considered independent from the previous one because, whenever the supraoccipital is exposed in lateral view, the lacuna can be either absent or present. The presence of a lacuna of ossification in the posteriorly exposed portion of the endocranium was firstly reported by Blot (1984) in *Pycnodus*. Ulterior observations have confirmed the presence of such a lacuna in *Oropycnodus* (Poyato-Ariza & Wenz 2002: fig. 11B) and its absence in *"C." gridellii*, *Polazzodus*, *Sylvienodus*, and *Tergestinia* (Fig. 7A-F). The poor state of preservation of this region as commented in the previous character does not allow assessment in *Scalacurvichthys* (coded as ?).

15(19). Infraorbitals: reduced to tubular ossifications around infraorbital sensory canal (0); anterior infraorbital enlarged (1); small plates (2); absent (3). This character is coded as absent (3) in some taxa revised for the present analysis because, even though these bones are tubular and easily lost during fossilization, complete absence of any indication of their presence in the numerous, well preserved specimens of *Polazzodus*, *Sylvienodus*, and *Tergestinia* strongly indicates that they have been altogether lost in these genera (coded as 3, state added for the present analysis). They also seem absent in the holotype of *"C." gridellii*, but, since this is the only known specimen, it has been conservatively coded as unknown (?) in this form.

16(18). Anterior portion of infraorbital sensory canal: closely surrounding orbit (0); descending towards ethmoid region (1). Not applicable in *Polazzodus*, *Sylvienodus*, and *Tergestinia* (see previous character).

17(20). Infraorbital ornamentation: present in all infraorbitals (0); present only in posteriormost one (1); absent in all infraorbitals (2). See comments on previous character.

18(21). Suborbitals: mosaic of small plates (0); absent as independent ossifications (1).

19(22). Preopercular and hyomandibular: preopercular single, hypertrophied; hyomandibular deep, unornamented (0); one high preopercular in close contact with small ornamented portion of hyomandibular, at same superficial level (1); preopercular reduced, about as high as the ornamented portion of hyomandibular (2); preopercular additionally reduced, clearly lower than ornamented portion of hyomandibular (3). State 3 has been added for the present analysis because the preopercular bone is especially reduced in height in some genera, to the point that its main body (i.e., not including the anterior ascending process) is unmistakably lower than the ornamented portion of the hyomandibular. This is clearly visible in all well preserved specimens of *Polazzodus* (Poyato-Ariza 2010: figs. 2, 4) and *Pycnodus* (e.g., Poyato-Ariza & Wenz 2002: fig. 10). Unfortunately, this region is not very well preserved in the holotype and only specimen of "*Coelodus*" *gridellii*, but observable portions of the dorsal border of the preopercular bone indicate that it is not especially low, about as high as the ornamented portion of the hyomandibular (state 2). Although the anterior part of the preopercular bone is uniquely partially fused to the hyomandibular in *Sylvienodus*, its unfused surface clearly corresponds to state 2 (Poyato-Ariza 2013: fig. 3). The region is never well preserved in the numerous, but delicately ossified, specimens of *Tergestinia*, but the visible portions of the dorsal border of the preopercular bone indicate that it is very reduced, lower than the ornamented portion of the hyomandibular (state 3; e.g., holotype, MCSNT T.204).

20(23). Condyle in articular head of hyomandibular: absent (0); present (1).

21(24). Opercular bone: reduced (0); extremely reduced (1). An extremely reduced, narrow, opercular bone is observable in *"C." gridellii*, *Polazzodus* (Poyato-Ariza 2010: 655), *Sylvienodus* (Poyato-Ariza 2013: fig. 3) and specimen MCSNT T.204 of *Tergestinia* (counterpart of the holotype; coded as 1 for this genus).

22(25). Branchiostegal rays: two, thin and separated (0); two, relatively large and in contact (1); absent (2); three (3). Poyato-Ariza & Wenz (2002: 167) pointed that when branchiostegal rays are not observed, such small, delicate bones may be absent due to taphonomic reasons. In some cases, at least fragments of them can be observed in *Oropycnodus* (Poyato-Ariza & Wenz: fig. 17) and *Pycnodus* (Blot 1987: 35; pers. obs.). The large number of well-ossified and well-preserved specimens of *Polazzodus* observed with no traces of branchiostegal rays (Poyato-Ariza 2010: 655) is a reasonable indication that they are lost in at least this genus and, for the same reason, in *Sylvienodus* and *Tergestinia* (coded as 2, state added for the present analysis). The imperfect preservation of the only specimen of *"C." gridellii* prevents for such criterion to be applied to this genus (coded as ?). State 3 (three branchiostegal rays) is added for *Turboscinetes* according to Ebert (2016).

23(26). Morphology of premaxillary and dentary teeth: robust, barely incisiform (0); very flattened, fully incisiform (1); molariform (2); incisiform & bifurcated (3). The anterior region of the skull is unfortunately missing in the type and only specimen of *"C." gridellii*, so all characters concerning dentition and other features of the oral region are coded as unknown [?]. *Haqelpycnodus* presents small but robust, not fully incisiform teeth (Taverne & Capasso 2018a: Figs. 10, 11; coded as 0).

24(90). Morphology of premaxilla: small, with long, slender process continuous with anterior border of main body of bone (0); large, rounded, horizontally expanded, with short, robust process emitted by posterior region of the bone (1).

25(27). Number of premaxillary teeth: 2 (0); 3 (1); at least 8, arranged in at least two rows (2); 1 (3). State 3, only one premaxillary tooth, is added for the present analysis. This state is present in *Polazzodus*, *Sylvienodus*, and *Tergestinia* (see Poyato-Ariza 2010: 656 for a justification that this is not a preservational artifact).

26(28). Morphology of maxilla (outline): ovoid (0); reniform (1); straight oral border (2); elongated oval (3); oval with dorsal notch (4); axe-blade like (5). See Poyato-Ariza (2010: 656, fig. 5B; 2013: 94-95) for a full description of the very particular morphology of the maxilla in *Polazzodus* and *Sylvienodus* (state 5, added for this analysis; see Poyato-Ariza 2013: fig. 2 for a comparison of the maxillary outline in these two genera and *Pycnodus*). This confirms the remarkable variability of this bone in pycnodonts, in which it is always edentulous and very loosely articulated to the premaxilla; it is relatively rare for it to be preserved. The maxilla in *Thiollierepycnodus* as illustrated by Ebert (2019: fig. 4)

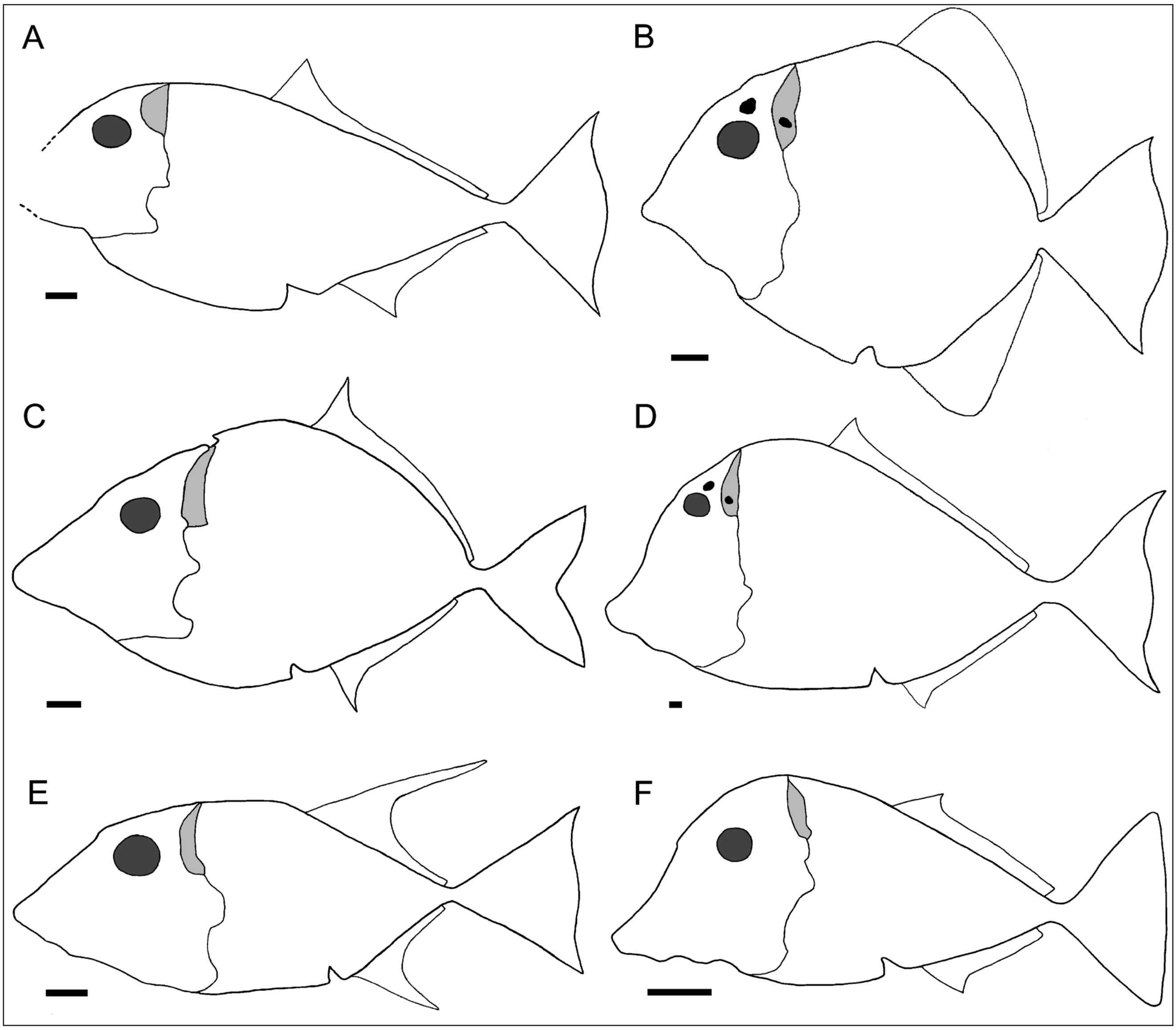

Fig. 7 - Simplified body outline in: A) *Polazzodus gridellii* n. comb., formerly "*Coelodus*" *gridellii* (type and only known specimen anteriorly incomplete); B) *Oropycnodus ponsorti*; C) *Polazzodus coronatus*; D) *Pycnodus apodus*; E) *Sylvienodus laveirensis*; F) *Tergestinia sorbinii*. The eye is shown in dark grey and the posteriorly exposed portion of the endocranium in light grey. The parietal process, present in all genera, is omitted for clarity; the dermocranial fenestra and the postcephalic lacuna are depicted in black when present. The pectoral and pelvic fins, very similar in all genera, are omitted for clarity. Idealized restorations based mostly on the corresponding type material, completed with observations on specimens MNHN MTA-42 and NHML P.30037 (*Oropycnodus*), NHMUK P.1634 (*Pycnodus*), IST-MDT 592-6 & 580 (*Sylvienodus*), and MCSNT T.201-202 (*Tergestinia*). See text and Poyato-Ariza & Wenz 2002: 189 for comments on the shape of the anal fin of *Oropycnodus*. Line bars represent 5 mm.

is ovoid rather than reniform (i.e., there is no constriction in the middle; coded as 0).

27(new). Crenulations on anteroventral border of maxilla: absent (0); present (1). All pycnodonts whose maxilla is known exhibit a smooth border, whatever the contour morphology. Only *Sylvienodus* presents crenulations on the anteroventral border of this bone (see Poyato-Ariza 2013: 94-95, fig. 2 for additional details).

28(29). Morphology of vomerine teeth: circular to subcircular contour (0); oval contour (1); reniform contour (2); triangular contour on the main row; (3) oval, very elongated (4). Among the pycnodonts included in this analysis, state 3 is present in *Polazzodus* only (Poyato-Ariza 2010: 656, fig. 5D).

29(30). Arrangement of vomerine teeth in regular rows: present (0); absent anteriorly, present posteriorly (1).

30(31). Number of vomerine tooth rows: 5 (0); 3 (1); 6 (2).

31(32). Number of teeth in principal vomerine tooth row: 10 or more (0); 8 or 9 (1); 7 or less (2).

Unlike Cawley & Kriwet (2017), this character is coded as unknown (?) for *Scalacurvichthys* because the vomer of the single known specimen is only partially exposed in lateral view and is covered to a degree by the lower jaw posteriorly (Cawley & Kriwet 2017, figs. 2-3), so that the principal tooth row is not fully visible and there may be more than the seven teeth reported by those authors. Vomerine dentition characters are also coded as ? for *Libanopycnodus* because only the most lateral row is exposed, and only in lateral view (Taverne & Capasso 2018b, figs. 3, 4).

32(33). Alternation of teeth on main vomerine tooth row: absent (0); present (1).

33(34). Number of dentary teeth: 4 (0); 3 (1); 2 (2). There are currently no known pycnodonts with only one dentary tooth. *Polazzodus* and *Tergestinia* have a single premaxillary tooth (see character 27 above), but they clearly show two teeth on the dentary (state 2).

34(35). Morphology of prearticulary teeth: oval contour (0); circular contour (1); sigmoid to drop-shaped contour (2); extremely elongated in contour, long axis perpendicular to row axis (3); oval, elongated, long axis of teeth coincident with row axis (4). Characters 35-38 are unknown in *Sylvienodus* because the prearticulary teeth are not sufficiently exposed in any observed specimen.

35(36). Arrangement of prearticular teeth in regular rows: present (0); absent anteriorly, present posteriorly (1); absent (2). Only the posterior part of the prearticulars is exposed in *Libanopycnodus* (Taverne & Capasso 2018b, figs. 5, 6; coded as ?).

36(37). Number of prearticular tooth rows: 3 (0); 2 (1); 5 or 6 (2). The prearticular tooth rows are different in the holotype and the paratype of *Haqelpycnodus* (Taverne & Capasso 2018a: 124, Figs. 10, 11, 13; coded as ?). "There are three rows of teeth present in the prearticular bone" in *Scalacurvichthys* according to Cawley & Kriwet (2018: 665, figs. 1-3). However, the left prearticular of the holotype and only specimen, partially visible in medial view, is largely covered by the right prearticular and the main tooth row is not exposed. Therefore, it is not possible to be certain of the number of prearticular tooth rows and it is coded as unknown (?) for this genus.

37(38). Number of teeth on main prearticular tooth row: 8 or 9 (0); 7 or fewer (1); 10 or more (2). See character 35 for *Libanopycnodus*. Incompletely prearticular dentitions in articulated specimens of *Polazzodus* have 7 teeth at the most, but they are never observable in their entirety; in turn, complete specimen MPCM 10879 clearly shows 8 (Poyato-Ariza 2010: 657, fig. 5F; state 0). Although the prearticular tooth plate is never observed in *Tergestinia* in its entirety, there is no room before the mandibular articulation for more than 7 teeth on the main row. Coded as ? for *Scalacurvichthys* (see previous character).

38(39). Coronoid process: high, straight dorsal border (0); high, club shaped (1). The morphology that corresponds to state 0 is suggested by the observable mandibular portion of the lectotype and fully observable in specimen IST-MDT-580 of *Sylvienodus*. As shown by Cawley & Kriwet (2018: figs. 2-3), the coronoid process of *Scalacurvichthys* is clearly not club-shaped, as it lacks the bulky head and the narrowing that define such morphology (compare with Poyato-Ariza & Wenz 2002: fig. 23B and 2004: figs. 5, 9B), so it is coded as 0 for this genus.

39(40). Crenulations in vomerine and prearticular teeth: occasionally present, weak (0); absent (1); present in most teeth, strong (2). Vomerine and especially prearticular teeth are seldom exposed in *Sylvienodus*. Nonethess, paralectotype LNEG-MG 6658 shows three teeth, two on the vomer and one on the prearticular, all three with strong crenulations. See Poyato-Ariza (2013: 95) for additional details on the strong crenulations observed in this taxon (state 2).

40(41). Groove on vomerine and prearticular teeth: absent (0); present (1).

41(42). Number of vertebrae (epichordal elements excluding those of the caudal endoskeleton): 30–34 (0); 35 or more (1); 25–29 (2); 24 or fewer (3). The number of vertebrae in *Sylvienodus*, 22-23, is quite reduced for a pycnodont (Poyato-Ariza 2013: Table 1; state 3). A maximum number of 29 is consistently observed in *Tergestinia* (13 abdominal, 15-generally 16 caudal excluding those of the caudal endoskeleton).

42(43). Neural and haemal corresponding arcocentra: not surrounding notochord (0); surrounding notochord partially (1); surrounding notochord completely (2). Adult specimens of *Flagellipinna* are reported to have the arcocentra surrounding the notochord completely but restored with all arcocentra surrounding the notochord partially only (Cawley & Kriwet 2019: figs. 1, 2; coded as 1). Same applies to *Sigmapycnodus* (Taverne & Capasso 2008b: 23, figs.

12-14; coded as 1). The lectotype of *Sylvienodus laveirensis* clearly shows that they surround the notochord completely (state 2).

43(44). Neural and haemal adjacent arcocentra: simple contact (0); complex contact (1); hyper complex contact (2); expanded and imbricate (3). The last caudal vertebrae show a hyper complex contact in *Flagellipinna*, but it is puzzling restored with overlapping arcocentra (Cawley & Kriwet 2019: figs. 7 & 2 respectively; coded as 2 & 3). This character is unclear in *Sigmapycnodus* too; it is described as "hypercomplex" by Taverne & Capasso (2008b: fig. 23), but their photos and restoration (op. cit.: 12-14, 20), show only 2-3 interdigitations (complex contact only), and some vertebrae appear separated, without contact (coded as 1 for the vertebrae actually in contact).

44(45). Sagittal flanges on neural and haemal spines: anterior, small and short (0); anterior, large and long (1); anterior and posterior (2). Modified in *Potiguara* from 0&1 to 1 because these flanges cannot be simultaneously short and long, and they are long as described by Machado & Brito (2006: 2) in relation with the character as originally used by Poyato-Ariza & Wenz (2002, 2004).

45(46). Number of autogenous anterior neural spines: 10 or more (0); 7–9 (1); 6 or fewer (2). At most six autogenous neural spines can be counted in the holotype of *"C." gridellii* (state 2). This character is difficult to determine in *Sylvienodus*; however, paralectotype LNEG-MG 6658 shows that the seventh neural spine is autogenous and the eighth is fused (state 1).

46(47). Relative length of last neural spine not supporting precurrent caudal fin rays: slightly shorter than previous ones (0); less than half as long as preceding spines (1); vestigial (2).

47(48). Number of epichordal elements of caudal endoskeleton: primitive (?); 6 to 8 (1); 4 or 5 (2); 3 or fewer (3). The state of preservation in *Libanopycnodus* does not allow verification (Taverne & Capasso 2018b: fig.8). Most caudal skeleton characters are coded as ? in *Sigmapycnodus* because of the incompleteness and very poor state of preservation (Taverne & Capasso 2008b: figs. 21, 22). It is difficult to discern between 6 and 7 epichordal elements in *Tergestinia*; specimen MCSNT T.17 seems to show a maximum of 6 (state 1 in any case). There seem to be 6 epichordal elements in the caudal skeleton of the holotype of *"C." gridellii* (state 1). According to Ebert (2016: Fig. 11), there are 4, maybe 5, epichordal elements supporting the fin exoskeleton, so it is coded as 2 for this genus.

48(49). Relative development of hypochordal elements of caudal endoskeleton: only slightly enlarged (0); enlarged, plate-like (1); one hypertrophied element (2); two hypertrophied elements (3). For the present analysis, we consider that "hypertrophied elements" correspond to those that are clearly larger than the normal size for their position in the series and clearly show at least one longitudinal ridge (suggesting a possible compound origin by fusion of two plates). In this sense, only *Oropycnodus* and *Pycnodus* among the genera re-evaluated for this analysis present state 3. *Scalacurvichthys* is coded as 0 after Cawley & Kriwet 2018 (fig. 4A, B; the camera lucida drawing on C does not seem to correspond clearly to the photos on A and B and is confusing and hard to interpret). *Turboscinetes* is coded as 1 because hypochordal element 6 and very likely 7 (party under the fin rays) of the caudal endoskeleton are enlarged and plate-like (Ebert 2016: Fig. 11).

49(50). Number of hypochordal elements of caudal endoskeleton: 9–11 (0); 12–13 (1); 6–8 (2). See character 47 for *Libanopycnodus*.

50(51). Diastema: absent (0); present (1).

51(52). Cleithrum: curved, anteroventral limb subvertical, expanded (0); two small posterior expansions framing a shallow notch for the insertion of the fin (1); two large posterior expansions framing a deep notch for the insertion of the fin plus anterior elongation of the anteroventral limb (2). The morphology of the cleithrum in the genera re-evaluated for the present analysis has shown interesting variations (Fig. 8). The simple, subvertical cleithrum broadly present in other Pycnodontidae is not observed among the revised genera. State 1 corresponds to *Pycnodus*, whose cleithrum presents two short posterior processes, upper and lower, that frame a high but shallow notch for the insertion of the fin (e.g., Poyato-Ariza & Wenz 2002: fig. 10; present paper: Fig. 8A); this also seems to be the morphology in *Oropycnodus* (although the preservation of this bone in this taxon is not good), *Sylvienodus*, and *Tergestinia* (Fig. 7). The morphology of the cleithrum in *Polazzodus* presents remarkable additional modifications; the two posterior processes are more robust and expanded, so that the notch for the insertion of the fin is quite deeper. As a matter of fact, the lower process is formed as an ex-

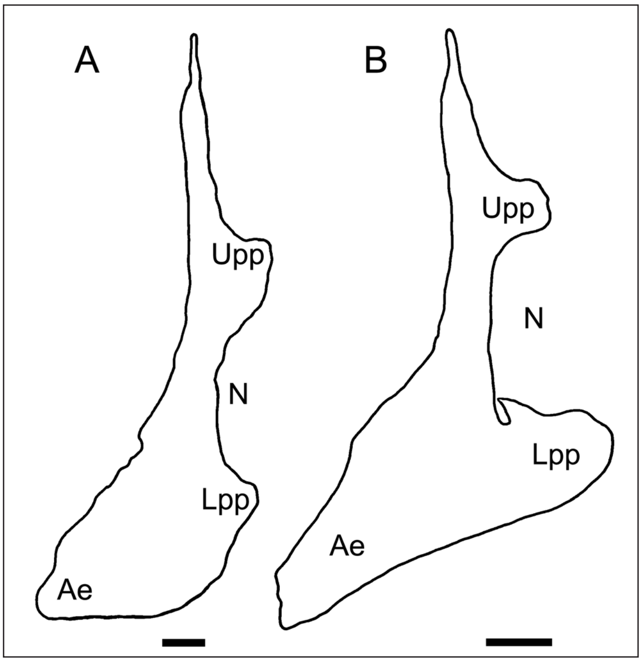

Fig. 8 - Restored comparative outline of the cleithrum in: A) *Pycnodus apodus*, based on a camera lucida drawing of transferred specimen NHMUK P.1634; B) *Polazzodus coronatus*, based on a camera lucida drawing of the holotype, MPCM-13464. Ae) anteroventral elongation of the anteroventral limb of the bone; Lpp) lower posterior process; N) large notch for the articulation of the endochondral girdle and insertion of the pectoral fin; Upp) upper posterior process. Notice the small notch, practically closed, in the anterodorsal border of the lower posterior process in B. Line bars represent 2 mm.

pansion of the whole posteroventral angle between the limbs of the bone. In addition, the anteroventral part of the bone is elongated anteriorly, so that the bone is crescent-shaped rather than subvertical (Poyato-Ariza 2010: fig. 6; present paper: Fig. 8B). The holotype of *"C." gridellii* shows a cleithrum whose morphology is similar to that of *Polazzodus* (state 2). The cleithrum of *Scalacurvichthys*, as seen in Cawley & Kriwet (2018: figs. 2A-3) corresponds to the morphology of the primitive state (coded as 0).

52(54). Position of pelvic fins (ratio prepelvic distance/standard length): 45–55% (0); more than 55% (1); less than 45% (2). Although the type and only specimen of *"C." gridellii* is incomplete, an estimation (for comparative purposes) of 55mm of prepelvic length and of 104 mm in standard length results in 52,3% (state 0).

53(55). Position of dorsal fin (predorsal length/standard length): 60%–69% (0); less than 49% (1); 50%–59% (2); 70%–79% (3). Although the type and only specimen of *"C." gridellii* is incomplete, an estimation of 53mm of predorsal length and of 104 mm in standard length results in 51% (state 2). Correct orientation of the holotype of *Thiollierepycnodus* (Ebert 2009: fig. 2) places the predorsal length at about 67-68% (state 0).

54(56). Number of dorsal axonosts: 30–39 (0); 40–49 (1); 50–59 (2); 60 or more (3). The number of dorsal axonosts in *Tergestinia* is variable, but never more than 52 or less than 50 (state 2). The state of preservation prevents from an accurate account in *"C." gridellii*, but an estimation of some 52-54 elements places it safely within the interval of state 2. In *Scalacurvichthys* "(…) disarticulation seems likely" in the dorsal fin (Cawley & Kriwet 2018: 666). The posteriormost dorsal fin rays and axonosts, faintly preserved as impressions, shown by the holotype and only specimen (Cawley & Kriwet op. cit.: fig. 1) are progressively more separated from their anatomic position; the whole posterodorsal border of the body appears completely eroded out and blurred in the specimen. The partial preservation and disarticulation are indications that the posteriormost portion of the fin, maybe even quite long, has been lost during fossilization. As a consequence, it is not likely that there are only 11 axonosts in its dorsal fin (coded as ? for this genus).

55(57). Dorsal axonost not supporting lepidotrichium (free axonost): absent (0); present (1).

56(58). Morphology of dorsal and anal fins: primitive (?); strip-like (1); falcate to acuminate (2); sigmoid outline (3); rounded in center (4); rounded anteriorly (5); extremely acuminate, higher anteriorly than it is long (6). There is a remarkable variability in shape among the different genera, but the dorsal and anal fin of each particular taxon normally present the same contour shape regardless of their different length. Although this may not seem the case in the type material of *Oropycnodus* (Fig. 2), this is a preservational artifact; whenever well observable in its entirety, the anal fin of this genus has the same shape than that of the dorsal fin (e.g., NHML P.30037; Poyato-Ariza & Wenz 2002: 189), that is, rounded anteriorly; so it has been restored on Fig. 7B. Most lepidotrichia of these fins in *Libanopycnodus* are lost, none preserved in its entirety; the restoration and description of the fins shape cannot be corroborated (Taverne & Capasso 2018b: figs. 1,2; coded as ?). See Poyato-Ariza (2013: 96-97; fig. 4) for a detailed description of the peculiar dorsal and anal fins of *Sylvienodus*. See also Fig. 7 in the present paper for a comparison of different genera. Due to inadequate preservation of this region, *Scalacur-*

vichthys is coded as ? (see comments in character 54).

57(59). Position of anal fin (preanal length/ standard length): 70%–79% (0); 50%–59% (1); 60%–69% (2); 80%–89% (3). The deformations presented to some extent by most specimens of *Polazzodus* makes this percentage quite variable. The lowest percentage is 61,74% in a clearly deformed specimen and 64,90-68,33% in apparently non-deformed specimens (Poyato-Ariza 2010: table 1). The highest percentages are 71,33% in the holotype and 74,75% in an apparently non-deformed specimen (idem). Such variation makes advisable to code this character as 0 & 2 simultaneously in this genus (this character is processed as unordered). For analogous reasons, it has been coded also 0&2 in *Sylvienodus* (see Poyato-Ariza 2013: Table 1 for further details). Correct orientation of the holotype of *Thiollierepycnodus* (Ebert 2009: fig. 2) places the preanal length at about 61-62% (state 2).

58(60). Number of anal axonosts: 20–29 (0); 10–19 (1); 30–39 (2); 40–49 (3); 50 or more (4); 9 or fewer (5). The holotype of *Tergestinia* shows 34-35 anal axonosts (state 2). The state of preservation prevents from an exact account in *"C." gridellii*, but an estimation of some 35-37 gets it safely within the interval of state 2. The holotype of *Polazzodus coronatus* has 41 anal axonosts, although all other specimens have less than 39 (Poyato-Ariza 2010: table 1; coded as 2&3).

59(61). Urodermals: one (0); two (1); absent (2). When present, urodermals are paired elements placed lateral to the proximal portions of the fin rays and/or the hypochordal elements (e.g., Poyato-Ariza & Wenz 2002: Figs. 24-27, 29, 30). However, the element described and illustrated as a urodermal by Taverne & Capasso (2018a,b) in *Haqelpycnodus* is an unpaired osseous element not lateral to fin rays or hypochordal elements; could be a fragment of the broken last epichordal element. For these reasons, it has been coded as unknown (?) in this genus. See Poyato-Ariza (2013: 97; fig. 5) for the description of the single urodermal of *Sylvienodus*.

60(62). Number of caudal principal fin rays: primitive (?); 9 or fewer (0); 10–19 (1); 20–25 (2); 26–35 (3); 36 or more (4). Whenever accurately observable, specimens of *Tergestinia* show 8 caudal principal rays in the upper lobe and 10-11 in the lower lobe, accounting for a total of 18-19 (mostly 19; state 1). The holotype of *"C." gridellii* seems to show 21-22 principal caudal fin rays (9 in the upper lobe and 12-13 in the lower lobe; state 2).

61(63). Morphology of caudal fin: distal border convex (0); distal border concave (1); double emarginated (2); vertical (3); forked (4); distal border vertical, straight (5). See Fig. 7 for comparison among the genera revised for this analysis. *Polazzodus* has a forked caudal fin that is unique among Pycnodontidae (state 4, new in the present analysis; Fig. 7C). In turn, *Tergestinia* has a caudal fin with a distal border that is vertical and straight (Fig. 7F), so state 5 was added for the present analysis as well. The distal border of the caudal fin is not perfectly preserved in the holotype of *"C." gridellii* (Fig. 1), but the observable portion strongly suggests it is double emarginated (Fig. 7A). This is not the case of *Libanopycnodus*, where only the basal portion of the fin rays is preserved (Taverne & Capasso 2018b: fig. 8; coded as ?).

62(64). Ossification of scales: complete in all scales (0); complete in abdominal scales, incomplete in caudal scales (1); complete in ventral scales and in some dorsal scales (2); complete in ventral scales, incomplete in dorsal scales (3); incomplete in all scales (4).

63(65). Distribution of scales: only abdominal region (0); whole body except caudal pedicle (1); abdominal region plus part of caudal region (2); whole body (3).

64(66). Arrangement of scales: rows in same direction (0); rows in different directions (1).

65(67). Ornamentation: tubercles (0); ridges (1); reticulation (2). Some taxa show different ornamentations simultaneously, such as the tubercles and reticulation of *Sylvienodus* (IST-MDT 592). Because this character refers to ornamentation on the dermal skull bones (not only on scales, which are rarely ornamented in pycnodontids), it is coded as 0 for *Haqelpycnodus* (Taverne & Capasso 2018a: 123) and 1 for *Turboscinetes* (Ebert 2016: Fig. 6).

66(69). First dorsal ridge scale: about same size as subsequent ridge scales (0); larger than subsequent ridge scales (1). In *Scalacurvichthys* (Cawley & Kriwet 2018: figs. 1-3), the gap between the dermal supraoccipital and the first visible dorsal ridge scale strongly suggest that the latter is actually the second dorsal ridge scale, and the first dorsal ridge scale, normally occupying the area of that gap, has been lost during fossilization in this partially disarticulated specimen. This interpretation is supported by the fact that the whole dorsal ridge scale series is partially disarticulated, broken, not entirely preserved (coded as ? for this genus). The argument that this scale contacts the dermal supraoccipital anteroventrally and that it is incorporated into the skull roof (Cawley & Kriwet 2018: 667) does not support its interpretation as the real first dorsal ridge scale, because such contact also occurs in the second dorsal ridge scale of other pycnodontids, such as *Polazzodus* (Poyato-Ariza 2010: fig. 3), whereas the real incorporation of the actual first dorsal ridge scale into the skull roof involves a tight structural continuity with the dermal supraoccipital bone, with no gap between them (e.g., Poyato-Ariza & Wenz 2002: figs. 6-9; 2004: figs. 4-5; Poyato-Ariza 2010: fig. 3).

67(new). Morphology of second dorsal ridge scale: similar to subsequent dorsal ridge scales (0); very long and large, with a central longitudinal ridge and a conspicuous anterior hook (1). State 1 accounts for the particular morphology of the second dorsal ridge scale in *Polazzodus* (for additional information see Poyato-Ariza 2010: 660-661; fig. 8). The second ridge scale ("first dorsal ridge scale" in Cawley & Kriwet 2018: figs. 1-3) of *Scalacurvichthys* is broken, only partially preserved; the restoration in Cawley & Kriwet (op. cit.: figs. 2B, D) is not straightforward when compared to the photos (op. cit.: figs. 2A, 3). For this reason, it has been coded as ? for the present analysis.

68(70). Scutellum-like contour scales: absent (0); present, dorsal only (1); present, ventral only (2); present, dorsal and ventral (3).

69(71). Number of differentiated dorsal ridge scales: 18 or more (0); 15 to 17 (1); 10 to 14 (2); 7 to 9 (3). The number of dorsal ridge scales is about 11 in *Tergestinia*. Although 9 dorsal ridge scales are shown by the holotype and only specimen of *Scalacurvichthys* (Cawley & Kriwet 2018: fig.1), the loss of the first dorsal ridge scale (as discussed in character 66 above) and the imperfect preservation of the whole series, with a complete loss of the posteriormost elements, are strong arguments for a total number of dorsal ridge scales well over 9. In other words, there can be no certainty that there were only 9 (coded as ?).

70(72). Arrangement of dorsal ridge scales: dorsal contour scales in close contact with each other (0); point contact (1); separated from each other (2). This character is rarely observable in *Sylvienodus laveirensis*; paralectotype LNEG-MG 6658 shows dorsal ridge scales that are in point contact with each other. It is coded as 2 for *Turboscinetes* because this character refers to the standard scales of the series, not including the anteriormost, enlarged ones (accounted for in characters 66 and 67) and mostly in contact because they are enlarged.

71(73). Number of spines on midline of dorsal ridge scales: 3 or more (0); midline serrated (1); 1 or 2 (2); no spines on dorsal contour scales (3). Consistently coded according to the maximum number observed in any scale of any specimen (the number of spines increases with age of specimen). As for the previous character, it is seldom visible in *Sylvienodus laveirensis*, but paralectotype LNEG-MG 6658 shows dorsal ridge scales that present a serrated midline (see also Poyato-Ariza 2013: fig. 6A). See Taverne & Capasso (2018b: figs. 1, 10) for the serrated midlines of the posteriormost scales of the series in *Libanopycnodus* (coded as 1).

72(74). Distribution of spines on midline of each dorsal ridge scale: all along midline, or centered if only one spine present (0); no spines on dorsal contour scales (1); posterior region (at most two thirds) of midline (2); anterior region (at most two thirds) of midline (3).

73(75). Contact of spines on each dorsal ridge scale: separated from each other (0); no spines on dorsal contour scales (1); in contact with each other (2).

74(76). Relative size of anterior and posterior spines on each dorsal ridge scale: similar in size (0); no spines on dorsal contour scales (1); spines of increasing size in cephalocaudal sense (2).

75(91). First ventral keel scale: smaller than subsequent scales (0); larger than subsequent scales (1).

76(77). Number of ventral keel scales: 22 or more (0); 18 to 21 (1); 15 to 17 (2); 10 to 14 (3). The holotype of "*C.*" *gridellii* shows at most 14 ventral keel scales: 11-12 before the cloaca, remarkably longer in caudal sense, the anteriormost ones less perfectly preserved, plus 2 after the cloaca (coded as 3). Because of imperfect preservation and uncertainty of description of the ventral keel scales in *Flagellipinna*, *Haqelpycnodus* and *Libanopycnodus*, their corresponding characters are all coded as unknown. A complete series of ventral keel scales is never clearly observed in any specimen of *Tergestinia*, but a maximum estimation of 12 of them can be made on the basis of the number of corresponding flank scale rows. With the 2 post-cloacal scales, this accounts for an estimated maximum number of 14 ventral keel scales (coded as 3 for this genus; similar estimation for *"C." gridellii*). The disarticulation and loss of the anteriormost ventral keel scales in *Scalacurvichthys* (Cawley & Kriwet 2018: fig. 1) renders the number impossible to be estimated because flank scales rows are also disarticulated and incomplete (coded as ?).

77(78). Arrangement of ventral keel scales: close contact with each other (0); point contact (1). The ventral keel scales are remarkably elongated in *"C." gridellii*, resulting on a point contact with each other. A close contact can be observed in the ventral keel scales shown by specimen MCSNT T.11 of *Tergestinia* (coded 0 for this genus).

78(79). Number of spines on the midline of ventral keel scales: 4 or more (0); 1 to 3 (1); no spines on ventral keel scales (2). Consistently coded as the maximum number observed in any scale of any specimen, usually in the postcloacal ventral keel scales of larger individuals (the number of spines increases with age). Characters 78-80 in *"C." gridellii*: at least one postcloacal scale of the holotype shows two spines on the posterior region of the midline, separated from each other and increasing in size cephalocaudally.

79(80). Distribution of spines on midline of ventral keel scales: all along midline, or centered if only one spine present (0); no spines on ventral keel scales (1); posterior region (at most two thirds) of midline (2). Although this character is coded as 1 (no spines) by Ebert (2016) for *Turboscinetes* this must be a typing mistake, because the author states that "Spines on the ventral keel scales are only present on the posteriormost two thirds…" (op. cit.: p. 33). It has therefore been coded as 2 in this genus for the present analysis.

80(81). Contact of spines on each ventral keel scale: separated from each other (0); no spines on ventral keel scales (1); in contact with each other (2); imbricate (3).

81(82). Relative size of anterior and posterior spines on each ventral keel scale: spines of increasing size cephalocaudally (0); no spines on ventral keel scales (1).

82(83). Several scales attached to contour scales: no (0); yes (1).

83(84). Number of post-cloacal ventral keel scales: more than 6 (0); 5 or 6 (1); 3 or 4 (2); two (3). The holotype of "*C.*" *gridellii* and quite a number of specimens of *Tergestinia*, including paratypes MCSNT T.66 and T.201/202, exhibit 2 ventral keel scales posterior to the cloaca (state 3 for both taxa). Coded as state 2 (three scales) for *Turboscinetes*, being the number shown by adult specimen in Ebert (2016: fig. 16). *Scalacurvichthys* is reported to have only one (Cawley & Kriwet 2018), but the ventral region between the cloaca and the anal fin is disarticulated, blurry, only partially preserved, so that it is impossible to be sure that there was only one post-cloacal keel scale. This is supported by the fact that there is an ample space before the anal fin; even a fragment of matrix in this area is completely lost (Cawley & Kriwet op. cit.: figs. 1, 5A), so that the actual number cannot be precisely established (coded as ?).

84(85). Number of anterior cloacal modified scales: mosaic of little scales (0); two (1); one (2); anterior cloacal scales not modified (3); three (4). Characters 85-89 in *Sylvienodus*: see Poyato-Ariza (2013: 98; fig. 6B) for a detailed description and restoration of the cloaca. The holotype of *Tergestinia* (MCSNT T.203) shows a single modified anterior cloacal scale (state 2). Only the roofing cloacal scales of *Flagellipinna* are described and restored by Cawley & Kriwet (2019), so that the complete structure of the cloaca is actually unknown. The inadequate preservation of the broken, partially lost cloaca in *Scalacurvichthys* (Cawley & Kriwet 2018: fig. 5A; their restoration on fig. 5B is difficult to make correspond to the photograph) does not allow an accurate estimation (conservatively coded as ? for the present analysis).

85(86). Number of posterior cloacal modified scales: mosaic of little scales (0); three (1); two (2); one (3); no scales, posterior part of anal notch formed by a rib (4). See comments on previous character for *Scalacurvichthys* (coded as ?).

86(87). Bifid scale in cloaca: absent (0); present (1); present plus several comma-shaped scales (2). A short, thin scale, ventrally bifid, is forming the roof of the cloacal notch in *Nursallia*, *Oropycnodus* (Poyato-Ariza & Wenz 2002: fig. 42), *Polazzodus* (Poyato-Ariza 2010: fig. 9), *Pycnodus* (Blot 1987: pl.22, fig.2), and *Sylvienodus* (Poyato-Ariza 2013: fig. 6). The bifid scale in the cloaca of *Tergestinia* is clearly shown by the holotype and also, in different degrees of preservation, in a number of paratypes. The cloaca of the type and only specimen of *"C." gridellii* is badly preserved. The presence of a bifid scale is strongly indicated by the morphology and arrangement of the preserved fragments, yet it is conservatively coded as unknown (?) because there is no direct evidence. This ventrally bifid scale is not to be mistaken with the large, dorsally bifid long structures reported by Cawley & Kriwet (2018) flanking the cloaca in the single known specimen of *Scalacurvichthys* (op. cit.: fig. 5; coded as 0). Not only their relative size and structure is completely different, also the fact that they are poorly preserved and dubiously restored in their illustration. They also cite such structures in *Stemmatodus* and *Proscinetes* (op. cit.: figs 7, 8), in a single specimen each, also poorly preserved and illustrated. Such structure may simply represent standard flank scales ventrally fused in particular individual variations. The future of these structures as an useful character in pycnodont phylogeny requires previous confirmation and individual variation screening in further, better preserved specimens. The restoration of the cloacal remains, very poorly preserved, in *Libanopycnodus* (Taverne & Capasso 2018b: fig. 11) shows a sort of broken, partially preserved scale described as "bifid", but the poor preservation of the region suggest strong caution (coded as ?). In addition, the morphology of this scale, as tentatively restored, does not correspond to that of the actual bifid scale of the other genera.

87(88). Post-cloacal notch: absent (0); present (1).

88(89). Supracloacal scale: absent (0); present, contacting only cloacal scales (1); present, contacting also non-differentiated scales adjacent to cloacal scales (2). This character is coded as 0 in *Turboscinetes* because there is no supracloacal scale as defined by Poyato-Ariza & Wenz (2004: 364). This is so because the scale contacting several scales, as seen in Ebert (2016: Fig. 16), does not contact cloacal scales; the scales that the supposed supracloacal scale is contacting ventrally are not cloacal scales, because they are not part of the actual border of the cloaca. This feature simply seems to correspond to a slight alteration of the scale rows between the pelvic fin and the cloaca; the cloacal scales of *Turboscinetes* do not contact a single scale dorsally.

Ebert (2016: 53) added three new characters. These have not been taken into account for different reasons: his number 92, about fringing and basal fulcra, because it does not take into account the very relevant individual variation in these structures; his number 93, about ethmoid commissure, because the very delicate bones in this region are easily lost, so that this can mislead to an absence that is just preservational; and his number 94, complete scale rows posterior to the cloaca, because it is wrongly polarized (i.e., basal pycnodonts certainly have more than one complete row posterior to the cloaca).

Analysis

The data matrix (Table 1) was processed by PAUP program 3.1.1 in an iMac 8 computer at the Unidad de Paleontología, Universidad Autónoma de Madrid. General heuristic search was used to run the analysis.

Multiple states are interpreted as polymorphisms (default settings), according to the observations in the list above. Because the Pycnodontidae is a monophyletic clade (Poyato-Ariza & Wenz 2002), the ingroup is made a monophyletic sister group to the outgroup.

Additivity

Characters 13, 17, 19, 31, 33, 35, 42-46, 48, 51, 54, 62, 69, 70, 76, 78, 83, 85, 86, and 88 were processed as ordered. All other multistate characters were processed as unordered. For a justification on ordering particular characters in pycnodonts, see Poyato-Ariza & Wenz (2002: 142); for a discussion on the methodological sense of ordering characters in a cladistic analysis, see Poyato-Ariza (2005b: 544, with abundant references). Further arguments to favour the additivity of multistate characters can be provided at present. The relevance of ontogenetic restrictions in evolutionary processes has been widely established in the last decades, stressing the relevance of heterochrony in explicit phylogenetic contexts as a mechanism for constraining directionality and patterns in morphological evolution (e.g., Alberch 1980; Maynard Smith et al. 1985; Alberch & Blanco 1996; Baguñà & García-Fernández 2003; Smith 2003; Laubichler & Maienschein 2007). Admittedly, the relationships between ontogeny and phylogenetic systematics have long been regarded as enormously complicated (e.g., De Queiroz 1985; Kluge 1985; Kluge & Strauss 1985), way far of the scope of the present paper. It is worth noticing, though, that ontogeny provides empirical evidence

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Outgrup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abdobalistum	0	0	0	?	0	0	0	?	?	0	1	?	0	0	1	1	?	?	?	?	0	?	0	0	?	?	?	?	0	?
Akromystax	0	0	0	1	0	2	1	0	1	1	1	0	0	0	?	?	?	1	2	0	0	?	2	1	2	?	?	4	0	1
Anomoeodus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
“Coelodus” gridellii	1	0	0	1	?	?	1	0	0	0	1	0	2	1	?	?	?	1	2	0	1	2	?	?	?	?	?	?	?	?
Coelodus saturnus	1	2	0	?	0	0	1	?	0	?	1	?	0	0	?	?	?	1	?	?	?	?	1	0	?	?	?	1	0	0
Flagellipinna	0	2	0	2	0	0	1	0	0	0	1	?	0	0	2	0	0	1	1	?	0	0	3	0	0	1	0	1	?	?
Haqelpycnodus	3	2	0	2	1	0	0	0	0	1	1	?	0	?	1	1	?	1	1	?	0	1	0	0	0	?	?	1	0	?
Iemanja	1	?	0	?	0	1	0	0	0	0	1	?	0	0	?	?	?	?	1	1	0	?	?	?	?	3	0	2	1	0
Libanopycnodus	1	0	0	0	1	0	?	0	0	0	1	?	0	0	1	?	?	1	1	?	0	1	1	0	0	?	?	?	?	?
Neoproscinetes	0	0	0	1	1	0	1	0	0	0	1	?	0	0	0	1	1	1	1	1	0	0	1	0	0	1	0	1	0	1
Nursallia? goedeli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nursallia gutturosum	0	2	0	0	0	0	1	1	1	0	?	0	0	0	1	0	0	1	1	0	0	?	0	0	0	0	0	0	0	0
Nursallia veronae	0	2	0	0	0	0	1	1	?	0	1	?	0	0	?	?	?	?	?	?	0	?	0	0	0	?	?	0	0	1
Ocloedus	0	2	0	2	1	0	0	0	0	1	1	1	0	0	0	1	1	1	2	0	0	0	1	0	0	?	?	1	0	0
Oropycnodus	0	2	0	1	0	0	0	0	0	1	1	1	1	2	0	1	?	1	2	?	1	?	1	0	0	?	?	1	0	?
Palaeobalistum	1	1	0	0	0	0	1	?	?	?	?	1	0	0	2	?	0	?	?	?	0	?	?	0	?	?	?	0	0	?
Polazzodus	1	0	0	1	0	0	1	0	0	0	1	0	1	1	3	-	-	1	3	0	1	2	1	0	3	5	0	3	0	0
Potiguara	0	2	0	2	1	0	0	0	0	1	1	?	0	0	?	?	?	?	?	?	?	?	?	0	?	?	?	1	0	0
Proscinetes	0	2	0	2	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	1	1	0	0	?	?	1	0	1
Pycnodus	1	0	0	0	0	0	1	0	0	1	1	0	1	2	1	1	0	1	3	0	0	0	1	0	0	1	0	0	0	0
Scalacurvichthys	1	0	0	1	1	0	0	0	0	0	1	0	?	?	?	?	?	1	0	?	0	?	1	0	0	?	?	1	0	?
Sigmapycnodus	1	?	?	?	0	?	?	0	?	?	1	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Stemmatodus	1	0	0	0	1	0	0	0	0	0	1	?	0	0	0	1	1	1	2	0	0	0	1	0	0	2	0	0	0	0
Stenamara	3	0	1	1	1	0	0	0	0	0	1	?	0	0	0	1	?	?	?	0	0	?	?	0	?	?	?	?	?	?
Sylvienodus	1	1	0	1	1	0	1	0	0	0	1	1	1	1	3	-	-	1	2	0	1	2	1	0	3	5	1	1	0	?
Tepexichthys	0	2	0	1	1	0	0	0	0	1	1	1	0	0	0	1	2	1	1	0	0	?	1	0	1	4	0	0	0	2
Tergestinia	1	3	0	1	1	0	1	0	0	0	1	0	1	1	3	-	-	1	3	?	1	2	1	0	3	?	?	1	0	0
Thiollierepycnodus	0	2	0	2	0	0	1	0	0	0	1	?	0	0	0	1	1	1	1	0	0	1	3	0	0	0	0	0	?	?
Turbomesodon praeclarus	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	?	1	0	0	1	0	1	0	1
Turbomeodon relegans	0	2	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	?	1	0	0	1	0	1	0	?
Turboscinetes	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	3	1	0	1	1	0	1	0	0

Table 1 - Data matrix showing the character states as coded for the pycnodontid taxa included in the present analysis. Numbers with more than one digit represent polymorphisms. Dash indicates non-applicable.

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Outgrup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	0	0	0	?
Abdobalistum	?	?	?	0	0	0	?	?	0	1	1	1	1	1	2	1	?	2	0	0	0	?	0	3	0	1	1	4	2	5
Akromystax	?	0	0	?	0	?	?	0	0	0	2	2	0	1	1	0	2	2	1	0	0	0	1	2	0	5	1	2	1	2
Anomoeodus	?	?	?	2	1	2	2	?	0	1	?	0	0	1	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
“Coelodus” gridellii	?	?	?	?	?	?	?	0	?	?	2	1	0	1	2	2	1	2	0	0	2	1	2	2	0	2	2	2	2	2
Coelodus saturnus	0	0	?	3	0	0	2	?	1	1	0	1	0	1	1	0	?	2	0	1	0	?	?	3	0	2	?	3	?	3
Flagellipinna	?	?	2	0	?	?	?	0	1	0	?	1	23	2	2	?	?	?	?	?	0	?	3	?	0	2	1	?	?	?
Haqelpycnodus	?	?	1	2	0	?	?	?	0	0	0	0	0	1	1	0	1	1	1	0	0	1	2	0	0	1	0	3	?	3
Iemanja	?	0	?	1	2	?	?	0	1	0	2	1	3	2	1	0	2	1	2	0	0	?	0	1	?	?	2	3	2	3
Libanopycnodus	?	?	?	0	?	0	?	0	0	1	2	0	0	1	1	0	?	1	?	?	0	1	0	1	?	?	0	2	0	2
Neoproscinetes	1	1	1	0	0	0	1	1	1	0	0	1	1	1	1	1	2	1	2	0	0	0	2	1	?	1	2	2	2	3
Nursallia? goedeli	?	?	?	?	?	?	?	?	?	?	?	2	2	1	?	1	2	2	2	?	?	?	?	?	?	2	?	4	1	4
Nursallia gutturosum	2	0	2	0	0	0	0	0	1	0	2	2	2	1	2	2	2	2	2	0	0	0	2	3	0	2	2	4	?	2
Nusallia veronae	1	0	2	?	0	?	0	?	1	0	2	2	2	?	?	2	2	2	2	0	0	0	2	3	0	2	2	4	2	4
Ocloedus	0	0	2	0	0	0	0	0	0	1	2	0	0	1	1	0	2	1	1	0	0	1	2	0	0	2	2	2	1	2
Oropycnodus	2	0	2	0	0	0	1	0	0	0	2	2	1	1	2	0	1	3	0	0	1	0	2	3	0	5	2	4	2	3
Palaeobalistum	1	0	?	0	0	0	0	?	1	0	?	?	?	?	?	?	?	1	0	0	?	0	0	?	?	?	1	?	?	4
Polazzodus	2	0	2	0	0	0	0	0	0	1	2	1	0	1	2	2	1	2	0	0	2	1	2	2	0	2	02	23	2	2
Potiguara	0	0	?	0	0	0	?	0	0	?	2	?	0	1	1	0	2	1	0	0	?	?	1	3	?	?	2	3	1	?
Proscinetes	1	1	2	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	0	0	1	2	12	1	2	2	3	1	3
Pycnodus	1	0	2	0	0	0	2	0	1	0	2	2	1	1	2	2	1	3	0	0	1	0	1	2	0	1	1	3	2	3
Scalacurvichthys	?	0	2	0	0	?	?	0	0	0	3	0	0	1	1	1	2	0	0	0	0	?	0	?	0	?	0	?	?	3
Sigmapycnodus	?	?	0	?	?	?	?	1	?	?	1	1	1	1	?	0	?	?	?	?	0	?	1	?	?	?	1	?	?	?
Stemmatodus	1	0	2	0	0	0	2	0	0	0	2	0	0	1	2	0	2	0	0	0	0	0	0	0	1	1	2	2	1	2
Stenamara	?	?	?	0	0	1	0	0	?	0	2	0	0	1	1	0	3	0	2	0	0	2	0	0	1	?	2	0	1	2
Sylvienodus	1	0	2	?	?	?	?	0	2	0	3	2	0	1	1	0	2	1	0	0	1	1	0	0	0	6	02	2	0	2
Tepexichthys	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	1	2	1	0	0	0	0	2	02	0	2	1	02	2	3
Tergestinia	1	0	2	2	0	0	1	0	2	1	2	1	0	1	2	0	1	2	0	0	1	0	2	2	0	1	2	2	2	1
Thiollierepycnodus	0	0	0	0	?	?	?	?	0	0	1	0	0	1	1	0	?	0	0	0	0	2	0	1	1	2	2	3	1	2
Turbomes. praeclarus	0	0	2	0	0	0	1	1	0	1	0	0	0	1	1	0	3	0	2	0	0	0	0	0	0	4	2	0	1	2
Turbomes. relegans	0	0	2	0	0	0	1	0	0	1	0	0	0	1	1	0	3	0	0	0	0	0	0	01	1	3	2	2	1	2
Turboscinetes	1	0	1	0	0	0	?	0	1	1	02	0	0	1	1	0	1	1	0	0	0	0	3	1	1	2	2	02	0	1

Table 1 - Data matrix showing the character states as coded for the pycnodontid taxa included in the present analysis. Numbers with more than one digit represent polymorphisms. Dash indicates non-applicable.

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
Outgrup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abdobalistum	0	3	2	1	?	1	0	2	1	0	2	0	0	1	0	2	0	2	1	1	1	1	?	?	?	?	?	?
Akromystax	2	2	0	0	0	0	0	0	2	0	0	0	2	2	1	3	0	0	0	3	0	0	3	4	2	0	0	0
Anomoeodus	?	2	0	0	2	?	?	0	?	?	?	?	?	?	0	?	0	1	0	2	0	0	?	3	2	0	0	0
"Coelodus" gridellii	2	4	0	0	0	1	0	0	2	1	3	1	1	1	0	3	1	1	2	0	0	0	3	?	?	?	0	0
Coelodus saturnus	2	2	0	0	?	?	0	?	2	2	3	1	1	1	0	?	?	?	?	?	?	0	?	?	?	?	?	?
Flagellipinna	?	1	2	0	2	0	0	0	1	0	0	0	0	0	0	?	0	?	?	?	?	0	3	?	?	0	0	?
Haqelpycnodus	2	3	0	0	0	0	0	0	2	2	0	0	0	2	?	?	?	0	0	0	0	0	3	1	2	0	0	0
Iemanja	?	2	0	0	1	?	?	0	?	0	?	?	?	?	0	?	?	?	?	?	?	0	?	?	?	?	0	?
Libanopycnodus	?	3	0	0	0	1	0	0	2	0	1	0	0	0	0	?	?	1	0	0	0	0	?	?	?	?	?	?
Neoproscinetes	1	2	0	0	1	?	0	0	2	2	2	3	0	2	0	1	1	0	2	0	?	0	3	1	2	?	0	0
Nursallia? goedeli	3	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nursallia gutturosum	3	2	2	0	1	1	0	0	1	1	?	?	?	?	0	2	0	?	?	0	0	0	3	?	?	?	0	?
Nursallia veronae	3	1	2	0	01	1	0	3	2	1	3	1	1	?	0	3	1	?	?	?	?	0	2	?	?	1	0	?
Ocloedus	2	2	0	0	0	0	0	0	2	1	0	2	2	2	0	2	0	0	2	2	0	0	3	2	2	0	0	0
Oropycnodus	2	4	0	0	012	1	0	1	3	1	3	1	1	1	0	3	1	0	2	2	0	0	3	1	2	2	1	0
Palaeobalistum	?	0	3	1	0	?	0	0	1	1	2	0	0	1	0	1	0	0	0	0	?	0	3	?	?	?	?	?
Polazzodus	4	4	0	0	0	1	1	0	2	1	3	1	1	1	0	2	0	0	0	0	0	?	?	2	3	1	0	0
Potiguara	?	?	?	?	?	1	?	?	?	?	3	1	1	1	?	?	?	0	0	2	0	0	?	?	?	?	?	?
Proscinetes	1	2	0	0	1	1	0	0	1	2	3	1	1	1	0	1	1	0	2	0	0	0	3	1	1	0	0	0
Pycnodus	2	4	0	0	02	1	0	1	3	1	3	1	1	1	0	3	1	0	2	0	0	0	3	2	3	1	0	0
Scalacurvichthys	0	4	0	0	01	?	?	0	?	?	3	1	1	1	?	?	0	1	2	0	0	0	?	?	?	0	0	0
Sigmapycnodus	?	3	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Stemmatodus	1	3	0	0	2	0	0	0	2	0	0	2	2	2	0	3	0	0	0	2	0	0	3	2	4	0	0	0
Stenamara	?	2	0	0	?	0	0	0	2	0	0	0	2	2	0	1	0	?	?	?	0	0	2	2	3	0	0	0
Sylvienodus	2	4	0	0	02	0	0	0	2	1	1	0	2	0	0	2	0	0	2	2	0	0	3	2	2	1	0	0
Tepexichthys	1	2	0	0	1	0	0	0	1	0	3	1	1	1	0	1	0	0	0	2	0	0	1	1	3	0	0	0
Tergestinia	5	4	0	0	2	0	0	1	2	1	3	1	1	1	0	3	0	1	0	?	?	0	3	2	3	1	0	0
Thiollierepycnodus	2	3	2	0	1	0	?	0	0	02	3	1	1	1	?	0	0	1	2	-	-	0	0	?	?	0	0	?
Turbomesodon praeclarus	0	2	0	0	2	0	0	0	1	1	0	2	0	2	0	1	0	0	0	2	0	0	1	2	3	0	0	2
Turbomesodon relegans	2	2	0	0	2	0	0	0	1	12	0	2	0	2	0	1	0	0	0	2	0	0	1	2	3	0	0	1
Turboscinetes	2	3	0	0	1	1	0	0	01	2	3	1	1	1	0	1	1	1	1	1	1	0	2	1	23	0	0	0

Table 1 - Data matrix showing the character states as coded for the pycnodontid taxa included in the present analysis. Numbers with more than one digit represent polymorphisms. Dash indicates non-applicable.

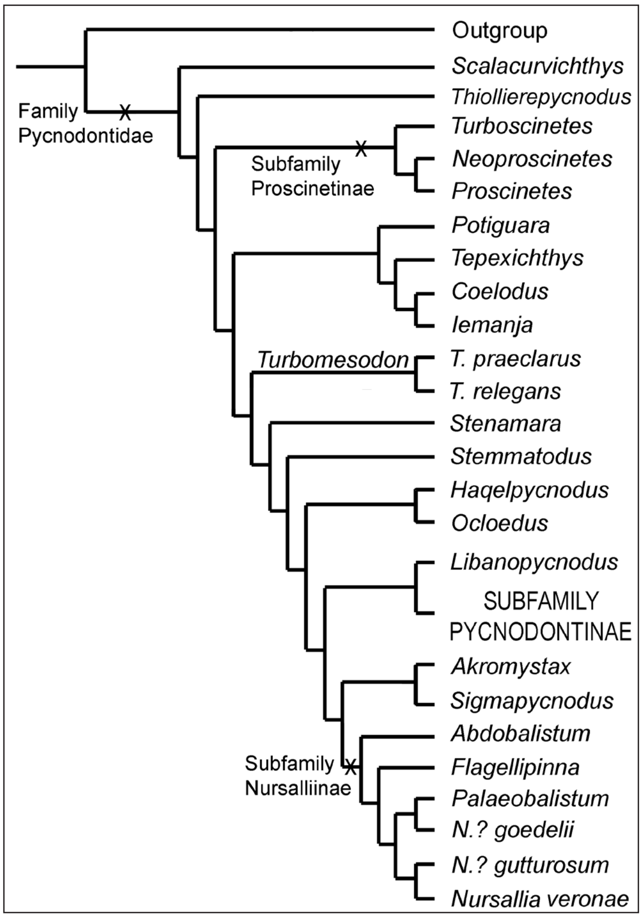

Fig. 9 - Single tree of Pycnodontidae interrelationships as provided by the cladistic analysis (*Anomoeodus* removed; for trees with this genus included, see Supplement 1). Unlike Ebert (2016), the three subfamilies within the family Pycnodontinae are defined as monophyletic groups, as in any Natural Classification. See supplements 2 and 3 for a detailed account of character distribution in all nodes and terminal branches. See Figure 10 for details on the content, definition, and interrelationships of the subfamily Pycnodontinae.

of character transformation (e.g., Williams et al. 1990). Such evidence is available for pycnodonts as well; for instance, adult specimens of *Turbomesodon praeclarus* (including the type series) show completely ossified flank scales in the ventral region of the abdomen, whereas those scales are incompletely ossified (i.e., scale bars only) in a very juvenile specimen (Poyato-Ariza & Wenz 2004: fig. 2B; pers. obs.), clearly pointing towards heterochrony in the reduction of scales ossification. Therefore, it seems sensible to apply ontogenetic restrictions to character transformation by ordering characters with a clear ontogenetic direction. In other words, additivity of multistate characters implies that not any transformation is equally probable because there are constraining ontogenetic restrictions.

Results

The cladistic analysis, including all taxa and characters in the data matrix (Table 1), resulted on 3 trees of minimal length (508 steps). The strict consensus tree (Supplement 1, p.2) contains a politomy involving several genera. The 50% majority rule consensus tree (Supplement 1, p.3) solves this politomy except for *Anomoeodus*. The removal of this genus, very incompletely known, results on a single most parsimonious tree of 501 steps (Fig. 10). This is the result that will be discussed herein because the removal of *Anomoeodus* solves the relationships without affecting the topology of the tree. The consistency index (CI) is 0,415 and the homoplasy index (HI) is 0,649. For other indices, see Supplements 2-3.

Since the present contribution is focused on the subfamily Pycnodontinae (Fig. 10), the discussion below only provides a detailed account of the relationships and character distribution for this clade and the taxa within. The different parts of the discussion refer directly to the characters defining the tree nodes as they are listed in the caption of Fig. 10. The characters commented in the discussion constitute the core of the diagnosis for the different taxa in the Sytematic Palaeontology section further on. For complete lists of the characters defining all nodes and terminal branches in the cladogram (Fig. 9), see Supplements 2 and 3 (respectively, ACCTRAN and DELTRAN optimizations).

Discussion

Subfamily Pycnodontinae

This is a monophyletic group that includes *Oropycnodus*, *Pycnodus*, *"C." gridellii*, *Polazzodus*, *Sylvienodus*, and *Tergestinia* (Fig. 10). According to the present analysis, *Scalacurvichthys naishi* is not a "well-resolved member of the subfamily Pycnodontinae" (Cawley & Kriwet 2018: 659). As a matter of fact, it appears in the most basal position among pycnodontids (Fig. 9). This confirms the opinion that "it is really difficult to agree with the placement of *S. naishi* within Pycnodontinae" (Taverne & Capasso 2018a: 132). Taverne & Capasso (2018b: 27) "confidently conclude that *Sigmapycnodus* gen, nov. belongs to the subfamily Pycnodontinae", but the present analysis places this incompletely known genus clearly out of it. *Haqelpycnodus* is not "the direct plesiomorphic sister-lineage of the subfamily Pycnodontinae (sic)" (Taverne & Capasso 2018a: 131) but the sister-group of *Ocloedus*. *Libanopycnodus* does not have "a systematic position within Pycnodontinae" (Taverne & Capasso 2018b: 25) but as stem-group Pycnodontinae. The characters defining the node (*Libanopycnodus* + Pycnodontinae) do not include any autapomorphy or any tipically pycnodontin character, and for this reason, the genus is excluded from the subfamily. The Pycnodontinae are one of the most derived clades within the family Pycnodontidae (Fig. 9) and consequently within the order Pycnodontiformes.

There are two autapomorphic characters that allow distinct diagnosis of all genera within the Pycnodontinae. The endocranium is not completely covered by the shortened dermal skull, so that the former is posteriorly exposed in lateral view (e.g., light grey colour in Fig. 7). The degree of the exposure varies, but such exposure of the endocranium in lateral view is a unique character of the subfamily. It particularly involves the supraoccipital, visible in lateral view all throughout the posterior border of the parietal. It should facilitate diagnosis of articulated specimens in a very good state of preservation. It is considered an autapomorphy because the homologies of the region exposed in *Scalacurvichthys* remains to be tested (see comments on character 13 above). This character is re-defined to diagnose Pycnodontinae as the presence of a thin, laminar supraoccipital exposed all along the posterior border of the skull roof.

The peculiar morphology of the cleithrum is another clear autapomorphy of the subfamily. This bone presents two posterior expansions that frame the notch for the pectoral fin (e.g., Fig. 8). The relative development of these expansions differs, but their presence is distinctive of the subfamily. It should facilitate diagnosis even of disarticulated specimens, provided the cleithrum is exposed and relatively well preserved.

A uniquely derived character (not autapomorphic) of this clade is the reduction in ossification of the flank scales into a single bar, forming what Nursall (1996) described as clathrate pattern. Other uniquely derived characters include the absence of infraorbital bones and of branchiostegal rays, and, very typically, the vertical reduction of the preopercular bone, which is especially low. This is in accordance with a corresponding expansion of the

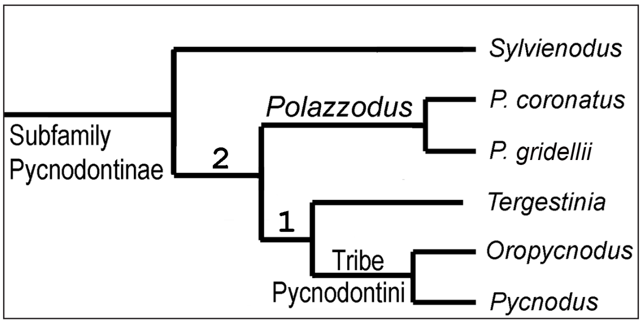

Fig. 10 - Phylogenetic relationships of the subfamily Pycnodontinae. Character distribution is as follows:

Subfamily Pycnodontinae: 4(1), 13(1,A), 14(1,A), 15(3), 21(1), 22(2), 25(3), 51(1,A), 62(3→4), 70(1), and 79(2) with ACCTRAN; 13(1,A), 14(1,A),15(3), 19(2), 21(1), 22(2), 25(3), 42(1), 51(1,A), 70(1), and 86(1) with DELTRAN.

Node 1, *Tergestinia* + Pycnodontini: 26(5→1), 37(1), 52(0,R), 60(2→1), 65(2), and 68(1) with ACCTRAN; 37(1), 52(0,R), 56(2→1), 68(1) and 76(3) with DELTRAN.

Node 2, *Polazzodus* + (*Tergestinia* + Pycnodontini): 5(0,R), 19(3), 45(2), 47(2→1), 48(2), 53(2), 54(2), 59(2), 71(3), 72(1), 73(2→1), 74(1), 76(3), and 85(3) with ACCTRAN; 12(1,R), 19(3), 45(2), 47(2→1), 48(2), 53(2), 54(2), 59(2), 71(3), 72(1), 73(2→1), 74(1), and 85(3) with DELTRAN.

Sylvienodus: 2(1), 12(1), 27(1,A), 39(2), 40(0,R), 41(3), 42(2), 54(0,R), 56(1→6), 66(0,R), and 80(2) with ACCTRAN; 2(1), 26, 27(1,A), 39(2),41(3), 42(2), 54(0,R), 56(2→6), 79(2) and 80(2) with DELTRAN.

Polazzodus: 28(1→3), 31(2), 37(0,R), 46(2), 51(2,A), and 56(2) with ACCTRAN; 46(2), 51(2,A), and 66(1) with DELTRAN. *P. coronatus*: 61(2→4), 67(1,A), 76(3→2), and 79(0,R) with ACCTRAN; 5(0,R), 19(3), 26(5), 28(1→3), 31(2), 40(1), 61(2→4), and 67(1,A) with DELTRAN. *P. gridellii* n. comb.: 13(2A), 19(3→2), 77(1), and 78(1) with ACCTRAN; 13(2,A), 76(3), 77(1), 78(1), and 79(2) with DELTRAN.

Tergestinia: 2(3), 5(1), 34(2), 39(2), 61(2→5), 66(0,R), 78(1), and 79(0,R) with ACCTRAN; 2(3); 19(3), 34(2); 39(2), 40(1), 60(2→1), 61(2→5), 65(2), and 78(1) with DELTRAN.

Tribe Pycnodontini: 10(1), 14(2,A), 15(0,R), 22(0,R), 25(0,R), 40(0,R), 42(2), 43(1), 48(3), 58(3), 60(1→3), 68(1), 69(3), and 77(1) with ACCTRAN; 5(0,-R), 10(1), 14(2,A), 25(0,R), 42(2), 43(1), 48(3), 60(1→3), 66(1), 69(3), 77(1), and 79(2) with DELTRAN.

Oropycnodus: 1(0,R), 2(2), 7(0,R), 12(1), 19(3→2), 31(2), 54(3), 56(5), 58(4), 80(2), 84(2→1), 85(3→2), 86(2), and 87(1,A) with ACCTRAN; 1(0,R), 2(2), 7(0,R), 12(1), 15(0,R), 21(1), 31(2), 37(1), 39(0,R), 54(3), 56(5), 58(4), 80(2), 84(2→1), 85(3→2), 86(2), and 87(1,A) with DELTRAN.

Pycnodus: 4(0,R), 15(1), 21(0,R), 28(0,R), 37(2), 39(1), 46(2), 53(2→1), 57(2→1), and 58(4→3) with ACCTRAN; 4(0,R), 15(1), 19(3), 21(0,R), 22(0,R), 28(0,R), 37(2), 39(1), 46(0→2), 53(2→1), 57(2→1), and 58(2→3) with DELTRAN.

A indicates autapomorphy; R indicates reversion; arrows specify particular state changes in certain characters.

exposed, ornamented portion of the hyomandibular bone; the preopercular is never higher than the ornamented portion of the hyomandibular bone. One more among the many characters of the subfamily (Fig. 10) is the presence of a bifid scale in the cloaca, typical of the group, but not autapomorphic because it is also reported in *Nursallia veronae* (Poyato-Ariza & Wenz 2002: 203). According to Article 50.3.1 of the International Code of Zoological Nomenclature, the author of the subfamily Pycnodontinae is the author of the type genus: Agassiz, 1833. This monophyletic group was formally granted subfamiliar rank and diagnosed for the first time by Poyato-Ariza & Wenz (2002).

Tribe Pycnodontini

Oropycnodus and *Pycnodus* are sister genera, with the autapomorphic presence of a postcephalic lacuna (Fig. 7B, D, dark grey). Other shared derived characters include the presence of a dermocranial fenestra (convergent with other pycnodonts), two hypertrophied hypochordal elements in the caudal endoskeleton, and scutellum-like dorsal contour scales. Other useful derived characters lie in the further reduction of the number of contour ridge scales: 7-9 dorsal and 10-14 ventral.

Within the tribe, *Oropycnodus* (Fig. 2) is diagnosed by the autapomorphic presence of a post-cloacal notch (Poyato-Ariza & Wenz 2002: fig. 42). Uniquely derived characters within the subfamily include: reduction of the number of teeth on the principal vomerine tooth row to 7 or less, presence of more than 60 dorsal axonosts, anteriorly rounded dorsal fin, and presence of several comma-shaped scales flanking the cloacal bifid scale. It is also readily distinguishable from fellow pycnodontins because it is the only genus of this subfamily to present a high, discoid body and a caudal pedicle that is not well differentiated. Curiously enough, *Pycnodus* (Fig. 4), the type and longest-known genus, has no autapomorphic characters of its own, but can be readily diagnosed by a unique combination of characters. These include a low body with dorsal apex between the skull and the point of insertion of the dorsal fin plus absence of ventral apex (i.e., straight lower border of the body), providing the typical truncated-like body contour of this genus (Figs. 4, 7D). This, together with the strip-like dorsal and anal fin contour (i.e., very low with very few anterior fin rays somewhat longer than the rest) allows ready identification of complete, well preserved specimens. Other characters are: preopercular additionaly reduced, lower than the ornamented portion of the hyomandibular bone; opercular bone relatively more developed than in other pycnodontins (e.g., Poyato-Ariza & Wenz 2002: fig. 10); vomerine teeth circular to subcircular in occlusal contour (not implying that all vomerine teeth with this morphology can be simply assessed to this genus), 10 or more teeth on main prearticular tooth row (idem); last neural spine not supporting precurrent caudal fin rays vestigial; predorsal length less than 49% of standard length; preanal length 50-59% of standard length; and 40-49 anal axonosts.

Polazzodus coronatus and "*C.*" *gridellii*, a valid species, are sister-groups. As a consequence, the latter is removed to the genus *Polazzodus*, forming *Polazzodus gridellii* n. comb. The genus has an autapomorphic cleithrum morphology as described in character 51 above (Fig. 8B). Other derived characters shared by its two species include a vestigial last neural spine not supporting precurrent caudal fin rays and acuminate shape of dorsal and anal fins. The maxilla is axe-shaped (see description in character 26 above), readily distinguishable from that of *Sylvienodus* because the anterior border is smooth in *Polazzodus*. These characters have been combined herein with those in the diagnosis by Poyato-Ariza (2010) in order to provide an emended diagnosis for the genus and its species.

Polazzodus coronatus, the type species, has an autapomorphic shape of the second dorsal ridge scale as described above for character 67. In addition, it presents further reduction of the preopercular bone in height; 7 teeth on the main vomerine row, of triangular contour; groove on vomerine and prearticular teeth; forked caudal fin (unique among pycnodontids); and spines on midline of ventral keel scales distributed all along midline. In addition, it presents an olfactory fenestra on the premaxilla (Poyato-Ariza 2010: fig. 5) never reported in other pycnodonts. This feature may be related with the configuration of the whole nasal cavity (Poyato-Ariza 2010: 656), and it has been used as an additional character in the diagnosis below. Characters involving ventral keel scales are used as well because they are different in the two species of the genus.

Polazzodus gridellii n. comb. presents an autapomorphy, the endocranium largely exposed posteriorly as described in character 13 above, plus a unique combination of derived characters: preopercular bone about as high as the ornamented portion of dermohyomandibular bone; 13-14 ventral keel scales in point contact with each other, bearing at most two spines, placed on the posterior region of their midline. The shape of the distal border of the caudal fin is also used in the diagnosis because it is different from that of the other species.

Sylvienodus is diagnosed in the present analysis by the autapomorphic presence of crenulations on the anteroventral border of the maxilla plus: dorsal apex in point of insertion of dorsal fin; axe-shaped maxilla; strong crenulations and absence of a groove on vomerine and prearticular teeth; 22-23 vertebrae, a very low number among pycnodonts; arcocentra surrounding notochord completely; 37 dorsal axonosts, quite a short dorsal fin for a pycnodontid; and dorsal and anal fins extremely acuminate, with anteriormost fin rays much longer than the rest, so that the dorsal fin is higher than it is long. These characters are combined with others in the original description (including two clearly unique to *Sylvienodus* among pycnodonts) in order to elaborate the emended diagnosis provided below.

Tergestinia lacks autapomorphies of its own but presents a unique combination of characters including: maximum body height placed in skull, i.e., its head is higher than its body; preopercular bone height reduced, lower than the ornamented portion of the hyomandibular bone; prearticular teeth sigmoid to drop-shaped in contour; strong crenulations plus groove on vomerine and prearticulary teeth; 18-19 caudal principal fin rays, 8 in the upper lobe, 10-11 in the lower lobe; caudal fin with vertical distal border, therefore with overall triangular shape; and 1-3 centered spines on larger ventral keel scales. These are the characters used in the emended diagnosis presented below. The size of this genus is remarkably small for a pycnodont, less than 50 mm in fully-ossified, apparently adult individuals with branched fin rays. As a consequence, this character is also used in its emended diagnosis below. According to the present analysis, *Tergestinia* is a well-established member of the Pycnodontidae, so the analysis validates removal of the genus from the "family Tesgestiniidae" erected by Capasso (2000). All of the numerous characters used to diagnosed such a family by Capasso (op.cit.: 265-267) are broadly present in the Pycnodontinae and/or Pycnodontidae, even in higher-rank taxa.

Other comments

According to the results of the present analysis, the fossil record of the Pycnodontinae as initially defined by Poyato-Ariza & Wenz (2002) is increased in diversity up to 5 genera and expanded back in time into the Mesozoic. The Italian genera (*Pycnodus*, *Polazzodus*, and *Tergestinia*) form a clade together with the geographically close *Oropycnodus*. The oldest pycnodontin fish is also the most basal one: *Sylvienodus*, from the Cenomanian of central Portugal. With the present evidence, the origin of the subfamily can be placed in the westernmost Tethys. According to these data, a very simple biogeographic pattern infers that, from this westernmost part of the Tethys, the lineage formed by the Italian genera plus *Oropycnodus* diverged and diversified towards the north-east during the Late Cretaceous. The Cenozoic pycnodontins, *Tergestinia* + (*Pycnodus* + *Oropycnodus*), are also the most derived ones. The present phylogeny of the Pycnodontinae is congruent with the temporal distribution of its fossil record.

These results indicate that that pycnodonts were still diversifying during the Late Cretaceous in the Western Tethys, whereas their general diversity and geographic distribution were declining. With the current data this constitutes, nonetheless, the final diversification of the Pycnodontiformes.

"*Pseudopycnodus*" remains a very problematic genus. The holotype of "*P. nardoensis*" is actually the only specimen of the type series (ICZN 1999: Art. 73.1.2). Unfortunately, the holotype is very incomplete and poorly preserved. This only type specimen is indistinguishable from *Pycnodus*, as already discussed by Taverne (1997). Additional specimens by Taverne (2003) and Taverne & Capasso (2012) exhibit heterogeneous characters and provenance (see Material section above), so that such additional material may or may not belong to the same taxon. The short diagnosis of "*Pycnodus nardoensis*" by Taverne (1997: 439), based on the only type specimen, contains characters that are not really visible in the specimen (arrangement of the frontals in relation to the orbit: fig. 1 in that paper shows that the anterior portion of the frontal is missing and the orbit is simply not preserved), unknown in *Pycnodus* (endocranial fossae), or based on an idealized restoration of a damaged, cracked area (sphenotic bones) without photographs or precise comparisons. Subsequent emended diagnoses by Taverne (2003) and Taverne & Capasso (2012) for "*Pseudopycnodus nardoensis*" (no diagnosis for the genus) fail to provide a uniquely derived combination of characters as well. Such diagnoses are in fact lengthy descriptions with many primitive and derived characters that are broadly present in pycnodontiforms, pycnodontids, and/or pycnodontins. As a consequence, and until detailed revision of the taxonomic status of the different specimens is carried out, "*Pseudopycnodus*" is considered *nomen dubium* (i.e., "a name of unknown or doubtful application"; ICZN 1999: 111), and so is "*P. nardoensis*".

SYSTEMATIC PALAEONTOLOGY

Subclass **ACTINOPTERYGII** Cope, 1887
(sensu Rosen et al. 1981)
Infraclass **NEOPTERYGII** Regan, 1923
(sensu Rosen et al. 1981)
Order **Pycnodontiformes** Berg, 1937
(sensu Nursall 1996)
Family Pycnodontidae Agassiz, 1833
(sensu Nursall 1996)
Subfamily Pycnodontinae Agassiz, 1833

Diagnosis (emended from Poyato-Ariza & Wenz, 2002): Pycnodontid fishes with two autapomorphies: dermal skull posteriorly shortened so that the supraoccipital bone is posteriorly exposed in lateral view as a thin blade along the posterior border of the skull roof; and presence of two posterior expansions in the cleithrum that frame dorsally and ventrally a high notch for the insertion of the pectoral fin. Unique combination of other derived characters: infraorbital bones and branchiostegal rays absent; flank scales reduced to an osseous bar in a clathrate pattern of squamation; preopercular bone reduced in height, as high as the exposed, ornamented portion of dermohyomandibular bone or lower, ornamented portion of dermohyomandibula expanded accordingly in height; and presence of a bifid scale dorsally roofing the cloaca.

Taxa included (from basal to derived): *Sylvienodus*, *Polazzodus*, *Tergestinia*, and Tribe Pycnodontini: *Pycnodus* (type genus) and *Oropycnodus*.

Sylvienodus

Diagnosis (emended from Poyato-Ariza, 2013): Pycnodontin fish with the following autapomorphies: anterior border of axe-shaped maxilla ornamented with crenulations; parietal peniculus very small and short, with 4 or less posterior branches; and presence of oval notch between 1st and 2nd dorsal ridge scales. Unique combination of other characters: ovoid body shape; dorsal apex in point of insertion of dorsal fin; dermocranial fenestra absent; postcephalic (supraoccipital) lacuna absent; groove on vomerine and prearticular teeth absent; 22-23 vertebrae counted as neural spines, caudal skeleton excluded; arcocentra surrounding notochord completely; 37 dorsal and 33 anal axonosts; dorsal and anal fins extremely acuminate, anteriormost fin rays much longer than the rest; and 15 ventral keel scales.

Type and only species: *Sylvienodus laveirensis* (Vega-Ferreira, 1961). Late Cretaceous (late Cenomanian) of Laveiras, Vale do Tejo, Portugal. Same diagnosis as genus.

Polazzodus

Diagnosis (emended from Poyato-Ariza, 2010): Pycnodontin fish with an autapomorphic cleithrum morphology consisting of: expansion of dorsal and ventral posterior processes; deep notch for the insertion of the fin; expansion of the posteroventral angle between the limbs of the bone; and anterior elongation of the anteroventral limb so that the bone is not subvertical. Unique combination of derived characters: postcephalic (supraoccipital) lacuna absent; anterior border of axe-shaped maxilla smooth; last neural spine not supporting precurrent caudal fin rays reduced to vestigial; and acuminate dorsal and anal fins.

Type species: *Polazzodus coronatus* by original designation (ICZN article 68.2).

Other species: *Polazzodus gridellii* n. comb.

Ocurrence: Late Cretaceous of Polazzo (Gorizia).

Comments. cf. *Polazzodus* sp., from the Albian-Cenomanian of Mrzlek near Solkan, Slovenia (Križnar 2014). The relative width of the teeth from the main row of the prearticular dentition assessed to cf. *Coelodus* sp. by Križnar (2014, fig. 4E) is closer to that of *Polazzodus* (2,5 to 3 times wider than long) that to that of *Coelodus* (3 to 5 times wider than long). The observable features of the vomerine and prearticular teeth assessed to Pycnodontidae gen. et sp. indet by Križnar (2014, fig. 4D, F, G) are consistent with the vomerine and prearticular dentitions of *Polazzodus* as well. The small size of the bones and the low number of teeth on each row are indication of a very early ontogenetic stage (e.g., Poyato-Ariza & Wenz 2002, 2004; pers. obs.). This suggests that all those remains can also be considered cf. *Polazzodus* sp., rendering *Coelodus* actually absent in the Slovenian locality of Mrzlek, and the actual diversity of pycnodonts in that locality reduced to a single form, the genus *Polazzodus*.

Polazzodus coronatus

Diagnosis (emended from Poyato-Ariza, 2010): *Polazzodus* with one autapomorphy: very long and large second dorsal ridge scale with a central longitudinal ridge and a conspicuous anterior hook. Unique combination of other characters: preopercular bone lower than exposed, ornamented portion of hyomandibular bone; presence of olfactory fenestra on premaxilla; teeth on main vomerine row with triangular contour; 7 teeth on the main vomerine row; weak crenulations and groove present on well preserved, unworn vomerine and prearticular teeth; forked caudal fin; 15-16 ventral keel scales (2 of them postcloacal), in close contact with each other; and 2-4 spines on midline of ventral keel scales distributed all along midline.

Type locality: Polazzo (Gorizia), NE Italy.
Age: Late Cretaceous (early Santonian).

Comments. The specimen described and figured by d'Erasmo (1952: "esemplare n.4") as *Palaeobalistum* shows no differences from *Polazzodus coronatus* and presents the same morphology in head, body, and dorsal ridge scales, so it is moved to this species. There is no *Palaeobalistum* in the Carso Triestino.

Polazzodus gridellii n. comb.

Figs. 1, 7A

1952 *Coelodus gridellii* d'Erasmo pro parte, p. 84-89, pl. 1, fig.1
2010 "*Coelodus*" *gridellii* pro parte – Poyato-Ariza, p. 650, 662

Diagnosis: *Polazzodus* with one autapomorphy, endocranium (laminar supraoccipital) very largely exposed by posterior expansion plus concavity in the posterior border of dermal skull, and the following unique combination of characters: preopercular bone about as high as ornamented portion of dermohyomandibular bone; double emarginated caudal fin; 13-14 ventral keel scales (2 of them postcloacal); precloacal ventral keel scales very elongated and in point contact with each other; and at most 2 spines on their midline, placed on the posterior part of it.

Type locality: near Polazzo, Carso Isontino, NE Italy (destroyed during World War I).

Age: Late Cretaceous (early Santonian).

Holotype: MCSNT-12366 ("*Coelodus*" *gridellii*, "Esemplare N. 1" in d'Erasmo 1952: 84); the only specimen currently known.

Tergestinia

Diagnosis (emended from Capasso 2000): Very small, less than 50 mm, pycnodontin fish with the following unique combination of characters, most of them derived: head higher than body, maximum body height placed in posterior part of skull; postcephalic (supraoccipital) lacuna absent; preopercular bone very reduced, lower than ornamented portion of hyomandibular bone; prearticular teeth with sigmoid to drop-shaped contour; presence of strong crenulations and a groove on vomerine and prearticulary teeth; 18-19 caudal principal fin rays, 8 in upper, 10-11 in lower lobe; caudal fin triangular, with vertical distal border;; and presence of 1-2 spines centered in the midline of larger ventral keel scales.

Type and only species: *Tergestinia sorbinii* Capasso, 2000. Paleogene (early Paleocene) of Trebiciano near Trieste, northeastern Italy. Same diagnosis as genus.

Tribe **Pycnodontini** new

Diagnosis: Pycnodontinae fishes with one autapomorphy: presence of a postcephalic lacuna in the portion of the supraoccipital bone posteriorly exposed. Unique combination of other derived characters: dermocranial fenestra present (convergent with other pycnodontids); two hypertrophied hypochordal elements in the caudal skeleton; scutellum-like dorsal contour scales; 7-9 dorsal ridge scales; 10-14 ventral keel scales.

Genera included: *Pycnodus* (type genus) and *Oropycnodus*.

Pycnodus

Diagnosis: As in Poyato-Ariza & Wenz (2002).

Type species: *Pycnodus apodus* (Volta, 1809), only species known from articulated remains; early to middle Eocene of Bolca (Italy). Same diagnosis as genus. Numerous nominal species based on isolated dentitions, all in need of revision (*nomina dubia*).

Oropycnodus

Diagnosis: As in Poyato-Ariza & Wenz (2002).

Type and only species: *Oropycnodus ponsorti* (Heckel, 1854). Paleocene (Montian) from Mont-Aimée (France). Same diagnosis as genus.

CONCLUSIONS

A number of new derived pycnodontid genera have been described in recent years, some of them ascribed to the subfamily Pycnodontinae as erected by Poyato-Ariza & Wenz (2002) for *Pycnodus* and *Oropycnodus*. The Pycnodontinae are one of the most derived pycnodont clades. The results of the present revision confirm that *Polazzodus*, *Sylvienodus*, and *Tergestinia* do belong to this subfamily. The fossil record of the Pycnodontinae is pushed back into the Late Cretaceous; the oldest pycnodontin is *Sylvienodus*, from the late Cenomanian of Portugal. The three Italian pycnodontin genera (*Pycnodus*, *Polazzodus*, and *Tergestinia*) present different origins, being more closely related to French or Portuguese forms than they are to each other. The increasing number of new genera and their different biogeographic origin confirm that the most derived pycnodonts were still diversifying in the Western Tethys during the latest Late Cretaceous (Santonian to Maastrichtian), even though their global diversity was declining (see Poyato-Ariza & Abad 2013 for details). This is because such late diversification is small and limited to their last geographical area, so that the decline in global diversity of pycnodonts during the latest Late Cretaceous is still evident. The results provided by the present revision suggest that the reduction of their geographical area of distribution is the key factor in such decline. If confirmed, we can expect that pycnodontids will continue to increase their known diversity in Late Cretaceous-Cenozoic beds from the Tethys and peritethyan areas in the future.

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