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STUDIES ON PYCNODONT FISHES (I): EVALUATION OF THEIR PHYLOGENETIC POSITION AMONG ACTINOPTERYGIANS

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Abstract. One of the main pending, unsolved problems concerning the study of the pycnodont fishes is their phylogenetic relationships with other major actinopterygian groups. The Pycnodontiformes have often been proposed as the sister group of the Telostei or the Teleosteomorpha. The first extensive cladistic analysis on pycnodont relationships is hereby attempted by coding Pycnodontiformes into a previously existing data matrix with major neopterygian groups: Lepisosteiformes, Semionotiformes, Macrosemiiformes, Halecomorphi, and Teleostei.

This analysis has resulted on the Pycnodontiformes having an unexpected position as the most basal Neopterygii among the groups included. Therefore, pycnodonts are not the sister-group of teleosteans, and they are not holosteans either. The phylogenetic relationships and the definition of the Holostei and the Gynglimodi are not affected by the inclusion of the Pycnodontiformes, but the basal position of the latter among Neopterygii may affect the definition of this traditional major actinopterygian group. A collateral consequence of these results is that the Halecostomi can be re-defined as the clade formed by [Holostei + Teleostei].

The phylogenetic relationships of pycnodonts should, consequently, be solved among basal neopterygian groups, mostly from the Triassic, as well as relevant non-neopterygian actinopterygians in order to confirm the neopterygian affinities of the Pycnodontiformes and to verify the definition and diagnosis of the Neopterygii and the Halecostomi.

Introduction

Scientific literature on pycnodontiform fishes, briefly called pycnodonts (Figs 1-3), has been unusually abundant in the last two decades. Numerous new taxa have been described, either by discovery of new material or by revision of existing material; in chronological order, see, for instance, Nursall (1999a), Poyato-Ariza & Wenz (2002), Taverne (2003), Kriwet (2004), Machado & Brito (2006), Poyato-Ariza & Bermúdez-Rochas (2009), Poyato-Ariza (2010, 2013), and Koerber (2012). In addition, there have been extensive appraisals of this group from different approaches: systematic/taxonomic (Nursall 1996a; Poyato-Ariza & Wenz 2002), palaeoecologic (Nursall 1996b), anatomic (Nursall 1999b), functional (Kriwet 2001, 2005), evolutionary (Poyato-Ariza 2005), ecomorphologic (Poyato-Ariza & Martín-Abad 2013), and palaeobiogeographic (Martín-Abad & Poyato-Ariza 2013). Such research on pycnodonts, very intense and wide-ranging in comparison with that of preceding decades, has resulted on a new, deeper understanding of this remarkable group of fishes. As is usually the case in any field of Science, new discoveries and interpretations have originated new issues and raised new questions. Accordingly, there are, at present, several pycnodont problems that require revision. With this purpose, this is the first of a series of papers devoted to contend with current issues involving pycnodontiform fishes.

The most obvious pending gap in the knowledge of the Pycnodontiformes is their phylogenetic position among actinopterygians, which has largely been a matter of debate but ultimately unsolved. Although some papers state quite matter-of-factly that pycnodonts are stem-group teleosteans (e.g., Friedman 2012: 117, fig. 1), this hypothesis has never been properly tested on the basis of an extensive cladistic analysis (see below).

There is a reason for the difficulty of approaching such task. Pycnodonts are a monophyletic clade, very strongly defined by a high number of autapomorphies, some of them quite remarkable and unmistakable (Nur-

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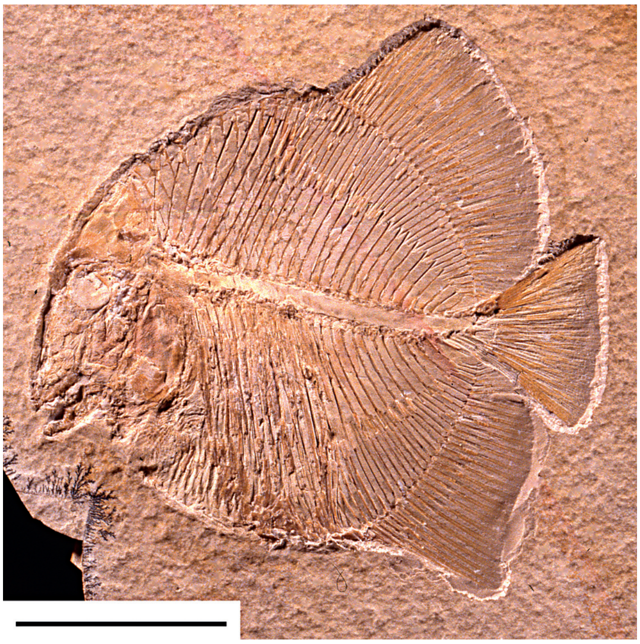

Fig. 1 - *Turbomesodon relegans* (incorrectly called *Macromesodon macropterus* for a long time, see Poyato-Ariza & Wenz 2004), probably one of the most typical pycnodonts, from the Late Jurassic of Solnhofen, Germany; holotype, Natural History Museum, London, specimen P.5546; photo courtesy P. Forey, modified from Poyato-Ariza & Wenz (2004); scale bar: 5 cm. It is a relatively derived genus that belongs to the Pycnodontidae.

sall 1996a; Poyato-Ariza & Wenz 2002). These characters do provide a definite "pycnodont look" that makes these fishes easily recognizable (Nursall 1999b; Poyato-Ariza 2005; present paper: Fig. 1). However, these numerous morphologic peculiarities, on the other hand, render the study of their relationships with other actinopterygians very difficult to approach, because characters shared with other groups can be veiled by the overwhelming pycnodont features and the impressive degree of characters evolution within the group. Only Nursall (1996a) attempted a detailed discussion of the systematic position of the Pycnodontiformes, proposing them as the sister group of the Teleostei. That paper revealed interesting similarities between both groups. This hypothesis, however, was based on a hand-made tree and a discussion of ad-hoc character distribution, without the support of a cladistic analysis. Therefore, potential convergences between pycnodonts and teleosts could not be tested. A more recent approach to this sister-group relationships hypothesis (Nursall 2010) was based on a new analysis of ad-hoc character distribution and a "synapomorphy relationships analysis" mixing anatomic and functional characters. The sister-group relationship proposed, in this case, for the Teleosteomorpha and the newly erected Pycnodontomorpha was not based on a cladistic analysis, so it was not tested to be the most parsimonious solution. In all, both studies have shown remarkable similitudes between pycnodonts and teleosts, and have provided a phylogenetic hypothesis worth to be tested.

The only previously available cladistic analysis for pycnodont relationships is the one by Gardiner et al. (1996). There, pycnodonts appeared as the sister-group of the Telostei. This was, however, a very limited analysis in the number of characters and taxa used: only 37 characters and only 12 genera to represent all neopterygians. In that study, the only genus chosen to represent pycnodonts was *Microdon* (which, incidentally, is an invalid genus as a pycnodont and was replaced with *Proscinetes* by Gist (1848: 185). Moreover, character discussion in that paper is confusing because it often refers to genera that are not included in the analysis itself. In addition, character coding for pycnodonts is never clearly explained or discussed, although it seems to have been based on *Neoproscinetes* rather than on *Proscinetes*, since the former is much more often mentioned than the latter. Furthermore, the only anatomic illustrations in the paper are from *Neoproscinetes* (op. cit.: figs 5-6). This choice of genera is not appropriate for pycnodonts, since both *Proscinetes* and *Neoproscinetes* are taxa highly derived within the group (e.g., Poyato-Ariza & Wenz 2002, present paper: fig. 4), therefore unsuited to be relied upon with the general pycnodont condition. Problematic characters mentioned by Gardiner et al. (1991), such as the interpretation of the posterolateral bones of the skull roof, are largely due to the derived condition of those genera among Pycnodontiformes, so that the general condition for pycnodonts appears logically unclear. Furthermore, that analysis supported the paraphyly of the Holostei, recently shown to be a monophyletic group (Grande 2010), so that the relationships of the pycnodonts would better be revised on the light of such new phylogeny of actinopterygian groups.

To sum up, there is no clear evidence that the most parsimonious phylogenetic position of the pycnodonts is as sister group of the teleosts (Teleosteomorpha). Therefore, the present paper aims to provide a test of such sister-group relationship by means of a new cladistic analysis, based on one of the most recent, extensive neopterygian analysis available.

Recent comprehensive analyses of neopterygian groups (i.e., Grande & Bemis 1998; Grande 2010; López-Arbarello 2012) have not coded pycnodonts, so their position logically appears unsolved in the corresponding summarizing phylogenetic hypotheses. The present paper aims to include pycnodonts in the data matrix by Grande (2010), so that their phylogenetic position can, for the first time, be based on the results of a comprehensive cladistic analysis. The analysis by Grande (2010) is preferred, for the present purpose, over that by López-Arbarello (2012) because the former is

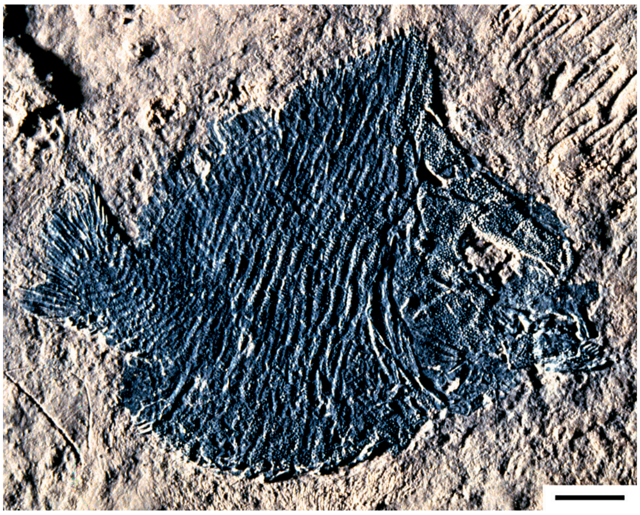

Fig. 2 - The brembodontid *Gibbodon cenensis*, a basal pycnodont, from the Late Triassic of Zorzino, Italy; holotype, Museo Civico di Scienze Naturale "E. Caffi", Bergamo, specimen 3317; photo courtesy F. Confortini, M. Malzanni, A. Paganoni; scale bar: 5 mm.

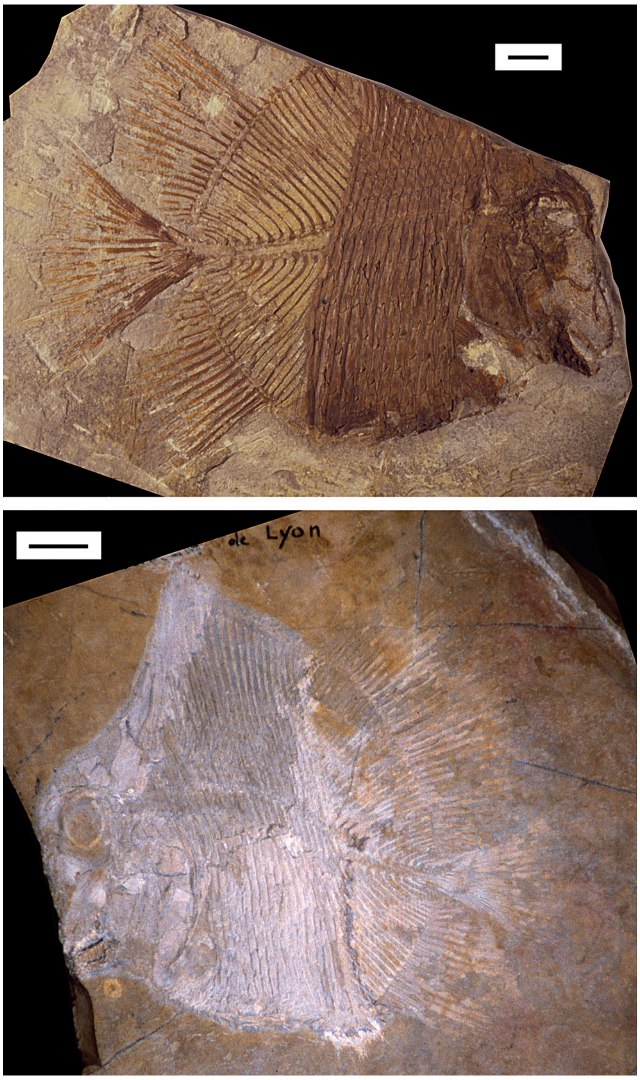

Fig. 3 - Specimens of the basal pycnodont genus *Macromesodon*, incorrectly called *Eomesodon* for a long time (see Poyato-Ariza & Wenz 2004). Above, holotype of *M. macropterus* (incorrectly called *E. gibbosus* for a long time), from the Late Jurassic of Solnhofen, Germany; Bayerischen Staatssammlung für Paläontologie und historische Geologie, München, Germany, specimen AS VII 345; photo Bergmeier, courtesy B. Reichenbacher, modified from Poyato-Ariza & Wenz (2002). Below, *M. surgens*, from the Late Jurassic of Cerin, France; Muséum d'Histoire naturelle, Lyon, France, specimen ML 15660; photo Serrette, courtesy S. Wenz, modified from Martín-Abad and Poyato-Ariza (2013b). Scale bars: 1 cm.

more inclusive and also because the latter focused on the relationships of the Ginglymodi rather than on those of all major neopterygian groups; it resulted on an undetermined position for the Teleostei, a clade that is fundamental for testing the sister-group relationships of the Pycnodontiformes. The major neopterygian groups represented in the analysis herein are, therefore, those in Grande (2010): Lepisosteiformes, Semionotiformes, Macrosemiiformes, Halecomorphi, and Teleostei, with the addition of the Pycnodontiformes (Tab. 1).

Material and methods

Material

The data matrix from Grande (2010) was completed for pycnodonts with bibliographic references and direct anatomic information, the latter as gathered during the studies by Poyato-Ariza & Wenz (2002, 2004, 2005) and Poyato-Ariza (2005, 2010); see those papers for detailed lists of the material directly observed.

Nomenclature

The terms "pycnodont" and "pycnodontiform" are unequivocally equivalent in the specialised literature, both being used for referring to the fishes of the order Pycnodontiformes. See, for instance (in chronological order): Nursall (1964, 1996a, b, 1999a, b, 2010), Tintori (1981), Figueiredo & Silva-Santos (1991), Hooks et al. (1999), Kriwet (1999, 2001, 2005, 2008), Poyato-Ariza & Wenz (2002, 2004, 2005), Delsate & Kriwet (2005), Kriwet & Schmitz (2005), Poyato-Ariza (2005, 2010), Machado & Brito (2006), Everhart (2007), Cavin (2008), Cavin et al. (2009), Kocsis et al. (2009), Poyato-Ariza & Bermúdez-Rochas (2009), and Shimada et al. (2010). Therefore, in this paper "pycnodont" is used to refer to any taxon of the order Pycnodontiformes and "pycnodonts" is used to refer to all taxa of the order Pycnodontiformes.

In the present paper, the terms "teleosteans", "Teleosteomorpha", and "Teleostei" are used sort of indifferently because all teleosteomorphs included in the analysis are teleosteans.

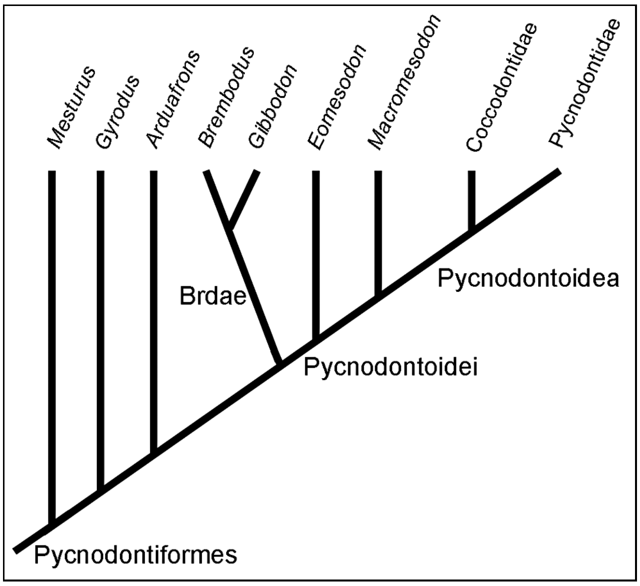

Fig. 4 - Cladogram of pycnodont interrelationships to show the primitive genera mentioned in the present paper. Simplified from Poyato-Ariza & Wenz (2002), with nomenclature for *Macromesodon* corrected after Poyato-Ariza & Wenz (2004). Brdae, Brembodontidae.

The superordinal rank of the pycnodonts, based on the congruence of the characteristics distinguishing the taxon as proposed by Nursall (2010), is not followed in the present series of papers because congruence of features is not considered an adequate criterion for assessing hierarchical categories. Such assessment is better based on congruence of phylogenetic relationships instead (i.e., Principles of Subordination and Coordination). For the time being, pending a definitive assessment of their phylogenetic relationships, it seems more suitable to consider the Pycnodontiformes in their traditional sense (Nursall 1996a).

For the present series of papers, a "basal pycnodont" is any non-pycnodontoid taxon (Fig. 4), whereas pycnodontoid taxa are considered "derived pycnodonts" (i.e., members of the superfamily Pycnodontoidea). The better known basal pycnodonts are *Mesturus*, *Gyrodus*, *Arduafrons*, and the Brembodontidae (Tintori 1981; Lambers 1991, 1992; Nursall 1999a; present paper, Fig. 2), and also *Macromesodon* as diagnosed by Poyato-Ariza & Wenz (2004; present paper, Fig. 3).

Character coding

For the present analysis, the data matrix for neopterygian fishes by Grande (2010: Appendix A) is completed by coding the corresponding character states for the Pycnodontiformes. All characters are included as in the original publication; they are not revised because the aim of this paper is to provide a tentative position for pycnodonts in that phylogeny, which included most major neopterygian groups and restored the Holostei as a monophyletic clade. Only very few problematic characters or states are treated differently (see comments in the list of characters below), when there was a real difficulty on their definition, or when they could be clearly improved for pycnodonts. Such changes have been kept to a minimum in order to preserve as much of the original analysis as possible. New states have been added when they were necessary to account for the distinct, deep morphologic modifications of the Pycnodontiformes (e.g., characters 5, 6, 7)

The controversy on how to approach the coding of higher-rank taxa in phylogenetic analyses is well known in cladistic literature (see subsequent references in this section). There are two groups of approaches, both of which basically aim to assess the plesiomorphic state of the higher taxon concerned (e.g., Prendini 2001). They differ essentially on how to proceed in order to obtain such ancestral assessment. Since there is no consensus on their use, or even on their denominations, both will be briefly explored herein.

A) The first approach is to use the higher taxon as a single unit, a terminal taxon on itself. This has been called groundplan analysis (Yeates 1995; Griswold et al. 1998), summary terminals (Nixon & Carpenter 1996), ancestral method (Bininda-Emons et al. 1998) or supraspecific method (Prendini 2001). The correct use of this approach obviously requires that the monophyly of the group is well established (e.g., Bininda-Emons et al. 1998). This method will herein be called the "extensive" approach, since it involves a broad knowledge of the group and of the evolution of each particular character within it in order to assess the correct ancestral state.

B) The second group of approaches consists of representing the higher taxon with a survey of some or even one of its significant constituent species. It has been called exemplar (Mishler 1994; Yeates 1995; Bininda-Emons et al. 1998 when only one taxon is used), democratic (Bininda-Emons et al. 1998 when several taxa are used) or species (Prendini 2001) method. The use of all the lower rank taxa within the group is consistently discouraged because it is impractical (Donoghue 1994; Mishler 1994; Nixon & Carpenter 1996; Rice et al. 1997) since the number of possible cladistic arrangements increases very rapidly with the addition of taxa (Felsestein 1978; Prendini 2001). This particular approach requires a significantly substantial knowledge of at least some lower rank taxa within the higher rank group, and the choice of taxa that are as basal as possible within the group, so that their character combinations represent the groundplan of the higher taxon as closely as possible (Yeates 1995; Griswold et al. 1998) or that they exhibit the greatest number of plesiomorphic states (Prendini 2001). Derived taxa should be avoided because their character combinations may differ greatly from the plesiomorphic condition of the higher taxon

(Griswold et al. 1998; Prendini 2001). This group of methods will herein be called the "representative" approach, since they involve the choice of certain selected lower taxa to represent the higher taxon.

Some practical studies have shown that the extensive (ancestral) method "...performed the best, always maintaining the correct topology when monophyletic taxa were represented" (Bininda et al. 1998: 101), but, as a matter of fact, there is no consensus on the advantages and disadvantages of each particular method in the literature; see, for instance, the disagreements among Yeates (1995), Rice et al. (1997), Bininda-Emonds et al. (1998), Wiens (1998), and Prendini (2001). Some authors encourage to use always the extensive or the representative approach, and there are significant arguments to support either one (e.g., Rice et al. 1997; Wiens 1998; Prendini 2001).

It must be noted that this methodological choice is especially important for the correct treatment of some very large data sets in molecular phylogeny (see any of the references cited in this section). For morphologic studies with smaller data sets, rather than always choosing the same approach on the basis of debatable arguments that are not agreed upon, it seems more practical to choose the method according to the real level of knowledge on the particular high taxon involved in the study. That is, whether the group is well known in its entirety or if it is accurately known from a few of its taxa only. In the case of the pycnodonts, the extensive method seems advisable for four particular reasons in this case:

1) Pycnodonts are very well, comprehensibly known as a group, and most of its genera known from articulated specimens have been widely described and figured. Furthermore, character evolution within the group is very well established (Nursall 1996a, 1999a; Poyato-Ariza & Wenz 2002, 2004, 2005).

2) The Pycnodontiformes form a very strong clade supported by 48 synapomorphies (Poyato-Ariza & Wenz 2002: 206), most of which are autapomorphies. In other words, their monophyly is not questioned and is commonly agreed upon, so that the use of this monophyletic supraspecific taxon in the correct sense discussed by Bininda et al. (1998) is assured. This is also why additional "pycnodont" characters are not added to the analysis; there is no need for them.

3) Unfortunately, even in the best known basal pycnodont genera (i.e., *Mesturus*: Nursall 1999a), large parts of their anatomy are not accessible due to a preservational bias and because their complete thick squamation conceals the axial and apendicular skeletons. This implies that additional information must be retrieved from additional taxa, wherever accessible. In turn, other genera, more derived, show the axial and caudal endoskeletons, but their endocranium and other structures are not known. This means that if several particular pycnodont genera were to be chosen for a representative approach, the percentage of unknown character states in the data matrix would significantly increase. Therefore, in this case the option of the extensive method is a sound strategy of safe taxonomic reduction in order to ameliorate the problem of the obfuscatory effect of the missing data (Wilkinson 1995).

4) Finally, the particular evolutionary history of the Pycnodontiformes resulted on far-reaching changes in character states in most members of the group, so that the use of only certain genera risks the wrong interpretation of the ancestral state more than in other groups. That is, the representative methods, in the case of the pycnodonts, would involve a higher risk of "inadequate sampling" in the sense of Prendini (2001: 292) or of "not representative sample" in the sense of Wägele (2005: 273).

Therefore, characters are coded for Pycnodontiformes as a whole by inferring the state in their common ancestor, a method that "is the most likely to maintain the correct topology because it attempts to infer the character states of the groundplan (the ideal scenario from first principles)." (Bininda et al. 1998: 129). Most usages of this approach have been criticized for not providing any detailed description of the method (e.g., Yeats 1995; Prendini 2001). Therefore, in order to specify such detailed description of the particular method used herein, precise criteria to assess the ancestral state for character coding in Pycnodontiformes are stipulated as follows:

1- Coded as present in all genera where the character is accessible, that is, the common condition shared by all pycnodonts.

2- If the condition is heterogeneous within the group, it is coded as it appears in all basal genera (Fig. 4) where the character is accessible. This is the generalized condition for basal pycnodonts, that is, the ancestral pycnodont condition regardless of ulterior character evolution within the group.

3- If the character is not accessible in the most basal pycnodonts (Fig. 4), it is coded as it is observed in the most basal genera where the character is accessible, that is, generalized condition for the most basal pycnodonts where it can be verified.

These criteria are ordered from more to less decisive in order to assess the ancestral pycnodont state; that is, the preferred criterion is always 1, then 2 if 1 is not verifiable, finally 3 if 2 is not verifiable either. Ultimately, this extensive method of assessing the ancestral state for pycnodonts ensures, in the present analysis, to "make use of all the available data and take into account whatever is known about phylogenetic relationships within well-supported subtrees" (Rice et al. 1997: 562). This extensive search within the group also en-

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	31	32	33	34	35
0	0	?	0	2	2	2	1	0	0	1	1	1	0	0	0	1	2	1	0	0	0	0	0	?	0	?	0	0	0	?	0	0	0	0

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	61	62	63	64	65	66	67	68	69	70
1	0	0	0	0	0	0	2	0	0	0	0	0	1	0	1	0	1	0	1	1	N	1	0	1	0	0	0	1	N	N	1	1	0	2

71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
N	0	0	2	1	1	0	0	?	?	?	0	0	?	1	0	0	1	1	0	?	?	0	0	1	?	0	0	?	0	0	1	?	N	0

Tab. 1 - Small data matrix showing the character states as coded for the Pycnodontiformes in this analysis. All other characters in the data matrix processed in the present analysis are as in Grande (2010: Appendix 1).

sures to avoid common sources of errors such as choice of not representative samples of individuals and/or species, lack of monophyly of the terminal taxa (i.e., non-monophyletic genera to represent the group) or coding for character states that are not of the ground pattern but autapomorphies of a subset of species (Wägele 2005). It also diminishes the risk of exponential increase in possible cladistics arrangements with the addition of taxa (Felsenstein 1978).

Therefore, the comments in the subsequent list of characters are focused on the coding in pycnodonts according to the extensive approach, with the precise 3-criteria method described above.

List of characters

This section presents the list of characters used in the present analysis; they are listed with the same number as they appear in Grande (2010). Data for the present analysis are retrieved from the descriptions and illustrations of particular genera in the corresponding papers cited below, and from the specimens studied for the analyses by Poyato-Ariza & Wenz (2002, 2004, 2005). In addition, whenever any additional noteworthy specimen or reference is relevant for the understanding of a particular structure, it is discussed in the corresponding character.

The coding for pycnodonts is the state that appears underlined for each character in the list. Characters that are not underlined below indicate that their state in pycnodonts is unknown (coded as?). Characters are often commented for clarification in pycnodonts. Absence of comments indicates a clear common condition for all pycnodonts where it is accessible. A small data matrix showing the character states as coded for pycnodonts in this analysis is provided by Tab. 1.

(1) *Preorbital snout length-to-postorbital head length ratio* [0 = less than 1.2; 1 = of 1.5 or greater]. It is about 1.48 in *Mesturus* as restored by Nursall (1999a: fig. 3), 0.7 in *Gyrodus* as restored by Lambers (1991, 1992: fig. 9), and 0.8 in the holotpye of *Brembodus*. Most other pycnodonts have a ration consistently under 1.2, usually under 1.0 (e.g., 0.57 in *Turbomesodon*; pers. obs.). Therefore, although it is 1.48 in *Mesturus*, since it is still under 1.5, and it is under 1.2 in most other pycnodonts, basal and derived, it is coded as 0.

(2) *Large, firmly anchored, pointed conical teeth covering the dermal bones of the skull* [0 = absent; 1 = present].

(3) *Ampullary electroreceptors* [0 = present; 1 = absent].

(4) *Elongation of rostral region anterior to lower jaw symphysis* [0 = extends anterior to dentary symphysis by less than 20% of mandibular length; 1 = extends well anterior to dentary symphysis by more than 50% of mandibular length].

(5) *Posterior extent of median rostral bone* [0 = with lamellar bone component separating the nasals, at least anteriorly; 1 = a simple tube at the anterior end of snout with no internasal lamella; 2 = no autogenous median rostral]. A median rostral is absent in all pycnodonts where the ethmoid region is accessible and well preserved, so a new character state is added for the absence of this bone (state 2).

(6) *Premaxilla immovably attached to braincase by means of a long nasal process tightly sutured to the frontals* [0 = no; 1 = yes; 2 = attached to braincase by means of a long ascending process articulated to the mesethmoid]. As discussed by Poyato-Ariza & Wenz (2002: 168), the long premaxillary process of the pycnodonts is a derived state, not homologous to the deep nasal process of *Amia*, for instance. Furthermore, in all pycnodonts this ascending process is very superficial and forms a long attachment of the premaxilla to the braincase. It does not suture with the frontals because the mesethmoid of pycnodonts is highly hypertrophied and forms a large portion of the braincase (Nursall 1996a: 129; 1999b: 193; Poyato-Ariza & Wenz 2002: 154-155), largely separating the premaxilla from the frontals. As a consequence, the long ascending process of each premaxilla articulates with the mesethmoid, not with the frontals. The premaxillae in the Mesturidae are largely covered by dermal tesserae (Nursall 1999a), so the precise morphology of the bone is unknown. In *Gyrodus*, the bone does have the same process as in other pycnodonts, already very elongated (Lambers 1991, 1992: figs. 9, 15). Therefore, a new character state has been added to accommodate the particular morphology and way of attachment of the pycnodont premaxilla (state 2).

(7) *Nasal process of premaxilla forms much of the ornamented dermal roof in the snout region* [0 = no; 1 = yes; 2 = unornamented, but forming much of the dermal cover of the snout region]. The premaxilla is usually devoid of ornamentation in pycnodonts, but it does form much of the dermal roof in the snout region. As a character, this one seems linked to number 6; in a similar manner, a new character state has been added for the premaxilla of pycnodonts, which forms much of the dermal cover of the snout region but is devoid of ornamentation (state 2).

(8) *Anterior portion of premaxilla lining the nasal pit and pierced by a large foramen for the olfactory nerves* [0 = no; 1 = yes]. The premaxilla does not line the nasal pit, but roofs it, because the bone is superficial in its entirety (e.g., Poyato-Ariza & Wenz 2004: figs. 4, 5), and it is devoid of any foramen for the olfactory nerves, except in the derived *Polazzodus* (Poyato-Ariza 2010: fig. 5A,B).

(9) *Premaxillary width to length ratio based on dorsally exposed region (mean value)* [0 = 0.95-0.28; 1 = 0.18-0.02]. As a character, this one seems linked to numbers 6 and 7 because the key morphologic feature is the elongation of the process of the premaxilla. This ratio is about 0.14 in *Gyrodus* (based on Lambers 1991, 1992: fig. 15), and very similar in most other pycnodonts, such as *Turbomesodon* and *Ocloedus*.

(10) *Flank scale morphology* [0 = absence of †obaichthyd-type scale, 1 = presence of †obaicththyd-type scale].

(11) *Number of teeth in outer premaxillary tooth row* [0 = usually four to 18; 1 = usually one to four].The single premaxillary tooth row of pycnodonts is herein considered homologous to the outer premaxillary tooth row of Lepisosteiformes, the closest to the oral border of the bone. There is a single premaxillary tooth row in pycnodonts, bearing three teeth in basal forms such as *Brembodus*, *Gibbodon*, and some *Mesturus* (see Poyato-Ariza & Wenz 2002: 169-170 for further comments in this genus). The number of premaxillary teeth is reduced to two in most other pycnodonts.

(12) *Tube-like canal bearing anterior arm on antorbital* [0 = absent; 1 = present]. In *Mesturus* and *Gyrodus*, the whole region is covered by tesserae, and the antorbital is not distinguishable; preservation prevents from observation in most other pycnodonts. Whenever preserved, though, the antorbital is an entirely tubular bone, including the anterior arm (dorsally oriented due to the general vertical elongation of the skull; e.g., Nursall 1999b: fig. 9).

(13) *Number of extrascapulars* [0 = one on each side; 1 = more than one on each side; 2 = no autogenous extrascapulars]. In the most basal pycnodonts, including Mesturidae, *Gyrodus*, and *Macromesodon*, there is more than one extrascapular on each side (e.g., Poyato-Ariza & Wenz 2002: 159).

(14) *Supraorbital bone/bones* [0 = absent; 1 = present].

(15) *Circumorbital ring* [0 = incomplete (lateral edge of frontal or nasal makes up part of orbital margin, or anterior part of ring absent); 1 = complete (frontal and nasal margins excluded from orbital margin by circumorbital bones)].

(16) *Dermosphenotic participation in orbital margin* [0 = dermosphenotic reaches orbital margin; 1 = dermosphenotic does not reach orbital margin]. A dermosphenotic is not described in *Mesturus*; in the Mesturidae *Micropycnodon* it does reach the orbital margin (Nursall 1999a: fig. 7), and so does in *Gyrodus* (Lambers 1991, 1992: fig. 9) and all other pycnodonts where the bone is observed, in which, as a matter of fact, the dermosphenotic does form a significant part of the orbit (e.g., *Polazzodus*, *Turbomesodon*).

(17) *Anterior extent of preopercle* [0 =not reaching below anterior part of the orbit; 1 = reaching below anterior part of the orbit]. The evolution of this character within pycnodonts is rather interesting. The anterior extent of the preopercular bone does reach below the anterior part of the orbit in most of the basal forms, namely *Mesturus*, *Arduafrons*, and the Brembodontidae. In *Gyrodus*, however, as in all derived genera where this character is accessible, it does not reach below the anterior part of the orbit. Since it is 1 in most observed basal forms, including *Mesturus*, it is coded as 1, implying an independent character reversion within the order.

(18) *Suborbital bones in adults (mean value)* [0 = 1 to 8; 1 = more than 8; N = inapplicable due to absence in Grande (2010) modified into 2 = absence or zero suborbitals]. Because absence also concerns the number of suborbitals, this character is coded as 2 instead of inapplicable (state modified from N to 2, zero suborbitals). In other words, morphological features are inapplicable when there is absence, but absence itself is considered an applicable character state. Orbitals are absent in all pycnodonts; the dermal tesserae of *Mesturus* are not homologous to true suborbitals.

(19) *Interopercle* [0 = present; 1 = absent]. This is a clear character coding for pycnodonts, since the interopercular bone is absent from the most basal forms as part of the profound modifications of their opercular region.

(20) *Position of anteriormost lacrimal* [0 = part of orbital ring; 1 = well anterior to orbital ring]. The orbital ring as formed by all infraorbitals, including lacrimal, is displaced ventrally in pycnodonts due to the vertical elongation of the skull, but it is not extended anterior to the orbit.

(21) *Number of lacrimal bones* [0 = only a single lacrimal; 1 = a series of 3 or more lacrimals].

(22) *Dermosphenotic/sphenotic association* [0 = closely associated with each other (i.e., contacting or fused to each other); 1 = not in contact with each other]. Whenever both the dermosphenotic and the autosphenotic are observable, which is rarely among pycnodonts, they are closely associated, in contact (e.g., *Micropycnodon*: Nursall 1999a: fig. 7; *Turbomesodon*: Poyato-Ariza & Wenz 2004: fig. 7; *Polazzodus*: Poyato-Ariza 2010: fig. 3).

(23) *Sphenotic with small dermal component* [0 = no; 1 = yes]. Whenever observable, the autosphenotic of pycnodonts appear entirely in a profound level, with no parts forming the skull roof and no traces of ornamentation.

(24) *Supraorbital canal incorporated into premaxilla* [0 = no; 1 = yes].

(25) *Junction of supraorbital canal with infraorbital canal* [0 = within (or at least including) frontal bone; 1 = exclusively within dermopterotic bone]. This character is very problematic. As defined, no difference seems to exist between the condition in *Lepisosteus* and in *Semionotus*; in both cases, the real junction occurs in the dermopterotic, but there is a portion from the frontal "involved", which corresponds to the trajectory of the posterior part of the supraorbital canal in the frontal. In other words, the "branch to the frontal" in Grande (2010: 764), is not a real branch, but the posterior part of the supraorbital canal in the frontal bone. However, it is coded by Grande (op. cit.) as 1 in *Lepisosteous* and as 0 in *Amia* and *Semionotus*. The arrangement of these canals in pycnodonts is indistinguishable from the one present in any of these genera, so it is coded as unknown, but due to lack of precision in character definition, not to lack of information in the fossil pycnodont material. As a test, the analysis was run with and without this character (see Discussion below), which would be better not considered until further revision.

(26) *Commissure between right and left supraorbital canal within frontal* [0 = absent; 1 = present].

(27) *Vertebrae fused into adult occipital condyle* [0 = no vertebral centra fused into condyle; 1 = one vertebral centrum fused into condyle during early ontogeny; 2 = two vertebral centra fused into condyle during early ontogeny; 3 = normally more than three]. Only arcocentra (neural and haemal arches) are ossified in pycnodonts; the lack of accurate ontogenetic series prevents from knowing how many arcocentra, if any, are fused into the occipital condyle of adult individuals. Therefore, it has been coded as unknown in the group.

(28) *Supraoccipital bone* [0 = absent; 1 = present]. This is admittedly a problematic character. There is a very large bone traditionally called "supraoccipital" in pycnodonts (e.g., Nursall 1996a, 1999a, 1999b; Poyato-Ariza & Wenz 2002), whose morphology and vertical extension are typical, unique of the order. The presence of a supraoccipital crest is proposed to be a synapomorphy shared by pycnodonts and teleosts by Nursall (1996a: 144). This bone, however, is proven to be the supraotic by Maisey (1999), and considered not homologous of the supraoccipital bone of teleosts by Arratia (1999) and Kriwet (2001). As a test, the analysis was also run with this character coded as 1 (present) for pycnodonts (see Discussion below). This endochondral bone, deep and unornamented, must not be confused with the dermal supraoccipital bone, a unique superficial, ornamented structure of pycnodonts (Nursall 1996a; Poyato-Ariza & Wenz 2002).

(29) *Pterotic* [0 = present; 1 = absent]. Nursall (1999a: 172, figs. 17, 20) claimed the presence of an autopterotic, distinct from the dermopterotic, in *Mesturus* as in the more derived *Neoproscinetes* and *Pycnodus*. There is also evidence of its presence in *Polazzodus* (Poyato-Ariza 2010: 653, fig. 3).

(30) *Intercalar ossification in the otic region* [0 = present; 1 = absent]. An intercalar ossification is described and illustrated in *Mesturus* by Nursall (1999a: 175, fig. 14), who specifies that its presence represents the primitive condition.

(31) *Anterior myodome* [0 = present; 1 = absent]. A posterior myodome is described an illustrated in *Mesturus* by Nursall (1999a), but there is no mention of an anterior myodome; consequently, this character is coded as unknown, because no other description or observation of this part of the pycnodont braincase are available.

(32) *Posttemporal fossa* [0 = present; 1 = absent]. The presence of a posttemporal fossa is explicitly cited in *Mesturus* by Nursall (1999a: 172).

(33) *Opisthotic bone* [0 = present; 1 = absent]. An ossified, autogenous opisthotic bone is described and illustrated in *Mesturus* by Nursall (1999a: 175, figs. 14, 17).

(34) *Predorsal length* [0 = 70% or less of standard length; 1 = 75% or more of standard length]. Dorsal fin is usually long in pycnodonts, therefore inserted at 70 or less of standard length. Among basal

forms, predorsal length is 65%-70% in *Arduafrons*, *Gyrodus* and *Mesturus*, and about 50% in *Brembodus*. Other pycnodonts have smaller predorsal lengths, even below 50% (e.g., *Akromystax*). Only very occasionally, in highly derived forms such as *Ichthyoceros*, the predorsal length can attain 75%. This variation in pycnodonts is not correlated with the more or less elevated shape of the body (see also Poyato-Ariza & Wenz 2002 and Poyato-Ariza 2005).

(35) *Ethmoid ossifications* [0 = present; 1 = absent]. There is one large, hypertrophied mesethmoid in all pycnodonts, playing a key structural role in the whole anterior region of the skull.

(36) *Vomer differentiated and molded to underside of ethmoid region* [0 = no; 1 = yes]. A differentiated vomer is the teeth-bearing bone that forms most of the palate and the underside of the ethmoid region in all pycnodonts.

(37) *Vomer median or paired in adults* [0 = median; 1 = paired]. The vomer in pycnodonts, just commented in the previous character, is median (single, unpaired) in all adult specimens observed.

(38) *Flank scales with large prominent posteriorly pointing spines* [0 = no; 1 = yes].

(39) *Tooth organization of dentary* [0 = dentary teeth in a single row and all of similar size; 1 = in addition to a lateral single row of similar sized teeth, there is a medial row of much larger fangs; 2 = a pavement of small similar sized teeth not in rows; 3 = no teeth on dentary].

(40) *Collective shape of laterally expanded part of vomerine heads* [0 = not forming an equilateral triangle; 1 = forming a shape roughly like an equilateral triangle]. The anterior head of the vomer does not form the peculiar triangular lateral expansion of the Lepisosteiformes, so it has been coded as 0. Grande (2010) groups into the primitive state also the taxa where the anterior part of the vomer is not expanded forming heads, so the wording of the character should probably be revised.

(41) *Plicidentine tooth structure* [0 = absent; 1 = present].

(42) *Lacrimomaxillary bone series present/absent* [0 = absent; 1 = present].

(43) *Marginal teeth of upper jaw* [0 = conical teeth of moderate to large size; 1 = microteeth; 2 = no teeth on margin of upper jaw]. The "upper jaw" in Grande (2010) are "the maxillary elements, whether autogenous or fused to other bones" (op. cit.: 775). According to this, marginal teeth are absent in pycnodonts, since the maxilla is toothless in all of them.

(44) *Size of adult autogenous maxilla* [0 = a large, well ossified bone making up half or more of the biting surface of the upper jaw; 1 = either absent, or a series of relatively minute (atrophied) bones (...)].

(45) *Maxilla with well-developed anterior articular process* [0 = yes; 1 = no]. A distinct anterior articular process is visible whenever the delicate maxilla is observable in its entirety (e.g., *Gyrodus* in Lambers 1991, 1992: fig. 15A; *Polazzodus* in Poyato-Ariza 2010: fig. 5B), although sometimes the process is visible in medial view only (e.g., *Turbomesodon*, pers. obs.).

(46) *Mobility of maxilla* [0 = present; 1 = absent]. The maxilla is very loosely attached in all pycnodonts, therefore likely to have presented high mobility (see, for instance, Kriwet 2001: fig. 10).

(47) *Supramaxilla* [0 = absent; 1 = present].

(48) *Position of lower jaw/quadrate articulation* [0 = under or posterior to orbit; 1 = in advance of the orbit].

(49) *Lower jaw articulation single versus double* [0 = single articulation between the suspensorium and lower jaw, consisting of an articulation between articular and quadrate; 1 = double articulation between the suspensorium and lower jaw, consisting of an anterior condyle of the quadrate and an anterior condyle of the symplectic, both articulating with an articular element or elements of the lower jaw]. This is a fascinating character in pycnodonts. Unfortunately, the articular area of the suspensorium is not accessible in the most basal forms; however, in all taxa where it is, it consistently appears double, exactly as described for the derived state. The particular modifications in shape and orientation of the quadrate and the symplectic, and of their articular surfaces as extensively described by Kriwet (2005: 157-158) are consistent with the other modifications of the vertically enlarged skull of pycnodonts and the high mobility of the mandibular articulation. Poyato-Ariza & Wenz (2002: 207) considered the double mandibular articulation of pycnodonts as homologous to that of Halecomorpha. Whenever observable, both the symplectic and the quadrate participate in the mandibular articulation, and both present a distinct anterior condyle (e.g.: *Pycnodus*, Kriwet 2001: fig. 2; *Turbomesodon*, Poyato-Ariza & Wenz 2004: fig. 10).

(50) *Mandibular length as a percentage of head length (mean value)* [0 = less than 43%; more than 44%].

(51) *Type of mandibular coronoid process* [0 = absent or of a single bone, 1 = compound structure involving more than one bone]. Whenever observable, the coronoid process (i.e., the most elevated region of the lower jaw) of pycnodonts is seen to be formed by, at least, the prearticular and angular bones. In *Mesturus*, the dentary and the surpraangular are also part (Nursall 1999a: fig. 5). The coronoid process extends vertically to form a distinct structure of variable morphology within the group.

(52) *Prearticular* [0 = present; 1 = absent]. A prearticular is present in all pycnodonts, being the highly developed bone that bears the molariform teeth and constitutes the coronoid process of the lower jaw.

(53) *Supraangular* [0 = absent; 1 = present]. See, for instance, *Mesturus* in Nursall (1999a: fig. 5).

(54) *Type of dentary symphysis* [0 = symphysis occurs between the recurved anterior ends of right and left dentary; 1 = symphysis occurs along medial surface of anterior right and left dentary with anterior ends pointing anterior].

(55) *Coronoid bones* [0 = present as separate ossifications; 1 = not present].

(56) *Extent of teeth on dentary (excluding coronoid tooth plates)* [0 = tooth row extends over a third of the length of the dentary; 1 = tooth row is present on only the anterior one-third or less of dentary].

(57) *Coronoid tooth morphology* [0 = small, conical, pointed teeth; 1 = robust broadly or bluntly tipped teeth]. Not applicable to pycnodonts, because the coronoid bones are absent.

(58) *Mentomeckelian bone* [0 = present; 1 = absent].

(59) *Laterally sliding articulation between metapterygoid and the "basipterygoid process" (= parasphenoid-prootic process) in adults* [0 = absent; 1 = present].

(60) *Quadrate/metapterygoid contact or close association* [0 = present; 1 = absent]. The quadrate and the metapterygoid are broadly separated by the entopterygoid in all pycnodonts where this region is accurately preserved; see, for instance, Nursall & Maisey (1991: fig. on p.131), Lambers (1991, 1992: fig.14; label Mpt is incorrect in fig. 14b, as p. 79 of the text specifies that the bone is the entopterygoid), Nursall (1999b: fig.5), Kriwet (2001: figs. 1A, 10; 2005, figs. 1, 22A, 27C), Poyato-Ariza & Wenz (2004, figs. 4, 5, 10; 2005: fig. 3) and Poyato-Ariza (2010: fig. 4).

(61) *Part of dorsal surface of ectopterygoid ornamented and forming part of the skull roof* [0 = no; 1 = yes].

(62) *Length of ectopterygoid relative to endopterygoid* [0 = less than twice the length of the endopterygoid; 1 = more than twice the length of the endopterygoid].

(63) *Ectopterygoid participation in palatal surface area* [0 = ectopterygoid forms half or less of the palatal region; 1 = ectopterygoid forms the majority of the palatal region].

(64) *Autopalatine* [0 = present; 1 = absent]. Both the dermo- and the autopalatine are absent in all pycnodonts where this region is accessible and well preserved.

(65) *Endopterygoid/dermopalatine association* [0 = endopterygoid sutured to dermopalatine anteriorly; 1 = endopterygoid not in contact with any dermopalatine]. Not applicable to pycnodonts (see previous character).

(66) *Dermopalatine teeth* [0 = adults with very large fangs or large crushing teeth on dermopalatine (i.e., teeth as large as any in the

premaxilla and dentary); 1 = adults with only very small teeth on dermopalatine (i.e., smaller than the large teeth of premaxilla and dentary); 3 = both jaw teeth and dermopalatine teeth are very tiny]. Not applicable (see character 64).

(67) *Symplectic* [0 = absent; 1 = present].

(68) *Symplectic bone shape* [0 = slightly curved tube or splint; 1 = hatchet shaped; 2 = L-shaped; irregularly shaped subrectangular bone with two ventrally pointed arms]. The symplectic is rarely observed in its entirety in pycnodonts, because it is largely concealed by the quadrate and the preopercular bone in lateral view; when it is visible in medial view, it appears as a bone of a shortened hatchet shape, more similar to state 1 than to any of the others (e.g., Nursall & Maisey 1991: fig. on p. 131).

(69) *Symplectic/quadrate articulation* [0 = present; 1 = symplectic separated from quadrate by a quadratojugal].

(70) *Quadratojugal* [0 = plate-like; 1 = splint-like bone articulating with the anterior limb of the preopercle; 2 = absent].

(71) *Exposed, anterodorsal projection of subopercle* [0 = little or no narrow projection extending dorsally; 1 = forming an elongate process extending one third to two thirds the way up along the anterior edge of the opercle]. Not applicable to pycnodonts because the subopercular bone is always absent in this group.

(72) *Ventral limb depth of L-shaped preopercle* [0 = ventral limb narrow or absent; 1 = ventral limb deep, massively developed, and exposed, forming a major part of the ornamented dermal surface of the ventrolateral region of the skull]. The ventral limb of the preopercle is totally absent in all pycnodonts. Further revision of character state distribution among neopterygians may suggest division of state 0 into "ventral limb narrow" and "ventral limb absent".

(73) *Exposure of dorsal limb of preopercle* [0 = mostly exposed, forming a significant part of the ornamented lateral surface of the skull anterior to the opercle; 1 = entirely covered or nearly entirely covered by other dermal bones in adults]. There are no distinct limbs in the preopercle of pycnodonts; however, this bone is always forming a significant part of the ornamented lateral surface of the skull.

(74) *Number of branchiostegal rays* [0 = more than 4; 1 = usually 4; 2 = usually 3; 3 = usually 1 or 2; 4 = none]. The basal pycnodonts *Mesturus* and *Gibbodon* have 3 branchiostegal rays; other pycnodonts, more derived, where this region is well preserved have 2 (see character 30 in Poyato-Ariza 2002 for further comments on the branchiostegal rays of these fishes). The reduction of the number of branchiostegal rays from 3 to 2 occurs independently within the Pycnodontiformes; as a matter of fact, it is a synapomorphy of the suborder Pycnodontoidei (Poyato-Ariza & Wenz 2002: 210). Therefore, it has been coded as state 2 (3 branchiostegal rays), because such is the primitive state for pycnodonts.

(75) *Gular* [0 = present; 1 = absent].

(76) *Articular ossifications* [0 = a single ossification; 1 = two separate ossifications; 3 = absent]. All pycnodonts with a well-preserved lower jaw show a massive tooth-bearing prearticular plus a small articular bone.

(77) *Basihyal tooth plate ("tongue bone") consisting of a mosaic of bony plates ("entoglossals")* [0 = absent; 1 = present].

(78) *Urohyal* [0 = absent; 1 = present]. Re-examination of the material allows re-interpretation of the urohyal in *Turbomesodon* (Poyato-Ariza & Wenz 2004), the only one reported in pycnodonts so far, as a hypohyial, very much as in *Gyrodus* (Lambers 1991, 1992). Therefore, the urohyal is considered absent in pycnodonts.

(79) *Uncinate processes on epibranchials* [0 = absent; 1 = present].

(80) *Tooth plates associated with second and third hypobranchials* [0 = yes; 1 = no].

(81) *Gill raker morphology* [0 = simple small bits of bone bearing small conical teeth; 1 = rows of long, deeply serrated, laterally compressed gill rakers of a unique shape; 2 = rows of blade-like gill rakers].

(82) *Opisthocoelus vertebral centra* [0 = absent; 1 = present].

(83) *Number of ural centra* [0 = count of four or more; 1 = normally two or less]. The number of ural centra is admittedly difficult to precise because only arcocentra are ossified, and the evidence on the number of real hypurals is scarce and contradictory (see Poyato-Ariza & Wenz 2002: 184-185 for details). However, the consistently high number of epi- and hypochordal elements supporting caudal fin rays strongly indicates that pycnodonts present state 0.

(84) *Articulation of proximal end of pleural ribs with vertebral parapophysis* [0 = posterior to parapophyses; 1 = anteroventral to parapophyses, 2 = distal tip of parapophyses].

(85) *Neural spine type in caudal region* [0 = absent; 1 = median; 2 = paired; 3 = both median and paired].

(86) *Uroneural arches modified as elongate uroneurals* [0 = no; 1 = yes]. The original wording of the character should probably be revised, since there are no such structures as "uroneural arches" but neural arches modified as uroneurals. This is probably a simple mistake in the original phrasing of the character, since the whole discussion in Grande (2010: 787) correctly refers to neural arches or uroneurals, never to "uroneural arches",

(87) *Caudal fin ray branching* [0 = two or more unbranched principal rays in caudal fin; 1 = normally all principal rays of caudal fin are branched]. All pycnodonts with well-preserved caudal fin rays show one unbranched principal fin ray in each lobe; each of these unbranched fin rays is the longest of the respective lobe.

(88) *Number of principal caudal fin rays in adults* [0 = 11-13 (but usually 12); 1 = usually more than 12; 2 = usually less than 12].

(89) *Fin ray to pterygiophore ratios of dorsal and anal fins* [0 = 2:1 or greater; 1 = about 1:1].

(90) *Fulcra on caudal fin primarily of fringing type* [0 = absent; 1 = present]. The polarization of this character by Grande (2010) is in need of revision, since, as discussed by the same author, basal forms do have fringing fulcra, outgroup included.

(91) *Posttemporal penetration by lateral line canal* [0 = present; 1 = absent]. The posttemporal is not accurately observable in pycnodonts.

(92) *Ventral process of posttemporal bone* [0 = absent; 1 = weakly developed; 2 = well developed as a ventral rod-like process suturing to intercalar process; 3 = developed as a flat flange]. See previous character.

(93) *Supracleithrum with a concave articular facet for articulation with the posttemporal* [0 = no; 1 = yes].

(94) *Medial wing on cleithrum* [0 = absent; 1 = present].

(95) *Clavicles* [0 = well developed; 1 = absent].

(96) *Anterior and posterior "clavicle elements"* [0 = absent; 1 = present]. These elements are hardly preserved in fossils, so the character is conservatively coded as unknown for pycnodonts.

(97) *Medial processes of supracleithrum* [0 = absent; 1 = present].

(98) *A series of diplospondylous spool-shaped vertebrae in preural caudal region* [0 = absent; 1 = present].

(99) *Number of hypobranchials* [0 = 3 hypobranchials; 1 = 4 hypobranchials].

(100) *Long epineural intermuscular bones* [0 = absent; 1 = present].

(101) *Premaxillary tooth row curves anteriorly at symphysis and laterally onto projecting horns as it nears frontal* [0 = no; 1 = yes].

(102) *Dermosphenotic attachment to skull roof in adult sized individuals* [0 = loosely attached on the skull roof or hinged to the side of skull roof; 1 = tightly sutured into skull roof forming part of it].

(103) *Anterior part of body and top of head usually with large dark spots* [0 = no; 1 = yes].

(104) *Anterior end of first coronoid curves medially and expands broadly to a flat symphysis* [0 = no; 1 = yes]. Not applicable in pycnodonts due to absence of coronoid bones.

(105) *Lateral process of basioccipital* [0 = absent; 1 = present].

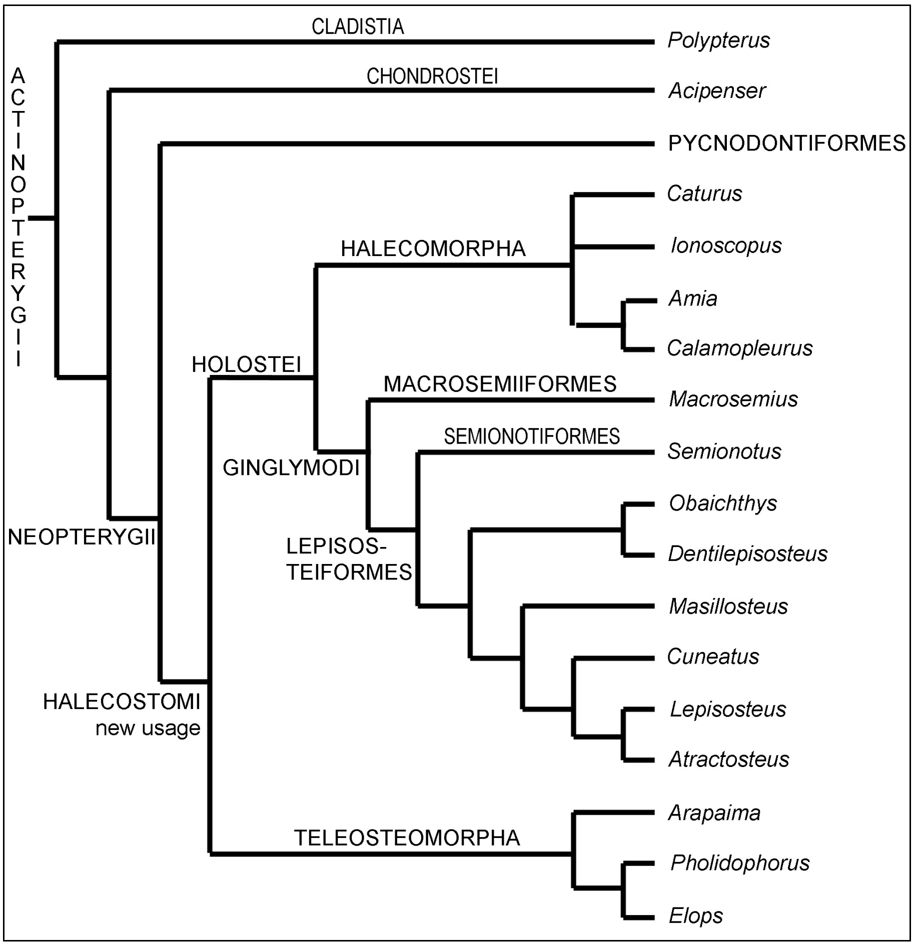

Fig. 5 - Strict consensus tree showing the basal position of pycnodonts among the neopterygian groups included in the analysis. Most of the unsolved nodes in this analysis are within *Atractosteous*; the interrelationships of the species of *Atractosteus*, *Lepisosteus*, and other lepisosteiform genera are not shown because they are presented in detail by Grande (2010); see also that paper for further information on the nodes of the cladogram that do not involve pycnodonts. Note: the interrelationships of teleosteomorphs appear sort of "inverted", with *Pholidophorus* instead of *Arapaima* as the sister group of *Elops* because this analysis does not include the characters that clarify teleosteomorph interrelationships, which is not the aim of Grande (2010) or the present paper.

Results

Cladistic analysis

The data matrix was processed by PAUP program 3.1.1 in an iMac 8 computer at the Unidad de Paleontología, Universidad Autónoma de Madrid. In all analyses, multiple states were interpreted as uncertainty. As in the original analysis, all characters were run as unordered and the heuristic search was rooted with *Polypterus* and *Acipenser* as the outgroup (Grande 2010: 741, appendix A). The search for the most parsimonious trees was heuristic, general option.

The number of shortest trees obtained was 176, as in the original analysis (Grande 2010: 741), each of them with a length of 199 steps; they are logically longer than the original analysis (180 steps) because an additional taxon, the Pycnodontiformes, was coded into the matrix. The consistency index (CI) was 0.643 and the retention index (RI) was 0.886, both barely lower than those of the original analysis.

The strict consensus tree is shown on Fig. 5; uncertainties involve mostly the different species of *Atractosteus*, as in the original analysis, and they do not appear on the figure. Because the position of the Pycnodontiformes is solved and unequivocal, only the strict consensus tree will be discussed. Such invariable position of the group in all 176 most parsimonious trees implies that further analyses with additional options or computer programs are not necessary, at least with the present data matrix.

In the present analysis, the phylogenetic relationships and the definition of the Holostei and the Ginglymodi are the same as in Grande (2010), so the inclusion of the Pycnodontiformes does not affect the interrelationships of the other neopterygian groups. Therefore, only the position of the pycnodonts will be discussed below; for additional information on other nodes, see Grande (2010).

The position of pycnodonts

In the present analysis, the Pycnodontiformes appear consistently as the most basal group among all the neopterygians included in the analysis (Fig. 5). This is quite an unexpected, but very interesting and challenging result: pycnodonts are not the sister-group of the Teleostei or Teleosteomorpha, and do not belong to the Holostei either.

The unambiguous characters shared by the pycnodonts plus all other neopterygians (Fig. 5) are: 36(1), differentiation of vomer, molded to underside of ethmoid region; 58(1), absence of mentomeckelian bone; 67(1), presence of symplectic; 70(2), absence of quadratojugal; 89(1), a 1:1 fin ray to prterygiophore ratio in dorsal and anal fins; and 95(1), absence of clavicles. All but 58 and 95 are autapomorphic. With Acctran optimization, the node is also defined by characters 3(1), 31(0, reversion), 51(1), 53(1), 79(1), and 92(2, reversion from 3). The Deltran optimization does not include any additional character.

Unambiguous characters shared by [Holostei + Teleostei] and not present in the Pycnodontiformes (Fig. 5) are: 13(0, reversion), a single extrascapular bone on each side of the skull roof; 15(1), circumorbital ring complete, with the frontal and nasal bones excluded from the orbital margin by the circumorbital bones; 19(0, reversion), presence of interopercle; and 33(1), absence of opisthotic bone. None of them is autapomorphic. In addition, the Acctran optimization adds characters 14(1), 43(0, reversion from 2), 47(1), and 102(0, reversion), and the Deltran, characters 3(1), 65(0, reversion), 74(0, reversion from 4), 79(1), and 92(2, reversion from 3).

Discussion

Pycnodonts and teleosteans

The basal position of the Pycnodontiformes among the major neopterygian groups included in this analysis necessarily implies that all the characters allegedly shared by teleosts and pycnodonts (Nursall 1996, 2010; Gardiner et al. 1996) are actually not synapomorphic. They may be:

- not homologous, such as the supraoccipital bone;
- convergent, such as the mobile maxilla or the unpaired vomer;
- more general conditions, such as the dermosphenotic in series with the infraorbitals or the absence of clavicle; or
- incorrectly interpreted in pycnodonts, such as the premaxilla with a small nasal process (see Poyato-Ariza & Wenz 2002: 168).

Admittedly, the supraoccipital is an especially problematic issue. Nursall (1996a) proposed that a supraoccipital crest is a synapomorphy of pycnodonts and teleosteans, but the corresponding bones in both groups are not considered homologous by Maisey (1999), Arratia (1999), and Kriwet (2001); this is how it was coded for pycnodonts in the present analysis (see discussion of character 28 above). Nonetheless, a further test seemed pertinent for confirmation within a phylogenetic context. With this purpose, a new analysis was run after changing the coding of character 28 in pycnodonts from 0 to 1 (supraoccipital bone present). The result of the analysis was the same, so this character did not alter the phylogenetic relationships of pycnodonts and teleosts, which did not appear as sister groups even when considering their supraoccipital bone as homologous; it was simply interpreted as a convergence between pycnodonts and teleosts, and an additional step was added (200 in total in this case).

A collateral implication of these results is that the taxonomic status of the pycnodonts as "Pycnodontomorpha" is unsupported, because they are not the sister group of the Teleosteomorpha.

Pycnodonts and halecomorphs

The double mandibular articulation in pycnodonts was considered homologous to that of halecostome fishes by Poyato-Ariza & Wenz (2002: 207), although the Pycnodontiformes were not included in the Halecomorphi in their classification. The results of the present analysis clearly indicate that the double articulation of the lower jaw with the quadrate and the symplectic is a convergence between Pycnodontiformes and Halecostomi, as confirmed by the distribution of character 49 with both Acctran and Deltran. Although the elements forming the double articulation in the upper jaw are still anatomically homologous (see also Nursall 1996a: 131), this convergence would nicely explain the remarkable morphologic peculiarities of the double mandibular articulation in pycnodonts as discussed by Nursall & Maisey (1991), Gardiner et al. (1996), and Kriwet (2001, 2005).

Neopterygii and Halecostomi

The most basal position of the Pycnodontiformes among the major neopterygian groups included in this analysis raises interesting questions on the definition of the Neopterygii. Traditional neopterygian characters include upper pharyngeal dentition consolidated, premaxilla with internal process lining the anterior part of nasal pit, symplectic developed as an outgrowth of hyomandibular cartilage, fin rays equal in number to their supports in the dorsal and anal fins, and clavicle lost or reduced (e.g, Lauder & Liem 1983; Nelson 2006). The node of the Neopterygii including Pycnodontiformes (Fig. 5) is better defined than the node formed by [Holostei + Teleostei]; respectively, six unambiguous synapomorphies, four of which are autapomorphies, versus four unambiguous characters, none of them autapomorphic. Therefore, it seems advisable to define Neopterygii including Pycnodontiformes. Incidentally, this implies that the reduction of the ray-pterygophore ratio to 1:1 on dorsal and anal fins would still be part of the definition and diagnosis of the Neopterygii, a name that etymologically means "new wings"; this is one of the most typical traditional characters mentioned above. Furthermore, the clade formed by [Holostei + Teleostei] can be considered as the Halecostomi (new usage), which has always been a more inclusive group than the Neopterygii (Fig. 5).

In any case, the results of the present analysis suggest that the definition and composition of the Neopterygii (and probably of the Halecostomi) will need to be revised by further analyses including additional basal groups, both neopterygians and non-neopterygian actinopterygians. Such analysis would provide additional insight into the evolution of certain characters, such as the number of pairs of extrascapular bones (number 13), the loss of interopercle (number 19), the absence of supramaxilla (number 47), and the possible correlation of the presence of a medially fused vomer (number 37) with molariform dentition, which are observed in several basal neopterygians (Tintori, pers. comm. 2015). The outgroup in the analysis by Grande (2010) is formed by living forms only (*Acipenser*, *Polypterus*) in order to have their ontogenetic information available. However, such evolutionary lines have had a very long history implying potential independent evolution of many characters, so the polarization should be revised with a fossil outgroup.

Conclusions

The Pycnodontiformes are the most basal group among the neoptergyian fishes included in the analysis: Lepisosteiformes, Semionotiformes, Macrosemiiformes, Halecomorphi, and Teleostei. This implies that they are not the sister-group of the telosteans (either Teleostei or Teleosteomorpha), as often considered previously. All the putative synapomorphies of pycnodonts and teleosts are convergences, misinterpretations, or not homologous (e.g., supraoccipital bone). Pycnodonts are not even Holostei, as might have been expected if not sister group of teleostean fishes.

The Halecostomi seemed deemed to be paraphyletic since the "resurrection" of the Holostei as a monophyletic group by Grande (2010), but the inclusion of the Pycnodontiformes as basal neopterygians implies that it is possible to re-define the Halecostomi as the clade formed by [Holostei + Teleosteomorpha]. According to the present analyisis (Fig. 5), the Halecostomi is a group distinct from, and more inclusive than, the Neopterygii, as has traditionally been the case, although, in this new usage, it includes all the Holostei (sensu Grande 2010) and the Teleosteomorpha.

According to the results of the present paper, the classification of the pycnodonts among major actinopterygian groups is as follows:

- **Actinopterygii** Cope, 1887 (sensu Rosen et al. 1981)
  - **Neopterygii** Regan, 1923 (sensu Rosen et al. 1981)
    - PYCNODONTIFORMES Berg, 1937 (sensu Nursall 1996a)
    - **Halecostomi** Regan, 1923 (new usage)
      - **Holostei** Müller, 1844 (sensu Grande 2010)
        - **Halecomorpha** Cope, 1872 (sensu Patterson 1973)
        - **Ginglymodi** Cope, 1872 (sensu Grande 2010)
      - **Teleosteomorpha** Arratia, 2000
        - **Teleostei** Müller, 1844 (sensu Arratia 2004)

The unexpected position of the Pycnodontiformes as basal neopterygians needs to be confirmed on the basis of additional analyses including more basal groups and a revised list of characters. This should be the focus of future research on pycnodont relationships among actinopterygians. In this context, Triassic pycnodonts acquire special relevance. All Triassic Pycnodontiformes known from published articulated specimens are from Italy: two genera from the Late Triassic (Norian: *Brembodus* and *Gibbodon*: Tintori 1981) and an especially interesting, unnamed form from the lower Norian (Nursall 2010). Additionally, such an analysis would help to re-define the composition of the Neopterygii and to precise the phylogenetic relationships of its most basal groups, currently far from accurately comprehended.

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