Pycnodont fishes: morphologic variation, ecomorphologic plasticity, and a new interpretation of their evolutionary history

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ABSTRACT—Some examples of morphologic variation of body and fins morphology in Pycnodontiformes are shown; not all are butterfly fish-like, as the common place assumes. Pycnodonts are characterized by a heterodontous dentition; teeth on the vomer and the prearticulars are molariform, yet of diverse shapes, whereas teeth on the premaxilla and the dentary do exhibit even more diverse morphologies. This morphologic variation is also analyzed, and the inaccuracy of another common place, the “crushing” or “durophagous” dentition of the pycnodonts, is explained: these terms refer to function, not to form.

The ecomorphologic evaluation of both sources of morphologic variation, body and dentition, indicate that pycnodonts may have been adapted to a large variety of potential diets and environments. The environment of pycnodont fishes is often believed to have been reefal, but this is not necessarily the case, since their adaptations are not exclusively functional in reefs or even in marine environments only. Examples of freshwater pycnodonts are mentioned, showing that these fishes are potentially misleading palaeoenvironmental indicators: their mere presence in any given locality is not an unambiguous indication of its palaeoenvironment.

The ecomorphologic plasticity of pycnodonts was a key factor for their success as a group. This, together with a re-evaluation of their fossil record, leads to a new interpretation of the evolutionary history of the Pycnodontiformes.

INTRODUCTION

Pycnodontiform fishes are familiar to many palaeontologists, no matter their speciality, and to many Palaeontology students and amateurs as well. Complete specimens are largely present in most Triassic to Eocene conservational fossil-Lagerstätten, mostly from Europe and America. In addition, isolated dentitions are known from an impressive number of localities worldwide, Africa and Asia included. Curiously enough, the only published Asian pycnodont specimen is an isolated vomer named Tibetodus (Young and Liu, 1954). Only Australia and Antarctica lack pycnodont record, at least for the time being. Comprehensive reviews of this order can be found in Nursall (1996b, 1999) and Poyato-Ariza and Wenz (2002).

These fishes have a very distinct anatomic bauplan, with many autapomorphies, such as: presence of dermic supraoccipital and of differentiated contour and cloacal scales; absence of subopercular and interopercular, with preopercular much more developed than opercular; etc. For further details on diagnostic anatomic characters of pycnodonts, see Nursall (1996b, 1999) and Poyato-Ariza and Wenz (2002). These autapomorphies define pycnodonts as a strong clade, and, at the same time, they determine a well established, distinguishable basic anatomic pattern. But within this distinctive, recognizable bauplan, the morphologic variation found is, as we will see in the present paper, unexpectedly high.

This group of fishes presents an impressive temporal and spatial fossil record that is re-evaluated in the present paper. Their record ends in the Cenozoic; the Pycnodontiformes left no known descendants, direct or indirect. All other Actinopterygian fish groups, and specifically all teleostean Recent groups of analogous shape (e.g., Chaetodontidae), are phylogenetically related...
very distantly, only because of their sharing a remote common ancestor, constituting a nice example of general morphological convergence.

The purpose of the present paper is to present a new overview of the diverse morphological variation found in these fishes, and its ecomorphologic implications, relating this variation with the environments that pycnodonts could have occupied. At the same time, some widespread common places about pycnodonts will be proven inaccurate: for instance, that all pycnodonts are high bodied and round, like the Recent butterfly fishes. And, prolonging this analogy, that they are certainly marine, linked to coral or other reefs, and are therefore reliable palaeoenvironmental indicators. Another inaccuracy about pycnodonts is that their dentition is crushing or durophagous. All these common places about these fishes reflect their reality, but are imprecise, present numerous exceptions and need to be revised and redefined.

**MORPHOLOGIC VARIATION OF BODILY SHAPE**

1.- The common place: *all pycnodonts are butterfly fish-like.*

The most common inaccuracy about pycnodonts is that they are all morphologically similar to the Recent Chaetodontidae, that is, that they all have high and round body and very long dorsal and anal fins. However, this is an overgeneralization with many exceptions. It is right that many of the most spread and best-known pycnodonts present this morphology. Therefore, the descriptions of pycnodonts in general textbooks are based on taxa that present a chaetodontid-like morphology. Obviously, general textbooks need to simplify their descriptions, so they cannot enter into details of morphologic variations. In some cases, the general description is nonetheless done with the necessary caution: "The pycnodontiforms (...) are mostly deep-bodied forms with long dorsal and anal fins" (Benton, 2000: 174). But, in other cases, the wording does not seem to leave room for exceptions: "in these peculiar fishes the body was extremely deep and narrow, near circular in outline when seen in side view, with long dorsal and anal fins" (Romer, 1966: 59); "they are characterized by a deep, narrow body; the dorsal and anal fins are long" (Carroll, 1988: 109). This is usually illustrated with examples of taxa that, effectively, remind butterfly fishes quite nicely; usually *Proscinetics*, (formerly *Microdon*; see Poyato-Ariza and Wenz, 2002), as in Romer (1966: fig.87) and Carroll (1988: fig.6-28, is the same one); in Benton (2000), fig.7.8.d is the same one again, a restoration of *Proscinetics* dating back to Woodward (1916). This way, the representative examples used for explaining the overall morphology of pycnodonts can be mistaken as a kind of general rule for all of them. The point is that these typical examples are excellent for describing the general morphology of many pycnodonts, but this general morphology, nonetheless, does not necessarily apply to all the pycnodont taxa; far from that. The idea that *all pycnodonts are butterfly fish-like* is inaccurate because a number of pycnodonts do not present this particular body morphology, as shown below.

Brief, the body shape of many pycnodontiforms is effectively high and round, and the dorsal and anal fins are long, such as the very typical *Oropycnodus* (Fig. 1A), but there are, however, many other morphologies among these fishes. This will not be an exhaustive catalogue of body and fin morphologies in pycnodontiforms, just a few examples of the morphological variation that does occur within this group, that is, some examples of exceptions, in several aspects, to this common place about body shape in pycnodonts.

2.- Examples of bodily morphologic variation.-

Although not a single known pycnodont has a completely fusiform body, not all of them have a especially high one. There are a number of taxa with a maximum body height to standard length ratio between 50 and 70%, which are not remarkably high bodies. This is the case, for example, of the type genus of the type family, *Pycnodus* (Fig. 1B), and the similar *Tergestinia*; the oval *Coelodus saturnus* and *lemanja palma*; the nice, rare *Palaeobalistum* (Figs. 1C, D); the balistid-shaped *Mesturus*, the bizarre *Coccodus* and *Trewavasias* (Fig. 1E); even the very typical *Steinmatodus* is not specially high-bodied (Fig. 1F). In addition, more exceptions will come from undescribed new taxa from the Lebanon and Italy (pers. obs.). Therefore, many pycnodonts are effectively high-bodied, but a number of them are not.

As a side note of some historic interest, the first pycnodont ever figured, two centuries ago, was not one of those typically high-bodied, butterfly fish-like taxa, but one of the just-mentioned exceptions. The first illustrated pycnodont was, at the time, called like the Recent *Diodon orbicularis* (VOLTA, 1809: pl. 40). It is known today as *Palaeobalistum orbiculatum*. The long, complicated nomenclatural history of this extraordinary taxon is examined by Poyato-Ariza and Wenz (2002). This pycnodont is shown by Fig. 1C, and a recent photograph of the original illustration of the same specimen, by Fig. 1D behind. This is, still today, the only known specimen of this intriguing genus and species.

Many pycnodonts are effectively high-bodied, that is, they present a maximum body height to standard length...
ratio around 90%, with variations from 70 to about 120%. But, again, although in many cases the body outline in lateral view is effectively more or less round (Fig. 1A), there is a number of high-bodied pycnodonts whose body outline is not round. For instance, the unusual, nearly triangular *Ichthyoceros* (Fig. 2G); the primitive *Arduafrons* (Fig. 2H), *Gibbodon*, and all other genera with a conspicuous dorsal apex, such as *Eomesodon* and *Macromesodon* (Fig. 2I); *Stenamara minia*, which is oval and notably higher than it is long; plus undescribed new taxa with polygonal body outlines from the Lebanon (pers. obs.). Therefore, although many pycnodonts effectively present a roughly circular body outline in lateral view, not all high-bodied pycnodonts have this precise morphology.

Another inaccuracy involves the shape of the dorsal and anal fins; again, the general case is not necessarily always the case. That is, many pycnodonts effectively exhibit very long dorsal and anal fins, but a number of them do not. As indicated by the number of axonosts (easier to count than the number of fin rays, but closely related to them), the variation in the length of the dorsal and anal fins is enormous among pycnodonts: the longest dorsal fins have up to about 60 axonosts, and the longest anal ones, up to about 50; but the shortest ones can present as few as six axonosts only. Especially short fins are present, for instance, in *Coccodus*, *Gibbodon*, and *Ichthyoceros*, but the observed length of the fins covers most of the range between these shortest ones and the longest ones (present in *Abdobalistum*, *Coelodus*, *Nursallia*, and *Oropycnodus*). For more details, see characters 66 and 70 in Poyato-Ariza and Wenz (2002; column numbers 65 and 66 are erroneously inverted in the data matrix, appendix 3, of that paper). In addition to this noticeable variation in length, the variation in shape of even the
longest fins is also remarkable, actually quite complicated to be accounted for (Poyato-Ariza and Wenz, 2002: character 68): strip-like, falcate, acuminate, sigmoid, round in the centre, round in the middle, and square (Fig. 2A).

It is worth mentioning here yet another source of morphologic variation: the caudal fin. Like the dorsal and anal fins, the caudal in pycnodonts presents a highly variable number of fin rays, ranging from seven in Ichthyocecoros to nearly 40 in Abdoabalistum. And the caudal fin morphology is very variable and complicated to be accounted for as well (Poyato-Ariza and Wenz, 2002: character 73): stalked or deeply forked; distal border convex, that is, fan-shaped; distal border concave, that is, semi-lunate; distal border straight; double emarginated; and vertical, which is much higher than it is long (Fig. 2B). Therefore, the dorsal, anal, and caudal fins of pycnodonts are extremely variable both in length and in morphology.

3.- Ecomorphologic implications.-

The spectrum of the body and fins morphologic variations briefly outlined above results rather unexpected in this group of fishes, and very interesting from an ecomorphologic point of view, due to its implications on the potential modes of locomotion that can be inferred. Body and fins shape determine a simple, yet quite interesting morphospace in fishes. This functional morphospace is nicely represented by Webb (1984) for teleosts as a triangle (Fig. 2C) that summarizes the possible morphologies observed in the body and fins, relating them with the correspondingly observed modes of swimming. Form and function are, of course, related: in the case of the fishes, the morphology of the body and fins is related with the corresponding mode of locomotion. In this triangular morphospace, specialists occupy the apices, whereas the centre is occupied by generalists. The latter can alternatively use different modes of swimming, although they are not specialists on any of them; they present body and fin morphologies that are intermediate among those of the specialists in the corners. These three specialists are: for accelerating, upper corner; for cruising, bottom left corner (both extremely fusiform); and, the most interesting ones for us, for manoeuvring, bottom right corner. The typical high-bodied, round pycnodonts with very long dorsal and anal fins are just the paradigm of morphologic adaptations for manoeuvring. This morphology is analogous to that of the Chaetodontidae, precisely the example used by Webb (1984). But, as we just saw above, there are other body and fin shapes in pycnodonts; actually, the Pycnodontiformes as a whole would roughly occupy, in this triangular space, a morphospace that spreads from the specialists for manoeuvring in one corner to a good part of the generalists in the centre (Fig. 2C).

Brief, the variation in body and fins form in pycnodonts indicates that part of them are specialists for a swimming mode based on manoeuvring, but another part are generalists, and their bodily morphologies “represent a compromise between more than one mode of propulsion” (Wootton, 1990: 20). Therefore, they could combine or switch to one or another mode of propulsion according to their needs, without being, of course, as effective as specialists.

It is interesting to consider briefly what this implies in terms of the possible original environment of pycnodonts. On the first place, generalists that are capable of several modes of propulsion may have lived in a large variety of potential environments, as Recent generalist fishes dwell in: bottom, shore and open waters in rivers, ponds, and lakes; marine coasts, deltas, wetlands... the only clear exceptions are pelagic waters and strong currents. But, if these are the potential possible environments for generalists, even the specialists in manoeuvring do occupy a variety of environments: reefs, of course, but also rocky shores and bottoms, beds of vegetation, even open sand. This is the case of, for instance, the Recent Acanthuridae (Küttler & Debelius, 2001) or the Ephippidae (notably Zabidus, Chaetodipterus, Ephippus or Drepane, which dwell in open sand). This shows that this particular shape is not necessarily associated with reefs (Bellwood, pers. comm., 2004). In sum, a generalised morphology, and even a round body, are effective in many environments in marine, brackish, and fresh waters.

Therefore, the environments that may have been potentially inhabited by pycnodonts are very variable, not only reefal or even exclusively marine. As inferred from the brief ecomorphological analysis of body shape and locomotion just presented, pycnodonts may have dwelt in practically all aquatic environments except openly pelagic waters and strong currents.

MORPHOLOGIC VARIATION OF DENTITION AND JAWS

1.- Heterodonty in pycnodonts.-

The Pycnodontiformes present heterodontous dentition (Fig. 3): there are teeth of different shape in the same individual. In general, the teeth on the premaxilla and the dentary are similar among them (e.g., Figs. 3A, B), but different from the teeth on the vomer (e.g., Figs. 3C, D) and on the prearticular (e.g., Figs. 3A, B), a bone that forms a well developed coronoid process (e.g., Fig. 3C). The teeth on the premaxilla and the dentary may present
remarkably diverse morphologies in the different taxa. In contrast, the vomerine and prearticular teeth in all known pycnodonts have a low, large, hard, robust crown. These teeth are molariform, because they remind the shape of the molars of mammals, without implying, of course, any relationship of homology. In most cases, the molariform teeth are arranged forming distinct rows on the vomer (normally 3 or 5 rows) and the prearticular (normally 2-6 rows).

2.- The common place: the dentition of pycnodonts is durophagous.-

The dentition of pycnodonts is often described as crushing or durophagous, and this is another inaccuracy about these fishes. There is good ecomorphologic empiric evidence that crushing performance has a direct relationship with the biting force, which depends on the size of the biting muscles (e.g., WAINWRIGHT and BELLWOOD, 2002). In pycnodonts, the large insertion surfaces observed in the lower jaw provide an accurate idea of the big size of the corresponding muscles, notably the adductor mandibulae, which closes the lower jaw and is attached to the mandible at the base of the coronoid process; both the coronoid process and this area of insertion are particularly big in these fishes. The crushing performance was carried out by the molariform vomerine and prearticular teeth, a shape better suited for crushing purposes. In addition, these molariform teeth usually present large worn surfaces in adult specimens (Fig. 3), which is a clear indication of the intense grinding action that they have must carried out during the lifetime of the animal. But the premaxillary and dentary teeth are not molariform (with the exception of Akromystax), and their morphology is therefore not suited for this crushing function; therefore, not all the teeth in pycnodonts are adapted for crushing.

At this point, let us note that crushing is a feeding action, a mechanism, not a morphology; it is function, not form. The statement teeth are crushing mistakes form and function, as a good colleague remarked (BELLWOOD, pers. comm., 2002). Crushing is the function of the teeth, whose form is molariform. For a similar reason, the statement teeth are durophagous is also inaccurate. In this case, the term refers to a certain diet or to an organism with a certain diet, not to a morphology of any part of that animal. And, furthermore, some Recent forms that do present molariform teeth do not have a durophagous diet, such as the genus Mola or plankton feeding balistids (BELLWOOD, pers. comm., 2004). Therefore, when referring to the shape of the teeth on the vomer and prearticular of the pycnodonts, we must use the term molariform. We must not use the terms crushing, which refers to the function, that is, a mechanic chewing action, or durophagous, which refers to a diet consisting on hard items, or to an animal that has such a diet. All these terms are obviously related among them to a great extent, but each one is to be used for what it precisely refers to. Clarity and precision are essential in science, specially when involving conceptual issues, as is the case here.

Fig. 3. Dentition and its variation in pycnodontiform fishes. Red arrows point premaxillary teeth; green arrows, dentary teeth; yellow arrows, vomerine teeth; blue arrows, prearticular teeth; pink arrows, the coronoid process. A, typical heterodontous dentition as seen in Gyrodus, specimen in private collection, anterolateral view; anterior part to the left, posterior part to the right. B, incisiform teeth on premaxilla and dentary, and oval, crenulated molariform teeth with a large central groove on the prearticular, as shown by Oceloedus subdisces, specimen MGSB 20659, modified from Poyato-Ariza and Wenz (2002: fig. 22C); scale bar represents 5mm. C, incisiform teeth on premaxilla and dentary, rounded to oval teeth on the vomer and high, club-shaped coronoid process on the lower jaw as shown by Proscinetes sp., specimen FSL 400047; scale bar represents 5mm. D, detail of C in ventrolateral view to observe the morphology of the incisiform teeth, and the alternation of the vomerine teeth on the median tooth row. E, cutting-edged teeth on the premaxilla and dentary as shown by Mesturus verrucosus, specimen in private collection. F: dentition of Macromesodon macroperus specimen in private collection; notice cylindrical teeth on premaxilla and dentary, and vomerine molariform teeth rounded in contour. G: robust, cylindrical teeth on premaxilla and dentary and rounded, worn out molariform teeth on the vomer and prearticular as shown by Mesturus verrucosus, specimen in private collection. H: high, styliform teeth on the premaxilla and dentary, with bifurcated crowns on the premaxilla, as shown by Gibbidon censens, holotype, specimen MCSNB 3317; scale in cms. I: molariform teeth on the premaxilla and pseudo-molariform teeth on the dentary as shown by Akromystax tilmachiton, holotype, specimen MNHN HAK 318; notice also the short, but enlarged mouth gap, and the extremely high coronoid process (actually getting out of the picture, on the top right corner); scale in mms. J, rounded molariform teeth as seen on the elongated jaws of Lemanja palma; holotype, specimen MNHN BCE 166a. K, vomerine tooth plate of cf. Paramicrodon; specimen JISL 91 (private collection; cast available at MCNA), occlusal view, anterior end towards the top; total length of bone as preserved: 35mm; photo courtesy J. C. Corral. L, left prearticular bone of Neoprosocinetes penvalai, specimen MNHN BCE-104, occlusal view, anterior end towards the right; total length of bone as preserved: 33mm. M: elongated prearticular teeth of Coelodus saturnus, holotype, NMW.XXXIII; photo Schumacher, courtesy O. Schulte; scale bar represents 10mm. N: vomerine teeth with triangular contour as shown by Cocodus arnatus, specimen in private collection, modified from Poyato-Ariza and Wenz (2002: fig. 22D). A, F, G: photos courtesy K. Frickinger, Emmering, Germany. B, C, D, I, J, L, N: photos Serretti, Paris. Some original photos did not have scale. Abbreviations of institutions: FSL, Faculté des Sciences de Lyon; MCNA, Museo di Ciencias Naturales de Álava; MCSNB, Museo Civico di Storia Naturale di Bergamo; MGSB, Museu Geològic del Seminari Conciliar de Barcelona; MNHN, Muséum national d'Histoire naturelle de Paris; MPCM, Museo Paleontologico Citadino di Monfalcone, Italy; NMW, Naturhistorisches Museum in Wien.!
3.-Examples of morphologic variation in dentition and jaws.-

In addition to their normal heterodontous condition, pycnodontiforms do exhibit a high variation on the morphology of their teeth when different taxa are compared among them. This variation affects the teeth on the premaxilla and dentary, the teeth on the vomer and prearticular, and, interestingly, the overall morphology of the jaws as well.

3a.- Variation on premaxillary and dentary teeth.-

The extent of the morphologic variation of the premaxillary and dentary teeth is such that it is very hard to account for in distinct character states, as there are many intermediate states (Poyato-Ariza and Wenz, 2002: character 32). In many pycnodonts, these teeth are incisiform, that is, they have a shape that reminds that of the mammalian incisives, without implying any relationship of homology. The crown of the incisiform teeth is flattened, enlarged, with a labial side that is flat to slightly convex, and a lingual side that is clearly concave (Figs. 3B-D). Their occlusal edge varies from robust to sharp. These incisiform teeth can be of similar size or of very different relative sizes within the same single bone. An extreme variation of this incisiform morphology results on teeth whose crown is very thin, larger than high, with a sharp edge (Fig. 3E), quite fit for cutting. Non-incisiform morphologies include: smaller but robust teeth, roughly cylindrical, with a flattened lingual side (Fig. 3F); big, very robust, cylindrical, with round occlusal ends (Fig. 3G); big, very robust, curved, peg-like (Fig. 3A); high, styliform, and even complex crowns, bifurcated once or twice (Fig. 3H); even molariform teeth on the premaxilla are known as well (Poyato-Ariza and Wenz, in press; present paper, Fig. 3I).

3b.- Variation on vomerine and prearticular teeth.-

The morphologic variation of the molariform teeth on the vomer and prearticular is more limited, yet also interesting. They are often smooth (Figs. 3C, D), although this may be due to the grinding action (Figs. 3A, G); but, when unworn, they can also be lightly to heavily crenulated (Fig. 3B), or present a central papilla (Gyrodus), ridge (Mesturus leedsi) or groove (Fig. 3B). As for their outline in occlusal view, in some taxa all molariform teeth are round (Figs. 3C, D, F, J), whereas in other taxa, the largest teeth are oval (Figs. 3A, B, E, K, L). But this contour may as well be very elongated in transversal (Fig. 3M) or longitudinal (Fig. 3I) sense, or be even roughly triangular (Fig. 3N). Another source of variation: the molariform teeth are normally arranged in rows (Figs. 3A, B, E-G, K, M, N), but in some cases the rows are altered (Fig. 3L, also Anomoeodus), there is alternation of teeth on the main vomerine row (Figs. 3C, D) or the tooth plates are patchy, the teeth do not form rows (Fig. 3I).

3c.- Variation on jaw morphology.-

Pycnodonts normally have a relatively small mouth gape. But there are notable variations in jaw shape. In the first place, in the length of the jaws, that can be short (Figs. 3H, I, L), moderately elongated (Figs. 3C-H) or very elongated (Fig. 3J). This variation in jaw length is usually related with the number of vomerine and prearticular teeth and with the prognathism of the whole bucco-ethmoidal region. Another source of variation of the lower jaw morphology is the shape and development of the coronoid process. It is normally robust in all pycnodonts, but it can also be blunt (Figs. 3F, L) or club-shaped (Fig. 3C). As for its relative height, it is quite variable (Figs. 3C, F, L), from very low (Coccodus: Poyato-Ariza and Wenz, 2002: fig. 23C) to extraordinarily high, making the lower jaw higher than it is long (Fig. 3I; Poyato-Ariza and Wenz, in press). This implies a considerable variation of both the biting forces applied and the exact point where these forces are applied (see, for instance, Kriwet, 2001, and Wainwright and Bellwood, 2002, for biomechanics of the mandible).

4.- Feeding strategies in pycnodonts.-

Their anatomic structure did not allow effective jaw protrusion, which is an evolutionary achievement of advanced teleosts (e.g., Moyle and Cech, 1988; Woottton, 1990; Helfman et al., 1997). In addition, the body morphology adapted for manoeuvring involves that they could not gain enough speed to use body propulsion to overtake their prey. Consequently, ram and suction feeding, which are based on body propulsion and jaw protrusion, could not be their primary feeding strategy. Pycnodonts must have captured their food items chiefly by manipulation, the method “in which the jaws are directly applied to the prey and used to remove it from the substratum” (Wainwright and Bellwood, 2002: 37); the premaxillary and dentary teeth had a prehensile function (Nursall, 1996b, 1999).

Kriwet (2001) claimed that pycnodonts were able of protruding jaws, and therefore of suction feeding. In pycnodonts, the maxilla probably rotated anterovertrally (Nursall, 1999), but the movements of the oral bones were considerably more limited than in teleosts, where the morphofunctional relationships of premaxilla and maxilla are quite different. The pycnodont premaxilla is radically unlike that of teleosts; it lacks the anatomic connection with the maxilla used during the protrusion process (descending process; e.g., Helfman et al., 1997), and there is no articulation between premaxilla and maxilla (Kriwet, 2001; pers. obs.), as needed for true protrusion.
The anatomic connections of the premaxilla with the vomer and the mesethmoid indicate that the premaxilla could move only very slightly forward (Kriwet, 2001; pers. obs.), if any at all. In addition, this movement would result in a reduction of the mouth gape, useful for manipulation but inadequate for suction. In any case, protrusion in pycnodonts, even if it did occur, is not comparable to protrusion in teleosts (Kriwet, 2001). Pycnodonts were probably able of limited suction by some expansion of the bucco-pharyngeal cavity (op. cit., Nursall, 1999), but not by effective jaw protrusion; such limited suction without protrusion does occur in other non-teleostean lineages as well (e.g., Helfman et al., 1997). But the primary feeding strategy of pycnodonts must have been manipulation, as strongly indicated by their solid and steady oral bones (Nursall, 1996a) and their dental ecomorphology (e.g., prehensile function of anterior teeth). Pycnodonts are anatomically unable to have used ram or suction as primary feeding strategies; they must have relied mostly on manipulation, with very limited and occasional assisting ram and/or suction. Manipulation is the rarest primary feeding strategy among Recent teleosts, precisely because they are capable of factual jaw protrusion (pipette mouth; e.g., Helfman et al., 1997), used in suction and ram; and they are capable of effective acceleration to overtake preys as well. But pycnodonts, generalised to specialist for manoeuvring, incapable of efficient protrusion, with their limited suction capacity and robust mouth structure, were best fitted for manipulation than for any other feeding strategy.

Manipulation allows for a broad range of vegetal and animal food sources, involving a surprisingly varied array of particular techniques and potential evolution. This is better understood by comparison with Recent fishes that present this feeding strategy. Some herbivores, as the surgeonfish (Acanthuridae) show “single rows of complex crowned teeth” (Wainwright and Bellwood, 2002: 40); this is the case of Gibbodon, described above. Some butterfly fishes possess elongated jaws; they are “biting predators, often using their long jaws to reach invertebrates that are taking refuge inside the complex habitat” (Wainwright and Bellwood, 2002: 45); this could be the case of the long-snouted pycnodonts mentioned above. Detailed Recent analogous may be endless, but, for our purpose, it is more interesting to consider the diversity of precise feeding strategies and the corresponding diets and morphologic variations at group level. For instance, Chaetodontidae and Pomacanthidae exhibit a surprisingly diversified array of feeding strategies as predators at group level, ranging from benthic preys to zooplankton in open waters. Among the benthic preys, there are sponges, algae, zoanthids, coral, polychaetes, and other invertebrates. The corresponding jaw shape and dentition in the preying fishes is considerably diverse (Wainwright and Bellwood, 2002).

From the morphologic diversity found in pycnodonts, their possible precise feeding strategies could have been, at least potentially, quite diversified within their general manipulation strategy (with occasional and very limited ram-suction). This is a combination of the highly specialised durophagy analysed by Nursall (1996a, 1999) and the omnivorous diet based on suction strategy proposed by Kriwet (2001). More ample than the former, and more restrained than the latter, assimilates both into a new integrating interpretation.

5.- Ecomorphologic implications.

It is not possible to analyse in detail, within the global scope of the present paper, the enormous ecomorphologic implications of the variations in the dentition and jaws shape and in the feeding strategies for each particular pycnodont taxon. Yet some interesting, general inferences at group level are worth discussing.

The action of the molariform teeth on the vomer and prearticular is most likely a crushing and grinding one in all cases; still, their morphologic variations probably involve variations on the precise biomechanics: diverse types of particular grinding actions may have been used according to the precise food source and the specific tooth morphology.

Ecomorphologically, the premaxillary and dentary teeth are even more variable; some morphologies seem more generalist than others. The typically incisiform teeth were probably the most generalist type, in the sense that they may have been applied to a variety of functions with diverse efficiency: biting, scraping, grazing, picking, rasping, gripping, grasping, and clipping, depending on the food source availability. We could consider this as a generalist durophagous diet, that would be based on a potentially varied and adaptable manipulation feeding strategy (e.g. Ocloedus, Proscinetes, Turbomesodon). Other morphologies, on the other hand, seem more suitable for more specialized actions, such as: intensive breaking of large, very hard food items (e.g., Mesturus); grasping or scraping large hard food items (e.g., Gyrodus); crushing small but very hard food items (e.g., Akromys-tax; Poyato-Ariza and Wenz, in press); searching for food items into cracks with their elongated mouth (e.g., lemanja); grazing or scraping delicate surfaces, even cutting soft items (e.g., Gibbodon, Testesinio, new Italian genus with cutting edged premaxillary and dentary teeth; Poyato-Ariza, work in progress). These more specialised manipulation feeding strategies would probably involve specialised durophagous diets, different in
each case, yet diversified as an ensemble. Consequently, a large variety of hard food sources, and even plants (by cutting-crushing), can be envisaged to have formed the diet of the pycnodonts as a group.

In turn, the length/height ratio of the lower jaw has a relevant role in the strength of the biting action, and on the precise place where this action is exerted (e.g., Wainwright et al., 2000). The variations of this ratio in pycnodonts involves different possibilities for specific mandibular action. This is yet another source of potential variation for different particular types of general or specialised feeding strategies, and therefore for the degree of specialization and the diet diversification.

Concerning the precise food sources, a generalist durophagous diet can be potentially very varied, and the different specialist durophagous diets probably consisted on comparatively diverse food sources. The potential diet of the different pycnodonts may have included (exclusively or combined): corals, rudists and other reeal organisms, echinoids, crinoids, and brachiopods as strictly marine organisms; and bivalves, gastropods, decapods, and even plants as marine, brackish, and freshwater organisms. The direct evidence of diet in pycnodonts is very rare, and, yet, it accounts for a remarkable variation: corals, echinoids, bivalves, gastropods, decapods, even little actinopterygians (Nursall, 1996a; Kriwet, 2001; Poyato-Ariza and Wenz, 2002: fig. 5B). The hypothesis that the observable stomach contents are monospecific, and therefore, that pycnodont species were very selective (Kriwet, 2001) is not supported by the known data. The direct fossil evidence on which it is based is very scarce, and therefore not significant enough. These remains are not identified at specific, generic, familial, or ordinal level, and they are consequently not proven to be monospecific.

And, on top of that, the diet of fishes does vary ontogenetically, seasonally, yearly, and according to individual taste, food availability, behaviour, etc. (cf. Poyato-Ariza, this volume). In any case, and although more direct evidence is necessary to have a clear idea of the actual diet of each particular taxon, the evidence that we do have at this point confirms the ecomorphologic inferences about the potentially highly varied diet of the pycnodonts as a group. This is not far from Kriwet’s (2001) claim that pycnodonts as a group were omnivorous, but needs to be precised: it seems better to consider them as generalised to specialised durophagous. They could hardly eat plankton, filter detritus, or actively hunt large fishes, for instance. They cannot be considered omnivorous in strict sense, since no single pycnodont species is proven to have had such diet. But, even so, their potential array of preys was most likely very large.

**FORM, FUNCTION, AND ENVIRONMENT IN PYCNODONTS**

The preceding sections evidence that the morphology in pycnodonts is more varied than usually thought. Variation in form is obviously linked to variation in function: the relationships between form and function are very complex, and not the main issue herein. As inferred from their morphological variations, the particular associated functions were probably more varied than previously thought. These functional variations are framed within generalised to manoeuvring specialised locomotion, and manipulation primary feeding strategy, but they can potentially be very diverse within those limits. In addition to the group as a whole, the line of research for future biomechanic analyses should be also focused on the distinct specific taxa and on the differences among them, integrated in the frame of their phylogenetic relationships.

Most interesting for this paper is the fact that, a particular function is not necessarily associated to a particular environment. This is so because each specific function is actually performed in any given environment only through the filter of multiple interacting factors: chemical and physical conditions, food and space availability, animal behaviour, predator pressure, anti-predator strategies of the preys, and so on. Therefore, there is not an univocal relationship between function and environment. Only a study of the whole ecosystem and, in the case of fossils, of the geological (notably the sedimentological) setting, can provide an accurate hypothesis of relationship between the inferred function and the particular environment where it was performed. Ecomorphologic studies provide useful patterns to associate morphology and use of the habitat (e.g., Wainwright and Bellwood, 2002), even in fossils, with the necessary cautions (cf. Poyato-Ariza, this volume). But it is essential to implement a thorough study of the whole associated community and of the original depositional environment.

In pycnodonts, their variations in form imply that the particular functions that they may have performed were probably quite variable: more generalised in some of them, more specialised, in different directions, in some others. The important point is that those functions were not necessarily linked to any particular environment. Pycnodonts were obviously not adapted to strong currents or to open pelagic waters, but, other than that, they could have potentially dwelt in any kind of environment. The misassumption that pycnodonts were strictly durophagous organisms that lived only on reefs is not supported by evidence: their ecomorphologic adaptations in locomotion modes and feeding strategies made pycnodonts poten-
Ecomorphology and Evolutionary History of Pycnodonts

1.- Ecomorphologic plasticity, success, and extinction.

The evidence presented above shows that Pycnodontiformes, as a group, are not as specialised as they may seem, in particular ecologically. The more generalist forms, which could exploit diverse modes of locomotion and diets, were potentially adaptable to a variety of niches. And the different specialist forms had diverse particular adaptations, so that they could have occupied a range of niches. This explains the evolutionary success of this group, and, as a result, its impressive fossil record, notably large both in time and in space. Their ecomorphologic plasticity was obviously a key factor for their evolutionary success as a group.

However, an stimulating apparent paradox arises at this point. If they were not so highly specialised as a whole, and were potentially adaptable and successful... what can account for their extinction? It is clear that pycnodonts "were excluded competitively under changing conditions by more rapidly diversifying teleosts" (Nursall, 1996a: 121), but a precise hypothesis for the cause and mechanisms of this faunal replacement seems necessary. It has been suggested that "prey specification may have made pycnodonts extremely vulnerable to changes in the environment and to competition by teleosts" (Kriwet, 2001: 162). But, as seen above, pycnodonts were more adaptable than previously thought, and not such a prey-specific group. Therefore, a new, more precise hypothesis to account for their extinction is necessary. Before that, in order to have a clear picture of their diversity throughout time and space, we will outline their fossil record, that is, their evolutionary history.

2.- The pycnodont fossil record as witness of their evolutionary history.

The present list is not exhaustive, and is focused on the record of complete specimens; only the isolated denticles that are significantly relevant in their general temporal or geographic distribution are mentioned. The data are based on and updated from citations and references in: Nursall (1996a), Poyato-Ariza and Wenz (2002, 2004, in press), Poyato-Ariza and Nursall (work in progress); also on personal observations and on personal communications (all 2004) by: Applegate and Blanco-Piñón on Mexican material; Machado on Brazilian material; Nursall on the putative Oligocene record; Tintori (also Delsate and Kriwet, in press), on Triassic material. The localities, with their corresponding taxa, are listed below in chronological order, from older to younger.

The oldest fossil record of a pycnodont dates from the Late Triassic (Norian) of Europe. From Zorzino, in northern Italy, come the genera Brembodus and Gibbodon. "Eomesodon" hoeferi is from the Norian as well. In this case, the original type material is from Hallein, Austria, but it is also known from Zorzino, in the same...
The Early to Middle Jurassic record is extremely scarce and the remains, very incomplete: a couple of dentitions from the Bathonian of Oxfordshire in the United Kingdom (cf. Proscinetes) and very partial remains (Mesturus leedsi), from the Callovian of Peterborough in the United Kingdom, which is a little younger, latest middle Jurassic. But this must be, to a good extent, a taphonomic bias, since the Late Jurassic has provided a fairly diversified pycnodont fauna with a large distribution: unspecified Late Jurassic from Torre d’Orlando in Italy (Ocloedus costae); Lower Lias of Barrow-on-Soar in the United Kingdom (Eomesodon liassicus); Kimmeridgian of Cerin in France (Macromesodon surgens as well as Proscinetes with many species, some of them possibly other genera; this is the oldest well-dated record of the Pycnodontidae); the Tithonian of Canjuers in France (Mesturus sp.); the well diversified Tithonian fauna from the Solnhofen area in Germany (which contains Arduafrons, Gyrodus, Mesturus, Macromesodon gibbosus as well as the Pycnodontidae Proscinetes elegans and Turbomesodon relegans, plus probably some new taxa); and the Portlandian from Dorset in the United Kingdom (the incomplete P. barnesi and E. depressus?). Surprisingly, pycnodonts are also known from a single partial specimen from the Oxfordian of Quebrada del Profeta, in Chile (Mesturus cordillera in Kriwit, 2000; Gyrodus sp. in Poyato-ArizA and Wenz, 2002). By the end of the Jurassic pycnodonts were diversified all over Europe and already present in South America.

The Late Jurassic and the Cretaceous contain the highest taxonomic and morphologic diversity and the largest geographic distribution of the Pycnodontiformes. By the Cretaceous, they were already in Asia, although, as we saw in the introduction, the only remains from this continent is an isolated vomer, Tibietodus, unfortunately with an undetermined Jurassic-Cretaceous age. They were also all over the Americas at least already during the latest Early Cretaceous. In North America, Hadrodus may not be a pycnodont, but Nonaphalagodus, Paramicrodon, and other isolated dentitions reveal a diversified pycnodont fauna from the Albain of the Trinity Division in Texas. In South America, they are known from the Aptic-Albain of the Santana Formation in Brazil (Lemanja, Neoprosclinetes); from the Aptic-Albain of Rosário do Catete in Brazil (Camposichthys); and from the middle to upper Albain of Tepeix de Rodriguez, in Mexico (Tepexichthys plus a large array of new taxa). Together with South-America, the largest known record of pycnodonts from the Early Cretaceous is from Europe: undetermined Early Cretaceous of Torre d’Orlando, Italy (Stemmatoles); Valanginian-Berriasian from El Montsec, Spain (Ocloedus subdiscus); Berriasian-Barremian from Bernissart, Belgium (Turbomesodon bernissartensis); Barremian from Uña, Spain (Anomoedus narsilli); late Barremian from Las Hoyas, Spain (Stenamara, Turbomesodon praecolus); lower Aptian of Helgoland, Germany (Paramesturus, provided it is a pycnodont).

So, the Early Cretaceous presents a diversity that is globally similar to that of the Late Jurassic, but a considerably larger geographic distribution. The Late Cretaceous contains a still greatly diversified pycnodont record, although their diversity begins to decrease after the Turonian. They also present still a vast geographic extension. The Late Cretaceous record includes: the Cenomanian from Sussex in the United Kingdom (Anomoedus willetti); the late Cenomanian of Jebel Tsefalt in Morocco (Nursallia gutturosus); the Cenomanian of the Lebanon (Hadjoula, Haqel, en Namoura), that contains an amazingly diversified pycnodont fauna (Akromystax, Cocododus, Ichthyoceras, Nursallia goedeli, Proscinetes, Trewavasia, plus many new taxa); the lower Turonian of Vallecillo in Mexico (Nursallia sp.); Turonian from Sergipe and Rio Grande do Norte in Brazil (Nursallia flavellatum? and Ocloedus rosadai, respectively), the only known occurrences in the Late Cretaceous of South America; the Turonian of Laveira in Portugal ("Pycnodus lavairensi"); the Turonian-Santonian of Slovenia (Coeldus); the Coniacian from the Niobar Formation in Kansas (Micropycnodon); the Santonian from Polazzo, in Italy (undescribed new genus, Poyato-ArizA, work in progress); the Maastrichtian from the Netherlands (Anomoedus subelavatus); and the upper Maastrichtian from Albaina in Spain (Pycnodontidae indet. plus cf. Anomoedus and cf. Paramicrodon). Let us remark that most of the numerous references to isolated pycnodont dentitions from the Late Jurassic and the Cretaceous are not mentioned herein, but are numerous, specially from the Cretaceous of Europe.
The Cenozoic witnesses a drastic decrease in the diversity and geographic distribution of the pycnodonts, and eventually their extinction. Complete specimens are known in south-central Europe only. The oldest Cenozoic record is from the Paleocene (Montain) of Mont-Aimé, in France (Oropycnodus) and Trebiciano in Italy (Tergestinia). Still in the Paleocene, but a little younger, there is an African occurrence from the Landenian of Wurno, Nigeria (isolated dentition assessed to Pycnodus). Then comes their last records. The most reliable ones date from early to middle Eocene. Regarding complete specimens, the Eocene pycnodont record is still relatively diversified, but from a single locality, Monte Bolca, in Italy (Nursallia veronea, Palaebalistum, Pycnodus apodus), curiously geographically not far from their oldest records in the Triassic. In addition to these complete specimens, isolated dentitions are known from France and the United Kingdom (cf. Pycnodus). But the lower-middle Eocene has also provided pycnodont record in Africa, unfortunately isolated dentitions again, mostly from Tamagüélet in Mali, but also from Tocqueville in Algeria, Mokattam in Egypt, and Gafsa in Tunisia (all assessed to Pycnodus). There is an unconvincing Oligocene record of a pycnodont. It is from Hungary, a Pycnodus-like dentition found during a student excursion. It is interesting to know that at least one pycnodont has been cited in Europe after the Eocene, but, in any case, there is no well studied record of pycnodontiform fishes after the lower-middle Eocene (Ypresian and Lutetian), and no citations at all after the Oligocene.

In sum, the pycnodont record indicates that their origin, radiation centre, and last refuge were all related with the Tethys sea. They did reach an impressive diversity, a vast geographic extension, and a long record that covers at least 150 million years. Their evolutionary success is obvious. They did not suffer a mass extinction event, but a long, progressive, slow decline in diversity and distribution that began in the Late Cretaceous after the Turonian, and that would eventually lead to their extinction in the Paleogene.

3.- A new hypothesis for their extinction.-

It could seem paradoxical that such a diversified group, potentially adaptable to many different environments, declined in diversity during the Late Cretaceous, to become finally extinct after their last records in the Paleogene. It is obvious that the adaptations of the pycnodonts were effective enough to account for a long evolutionary success, but not effective enough to overcome the concurrence of the teleosts. But why? The main teleostean lineages can be traced at least back in the Jurassic, and they greatly developed during the Early Cretaceous. Their main radiation began in the Late Cretaceous, when pycnodonts were still enormously diversified and largely distributed. This was the time when concurrence between pycnodonts and teleosts became decisive. Locomotion was probably one of the key factors; pycnodonts do not occupy two of the three specializations in the functional morphospace of Recent teleosts (Fig. 2C). But these two specializations, accelerating and cruising, are truly effective in a limited number of environments. So another, more important key factor must lie in their feeding strategies; more particularly, in how these strategies could have evolved.

Euryphy can be defined as the possibility to adapt to many different food sources in an effective manner. It is an important feature of ubiquitous fishes, as omnivore fishes have better chances to get more amply distributed than specialists (Lowe-McConnell, 1987). This is a key factor in the success of teleostean fishes, and is revealing when evolutionary processes involving Recent teleosts are studied.

For instance, in addition to manipulation, chaetodontids can use effective suction and ram feeding when acting as predators of midwaters (Wainwright and Bellwood, 2002). Acanthuridae mostly feed from the benthos by biting preys that are attached, but a large variety of morphological variations, including mechanics of the jaws and oral jaw dentition, has resulted on a considerable radiation within this general feeding pattern (op. cit.). Even more interestingly, the feeding mode has changed drastically as “part of a trophic radiation within the family” in, for instance, Serranidae and Labridae (op. cit.: 48). This way, fishes that feed on “firmly attached prey category often give rise to zooplanktivores (e.g., Acanthuridae, Chaetodontidae, Pomacentridae, and Balistidae)” (op. cit.: 48). These examples evidence how a change in the primary feeding strategy from manipulation to ram and/or suction is related with a trophic radiation. This way, teleosts exhibit today a wide adaptative radiation in feeding habits, occupying many trophic roles from detritivores to carnivores (e.g., Wootton, 1990).

Therefore, teleosts have achieved major changes in their feeding strategies in several groups, and this is certainly a key factor of their evolutionary success and radiation. Pycnodonts, whose jaw anatomy was very different, could not achieve such changes. Their bones and teeth were adapted to general and specialised manipulation and durophagy. This strategy was adaptable and efficient enough to account for their success, because of the large array of environments that it enabled pycnodonts to inhabit, as we have previously seen. However, “the jaw structure, once established in the pycnodonts, remained remarkably constant” (Nursall, 1996a: 121).
This implies that the variations in the basic anatomy of the jaws in these fishes was not comparable, by far, with those of teleosts. Even the anatomic variations cited by Kriwet (2001) and in the present paper did not allow pycnodonts to change their primary feeding strategy. They were anatomically unable to switch from their primary manipulation feeding strategy to the radically different primary ram and/or suction. Teleosts, mostly due to their capacity for effective jaw protrusion, related with the anatomic plasticity of their oral region, can change their feeding strategies drastically as part of their evolutionary process. Pycnodonts could not change their primary feeding strategies, from manipulation to ram or suction, so this could not be part of their evolutionary process. This is hypothesised here to have been the key factor in their extinction.

Pycnodonts were capable of a certain euryphagy within the ample boundaries of their essentially durophagous, yet potentially diversified, diet, and their primarily manipulation feeding strategy, which was also potentially diversified, as we saw above. This explains their long evolutionary success. But they were not as effective as teleosts at euryphagy, since teleosteans can switch from manipulation to ram and suction. Pycnodonts could adapt to changing environments less effectively than teleosts could. In other words, pycnodonts were successful and competitive while the environmental changes were limited, that is, during the Late Jurassic–Early Cretaceous times. But they were not competitive enough with teleosts when needing to adapt to the new, drastically changing environments of the Late Cretaceous and the Cenozoic due to the opening of the Atlantic ocean and the subsequent regression of the Tethys sea (e.g., Behrensmeier et al., 1992; Smith et al., 1994; Bellwood and Wainwright, 2002; see also for the discussion below).

During the Cretaceous and the Early Cenozoic there was a wide marine connection through the Tethys seaway. Pycnodonts were essentially cosmopolitan during the Cretaceous. There was a progressive Mesozoic Marine Revolution that included antipredator adaptations in many invertebrate groups that were food sources for pycnodonts, but these could probably, in turn, develop new adaptations. The opening of the Atlantic radically changed the situation. The Late Cretaceous witnessed the progressive separation of Africa and south America; by the end of the Cretaceous, the Atlantic was wide open. During the Late Cretaceous, the pycnodont faunas became increasingly distinct while being competitive with the teleostean concurrence in the least changing environments, maintaining a specially high diversity in the Tethys domain. Pycnodont diversity begin to decrease clearly during the middle Late Cretaceous. This tendency did not change especially at the K/T boundary; it simply continued decreasing slowly during the Early Cenozoic, when pycnodonts dwelt in the Tethys domain and disappeared from the Atlantic domain (except a relict population in Mali). The last pycnodont refuges are mostly related with the Tethys sea (southern Europe and northern Africa), whose environments had been changing less radically than those of the Atlantic ocean, which continued to spread significantly during the Early Cenozoic. By the Miocene, the Tethys was reduced to a narrow channel with seas in peripheral basins, the Parathetys. In the meantime, most Recent teleostean groups had effectively radiated, and a Cenozoic Marine Grazing Revolution had occurred (Bellwood and Wainwright, 2002: 28–29), achieved by the teleosts only. They accomplished their impressive radiation, and pycnodonts eventually became extinct. There is certainly no record of pycnodonts after the Terminal Tethyan Event in the Early Miocene.

In sum, the inability, due to anatomic constraints, to develop radically different feeding strategies, that is, to switch primary feeding strategies during their evolutionary history, like many teleostean groups did, is hypothesised here as the crucial factor to explain the decline and final extinction of the pycnodontiform fishes.

**CONCLUSIONS**

Ecomorphologically, pycnodonts are more variable than previously thought. Some of them were generalist, both in their mode of locomotion and/or in their durophagous feeding strategy. Even though essentially within the limits of durophagy, the potential diet of these animals was very varied, both for general durophagous and for the different specialist durophagous. Pycnodonts may have fed on corals, rudists and other reefal organisms, echinoids, crinoids, and/or brachiopods in marine environments, and bivalves, gastropods, decapods and other crustaceans, and/or plants in marine, brackish, and freshwater environments. The direct evidence of digestive remains that we presently know confirms the ecomorphologic indications that the diet of these fishes was highly varied.

The ecomorphologic inferences in pycnodonts presented in this paper have relevant environmental implications. The palaeoenvironments of pycnodonts were not necessarily reefal. The misassumption that they were such comes from a misconstrued line of reasoning. Specialists do discuss the possible environments of pycnodonts with caution: "Location was generally coastal, with the possibility of freshwater or estuarine conditions" (Nursall, 1996a: 117). Authors of general
textbooks usually present the environment of pycnodonts in a very general manner, e.g., "...quiet reef waters (...) may have been a favourite environment" (Romer, 1966: 59); "...this group probably lived in quiet reef waters" (Carroll, 1988: 109). When this generalization is mistaken as the only possibility, the result is that one may think that pycnodonts were exclusively reefal. But they were not. The palaeoenvironment of pycnodonts was not, by any means, necessarily restricted to reefs. As a matter of fact, "in both evolutionary and ecological terms, coral reefs represent only one of a range of suitable habitats" even in Recent groups that are effectively adapted to this environment (Bellwood and Wainwright, 2002: 31). Furthermore, the palaeoenvironment of pycnodonts was not necessarily restricted to marine conditions either (Poyato-Ariza et al., 1998). As a consequence, these fishes can be misleading when used as sole indicators of their original environment. Their mere presence is not, by itself, an unambiguous indication of the palaeoenvironment of their locality. They are useful only as one more part of the large, comprehensive analysis of the original community; this and the geological data, including the sedimentologic environment and processes, are the only base for a reliable, sound palaeoecological restoration. Pycnodonts, and fishes in general, are potentially misleading palaeoenvironmental indicators.

The brief, overall account of the morphologic variations in pycnodont fishes and the very general ecomorphologic implications inferred from these variations presented in this paper reveal that pycnodonts were more diversified and adaptable than previously thought. As a group, they could adapt quite well to their environments, both through generalised strategies and through several different specialised strategies. Their ecomorphologic plasticity accounts for their success as a group, explaining why they flourished to a great extent during the Late Jurassic and the Cretaceous. But they had to face the concurrence of the teleosts, which were drastically evolving at the time. Teleost fishes were developing the anatomic capacities (especially jaw protrusion) that would enable them to effectively change their locomotion modes and, most importantly, their primary feeding strategies. They were therefore able to effectively adapt to new, drastically changing environments. This marked the decline of the less adaptable pycnodonts, anatomically unable to accelerate, cruise, and, more significantly, to effectively protrude jaws. They were therefore unable to switch their primary feeding strategies, as teleosts were. So, pycnodonts slowly lost geographic distribution during the Late Cretaceous as their environments significantly changed, remaining still quite diversified in the least changing environments, basically the Tethys domain, to become finally extinct during the Cenozoic, with the regression of the Tethys sea. Teleosts could adapt to the drastic environmental changes much more effectively, mostly by major changes in their feeding strategies, and thus, they radiated during the Late Cretaceous and the Cenozoic, becoming the most diversified and widespread fishes. The incapacity to switch primary feeding strategies during their evolutionary history, like many teleosts, was a critical factor in the extinction of the pycnodonts.

We should not be surprised to discover a high morphologic variation, and, consequently, ecomorphologic plasticity, in such a supposedly specialised and homogeneous group as the Pycnodontiformes, as only that can account for their evolutionary success. The fact is, the more pycnodonts that are described, and the more carefully that they are studied, the greater their morphologic variations are. And, as their localities of origin are more precisely known, their palaeoenvironments are better understood. These beautiful fishes will undoubtedly provide more interesting scientific surprises in the near future.

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REFERENCES


Added in proof: a new, significant record of Pycnodontidae in Asia is reported by Rana and Kumar (in press) from the Late Cretaceous of India. This is only the second Asian record of pycnodonts, after Tibetodus. It confirms their presence in this continent and indicates that they were more diversified and spread in it than we previously thought. However, since the Indian subcontinent was narrowly related to Africa and Antarctica during a good part of the Mesozoic, it would be even more interesting to make new discoveries of pycnodonts at the North of India-Tibet, where they are absent so far.