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Author: Capasso, Luigi

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Growth and aging in †pycnodonts (Actinopterygii: †Pycnodontomorpha)

LUIGI CAPASSO

The University Museum of Chieti, State University "Gabriele d'Annunzio" of Chieti and Pescara, Piazza Trento e Trieste, no. 1, Chieti 66100, Italy (e-mail: l.capasso@unich.it)

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Abstract. This paper presents the first analytical examination of the evidence of growth and aging in pycnodonts. Preliminarily, the author discusses the difficulties of evaluating auxological phenomena in animals that do not have current descendants and in which the anatomical traits typical of juveniles persist in adults (neoteny), as an evolutionary strategy. The author collected biometric data on juvenile and corresponding adult subjects of only 15 pycnodont species. Despite this scarcity of species, the author demonstrates that there does not seem to exist a single pattern of somatic growth. However, at least two characters (one skeletal and one dental) seem common to all the examined species: (i) the relative dimensions of the orbit decrease in a constant, sometimes conspicuous manner with respect to the total body dimensions, and (ii) the width of the interdental diastemas is noticeably reduced during growth. At least two phenomena seem to be present also in aging: (i) bone hypotrophy (detectable only through radiological means) and (ii) the depletion of ameloblastic activity leading to the cessation of polyphyodontia. However, the inability to replace worn teeth may have played a role in causing natural death in aged pycnodonts by interfering with their ability to feed themselves.

Keywords: Aging, Auxology, Bone hypotrophy, Maturation phases, Pycnodonts

Introduction

Cloutier (2010) was the first to systematically analyze the palaeontological evidence of auxological processes (the term "ontogenetic" is inappropriate, as it refers to the growth and changes that occur in the embryo) in fossil fish, asserting that: "Although fossilised ontogenies are fairly rare, size series of relatively complete specimens of more than 90 fish species have been documented in the literature. These fossilised ontogenies are known for most major phylogenetic groups of fishes, and have a broad stratigraphic range extending from the Silurian to the Quaternary, with good representation during the Devonian." Unfortunately, none of these 90 cases found in literature by Cloutier (2010) concerned pycnodonts. Nevertheless, these cases exist.

From a theoretical point of view, I can divide the data analysis of the growth processes of pycnodonts into at least two main chapters: the growth of the skeleton and that of the teeth. This subdivision certainly has an ontogenetic reason, based on the different embryonic origins of the skeleton (of mesodermal origin) compared to the teeth (of ectodermal origin). However, there are also additional reasons that suggest this subdivision. In fact, the growth process of the skeleton must also be related to the phenomenon of neoteny, a characteristic of the pycnodont skeleton which has repeatedly been taken into consideration to explain a certain degree of immaturity in the skeleton of these fishes, which is evident also in the larger individuals. On the other hand, the growth process of dentition must be evaluated with great caution since it not only has a meaning of growth, but also a meaning of "replacement activity of worn teeth": this is because pycnodonts are polyphyodont animals (Capasso, 2021b). Furthermore, all these evaluations cannot benefit from comparative anatomy and physiology due to the simple but crucial fact that pycnodonts are completely extinct, and no correlatives are still alive today.

Indeed, the purpose of this synthesis is to report all the cases of pycnodonts present in literature regarding the differences between juvenile individuals and corresponding adult individuals, including the addition of some new data. Only at least 15 species are involved and the differences, beyond the obvious dimensional ones, are above all morphological. Notwithstanding, differences in proportions between the various parts of the body are often evident, which suggests the presence of a differentiated growth pattern, both in speed and in rhythm, as also happens in many other living vertebrates.

Furthermore, for the first time I propose an auxological synthesis, attempting to interpret the variations of the main biometric measures, as well as of the indices that can be derived from them, with regard to a number of pycnodont species. Regarding the evidence demonstrating skeletal growth in pycnodonts, after having discussed in general the possible role of neoteny, I report the differences between juveniles and adults in 15 species, as well as those present in specialised literature, integrating them with some punctual new insights, based on direct examination of new data, and ending with a discussion on the phenomenon of dental growth. In addition, in the final part of this paper I will discuss the first palaeontological evidence that could be connected to aging processes, both in the bones and in the teeth of some pycnodonts, even if in this specific field any available information is very scarce.

Material and methods

The material used for this work are come from the public Museums and Collections, as indicated in Table 1. The additional specimens, from part of the "Luigi Capasso Public Collection" (LCPC) were used for this study (Table 1). This is a Public Collection that was established two centuries ago, and is protected by the Italian State. It is legally registered by two Decrees of the Ministry for Cultural Heritage, such as the no. 14, dated October 11, 1999, and no. 6259-A, dated April 29, 2020, both according to Italian law 1089/39 for the protection of the National Cultural Heritage. The specimens of this Collection were publicly accessible for studies on the basis of the Article 30 of Italian law No. 42/2004.

I have taken the main biometric measurements on all the examined fossils according to codified methods (Tortonese, 2000). In particular, I focused on the general proportions of the body that allow me to distinguish a general somatic model. The length measurements (standard length, SL and total length, TL) are related to the maximum thickness of the fish, i.e., the maximum body depth (total depth, TD). Walker *et al.* (2013) introduced the so-called "Fineness Ratio" (FR) i.e., a measurement of how elongated a fish is in relation to its body bepth. A high FR describes a spindle-shaped fish with an elongated and low body shape, while a smaller FR describes a disc-shaped fish, with an elevated and short body. In addition to these measurements, the total length of the head (HL) and the maximum length of the orbit (OL) were also recorded and related to the TL. The reference points that have allowed the detection of all the measurements mentioned are shown in the Figure 1.

Observations

In this chapter the information I have gathered from the literature but also from some new observations is summarised and organised as follows: skeletal growth, dental growth, and signs of aging.

Skeletal growth and maturation phases

Pycnodonts as neotenic animals.—The pycnodont skeleton has an extremely simple structure and organization, although this does not mean that the pycnodonts are to be considered primitive (Capasso, 2021a). Indeed, almost every part of the skeleton shows a reduced number of bones and simplification of the relationships between the various elements. This situation is evident first of all in the axial skeleton, where the notochord is never completely covered by the arcocentra, and the skeleton of the tail is also very simplified. The greatest simplification is seen, however, in the vertebral column and the skull; e.g. the opercular series is made up of only five elements (i.e., operculum, preopercle, two or three branchial rays, anterior ceratoyal). This generalised simplification has been interpreted as the consequence of systematic *neoteny*, as the persistence of juvenile, immature characters in adults (Capasso, 2021a).

Neoteny is not a primitive trait, as has been demonstrated in particular for some extant amphibians. These adopted the evolutionary pattern of their body when they were in conditions of environmental difficulties, especially due to the lack of food. In reality, neoteny involves the slowing down of the maturation phases, such as by interrupting or lengthening the growth phase of the whole organism, or parts of it. Nursall (1999) proposed that neoteny might have been an evolutionary strategy adopted by the pycnodonts for environmental adaptation on a genetic basis, through the phenotypic expression of suppressor genes. Of course, beyond discovering that the pycnodont skeleton remained largely immature throughout the lives of the single individuals, I still do not have enough evidence to demonstrate what the environmental factors might have been to favour this on such a general scale. Indeed, all pycnodont populations in all of the seas of the Earth, including continental freshwaters, expressed this same condition, regardless of the characteristics of the environment in which they lived and the era in which they developed.

In conclusion, when evaluating the possible auxological value of an anatomical character in a pycnodont in a presumed growth phase, it is always necessary to take into account the possible interference of neoteny.

Examples of skeletal growth and maturation phases: The case of Pycnodus apodus.—The question of morphological variability, and perhaps also functional and even

Table 1. List of the specimens examined ad discussed in this paper, with indication of the repository and number of inventory, and with reference to the Figure number on this paper.

Genus and species (in alphabetical order)	Location	Dating	Repository: Collection acronym, and inventory number	Figure(s) in which the specimen is reproduced in this paper
Anomoeodus sp. ind.,	Malyn, Zhitomir, Ukraine	Late Ctretaceous/ Eocene	“Luigi Capasso Public Collection”: LCPC # S-2017	29
Coccodus insignis	Haqel, Lebanon	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # S-399	16
Coccodus insignis	Haqel, Lebanon	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # S-161	17
“*Coelodus*” *danae*	Profeti, Caserta, Italy	Early Cretaceous	Paleontological Collection of the Paleontological Museum of the University of Naples: MPUN-Pr. no. 055 (*)	8
“*Coelodus*” *danae*	Profeti, Caserta, Italy	Early Cretaceous	Paleontological Collection of the Paleontological Museum of the University of Naples: MPUN-Pr. no. 075 (*)	9
“*Coelodus*” *danae*	Profeti, Caserta, Italy	Early Cretaceous	Paleontological Collection of the Paleontological Museum of the University of Naples: MPUN-Pr. no. 073 (*)	10
Flagellipinna rhomboides	Haqel, Lebanon	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # S-1927	4
Flagellipinna rhomboides	Haqel, Lebanon	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # S-1925	5
Globanomoeodus dentespassim	Waco Lake, Texas, U.S.A	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # S-1839	30 and 31
Gregoriopycnodus bassanii	Pietraroja, Italy	Early Cretaceous	“Luigi Capasso Public Collection”: LCPC # A-15	12
Gregoriopycnodus bassanii	Pietraroja, Italy	Early Cretaceous	“Luigi Capasso Public Collection”: LCPC # I-215	13
Gregoriopycnodus bassanii	Pietraroja, Italy	Early Cretaceous	“Luigi Capasso Public Collection”: LCPC # I-32	14
Gregoriopycnodus bassanii	Pietraroja, Italy	Early Cretaceous	“Luigi Capasso Public Collection”: LCPC # I-77	15
Gyrodus jurassicus	Solnhofen, Germany	Late Jurassic	“Luigi Capasso Public Collection”: LCPC # S-1999	28
Neoproscinetes penalvai	Cearà, Brazil	Early Cretaceous	Paleontological Collection of the University Museum of the State University “Gabriele d’Annunzio, Chieti, Italy: MSUC # 20089	27
Neoproscinetes penalvai	Cearà, Brazil	Early Cretaceous	“Luigi Capasso Public Collection”: LCPC # S-1935	26
Njoerdichthys dyckerhoffi	Lower Saxony, Germany	Late Ctretaceous	Geosciences Collection of the University of Bremen, Germany: GSUB no. V2303 (^)	20
Njoerdichthys dyckerhoffi	Lower Saxony, Germany	Late Ctretaceous	Geosciences Collection of the University of Bremen, Germany: GSUB no. V2304 (^)	21
Nursallia veronae	Monte Bolca, Italy	Eocene	Museo Civico di Storia Naturale di Verona: MCSNV, no. II – D – 173 – Vr (°)	23
Nursallia veronae	Monte Bolca, Italy	Eocene	Paleontological Collection of the Field Museum of Natural History of Chicago, U.S.A.: FMNHC no. PF 3256 (‡)	22
Paranursallia gutturosa	Vallecillo, Mexico	Late Ctretaceous	Paleontological Collection of the University Museum of the State University “Gabriele d’Annunzio, Chieti, Italy: MSUC # 213804	24
Paranursallia gutturosa	Vallecillo, Mexico	Late Ctretaceous	Paleontological Collection of the University Museum of the State University “Gabriele d’Annunzio, Chieti, Italy: MSUC # 213805	25
Pseudopycnodus nardoensis	Nardò, Lecce, Italy	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # I-467	6
Pseudopycnodus nardoensis	Nardò, Lecce, Italy	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # I-468	7
Pycnodus apodus	Monte Bolca, Italy	Eocene	Muséum national d’Histoire naturelle, Paris (France); Collection: Paleontology (F); Fossil specimen MNHN.F.BOL.131	2
Undetermined	Gara Sbaa, Morocco	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # S-1009	18
Undetermined	Gara Sbaa, Morocco	Late Ctretaceous	“Luigi Capasso Public Collection”: LCPC # S-1227	19

(*) Courtesy of Maria Carmela Del Re. (^) Courtesy of J. J. Cawley. (°) Courtesy of Stefano Pisani. (‡) Courtesy of William Simpson.

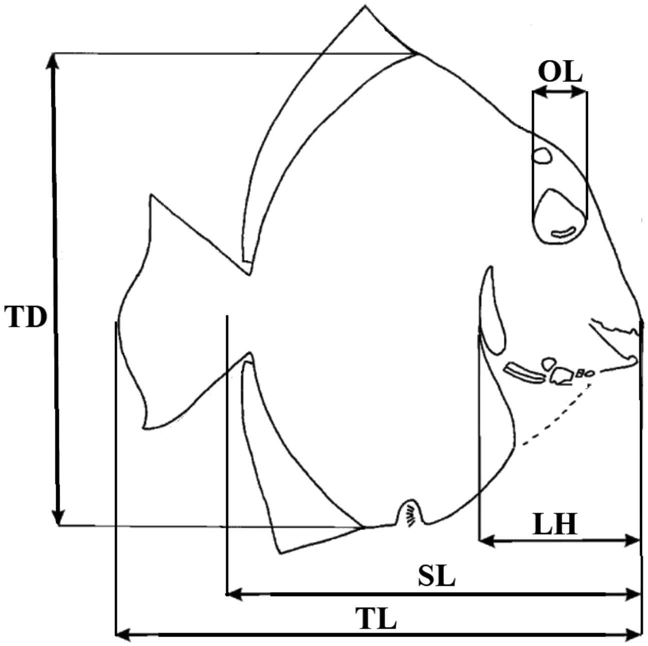


Figure 1. Schematic illustration of the landmarks used to take the measurements. TD, maximum depth of the body; SL, standard length; TL, total length; LH, length of the head; OL, length of the orbit.

Figure 2. *Pycnodus apodus* of the Eocene of Monte Bolca, northern Italy. This is a species known also through small specimens, with this specimen being the smallest of all those known, with a total length of only 33 mm (Muséum national d'Histoire naturelle, Paris (France); Collection: Paleontology (F); Fossil specimen MNHN.F.BOL131).

ecological variability, linked to auxological processes within the individual species of pycnodonts had already been raised and addressed in detail by Blot (1987). In fact, the pycnodonts collected from the famous Eocene deposit of Monte Bolca (northern Italy) were revised by Blot (1987), and among those attributable to the genus *Pycnodus*, these appeared to belong to two different species: *Pycnodus apodus* (Volta) (not *Pycnodus platessus* Agassiz), which is characterised by a body length twice its height, and *Pycnodus gibbus* Agassiz, which is characterised by a body length one and a half times its height. It follows that *P. gibbus* has a greater general body shape, though short, while *P. apodus* has a more tapered, elongated body.

Blot (1987) examined a total of 50 specimens attributed to both *Pycnodus apodus* and *Pycnodus gibbus* based on the classifications shown on the tags and catalogues of the museums and collections to which they belonged. These samples included specimens of very different sizes: the smallest was only TL = 33 mm (Muséum National d'Histoire Naturelle, Paris, No. 0130-0131) (Figure 2), the largest with a TL = 295 mm (Civic Museum of Natural History of Verona; no. II D 170-171). For all of these specimens, Blot (1987) carried out a complete metric analysis showing, among other things, that in the smaller specimens the body was relatively higher in relation to the length, and the individuals had a more oval and shortened general appearance. At the same time, for the larger specimens, the height of the body was less than the length, and the individuals had a more tapered general appearance (high value of the Fineness Ratio).

On the basis of these data, Blot (1987) demonstrated that the two presumed species, namely *Pycnodus apodus* and *Pycnodus gibbus*, are in reality only one species; namely *P. apodus*. *Pycnodus gibbus* corresponds to a body morphology that is characteristic of the younger developmental phases of *P. apodus*, which were characterised in particular by a more angular morphology of the frontal profile, as well as by a general morphology of a greater and shorter body (low value of Fineness Ratio).

Blot (1987) also reconstructed a graphic scheme that demonstrated the evolution of the general shape of the body during the growth of *Pycnodus apodus* (Figure 3). At the present state of our knowledge, this scheme represents the only known example of progressive, almost continuous metrical variation linked to the age of the individuals within the pycnodonts.

In addition to metric differences, which are evidently linked to the growth phase, as I have already indicated, Blot (1987) underlined that between the two alleged species there were also small morphological differences. The documented morphological differences between the smaller (juvenile) the larger (adult) individuals referred to a greater relative size of the orbit, and a deeper body shape (see Table 2 for the complete set of measurements). The more angular aspect of its frontal profile, and this major 'gibbosity' was not always well correlated to the general somatic measurements and indices, as Blot (1987) demonstrated by relating the length of the body, the body

Table 2. Main biometric measurements of the 10 species of pycnodonts considered in this paper for the auxometric evaluations, being able to have specimens of adults and determined juveniles belonging to the thick species; next to each specimen the deposit coordinates of the Museums and Collections to which they belong are indicated. TD, maximum depth of the body; SL, standard length; TL, total length; LH, length of the head; OL, length of the orbit (see Figure 1).

Species	Specimen	Repository	Measures (in mm)				
			TL	SL	TD	LH	OL
Gara Sbaa undetermined species	Juvenile	LCPC #S-1009	26	23	16	8	5
	Adult	LCPC #S-1227	81	72	40	26	8
Coccodus insignis	Juvenile	LCPC #S-399	45	39	26	16	—
	Adult	LCPC #S-161	122	115	55	38	—
Flagellipinna rhomboides	Juvenile	LCPC #S-1927	43	39	35	16	9
	Adult	LCPC #S-1094	124	113	134	49	13
Gregoriopycnodus bassanii	Juvenile	LCPC #A-15	51	46	30	15	10
	Adult	LCPC #I-215	290	277	188	78	32
"*Coelodus*" *danae*	Juvenile	MPUN #Pr-055	14	12	9	4	2
	Adult	MPUN #Pr-075	60	50	22	19	6
Njoerdichthys dyckerhoffi	Juvenile	GSUB #V-2303	27	24	30	9	5
	Adult	GSUB #V-2304	48	—	38	17	5
Nursallia veronae	Juvenile	FMNHC #PF-3256	21	19	18	9	4
	Adult	MCSNV # II-D-173-Vr	323	298	231	118	26
Paranursallia gutturosa	Juvenile	MSUC # 213804	99	94	84	41	14
	Adult	MSUC # 213805	370	348	248	110	26
Pseudopycnodus nardoensis	Juvenile	LCPC # I-467	34	28	16	10	4
	Adult	LCPC #I-468	199	178	78	66	14
Pycnodus apodus	Juvenile	NHMP #0130	33	29	22	10	5
	Adult	MCSNV # II-D-170-Vr	295	262	121	81	18

height, and the gibbosity angle value (in degrees) of the frontal profile. To explain these small differences, Blot (1987) hypothesised the role of sexual dimorphism, in the sense that female individuals might also have had a smaller body size, with a taller body and a more humped frontal profile.

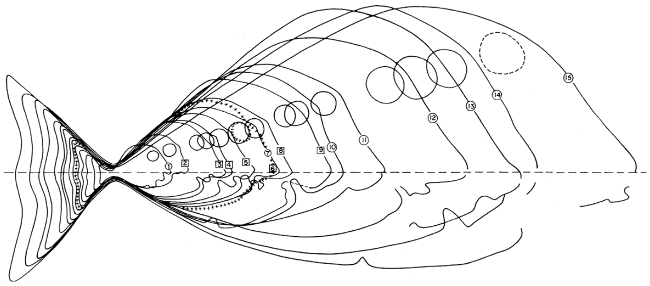


Figure 3. Evolution of the general shape of the body during somatic growth in the species *Pycnodus apodus* of the Eocene of Monte Bolca, northern Italy. Modified from Blot (1987).

More recently, Cawley *et al.* (2018) reviewed this same population (integrating a couple of further individuals, to a total of 52 specimens). Although Cawley *et al.* (2018) considered a greater number of measurements and used more refined data-processing methods, the conclusions they reached were exactly the same as those proposed by Blot (1987), even if "the analyses revealed that the variations of the body shape, morphometric and meristic characters cannot be used to distinguish different morphotypes. On the contrary, the present results show a remarkable link between shape and size, related to ontogeny."

Examples of skeletal growth and maturation phases: The case of Flagellipinna rhomboides.—Cawley and Kriwet (2019) described the new species *Flagellipinna rhomboides*, from the Cenomanian of Haqel (Lebanon), and they identified a slightly smaller specimen that certainly belonged to the same species, but which they interpreted as juvenile or sub-adult. They listed the following characteristics that distinguished the assumed juvenile from the adults: (i) poorly ossified dermal skull roof bones and mesethmoid; (ii) relatively large orbit; (iii) shorter preorbital distance; (iii) dorsal fin lacking the whip-like extension of the larger specimens (adults); (iv) notochord that was only partially surrounded by the arcocentra; (v) bar-scales that did not cover the ventral flank posterior to the post-coelomatic bone; (vi) dorsal ridge scales that lacked spines; and (vii) the first dorsal ridge scale located further from the skull roof (Figures 4, 5). They interpreted the combination of these characters as a small juvenile specimen, in the process of maturing.

As for the morphological differences demonstrated in *Pycnodus apodus* of the Eocene of Bolca, also for *Flagellipinna rhomboides* of the Cretaceous of Lebanon, some of the morphological differences that distinguish the assumed juveniles from adults were interpreted as indicators of environmental adaptations characteristic of the juvenile stages of these fish. In particular, the structure of the muzzle and that of the 'nape' area were interpreted as arising from the presumed differences in their ways of obtaining food when feeding, and ultimately in the differences in the habitats that would have characterised the adults compared to the juveniles. Indeed, Cawley and Kriwet (2019) also stated: "The interpretation of the smallest specimen of *Flagellipinna*, gen. nov., being a juvenile raises interesting questions regarding ontogeny and change in ecology during the growth of this fish. The juvenile has an even deeper body shape than the adult, along with a shift in skull position and shape, indicating that it was a more typical durophagous pycnodont that lived in shallower reef habitats and may have moved into deeper waters to feed from the crevices of the reef edge as it became older. Of course, more specimens of *Flagellipinna*, gen. nov., are necessary in order to confirm the validity of these morphological changes throughout its ontogeny, but this interpretation is supported by similar ontogenetic changes observed in modern taxa." However, in the paragraph relating to the "Discussion" I will set out the elements that contradict this hypothesis.

Figure 4. *Flagellipinna rhomboides* from the Cenomanian of Haqel: a very juvenile specimen, with total length = 43 mm (LCPC # S-1927).

Figure 5. *Flagellipinna rhomboides* from the Cenomanian of Haqel: an adult specimen, with total length = 100 mm (LCPC # S-1925).

In addition to the morphological variations, the comparison between the assumed juvenile subject and adult subject also demonstrates the existence of biometric differences. Cawley and Kriwet (2019), as reported above, concluded that the sub-adult of this species was taller and shorter in body than the adults. Notwithstanding, it must be emphasised that the SL of this subject presumed as juvenile or sub-adult is 70.4 mm: a dimension only slightly smaller than the considered adult holotype, which has a SL = 97.2 mm. By comparing these subjects, Cawley and Kriwet (2019) deduced that the smaller subject had a taller body than the larger subject. However, Taverne and Capasso (2020) had the opportunity to examine a number of larger adults (the major has a SL = 124 mm) obtained from the same site, showing that taphonomic distortions can also lead to important errors in the biometric evaluation of this type of pycnodont, as was demonstrated, for example, in specimen LCPC # S-1077. In addition, I recently had the opportunity to collect at Haqel a truly smaller size specimen of *Flagellipinna* which has a SL = 39 mm, which can actually be considered very juvenile. Therefore, on the basis of these new data, the interpretations proposed by Cawley and Kriwet (2019) must be revised. In particular, the auxological tendency of *Flagellipinna* can be defined as analogous to that observed in *Gregoriopycnodus*, with juveniles having a more elongated and less deep body than the adults. Such as *Flagellipinna* growth pattern corresponds to an "Auxological Decrease of the Fineness Ratio" (pattern ADFR).

On the basis of new *Flagellipinna rhomboides* specimens recently collected (Figures 4, 5), in fact, I noted that in this species the proportions of the major somatic measures are reversed with respect to what was observed in most of the other cases presented in this paper. The maximum body depth (TD) with respect to both the standard length (SL) and the total length (TL) is lower in juvenile subjects and increases in adult ones. This means that juvenile subjects have a relatively more elongated body than adults: an auxological situation which is exactly the contrary to what was already described, for example, in the cases of *Pycnodus apodus*.

On the contrary, the tendency towards a progressive reduction of the relative dimensions of the orbit remains confirmed also in *Flagellipinna rhomboides*: greater in juvenile subjects than in adults, as is evident from the examination of the biometric data reported in Tables 3, 4.

Examples of skeletal growth and maturation phases: The case of Pseudopycnodus nardoensis.—A revision of the species *Pseudopycnodus nardoensis* (originally described by Taverne 1997, on the basis of an imperfect specimen from the Late Cretaceous of Apulia, Italy) was based on a series of new specimens collected around the town of Nardò (Province of Lecce, southern Italy). These new specimens consisted of a series of medium sized, presumably adult individuals that were more or less complete, with total lengths ranging from about 150 mm to 250 mm (Taverne and Capasso, 2012). These included just one juvenile, probably particularly young individual, with a total length of about 34 mm. As reported by Capasso (2021a) there were a few morphological differences that characterised this juvenile compared to the adults. First of all, the juvenile specimen of the above-mentioned species has a very short body morphology, with a relatively tall trunk; on the contrary, the adults have a much more tapered, lower and longer, near fusiform, body shape. A measure of this morphological evolution that is evidently associated with growth is seen by the index that relates the standard length to the maximum body depth of the body ([TD/SL] × 100): this is 57.1% in the juvenile, and 43.8%, in the adults. The Fineness Ratio is 2.1 in the juvenile subject and is 2.6 in the adult one. In addition, in the juvenile specimen the head is shorter, and above all, the profile of the forehead is much more vertical, while in the adults the forehead is more oblique, so much so that the muzzle extends far forward. Finally, the orbit of the juvenile individual is more rounded (Figures 6, 7) and much wider than that of the adults (Tables 3, 4).

As can be seen, for *Pseudopycnodus nardoensis* the morphological differences that transform the body proportions during auxological growth are repeated almost identically with respect to what we have seen for *Pycnodus apodus*. Obviously, none of these differences leads us to assume that these are the expression of adaptations to different environments between the young and adult individuals of this species.

Examples of skeletal growth and maturation phases: The case of Turbomesodon preclarus.—Poyato-Ariza and Wenz (2004) established the new taxon *Turbomesodon preclarus*, which they collected in the lithographic limestone of the Solnhofen area (Germany), dated to the Late Jurassic. They also described a specimen that certainly belonged to this species but which had very small dimensions, having a total length of 24 mm, whereby they indicated that this specimen is "one of the smallest known specimens of pycnodonts in the world". The analysis of the characteristics of this specimen made it possible to make some auxological observations. Indeed, the juvenile specimen is characterised by the following three differences that distinguish it from the adults of the same species: (i) the juvenile shows a growing vomer with no more than eight teeth on its lateral row, compared to the nine teeth in the lateral row of the vomer of the adults; (ii) both the adults and the only juvenile have 15 dorsal ridge scales and 22 ventral keel scales, but in the adults, all of these contour scales have distal crests, with up to five spines that increase in size in the cephalocaudal direction; the juvenile shows only up to three spines on the dorsal and ventral contour scales, which clearly indicates an auxological increase in their number; finally (iii) the trajectory of the supraorbitary sensory canal is curved in the juvenile, to roughly follow the orbital curvature of the bone, and is closer to the midline in the anterior region.

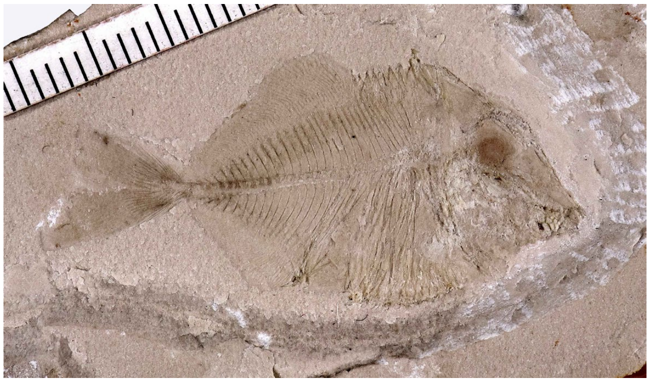


Figure 6. *Pseudopycnodus nardoensis* from the Upper Cretaceous of Lecce, southern Italy: a very juvenile specimen, with total length = 34 mm (LCPC # I-467).

Figure 7. *Pseudopycnodus nardoensis* from the Upper Cretaceous of Lecce, southern Italy: an adult specimen, with total length = 199 mm (LCPC # I-468).

Poyato-Ariza and Wenz (2004) also discussed possible explanations for the difference in trajectory of the supraorbitary sensory canal in the adults compared to the juvenile specimen: "the most plausible interpretation for the bones of this region in *Turbomesodon* is that the dermosphenotic bone is in part present as an independent plate, and in part fused to the dermopterotic. This interpretation is confirmed by the juvenile specimen, which shows the junction of the infraorbitary and supraorbitary sensory canals in a large plate posterior to the frontal, plus a small, ventral, independent triangular plate carrying the postorbital portion of the infraorbital canal." In addition, no biometric data useful for auxometric evaluations was detected in this species.

*Examples of skeletal growth and maturation phases: The case of "*Coelodus*"* danae.—Further, it is worth noting the case of "*Coelodus*" *danae*, described by Bravi (1996). This is well known through a large population sample where the detailed morphological and metric setup demonstrates two distinct adult morphotypes, which represent the two anatomical configurations distinguished by sex (Capasso *et al*., 2021). The analysis of this population that included over 130 specimens collected in the Early Cretaceous limestone of Profeti (little town near Caserta, southern Italy) made it possible to trace some very small individuals. The smallest of these had a total length of only 14 mm, which indeed represents the smallest specimen of the pycnodonts known to date (Figure 8). I describe the morphological characteristics that distinguish the supposed adult male morphotype (Figure 9) from the adult female one (Figure 10) (Capasso *et al*., 2021).

In particular, the dermal elements (i.e., the scales) of the anal region consist of two small scales that are positioned posterior to the anus and anterior to the beginning of the anal fin. These are almost constant, and show only minimal differences across these two morphotypes. One such difference is seen for the "long morphotype", where the anterior scale is smaller, and is surmounted by two spinous processes; in the "short morphotype", it is a little more robust and surmounted by three spinous processes. However, the posterior scale is more robust and surmounted by three spinous processes in both of these morphotypes. Also, these spinous processes, and especially those for the posterior anal scales, are longer for the "short morphotype" than for the "long morphotype". In this regard, however, it is particularly interesting to note that these small differences were not observed in the juvenile individuals (Figures 8–10).

Thus, it is precisely the absence of all of these characteristics in the smaller sized specimens that represents the fundamental criteria to be taken into account when analysing and conferring value to sexual dimorphism of fossil specimens (Capasso *et al*., 2021). Indeed, in assessing the sexual value of each character, its auxological evolution must also be considered, so as to ascertain its possible absence in the youngest individuals (i.e., those of the smallest sizes) (Horner and Goodwin, 2006). Therefore, it is very important to emphasise that in the smaller individuals, which correspond to the juvenile stages of auxological development of the "*Coelodus*" *danae* species, none of the morphological aspects that characterise each morphotype of the adult phases is present. This observation shows that the characteristics of the variability were configured during growth.

In addition to the morphological variations, the comparison between juvenile subjects and adult subjects also demonstrated the existence of biometric differences. In particular, I noted that in this species the maximum depth of the body (TD) with respect to the standard length (SL)

Table 3. The first attempt of an auxometric evaluation of the main biometrical measures of some species of pycnodonts. Only those species have been selected for which juvenile specimens and adult specimens undoubtedly pertaining to the same taxon are known. Only two specimens were taken into consideration for each species: one juvenile and one adult. In the event that several specimens are known, the smallest size was considered as "juvenile" and the largest size as "adult" (see Table 2 for the identification of examined specimens). Two growth patterns were observed: (i) the model with an auxological increase in fineness ratio, observed in the species *Flagellipinna rhomboids* and *Gregoriopycnodus bassani* and (ii) the model with auxological decrease in fineness ratio, observed in species *Coccodus insignis*, "*Coelodus*" *danae*, Gara Sbaa undetermined species, *Njoerdichthys dyckerhoffi*, *Nursallia veronae*, *Paranursallia gutturosa*, *Pseudopycnodus nardoensis* and *Pycnodus apodus*. TD, maximum depth of the body; SL, standard length; TL, total length; LH, length of the head; OL, length of the orbit. (1) In the case of *Coccodus insignis* the TD has been replaced with the maximum distance between the apices of the lower spines of the cleitra. (2) The largest sized individual present in this population belongs to the "long" morphotype, interpreted as an adult male (Capasso *et al.*, 2021). (3) Both TL and SL were measured on the reconstruction proposed by Cawley *et al.* (2020).

Species	Ratio TL/TD Fineness Ratio		Ratio (TD/SL)×100 (%)		Ratio (LH/TL)×100 (%)		Ratio (OL/TL)×100 (%)	
	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult
Coccodus insignis	1.7 (1)	2.2 (1)	66.7 (1)	47.8 (1)	35.6	31.1	—	—
"*Coelodus*" *danae*	1.6	2.8 (2)	71.7	61.4 (2)	28.6	38.0 (2)	14.3	10.0 (2)
Flagellipinna rhomboides	1.2	1.1	89.7	118.6	37.2	39.5	20.9	10.5
Gara Sbaa undetermined species	1.6	2.0	69.6	55.6	30.8	32.1	19.2	9.9
Gregoriopycnodus bassanii	1.5	1.7	65.2	67.9	29.4	26.9	19.6	11.0
Njoerdichthys dyckerhoffi (3)	0.9	1.3 (3)	127.6	— (3)	33.3	35.4 (3)	18.5	10.4 (3)
Nursallia veronae	1.2	1.4	94.7	77.5	42.9	36.5	19.0	7.4
Paranursallia gutturosa	1.2	1.5	89.4	71.3	41.4	29.7	14.1	7.0
Pseudopycnodus nardoensis	2.1	2.6	57.1	43.8	29.4	22.2	11.8	7.0
Pycnodus apodus	1.5	2.4	75.9	46.2	30.3	27.5	15.2	6.1

is greater in juvenile subjects (71.7%) and decreases in adults (61.4%), without distinction of sex. This means that juvenile subjects have a relatively taller yet less lengthier, overall stocky, rounded body than adults: an auxological situation exactly compliant with that found in most of the cases reported in this paper. Also in the case of the "*Coelodus*" *danae* the tendency towards the progressive reduction of the relative dimensions of the orbit remains confirmed: greater in juvenile subjects (14.3%) than in adults (10.0%), as is evident from the examination of the biometric data listed in Tables 3 and 4.

Examples of skeletal growth and maturation phases: The case of Arduafrons prominoris.—Frickhiner (1991) reported that the anal fin margin of the *Arduafrons* from the Late Jurassic of the Solnhofen area (Germany), tended to be concave upon maturity, through a comparison of different sized specimens from the same site.

Subsequently, Nursall (1999) studied in detail all known specimens belonging to this species. In particular, the comparison between the largest (presumably adult) specimen, at about TL = 500 mm, and a smaller (and presumably younger) specimen, at only TL = 190 mm, highlighted a series of differences that therefore had an auxological basis (Figure 11). The observed changes in growth included the following characters (Nursall, 1999): (i) increased prognathism; (ii) increased height of the apical crest; (iii) slimming of the postabdominal, ventral body contour; (iv) elongation of the anterior fin rays of the dorsal and anal fins, to provide what must have been the more characteristic adult shape; and (v) increasing convexity of the caudal fin. Nursall (1999) thus suggested that "changes such as these are to be expected as fish mature and take on sexual characteristics".

Examples of skeletal growth and maturation phases: The case of Gregoriopycnodus bassanii.—The species *Gregoriopycnodus bassanii* was described by D'Erasmo (1914–1915) on the basis of a single adult specimen (standard length = 380 mm) collected from the Albian limestone of Pietraroja (Province of Benevento, southern Italy). This was recently revised by Taverne *et al*. (2020), who examined a certain number of specimens from the same location, and also assessed the morphological variability among the individuals, which included a particularly small specimen (standard length = 48 mm).

Table 4. Percentage variation of the ratio (OL/TL)×100 during growth in the nine species of pycnodonts studied in this paper. The most constant somatometric difference between juvenile individuals and adult individuals, present in all the species examined, is that which expresses the dimensional relationship of the orbit with respect to the total length of the body: in juvenile subjects, in fact, the orbit is always proportionally much larger than in adults of the same species. (1) The largest sized individual present in this population belongs to the "long" morphotype, interpreted as an adult male (Capasso *et al*., 2021). (2) Both TL and SL were measured on the reconstruction proposed by Cawley *et al.* (2020).

Species (in alphabetical order)	Ratio (OL/TL) ×100 (%)		Percentage variation of the Ratio (OL/TL)×100 during growth
	Juvenile	Adult	
"*Coelodus*" *danae*	14.3	10.0 (1)	— 4.3
Flagellipinna rhomboides	20.9	10.5	— 10.4
Gara Sbaa undetermined species	19.2	9.9	— 9.3
Gregoriopycnodus bassanii	19.6	11.0	— 8.6
Njoerdichthys dyckerhoffi	18.5	10.4 (2)	— 8.1
Nursallia veronae	19.0	7.4	— 11.6
Paranursallia gutturosa	14.1	7.0	— 7.1
Pseudopycnodus nardoensis	11.8	7.0	— 4.8
Pycnodus apodus	15.2	6.1	— 9.1

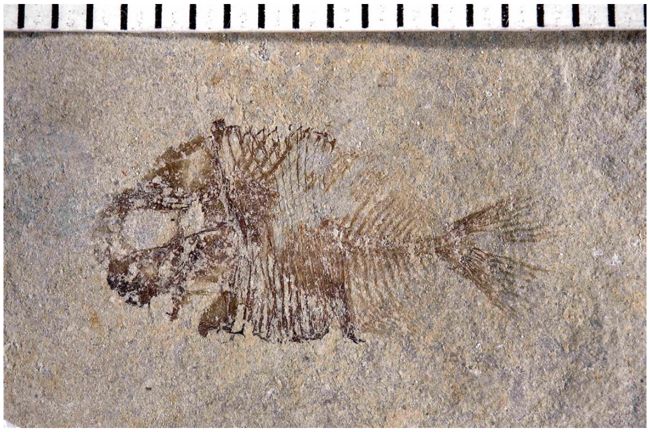


Figure 8. The smallest pycnodont known today is this specimen belonging to the species "*Coelodus*" *danae*, from the Early Cretaceous limestone of Profeti, Caserta, southern Italy, with Total Length = 14 mm (MPUN – Pr.55). Courtesy of Maria Carmela Del Re.

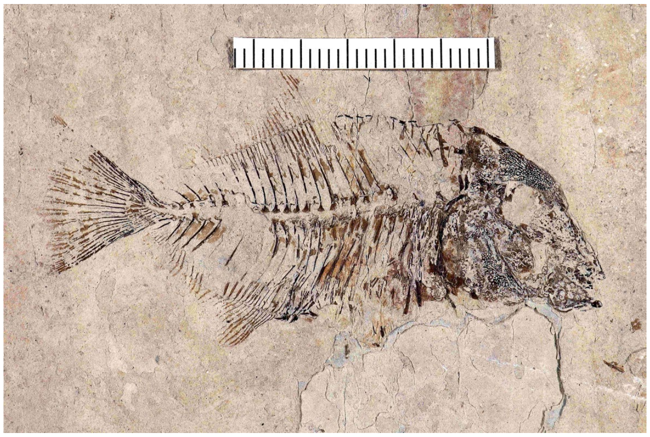


Figure 9. "*Coelodus*" *danae*, from the Early Cretaceous limestone of Profeti, Caserta, southern Italy: an adult individual of male morphotypes (MPUN – Pr.75). Courtesy of Maria Carmela Del Re.

In regards to *Gregoriopycnodus*, a special auxological pattern was observed, opposed to that described in other pycnodonts (Figures 12, 13): the juvenile specimen was more elongated, with a longer body, and the head was also slightly more prominent forward. Indeed, the measurement of the total depth of the body in the adult was 67.9% of the standard length, while in the juvenile, it was 65.2% of the standard length. Even the head was a little more elongated in the juvenile: in adults, the length of the head was 26.9% of the total length, while in the juvenile it was 29.4%. Finally, also in the case of *Gregoriopycnodus bassanii*, on the basis of the large number of specimens examined by Taverne *et al.* (2020), the tendency towards the progressive auxological reduction of the relative dimensions of the orbit was confirmed (Figures 12, 13): greater in juvenile subjects (19.6% of the TL) than in adults (11.0% of the TL), as is evident from the examination of the biometric data shown in Tables 3 and 4.

In addition, there were differences also at a morphological level. First, for the juvenile specimen, I noted how the arcocentra of the pre-caudal region was underdeveloped which left a large portion of the notochord uncovered; in the adults, on the other hand, the notochord was almost completely covered in this region. This is certainly a well explainable characteristic that is typical of skeletal immaturity of juvenile subjects, notwithstanding possible interference deriving from neoteny. Furthermore, the frontal profile of the fish also changed with age: in the adults, the anterior margin of the frontal bone and the mesethmoid was much more vertical than in the juvenile.

Finally, we were also able to compare the dental characteristics, given the high number of dentitions, especially vomerine, that were dispersed in the strata in the Pietraroja site (Figures 14, 15). As demonstrated by Capasso (2021a), I can assert that the dentitions of smaller

Figure 10. "*Coelodus*" *danae*, from the Early Cretaceous limestone of Profeti, Caserta, southern Italy: an adult individual of female morphotypes (MPUN – Pr.73). Courtesy of Maria Carmela Del Re.

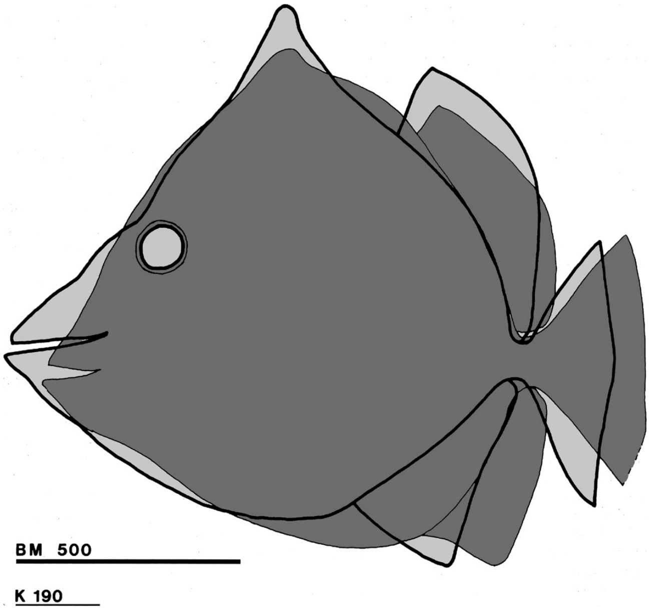


Figure 11. Outline of the largest (BM, with total length = 500 mm) and smallest (K, with total length = 190 mm) specimens of *Arduafrons prominoris*, compared to illustrate the proportional changes due to morphological variations in the body shape that occurred during growth. Modified from Nursall (1999).

Figure 12. *Gregoriopycnodus bassanii* from the Early Cretaceous of Pietraroja, southern Italy: a juvenile subject (standard length = 40 mm) (LCPC # A-15).

Figure 13. *Gregoriopycnodus bassanii* from the Early Cretaceous of Pietraroja, southern Italy: an adult subject (standard length = 380 mm) (LCPC # I-215).

sized subjects, as probably younger types, showed less teeth (six in young, eight in adult specimens) pertaining to the central vomerine row; in addition, in younger individuals the teeth were very well spaced from each other, even in the same row.

Examples of skeletal growth and maturation phases: The case of Phacodus *sp. ind.*—Cavin *et al.* (2020) described a fragment of prearticular and a fragment of vomer referred to cf. *Phacodus* that were collected from the Lower Campanian, Late Cretaceous, continental deposits of the Villeveyrac (L'Olivet site, southern France). The specimens were very small in size and corresponded to tiny individuals of pycnodonts, presumed juvenile. The differences between these juvenile speci-

Figure 14. Vomerine dentition of *Gregoriopycnodus bassanii*, from the Early Cretaceous of Pietraroja, southern Italy: a juvenile specimen with few dental elements in each row and the presence of diastemas between the teeth (LCPC # I-32).

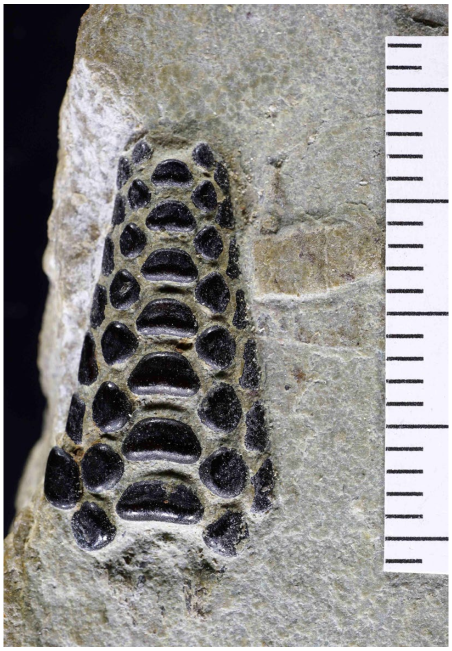


Figure 15. Vomerine dentition of *Gregoriopycnodus bassanii*, from the Early Cretaceous of Pietraroja, southern Italy: an adult individual (LCPC # I-77).

mens and the adults are in their general dimensions, in the lower number of teeth, and in the larger diastema between the teeth of the same row.

Examples of skeletal growth and maturation phases: The case of Coccodus insignis.—Taverne and Capasso (2014) reported that in juvenile subjects of *Coccodus insignis* there is a small intermediate spine located between the two posterior spines of the cleithrum; this accessory plug disappears in adults. Furthermore, adult individuals have a more tapered general body shape; in fact, by relating the total depth (in the case of *C. insignis* the TD was replaced with the maximum distance between the apices of the lower spines of the cleitra) (×100) with the standard length, I obtained a value of approximately 66.7% in juvenile subjects (Figure 16), and approximately 47.8% in adults (Figure 17; Table 2).

Examples of skeletal growth and maturation phases: The case of the indeterminate species from Gara Sbaa, Morocco.—Cavin *et al.* (2010) first described the fossil fish complex from the laminated Cenomanian dolomitic limestones of Gara Sbaa, (Kem Kem Valley, Morocco) where they also reported the presence of unidentified pycnodonts, and Capasso (2020) identified the presence of *Paranursallia guttorosa*. However, a large sample of finds concerns a new and characteristic species that is currently being studied from a taxonomic point of view by myself and my colleague Louis Taverne. This population sample is characterised by a significant number of young, small or very small sized specimens, which offers the possibility to consider some aspects of growth of not only the skeleton, but of some soft organs which are exceptionally well preserved. For these reasons, it is very interesting to cite here some of my preliminary observations concerning the possible phases of growth of the soft organs of the pycnodonts. At Gara Sbaa, the bones were generally poorly preserved, including those of fossil fish. Instead, and exceptionally, some soft tissues were well preserved. Among these, the sometimes perfect conservation of the eyeballs stands out. Beyond the anatomical characterization of these remains, which might become part of the systematic and taxonomic study of the new species, the presence of a large number of juveniles in the Gara Sbaa pycnodont population allowed for a comparative assessment of the state of development of the eyeballs in the young compared to the adults, which represents an absolutely exceptional condition.

First of all, there were no morphological differences, and the ocular bulbs have a somewhat circular profile in both adults and young. The position of the eyeball inside the orbit is also the same: the eye occupies the central part of the orbit, although it is in contact with the upper edge. The differences are metric: in the young (Figure 18), the eyeballs are proportionally larger than in the adults. In the adult shown in Figure 19 (TL = 81 mm), the total length of the orbit is 7.7 mm; in the juvenile shown in Figure 18 (TL = 26 mm), the total length of the orbit is 5 mm. Simi-

Figure 16. *Coccodus insignis*, from the Cenomanian of Haqel, Lebanon: a juvenile individual (LCPC # S-399).

Figure 17. *Coccodus insignis*, from the Cenomanian of Haqel, Lebanon: an adult individual (LCPC # S-161).

lar proportions were also noted in other individuals, and this allowed us to confirm that in the juveniles, the orbit has a size that represents about 19.2% of the TL, while in adults, it represents only about 9.9% of the TL. This is a significant difference, which highlights how in the young pycnodonts collected in this site, the orbit (and consequently, the eyeballs) showed relatively greater development compared to adults (Figures 18, 19).

In addition, the same somatometric pattern, which was observed and described in the majority of the other pycnodonts, is repeated for this indeterminate species from Gara Sbaa (Figures 18, 19): the juvenile specimen was shorter and taller, overall stockier than that of the adults. Indeed, the measurement of the maximum depth of the body in the adult was 55.6% of the standard length, while in the juvenile it was 69.6% of the standard length. The head was also a little more elongated: in adults the length of the head was 32.1% of the total length, while in juveniles it was 30.8% (Table 3).

Summarising, also for this undetermined species I confirm the existence of a growth pattern of Auxological Increasing of Fineness Ratio (AIFR).

Examples of skeletal growth and maturation phases: The case of Gyrodus hexagonus.—Lambers (1991) described a series of auxological changes also in *Gyrodus hexagonus* of the Late Jurassic of the Solnhofen area (Germany), which are more or less the same as those described by Nursall (1999) for *Arduafrons prominoris* collected in the same site. Also in this case, Lambers (1991) suggested that the differences between juveniles and adults are linked to maturation and growth into the two morphotypes, which represent the two mature morphologies linked to both sexes.

Examples of skeletal growth and maturation phases: The case of Apomesodon gibbus.—Poyato-Ariza and Wenz (2002) reported a variation in the number of axonosts of the dorsal fin in *Apomesodon gibbosus*: in a smaller specimen (SL = 100 mm) there were 30 axonosts, while in a larger specimen (SL = 360 mm) there were 37 axonosts. Consequently, this appeared to be linked to the length of the specimen, and therefore to age as Poyato-Ariza and Wenz (2002) commented: "the number of dorsal axonosts increases with age, a feature that is highly unusual in actinopterygian". However, this condition has not been observed in other genera (e.g. *Macromesodon, Proscinetes*). These variations between the number of axonosts and the size of the fish are observed, however, only in the dorsal fin and not in the anal fin, also in the same genus *Apomesodon*.

Examples of skeletal growth and maturation phases: The case of Njoerdichthys dykerhoffi.—Recently, Cawley *et al.* (2020) illustrated a juvenile specimen of the new species *Njoerdichthys dyckerhoffi*, from the Turonian (Late Cretaceous) of the Lower Saxony, (Germany). On the basis of the high definition images kindly supplied by J. J. Cawley, it would appear that also in this case the juvenile

Figure 18. An indeterminate species of pycnodont from the Cenomanian dolomitic limestone of Gara Sbaa, Morocco: a juvenile individual (standard length = 26 mm) with a large relative size of the remains of the eyeball (LCPC # S-1009).

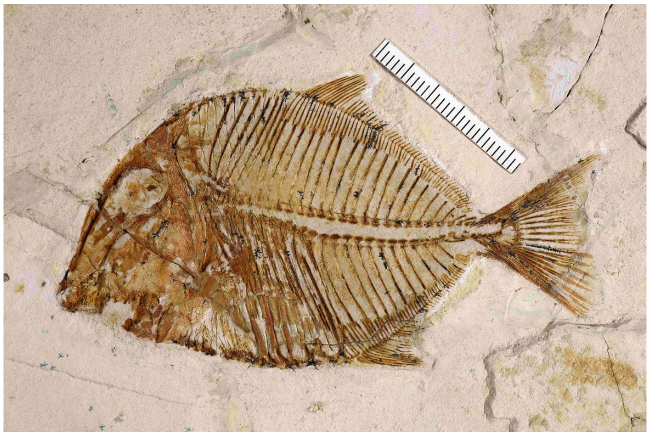


Figure 19. An indeterminate species of pycnodont from the Cenomanian dolomitic limestone of Gara Sbaa, Morocco: an adult individual (standard length = 81 mm) (LCPC # S-1227).

specimen is characterised by a more vertical front profile, featuring a slit of the mouth facing downwards instead of frontwards, even if these morphological differences might be correlated with or emphasised by taphonomic distortions. Certainly, also in the case of *N. dyckerhoffi*, the juvenile specimen shows a proportionally much larger orbit than the adult individuals of the same species (Figures 20, 21). In fact, the length of the orbit represents about 18.5% of the TL in the youngest specimen, while in the adult it represents only 10.4% of the TL (although the TL of the adult was estimated on the basis of a reconstruction of a partial individual) (Tables 3, 4).

The juvenile specimen of the *Njoerdichthys dyckeroffi* species has a short body morphology, with a relatively high trunk; in contrast, adults have a relatively elongated body shape. Indeed, this is the same situation that characterises most of the cases considered in this paper, thus corresponding to a growth pattern of Auxological Increasing of Fineness Ration (Table 3).

Examples of skeletal growth and maturation phases: The case of Nursallia veronae.—The species *Nursallia veronae* was first described in 1987 by Blot on a single adult specimen (TL = 298 mm) conserved at the Civic Museum of Natural History of Verona (no. II-D-173-Vr). In recent times, my colleague Martin Ebert has identified a second specimen, certainly juvenile (TL = 21 mm) in the collections of the Field Museum of Natural History in Chicago which, thanks to the collaboration of William Simon, has also allowed me to perform a first auxological evaluation on this very rare pycnodont of the Ypresian of Monte Bolca (Figures 22, 23). The juvenile specimen has an almost perfect circular lateral outline, much shorter and taller than the adult holotype. Indeed, the measurement of the maximum depth of the body in the adult was 77.5% of the standard length, while in the juvenile, it was 94.7% of the standard length (Table 3).

Furthermore, in this species the reduction of the dimensions of the orbit associated with the progress of aging is very evident: the maximum length of the orbit, in fact, represents as much as 19.0% of the TL in the juvenile, while it drops to about half of this value, i.e., 7.4%, in the adult holotype (Table 4).

Examples of skeletal growth and maturation phases: The cases of Paranursallia gutturosa.—*Paranursallia gutturosa* was first described in the Cenomanian deposit of Jebel Tselfat, Morocco by Arambourg (1954). In this location *P. gutturosa* is abundantly found and a preliminary examination of a few dozen specimens allowed me to observe the presence of two different morphotypes that could correspond to both sexes (Capasso, 2023). *Paranursallia gutturosa* has also recently been reported in a second location in Morocco: the Cenomanian dolomitic limestones of Gara Sbaa, in south-eastern Morocco (Capasso, 2020), and has also been reported in many locations of the Cenomanian of Italy: Floresta, Sicily (Leonardi, 1966), Passo del Furlo, Marche (Capasso, 2007), and Bomba Quarry, near Cinto Euganeo, Veneto (Amalfitano *et al*., 2020). Finally, a real population of *P. gutturosa* was recently identified in the limestones of Vallecillo, Nuevo Leon, Mexico, dated to the final Cenomanian-middle Turonian (Stinnesbeck *et al*., 2019).

Despite this truly transcontinental geographic distribution, *Paranursallia gutturosa* shows strict morphological constancy. The only differences recorded between the specimens of the different locations are those of a dimen-

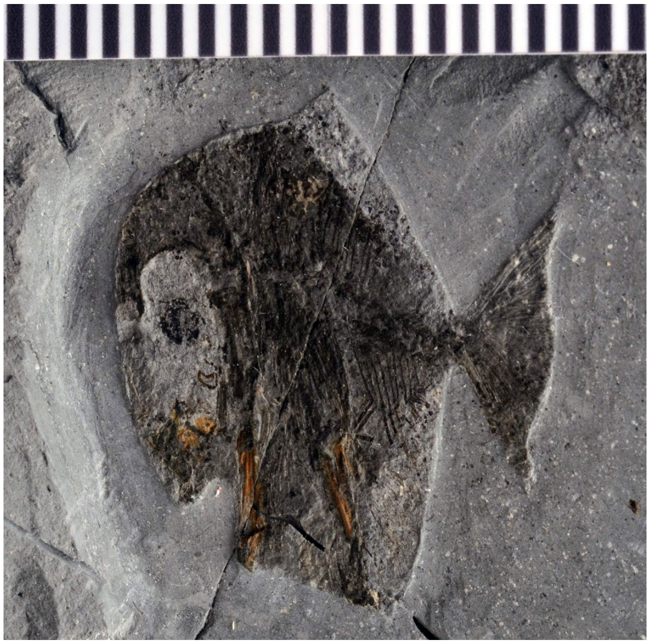


Figure 20. *Njoerdichthys dyckerhoffi*, from the Turonian (Late Cretaceous) of the Lower Saxony, Germany: a juvenile individual. Courtesy of J. J. Cawley (GSUB # V-2303).

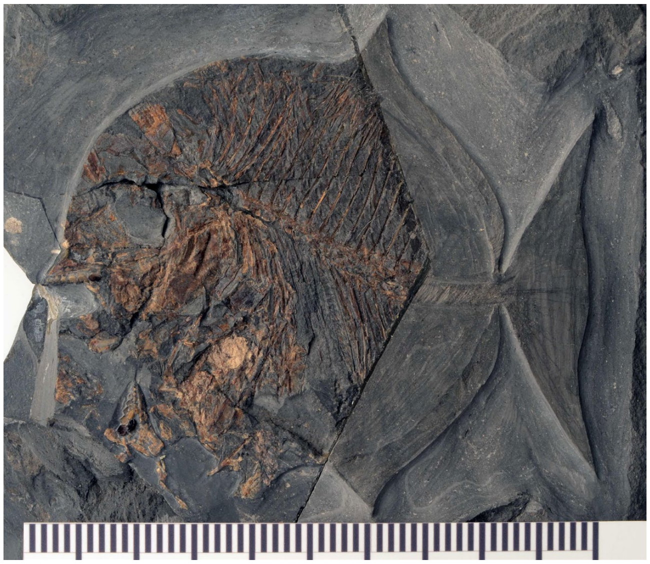


Figure 21. *Njoerdichthys dyckerhoffi*, from the Turonian (Late Cretaceous) of the Lower Saxony, Germany: an adult individual. Courtesy of J. J. Cawley (GSUB # V-2304).

Figure 22. *Nursallia veronae*, from the Ypresian (Eocene) of the Monte Bolca, Italy: a juvenile individual. Field Museum of Natural History in Chicago, no. FMNH – PF 3256, courtesy of William Simpson (FMNHC # PF-3256).

Figure 23. *Nursallia veronae*, from the Ypresian (Eocene) of the Monte Bolca, Italy: an adult individual. Holotype of the Museo Civico di Storia Naturale di Verona, no. II-D-173-Vr., courtesy of Stefano Pisani, Musei Civici di Verona (Italy) (MCSNV # II – D – 173 – V).

sional order. Indeed, much larger dimensions have been observed in the populous colony of Vallecillo, Central America, than those observed in the Tethys area. In fact, Stinnesbeck *et al.* (2019) demonstrated that out of a sample of over 90 individuals of *P. gutturosa*, most of the specimens had a total length between 100 and 150 mm (18 specimens), but at least one third of the individuals had a total length between 300 and 400 mm, while some specimens (although incomplete) had a total length of 650 mm or more, which can be interpreted as truly gigantic for this species (Figures 24, 25).

In regards to the Vallecillo population, thanks to the large number of specimens collected and their good state of conservation, a detailed observation of the taphonomic processes of this population was possible, including the possibility to detect the presence of two different morphotypes characterised by a conspicuous difference in length of the dorsal fin, which have been interpreted as possible sexual variants (Stinnesbeck *et al.*, 2019).

Nevertheless, "Size distribution identified in the Vallecillo specimens does not result from sexual dimorphism, e.g. small individuals being females and large individuals being males" (Stinnesbeck *et al.*, 2019). However, these same authors did not conduct a detailed examination of possibly growth-related morphological and biometric variations. I also managed to access two specimens of very different dimensions from this same location, one with TL = 99 mm and one with TL = 370 mm: a difference that could only be documented in the Vallecillo population. The results of the biometric evaluations, including the calculation of the main somatic indices, are reported in Table 3. I noted that, as in the majority of the pycnodonts that I have been able to analyse in this study, the species *Paranursallia guttorosa* also shows a somatic growth pattern in which juvenile subjects have a more rounded body and tend to become more elongated in the adult stage (Fineness Ratio increasing during growth pattern). Furthermore, in *P. gutturosa* the tendency to reduce the dimensions of the orbit while increasing in age is very evident: in juveniles I observed that the length of the orbit represents about 14.1% of the TL, while in adults this value decreases to below half (7%) (Table 4).

Examples of skeletal growth and maturation phases: The cases of the gular scales.—The presence of scales or bone tesserae covering the snout, cheek, and gular region represents a distinctive character, of high taxonomic value for the Pycnodontomorpha of the order Gyrodontiformes. Nonetheless, this trait may occasionally appear also in some species belonging to the order Pycnodontiformes.

Nursall (2010) reported that in species pertaining to Pycnodontidae, the snout, cheek and gular regions in adults are naked, while juvenile specimens (or in any case regarding immature individuals), often have scattered, vestigial scales on the cheek, which are gradually lost during growth.

Dental growth and maturation phases

The dentition of the pycnodonts has been considered unique by many authors, in the sense that the set of teeth of a given individual are the result of a single dental generation. However, this view does not explain the following two problems: (i) how the dentition of a young and a sub-adult specimen, which is evidently made up of fewer and smaller teeth than the adult (see Figures 14, 15), reaches the anatomical maturity and functionality of the adult; and (ii) whether, and in what way the worn teeth, due to their use in chewing, are replaced (alternatively, how can an individual survive when their teeth are so

Figure 24. *Paranursallia gutturosa*, from the Turonian (Late Cretaceous) of Vallecillo, Mexico: a juvenile individual. Paleontological Collection of the University Museum of the State University "Gabriele d'Annunzio, Chieti, Italy, no. MSUC # 213804.

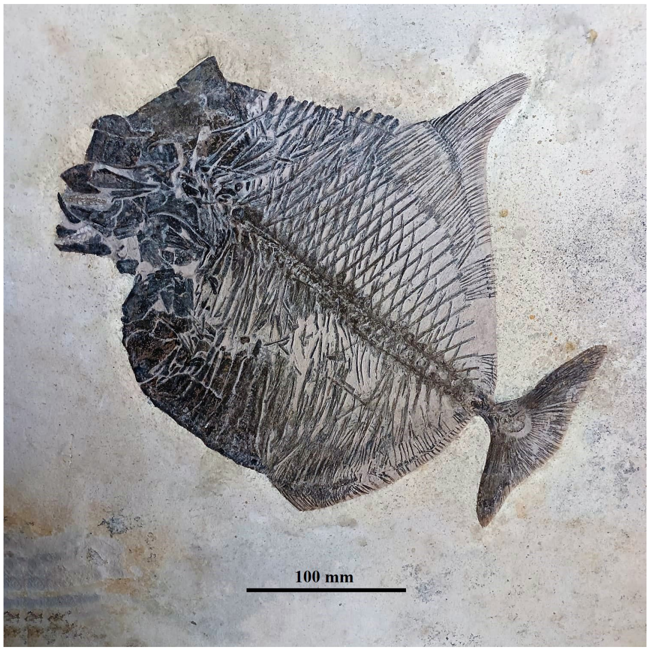


Figure 25. *Paranursallia gutturosa*, from the Turonian (Late Cretaceous) of Vallecillo, Mexico: an adult individual. Paleontological Collection of the University Museum of the State University "Gabriele d'Annunzio, Chieti, Italy, no. MSUC # 213805.

worn and ultimately become useless for chewing)?

These two problems refer to two separate and quite distinct phenomena: (i) the growth and maturation of dentition, which reaches the configuration of adult dentition through an auxological process that has set stages and modalities and characteristics for each species; and (ii) the possibility that some (or even all) of the individual teeth might be replaced after the final configuration has been reached when the auxological process has ended; i.e., when the typical configuration of the adult is attained. The second of these can only be realised if the ameloblasts (cells responsible for the synthesis of dental crowns) persist also in the adults. Thus, the first phenomenon relates to the auxology of the dentition, while the second relates to dental replacement.

Woodward (1895) suggested that new teeth are added to the dentition from behind in pycnodonts, and this mechanism would also be the basis for the growth of dentition, which would enable the size of the dental sets to increase along with auxological growth processes. Nursall (1996b) also assumed that there was a single generation of teeth, and new teeth are added to the dentition from behind, just during the growth of each individual.

In support of this hypothesis and of this growth model, data have now been collected concerning the wear patterns of adult dentition, above all through an extensive analysis by Kriwet (2005) on a large number of pycnodont dental apparatuses, both of prearticular and of vomer. As he stated: “wear patterns first occur on anterior teeth and then move posteriorly to the larger posterior teeth with age. Consequently, anterior teeth are mostly smooth, whereas posterior teeth exhibit their original ornamentation. The tooth ornamentation is generally well preserved in juvenile specimens; the ornamentation of teeth is completely lost in senile specimens”. This pattern of dental abrasion can be easily explained by noting that the anterior teeth, both prearticular and vomerine, erupt first, and therefore are used for chewing for a longer time compared to the posterior teeth which erupt later in the life of the same individual, and therefore are less worn. So the model proposed by Woodward (1895) to explain the growth of dentition in pycnodonts during auxological processes agrees with the theory of single dental generation, with progressive addition of new dental elements from behind. This model was supported by both Thurmond (1974) and Nursall (1996a).

It thus appears that in the pycnodonts there was a growth pattern of dentition that allowed the anterior teeth (which were mobile and prehensile) to grow locally at the expense of the dental gems in the dental bones and in the premaxillae, while the posterior teeth grew to reinforce the new teeth from behind. In my opinion, a very similar model is observed in manatees (Capasso, 2021b): these have no incisor or canine teeth anteriorly, but just a set of cheek teeth, which are not clearly differentiated from a morphological point of view. The molar teeth, however, are continuously replaced throughout their life with new teeth that grow at the rear as the older teeth fall out forwardly in the mouth (Capasso, 2021b). This process is called “hind molar progression” or “marching molars” (Whitlock *et al*., 2013).

At the same time as the growth phenomena however, cases of tooth replacement are also well documented. For example, in describing the new species of pycnodont *Akromystax tilmachiton* of the Cretaceous of Lebanon, Poyato-Ariza and Wenz (2005) identified a specimen in which some dental gems were present inside the bones. These included two teeth: one located in the prearticular, posteriorly, which was interpreted as a tooth in development that was about to be added to the series of prearticular teeth from behind; the other was located below a tooth that had already erupted within the dental bone, and was interpreted as a case of replacement. However, the described model does not exclude the hypothesis that worn teeth had the possibility of being replaced, which must be expected above all for the front teeth.

In fact, I have recently been able to provide the definitive demonstration that pycnodonts are polyphyodont animals, through radiographic highlights of dental gems in various states of maturation. These gems were present in both the prearticular and the vomer of at least some of the Cretaceous genera, such as *Neoproscinetes* and *Phacodus*, and in one Eocene genus, *Pycnodus* (Capasso, 2021a). For the first time, I used classical radiographic techniques as well as micro-tomographic techniques on fossil remains of pycnodonts, which clearly demonstrated how the dental gems are invariably present, even in subjects where the maximum body size had been reached, as foreseen by the respective species, and which therefore must be considered adults (Figures 26, 27). Based on the radiographic evidence, I confirmed that polyphyodonty in pycnodonts involved differentiated auxological mechanisms in young subjects compared to adults (Capasso, 2021b).

All these new data provide palaeontological evidence that demonstrates how the replacement of worn, deciduous teeth by newly formed dental gems was common to many species and genera of the pycnodonts. This also seems to be a frequent observation, as whenever numerous samples are available, concrete evidence can be found in support of dental replacement. In summarising all these observations, it can be clearly stated that the pycnodonts were polyphyodonts (Capasso, 2021b).

Possible signs of aging

The skeleton of pycnodonts remained in a backward

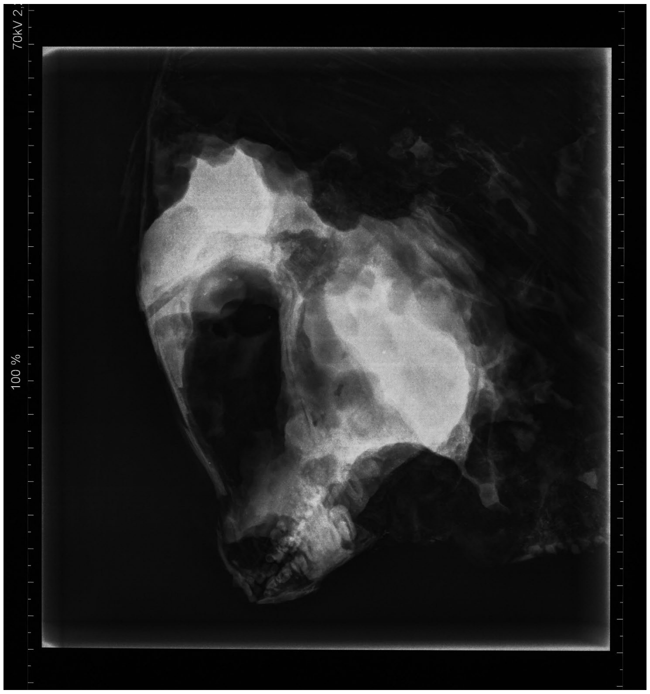


Figure 26. X-ray taken in lateral-lateral projection of the head region of an adult specimen of *Neoproscinetes penalvai* (Cretaceous, Brazil), TL = 370 mm; note the presence of dental gems both at the premaxillary level and at the level of the vomer. Note also how the dental gems in the vomer are particularly abundant, and also occupy the upper part of the bony lamina that connects with the parasphenoid; it should also be noted how the dimensions of these dental gems in the context of the vomer present extensive variable dimensions, demonstrating different degrees of development and maturation. LCPC # S-1935.

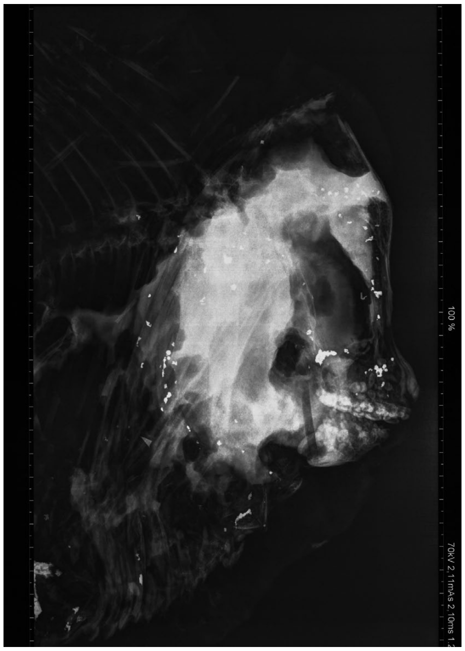


Figure 27. X-ray taken in lateral-lateral projection of the head region of an adult specimen of *Neoproscinetes penalvai* (Cretaceous, Brazil), TL = 360 mm; note the presence of dental gems both at the premaxillary level and at the level of the vomer. University Museum of Chieti, MSUC # 20089.

stage of maturation even in adults, which did not allow us to use the morphology of the skeleton as a whole, nor that of the individual bones that compose it, to search for possible alterations linked to aging. Therefore a careful investigation of the specimens' teeth provided us with some indication in this regard.

First of all, I observed that the worn teeth of pycnodonts are well known. These mainly regarded all posterior teeth with an abraded chewing surface, furrowed by deep striations due to extensive chewing of very hard foods (Figure 28). This wear could lead to the disappearance of the enamel: the crown, in this case, appeared incomplete, i.e., the highest part of the masticatory surface had disappeared through a process that produced microtraumas, without violent detachments, but with rounded edges (Figure 29). These teeth may have simply been waiting to be replaced by new teeth underneath, and this is a characteristic of polyphyodont animals. Equally however, this possibility couldn't last indefinitely, as the ameloblastic tissue tends to disappear, depleting itself with the aging process of the individual. In this regard however, we have no data (at the moment) of the extent of this phenomenon. For example, we do not know if the persistence in adults of ameloblastic cells and tissue was common to many or all of the pycnodonts, or if the phenomenon was restricted hypothetically to a certain period of time. Above all, we do not know how long the amelogenetic capacity persisted in the adults, over their lifespan. For some fossil reptiles of the Cretaceous (e.g. *Tyrannosaurus*), it has been demonstrated that when the amelogenetic potential ceases, the individual dies because it can no longer eat. This is due to the fact that worn and fallen teeth are no longer replaced, meaning that the dentition becomes ineffective to capture and eat any prey (D'Anastasio *et al*., 2002).

In this regard, a particularly preliminary study that was conducted on a single prearticular specimen with few teeth (*Globoanomoeodus*, from the Cretaceous of Texas) allowed me to identify some radiological characteristics that could presumably configure the appearance of dental senescence in pycnodonts (Capasso, 2021b). This specimen (Figures 30, 31) is characterised, among other things, by (i) a small number of teeth, with (ii) shapes and (iii) dimensions that are very different from each other, and which (iv) have almost completely lost their characteristic arrangement of ordered rows. Conventional radiographic examination of this specimen also demonstrated

Figure 28. Pycnodonts' dental wear. Isolated tooth of *Gyrodus jurassicus* from the Kimmeridgian of Solothurn, Switzerland: the tooth has a flattened occlusal surface, affected by deep striations, with a thinned and translucent dentin layer, so as to show the underlying pulp cavity (LCPC # S-1999).

Figure 29. Some isolated teeth of *Anomoeodus* sp. ind. from Upper Cretaceous-Eocene of Malyn, Zhitomir, Ukraine: the teeth show subcircular perforations of the most apical part of the crowns, consistent with the results of advanced dental wear (so-called "*perforating wear*") (LCPC # S-2017).

Figure 30. Inner face of left prearticular, with dentition, of *Globanomoeodus dentespassim* from the Del Rio Formation, of the Cenomanian of Waco Lake, Texas, U.S.A. (LCPC # S-1839).

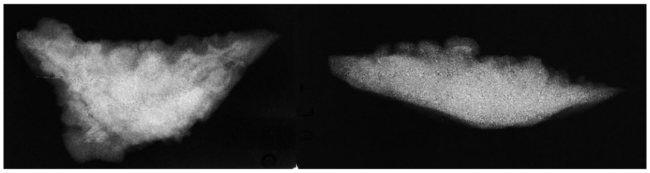


Figure 31. Radiographs of the same specimen of Figure 30, showing the total absence of dental gems, the extreme thinness of the bone, and the atrophy of the spongy tissue, with the collapse of the cortical bone of the external and internal surfaces, both in lateral projection (left) as in dorso-ventral projection (right). These are all radiological signs of the exhaustion of ameloblastic activity, and the atrophy of the old bone, indicating the possible advanced age of the individual.

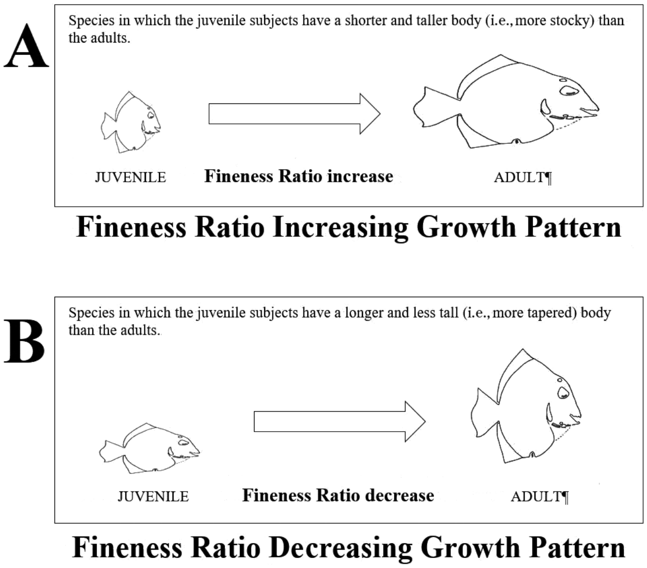
changes in the bone: the extreme thinness of the bone, and the atrophy of the spongy tissue, due to the collapse of the cortical bone of the external and internal surfaces. Overall, these are all radiological signs of atrophy, typical of old bones. The sum of these characteristics, both dental and skeletal, define an 'atrophic' prearticular specimen, which is fully compatible with the dentition of an old individual. In addition, the ameloblastic activity might have been exhausted and thus only few residual teeth survived, arranged in a rarefied and disordered way, while at the same time the bone that supported them became hypotrophic (Capasso, 2021b).

In conclusion, having ascertained that the ameloblastic activity that leads to the formation of the first dentition in juvenile subjects continues for a long time even in the adult, I will have to consider the possibility that at least part of the dental characteristics of the pycnodonts might be linked to the variability of aging, rather than genetics, with the resulting taxonomic reflexes. Only an extensive examination of a large quantity of finds will make it possible to at least carry out further studies so as to provide answers to these new questions in the future, from this new viewpoint.

Discussion

Although the total number of pycnodont species examined here is relatively low, this first study demonstrates that most of the differences, both morphological and biometric, between juvenile subjects and adult subjects belonging to the same species are not constant, but generally vary from one species to another.

In most species (i.e., *Coccodus insignis*, "*Coelodus*" *danae*, Gara Sbaa undetermined species, *Njoerdichthys dyckerhoffi, Nursallia veronae*, *Paranursallia gutturosa*, *Pseudopycnodus nardoensis* and *Pycnodus apodus*) the younger individuals have a body shape with a rounded lateral profile; they are characterised by a relatively less lengthy and elevated body, compared to the corresponding adults which have a more tapered body that is more elongated and less elevated. This condition (Figure 32A) is reflected in a biometric datum based on the proportion obtained between the total depth of the body (TD) with respect to both the standard length (SL) and the total length (TL), which also results in the calculation of the Fineness Ratio. In fact, in the species whose juveniles have a shorter and taller appearance, the relative indices show lower values in young subjects than in adults. However, despite the fact that this condition is present in eight of the species examined, in the two remaining species (*Flagellipinna rhomboides*, *Gregoriopycnodus bassani*), the exact opposite situation occurs (Figure 32B). In summary, two growth patterns were observed: (i) an auxological decrease of the fineness ratio, that involved just two studied genera, and (ii) an auxological increase of the fineness ratio, that involved the remaining part (eight cases) of the studied genera. These variations are also reflected in the relative proportions of the length of the head compared to the total length of the body, confirming that there are two subgroups of pychnodonts: one in which somatic growth involves a sort of "lengthening" of body proportions, the other in which the opposite occurs.



Species in which the juvenile subjects have a shorter and taller body (i.e., more stocky) than the adults.

Fineness Ratio Increasing Growth Pattern

Species in which the juvenile subjects have a longer and less tall (i.e., more tapered) body than the adults.

Fineness Ratio Decreasing Growth Pattern

Figure 32. Two growth patterns were observed in the examined species of pycnodonts. **A**, the model with an auxological increase in fineness ratio, observed in the species *Flagellipinna rhomboids* and *Gregoriopycnodus bassani* in Table 3 and **B**, the model with auxological decrease in fineness ratio, observed in species *Coccodus insignis*, "*Coelodus*" *danae*, Gara Sbaa undetermined species, *Njoerdichthys dyckerhoffi*, *Nursallia veronae*, *Paranursallia gutturosa*, *Pseudopycnodus nardoensis* and *Pycnodus apodus* in Table 3.

The only parameter that undergoes variations in all the species studied here is the size of the orbit: invariably the juveniles have larger orbits than the corresponding adults. In fact, the ratio between the maximum length of the orbit (OL) and the total length (TL) takes on conspicuously higher values in juveniles than in adults, among all the species examined (Table 4). Nevertheless, in some species I observed a very significant reduction in the relative dimensions of the orbit during growth: in *Nursallia veronae* and in *Pycnodus apodus*, the only species of Eocene age, in the undetermined species in Gara Sbaa, and in *Flabellipinna rhomboids*, as in *Paranursallia gutturosa* of the Late Cretaceous, the relative dimensions of the orbit are almost halved during growth. In other species, the reduction is much less (*Pseudopycnodus nardoensis*). Nonetheless, I can assert that the reduction in the dimensions of the orbit is an auxological characteristic (the only one demonstrated up to now) which is present in all pycnodonts.

The differences between juveniles and adults both in the general shape of the body and in the dimensions of the orbit have been the object of possible interpretations, at least as regards the genera *Flagellipinna* and *Pycnodus*. In fact, Cawley *et al.* (2018) asserted that the small morphological differences between the young and the adults of the species *Pycnodus apodus* of the Eocene of Bolca might have also led to differences in habitats, in the sense that juvenile individuals occupied different habitats from the adults, as still happens today for some fish species that are characteristic inhabitants of coral reefs: "The morphological differences between juvenile and adults may be due to the occupation of different habitats with juveniles sheltering among cover and adults being better adapted to a roaming lifestyle, swimming over the benthos to feed."

In general, Goatley *et al.* (2010) reported that the large eye size of the pycnodonts was related to behavioral flexibility and possible nocturnal behavior. On the other hand, in many species of Acticopterygii, both living (Pankhurst and Montgomer, 1990) and fossils (Cloutier, 2010), the juvenile forms are specifically characterised by the different proportions of the various parts of the body. In this study, the orbit size was relatively prevalent, regardless of the environment occupied by the various species, and above all, by any nocturnal habits of the younger and immature forms.

Although supported by comparisons with some current species (i.e., *Gomphosus varius*, cited by Myers, 1999), the hypothesis that the morphological differences demonstrated between the juvenile and adult stages of these pycnodonts are an expression of adaptations to different environments and to different eating habits does not really seem sustainable in light of the auxological laws currently accepted by the scientific community. The process of functional maturation and anatomical growth of juveniles represents an asynchronous process by organs and apparatus; this implies that the rhythms and methods of growth of the individual parts of the same body, as well as of the individual organs and systems (which also corresponds to maturation of individual functions related to the individual anatomical structures) are different. Thus, each organ and each system grows with different modes and speeds. This means that every organ, every apparatus, every part of the body will have its own growth curve, which will not coincide with the general growth curve of the whole organism; of the overall body dimensions. This implies that some organs or parts of the body will reach their maximum development before others, which will create specific body proportions that characterise each evolutionary stage, and which will not correspond to those of the adults. This implies that growth as a whole occurs at different times and in different ways within each individual. In general, growth that is differentiated by apparatus or body section is not affected by environmental factors, except when reduced food intake or pathological conditions result in a generalised slow down of growth.

The growth of living beings as an asynchronous phenomenon is regulated by general laws that have been validated for all animals, and that are homogeneous at least in vertebrates (West *et al.*, 2001), including fish (Kimura, 1980). Certainly there are some possible exceptions, and there are really no reasons to suggest that the pycnodonts might have escaped these general laws, which have indeed also been verified with regard to the growth of a large number of fossil fish species (Cloutier, 2010). Thus, at the moment there is no evidence to show that these general laws of body growth do not apply to the pycnodonts, or apply differently, and the arguments put forward by both Cawley *et al.* (2018) for *Pycnodus apodus* and Cawley and Kriwet (2019) for *Flagellipinna rhomboides* do not seem convincing to the author. To all this I must add that Cawley and Kruwet (2019) based their observations (and consequently their inferences) on measurements performed on a subject erroneously considered juvenile, but in reality was almost adult. Finally, more convincingly, both the young and the adults fossilised in the same geological facies, and this clearly indicates that they shared the same habitat.

The differences between juveniles and adults have also been examined at the dental level and, also in this case, these differences seem to be common to all the species examined, thus assuming a general auxological value. In particular, I can therefore conclude that the presence of diastemas between the teeth is a juvenile characteristic in many species, and moreover, it is also observed in the genus *Phacodus* of the Upper Cretaceous of Morocco, as well as in the species *Gregoriopycnodus bassanii*, of the Lower Cretaceous of South Italy, and others.

Finally, as regards the process and rhythms of aging, though information collected is very limited and thus does not allow me to draw any conclusions, the first traces of bone hypotrophy have been found, and any in-depth studies on this topic will involve the use of more sophisticated investigation technologies (Computerised Axial Tomography, Nuclear Magnetic Resonance, Micro-tomography) which can be extended to larger samples. Furthermore, as with other polyphyodont species, I identified the first fossil evidence that depletion of ameloblastic activity may have played an important role in causing natural death in aged pycnodonts by interfering with their ability to feed themselves.

Conclusions

The reconstruction of the auxological processes in pycnodonts must necessarily be based on the comparative examination of juvenile and adult specimens certainly belonging to the same species: a rather rare condition which, during the preparation of this article, I was able to verify only for 10 valid species, drawing from literature with some new observations. Although this sample represents a small part of the totality of pycnodonts, some preliminary conclusions can still be drawn, based on both morphological and morphometric comparative findings.

First of all, it can be concluded that most of the metric-type auxological variations do not show the same growth pattern in all the species examined. As far as the general body shape, the most common pattern (which I found in eight out of 10 species) shows that juveniles have a more elevated shape than adults, such as an increasing auxological fineness ratio pattern (Figure 32). However, only two species show an opposite trend, with young individuals having a more tapered body, that is elongated and low; this pattern appears to be rarer and was observed in *Flagellipinna* and *Gregoriopycnodus*. However, it must be emphasised that the case of *Njoerdichthys* is doubtful, since the adult's TL was estimated on a reconstruction; after all, even the case of *Flagellipinna* is somewhat controversial, considering that some authors (Cawley and Kriwet, 2019) hypothesised the presence of a different model. There is no doubt, however, that in *Gregoriopycnodus bassanii* the juvenile individuals have a more tapered body than the adults.

From the overall comparative examination of the biometric and morphological data, only two variables behave in the same way during growth in all the species examined: (i) the morphological dental variable and the (ii) skeletal metric variable. In regards to dentition, especially the vomerine one, I asserted that in young individuals the teeth are separated from each other by a large diastema which tends to decrease as the subject ages. Regarding the metric proportions of the body, as a reflection of sections of the skeleton, the dimensions of the orbit are relatively larger in juveniles than in adults. Even if this variable takes on more accentuated values in some species and less in others, it is constantly present in all the observed species. I have demonstrated the maximum expression of this auxological tendency in *Nursallia veronae*, the minimum in "*Coeodus*" *danae* (Table 4).

As regards changes linked to aging, the information collected is even scarcer, but some trends seem to be already outlined. Even in this case two significant variables were identified: one of the bone type and one of the dental type. At the bone level, I documented the presence of significant bone hypotrophy, with a reduction of the spongy bone and thinning of the cortical bone in the case of almost edentulous pre-articular bone. This hypotrophy is a common feature in many vertebrates and is analogous to senile osteopenia also documented in all mammals. At the dental level, the first case of possible exhaustion of ameloblastic activity was documented. In fact, since pycnodonts are polyphyodont animals, and since the ameloblastic cells persist in the adult in finite numbers, the capacity to replace worn teeth is exhaustible. This phenomenon results in the individual no longer being able to feed itself, leading the elderly subject to death. Naturally, these first observations only represent the starting point for further investigations, which however require new laboratory methods and techniques, in particular radiographic and microtomographic examination of the fossils.

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References

Amalfitano, J., Giusberti, L., Fornaciari, E. and Carnevale, G., 2020: Upper Cenomanian fishes from the Bonarelli level (OAE2) of Northeastern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, vol. 126, p. 261–312.

Arambourg, C., 1954: Les Poissons crétacés du Jebel Tselfat (Maroc). *Notes et Mémoires, Service géologique du Maroc*, vol. 118, p. 1–188.

Blot, J., 1987: L'Ordre des Pycnodontiformes. *Studi e ricerche sui giacimenti terziari di Bolca*, 5, p. 1–211.

Bravi, S., 1996: *Ricerche sui livelli ad ittioliti in facies di piattaforma carbonatica dell'Italia meridionale*, 396 p. Tesi di Dottorato, Università di Napoli Federico II, Naples.

Capasso, L., 2007: Segnalazione dell'Actinopterigio *Nursallia gutturosum* (Arambourg, 1954) nelle radiolariti bituminose cenomaniane del Passo del Furlo, Pesaro. *Atti del Museo Civico di Storia Naturale di Trieste*, vol. 53, p. 187–196.

Capasso, L., 2020: Segnalazione del picnodontiforme *Paranursallia gutturosa* (Arambourg, 1954) nei calcari dolomitici del Cretaceo superiore di Gara Sbaa, Marocco sudorientale. *Atti del Museo Civico di Storia Naturale di Trieste*, vol. 61, p. 153–162.

Capasso, L., 2021a: Pycnodonts: an overview and new insights in the Pycnodontomorpha Nursall, 2010. *Occasional Paper of the University Museum of Chieti*, *Monographic Publications*, vol. 1, p. 1–223.

Capasso, L., 2021b: Pycnodonts were polyphyodont animals. *Thalassia Salentina*, vol. 43, p. 53–70.

Capasso, L., 2023: Biodiversity of †pycnodonts (Actinopterygii) during the Cenomanian–Turonian (Upper Cretaceous). *Historical Biology*, doi: 10.1080/08912963.2023.2221269.

Capasso, L., Del Re, M. C., Bravi, S. and Taverne, L. P., 2021: Sexual dimorphism in a population of Pycnodontiformes of the Aptian (Lower Cretaceous) from Profeti (Province of Caserta, Southern Apennines, Italy). *Bollettino del Museo Civico di Storia Naturale di Verona (Geologia, Paleontologia, Preistoria)*, vol. 45, p. 31–41.

Cavin, L, Garcia, G. and Valentin, X., 2020: A minute freshwater pycnodont fish from the Late Cretaceous of southern France: Palaeoecological implications. *Cretaceous Research*, doi:10.1016/j.cretres.2019.104242.

Cavin, L., Tong, H., Boudad, L., Meister, C, Piuz, A., Tabouell, J. *et al*., 2010: Vertebrate assemblages from the early Late Cretaceous of Southeastern Morocco: an overwiew. *Jounal of African Earth Sciences*, vol. 57, p. 391–412.

Cawley, J. J. and Kriwet, J., 2019: A new genus and species of pycnodontid fish *Flagellipinna rhomboides*, gen. et sp. nov. (Neopterygii, Pycnodontiformes), from the Upper Cretaceous (Cenomanian) of Lebanon, with notes on juvenile form and ecology. *Journal of Vertebrate Paleontology*, doi: 10.1080/02724634.2019.1614012.

Cawley, J. J., Lehmann, J., Wiese, F. and Kriwet, J., 2020: *Njoerdichthys dyckerhoffi* gen. et sp. nov. (Pycnodontiformes, lower Turonian) northward migration caused by the Cretaceous Thermal Maximum. *Cretaceous Research*, doi: 10.1016/j.cretres.2020.104590.

Cawley, J. J., Marramà, G., Carnevale, G. and Kriwet, J., 2018: A quantitative approach to determine the taxonomic identity and ontogeny of the pycnodontiform fish *Pycnodus* (Neopterygii, Actinopterygii) from the Eocene of Bolca Lagerstätte, Italy. *PeerJ*, doi:10.7717/peerj.4809.

Cloutier, R., 2010: The fossil record of fish ontogenies: Insights into developmental patterns and processes. *Seminars in Cell & Developmental Biology*, vol. 21, p. 400–413.

D'Anastasio, R., Pierfelice, L., Di Fabrizio, A. and Capasso, L., 2002: The cessation of tooth replacement in a aged tyrannosaur. *Journal of Paleopathology*, vol. 14, p. 133–137.

D'Erasmo, G., 1914-15: La fauna e l'età dei calcari a ittioliti di Pietraroia. *Paleontographia Italica*, vol. 20, p. 29–86.

Frickhinger, K. A., 1991: *Fossilien-Atlas Fische*, 1088 p. Mergus Verlag, Melle.

Goatley, C. H. R., Bellwood, D. R. and Bellwood, O., 2010: Fishes on coral reefs: changing roles over the past 240 million years. *Paleobiology*, vol. 36, p. 415–427.

Horner, J. and Goodwin, M., 2006: Major cranial changes during *Triceratops* ontogeny. *Proceedings of the Royal Society B: Biological Sciences*, vol. 273, p. 2757–2761.

Kimura, D. K., 1980: Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*, vol. 77, p. 765–776.

Kriwet, J., 2005: A comprehensive study of the skull and dentition of pycnodont fishes. *Zittelliana*, vol. A45, p. 135–188.

Lambers, P. H., 1991: The Upper Jurassic actinopterygian fish *Gyrodus dichactinius* Winkler 1862 (*Gyrodus hexagonus* Blainville 1818) from Solnhofen, Bavaria and anatomy of the genus *Gyrodus* Agassiz. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, vol. 94, p. 489–544.

Leonardi, A., 1966: L'ittiofauna cenomaniana di Floresta, Messina. *Palaeontographia Italica*, vol. 60, p. 31–67.

Myers, R. F., 1999: *Micronesian Reef Fishes: A Comprehensive Guide to the Coral Reef Fishes of Micronesia*, 330 p. Coral Graphics, Barrigada.

Nursall, J. R., 1996a: The phylogeny of pycodont fishes. *In*, Arratia, G. and Viohl, G. *eds*., *Mesozoic Fishes—Systematics and Palaeoecology*, p. 125–152. Verlag Dr. Friedrich Pfeil, München.

Nursall, J. R., 1996b: Distribution and ecology of pycnodont fishes. *In*, Arratia, G. and Viohl, G. *eds*., *Mesozoic Fishes—Systematics and Paleoecology*, p. 115–124. Verlag Dr. Friedrich Pfeil, München.

Nursall, J. R., 1999: The pycnodontiform bauplan: the morphology of a successful taxon. *In*, Arratia, G. and Schultze, H.-P. *eds*., *Mesozoic Fishes 2—Systematics and Fossil Record*, p. 189–214. Verlag Dr. Friedrich Pfeil, München.

Nursall, J. R., 2010: The case for pycnodont fishes as the fossil sister-group of teleosts. *In*, Nelson, J. S., Schultze, H.-P. and Wilson, M. V. H. *eds*., *Origin and Phylogenetic Interrelationships of Teleosts*, p. 37–60. Verlag Dr. Friedrich Pfeil, München.

Pankhurst, N. W. and Montgomery, J. C., 1990: Ontogeny of vision in the Antarctic fish Pagotheria borchgrevinki (Nototheniidae). *Polar Biology*, vol. 10, p. 419–422.

Poyato-Ariza, F. J. and Wenz, S., 2002; A new insight into pycnodontiform fishes. *Geodiversitas*, vol. 24, p. 139–248.

Poyato-Ariza, F. J. and Wenz, S., 2004: The new pycnodontid fish genus *Turbomesodon*, and a revision of *Macromesodon* based on new material from the Lower Cretaceous of Las Hoyas, Cuenca, Spain. *In*, Arratia, G. and Tintori, A. *eds*., *Mesozoic Fishes 3—Systematics, Paleoenvironments and Biodiversity*, p. 341–378. Verlag Dr. Friedrich Pfeil, München..

Poyato-Ariza, F. J. and Wenz, S., 2005: *Akromystax tilmachiton* gen. et sp. nov., a new pycnodontid fish from the Lebanese Late Cretaceous of Haqel and En Nammoura. *Journal of Vertebrate Paleontology*, vol. 25, p. 27–45.

Stinnesbeck, E. S., Rust, J. and Herder, F., 2019: Paleobiology and taphonomy of the pycnodont fish *Nursallia gutturosum*, based on material from the Latest-Cenomanian-middle Turonian Vallecillo platy limestone, Mexico. *Paläontologische Zeitschrift*, vol. 93, p. 659–668.

Taverne, L., 1997: Les poissons crétacés de Nardò. 5°. *Pycnodus nardoensis* sp. nov. et considérations sur l'ostéologie du genre *Pycnodus* (Actinopterygii, Halecostomi, Pycnodontiformes). *Bollettino del Museo Civico di Storia Naturale di Verona*, vol. 21, p. 437–454.

Taverne, L. P. and Capasso, L., 2012: Les poissons crétacés de Nardò. 35°. Compléments à l'étude des halécostomes *Belonostomus* (Aspidorhynchiformes) et *Pseudopycnodus* (Pycnodontiformes). *Bollettino del Museo Civico di Storia Naturale di Verona (Geologia Paleontologia Preistoria)*, vol. 36, p. 25–44.

Taverne, L. and Capasso, L., 2014: Ostéologie et phylogénie des Coccodontidae, une famille remarquable de poissons Pycnodontiformes du Crétacé supérior marin du Liban, avec la description de deux nouveaux genres. *Palaeontos*, vol. 25, p. 3–43.

Taverne, L. and Capasso, L., 2020: New data on the osteology and relatioships of *Flagellipinna rhomboides*, a pycnodont fish (Pycnodontidae), from the Cenomanian (Upper Cretaceous) of Lebanon. *Geo-Eco-Trop*, vol. 44, p. 175–184.

Taverne, L., Capasso, L. and Del Re, M. C., 2020: Osteology and phylogenetic relationships of *Gregoriopycnodus bassanii* gen. nov., a pycnodont fish (Pycnodontidae), from the marine Albian (Lower Cretaceous) of Pietraroja (sothern Italy). *Geo-Eco-Trop*, vol. 44, p. 161–174.

Thurmond, J. T., 1974: Lower vertebrate faunas of the Trinity Division in north-central Texas. *Geoscience and Man*, vol. 8, p. 103–129.

Tortonese, E., 2000: *Osteichthyes: pesci ossei.*, vol. 1, p. 543. Calderini Editore, Bologna.

Walker, J. A., Alfaro, M. E., Noble, M. M. and Fulton, C. J., 2013: Body fineness ratio as a predictor of maximum prolonged- swimming speed in coral reef fishes. *PLoS ONE*, doi: 10.1371/journal.pone.0075422.

West, G. B., Brown, J. H. and Enquist, B. J., 2001: A general model for ontogenetic growth. *Nature*, vol. 413, p. 628–631.

Whitlock, J. A. and Richman, J. M., 2013: Biology of tooth replacement in amniotes. *International Journal of Oral Science*, vol. 5, p. 66–70.

Woodward, A. S., 1895: *Catalogue of the Fossil Fishes in the British Museum (Natural History)*, vol. 3, 540 p. Trustees of the British Museum, London.