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Sylvienodus, a new replacement genus for the Cretaceous pycnodontiform fish "*Pycnodus*" *laveirensis*

Sylvienodus, *un nouveau genre de remplacement pour le poisson pycnodontiforme crétacé* « Pycnodus » laveirensis

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ABSTRACT

Sylvienodus nov. gen. is erected as replacement for "*Pycnodus*" *laveirensis*, from the marine Cenomanian, Late Cretaceous, of Laveiras, Portugal. Significant differences between *Sylvienodus* and *Pycnodus* include: absence of dermocranial fenestra, a single premaxillary tooth, simple contact of arcocentra, extremely falcate dorsal and anal fins, lesser enlargement of hypochordal elements on caudal endoskeleton, simpler dorsal ridge scales, oval notch between 1st and 2nd dorsal ridge scales, and a single post-cloacal ventral keel scale. After the removal of the species *laveirensis*, the genus *Pycnodus* is considered restricted to the Eocene; its type species, *P. apodus*, is the only one known from complete specimens. *Sylvienodus laveirensis* is provisionally assigned to the Pycnodontinae, pending revision of this subfamily.

Mots clés :
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Laveiras
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Phylogénie

RÉSUMÉ

Sylvienodus nov. gen. est un genre de remplacement créé pour « *Pycnodus* » *laveirensis*, du Cénomanien, Crétacé supérieur marin de Laveiras, Portugal. Parmi les différences les plus significatives entre *Sylvienodus* et *Pycnodus*, on peut citer l'absence de fenêtre dermocrânienne, une seule dent au prémaxillaire, un contact simple entre les arcocentres, les nageoires dorsale et anale de morphologie falciforme extrême, des éléments hypochordaux dans l'endosquelette caudal moins élargis, des écailles faîtières dorsales plus simples, une encoche ovale entre la première et la deuxième écaille faîtières dorsales et une seule écaille faîtière ventrale post-cloacale. Si l'on excepte « *P.* » *laveirensis*, le genre *Pycnodus* est considéré restreint à l'Éocène ; l'espèce-type, *P. apodus*, est la seule connue par des échantillons complets. *Sylvienodus laveirensis* est considéré provisoirement comme un Pycnodontinae, en attendant une révision de cette sous-famille.

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1. Introduction

Pycnodontiformes are an order of fossil non-teleostean neopterygian actinopterygians. They appear in the Norian (Late Triassic), and are common in Mesozoic beds, especially Late Jurassic and Cretaceous. The last locality with uncontestable, complete pycnodont remains is Monte Bolca, from the Eocene (see Poyato-Ariza, 2005 for an account of their fossil record). Pycnodonts have many autapomorphies that characterize a very distinctive body plan and make the group easily recognizable, including heterodont dentition with molariform teeth, significant modifications in the opercular region, peculiar patterns of the squamation, and morphologic differentiation of cloacal and marginal scales (Nursall, 1996; Poyato-Ariza and Wenz, 2002).

The genus *Pycnodus* is one of the latest occurrences of the group. The type species comes from the Eocene Monte Bolca (Blot, 1987). With the exception of *P. laveirensis*, whose revision is the aim of the present paper, all nominal species of *Pycnodus* from Cretaceous beds were based on isolated dentitions (Woodward, 1895); as noted by Blot and Voruz in Blot (1987); these species have been removed to other genera. The only other species of *Pycnodus* represented by articulated material is the type species. Comparisons with species based on isolated dentitions only will not be done in order to avoid parataxonomical problems and because most of the characters in the revised diagnosis of the genus (Poyato-Ariza and Wenz, 2002, p. 222) are not dental. In addition, according to the statement of the principle of typification "...the name-bearing type of a nominal taxon provides the objective standard of reference for the application of the name it bears" (ICZN, 1999, p. 63, Article 61.1). Therefore, the standard reference for comparisons with *Pycnodus* is its type species, for which the name "*Pycnodus platessus*" has been broadly used; the valid name, however, according to the rules of the ICZN (1999) is *Pycnodus apodus* (Poyato-Ariza and Wenz, 2002, p. 152).

Pycnodus laveirensis was erected in 1961 by Veiga Ferreira for six small individuals from a Turonian (Late Cretaceous) outcrop 340 m east of Laveiras, Caixas, Portugal. He considered that the size and placement of the dorsal and anal fins, the shape of the caudal fin, and the number of fin rays were so different from "*P. platessus*" as to justify erecting a new species. Jonet (1964) added more features to the description provided by an additional specimen, notably from the dentition. Poyato-Ariza and Wenz (2002), on the basis of literature only, pointed out that the specimens of "*P.*" *laveirensis* might be juvenile, so the species was considered *nomen dubium* and in need of revision.

This paper provides such a revision of *P. laveirensis* Veiga Ferreira, 1961 by direct examination of the available type material and other specimens as part of a review of the subfamily Pycnodontinae (Poyato-Ariza, 2010, work in progress). Observations show that not all specimens are juvenile, confirm the valid status of the species, and indicate that a new replacement genus is needed to account for the numerous, substantial differences between the Portuguese material and *Pycnodus apodus*. The new replacement genus is *Sylvienodus*, and will be used instead of "*P.*" *laveirensis* in the rest of the text.

Because the Portuguese specimens have been previously figured and described, the present paper will focus on the characters that differentiate *Sylvienodus* nov. gen. from *Pycnodus*; all new characters observed in the material are signaled. Comparisons will be focused mostly on the genera that present more derived characters in common, such as the occipital region, the squamation pattern, and the cloaca; these are the monotypic *Oropycnodus*, *Polazzodus*, and *Tergestinia*.

2. Material and methods

The material examined includes the type series, which was figured by Veiga Ferreira (1961). However, there was no mention of holotype or name-bearing type in that paper. Therefore, the specimens in the original description are a type series of syntypes according to articles 72.1 and 73.2 of the ICZN (1999). Article 74.1 of the ICZN (1999) provides the grounds for the designation of a lectotype chosen from the syntypes to become the unique name-bearer. In accordance with the provisions by the ICZN (1999), specimen 6659 from the Laboratorio Nacional de Energia e Geologia, Museu de Geologia in Lisbon (Veiga Ferreira, 1961, Plate 4, figure 16; present paper, Figs. 1–5) is herein explicitly designed as the lectotype of the species *Sylvienodus laveirensis*. It is chosen as the lectotype because it is an adult specimen, and, although it lacks the anterodorsal part of the skull, it is very well preserved and clearly shows key differences from *Pycnodus*, such as the absence of dermocranial fenestra and the shape of the dorsal and anal fins. The rest of the syntypes become paralectotypes according to recommendation 74F of the ICZN (1999). In addition to the available specimens of the type series, all other available specimens were observed for this revision.

The material comes from an outcrop 340 m east of Laveiras, concelho de Oeiras, Vale do Tejo, some 15 km west of Lisbon. The age of the locality was Middle Turonian according to Veiga Ferreira (1961), although it is nowadays considered Upper Cenomanian (Berthou, 1973; Costa-Pereira, pers. comm., 2011; Ramalho, pers. comm., 2011). These beds are marine according to Veiga Ferreira (1961), as confirmed by the accompanying fauna mentioned by Jonet (1964): rudists, marine bivalves such as *Ostrea*, and Cidaridae echinoderms. The material revised is housed in two institutions in Lisbon: Laboratorio Nacional de Energia e Geologia, Museu de Geologia (LNEG–MG: 4716, 6658, 6659) and Instituto Superior Técnico, Museu Décio Thadeu (IST–MDT: 527, 580, 583.1–6, 589, 591, 592, 617). They were observed under a binocular microscope at each institution; drawings were made using a camera lucida at LNEG–MG. In addition, previous observations of *P. apodus*, *Oropycnodus*, *Polazzodus*, and *Tergestinia* were used for comparison; see Blot (1987), Capasso (2000), Poyato-Ariza and Wenz (2002), and Poyato-Ariza (2010) for detailed descriptions and figures. For the particular nomenclature of pycnodont anatomy, see Nursall (1996) and Poyato-Ariza and Wenz (2002).

Fig. 1. *Sylvienodus* nov. gen. from the Cenomanian of Laveiras, Portugal. Specimen LNEG–MG 6659, lectotype of *S. laveirensis* nov. comb. Left side, lateral view. Scale bar represents 5 mm. Photo by J.P. Ferreira Vicente, courtesy M. Ramalho, provided by S. Gabriel.
Fig. 1. *Sylvienodus* nov. gen. du Cénomanien de Laveiras, Portugal. Échantillon LNEG–MG 6659, lectotype de *S. laveirensis* nov. comb. Côté gauche, vue latérale. L'échelle représente 5 mm. Photo de J.P. Ferreira Vicente, avec l'aimable permission de M. Ramalho, fournie par S. Gabriel.

3. Systematic paleontology

Order PYCNODONTIFORMES Berg, 1937
Family PYCNODONTIDAE sensu Nursall, 1996
cf. Subfamily PYCNODONTINAE Poyato-Ariza and Wenz, 2002
Sylvienodus nov. gen. (Figs. 1–6)

Diagnosis: Pycnodontin neopterygian with the following autapomorphies: anteroventral border of maxilla ornamented with crenulations; parietal peniculus present but small, short, with only up to 4 posterior branches; extremely falcate dorsal and anal fins; 1st and 2nd dorsal ridge scales forming an oval notch between them. Unique combination of primitive and derived characters: very small size, less than 60 mm in SL; body outline ovoid, maximum body height less than 50% of SL; dermocranial fenestra absent; dermopterotic bone very large; postcephalic lacuna in posteriorly exposed portion of endocranium absent; premaxillary bone with a single tooth and no olfactory fenestra; ax-shaped maxilla; 22–23 vertebrae counted as neural spines, caudal endoskeleton excluded; about 37 dorsal and 33 anal axonosts; 17–18 principal caudal fin rays (1 unbranched plus 7 branched in upper lobe, 9–10 branched plus 1 unbranched in lower lobe); 4 epichordal and 9 hypochordal elements in the caudal endoskeleton, number 8 and 9 slightly larger than the rest; 12 dorsal ridge scales, devoid of spines or ornamentation.

Etymology: From *Sylvie*, in homage to Dr. Sylvie Wenz, and *–nodus*, the last part of *Pycnodus*, the genus it was previously referred to.

Type species: *Sylvienodus* (*Pycnodus) laveirensis* (Veiga Ferreira, 1961).

Sylvienodus laveirensis nov. comb. (Figs. 1–6)
Diagnosis: As for genus (monospecific genus).
Type locality: Laveiras, Vale do Tejo, Portugal.
Lectotype: Specimen 6659 in the Laboratorio Nacional de Energia e Geologia, Museu de Geologia, Lisbon, Portugal (Veiga Ferreira, 1961, Plate 4, figure 16). It is nearly complete, lacking the anterodorsal part of the head and the distal part of the caudal fin (Figs. 1–5).

Paralectotypes: Specimens 4716 and 6658 in the Laboratorio Nacional de Energia e Geologia, Museu de Geologia, Lisbon, Portugal; 527 and 592 in the Instituto Superior Técnico, Museu Décio Thadeu, Lisbon, Portugal (Veiga Ferreira, 1961, respectively: Plate 4, figure 15, upside down; Plate 6, figure 20; Plate 8, figure 22; and Plate 1, figure 7; syntypes on Plate 2, Figure 12 and on Plate 5, Figure 18 were never found).

Other material (topotypes): Specimens 580 (Fig. 6), 583.1–6, 589, 591, and 617 in the Instituto Superior Técnico, Museu Décio Thadeu, Lisbon, Portugal.

Age: Upper Cenomanian (Upper Cretaceous).

Etymology: The specific name is the Latin adjective meaning "from Laveiras", the type and only locality where it is known.

4. Description and comparison

The present description focuses on the anatomic features that differentiate the new genus from *Pycnodus* as represented by its type species, *P. apodus*. Some relevant characters of the most inclusive Pycnodontidae as defined by Poyato-Ariza and Wenz (2002, node 23 in fig. 43 and pp. 215–216) are also addressed in this section. For further description of the Portuguese material, see Veiga Ferreira (1961) and Jonet (1964).

4.1. General features

Sylvienodus nov. gen. is a tiny fish; the estimated standard length (SL) of the lectotype, LNEG–MG 6659, is 57 mm. In spite of this, it does not seem juvenile, as it is well ossified and the dermal bones show remarkable ornamentation of tubercles and grooves. Dorsal and anal fin rays are barely bifurcated, just once or twice, but this also occurs in *Pycnodus*, *Polazzodus*, and *Tergestinia* (Blot, 1987; Poyato-Ariza, 2010; pers. obs.). This is not considered a juvenile feature for these genera; even the largest specimens of

Pycnodus, well above 200 mm, have barely bifurcated dorsal and anal fin rays. Caudal fin rays in all these genera are more bifurcated, especially in larger specimens, although the exact number of bifurcations in *Sylvienodus* is unknown because all specimens lack the distal part of this fin. Caudal fin rays are bifurcated 4–5 times in the specimen illustrated by Jonet (1964, p. 15–17; pl. 2, fig. 1), comparable to the preserved part of the caudal fin of the lectotype, which is additional evidence that they are adults. Paralectotypes LNEG–MG 4716 and 6658 of *Sylvienodus* are smaller, less ossified and less ornamented, probably subadult to juvenile, as are most specimens from IST–MDT except 527, 580, and 592.

The overall shape of the body, without the fins, in larger specimens is ovoid, more similar to *Polazzodus* than to the typical truncated shape of *Pycnodus* and *Tergestinia*. *Sylvienodus* is low for a pycnodont, about 41% of the estimated SL in the lectotype; it is 47–46% in younger specimens, so the body is always less than half as high as it is long. The maximum body height is reached at the posteriormost part of the skull or slightly posterior to it, always well before the point of insertion of the dorsal fin. The head is about 32% of the standard length in the lectotype and very similar in other specimens; head height is about 123% of head length in the lectotype, and 115–130% in other specimens. In other words, the head is higher than it is long (see Table 1 for further measures, proportions, and meristic characters).

Size itself is a feature with little taxonomic value; however, the difference between *S. laveirensis* and *P. apodus* is really remarkable. In percentage, the SL ratio of the only remaining syntype of the latter and the lectotype of the former is about 360%. This is a remarkable size difference, certainly not of intrageneric variation in pycnodonts. The SL ratio of the holotype of *Polazzodus* and the lectotype of *Sylvienodus* is about 130%; the only other advanced pycnodontid of comparable small size is *Tergestinia*.

4.2. Endocranium and skull roof

The endocranium, as in all pycnodontins, is posteriorly exposed, the supraoccipital bone largely showing behind the posterior border of parietal and dermopterotic. The exposed portion is large but delicate, never entirely preserved; the postcephalic lacuna present in *Pycnodus* and *Oropycnodus* seems absent in *Sylvienodus* nov. gen.

The skull roof consists of frontal, parietal, small dermosphenotic, and large dermopterotic. The frontal is elongated, as in most pycnodonts, its postorbital part short, only slightly expanded. The parietal is larger than in *Pycnodus*, where the main body of this bone is comparatively slender. Unlike other pycnodonts with parietal peniculus, in *Sylvienodus* it is very small, short, with very few branches; only 4 in the lectotype. The posterolateral part of the skull roof is incomplete and/or imperfectly preserved, but a brief description can be provided from observations in the lectotype and LNEG–MG 4716. The dermosphenotic is very small, but present; it is apparently absent in *Pycnodus*. It forms the posterodorsal corner of the orbit, versus the posteroventral corner in *Polazzodus*. In turn, the dermopterotic, placed lateral to the parietal, is, as in *Polazzodus*, remarkably large, unlike the much narrower dermopterotic of *Pycnodus* (Blot, 1987; Nursall, 1999; pers. obs.).

All published and observed specimens of *Sylvienodus* lack the dermocranial fenestra of *Pycnodus* ("fosse supratemporale" of Blot, 1987, fig. 6; pers. obs.). This is a very distinctive feature among pycnodonts. Its observation in *Sylvienodus* can be misleading because there are areas of the skull roof heavily ornamented, with deep grooves filled with matrix, and some parts of the bones may be missing, forming small, irregular gaps (e.g., lectotype). This is the reason why an accurate figure of the skull roof is not provided. However, the regular, well-defined dermocranial fenestra anterior to the parietal, posterior to the frontal, and ventral to the dermal supraoccipital (Blot, 1987, fig. 6; Poyato-Ariza and Wenz, 2002, fig. 11B) never appears in *Sylvienodus*, where the corresponding area is always ossified. When present, this fenestra is large, about half the size of the orbit, so it is conspicuous and very characteristic. This remarkable difference provides strong support for removal of the Portuguese species from *Pycnodus*. It is also absent in *Polazzodus* and *Tergestinia*, but present in *Oropycnodus*. The dermal supraoccipital bone closes the skull roof posteriorly, as in all pycnodonts; it is long, with a pointed anterior end, and posteriorly large, encasing the transversal extrascapular commissure (which partially pierces the parietal as well); extrascapulars are absent as independent ossifications.

4.3. Oral region

The premaxilla and the dentary, as seen in LNEG–MG 6658, IST–MDT-580, 592 and the specimen described and illustrated by Jonet (1964, p. 15–17, fig. 2; pl. 2, figs. 1–2) have, respectively, 1 and 2 teeth. A single premaxillary tooth is another difference from *Pycnodus*, which has 2. As in all Pycnodontoidea but *Akromystax*, the premaxillary and dentary teeth are incisiform; in *Sylvienodus*, the premaxillary tooth is larger than the dentary teeth, of which the 1st one is much larger than the 2nd one. *Polazzodus* has only 1 premaxillary tooth as well, but its crown is shorter, larger, and thinner than in *Sylvienodus*. The premaxillary process of *Polazzodus* is relatively longer and thinner, and it has an olfactory fenestra that is absent in *Sylvienodus*. The premaxilla of the new genus is more similar to that of *Tergestinia*, the only other pycnodont with a single premaxillary tooth. The main difference is that this tooth is comparatively shorter in meso-distal dimension and higher between the insertion and the occlusal border in *Tergestinia*.

The morphology of the maxilla is another remarkable feature of the new genus (Fig. 2). It has a conspicuous dorsal process, with a distinct and robust articular head for the premaxilla; the posterior and ventral borders of the bone are nearly straight, and the anterior one, very concave (lectotype, LNEG–MG 6658, IST–MDT-580, 583(2), 591). The maximum width is reached in the ventralmost part, which presents a long, pointed anterior projection. This peculiar "ax-shaped" morphology of the maxilla is known in *Polazzodus* only among pycnodonts; the articular head is shorter and stouter in *Sylvienodus* than in *Polazzodus* (Fig. 2A-B). The maxilla is reniform in *Pycnodus* (Fig. 2C). A unique

Table 1
Relevant measures, proportions, and meristic characters of the articulated specimens of the type series of *Sylvienodus laveirensis* n. gen.
Tableau 1
Mesures, proportions et caractères méristiques remarquables des échantillons articulés de la série type de *Sylvienodus laveirensis* n. gen.

	LectotypeMGL 6659	MGL4716 juv	MGL6658 juv	IST 527
SL	55 est	29	25.9	41 est
PDL	31	20	16.8	25.5
%SL	56.4	68.9	64.8	62.2
PAL	37	22	18.9	29
%SL	67.3	75.8	72.9	70.7
PCL	20	–	11.0	15.3
%SL	36.4	–	42.4	37.3
PVL	31	–	–	22.5
%SL	56.4	–	–	54.9
HH	21.5	13.7	13.2	17
%SL	39.1	47.2	50.9	41.4
HL	17.5	10.2	11.6	13
%SL	32	35.2	44.7	31.7
MBH	23.5	13.5	11.2	16.5 est
%SL	41.2	46.5	43.2	40.2
%HH/HL	123	134	114	130
DAX	37	>34	–	–
AAX	33	>31	–	>31
V(D)	22	23	23	–
A+C	12+11	12+11	12+11	(–)+12
EPCA	5	–	(4)	>3
HYCA	9	9	9	9
DRS	12 est	–	12 est	–
VKS	15	–	–	15
PSCL	2	–	2	2

All measures in millimetres. Abbreviations in first column, from top to bottom, read: SL: standard length; PDL: predorsal length; %SL: percentage of the measure above to standard length; PAL: preanal length; PCL: prepectoral length; PVL: prepelvic length; HH: head height; HL: head length; MBH: maximum body height; %HH/HL: percentage of head height to head length; DAX: number of dorsal fin axonosts; AAX: number of anal fin axonosts; V(D): number of vertebrae, counted as dorsal elements excluding the epichordal elements of the caudal endoskeleton; A+C: number of abdominal plus caudal vertebrae, counted as in V(D) above; EPCA: number of epichordal elements of caudal endoskeleton; HYCA: number of hypochordal elements of caudal endoskeleton; DRS: number of dorsal ridge scales (including the first one, incorporated to the skull roof, counted separately); VKS: total number of ventral keel scales; PSCL: number of post-cloacal ventral keel scales. Institutional abbreviations: MGL: Museu Geológico de Lisboa; ITSL: Instituto Técnico Superior de Lisboa. Other abbreviations: est: measure(s) estimated, therefore related proportions are estimated as well; inc: incomplete specimen; juv: juvenile or subadult specimen. The estimations of the standard length are acceptable: in the lectotype the premaxilla is missing but the dentary is present and observable in its entirety; in IST-527, only the anteriormost tip of the premaxilla is missing. All specimens listed, other than the lectotype, are paralectotypes.
Toutes les mesures sont en millimètres. Les abréviations de la première colonne, du haut en bas, sont : SL : longueur standard ; PDL : longueur pré-dorsale ; %SL : pourcentage de la mesure en haut sur la longueur standard ; PAL : longueur pré-anale ; PCL : longueur pré-pectorale ; PVL : longueur pré-pelvienne ; HH : hauteur de la tête ; HL : longueur de la tête ; MBH : hauteur maximale du corps ; %HH/HL : pourcentage de la hauteur de la tête sur sa longueur ; DAX : nombre d'axonostes de la nageoire dorsale ; AAX : nombre d'axonostes de la nageoire anale ; V(D) : nombre de vertèbres, comptées comme les éléments dorsaux, à l'exception des éléments épichordaux de l'endosquelette caudal ; A+C : nombre de vertèbres abdominales plus caudales, comptées comme V(D) en haut ; EPCA : nombre d'éléments épichordaux de l'endosquelette caudal ; HYCA : nombre d'éléments hypochordaux de l'endosquelette caudal ; DRS : nombre d'écailles faîtières dorsales (à l'inclusion de la première, incorporée dans le toit crânien) ; VKS : nombre total d'écailles faîtières ventrales ; PSCL : nombre d'écailles faîtières ventrales post-cloacales. Abréviations des institutions : MGL : Museu Geológico de Lisboa ; ITSL : Instituto Técnico Superior de Lisboa. Autres abréviations : est : mesure(s) estimée(s) ; en conséquence les proportions correspondantes sont aussi une estimation ; inc : échantillon incomplet ; juv : individu juvénile ou sub-adulte. Les estimations des longueurs standard sont acceptables ; chez le lectotype, le prémaxillaire manque, mais le dentaire est présent et visible dans son intégralité ; chez IST-527, seule l'extrémité la plus antérieure du prémaxillaire manque. Tous les échantillons dans le tableau, autres que le lectotype, sont des paralectotypes.

character of *Sylvienodus* is the crenulated ornamentation on the anterior border, presented since early ontogenetic stages (e.g., juvenile IST–MDT-591).

Vomerine and prearticular teeth are seldom visible; IST–MDT-580 shows 9 exposed vomerine teeth, all small, rounded to oval in occlusal contour and bearing crenulations where unworn (also IST–MDT-592). These crenulations are strong, placed around the crown. Two vomerine and one prearticular teeth exposed in the juvenile IST–MDT-583(6) confirm such shape and ornamentation.

The coronoid process is large, with a straight, inclined anterodorsal border (IST–MDT-580); it is so high that the mandible is nearly as high as it is long. This shape is quite similar to that of derived pycnodontids such as *Polazzodus* and *Pycnodus*.

4.4. Opercular region

The opercular bone is present, but greatly reduced (lectotype, IST–MDT-592); it is placed rather high, not reaching the preopercular ventrally (Fig. 3). In shape, extension and position, it is much more like that of *Polazzodus* and *Oropycnodus* than that of *Pycnodus*. The preopercular is about as high as the exposed, superficial part of the dermohyomandibula, and, curiously enough, the two bones are partially fused anteriorly. This partial fusion, first reported in pycnodonts, is observed in juvenile (LNEG–MG 4716) and adult individuals (lectotype; Fig. 3), although there is individual variation; IST–MDT-592 and juvenile IST–MDT-591 have an autogenous preopercular showing a very long, thin anterior ascending process. The relationship between the preopercular and the dermohyomandibular is very

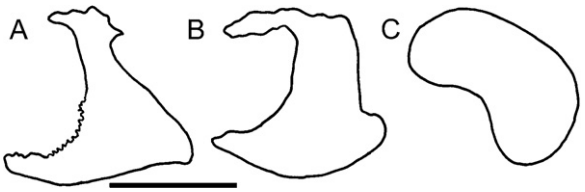

Fig. 2. Comparative outlines of the maxilla in three pycnodont genera. A. *Sylvienodus* nov. gen., from a camera lucida drawing of the lectotype, LNEG–MG 6659. Scale bar represents 1 mm. B. *Polazzodus*, from a camera lucida drawing of paratype 12264, Museo Paleontologico Cittadino di Monfalcone, Italy. C. *Pycnodus*, based on Blot, 1987, figs. 2, 3, and 10B, and on personal observations. All left side, lateral view, anterior to the left. B and C not to scale for comparative purposes.

Fig. 2. Contours comparatifs du maxillaire dans trois genres de pycnodontes. A. *Sylvienodus*, d'après un dessin à la chambre claire du lectotype, LNEG–MG 6659. L'échelle représente 1 mm. B. *Polazzodus*, d'après un dessin à la chambre claire du paratype 12264, Museo Paleontologico Cittadino di Monfalcone, Italie. C. *Pycnodus*, adapté de Blot, 1987, figs. 2, 3, and 10B, et d'après observations personnelles. Tous envisagés du côté gauche, vue latérale, région antérieure vers la gauche. B et C ne sont pas représentés à la même échelle pour des raisons de comparaison.

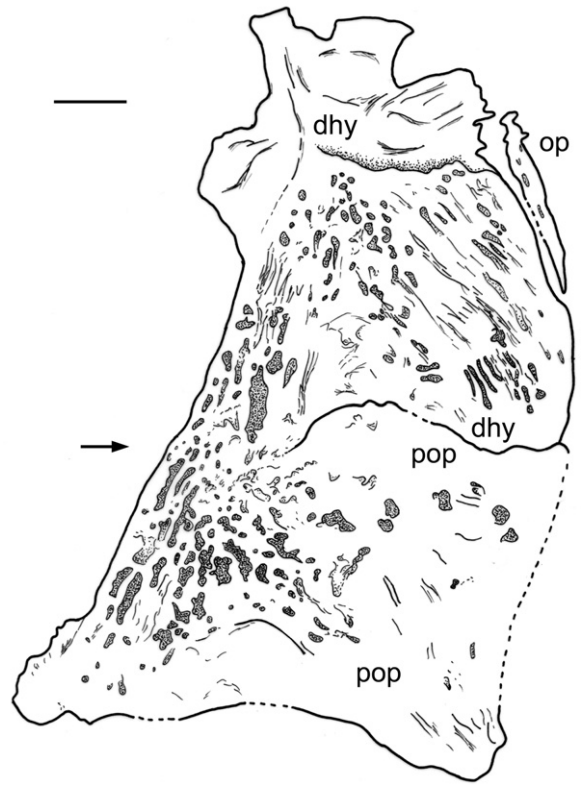

Fig. 3. *Sylvienodus* nov. gen. Opercular region of lectotype, LNEG–MG 6659, camera lucida drawing. Abbreviations: dhy: dermohyomandibular bone; op: opercular bone; pop: preopercular bone. Note the partial fusion in the anterior region between dhy and pop, pointed by an arrow. Left side, lateral view. Scale bar represents 1 mm.

Fig. 3. *Sylvienodus* nov. gen. Région operculaire du lectotype, LNEG–MG 6659, dessin à la chambre claire. Abréviations : dhy : os dermohyomandibulaire ; op : os operculaire ; pop : os préoperculaire. On remarquera la fusion partielle dans la région antérieure entre dhy et pop, signalée par une flèche. Côté gauche, vue latérale. L'échelle représente 1 mm.

peculiar in pycnodonts; the former is progressively smaller from primitive to derived forms, and the latter is progressively more exposed superficially, with an increasing ornamented portion tightly articulated with the preopercular ("dermalization of the hyomandibular body" sensu Nursall, 1996, p. 138–139). In this context, this partial fusion in some specimens of *Sylvienodus* is unique, but not very surprising.

4.5. Axial skeleton

There are 23 vertebrae in the lectotype, counted, as in other pycnodonts, as neural spines not forming part of the caudal skeleton. This includes 12 abdominal and 11 caudal vertebrae (Table 1). This number is lower than in *Pycnodus*, *Polazzodus* and *Tergestinia* (mostly 29). Paralectotype LNEG–MG 4716 has 23, although not as clearly countable as the lectotype. Other specimens (LNEG–MG 6658 and IST–MDT-4716) have 23. There are 7 anterior autogenous neural spines (IST–MDT-617; the 7th spine is arranged very tightly to the corresponding arch, with a suture between them). The number of caudal centra, excluding caudal endoskeleton, is 11–12.

Neural and haemal spines have anterior sagittal flanges, as in most pycnodontids. The arcocentra surround the notochord, closing the notochordal canal in lateral view, as in some other pycnodonts. Caudal arcocentra surround the notochord completely since earlier ontogenetic stages, but abdominal vertebrae leave a little aperture for the notochordal canal in lateral view in younger specimens (e.g., LNEG–MG-4716). The contact of each arcocentrum with the adjacent ones is simple, not interdigitated, by means of a single projection; quite different from the complex, interdigitated contact of *Pycnodus*. This dissimilarity is very significant for pycnodonts.

4.6. Paired, dorsal, and anal fins

Paired fins are rarely and partially preserved. There are at least 20 pectoral fin rays in the lectotype, evidence of a much larger pectoral than pelvic fin. IST–MDT-580 shows 22 right and 20 left long, robust pectoral radials, a confirmation of the ample width of the fin. IST–MDT-583(1) and 583(7) show remains of a tiny pelvic fin, with very few lepidotrichia; it is inserted before the first scale row anterior to the cloaca.

Another unique character of *Sylvienodus* nov. gen. is the shape of the dorsal and anal fins (Figs. 1 and 4). The lectotype, the only observed specimen where the very delicate fin rays are entirely preserved, shows extremely acuminate fins. The dorsal one has 3 short precurrent fin rays, unsegmented and unbranched. Then, there are 37 segmented fin rays; the first 6–7 of them are much longer than the rest. These fin rays are so long that they make the dorsal fin higher than it is long; these rays are about 8 times longer than the shortest fin rays, which form most of the fin (e.g., the 4th segmented fin ray is about 7,8 times longer than the 17th). The anal fin is very similar, with only 1 precurrent, unsegmented fin ray and 33 segmented fin rays, the longest of which are the first 4–5; they are not as long as the dorsal ones, so that the fin is a little lower than it is long.

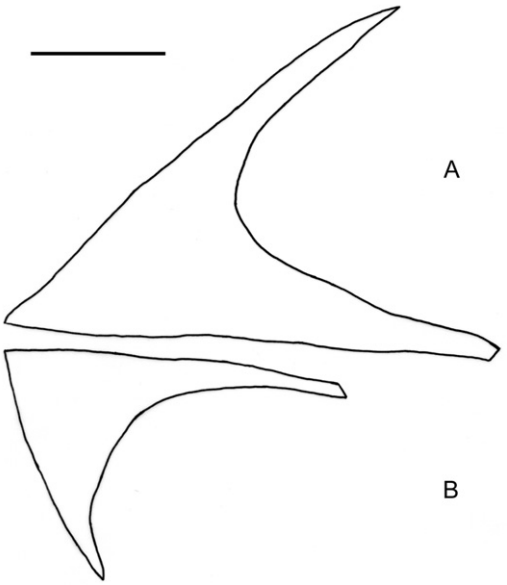

Fig. 4. *Sylvienodus* nov. gen. Idealized contour of the dorsal (A) and anal (B) fins, based on a camera lucida drawing of lectotype, LNEG–MG 6659. Left side, lateral view. Line bar represents 5 mm for both fins.
Fig. 4. *Sylvienodus* nov. gen. Contour idéalisé des nageoires dorsale (A) et anale (B), d'après un dessin à la chambre claire du lectotype, LNEG–MG 6659. Côté gauche, vue latérale. L'échelle représente 5 mm pour les deux nageoires.

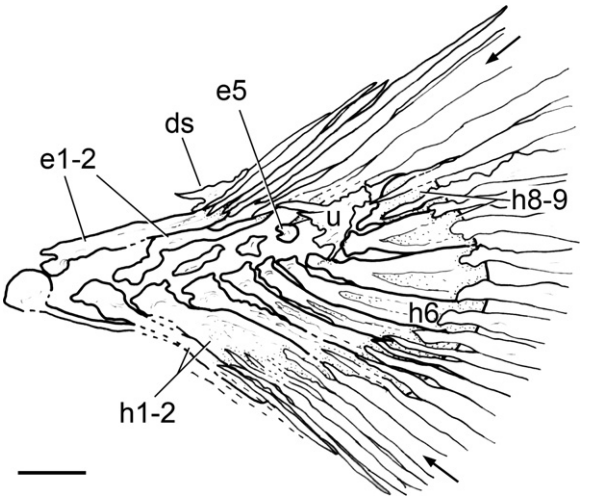

Fig. 5. *Sylvienodus* nov. gen. Caudal skeleton, camera lucida drawing of lectotype, LNEG–MG 6659. Left side, lateral view. Abbreviations: ds: dorsal scute; e1–5: epaxial elements 1 to 5; h1–9: hypaxial elements 1 to 9; u: urodermal. Arrow points the main principal fin ray on each lobe. Line bar represents 1 mm.
Fig. 5. *Sylvienodus* nov. gen. Endosquelette caudal, dessin à la chambre claire du lectotype, LNEG–MG 6659. Côté gauche, vue latérale. Abréviations : ds : écusson dorsal ; e1–5 : éléments épaxiaux 1 à 5 ; h1–9 : éléments hypaxiaux 1 à 9 ; u : urodermal. Les flèches signalent le rayon principal sur chaque lobe. L'échelle représente 1 mm.

This dorsal and anal fin morphology is an autapomorphy of *Sylvienodus* among pycnodonts; compare Fig. 4 herein with fig. 34 in Poyato-Ariza and Wenz (2002). The most similar is the acuminate shape, in, for instance, *Gyrodus* or *Proscinetes* (e.g., op. cit., figs. 5, 34B), but the acumination in *Sylvienodus* is extreme, unique in pycndonts. In *Pycnodus*, the dorsal and anal fins are slightly falcate, with the anteriormost segmented fin rays only about twice longer than the rest of the series. Yet another remarkable difference: *Sylvienodus* has fewer axonosts than *Pycnodus*; about 37 dorsal and 33 anal in the former, and about 58 and 45 in the latter.

4.7. Caudal fin and endoskeleton

The caudal fin of the lectotype lacks the distal part. This fin is entirely preserved only in the specimen illustrated by Jonet (1964, p. 15–17; pl. 2, fig. 1); its distal contour shows that it is double emarginated, very much as in *Pycnodus* and *Oropycnodus*, unlike the forked caudal fin of *Polazzodus* or the straight distal border of *Tergestinia*. Fringing fulcra are absent; there are 5 dorsal and 7–8 ventral precurrent fin rays in the lectotype; respectively, 4 and 4 in juvenile LNEG–MG 4716. Adults of *Pycnodus* have 9–11 precurrent rays on each lobe, yet another difference. In *Sylvienodus*, there is 1 longest, segmented, unbranched principal caudal ray on each lobe plus 6 segmented, branched rays in the upper one, and 9–10 in the lower one, a total of only 17–18 principal caudal fin rays (about 21 in *Pycnodus* and *Polazzodus*). One large, thin, irregular urodermal with several projections is seen on the lectotype and LNEG–MG-4716. The former also shows a dorsal caudal scute (corresponding ventral part missing).

The caudal endoskeleton (Fig. 5) is close in some features, but dissimilar in others, to that of *Pycnodus* and similar genera. There are 5 epichordal elements (e.g., lectotype), versus 6 in *Pycnodus*, *Oropycnodus*, and *Polazzodus*. There are only 9 hypochordal elements (e.g., lectotype, IST–MDT-583(5), 617), unlike 10–11 in the mentioned genera. The most developed hypochordal elements are the 8th and 9th, as in *Pycnodus* and the others; however, these hypochordal elements are only enlarged in *Sylvienodus*, not hypertrophied as in *Pycnodus* and other genera, that is, extremely wide, with a central, additional ridge (compare Fig. 5 herein with, for instance, figs. 27, 28 and Plates 14, 15 in Blot, 1987 and figs. 26 and 29 in Poyato-Ariza and Wenz, 2002).

4.8. Squamation

Sylvienodus nov. gen. has a clathrate squamation pattern, like most derived pycnodonts (Nursall, 1996). The lectotype and LNEG–MG-6658 show 6 complete flank scale rows plus at least 2 incomplete rows. Each complete flank row is composed of about 6 thin, long scales.

Contour scales are never well preserved, but their main features can be outlined from different specimens (e.g., lectotype, paralectotype IST–MDT-527). There are 12 dorsal ridge scales. Their morphology is mostly rather simple: thin and elongated, with a crenulated dorsal border. They are different from the elaborated scutellum-like dorsal ridge scales of *Pycnodus*. The 1st dorsal ridge scale is incorporated into the skull roof, as in all pycnodonts. The 2nd dorsal ridge scale has a long, stout anteroventral projection; the

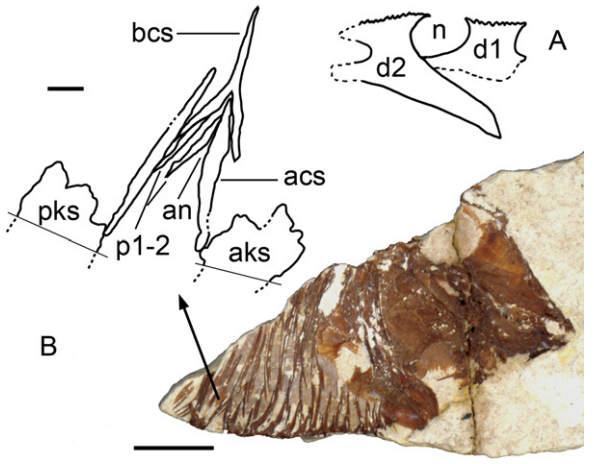

Fig. 6. *Sylvienodus* nov. gen. Contour scales. A. Idealized restoration of dorsal ridge scales 1 and 2 to show the notch formed between them. Right side, lateral view. Restored mostly from specimens LNEG–MG 6658 and IST–MDT 527. B. Specimen IST–MDT-580. Below, direct 2D scan of specimen, courtesy M.F. Costa-Pereira; above, sketch of cloacal scales rendered in Adobe Illustrator® by H. Martín-Abad from the same scan. Right side, lateral view. Abbreviations: acs: anterior cloacal scale; aks: anterior ventral keel scale; an: anal notch; bcs: bifid cloacal scale; d1: dorsal ridge scale 1; d2: dorsal ridge scale 2; n: notch between dorsal ridge scales 1 and 2; p1–2: posterior cloacal scales 1 and 2; pks: posterior ventral keel scale. Line bars represent 1 mm (above) and 5 mm (below).

Fig. 6. *Sylvienodus* nov. gen. A. Reconstitution idéalisée des écailles faîtières dorsales 1 et 2, pour montrer l'encoche formée entre les deux. Côté droit, vue latérale. Reconstitué principalement d'après les spécimens LNEG–MG 6658 and IST–MDT 527. B. Spécimen IST–MDT-580. Au-dessous, scan 2D direct du spécimen, fourni par M.F. Costa-Pereira ; au-dessus, dessin de détail du cloaque préparé par H. Martín-Abad à l'aide d'Adobe Illustrator® à partir du même scan. Côté droit, vue latérale. Abréviations : acs : écaille cloacale antérieure ; aks : écaille faitière ventrale antérieure ; an : encoche anale ; bcs : écaille cloacale bifide ; d1 : écaille faîtière dorsale 1 ; d2 : écaille faîtière dorsale 2 ; n : encoche formée entre les écailles faîtières dorsales 1 et 2 ; p1–2 : écailles cloacales postérieures 1 et 2 ; pks : écaille faîtière ventrale postérieure. Les échelles représentent 1 mm (au-dessus) et 5 mm (au-dessous).

dorsal part resembles the scutellum-like scales of *Pycnodus* more than the rest of the series. The anterior and posterior borders of this scale are rather curved, the anterior one forming an oval notch with the posterior border of the first scale (MGB 6658, IST–MDT-527, 583(1); in the lectotype, the notch is deformed due to displacement of the 2nd dorsal ridge scale). Such a notch (Fig. 6A) is apparently unique among pycnodonts.

There are 15 ventral keel scales, 2 post-cloacal. IST–MDT-580 shows 5 under the cleithrum, 8 between cleithrum and cloaca, and 2 after the cloaca. Unfortunately, the specimen is broken, so their distal border is missing. In general, these scales are very simple, although larger than the dorsal ridge scales. The anteriormost ones seem to bear a single spine on the center of the distal border, whereas the rest of the series bear spines in increasing number, from 2 short to 3–4 long, curved spines, placed on the posterior part of the distal border, of increasing size and in close contact with each other (e.g., IST–MDT-583(2), 583(7), lectotype). In sum, the ventral keel scales are very much like those of many pycnodonts, such as *Ocloedus*, *Turbomesodon* and *Polazzodus*, but a bit smaller. They are not like the scutellum-like ventral keel scales of *Abdobalistum*; the ventral keel scales of *Pycnodus* are even simpler, with no more than 3 small spines.

The cloaca (Fig. 6B) is seldom preserved. Specimen IST–MDT-580 shows a cloaca with a bifid scale, a derived character state within Pycnodontidae (Poyato-Ariza and Wenz, 2002). In addition to the bifid scale, *Syvienodus* has 1 long, robust anterior and, differently from other genera, 2 short and thin posterior cloacal scales, all of them long and straight (Fig. 6B).

5. Discussion and conclusions

The taxon revised herein was considered a species of *Pycnodus* as understood at that time by Veiga Ferreira (1961) and Jonet (1964). *P. laveirensis* was a *nomen nudum* in Poyato-Ariza and Wenz (2002), although they did not include it in their phylogenetic analysis because the material could not be studied at the time. The species was confirmed as a valid one, belonging to *Pycnodus*, by Machado et al. (2010) in a preliminary report of a redescription that was never finished (Machado, pers. comm. 2011). The present revision, based on all the material from the Laboratorio Nacional de Energia e Geologia, Museu de Geologia and the Instituto Superior Técnico, Museu Décio Thadeu (Lisbon, Portugal) available at the time of study (August–November 2011), agrees in considering it a valid species, based on adult individuals (unlike hypothesized by Poyato-Ariza and Wenz, 2002). However, it disagrees with Machado et al. (2010) in not considering it a species of *Pycnodus* by providing a number of characters that are significantly different from *Pycnodus* at the generic level, including several autapomorphies plus a unique combination of characters different from the emended diagnosis of the genus by Poyato-Ariza and Wenz (2002, p. 222).

Sylvienodus differs from *Pycnodus* in presenting: very small size, up to 6 cm in SL (3–4 times smaller); ovoid rather than truncated body outline; postcephalic lacuna absent; larger parietal; ax-shaped rather than reniform maxilla; small opercular bone, not reaching the preopercular ventrally; 22–23 vertebrae rather than 28–29 (counted as dorsal spines, caudal endoskeleton excluded); 37 rather than 58 dorsal and 33 rather than 45 anal axonosts; 17–18 rather than 21 principal caudal fin rays; 5 rather than 9 epichordal and 9 rather than 10 hypochordal elements in the caudal endoskeleton; 12 rather than 9 dorsal ridge scales; presence of oval notch between dorsal ridge scales 1 and 2; 15 rather than 11 ventral keel scales; and 2 posterior cloacal scales rather than 1. Furthermore, and especially relevant for a pycnodontid at the generic level: dermocranial fenestra absent; 1 premaxillary tooth rather than 2; contact between arcocentra simple rather than interdigitated; dorsal and anal fins extremely rather than slightly falcated; largest hypochordal elements in caudal endoskeleton enlarged rather than hypertrophied; and dorsal ridge scales simple, with crenulated dorsal border, rather than scutellum-like. All these differences support the removal of the Portuguese material from *Pycnodus* and the erection of *Sylvienodus* as a replacement genus.

Pending a revision of its phylogenetic relationships, *Sylvienodus* nov. gen. is provisionally attributed to the

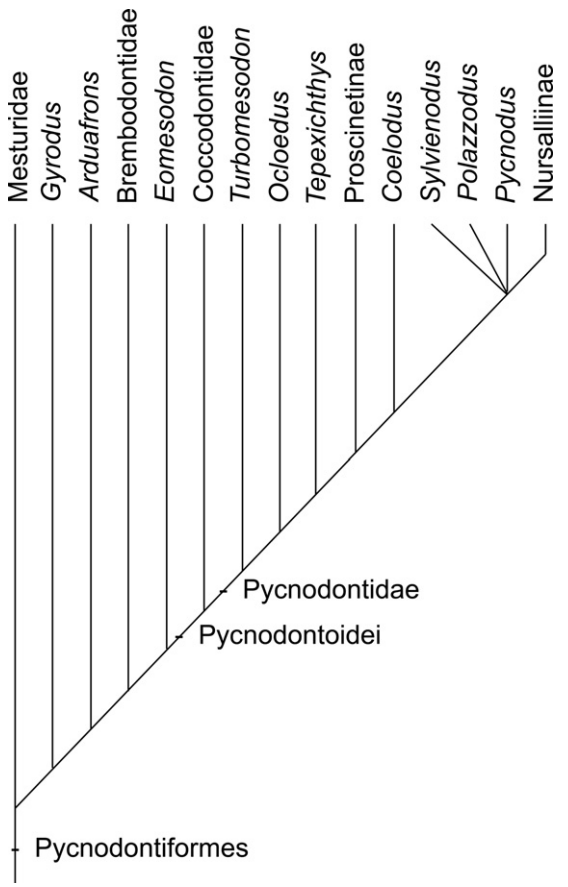

Fig. 7. Expected phylogenetic position of *Sylvienodus* nov. gen. among Pycnodontiformes. Simplified from Poyato-Ariza and Wenz (2002).
Fig. 7. Position phylogénétique attendue pour *Sylvienodus* nov. gen. parmi les Pycnodontiformes. Simplifié d'après Poyato-Ariza et Wenz (2002).

Pycnodontinae because it has a significant autapomophy of the subfamily as defined by Poyato-Ariza and Wenz (2002), the presence of a postcephalic lacuna, although it lacks other diagnostic features. *Tergestinia* Capasso, 2000 and *Polazzodus* Poyato-Ariza, 2010, also present some, but not all, of the diagnostic characters of the Pycnodontinae. *Sylvienodus* confirms that the diagnosis of the subfamily and the character distribution in the most inclusive pycnodontids are in need of revision. This, together with the currently unsolved taxonomic problems presented by other nominal species from Italy (Poyato-Ariza, 2010), suggests taking this subfamilial assessment with caution until the phylogenetic relationships of these forms (Fig. 7) are re-evaluated.

The removal of *laveirensis* from *Pycnodus* has interesting consequences for the temporal distribution of this genus. The type species, *P. apodus*, is from the lower Eocene of Monte Bolca, in Italy. Some nominal species, whose generic assessment needs confirmation, are also from the Eocene (Longbottom, 1984). A few Cretaceous isolated dentitions of dubious generic assessment (Woodward, 1895) are *nomina dubia* at best, all in need of revision. Interestingly, articulated material from the new locality of Gara Sbaa (Martill et al., 2011) was preliminarily identified as a new species of *Pycnodus*; it is Late Cenomanian to Early Turonian (op. cit.), very close, or alike, in age to Laveiras. There are no detailed descriptions in that first report, but interesting features can be observed in the specimen illustrated (Martill et al., 2011, fig. 8C). As seen in that figure, the pycnodont from Gara Sbaa resembles *Sylvienodus* rather than *Pycnodus* in at least these characters: size, about 6 cm; contour of the body ovoid, not truncated; dermocranial fenestra absent; contact between arcocentra simple, not interdigitated; and closer meristic accounts in number of vertebrae (about 24 rather than 28–29), dorsal axonosts (about 43 rather than 58), anal axonosts (about 30 rather than 45), and dorsal ridge scales (some 12–14 rather than 9). Detailed study of the pycnodont from Gara Sbaa may show additional differences from *Pycnodus*, so it may be closer to *Sylvienodus* than to *Pycnodus*. In any case, the absence of dermocranial fenestra alone is a strong indication that the new Moroccan material does not belong to *Pycnodus*.

Consequently, the genus *Pycnodus* is considered restricted to the Eocene; as currently understood, the only valid species of *Pycnodus* based on complete, articulated material, is the type species, *P. apodus*. In turn, *Sylvienodus* nov. gen., as diagnosed here, is known only from the Cenomanian of Laveiras, Portugal. This confirms that the diversity of pycnodonts is higher than we used to think, as suggested by Poyato-Ariza (2005), and that the more we know about them, the more restricted their genera and species happen to be, both in time and space.

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