



## Osteology and relationships of *Brauccipycnodus pillae* gen. nov. from the Albian (Lower Cretaceous) of Pietraraja (Campania, southern Italy)

### Ostéologie et relations de *Brauccipycnodus pillae* gen. nov. de l'Albien (Crétacé inférieur) de Pietraraja (Campanie, Italie du Sud)

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**Résumé:** L'ostéologie et les relations phylogénétiques de *Brauccipycnodus pillae* gen. nov., un poisson pycnodonte de l'Albien marin (Crétacé inférieur) de Pietraraja (Campanie, Italie du Sud), sont étudiées en détails. Le nouveau genre appartient à la famille des Pycnodontidae, comme le montre la présence d'un processus en brosse sur le pariétal. Au sein de la famille, *Brauccipycnodus* est un membre d'un sous-groupe primitif caractérisé par des écussons dorsaux portant de fortes épines, par le contour faiblement crénelé des dents vomériennes et préarticulaires et par la présence de deux axonostes libres devant le premier ptérygophore dorsal. Une analyse phylogénétique montre que la position systématique de *Brauccipycnodus* est intermédiaire entre celle d'*Akromystax* et de *Stemmatodus*, d'une part, et celle de *Stenamara* et de *Turbomesodon*, d'autre part.

Mots-clés: Pycnodontiformes, Pycnodontidae, *Brauccipycnodus pillae* gen. nov., ostéologie, phylogénie, Albien marin, Pietraraja, Campanie, Italie du Sud.

**Abstract:** The osteology and the phylogenetic relationships of *Brauccipycnodus pillae* gen. nov., a pycnodontiform fish from the marine Albian (Lower Cretaceous) of Pietraraja (Campania, southern Italy), are studied in details. The new genus belongs to the family Pycnodontidae, as shown by the presence of a brush-like process on the parietal. Within the family, *Brauccipycnodus* is a member of a primitive subgroup characterized by dorsal ridge scutes bearing strong spines, by vomerine and prearticular teeth with a weakly crenulated contour and by the presence of two free axonosts before the first dorsal pterygiophore. A phylogenetical analysis shows that the systematic position of *Brauccipycnodus* is intermediate between that of *Akromystax* and *Stemmatodus*, on the one hand, and that of *Stenamara* and *Turbomesodon*, on the other hand.

Key words: Pycnodontiformes, Pycnodontidae, *Brauccipycnodus pillae* gen. nov., osteology, phylogeny, marine Albian, Pietraraja, Campania, southern Italy.

## INTRODUCTION

Pietraraja is a little village in the Benevento province (Campania, southern Italy) in which richly fossiliferous marine Aptian deposits were discovered three centuries ago. These layers contain the most famous European Lower Cretaceous fossil fish community. The main study of this ichthyofauna was conducted by D'ERASMO (1914, 1915) who published a monograph divided in two volumes. The historical account of the geological and paleontological investigations in Pietraraja is related by CAPASSO (2007) in a richly illustrated book.

Two different species of pycnodontid fishes are present in the Albian deposits of Pietraraja.

Pycnodontomorpha are by far the largest lineage within fossil Neopterygii. The group contains around 50 genera and more than 650 nominal species. Their first occurrence dates back to the Late Triassic and they disappear during the Eocene (POYATO-ARIZA & MARTIN-ABAD, 2013). They reach a nearly worldwide distribution during the Late Cretaceous. Most of them are deep-bodied fishes. They bear molariform teeth on the vomer and the prearticulars and generally have a durophagous mode of feeding (NURSALL, 1999).

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The first pycnodontid species from Pietraraja is represented by numerous specimens and was erroneously reported by D'ERASMO (1914) to *Coelodus costae* HECKEL, 1856, another pycnodontid fish already known from the Hauterivian-Barremian of Castellammare di Stabia, in Campania (BASSANI & D'ERASMO, 1912), and called now *Costapycnodus costae* (TAVERNE *et al.*, 2019). That first pycnodontid from Pietraraja was recently re-studied (TAVERNE *et al.*, 2020) and is presently known under the name *Gregoriopycnodus bassanii* (D'ERASMO, 1914).

The second species was discovered more recently and was described on the basis of the holotype only (CAPASSO, 2007). It was labelled *Proscinetes pillae* CAPASSO, 2007.

The aim of our present paper is to re-study in a detailed way the osteology and the systematic relationships of this last fish. We will see that it does not belong to the genus *Proscinetes* GISTEL, 1848 but represents a new genus.

## MATERIAL AND METHODS

The two specimens hereafter described belong to the CAPASSO registered collection (CLC). They were studied with a stereomicroscope Leica Wild M 8. The figures were drawn by the first author (L. T.) and the photos made by Mr. Luciano LULLO, from the University of Chieti-Pescara. Aspersions with ethanol and razing light were used to improve some observations.

The Capasso collection (CCL) in Chieti (Italy) is legally registered by a decree of the Ministero per I Beni e le Attività Culturali under the date of October 11<sup>th</sup> 1999, following the disposition of the Italian law 1089/39. The Soprintendenza per I Beni Archeologici dell'Abruzzo-Chieti has authorized the authors to study this collection by two letters bearing the dates of May 5<sup>th</sup>, 2011 (ref.: MBAC-SBA-ABR PROT 0004537 05/05/2011 Cl. 34.25.01/2.1) and July 30<sup>th</sup>, 2014 (ref.: MBAC-SBA-ABR PROT 0005618 31/07/2014 Cl. 34.25.01/2.1).

### List of abbreviations used in text-figures

AN	=	angular
ART	=	articular
APTE	=	autopterotic
ASPH	=	autosphenotic
AX 1, 2	=	dorsal free axonosts 1 and 2
BO	=	basioccipital
BRSTG	=	branchiostegal rays
CHY a., p.	=	ceratohyal (anterior, posterior)
CLT	=	cleithrum
DHYOM	=	dermohyomandibula
DN	=	dentary
DPTE	=	dermopterotic
DSOC	=	dermosupraoccipital
DSPH	=	dermosphenotic
ECPT	=	ectopterygoid
ENPT	=	entopterygoid (= endopterygoid)
EPCO 1-6	=	epichordals 1 to 6
EXO + SYN	=	exoccipital fused with synarcual
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HP 15	=	haemal spine (fifteenth)
HYCO 1-10	=	hypochordals 1 to 10
HYOM	=	hyomandibula
IHY	=	interhyal
IC	=	intercalar
IORB (1)	=	infraorbital (first)
LEP	=	lepidotrichium (= ray)
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
NA	=	nasal
NP 31	=	neural spine (thirty first)

OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PCLT	=	postcleithrum
PCOEL	=	postcoelomic bone
PELV	=	pelvic (= ventral) rays
PMX	=	premaxilla
POP	=	preopercle
PRART	=	prearticular
PRFR	=	prefrontal
PS	=	parasphenoid
PSPH	=	pleurosphenoid
PT	=	posttemporal
QU	=	quadrate
RAD	=	pterygiophores (= radials, axonosts)
RI	=	rib
SC	=	scales
SCL	=	sclerotic bone
SCU d. 13	=	thirteenth and last scute of the dorsal ridge
SCU v. 15	=	fifteenth precloacal scute of the ventral keel
SCU v. 16-17	=	postcloacal scutes of the ventral keel
SOC	=	supraoccipital (= supraotic)
ST	=	supratemporal
SY	=	symplectic
PT	=	posttemporal
UD 1, 2	=	urodermal 1 and 2
VO	=	vomer
b. pr.	=	brush-like process of the parietal
br.	=	broken
t. f.	=	temporal (cranial) fenestra

## SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885

Series Neopterygii REGAN, 1923

Division Halecostomi REGAN, 1923 *sensu* PATTERSON, 1973

Superorder Pycnodontomorpha NURSALL, 2010

Order Pycnodontiformes BERG, 1937 *sensu* NURSALL, 2010

Family Pycnodontidae AGASSIZ, 1833 *sensu* NURSALL, 1996

Genus *Brauccipycnodus* gen. nov.

Type-species: *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. (by monotypy).

### Diagnosis

As for the species (monospecific genus)

### Etymology

The name of the new genus is chosen in honour of Niccolo BRAUCCI (1719-1774), a medical physician, professor at the University of Naples, who was the first scientist to have studied the fossil fishes from Pietraraja (CAPASSO, 2007 : 14, fig. 1). Unfortunately, his premature death did not allow the publication of this manuscript. The generic name *Pycnodus* is added to his patronym.

Species *Brauccipycnodus pillae* (CAPASSO, 2007)

### Synonymy

*Proscinetes pillae*, sp. nov. – In: CAPASSO, 2007: 177, fig. 134.

### Emended diagnosis

Small sized and deep-bodied pycnodontid fish. Maximum body depth around eight tenths of the standard length. Large head, with short preorbital and postorbital regions. Wide orbit. Large temporal fenestra. Narrow dermosupraccipital. Supraoccipital visible in the temporal fenestra. Small brush-like process on parietal. Long prefrontal with a slightly broadened anterior extremity. Hypertrophied pleurosphenoid forming an interorbital bony septum. Vomer with 3 rows of teeth, 5 teeth in the lateral rows and 6 teeth in the middle row. Parasphenoid outpacing the rear of the skull. Exoccipital, basioccipital and intercalar exposed behind the dermopterotic. Exoccipital fused with a synarcual. Mouth gape obliquely oriented. Premaxilla with 2 incisiform teeth. Short dentary with 2 incisiform teeth. Coronoid process moderately developed. Prearticular with 3 rows of teeth, 6 in the upper row, 4 in the middle row and 5 in the lower row. Vomerine and prearticular teeth with a weakly crenulated contour. Dermosphenotic sutured with dermopterotic and frontal. Large triangular first infraorbital. Tubular infraorbitals present. Preopercle much larger than the exposed region of hyomandibula-dermohyomandibula. Small opercle. Notochord partly surrounded by neural and haemal arches. 31 neural spines before the epichordal series. First 8 neural spines autogenous. 15 haemal spines before the hypochordal series. Anterior bony wing on the neural and haemal spines. Neural and haemal arches connected by one pre- and one postzygapophysis. 13 pairs of ribs. Postcoelomic bone not reaching the axial skeleton. Two free axonosts before the first dorsal pterygiophore. Falcate dorsal fin with 61 rays and 58 pterygiophores. Origin of dorsal fin located at the highest point of the dorsal profile. Falcate anal fin with 39 rays and 38 pterygiophores. Origin of the anal fin located behind the lowest point of the ventral profile. 6 epichordals. 10 hypochordals. 2 urodermals. Caudal fin with a convex posterior margin, 21 principal rays, 2 dorsal and 5 ventral procurrent rays. Second dorsal procurrent ray hypertrophied. Body scales only in the abdominal region. 15 rows of flank scales. Bar-scales dorsally and ventrally. One row of complete scales ventrally. 13 dorsal ridge scutes, with strong spines. 17 ventral keel scutes with strong spines, 15 before and 2 behind the cloaca. 3 cloacal scales, one anterior, one above and one posterior to the cloaca.

### Holotype

Sample CLC I-125, a complete and well preserved specimen (Fig.1; CAPASSO, 2007: fig. 134). Total length: 67mm. Standard length: 54 mm.



Figure 1: *Braucippycnodus pillae* (CAPASSO, 2007) gen. nov. Holotype CLC I-125. Total length: 6.7 cm.

## Other material

Sample CLC I-347, an isolated and well preserved skull (Fig. 2).



**Figure 2:** *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. Specimen CLC I-347, an isolated skull.

## Formation and locality

Marine Albian (Lower Cretaceous) of Pietraraja, Benevento province, Campania, southern Italy.

## Morphometric data

The morphometric data are given in percentage (%) of the standard length (54 mm) of the holotype.

Length of the head (opercle included) .....	35.0 %
Depth of the head (in the occipital region) .....	52.3 %
Maximum depth of the body (at the dorsal apex) .....	82.2 %
Prepelvic length .....	66.0 %
Predorsal length .....	58.9 %
Basal length of the dorsal fin .....	51.8 %
Preanal length .....	75.1 %
Basal length of the anal fin .....	36.0 %
Depth of the caudal peduncle .....	7.6 %

## Osteology

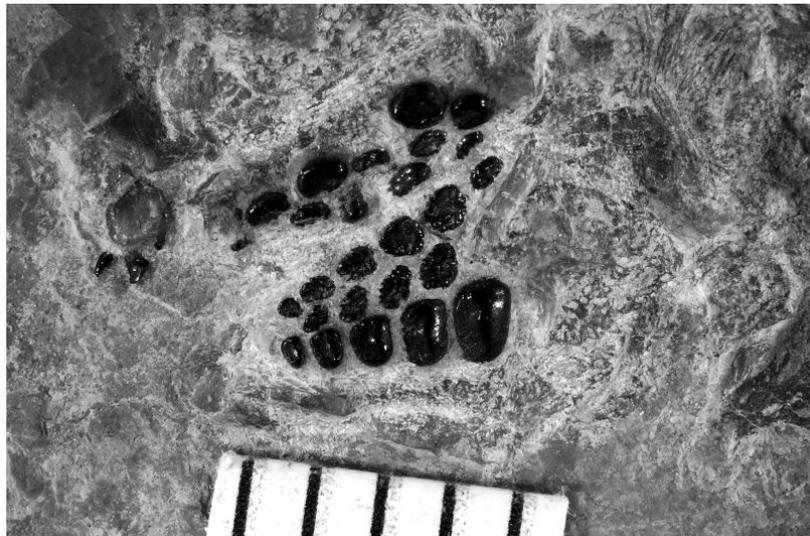
### *The skull* (Figs 2-6)

The dermal bones of the skull are strongly ornamented with some ridges and numerous alveoli that often are arranged in long rows. The mouth gape is ventrally inclined. The orbit is wide. The preorbital region is only 1.3 longer than the postorbital region.



The mesethmoid is a very large bone with a “T”-like transversal section. It is covered by a narrow and strongly ornamented prefrontal that is broadened at the level of its anterior extremity. A very short tubular nasal is visible just before the frontal in the holotype. The presence of such a bone is extremely rare in pycnodont fishes but, however, is known in some of them (POYATO-ARIZA & WENZ, 2004: figs 4, 5). There are three rows of teeth on the vomer of the holotype but only two rows are visible on sample CLC I-347. The external row of both specimens contains 5 ovoid teeth but the first tooth of the holotype is lost and only its alveolus is preserved. The middle row has 6 teeth, three large anterior and three smaller posterior ones. These vomerine teeth exhibit a few weakly marked tubercles on their contour.

As usual, the skull roof is formed by the paired frontals, parietals and dermopterotics and by the unpaired dermosupraoccipital. The dermosphenotic is not a free bone. It is articulated with the frontal and the dermopterotic and is integrated at the lateral margin of the skull roof. The frontal of the holotype is slightly arched, a feature probably accentuated by a break and a small deformation of the substratum. There is a temporal fenestra opened between the frontal, the parietal and the dermosupraoccipital. The upper region of the supraoccipital (= supraotic for some authors, see for instance KRIWET, 2005: fig. 13) is visible in the fenestra. The parietal bears a small posterior brush-like process (= parietal peniculus) on the holotype but the process is not visible on sample CLC I-347. In this specimen, the substratum just behind the parietal is damaged. Parts of the cephalic sensory canals are clearly visible on the holotype. The supraorbital canal is exposed at the junction of the frontal and the dermopterotic. The otic canal passes from the dermosphenotic to the dermopterotic. The upper portion of the preopercular canal and the lower portion of the extrascapular canal also are visible on the dermopterotic, both being connected to the otic canal. A supratemporal is present on the holotype, just behind the parietal. It seems composed of three small bar-like scales fused to an underlying thin bony plate.



**Figure 5:** *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. Vomer and prearticular of holotype CLC I-125.

The orbitosphenoid is pressed against the posterior border of the mesethmoid and delimits the anterior margin of the orbit. In the holotype, a very wide pleurosphenoid is visible in the orbit, forming an almost complete bony interorbital septum, and a well developed autosphenotic is present along the posterior margin of the orbit. Such a hypertrophied pleurosphenoid is unknown in other pycnodontid fishes. No bone is visible in the orbit of sample CLC I- 347. The trabecular toothless part of the parasphenoid is obliquely oriented.

The most posterior part of the endocranium appears on the holotype and is separated from the pre-occipital region of the braincase. This occipital portion is supported by the elongate parachordal region of the parasphenoid. The exoccipital is fused to a synarcual on which the first three neural spines are articulated. Two opened foramina, probably for the glossopharyngeal (IX) and the vagal (X) nerves, are visible at the anterior margin of the exoccipital. A small intercalar and a knob-like basioccipital are also present.

The metapterygoid and the entopterygoid are large bones. A small ectopterygoid is also visible. Both the quadrate and the symplectic are articulated on the lower jaw.

The premaxilla is rather short and particularly thin. It bears two small incisiform teeth. The plate-like toothless maxilla is preserved on both available specimens. It has an irregular contour, with a small posterior ventral process. The dentary is reduced to its short ventral branch and bears also two incisiform teeth. The angular covers only a small part of the prearticular, as it is clearly visible on sample CLC I-347. The posterior ventral corner of the lower jaw is formed by the articular. The prearticular is triangle-shaped, with a deep but

moderately marked coronoid process. There are three rows of teeth. The upper and the middle rows contain respectively 6 and 4 small rounded teeth. The lower row is formed by 5 larger ovoid teeth. The periphery of all those teeth bears a few poorly developed tubercles.

As already written, the dermosphenotic is integrated to the skull roof. A series of short tubular posterior infraorbitals and a great part of a large triangular first infraorbital are visible on the holotype. A sclerotic bony ring is also present.

The exposed region of the hyomandibula-dermohyomandibula is much smaller than the deep and broad preopercle which is the largest bone of the skull. The opercle is present but, as always in pycnodonts, is much smaller than the preopercle. There are two thin branchiostegal rays pressed the one against the other.

The anterior ceratohyal is preserved on both specimens. The anterior extremity is narrow but the posterior margin is enlarged and rounded. The smaller posterior ceratohyal and the interhyal are visible on the holotype.

The preopercle of the holotype is crushed. Some parts are missing. Underlying branchial bones, long, thin and acuminate gill rakers and a few small hook-like branchial teeth are exposed.

#### ***The girdles*** (Figs 2-4)

The shape of the cleithrum is similar to the one of *Stemmatodus rhombus* AGASSIZ, 1839 as figured in NURSALL (1996: fig. 11 C). The hypercleithrum (= supracleithrum) is long and narrow. A small rod-like posttemporal is visible just behind the dermopterotic. The pectoral fin is supported by 6 pterygiophores (= radials) and contains 31 short rays.

Fragments of 5 ventral fin rays are visible in the cloacal vestibule.

#### ***The axial skeleton*** (Figs 1, 6-8)

As usual, the vertebral axis progressively elevates from the caudal region to reach the head at the orbit level. A large part of the notochord is surrounded by the dorsal and ventral arcocentra. There are 31 neural and 15 haemal spines respectively before the epichordal and the hypochordal series. All these spines have an anterior wing-like expansion and branched distal extremities. The first 8 neural spines are autogenous, 3 being articulated on the large synarcual and 5 on the first neural arches. The first haemal spine is extremely short. The articulation between the spines is formed by only one zygapophysis. There are 13 paired ribs. They are broadened in their upper region by posterior wing-like flanges.

The postcoelomic bone is elongated but does not reach the axial skeleton. It rests on the anterior border of the first short haemal spine.

#### ***The dorsal and anal fins*** (Figs 6-8)

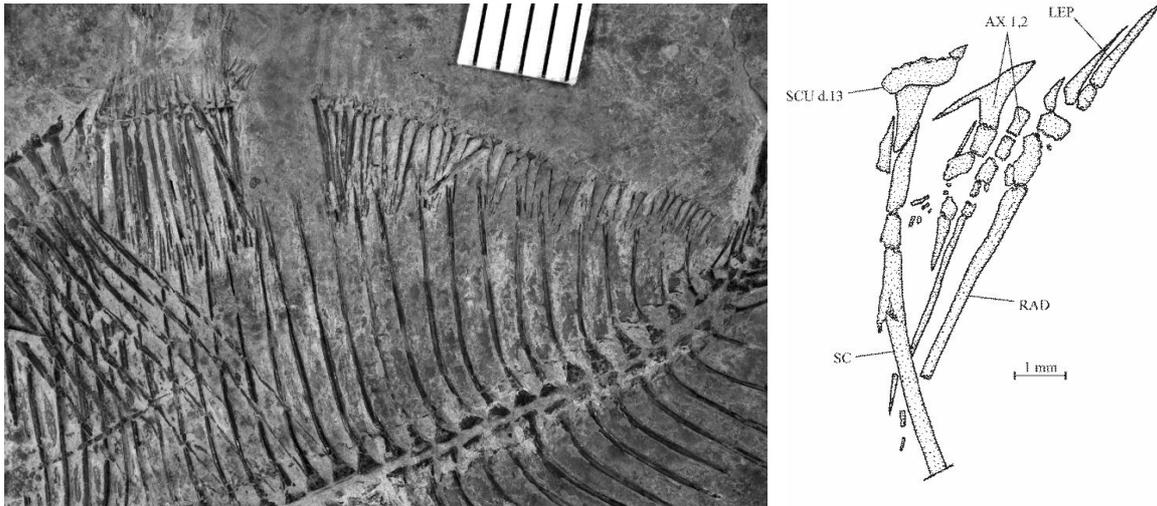
There are two free axonosts before the first dorsal pterygiophore. The first free axonost is composed of two branches, the usual ventral branch and a short, narrow dorsal branch that bears of few microspines on its upper margin. Such a morphology suggests that the first free axonost has probably captured the last dorsal ridge scute. The second free axonost is rod-like.

The dorsal fin contour is falcate (POYATO-ARIZA & WENZ, 2004: fig. 34 B). The dorsal fin contains 50 pterygiophores but a few ones are lost at the level between the fifteenth and the eighteenth neural spines. The length of this empty space represents eight missing axonosts. So the total number of dorsal pterygiophores must be of about 58. The first three dorsal pterygiophores bear a series of 6 short pointed rays. Each following pterygiophore bears only one ray. The posterior rays are lost. However, the total number of dorsal rays can be estimated of about 61, 6 short and pointed rays and 55 long, segmented and branched rays. The origin of the dorsal fin is located at the highest point of the dorsal profile.

The anal fin also has a falcate contour. There are 38 pterygiophores, the last ones being preserved only as imprints. Both the first and the second pterygiophores bear a small pointed ray. A third small pointed ray articulates on both the second and the third pterygiophores. This third pterygiophore also bears the first long, segmented and branched ray. The following pterygiophores bear only one ray each. The last rays are missing but the total number of anal rays can be estimated of about 39, 3 short pointed rays and 36 long, segmented and branched rays.

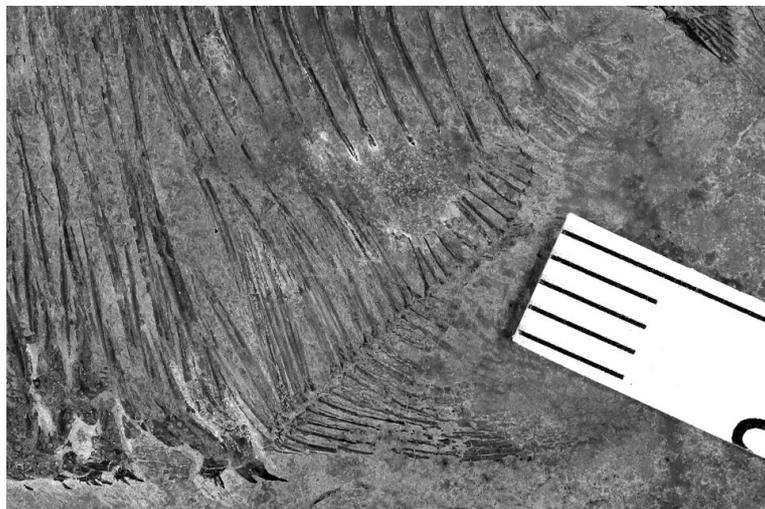
#### ***The caudal endoskeleton and fin*** (Figs 9-10)

The caudal peduncle is short. There are 6 epichordals, 10 hypochordals and 2 urodermals in the caudal endoskeleton. The first two epichordals have long neural spines. The four following ones are much shorter. The eighth and the ninth hypochordals are broadened but not really hypertrophied.



**Figure 6:** *Brauccipynodus pillae* (CAPASSO, 2007) gen. nov. Dorsal fin of holotype CLC I-125.

**Figure 7:** *Brauccipynodus pillae* (CAPASSO, 2007) gen. nov. The two free dorsal axonosts of holotype CLC I-125, just before the first dorsal pterygiophore.



**Figure 8:** *Brauccipynodus pillae* (CAPASSO, 2007) gen. nov. Anal fin of holotype CLC I-125.

The caudal fin has a convex distal margin (POYATO-ARIZA & WENZ, 2002: fig. 36 B). There are 21 principal caudal rays, 2 dorsal and 5 ventral procurrent rays (= basal fulcra). The most external dorsal and ventral principal rays are segmented and pointed. The nineteen others are segmented and branched. The fourth principal ray from the upper margin of the fin has an elongate claw-like proximal extremity that overhangs the three last epichordals. The second dorsal procurrent ray is hypertrophied. A similar but less pronounced hypertrophy also exists on the second ventral procurrent ray.

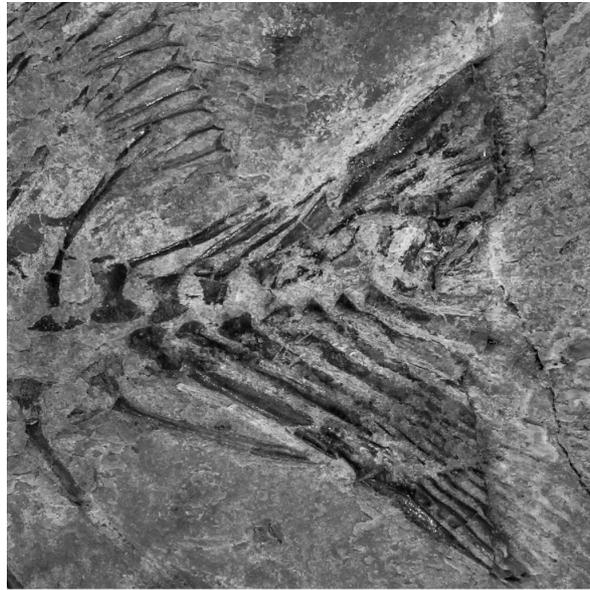
#### ***The squamation*** (Figs 11-14)

There are flank scales only in the abdominal region of the body. The most ventral ones are complete but all the other scales are reduced to the bar-like elements. The flank scales are ranged in 15 rows. A series of small tubular scales carrying the lateral sensory line are associated the bar-scales that support the dorsal ridge scutes.

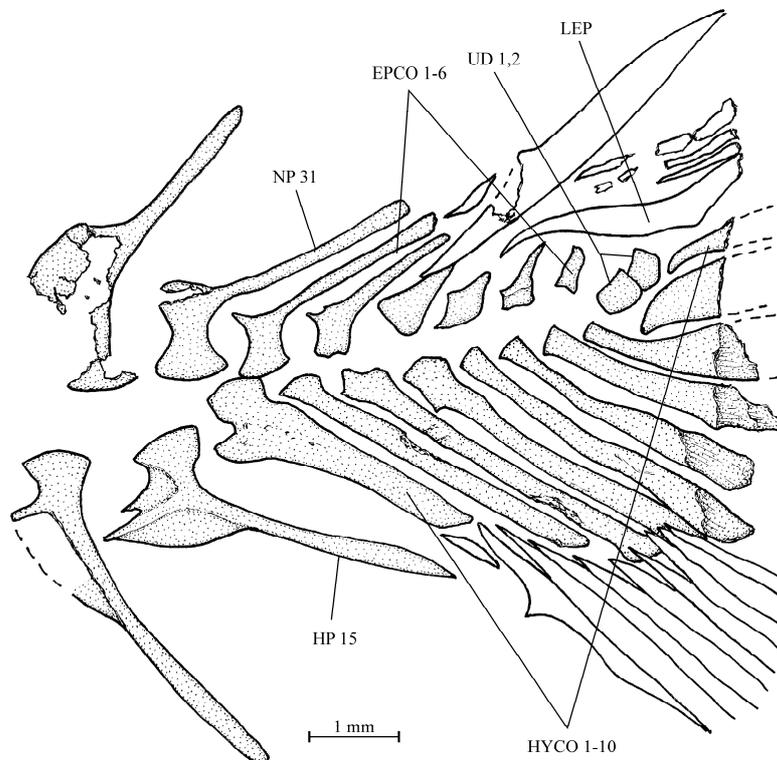
The dorsal ridge is formed by 13 scutes that bear three or four well developed spines on their upper margin, except the first one that is articulated on the dermosupraoccipital. This first scute is not larger than the following ones.

The ventral keel contains 17 scutes, 15 before and 2 behind the cloaca. The best preserved precloacal scutes bear two or three strong spines. The first postcloacal scute bears four spines and the second postcloacal scute only two very large spines. This second postcloacal spine is articulated on the ventral extremity of the postcoelomic bone.

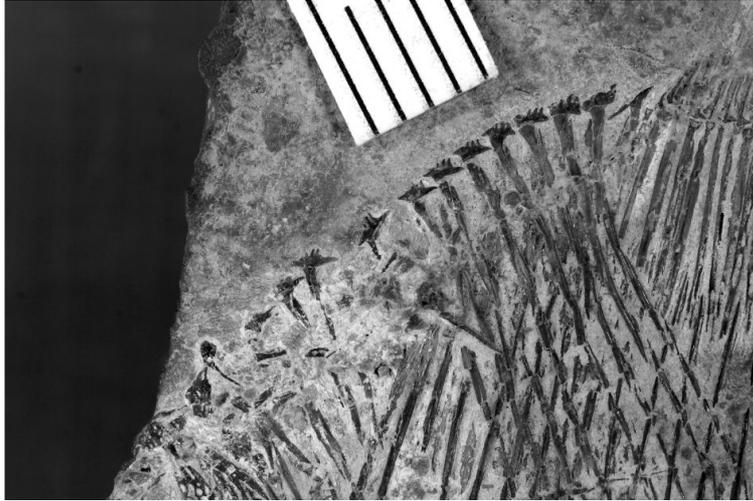
Three small modified scales, not in contact with the ventral scutes, are associated with the cloacal region. One scale is anterior and one is posterior to the cloaca. An extremely reduced third scale overhangs the cloaca. Behind the cloaca, two scales are associated with the first postcloacal scute. There are still two other posterior scales resting on the postcoelomic bone. No bifid scale is present in the cloacal region.



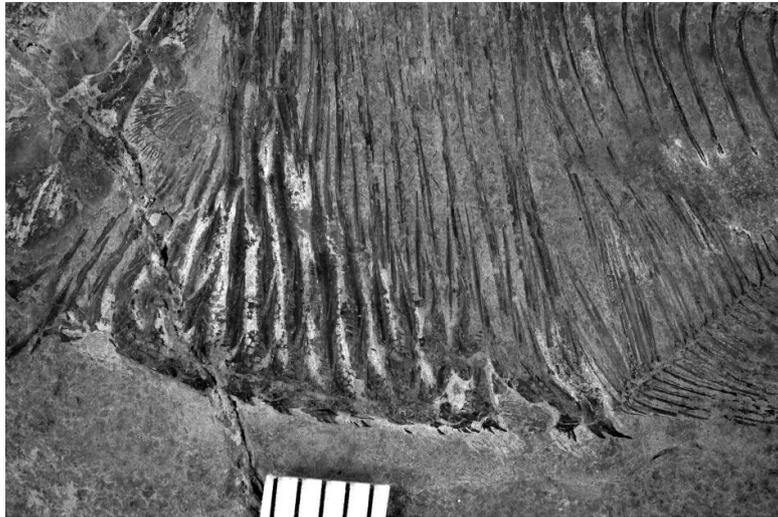
. **Figure 9:** *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. Caudal region of holotype CLC I-125.



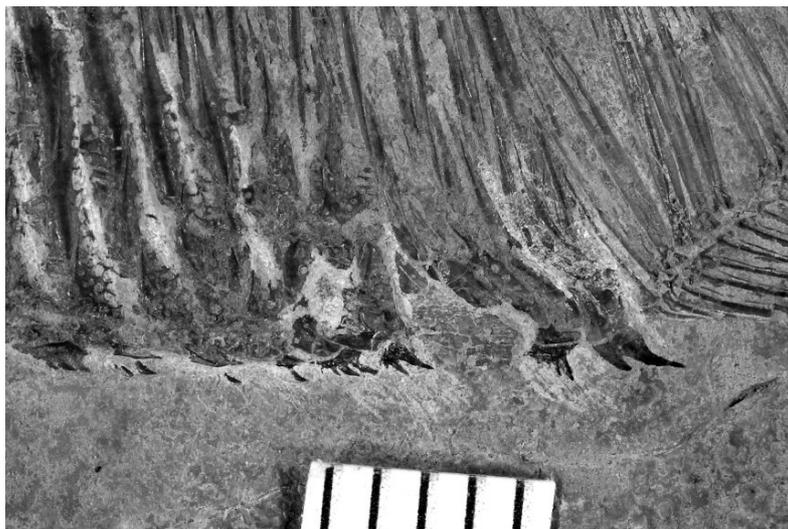
**Figure 10:** *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. Caudal skeleton of holotype CLC I-125.



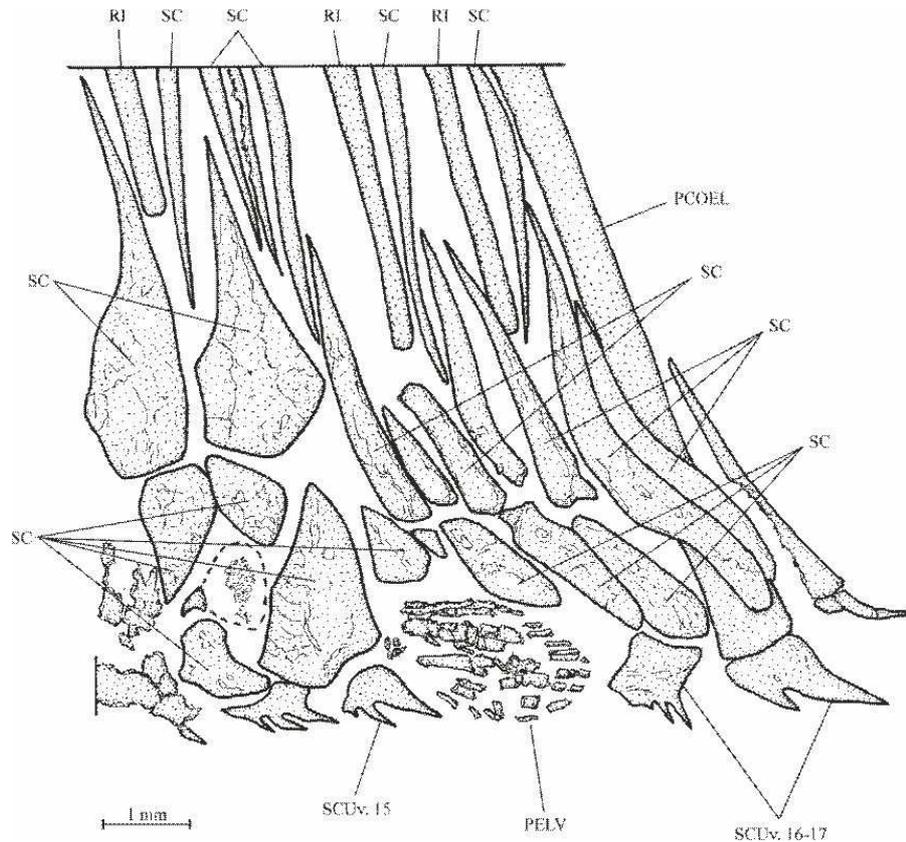
**Figure 11:** *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. Dorsal ridge scutes of holotype CLC I-125.



**Figure 12:** *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. Ventral keel scutes of holotype CLC I-125.



**Figure 13:** *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. Cloacal region of holotype CLC I-125.



**Figure 14:** *Brauccipycnodus pillae* (CAPASSO, 2007) gen. nov. Cloacal scales and ventral fins of holotype CLC I-125.

## DISCUSSION

### *Brauccipycnodus* within Pycnodontiformes

The parietal brush-like process (= parietal peniculus) present in *Brauccipycnodus pillae* indicates that this fish belongs to the family Pycnodontidae (POYATO-ARIZA & WENZ, 2002, character 14[1]).

### *Brauccipycnodus* and *Proscinetes*

CAPASSO (2007: 177) ranged the species *pillae* in *Proscinetes* principally because this species shares two important characters with the genus, *i. e.*, the presence of two anterior free axonosts before the first dorsal pterygiophore and the notochord not completely surrounded by the neural and haemal arcocentra.

However, these two features also occur in other pycnodontid genera and the cranial skeleton of *Proscinetes* greatly differs from the one of *Brauccipycnodus*.

The skull of *Proscinetes* is known in two species from the Upper Jurassic of Europe, *Proscinetes elegans* (AGASSIZ, 1833) and *Proscinetes bernardi* (THIOLLIÈRE, 1852). The genus is devoid of temporal fenestra and of prefrontal and it has an extrascapular included in the skull roof near the dermopterotic (DE SAINT-SEINE, 1949: fig. 41; POYATO-ARIZA & WENZ, 2002: fig. 8B; EBERT, 2013: fig. 11). Moreover, the dorsal ridge scutes of *Proscinetes* are devoid of spines. These four marked differences are enough to show that the species *pillae* can not be included in the genus *Proscinetes*.

### *Brauccipycnodus* and *Gregoriopycnodus*

It is interesting to compare *Brauccipycnodus* and *Gregoriopycnodus* since they are present together in the Pietraraja deposits. The data concerning *Gregoriopycnodus* come from TAVERNE *et al.* (2020). Both genera

have a brush-like process on the parietal and thus belong to the family Pycnodontidae. Both fishes also exhibit a temporal fenestra and a dermosphenotic sutured with the frontal and the dermopterotic. However, the differences are numerous.

In *Gregoriopycnodus*, the preorbital region of the skull is proportionally longer, the metapterygoid and the opercle larger, the maxilla smaller, the coronoid process of the lower jaw more marked than in *Brauccipycnodus*. The prefrontal of *Gregoriopycnodus* is short and partly fused with the mesethmoid; the one of *Brauccipycnodus* is longer and is not fused with the mesethmoid. No pleurosphenoid is visible in the orbit of *Gregoriopycnodus*, while the one of *Brauccipycnodus* is hypertrophied and completely fills the orbit. The parasphenoid of *Brauccipycnodus* markedly outpaces the rear of the skull; that is not the case in *Gregoriopycnodus*. The exoccipital and the synarcual are fused to the rear of the skull in *Gregoriopycnodus* while the basioccipital and the exoccipital, fused to a synarcual, are separated from the skull in *Brauccipycnodus*. *Gregoriopycnodus* has more teeth on the vomer and the prearticular than *Brauccipycnodus*. The contour of the vomerine and prearticular teeth is not crenulated in *Gregoriopycnodus* contrarily to the case of *Brauccipycnodus*.

*Gregoriopycnodus* has 5 autogenous neural spines, a postcoelomic bone that reaches the vertebral axis, no free dorsal axonost, 49 to 52 dorsal rays supported by 49 to 50 pterygiophores, 13 rows of flank scales, no spines on the dorsal ridge scutes, 14 or 15 ventral keel scutes, with only one postcloacal scute. For all these characters *Brauccipycnodus* differs from *Gregoriopycnodus*. The two fishes also have a completely different pattern of the scales located in the cloacal region.

It is clear that *Gregoriopycnodus* and *Brauccipycnodus* represent two totally different genera of Pycnodontidae.

### ***Brauccipycnodus* within Pycnodontidae**

We principally use hereafter the phylogeny elaborated by POYATO-ARIZA & WENZ (2002, 2004, 2005) and more accessorially the phylogenetic hypotheses of KRIWET (2005), EBERT (2016) and CAWLEY & KRIWET (2017). We also use some information from two of our own recent papers (TAVERNE & CAPASSO, 2013; TAVERNE *et al.*, 2019).

Within the family Pycnodontidae, *Brauccipycnodus* belongs to the primitive subgroup that exhibits strong spines on the upper margin of the dorsal ridge scutes (POYATO-ARIZA & WENZ, 2002, character 90 [1, 2, 3]). The subgroup contains the genera *Akromystax* POYATO-ARIZA & WENZ, 2005, *Stemmatodus* HECKEL, 1854, *Stenamara* POYATO-ARIZA & WENZ, 2000, *Turbomesodon* POYATO-ARIZA & WENZ, 2004, *Ocloedus* POYATO-ARIZA & WENZ, 2002, *Rhinopycnodus* TAVERNE & CAPASSO, 2013 and *Costapycnodus* TAVERNE *et al.*, 2019.

The Lebanese *Hagelichthys* TAVERNE & CAPASSO, 2018 has also the dorsal ridge scutes ornamented with strong spines (TAVERNE & CAPASSO, 2018: fig. 19). However, this genus belongs to a more evolved assemblage of Pycnodontidae (*ibid.* 2018: 130-131) and, in that case, the character is considered as a reversion.

The presence in *Brauccipycnodus* of weakly developed crenulations on the contour of the vomerine and prearticular teeth confirms that this genus is a primitive member of the family. Indeed, this feature disappears in *Proscinetes* and in the more specialized Pycnodontidae (POYATO-ARIZA & WENZ, 2002, node 20, character 49[0]).

The less specialized genus of the subgroup is *Akromystax*. It still has a horizontal mouth gape (POYATO-ARIZA & WENZ, 2005, character 5 [0]), a small independent extrascapular associated with the parietal (*ibid.*, 2005, character 16[0]) and a row of complete scales below the dorsal ridge scutes (*ibid.*, 2005: fig. 2).

*Brauccipycnodus* and the other genera of the primitive subgroup have an oblique mouth gape (*ibid.*, 2005, character 5 [1]), the extrascapular incorporated in the parietal (*ibid.*, 2005, character 16 [1]) and they have already lost the complete scales below the dorsal ridge scutes.

In this remaining subgroup, *Brauccipycnodus*, *Stemmatodus*, *Stenamara* and *Turbomesodon* share a very peculiar character. They have a few free axonosts before the dorsal fin origin and the first dorsal pterygiophore (POYATO-ARIZA & WENZ, 2004, node 1, character 57 [1]). *Ocloedus*, *Rhinopycnodus* and *Costapycnodus* do not exhibit such a feature.

In *Stemmatodus*, the scales located just below the dorsal ridge scutes are reduced but still preserved a wing-like component associated with the bar-like element (BASSANI & D'ERASMO, 1912: fig. 10; TAVERNE *et al.*, 2019: fig. 25). *Brauccipycnodus*, *Stenamara* and *Turbomesodon* exhibit only the bar-like element of these scales and no more a wing-like component (POYATO-ARIZA & WENZ, 2002: fig. 3 D, 2004: fig. 3).

*Stenamara* and *Turbomesodon* share two other peculiar features. Their epichordal series is reduced to 3 or less elements (POYATO-ARIZA & WENZ, 2005, node 2, character 48 [3]) and they exhibit the reverse condition of having 3 to 6 postcloacal ventral keel scutes (POYATO-ARIZA & WENZ, 2002: fig. 41 D, 2004: figs 12, 14, node 2, character 84 [2]).

*Brauccipycnodus* and *Stemmatodus* have 4 to 6 elements in the epichordal series (NURSALL, 1999: fig. 10 B; TAVERNE *et al.*, 2019: fig. 23) and only 2 postcloacal ventral keel scutes (POYATO-ARIZA & WENZ, 2002: fig. 41 C).

Thus, within the phylogeny of Pycnodontidae, *Brauccipycnodus* must be positioned between the primitive genera *Akromystax* and *Stemmatodus*, on the one hand, and the more evolved genera *Stenamara* and *Turbomesodon*, on the other hand.

### The generic validity of *Brauccipycnodus*

In the subgroup of Pycnodontidae that contains *Brauccipycnodus*, *Akromystax*, *Stemmatodus*, *Stenamara* and *Turbomesodon*, *Akromystax* and *Brauccipycnodus* are the only ones that have a temporal fenestra. But these two genera are quite different. That is enough to confirm the validity of the genus *Brauccipycnodus*.

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