



Osteology and phylogenetic relationships of *Gregoriopycnodus bassanii* gen. nov., a pycnodont fish (Pycnodontidae) from the marine Albian (Lower Cretaceous) of Pietraroja (southern Italy)

Ostéologie et relations phylogénétiques de *Gregoriopycnodus bassanii* gen. nov., un poisson pycnodonte (Pycnodontidae) de l'Albien marin (Crétacé inférieur) de Pietraroja (Italie du Sud)

Louis TAVERNE¹, Luigi CAPASSO² & Maria DEL RE³

Résumé: L'ostéologie et les relations phylogénétiques de *Gregoriopycnodus bassanii* gen. nov., un poisson pycnodonte de l'Albien marin (Crétacé inférieur) de l'Italie du Sud, sont étudiées en détails. Ce genre fossile appartient à la famille des Pycnodontidae, comme le montre la présence d'un peniculus branchu sur le pariétal. *Gregoriopycnodus* diffère des autres genres de la famille par son préfrontal court, en forme de plaque et qui est partiellement soudé au méséthmoïde. Au sein de la famille, la position systématique de *Gregoriopycnodus* est intermédiaire entre celle de *Tepexichthys* et *Costapycnodus*, d'une part, et celle de *Proscinetes*, d'autre part.

Mots-clés: Pycnodontiformes, Pycnodontidae, *Gregoriopycnodus bassanii* gen. nov., ostéologie, phylogénie, Albien marin, Italie du Sud

Abstract: The osteology and the phylogenetic relationships of *Gregoriopycnodus bassanii* gen. nov., a pycnodont fish from the marine Albian (Lower Cretaceous) of Pietraroja (southern Italy), are studied in details. This fossil genus belongs to the family Pycnodontidae, as shown by the presence of a branched peniculus on the parietal. *Gregoriopycnodus* differs from the other genera of the family by its short and plate-like prefrontal that is partly fused to the mesethmoid. Within the family, the systematic position of *Gregoriopycnodus* is intermediate between that of *Tepexichthys* and *Costapycnodus*, on the one hand, and that of *Proscinetes*, on the other hand.

Key words: Pycnodontiformes, Pycnodontidae, *Gregoriopycnodus bassanii* gen. nov., osteology, phylogeny, marine Albian, southern Italy.

INTRODUCTION

The marine Albian layers of Pietraroja, a little village in the Benevento province (Campania, southern Italy), contain the most famous fossil fish assemblage in Europe for the Lower Cretaceous times. These deposits are known since at least the 18th century but the true scientific investigations on the site began with the excavations performed there between 1850 and 1867 by Oronzo Gabriele COSTA, the father of the Italian paleoichthyology, and his collaborators (CAPASSO, 2000, 2007).

D'ERASMO (1914, 1915) provided the only general study of the ichthyofauna from Pietraroja in a monograph published in two volumes. In the first part (1914) of his work he mentioned the presence of two different pycnodont fishes, *Coelodus costae* HECKEL, 1856, a species already known from the Hauterivian-Barremian of Castellammare di Stabia (COSTA, 1850; BASSANI & D'ERASMO, 1912), and *Palaeobalistum bassanii* D'ERASMO, 1911, a species he erected three years sooner on the basis of only one badly preserved specimen, with a crushed skull, previously discovered by COSTA and labelled by him *Rhombodus aculeatus* but never studied nor published (D'ERASMO, 1911). *Palaeobalistum bassanii* was recently ranged but with some doubt in the genus *Proscinetes* GISTEL, 1848 by POYATO-ARIZA & WENZ (2002: 151).

¹Royal Institute of Natural Sciences of Belgium, Directorate Earth and History of Life, Vautierstreet, 29, B-1000 Brussels, Belgium. E-mail: louis.taverne@skynet.be

²Museo Universitario dell'Università "G. d'Annunzio" di Chieti-Pescara, Piazza Trento e Trieste, 1, I-661000 Chieti, Italy. E-mail: lcapasso@unich.it

³Museo di Paleontologia, Centro Musei delle Scienze Naturali e Fisiche, Università degli Studi « Federico II », Largo San Marcellino, 10, I-80138 Napoli, Italy. E-mail: mardelre@unina.it

Since 1980, new excavations were conducted around Pietraraja and new fossil fish specimens were collected. Almost all the pycnodonts pertaining to this newly discovered material were labelled *Coelodus costae* but were not studied until now (CAPASSO, 2007: fig. 127-132). Only one sample become the holotype of a new pycnodont species, *Proscinetes pillae* CAPASSO, 2007 (ibid., 2007: 177-178, fig. 134A-G).

Our recent revision of “*Coelodus*” *costae* from Castellammare di Stabia (TAVERNE *et al.*, 2019) led us to conclude that this species belonged neither to *Coelodus* nor to *Ocloedus* POYATO-ARIZA & WENZ, 2002 but represented a new genus of Pycnodontidae, *Costapycnodus* TAVERNE *et al.*, 2019.

The aim of the present paper is to re-describe in a much more detailed way than previously the osteology of the specimens from Pietraraja referred to “*Coelodus*” *costae*, to compare this material with *Costapycnodus costae* (HECKEL, 1856) from Castellammare and to determine its systematic position within Pycnodontiformes.

As shown hereafter, our study of these samples reveals that they belong neither to the true species *costae* nor to the genus *Costapycnodus*. They represent a new genus. We have also seen that the morphological and anatomical data of the unique sample of “*Palaeobalistum*” *bassanii* totally correspond to those of the so called “*Coelodus*” *costae* from Pietraraja. The differences invoked by D’ERASMO (1914) to justify the erection of this new species simply are the result of the bad preservation and of the distortions due to the fossilisation. The specific name *bassanii* is thus available and must be used for the material from Pietraraja formerly reported to the species *costae*.

Our researches also show that the holotype and unique specimen of “*Proscinetes*” *pillae* did not belong to *Proscinetes* but represent another new genus. Its description will be the subject of a forthcoming paper (TAVERNE & CAPASSO, work in progress).

MATERIAL AND METHODS

The material hereafter studied belongs to the collections of the Museum of Paleontology of the Università degli Studi di Napoli Federico II (MPUN) and to the CAPASSO collection (CLC) in Chieti.

The specimens were studied with two stereomicroscopes, a Nikon SMZ 1500 and a Leica Wild M 8. The figures are drawn by the first author (L. T.) with a camera lucida and photos. The photos are made by Mr. Luciano LULLO, from the Università “G. d’Annunzio” di Chieti-Pescara.

The CAPASSO collection is legally registered and was declared part of the Italian cultural heritage by a decree of the Ministero per I Beni e le Attività Culturali under the date of October 11th 1999, following the disposition of the Italian law of cultural heritage protection N° 1089/1939. The specimens of this collection were also subject to prescription in order of conservation and availability to the studies on the basis of the article 30 of the Italian law N° 42/2004. 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 5th, 2011 (ref.: MBAC-SBA-ABR PROT 0004537 05/05/ 2011 Cl. 34.25.01/2.1) and July 30th, 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
BO	=	basioccipital
BRSTG	=	branchiostegal rays
CHY a., p.	=	ceratohyal (anterior, posterior)
CLO	=	cloaca
CLT	=	cleithrum
DHYOM	=	dermohyomandibula
DN	=	dentary
DPTE	=	dermopterotic
DSOC	=	dermosupraoccipital
DSPH	=	dermosphenotic
ECPT	=	ectopterygoid
ENPT	=	entopterygoid (= endopterygoid)
EPCO 1-4	=	epichordals 1 to 4
EXO	=	exoccipital
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HHY	=	hypohyal

HP 1, 14	=	haemal spine (first, fourteenth)
HYCO 1-10	=	hypochochordals 1 to 10
HYOM	=	hyomandibula
IORB	=	infraorbital
LEP	=	lepidotrichium (= ray)
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
NP 33	=	neural spine (thirty third)
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PCOEL	=	postcoelomic bone
PMX	=	premaxilla
POP	=	preopercle
PRART	=	prearticular
PRFR	=	prefrontal
PS	=	parasphenoid
PT	=	posttemporal
QU	=	quadrate
RAD	=	pterygiophores (= radials)
RI	=	ribs
SC	=	scales
SC clo.	=	cloacal scales
SCU d.	=	scutes of the dorsal ridge
SCU v.	=	scutes of the ventral keel
SOC	=	supraoccipital (= supraotic)
ST	=	supratemporal (= scale associated to the first dorsal scute)
SY	=	symplectic
SYN	=	synarcual
PT	=	posttemporal
UD 1-3	=	urodermals 1, 2 and 3
VO	=	vomer
br. l. pr.	=	brush-like process (branched peniculus) of the parietal
f. IX:	=	foramen for the glossopharyngeal nerve (IX)
f. X	=	foramen for the vagus nerve (X)
l. l. c.	=	lateral line sensory canal
t. f.	=	temporal (= dermocranial) 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 *Gregoriopycnodus* gen. nov.

Type species: *Gregoriopycnodus bassanii* (D'ERASMO, 1914)

Etymology

The name of the new genus is dedicated to Gregorio CAPASSO (1794-1860) who was a friend and a collaborator of Oronzo Gabriele COSTA. He helped him during the excavations at Pietraroja. Gregorio CAPASSO is also the great-great grandfather of the second author (L. C.) and the initiator of the CAPASSO collection. The generic name *Pycnodus* is added.

Diagnosis

The same as the species (monospecific genus).

Species *Gregoriopycnodus bassanii* (D'ERASMO, 1914)

Diagnosis

Middle sized and deep-bodied pycnodontiform fish belonging to the family Pycnodontidae. Maximum body depth around eight tenths of the standard length. Large head, with a long preorbital and a short postorbital region. Large temporal fenestra. Small, narrow dermosupraccipital. Supraoccipital visible in the temporal fenestra. Brush-like process on parietal. Prefrontal short, with a plate-like anterior extremity and partially fused to the mesethmoid. Dermosphenotic sutured with dermopterotic and frontal. Tubular infraorbitals present. Basioccipital, exoccipital and synarcual fused and exposed behind dermopterotic. Mouth gape obliquely oriented. Premaxilla with 2 incisiform teeth. Short dentary with 2 incisiform teeth. Coronoid process strongly developed. Preopercle much larger than the exposed region of hyomandibula-dermohyomandibula. Well developed opercle. Notochord almost completely surrounded by neural and haemal arches. 30-33 neural spines before the epichordal series. First five neural spines autogenous. 13-14 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. 12 or 13 pairs of ribs. Postcoelomic bone reaching the axial skeleton. Falcate dorsal fin with 49-52 rays and 49-50 pterygiophores. Origin of dorsal fin located at the highest point of the dorsal profile. Strip-like anal fin with 39-42 rays and 36-39 pterygiophores. Origin of the anal fin located behind the lowest point of the ventral profile. 4-5 epichordals. 9-10 hypochordals. 3 large and irregularly shaped urodermals. Double emarginated caudal fin, with 20-22 principal rays, 2 dorsal and 4-5 ventral procurrent rays. Body scales only in the abdominal region. Bar-scales dorsally and complete scales ventrally. 13-14 dorsal ridge scutes, devoid of spines. 13-14 pre- and 1 large postcloacal ventral keel scutes. 6 cloacal scales, two anterior, two above and two posterior to the cloaca. No bifid cloacal scale.



Fig. 1: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Holotype MPUN M 343.
Total length: 38 cm.

Synonymy

Palaeobalistum Bassanii. In D'ERASMO, 1911: 798.

Coelodus Costai HECKEL. In D'ERASMO, 1914: 36(64), pl. 6(3), figs 2, 3, pl. 7(4).

Palaeobalistum Bassanii n. sp. In D'ERASMO, 1914: 43(71), pl. 8(5).

? *Proscinetes bassanii* (D'ErasmO, 1914). In POYATO-ARIZA & WENZ, 2002: 151.

? *Proscinetes bassanii* (D'ERASMO). In CAPASSO, 2007: 127, fig. 133.

Holotype

MPUN M 343. A nearly complete but badly preserved specimen, with an imperfect skull (Fig. 1; D'ERASMO, 1914: pl. 8(5); CAPASSO, 2007: fig. 133). The top of the dorsal profile is lost. Total length: 38 cm. It is to be noted that D'ERASMO (1911, 1914) did not officially design this sample as a holotype.

Paratypes

CLC I-51. A well preserved complete specimen (Fig. 2; CAPASSO, 2007: fig. 128). Total length: 30 cm.

CLC I-215. A well preserved complete specimen (Fig. 3; *ibid.* 2007: fig. 127). Total length: 29 cm.

CLC I-347 (former A-15). A small well preserved complete specimen (Fig. 4; *ibid.*, 2007: fig. 130). Total length: 4 cm.

MPUN M 19260. A well preserved and nearly complete specimen. Only the tail is missing. Total length: 14 cm.

MPUN M 19280. A well preserved complete specimen. Total length: 32 cm.

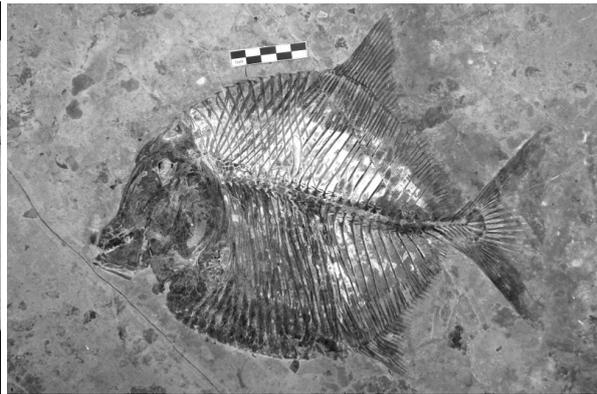
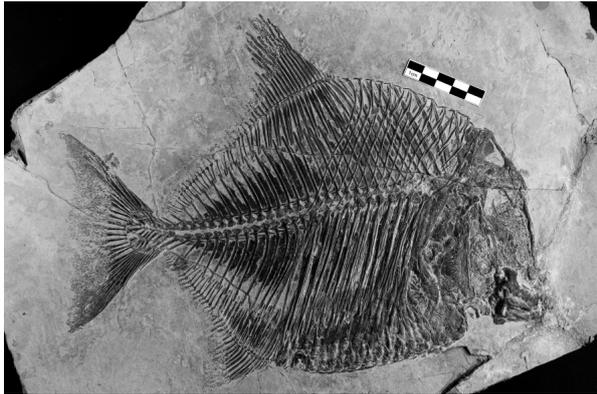


Fig. 2: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Paratype CLC I-215. **Figure 3:** *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Paratype CLC I-51.

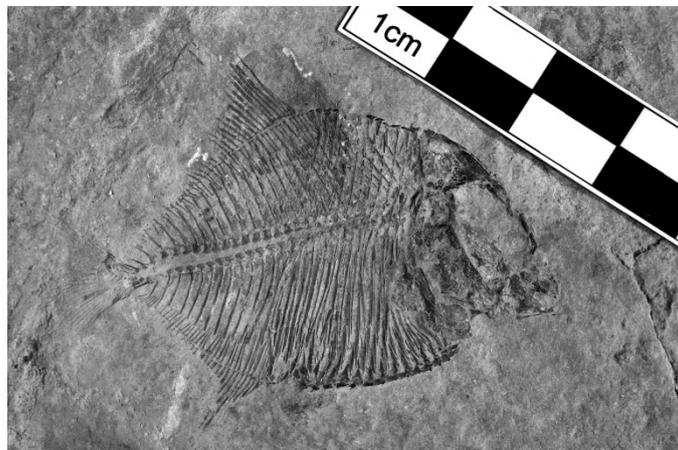


Figure 4: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Paratype CLC I-347 (former A-15).

Other material

CLC I-31. Two isolated prearticulars in oral view (*ibid.*, 2007: fig. 129B).

CLC I-77. An isolated vomer in oral view (Fig. 8; *ibid.* 2007: fig. 129D).

CLC I-115. An isolated prearticular in oral view (Fig. 9).

CLC I-220. Two isolated prearticulars in oral view (Fig. 10).

CLC I-233. A crushed head and the abdominal region of the body.

CLC I-347. A badly preserved skull.

Formation and locality

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

General morphology and morphometric data (Fig. 2)

The fish is deep-bodied, the maximum body height being approximately equal to eight tenths of the standard length. The dorsal apex is located at the origin of the dorsal fin but is weakly marked. The ventral profile is rounded.

The morphometric data are given in % of the standard length (23.5 cm) of paratype CLC I-51, the best preserved specimen of all the series.

Length of the head (opercle included)	34.6 %
Depth of the head (in the occipital region)	51.4 %
Maximum depth of the body (origin of the dorsal fin)	78.4 %
Prepelvic length	63.2 %
Predorsal length	55.6 %
Basal length of the dorsal fin	56.8 %
Preanal length	71.9 %
Basal length of the anal fin	40.0 %
Depth of the caudal peduncle	8.6 %

Osteology

The skull (Figs 5-10)

The head is high, triangular in shape, with a rather small orbit, an elongate preorbital region and a short postorbital region. The mouth gape is inclined ventrally. The dermic bones of the skull are strongly ornamented with small alveoli and a few thin ridges.

The mesethmoid is a very large and long bone, with a “T”-shaped transverse section, the anterior margin being broadened. A short, broadened, spatula-like and strongly ornamented prefrontal is fused to the anterior extremity of the underlying mesethmoid. The vomer is a long, narrow and triangular bone. Its teeth are arranged in five rows. Their contour is not crenulated. The size of all these teeth regularly increases in the cephalocaudal sense. The median teeth are transversally elongate, with a reniform contour, while the lateral teeth are smaller and more or less ovoid. There are 7 teeth in the middle row and in the two most lateral rows and 8 teeth in the two rows lying between.

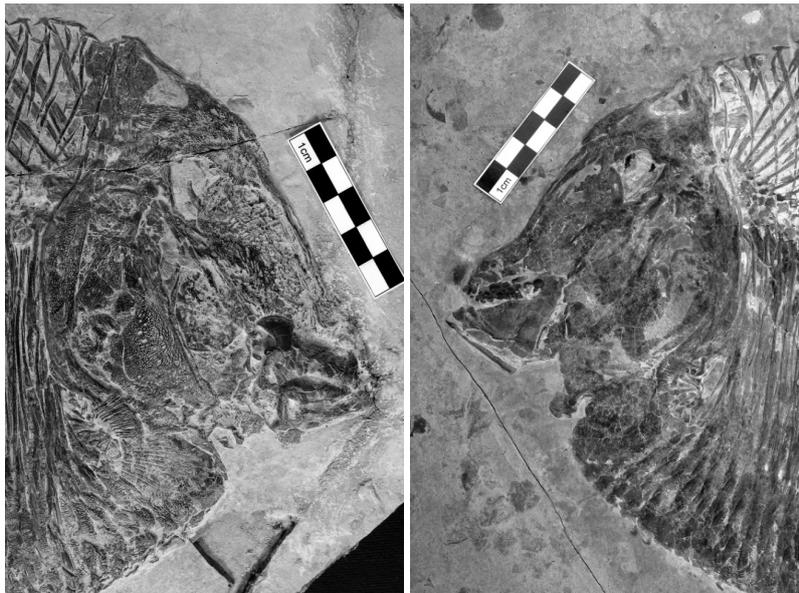


Figure 5: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen.nov. Head region of paratype CLC I-51. **Figure 6:** *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Head region of paratype CLC I-215.

The skull roof is formed by paired frontals, parietals and dermosupraoccipital. There is a large temporal (= intracranial) fenestra between the frontal, the dermosupraoccipital and the parietal. A part of an endocranial bone is visible in the temporal fenestra. This bone is interpreted as a supraoccipital by a few ones and as a supraotic by some others. The frontal is short but rather broad. The parietals bears a posterior brush-like process (= branched peniculus). The dermosupraoccipital is reduced to a thin rod-like bone located above the temporal fenestra. Its posterior extremity is a little broader and ends in a small spine. A short canal is visible on the posterior extremity of the dermosupraoccipital in sample CLC I-51. This tubular canal carries the beginning of the lateral line. The dermosupraoccipital is well developed and as deep as long. There is no trace of a small independent extrascapular associated with the dermosupraoccipital. The sensory canals of the skull roof are not visible.

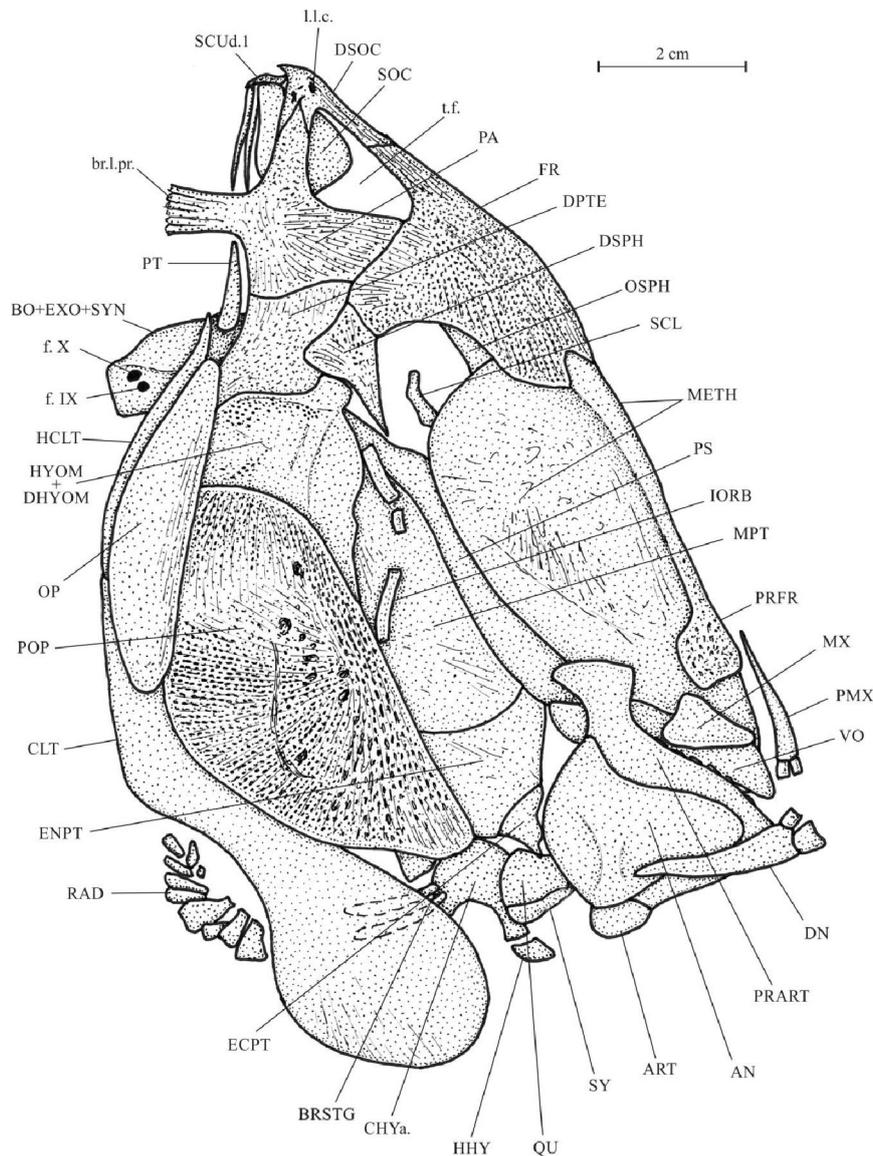


Figure 7: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Reconstruction of the skull and the pectoral girdle, principally based on paratype CLC I-51 to which the scale refers, completed with specimens CLC I-215 and CLC I-233.

A large synarcual is visible behind the rear of the skull on some specimens (for instance CLC I-51). The exoccipital and the basioccipital seem fused to this synarcual. Two foramina are present. They probably serve for the glossopharyngeal (IX) and the vagal (X) nerves.

The parasphenoid is elongated, toothless and inflected downwards below the orbit. A small orbitosphenoid is pressed against the mesethmoid and the frontal. The autosphenotic is completely or almost completely hidden by the dermosphenotic. No pleurosphenoid and no basisphenoid are visible. The prootic is covered by the hyomandibula.

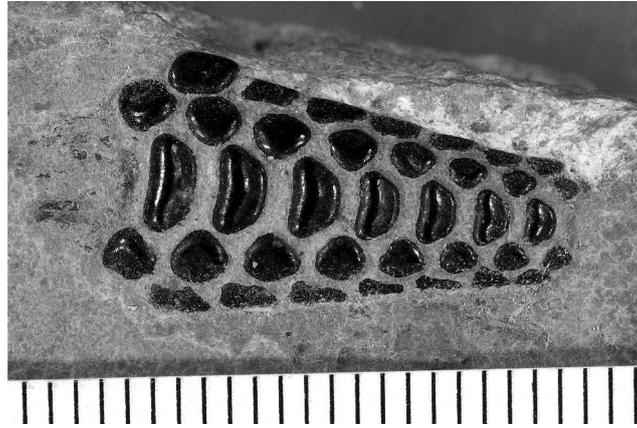


Figure 8: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Vomer (specimen CLC I-77).

The metapterygoid, the entopterygoid and the ectopterygoid are well exposed between the anterior margin of the preopercle and the parasphenoid. The metapterygoid is deeper than the entopterygoid. The ectopterygoid is a small bone. The quadrate is rather small. Both the quadrate and the symplectic articulate with the lower jaw. The premaxilla is narrow and not very elongate. It bears 2 small incisiform teeth. The maxilla is small, toothless, longer than deep but broader posteriorly than anteriorly. Its posterior margin is slightly concave.

The dentary is more massive than the premaxilla. It is reduced to its ventral branch and it bears 2 incisiform teeth, the first one enlarged and the second one small. The prearticular is triangle-shaped, with a well marked and very strong coronoid process. The prearticular dentition consists of three longitudinal rows. In some rare cases (for instance sample CLC I-115), the middle row is partly subdivided into two rows of smaller teeth. In each row, the size of the teeth increases from the anterior to the posterior region of the bone. The upper row contains 8 to 11 teeth and the middle one 8 to 11 teeth. The teeth of the lower row are by far the largest. There are 7 or 8 teeth in this lower row. They are dorso-ventrally elongated, with rounded dorsal and ventral borders. The contour of all these teeth is not crenulated. The angular is wide, triangular and its covers a great part of the prearticular. The posterior part of the angular bears a large and deep fossa. A small knob-like articular forms the posterior ventral corner of the lower jaw.



Figure 9: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Prearticular teeth (specimen CLC I-115).

Figure 10: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Two prearticulars (specimen CLC I-220).

The well developed dermosphenotic is not a free bone. It is firmly articulated with the dermopterygoid and the frontal, forming the posterior margin of the orbit. The ventral extremity of the dermosphenotic is elongated into a sharp point. Three tubular posterior infraorbitals are clearly visible on the metapterygoid in sample CLC I-

51. The most dorsal and the most ventral infraorbitals are long, while the middle one is short. Sclerotic bones are present.

The exposed dorsal region of the hyomandibula-dermohyomandibula is much smaller than the preopercle. A knob-like dorsal process is present on the upper margin of the hyomandibula. The preopercle is the largest dermic bone of the skull. It covers a great part of the cheek and is deeper than long. Its ventral region is much broader than its dorsal part. The broad, deep and crescent-like opercle is much smaller than the preopercle as in other pycnodont fishes. There are two long branchiostegal rays.

Each hyoid bar contains one hypohyal, a large triangular anterior ceratohyal, a smaller posterior ceratohyal and a thin interhyal.

The girdles (Figs 5-7)

The cleithrum looks like the one figured by NURSALL (1996: fig. 11b) for *Proscinetes*, with a narrow dorsal branch, a still narrower region at the level of the pectoral fin and a very broad ventral region. The hypercleithrum (= supracleithrum) is a long and very thin bone. The posttemporal is small and pressed against the parietal and the dermopterotic. The short pectoral fin contains 25 or 26 rays and is supported by about 10 pterygiophores. Fragments of the ventral fin are visible in the cloacal vestibule.

The axial skeleton (Figs 1-4)

The axial skeleton progressively raises up from the tail to the head, reaching there the orbit level. The notochord is almost completely surrounded by the dorsal and ventral arcocentra that are the only components of the vertebrae. There are 30 to 33 neural spines and 13 or 14 haemal spines before the caudal endoskeleton. The first five neural spines are autogenous and articulated on the large synarcual. The neural and haemal spines develop an anterior sagittal wing-like expansion. The neural arches are connected together by one well developed pre- and postzygapophysis. The same situation exists in the haemal arches of the caudal region. There are 12 or 13 pairs of ribs that are slightly broadened in their upper region. The postcoelomic bone is a long, strong bone that dorsally reaches the vertebral axis.

The dorsal and anal fins (Figs 11, 12)

The dorsal fin has a falcate contour (POYATO-ARIZA & WENZ, 2002: fig. 34B) and its origin is positioned at the higher point of the dorsal profile. The fin contains 49 to 52 rays and is supported by 49 or 50 pterygiophores (axonosts). The first five or six rays are reduced to short spines. The first long ray is segmented and pointed, the following ones being segmented and branched. There is no free dorsal pterygiophore before the dorsal fin.

The anal fin has a strip-like contour (POYATO-ARIZA & WENZ, 2002: fig. 34 A2). Its origin is located behind the lowest point of the ventral profile. There are 36 to 39 pterygiophores and 39 to 42 rays. The first four, five or six rays are reduced to small spines. As in the dorsal fin, the first long ray is segmented and pointed, the other rays being segmented and branched.

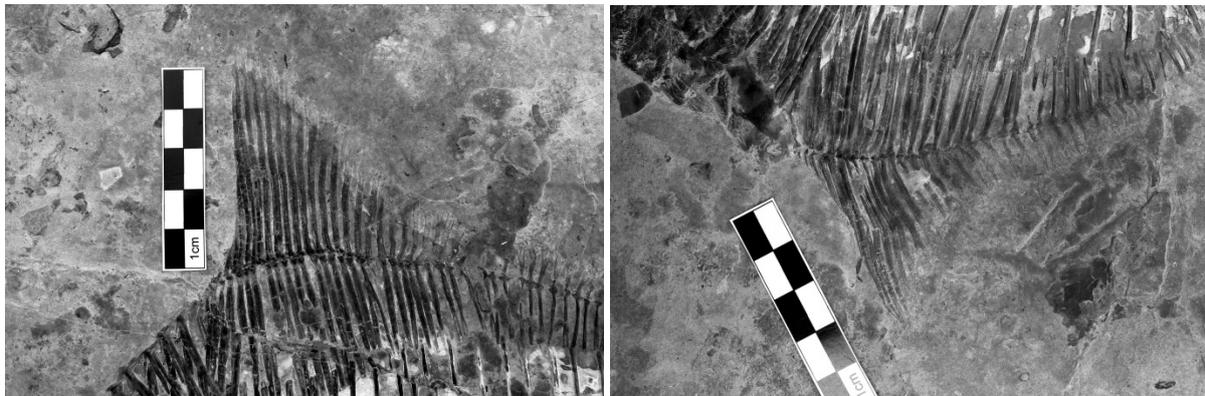


Figure 11: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Dorsal fin of paratype CLC I-215. **Figure 12:** *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Anal fin of paratype CLC I-215.

The caudal skeleton (Figs 13-15)

The caudal peduncle is very short, the dorsal and anal fins ending close to the caudal fin. The caudal endoskeleton contains 4 or 5 epichordals, 9 or 10 hypochordals and 2 or 3 large and irregularly shaped urodermals. In some specimens (CLC I-51), there are a series of small accessory urodermals. Two or three posterior hypochordals are broadened but not really hypertrophied.

The caudal fin is large, with a double emarginated posterior border (POYATO-ARIZA & WENZ, 2002: fig. 36E). There 20-22 principal rays, 2 dorsal and 4 or 5 ventral procurrent rays (= basal fulcra). The most external dorsal and ventral principal rays are segmented and pointed. The other principal rays are segmented and branched. The two dorsal procurrent rays are broadened.

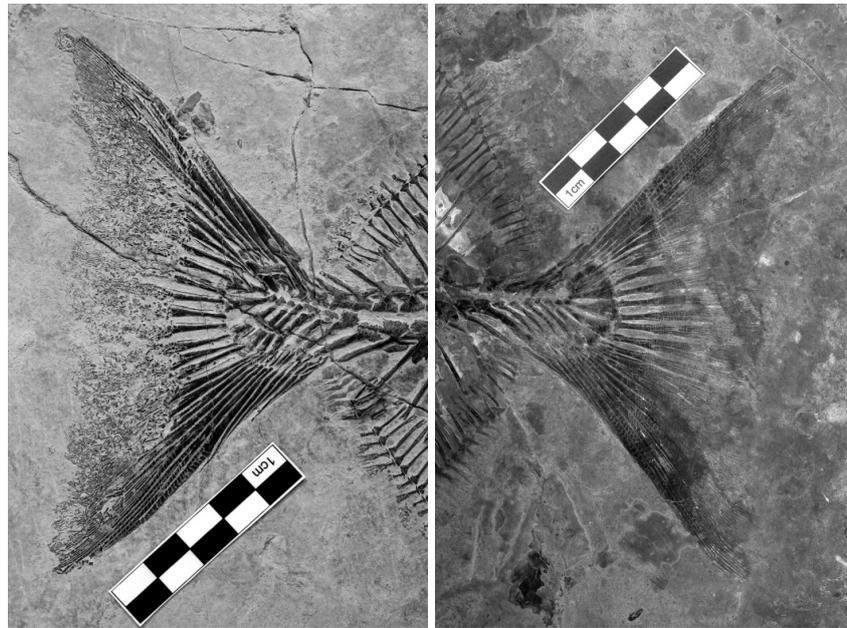


Figure 13: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Tail region of paratype CLC I-51.

Figure 14: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Tail region of paratype CLC I-215.

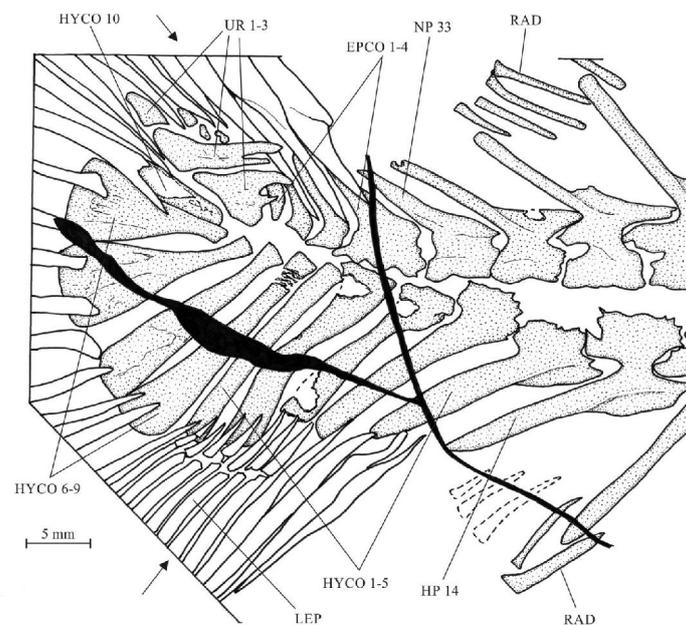


Figure 15: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Caudal skeleton of paratype CLC I-51. The two arrows point on the most external dorsal and ventral principal rays.

The squamation (Figs 16-19)

There are flank scales only in the abdominal region of the fish, anterior to the origin of the dorsal and anal fins. The scales located near the ventral margin of the body are complete, while all the other scales are reduced to their bar-like components. The ventral complete scales are strongly ornamented. There are 13 vertical rows of bar-scales.

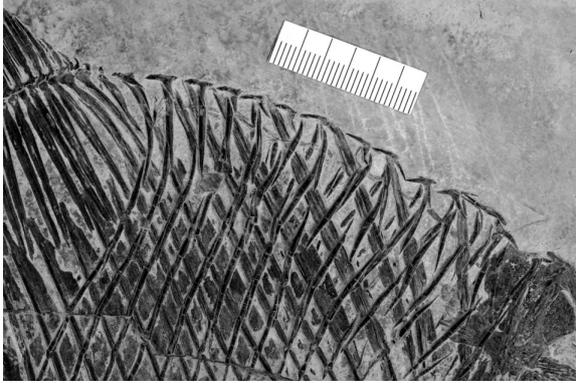


Figure 16: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Dorsal ridge scutes of paratype CLC I-51.

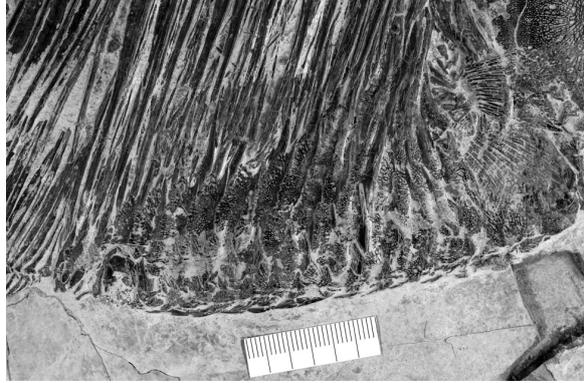


Figure 17: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Ventral keel scutes of paratype CLC I-51.

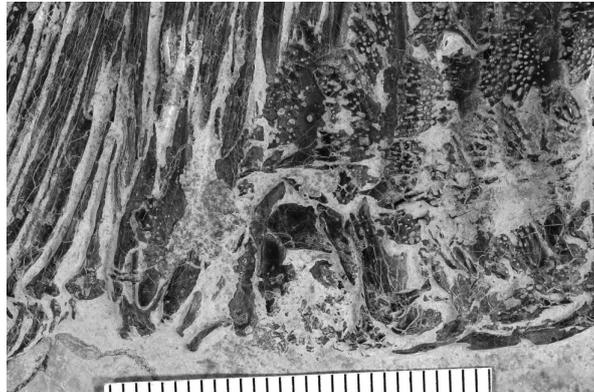


Figure 18: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Cloacal region of paratype CLC I-51.

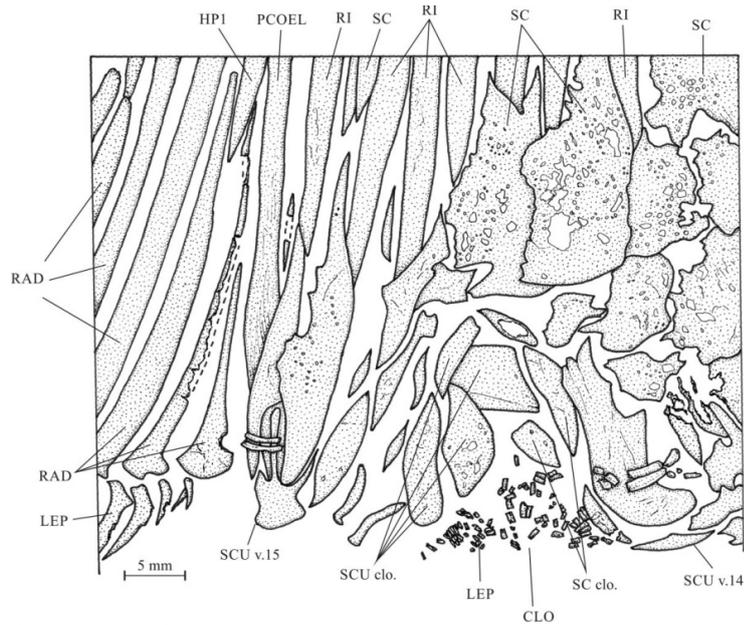


Figure 19: *Gregoriopycnodus bassanii* (D'ERASMO, 1911) gen. nov. Cloacal scales of paratype CLC I-51.

A series of tubular scales located near the dorsal margin of the body carries the lateral line sensory canal between the dermosupraoccipital and the origin of the dorsal fin.

There are 13 or 14 dorsal ridge scutes between the dermosupraoccipital and the origin of the dorsal fin. All these scutes have approximately the same size. They are devoid of spines on their upper margin and are associated with a pair of bar-scales. The first scute is in contact with the dermosupraoccipital and is not larger than the following scutes. This first scute is not only associated with a pair of bar-scales but also with a small complete scale that forms a sort of supratemporal lying along the parietal and the dermosupraoccipital.

The ventral keel contains 13 or 14 scutes before the cloaca and only 1 scute behind the cloaca. Most precloacal scutes are devoid of spines on their ventral margin but a few ones bear two or three small spines. The postcloacal scute is the largest of the series. This scute bears three dorsal arms that articulate with the postcoelomic bone and with the two last ventral scales.

The scales in the cloacal region have very different sizes. Most of them also have extremely irregular contours. The cloaca is surrounded by 6 scales that have no contact with the ventral keel scutes, 2 anterior, 2 dorsal and 2 posterior. There are also a few small comma-shaped scales above and behind the cloaca. No bifid cloacal scale is present. There are still two other complete scales behind the cloaca but they are connected with the postcloacal ventral keel scute and they are partially covering the ventral extremity of the postcoelomic bone.

DISCUSSION

Gregoriopycnodus bassanii and the genus *Palaeobalistum*

In his two descriptions of the species *bassanii*, D'ERASMO (1911, 1914) refers the unique specimen to the genus *Palaeobalistum* DE BLAINVILLE, 1818. Today, this genus contains only one valid species, *Palaeobalistum orbiculatum* DE BLAINVILLE, 1818 from the Eocene of Monte Bolca (POYATO-ARIZA & WENZ, 2002: 150) that is now included in the tribe Nursalliini. This tribe is characterized by a series of synapomorphies, such as the neural and haemal arches in hyper-complex contact, vestigial neural and haemal spines directly preceding the caudal endoskeleton, two or three hypertrophied elements in the caudal endoskeleton, a vertical caudal fin, etc. It is clear that *Gregoriopycnodus bassanii* does not exhibit these evolved characters and belongs neither to *Palaeobalistum* nor to any other genus of Nursalliini.

Gregoriopycnodus bassanii and the genus *Proscinetes*

POYATO-ARIZA & WENZ (2002: 151) refer with some doubt "*Palaeobalistum*" *bassanii* to *Proscinetes*, a genus belonging to the family Pycnodontidae.

The skull of this genus is known in two species, *Proscinetes elegans* (AGASSIZ, 1833) and *Proscinetes bernardi* (THIOLLIÈRE, 1852), both from the Upper Jurassic of Europe (DE SAINT-SEINE, 1949: fig. 41; POYATO-ARIZA & WENZ, 2002: fig. 8B; EBERT, 2013: fig. 11).

These two fishes are devoid of temporal fenestra and of prefrontal and they have an extrascapular included in the skull roof near the dermopterotic, three important cranial differences separating them from *Gregoriopycnodus bassanii*. That is enough to show that the Italian pycnodont fish can not be included in the genus *Proscinetes*.

Gregoriopycnodus bassanii and *Costapycnodus costae*

As already written, most pycnodont specimens from Pietraraja studied by D'ERASMO (1914) were referred by him to "*Coelodus*" *costae*, a species previously described from Castellammare di Stabia and now reported to the genus *Costapycnodus*. Many newly discovered samples from Pietraraja were also reported to the species *costae* (CAPASSO, 2007).

The data concerning *Costapycnodus costae* hereafter used come from TAVERNE *et al.* (2019).

Gregoriopycnodus bassanii and *Costapycnodus costae* have a rather similar general morphology, a brush-like process on the parietal and a temporal fenestra but the two fishes differ by many osteological details. *C. costae* has a longer frontal, a longer and not plate-like prefrontal, a smaller temporal fenestra, less teeth rows on the vomer, a different shape of the preopercle, a much more reduced opercle, a larger maxilla, a shorter metapterygoid, a less developed coronoid process on the prearticular, a notochord less constricted by the arches, less neural and haemal spines before the caudal skeleton, less pterygiophores in the dorsal fin, smaller regular urodermals, a totally different distribution of the scales in the cloacal region and two postcloacal ventral keel scutes.

Clearly, with such an amount of differences, it is not possible to consider *G. bassanii* and *C. costae* as synonyms.

The generic validity of *Gregoriopycnodus*

Gregoriopycnodus differs from all other known pycnodontiform genera by the shape and the size of its prefrontal that is reduced, broadened, plate-like and fused to the anterior corner of the mesethmoid. This specialized character is enough to justify the peculiar generic status of *Gregoriopycnodus*.

Gregoriopycnodus within Pycnodontiformes

In our comments in this chapter and in the next one, we follow principally the phylogeny of the Pycnodontiformes proposed 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 our own observations on some recently described pycnodont genera.

A brush-like process (= branched peniculus) is attached to the parietal of *Gregoriopycnodus bassanii*. Such a feature is the main synapomorphy characterizing Pycnodontidae (POYATO-ARIZA & WENZ, 2002, node 13, character 14[1]). *G. bassanii* can thus be ranged confidently in that family.

Gregoriopycnodus within Pycnodontidae

Akromystax POYATO-ARIZA & WENZ, 2005, *Stemmatodus* HECKEL, 1854, *Stenamara* POYATO-ARIZA & WENZ, 2000, *Ocloedus* POYATO-ARIZA & WENZ, 2002, *Turbomesodon* POYATO-ARIZA & WENZ, 2004 and *Rhinopycnodus* TAVERNE & CAPASSO, 2013 represent a primitive group of Pycnodontidae. They preserved the plesiomorphic state of having several strong spines on the dorsal ridge scutes (POYATO-ARIZA & WENZ, 2002, node 16, character 92[2]; cf. BASSANI & D'ERASMO, 1912: fig. 10; KRIWET *et al.*, 1999: pl. 1, fig. 1; POYATO-ARIZA & WENZ, 2000: 255, 2002: fig. 33C, 2004: figs 3, 13, 2005: fig. 2; TAVERNE & CAPASSO, 2013: fig. 8; TAVERNE *et al.*, 2019: figs 24, 25).

Gregoriopycnodus and the more specialized Pycnodontidae present the apomorphic condition of having the dorsal ridge scutes devoid of large spines on the upper margin (POYATO-ARIZA & WENZ, 2002, node 19, character 92[0]).

There is however two exceptions, *Haqelpycnodus* TAVERNE & CAPASSO, 2018 and *Flagellipinna* CAWLEY & KRIWET, 2019, both from the Cenomanian of Lebanon. *Haqelpycnodus* exhibits a series of advanced characters, such as the posterior region of the endocranium well exposed, the ventral margin of the dermopterotic and of the dermosphenotic located at the level of the orbital lower border, a well visible *dilatator fossa* and an almost bifid cloacal scale (TAVERNE & CAPASSO, 2018: figs 9, 21), but has also the dorsal ridge scutes that bear strong spines (*ibid.*, 2018: fig. 19), a primitive situation that probably represents in that case a reversion. *Flagellipinna* has a few spines on the dorsal ridge scutes (CAWLEY & KRIWET, 2019: fig. 9) but also exhibits an hyper-complex contact between some neural and haemal arches (*ibid.*, 2019: fig. 7), a highly specialized character only known in the members of the tribe Nursalliini and in three other genera of Pycnodontinae. Bar scales cover not only the abdominal region but also the caudal region in *Flagellipinna* (*ibid.*, 2019: 11, fig. 1C, D), another advanced character only present in Nursalliini.

Pycnodontinae are the most specialized assemblage within the group devoid of strong spines on the dorsal ridge scutes. The presence of a bifid cloacal scale is the main apomorphy characterizing this subfamily (POYATO-ARIZA & WENZ, 2002, node 23, character 104[2]). *Gregoriopycnodus* does not possess a bifid cloacal scale and in consequence does not belong to the Pycnodontinae. However, the bifid cloacal scale is lost in some Pycnodontinae belonging to the tribe Nursalliini. But we have already seen that *Gregoriopycnodus* does not exhibit the specialized features characterizing the Nursalliini.

The systematic position of the new Italian genus is thus be searched in an intermediate subgroup comprising the genera *Proscinetes*, *Coelodus* HECKEL, 1854, *Neoproscinetes* FIGEIREDO & DA SILVA SANTOS, 1987, *Iemanja* WENZ, 1989, *Tepexichthys* APPLIGATE, 1992, *Turbomesodon* POYATO-ARIZA & WENZ, 2004, *Turboscinetes* EBERT, 2016, *Scalacurvichthys* CAWLEY & KRIWET, 2017, *Haqelpycnodus* and *Costapycnodus*. Two characters allow the problem to be solved.

Tepexichthys exhibits strong crenulations on the margin of its vomerine and prearticular teeth (APPLIGATE, 1992: fig. 10B). That is the primitive condition within Pycnodontomorpha (POYATO-ARIZA & WENZ, 2002, node 1, character 49[2]). *Costapycnodus* still has weakly developed crenulations on some vomerine teeth but not on the prearticular teeth (TAVERNE *et al.*, 2019: 59, 60, figs 8, 9), a more advanced situation (POYATO-ARIZA & WENZ, 2002, node 5, character 49[1]). *Gregoriopycnodus* and the remaining

members of the subgroup share the still more apomorphic condition of having completely lost the crenulations on the vomerine and prearticular teeth (ibid., 2002, node 20, character 49[0]).

Proscinetes and the more evolved Pycnodontidae possess another apomorphic feature. The first scute of the dorsal ridge series is larger than the following ones (ibid., 2002, node 20, character 86[2]). This evolved feature is not yet present in *Tepexichthys*, *Costapycnodus* and *Gregoriopycnodus* (APPLEGATE, 1992: figs 3, 4; TAVERNE *et al.*, 2019: figs 1, 5, 6).

Thus, the systematic position of *Gregoriopycnodus* within Pycnodontidae is intermediate between *Tepexichthys* and *Costapycnodus*, on the one hand, and *Proscinetes*, on the other hand.

REFERENCES

- APPLEGATE S. P., 1992 - A new genus and species of pycnodont from the Cretaceous (Albian) of Central Mexico, Tepexi de Rodriguez, Puebla. *Universidad Nacional Autónoma de México, Instituto de Geología, Revista*, 10, 2: 164-178.
- CAPASSO, L., 2000. Storia della Paleontologia Italiana. *Atti del Museo Civico di Storia Naturale di Trieste*, 48: 251-260.
- CAPASSO, L., 2007. *Pietraroja pietre e memorie*. Ed. Paper's World, Teramo: 181 p.
- CAWLEY, J. J. & KRIWET, J., 2017. A new pycnodont fish, *Scalacurvichthys naishi* gen. et sp. nov., from the Late Cretaceous of Israël. *Journal of Systematic Palaeontology*, DOI: 10.1080/14772019.2017.1330772: 15 p.
- CAWLEY, J. J. & 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: 16 p.
- COSTA, O. G., 1850. Paleontologia del Regno di Napoli. Parte 1. *Atti dell'Accademia Pontaniana*, Napoli, 5: 1-203.
- D'ERASMO, G., 1911. Risultati ottenuti dallo studio di alcuni Actinopterygii del calcare cretaceo di Pietraroja in provincia di Benevento. *Atti della Società Italiana per il progresso delle Scienze*, 4 Reunione (Napoli, Dic. 1910), Roma: 797-800.
- D'ERASMO, G., 1914. La fauna e l'età dei calcari a ittioliti di Pietraroja. Parte I. *Palaeontographica Italica, Memorie di Paleontologia*, Pisa, 20: 29-86.
- D'ERASMO, G., 1915. La fauna e l'età dei calcari a ittioliti di Pietraroja. Parte II. *Palaeontographica Italica, Memorie di Paleontologia*, Pisa, 21: 59-111.
- DE SAINT-SEINE P., 1949. Les poissons des calcaires lithographiques de Cerin (Ain). *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 2: 1-357.
- EBERT, M., 2013. The Pycnodontidae (Actinopterygii) in the Late Jurassic: 1) the genus *Proscinetes* GISTEL, 1848 in the Solnhofen Archipelago (Germany) and Cerin (France). *Archaeopteryx*, 31: 22-43.
- EBERT, M., 2016. The Pycnodontidae (Actinopterygii) in the Late Jurassic: 2) *Turboscinetes* gen. nov. in the Solnhofen Archipelago (Germany) and Cerin (France). *Archaeopteryx*, 33: 12-53.
- KRIWET, J., 2005. A comprehensive study of the skull and dentition of pycnodont fishes. *Zitteliana*, A45: 135-188.
- NURSALL, J. R., 1996. The phylogeny of pycnodont fishes. In: ARRATIA, G. & VIOHL, G. (eds) *Mesozoic Fishes – Systematics and Paleocology*, Verlag Dr. F. Pfeil, München: 125-152.
- POYATO-ARIZA, F. J. & WENZ, S., 2002. A new insight into pycnodontiform fishes. *Geodiversitas*, 24, 1: 139-248.
- POYATO-ARIZA, F. J. & 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. & Tintori A. (eds) *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*, Verlag Dr. F. Pfeil, München: 341-378.
- POYATO-ARIZA, F. J. & 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*, 25, 1 : 27-45.
- TAVERNE, L., CAPASSO, L. & DEL RE, M., 2019. The pycnodont fishes from the Lower Cretaceous of the Capo d'Orlando, near Castellammare di Stabia (Naples, Campania, southern Italy), with the description of the new genus *Costapycnodus*. *Geo-Eco-Trop*, 43, 1: 53-74.