Geo-Eco-Trop., 2019, 43, 1 : 53-74

GEO - ECO - TROP
http://www.geoecotrop.be

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*

Les poissons pycnodontes du Crétacé inférieur du Capo d'Orlando, près de Castellammare di Stabia (Naples, Campanie, Italie du Sud), avec la description du nouveau genre *Costapycnodus*

Louis TAVERNE [1], Luigi CAPASSO [2] & Maria DEL RE [3]

Résumé: *Costapycnodus costae* (HECKEL, 1856), du Crétacé inférieur du Capo d'Orlando (Castellammare di Stabia, Campanie, Italie du Sud), fut premièrement identifié à *Stemmatodus rhombus* et, après cela, décrit comme *Coelodus costae*. Plus récemment, l'espèce fut rangée avec quelques doutes dans le genre *Ocloedus* mais elle demeurait en besoin de révision. Le squelette de *Costapycnodus costae* est étudié ci-après en détails. Les os dermiques crâniens sont fortement ornementés. Il y a un processus en brosse sur le pariétal, ce qui atteste que *C. costae* appartient à la famille des Pycnodontidae. Le préfrontal est bien développé. Le dermosphénotique n'est pas un os libre; il est inclus dans la paroi latérale du toit crânien. Une fenêtre temporale est présente. L'exoccipital est visible en arrière du dermoptérotique et est fusionné avec un synarcual. Le prémaxillaire et le dentaire portent chacun deux dents en forme d'incisive. Le maxillaire est réniforme, avec une encoche dans son bord postérieur. Le préoperculaire est plus vaste que la partie exposée de l'hyomandibulaire. L'operculaire est fortement réduit. Des comparaisons sont faites avec *Stemmatodus rhombus*, *Ocloedus subdiscus* et *Coelodus saturnus*. Les données ostéologiques montrent que *C. costae* représente un nouveau genre de poisson pycnodonte. La position systématique de *C. costae* au sein de la famille des Pycnodontidae est discutée.

Mots-clés: Pycnodontiformes, Pycnodontidae, *Costapycnodus costae* gen. nov., ostéologie, relations phylogénétiques, Crétacé inférieur marin, Capo d'Orlando, Castellammare, Campanie, Italie du Sud.

Abstract: *Costapycnodus costae* (HECKEL, 1856), from the Lower Cretaceous of the Capo d'Orlando (Castellammare di Stabia, Campania, southern Italy), was firstly identified as *Stemmatodus rhombus* and, after that, described as *Coelodus costae.* More recently, the species was ranged with some doubt in the genus *Ocloedus* but remained in need of revision. The skeleton of *Costapycnodus costae* is here studied in details. The dermic bones of the skull are strongly ornamented. There is a brush-like process on the parietal, attesting that *C. costae* belongs to the family Pycnodontidae. The prefrontal is well developed. The dermosphenotic is not a free bone but is included in the lateral wall of the skull roof. A temporal fenestra is present. The exoccipital is visible behind the dermopterotic and is fused to a synarcual. Both the premaxilla and the dentary bear two incisiform teeth. The maxilla is reniform, with a notch in its posterior margin. The preopercle is wider than the exposed part of the hyomandibula. The opercle is strongly reduced. Comparisons are done with *Stemmatodus rhombus*, *Ocloedus subdiscus* and *Coelodus saturnus*. The osteological data show that *C. costae* represents a new genus of pycnondontid fish. The systematic position of *C. costae* within the family Pycnodontidae is discussed.

Key words: Pycnodontiformes, Pycnodontidae, *Costapycnodus costae* gen. nov., osteology, systematic position, marine Lower Cretaceous, Capo d'Orlando, Castellammare, Campania, southern Italy.

INTRODUCTION

With more than 50 genera, Pycnodontomorpha are by far the largest lineage within the fossil neopterygian fishes. Most of them are marine fishes, with a deep and laterally flattened body, and a durophagous mode of feeding. They appear during the Late Triassic and survive till the Middle Eocene (NURSALL, 1996a; KRIWET, 2001; MARTIN-ABAD & POYATO-ARIZA, 2013; POYATO-ARIZA & MARTIN-ABAD, 2013). Pycnodontomorpha are generally considered as closely allied to Teleostei (NURSALL, 2010) but they are placed as basal Neopterygii in a recent phylogenetical analysis (POYATO-ARIZA, 2015).

---

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

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

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

Our present paper deals with the Pycnodontidae from the marine Lower Cretaceous of the Capo d'Orlando, near Castellammare di Stabia, in the region of Naples (Campania, southern Italy) and more particularly with a fish that is presently named *Ocloedus costae* (HECKEL, 1856), "a species in need of revision" (cf. POYATO-ARIZA & WENZ, 2002: 152). Indeed, its osteology is too poorly known to be sure of its actual generic attribution.

Ocloedus costae has a rather complicated story. The first two specimens discovered of *O. costae* were mistakenly reported by COSTA (1850: 102-105, pl. 4, fig. 8, pl. 5, fig. 1) to *Pycnodus rhombus* AGASSIZ, 1839, another species from the Lower Cretaceous of Castellammare. Four years later, *P. rhombus* was designed as the type-species of a new genus, *Stemmatodus* HECKEL, 1854. Unfortunately, HECKEL (1854: 455) did the same mistake as COSTA (1850). He ranged in this new genus not only the holotype of *P. rhombus* but also the two specimens of false *P. rhombus* previously described by COSTA (1850). However, he became quickly aware of his error and erected, two years later, the new species *costae* for these two samples (HECKEL, 1856: 203), a species that he included in the genus *Coelodus* HECKEL, 1854. Other specimens from Castellammare were referred to *Coelodus costae* much later (WOODWARD, 1895: 252; BASSANI & D'ERASMO, 1912: 44-49). Recently, *C. costae* was reported to *Ocloedus* POYATO-ARIZA & WENZ, 2002, a newly erected genus, with *Ocloedus subdiscus* (WENZ, 1989) from the Berriasian-Valanginian of Spain as type-species (POYATO-ARIZA & WENZ, 2002: 149).

The aim of our paper is thus to describe in a detailed way the skeleton of *Ocloedus costae*, to compare this fish with *Stemmatodus rhombus*, *Ocloedus subdiscus* and *Coelodus saturnus*, and to precise its systematic position within the phylogeny of the Pycnodontiformes. We will see so that *O. costae* does not belong to *Ocloedus* but must be included in a new genus.

HECKEL (1856) did not designate expressly a holotype for his new species *costae*. Concerning this fish, WOODWARD (1895: 252) only wrote "Type. Nearly complete fish". That was an imprecise indication. He very probably referred to the samples firstly illustrated by COSTA (1850: pl. 4, fig. 8), a specimen having lost its tail. The second sample figured by COSTA (1850, pl. 5, fig. 1) is a complete one. We will take the opportunity of our paper to officially designate a holotype and a few paratypes for the species *costae*.

It is also to be noted that D'ERASMO (1914: 36-42, pl. 6(3), figs 2, 3, pl. 7(4), figs 1-15) described as *Coelodus costae* a few badly preserved and incomplete specimens of pycnodontid fishes from the marine Albian deposits of Pietraroja (Campania, southern Italy). Later, complete and much better preserved sample of the same fish were found at Pietraroja. These beautiful but still undescribed specimens (CAPASSO, 2007: figs 127, 128, 130, 132) were also labelled *Coelodus costae*. Indeed, their general morphology is very close to that of the true *C. costae*. However, the specimens from Pietraroja differ by many osteological characters from the true *costae*. They do not belong to that species and represent another new genus (TAVERNE & CAPASSO, work in progress).

D'ERASMO (1910: 6-7) also pointed out the presence of fragments of a pycnodont fish in the Upper Cretaceous deposits of Lecce (Puglia, southern Italy). He reported these remains to a *Coelodus* sp. Later, he described a more complete specimen from the same deposits and the same region (Alessano, Lecce) and ranged it in the species *Coelodus costae* (D'ERASMO, 1922: 3-7, pl. 1, fig. 1), spelled by him *costai*. Today, the pycnodont fish from the Upper Cretaceous of the province of Lecce (Nardò, Alessano) is known as *Pseudopycnodus nardoensis* (TAVERNE, 1997), a fish that also strongly differs from the true *O. costae* (TAVERNE, 1997, 2003; TAVERNE & CAPASSO, 2012).

Some bones and other fragments reported to *Coelodus costae* are mentioned from the marine Cenomanian-Turonian of Comen (Slovenia) by D'ERASMO (1946: 17-19, figs 4, 5) but that material needs to be revised before doing a precise specific determination. However, the lapse of time separating the geological deposits of Castellamare and Comen, about 40 millions years, makes improbable an attribution of the pycnodont material from Comen to *O. costae*.

The presence of fossil fishes in the locality of Castellammare (Capo d'Orlando) was firstly quoted by BREISLAK (1798: 25) but the principal study of that ichthyofauna is due to BASSANI & D'ERASMO (1912) who published a small monograph on the subject more than a century ago The two authors reported these fishes to nine species, the pycnodont *Stemmatodus rhombus* being by far the most abundant. The story of the discovery of that fish fauna is related by LEUCI (1976). The paleoenvironment of the Castellammare fossil fish plattenkalk was a shallow lagoon and the age of the deposits is comprised between the Upper Hauterivian and the Lower Barremian as shown by the microfossil fauna (DE CASTRO, 1962; CHERCHI *et al.*, 1978; VELIC, 1988). The biostratigraphy and the depositional conditions of the fossil fish level of Castellammare are studied in a very detailed way in BRAVI & DE CASTRO (1995).

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).

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. Some photos are made by Mr. Luciano LULLO, from the Università "G. d'Annunzio" di Chieti-Pescara. Other photos are provided by Dr. Maria Angela DEL RE, from the MPUN.

List of abbreviations used in text-figures

AN = angular
ART = articular
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 1-5 = epichordals 1 to 5
EXO = exoccipital
FR = frontal
HCLT = hypercleithrum (= supracleithrum)
HHY = hypohyal
HP 12 = haemal spine (twelfth)
HYCO 1-9 = hypochordals 1 to 9
HYOM = hyomandibula
IHY = interhyal
IORB = infraorbital
LEP = lepidotrichium (= ray)
METH = mesethmoid
MPT = metapterygoid
MX = maxilla
NP 25, 28 = neural spine (twenty fifth, twenty eighth)
OP = opercle
OSPH = orbitosphenoid
PA = parietal
PCLT = postcleithrum
PCOEL = postcoelomic bone
PMX = premaxilla
POP = preopercle
PRART = prearticular
PRFR = prefrontal (= lateral dermethmoid ?)
PS = parasphenoid
PSPH = pleurosphenoid
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 1-2 = urodermal 1 and 2
VO = vomer
br. l. pr. = brush-like process of the parietal
f. X = foramen for the vagus nerve (X)
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 ***Costapycnodus*** gen. nov.

Type species: *Coelodus costae* HECKEL, 1856

Etymology

The name of the new genus is dedicated to Oronzo Gabriele COSTA (1789-1867), the father of the Italian paleoichthyology and also the first scientist having described the pycnodont fish hereafter studied. The generic name *Pycnodus* is added.

Diagnosis

The same as the species (monospecific genus).

Species ***Costapycnodus costae*** (HECKEL, 1856) new comb.

Emended diagnosis

Small-sized and deep-bodied pycnodont fish. Maximum body depth comprised between 7 and 8 tenths of the standard length. Dermal bones of the skull ornamented with ridges and tubercles. Large head, with a short postorbital and a long preorbital region. Small dermosupraoccipital. Temporal (= dermocranial) fenestra present and supraoccipital (= supraotic) visible in the fenestra. Brush-like process of the parietal present, weakly developed. Prefrontal present. Dermosphenotic included in the lateral wall of the skull roof. Exoccipital exposed behind the skull and fused with a synarcual. Mouth gape obliquely oriented. Premaxilla and dentary with 2 incisiform teeth. Maxilla reniform, with a notch in the posterior margin. Preopercle larger than the exposed region of the hyomandibula-dermohyomandibula. Opercle reduced, extremely narrow. Prearticular bearing three rows of crushing teeth, 10 to 12 teeth in the upper row, 8 to 10 teeth in the middle row and 6 to 7 teeth in the lower row. Notochord almost completely surrounded by neural and haemal arches in the abdominal region and incompletely surrounded in the caudal region. 28-29 neural spines before the epichordal series. First five neural spines autogenous. 12 haemal spines before the hypochordal series. Postcoelomic bone reduced, not reaching the axial skeleton. Dorsal fin falcate, 47-48 rays, 44-45 pterygiophores. Origin of the dorsal fin located at the highest point of the dorsal profile. Anal fin strip-like, 38-39 rays, 35-37 pterygiophores. Origin of the anal fin located behind the lowest point of the ventral profile. 4-5 epichordals. 9-10 hypochordals, with three elements slightly broadened. 2 urodermals. Caudal fin double emarginated, with 19-20 principal rays. Scales only in the abdominal region. Scale bars on the flank. Complete scales in contact with the ventral keel scutes. 12-13 dorsal ridge scutes, most with a smooth upper margin, some with a few tiny spines. 15 ventral keel spiny scutes, 13 precloacal, 2 postcloacal. 3 modified cloacal scales, 1 anterior, 2 posterior to the cloaca.

Synonymy

Pycnodus rhombus, Ag. *in* COSTA, 1850: 102, pl. 4, fig. 8, pl. 5, fig. 1.
Coelodus Costae Heck. *in* HECKEL, 1856: 203.
Coelodus costae, Heckel *in* WOODWARD, 1895: 252.
Coelodus Costae Heck. *in* BASSANI & D'ERASMO, 1912: 44(224), pl. 5, figs 4, 5.

Holotype

MPUN M 662, a nearly complete specimen having lost the tail (Fig. 1; COSTA, 1850: pl. 4, fig. 8; BASSANI & D'ERASMO, 1912: pl. 5, fig. 5). Total length: 82 mm.

Paratypes

MPUN M 652, a complete specimen (Fig. 2; COSTA, 1850, pl. 5, fig. 1). Total length: 102 mm.
MPUN M 654, a complete specimen (Fig. 3; BASSANI & D'ERASMO, 1912: pl. 5, fig. 4). Total length: 101 mm.
MPUN M 671, a complete specimen (Fig. 4). Total length: 60 mm.

Formation and locality

Marine Upper Hauterivian-Lower Barremian (Lower Cretaceous) of the Capo d'Orlando, Castellammare (Naples, Campania, southern Italy).

General morphology and morphometric data (Figs 1-5)

The fish is deep-bodied, the maximum body height being equal to seven or eight tenths of the standard length. The dorsal and ventral profiles are rounded.

The morphometric data are measured as shown in TAVERNE & CAPASSO (2018: fig. 5) and are given in % of the standard length of the four fishes (MPUN M 668: 78 mm, M 652: 83 mm, M 654: 82 mm, M 671: 51 mm).

	668	**652**	**654**	**671**
Length of the head (with opercle)	37.8 %	35.4 %	36.8 %	37.3 %
Depth of the head (occipital region)	51.4 %	52.0 %	56.8 %	55.1 %
Maximum depth of the body	74.1 %	80.0 %	80.0 %	72.8 %
Prepelvic length	59.5 %	62.9 %	56.8 %	61.4 %
Predorsal length	64.9 %	65.1 %	63.2 %	66.4 %
Basal length of the dorsal fin	46.5 %	51.4 %	53.7 %	47.5 %
Preanal length	70.3 %	71.4 %	67.4 %	?
Basal length of the anal fin	36.8 %	35.4 %	37.4 %	?
Depth of the caudal peduncle	10.8 %	14.3 %	13.2 %	12.0 %

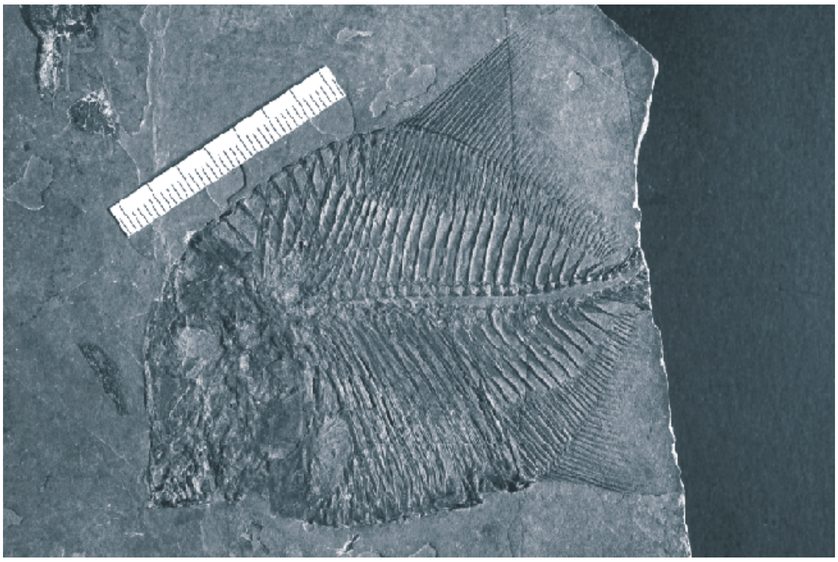

Figure 1. *Costapycnodus costae* (HECKEL, 1856). Holotype MPUN M 662. The scale is in millimetre.

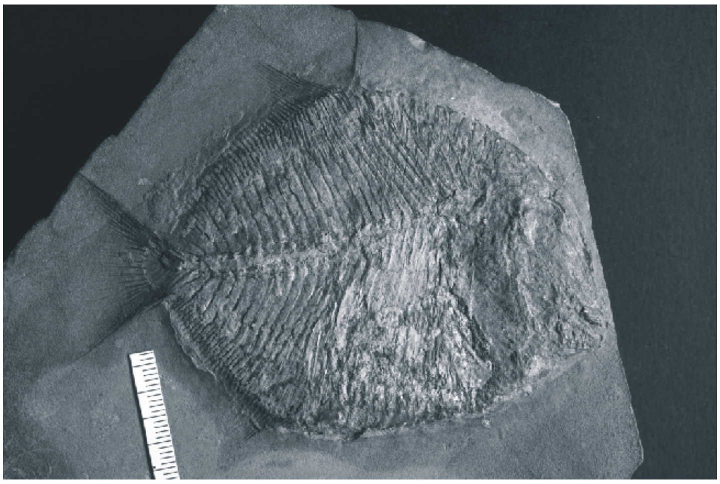

Figure 2. *Costapycnodus costae* (HECKEL, 1856). Paratype MPUN M 652. The scale is in millimetre.

Figure 3. *Costapycnodus costae* (HECKEL, 1856). Paratype MPUN M 654. Total length: 101 mm.

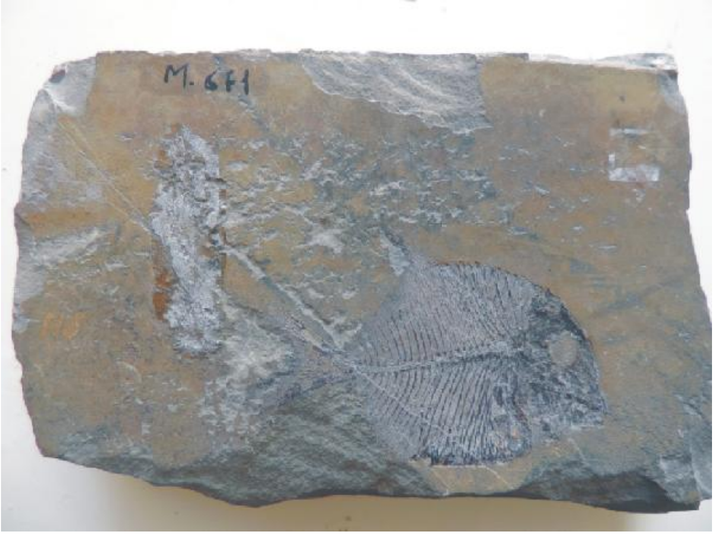

Figure 4. *Costapycnodus costae* (HECKEL, 1856). Paratype MPUN M 671. Total length: 60 mm.

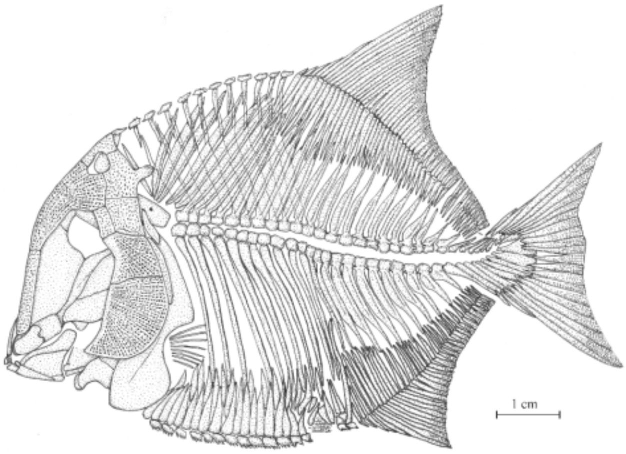

Figure 5. *Costapycnodus costae* (HECKEL, 1856). Reconstruction based on the holotype and the three paratypes. The scale refers to the holotype.

Osteology

The skull (Figs 6-9)

The skull is nearly 1.5 as deep as long. The orbit is small and the preorbital region much more elongated than the postorbital part of the cranium. The mouth gape is inclined ventrally. The dermal bones of the skull are ornamented with alveoli, ridges and small tubercles.

The mesethmoid is hypertrophied and "T"-shaped in cross section, as usual in pycnodont fishes. The antero-dorsal margin of the bone is covered by a long, narrow and strongly ornamented prefrontal. The vomer is well developed and bears three rows of teeth. The preservation is not good enough to allow a precise count of the teeth in each row. However, there are at least 10 teeth in the left lateral row of the holotype MPUN M 668. These teeth have a concave anterior margin and a rounded posterior border. The last and biggest teeth of the left lateral row bear small tubercles on their oral outline in the holotype and in paratype MPUN M 652.

The dermosupraoccipital and the paired frontals, parietals and dermopterotics form the skull roof. A large temporal (= dermocranial) fenestra is open between the frontal, the dermosupraoccipital and the parietal. The top of a large endochondral bone is visible in the fenestra. Some consider that bone as a supraoccipital (NURSALL, 1999: fig. 22) and others as a supraotic (MAISEY, 1999: fig. 15). The parietal bears a short posterior brush-like process (= branched peniculus). The dermosupraoccipital has a pointed posterior extremity to which the first dorsal ridge scute is articulated. The dermopterotic is almost quadrangular, as deep as long. The autosphenotic is completely hidden by the dermosphenotic.

The exoccipital is exposed behind the dermopterotic and is fused to a large synarcual as in the Lower Cretaceous *Neoproscinetes penalvai* (DA SILVA SANTOS, 1970) but, in the case of this Brazilian pycnodont fish, the composed exoccipital-synarcual is lying on a posterior expansion of the parasphenoid (MACHADO, 2008: figs 2 B, 4). There is no posterior expansion of the parasphenoid in *Costapycnodus costae*. The exoccipital of paratype MPUN M 654 exhibits a broad foramen for the vagus nerve (X).

The parasphenoid is elongated, toothless and inflected downwards below the orbit. The orbitosphenoid and the pleurosphenoid are well visible in the orbit of the holotype and paratype MPUN M 654. They are small bones pressed against the frontal. The orbitosphenoid reaches the posterior margin of the mesethmoid.

The premaxilla is a long, thin, rod-like bone that bears two small incisiform teeth. The maxilla is preserved in paratype MPUN M 654. It is a reniform bone, with a notch in its posterior margin. The dentary is rather short and reduced to its ventral branch. It bears two incisiform teeth, the first one being the largest. The articular is small. The angular is lost in all the specimens except in paratype MPUN M 671 that has preserved a part of the bone. The prearticular is triangular in shape, with a well marked coronoid process as seen on paratype MPUN M 652. The coronoid process is lost on the holotype, due to the fossilisation. The prearticular bears three rows of crushing teeth. In the three rows, the teeth increase in size from the anterior to the posterior region of the bone. There are 6 to 7 teeth in the lower row that is also the main row, 8 to 10 teeth in the middle row and 10 to 12 teeth in the upper row. In the lower and the middle rows, the teeth are transversally elongated, with rounded upper and lower margins. The teeth of the lower row are broader than those of the middle row. The contour of the teeth is not crenulated. In the holotype, the teeth of the lower row are lost and only their sockets are preserved.

Both the quadrate and the symplectic articulate with the lower jaw. Large parts of the wide metapterygoid and entopterygoid are visible between the preopercle and the parasphenoid. A small ectopterygoid is present.

The dermosphenotic is the only preserved element of the orbital series. It is a large and ornamented bone that is sutured with the frontal and the dermopterotic and is included in the lateral wall of the skull roof.

The preopercle is the largest bone of the skull. It is almost as broad in its upper region than in its lower one. The opercle is extremely reduced, forming a long and very thin bar-like piece. The hyomandibula-dermohyomandibula is articulate to the preopercle that covers the ventral branch of the bone. The exposed part of the hyomandibula-dermohyomandibula is wide but not as wide as the preopercle.

The hyoid bar is well preserved on the holotype, with the hypohyal, the large anterior ceratohyal and the smaller posterior ceratohyal. There are two branchiostegals rays.

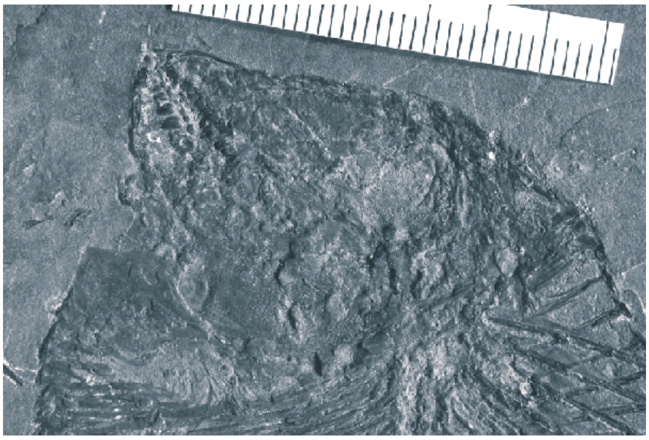

Figure 6. *Costapycnodus costae* (HECKEL, 1856). Head region of holotype MPUN M 662.

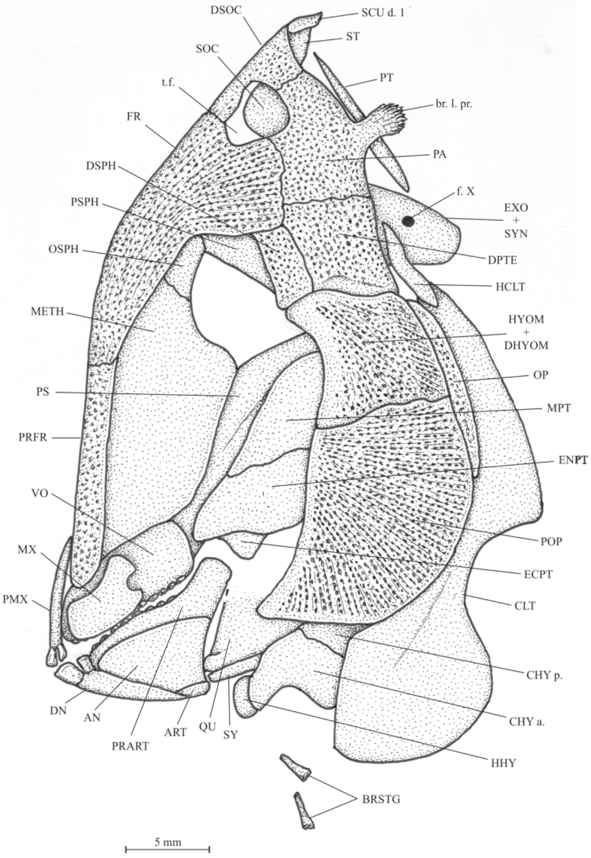

Figure 7. *Costapycnodus costae* (HECKEL, 1856). Skull and pectoral girdle of holotype MPUN M 662.

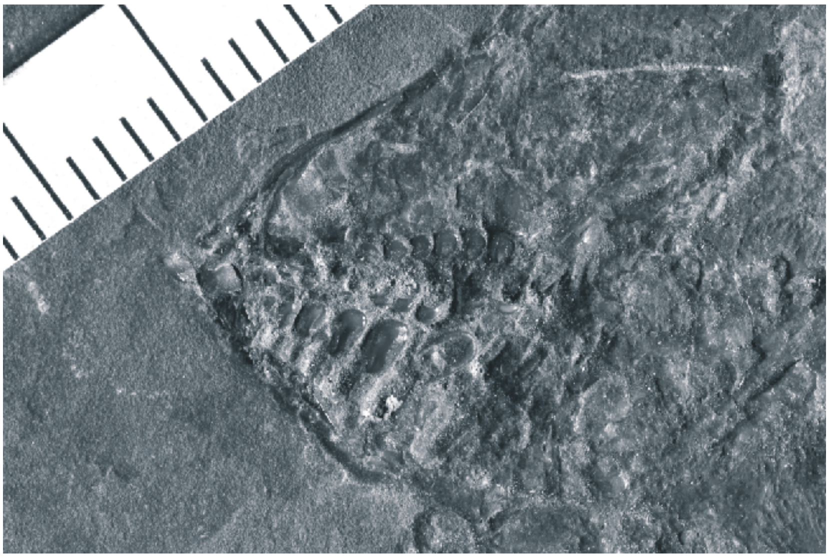

Figure 8. *Costapycnodus costae* (HECKEL, 1856). Vomer and lower jaw (internal view) of holotype MPUN M 662.

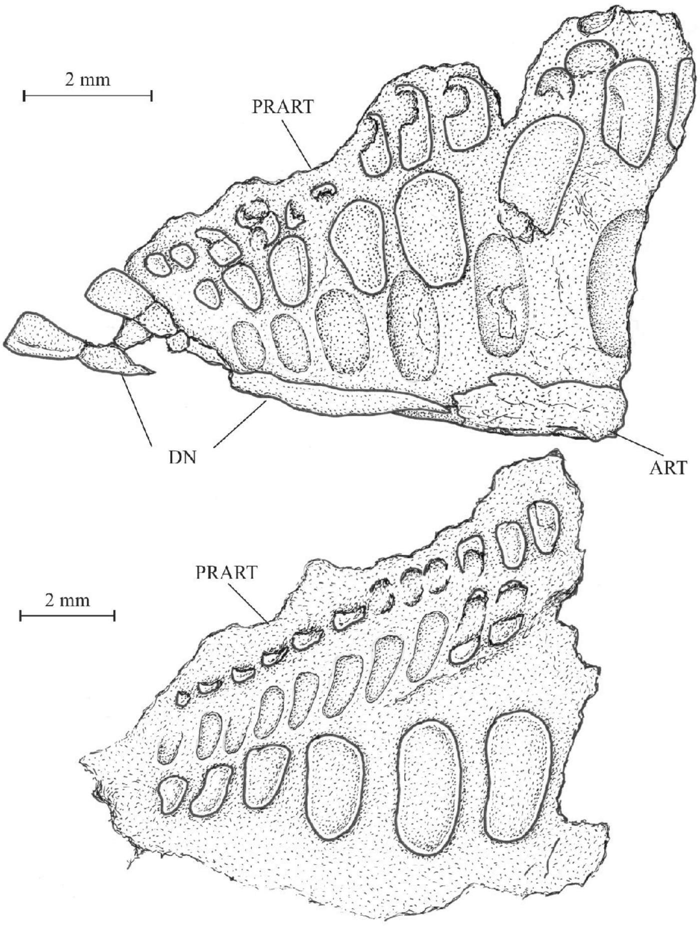

Figure 9. *Costapycnodus costae* (HECKEL, 1856). Lower jaw (internal view) of holotype MPUN M 662 (above) and of paratype MPUN M 654 (below).

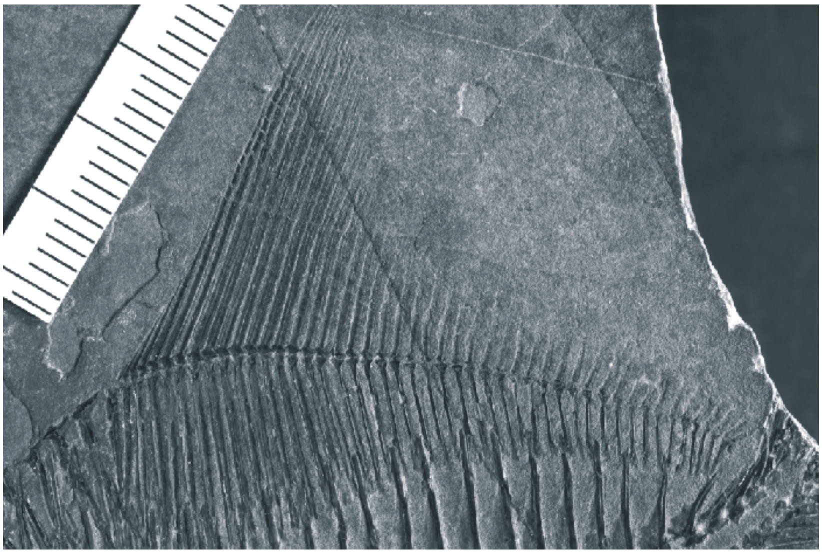

Figure 10. *Costapycnodus costae* (HECKEL, 1856). Dorsal fin of holotype MPUN M 662.

The girdles (Fig. 7)

The cleithrum is very similar in shape to the one of *Proscinetes elegans* (AGASSIZ, 1833) as figured by NURSALL (1996b: fig. 11b), with a very broad ventral part and an extremely narrow region at the level of the notch for the pectoral fin. The hypercleithrum (= supracleithrum) is well developed. The posttemporal is reduced to a thin rod-like element. The pectoral radials are not visible. The preservation of the pectoral fin is never good enough to count the rays.

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

The axial skeleton (Figs 1-5)

Starting from the caudal skeleton, the vertebral axis progressively elevates to reach anteriorly the level of the orbit. The dorsal and ventral arcocentra are the only elements constituting the vertebrae. In the abdominal region, the neural and haemal arches surround almost completely the notochord but, in the caudal region, the greatest part of the notochord is not enclosed by the arches. There are 28 or 29 neural spines before the epichordal series and 12 haemal spines before the hypochordal series. The first 5 neural spines are autogenous and rest on the synarcual. All the neural and haemal spines bear a well developed sagittal flange. In the caudal region, the neural arches are connected together by one small pre- and postzygapophysis. The same character also exists at the level of the haemal arches in the caudal region.

There are 11 pairs of ribs. They are slightly broadened in their upper part.

The postcoelomic bone is strongly reduced. It does not reach the vertebral axis and has only the half of the usual length of a postcoelomic bone. A reduced postcoelomic bone separated from the axial skeleton is known in some other pycnodont fishes, such as *Turboscinetes egertoni* (THIOLLIÈRE, 1852) from the Upper Jurassic of France and Germany, *Turbomesodon praeclarus* POYATO-ARIZA & WENZ, 2004 from the Lower Cretaceous of Spain or *Scalacurvichthys naishi* CAWLEY & KRIWET, 2017 from the Upper Cretaceous of Israël (POYATO-ARIZA & WENZ, 2004: figs 3, 12; EBERT, 2016: fig. 16 A, B; CAWLEY & KRIWET, 2017: figs 1, 5A).

The dorsal and anal fins (Figs 1-5, 11)

The dorsal fin has a falcate contour (POYATO-ARIZA & WENZ, 2002: fig. 34B) and its origin is located at the higher point of the dorsal profile. The fin is supported by 44 or 45 pterygiophores (axonosts). There are 47 or 48 rays. The first 5 or 6 rays are reduced to spines shorter than the following segmented rays. The two last short spiny rays are already segmented. The first long ray is segmented and pointed. The other rays are segmented and branched. There is no free dorsal pterygiophore before the dorsal fin.

The anal fin is strip-like (contour A 2 of POYATO-ARIZA & WENZ, 2002: fig. 34) and begins behind the lowest point of the ventral profile. The fin is supported by 35 to 37 pterygiophores and contains 38 or 39 rays. The first 4 or 5 rays are short spines, the two last of them being segmented. As in the dorsal fin, the first long ray is segmented and pointed, the following ones being segmented and branched.

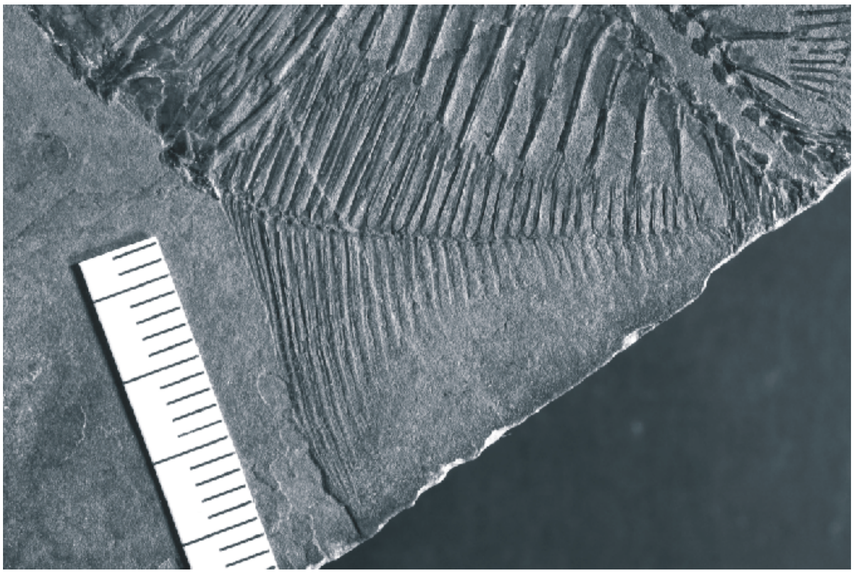

Figure 11. *Costapycnodus costae* (HECKEL, 1856). Anal fin of holotype MPUN M 662.

The caudal skeleton (Figs 12-14)

The caudal peduncle is extremely short, the dorsal and anal fins ending close to the tail.

Figure 12. *Costapycnodus costae* (HECKEL, 1856). Caudal region of holotype MPUN M 662.

The caudal endoskeleton is formed by 4 or 5 epichordals, 9 or 10 hypochordals and 2 urodermals. Three posterior hypochordals are broadened but there is no real hypertrophy. There are only 8 hypochordals preserved in holotype, the uppermost elements being lost.

The contour of the caudal fin is double emarginated (type E of POYATO-ARIZA & WENZ, 2002: fig. 36). There are 19 or 20 principal rays, 2 dorsal and 2 ventral procurrent rays. The more external dorsal and ventral principal rays are segmented and pointed. The 17 or 18 other principal rays are segmented and branched. The second procurrent ray of each lobe is markedly broadened.

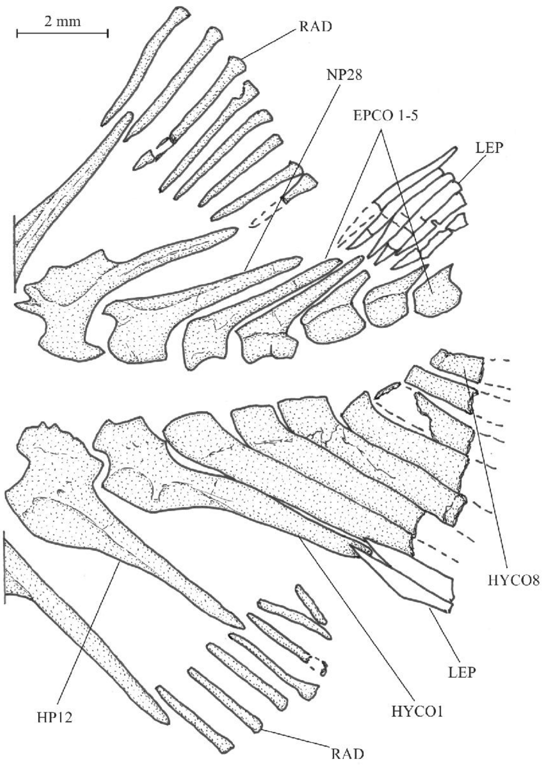

Figure 13. *Costapycnodus costae* (HECKEL, 1856). Caudal skeleton of holotype MPUN M 662

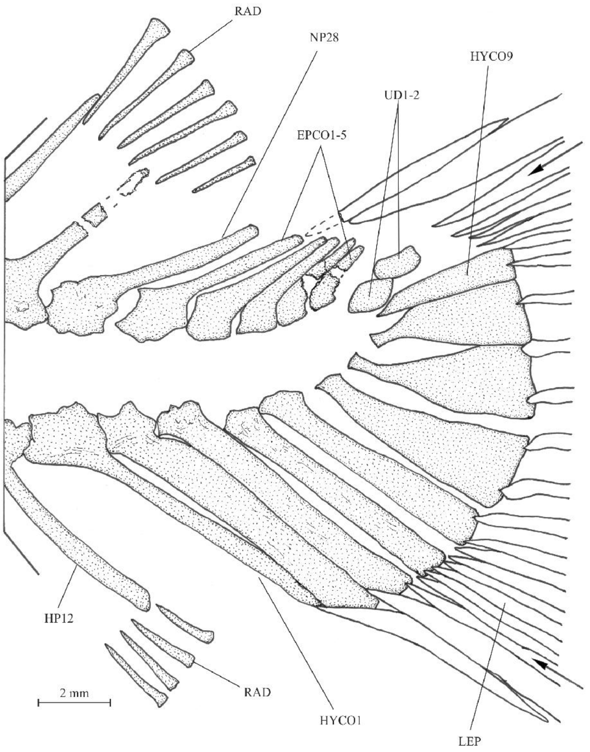

Figure 14. *Costapycnodus costae* (HECKEL, 1856). Caudal skeleton of paratype MPUN M 654. The arrows point on the most external principal caudal rays.

The squamation (Figs 15-18)

There are flank scales only in the abdominal region of the body, anterior to the origin of the dorsal and anal fins. The most ventral scales that contact the ventral keel scutes are complete. All other scales are reduced to their bar-like component. There are 11 vertical rows of bar scales.

The dorsal ridge contains 12 or 13 scutes. Most of them are devoid of spines on their straight upper margin but some rare scutes possess a few tiny spines. The first dorsal scute is articulated with the dermosupraoccipital and is not larger than the following scutes. All the dorsal scutes are lying on an elongate and vertically oriented scale and are associated with a pair of bar-scales. The scale (= supratemporal) associated to the first dorsal scute is small and triangle-shaped.

There are 15 scutes in the ventral keel, 13 precloacal and 2 postcloacal. On the best preserved scutes, we can observe from 1 to 4 well developed spines on the lower margin.

The cloacal vestibule is surrounded by 3 modified scales (not in contact with the ventral scutes, as defined in POYATO-ARIZA & WENZ, 2002), one anterior and two posterior to the cloaca. There is no bifid cloacal scale.

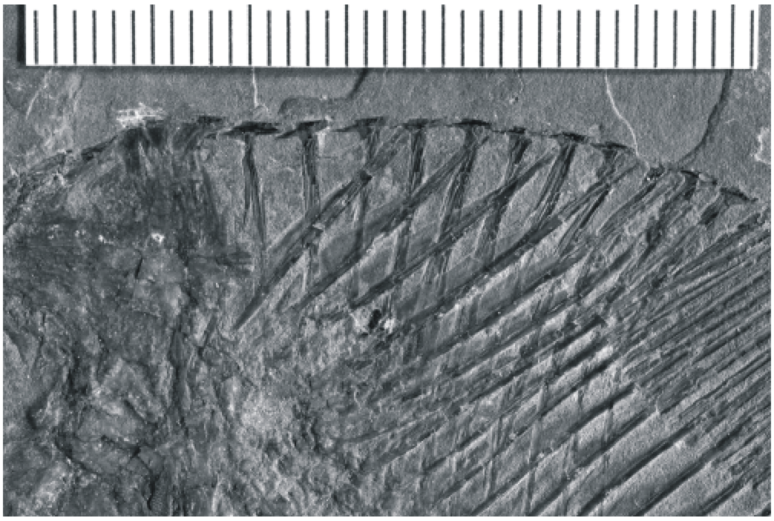

Figure 15. *Costapycnodus costae* (HECKEL, 1856). Dorsal ridge scutes of holotype MPUN M 662.

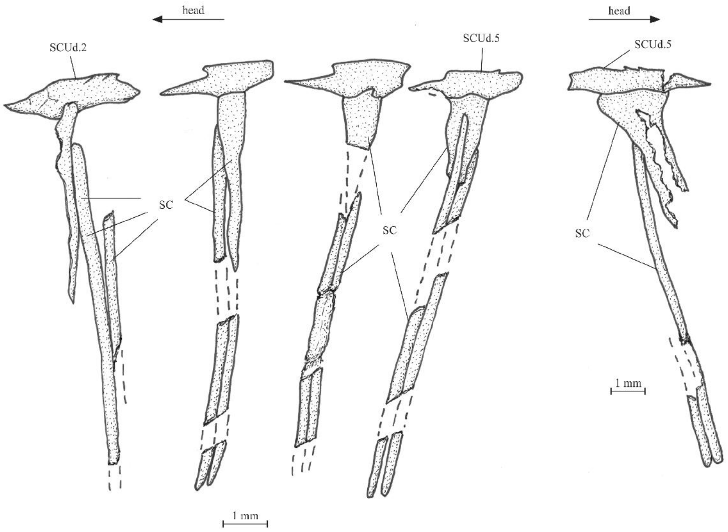

Figure 16. *Costapycnodus costae* (HECKEL, 1856). Dorsal ridge scutes 2 to 5 of holotype MPUN M 662 (left) and dorsal ridge scute 5 of paratype MPUN M 652 (right).

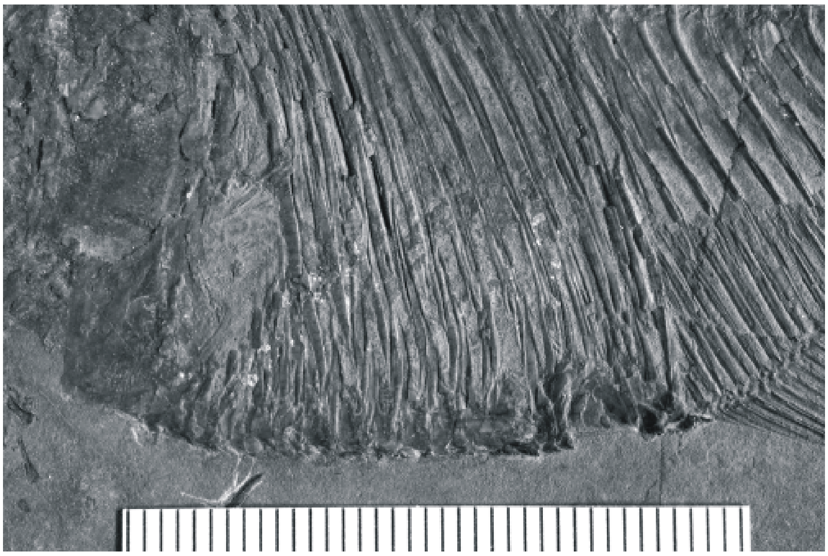

Figure 17. *Costapycnodus costae* (HECKEL, 1856). Ventral margin of the abdominal region of holotype MPUN M 662.

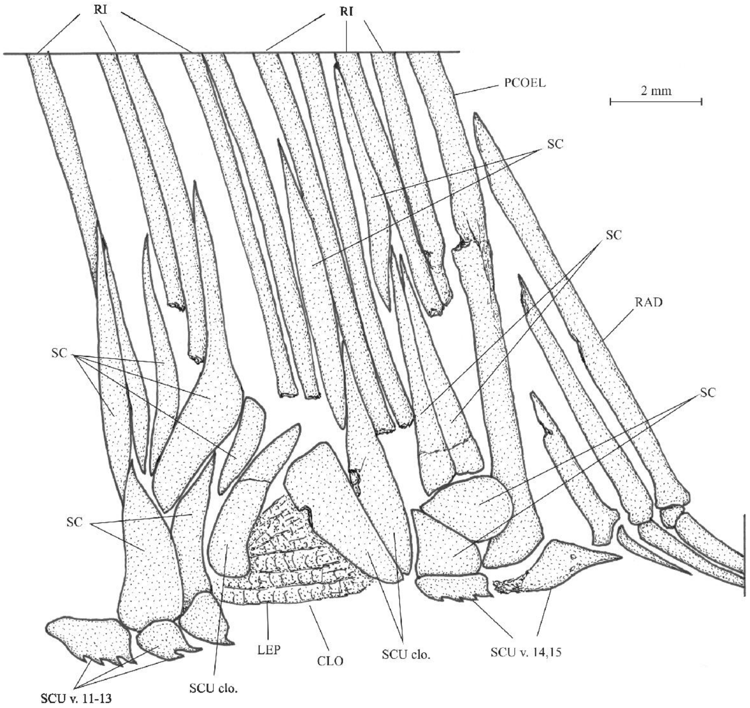

Figure 18. *Costapycnodus costae* (HECKEL, 1856). Scales of the cloacal region of holotype MPUN M 662.

DISCUSSION

Costapycnodus costae within Pycnodontiformes

There is a general agreement among the specialists to consider the presence of a brush-like process on the parietal (branched peniculus) as the main apomorphy characterizing Pycnodontidae (POYATO-ARIZA & WENZ, 2002, node 13, character 14[1]). *Costapycnodus costae* exhibits such a process and can thus be ranged confidently in that family.

Costapycnodus costae* and *Ocloedus subdiscus

As previously mentioned, the species *costae* was ranged in the recently erected genus *Ocloedus*, but with some doubt, by POYATO-ARIZA & WENZ (2002: 149). It is thus important to compare *Costapycnodus costae* and the Spanish Lower Cretaceous *Ocloedus subdiscus*, the type-species of the genus. The data on *O. subdiscus* come from WENZ (1989), KRIWET *et al.* (1999) and POYATO-ARIZA & WENZ (2002).

Both species have a brush-like process on the parietal, a temporal fenestra in the skull roof and the same general morphology. However, the differences between them are numerous as shown hereafter.

O. subdiscus has the dermopterotic and the dermosphenotic completely fused in one unique bone. The opercle is well developed. The preopercle is rather narrow. The prefrontal is absent. There are five rows of teeth on the vomer. The main prearticular tooth row contains 8 teeth. The teeth of the prearticular lateral tooth rows have crenulated margins. The postcoelomic bone reaches the axial skeleton. There are respectively 40 to 41 and 32 to 33 rays in the dorsal and anal fins. The origin of the dorsal fin is located behind the highest point of the dorsal profile. The dorsal ridge scutes bear strong spines on their upper margin.

Costapycnodus costae differs from *O. subdiscus* for all these features and, thus, can not be ranged in the genus *Ocloedus*.

Costapycnodus costae* and *Stemmatodus rhombus (Figs 19-22)

The data concerning *Stemmatodus rhombus* hereafter mentioned come from POYATO-ARIZA & WENZ (2002), KRIWET (2004) and from our own observations on specimens MPUN M 629, MPUN M 669, CLC A-30 and CLC A-31, all four from Castellammare di Stabia.

Figure 19. *Stemmatodus rhombus* (AGASSIZ, 1839). Specimen CLC A-31, from Castellammare

S. rhombus has a brush-like process and, thus, belongs to the family Pycnodontidae as *Costapycnodus costae*.

As previously stated, COSTA (1850) and HECKEL (1854) confused *C. costae* and *S. rhombus*. However, the two species greatly differ as shown by the following comparison.

Indeed, *S. rhombus* has a well developed opercle and does not present a temporal fenestra. *S. rhombus* also exhibits in the skull roof a rare apomorphy, the apparent division of the dermopterotic in two separated but associated bones, one dorsal and one ventral. This ventral element seems the result of the integration of an extrascapular in the lateral wall of the skull roof, near the original dermopterotic (POYATO-ARIZA & WENZ, 2002: fig. 12 B). Such a division of the dermopterotic is known in only three other pycnodont fishes, *Proscinetes bernardi* (THIOLLIÈRE, 1852) from the Upper Jurassic of France and Germany (EBERT, 2013: fig. 11, with the large ventral dermopterotic called "dermosphenotic 2"), *Akromystax tilmachiton* POYATO-ARIZA & WENZ, 2005 from the Upper Cretaceous of Lebanon (POYATO-ARIZA & WENZ, 2005: fig. 6 B) and *Polazzodus coronatus* POYATO-ARIZA, 2010 from the Upper Cretaceous of Italy (POYATO-ARIZA, 2010: fig. 3). However, this feature is less developed in these three pycnodonts than in *S. rhombus* where the dermopterotic-extrascapular becomes as wide or wider than the true dermopterotic.

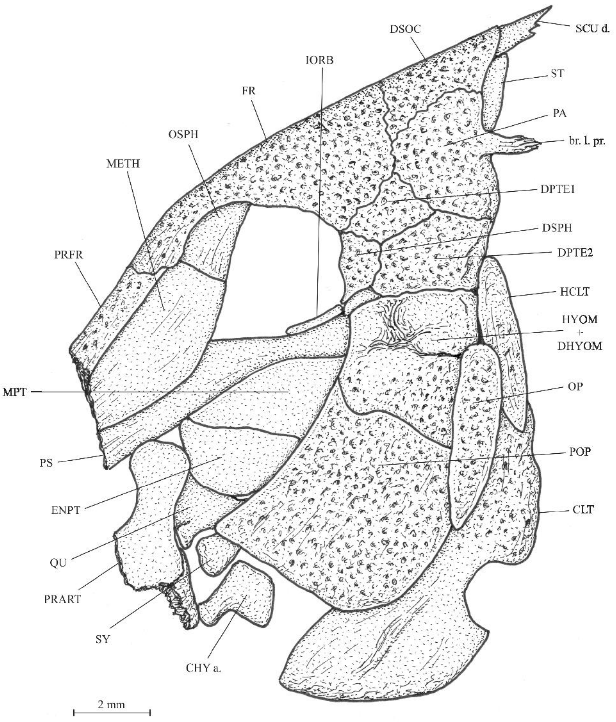

Figure 20. *Stemmatodus rhombus* (AGASSIZ, 1839). Skull (the snout is missing) and pectoral girdle of specimen MPUN M 629, from Castellammare.

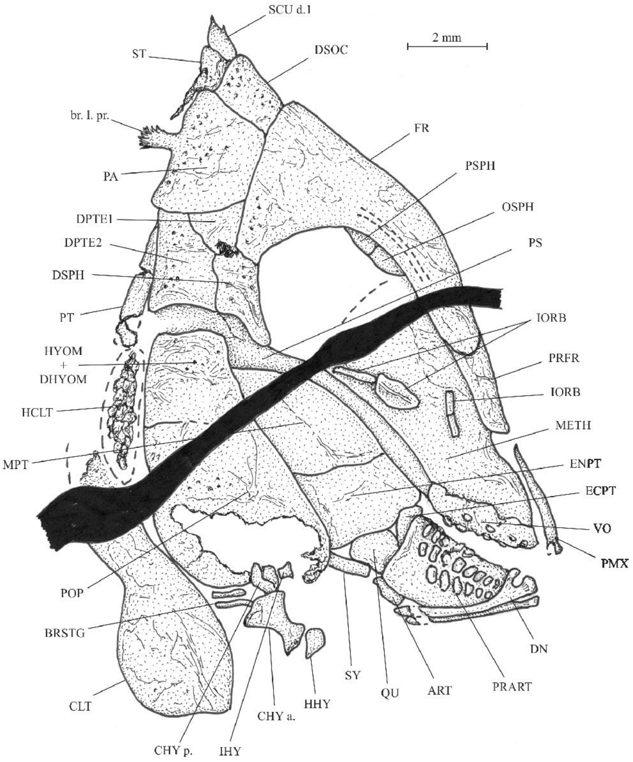

Figure 21. *Stemmatodus rhombus* (AGASSIZ, 1839). Skull and pectoral girdle of specimen CLC A-31, from Castellammare.

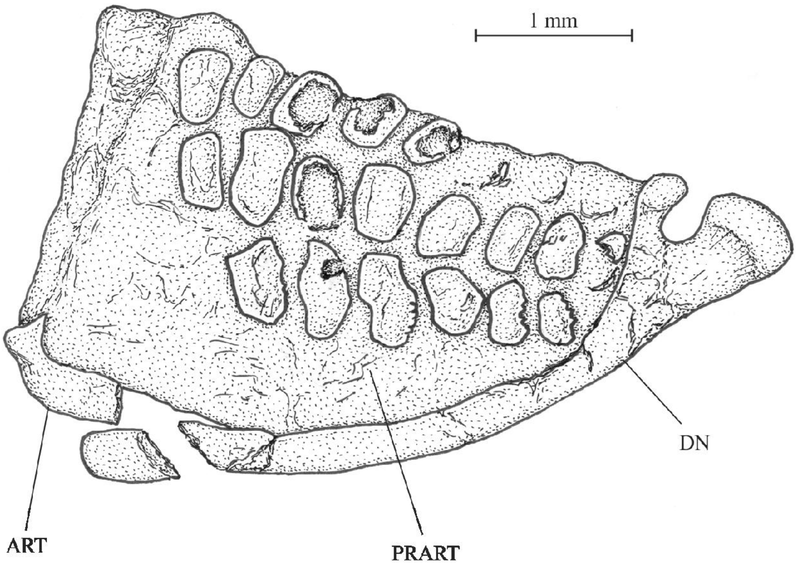

Figure 22. *Stemmatodus rhombus* (AGASSIZ, 1839). Left lower jaw of specimen CLC A-31, from Castellammare, in inner view.

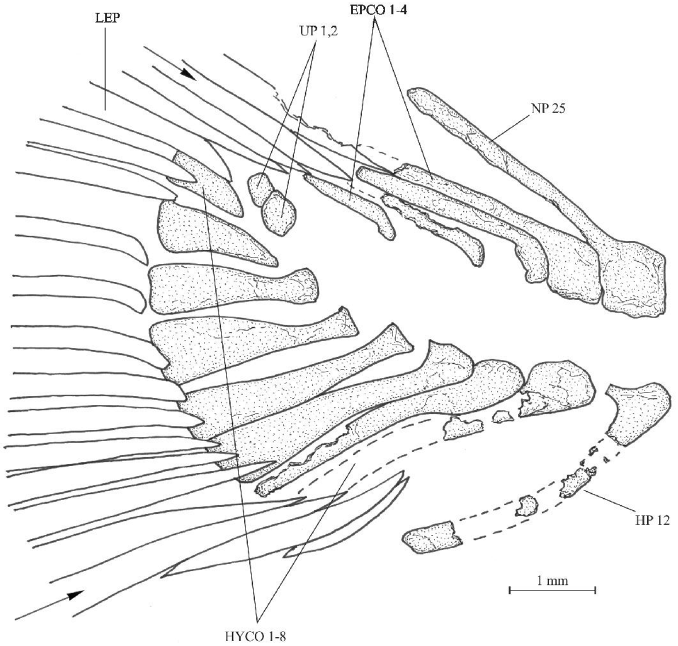

Figure 23. *Stemmatodus rhombus* (AGASSIZ, 1839). Caudal skeleton of specimen CLC A-31, from Castellammare. The arrows point on the most external principal caudal rays.

The vomerian and the prearticular teeth of *S. rhombus* are rather small and flat, with a shallow apical depression and an irregular contour that is weakly crenulated. The dentary bears two teeth, the first one being strongly enlarged.

There is a free axonost before the dorsal fin in *S. rhombus*.

The caudal skeleton of *S. rhombus* contains 4 epichordals, 8 hypochordals and 2 urodermals. There are 16 principal rays in the caudal fin.

The dorsal ridge scutes of *S. rhombus* bear a series of strong spines. The scales supporting these scutes still exhibit a rather well developed wing-like component on each side of the bar like element. *S. rhombus* also is devoid of postcloacal modified scales (as defined by POYATO-ARIZA & WENZ, 2002: 203).

For all these characters, *C. costae* is completely different from *S. rhombus*. The two species can easily be distinguished the one from the other.

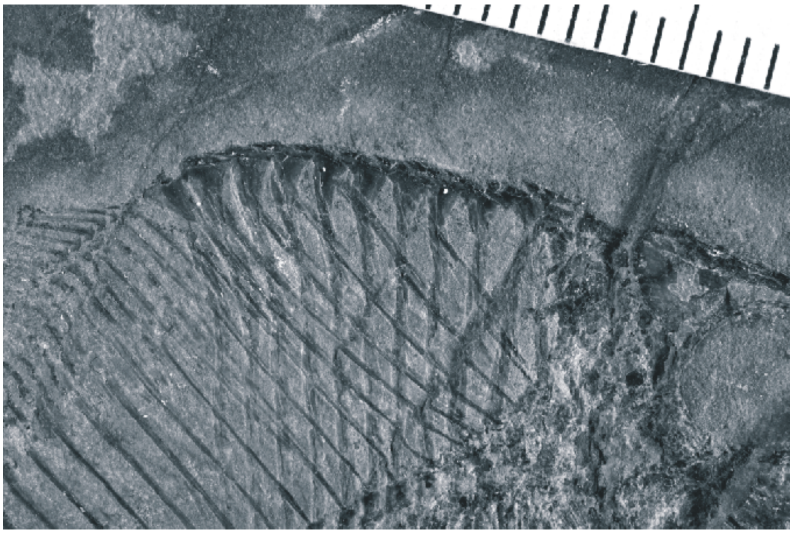

Figure 24. *Stemmatodus rhombus* (AGASSIZ, 1839). Dorsal ridge scutes of specimen CLC A-31, from Castellammare.

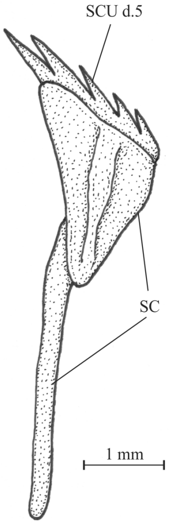

Figure 25. *Stemmatodus rhombus* (AGASSIZ, 1839). Fifth dorsal ridge scute of specimen CLC A-31, from Castellammare.

Costapycnodus costae* and *Coelodus saturnus

As previously mentioned, *Costapycnodus costae* was originally ranged by HECKEL, 1856 in the genus *Coelodus*.

Coelodus saturnus HECKEL, 1854, from the Turonian-Santonian of Komen, Slovenia, is not only the type-species of the genus and but also the unique species presently included in the genus. The presence of a brush-like process indicates that the species is a member of the family Pycnodontidae. Unfortunately, its skull is partly and badly preserved and was never really studied. So, comparisons with *Costapycnodus costae* are not easy. The data on *Coelodus saturnus* come from HECKEL (1856) and POYATO-ARIZA & WENZ (2002).

We do not know if a temporal fenestra is present or not in *C. saturnus* but the prefrontal is missing. There are more than 30 vertebral segments before the tail region. *Coelodus saturnus* also has a unique dental specialization within Pycnodontidae. Its prearticular teeth are straight, extremely elongated in vertical sense and pressed the ones against the others.

These few differences between the two species are sufficient to indicate that *Costapycnodus costae* does not belong to the genus *Coelodus.*

***Costapycnodus costae* within Pycnodontidae**

The phylogeny within Pycnodontomorpha and more particularly within the family Pycnodontidae was studied several times during the recent years (NURSALL; 1996b, 2010; POYATO-ARIZA & WENZ, 2002, 2004, 2005; KRIWET, 2005; MACHADO & BRITO, 2006; TAVERNE & CAPASSO, 2012; EBERT, 2016; CAWLEY, J. J. & KRIWET, J., 2017; etc.).

However and unfortunately, these studies conduct to divergent results. For instance, in the phylogeny proposed by POYATO-ARIZA & WENZ (2002, 2004, 2005), the presence of a temporal (= dermocranial) fenestra is a homoplasious character (ibid., 2002: 156, character 12[1]) that occurs at different levels within the family Pycnodontidae and *Akromystax* POYATO-ARIZA & WENZ, 2005, a fish that exhibits a temporal fenestra (POYATO-ARIZA & WENZ, 2005: fig. 3 A, B), appears as the most basal genus of the family. EBERT (2016) proposes a quite different phylogenetic hypothesis for the Pycnodontidae, a hypothesis in which the presence or the absence of a temporal fenestra plays a major role (ibid., 2016: 35, character 11[1, 2]). He ranges the genera having a temporal fenestra in one group, his "Paraphyletic Group B" (ibid., 2016: 43, character 11[1], fig. 21) that also includes the subfamily Pycnodontinae minus the Nursalliinae. However, he also ranges in that Paraphyletic Group B two genera without a temporal fenestra, *Polazzodus* POYATO-ARIZA, 2010 (POYATO-ARIZA, 2010: figs 2, 3) and *Sylvienodus* POYATO-ARIZA, 2013 from the Upper Cretaceous of Portugal (POYATO-ARIZA, 2013: 94). *Akromystax* is no more the most basal member of the family but the most basal genus of the Paraphyletic Group B. The other genera devoid of temporal fenestra are reported to the new subfamily Turboscinetinae (ibid., 2016: 43, character 11[0], fig. 21). Four genera are positioned betwen the two groups. One of these, *Tepexichthys* APPLEGATE, 1992 from the Lower Cretaceous of Mexico bears a temporal fenestra (APPLEGATE, 1992: fig. 9), the three others no. *Rhinopycnodus* TAVERNE & CAPASSO, 2013 from the Upper Cretaceous of Lebanon becomes the basal genus of the family. So, even in the phylogenetic hypothesis of EBERT (2016), the temporal fenestra appears at different levels and seems rather to be an homoplasious character than really an autapomorphy defining one precise subgroup of pycnodontid fishes. Personally, we think that the presence of a temporal fenestra is a manner for alleviating the heavily ossified skull of some Pycnodontidae and is homoplasious within the family. That is the principal reason that leads us to follow preferably the hypothsis of POYATO-ARIZA & WENZ (2002, 2004, 2005) than that of EBERT (2016) in our quest of the systematic position of *Costapycnodus costae* within Pycnodontidae.

The new Italian genus is devoid of the apomorphies characterizing Pycnodontinae, such as the bifid cloacal scale, the well visible *dilatator fossa* surrounded by the dermosphenotic and the dermopterotic, etc. Its relationships clearly are to be found within the more primitive Pycnodontidae.

Three characters allow more particularly to precise the exact systematic position of *Costapycnodus* within that primitive assemblage.

(1) The new genus has the lower point of its ventral margin located before the origin of the anal fin (POYATO-ARIZA & WENZ, 2002, character 4[1]). The same morphology exists from *Akromystax* (POYATO-ARIZA & WENZ, 2005: Figs 1, 2) to *Ocloedus* (WENZ, 1989: pl. 1, fig. 1). In *Rhinopycnodus* (TAVERNE & CAPASSO, 2013: figs 1, 2), *Tepexichthys* (APPLEGATE, 1992: figs 3, 4) and the more advanced genera, the origin of the anal fin is located at the level of the lower point of the ventral profile (POYATO-ARIZA & WENZ, 2002, character 4[2]). It is to be noted that *Ocloedus* is also quoted 4[2] in POYATO-ARIZA & WENZ (2002: 235). However, The photos of the holotype shown in WENZ (1989: pl. 1, fig. 1) and in KRIWET *et al.* (1999: pl. 1, fig. 4) indicate that the origin of the anal fin is located a little behind the ventral apex positioned at the cloacal level.

(2) *Costapycnodus* still possesses two urodermals in the caudal skeleton, a plesiomorphic feature (POYATO-ARIZA & WENZ, 2002, node 10, character 71[2]) present in the most primitive members of the family, once again from *Akromystax* (POYATO-ARIZA & WENZ, 2005: fig. 8) to *Ocloedus* (KRIWET *et al.*, 1999: fig. 5). *Rhinopycnodus* (TAVERNE & CAPASSO, 2013: fig. 7)*, Tepexichthys* (APPLEGATE, 1992: fig. 7) and the more evolved genera share the apomorphic condition of having only one urodermal (ibid., 2002, node 19, character 71[3]), except *Proscinetes* GISTEL, 1848, from the Upper Jurassic and the Lower Cretaceous of Europe, that preserves two urodermals (ibid., 2002: fig. 24 B; NURSALL, 1999: fig. 10 A; EBERT, 2013: fig. 12) and *Potiguara* MACHADO & BRITO, 2006, from the Upper Cretaceous of Brazil, that also has two urodermals (MACHADO & BRITO, 2006: fig. 3).

(3) The less advanced Pycnodontidae exhibit a series of strong spines posteriorly inclined on their dorsal ridge scutes (POYATO-ARIZA & WENZ, 2002, nodes 1, 3, character 90[1, 2, 3]. Such a morphology exists from *Akromystax* (POYATO-ARIZA & WENZ, 2005: fig. 2) to *Ocloedus* (KRIWET *et al.*, 1999: 46; POYATO-ARIZA & WENZ, 2002: fig. 38 A). In *Tepexichthys* and the more specialized genera, these spines are lost (ibid., 2002, node 19, character 90[0]). There are however three exceptions in this last group.

Neoproscinetes DE FIGUEIREDO & DA SILVA SANTOS, 1987, from the Lower Cretaceous of Brazil, develops one or two spines anteriorly inclined on the dorsal ridge scutes (NURSALL & MAISEY, 1991: fig. p. 126). *Haquelpycnodus* TAVERNE & CAPASSO, 2018, from the Upper Cretaceous of Lebanon, has well marked spines on its dorsal ridge scutes (TAVERNE & CAPASSO, 2018: fig. 19). That probably is a reversion. Some Pycnodontinae with scutellum-like dorsal ridge scutes bear microspines on their upper margin (BLOT & VORUZ, 1987; fig. 29; CAPASSO, 2000: 285, fig. 22).

For this character, *Costapycnodus* and *Rhinopycnodus* seem intermediate between the two groups. Most of their dorsal ridge scutes are devoid of spines but a few small spines are preserved on some rare scutes (Fig. 16; TAVERNE & CAPASSO, 2013: fig. 8).

So, characters (1) and (2) indicate that *Costapycnodus* belongs to the basal group of Pycnodontidae, an assemblage comprising the genera *Akromystax* to *Ocloedus*, and not to the crown group including *Rhinopycnodus*, *Tepexichthys* and the more advanced genera. Character (3) shows that *Costapycnodus* is more evolved than *Ocloedus* and allows to place the new Italian genus between *Ocloedus*, on the one hand, and *Rhinopycnodus*, on the other hand, within the phylogeny of the family.

The generic validity of *Costapycnodus*

Costapycnodus costae is one of the four species of Pycnodontidae having the postcoelomic bone reduced and not reaching the axial skeleton. The other species are *Turboscinetes egertoni*, *Turbomesodon praeclarus* and *Scalacurvichthys naishi*, three fishes that greatly differ from *C. costae*.

In all Pycnodontidae, the opercle is a small, narrow and vertically oriented bone. But a so important atrophy of the opercle as in *Costapycnodus costae* is almost unique in the family (POYATO-ARIZA & WENZ, 2002, character 28[2]). This reduction seems even more pronounced than in *Oropycnodus ponsorti* (HECKEL, 1854) from the Paleocene of France (ibid., 2002, fig. 17B).

With 6 to 7 teeth in the main prearticular tooth row (ibid., 2002, character 46[1]), *Costapycnodus costae* also differs from the other members of the family. They have all 8 or more teeth in this row (ibid., 2002, character 46[2, 3]), except *Oropycnodus ponsorti* that also exhibits 7 or less teeth in the concerning prearticular row.

So, *C. costae* and *O. ponsorti* share two very rare characters (28[2] and 46[1]) for the family. However, the two species can in no way be ranged in the same genus. They differ in too many anatomical features. *O. ponsorti* belongs to the Pycnodontinae. As the other members of this subfamily, it has the endocranium posteriorly exposed, the exposed part of the hyomandibula-dermohyomandibula as wide as the preopercle, a bifid cloacal scale, only one urodermal, some hypertrophied elements in the hypochordal series and no more than 9 dorsal ridge scutes that are all scutellum-like shaped (POYATO-ARIZA & WENZ, 2002: figs 11 B, 17B, 29 B, 42 B).

The osteology of *Costapycnodus* not only shows that it greatly differs from *Ocloedus* but also that it is a valid genus within the family Pycnodontidae.

ACKNOWLEDGMENTS

We greatly thank Prof. Dr. Maria Rosaria GHIARA, head of the museums of the Universita degli Studi di Napoli Federico II, for allowing us the access to the material studied in the present paper. We are also grateful to Mr. Luciano LULLO, from the Universita di Chieti-Pescara, and to Mr. Adriano VANDERSYPEN, from the Royal Institute for Natural Sciences of Belgium, for their technical help and to the anonymous reviewers who have read and commented our text.

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 Geologia*, *Revista*, 10 (2): 164-178.

BASSANI, F. & D'ERASMO, G., 1912. La ittiofauna del calcare cretacico di Capo d'Orlando presso Castellammare (Napoli). *Memorie del Societa Italiana delle Scienze*, Roma, serie 3, 17: 184-243.

BLOT, J. & VORUZ, C., 1987. L'ordre des Pycnodontiformes. Chapitre 1. Famille des Pycnodontidae (Agassiz, 1833). *Museo Civico di Storia Naturale di Verona*, *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 5: 11-86.

BRAVI, S. & DE CASTRO, P., 1995. The Cretaceous fossil fishes level of Capo d'Orlando, near Castellammare di Stabia (NA): biostratigraphy and depositional environment. *Memorie di Scienze Geologiche*, Padova, 47: 45-72.

BREISLAK, S., 1798. Topografia fisica della Campania. Stamperia di Antonio BRAZZINI, Firenze: XII + 368 p.

CAPASSO, L., 2000. *Tergestina sorbinii* gen. nov., sp. nov., del Paleocene inferiore di Trebiciano, Trieste (Pisces, Pycnodontiformes). *Atti del Museo Civico di Storia Naturale di Trieste*, 48: 261-289.

CAPASSO, L., 2007. Pietraroja pietre e memorie. Ed. Paper's World, Teramo: 1-181.

CHERCHI, A., DE CASTRO, P. & SCHROEDER, R., 1978. Sull'eta dei livelli ad Orbitolinidi della Campania e delle Murge baresi. *Bollettino della Societa Naturalisti di Napoli*, 87: 1-17.

COSTA, O. G., 1850. Paleontologia del Regno di Napoli. Parte 1. *Atti dell'Academia Pontaniana*, Napoli, 5: 1-203.

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.

DE CASTRO, P., 1962. Nuove osservazioni sul livello ad Orbitolina in Campania. *Bollettino della Societa Naturalisti di Napoli*, 71: 103-135.

D'ERASMO, G., 1910. Sopra alcuni avanzi di pesci cretacei. *Atti della Reale Accademia delle Scienze fisiche e matematiche di Napoli*, serie 2a, 15 (5): 1-8.

D'ERASMO, G., 1914. La fauna e l'età dei calcari a ittioliti di Pietraroia. Parte I. *Palaeontographica Italica*, *Memorie di Paleontologia*, Pisa, 20: 29-86.

D'ERASMO, G., 1922. Contributo alla Ittiolitologia dell'Italia Meridionale. I. – Un Picnodonte (*Coelodus costai* Heckel) del calcare cenomanian di Alessano, in provincia di Lecce. *Memoria della Reale Accademia delle Scienze fisiche e matematiche di Napoli* (1920): 3-5.

D'ERASMO, G., 1946. L'ittiofauna cretacea dei dintorni di Comeno nel Carso Triestino. *Atti della Reale Accademia delle Scienze fisiche e matematiche della Società Reale di Napoli*, serie 3a, 2 (8): 1-136.

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.

HECKEL, J., 1854. Über den Bau und die Eintheilung der Pycnodonten, nebst kurzer Beschreibung einiger neuen Arten derselben. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften*, *Mathematisch-Naturwissenschafliche Klasse*, Vienna, 12 (3): 433-464.

HECKEL, J., 1856. Beiträge zur Kenntniss der fossilen Fische Osterreichs. *Denkschriften der kaiserlichen Akademie der Wissenschaften*, *Mathematisch-Naturwissenschafliche Klasse*, Vienna, 11: 187-214.

KRIWET, J., 2001. Palaeobiogeography of pycnodontiform fishes (Actinopterygii, Neopterygii). *In*: MELENDEZ, G., HERRERZ, Z., DELVENE, G. & AZANZA, B. (eds) *Los fósiles y la paleogeographia. XII Jornadas de la Sociedad Española de Paleontologia*: 121-130. Universidad de Zaragoza, Zaragoza.

KRIWET, J., 2004. Dental morphology of the pycnodont fish +*Stemmatodus rhombus* (AGASSIZ, 1844) (Neopterygii, +Pycnodontiformes) from the Early Cretaceous, with comments on its systematic position. *Transactions of the Royal Society of Edinburgh*, *Earth Sciences*, 94: 145-155.

KRIWET, J., 2005. A comprehensive study of the skull and dentition of pycnodont fishes. *Zittelliana*, A45: 135-188.

KRIWET, J., POYATO-ARIZA, F. J. & WENZ, S., 1999. A revision of the pycnodont fish *Coelodus subdiscus* Wenz 1989, from the Early Cretaceous of Montsec (Lleida, Spain). *Trebals del Museu de Geologia de Barcelona*, 8: 33-65.

LEUCI, G., 1976. La collezione di ittioliti di Castellammare di Stabia, Napoli. *Atti dell' Academia Pontaniana*, 25: 1-25.

MACHADO, L. P. , 2008. The braincase of *Neoproscinetes penalvai* (Pycnodontiformes, Pycnodontidae). *In*: ARRATIA, G., SCHULTZE, H. P. & WILSON, M. V. H. (eds) Mesozoic Fishes 4 – Homology and Phylogeny, Verlag Dr. F. PFEIL, München: 167-180.

MACHADO, L. P. & BRITO, P. M., 2006. The new genus *Potiguara* (Actinopterygii: Pycnodontiformes) from the Upper Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, 26 (1): 1-6.

MAISEY, J. G., 1999. The supraotic bone in neopterygian fishes (Osteichthyes, Actinopterygii). *American Museum Novitates*, 3267: 1-52.

MARTIN-ABAD, H. & POYATO-ARIZA, F. J., 2013. Historical patterns of distribution in Pycnodontiform and Amiiform fishes in the context of moving plates. *GeologicaBelgica*, 16 (4): 217-226.

NURSALL, J. R., 1996a. Distribution and ecology of pycnodont fishes. *In*: ARRATIA, G. & VIOHL, G. (eds) Mesozoic Fishes – Systematics and Paleoecology, Verlag Dr. F. PFEIL, München: 115-124.

NURSALL, J. R., 1996b. The phylogeny of pycnodont fishes. *In*: ARRATIA, G. & VIOHL, G. (eds) Mesozoic Fishes – Systematics and Paleoecology, Verlag Dr. F. PFEIL, München: 125-152.

NURSALL, J. R., 1999. The family +Mesturidae and the skull of pycnodont fishes. *In*: ARRATIA, G. & SCHULTZE, H. P. (eds) Mesozoic Fishes 2 – Systematics and Fossil Record, Verlag Dr. F. PFEIL, München: 153-188.

NURSALL, J. R., 2010. The case for pycnodont fishes as the fossil sister-group of teleosts. *In*: NELSON, J. S., SCHULTZE, H.-P. & WILSON, M. V. H. (eds) Origin and phylogenetic interrelationships of teleosts, Verlag Dr. F. PFEIL, München: 37-60.

NURSALL, J. R. & MAISEY, J. G., 1991. *Neoproscinetes* Figueiredo & Silva Santos1987. *In*: MAISEY J. G. (ed.) Santana Fossils. An illustrated atlas. T. F. H. Publications, Neptune City: 124-136.

POYATO-ARIZA, F. J., 2010. *Polazzodus*, gen. nov., a new pycnodont fish from the Late Cretaceous of northeastern Italy. *Journal of Vertebrate Paleontology* 30(3): 650-664.

POYATO-ARIZA, F. J., 2013. *Sylvienodus*, a new replacement genus for the Cretaceous pycnodontiform fish "*Pycnodus*" *laveirensis*. *Comptes Rendus Palevol* 12: 91-100.

POYATO-ARIZA, F. J. 2015. Studies on pycnodont fishes (I): evaluation of their phylogenetic position among actinopterygians. *Rivista Italiana di Paleontologia e Stratigrafia*, 121 (3): 329-343.

POYATO-ARIZA, F. J. & MARTIN-ABAD, H., 2013. History of two lineages: Comparative analysis of the fossil record in Amiiformes and Pycnodontiformes (Osteichthyes, Actinopterygii). *Spanish Journal of Palaeontology*, 28 (1): 79-90.

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., 1997. Les Poissons Crétacés de Nardo. 5°. *Pycnodus nardoensis* sp. nov. et considérations sur l'ostéologie du genre Pycnodus (Actinopterygii, Halecostomi, Pycnodontiformes). *Bollettino del Museo Civico di Storia Naturale di Verona*, 21: 437-454.

TAVERNE, L, 2003. Les poissons crétacés de Nardo. 15°. Etude complémentaire de *Pseudopycnodus nardoensis* (Taverne, 1997) nov. gen. (Actinopterygii, Halecostomi, Pycnodontiformes). *Bollettino del Museo Civico di Storia Naturale di Verona*, *Geologia Paleontologia Preistoria*, 27: 15-28.

TAVERNE, L. & CAPASSO, L., 2012. Les poissons crétacés de Nardò. 35°. Compléments à l'étude des halécostomes *Belonostomus* (Aspidorhynchiformes) et *Pseudopycnodus* (Pycnodontiformes). *Bollettino del Museo Civico di Storia Naturale di Verona*, *Geologia Paleontologia Preistoria*, 36: 25-44.

TAVERNE, L. & CAPASSO, L., 2013. Osteology and relationships of *Rhinopycnodus gabriellae* gen. et sp. nov. (Pycnodontiformes) from the marine Late Cretaceous of Lebanon. *European Journal of Taxonomy*, 67: 1-14.

TAVERNE, L. & CAPASSO, L., 2018. Osteology and phylogenetic relationships of *Haqelpycnodus picteti* gen. and sp. nov., a new pycnodont fish genus (Pycnodontidae) from the marine Late Cretaceous tropical sea of Lebanon. *Geo-Eco-Trop*, 42 (2): 117-132.

VELIC, I., 1988. Lower Cretaceous benthic foraminiferal biostratigraphy of the shallow-water carbonates of the Dinarides. *Revue de Paléobiologie*, Volume special 2, "Benthos '86": 467-475.

WENZ, S., 1989. Une nouvelle espèce de *Coelodus* (Pisces, Pycnodontiformes) du Crétacé inférieur du Montsech (Province de Lérida, Espagne) : *Coelodus subdiscus* n. sp. *Geobios*, 22 (4) : 515-520.

WOODWARD, A. S., 1895. Catalogue of the fossil fishes in the British Museum (Natural History). Part III. Trustees of the British Museum (Natural History), London: I-XXXIX + 1-544.