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A revision of the pycnodontid fish *Coelodus subdiscus* Wenz 1989, from the Early Cretaceous of Montsec (Lleida, Spain)

Jürgen KRIWET*, Francisco José POYATO-ARIZA** and Sylvie WENZ***

RESUMEN

KRIWET, J., POYATO-ARIZA, F.J. y WENZ, S. Revisión del pez pycnodóntido *Coelodus subdiscus* Wenz 1989, del Cretácico inferior del Montsec (Lleida, España).

La revisión de *Coelodus subdiscus* Wenz 1989 (Cretácico inferior del Montsec, Lleida) proporciona nueva información sobre su anatomía, especialmente sobre los esqueletos craneal y caudal y sobre la cloaca. El hueso parietal presenta una extensión digitada, el proceso parietal, y parece constar de dos partes fusionadas, parietal y supratemporal. Se discute la identificación del hueso en el margen posterodorsal de la órbita. Descrito como dermopterótico, parece consistir en un complejo de dermopterótico más dermosfenótico. Ello se evidencia por la unión en este hueso de los canales sensoriales infraorbitario y supraorbitario. Se figuran las denticiones prearticular y vomeriana, y se indica la presencia de grandes dientes branquiales con forma de gancho. Se describen en detalle, por primera vez, el esqueleto caudal, las escamas del borde del cuerpo y las que forman la cloaca. Para evitar forzar homologías, aún por establecer, con los teleósteos, se utilizan para el endoesqueleto caudal los términos "elementos epi- e hipocordales". Hay 4 epi- y al menos 12 elementos hipocordales, y dos grandes urodermales, estrechamente articulados. Las fulcras están ausentes. La cloaca está formada por una escama diferenciada anterior y dos posteriores. Se presenta una revisión taxonómica y una nueva diagnosis de *Coelodus subdiscus*.

Palabras clave: Actinopterigios, Pycnodontiformes, *Coelodus subdiscus*, Cretácico inferior, Montsec, España.

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ABSTRACT

The revision of *Coelodus subdiscus* Wenz 1989 (Early Cretaceous of Montsec, north-eastern Spain) has yielded new information on its anatomy, notably on cranial and caudal skeletons and cloaca. The parietal bone has a brush-like extension, the parietal process, and seems to consist of two different fused portions, parietal and supratemporal. The identification of the bone in the postero-dorsal margin of the orbit is discussed. It was described as dermopterotic, but seems to be a complex bone consisting of dermopterotic plus dermosphenotic. This is evident by the junction of the infraorbital and supraorbital sensory canals in this bone. The prearticular and vomerine dentitions are figured, and the presence of large, hook-shaped branchial teeth is indicated. The caudal skeleton, ridge scales, and cloaca are described in detail for the first time. To avoid forcing homologies that are not established yet with teleosts, the terms "epi- and hypochordal elements" are used for the caudal endoskeleton. There are 4 epi- and at least 12 hypochordal elements, and two large, tightly articulated urodermals. Fringing fulcra are absent. The cloaca is formed by one anterior and two posterior differentiated scales. A taxonomical review and a new diagnosis of *Coelodus subdiscus* are presented.

Key words: Actinopterygii, Pycnodontiformes, *Coelodus subdiscus*, Early Cretaceous, Montsec, Spain.

INTRODUCTION

Pycnodontiform fishes usually have a highly rounded and laterally flattened body (Pl. 1, figs. 1, 4). The vomer and the prearticulars bear more or less regularly arranged tritoral teeth (Pl.1, figs. 2, 3). A single row of styliform or incisiform grasping teeth is developed on the dentalosplenials and premaxillae. Pycnodonts are interpreted as inhabitants of shallow waters of the Tethyan Sea and the developing Atlantic Ocean (Nursall, 1996a), although lacustrine pycnodontiforms do occur in the Early Cretaceous of Las Hoyas, Cuenca, Spain (Poyato-Ariza *et al.*, 1998). Their fossil record dates back as far as Upper Triassic (Norian) from northern Italy (Tintori, 1981) and Austria (Gorjanovic-Kramberger, 1905), and the last pycnodonts are recorded with highly derived forms in Paleogene strata (Eocene) of Europe and Africa (Blot, 1980; Longbottom, 1984). The pycnodontid *Coelodus subdiscus* Wenz 1989, object of revision in this paper, is only known from two localities in north-eastern Spain, in the Montsec area.

The examined material comes from the localities of "La Pedrera" and "La Cabrua", near Santa Maria de Meià in the Serra del Montsec (province of Lleida, Catalonia, Spain). The former is the type locality, also known as "La Pedrera de Meià" and "La Pedrera de Rúbies" (Gómez-Alba, 1997). The age of the limestone beds was given by Vidal (1902) as Kimmeridgian. Later, Peybernès & Oertli (1972) and Brenner *et al.* (1974) attributed a late Berriasian to early Valanginian age to the fossiliferous strata. The fish fauna includes chondrichthyans (only hybodonts; Vidal, 1915; Gómez-Pallerola, 1985, 1988, 1992; Soler-Gijón & Poyato-Ariza, 1995), a sarcopterygian and many actinopterygians (e.g., Sauvage, 1903; Vidal, 1915; Wenz, 1964, 1988, 1991; Poyato-Ariza, 1991; Wenz & Poyato-Ariza, 1994). Pycnodont fishes are rather abundant. They are represented by adult and juvenile specimens.

Vidal (1902) was the first to present well-preserved fossil plants and fishes from "La Predrera de Santa Maria de Meià" in a session at the Real Academia de Ciencias y Artes de Barcelona. He mentioned a pycnodont fish, *Microdon*, as a species close to *M. egertoni*, in a faunal list. *Microdon* (=*Proscinetes*) *egertoni* was originally described from upper Kimmeridgian limestones of Cerin in France (Thiollière, 1854). Sauvage (1903) also identified the Spanish specimen as *Microdon* aff. *egertoni*. The specimen is preserved as an impression only. Following Sauvage (1903) the pycnodont fishes from Montsec were determined as *Microdon* aff. *egertoni* by most authors (e.g., Broili, 1932). In 1968, Wenz indicated the presence of *Coelodus* in Montsec, and in 1989a this author described the new species *Coelodus subdiscus*. At the same time, she stated that the presence of *Proscinetes* in Montsec was not verified. This statement was reinforced by Wenz (1991) and Wenz & Poyato-Ariza (1994) and is confirmed herein.

The original description of *Coelodus subdiscus* from the famous Early Cretaceous vertebrate outcrops of Montsec in eastern Spain was based on material housed in the collections of the Muséum national d'Histoire naturelle in Paris (e.g., the holotype, Pl. 1, fig. 4) and in several Spanish collections (e.g., Museu de Geologia de Barcelona, Museu de Geologia del Seminari de Barcelona, Institut d'Estudis Ilerdencs in Lleida). The present revision is based on new material and on new preparations of the previously studied material.

MATERIAL

The specimens for this study are housed in the Museu de Geologia de Barcelona (MGB), the Museu de Geologia del Seminari de Barcelona (MGSB), and the Muséum national d'Histoire naturelle in Paris (MNHN). In addition, several private collections and an isolated prearticular dentition, which is housed in the Institut of Palaeontology of the Free University of Berlin (IPFUB), were examined.

The MNHN material comprises 37 specimens: MSE 290a-b (skull and body); MSE 291a-b (skull and dorsal part of the body, eroded); MSE 292 (early juvenile specimen); MSE 293 (isolated prearticular dentition); MSE 294 (dentition); MSE 295 (fragmentary prearticular dentition); MSE 296 (isolated teeth, pycnodont indet.); MSE 297a-b (prearticular dentitions); MSE 299a-b (isolated teeth, pycnodont indet.); MSE 300a-b (specimen lacking unpaired fins); MSE 302a-b (specimen lacking snout and caudal fin); MSE 303a-b (prearticular and vomerine dentition); MSE 305 (fragmentary specimen, pycnodont indet.); MSE 306 (fragmentary specimen, pycnodont indet.); MSE 307 (isolated teeth, pycnodont indet.); MSE 341a-b (holotype); MSE 374 (isolated teeth, *Coelodus* sp.); MSE 433 (fragmentary specimen, pycnodont indet.); MSE 437 (prearticular and vomerine dentition); MSE 439a-b (isolated skull); MSE 440 (badly preserved specimen); MSE 441 (prearticular and vomerine dentition); MSE 442 (acid prepared specimen, figured by Wenz 1989a); MSE 465 (isolated teeth, pycnodont indet.); MSE 652a-b (incomplete specimen); MSE 653a-b (incomplete specimen); MSE 654a-b (fragmentary specimen, pycnodont indet.); MSE 655; MSE 656; MSE 721a-b (prearticular teeth); MSE 818a-b (dentition); MSE 821 (prearticular dentition); MSE 824 (vomerine dentition); MSE 831 (isolated teeth, pycnodont indet.); MSE 837a-b (fragmentary specimen, pycnodont indet.); MSE 944 (isolated prearticular teeth); MSE 965 (complete specimen, acid prepared).

The MGB material consists of 13 more or less completely articulated specimens: 127, 536, 537-1, 537-2, 599, 602, 609 a, 609 b, 29455 a, 29455 b, 30339, 30345 and 30377.

The MGSB material comprises seven specimens: 8997, 13.376 A + B, 20.658, 27.298, 27.299 (only impression of skull), 56.216 (parts of skull and anterior body) and 20659 (paratype; skull exhibiting vomerine dentition).

ABBREVIATIONS AND TERMINOLOGY

The following abbreviations are used: **a**, anterior cloacal scale; **af**, anal fin rays; **amf**, anterior median flange of neural spine; **ap**, anal pterygiophores; **ax 1-3**, anal axonosts 1-3; **ang**, angular; **art**, articular; **br**, branchiostegal rays; **ch**, ceratohyals; **cl**, cleithrum; **cp**, coronoid process; **den**, dentary; **df**, dermocranial fenestra; **dfr**, dorsal fin rays; **dp**, dorsal pterygiophores; **dpf**, compound bone consisting of dermopterotic, parietal and frontal bones; **dpt**, dermopterotic; **dptsp**, compound bone consisting of dermopterotic and dermosphenotic; **dso**, dermosupraoccipital; **dsp**, dermosphenotic; **e1-4**, epicohordal elements 1 to 4; **ec**, ectopterygoid; **enp**, entopterygoid; **f**, frontal; **fi**, anal fin; **h1** - **h12**, hypochordal elements 1 to 12; **hp**, hypohyal; **hyo**, hyomandibular; **io**, infraorbital ossicles; **isl**, infraorbital sensory line; **met**, mesethmoid; **mpt**, metapterygoid; **op**, operculum; **p1**, posterior cloacal scale 1; **p2**, posterior cloacal scale 2; **pa**, parietal; **pb**, postcoelomic bone; **pfb**, pectoral fin bases; **pm**, premaxilla; **pop**, preoperculum; **pp**, parietal process; **pr**, prearticular; **prr**, principal caudal fin rays; **ps**, parasphenoid; **psl**, parietal branch of sensory line; **pvf**, pelvic fin; **q**, quadrate; **sc**, scales; **scl**, supracleithrum; **st**, supratemporal; **stpa**; supratemporal portion of parietal bone; **sym**, symplectic; **tsl**, temporal branch of sensory line; **ud1-2**, urodermals 1 and 2; **v**, cloacal vestibule; **vo**, vomer; **vrs**, ventral ridge scales.

Other abbreviation is **SL** for standard length.

The terms “pycnodont” for Pycnodontiformes and “pycnodontid” for Pycnodontidae are used from now on, following Nursall (1996b).

SYSTEMATIC PALAEONTOLOGY

Osteichthyes Huxley 1880
Actinopterygii Klein 1885
Neopterygii Regan 1925
Pycnodontiformes Berg, 1937
Pycnodontoidei Nursall 1996b
Pycnodontidae *sensu* Nursall 1996b
Genus *Coelodus* Heckel, 1854

Type species: *Coelodus saturnus* Heckel, 1854 from the Cenomanian of Goriansk, Slovenia.

Coelodus subdiscus Wenz, 1989

1902 *Microdon* aff. *egertoni* Thiollière; Vidal: 10.
1903 *Microdon* aff. *egertoni* Thiollière; Sauvage: 10; pl. 4, fig. 4.
1905 *Microdon egertoni* Thiollière; Font: 323; fig. 214.
1908 *Microdon egertoni* Thiollière; Font: 95, lower figure.
1926 *Microdon egertoni* Thiollière; Font: 241; fig. 214.
1932 *Microdon* aff. *egertoni* Thiollière; Broili: pl. 1, fig. 2.
1953 *Microdon* aff. *egertoni* Thiolière [*sic*]; Bataller: pl. 7, fig. 2.
1968a *Coelodus*; Wenz: 118.
1981 *Coelodus* sp.; Lacasa: 70, 123; pl. 54, lower figure.
1981 *Microdon* aff. *egertoni* Thiollière; Lacasa: 70, 124; pl. 55.
1982 *Microdon* aff. *egertoni* Thiollière; Gómez-Pallerola: 205, fotos 12 & 13.
1984 ? *Microdon* aff. *egertoni* Thiollière; Barale *et al.*: tab. 2.
1984 *Coelodus* n. sp.; Barale *et al.*: tab. 2.
1988 *Coelodus* sp.; Gómez-Alba: 682; pl. 338, fig. 3.
1989 *Coelodus* sp.; Viohl: fig. 14.
1989a *Coelodus subdiscus* Wenz: 516; pl. 1; text-fig. 1.
1990 *Coelodus*; Muñoz: 97, upper figure.
1991 *Coelodus subdiscus* Wenz; Gómez-Alba: 28.
1991 *Coelodus subdiscus* Wenz; Wenz: 113, photo 3-4.
1992 *Coelodus subdiscus* Wenz; Gómez-Alba: 190-191.
1992 Pycnodontidae; Gómez-Alba: 209-210.
1994 *Coelodus subdiscus* Wenz; Wenz & Poyato-Ariza: 210.
1995 *Proscinetes*; Wenz & Poyato-Ariza: 50.
1995 *Coelodus*; Wenz & Poyato-Ariza: 50; fig. 22/1-2 (as *Coelodus subdiscus*).
1996a *Coelodus*; Nursall: 116.
1997 *Coelodus subdiscus* Wenz; Gómez-Alba: 84.
1997 Pycnodontidae; Gómez-Alba: 98.
1999 *Coelodus subdiscus*; Poyato-Ariza *et al.*: 509.

Holotype

MNHN MSE 341 (Muséum national d'Histoire naturelle de Paris: Pl. 1, fig. 4), complete specimen.

Locus typicus

La Pedrera de Santa Maria de Meià, Serra del Montsec, Province of Lleida, E-Spain.

Stratum typicum and age

Lithographic limestones of La Pedrera de Rúbies (Unit N2 by Peybernès, 1976); Berriasian-Valanginian.

Geographic and stratigraphic distribution

Species only known from the type locality and from the nearby locality of "La Cabrua", same age and formation.

Diagnosis (emended from Wenz, 1989a)

A species of *Coelodus* with the following combination of characters: standard length up to 230 mm. Maximum body depth 60 to 80% of SL, head length about 22% of SL. Teeth of the main row of the prearticulars subrectangular in outline with two medio-labial arranged tubercles in the posterior part of the jaw. About 11 pairs of long and alate ribs. Postcoelomic bone connected to the 12th ventral arcocentrum. The dorsal and anal fins are long and falcate. Both are situated behind the deepest points of the body. Dorsal fin with about 40 to 41, anal fin with about 32 to 33 fin rays. Dorsal fin about 66% of SL, anal fin about 50% of SL. Twenty-six to twenty-seven vertebrae, excluding those of the caudal endoskeleton. Seven to 8 anterior-most neural spines separated from their arcualia. Four epi- and at least 12 hypochordal elements in the caudal endoskeleton. Two large urodermals. Fringing fulcra absent. Squamation peltate, with 12 dorsal and 17 ventral ridge scales, 2 of them postanal. Dorsal ridge scales with up to 4 spines, ventral with up to 3 spines, in both cases posteriorly placed and oriented. Cloaca formed by 1 anterior and 2 posterior modified scales, the first posterior one ovoid and very small.

Description

Dermocranium

The skull roof of *Coelodus subdiscus* shows the typical arrangement of pycnodontid fishes (Fig. 1, Pl. 2). It is composed of an unpaired median dermosupraoccipital, paired parietals and frontals. The dermosupraoccipital (Nursall, 1996b, 1999) is a dermal bone, and is not homologous to the chondral supraoccipital bone of teleosts (Patterson, 1977). It roofs the post-temporal fossae and overlies the supraoccipital crest of the endocranium. The dermosupraoccipital bone is an autapomorphic character for pycnodonts (Nursall, 1996b, 1999). In the skull roof, the dermosupraoccipital bone interdigitates with the paired frontals antero-medially and is bordered by the paired parietals ventro-laterally. The frontals lie in the midline of the skull and are the largest of the dermal bones. The suture between the left and right frontal bones is

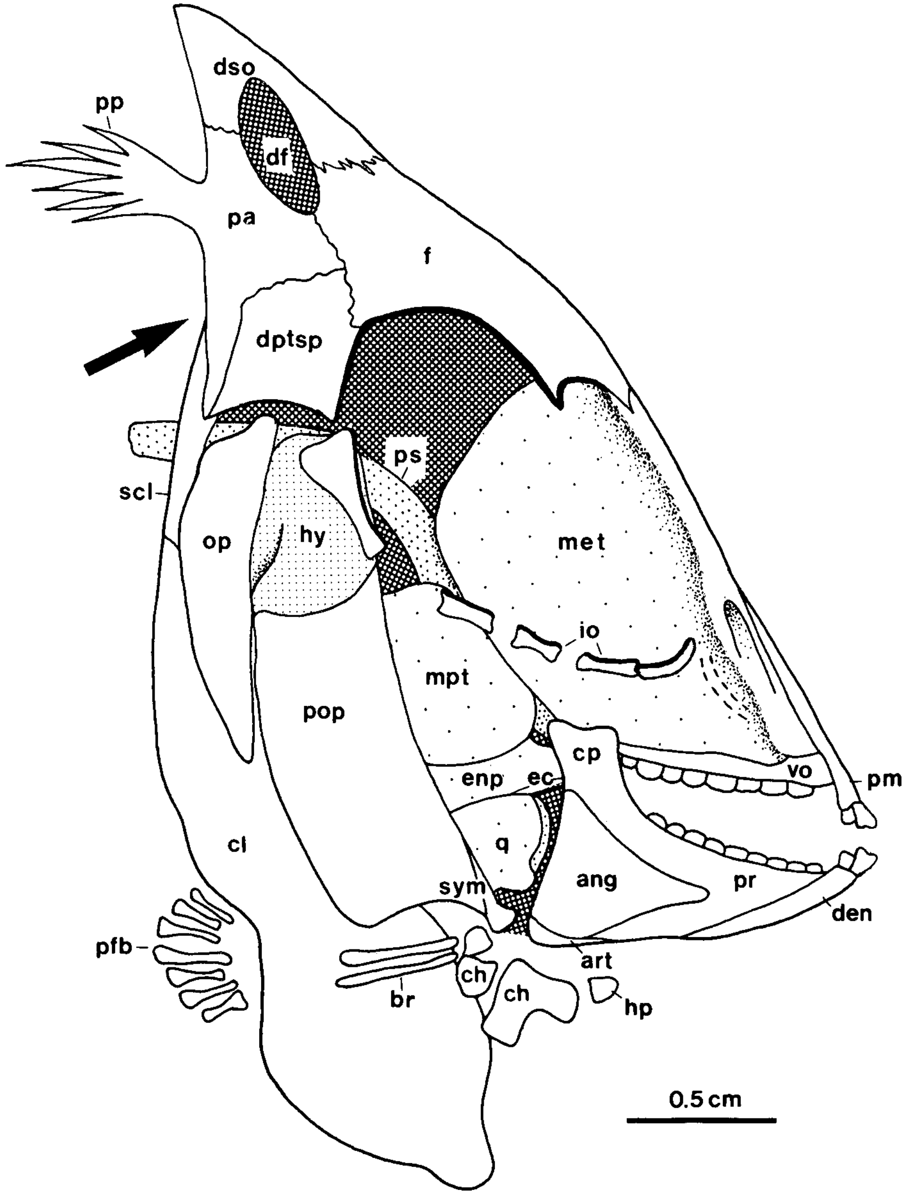

Fig. 1. *Coelodus subdiscus* Wenz, 1989. Restoration of the skull. Arrow points to the position of the vertebral column. Mostly from the holotype and specimens MNHN MSE 442, 965, MGB 537-1, MGB 30345, and MGSB 13.376B. Right side, lateral view.

Fig. 1. *Coelodus subdiscus* Wenz, 1989. Reconstrucción del cráneo. La flecha señala la posición de la columna vertebral. Principalmente del holotipo y de los ejemplares MNHN MSE 442, 965, MGB 537-1, MGB 30345 y MGSB 13.376B. Lado derecho, vista lateral.

straight. The frontals form the dorsal and antero-dorsal bony margin of the orbits and are contiguous with the parietals posteriorly. The parietals form most of the posterior margin of the dermal skull, and a brush-like extension, the parietal process, arises posteriorly from each parietal. It is assumed that parts of the epaxial musculature inserted on the ossified extensions of this peniculus. Other epaxial musculature was probably attached to the lateral post-temporal fossae.

The dermosupraoccipital, frontals, and parietals form the bony margin of a fenestra in the lateral wall of the dermocranium (Figs. 1, 2, Pl. 2). This dermic fenestra is oval to subcircular in outline, with its long axis directed antero-ventrally. The presence of such a fenestra is a derived character for pycnodontids (Nursall, 1996b), and is shared by *Coelodus*, *Tepexichthys*, and *Pycnodus*.

The postero-dorsal margin of the orbit is formed by a rectangular bone (Fig. 2). It is contiguous with the postero-ventral part of the frontal. In the skull reconstruction by Wenz (1989a: Fig. 1) this bone is called dermosphenotic and it borders posteriorly a smaller bone labelled as dermopterotic. The „dermopterotic“ of Wenz (1989a) is in fact the ventral extension of the parietal, and probably corresponds to the fused supratemporal (extrascapular bone), since this portions carries parts of the sensory canal (Figs. 1, 2). According to its articulation to the parietal and frontal bones, the rectangular bone in front of the ventral extension of the parietal can be regarded partially as the dermopterotic bone. Nevertheless, the position of the angle of the infraorbital canal between the circumorbital and otic parts of the sensory canals in its antero-ventral part indicates the presence of the dermosphenotic bone. Therefore, this bone seems to be a compound bone consisting of dermosphenotic and dermopterotic. Unfortunately, there are no growth series to study the development of these bones and their fusion (parietal/supratemporal and dermosphenotic/ dermopterotic).

In the posterior margin of the orbit the club-like posterior infraorbital bone (dermosphenotic of Nursall, 1999) is positioned (Fig. 1). The cheeks are naked but bear tubular infraorbital ossicles for the infraorbital sensory canal. Supraorbitals are absent, a typical feature of pycnodont fishes that is also found in other forms, such as *Amia*.

There is no unpaired dermethmoid or nasal bone overlying the frontal plate of the mesethmoid bone. Lateral ethmoids like in *Iemanja* (Wenz, 1989b; pers. obs.) are also absent.

The dermal cover of the skull has a pitted ornamentation. Tubercles may occur in larger specimens (e.g., MGB 609b).

Endocranium

The endocranium of *Coelodus subdiscus* is poorly preserved. A cracked, endochondral structure dorso-ventrally and antero-ventrally to the dermopterotic/ dermosphenotic may represent parts of the pterotic and sphenotic respectively. The paired exoccipitals are fused together with the anteriormost dorsal arcualia (two to three). This bony block (= synarcual; Nursall & Maisey, 1991) surrounds the neural canal. The mesethmoid of pycnodonts is a large, unpaired median bone, which separates the orbits, and supports the snout. The anterior margin forms a plate-like expansion, which supports the premaxillae. In *Coelodus subdiscus*, there is no nasal depression on the anterior surface of the plate-like expansion of the mesethmoid to house the process of the premaxilla. The ventral border of the mesethmoid envelops the anterior portion of the parasphenoid and the dorsal crest of the vomer, and is laterally exposed (Nursall, 1999).

There are two antero-posteriorly placed sclerotic bones in each orbita.

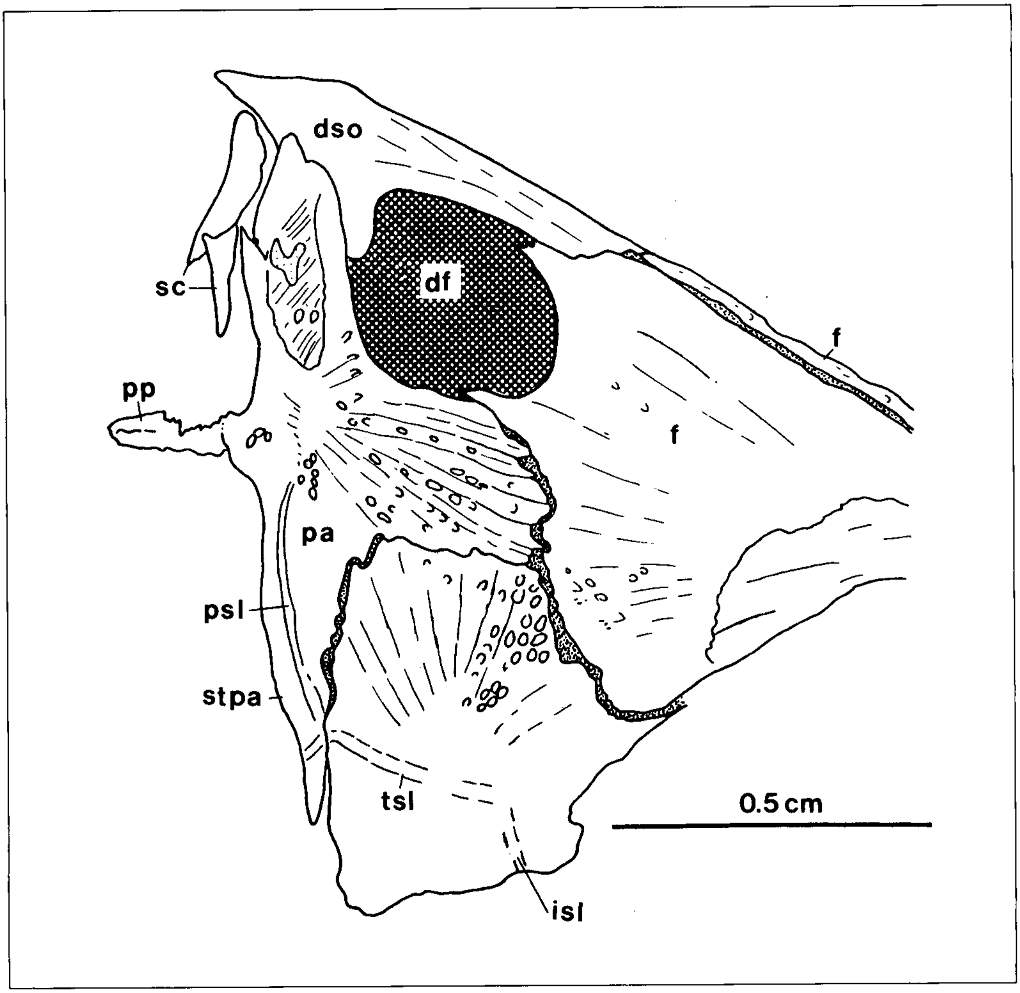

Fig. 2. *Coelodus subdiscus* Wenz, 1989. Camera lucida drawing of the occipital region of specimen MGSB N° 13.376B showing the juction of the sensory canals in the complex bone consisting of the dermopterotic and dermosphenotic. Right side, lateral view.

Fig. 2. *Coelodus subdiscus* Wenz, 1989. Dibujo a cámara clara de la región occipital del ejemplar MGSB N° 13.376B mostrando la unión de los canales sensoriales en el hueso compuesto consistente en dermopterótico más dermosfenótico. Lado derecho, vista lateral.

Parasphenoid and vomer

The base of the neurocranium is composed of two dermal bones, the parasphenoid and the vomer. The parasphenoid is edentulous, very long and inflected downward below the orbit as in other pycnodonts. This is an unusual condition in fishes (Nursall & Maisey, 1991). It reaches posteriorly behind the occipital margin of the skull below the level of the notochord (Fig. 1). An oval fenestra in the complex ventral keel of the parasphenoid (a synapomorphy of Pycnodontidae; Nursall, 1996b) was not observed due to the poor preservation of the parasphenoid in all studied specimens of *Coelodus subdiscus*. The oral surface of the vomer is strongly convex from side to side.

Jaw apparatus and mandibular articulation

Maxillae are not preserved in the examined specimens. Because of the loose attachment of the maxillae to the skull they are easily lost in pycnodonts after death. Supramaxillae are lacking in pycnodont fishes (Nursall, 1996b).

The premaxillary process roofs the snout anteriorly and makes up one third of the length of the anterior plate-like expansion of the mesethmoid (Fig. 1, Pl. 2). There is some confusion about the homology of the nasal process of the premaxillary within neopterygian fishes, e.g., in *Amia* (Grande & Bemis, 1998). The nasal process in teleosts always forms the most profound part of the nasal cavity. But in pycnodonts, the process is completely superficial and is actually like the superficial position of the ascending process. To avoid any homological implications with the ascending process of teleosts we suggest to call this structure premaxillary process.

The lower jaw is rather massive and consists of paired dentalosplenials, prearticulars, angular, and articular bones (Figs. 1, 3, Pl. 2). The well-developed coronoid process is fused laterally to the prearticular bone. Here, the massive mandible musculature must have been inserted. The angular is roughly triangular in outline in lateral view. The articular forms the postero-ventral part of the mandibular arch. The dentalosplenial is long and slender, its posterior end being pointed and single.

A special feature of pycnodonts is a double mandibular articulation with two pairs of bones. The double jaw articulation is also found in *Coelodus subdiscus* (Fig. 3). The articular facet of the quadrate is convex (condylar) and shows a rugose surface. It articulates with the concave posterior articular facet of the angular bone. The articular facet of the angular is marked by a rugose structure, which indicates some kind of articular cartilage commonly existing on condylar fossae surfaces, and articulates also with the symplectic. This double jaw articulation may relate pycnodonts to halecomorphs *sensu* Patterson, 1973 (Nursall & Maisey, 1991). In halecomorphs, however, (e.g., *Amia*, *Caturus*) the elements of the double mandibular articulation lie side by side. *Coelodus* as well as all other pycnodonts is unique since the two articulation pairs are positioned dorso-ventrally (Nursall, 1996b). In some pycnodonts an additional articular facet exists between quadrate and symplectic, e.g., in *Pycnodus*. This indicates a very complex functional pattern of jaw movements in these forms.

Dentition

The maxillae and the pterygoquadrate arcade of pycnodont fishes are toothless. In *Coelodus subdiscus*, each premaxillary and dentary bone bears two incisiform grasping teeth, the anterior one being remarkably bigger than the posterior one (Pl. 1, figs. 1, 2). The vomerine teeth are arranged in five longitudinal rows with closely placed teeth (Pl. 1, fig. 4). The teeth of the main row are about twice as broad as long, transversally elongated and oval in outline. An apical linear and narrow indent with crenulated margins is developed. The teeth of the lateral rows are elongated, with rounded crown extremities. The long axis of the teeth is set obliquely to the long axis of the vomer. No lateral teeth are inserted into spaces between main teeth as in *Proscinetes*. All teeth decrease in size slightly from posterior to anterior.

Each prearticular dentition consists of three longitudinal rows of crushing teeth (Pl. 2, figs. 1, 2; Pl. 3) and agrees well with that described by Woodward (1893, 1895a, 1895b, 1917) for *Coelodus*. It comprises one principal series of transversally elongated and subrectangular teeth. The main teeth are much broader than any of the lateral tooth rows. They are about 1.4 times as broad as long on average (Tab. 1). In occlusal view, they expose in the posterior part of the prearticular a very shallow apical indent, which may have crimped walls. Further anteriorly the occlusal surface exhibits two latero-medially placed rounded tubercles (Pl. 3, fig. 1). The main row is flanked laterally by two tooth rows. Teeth of the first and second lateral row are similar in

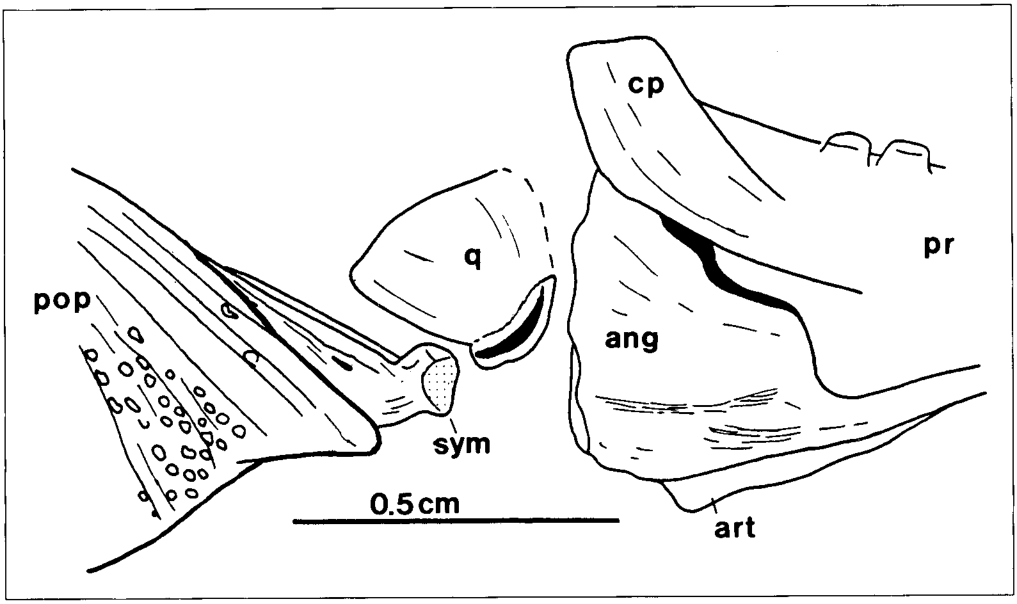

Fig. 3. *Coelodus subdiscus* Wenz, 1989. Camera lucida drawing of lower jaw articulation, based on specimen MNHN MSE 442. Right side, lateral view.

Fig. 3. *Coelodus subdiscus* Wenz, 1989. Dibujo a cámara clara de la articulación de la mandíbula inferior, basado en el ejemplar MNHN MSE 442. Lado derecho, vista lateral.

morphology. The long axes of the teeth are orientated obliquely. Teeth of the first lateral row are oval to subcircular in outline. They are about 1.6 times as broad as long (Tab. 1). All tooth crowns exhibit a shallow indent with crimped margins. The indent follows slightly the outer tooth contour. In the anterior part of the prearticular the teeth of the first lateral row are set with their long axes obliquely. The second (outer) lateral row is composed of more rectangular to subcircular teeth. They are almost as broad as long (Tab. 1). All tooth crowns have an apical indent. No additional intercalated teeth between the tooth rows are present. The aw/l index (average of width/length ratio) was calculated for an isolated left prearticular dentition, which is shown on Plate 3 (Tab. 1).

MR

Width	Length	w/l
1.81	1.47	1.23
1.45	1.02	1.42
1.06	0.79	1.34
0.86	0.58	1.48
0.61	0.46	1.33

aw/l index: 1.36

1.LR

1.72	0.82	2.10
1.31	0.81	1.62
1.41	0.59	1.93
1.00	0.65	1.54
0.93	0.60	1.55
0.80	0.53	1.51
0.65	0.44	1.48
0.57	0.44	1.30

aw/l index: 1.63

2.LR

1.02	1.26	0.81
0.99	0.81	1.22
0.91	0.92	0.99
0.76	0.72	1.10
0.65	0.73	0.90
0.61	0.73	0.84
0.46	0.71	0.65
0.35	0.54	0.65

aw/l index: 0.90

Tab. 1. Measurements of left prearticular teeth of *Coelodus subdiscus* (IPFUB, without number) in mm, from posterior to anterior, showing the average of width/length ratio (aw/l index) of tooth rows. MR = main tooth row, 1.LR = first lateral tooth row, 2.LR = second lateral tooth row.

Tab. 1. Medidas de los dientes del prearticular izquierdo de *Coelodus subdiscus* (IPFUB, sin número) en mm, de posterior a anterior, mostrando la media del cociente anchura/longitud (índice aw/l) de las filas de dientes. MR = fila principal, 1.LR = primera fila lateral, 2.LR = segunda fila lateral.

Branchial teeth

A review of branchial teeth in pycnodontids is given by Kriwet (1999). Woodward (1917) already indicated the presence of hook-shaped teeth in the branchial chamber of articulated specimens of *Coelodus subdiscus* and others. Several specimens in the collections of the Museu de Geologia de Barcelona and Museu de Geologia del Seminari de Barcelona also show those hook- or claw-shaped branchial teeth, which are situated at the level of the preoperculum.

Opercular series

The opercular series consists of two short and acinaciform branchiostegal rays (a common feature in pycnodonts; Lambers, 1991, fig. 13; Nursall, 1996b), a rather large preoperculum, and a smaller and narrow operculum fixed to the posterior border of the preoperculum (Fig. 1, Pl. 2). Inter- and suboperculum are absent. The preoperculum belongs functionally to the suspensorium. It is reduced in size and was called "préopercle 2" by Wenz (1989a). The structure called "préopercle 1" by Wenz (1989a) is the so-called dermohyomandibular of Nursall (1996b), and represents the expanded and enlarged upper part of the hyomandibular (see below).

Pterygoquadrate arcade

The pterygoquadrate arcade consists of the quadrate, metapterygoids, entopterygoids, and ectopterygoids (Fig. 1). The paired metapterygoids are rather large and cover the dorsal portions of the entopterygoids (= ectopterygoid of Wenz, 1989a). The ectopterygoid bone is a very delicate structure and is not preserved in most specimens. Nevertheless, in a few specimens a splint like structure at the antero-dorsal part of the quadrate and in front of the entopterygoid may represent the ectopterygoid bone, similar to the condition seen in *Gyrodus*, *Macromesodon,* and *Neoproscinetes.* The placement of the pterygoid bones above each other has been proposed as a synapomorphy for pycnodont fishes (Lambers, 1991; Nursall, 1996b, 1999). The quadrate is rather large and situated ventrally to the entopterygoid.

Hyomandibular and symplectic

Anatomically, the hyomandibular and symplectic bones belong to the hyoid arch of the branchial skeleton. The hyomandibular bone is attached to the medial surface of the preoperculum. The head of the hyomandibular has no condylar process for articulation with the endocranium, but shows a structure characteristic of dermal bones at its upper part, so that in derived pycnodontiforms, the upper part of the preoperculum is reduced and the upper part of the hyomandibular is ornamented and exposed in the surface plane. This condition is also found in *Coelodus subdiscus* (Fig. 1, Pl. 2), where the hyomandibular is superficial and shows a similar reticulated ornamentation to that of the dermal skull bones. The development of a dermohyomandibular is a peculiar feature in the evolution of pycnodonts and is a synapomorphy for Pycnodontidae (Nursall, 1996b; 1999).

In pycnodontiforms, a small bone at the antero-ventral border of the preoperculum corresponds to the symplectic bone. The symplectic of *Coelodus subdiscus* is a massive and robust bone tightly articulated to the anteroventral extremity of the preoperculum (MNHN MSE 442; Fig. 3, Pl. 2). The lack of fusion between both bones is confirmed by MNHN MSE 965, where the symplectic is detached and missing, and the antero-ventral end of the preoperculum is a thin blade that exhibits a groove for the articulation with the symplectic.

Squamation

The scale covering of *Coelodus subdiscus* is notably reduced, corresponding to Nursall's (1996b) peltate pattern: scales only in the abdominal region, complete scales only in the ventral abdominal region. When scale rows are more or less accurately countable (e.g., MNHN MSE 965), there seems to be only about 11 of them, all placed between the head and the points of insertion of the dorsal and the anal fins. In dorso-ventral sense, each scale row is formed by: one series of dorsal ridge scales (see description later on); about five lines of scales that are reduced to the scale bar; a hiatus on the rib region, so that all scale rows are incomplete; one line of stout, high, not completely reduced scales; two lines of complete scales; and one series of ventral ridge scales (see description later on). Only the largest totally or partially complete scales show some ornamentation; in well-preserved specimens (MNHN MSE 442, 965; e.g., Fig. 4) there are sparse small grooves, and there is also an irregularly waved posterior border.

All observed specimens exhibit 12 dorsal ridge scales (Pl. 1, fig. 1). The anteriormost one is enlarged, and articulates tightly with the posterior border of the dermosupraoccipital. The dorsal ridge scales present up to four straight to slightly curved spines of increasing size in cephalocaudal sense, and posteriorly placed and oriented. The morphology and arrangement of the spines on the ventral ridge scales is similar, but there are never more than three of them in each scale. The ventral ridge scales (Fig. 4, Pl. 2) are accurately countable in very few specimens (e.g., MNHN MSE 965); there seem to be about 17 of these scales. Some 15 are placed between the cleithrum and the cloaca, and there are only 2 between the cloaca and the anal fin (Fig. 4).

The scales flanking the anus are differentiated in pycnodonts, forming a distinctive cloaca (Nursall, 1996b). This region is nicely preserved in specimen MNHN MSE 965 of *Coelodus subdiscus* (Fig. 4). The cloacal vestibule is relatively broad, but very low. It is dorsally limited by three differentiated scales, one anterior and two posterior to the anal notch. The anterior one is the largest of them, yet smaller than an average non-cloacal complete scale. The two posterior cloacal scales are arranged obliquely to the anterior one; the first posterior cloacal scale is more or less ovoid in shape and remarkably small. As in other pycnodontiforms, the modified cloacal scales lack their corresponding ventral ridge scales.

Axial skeleton

The only ossified elements of the vertebral centra in pycnodont fishes are the dorsal and ventral arcocentra; neither autocentra nor chordacentra have ever been found. In *Coelodus subdiscus*, there are 26-27 vertebrae, excluding those forming part of the caudal endoskeleton. The arcocentra are relatively small; each one is in small contact with its anterior and posterior neighbours. The dorsal and ventral arcocentra do not

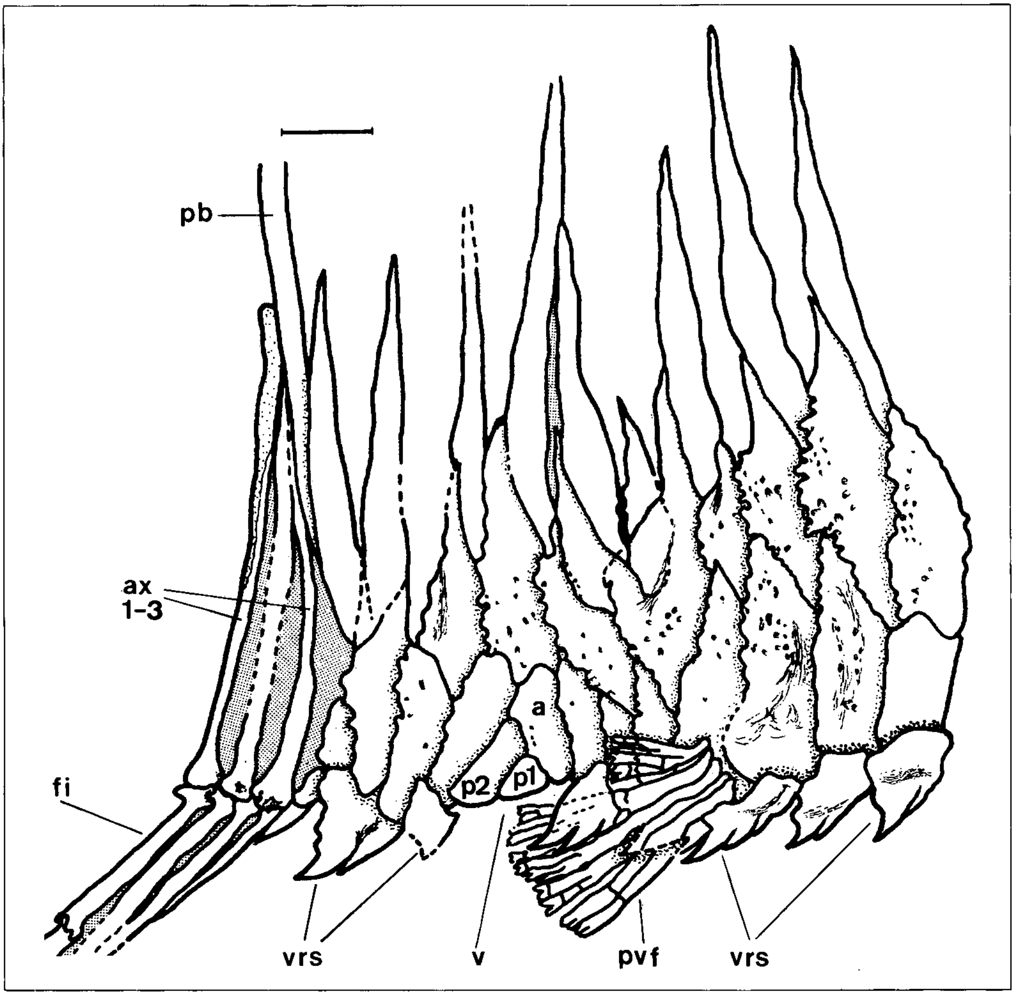

Fig. 4. *Coelodus subdiscus* Wenz, 1989. Camera lucida drawing of the cloacal region as preserved on specimen MNHN MSE 965. The ridge scales under the pelvic fin are visible by partial transparence and/or their relief. Scale bar equals 2 mm. Right side, lateral view.

Fig. 4. *Coelodus subdiscus* Wenz, 1989. Dibujo a cámara clara de la región cloacal como está preservada en el ejemplar MNHN MSE 965. Las escamas del borde ventral son visibles bajo la aleta pelviana por transparencia parcial y/o su relieve. La línea de escala equivale a 2 mm. Lado derecho, vista lateral.

entour the notochord at all, leaving a large, open notochordal canal. The neural and haemal spines are long and thin. Practically all spines bear anterior saggital flanges; when well preserved, these flanges show to be quite long, occupying about one half of the length of the corresponding spine, and also large, each one contacting with the anterior spine (Plate 1, fig. 4). The anteriormost neural spines of pycnodont fishes are separated from their corresponding arcocentra. In *Coelodus subdiscus*, there are 7 to 8 of them.

Sensory canals

The sensory canals of *Coelodus subdiscus* correspond to the pycnodont pattern (Nursall, 1999). There are two lateral lines on the body. The main lateral line runs from the skull to the caudal peduncle more or less parallel to the notochord, the dorsal lateral line is situated just below the dorsal ridge scales (Plate 1, fig. 1). Traces of the sensory canals of the skull are recognized only partly due to the massiveness and mode of preservation of the dermal bones. Traces of the dorsal limb of the supraorbital sensory canal are recognized in the frontals. The angle of the infraorbital canal between the supraorbital and temporal canals is situated in the large and rectangular bone in the postero-dorsal margin of the orbit, which is assumed to be a compound bone consisting of the dermosphenotic and dermopterotic. The infraorbital sensory canal is carried by the infraorbital ossicles to the snout. The ventral extension of the parietal bone carries the parietal branch of the sensory canals and is therefore recognized as the supratemporal fused with the parietal bone.

Caudal fin

The caudal fin of *Coelodus subdiscus* is slightly forked, with a central convexity. There is no distinctive caudal peduncle. The caudal fin forms together with the anal and dorsal fins an effective rudder. A schematic restoration of the caudal endoskeleton of *Coelodus subdiscus* is depicted on Fig. 5. In interpreting the systematic and phylogenetic relationships of actinopterygian fishes the caudal endoskeleton forms an important structural system (e.g., Nybelin, 1963; Arratia, 1991). Generally, the caudal endoskeleton can be divided into epi- and hypochordal elements. Nybelin (1963) distinguished preural and ural regions of the caudal skeleton in actinopterygian fishes. This scheme was accepted by most authors for the caudal skeleton of Recent halecomorphs (e.g., Schultze & Arratia, 1986; Grande & Bemis, 1998), and for Recent and fossil teleosts (e.g., Arratia, 1991; Arratia, 1997; Schultze & Arratia, 1989). Following these publications, the first preural centrum is by definition that vertebra bearing the last haemal arch that serves as the last passage of the caudal artery (Schultze & Arratia, 1986). This artery bifurcates behind this last haemal arch, which is called parhypural, into two arteriae pinnales. The bifurcation of the artery characterizes the boundary between preural and ural regions. Nevertheless, the caudal endoskeleton of pycnodontiforms seems to be much more simpler in structure compared to the one found in teleosteans (e.g., absence of epurals and uroneurals), and it also significantly differs from that of *Amia*, for instance. In most studied specimens of *Coelodus subdiscus* it is quite difficult to distinguish hypural bones sensu stricto from ray-bearing preural vertebral segments. But specimen MNHN MSE 965 shows some of the hypochordal elements in latero-dorsal view. One element (hypochordal element 2 in our restoration) exhibits an open canal and would therefore be a true haemal arch. The head of the following hypochordal element is completely convex, without traces of an open canal, but with a lateral groove, maybe for the already bifurcated caudal vein

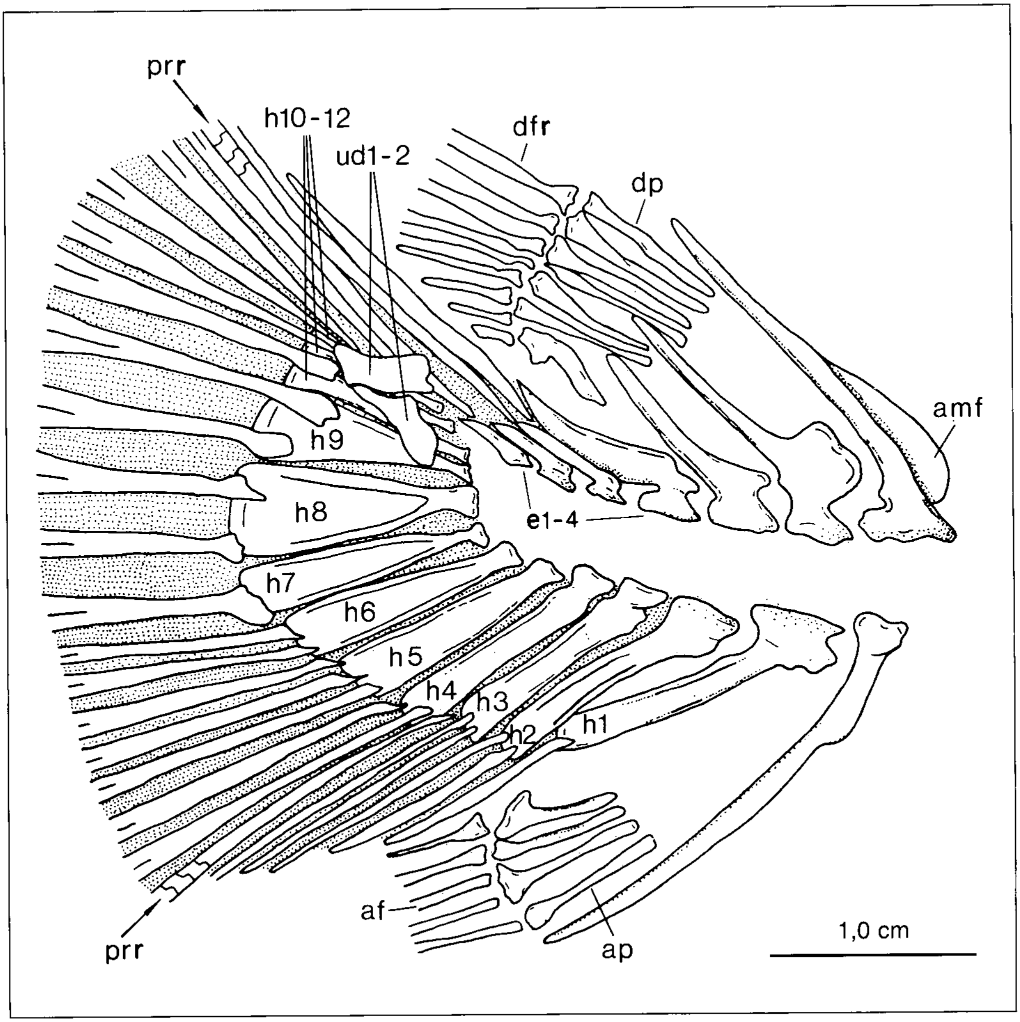

Fig. 5. *Coelodus subdiscus* Wenz, 1989. Restoration of the caudal skeleton based on specimens MGB 537-1, MGB 609a, MGB 29455a, and MNHN MSE 965. Arrows point to first and last principal caudal fin rays. Right side, lateral view.

Fig. 5. *Coelodus subdiscus* Wenz, 1989. Recostrucción del esqueleto caudal basada en los ejemplares MGB 537-1, MGB 609a, MGB 29455a y MNHN MSE 965. Las flechas indican los radios principales caudales primero y último. Lado derecho, vista lateral.

and would therefore correspond to the first hypural of Nybelin (1963). Nevertheless, we prefer to use the terms epichordal and hypochordal elements for the pycnodontiform caudal endoskeleton instead of the terms like hypurals, urals, and preurals, to avoid forced homologies with teleosts, since the phylogenetic relationships of pycnodontiforms are not clear at all, and homologies are still to be established.

Ossified vertebral centra are absent in the caudal endoskeleton of *Coelodus subdiscus*, like in all vertebra of every other known pycnodontiform. Only dorsal and ventral arcocentra are developed. There are 4 small epichordal elements. Specimen MNHN MSE 965 exhibits at least 12 hypochordal elements participating in the caudal endoskeleton. The first one is a normal haemal spine that supports the first ventral precurrent fin ray, and is completely separated from the second one. Hypochordal elements two to six are stout and tightly arranged; only the sixth is slightly enlarged. Only the first and second ones show a small anterior laminar expansion. Hypochordal elements number seven to nine articulate with their neighbours only distally; number eight is the most enlarged one of the whole series. The tenth element and the subsequent ones are again tightly arranged, and become progressively shorter and thinner. The presence of an eventual 13th hypochordal element requires confirmation. There is no diastema in the caudal endoskeleton of *Coelodus subdiscus*.

The caudal exoskeleton of *Coelodus subdiscus* consists of two dorsal precurrent rays, nine dorsal principal fin-rays, ten ventral principal rays, always one dorsal and ventral segmented and unbranched fin-ray, and about four or five simple ventral precurrent rays (Fig. 5). The ventral fin lobe has always more rays than the dorsal one. The segmentation of the principal rays is step-like. There are two large urodermals, lying over the proximal region of the last hypochordal elements (9th and on). Both form a long, tight, and sigmoid articulation with each other.

CONCLUSIONS

Wenz (1989a) based her study of *Coelodus subdiscus* on well-preserved specimens from the famous vertebrate localities of Montsec in Catalonia, northeastern Spain. She assigned this species to the family Pycnodontidae. Pycnodontidae *sensu* Wenz (1989a) is characterised by the presence of a fenestra in the lateral wall of the dermocranium, a derived character within pycnodont fishes. A dermic fenestra is also developed in *Tepexichthys* and *Pycnodus*. These three pycnodonts belong together with *Macromesodon*, *Proscinetes*, *Neoproscinetes*, *Anomoeodus*, *Stemmatodus*, and *Iemanja* to the family Pycnodontidae *sensu* Nursall (1996b). *Anomoeodus*, *Coelodus*, *Tepexichthys*, *Trewavasia*, and *Pycnodus* form a group within Pycnodontidae characterised *inter alia* by the presence of large, hook-shaped branchial teeth. Tooth-like structures on gill rakers of *Gyrodus hexagonus* have been figured by Lambers (1991). But as pointed out by him, these structures do not correspond to branchial teeth but are rather small denticles. Branchial teeth are also found in *Lepidotes* s. l. and amiid fishes (e.g., *Amia*). *Coelodus subdiscus* differs from other *Coelodus* species (e.g., *C. costae*, *C. grandis*, *C. jourdani*, *C. saturnus*) in the body outline, the number of fin rays in the unpaired fins, the number of neural and haemal spines and the number of the abdominal autogenous neural arches (Wenz, 1989a; pers. obs.). From other Early Cretaceous species that are based on isolated dentitions only (e.g., *C. hirudo*, *C. laevidens*, *C. mantelli*, and *C. multidens*), *C. subdiscus* is distinct in the morphology mainly of the prearticular teeth. In no other *Coelodus* species, teeth with two latero-medially arranged tubercles have been found so far. Therefore, the combination of characters mentioned in the diagnosis distinguishes *C. subdiscus* from all known *Coelodus* species.

The cranial and caudal anatomy corresponds well to that found in other pycnodontids. A striking feature of the skull of *Coelodus subdiscus* is the rather low number of dermal bones in the lateral wall of the skull roof. The posterior margin of the cranium is formed mostly by the parietal bone, with its parietal process projecting posteriorly. The main lateral line enters the skull through the ventral extension of the parietal bone. This extension also carries the supratemporal commissure, which is exceptional for the parietal bone in actinopterygians. Therefore, this part of the parietal bone is interpreted as a supratemporal bone fused to the parietal. This condition is found in other pycnodonts (e.g., *Pycnodus*). Amiid fishes and many teleosts have a single supratemporal on each side of the skull. Some teleosts have even lost the supratemporals. Many halecomorphs and *Pachycormus* also have a single pair of supratemporal bones. In contrast to that, gars, palaeoniscids, *Polypterus*, and many sarcopterygians have two or more supratemporals lying on each side of the skull. This condition was assumed to be plesiomorphic by Wiley (1976). How many supratemporals were present in *Coelodus* is not clear at present.

In *Coelodus subdiscus* the lateral line continues forward through a larger bone that forms most of the posterior border of the orbit (Fig. 2). This bone carries the junction of the infraorbital, supraorbital and temporal portions of the lateral line. The bone under question was described by Nursall (1999) and others (e.g., Wenz, 1989a) for pycnodont fishes as dermopterotic bone. But the post-orbital junction of the orbital and temporal portions of the neuromast system is located in the dermosphenotic in actinopterygians (Fig. 6 A-H). Because of this and because of its topographic position, this bone is interpreted at least in *Coelodus subdiscus* as a compound bone that is formed by the fusion of the dermosphenotic and at least parts of the dermopterotic. This condition is also found in the primitive semionotid *Acentrophorus* (Fig. 6, C). Fusion of several dermal skull elements to a compound bone is also found in other actinopterygian fishes, e.g., the frontals, parietals and dermopterotics are fused to a single complex in *Dapedium (*Wenz 1968b; Thies, 1988) (Fig. 6, D). In *Coelodus subdiscus*, the infraorbital canal is carried by the posterior infraorbital ossicle, a rather large and club shaped bone in the postero-ventral margin of the orbit, to the cheek and the ethmoidal commissure. This bone was interpreted so far as the dermosphenotic but is here reconsidered as the posterior infraorbital.

The cloaca and ridge scales of *Coelodus subdiscus* are described herein for the first time, allowing future comparison with other pycnodontiforms. The number, morphology, and arrangement of cloacal and ridge scales are very diverse within pycnodontiforms, and have a high interest for taxonomic and phylogenetic purposes (Nursall, 1996b; Poyato-Ariza & Wenz in press, work in progress).

Although it was possible to reconstruct the caudal endoskeleton of *Coelodus subdiscus*, the detailed structure and homologies of the caudal endoskeleton of pycnodontiforms are not clear at all. Problems are the distinction between haemal spines and hypurals, and consequently the homologization of the hypochordal elements and of the ural and preural ones with those of the teleosts and of halecomorphs, and also the interpretation of the lack of uroneurals and epurals. Nursall (1999) comes to the conclusion that the caudal skeleton of pycnodonts is a "parateleostean" development. In fact, the structure of the endoskeleton of pycnodontiforms is not contradictory to that of teleosts and of halecomorphs. But it is quite simpler than the teleostean caudal skeleton, and their possible homologies remain to be tested.

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Fig. 6 Patterns of cephalic sensory canals of the occipital region in some fossil and Recent fishes. **A**. *Polypterus bichir*. **B**. *Moythomasia durgaringa*. **C**. *Acentrophorus* sp. **D**. *Dapedium pholidotum*. **E**. *Amia calva*. **F**. *Lepisosteus oculatus*. **G**. *Pholidophorus bechei*. **H**. *Leptolepis coryphaenoides*. Not to scale. All left side, lateral view. Modified from Nybelin (1966), Lehman (1966a & b), Moy-Thomas & Miles (1971), Wiley (1976), Gardiner (1984), Thies (1988), and Grande & Bemis (1998).

Fig. 6 Patrones de los canales sensoriales cefálicos de la región occipital en algunos peces fósiles y actuales. **A**. *Polypterus bichir*. **B**. *Moythomasia durgaringa*. **C**. *Acentrophorus* sp. **D**. *Dapedium pholidotum*. **E**. *Amia calva*. **F**. *Lepisosteus oculatus*. **G**. *Pholidophorus bechei*. **H**. *Leptolepis coryphaenoides*. No están a escala. Todos lado izquierdo, vista lateral. Modificado de Nybelin (1966), Lehman (1966a & b), Moy-Thomas & Miles (1971), Wiley (1976), Gardiner (1984), Thies (1988) y Grande & Bemis (1998).

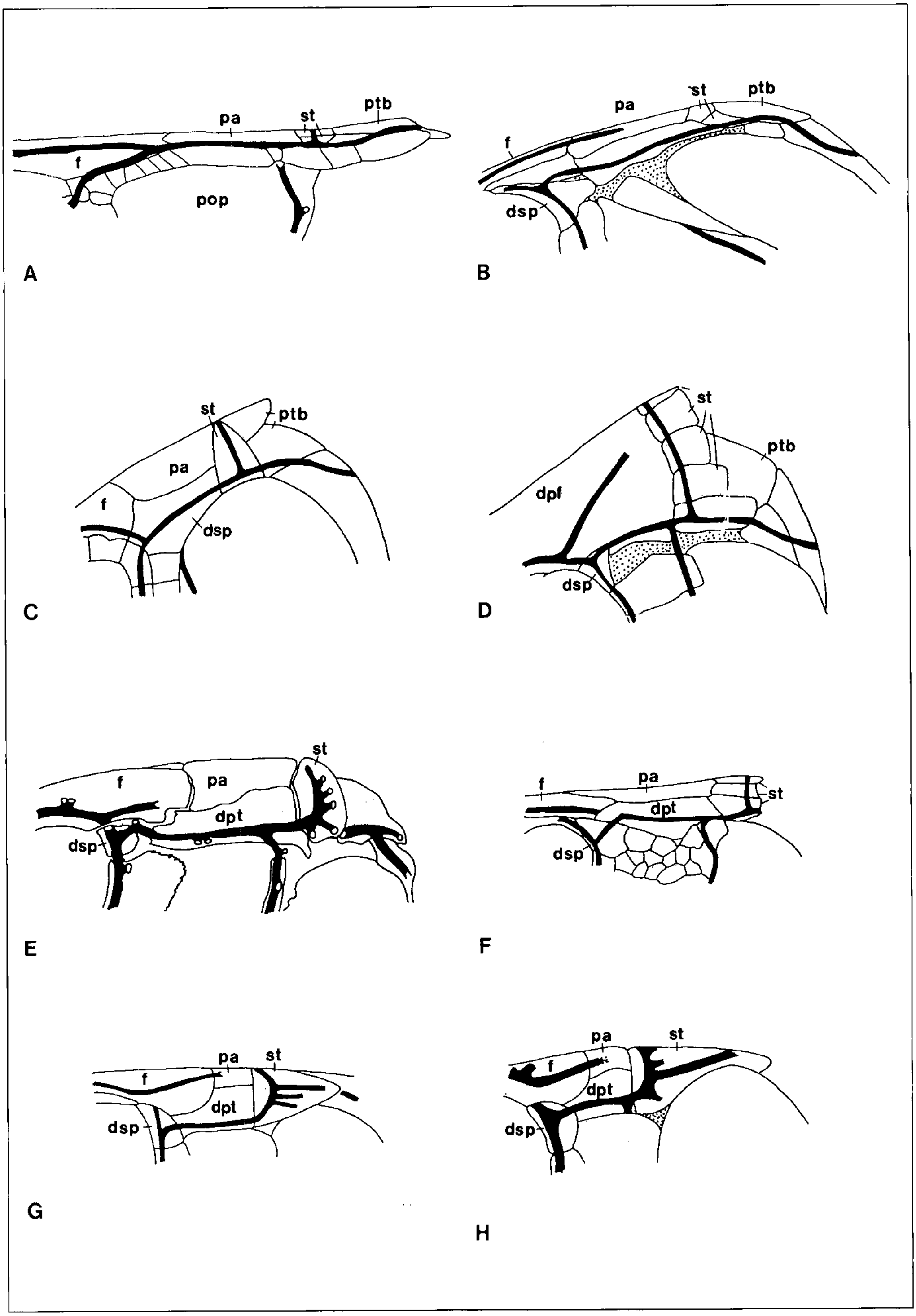
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Plate 1

Coelodus subdiscus Wenz, 1989. **1**. Specimen MGSB 20376a under ultraviolet light. Line bar equals 5 mm. Right side, lateral view. **2**. Detail of the prearticular and dentary of the same specimen under standard light. Line bar equals 1 mm. Left jaw, latero-occlusal view. **3**. Vomer of specimen MGSB 20659 (from Wenz, 1989a). Line bar equals 5 mm. Occlusal view. **4**. Holotype, MNHN MSE 341 (previously published only under ultraviolet light). Right side, lateral view. Photos Serrette (MNHN).

Lámina 1

Coelodus subdiscus Wenz, 1989. **1**. Ejemplar MGSB 20376a bajo luz ultravioleta. La línea de escala equivale a 5 mm. Lado derecho, vista lateral. **2**. Detalle del prearticular y el dentario del mismo ejemplar bajo luz estándar. La línea de escala equivale a 1 mm. Madíbula izquierda, vista latero-oclusal. **3**. Vómer del ejemplar MGSB 20659 (de Wenz, 1989a). La línea de escala equivale a 5 mm. Vista oclusal. **4**. Holotipo, MNHN MSE 341 (previamente publicado únicamente bajo luz ultravioleta). Lado derecho, vista lateral. Fotos Serrette (MNHN).

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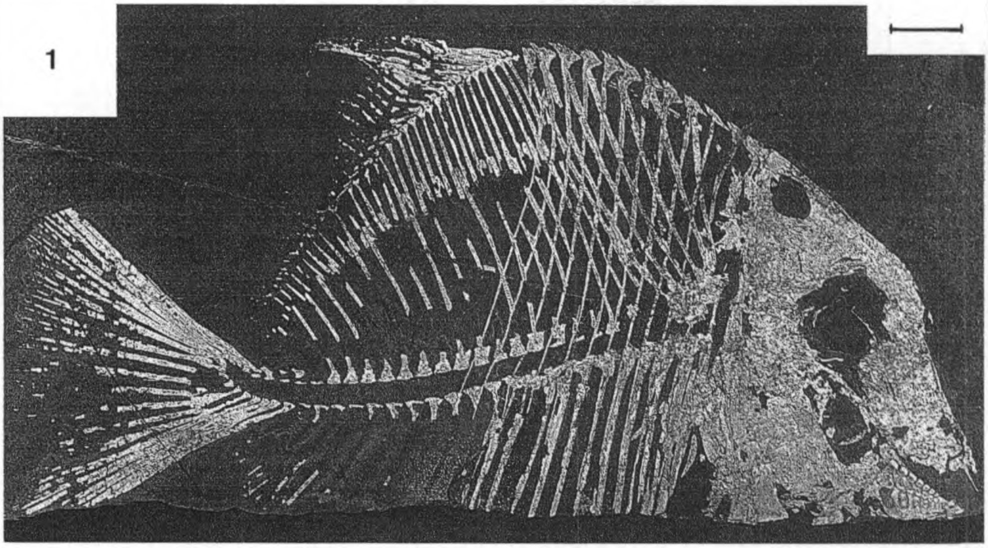

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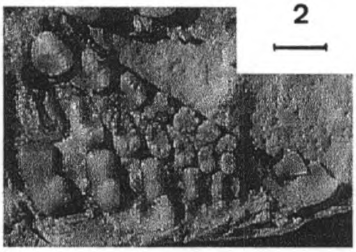

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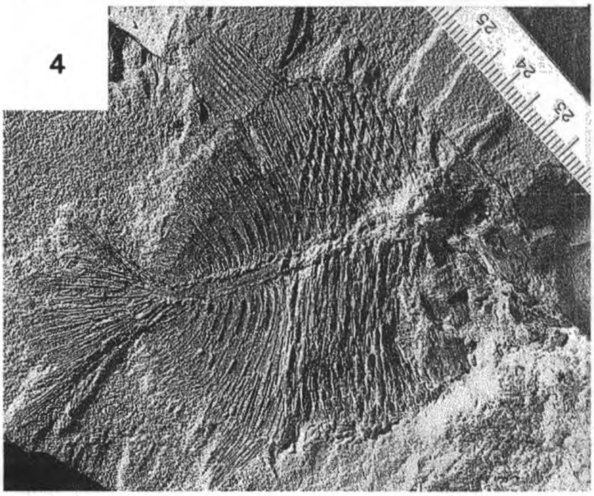

Plate 2

Coelodus subdiscus Wenz, 1989. Skull and anterior region of body of specimen MNHN MSE 341. Right side, lateral view. Photo Serrette (MNHN). From Wenz, 1989a. Line bars equals 5 mm.

Lámina 2

Coelodus subdiscus Wenz, 1989. Cráneo y región anterior del cuerpo del ejemplar MNHN MSE 341. Lado derecho, vista lateral. Foto Serrette (MNHN). De Wenz, 1989a. La línea de escala equivale a 5 mm.

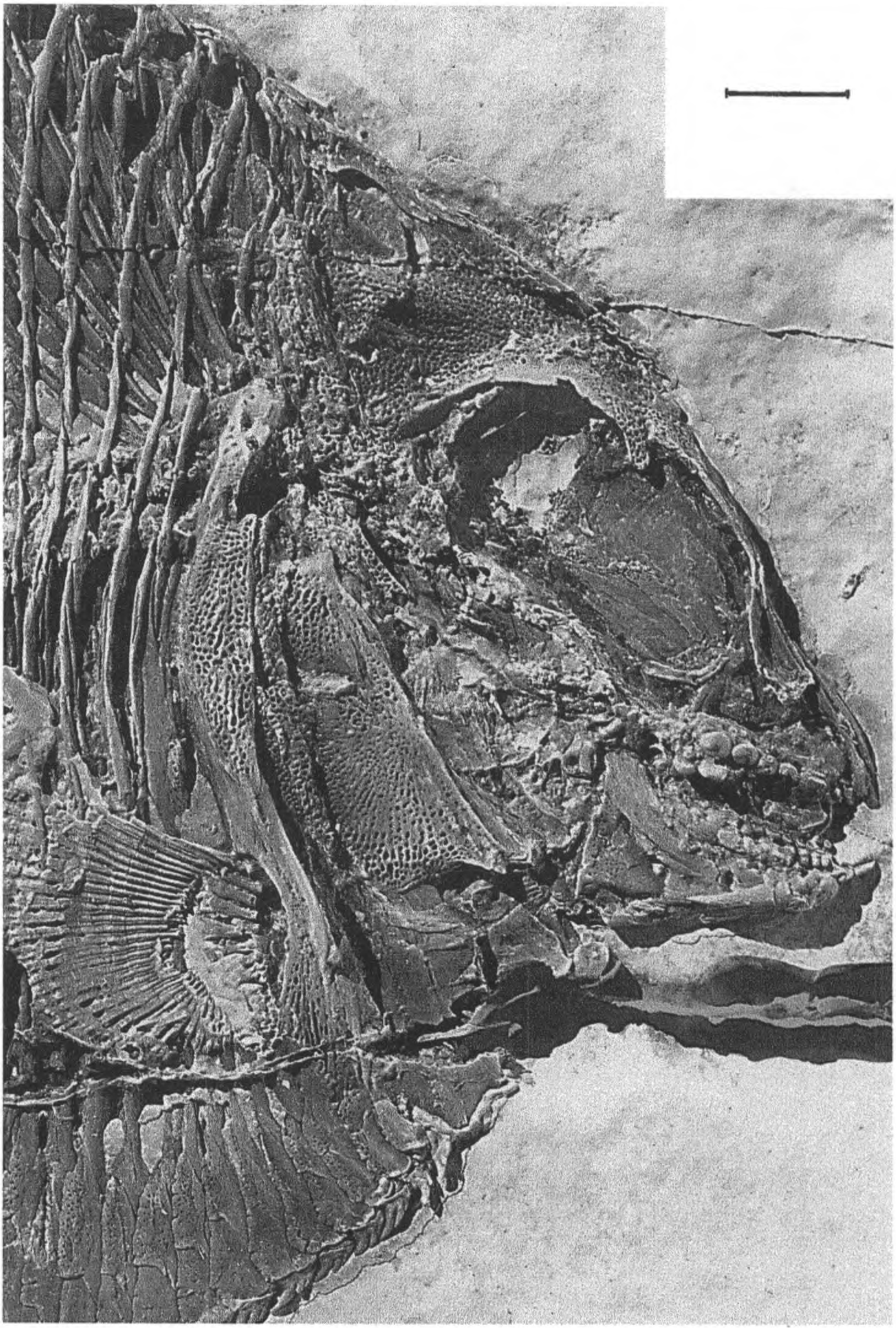

Plate 3

Coelodus subdiscus Wenz, 1989. Left prearticular dentition (SEM pictures) of specimen IPFUB (without number). **1**. Anterior portion, x 18. **2**. Posterior portion, x 18. **3**. Tooth of first lateral row, exhibiting the crenulated margin, x 58. **4**. Teeth of first and second lateral rows, x 28. **5**. Teeth of second lateral row, x 32.

Lámina 3

Coelodus subdiscus Wenz, 1989. Dentadura del prearticular izquierdo en vista oclusal (Fotos al miscroscopio electrónico de barrido) del ejemplar IPFUB (sin número). **1**. Parte anterior, x 18. **2**. Parte posterior, x 18. **3**. Diente de la primera fila lateral, mostrando el borde crenulado, x 58. **4**. Dientes de la primera y segunda filas laterales, x 28. **5**. Dientes de la segunda fila lateral, x 32.


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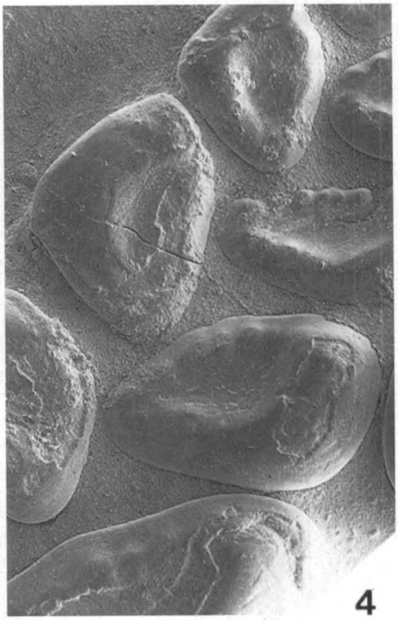
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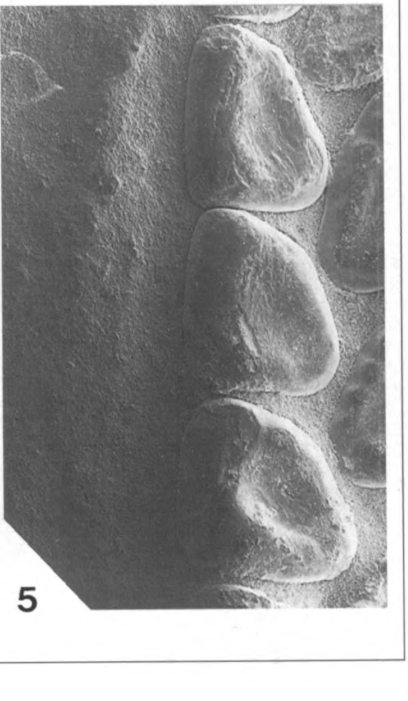
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