A new insight into pycnodontiform fishes

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ABSTRACT

The present paper provides a revision of the pycnodontiform fish genera that are based on articulated material. The results of the first cladistic analysis on the interrelationships of the order Pycnodontiformes Berg, 1937 are also presented: it is based on 105 characters for 33 taxa. The monophyly of the order, of the suborder Pycnodontoidei Nursall, 1996, and of the family Pycnodontidae Agassiz, 1833 *sensu* Nursall 1996b (in large sense) are confirmed; the "suborder Gyrodontoidei" appears, in contrast, as a paraphyletic group. The revision of the historic nomenclatural problems and the hypothesis of phylogenetic relationships show that the genera *Eomesodon* Woodward, 1918, *Coelodus* Heckel, 1854, and *Palaeobalistum* Blainville, 1818, as previously recognized, were not natural assemblages. The new genera *Apomesodon* n. gen., *Ocloedus* n. gen., *Oropycnodus* n. gen., and *Abdobalistum* n. gen., together with two new species (*Apomesodon surgens* n. gen., n. sp. and *Abdobalistum thyrsus* n. gen., n. sp.), are erected to locate former species of those non-monophyletic genera. The subfamilies Proscinetinae n. rank, Pycnodontinae n. rank, and Nursalliinae n. rank, are also proposed, together with the superfamily Pycnodontoidea n. rank, which gathers the sister-groups Coccodontidae and Pycnodontidae. A completely revised systematic palaeontology of the Pycnodontiformes is provided.

KEY WORDS
Actinopterygii,
Pycnodontiformes,
revision,
cladistics,
phylogeny,
new genera,
new species.

RÉSUMÉ

Un nouveau regard sur les poissons pycnodontiformes.

Ce travail présente une révision des poissons pycnodontiformes, fondée sur des spécimens en connexion sans tenir compte des dentures ou des dents isolées. Il a pour but d'établir les relations phylogénétiques au sein du groupe des Pycnodontiformes Berg, 1937 à l'aide d'une analyse cladistique prenant en compte 33 taxons et 105 caractères. La monophylie de l'ordre, du sous-ordre Pycnodontoidei Nursall, 1996 et de la famille Pycnodontidae Agassiz, 1833 *sensu* Nursall 1996b (au sens large) a été confirmée, ce qui n'est pas le cas du « sous-ordre Gyrodontoidei ». Les sous-familles Proscinetinae n. rank, Pycnodontinae n. rank et Nursalliinae n. rank ont été proposées ainsi que que la super-famille Pycnodontoidea n. rank, qui réunit les groupes-frères Coccodontidae et Pycnodontidae. Quatre genres (*Apomesodon* n. gen., *Ocloedus* n. gen., *Oropycnodus* n. gen. et *Abdobalistum* n. gen.) et deux espèces (*Apomesodon surgens* n. gen., n. sp. et *Abdobalistum thyrsus* n. gen., n. sp.) ont été créés pour les taxons exclus des genres *Eomesodon* Woodward, 1918, *Coelodus* Heckel, 1854 et *Palaeobalistum* Blainville, 1818, qui apparaissent comme non-monophylétiques. Ce travail s'achève par une mise à jour de la systématique paléontologique des Pycnodontiformes à la lumière des données nouvelles présentées ici.

INTRODUCTION

One of the most characteristic and popular fossils of many preservational Lagerstätten are the pycnodontiform fishes. They have been found in Triassic to Eocene strata all over the world. In general lines, a pycnodontiform is easily recognizable by its laterally compressed body, resulting in a more or less rounded outline, and by its well developed durophagous dentition, so that these fishes have always called the attention of both amateurs and professional palaeontologists. Pycnodontiforms have been known for a long time. The oldest plate that we have seen is Knorr (1768: pls 1755), containing a long philosophical dissertation on the nature of this "petrified animal". The first descriptions with scientific characters on what would later be pycnodont fishes are about two centuries old (e.g., Volta 1809, usually cited as 1796, but a note on the last page of the book explains that it was not published until 1809, which should be the valid date). Pycnodonts are a relevant part of many key classic palaeoichthyological works, such as

Blainville (1818), Agassiz (1833-43), Pictet (1854), Heckel (1856), Wagner (1862), Woodward (1895a), and Hennig (1906).

The order Pycnodontiformes was erected by Berg in 1937 (p. 1278) by giving the name only. Later on, a small diagnosis and a familiar arrangement are given by the same author in 1940 (p. 208-210, 413, 414 in the English translation of 1947). A most exhaustive account, with all genera known at the time, including their geographic and temporal distribution, was presented by Lehman (1966: 170-181). Some papers have extensively dealt with certain pyncodontiforms in the last decades (e.g., Blot 1987; Lambers 1991), but the first recent look at the ensemble of these fishes was not given until Nursall (1996a on their palaeoecology and distribution, 1996b on a detailed phylogenetic hypothesis, 1999a on the Mesturidae, 1999b on the pycnodontiform bauplan).

The aims of the present paper are to update their nomenclatural problems, and to accomplish the first cladistic analysis on the interrelatiohships of the order Pycnodontiformes. The phylogenetic

hypothesis by Nursall (1996b) is based in a discussion of the distribution of his proposed characters, rather than on a cladistic analysis *sensu stricto*. As acknowledged by this author, his hypothesized relationships "should provide directions for further analysis" (Nursall 1999b: 149). Facing works on certain pycnodontiforms from Spain and the Lebanon, both new and revised forms (Kriwet *et al.* 1999; Poyato-Ariza & Wenz 1995, 2000, work in progress), we found that they do not fit neatly into Nursall's phylogenetic hypothesis. This is due not only to the relatively high number of his *incertae sedis* forms, but also to incongruences in the distribution and in the polarity of the characters used by him when applied to the forms involved in our studies. We therefore realized that we needed to perform a cladistic analysis if we wanted to present coherent phylogenetic hypotheses for the taxa that we are describing and revising. Both the cladistic analysis and its taxonomic implications, including a new arrangement of the Pycnodontiformes, with several new taxa, are presented herein.

INSTITUTIONAL ABBREVIATIONS

ADR	private collection of Mr. Armando Díaz-Romeral, Cuenca;
BMM	Burgmeister Müller Museum, Solnhofen;
DGM-DNPM	Divisão de Geologia e Mineralogia, Departamento Nacional da produção Mineral, Rio de Janeiro;
FSL	Faculté des Sciences de Lyon;
IEI	Institut d'Estudis Ilerdencs, Lleida;
IGM	Instituto de geología, Universidad Nacional Autónoma de México (Departamento de Paleontología), México D. F.;
JM	Jura Museum, Eichstätt;
IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels;
MB	Museum Bergér, Harthof;
MCCM	Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain. Provisionally housed at the UAM for study;
MCSNB	Museo Civico di Scienze Naturale "E. Caffi" di Bergamo;
MCSNM	Museo Civico di Storia Naturale di Milano;
MCSNV	Museo Civico di Storia Naturale di Verona;
MGB	Museu de Geologia de Barcelona;
MGSB	Museu Geològic del Seminari Conciliar de Barcelona;
ML	Muséum d'Histoire naturelle, Lyon;
MNHN	Muséum national d'Histoire naturelle, Paris; HDJ, HAK, MSE, SLN, BCE, CRN, CNJ: abbreviations of localities in this collection.
MNHUB	Museum für Naturkunde, der Humboldt Universität, Berlin;
NHML	Natural History Museum, London;
NMW	Naturhistorisches Museum in Wien;
UAM	Universidad Autónoma de Madrid.

METHODS

Our characters are based, on the first place, on those presented by Nursall (1996b, re-taken in 1999b). We have not used those characters regarding the phylogenetic relationships of the Pycnodontiformes with other high taxa (1996b: characters 72-93), because the present paper does not address this issue. Regarding Nursall's sets of characters, many of them actually turn out to be different states of a same given character. For example, characters 25 ("The prehensile teeth are styliform"; Nursall 1996b: 133) and 40 ("Incisiform prehensile teeth"; Nursall 1996b: 135) are actually different states of a single character on the morphology of the prehensile teeth. We therefore gathered all the different states into discrete characters. Some of the characters, notably those concerning the contour scales and the cloaca, were substantially developed into additional characters, and we added some characters of our own as well. The result is the character data set discussed below and listed on Appendix 1. The correspondence of our characters with those of Nursall (1996b) is noted in the section below for each case wherever pertinent.

The characters were polarised by using the compound outgroup methodology by Maddison *et al.* (1984). The outgroup was formed by *Pteronisculus* (Nielsen 1942; Lehman 1952); *Semionotus* (Olsen & McCune 1991); *Dapedium* (Wenz 1968; Thies 1988; Thies & Herzog 1999); *Amia* (Allis 1897, 1898; Grande 1996; Grande & Bemis 1998), with unsolved relationships among them as shown on Fig. 1. In a few
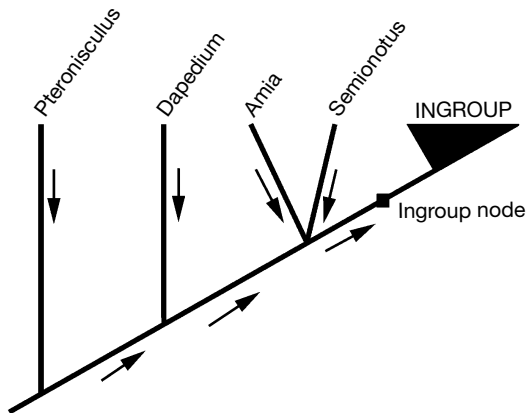
Fig. 1. — Tree showing the compound outgroup structure, with unsolved position for *Amia* Linné, 1766 and *Semionotus* Agassiz, 1832. Following Maddison *et al.* (1984), characters were polarised by assessing the states from terminal branches to the ingroup node, as indicated by the arrows.

cases only, the polarization resulted in an uncertainty. For those cases we used Arnold's (1981) method of considering the predominant state within the outgroup as the primitive state; this was applied to our characters 60, 68, and 72. Yet, characters 73 and 81 were unpolarizable, so that the outgroup state was coded as ? and all ingroup states were treated as unordered.

The data matrix was written in the MacClade program, version 3.0.4, and run using the PAUP program, version 3.1.1, in an IMac 8 computer at the Unidad de Paleontología, UAM. We used both the ACCTRAN and the DELTRAN options, with, as expected, some differences in the interpretation of the distribution of certain characters, as commented whenever appropriate. Characters 1, 5, 21, 22, 24, 25, 28, 34, 42, 52, 53, 58, 59, 60, 66, 71, 74, 75, 76, 88, 89, 94, 95, 96, and 101 were processed as ordered, and the rest, as unordered. We do believe that ordering characters has a biological meaning whenever the primitive state is the first (or the last) of a continuously increasing (or decreasing) series.

Whenever possible we have considered the ontogeny of the characters, always coding the state of each character from adult specimens; comments on their occasional ontogenetic variation are made when relevant for understanding the character. The intervals considered for meristic and continuous characters are problematic in general, as they usually involve subjective considerations. We tried to be as objective as possible, considering these characters with consistent criteria. The intervals for each state are chosen after gathering and comparing all observations. The intervals then established are those found to be most discriminating (most common figures) and less confusing (fewer taxa in between, and including most individual variations).

The material studied is listed below; it includes the pycnodontiform genera that are known from at least partially complete articulated remains. The purpose of this paper is to establish the phylogenetic relationships of confidently classified forms as a basis for further studies, and therefore doubtful forms are not included in the analysis, in order to avoid distortion in the data and in the subsequent results. We have considered only more or less complete, articulated specimens, and not isolated dentitions, to avoid problems of parataxonomy. Many pycnodontiform genera are monospecific. When this is not the case, we have included the type species and have considered other distinct, well established, confidently assessed species when they all provide information that is consistent in the character codification for the genus as a whole. The few cases where this information is not consistent are discussed in detail in the text. Some articulated forms that are not included in the analysis are nonetheless also listed here, with the corresponding explanation. Isolated dentitions are cited only when they regard the holotype of a type species.

Following Nursall (1996b), and the general use, we eventually use the term "pycnodont" for pycnodontiform.

The original drawings for the line figures were made by using a camera lucida attached to binocular microscopes at the JM, MNSNB, MCSNV, MNHN, NHML, NMW, and UAM. All drawings, informatic treatment, and legends of the illustrations were prepared by FJPA.

COMMENTED LIST OF PYCNO-DONTIFORM GENERA AND MATERIAL

The present list includes, in alphabetical order, the pycnodontiform genera that are known from articulated remains, exceptionally mentioning isolated dentitions only when pertinent. To avoid subsequent confusions, we include in the list the new taxa that are erected in the present paper for some species formerly assigned to *Coelodus*, *Eomesodon*, and *Palaeobalistum*. Some historic nomenclatural problems are addressed. The mode of designation is indicated especially to clarify the nomenclatural problems addressed by the present paper. Whenever necessary, we refer to the involved articles of the ICZN (*International Code of Zoological Nomenclature*, Fourth Edition 1999).

Each genus includes the list of observed material: one asterisk (*) indicates acid-treated specimen; two asterisks (**), transferred specimen. The list of institutional abbreviations is given after the Introduction.

The list of the genera depicted in the figures of the present paper is given in Appendix 2. To facilitate comparisons of species previously referred to different genera, Fig. 2 shows the holotype of *Coelodus saturnus*, type species of the genus (Fig. 2A), and one topotype specimen of *Ocloedus subdiscus* n. comb., formerly considered *Coelodus* (Fig. 2B). The part and the counterpart of a historic specimen of *Apomesodon surgens* n. gen., n. sp., together with *A. gibbosus* n. comb., and *Stenamara*, both previously referred to *Eomesodon*, are shown in Fig. 3. Finally, the holotype of *Palaeobalistum orbiculatum*, together with examples of *Abdobalistum* n. gen. and *Oropycnodus* n. gen., previously referred to *Palaeobalistum*, are shown in Fig. 4.

Genus *Abdobalistum* n. gen.

TYPE SPECIES. — By original designation: *Abdobalistum thyrsus* n. gen., n. sp. Early to middle Eocene from Monte Bolca, Italy. Only known species. Holotype by monotypy: NHML P 9830 (Fig. 4C, D).

MATERIAL EXAMINED. — Holotype of *Abdobalistum thyrsus* n. gen, n. sp. (complete, moderately well preserved). Only known specimen. This is the specimen
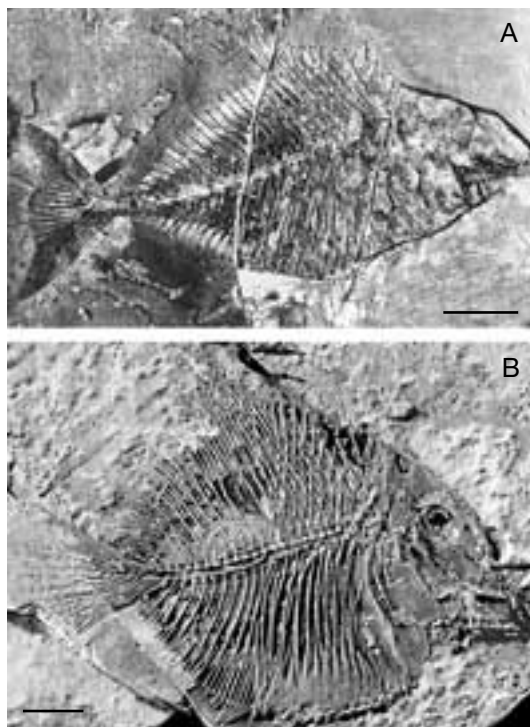

FIG. 2. — Forms previously referred to the genus *Coelodus* Heckel, 1854; **A**, *C. saturnus* Heckel, 1854, type species, holotype, NMW.XXXIII.2. Photo Schumacher, courtesy Ortwin Schultz; **B**, *Ocloedus subdiscus* n. comb., topotype MNHN MSE 965. Photo Serrette. Scale bars: A, 5 cm; B, 1 cm.

figured by Heckel (1856: pl. X) in his redescription of *Palaeobalistum orbiculatum* Blainville, 1818. It was erroneously designed by Blot (1987: 88-91) as the "type = lectotype" of "*Palaeobalistum orbiculatum*" (see under *Palaeobalistum* below).

Genus *Anomoeodus* Forir, 1887

TYPE SPECIES. — By monotypy: *Pycnodus subclavatus* Agassiz, 1833. Maastrichtian from the Netherlands (Agassiz 1833-1843: vol. II, pt. 1 p. 17, pt. 2 p. 198, pl. 72a, fig. 59). Holotype of *Anomoeodus subclavatus*: MNHN 1884-247-F (fragment of dentition, currently deteriorated).

OTHER SPECIES. — *A. angustus* (Agassiz, 1837), Cenomanian from Sussex, United Kingdom; *A. willetti* Woodward, 1893, same age and locality; *A. nursalli* Kriwet, 1999, Barremian from Uña, Cuenca, Spain; plus numerous nominal species based on isolated dentitions. See historic revision of this genus in Kriwet (1999).

MATERIAL EXAMINED. — *Anomoeodus angustus*: NHML 25780 (fragment of abdominal region and both prearticulars, well preserved). The holotype is specimen NHML P1616 (Agassiz 1833-1843: vol. II, pt. 2, p. 235, 246, pl. 66a, figs 14, 15), which was not included in the analysis because it is an isolated prearticular.

Genus *Apomesodon* n. gen.

TYPE SPECIES. — By original designation: *Mesodon gibbosus* Wagner, 1851. Early Tithonian of the "Solnhofener Plattenkalke", Bavaria, Germany. This species is explicitly referred by Wagner (1851: 52) as the *Gyrodus gibbosus* in Agassiz (1843: 236, name only, without description or illustration, therefore not available). Holotype of *Apomesodon gibbosus* n. comb. by monotypy: specimen figured by Wagner (1851: pl. 3, fig. 2) as *Mesodon gibbosus*. It is currently housed at the Bayerischen Staatssammlung für Paläontologie und Historische Geologie, München, Germany, specimen AS VII 346.

OTHER SPECIES. — ? *Apomesodon comosus* (Thiollière, 1858) n. comb. Kimmeridgian from Cerin, France; poorly preserved form previously described as a *Macromesodon* by Saint-Seine (1949). Specific name created by Thiollière (1858: 783) as "*Mesodon comosus* inédit". It certainly does not belong to *Macromesodon* because of its loricate scale pattern, so it is provisionally referred to *Apomesodon* n. gen. herein. *Apomesodon surgens* n. gen, n. sp., Kimmeridgian from Cerin, France; initially mentioned as "*Mesodon gibbosus*" by Thiollière (1858: 119), revisited and figured later under the same species name by Thiollière (1871: 33; 1873: 13, pl. 2, fig. 2) and Saint-Seine (1949: 105, 129-132, 313, figs 56-58, pl. 14, fig. A).

MATERIAL EXAMINED. — *Apomesodon gibbosus* n. comb.: FSL 93095, JM 4120 (Fig. 3C) / SOS 3570 (part and counterpart of the same complete specimen, with different labels); BMM, one complete, unlabelled specimen. *Apomesodon surgens* n. gen., n. sp. Holotype: ML 15443 (specimen figured by Thiollière in 1858). Other specimens: ML 15660, MNHN CRN-69 (counterpart of ML 15660, as shown by Fig. 3A, B; complete, well preserved skeleton).

Genus *Arduafrons* Frickhinger, 1991

TYPE SPECIES. — By monotypy: *Arduafrons prominoris* Frickhinger, 1991. Lower Tithonian from the "Solnhofener Plattenkalke" of Bavaria, Germany. See Nursall (1999a) for a description of this genus and species. Holotype of *Arduafrons prominoris* by subsequent designation: BMM 33a-b.

MATERIAL EXAMINED. — Holotype (complete specimen). Other specimens: MB (unlabelled); NHML

P8658 (both complete specimens). The incomplete specimen JM SOS 3309a-b is labelled as *Arduafrons*, but we interpret it as *Mesturus* due to the jagged suture of its scales, unique to this genus (Nursall 1999a).

Genus *Brembodus* Tintori, 1981

TYPE SPECIES. — By original designation: *Brembodus ridens* Tintori, 1981. Upper Norian from the Zorzino Limestone, Lombardy, Italy. Only known species. Holotype of *Brembodus ridens* by original designation: MSCNB 4898.

MATERIAL EXAMINED. — Holotype (complete, well preserved). Paratypes: MCSNB 4894 (prearticulars and dentaries in occlusal view); 4895 (some bones and fin rays, some vomerine teeth); 4896 (complete, subadult, mediocre preservation); 4897 (almost complete, bad preservation); 4899 (skull plus anterior region of body, good preservation); 4900 (almost complete, mediocre preservation); 4902 (fragment of skull with dentition); 4932 (right prearticular in occlusal view); and 4933 (complete, good preservation). Other specimens: 4859 (incomplete, juvenile); 4891 (fragment, subadult); 4892 (two specimens, both fragments of skull showing the vomer); 5157 (posterior region, bad preservation); and 6086 (almost complete, juvenile).

Genus *Camposichthys* Figueiredo & Silva-Santos, 1991

TYPE SPECIES. — By original designation: *Camposichthys riachuelensis* Figueiredo & Silva-Santos, 1991. Early Cretaceous from the Riachuelo Formation, Sergipe-Alagoas, Brazil. Only known species. Holotype of *Camposichthys riachuelensis*: Instituto de Biología da Universidade do Estado do Rio de Janeiro, Brazil (Figueiredo & Silva-Santos 1991: 370, pl. 1; single, quite incomplete, imperfect specimen). We did not include it in the analysis because this taxon is in need of revision, and we could not retrieve from the literature the necessary information for the analysis.

Genus *Coccodus* Pictet, 1850

TYPE SPECIES. — By monotypy: *Coccodus armatus* Pictet, 1850. Cenomanian from Hakel, Lebanon. Holotype of *Coccodus armatus* by monotypy: specimen described and figured by Pictet (1850: 51, pl. 9, fig. 9; head and fragment of body, showing prearticular bone, not vomer as described by Pictet 1850). Currently housed at the Muséum de Genève. According to Meister (1993), the holotype figured by Pictet has the catalogue number V-674, while its unfigured counterpart has V-733.
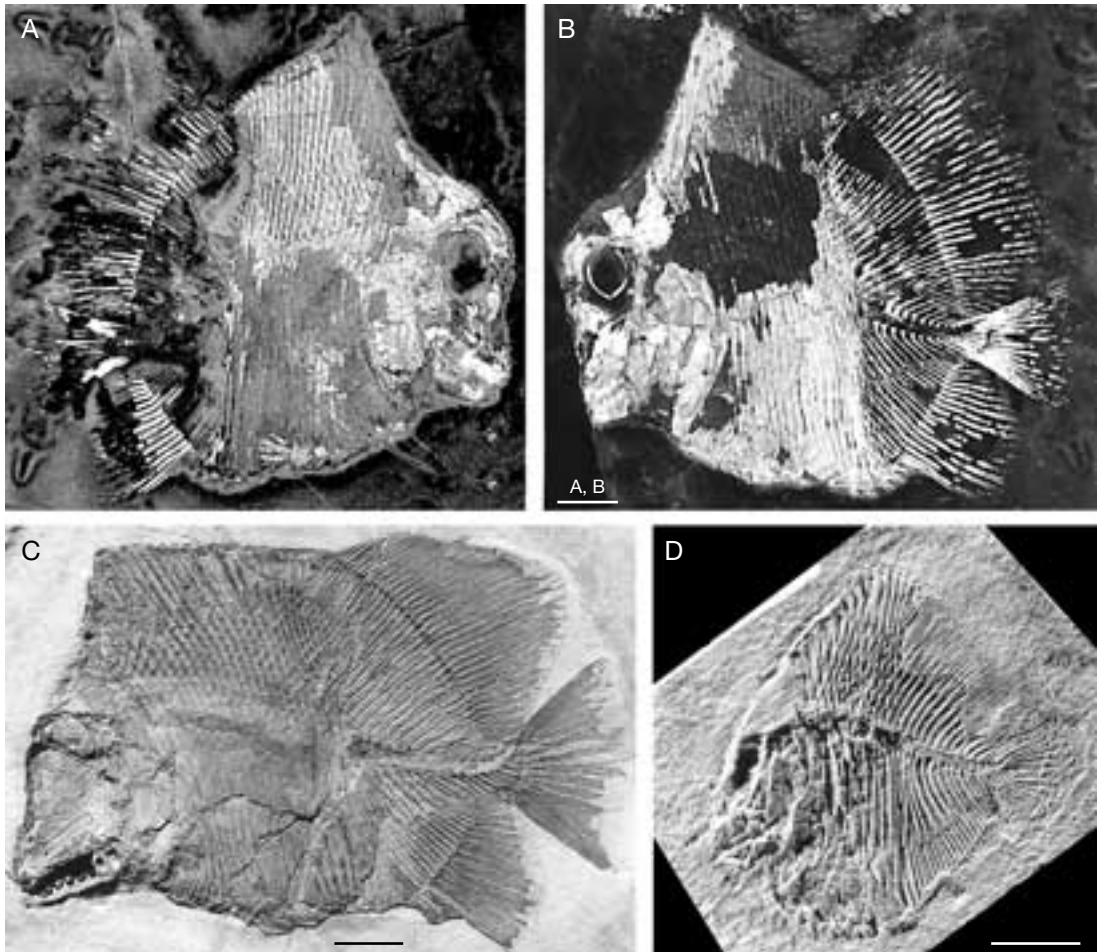
Fig. 3. — Forms previously referred to the genus *Eomesodon* Woodward, 1918; **A**, **B**, *Apomesodon surgens* n. gen., n. sp. Part and counterpart of the same specimen, currently housed in different collections; **A**, MNHN CRN 69; **B**, ML 15660. Photos Serrette, both under ultraviolet light; **C**, *Apomesodon gibbosus* n. comb., JM 4120. Photo courtesy G. Viohl; **D**, *Stenamara mia* Poyato-Ariza & Wenz, 2000, silicone cast of the holotype, LH – 14365. Photo Serrette, from Poyato-Ariza & Wenz (2000). Scale bars: A, B, D, 1 cm; C, 5 cm.

INVALID SPECIES. — "*Coccodus*" *lindstroemi* Davis, 1890, Cenomanian from Hakel, Lebanon. Holotype: State Museum, Stockholm, *in* Davis (1890: 565, pl. 22; nearly complete specimen). This enigmatic form is certainly not a *Coccodus*. We have not observed any pycnodontiform synapomorphy in this species. For example, the opercular region does not seem reduced, and the observed teeth are not typically durophagous. Therefore, *lindstroemi* is a valid specific name, but "*Coccodus*" *lindstroemi* is not a valid species. It is not considered as a pycnodontiform, remains in need of revision, and is consequently not included in the analysis.

OBSERVED MATERIAL. — *Coccodus armatus*: MNHN HDJ-534a-b (almost complete, dorsal view), 539** (almost complete; lateral view), 540 (almost complete, lateral view), 542 (almost complete, head in ventral view), 543a-b (complete, ventral view), 1299** (dentition and part of the skull, lateral view), 1300 (complete), 1301a (complete); HAK-319** (complete specimen, dorsal view, only skull remains after transfer preparation), 1935 (skull fragment in lateral view). NHML: 4742 (almost complete, lateral view, figured by Davis 1887), 13868, 13869 (spine), 47912 (very incomplete, with part of the mandible), 47913; "*C.*" *lindstroemi*: HAK-1936a-b (complete, well preserved).

Genus *Coelodus* Heckel, 1854

TYPE SPECIES. — By original designation: *Coelodus saturnus* Heckel, 1854. Turonian-Santonian (Ortwin pers. comm. 1999) from Komen, formerly Comeno, Slovenia. Holotype of *Coelodus saturnus*: NMW 1857.XXXIII.2 (Fig. 2A). The valid date for the generic name *Coelodus* is not 1856, since Heckel first mentioned it in 1854 (p. 435, with a diagnosis given on p. 449). In 1854, the species *C. saturnus* is explicitly designed as "als Typus". Both the genus *Coelodus* and the species *C. saturnus* are revisited by Heckel in 1856, where the holotype is figured for the first time (Heckel 1856: pl. 3, fig. 1; this plate caption reads "*Pycnodus Saturnus*", but this is surely a printing error, as in all parts of the text and in the original label of the specimen the name is "*Coelodus Saturnus*"). Again, *C. saturnus* is desiged as "als Typus" (Heckel 1856: 203). The holotype is shown in the present paper on Fig. 2A. Some isolated dentitions have also been referred to this species (Schultz & Paunoviæ 1997; Cavin *et al.* 2000).

NOMINA DUBIA. — *C. rosthorni* Heckel, 1854, Late Cretaceous from Komen, Slovenia; *C. suillus* Heckel, 1854, Late Cretaceous from the Island of Lesina, Dalmatia, Kroatia. They are named and described in 1854, figured by the same author later on, in 1856. Both species are based on fragmentary material, apparently indistinguishable from *C. saturnus*, and are probably conspecific with the type species.

INVALID NAMES. — "*Coelodus*" bassanii, for comments see ? *Proscinetes bassanii*. "*Coelodus*" ponsorti, for comments see *Oropycnodus* n. gen.

OTHER SPECIES. — For other species based on complete specimens formerly referred to this genus, see *Ocloedus* n. gen. There are numerous nominal species of *Coelodus* based on isolated dentitions from France, Istria, Dalmatia, Italy, Spain, United Kingdom, and South America. They are in need of revision, as probably many of them will eventually fit better in *Ocloedus* n. gen. (see diagnosis in the Systematics section below).

MATERIAL EXAMINED. — Holotype (articulated specimen; nearly complete fish, not well preserved; skull especially defective but showing an excellent prearticular dentition; good caudal endoskeleton). NHML P.5947 (juvenile specimen, imperfect preservation, previously referred to *C. suillus*).

Genus *Eomesodon* Woodward, 1918

TYPE SPECIES. — By original designation (Woodward 1918: 54): *Pycnodus liassicus* Egerton, 1855. Lower Lias from Barrow-on-Soar, Leicestershire, United Kingdom. Holotype of *Eomesodon liassicus*: NHML 19864.

OTHER SPECIES. — ? *Eomesodon barnesi* (Woodward, 1906), Portlandian (Portland Stone, Roach Bed) from Portland, Dorset, United Kingdom, and Middle Purbeck Beds from the Isle of Portland, Swanage, Dorset, United Kingdom. *E. depressus* ? Woodward, 1918. Upper Portlandian-lower Berriasian from Swanage, Dorset, United Kingdom; too incomplete to be sure it is a distinct species, therefore not included in the data matrix. *E. hoeferi* (Gorjanovic-Kramberger, 1905). As illustrated in its original description (Gorjanovic-Kramberger 1905: pl. 20, fig. 5; pl. 21, fig. 2) it looks like a juvenile form because of its very small size (holotype of about 23 mm in standard length), the apparently weak ossification, and the unbranched aspect of many fin rays (the few branched ones show one branching only). Unfortunately, the holotype seems to be currently missing, although additional specimens have been very recently found (Tintori pers. comm. 2000, work in progress). This species is therefore in need of revision.

MATERIAL EXAMINED. — *E. liassicus*: holotype (poorly preserved, incomplete specimen). Other specimens: NHML P 1336, P 5127. ? *E. barnesi*: holotype: NHML P.12511 (poorly preserved, incomplete specimen). Other specimens: NHML 6382: *E. depressus* ?: NMHL 10582 (very incomplete and poorly preserved individual).

Genus *Gibbodon* Tintori, 1981

TYPE SPECIES. — By original designation: *Gibbodon cenensis* Tintori, 1981. Upper Norian from the Zorzino Limestone, Lombardy, Italy. Holotype of *Gibbodon cenensis*: MCSNB 3317.

MATERIAL EXAMINED. — Holotype and only known specimen (complete, good preservation).

Genus *Gyrodus* Agassiz, 1833

TYPE SPECIES. — By subsequent designation: *Stromateus hexagonus* Blainville, 1818. Lower Tithonian from the "Solnhofener Plattenkalke" Bavaria, Germany. Holotype of *Gyrodus hexagonus* by monotypy: specimen described and figured by Knorr (1755: vol. I, pl. 22, fig. 1), which Blainville (1818: 322) explicitly referred to when creating his new species *Stromateus hexagonus*. This specimen is not any of those figured by Agassiz (1833: vol. II, pt. 1: 16; pt. 2: 184, 206, pl. 69c, figs 4, 5) or any of the four "type specimens" proposed by Lambers (1991). However, we could not find the type specimen in any of the studied collections.

OTHER SPECIES. — *G. circularis* Agassiz, 1843, early Tithonian from the "Solnhofener Plattenkalke" Bavaria, Germany; *Gyrodus* sp., Kimmeridgian from Cerin, France; the "*Mesturus verrucosus*" in Saint-Seine (1949) is actually *Gyrodus* sp. (Lambers 1991; pers.
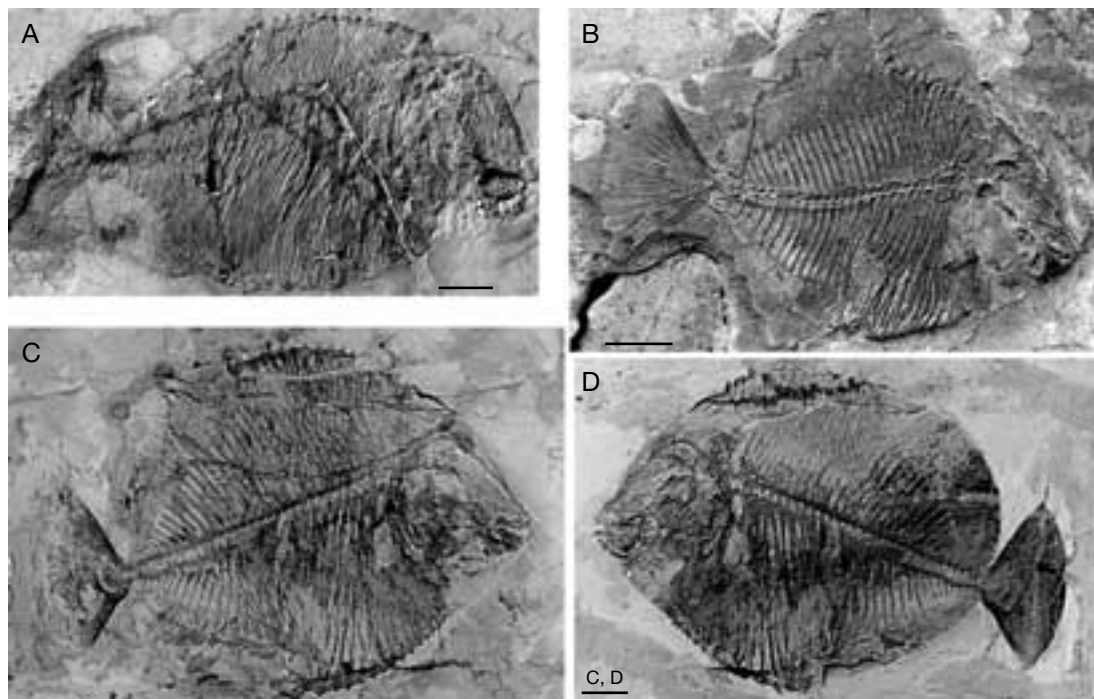
FIG. 4. — Forms previously referred to the genus *Palaeobalistum* Blainville, 1818; **A**, *P. orbiculatum* Blainville, 1818, type species, holotype, MNHN BOL 0523. Photo Serrette; **B**, *Oropycnodus ponsorti* n. comb., lectotype, NMW.1854.XXXIX.38. Photo Schumacher, courtesy Ortwin Schultz; **C, D**, *Abdobalistum thyrsus* n. gen., n. sp., part and counterpart of the holotype, NMHL P.9830a-b. Photos courtesy P. Forey. Scale bars: A, 5 cm; B-D, 2 cm.

obs.). *Gyrodus* sp., almost complete head with partially exposed vomerine and prearticular dentitions, Oxfordian from Quebrada del Profeta, Chile (Kriwet 2000). Plus numerous nominal species, in need of revision, based on isolated dentitions (e.g., Woodward 1895a). See Lambers (1991) for a revision of this genus. For "*Gyrodus*" *wagneri*, see *Proscinetes*? *wagneri*.

MATERIAL EXAMINED. — *G. hexagonus*: BMM 31, 32, 36; JM 3710, SOS 4303 (counterpart of 3710); NHML 1625**, 3772, 3773, 3774, 4633**, 37711; MNHN SLN 5a-b, 22 (juvenile specimen), 49, 206, 208, plus unlabelled cast, probably from the type of *G*. "*frontatus*".

Genus *Hadrodus* Leidy, 1858

TYPE SPECIES. — By subsequent designation: *Hadrodus priscus* Leidy, 1858. Cretaceous from Colombus, Mississippi, USA. "The genus and species are founded upon the fragment of a bone with two teeth, apparently a Pycnodont fish allied to *Placodus*" (Leidy 1858: 167). Holotype of *Hadrodus priscus*: isolated premaxilla figured in Leidy (1873: pl. 19, figs 17-20).

OTHER SPECIES. — *H. marshi* Gregory, 1950, based on premaxilla, prearticular, and fragments of skull roof, lower Senonian from the Niobrara Chalk, Smoky Hill River, Kansas, USA; *H. hewletti* (Applegate, 1970), Mooreville Chalk (Campanian) in Greene County, Alabama. Bell (1986) gathered in a single pycnodontiform taxon the dentitions named *Hadrodus* and the cranial roof named *Hadrodus hewletti* and described by Applegate (1970), who considered it as an acipenseriform. This material also includes some lepidotrichia, dorsal scutes, and vertebrae with arcocentra and apparently also autocentra. This fact, and the great resemblance of the skull roof and the dorsal scutes of *Hadrodus hewletti* with those of the Acipenseridae (e.g., compare Applegate 1970: figs 181, 184E with Hilton & Bemis 1999: figs 5, 6) indicate that these remains do not belong to a pycnodontiform (already suggested by Lambers 1991: 509). This genus is in need of revision, and is not included in the analysis.

Genus *Ichthyoceros* Gayet, 1984

TYPE SPECIES. — By original designation: *Ichthyoceros spinosus* Gayet, 1984. Cenomanian from Hakel,

OTHER SPECIES. — *M. gaynaisensis* Nursall, 1999, Turonian from the Eagle Ford Formation, Ellis County, Texas, USA. Holotype: United States National Museum, Washington D.C., USA.

Genus *Neoproscinetes*
Figueiredo & Silva Santos, 1987

TYPE SPECIES. — By monotypy: *Microdon penalvai* (Silva Santos, 1970). Aptian-Albian from the Romualdo Member, Santana Formation, Chapada do Araripe, Brazil. Only known species. Holotype of *Neoproscinetes penalvai*: DGN-DNPM 918 P.

MATERIAL EXAMINED. — Holotype (complete specimen). Other specimens: MNHN BCE-104* (three-dimensional isolated skull with detached prearticular), BCE 169 (complete specimen), BCE-237 (three-dimensional isolated skull).

Genus *Nursallia* Blot, 1987

TYPE SPECIES. — By original designation: *Nursallia veronae* Blot, 1987. Early to middle Eocene from Monte Bolca, Italy. Holotype of *Nursallia veronae*: MCSNV II. D. 172-173.

OTHER SPECIES. — *Nursallia flavellatum* ? (Cope, 1886), Continguiba Formation, upper Cretaceous from Sergipe / Alagoas, Brazil. One single specimen, very incomplete and not observed; it is nonetheless briefly discussed in the Results section below. *Nursallia* ? *goedeli* (Heckel, 1854), Cenomanian from Hakel, Lebanon. The species *Palaeobalistum goedeli* was erected by Heckel (1854: name p. 445, diagnosis p. 461) under the original spelling *goedelii*. It was later revisited and illustrated for the first time by Heckel (1856: 234; pl. II, figs 3-8; it is the specimen NMW 1858.III.21). Davis (1887) described three other specimens, two of them as the new nominal species *Palaeobalistum ventralis*. Woodward (1895a) considered that: "The form of the median fins and the extension of the squamation over the caudal region may even be regarded as necessitating the removal of the fish from the genus *Palaeobalistum*" (Woodward 1895a: 273), and that *P. ventralis* Davis, 1887 is a junior synonym of *P. goedeli* (Woodward 1895a: 274-275). The same author used the subsequent spelling *goedeli* (Woodward 1895a: 272). Since this incorrect subsequent spelling is in prevailing usage (Art. 33.3.1 of the ICZN), it is maintained herein. Hennig (1907) regarded *goedeli* and *ventralis* as two valid species of *Palaeobalistum*. Arambourg (1954) compared them with his new species *P. gutturosum*. Finally, Blot (1987) transferred both nominal species to his new genus *Nursallia*. Both specimens of *N. ventralis* ?, when compared with the holotype of *N.* ? *goedeli* have apparently more discoidal shape; long, low, falcate

dorsal and anal fins (incomplete in *N.* ? *goedeli*); large pectoral fin (unknown in *N.* ? *goedeli*); bar-reduced (not complete) scales partially covering the caudal region (complete scales in *N.* ? *goedeli*); incisiform teeth on the dentary (unknown in *N. goedeli*); similar caudal fin with enlarged to hypertrophied hypurals. The differences on body shape and in squamation indicate that *N.* ? *goedeli* and *N. ventralis* ? may not be conspecific. Pending revision of these and quite a few other Lebanese specimens previously assessed to *Palaeobalistum* and *Nursallia*, we have included in our analysis only the information provided by the holotype of *Nursallia* ? *goedeli*. *Nursallia* ? *gutturosum* (Arambourg, 1954), lower Cenomanian from Jebel Tselfat (localities of Aïn el Kerma and Sigda), Morocco.

MATERIAL EXAMINED. — *N. veronae*: holotype (complete adult specimen with unsatisfactory preservation); MCSNV T.830 (complete, very juvenile, well preserved specimen); *N.* ? *goedeli*: holotype, NMW 1858.III.21 (caudal region of a well preserved adult specimen). Other specimens: NHML: P.4001/ P.4781; P.61/P.62 (*Palaeobalistum goedeli* in Davis 1887); P.63; P.63a; P.4002 (Davis's 1887 unfigured specimen); 39231; 39232; P.65 (*Palaeobalistum ventralis* in Davis 1887). *N.* ? *gutturosum*: holotype, MNHN DTS 60a-b (complete specimen from Aïn el Kerma), paratypes DTS-61a-b (from Aïn el Kerma) and 231a-b (from Sigda). Other specimens: 63a-b, 94a-b (juvenile specimen), 231a-b, 232a-b, 233a-b, 235a-b, 236a-b, 237, 239, 241a-b, 313a-b, 314 (Sigda), DTS-57, 62a-b, 64a-b, 65, 66, 67, 68, 69, 170a-b, 229a-b, 234a-b, 311a-b, 312a-b (Aïn el Kerma). All complete or nearly complete specimens with unsatisfactory preservation.

Genus *Ocloedus* n. gen.

TYPE SPECIES. — By original designation: *Coelodus subdiscus* Wenz, 1989 (Fig. 2B). Berriasian-Valanginian from El Montsec, province of Lérida, Spain. Holotype of *Coelodus subdiscus*: MNHN MSE-341.

OTHER SPECIES. — *O. costae* (Heckel, 1856) n. comb., Late Jurassic from Torre d'Orlando, Italy; ? *Ocloedus rosadoi* (Silva Santos, 1963) n. comb., Late Cretaceous from Rio Grande do Norte, Brazil. Specific names originally assigned to *Coelodus*, and provisionally reassessed to *Ocloedus* n. gen. herein; species in need of revision. Many of the nominal species based on isolated dentitions previously referred to *Coelodus* (e.g., Woodward 1895a), may eventually prove to fit better here after revision.

MATERIAL EXAMINED. — *O. subdiscus* n. comb. Holotype: MNHN MSE-341 (complete, well preserved). Paratypes: MNHN MSE-442* (nearly complete

specimen), MGSB 20659* (skull). Other specimens: IEI LP-084a-b (skull and part of the body); MNHN-MSE-290a-b (skull and body), 291a-b (skull and dorsal part of the body, eroded), 292 (early juvenile specimen), 300a-b (specimen lacking unpaired fins), 302a-b (specimen lacking snout and caudal fin), 303a-b, 439a-b (isolated skull), 652a-b (incomplete specimen), 653a-b (incomplete specimen), 656, 965* (complete specimen; Fig. 2B); MGB 536, 537-1, 29455a-b, 30345, 30377; MGSB 8997 (complete specimen), 13.376a-b (skull and part of the body), 20.658 (complete skeleton), 27.298, 27.299 (only impression of skull), 56.216 (parts of skull and body); NHML 10996a-b, 10997, 10999 (used by Nursall 1999b, fig 2 to restore *Coelodus* sp.), 37497, 37500-1. *O. costae* n. comb.: NHML 1641, 1671a**, P.4394.

Genus *Oropycnodus* n. gen.

TYPE SPECIES. — By monotypy: *Palaeobalistum ponsortii* Heckel, 1854. Paleocene (Montian) from Mont Aimé, Chalons-sur-Marne, France. Lectotype of *Oropycnodus ponsorti* n. comb.: NMW 1854/XXXIX/38 (Fig. 4B). The original syntypes were NMW 1854/XXXIX/38 (Fig. 4B), 1854/XXXIX/39, and 1854/XXXIX/40. The first and the third were figured by Heckel (1856: pl. 11); the second one was studied, but not figured, by Heckel (1856). In the present paper, since we are creating a new genus for the specific name *ponsorti* (see Results and Systematics sections below), the former syntype 1854/XXXIX/38 (Fig. 4B) is herein explicitly designed as the lectotype, in accordance with the Article 74 of the ICZN. Therefore, the other syntypes, 1854/XXXIX/39 and 1854/XXXIX/40, become herein the paralectotypes (Art. 74.1.3). This specific name was created by Heckel (1854: 436), with a formal diagnosis (Heckel 1854: 461, 462), being assessed to the genus *Palaeobalistum*. It was later revisited and this time figured by the same author in 1856 (pl. 11, figs 1-15). The original spelling *ponsortii* was emended to *ponsorti* by Woodward (1895a: 272). We keep this subsequent incorrect spelling because it is in prevailing usage (Art. 33.3.1 of the ICZN). Later on, Woodward (1917) considered that *ponsorti* "is probably a species of *Pycnodus*" (Woodward 1917: 387). Finally, the specific name was transferred to the genus *Coelodus* by Blot (1987: 146, 147), and cited as such by Nursall (1999b: 195).

MATERIAL EXAMINED. — The lectotype and both paralectotypes. Other specimens: MNHN MTA 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 15, 16, 17, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49; NHML 30035, 30036*, 30037 (figured as 28292 by Woodward 1917: 387), 30038, 30039, 30040, 30042, 30043, 30044, 30045, 30046, 30047, P1638.

Genus *Palaeobalistum* Blainville, 1818

TYPE SPECIES. — By monotypy: *Palaeobalistum orbiculatum* Blainville, 1818 (Fig. 4A). Early to middle Eocene from Monte Bolca, Italy. Holotype of *Palaeobalistum orbiculatum*: MNHN BOL 0523. The name *Palaeobalistum orbiculatum* is based on the specimen MNHN BOL 0523, illustrated by Volta (1809 [1796]: pl. 40), who mentioned it as the Recent species *Diodon orbicularis* Bloch, 1785. This nominal taxon is available under Art. 12.2.7 of the ICZN and the specimen in MNHN is therefore the holotype by monotypy (Art. 73.1.2). Heckel (1856) redescribed *Palaeobalistum orbiculatum* based on a second specimen (NHML P9830), which is neither conspecific, nor even congeneric (see under *Abdobalistum* n. gen. above, and the Results section below). In his revision of *Palaeobalistum*, Blot (1987: 88-90) erred in considering that both the genus *Palaeobalistum* and the species *P. orbiculatum* were "*nomina nuda*", and instead considered that Heckel (1856) was the author of *Palaeobalistum orbiculatum*, typified by NHML P.9830. Furthermore, Blot (1987) established the nominal species *Palaeobalistum zignoi* typified by MNHN BOL 0523, i.e. a junior objective synonym of *Palaeobalistum orbiculatum*. The specific name *zignoi* is therefore an invalid name, and *Palaeobalistum* is a monotypic genus.

INVALID NAMES. — "*Palaeobalistum*" *bassanii* (D'Erasmo, 1914), for comments see ? *Proscinetes bassanii*. "*Palaeobalistum*" *flavellatum* (Cope, 1886), see *Nursallia flavellatum* ? above. "*Palaeobalistum*" *gutturosum* (Arambourg, 1954), also cited under this species name by Lehman (1966: fig. 166), see *Nursallia* ? *gutturosum* above. "*Palaeobalistum*" *ponsorti*, see under *Oropycnodus* n. gen. "*Palaeobalistum zignoi*" Blot, 1987, see under *Abdobalistum* n. gen.

MATERIAL EXAMINED. — MNHN BOL 0523 (holotype and only specimen; complete individual with skull badly preserved; Fig. 4A).

Genus *Paramesturus* Taverne, 1981

TYPE SPECIES. — By original designation: *Paramesturus stuehmeri* Taverne, 1981. Lower Aptian from Helgoland, Germany. Holotype of *Paramesturus stuehmeri*: Stühmer private collection, Helgoland n° 13 (skull plus anterior portion of body).

Genus *Proscinetes* Gistl, 1848

TYPE SPECIES. — By monotypy: *Microdon elegans* Agassiz, 1833 (Fig. 5A). Lower Tithonian from the "Solnhofener Plattenkalke" Bavaria, Germany. Holotype of *Proscinetes elegans*: Bayerischen Staatssamlung für Paleontologie und Historische
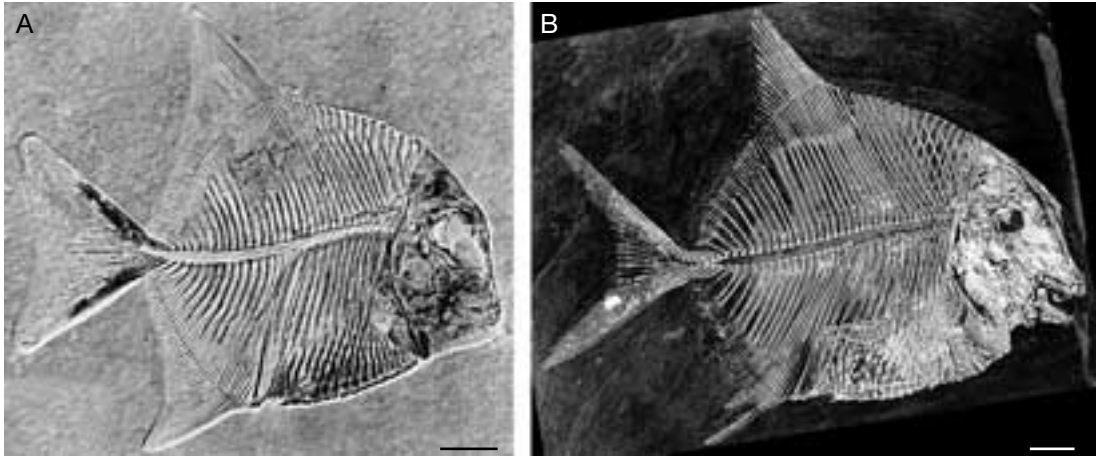
FIG. 5. — Two species of the genus *Proscinetes* Gistl, 1848; **A**, *P. elegans* (Agassiz, 1833), type species, specimen JM 1941.12.a. Photo courtesy G. Viohl; **B**, *P. bernardi* Thiollière, 1852, specimen ML 15288. Notice the stomach content, previously reported in this specimen by Nursall (1996a: 121) as "finely comminuted shell" in "*Microdon bernardi*"; it represents the first illustration of direct evidence of the diet in pycnodontiform fishes. Photo Serrette, under ultraviolet light. Scale bars: 1 cm.

Geologie, München, Germany after Woodward (1895a: 222). First mention by Agassiz in 1833 (vol. II, pt. 1, p. 16), later illustration by the same author in 1839 (pl. 69b, fig. 1).

OTHER SPECIES. — ? *Proscinetes bassanii* (D'Erasmo, 1914). This specific name is removed from both *Coelodus* and *Palaeobalistum* to this genus in the present paper. As explained at the end of the Results section below, it does not seem to show the characters of either genus. This assessment is to be taken with caution, this species being in need of revision. *P. bernardi* (Thiollière, 1852; figured in 1854; Fig. 5B), Kimmeridgian from Cerin, France; *P. egertoni* (Thiollière, 1852) (plate published in 1854), Kimmeridgian from Cerin, France; ? *P. itieri* (Thiollière, 1850), Kimmeridgian from Cerin, France; *P.* ? *radiatus* (Agassiz, 1839), late Portlandian to early Berriasian from Swanage, Dorsetshire, United Kingdom; *P. sauvanasi* ? (Thiollière, 1852), Kimmeridgian from Cerin, France; *P. thiollieri* ? (Saint-Seine, 1949), Kimmeridgian from Cerin, France; *P.* ? *wagneri* (Thiollière, 1852; plate published separately in 1853), Kimmeridgian from Cerin, France; plus numerous nominal species, in need of revision, based on isolated dentitions (e.g., Woodward 1895a; Saint-Seine 1949). *Proscinetes bernardi* and *P. egertoni* are herein regarded as valid species, as they present the same anatomic characters as *Proscinetes elegans*, with consistent differences on the meristic accounts. *Proscinetes itieri* may be a valid species, but the body shape is so different that it probably does not belong to the genus. The holotype of *P.* ? *radiatus*, as figured by Agassiz (1839: pl. 69c, figs 1, 2), shows

large spines on the ventral keel scales, with relative size and arrangement very different from those of *P. elegans*; therefore, it may not belong to *Proscinetes*. The species *P. thiollieri* ? is based on a poorly preserved specimen, and its validity remains to be tested. Same applies to the species *P. sauvanasi* ?. *Proscinetes* ? *wagneri* has traditionally been considered a species of *Proscinetes* (formerly *Microdon*; e.g., Woodward 1895a). Saint-Seine (1949) reassessed it to the genus *Gyrodus*, but we agree with Lambers (1991) that it does not belong to it. The general anatomic features of this species are in fact quite similar to those of the available species of *Proscinetes*. However, the occurrence of scale bars behind the level of the dorsal and anal fins indicates that *wagneri* may not belong to this genus. Therefore, considering the amount of issues to be solved at specific level in *Proscinetes*, for the codification of this genus in our analysis we have only used the type species plus *P. bernardi* and *P. egertoni*. We coded the anatomical characters as consistently present in the three species, and the meristic characters as present in the type species.

MATERIAL EXAMINED. — *Proscinetes elegans*: JM 1941.12 (Fig. 5A); MNHN SLN 205 (cast); *P. bernardi*: neotype, ML 15.199; other specimens, ML 15.194, 15.288 (Fig. 5B), 15916 (ex 15194 bis); *P. egertoni*: holotype, ML 15.275; other specimens, ML 15273, 15.390; "*P.*" *itieri*: holotype 15268, specimen 15267; *P.* "*thiollieri*": type and only specimen; "*P*". *wagneri* ML 15207, 15214, 15317; MNHN, CRN-31, 56; NHML P. 1636, P. 4649. *Proscinetes* sp.: FSL 400047 (nearly complete, partially disarticulated specimen showing dentition).

Genus *Pycnodus* Agassiz, 1833

TYPE SPECIES. — By subsequent designation (Blot 1987: 14): *Coryphaena apoda* Volta, 1809. As explained in the general introduction, the correct date of publication of the paper usually cited as Volta (1796) is 1809. Early to middle Eocene from Monte Bolca, Italy. Only syntype currently available of *Pycnodus apodus*: MNHN BOL 0094. This specimen was described and figured as the valid new species *Coryphaena apoda* by Volta (1809: 147, 148, pl. 35, figs 1-3; on this plate, fig. 1 is syntype MNHN BOL 0094; fig. 2 is another syntype, of unknown current location; fig. 3 is not a pycnodontiform). Volta (1809) erected this specific name because the pelvic fins were apparently absent in those specimens (Volta 1809: 148). Blainville (1818: 356) described it, without illustration but with explicit reference to Volta's specimens, as an invalid new species of the genus *Zeus*, *Z. platessus*. Later on, Agassiz (1833), on the basis of the two specimens figured by Volta (1809: pl. 35, figs 1, 2; explicitly cited by Agassiz 1833: vol. II, pt. 1: 17), erected the genus *Pycnodus*. Later on, two additional specimens were figured by Agassiz (1839). However, Agassiz (1833, 1839) used the specific name *platessus*, which is a junior objective synonyme of *apoda*. The invalid specific name *platessus* has been broadly used since, but it is not a *nomen oblitum* because Eastman (1905: 10) used the valid specific name *apodus* (in grammatical accordance with *Pycnodus*) with explicit reference to Volta (1809: pl. 35, fig. 1 only). For further synonymies, see Blot (1987: 14).

NOMEN DUBIUM. — "*Pycnodus laveirensis*" da Veiga Ferreira, 1961, Turonian from Alcântara and Laveiras, Portugal. This is a small, juvenile-like species. Both the validity of the specific name and its assessment to *Pycnodus* remain to be revised and tested.

OTHER SPECIES. — Numerous nominal species based on isolated dentitions, mostly from the Eocene (e.g., Longbottom 1984).

MATERIAL EXAMINED. — Syntype: MNHN BOL 0094-0095 (part and counterpart of a complete, well preserved individual). Other specimens: MNHN BOL 0124-0125, BOL 0126-0127, BOL 0130-0131, BOL 0134-0135 (all parts and counterparts of the same individuals); MCSNV B1 (fragment), II.D.167/168 (part and counterpart of subadult, complete specimen); II.D.170/171 (part and counterpart of large, complete specimen); II.D.180 (complete, subadult); T.309 (complete, juvenile); T.998/999 (part and conuterpart of juvenile specimen); I.G.135608/135609 (part and counterpart, almost complete, subadult); and I.G.135664 (almost complete, juvenile); NHLM P.44520** (complete subadult specimen, excellent preservation).

Genus *Stemmatodus* Heckel, 1854

TYPE SPECIES. — By original designation: *Pycnodus rhombus* Agassiz, 1839. Early Cretaceous from Torre d'Orlando, Naples, Italy. Heckel (1854) created, with a description, the generic name *Stemmatodus* for *Pycnodus rhombus* Agassiz, 1839, this species being explicitly designed by Heckel as "als Typus" (Heckel 1854: 455). Holotype of *Stemmatodus rhombus*: Bohemian Museum Prague (*fide* Heckel 1854 and Woodward 1895a). Heckel (1854) included in his new genus *Stemmatodus* the holotype plus some additional specimens previously described by Costa (1850) as *Pycnodus rhombus* as well. The latter material (which, as figured by Costa 1850: pl. 4, fig. 8; pl. 5, fig. 1, does not present the features that currently characterize *Stemmatodus*) would later become "*Coelodus*" *costae*, a species in need of revision. However, Heckel (1854: 457), when referring to the binomial species name, used the subsequent spelling *rhomboides* for the specific name. This is a demonstrably intentional emendation according to Art. 33.2.1 of the ICZN. *Stemmatodus* was later revisited and figured by Heckel (1856: pl. 2, figs 9-11), again with reference to *Pycnodus rhombus*, but using once more the subsequent spelling *rhomboides*. Later on, Woodward (1895a: 248) restored the original spelling *rhombus*, which is in prevailing usage since.

MATERIAL EXAMINED. — MNHN JRE 37, 38, 39, 40, 41, 42 (two specimens), 43 (two specimens), NHML 12001 (two specimens), 12002, 12003 (two specimens) 12004 (two specimens), P. 12006, 39775, 9672 (two specimens), 18600, 23152 (three specimens), 62200 (ex 1671), 1673, 43451 (two specimens), 45679 (two specimens), P. 1640 (all complete specimens).

Genus *Stenamara* Poyato-Ariza & Wenz, 2000

TYPE SPECIES. — By original designation: *Stenamara mia* Poyato-Ariza & Wenz, 2000. Upper Barremian from Las Hoyas, province of Cuenca, Spain. Holotype of *Stenamara mia*: MCCM LH-14365a-b.

MATERIAL EXAMINED. — Holotype and only known specimen (complete, unsatisfactory preservation), plus silicone peels of both part and counterpart (Fig. 3D).

Genus *Tepexichthys* Applegate, 1992

TYPE SPECIES. — By original designation: *Tepexichthys aranguthyorum* Applegate, 1992. Middle to upper Albian from the Tlayúa Formation, Tepexi de Rodríguez, Puebla, Mexico. Only known species. Holotype of *Tepexichthys aranguthyorum*: IGM 3286.

MATERIAL EXAMINED. — Casts of the holotype (complete specimen) at MNHN and UAM, both kindly donated by S. Applegate to the authors.

Genus *Trewavasia*
White & Moy-Thomas, 1941

Type species. — By monotypy: *Xenopholis carinatus* Davis, 1887. Cenomanian from Hakel, Lebanon. Holotype of *Trewavasia carinatus*: NHML 39239 (nearly complete specimen).

Material examined. — Holotype. Other specimens: NHLM P. 10700** (complete, excellent preservation), P.62617 (complete, good preservation); MNHN HAK-1934; MCSNM V 3046 A-B (both complete); NMW 1965/536 a**-b** (complete, excellent preservation).

DISCUSSION OF CHARACTERS

In this section of the paper, the characters used for the analysis are presented, and their states in the different pycnodont taxa are discussed in some detail. An abbreviated list of characters is given in Appendix 1; the complete data matrix is presented in Appendix 3. We basically follow Nursall's (1996b, 1999b) terminology for the anatomy of pycnodontiform fishes, occasionally including some new term of our own (e.g., "anal notch"). The terminology generally used for the actinopterygian skull roof is followed herein (see introduction to cranial characters below). Some particular epistemological problems are addressed in the corresponding characters.

General morphology
1 Body shape (as measured by the ratio maximum body height/standard length)
Fusiform, less than 40 % (0); intermediate, 40-70 % (1); discoid, 70-100 % (2); deep, more than 100 % (3). State 1 corresponds to *Coelodus saturnus* (Fig. 2A), *Iemanja*, *Mesturus*, *Palaeobalistum orbiculatum* (Fig. 4A), *Pycnodus*, and *Stemmatodus*. Most other pycnodonts are discoid in shape (state 2; e.g., Fig. 2B), although some of them are deeper than long (*Apomesodon surgens* n. gen., n. sp., Fig. 3A, B; *Stenamara*, Fig. 3D: state 3). This character partially includes Nursall's (1996a) character 100, "body form ovoid" for his Mesturidae.

2 Relative position of dorsal apex
Apex absent (0); before the point of insertion of the dorsal fin (1); in the point of insertion of the dorsal fin (2). Following Nursall's (1996a) character 43, we consider the dorsal apex as the highest point of the dorsal outline of the animal. Whenever the body form is typically fusiform, or the outline is only gently curved, it is difficult to distinguish an apex in a precise position, and we consider this as an absence of apex, that is, the primitive state. Regardless of the position of the dorsal fin, the apex may be before (e.g., *Apomesodon surgens* n. gen., n. sp., Fig. 3A, B; *Palaeobalistum orbiculatum*, Fig. 4A: state 1) or just in the point of insertion of the dorsal fin (e.g., *Ocloedus subdiscus* n. comb., Fig. 2B; *Oropycnodus ponsorti* n. comb., Fig. 4B: state 2). This character corresponds to Nursall's (1996a) character 95 *pro parte* ("eomesodontoid shape").

3 Morphology of dorsal prominence
Dorsal prominence absent (0); pointed, posterior border inclined (1); obtuse angle, posterior border (sub)horizontal (2); curved; anteriorly oriented (3); curved, dorsally oriented (4). A dorsal prominence is present, with different morphologies, in some pycnodontiforms. *Arduafrons*, *Apomesodon surgens* n. gen., n. sp., and *Gibbodon* present state 1, an acute, pointed dorsal prominence whose anterior and posterior borders are straight and markedly inclined (Fig. 3A, B). *Brembodus* (independently of the presence of a dorsal spine: see character 84), and *Apomesodon gibbosus* n. comb. present state 2, a dorsal prominence in obtuse angle, with both borders more or less straight, the anterior one being very inclined and the posterior one horizontal to subhorizontal (e.g., Frickhinger 1994: fig. 431; Fig. 3C). *Eomesodon liassicus* exhibits, in turn, a curved dorsal prominence that is anteriorly oriented, the anterior border being slightly sigmoid (state 3); the holotype, NHML 19864, and specimen NHML P.1336 show a dorsal prominence quite different from Gardiner's restoration (1960: fig. 51), and much more as that illustrated by Woodward (1916: fig. 21). Finally, ? *Eomesodon barnesi* and *Stenamara* present state 4, a dorsal prominence also curved, but dorsally oriented (Fig. 3D). This character also corresponds to Nursall's (1996a) character 95 *pro parte*.

4 Relative position of ventral apex

Apex absent (0); before the point of insertion of the anal fin (1); in the point of insertion of the anal fin (2). This character also corresponds to Nursall's (1996a) character 95 *pro parte*.

5 Mouth gape

Horizontal or subhorizontal (0); inclined (1); subvertical, opening downward (2). Most pycnodontiforms exhibit a mouth gape that is either more or less horizontal (e.g., *Coelodus saturnus*, Fig. 2A; *Palaeobalistum orbiculatum*, Fig. 4A) or inclined (e.g., *Ocloedus subdiscus* n. comb., Fig. 2B; *Apomesodon surgens* n. gen., n. sp., Fig. 3A, B). Only *Trewavasia* has a subvertical mouth gape that is clearly opening downward (Gayet 1984; pers. obs.).

6 Prognathism

Absent (0); present (1). In addition to the hypertrophy of the ethmoid region present in pycnodontiforms (see character 8), the jaws are prognathous, that is, projected anteriorly in *Apomesodon* n. gen. (Fig. 3A, B), *Arduafrons* (Nursall 1999a), *Eomesodon* (Frickhinger 1991, 1994; Fig. 3C), *Ichthyoceros* (Gayet 1984), and *Iemanja* (Wenz 1989a). In the different specimens of *Apomesodon gibbosus* n. comb. from Bavaria, the degree of prognathism seems to vary according to the size of the specimen and also maybe to the preparation (Frickhinger 1991, 1994; pers. obs.). In the case of *Gyrodus*, some specimens from Bavaria may eventually look prognathous, but we consider that it is due to the restoration of a faked outline of the specimen, not comparable to actual prognathism (e.g., Frickhinger 1994: fig. 436; pers. obs.). We therefore coded this character as 1 for *Apomesodon gibbosus* n. comb. and 0 for *Gyrodus*. This character is part of Nursall's "eomesodontoid shape" (Nursall 1996b: character 95, p. 145), but, as just mentioned, it is found not only in *Eomesodon*.

7 Caudal pedicle

Differentiated (0); not differentiated (1). In many pycnodontiforms there is a differentiated caudal pedicle; in these cases, the distal end of the dorsal and anal fin rays do not reach the caudal fin, and, when the endoskeleton is accessible, there are at least three neural and/or haemal spines not supporting any fin ray between the end of the dorsal and anal fins and the first precurrent caudal fin rays: e.g., *Coelodus saturnus* (Fig. 2A), *Pycnodus*. In some pycnodonts the caudal pedicle is not differentiated: the dorsal and anal fins end very close to the base of the caudal fin rays, sometimes overlapping them; the distal end of the last dorsal and anal fin rays reach the caudal fin; and the number of neural and haemal spines between the end of those fins and the beginning of the caudal endoskeleton is reduced to two or, more commonly, one. This is the case of *Ocloedus subdiscus* n. comb. (Fig. 2B), *Apomesodon* n. gen. (Fig. 3A-C), *Iemanja*, *Macromesodon*, *Oropycnodus ponsorti* n. comb. (Fig. 4B), *Proscinetes* (Fig. 5), *Stemmatodus*, *Tepexichthys*, and *Trewavasia*. See also figures on the caudal endoskeleton section below.

SKULL

The traditional terminology for actinopterygian cranial bones is followed herein. Anterior to posterior, the paired bones of the skull roof are called nasals (so far not observed in pycnodontiforms), prefrontals (often absent), frontals, parietals, and extrascapulars. This terminology is based on homologization of these bones within Actinopterygii. We herein interpret Nursall's (1999a) "marginal bones" as extrascapulars due to their topographic position and to their anatomic relationships with other bones, and also because of the presence of a sensory commissure in these bones in an undescribed specimen of *Mesturus* sp. from Canjuers (MNHN CNJ 130).

8 Antorbital and ethmoidal regions

Normal (0); hypertrophied (1). All observed pycnodonts present a hypertrophy of the region between the orbit and the snout. This region is much enlarged and ventrally expanded (anteriorly expanded in *Mesturus*). This involves significant anatomic modifications in the mesethmoid and the parasphenoid (Nursall 1996b: characters 5, 6, 1999b). This character is independent from

the relative prognathism of the snout (character 6; see data matrix).

9 Morphology of the frontal bones

Rectangular, long (0); curved, long (1); curved, short (2); curved, very broad (3). Primitively, the frontals are long, rectangular bones whose anterior border is anterior to or lies at the same level as the orbit. In the primitive state, the lateral border of the frontals at the level of the orbit is straight to faintly curved. Within pycnodontiforms, only *Gibbodon* presents the primitive state (Fig. 6). The profound modifications of the pycnodontiform skull include a strong curvature of the frontal bones in all other fishes of this order, although the relative morphology varies. The frontals are quite long, ventrally curved, their anterior border reaching well before the orbit, in *Brembodus* (Fig. 7), *Eomesodon liassicus*, and *Gyrodus* (state 1). They are shorter in most other pycnodontiform genera, where the anterior border of the frontals does not reach the ventral level of the orbit (e.g., *Oropycnodus ponsorti* n. comb., syntype NMW 1854/XXXIX/38; *Proscinetes*, Fig. 8: state 2). Finally, the studied specimens of *Nursallia veronae* and *N.* ? *gutturosum* exhibit frontal bones that are short, very curved and remarkably large (state 3). Together with the enlarged, conical dermal supraoccipital, the frontals form a hemispherical skull roof, and the orbit is placed midway between the dorsal and the ventral borders of the head (Fig. 9).

10 Prefrontal bones

Absent (0); present (1). There is a pair of prefrontal bones, distinct from the frontals and from the superficial portion of the mesethmoid, in *Ichthyoceros* (Gayet 1984; pers. obs.), *Nursallia* ? *gutturosum* (Fig. 9), and *Trewavasia*. Concerning *Nursallia* ? *gutturosum* we agree with Arambourg's (1954: 11; fig. 4; pl. 2, fig. 1) interpretation of the prefrontal, and disagree with Lambers (1991, 509-510), who considers that this bone is part of the mesethmoid. As shown by MNHN DTS 229 D, G; DTS 231 G; and DTS 235 G (which includes a revealing positive cast), both the arrangement and the ornamentation strongly
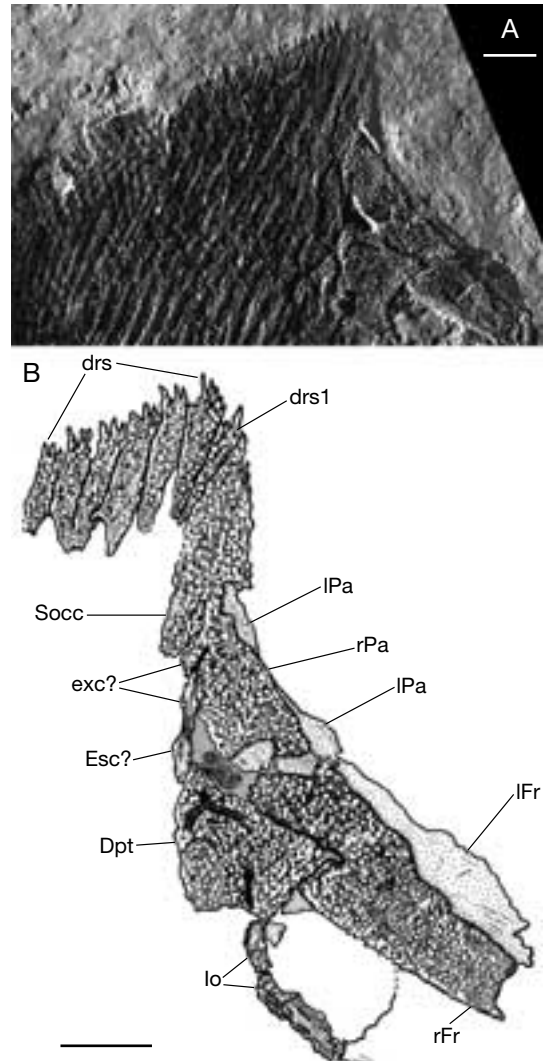
Fig. 6. — *Gibbodon cenensis* Tintori, 1981, holotype, MCSNB 3317, right side, lateral view; **A**, anterodorsal region. Photo courtesy F. Confortini, M. Malzanni, A. Paganoni; **B**, camera lucida drawing showing detail of the skull roof and anteriormost dorsal ridge scales. Abbreviations: **Dpt**, dermopterotic; **drs**, dorsal ridge scales; **drs1**, dorsal ridge scale 1; **Esc**, extrascapular bone; **exc**, extrascapular commissure; **Io**, infraorbitals; **lFr**, left frontal; **lPa**, left parietal; **rFr**, right frontal; **rPa**, right parietal; **Socc**, dermal supraoccipital. Scale bars: 5 mm.

suggest that this is a distinct paired bone, therefore a prefrontal. The ornamentation of this bone consists of ridges converging towards a point, the center of ossification. This is comparable to the ornamentation observed in other dermal bones of
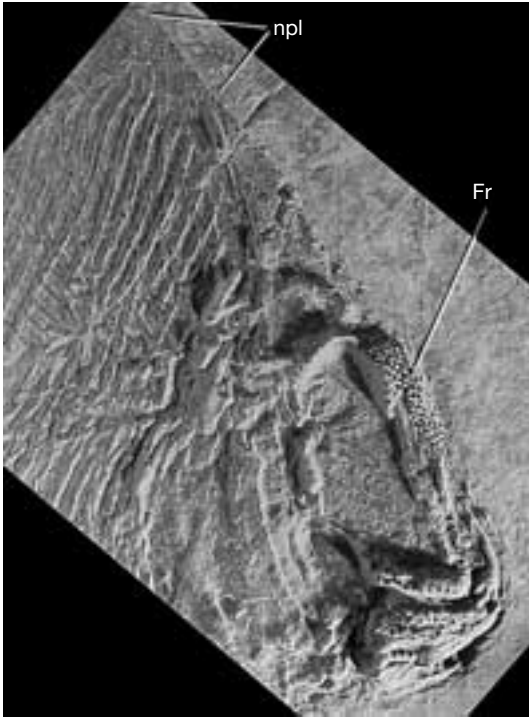
F IG . 7. — *Brembodus ridens* Tintori, 1981, holotype, MSCNB 4898, head and anterodorsal region of the body, right side, lateral view. Standard length of specimen: 118 mm. The original specimen is complete; the blanks on right upper and lower corners are due to reframing the original photograph. Photo courtesy F. Confortini, M. Malzanni, A. Paganoni. Abbreviations: **Fr**, frontal; **npl**, nuchal plates.

the skull (Fig. 9), including the frontal. This suggests two centers of ossification on each side, one for the frontal and one for the prefrontal. Unfortunately, this character cannot be verified in the holotypes of *Nursallia veronae* and *N.* ? *goedeli*. Specimen NMW 1965/536 a-b of *Trewavasia* presents a paired plate (there is one plate in the part and another one in the counterpart) that is anterior to the frontal and strongly ornamented. However, a small portion that is broken away shows what seems to be a partial fusion with the mesethmoid. In agreement with Gayet (1984), we still consider this bone as the prefrontal because it is paired, strongly ornamented and therefore dermal, and because the transverse part of the T section of the mesethmoid is clearly underlying it. In contrast, we have

found no trace of any prefrontal distinct from the superficial portion of the mesethmoid in the observed specimens of *Pycnodus*, contrary to both Blot's (1987) and Taverne's (1997) interpretations. From our point of view, both Blot's "préfrontal" (Blot 1987: figs 2, 6, 34) and Taverne's "dermethmoïde" (Taverne 1997: fig. 4) are actually the superficial, transversal part of the T section of the mesethmoid, as figured by Nursall (*in* Blot 1987: fig. 3) and noted by Lambers (1991). We confirm our interpretation also with personal observations on the holotype and on transfer specimens NHML P1634 and 44520 (Fig. 10).

11 Frontal spine

Absent (0); present, simple (1); present, compound (2). One simple, paired spine on the frontal bones is present only in *Trewavasia* (Gayet 1984; pers. obs.). In the holotype of *Ichthyoceros* the frontal spine is a compound structure, with a central, longer spine plus two shorter spines, one anterior and one posterior to it (Gayet 1984; pers. obs.; state 2). Minor variations of this compound spine are observed on specimen MCSNM 3046 of this genus. This character corresponds to Nursall's (1996a) character 56 *pro parte*.

12 Dermocranial fenestra

Absent (0); present (1). A well-defined fenestra in the dermocranium, bordered by the frontal, the parietal, and the dermal supraoccipital, is present in many pycnodonts (e.g., *Ocloedus subdiscus* n. comb., Fig. 2B; *Oropycnodus ponsorti* n. comb., Fig. 11). Our "dermocranial fenestra" corresponds to Nursall's "temporal fenestra" (1996a: character 116), but we prefer the former term in order to avoid possible confusions of this dermal fenestra with some non-homologous endocranial structures found in other fishes, including teleosts (e.g., post-temporal fossa, subtemporal fossa). In the holotype of *Gibbodon* (Fig. 6), the region anterolateral to the right parietal is badly preserved, and some fragments of the skull roof are missing. Nonetheless, the dark region depicted on Fig. 6B is not to be mistaken with a
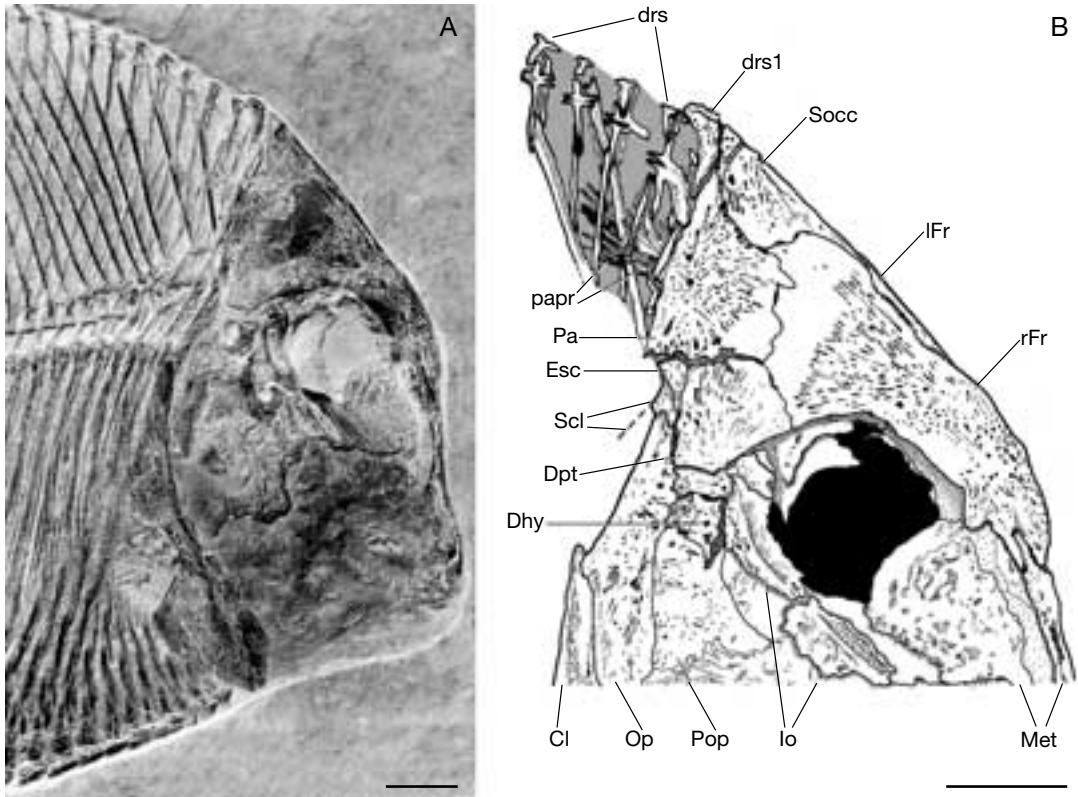
FIG. 8. — Skull of *Proscinetes elegans* (Agassiz, 1833), specimen JM 1941.12a; **A**, photo courtesy G. Viohl; **B**, camera lucida drawing showing detail of the dorsal part of the skull and anteriormost dorsal ridge scales. Both right side, lateral view. Abbreviations: **Cl**, cleithrum; **Dhy**, dermohyomandibular; **Dpt**, dermopterotic; **drs**, dorsal ridge scales; **drs1**, dorsal ridge scale 1; **Esc**, extrascapular; **Io**, infraorbitals; **lFr**, left frontal; **Met**, mesethmoid; **Pa**, parietal bone; **papr**, parietal process; **Pop**, preoperculum; **Op**, operculum; **rFr**, right frontal; **Scl**, supracleithrum (only partially depicted); **Socc**, dermal supraoccipital. Scale bars: 5 mm.

dermocranial fenestra, which is absent, since the left parietal is seen extending beneath this damaged region, and contacts along its entire posterior border with the dermosupraoccipital. The skull roof of *Abdobalistum thyrsus* n. gen., n. sp. NHML P.9830 is not very well preserved, but it shows bone remains or bone imprints all over this region of the skull roof, so that the fenestra was probably absent. For the same reason, it is considered also absent in *Nursallia veronae* (specimen MCSNV II.D.172, confirmed by juvenile specimen MCSNV T.830 [state 0]). Contrary to what is implied by the distribution of Nursall's (1996a: fig. 18) character 116, there is no dermocranial fenestra in *Stemmatodus* either (Fig. 12). Unfortunately, this region of the skull roof is lost

(and restored with plaster) in the holotype of *Coelodus saturnus*; still, some bone in the region anterior to the parietal process is preserved, suggesting that the fenestra might be absent. We have, nonetheless, conservatively coded this character as ? for this taxon, because this evidence is too weak and the preservation of this region is too bad and incomplete.

13 Parietal

Single (0); divided (1); absent (2). The parietal is a single paired bone (state 0) in most observed pycnodontiforms (e.g., Figs 6; 8; 9; 11; 12), including *Arduafrons* (Nursall 1999a; pers. obs.). The parietal is divided into several small paired plates only in *Mesturus*: Woodward 1895a, 1896;

Nursall 1999a; pers. obs. in *M. leedsi* NHML P.8383 and 8384, where this region is totally covered by small plates, which do not form rows as regular as those restored by Woodward 1896 (state 1). In *Trewavasia* the parietal is absent as an independent ossification (Gayet 1984; pers. obs. in MNHN 1991-3-3 and NMW 1965/536 a-b).

14 Parietal process

Absent (0); present (1). Some pycnodontiforms show a paired posterior, peniculated process at about the midpoint of the posterior border of the parietal bones (e.g., Figs 8; 11; 12). This process is not superficial, but formed by a prolongation of the profound part of the bone. For other denominations of this process, see Nursall (1996a: character 48). The primitive state is coded for *Apomesodon* n. gen., *Arduafrons*, *Brembodus*, *Eomesodon*, *Gibbodon*, *Ichthyoceros*, *Mesturus*, *Micropycnodon*, and *Paramesturus* because the posterior border of the parietal does not show any indication of the presence of a process, but needs former confirmation, as thick scales always cover the region immediately posterior to the parietal. This area is however accessible in specimen NHML P.3773a of *Gyrodus*. Here we can observe a left cranial skull roof in lateral view, without parietal process, while the scales are from the right side, in medial view (state 0). The posterior border of the parietal in *Abdobalistum thyrsus* n. gen., n. sp. NHML P.9830 does show remains of a process (pers. obs.), in agreement with the interpretations by Heckel (1856) and Woodward (1895a), and in disagreement with the interpretation by Blot (1987). The holotype of *Nursallia veronae* shows the base of a process, although it is not preserved in its entirety (state 1). We have conservatively coded this character as unknown in *Nursallia* ? *gutturosum* because, although Arambourg (1954) and Blot (1987) believe that there is no process, the available specimens actually show accurately preserved only the superficial part of the bone, and the postero-median border is never preserved clearly enough, unlike the above-mentioned genera.

15 Dermal supraoccipital

Absent (0); single (1); divided into two or more unpaired plates (2). All pycnodontiforms present one, or a series of, unpaired dermal supraoccipital(s) (Nursall 1996b; detailed description by Nursall 1999a). In most cases, this median bone is single (state 1; e.g., Figs 6; 8; 9; 11-13). However, *Mesturus* (Woodward 1895a, 1896; Nursall 1999a; pers. obs. in *M. leedsi* NHML P.8385), *Micropycnodon* (Hibbard & Graffham 1941; Dunkle & Hibbard 1946), and *Paramesturus* (Taverne 1981) show a series of two or more consecutive superficial, ornamented medial plates in the postero-dorsal region of the skull, which can be reliably interpreted as dermal supraoccipitals (state 2). We interpret that these extra supraoccipitals correspond to the "nuchal plate" of Nursall's (1999a). Whenever dorsal ridge scales are differentiated, the anteriormost one is incorporated onto the skull, in close contact with the posterior border of the dermal supraoccipital (see character 86). This arrangement of the first dorsal ridge scale (Figs 6; 8; 9; 11; 12) is not to be mistaken with the presence of extra supraoccipital plates or of any other extra dermal bone of the skull roof.

16 Supraoccipital spine

Absent (0); present, simple (1); present, compound (2). An unpaired spine on the supraoccipital is present only in: *Coccodus* (Fig. 13), where it is single, large and very stout (MNHN HAK 39, HDJ 319, HDJ 539; state 1); and in the holotype of *Ichthyoceros*, where the "épine postcéphalique" of Gayet (1984), unlike described by this author, is a compound structure, with a central, longer element plus two shorter elements, one anterior and one posterior to it (pers. obs. on holotype, MNHN HAK 106, directly and by transparency from the right side; state 2). Minor variations of this compound spine are observed on specimen MCSNM 3046 of this genus. This character includes Nursall's (1996a) character 62.

17 Extrascapulars hypertrophied

No (0); yes (1). Only in *Trewavasia* the pair of extrascapular bones are hypertrophied (Gayet
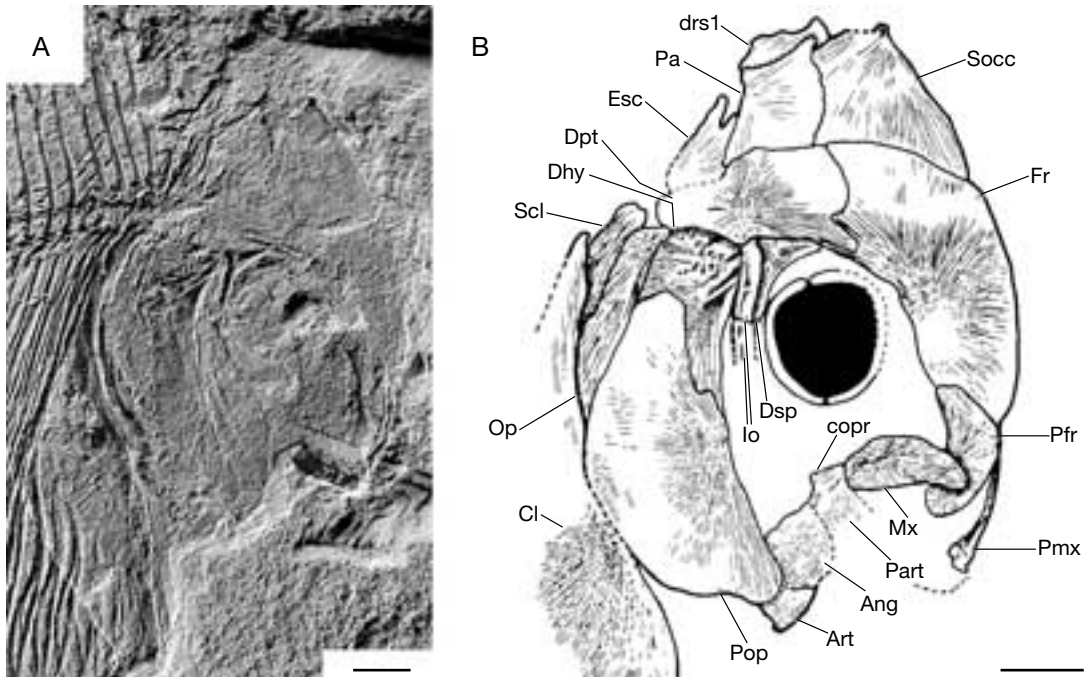
Fig. 9. — Skull of *Nursallia* ? *gutturosum* (Arambourg, 1954), specimen MNHN DTS 229 D, right side, lateral view; **A**, photo Serrette; **B**, interpretation of the bones of the skull, based on a camera lucida drawing and on the distribution of the ornamentation. Abbreviations: **Ang**, angular; **Art**, articular; **Cl**, cleithrum; **copr**, coronoid process; **Dhy**, dermohyomandibular; **Dpt**, dermopterotic; **drs1**, dorsal ridge scale 1; **Dsp**, dermosphenotic; **Esc**, extrascapular; **Io**, infraorbitals; **Fr**, frontal; **Mx**, maxilla; **Pa**, parietal; **Part**, prearticular; **Pfr**, prefrontal; **Pmx**, premaxilla; **Pop**, preoperculum; **Op**, operculum; **Scl**, supracleithrum; **Socc**, dermal supraoccipital. Scale bars: 5 mm.

1984; pers. obs. on MNHN 1991-3-3 and NMW 1965/536 a-b).

18 Extrascapular(s) fused to parietal
No (0); yes (1). There are two or more large pairs of extrascapular bones bordering the dermocranium posteriorly in: *Apomesodon gibbosus* n. comb. (JM SOS 3572 b), *Gyrodus* (Lambers 1991, 1992), *Mesturus* (Woodward 1895a, 1896; pers. obs. in *M. leedsi* NHML P.8383), *Micropycnodon* (Hibbard & Graffham 1941; Dunkle & Hibbard 1946), and *Paramesturus* (Taverne 1981). Extrascapulars are usually reduced in size and in number of pairs in most other pycnodontiforms. We consider that there has been a fusion of an extrascapular with the parietal whenever the latter shows evidence of a supratemporal commissure (e.g., *Apomesodon* sp. from Cerin MGNH 15433, Fig. 14A) or of sensory pores (e.g., *Ocloedus sub-*

discus n. comb. MSB 20659, *Proscinetes* JM 1941.12a, where the commissure extends also through the dermosupraoccipital, Fig. 8). The fusion may occur regardless of the presence of another small extrascapular. For instance, there is a supratemporal commissure in the parietal plus an independent extrascapular in *Eomesodon liassicus* (Gardiner 1960; pers. obs. in NHM 19864) and in *Tepexichthys* (Applegate 1992), whereas there is fusion with absence of an extrascapular as independent ossification (Fig. 14A) in *Apomesodon surgens* n. gen., n. sp. from Cerin (Saint-Seine 1949; pers. obs. in MGNH 15433 and 15660; MNHN CRN 69). Contrary to Tintori (1981), we have found no certain evidence of fusion in *Brembodus*, although we have found no remains of independent extrascapulars either (coded as ?). This character is difficult to evaluate in *Gibbodon* (Fig. 6). As mentioned

above, the region anterolateral to the right parietal on the holotype is badly preserved, and some fragments of the skull roof are missing. For this reason the number, arrangement, and morphology of the eventual extrascapulars are not known; however, a commissure in this region is very likely present, so there must be an independent extrascapular. In addition to it, the parietal exhibits a portion of the transversal commissure, so we have coded this character as 1. Nonetheless, further findings are necessary to confirm the exact number and arrangements of extrascapulars in *Gibbodon*.

19 Endocranium posteriorly exposed
No (0); yes (1). Nursall (1999b: 178, 179, fig. 20) describes a postorbital shortening of the dermocranium, with posterior exposure of the endocranium, in *Pycnodus*. Other than this genus, the derived state of this character is observed only in *Oropycnodus ponsorti* n. comb. (Fig. 11B). The exposed portion of the endocranium is always a faintly ossified lamina. A postcephalic lacuna in the ventral part, below the level of the parietal process, has been pointed in *Pycnodus* (Blot 1987: fig. 6; Nursall 1999a: fig. 178; pers. obs.). We signal here for the first time that also *Oropycnodus ponsorti* n. comb. has such a postcephalic lacuna (Fig. 11B). The weak ossification of the exposed part of the endocranium results in a defective preservation that prevents the identification of the precise bones that form this region; Nursall (1999a: 179) suggests that the lower part may be epioccipital.

20 Anterior portion of infraorbital sensory canal
Closely surrounding the orbit (0); descending towards the ethmoid region (1). The anterior part of the infraorbital sensory canal surrounds the orbit (primitive state) in *Gibbodon* (Fig. 6), *Gyrodus* (Lambers 1991, 1992), *Mesturus* (Nursall *in* Lehman 1966: fig. 164; Nursall 1999a), *Nursallia* ? *gutturosum* (Arambourg 1954), *Paramesturus* (Taverne 1981), and *Trewavasia* (Gayet 1984). The rest of the observed pycnodontiforms shows the derived

state, where the anterior part of the infraorbital canal is ventrally oriented over the mesethmoid, descending towards the ethmoid region (e.g., *Arduafrons* NHML P.8658; holotype of *Brembodus*; *Macromesodon*: Nursall *in* Lehman 1966: fig. 169; Nursall 1996b: figs 5, 6, 1999b: figs 8, 9).

21 Infraorbitals
Row of plates around the ventral and the posterior border of the orbit (0); mosaic of small plates (tesserae) partially covering the cheek (1); reduced to tubular ossifications around the infraorbital sensory canal (2); anterior infraorbital enlarged (3). Among pycnodontiforms, the primitive state is present only in *Eomesodon liassicus*, *Gibbodon* (Fig. 6), and *Paramesturus*. Whenever observable, the presence of infraorbital tesserae is always associated with the presence of tesserae covering the ethmoidal region (state 1). When the infraorbitals are reduced to tubular ossifications (state 2), the posteriormost one is more robust than the others, and occupies the posterior border of the orbit (see next character). The infraorbitals are reduced to tubular ossifications in *Apomesodon surgens* n. gen., n. sp. (e.g., ML 15433: Fig. 14A; state 2). In *Apomesodon gibbosus* n. comb. from Bavaria there are certainly tesserae (e.g., JM SOS 3570), but the infraorbital region exhibits both small plates and tubular infraorbitals in at least one specimen (FSL 93095, Fig. 14B). Therefore, we have coded this character as 1 and 2 simultaneously for this taxon. The anterior infraorbital is considerably enlarged, roughly triangular in shape, only in *Nursallia* ? *gutturosum*, *Abdobalistum thyrsus* n. gen., n. sp., and *Pycnodus* (Arambourg 1954; Blot 1987; pers. obs). This expanded anterior infraorbital is probably the antorbital (see Nursall 1999b: 199 for a discussion of the canal-bearing bones of this region in pycnodontiforms). This character corresponds to Nursall's (1996b) characters 22 *pro parte* and 47 *pro parte*.

22 Infraorbital ornamentation
Present in all infraorbitals (0); present only in the posteriormost one (1); absent in all infra-
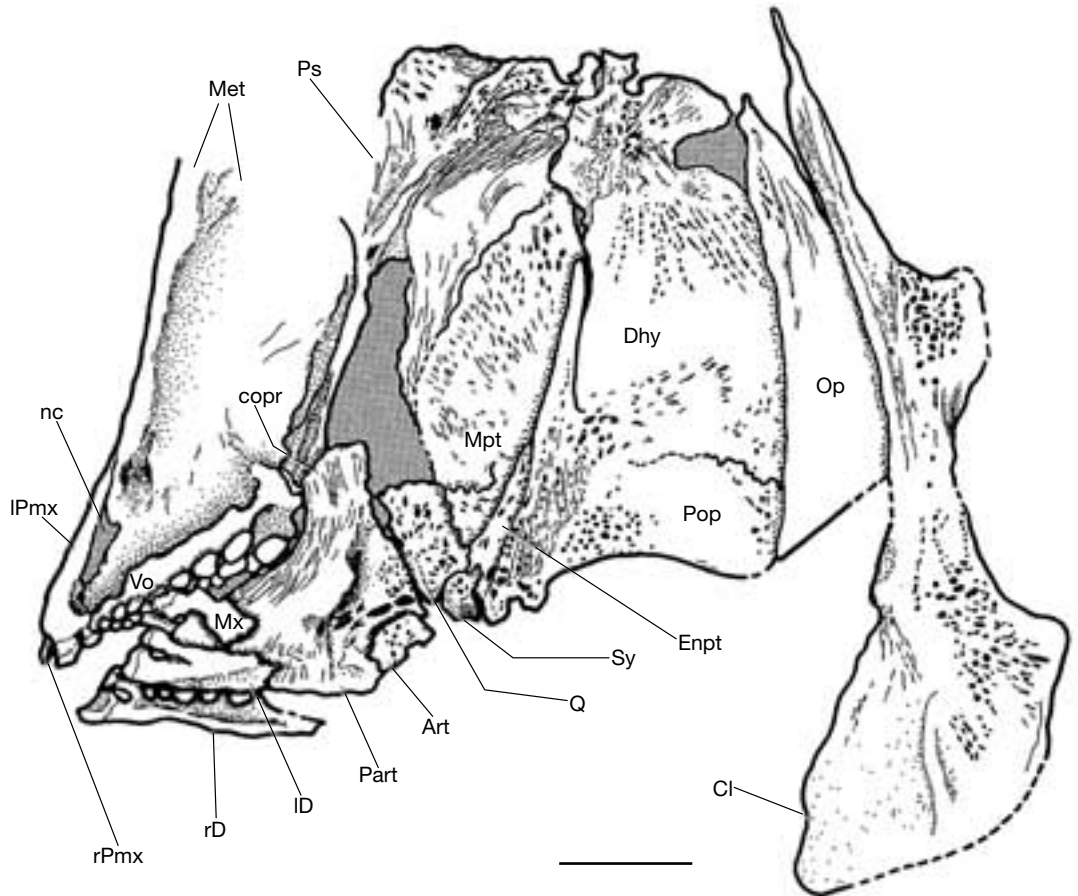
F_{IG}. 10. — *Pycnodus apodus* (Volta, 1809), camera lucida drawing of ventral region of skull plus cleithrum as shown by transferred specimen NHML P.1634, left side, lateral view; articular head of dermohyomandibular partially restored from a reverted camera lucida drawing of transferred specimen NHML P.44520; branchial teeth (illustrated by Nursall 1996a: fig. 23), ceratohyal, and basihyal not depicted. Abbreviations: **Art**, articular; **Cl**, cleithrum; **copr**, coronoid process; **Dhy**, dermohyomandibular; **Enpt**, entopterygoid; **ID**, left dentary; **lPmx**, left premaxilla; **Met**, mesethmoid; **Mpt**, metapterygoid; **Mx**, maxilla; **nc**, nasal capsule; **Part**; prearticular; **Pop**, preoperculum; **Ps**, parasphenoid; **Op**, operculum; **Q**, quadrate; **rD**, right dentary; **rPmx**, right premaxilla (tooth); **Sy**, symplectic; **Vo**, vomer. Scale bar: 5 mm.

orbitals (2). Whenever all infraorbitals but the last one are reduced to tubular ossifications (state 2 of previous character), the last one, more robust than the others, is ornamented (state 1), with two exceptions. In *Trewavasia* all infraorbitals are reduced, and yet all of them are ornamented (specimen NMW 1965/536 a-b; primitive state). On the contrary, in *Tepexichthys* the last infraorbital also lacks ornamentation according to Applegate (1992: 169, figs 8, 9; state 2).

23 Suborbitals

One or several rows (0); mosaic of small plates (1); absent as independent ossifications (2). We have not found suborbital bones forming a regular row in any observed pycnodontiform. Whenever present, the suborbital bones are arranged as a tesserae of small elements (state 1): *Arduafrons*, *Brembodus* (holotype, MCSNB 4898; worse preservation in specimens MCSNB 4899 and 4933), *Gyrodus*, *Ichthyoceros*, and *Mesturus* (Nursall *in* Lehman 1966: fig. 164;
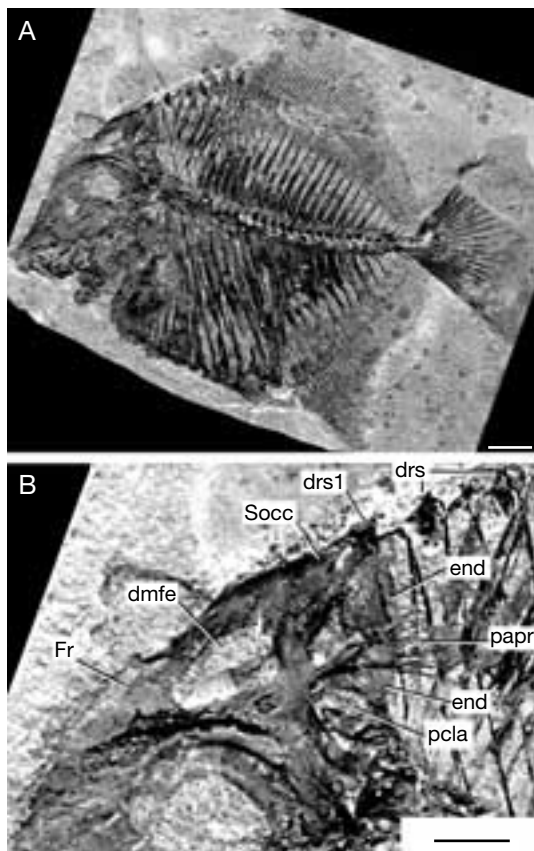
FIG. 11. — *Oropycnodus ponsorti* n. comb., paralectotype, NMW 1854.XXXIX.40, left side, lateral view; **A**, complete specimen. Photo Schumacher, courtesy Ortwin Schultz; **B**, detail of the posterior region of the skull roof. Abbreviations: **dmfe**, dermocranial fenestra; **drs**, dorsal ridge scales; **drs1**, dorsal ridge scale 1; **end**, endocranium (posteriorly exposed); **Fr**, frontal; **papr**, parietal process; **pcla** postcephalic lacuna; **Socc**, dermal supraoccipital. Scale bars: A, 1 cm; B, 5 mm.

Nursall 1999a; pers. obs.). This character corresponds to Nursall's (1996b) characters 22 *pro parte* and 47 *pro parte*.

24 Preopercular and hyomandibular

Preopercular single, smaller than opercular; hyomandibular deep, unornamented (0); preopercular single, hypertrophied; hyomandibular deep, unornamented (1); one large preopercular plus a small ornamented plate over the head of the hyomandibular (2); one large preopercular in close contact with a small ornamented portion of the hyomandibular, at the same superficial level (3); preopercular of similar size as the expanded, superficial, ornamented portion of hyomandibular (4). As remarked by Nursall (1996b, 1999b), all pycnodontiforms present a hypertrophied preopercular, larger than the opercular, and separated from the neurocranium by a lacuna. Whenever only such a large preoperculum is visible, and the hyomandibular is in a deeper plane, with no apparent ornamentation on its head, the character is coded as 1: *Apomesodon* n. gen. (Fig. 14A), *Arduafrons*, *Brembodus*, *Eomesodon*, *Gibbodon*, *Gyrodus*, and *Micropycnodon*. In turn, Nursall's restoration of *Mesturus verrucosus* shows a similar arrangement (1999b: fig. 3), but specimen NHML P.8383 of *Mesturus leedsi* clearly exhibits one large preopercular plus a small independent, dorsal, ornamented, plate placed over the deep head of the hyomandibular (Fig. 15). We think that the absence of this plate in the specimens of *Mesturus verrucosus* may be preservational. Pending confirmation by transfer preparations of good specimens, we have coded this character as 2 for *Mesturus*. An apparently more advanced state (3) is found in *Iemanja* (Fig. 16A, B), *Macromesodon* (Nursall 1996b: figs 5, 6, 1999b: fig. 9; Fig. 16C), *Neoproscinetes* (e.g., Nursall 1999a: fig. 7), *Nursallia* ? *gutturosum* (Fig. 9), and *Proscinetes* (Fig. 8). Here, the preopercular is of equivalent size to that of previous states, but it articulates closely anterodorsally with a small portion of the hyomandibular that is ornamented and in the same superficial plane; the rest of the hyomandibular is in a deeper plane, without ornamentation, and separated from the superficial portion by a generally well marked crest (Figs 8; 9; 16A-C). This character is observable only on specimen NMW 1965/536 a-b of *Trewavasia*. It shows a large, ovoid preopercular, and the hyomandibular seems to correspond also to state 3. This bone is, however, partially covered by the last infraorbital, and the whole region is cracked on one side, while it is preserved only as an imprint on the resin on the other side, so that this character needs confirmation in further specimens. Finally, in some pycnodonts we find state 4: the superficial,

ornamented portion of the hyomandibular is enlarged, about as large as the preopercular, which is reduced in relative size with respect to that of states 1-3. These two ornamented surfaces are separated by a characteristic sigmoid suture that forms an acute antero-dorsal process on the preopercular (Figs 10; 12; 17). This is the case of *Ocloedus subdiscus* n. comb. (Wenz 1989b; pers. obs. on MNHN MSE 442 and 965), *Oropycnodus ponsorti* n. comb. (syntype NMW 1854/XXXIX/38; Fig. 17), *Pycnodus* (Blot 1987; pers. obs. on NHML P.1634 and 44520; Fig. 10), and *Stemmatodus* (Nursall 1996b: fig. 22; pers. obs. on both specimens labelled MNHN JRE 39; Fig. 12). We interpret that, in these cases, the preopercular is divided into two plates, whose ensemble is of equivalent size to that of the hypertrophied preopercular of other pycnodontiforms, and the dorsal part is fused to the head of the hyomandibular. As for *Tepexichthys*, although its phylogenetic position in Nursall (1996b) implies that it would present the most derived state, we have conservatively coded it as ? because we could not interpret the character state either in Applegate (1992) or in the observed cast.

The sequence described by states 1-4 above is interpreted as a "dermalization" of the hyomandibular by Nursall (1996b: characters 49 and 109), but we rather believe it is a fusion of a small dermal plate (state 3), or of a large dorsal preopercular (state 4) to the head of the hyomandibular. We prefer this interpretation because of the presence of a small independent plate on state 2 (Fig. 15), and because the ensemble of the ornamented surfaces in state 4 is equivalent in size and shape to that of a standard pycnodont preopercular. An additional problem is that the apparent "dermalization" of the hyomandibular is a reticulation similar to that observed in dermal bones, but also to that of endochondral bones such as the quadrate, symplectic or retroarticular (e.g., Figs 10; 12), and this could be an effect of the acid treatment rather than a "dermalization" of these bones, with the important exception of unprepared specimens of *Stemmatodus*. This problem requires further investigation, especially when abundant, well-preserved ontogenetic series
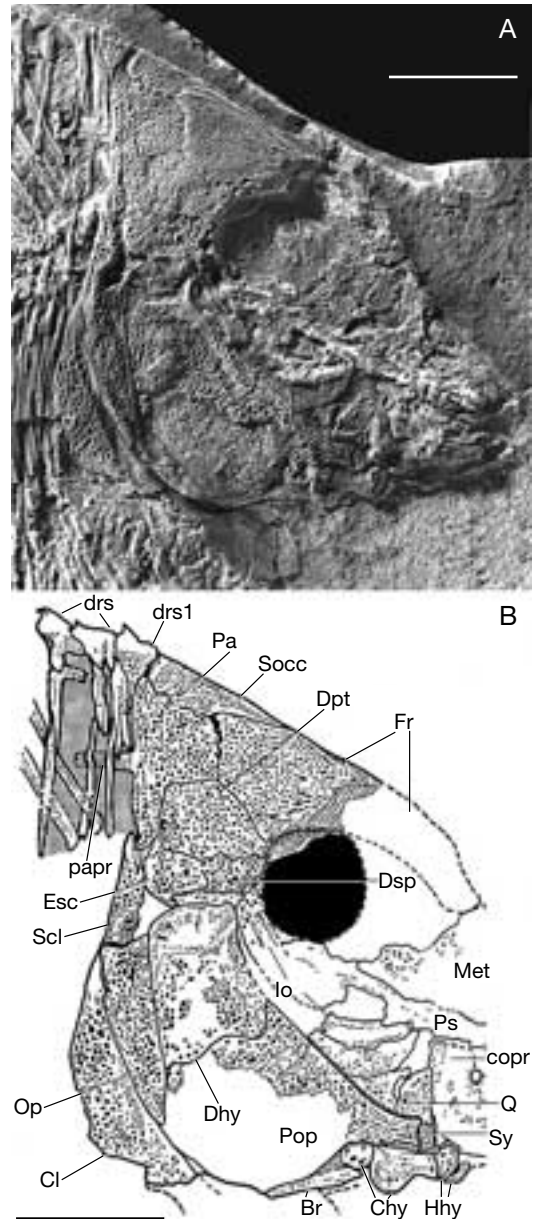
FIG. 12. — Skull of *Stemmatodus rhombus* (Agassiz, 1839), specimen MNHN JRE 39, right side, lateral view; **A**, complete skull, photo Serrette; **B**, detail of the posterior region, camera lucida drawing. Abbreviations: **Br**, branchiostegal ray; **Chy**, ceratohyals (anterior and posterior); **Cl**, cleithrum; **copr**, coronoid process; **Dhy**, dermohyomandibular; **Dpt**, dermopterotic; **drs**, dorsal ridge scales; **drs1**, dorsal ridge scale 1; **Dsp**, dermosphenotic; **Esc**, extrascapular; **Io**, infraorbitals; **Fr**, frontal; **Hhy**, hypohyals (dorsal and ventral); **Met**, mesethmoid; **Pa**, parietal; **papr**, parietal process; **Pop**, preoperculum; **Ps**, parasphenoid; **Op**, operculum; **Q**, quadrate; **Scl**, supracleithrum; **Socc**, dermal supraoccipital; **Sy**, symplectic. Scale bars: 5 mm.
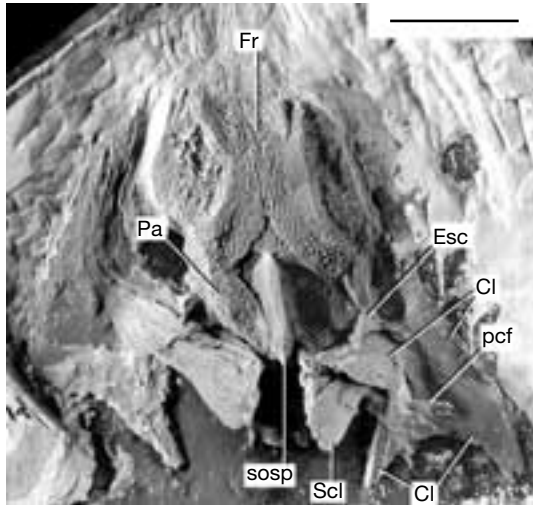
FIG. 13. — *Coccodus armatus* Pictet, 1850, transferred specimen MNHN HAK 39, skull and pectoral girdle in dorsal view. The presence of a big supraoccipital spine is marked by its large broken base. Photo Serrette. Abbreviations: **Cl**, cleithrum; **Esc**, extrascapular; **Fr**, frontals (fused in the midline); **Pa**, parietal; **pcf**, pectoral fin; **Scl**, supracleithrum; **sosp**, supraoccipital spine (distally broken). Scale bar: 1 cm.

will be available. In any case, and regardless of the preferred interpretation, the sequence of the morphology and arrangement of the preopercular(s) and hyomandibular can be divided into the four states presented above. We also think that the term "dermohyomandibula" of Nursall (1996a) should anyway be kept to be applied to the hyomandibular of states 3 and 4 herein, regardless of the preferred hypothesis on its origin. We interpret the term dermohyomandibular in a broad sense. To us, this name should be applied to this bone whenever there is a region, small as it may be, that is ornamented, forms part of the superficial plane of the head, is dorsally separated from the head of the bone by a more or less well marked ridge, and articulates with the preoperculum ventrally. This corresponds to states 3 and 4 herein. Nursall (1996b: character 109) applied the term in a more restricted sense, only when the ornamented region is enlarged (state 4 herein).

25 Opercular process of hyomandibular
Present, well developed (0); present, reduced (1); absent (2). No pycnodontiform where the opercu-
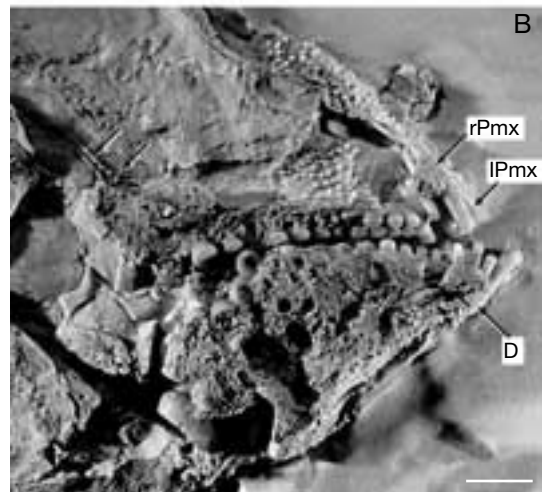
FIG. 14. — **A**, skull of *Apomesodon surgens* n. gen., n. sp., from specimen ML 15433, holotype. Right side, lateral view. Arrows on the left upper corner points at the portion of the supratemporal commissure piercing the parietal (**1**) and the dermopterotic (**2**); arrows on the ethmoidal region point at the tubular infraorbitals (**3**), the ossicle(s) of the ascending branch of the infraorbital sensory canal (**4**), and the ossicles of the ethmoid commissure (**5**). Photo Serrette, under ultraviolet light; **B**, *Apomesodon gibbosus* n. comb., ethmoidal and oral region of specimen FSL 93095. Arrows on the left point at the tubular infraorbitals. Photo Serrette. Abbreviations: **D**, dentary; **lPmx**, left premaxilla (tooth); **rPmx**, right premaxilla. Scale bars: A, 1 cm; B, 5 mm.

lar process is observable presents this structure as developed as in the outgroup. We have only seen an opercular process in *Gyrodus*, where this structure is present but considerably reduced (Fig. 18A; state 1). It is considered as a "vestigial process" in *Gyrodus* by Nursall (1996a: character 11). We therefore agree also with Lambers' interpretation of this structure in *Gyrodus* as illustrated by this author (Lambers 1991: fig. 11), but disagree, however, with his interpretation of this structure in *Gyrodus* as comparable to that of other pycnodontiforms: "The hyomandibulars of other pycnodontiforms (*Macromesodon*, *Proscinetes*, pers. obs.) are of the same type" (Lambers 1991: 516). We think that the posterior border of the hyomandibular of *Gyrodus* (Fig. 18A) is not comparable to the slightly curved posterior border of the hyomandibular that we find in all other pycnodontiforms where this character is observable (e.g., holotype of *Iemanja*, Fig. 16A; *Macromesodon* aff. *bernissartensis*, specimen MCCM LH-13483, Fig. 18B; *Neoproscinetes* as illustrated by Nursall & Maisey 1991: fig. on bottom of p. 131). In these cases, there is no process, and the slightly curved posterior border of the hyomadibular simply articulates with a medial grooved ridge of the opercular (as described for *Neoproscinetes* and "pycnodonts generally" by Nursall & Maisey 1991: 132). We have therefore coded this character as 2 for most cases where it is observable (and/or reported in the literature): *Iemanja*, *Macromesodon*, *Neoproscinetes*, *Proscinetes*, *Pycnodus*, *Stemmatodus*, and *Trewavasia*. A "modified opercular process" seems present in *Micropycnodon* after Dunkle & Hibbard (1946). In the hyomandibular of this form "the axis of the ventral limb is continued on the lateral face of the proximal head in the form of a distinct and broad ridge whose faceted dorsal extremity constitutes a modified opercular process" (Dunkle & Hibbard 1946: 169, figs 1, 2). We interpret this as a vestigial opercular process, comparable to that of *Gyrodus*, and have consequently coded this character as 1 for *Micropycnodon*. This feature is not described by Nursall (1999a). The head of the hyomandibular is not sufficiently well preserved or not accessible at all in the other studied pycnodontiforms.
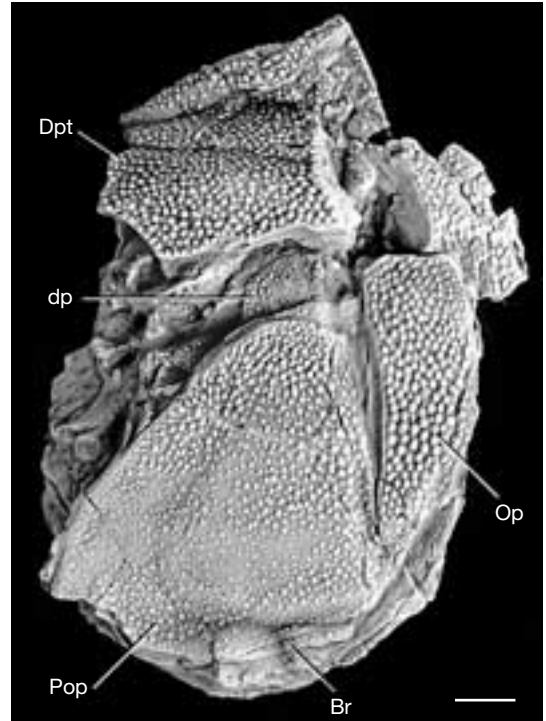
Fɪɢ. 15. — *Mesturus leedsi* Woodward, 1895, specimen NHML P.8383. Opercular region. Left side, lateral view. Photo courtesy P. Forey. Notice the pores of the different sensory canals. Abbreviations: **Br**, branchiostegal ray; **dp**, dorsal ornamented plate (dorsal preoperculum ?); **Dpt**, dermopterotic; **Op**, operculum; **Pop**, preoperculum. Scale bar: 2 cm.

26 Condyle in articular head of hyomandibular
Absent (0); present (1). Among pycnodontiforms where this region is observable, a distinct condyle in the articular head of the hyomandibular is present only in *Iemanja* (pers. obs. on holotype; Fig. 16A) and, even more developed, in *Neoproscinetes* (Nursall & Maisey 1991; pers. obs.).

27 Suboperculum and interoperculum
Present (0); absent (1). These bones are absent in all observed pycnodontiforms. This character is partially one of Nursall's (1996b) synapomorphies for the order Pycnodontiformes (his character 10 *pro parte*). We have observed differences in the way the reduction of the opercular series is achieved, so that we have separated Nursall's
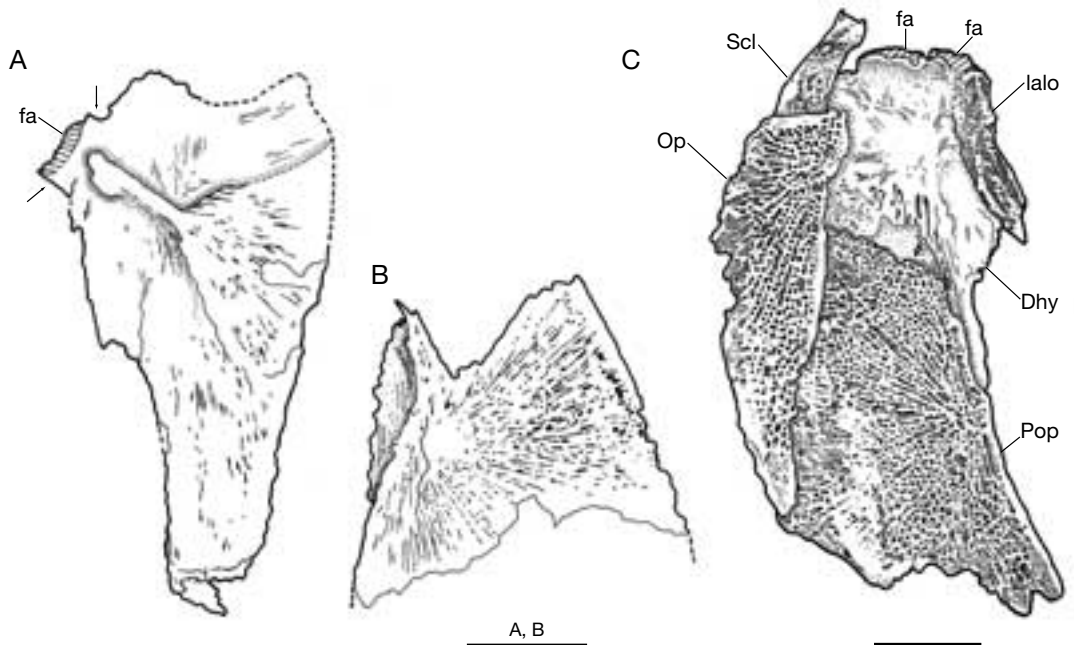
Fig. 16. — **A**, **B**, *Iemanja palma* Wenz, 1989, holotype, transfer prepared. Camera lucida drawings of the dermohyomandibular (**A**, the arrows indicate the condyle for articulation with the endocranium) and the preserved portion of the preopercular (**B**). Both left side, lateral view, drawn with specimen inclined to obtain a completely lateral view, as bones are disarticulated and displaced in the specimen; **C**, *Macromesodon* aff. *M. bernissartensis* Traquair, 1911. Opercular region of transferred specimen MCCM LH-16345. Right side, lateral view. The preopercular seems slightly displaced, revealing the crest of separation between this bone and the small, ornamented portion of the dermohyomandibular. Abbreviations: **Dhy**, dermohyomandibular; **fa**, facet for articulation with the endocranium; **Ialo**, last infraorbital; **Op**, operculum; **Pop**, preoperculum; **Scl**, supracleithrum. Scale bars: A, B, 1 cm; C, 5 mm.

character 10 into four different characters: this one plus the three following characters, concerning the opercular, the gular region, and the branchiostegal rays.

28 Opercular bone

Well developed (0); reduced (1); extremely reduced (2). Most pycnodontiforms present a reduced opercular bone, much smaller than the preopercular, narrow, roughly triangular, ventrally pointed, and vertically arranged between the preopercular and the cleithrum/supracleithrum (state 1; e.g., Figs 9; 10; 12; 15; 16). This includes *Pycnodus*; although Blot (1987: 34, fig. 11) describes and restores an opercular bone that is more developed than and dorsal to the preopercular bone, this interpretation is wrong, as already suggested by Wenz (1989b). Blot (1987) mistook the dermohyomandibular for the

opercular bone. In *Pycnodus* the operculum is present, and shows the standard pycnodontiform morphology, as seen in well preserved, transferred specimens (e.g., NHML P.44520, Fig. 10). This interpretation of the opercular bone in *Pycnodus* agrees with Lambers (1991: 513), but disagrees with Nursall (1996b: 148). The reduction of the operculum is extreme in *Oropycnodus ponsorti* n. comb. This bone is very seldom observed in this taxon; yet, syntype NMW 1854.XXXIX.38 (Fig. 17) shows that the operculum is reduced to a very thin rod (state 2).

29 Ossifications in gular region

Large gular plate (0); small, numerous tesserae (1); no ossifications (2). Some genera show a series of small plates on the gular region (*Arduafrons, Brembodus*, *Gibbodon*, *Gyrodus*, *Mesturus,* and *Micropycnodon*), but in most
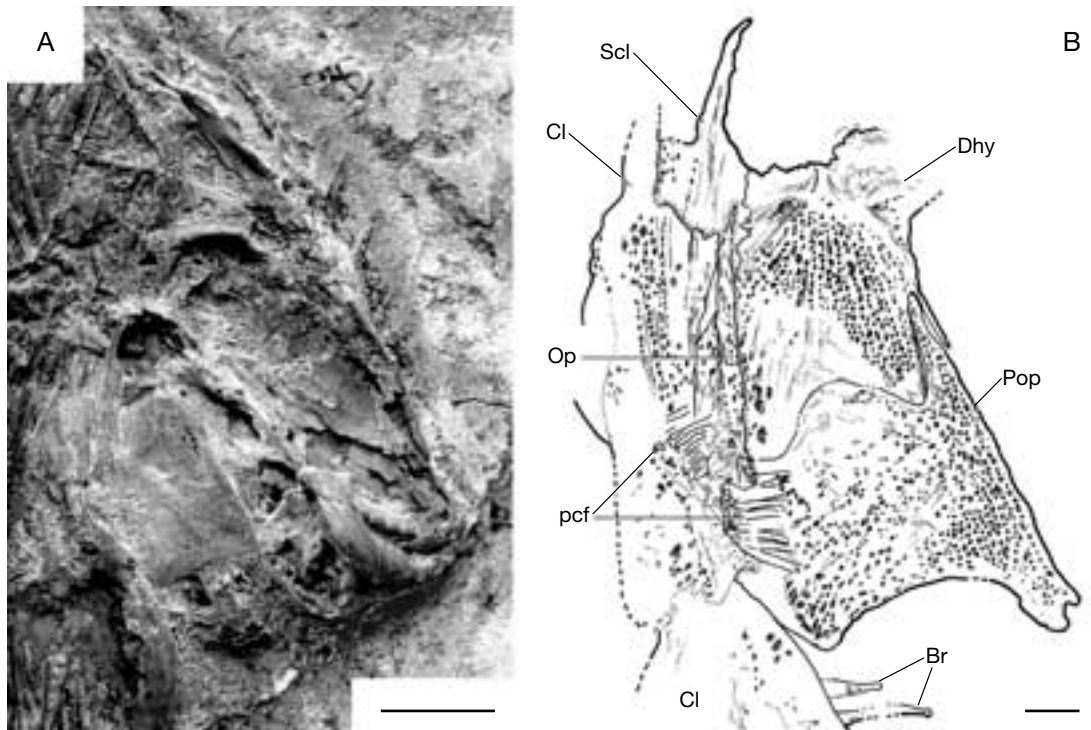
F<small>IG</small>. 17. — Skull of *Oropycnodus ponsorti* n. comb., lectotype, NMW 1854.XXXIX.38, right side, lateral view; **A**, complete skull. Photo Schumacher, courtesy Ortwin Schultz; **B**, camera lucida drawing showing detail of the opercular region. Abbreviations: **Br**, branchiostegal rays; **Cl**, cleithrum; **Dhy**, dermohyomandibular; **Op**, operculum; **pcf**, pectoral fin; **Pop**, preoperculum; **Scl**, supracleithrum. Scale bars: A, 1 cm; B, 2 mm.

observed pycnodontiforms the gular region exhibits no ossifications at all. This character corresponds to Nursall's (1996b) characters 10 *pro parte* and 22.

30 Branchiostegal rays

More than two (0); two, relatively large, in contact (1); two, thin, separated (2). Nursall restores two thin, separated branchiostegal rays for *Arduafrons* (Nursall 1999a: fig. 12, based on specimen NHML P8658). However, we consider that this region is not well enough preserved in any *Arduafrons* specimen to be certain of the number and arrangement of branchiostegal rays (coded as ?). *Gibbodon* (Fig. 19A) exhibits three broad branchiostegal rays, in close contact with each other, and the first one with the preopercular (primitive state). There are more than two branchiostegal rays in specimen JM SOS 3309a-b of *Mesturus*, the only specimen where this region is well preserved (state 0), although only two, thin and separated, are restored by Nursall (1999a: fig. 3). Also, specimen NHML P.8383 of *Mesturus leedsi* shows only one branchiostegal ray (the rest of the region is missing), but it is large, closely arranged to the preopercular (Fig. 15). All other pycnodontiforms present only two branchiostegal rays, but they are not alike in all genera. The rays may be relatively large and contact with each other throughout most of their length (e.g., *Proscinetes*, ML 15288; Fig. 19B), or, as in most cases, very thin and mostly or completely separated from each other (e.g., Fig. 17B). It is difficult to be certain whether, when not observed, the branchiostegal rays are actually absent or they simply lack due to preservational artefacts (similar case to the maxilla, character 35).
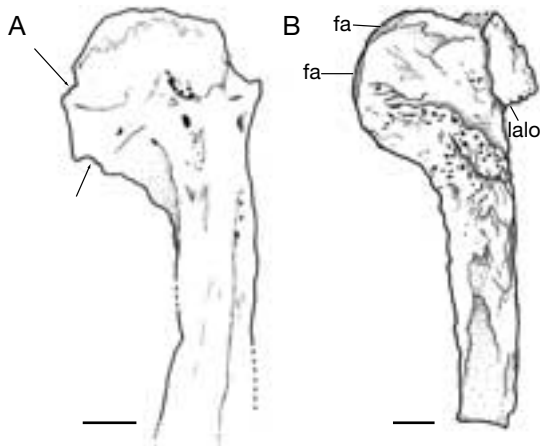
FIG. 18. — Camera lucida drawings of the hyomandibular as preserved in **A**, *Gyrodus hexagonus* (Blainville, 1818), specimen NHML P.3773a, transfer prepared. Left side, medial view. Arrows point the vestigial opercular process; **B**, *Macromesodon* aff. *M. bernissartensis* Traquair, 1911, specimen MCCM LH-16363, transfer prepared. Right side, lateral view. Abbreviations: **fa**, facet for articulation with the endocranium; **lalo**, last infraorbital. Scale bars: 2 mm.

DENTITION AND ORAL REGION
31 Premaxillary process
Profound (0); anteriorly placed, long, superficial (1). In the outgroup, the premaxillary process is profound and posterior to the tooth-bearing part of the bone, forming a cup for the ventral part of the nasal capsule (nasal process of *Amia*: see Grande & Bemis 1998: 80, 81, for a description and discussion of homologies; see Patterson 1973, 1975 and Thies 1988 for *Dapedium*), and is therefore placed in a profound plane. Among pycnodontiforms, the primitive state seems to be present only in *Gibbodon*, where the premaxilla is flat and expanded anteriorly (Fig. 19A), and no traces of any superficial process are present. However, the bone might be broken, and this character needs confirmation when additional specimens are found. In any case, the premaxilla of *Gibbodon* is very different to that of all other pycnodontiforms, including *Mesturus* (e.g., specimen MNHN CNJ 130). The premaxillary process in all observed pycnodonts but *Gibbodon* exhibits state 1: it is very elongated, thin, almost vertical and always superficial (e.g., Figs 10; 20A). The nasal capsule is formed mostly by the

mesethmoid, which is in the profound plane, and by the premaxillary process, which forms part of the surface plane, in continuity with the most superficial portion of the mesethmoid, closing the nasal capsule anterodorsally (Nursall 1996b: figs 5, 6; 1999a, fig. 7; 1999b, figs 3, 9; Figs 10; 20A) (state 1).

32 Morphology of premaxillary and dentary teeth
Small, triangular to conic (0); robust, columnar to hook-shaped (1); robust, barely incisiform (2); very flattened, fully incisiform (3). We have rearranged Nursall's (1996b) characters 1 *pro parte*, 25, and 40 into four distinct characters (numbers 32, 33, 34, and 42) by separating the number and the morphology of the premaxillary and the dentary teeth. In the present character we treat together the morphology of the teeth on the premaxilla and on the dentary because they are always similar. Some morphologies are, however, somewhat variable, individually and also probably ontogenetically, and are a little difficult to delimit. Teeth are robust, columnar-cylindrical to slightly hook-shaped (state 1) in *Arduafrons*, *Gyrodus*, *Mesturus* (e.g., Frickhinger 1994: figs 454, 454a; pers. obs.), *Paramesturus*, and *Trewavasia* (Fig. 20B). *Gyrodus* presents styliform teeth according to Lambers (1991) and Nursall (1996b), but some specimens, such as JM SOS 4303 and one figured by Frickhinger (1994: fig. 439), show more robust teeth, and an other specimen figured by Frickhinger (1994: figs 436-438) exhibits robust hook-shaped teeth. Further studies are necessary to determine if this variation found in *Gyrodus* is specific, ontogenetic, and/or individual. The crown of the teeth is small, yet quite robust, but slightly flattened, especially on their lingual side, (state 2) in *Apomesodon* n. gen. (Figs 14A, B; 21B), *Brembodus* (e.g., holotype), *Eomesodon*, *Gibbodon* (Fig. 19A), the two species of *Nursallia* where accessible (e.g., holotype of *N. veronae*, MCSNV II. D. 173), and *Abdobalistum thyrsus* n. gen., n. sp. These teeth could be considered barely incisiform, because they are eventually wider (side to side) than thick (labial to lingual), but they are clearly distinct
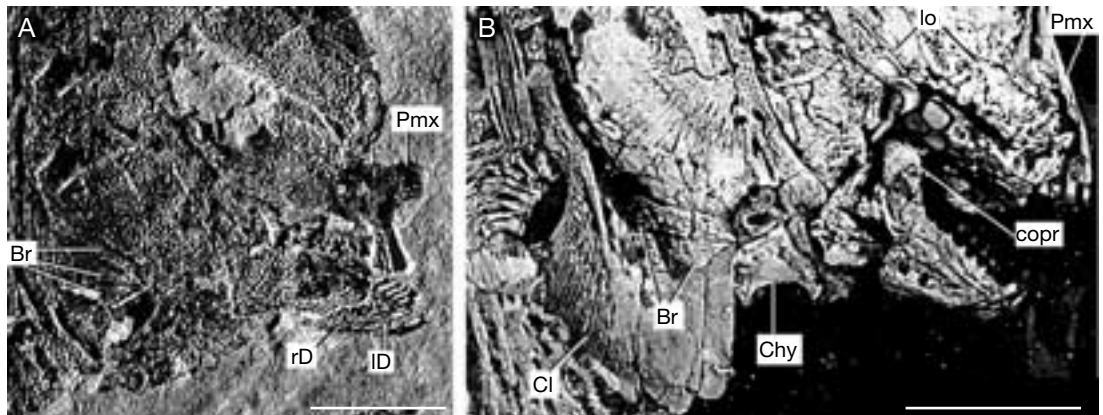
FIG. 19. — **A**, *Gibbodon cenensis* Tintori, 1981, holotype, MCSNB 3317, ventral region of the skull. Photo courtesy A. Paganoni, F. Confortini, M. Malzanni; **B**, *Proscinetes bernardi* Thiollière, 1852, specimen ML 15288, ventral region of the skull. Photo Serrette, under ultraviolet light. Abbreviations: **Br**, branchiostegal rays; **Chy**, anterior ceratohyal; **Cl**, cleithrum; **copr**, coronoid process; **Io**, infraorbitals; **ID**, left dentary; **Pmx**, premaxilla; **rD**, right dentary. Scale bars: A, 5 mm; B, 1 cm.

from what we consider fully incisiform. Premaxillary and dentary teeth are considered incisiform *sensu stricto* (state 3) only when they are extremely flattened, enlarged, with their labial side flat to slightly convex, and their lingual side markedly concave (e.g., Figs 10; 20A; 22C). They are flattened to the point that there the occlusal side is nearly dimensionless and reduced to just an edge. Initially, this edge is straight, but wear may lead to the occurrence of a small central concavity in the edge in larger specimens (e.g., *Proscinetes*, Fig. 20A). The first (anterior) incisiform tooth may be as large as the second (posterior) tooth (e.g., *Macromesodon*), or, most commonly, notably larger, both in the premaxilla and in the dentary (e.g., *Ocloedus subdiscus* n. comb., Kriwet *et al.* 1999; Fig. 22C; syntypes of *Oropycnodus ponsorti* n. comb.; *Pycnodus*; Fig. 10; and *Proscinetes*; Fig. 20A). The premaxillary and dentary teeth are more rarely observable in certain taxa, such as *Coccodus* and *Ichthyoceros*; still, specimens NHML P.4742 of the former genus and MCSNM V3045 of the latter exhibit typical fully incisiform teeth on the premaxilla. Unlike Tintori (1981) we consider that premaxillary and dentary teeth in *Brembodus* are not incisiform *sensu stricto* (see state 2 above).

33 Crown of premaxillary and dentary teeth

Simple (0); bifurcated (1). The crown of these teeth in *Gibbodon* is remarkable; it is clearly bifurcated, even twice branched in the premaxilla (Fig. 19A). It must be stressed that the concavity in the occlusal border of the incisiform teeth, due to wear, as described in the previous character, is not to be mistaken with an actually double or bifid cuspid (Fig. 19A). It does not seem possible that simple wear, which produces a large, but gently curved concavity (e.g., Fig. 20A), could be the cause of the extremely deep, narrow notch that produces the bifurcation.

34 Number of premaxillary teeth

More than three (0); three (1); two (2). In all pycnodontiforms, regardless of their number, premaxillary teeth are arranged in a single row. The upper jaw of *Trewavasia* was previously undescribed; we have observed three teeth (state 1) on transfer specimen NHML P.10700 (Fig. 20B), confirmed by observation of the right premaxilla on the other side of this specimen by transparency through the resin. There are two premaxillary teeth on specimen NHML P.4742 of *Coccodus* (state 2). According to Lambers (1991: 520) and Nursall (1999a: 158, fig. 3), there are three teeth on the premaxillary of
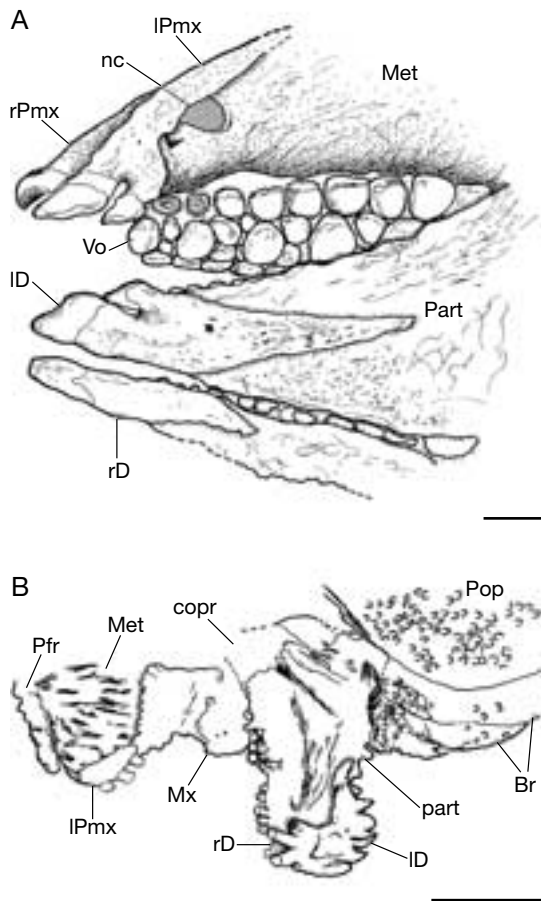
FIG. 20. — **A**, *Proscinetes* sp., camera lucida drawing of the oral region as shown by acid-treated specimen FSL 400047, left side, lateroventral perspective; **B**, *Trewavasia carinatus* (Davis, 1887), camera lucida drawing of oral region as shown by transfer specimen NHML P.10700. Left side, lateral view. Abbreviations: **Br**, branchiostegal rays; **copr**, coronoid process; **ID**, left dentary; **IPmx**, left premaxilla; **Met**, mesethmoid; **Mx**, maxilla; **nc**, nasal capsule; **Part**, prearticular; **Pfr**, prefrontal; **Pop**, preoperculum; **rD**, right dentary; **rPmx**, right premaxilla; **Vo**, vomer. Scale bars: 5 mm.

Mesturus, and that is what we have found in *M. leedsi* (NHML P.8384), but in *M. verrucosus* (the species restored by Nursall 1999a: fig. 3) there are only two premaxillary teeth in the cast of the holotype (NHML 49147) and on the specimen photographed by Frickhinger (1994: figs 454, 454A). This is also the case of *Mesturus* sp. MNHN CNJ 130. Pending further revision of this character in additional specimens of

M. verrucosus, we have coded this character as 1 and 2 simultaneously for *Mesturus*. We have not observed any pycnodontiform with a single premaxillary tooth.

35 Maxilla

Teeth-bearing, ornamented, elongated (0); edentulous, ornamented, ovoid (1); edentulous, ornamented, elongated (2); edentulous, unornamented, reniform (3); edentulous, unornamented, straight oral border (4); edentulous, unornamented, elongated oval (5). When observable, the maxilla of pycnodontiforms is always edentulous and generally unornamented (except for *Gyrodus* and *Mesturus*, states 1 and 2, respectively), and its morphology is highly variable. The most common type has a reniform shape (state 3: *Macromesodon macropterus*, *Neoproscinetes*, *Pycnodus*, and *Tepexichthys*, the latter with a notch). The other two morphologies are found only in one genus each (*Stemmatodus* and *Iemanja*, states 4 and 5, respectively). The interpretation of the maxilla of *Ichthyoceros* by Gayet (1984) is not confirmed by our observations, as we think that the bone she identified as such may be an infraorbital. Some specimens of *Brembodus* and the holotype of *Gibbodon* present remains of a maxilla, but its morphology is impossible to establish. Another problem that we have found is about the eventual absence of this bone; in pycnodontiforms, it is a loose, thin element, so that, when not observable, it is impossible to know whether it is really absent or simply lost during fossilization. This is the case of *Coccodus*, *Coelodus saturnus, Eomesodon, Micropycnodon, Nursallia veronae, Ocloedus subdiscus* n. comb., *Palaeobalistum orbiculatum, Oropycnodus ponsorti* n. comb., *Paramesturus, Proscinetes*, and *Trewavasia*. This character corresponds to Nursall's (1996b) characters 3, 33, 30, 46 *pro parte*, 123.

36 Morphology of vomerine teeth

Villiform to conic (0); circular to subcircular contour (1); oval contour (2); reniform contour (3); triangular contour (4). All observed pycnodontiforms possess crushing teeth on the vomer, including *Trewavasia*: it is doubtful in Gayet's
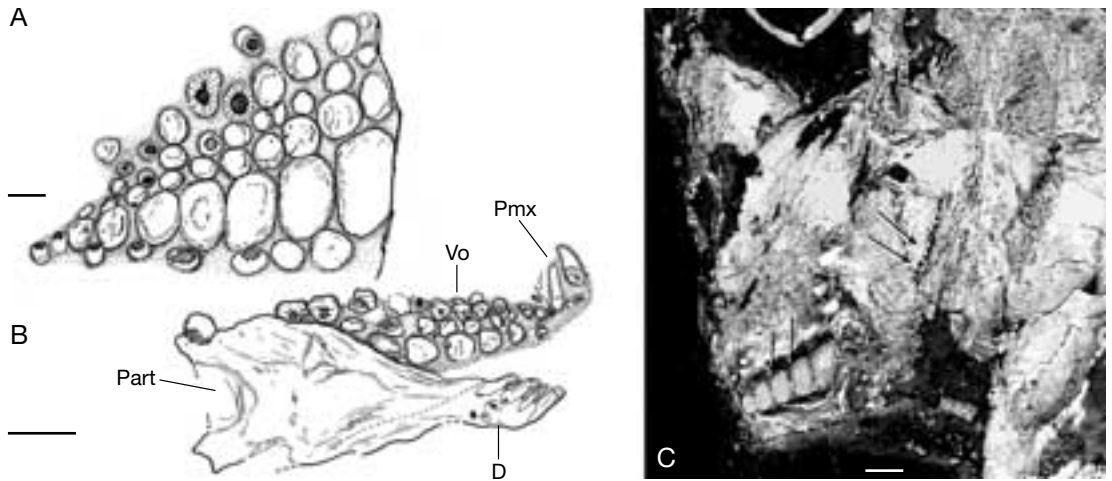
Fɪɢ. 21. — **A**, camera lucida drawing of the prearticular teeth as shown by the holotype of ? *Eomesodon barnesi* (Woodward, 1906), NHML 12511, right side, occlusal view; **B**, camera lucida drawing of the oral region of *Apomesodon surgens* n. gen., n. sp., specimen ML 15433, holotype, showing mostly the teeth on the dentary and on the vomer, right side, lateral view; **C**, anteroventral region of the skull of *A. surgens* n. gen., n sp., specimen ML 15660, showing crenulated oval teeth in occlusal view on the right prearticular (pointed by arrows on the left) and some small branchial teeth (pointed by arrows on the right), left side, lateral view. Abbreviations: **D**, dentary; **Part**, prearticular; **Pmx**, premaxillary teeth; **Vo**, vomerian teeth. Scale bars: 2 mm.

(1984) figures of specimen MNW 1965/636, where the teeth appear very partially depicted, but they are better observable when the specimen is inclined. Specimen NHML P.10700, where the vomer of the right side is seen by transparency of the resin, confirms the presence of real crushing teeth in this genus. The contour of the crushing vomerine teeth of pycnodontiforms in occlusal view is somewhat variable, and this variation needs to be established at a specific and individual level. This variation is more marked for some genera (e.g., isolated vomers assigned to *Gyrodus*). For our analysis, we have considered state 1 for circular to subcircular contour, occasionally slightly irregular: e.g., *Apomesodon gibbosus* n. comb., Fig. 14B; *Gyrodus* NHML 37792; holotype of *Nursallia veronae*; *Pycnodus*, Fig. 10; *Stemmatodus*, specimen NHML P.12006. State 2 is for an oval contour at least for the most posterior teeth of the principal row: e.g., *Apomesodon surgens* n. gen., n. sp., posteriormost teeth on principal row of specimen on Fig. 21B; *Coelodus saturnus*, Fig. 22A; *Ocloedus subdiscus* n. comb., Fig. 22B; *Proscinetes*, posteriormost teeth on principal row of specimen on Fig. 20A. In these

cases, the longest axis of the tooth is generally, but not always, the axis transverse to the longitudinal row. State 3 is for reniform teeth, at least for the most posterior ones of the principal row. Among the articulated specimens that we have observed, reniform teeth on the vomer are only exhibited by *Iemanja* (holotype, MNHN BCE 166). State 4, teeth triangular with softened rounded corners, is found only in *Coccodus* (e.g., Fig. 22D and NHML P.4742) and *Ichthyoceros* (specimen MCSNM V3045A-B). Note that the vomerine dentition of these two genera is described, and figured for *Coccodus*, for the first time in the present paper. This character corresponds to Nursall's 1996b character 2 *pro parte*.

37 Arrangement of vomerine teeth in regular rows
Absent (0); present (1); absent anteriorly, present posteriorly (2). The teeth on the vomer and on the prearticular are normally arranged in rows in pycnodontiforms. Some cases where the regularity of the anteriormost teeth is slightly disturbed are regarded as individual variations that affect the regular arrangement of some teeth in some rows, but do not form large, completely patchy
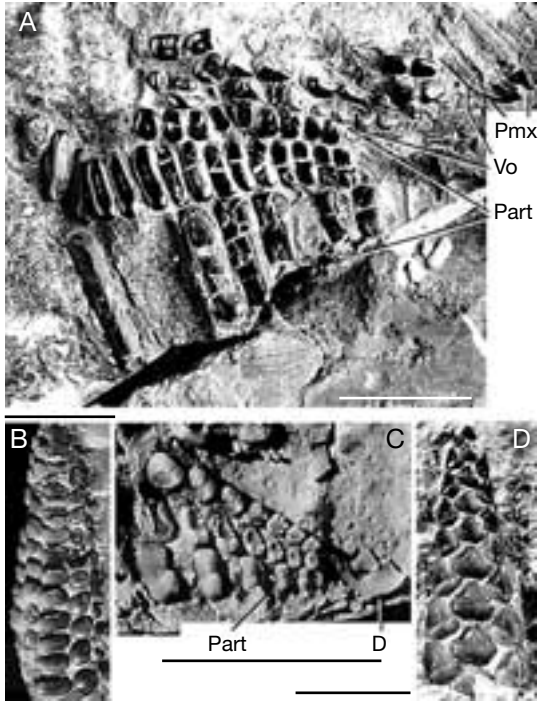
FIG. 22. — **A**, *Coelodus saturnus* Heckel, 1854, oral region of the holotype, NMW.XXXIII.2, right side, lateral view, with left prearticular in occlusal view. Photo Schumacher, courtesy Ortwin Schultz.; **B**, *Ocloedus subdiscus* n. comb., vomer of specimen MGSB 20659. Photo Serrette (from Wenz 1989b); **C**, *Ocloedus subdiscus* n. comb., lower mandible of specimen MGSB 20376a, left side, occlusal view. Photo Serrette (from Kriwet *et al*. 1999); **D**, *Coccodus armatus* Pictet, 1850, vomer in occlusal view (private collection). Photo Serrette. Abbreviations: **D**, dentary teeth; **Part**, prearticular teeth; **Pmx**, premaxillary teeth; **Vo**, vomerian teeth. Scale bars: A, 2 cm; B, 1 cm; C, D, 5 mm.

surfaces. This is also Longbottom's (1984) interpretation for some isolated *Pycnodus* dentitions, such as *P. maliensis* on her figs 3-8 and *P. zeaformis* on her figs 9-14. The arrangements of the vomerine and prearticular teeth in rows are treated in two distinct characters (this one and number 44) because they are not linked in the cases where they are totally or partially patchy (e.g., *Iemanja*). For the present character, the teeth on the vomer are arranged forming rows (state 1) in all observed pycnodontiforms except *Iemanja*, where the vomerine teeth are patchy anteriorly and arranged in rows posteriorly (Wenz 1989a; holotype, MNHN BCE 166; state

2). This character corresponds to Nursall's 1996b character 2 *pro parte*.

38 Number of vomerine tooth rows
Not arranged in rows (0); 3 (1); 5 (2). The number of tooth rows on the vomer is independent from the number of tooth rows on the prearticular, and are consequently treated as distinct characters (see character 45). All pycnodontiforms possess either three or five regular tooth rows on the vomer, with the exception commented below. Contrary to Woodward (1895a: 198, 266), who suggests that *Coccodus* has five tooth rows on the vomer, this genus does present only three of them (Fig. 22D). *Gibbodon* has three rows; the central one has very developed teeth, and the lateral one that is visible has small, pedicellated teeth (Fig. 19A). The only specimen of *Ichthyoceros* that shows the vomer in occlusal view is MCSNM V3045, exhibiting three tooth rows (state 1). *Mesturus leedsi* presents three regular rows plus two irregular rows lateral to the principal row (e.g., Woodward 1896; pers. obs. on NHML P.8385; coded as 2). The only studied articulated specimen of *Proscinetes* showing the vomer in occlusal view shows only three rows on this bone (Fig. 20A). There are probably three rows on the vomer of *Nursallia veronae*, as, although the bone is incompletely exposed, there does not seem to be room enough for five rows. Concerning state 2, the presence of five tooth rows on the vomer of articulated specimens of *Gyrodus* is confirmed by specimen NHML 37792. This state has also been coded for *Coelodus saturnus*. Its vomer (Fig. 22A) is only partially visible, and some teeth are missing. However, four rows can be identified at least in the anterior region, and the largest teeth seem to be those of the third row, which would be the median one. We can consequently deduce that the total number of rows on the vomer of *Coelodus saturnus* is five (state 2). The number of rows in *Trewavasia* (NHML P.10700, the only specimen where this region is accurately accessible, on the right side, by transparency of the resin) cannot be established, as the vomer is very incompletely exposed, and mostly in lateral view.

Micropycnodon is coded for the type species, *M. kansasensis* (state 2); *M. gaynaisensis* is an exceptional case of seven tooth rows on the vomer (Nursall 1999a).

39 Number of teeth in principal vomerine tooth row
Teeth not arranged in rows (0); seven or less (1); eight or nine (2); 10 or more (3). The number of teeth on the vomer and prearticular must be regarded with precaution. This number increases during ontogeny; for example, larger specimens of *Macromesodon* aff. *M. bernissartensis* from Las Hoyas show 11-12 vomerine teeth, whereas the juvenile specimen MCCM LH 91-110a exhibits at most seven (Poyato-Ariza & Wenz work in progress). This phenomenon was previously mentioned by Blot (1987) for *Pycnodus apodus*, and is herein confirmed by our personal observations. We have therefore counted the number of vomerine and prearticular teeth preferentially on the largest available specimens. Additionally, it is usually difficult to count an exact number of teeth due to the preservation conditions (e.g., anterior or posterior portions of the bone missing or concealed under other bones), and due also probably to individual variations that are not established at present. We have counted the teeth on the principal row whenever possible, but most articulate specimens show the tooth rows only laterally, especially in the case of the vomer. Consequently, we occasionally counted the number of teeth on a lateral row, bearing in mind that it may be slightly different (usually higher) from the number of teeth on the principal row. For these reasons we arranged the derived states on the basis of conservative intervals, rather than exact numbers. Available vomers exposed in occlusal view of *Brembodus* are probably incomplete anteriorly (e.g., remains of anterior teeth on MCSNB 4895). Specimens MCSNB 4892 and 4895 show at least seven teeth on the principal row; the latter has at least eight on the lateral row. However, the lateral row exhibits at least nine in MCSNB 4902, and at least 10 in the holotype and in specimens MCSNB 4899 and 4900. We therefore estimate that the principal row has more than seven teeth, so the character has been coded as 2 (eight or nine teeth). The holotype of *Gibbodon* has eight teeth on the main row of the vomer (Fig. 19A), although there might be one more anteriorly (state 2). Both specimens labelled MNHN JRE 39 of *Stemmatodus* exhibit eight or nine teeth on the principal row of the vomer (state 2). The presence of more than 10 teeth on the main row of the vomer in articulated *Gyrodus* is confirmed by specimen NHML 37792, and in articulated *Mesturus* by specimen NHML P.8385 of *M. leedsi,* and by the lateral row of NHML 37023 of *M. verrucosus* (state 3). The vomer of *Ichthyoceros* is very long; specimen MCSNM V3045 shows at least 13 teeth on the main row, plus those of the posterior part of the bone, which is concealed by the prearticulars (state 3). *Trewavasia* (NHML P.10700, the only specimen where the vomer is accessible) shows 11 teeth on the partially preserved lateral row, and at least 10 teeth on the also partially preserved main row, as seen by transparency of the resin on the left side (state 3).

40 Alternation of teeth on main vomerine tooth row
Absent (0); present (1). The teeth of the vomerine main row normally form a series of regularly increasing size in cephalocaudal sense. However, in *Neoproscinetes* (Nursall & Maisey 1991; pers. obs.) there is a regular alternation of one large and two small teeth within this row. Saint-Seine (1949) illustrates vomers presenting this character in four nominal species of *Proscinetes* from the Kimmeridgian of Cerin (*Microdon* in that paper; Saint-Seine 1949: figs 42, 47, 48, 50, pls 8B, 9D, E, 11B, C; see also, for instance, Woodward 1918: pl. 14, fig. 5). They are all, however, isolated vomers. The only articulated specimen of *Proscinetes* showing the vomer in occlusal view that we could study confirms, in any case, the presence of this character in this genus also (Fig. 20A). No other observed pycnodontiform presents such alternation.

41 Dentary
Well developed, relatively broad (0); small, posteriorly elongated and simple (1); small, posteriorly

bifid (2). In all pycnodonts the dentary is considerably reduced, but the precise state of this character is seldom observable with clarity, since it requires a good preservation of the posterior end of the dentary in ventro-lateral view. It could not be verified, for instance, in *Apomesodon gibbosus* n. comb., *Arduafrons*, *Micropycnodon*, *Palaeobalistum orbiculatum*, or *Paramesturus*. Most pycnodontiforms where the region is clearly seen show an elongated, single end of the dentary (e.g., Figs 10; 14B; 20A, B). The presence of the derived state of this character in *Gyrodus* is figured by Nursall (1996b: fig. 15), but no label of the illustrated specimen is indicated; we have clearly observed it in acid prepared specimen NHML P.4633 (state 2). The specimens NHML P.8383 of *Mesturus leedsi*, NHML 37025 of *M. verrucosus*, and MNHN CNJ 130 of *M.* sp. also exhibit a posteriorly bifid dentary, although it is relatively broader than in *Gyrodus* (state 2). This character corresponds to Nursall's (1996b) characters 26 (state 2 herein) and 41 (state 1 herein).

42 Number of dentary teeth

More than five (0); five (1); four (2); three (3); two (4). We have separated the number of the dentary teeth from that of the premaxillary teeth because they are different in *Apomesodon surgens* n. gen., n. sp. (four and two, Fig. 21B), *Brembodus* (four and three, respectively), *Gibbodon* (five and three; Fig. 19A), *Gyrodus* (four and two), *Mesturus* (two to three and four to five, respectively), and *Neoproscinetes* (three and two). Specimen NHML P.8383 of *Mesturus leedsi* shows four teeth on the dentary. In turn, specimen NHML P.37024 of *M. verrucosus* and specimen MNHN CNJ 130 of *Mesturus* sp. exhibit five dentary teeth, although there are four in Nursall's restoration of the type species (1999a: fig. 3). This character is therefore coded as 1 and 2 for *Mesturus*, pending study of the variation in *M. verrucosus*. Gayet (1984: fig. 2) restores six small teeth on the dentary of *Trewavasia*. The specimen illustrated by Gayet (1984), NMW 1965/536 actually shows three teeth on the left dentary, plus a gap between the

second and the third teeth. This gap is a portion of the border of the bone without the slightest trace of teeth or tooth bases. All other teeth visible in this specimen correspond to the right dentary (which is not accurately visible) and to the anterior part of the retroarticulars. We think that this genus has only three styliform to hook-shaped teeth on the dentary, as confirmed by transfer prepared specimen NHML P.10700 (Fig. 20B; there are two complete teeth plus the broken base of the third tooth; this number of teeth is confirmed by observation of the dentary of the other side of the same specimen by transparency of the resin). The gap mentioned above for the NMW specimen could be an individual variation or due to preservation; pending confirmation, we have coded this character as 3 (three teeth) for *Trewavasia*. The most common number of dentary teeth is two; they are visible, for instance, on specimen NHML P.4742 of *Coccodus*, on *Ocloedus subdiscus* n. comb. (Kriwet *et al.* 1999; Fig. 22C); on specimen MCSNM 3045A-B of *Ichthyoceros*; and on syntype NMW 1854/XXXIX/38 of *Oropycnodus ponsorti* n. comb. (state 4).

43 Morphology of prearticular teeth

Villiform to conic (0); circular contour (1); oval contour (2); sigmoid to drop-shaped contour (3); extremely elongated in contour (4). All pycnodontiforms present crushing teeth on the prearticular, but their contour present remarkable variations, as for the vomerine ones. We have nonetheless separated the morphology of the contour of the vomerine and of the prearticular teeth into two distinct characters (number 36 and the present one) because oval teeth on the prearticular are more common than on the vomer. A number of pycnodontiforms show only circular to subcircular teeth on the vomer, but oval teeth, at least the most posterior ones of the principal row, on the prearticular. This is the case of *Abdobalistum thyrsus* n. gen., n. sp., *Apomesodon* n. gen. (Figs 14B; 21C), *Coccodus*, *Eomesodon* (Fig. 21A), *Gyrodus*, *Nursallia* ? *gutturosum*, *Palaeobalistum orbiculatum*, *Pycnodus* (Fig. 10), and *Tepexichthys*. All observed pyc-

nodontiforms possess crushing teeth on the prearticular, including *Trewavasia*. Although it is doubtful in this genus according to Gayet's (1984) figures, where the teeth might be mistaken for the strong ornamentation of the bones, the presence of real crushing teeth on the prearticular of *Trewavasia* is confirmed by specimen NHML P.10700 on the left side (Fig. 20B), and also on its right side, seen by transparency of the resin; their contour in occlusal view is circular (state 1). Many dentitions assigned to *Gyrodus* show variation, as teeth on isolated prearticulars are mostly subcircular, but teeth on some articulated specimens (e.g., Frickhinger 1994: fig. 439; pers. obs. on NHML 37792) are oval (state 2). The prearticular dentition of *Ichthyoceros* is described and figured herein for the first time. Specimen MCSNM V3045 (Fig. 23A) exhibits state 3 in the teeth of the main row, with teeth that slightly vary from barely sigmoid to drop-shaped in contour. These teeth are arranged obliquely to the main axis of the bone and of the row, and present a tapering medial edge. Other than this genus, such teeth are found only in *Anomoeodus* (Dixon 1850: pl. 33; Woodward 1909: pl. 34; Kriwet 1999: fig. 7; pers. obs. on NHML 25780) among the articulated specimens studied. We have not observed any articulated pycnodont specimen showing reniform teeth on the prearticular. Among articulated pycnodonts, state 4 is found in *Coelodus saturnus* only. The teeth on the prearticular of the holotype (Fig. 22A) are extremely elongated in transversal sense (that is, perpendicularly to the longitudinal axis of the bone). The medium-sized teeth of the main row are about three times longer than wide (e.g., 16.9 mm long/4.9 mm wide), and the biggest ones are about five times longer than wide (e.g., 22.7 mm long/4.3 mm wide). The teeth of the main row are arranged in the same direction than the teeth of the adjacent lateral row, their major axis being parallel. This character corresponds to Nursall's (1996b) character 2 *pro parte*.

44 Arrangement of prearticular teeth in rows
Absent (0); present (1); absent anteriorly, present posteriorly (2). The teeth on the prearticular are
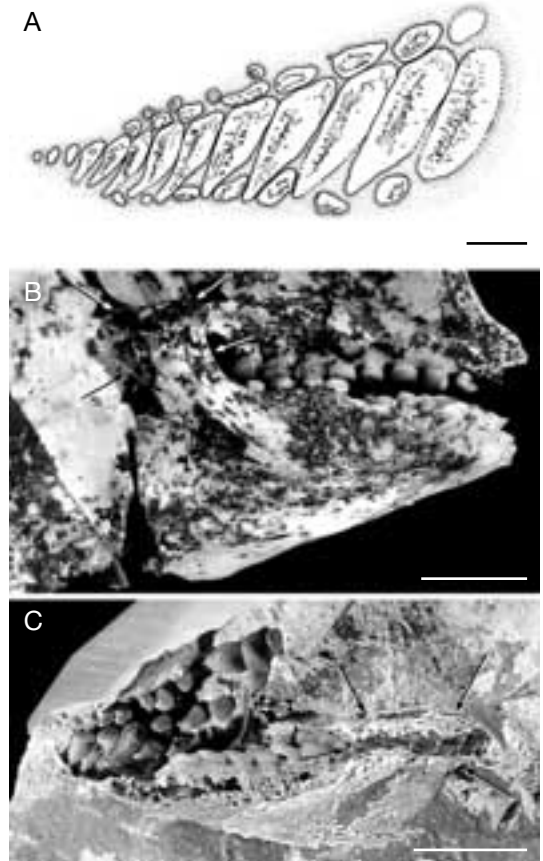
Fig. 23. — **A**, camera lucida drawing of the prearticular dentition as preserved in specimen MCSNM V3045A of *Ichthyoceros* Gayet, 1984. The anteriormost three teeth of the main row, as well as a few lateral teeth, have been restored from a camera lucida drawing of their impressions in the counterpart, MCSNM V3045B; right side, occlusal view; **B**, **C**, coronoid process, pointed by arrows, of *Neoproscinetes* Figueiredo & Silva Santos, 1987; **B**, specimen MNHN BCE 104, right side in lateral view, and *Coccodus* Pictet, 1850; **C**, specimen MNHN 1939/12, left side in lateral view (plus right prearticular visible in occlusal view). Photos Serrette. Scale bars: A, 1 mm; B, C, 1 cm.

arranged in rows in all observed pycnodontiforms, except in *Iemanja* (Wenz 1989a; pers. obs.), where they form a completely patchy surface (state 0), and in *Anomoeodus* (Kriwet 1999; pers. obs.), where they form rows in the posterior region, and are patchy in the anterior region (state 2).

45 Number of prearticular tooth rows
Not arranged in rows (0); two (1); three (2); four (3); five or six (4). The observed articulated

pycnodontiforms present two to five regular tooth rows on the prearticular. Two rows are present only in *Coccodus* and *Stenamara* (state 1). Three prearticular tooth rows (state 2) is the most common number (e.g., *Coelodus saturnus*, Fig. 22A; *Ocloedus subdiscus* n. comb., Fig. 22C; *Ichthyoceros*, Fig. 23A; *Stemmatodus*, specimen NHML P.12006). The presence of four tooth rows on the prearticular in *Gyrodus* is confirmed by articulated specimens NHML P.3774 and 37792 (state 3). Specimens MCSNB 4894 and 4932 of *Brembodus* have five tooth rows, the internal lateral row being irregular (it disappears anteriorly) on the right prearticular, and regular on the left prearticular (state 4). Kriwet (1999) presents a diagnosis of the prearticular of *Anomoeodus* where "medial or inner teeth" form "one to five more or less irregular rows"; "lateral or outer teeth" form "two or more rows", and "additional intercalated teeth between the tooth rows may occur" (Kriwett 1999: 217); this is rather confusing, probably due to the species *Anomoeodus nursalli*. We have coded this character as 4 for *Anomoeodus* on the basis of our personal observations on the most complete specimen we have seen, NHML 25780, *A. angustus* (which consists of both prearticulars and part of the ventral region of the body, and is figured by Kriwet 1999: fig. 7). It shows irregularities in the most lateral and in the medial rows, which are quite inconstant, but, in any case, there are at least five rows (state 4). *Mesturus leedsi* possesses three regular rows plus two irregular rows between the principal and the lateral ones (e.g., Woodward 1896; pers. obs. on NHML P.8383 and 8385) (state 4). The number of rows in *Trewavasia* (NHML P.10700, the only specimen where this region is accessible) cannot be established, as the prearticular is exhibited in lateral view on the left side (Fig. 20B), and imperfectly preserved on the right side. This character corresponds to Nursall's (1996b) character 2 *pro parte*.

46 Number of teeth on main prearticular tooth row
Teeth not arranged in rows (0); seven or less (1); eight or nine (2); 10 or more (3). We have separated the number of teeth on the prearticular and on

the vomer because they are not necessarily the same. For instance, there are eight prearticular teeth in *Ocloedus subdiscus* n. comb. and *Proscinetes*, but the number of vomerine teeth is 13 for the former and nine for the latter. See character 39 above; the criteria presented there concerning the ontogenetic increase of teeth number and the individual variations between the main and the lateral tooth rows are also applied to the present character. State 1, seven or fewer teeth on the main prearticular row, is found only in *Micropycnodon*, *Neoproscinetes*, and *Oropycnodus ponsorti* n. comb. Tintori (1981) does not give a number of prearticular teeth for *Brembodus*; specimen MCSNB 4894 has only seven teeth on the prearticulars of both sides (as illustrated by Tintori 1981: pl. 96, fig. 3), but these bones are probably incomplete posteriorly. In addition, nine teeth on the main prearticular row of specimen MCSNB 4932 can be counted. We have therefore coded this character as 2 for *Brembodus*. As additional information for the correspondence of the number of teeth on the lateral and on the main row in this genus, specimen MCSNB 4899 has at least eight teeth on the main row, which is concealed posteriorly; the lateral row is complete, exhibiting 12 teeth that correspond to the eight teeth of the main row, plus three more teeth beyond the level of the 8th tooth of the main row. The presence of eight to nine teeth on the main row of the prearticular in articulated *Gyrodus* is confirmed by specimen NHML 37792 (state 2). The holotype of *Nursallia veronae* has about nine teeth on its visible lateral row (coded as 2). Kriwet (1999) does not give a number of prearticular teeth in his diagnosis of *Anomoeodus*; specimen NHML 25780 of *A. angustus* shows eight teeth on the main row at the regularly arranged part of the prearticular (see character 44), which, added to the teeth of the patchy part, accounts for at least 10 teeth (state 3). The holotype of *Coelodus saturnus* exhibits 11 teeth (state 3), including the negative imprints of the missing teeth (Fig. 22A). This number is confirmed by the counterpart, the isolated dentition of the right side, as illustrated by Heckel (1856: pl. 3, fig. 2; it is currently housed in the Prirodoslovni Museum, Ljubljana, Slovenia – Ortwin pers. comm. 2000 – but was not directly

observed by the authors). There are at least 13 teeth on the main row of *Ichthyoceros*, as shown by specimen MCSNM V3045 (Fig. 23A); these teeth are also seen with difficulty by transparency of the resin on the right side of the transferred holotype. Specimen MNHN JRE 41 of *Stemmatodus* exhibits at least 10 teeth on the principal row of the prearticular, so it is also coded as three (10 or more). Specimen NHML P.10700 of *Trewavasia*, the only one of this genus where the prearticular is accessible, shows at least 11 teeth on the partially preserved lateral row (Fig. 20B; state 3).

47 Coronoid process

Low, curved (0); high, straight dorsal border (1); high, club-shaped (2); low, straight dorsal border (3). In the outgroup (except *Pteronisculus*, where it is absent), the coronoid process is low and small, formed by a curvature of the posterodorsal border of the mandible. Among pycnodontiforms, the primitive state (coronoid process practically absent) is found only in *Arduafrons* (Museum Bergér specimen) and *Ichthyoceros* (holotype, MNHN HAK 106). As pointed by Nursall (1996b: character number 8; 1999b), the coronoid process of pycnodontiforms (with the exceptions just mentioned) is formed by the prearticular, probably fused to the coronoid; the process is very stout and arises laterally. However, we have found that there are different sizes and morphologies of the coronoid process among pycnodontiforms. It is normally a strong posterolateral projection with straight or very slightly incurved anterior and posterior border; the dorsal border is generally more or less straight, usually strengthened (state 1; e.g., specimens MCSNB 4899, 4900, and 4932 of *Brembodus*). The dorsal and posterior borders usually form an acute angle (e.g., *Oropycnodus ponsorti* n. comb. MNHN MTA 49, NHML P.30045, Fig. 17A; *Stemmatodus* MNHN JRE 36), or are eventually gently curved (e.g., *Mesturus leedsi*, pers. obs.). In some cases, namely *Macromesodon* aff. *M. bernissartensis*, *Micropycnodon* (Hibbard & Dunkle 1946: pl. 8), *Neoproscinetes* (e.g., Figueiredo & Silva-Santos 1990: fig. 1, pl. 1, fig. 3), and *Tepexichthys* (Applegate 1992), it is club shaped (state 2), with

the anterior and posterior border concave, forming a neck, and the dorsal border rounded, forming a head (Fig. 23B). Finally, *Coccodus* presents state 3: a stout but low coronoid process, whose dorsal border is at the level of the prearticular teeth. This process is diagonally arranged, its dorsal border being straight and strengthened, forming an acute angle with the posterior border (MNHN 1939-12; Fig. 23C).

Note for characters 48-51

The ornamentation and accessory structures on the crushing teeth of the pycnodontiforms are to be regarded with caution. They probably show specific and individual variations, and, in addition, we think that the grinding activity of the crushing dentition during lifetime has a wearing effect that is usually quite difficult to evaluate. For instance, the strong, asymmetric ridges on some vomerine teeth of *Macromesodon* aff. *M. bernissartensis* LH 13483, and the gentle, asymmetric ridges on some dentary teeth of *Macromesodon bernissartensis* IRSNB 1218 A, are all interpreted as heterogeneous, individual results of the grinding effect, with no taxonomic value. Bearing this problem in mind, we have coded for a certain ornamentation or accessory structure on the vomerine and prearticular teeth only when it is well developed, regular, and broadly present on the specimens of the corresponding taxon. Papillae, crenulations, ridges, and grooves are treated as distinct characters because they occur in different combinations, not necessarily linked (see data matrix).

48 Central papilla on vomerine and prearticular teeth

Absent (0); present (1). Papillae on the teeth (state 1) of articulated specimens have been observed only in *Gyrodus*, whose teeth usually exhibit one well marked central papilla (e.g., Lambers 1991; although they look smooth on Frickhinger 1994: fig. 439; pers. obs.).

49 Crenulations on vomerine and prearticular teeth

Absent (0); occasionally present, weak (1); present in most teeth, strong (2). Some apparently

non-crenulated teeth may be the result of wear on weakly-crenulated teeth. Consequently, this character has been coded as 0 when no crenulations at all have been observed in any teeth of any individual of the corresponding taxon. The state 1 is for those taxa where at least one observed specimen show weak crenulations, often in a few teeth only, that are generally the posteriormost, unworn ones: *Apomesodon* n. gen. (Fig. 21B, C), *Anomoeodus* (Kriwet 1999; pers. obs.), *Coccodus* (e.g., NHML P.4742; MHNH HDJ 539; Fig. 22D), *Ocloedus subdiscus* n. comb. (Wenz 1989b; Kriwet *et al.* 1999; pers. obs. on MGSB 20659; Fig. 22B), *Eomesodon* (NHM 19864; Fig. 21A), vomer of the holotype of *Gibbodon* (Fig. 19A), *Ichthyoceros* (Gayet 1984; pers. obs. on MNHN HAK 298, on the holotype, MNHN HAK 106, splenial teeth seen by transparency, and on MCSNM V3045, Fig. 23A), *Macro-mesodon* aff. *M. bernissartensis* (MCCM LH 17345), *Abdobalistum thyrsus* n. gen., n. sp. (Blot 1987; pers. obs. on NHML P.9830), *Oropycno-dus ponsorti* n. comb. (prearticular of NHML P.30037 and 30045), and *Stemmatodus* (e.g., MNHN JRE 39, JRE 42; Fig. 12). State 2 consists of highly developed crenulations on most teeth. It is present, whenever teeth are observable and not excessively worn, in *Gyrodus* (Agassiz 1833: vol. 2, pls 67, 68; pers. obs., e.g., MNHN SLN 208; teeth are apparently smooth on Frickhinger 1994: fig. 439, probably due to wear), *Mesturus* (Woodward 1896, pers. obs.), *Micropycnodon* (Hibbard & Dunkle 1941: 172; Dunkle & Hibbard 1946: 170, pl. 8), and *Tepexichthys* (Applegate 1992).

50 Ridge on vomerine and prearticular teeth
Absent (0); present (1). Among the articulated studied pycnodonts, a strong ridge on the vomerine and prearticular teeth is present only in *Mesturus* (Woodward 1896; pers. obs.), where they are quite conspicuous.

51 Groove on vomerine and prearticular teeth
Absent (0); present (1). Among the studied articulated pycnodontiforms, a central groove on the crushing teeth is present in: *Anomoeodus* (Kriwet 1999; pers. obs.), *Coccodus* (e.g., NHML P.4742; MHNH HDJ 539; Fig. 22D), *Coelodus saturnus* (holotype, most teeth of the second lateral row and last four teeth visible in occlusal view on the first lateral row of the prearticular; Fig. 22A), *Ocloedus subdiscus* n. comb. (Wenz 1989b; Kriwet *et al.* 1999; pers. obs. on MGSB 20659 and MNHN MSE 965; Fig. 22B), *Gyrodus* (e.g., MNHN SLN 208, but see preceding character for comments on Frickhinger 1994: fig. 439), *Ichthyoceros* (Fig. 23A), *Mesturus* (Woodward 1896; pers. obs.), *Micropycnodon* (described as exhibiting "an apical pit" by Dunkle & Hibbard 1946: 170), and *Abdobalistum thyrsus* n. gen., n. sp. (Blot 1987: pl. 28; pers. obs. on NHML P.9830).

AXIAL SKELETON
52 Number of vertebrae
35 or more (0); 30-34 (1); 25-29 (2); 24 or less (3). We have consistently counted the neural arcocentra and/or the corresponding spines excluding those supporting caudal fin rays. According to Nursall (1999a), there are 34 vertebrae in *Arduafrons*, but this number does not include those of the long caudal pedicle, so that the total number falls above 35 (pers. obs.; coded as 0). *Ocloedus subdiscus* n. comb. (Fig. 2B) was reported to have 39 vertebrae by Wenz (1989b), but it in fact shows 28-29 (state 2). This must be due to a printing error, as the sum of the axial elements as reported by the same author (Wenz 1989b: 517) is 29, which is confirmed by our personal observations.

53 Neural and haemal corresponding arcocentra
Not surrounding notochord (0); surrounding notochord partially (1); surrounding notochord completely (2). Most pycnodontiforms present the primitive state, where the neural and haemal corresponding arcocentra do not surround the notochord at all, the notochordal canal being wide open (e.g., Fig. 24). In *Coccodus*, *Iemanja* (Fig. 25), *Neoproscinetes*, *Abdobalistum* n. gen., and *Trewavasia*, the neural and haemal arcocentra are somewhat enlarged and surround the notochord partially, constricting the notochordal

canal, which is, nonetheless, still open (state 1). Only in *Brembodus*, *Nursallia*? *goedeli* (Fig. 26A), *Nursallia*? *gutturosum* (Fig. 26B), *Nursallia veronae* (Fig. 26C), *Oropycnodus ponsorti* n. comb., and *Pycnodus* are the neural and haemal arcocentra in adult specimens very expanded, contacting with each other, and consequently constricting the notochord strongly in such a way that the notochordal canal is discontinuous in lateral view (state 2). The holotype of *Brembodus* clearly shows this character state in the caudal region, but it cannot be checked in the abdominal region; the specimens MCSNB 4896 and 6086a exhibit arcocentra that do not constrict the notochord, but these individuals are juvenile to subadults; larger individuals MCSNB 4901 and 4933 show arcocentra that constrict the notochord partially to completely. There seems, then, to occur an ontogenetic change in this character in *Brembodus*. This is also the case of *Pycnodus*, where the arcocentra of younger specimens are less expanded and do not surround the notochord (pers. obs.; see also Blot 1987: pls 1-10). We have therefore coded this character as 2 for *Brembodus* and *Pycnodus*. In some specimens of *Proscinetes*, a few arches, about 5-6, of the caudal region are occasionally more expanded than the rest, and 3-4 of them may surround the notochord completely, whereas the rest of the arches do not constrict the notochord at all. For instance, a large specimen of *Proscinetes bernardi* from Cerin (ML 15288) exhibits expansion on four caudal neural and haemal arches, two of which eventually surround the notochord (Fig. 24B). A subadult individual of *Proscinetes egertoni*, also from Cerin (ML 15390), does not show any trace of this phenomenon, and neither do the observed specimens of *P. elegans* from Bavaria (e.g., JM 1941.12a). However, Lambers (1991: fig. 22) illustrates this phenomenon in both *Proscinetes bernardi* and *P. elegans* (unspecified localities). At this moment, it is difficult to know if this phenomenon is due to specific, ontogenetic, and/or individual variation in this genus. In any case, we have coded the character as 0 for *Proscinetes*, because the vast majority of the arcocentra in all observed specimens, including
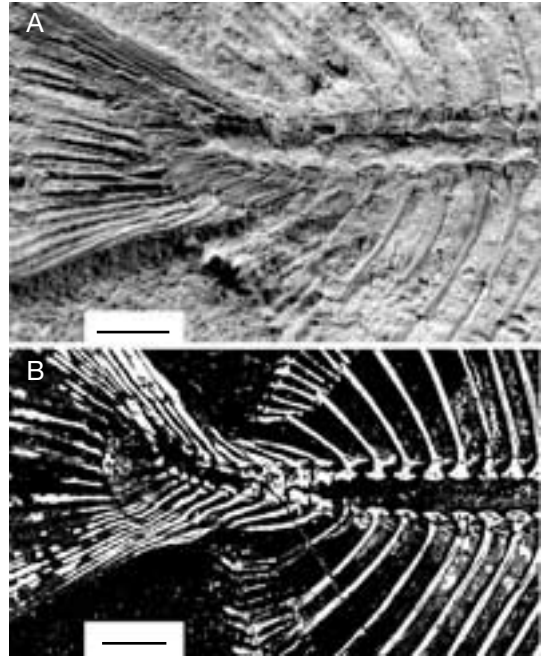
Fig. 24. — **A**, *Stemmatodus rhombus* (Agassiz, 1839), caudal region of specimen MNHN JRE 39. Photo Serrette; **B**, *Proscinetes bernardi* Thiollière, 1852, caudal region of specimen ML 15288. Photo Serrette, under ultraviolet light. Both right side. Scale bars: A, 2 mm; B, 5 mm.

the largest ones, are not expanded and do not surround the notochord. The holotype of *Nursallia veronae* only shows six vertebrae, all in the caudal region, all of them constricting the notochord completely; the state in juvenile specimen MCSNV T.830 is uncertain. Pending confirmation with further findings, this character has been coded as 2 for *Nursallia veronae*, because the relative expansion and the enclosure of the notochord are much stronger than in the individual cases of *Proscinetes* just described.

54 Neural and haemal adjacent arcocentra

Separated from each other (0); simple contact (1); complex contact (2); hyper-complex contact (3); expanded and imbricate (4). The only observed pycnodontiforms where each arcocentrum is clearly separated from the preceding and the subsequent ones are *Apomesodon* n. gen., *Arduafrons* (NHML P.8656), and *Eomesodon*,
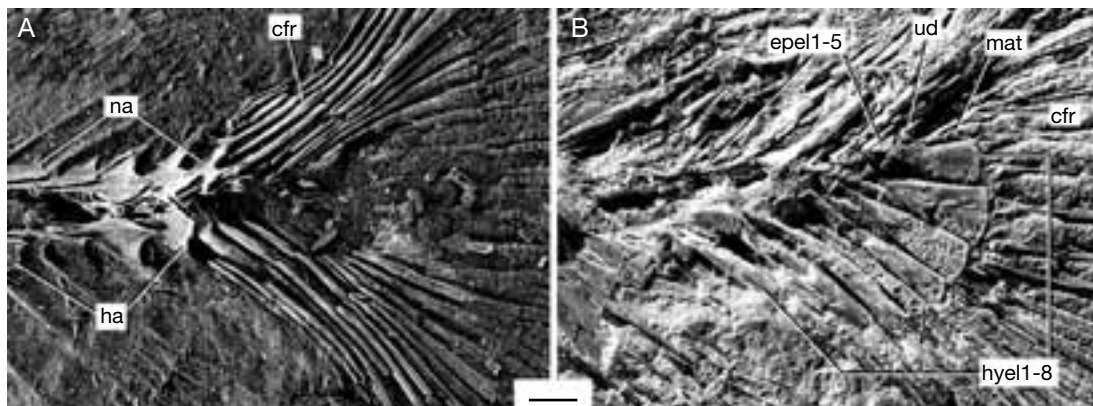
Fig. 25. — *Iemanja palma* Wenz, 1989, caudal region of the holotype, MNHN BCE 166, part (**A**, transferred) and counterpart (**B**). Both left side. Photos Serrette. Abbreviations: **cfr**, caudal fin rays; **epel**, epichordal elements; **ha**, haemal arcocentra; **hyel**, hypochordal elements; **mat**, matrix (in relief); **na**, neural arcocentra; **ud**, urodermal. Scale bar: 5 mm.

although the condition is unknown in *Gibbodon*, *Ichthyoceros*, *Mesturus*, *Micropycnodon*, *Palaeobalistum orbiculatum*, and *Paramesturus* because of their complete scale covering. In the rest, each arcocentrum contacts with its anterior and posterior neighbour by its more or less expanded base. In addition to the expanded base, state 1 corresponds to a contact by means of a small, anterior thickened zygapophysis in the base of the corresponding spine: *Brembodus*, *Coccodus*, *Coelodus saturnus* (Fig. 27A), *Ocloedus subdiscus* n. comb. (Fig. 27B), *Gyrodus*, *Macromesodon*, *Proscinetes* (Fig. 24B), *Stemmatodus* (Fig. 24A), *Stenamara*, *Tepexichthys*, and *Trewavasia*. In state 2 the contact is complex, by means of two or three pointed interdigitated zygapophyses, in *Neoproscinetes*, *Oropycnodus ponsorti*, *Abdobalistum thyrsus* n. gen., n. sp. (Blot 1987: fig. 43; pers. obs.), and *Pycnodus* (Blot 1987: fig. 18; pers. obs.). We consider as hyper-complex contact the cases of state 3, where there are three or more interdigitations between the arches: *Nursallia* ? *goedeli* (up to 11 interdigitations in the observable arcocentra of the caudal region; Fig. 26A), *Nursallia* ? *gutturosum* (Fig. 26B), and *Nursallia veronae* (Fig. 26C). There is ontogenetic variation in this character, as juvenile specimen MCSNV T.830 of the latter only presents one or two interdigi-

tations. Only *Iemanja* presents state 4, where there are no interdigitations, but the arches and the bases of the spines are greatly expanded and imbricate over the subsequent neighbour, except for the neural arches of the abdominal region (Fig. 25).

55 Sagittal flanges on neural and haemal spines
Absent (0); anterior, small and short (1); anterior, large and long (2); anterior and posterior (3); anterior and posterior with strengthened margins (4). This is a re-arrangement of Nursall's (1996b) characters 16 and 38. All observed pycnodontiforms bear anterior sagittal flanges on the neural and haemal spines, although they are apparently absent in *Arduafrons* (NMHL P.8658). The sagittal flanges are very small in: *Apomesodon* n. gen., *Brembodus* (Tintori 1981; pers. obs. on the caudal region of the holotype, on specimen MCSNB 4900 and on the neural, but not on the haemal, arches of subadult specimen MCSNB 4896), and in *Eomesodon*. Most pycnodontiforms exhibit state 2: large anterior sagittal flanges that are at least half as long as the corresponding spine, very often in contact with the anterior spine (e.g., Figs 2; 4B; 25; 27A). They may be difficult to observe, though, depending on the nature of the preservation.

For instance, there seems to be no flanges in most specimens of *Nursallia ? gutturosum*, but they are visible as faint impressions on the haemal spines of MNHN DTS 236 (Fig. 26B) and more clearly on MNHN DTS 241, on the neural and haemal spines (see also Arambourg 1954). They are difficult to observe also in *Stemmatodus*, but specimen NHML P.62201 exhibits only anterior, large and long sagittal flanges (state 2). *Iemanja* presents state 3, showing both anterior and posterior sagittal flanges (holotype; Fig. 25). Also *Gyrodus* has them, but in this case the flanges present thick, strengthened margins, at least on the caudal region (Lambers 1991: fig. 22; Nursall 1996b: fig. 17; pers. obs.). We consider this as a different state of derivation (state 4).

56 Number of autogenous anterior neural spines
Outgroup (?); most of them, including caudal ones (1); 10 or more (2); 7-10 (3); six or less (4). We could not polarize this character, because true neural spines are not formed on the abdominal vertebrae of *Amia* (the halves of the arches are not fused medially; Grande & Bemis 1998: 110, 111; pers. obs.), and they are not accessible in the other members of the outgroup. We have herein coded the data provided by Nursall (1999b: 195, table 1), confirmed by our personal observations, and added the character states for *Coelodus saturnus*, *Ocloedus subdiscus* n. comb. (both 7-8 autogenous spines, state 3), *Iemanja* (about nine spines, state 3), *Macromesodon* aff. *M. bernissartensis* (seven, state 3), *Nursallia ? gutturosum* (Fig. 9A; at most six spines, state 4), *Proscinetes elegans* (Fig. 8A), and *Stenamara* (Fig. 5B; both eight spines, state 3). The exact number in *Abdobalistum* n. gen. is difficult to precise, but there are six or less, as the seventh spine is fused to the arch (state 4). As pointed by Tintori (1981) and Nursall (1999b: 195), the case of *Brembodus* is quite remarkable; we have observed all neural spines, even those of the caudal region (caudal endoskeleton excluded: e.g., holotype) with their distal part separated from their basal part (but the haemal ones are not, at least in subadult specimen MCSNB 4896). This
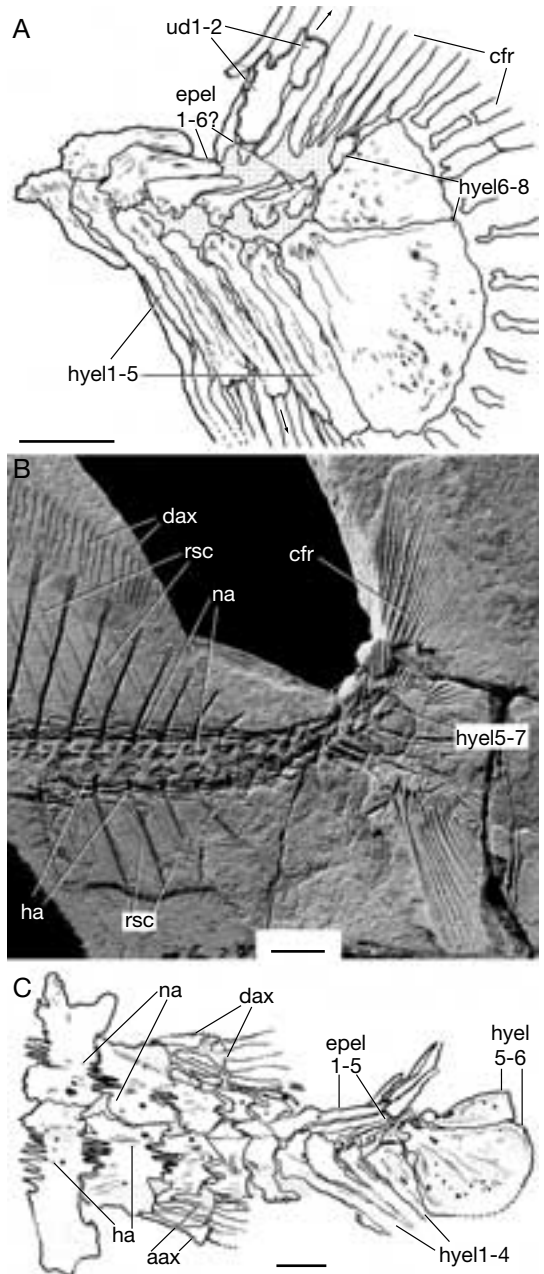
Fig. 26. — Axial and caudal skeleton of *Nursallia* Blot, 1987; **A**, *N.* ? *goedeli* Heckel, 1854, camera lucida drawing of the caudal region as shown by the holotype, NMW 1858.III.21. Arrows indicate upper and lower principal caudal fin rays; **B**, *N.* ? *gutturosum* (Arambourg, 1954), caudal region of the specimen MNHN DTS 236. Photo Serrette; **C**, *N. veronae* Blot, 1987, camera lucida drawing of the caudal region as shown by the holotype, MCSNV II. D. 172-173. All left side, lateral view. Abbreviations: **aax**, anal axonosts; **cfr**, caudal fin rays; **dax**, dorsal axonosts; **epel**, epichordal elements; **ha**, haemal arcocentra; **hyel**, hypochordal elements; **na**, neural arcocentra; **rsc**, reduced scales; **ud**, urodermals. Scale bars: 5 mm.

FIG. 27. — **A**, *Coelodus saturnus* Heckel, 1854, caudal region as shown by the holotype, NMW 1857.XXXIII.2. Photo Schumacher, courtesy Ortwin Schultz; **B**, *Ocloedus subdiscus* n. comb., camera lucida drawing of the caudal region as shown by specimen MNHN MSE 965. Both right side. Abbreviations: **aax**, anal axonost; **dax**, dorsal axonost; **di**, diastema; **epel**, epichordal elements; **ha**, haemal arcocentrum; **hyel**, hypochordal elements; **na**, neural arcocentrum; **sf**, sagittal flange; **ud**, urodermals. Scale bars: A, 1 cm; B, 2 mm.

FIG. 28. — **A**, camera lucida drawing of the caudal vertebrae and of the last dorsal and anal axonosts as shown by the holotype of *Eomesodon liassicus* (Egerton, 1855), NHML 19864. Notice some bifid neural and haemal spines; **B**, caudal region of specimen ML 15660 of *Apomesodon surgens* n. gen., n. sp. Notice some bifid dorsal axonosts. Photo Serrette, under ultraviolet light. Both left side. Abbreviations: **aax**, anal axonost; **dax**, dorsal axonost; **epel**, epichordal elements; **ha**, haemal arcocentrum; **hyel**, hypochordal elements; **na**, neural arcocentrum; **ud**, urodermals. In both A and B, arrows point some of the autogenous neural spines. Scale bars: 5 mm.

separation seems different from the separation of the complete spine from the corresponding basidorsal, as in the other cases, and has been coded separately (state 1). The interpretation of this character in *Eomesodon* is uncertain. According to Nursall (1999b: 195) "the same condition" as in *Brembodus* "obtains in *Eomesodon* spp." However, the holotype of *Eomesodon liassicus* (Fig. 28A) shows that most, but not all, of the caudal neural spines are fused. In this specimen, several neural and haemal spines are bifid, but this feature may or may not be related to the lack

of fusion. In addition, the spines of the caudal region are fused to their arches at least in specimens ML 15660 of *Apomesodon surgens* n. gen., n. sp. (Figs 3A, B; 28B) and specimens JM 4120 (Fig. 5A) and FSL 93095 of *Apomesodon gibbosus* n. comb., although ML 15660 shows some auto-
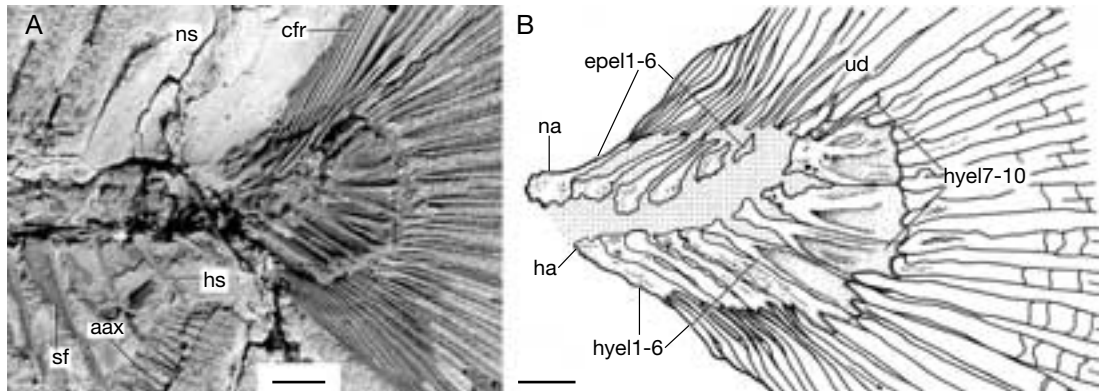
Fig. 29. — *Oropycnodus ponsorti* n. comb.; **A**, caudal region of specimen MNHN MTA 42. Photo Serrette; **B**, restoration of the caudal skeleton, mostly from camera lucida drawings of specimen in A and of lectotype NMW 1854/XXXIX/38 and paralectotype NMW 1854/XXXIX/40. Arrows on B indicate upper and lower principal caudal fin rays. Both left side. Abbreviations: **aax**, anal axonost; **cfr**, caudal fin rays; **epel**, epichordal elements; **ha**, haemal arcocentrum; **hs**, haemal spine; **hyel**, hypochordal elements; **na**, neural arcocentrum; **ns**, neural spine; **sf**, sagittal flange; **ud**, urodermal. Scale bars: A, 5 mm; B, 2 mm.

genous spines at the beginning of the caudal region (Fig. 28B). Pending further confirmation, we have coded this character as ? for *Apomesodon* n. gen. and *Eomesodon*, because, with the present evidence, it does not seem equivalent to the state in *Brembodus* and cannot be verified in the anteriormost vertebrae.

CAUDAL ENDOSKELETON

57 Relative length of last neural spine not supporting precurrent caudal fin rays
Same length as preceding spines (0); slightly reduced (1); less than half as long as preceding spines (2); vestigial (3). The last neural spine not supporting precurrent caudal fin rays is not accessible in most of the outgroup; in *Amia* and *Semionotus* it is not reduced in length. All observed pycnodontiforms where the caudal endoskeleton is accessible exhibit the last neural spine that does not support caudal fin rays somewhat reduced when compared to the average caudal neural spine (state 1; e.g., *Coelodus saturnus*, Fig. 27A; *Ocloedus subdiscus* n. comb., Fig. 27B; *Iemanja*, Fig. 25; *Oropycnodus* n. gen., Fig. 29; *Proscinetes*, Fig. 30A; *Stemmatodus*, Fig. 24A). This reduction is more manifest, the spine being less than half as long as the preceding ones (state 2), in *Neoproscinetes* (Nursall & Maisey 1991), *Nursallia* ? *goedeli* (Fig. 26A), and *Abdobalistum*

n. gen. The spine is vestigial, virtually nonexistent (state 3), in *Nursallia* ? *gutturosum* (Fig. 26B), *Nursallia veronae* (Fig. 26C), and *Pycnodus* (Blot 1987: fig. 27, pl. 24; Nursall 1996b: fig. 12E; pers. obs.).

58 Number of epichordal elements of caudal endoskeleton
Nine or more (0); six to eight (1); four or five (2); three (3). The number of epichordal elements in the caudal endoskeleton of pycnodontiforms is rather heterogeneous. We have consistently counted the epichordal elements that support caudal fin rays (both precurrent and principal). Although they are difficult to discern, there seem to be about four epichordal elements in the caudal endoskeleton of *Brembodus* (pers. obs. on the holotype; Nursall 1996b: fig. 12a; state 2). *Coccodus* has six of them (Fig. 30B), whereas *Apomesodon* n. gen. and *Eomesodon liassicus* present only three epichordal elements in the caudal endoskeleton (Figs 28B; 31; state 3). There are at least six in *Gyrodus* (pers. obs. on, for instance, NHML P.3772; Lambers 1991: fig. 25; state 1). The holotype of *Nursallia* ? *goedeli* certainly shows at least five; it is difficult to see whether the fifth one is broken or there is a sixth one, although the former possibility is more likely, because a distinct sixth basidorsal is not observable
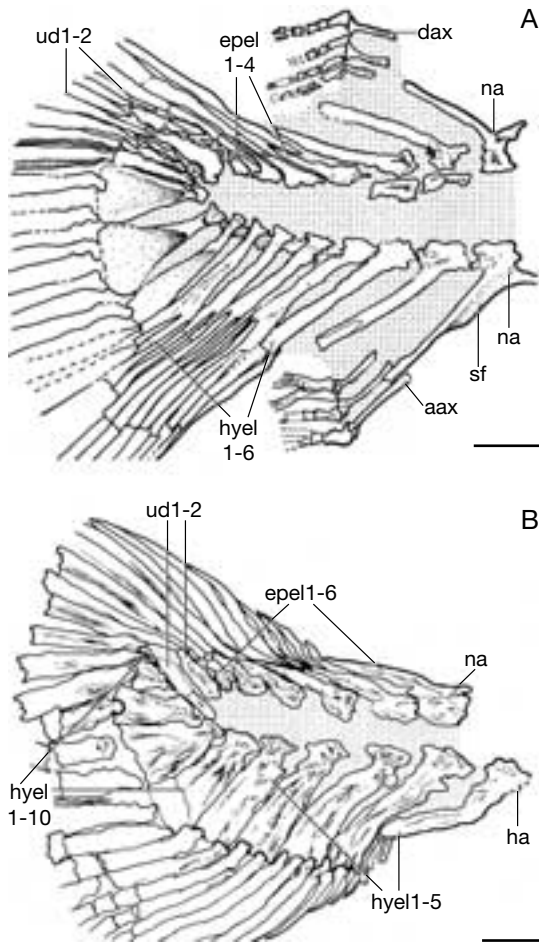
FIG. 30. — Camera lucida drawings of the caudal region as shown by **A**, specimen JM 1941.12a of *Proscinetes elegans* (Agassiz, 1833) (right side); **B**, specimen MNHN HDJ 540 of *Coccodus armatus* Pictet, 1850 (reverted left side). Abbreviations: **aax**, anal axonost; **dax**, dorsal axonost; **epel**, epichordal elements; **ha**, haemal arcocentrum; **hyel**, hypochordal elements; **na**, neural arcocentrum; **sf**, sagittal flange; **ud**, urodermals. Scale bars: 2 mm.
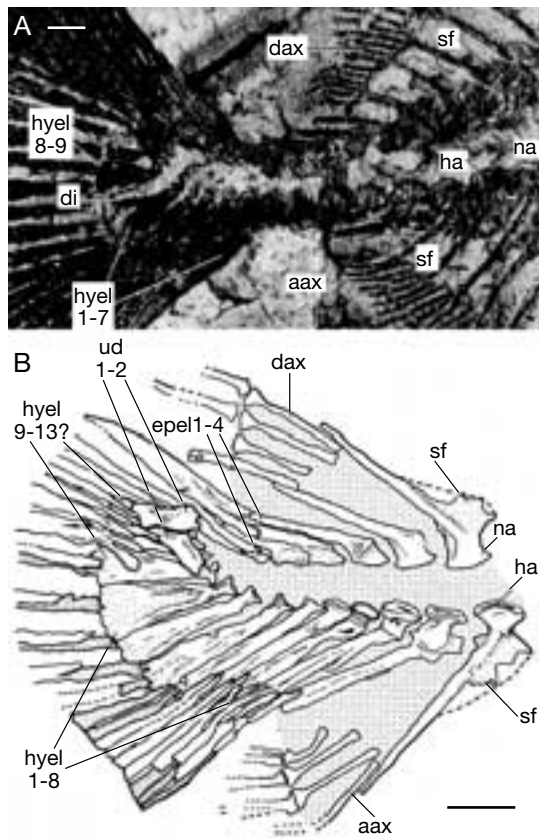

FIG. 31. — Camera lucida drawing of the caudal region as shown by specimen NHML P.5127 of *Eomesodon liassicus* (Egerton, 1855). Abbreviations: **aax**, anal axonost; **dax**, dorsal axonost; **epel**, epichordal elements; **ha**, haemal arcocentrum; **hyel**, hypochordal elements; **na**, neural arcocentrum; **pfr**, precurrent fin rays. Scale bar: 5 mm.

(Fig. 26A; state 2). Also *Nursallia veronae* has five elements (Fig. 26C), although the anteriormost ones are bent and broken, giving at a first sight the impression that there are more, as in Blot's interpretation (1987: fig. 60). There are four, at most five in specimens MNHN DTS 236 and especially 241 of *Nursallia ? gutturosum* (Fig. 26B; see also Arambourg 1954: fig. 9). *Oropycnodus ponsorti* n. comb. has at least six well

developed epaxial elements supporting caudal fin rays (e.g., MNHN MTA 42; NMW 1854/XXXIX/38; Fig. 29; state 1). Contrary to Blot's restoration (1987: fig. 46), we found that the number of epichordal elements in specimen NHML P.9830 of *Abdobalistum thyrsus* n. gen., n. sp. cannot be counted precisely (coded as ?). This region is not well preserved in any of the *Trewavasia* specimens studied, but a restoration taking elements from both sides of NMW 1965/536 a-b (Fig. 32A) results on eight of them (state 1; see also Gayet 1984: fig. 4).

Note on the hypochordal elements of pycnodontiforms
We agree with Lambers that: "It is very difficult to distinguish between the broadened haemal spines and the hypurals and therefore to determine the number of hypurals" (Lambers 1991: 527), and with Nursall that "it is often difficult to distinguish hypural bones from ray-bearing preural arches with certainty" (Nursall 1999b: 203). The latter illustrates an example of a specimen of *Tepexichthys* (Nursall 1999b: fig. 11) showing both open and collapsed haemal arches in the caudal region, and others interpreted as true hypurals, which would be only those elements showing "a grove for the branch of the caudal artery that passed lateral to it" (Nursall

1999b: 203). According to this interpretation, actual hypurals would be only the very last, considerably enlarged hypochordal elements. However, a specimen of *Ocloedus subdiscus* n. comb. exhibits a different morphology (Fig. 27B). In this case, haemal arches are also visible but they are dorsally open, whereas in the specimen of *Tepexichthys* they are dorsally closed. In addition, the first element showing a dorsal convex surface, and consequently no arch, and also a lateral groove for the corresponding arterial branch, is an element very anterior in the series, barely expanded, and only with difficultly made homologous with the corresponding element in *Tepexichthys*. The evidence for distinguishing the true hypurals of the pycnodont caudal endoskeleton is, then, not only very scarce (only two specimens), but also contradictory. Therefore, and to avoid forcing homologies within pycnodontiforms and of pycnodonts with teleosts and other Halecostomi, we have adopted Lambers' (1991) criterion of consistently counting all of the hypochordal elements supporting caudal fin rays (both principal and precurrents). We consider that the currently known evidence is too weak and conflicting to decide upon such an important issue as the nature and homologies of hypurals in pycnodonts.

59 Relative development of hypochordal elements of caudal endoskeleton

Only slightly enlarged (0); enlarged, plate-like (1); hypertrophied (2). The relative development of the hypochordal elements of the caudal endoskeleton and their number are not necessarily linked (see data matrix), and are consequently treated as distinct characters. Their development has consistently been regarded as the distal width of the largest elements of the series, which are generally close to the longitudinal axis of the body, in comparison with the distal width of the anteriormost ones and of the haemal spines. Their relative development is comparable to that of the outgroup, where the hypurals increase in width very slightly, forming a continuous series of tiny changes, and has been therefore coded as 0 in: *Brembodus* (Nursall 1996b: fig. 12a; pers.
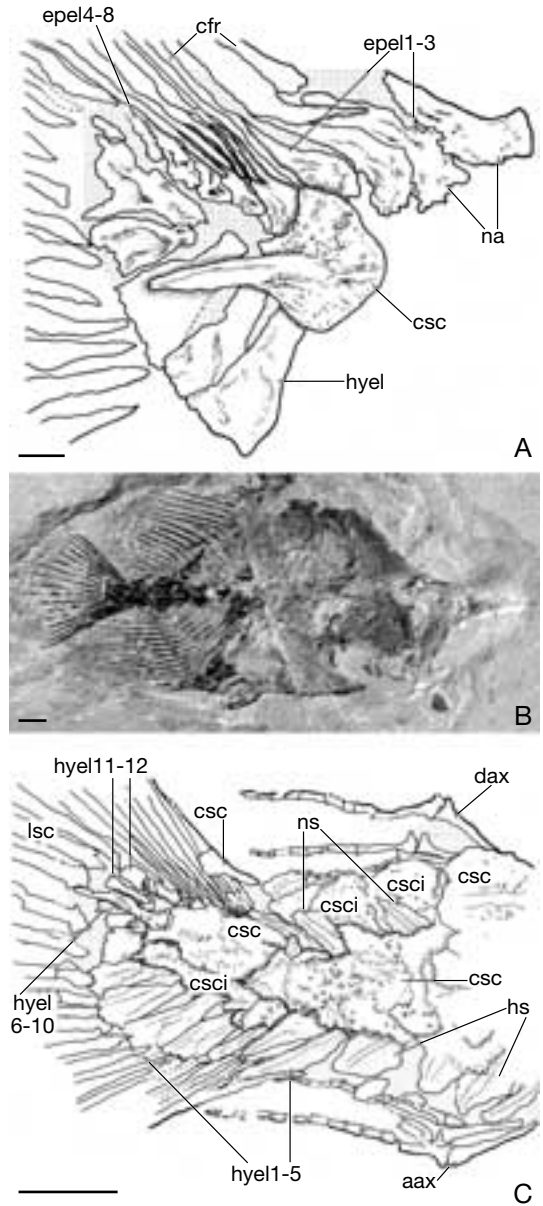
Fig. 32. — *Trewavasia carinatus* (Davis, 1887); **A**, caudal region of specimen NMW 1965/536 a-b, restored from camera lucida drawings of both the part and the counterpart; **B**, specimen NHML P.62617. Photo courtesy P. Forey; **C**, camera lucida drawing of the caudal region of the same specimen. Abbreviations: **aax**, anal axonost; **cfr**, caudal fin rays; **csc**, complete scale; **csci**, complete scale, inner face; **dax**, dorsal axonost; **epel**, epichordal elements; **hs**, haemal spines; **hyel**, hypochordal element(s); **lsc**, last scale of lateral line; **na**, neural arcocentra; **ns**, neural spines. Scale bars: A, 1 mm; B, 5 mm; C, 2 mm.

obs.), *Apomesodon* n. gen. (Fig. 28B), *Eomesodon* (Fig. 31), all species of *Macromesodon* (Nursall 1996b: fig. 12b; pers. obs.), *Stemmatodus* (Fig. 24A) and *Stenamara* (Poyato-Ariza & Wenz 2000: fig. 3; pers. obs). Many pycnodonts show large plates, such as *Coccodus* (Fig. 30B), *Ocloedus subdiscus* n. comb. (Fig. 27B), *Iemanja* (Fig. 25), *Proscinetes* (Figs 24B; 30A), and *Trewavasia* (Fig. 32). State 2 is for even larger, hypertrophied hypochordal elements, most of which present well marked longitudinal crests: *Coelodus saturnus* (Fig. 27A), the three nominal species of *Nursallia* (Fig. 26), *Oropycnodus ponsorti* n. comb. (Fig. 29), *Abdobalistum thyrsus* n. gen., n. sp. (Blot 1987: pls 28, 29; pers. obs.) and *Pycnodus* (Blot 1987: figs 27, 28, pls 24, 25; Nursall 1996b: fig. 12e, 1999b: fig. 10c; pers. obs.).

60 Number of hypochordal elements of caudal endoskeleton

14 or more (0); 12-13 (1); 9-11 (2); six to eight (3). Whenever there are many hypochordal elements in the caudal endoskeleton, their distal outline as an ensemble tends to be sigmoid, as it happens in most of the outgroup, *Apomesodon* n. gen. (Fig. 28B) and in *Eomesodon* (Fig. 31); condition unknown in *Arduafrons* and *Mesturus*. *Eomesodon* presents a remarkable contrast between the reduced number of its three epichordal elements and the high number of hypochordal elements, which, in addition, seems to vary between the different species: maybe a low number, at least seven (but probably some indeterminate number more) in the holotype of ? *E. barnesi* (coded as ?), 14 in *E. liassicus* (Fig. 31; state 0). The same feature is observed in *Apomesodon* n. gen.: about 11-12 in *A. gibbosus* n. comb. (e.g., FSL 93095) and 11 in *Apomesodon surgens* n. gen., n. sp. (Fig. 28B; both state 2). Smaller numbers of hypochordal elements, in general, form a shortened, simply curved distal outline (e.g., about 10 elements in a rounded outline in *Gyrodus* NHML P.3772). Two exceptions, where a higher number of hypochordal elements (12 or 13) are apparently forming a curved outline, are: *Trewavasia*, contrary to Gayet's restoration (1984: fig. 4; pers. obs. on specimen NHML

62617: Fig. 32B, C) and *Ocloedus subdiscus* n. comb. (Fig. 27B). The holotype of *Brembodus* has at least seven, probably eight elements (nine as restored by Nursall 1996b: fig. 12a, but in the specimen it is actually difficult to establish the exact number); in turn, MCSNB 4900 shows eight of them, so we conservatively coded as state 3 for this genus. The holotype of *Coelodus saturnus* (Fig. 27A) has at least nine, maybe 10 hypochordal elements (at most 11; this region is badly preserved; state 2), while at least 12, probably 13 are present in *Ocloedus subdiscus* n. comb. (Kriwet *et al.* 1999; Fig. 27B; state 1). The area of the last hypochordal elements in the holotype of *Nursallia veronae* is badly damaged; there are at least six elements (Fig. 26C), but there could be one, less probably two more that are not preserved. We have not found a pycnodontiform with more than 16 (normally no more than 13) or with less than six hypochordal elements in the caudal endoskeleton.

61 Diastema

Absent (0); present (1). A diastema in the caudal endoskeleton is absent in most pycnodontiforms, as the hypochordal elements are in contact. According to the relative width of these elements, this contact can range from very small, normally distal (e.g., *Stemmatodus*, Fig. 24A), to very tight, all along their borders (e.g., *Nursallia*, Fig. 26). The only exception that we have found is *Coelodus saturnus*, where there is a distinct diastema between the hypochordal elements 8 and 9, which are completely separated from each other (Fig. 27A; state 1).

GIRDLES AND FINS
62 Cleithrum

Two limbs in angle, anteroventral limb subhorizontal (0); curved, anteroventral limb subhorizontal, slightly expanded (1); curved, anteroventral limb subvertical, expanded (2); cleithrum with three limbs (3); cleithrum with four limbs (4). As pointed out by Nursall (1996b: character 14), in most pycnodontiforms the cleithrum is "large and palaform ventrally", but there are differences among the different genera. The

anteroventral limb is subhorizontal and points ahead in *Arduafrons* and *Mesturus* (state 1). Most pycnodontiforms exhibit a subvertical cleithrum, whose ventral limb points ventrally (state 2; e.g., Figs 8A; 9A); the relative expansion of the ventral limb is somewhat variable, being especially remarkable in, for instance, *Pycnodus* (Fig. 10). *Ichthyoceros* presents a highly derived cleithrum with three limbs that form a kind of an inverted T (state 3). Two of the limbs are considered homologous to the limbs of other pycnodontiform cleithra: a long, strong vertical one, with a broad, laminar posterior expansion; and a stout, narrow anteroventral one, in a straight angle with the vertical one, and about half as long. The third limb is directed posteriorly and slightly ventrally; it is narrow but stout, about as long as the vertical limb (pers. obs. on the holotype). The cleithrum of *Coccodus* (Fig. 13) is even more complex, with four limbs that merge ventrally behind the head (state 4, including Nursall's 1996b characters 64 *pro parte* and 65). The short, broad, vertical dorsal limb is homologous to the posterodorsal limb of other pycnodontiform cleithra, and articulates with the supracleithrum. The anteroventral limb is longer, narrower and pointed; it forms an approximately right angle with the vertical limb, and is homologous to the anteroventral limb of other pycnodontiform cleithra. The posteroventral limb points backwards and slightly towards the midline of the body. It is similar to the anteroventral one in length and shape, and forms a straight angle with the dorsal limb. The fourth limb, short and broad, extends ventrally below the abdominal cavity to meet its counterpart medially. The ensemble is a strong structure that probably functioned as the main support of the body.

63 Spines on cleithrum

None (0); one, hypertrophied (1); about 10 (2); about 50 (3). This character re-arranges Nursall's (1996b) characters 59 and 64 *pro parte*. The cleithrum of *Coccodus* (state 1), in addition to the four limbs described in character 59, bears a hypertrophied spine, hook-shaped, very large, curved backwards, lateroventrally projected

(Woodward 1895a; Nursall 1996b; pers. obs.) In *Trewavasia* (state 2) the cleithrum presents one straight, long spine on the centre, directed backwards, plus two smaller, hook shaped spines and about seven very small spines (Gayet 1984: fig. 2). In *Ichthyoceros* (state 3) there are about 50 small, hook-shaped spines, with two, probably three longer and stouter straight spines (pers. obs. on the holotype).

64 Position of pelvic fins (ratio prepelvic distance / standard length)

45-55% (0); more than 55% (1); less than 45% (2). The pelvic fins are placed about the middle of the body in the outgroup and in many pycnodontiforms (state 0). They are placed slightly posteriorly in *Brembodus*, *Coccodus*, *Ocloedus subdiscus* n. comb., *Gibbodon*, *Ichthyoceros*, *Macromesodon bernissartensis*, and *Proscinetes* (state 1). They are placed slightly anteriorly in ? *Eomesodon barnesi*, *Gyrodus,* and *Stenamara*. This character corresponds to Nursall's character 35.

65 Position of dorsal fin (predorsal length / standard length)

60%-69% (0); 40%-49% (1); 50%-59% (2); 70%-79% (3).

66 Number of dorsal axonosts

Less than 20 (0); 20-29 (1); 30-39 (2); 40-49 (3); 50-59 (4); 60 or more (5). There is a remarkable variation in the number of dorsal axonosts in *Apomesodon gibbosus* n. comb. (29-38), *Macromesodon macropterus* (36-44) and *Proscinetes elegans* (48-54). In the case of *Apomesodon gibbosus* n. comb., it seems linked to the length of the specimen, and therefore to the age: the number of dorsal axonosts increases with age, a feature that is highly unusual in actinopterygians. For instance, the unlabelled specimen at the BMM (about 100 mm in standard length) has at most 30, and specimen JM SOS 3570 (360 mm in standard length), about 37. We have coded the state of the character as found in the larger adult individuals (state 2). This phenomenon requires further confirmation in most abundant material of this species. In
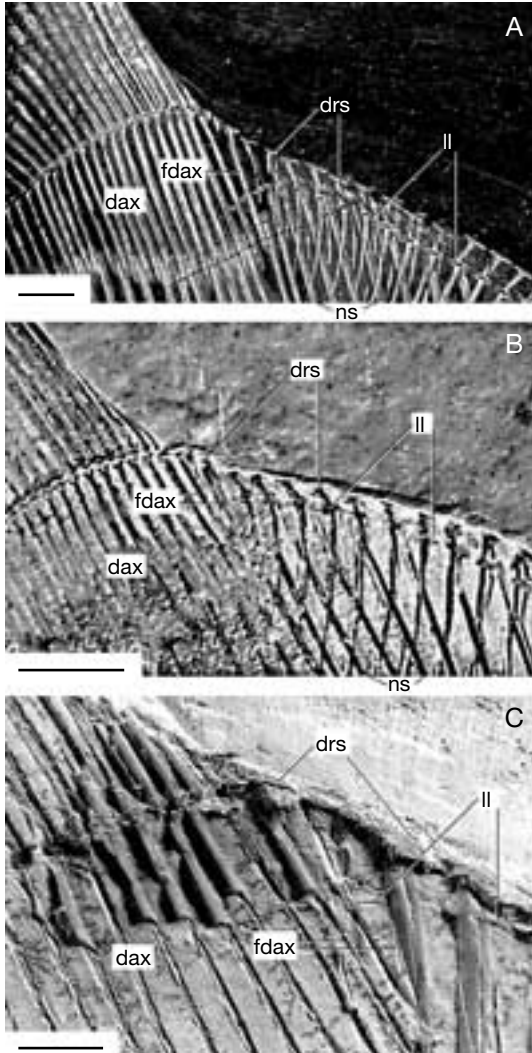
FIG. 33. — Zone of insertion of the dorsal fin of **A**, *Proscinetes bernardi* Thiollière, 1852, specimen MNHN CRN 15288, right side, lateral view. Photo Serrette, under ultraviolet light; **B**, *Proscinetes elegans* (Agassiz, 1833), specimen JM 1941.12a, right side, lateral view. Photo courtesy G. Viohl; **C**, *Macromesodon macropterus* (Agassiz, 1834), specimen MNHN SLN 54, reverted left side, lateral view. Photo Serrette. Abbreviations: **dax**, dorsal axonosts; **drs**, dorsal ridge scales; **fdax**, free dorsal axonost(s); **ll**, lateral line; **ns**, neural spines. Scale bars: 5 mm.

turn, a comparable variation is found, but does not seem linked to age in *Macromesodon* and *Proscinetes*. For instance, specimen MNB MBI.004.11 (87 mm in standard length) of the

former has 44 dorsal axonosts; in contrast, MNHN SLN 54 (135 mm in standard length), has at most 38. So we have coded 2 and 3 for the former and 3 and 4 for the latter.

67 Dorsal axonost not supporting lepidotrichium (free axonost)
Absent (0); present (1). We call "free axonost" the anteriormost one in the cases where it does not support any fin ray, but a ridge scale instead (Fig. 33). Such a free axonost is present in: *Brembodus* (Tintori 1981: pl. 100, fig. 2; pers. obs. on the holotype and on specimen MCSNB 4933); in the holotype of *Apomesodon surgens* n. gen., n. sp., but not in specimen ML 15660/MNHN CRN 69; *Macromesodon* (e.g., LH 14364); *Stemmatodus* (MNHN JRE 39, 41); and *Stenamara* (holotype; Fig. 3D). There is always at least one free axonost also in *Macromesodon* and *Proscinetes* (Fig. 33A), but eventually two in some individuals of *Macromesodon macropterus* (MNHN SLN 54; NHML P.9854; Fig. 33C) and *Proscinetes elegans* (JM 1941.12a; Fig. 33B).

68 Morphology of the dorsal and anal fins
Strip-like (0); falcate to acuminate (1); sigmoid outline (2); rounded in the centre (3); rounded anteriorly (4); square (5). See Fig. 34 for idealized contours of the fin shape. The morphology of the unpaired fins is sometimes very difficult to precise in pycnodontiforms, on the first place due to preservation reasons or to badly restored borders, but also because some morphologies may seem intermediate. For instance, it is occasionally difficult to distinguish between a strictly falcate fin and a strictly strip-like fin. This is the case of *Pycnodus*. We have considered falcate the cases where the anteriormost lepidotrichia are at least twice as long as the middle ones (state 1); and strip-like the cases where most lepidotrichia have similar length, although the anteriormost ones may occasionally be slightly longer (e.g., *Pycnodus*), it is still considered as state 0. We have treated together the morphology of the dorsal and of the anal fins into the same character even though their shape
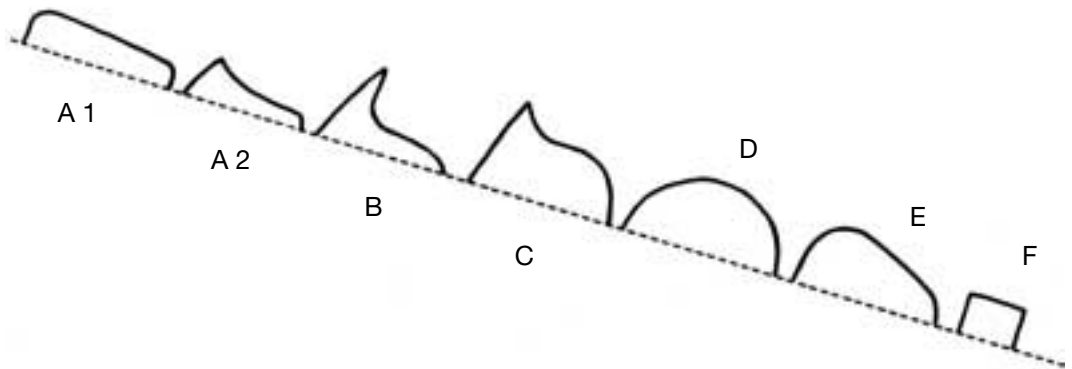
FIG. 34. — Idealized contours of the dorsal fin shape, left side in lateral view; **A**, strip-like (**A1** as in *Mesturus* Wagner, 1862, **A2** as in *Pycnodus* Agassiz, 1833); **B**, falcate to acuminate (as in *Gyrodus* Agassiz, 1833); **C**, sigmoid (as in *Macromesodon macropterus* [Agassiz, 1834]); **D**, rounded in the centre (as in *Macromesodon* aff. *M. bernissartensis* Traquair, 1911); **E**, rounded anteriorly (as in *Oropycnodus ponsorti* n. comb.); **F**, square (extrapolated from the anal of *Coccodus* Pictet, 1850).

is not linked in *Brembodus* (dorsal anteriorly rounded, anal falcate) and in the two species of *Apomesodon* n. gen. (dorsal rounded in the centre, anal anteriorly rounded; Fig. 3A-C). These three taxa have been simultaneously coded for both states. The shape of the anal fin is unknown in ? *E. barnesi* and *E. liassicus*. The anal fin is not complete in the holotype of *Nursallia veronae*, but the observable arrangement of the fin rays suggests that it is falcate to acuminate (anterior rays long and densely arranged; middle and posterior rays short and more separated), as the dorsal (state 1). Whenever well preserved, the anal fin of *Oropycnodus ponsorti* n. comb. is seen rounded anteriorly (e.g., NHML P.30037), as the dorsal (state 4). It is coded as 4 for *Trewavasia* mostly after specimens NHML P.62617 (Fig. 32B), and NMW 1965.636.a. The square type of fin (state 5) is formed by lepidotrichia of similar length, and about as long as the base of the fin. It is only found in *Coccodus* (seen by transparency on the original side of transfer specimen MNHN HDJ 539), where the morphology of the dorsal fin is unknown.

69 Position of anal fin (preanal length / standard length)
70%-79% (0); 50%-59% (1); 60%-69% (2); 80%-89% (3).

70 Number of anal axonosts
10-19 (0); 20-29 (1); 30-39 (2); 40-49 (3); 50 or more (4); 9 or less (5). The exact number of anal axonosts in *Nursallia veronae* cannot be counted precisely, but an estimation can be attempted. At least 44 can be counted in the holotype, while a good portion of the fin, corresponding to about 10 more rays, is eroded. So, the character can be coded as state 4 (50 or more). The number cannot be established in *Gibbodon* either, but personal observations on the holotype permit state 5 to be assigned, as there are certainly nine or less. As shown by Table 1, *Apomesodon gibbosus* n. comb. does not present in the anal fin the variation in the number of axonosts discussed above for the dorsal fin (see character 66). In contrast, *Macromesodon macropterus* (30-38) and *Proscinetes elegans* (42-48) do show a variation in the number of axonosts comparable to the variation of the dorsal fin mentioned above.

71 Urodermals
Not differentiated (0); a series of three or more (1); two (2); one (3); absent (4). Urodermals seem not to be differentiated in *Arduafrons*, *Gibbodon*, *Ichthyoceros*, and *Mesturus* (Fig. 35A; primitive state). When present, the urodermals of pycnodonts are either a series of small plates (state 1, Fig. 28B) or 1-2 rather broad plates (states 2-3 respectively, Figs 26A; 27B; 29B; 30A, B). In
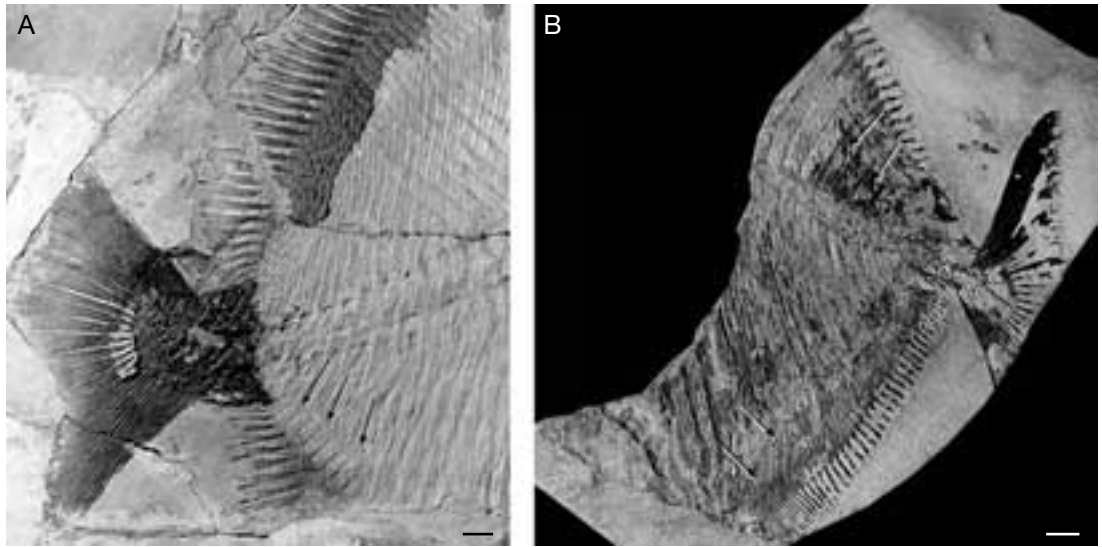
F_{IG}. 35. — **A**, caudal region of specimen NHML P.37023 of *Mesturus verrucosus* Wagner, 1862. Arrows indicate a change in the direction of the scale rows. Notice the rows of thin scales between the bases of the dorsal and anal fin rays, and the strong ornamentation of the scales. Right side. Photo courtesy P. Forey; **B**, holotype of *Nursallia* ? *goedeli* Heckel, 1854, NMW 1858.III.21, showing complete scales partially covering the caudal region (upper arrows) and a similar change in the direction of the scales rows (lower arrows). Left side. Photo Schumacher, courtesy Ortwin Schultz. Scale bars: 1 cm.

most cases their position is quite anterior, even anterior to the level of the last hypurals. It seems closer to the morphology and position of the urodermals *sensu stricto* of primitive forms (homologous to the ganoid scales and lateral to the space between the base of the epaxial basal fulcra and the first principal ray) than to those of the "urodermals" of teleosts, tendon bones lateral to the base of most principal dorsal rays (Arratia & Schultze 1992: 246). Nonetheless, the homologies of the pycnodontiform urodermals remain unclear. There are at least three urodermals forming a series in *Brembodus* (holotype and MCSNB 4933, although they are restored as two largely separated elements by Nursall 1996b: fig. 12a) and *Apomesodon* n. gen. (up to five or six: Fig. 28B; state 1). The number of urodermals is reduced to two in *Macromesodon bernissartensis*, *M.* aff. *M. bernissartensis*, *Nursallia* ? *goedeli*, *Ocloedus subdiscus* n. comb., *Proscinetes*, *Stemmatodus*, and *Stenamara* (state 2; Figs 24A; 26A; 27B; 30A). The case of *Coccodus* is remarkable, as this form, having lost the squamation, has

two urodermals in the caudal endoskeleton (MNHN HDJ 540, 543b, and its counterpart, 543a, shows at least one from the other side). In addition, the position and the arrangement of the two urodermals of *Coccodus* are rather unusual; they are very proximal, the first one being in contact with the last epichordal element, and the second one with the articular head of the last four hypochordal elements (Fig. 30B). There is only one urodermal in *Gyrodus*, *Iemanja* (*versus* Wenz 1989a, 1991 who mentions two; Fig. 25B), *Macromesodon macropterus*, *Neoproscinetes*, *Oropycnodus ponsorti* n. comb. (lectotype NMW 1854/XXXIX/38; Fig 29B), and *Tepexichthys* (state 3). Urodermals cannot be positively identified in *Coelodus saturnus*, but possible remains are seen. Urodermals are not preserved in any observed individual of *Nursallia veronae* (in need of confirmation), *Abdobalistum thyrsus* n. gen., n. sp. (in need of confirmation), *Pycnodus* (including transferred specimens), and *Trewavasia* (including transferred specimens), so they can be regarded as lost (state 4).
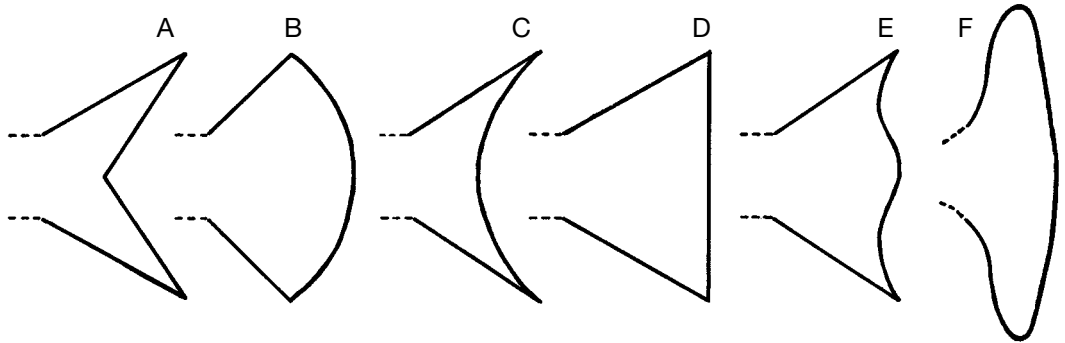
FIG. 36. — Idealized contours of the caudal fin shape, left side in lateral view; **A**, stalked (as in *Gyrodus* Agassiz, 1833); **B**, distal border convex (as in *Mesturus* Wagner, 1862); **C**, distal border concave (as in *Proscinetes* Gistl, 1848); **D**, distal border straight (as in *Apomesodon gibbosus* n. comb.); **E**, double emarginated (as in *Pycnodus* Agassiz, 1833); **F**, vertical (as in *Nursallia* Blot, 1987).

72 Number of principal caudal fin rays
20-25 (0); 9 or less (1); 10-19 (2); 26-35 (3); 36 or more (4). The holotype and the specimens MCSNB 4900, 4901, and 4933 of *Brembodus* have about 16-17. The most common number in *Gyrodus* is about 22-23, although specimen NHML 37039 exceptionally exhibits only 17 (coded as 0).

The correspondance in number between the caudal fin rays and the elements of the caudal endoskeleton is broadly discussed by Lambers (1991: 527). We have not used this character because, in the first place, it varies broadly within the same individual, from the central to the exterior fin rays, and also because it is linked to our characters 58-60 and 72 (it depends on the number and shape of the elements of the caudal endoskeleton and on the number of caudal fin rays).

73 Morphology of caudal fin
Outgroup (?); stalked (1); distal border convex (2); distal border concave (3); distal border straight (4); double emarginated (5); vertical (6). See Fig. 36 for idealized contours of the caudal fin. The caudal fin is stalked (deeply forked) only in *Gyrodus*. The state of preservation and eventual fake preparations make sometimes difficult the distinction between states 2, 3, 4, and 5; the most common is number 2 (distal border convex). The state 6, which we call vertical, is a very short and high caudal fin, five to six times higher than long.

Its upper and lower lobes are practically perpendicular to the axis of the body, and they define a vertical axis in the fin; the distal border of the fin is slightly convex (*Nursallia*: Figs 26B; 35B).

74 Fringing fulcra
Present, numerous (0); present, scarce (1); absent (2). Fringing fulcra in strict sense, that is, numerous, short, heavily imbricate fulcra covering all of the anterior border of the fin (state 0), are present only in *Brembodus* and *Gibbodon* among observed pycnodontiforms. They are present in all unpaired fins of the holotype of *Brembodus*, and specimen MCSNB 4933 exhibits them even on the pelvic fins. There seems to be ontogenetic variation in this character, because fringing fulcra are apparently absent in juvenile specimen MCSNB 6086 a, b; they are present at least in the anal fin of subadult individual MCSNB 4896. Numerous fringing fulcra are observed also in the upper and lower lobe of the caudal fin of the holotype of *Gibbodon*, whereas the anterior border of the dorsal and anal fins is not well preserved. However, reduced fringing fulcra have occasionally been described in pycnodontiforms. These are scarce, thin but relatively long, and are intercalated among the anterior fin rays (state 1). They may be found in dorsal, anal, caudal, and pelvic fins. By scoring previously this character separately for each fin we realized that, as far as it can be observable, the presence of intercalated fulcra is linked

in all these fins. Lambers mentions "possible basal fulcra on the caudal fin" of *Proscinetes elegans* (Lambers 1991: 527), and fringing fulcra on the anal fin of *Proscinetes bernardi* (Lambers 1991: 529, fig. 25b). We are not considering basal fulcra in this character, mainly because all of the putative basal fulcra we have observed in pycnodontiforms are actually small precurrent rays (as acknowledged by this author "it is difficult to discriminate between fulcra and lepidotrichia in *Macromesodon*", Lambers 1991: 527, which we apply to other observations). In turn, the structures labelled "fringing fulcra" in Lambers' mentioned illustration of *Proscinetes bernardi* cannot be interpreted as fringing fulcra; as illustrated, they rather correspond to parts of the left hemitrichia of the fin rays, as posterior fin rays in the same illustration show. In addition, we have never observed fringing fulcra in any *Proscinetes* specimen we have studied, including those where the anterior edges of the fins are well preserved (e.g., ML 15288; Fig. 24B). We have therefore coded this character as 2 (fringing fulcra absent) for *Proscinetes*. Lambers cites fringing fulcra on the dorsal and anal fin of *Eomesodon* sp. as well (Lambers 1991: 529, figs 25c, 26). We have also observed intercalated, thin fulcra in the border of the dorsal fin, treated with acid for this purpose, of specimen FSL 93095 of *Apomesodon gibbosus* n. comb. (formerly *Eomesodon*; state 1). We have not, however, observed fringing fulcra in any individual of the other species of *Apomesodon* n. gen., *A. surgens* n. gen., n. sp., including well preserved caudal fins with intact borders (e.g., ML 15660; Fig. 28B). They are also absent in *Eomesodon liassicus* (Fig. 31). Caudal fulcra are observed also in both species of *Mesturus* (NHML 37023 and 8383; Fig. 35A) (state 1). Fringing fulcra are certainly absent in the dorsal and anal fins, and in the dorsal lobe of the caudal fin of *Arduafrons* (NHML P.8656); it is unknown in the pelvics and in the ventral lobe of the caudal (coded as 2).

SCALES

75 Ossification of scales

Complete in all scales (0); complete in abdominal scales, incomplete in caudal scales (1); complete in ventral scales, incomplete in dorsal scales (2); incomplete in all scales (3); scales absent (4).

We have rearranged Nursall's (1996b) characters 39, 44, 60, and 98 because they are actually different states of only two characters: ossification and distribution of scales. This is so because Nursall's (1996b) character 39 is "body incompletely scaled", corresponding to his patterns loricate, peltate, clathrate, and apertate. His characters 44, 60, and 98 are "peltate or clathrate", "apertate", and "loricate", respectively. Nursall's terminology of scales patterns (imbricate, loricate, peltate, clathrate, and apertate, Nursall 1996b: fig. 19) is useful for description. Its results, however, are unsatisfactory when used as states of characters because the patterns deal at the same time with two different aspects of the scales: ossification and distribution. For instance, the distribution of the scales in the loricate and peltate patterns is the same, but not their ossification (compare *Apomesodon* n. gen., Fig. 3A-C, with *Ocloedus subdiscus* n. comb., Fig. 2B). At the same time, complete scales may form either imbricate or loricate patterns (compare *Palaeobalistum*, Fig. 4A, with *Apomesodon* n. gen., Fig. 3A-C). In addition, the five Nursall patterns do not cover all of the possible existing patterns resulting from the multiple combinations of the ossification and the distribution of the scales. For instance, the holotype of *Nursallia* ? *goedeli* exhibits complete scales all over the caudal region, except in the caudal pedicle, where scales are completely absent (Fig. 35B). Two more examples that cannot be coded following Nursall's patterns: *Nursallia* ? *gutturosum* (Arambourg 1954; pers. obs.) is not peltate *sensu stricto*, since some scales partially cover the caudal region (Fig. 26B), and *Abdobalistum thyrsus* n. gen., n. sp. (Blot 1987; pers. obs. on NHML P.9830) is not clathrate *sensu stricto* for the same reason. It must be noticed at this point that Nursall (1996b: 137) indicates that "this character (partially scaled body) will have to be re-evaluated if *Palaeobalistum* and *Nursallia* are considered to be pycnodontids."

Consequently, we have gathered Nursall's (1996b) different character states (his characters

39, 44, 60, and 98) and then split them into two characters: one for the different patterns of ossification of the scales, and another one for the different patterns of distribution of the scales over the body, because, as just discussed, these two characters are not necessarily linked. This allows dealing with, for instance, complete scales that may cover the whole body (e.g., *Mesturus*, *Palaeobalistum orbiculatum*) be restricted to the anterior half (*Apomesodon* n. gen., *Eomesodon*), or cover all the body but the caudal pedicle (*Nursallia* ? *goedeli*); and also with partially ossified scales that may cover much of the caudal region (e.g., *Nursallia* ? *gutturosum*) or be restricted to the region anterior to the dorsal and anal fins (e.g., *Pycnodus*).

Concerning the present character, ossification of the scales, the primitive state, ossification complete in all existing scales, is found in Nursall's patterns imbricate and loricate, plus *Arduafrons* and *Trewavasia*. We have not seen difference in the ossification pattern between the abdominal and the caudal scales in *Brembodus* (e.g., holotype), and have therefore coded this character as 0 for this genus, despite Tintori's (1981) description of the ossification of the scales as reduced in the caudal region; they are thinner, but still completely ossified (pers. obs.). The case of the holotype of *Nursallia* ? *goedeli* (Fig. 35B) is similar: the ossification of the scales in the caudal region is complete. Although the posteriormost scales are smaller and thinner, they are all completely ossified (state 0). State 1 has only been observed in *Nursallia veronae*. State 2, ossification complete in the scales of the ventral region of the body, and incomplete in the dorsal ones, which are reduced to scale bars, is found in the peltate pattern plus the not-peltate *Nursallia* ? *gutturosum*. State 3, ossification incomplete in all scales, which are reduced to scale bars, in the clathrate pattern plus *Abdobalistum* n. gen.; state 4, scales absent, in the apertate pattern (*Coccodus* only).

76 Distribution of scales

Whole body (0); whole body except caudal pedicle (1); abdominal region plus part of the caudal region (2); only abdominal region (3); body naked (4). The primitive state, scales covering the whole body, including the caudal pedicle (Nursall's 1996b imbricate pattern *sensu stricto*), is found in *Arduafrons* (NHML P.8658), *Brembodus* (e.g., holotype), *Gibbodon*, *Gyrodus*, *Ichthyoceros*, *Mesturus* (Fig. 35A), and *Palaeobalistum orbiculatum* (Fig. 4A). The caudal pedicle is devoid of scales, but the rest of the caudal region, including the regions adjacent to the dorsal and anal fins, is scaled (state 1; not found among Nursall's 1996b patterns) in *Nursallia* ? *goedeli* (Fig. 35B). The scales cover the whole body, except the caudal pedicle and the region adjacent to the dorsal and anal fin (state 2; not found among Nursall's 1996b patterns either) in *Nursallia* ? *gutturosum* (Arambourg 1954; pers. obs.; Fig. 26B), *N. veronae* (Blot 1987; pers. obs.), *Abdobalistum* n. gen. (Blot 1987; pers. obs. on NHML P.9830), and *Trewavasia* (Gayet 1984; pers. obs.; Fig. 32). The rest of the studied pycnodontiforms exhibits scales that are restricted to the region before the insertion of the dorsal and the anal fins (state 3; loricate, peltate, and clathrate patterns), except *Coccodus*, who exhibits a naked body (apertate pattern; state 4).

77 Arrangement of scales

Rows in the same direction (0); rows in different directions (1); not forming rows (2); scales absent (3). In state 1 the scale rows of the dorsal and ventral caudal region, covering the endoskeleton of the dorsal and anal fins, are arranged in a different direction from that of the rest of the body, forming a V-shaped discontinuity in the scale rows. Contrary to Blot's statement that "ces rangées d'écailles sont continues et ne présentent en aucune manière la disposition en chevron" (1987: 114, 115) in specimen NHML P.37023 of *Mesturus verrucosus*, its counterpart clearly exhibits this state, as shown by Fig. 35A. State 1 is also present in the holotypes of *Nursallia* ? *goedeli* (Fig. 35B), *Palaeobalistum orbiculatum* (Blot 1987: 114; pers. obs.; Fig. 4A), and *Abdobalistum* n. gen. (Blot 1987: pls 26, 27; pers. obs.; Fig. 4C, D). We agree with Nursall (1996b: character 58) about the scales not forming rows for *Ichthyoceros* (state 2), due to the hexagonal to
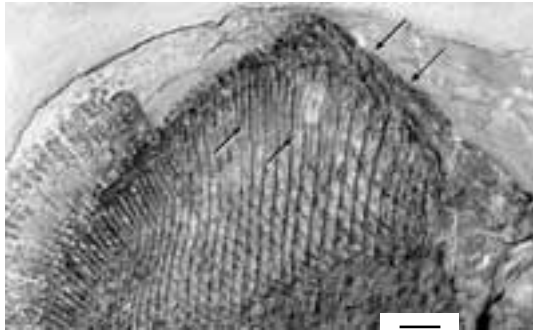
FIG. 37. — *Arduafrons prominoris* Frickhinger, 1991. Detail of the dorsal region of the body of the holotype, NHML P.8658, showing the nuchal plates (arrows on the right), the doubling of the scales rows (arrows on the left), the rows of thin scales between the bases of the dorsal fin rays, and the strong ornamentation of both scales and bones. Scale bar: 1 cm.

irregular form of the scales and to the lack of thickened anterior edges (pers. obs.), but we disagree for *Trewavasia*, which show the scales arranged in rows in Gayet (1984: pl. 2, fig. 1) and on observed specimens (MNHN 1991-3-3, and P.62617, Fig. 32B; NMW 1965/536 a-b); we coded 0 for this genus. This character partially corresponds to Nursall's (1996b) character 58.

78 Suture between scales of the same row
Not jagged (0); jagged (1). The suture between the scales of the same row, in external view, is jagged only in *Mesturus* (Nursall 1996b: character 101, 1999a: fig. 2; pers. obs.).

79 Scale rows
Simple (0); double (1). This character is taken from Nursall's (1999a) diagnosis of the genus *Mesturus*; as described by this author, the "scales rows bifurcate dorsally, anterior to the dorsal fin, and ventrally above the anal fin, in each case the doubling extending for a depth of four or five scales" (Nursall 1999a: 155, fig. 2; pers. obs.; Fig. 35A). Similar double scale rows are also present in at least the holotype of *Arduafrons* (Nursall 1999a: 168; Fig. 37). In turn, the holotype of *Palaeobalistum orbiculatum*, MNHN BOL 0523 shows several rows in the anterodorsal region of the body that seem to be double too. These rows, which are slightly curved, seem to double at a cer-

tain point as in *Arduafrons* and *Mesturus*, apparently with the same depth.

80 Scale rows between the bases of the lepidotrichia of the dorsal and anal fins
Absent (0); present (1). There are several rows of scales (up to eight, eventually 10 or more) placed between the proximal areas of the dorsal and anal lepidotrichia in *Arduafrons* (Fig. 37), *Brembodus*, *Gibbodon* (e.g., dorsal, anal, and caudal fins of the holotypes of these three genera), *Gyrodus* (Lambers 1991; pers. obs.), and *Mesturus* (e.g., NHML 37023; Fig. 35A). This character corresponds to Nursall's (1996b) character 23.

81 Ornamentation
Outgroup (?); ridges (1); reticulation (2); tubercles (3); small spines (4). The ornamentation of the dermal bones and the scales of *Iemanja* (Fig. 16A, B), *Macromesodon macropterus*, *Neoproscinetes*, *Nursallia* ? *gutturosum* (Fig. 9), *Proscinetes* (Fig. 8) and *Tepexichthys* (cast of holotype) is formed by ridges. These ridges may be more or less irregular and ordered. They are quite shallow in, for instance, *Neoproscinetes*; deeper and more regular, with occasional punctuations, in *Nursallia* ? *gutturosum*. However, we consider that these are minor variations of the same type of ornamentation (state 1). Reticulation, with well developed crests that limit deep, more or less large grooves (state 2) is shown by *Ocloedus subdiscus* n. comb., *Macromesodon* cf. *M. bernissartensis,* and *Stemmatodus* (Figs 2B; 12). Many pycnodontiforms exhibit tubercles (state 3): *Arduafrons* (Fig. 37), *Brembodus* (Fig. 7), *Apomesodon surgens* n. gen., n. sp. (Fig. 14A), *Gibbodon* (Fig. 6), *Gyrodus*, *Mesturus* (Fig. 35A), *Micropycnodon*, *Nursallia* ? *goedeli* (Fig. 35B), *Palaeobalistum orbiculatum* (Fig. 4A), *Abdobalistum* n. gen. (Fig. 4C, D) and *Trewavasia* (Fig. 32B). *Coccodus* exhibits both tubercles and strong, mostly parallel ridges (e.g., MNHN NAK 319, 359; Fig. 13; coded as 1, 3). *Apomesodon gibbosus* n. comb. presents coarse tubercles and also spines on the acid prepared bony surfaces of specimen FSL 93095 (Fig. 14B; coded as 3 and 4). The ornamentation of dermal bones and

scales consists of spines in *Ichthyoceros* (state 4). There are two types of ornamentation also in *Nursallia veronae*, as shown by the frontal bone of the holotype (coded as 1 and 3). *Oropycnodus ponsorti* n. comb. is even more variable, as it exhibits delicate ridges on the surface of the prearticular and tubercles on the imprints of the external surface of the skull roof bones of specimen NHML P.30045; tubercles on the frontals of paralectotype NMW 1854/XXXIX/39, and reticulation on the skull bones and on the scales of the latter and also of the lectotype and of paralectotype NMW 1854/XXXIX/40 (coded as 1, 2 and 3). *Pycnodus* presents states 2 and 3: for instance, the holotype, MNHN BOL 95, shows reticulation on most of the frontal, and tubercles on the bones around the dermocranial fenestra.

82 Large spines on scales
None (0); one (1); several (2). Small spines on the scales, similar to the ones found on the skull bones, are accounted for as ornamentation in the preceding character. However, exceptionally large, very conspicuous spines may also be present. In *Trewavasia* (state 1) there is a short, stout spine on the posterior border of each scale, corresponding to a conspicuous longitudinal keel on the scale (Gayet 1984; Nursall 1996b: character 57; Fig. 32). In *Ichthyoceros* (state 2) there is one large spine on the centre of each scale, plus several smaller, yet conspicuous, spines on each scale (Gayet 1984; the number of small spines is three to ten, depending on the size and position of the scale: pers. obs. on the holotype).

83 Nuchal plates
Absent (0); present (1). We consider nuchal plates *sensu stricto* the anteriormost ridge scales when they are elongated and imbricated, forming at least one distinct row that is obliquely oriented with respect to the other scale rows in the anterodorsal border of the body, just behind the occiput. These are the thick, ornamented nuchal plates between the occiput and the highest point of the body in *Apomesodon* n. gen. (Fig. 3A-C), *Arduafrons* (Fig. 37), *Brembodus* (Fig. 7), *Eomesodon* (Fig. 3A-C), and *Gibbodon* (Fig 6).

This character is a re-elaboration of Nursall's (1996b) characters 43 and 94 *pro parte*. See character 86 for further comments.

84 Dorsal spine formed by nuchal plates
Absent (0); present (1). A dorsal spine, distinctly formed by nuchal plates and placed between the occiput and the dorsal fin is present only in *Brembodus* (Tintori 1981; pers. obs.). It is of apparently very variable shape and length. This character corresponds to Nursall's (1996b) character 94 *pro parte*.

CONTOUR SCALES
In pycnodontiforms, the scales that form the contour of the body in lateral view are usually distinctly differentiated, being in this case called dorsal ridge and ventral keel scales. These differentiated contour scales are large and strengthened, presenting a crest, usually spined. Nursall (1996b: character 12) indicates that: "The counts and shapes of these (dorsal ridge and ventral keel scales) are often important in familial, generic or specific identification" (Nursall 1996b: 131). We have largely expanded his idea into our characters 85-99 to account for the possible variations in the differentiation and form of the differentiated contour scales, their number, and the number and arrangement of the spines often observed on their midline. Each of these characters, as proven by observations, is independent for the dorsal and for the ventral contour scales (see data matrix), and therefore we have made separate series of characters for them.

Both the number of contour scales and the number of their spines increase during ontogeny in pycnodontiforms, as shown by the following three examples. Juvenile specimens of *Gyrodus hexagonus*, such as MNHN SLN 22 (28 mm in standard length) exhibit 13 dorsal ridge scales with 1-2 spines, and about 23 ventral keel scales with 2-3 spines. Larger specimens, such as JM SOS 4303 (123 mm) present 17 dorsal ridge scales with up to about six spines, and 28-29 ventral keel scales, with 4-5 spines. The juvenile *Apomesodon gibbosus* n. comb. from the collection Schäfer (Kiel), as illustrated by Frickhinger
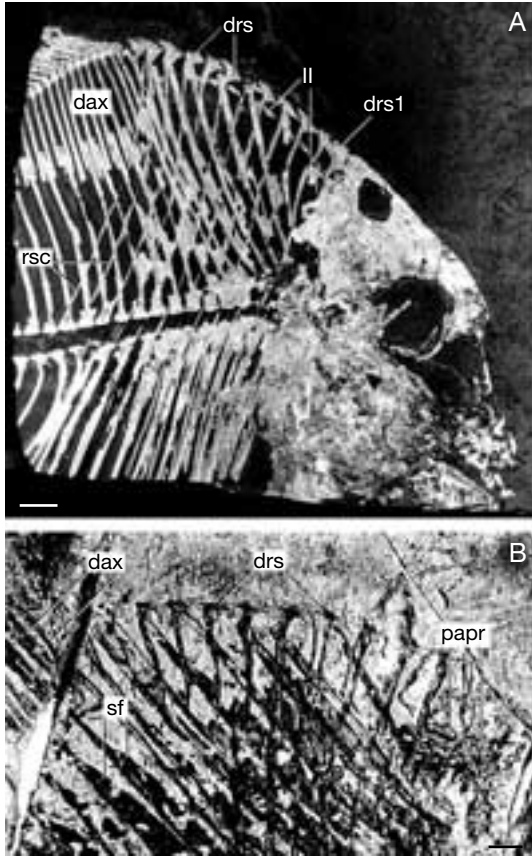
Fig. 38. — Anterodorsal region of the body in **A**, *Ocloedus subdiscus* n. comb., specimen MGSB 20376b. The incompleteness of the posterior region of the dermosupraoccipital allows observation of the shape of the first dorsal ridge scale, which is normally in a very close contact with this bone. Reverted left side, lateral view. Photo Serrette, under ultraviolet light; **B**, *Coelodus saturnus* Heckel, 1854, holotype, NMW 1857.XXXIII.2. Right side, lateral view. Photo Schumacher, courtesy Ortwin Schultz. Abbreviations: **dax**, dorsal axonosts; **drs**, dorsal ridge scales; **drs1**, dorsal ridge scale 1; **ll**, lateral line; **papr**, parietal process; **rsc**, reduced scales; **sf**, sagittal flanges. Scale bars: A, 5 mm; B, 1 cm.

(1994: fig. 432, 60 mm in total length) presents at most 14 dorsal ridge scales; the specimen from the collection Leich (Frickhinger 1994: fig. 431, 195 mm in total length), at most 17; and the large JM SOS 4120a-b (365 mm in standard length), at least 21. The only known juvenile specimen of *Macromesodon* aff. *M. bernissartensis* (LH 91-0110, 21 mm in standard length) exhibits 2-3 spines on the posteriormost ventral keel

scales, whereas adult specimens (e.g., LH 13483 a, b, about 95 mm) show 4-5. We therefore coded the states of the characters concerning the contour scales only in larger, adult specimens. These characters are to be considered with great precaution when described from smaller, juvenile individuals only.

85 Contour scales
Not differentiated (0); differentiated (1); absent (2). Most observed pycnodontiforms (including *Mesturus verrucosus*, specimen NHML 37023, and *Iemanja*, MNHN 1160 P) show contour scales that are morphologically different from all other scales of the body. They are placed dorsally between the occiput and the insertion of the dorsal fin, and ventrally between the cleithrum and the insertion of the anal fin (state 1). They are normally stout and large, with a strengthened border that forms a crest. The only exception seems to be *Paramesturus*, where the few preserved contour scales do not appear differentiated according to Taverne's restoration (1981: fig. 3B; state 0). Contour scales, as all other scales, are absent in *Coccodus* (state 2).

86 First dorsal ridge scale
Contour scales not differentiated (0); about same size than subsequent ridge scales (1); larger than subsequent ridge scales (2); absent (3). The anteriormost dorsal ridge scale, if present, is always incorporated onto the skull, in close contact with the posterior border of the dermal supraoccipital. The first dorsal ridge scale is not to be mistaken with a nuchal plate because it is not especially elongated, and does not imbricate forming part of a series of different direction from that of the other dorsal ridge scales. This first dorsal ridge scale can be of similar size and morphology to that of the subsequent dorsal ridge scales (state 1; e.g., *Gibbodon*, Fig. 6; *Ocloedus subdiscus* n. comb., Fig. 38A; *Stemmatodus*, Fig. 12) or different, larger than them (state 2; e.g., holotype of *Ichthyoceros*; *Mesturus* NHML P.8385, Nursall 1999a: figs 3, 4; *Oropycnodus ponsorti* n. comb. NHML P.30037, Fig. 11; *Proscinetes*, Fig. 8; in any case, it is never elongated or oriented in a different direction, as

nuchal plates are). The first, enlarged dorsal ridge scale corresponds to Nursall's (1996b: 147) "post-parietal bone" and (1999a) "nuchal plate". We nonetheless prefer not to name it like one or the other in order to avoid confusion, respectively, with an actual skull roof bone and with nuchal plates *sensu stricto* as defined in character 83, as it is not homologous to any of these structures.

87 Scutellum-like contour scales

Contour scales not differenciated (0); present, dorsal only (1); present, ventral only (2), present, dorsal and ventral (3); contour scales absent (4). In the scutellum-like contour scales the most distal border is relatively short, there is a constriction between the distal part and the base, and the base is expanded, larger than the distal border. The distal part is cornered by spine-like structures, that do not seem homologous to the spines placed along the midline that are accounted for by character 90. There are standard ventral keel scales in *Oropycnodus ponsorti* n. comb. and *Pycnodus*, but we also find dorsal scutellum-like contour scales (state 1; Blot 1987; pers. obs.). The case of *Abdobalistum* n. gen. is the converse; it exhibits standard, pointed ridge scales on the dorsal border, and scutellum-like scales ventrally. We have not seen any pycnodontiform with both dorsal and ventral scutellum-like contour scales other than *Nursallia veronae*, as shown by juvenile specimen MCSNV T.830. However, in the holotype the dorsal border of the body is broken and the ventral border is badly preserved, so this character requires further confirmation in adult specimens.

88 Number of differentiated dorsal ridge scales

Dorsal contour scales not differentiated (0); 18 or more (1); 15 to 17 (2); 10 to 14 (3); seven to nine (4); one or two (5); dorsal contour scales absent (6). Characters 88-93 are herein coded for *Neoproscinetes* following the restoration by Nursall & Maisey (1991, unnumbered fig. on p. 126), as we have not observed any specimen or photography of this genus where the dorsal rigde scales are accurately preserved. The maximum number (state 1) is observed in *Arduafrons*,

Apomesodon n. gen., and *Mesturus* among the forms where the dorsal ridge scales can be counted. State 2 is more abundant: ? *Eomesodon barnesi* (unknown in *E. liassicus*), *Gyrodus*, *Macromesodon*, *Stemmatodus*, etc. The holotype of *Brembodus* shows at least 10 dorsal ridge scales, and there are 12 in specimen MCSNB 4933. There are 11 after the apex in the holotype of *Gibbodon*. The holotype of *Nursallia veronae* has about 12, estimation confirmed by juvenile specimen MCSNV T.830 (all state 3). Specimen NMW 1965/536 a-b of *Trewavasia* has two scales: the first, large one incorporated to the skull roof, plus a second one with many spines (see also Fig. 32B; state 5, also present in *Ichthyoceros*).

89 Arrangement of dorsal ridge scales

Contour scales in close contact with each other (0); point contact (1); separated from each other (2); dorsal contour scales absent (3). The contact between the dorsal ridge scales varies from a close one (primitive state; e.g., *Gibbodon*, Fig. 6; *Stemmatodus*, Fig. 12) or a point one (state 1; e.g., *Ocloedus subdiscus* n. comb., Fig. 38A; *Oropycnodus ponsorti* n. comb., Fig. 11), to be completely separated (state 2; e.g., *Coelodus saturnus*, Fig. 38B; *Proscinetes*, Fig. 33A, B). Although this character may be somewhat misleading when the preservation and/or preparation of the dorsal border of the body are not good, *Macromesodon macropterus* consistently shows the anteriormost dorsal ridge scales separated from each other, whereas the posteriormost ones are in point contact with each other (Fig. 33C). It has been coded as 1, 2 for this species.

90 Number of spines on dorsal ridge scales

No spines on dorsal contour scales (0); one or two (1); three or four (2); five or more (3); midline serrated (4); dorsal contour scales absent (5). Most differentiated contour scales of pycnodonts exhibit spines placed along the midline (distal border in lateral view) of the scale. We counted the number of spines on the contour scales as the most common maximum number in most scales and individuals. This number is generally found in the

A B
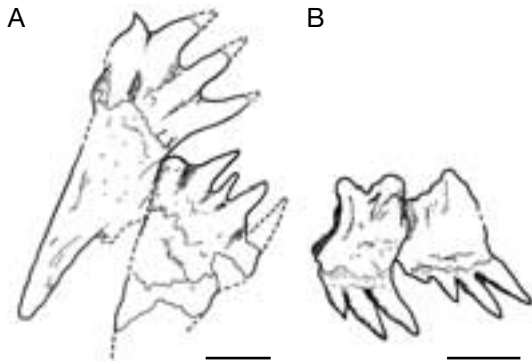
FIG. 39. — *Apomesodon surgens* n. gen., n. sp. Camera lucida drawings from specimen ML 15660; **A**, two consecutive dorsal ridge scales, placed just posterior to the apex; **B**, two consecutive postcloacal ventral keel scales. Notice the progressively increasing size of the spines in this case. Both left side, lateral view. Scale bars: A, 1 mm; B, 2 mm.

posterior scales of each series. Occasionally, one or two scales in some individuals may show one very small, additional spine, but we did not consistently account for it. It is to be remarked that the eventual absence of spines on the midline of the contour scales of pycnodontiforms must be taken with caution, as it may simply be the result of preservation, or, most commonly, of the absence of a proper preparation of the borders of the body. All studied pycnodontiforms exhibit spines along the midline of the dorsal ridge scales (states 1-4), with the exception of *Coelodus saturnus* (Fig. 38B), *Proscinetes* (Fig. 33A, B), *Pycnodus*, *Oropycnodus* n. gen. (Fig. 11), and *Tepexichthys* (primitive state). The "spines" seen in *Pycnodus* and *Oropycnodus* n. gen. are part of the scutellum-like structure of their contour scales, forming the corners of their distal part, as explained in character 87, and we do not consider them homologous to the midline spines seen in other genera. The fifth dorsal scale of *Abdobalistum* n. gen. NHML P.9830 shows two spines (state 1). At least one well-preserved dorsal ridge scale in specimen NHML 37023 of *Mesturus verrucosus* shows three spines (four spines after Nursall 1999a: fig. 2; state 2). The best preserved dorsal ridge scales in *Brembodus* are those of specimen MCSNB 4933; when well observable, they exhibit at least five small spines (state 3). The spines of the second ridge scale of *Trewavasia* are

tiny and very numerous (Gayet 1984; pers. obs.), so that we consider its dorsal ridge scales as serrated (state 4), and, as shown by NMW 1965/636 b, also the first scale has some spines, contrary to Gayet's (1984: fig. 6) restoration.

91 Distribution of spines on dorsal ridge scales
No spines on dorsal contour scales (0); all along the midline, or centered if only one spine present (1); posterior region (at most two thirds) of the midline (2); anterior region (at most two thirds) of the midline (3); dorsal contour scales absent (4). One well-preserved dorsal ridge scale in specimen NHML 37023 of *Mesturus verrucosus* shows the spines distributed all along the midline, as in Nursall 1999a: fig. 2. The small spines seen on specimen MCSNB 4933 of *Brembodus* and those of *Abdobalistum* n. gen. NHML P.9830 are also distributed all along the midline (state 1, the most abundant among pycnodonts). State 2 is present only in *Macromesodon* (Fig. 33C), *Ocloedus* n. gen. (Fig. 38A), and *Stemmatodus* (Fig. 12).

92 Contact of spines on each dorsal ridge scale
No spines on dorsal contour scales (0); separated from each other (1); in contact with each other (2); dorsal contour scales absent (3). The most observed state among pycnodontiforms is state 1. For instance, in *Abdobalistum* n. gen. NHML P.9830, only the fifth dorsal scale show spines; they are separated, and so are in *Brembodus* MCSNB 4933, *Gibbodon* (Fig. 6); even in *Macromesodon* the spines are slightly separated (Fig. 33C). State 2, dorsal ridge spines in contact, is more rare: e.g., *Ocloedus* n. gen. (Fig. 38A), *Stemmatodus* (Fig. 12).

93 Relative size of anterior and posterior spines on each dorsal ridge scale
No spines on dorsal contour scales (0); similar size (1); spines of increasing size in cephalocaudal sense (2); dorsal contour scales absent (3). In most cases where there are spines on each dorsal ridge scale, and they do not form a series of increasing size as in state 2, the spines have similar size (e.g., *Gibbodon*, Fig. 6; state 1). In *Apomesodon surgens* n. gen., n. sp. (Fig. 39A),
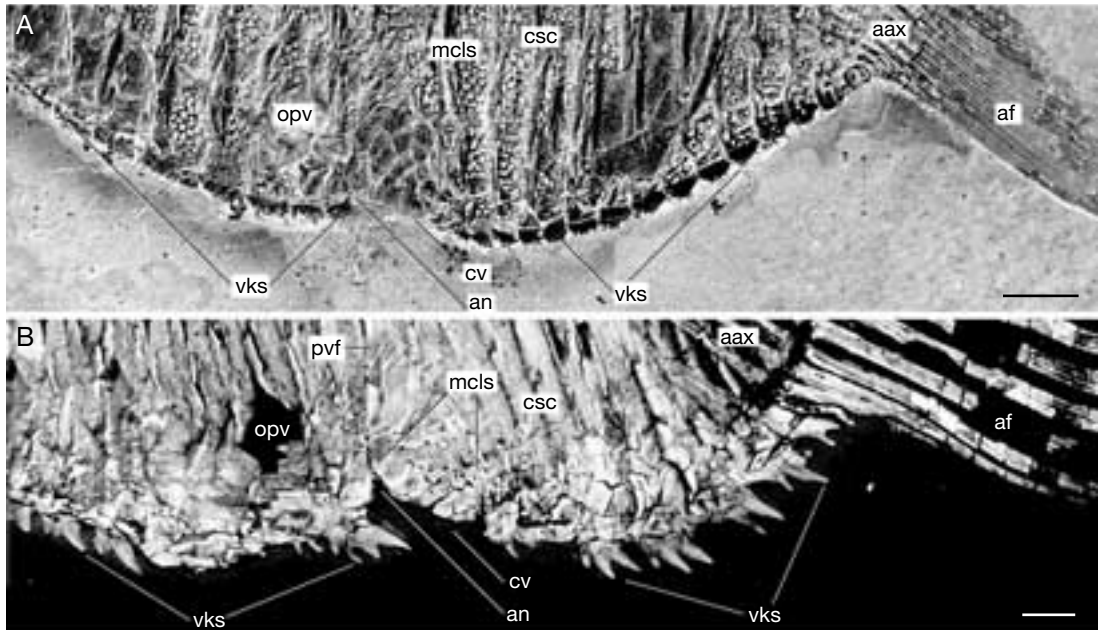
FIG. 40. — Ventral keel scales and mosaic cloacae; **A**, specimen JM 3710 of *Gyrodus hexagonus* (Blainville, 1818). Photo courtesy G. Viohl; **B**, specimen ML 15660 of *Apomesodon surgens* n. gen., n. sp. Photo Serrette, under ultraviolet light. Both left side, lateral view. Abbreviations: **aax**, anal axonosts; **af**, anal fin; **an**, anal notch; **csc**, complete scales; **cv**, cloacal vestibule; **mcls**, mosaic cloacal scale; **opv**, opening for pelvic fin; **pvf**, pelvic fin; **vks**, ventral keel scales. Scale bars: A, 5 mm; B, 2 mm.

there are different sizes, but still they do not form a series of increasing size, so it is coded also as 1. Two examples of spines of clearly increasing size in cephalocaudal sense are *Macromesodon* (Fig. 33C) and *Ocloedus* n. gen. (Fig. 38A).

94 Number of ventral keel scales
Not differentiated (0); 22 or more (1); 18 to 21 (2); 15 to 17 (3); 10 to 14 (4); two or three (5); ventral keel scales absent (6). The account of the ventral keel scales does not include the scales that are modified to form the cloaca (see characters 102-104); some examples of ventral keel scales are illustrated on figures 39B and 40-42. A large number of ventral keel scales (22 or more) is observed in *Arduafrons*, *Apomesodon gibbosus* n. comb., *Gyrodus* (Fig. 40A), and *Mesturus*. This number is reduced in other pycnodonts; for instance, *Ocloedus* n. gen. has at most 17 ventral keel scales (Kriwet *et al.* 1999; Fig. 2B; state 3); the lectotype of *Oropycnodus ponsorti* n. comb., NMW 1854/XXXIX/38, has about 12 ventral

keel scales (Fig. 4B). The most extreme reduction in this number, whenever ventral keel scales are present, is seen in *Ichthyoceros* (holotype and specimen MCSNM 3045A-B) and *Trewavasia* (contrary to Gayet 1984, there are only two in *Trewavasia*: holotype; NMW 1965/636; Fig. 32B).

95 Arrangement of ventral keel scales
Close contact with each other (0); point contact (1); ventral keel scales absent (2). Differently from the dorsal ridge scales, the ventral ones have never been observed separated from each other; they always appear contacting each other. They are usually in close contact (e.g., Figs 40; 41). They are in point contact, although under the overlying scales of the immediately dorsal row (visible by inclining the specimens), in the type series of *Oropycnodus ponsorti* n. comb. (Figs 4B; 43) and in *Proscinetes* (Fig. 5). This character is not applicable to *Trewavasia* because, although ventral keel scales are differentiated, there are

only two, the first one before the cloaca and the second one after the cloaca (specimen NMW 1965/636).

96 Number of spines on ventral keel scales

No spines on ventral keel scales (0); seven or more (1); four to six (2); one to three (3); ventral keel scales absent (4). Among the studied pycnodontiforms, all but *Eomesodon liassicus* and partially *Tepexichthys* exhibit spines on the midline of the ventral keel scales (e.g., Figs 40-42). *Tepexichthys* only shows spines (four of them) on the four posteriormost ventral keel scales, and no spines on the other scales, according to Applegate's (1992: fig. 4) restoration; it has therefore been coded as 0 and 2. The bad preservation does not allow good observation of this character in the holotype of *Gibbodon*, but the maximum number of spines does not seem to exceed three (state 3); unfortunately, no estimation can be given for any observed specimen of *Brembodus*. Exceptionally, one single scale of one single specimen of *Stemmatodus* (NHML P.45679) exhibits eight spines, but in all other cases the number is four to six (state 2). The specimens of the type series of *Oropycnodus ponsorti* n. comb. have up to five to six spines (state 2). In *Trewavasia* there is a longitudinal midline groove, with two serrated edges, plus two or three posterior spines in, at least, the last ventral keel scales (Gayet 1984: figs 7, 8; pers. obs.). We have therefore coded this character as 1 for this genus. Only in the juvenile specimen of *Nursallia veronae* can this character be verified (there is at least one spine), but because of the ontogenetic changes mentioned above, characters 96-99 have been coded as ? for this taxon.

97 Distribution of spines on ventral keel scales

No spines on ventral keel scales (0); all along the midline, or centered if only one spine present (1); posterior region (at most two thirds) of the midline (2); ventral keel scales absent (3). The cases where the spines are distributed all along the midline of each ventral keel scale are rare (e.g., *Gyrodus*, Fig. 40A). They are mostly distributed only in the posteriormost part of the scale, at most the posteriormost two thirds, leaving a smooth anteriormost part of the ventral midline (e.g., Figs 40B; 41). Due to the highly derived nature of the ventral keel scales of *Trewavasia*, just explained above, we have coded this character as 1 and 2 for this genus.

98 Contact of spines on each ventral keel scale

No spines on ventral keel scales (0); separated from each other (1); in contact with each other (2); ventral keel scales absent (3). They are separated (state 1) in, for instance, *Apomesodon* n. gen. (Fig. 40B), *Gyrodus* (Fig. 40A), and *Proscinetes* (Fig. 41A). The anteriormost ventral keel scales of *Anomoeodus* (NHML 25780) show spines in contact (state 2). Some other examples of contacting spines on each ventral keel scale are *Ocloedus* n. gen. (Fig. 41B), *Oropycnodus* n. gen. (Fig. 42), and *Stemmatodus* (Fig. 41C).

99 Relative size of anterior and posterior spines on each ventral keel scale

No spines on ventral keel scales (0); all spines of similar size (1); spines of increasing size in cephalocaudal sense (2); ventral keel scales absent (3). In contrast with its dorsal scales (Fig. 39A), *Apomesodon surgens* n. gen., n. sp. shows the spines of each ventral keel scale forming a series of increasing size in cephalocaudal sense (Figs 39B; 40B); this is state 2, the most common one in pycnodonts (e.g., Figs 41; 42).

100 Several scales attached to the contour scales

No (0); yes (1); contour scales absent (2). Among studied pycnodontiforms, only the holotype of *Abdobalistum* n. gen. exhibits several thin, long scale bars joined to each dorsal and ventral contour scale forming a kind of "bouquet" (Blot 1987: fig. 48, pls 26, 27; pers. obs.; Fig. 4C, D). The scale bars are probably attached, but not fused, to the contour scales, but the unsatisfactory state of preservation prevents from certainty in this matter.

CLOACA

Nursall (1996b) first pointed the importance of the cloaca in pycnodonts. Our characters 101-
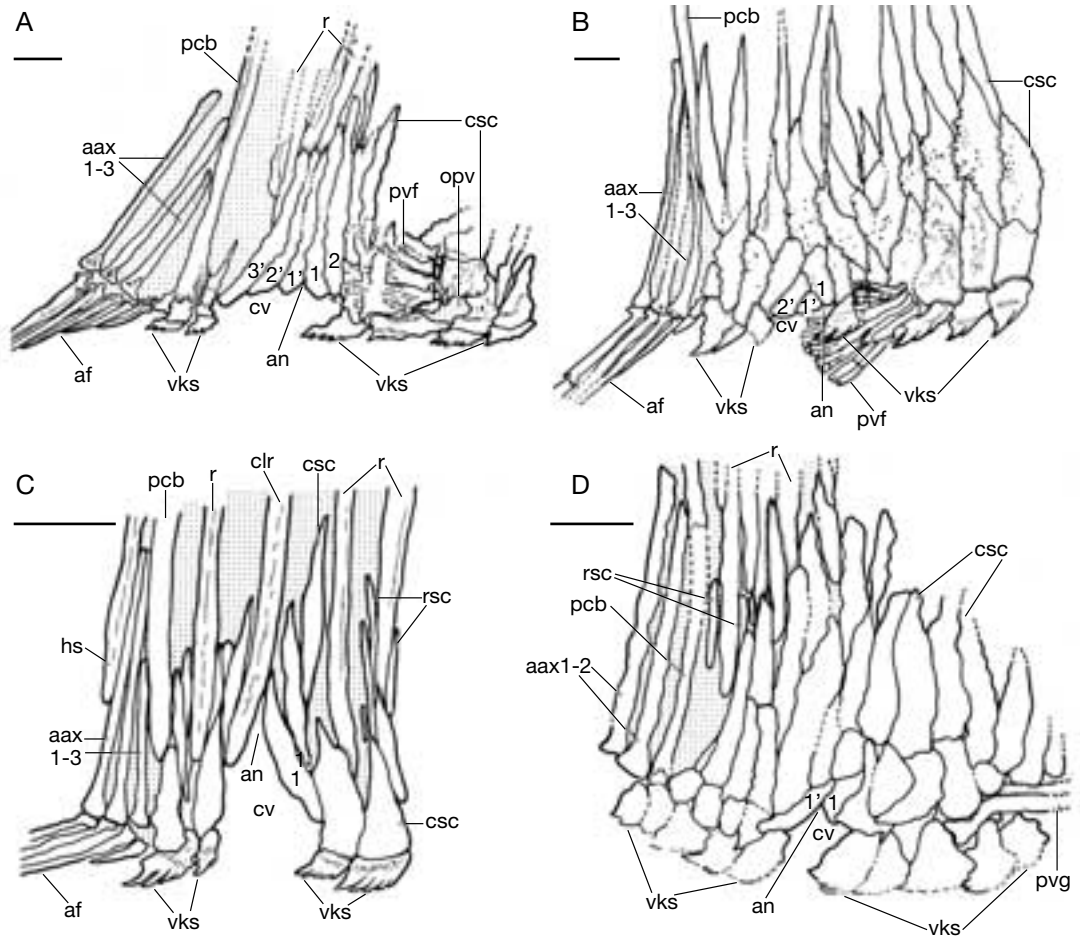
FIG. 41. — Non-mosaic cloacae without bifid scale; **A**, *Proscinetes elegans* (Agassiz, 1833), camera lucida drawing from specimen JM 1941.12a, right side, lateral view; **B**, *Ocloedus subdiscus* n. comb., camera lucida drawing from specimen MNHN MSE 965. Modified from Kriwet *et al.* 1999. Ribs not depicted. Ventral keel scales under pelvic fin partially visible by transparency and in relief. Right side, lateral view; **C**, *Stemmatodus rhombus* (Agassiz, 1839), restoration mostly from camera lucida drawings of specimens NHML P9672 and 43451, reverted left side, lateral view; **D**, *Stenamara mia* Poyato-Ariza & Wenz, 2000, camera lucida drawing of silicone peel from the holotype, MCCM LH-14365. Remains of some pelvic and anal fin rays not depicted. Reverted left side, lateral view (right side on original specimen). Abbreviations: **aax**, anal axonosts; **af**, anal fin; **an**, anal notch; **clr**, cloacal rib; **csc**, complete scale(s); **cv**, cloacal vestibule; **hs**, haemal spine; **opv**, opening for pelvic fin; **pcb**, post-coelomic bone; **pvf**, pelvic fin; **pvg**, pelvic girdle; **r**, rib(s); **rsc**, reduced scales; **vks**, ventral keel scale(s); **1**, **2**, anterior modified cloacal scales; **1'**, **2'**, **3'**, posterior modified cloacal scales. Scale bars: A-C, 2 mm; D, 5 mm.

104 are re-elaborated from Nursall's (1996b) character 13: "The position of the cloacal aperture is marked by modified scales" (Nursall 1996b: 131). The modification of these scales (Figs 40-42) can be accounted as differences in size and morphology with respect to the scales of adjacent areas, and also as differences in their arrangement. These modifications include, for instance, a reduction in size, with irregular shapes (e.g., Fig. 40) to elongation and/or curvature of the shape (e.g., Fig. 41A). In addition, the scales that form the border of the cloaca lack thickened borders, spines, and crests, and consequently cannot be considered as differentiated keel scales, and there are no keel scales that correspond to them.
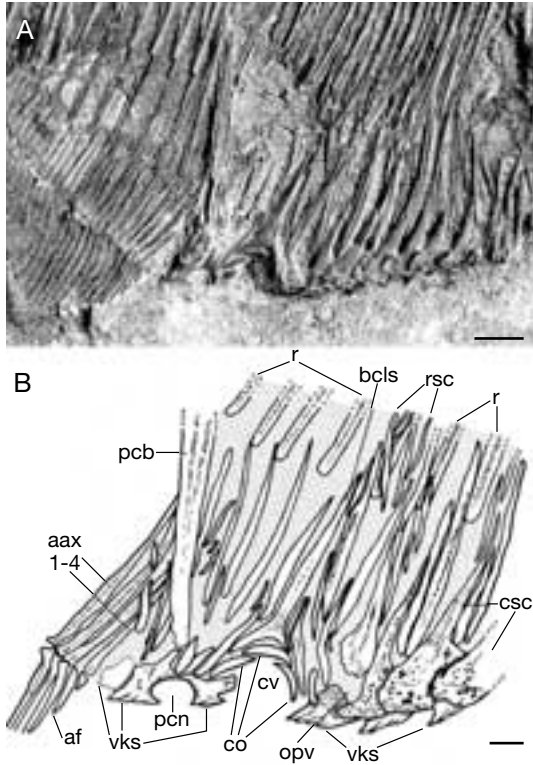
FIG. 42. — *Oropycnodus ponsorti* n. comb., non-mosaic cloaca with bifid scale; **A**, cloacal region of the lectotype, NMW 1854.XXXIX.38. Photo Schumacher, courtesy Ortwin Schultz; **B**, restoration of the cloacal region, mostly after a camera lucida drawing of the lectotype, illustrated in A, with information taken from camera lucida drawings of the paralectotypes, NMW 1854.XXXIX.39 and NMW 1854.XXXIX.40, and, topotypes NHML P1638, P3004, and P.30037. Both right side, lateral view. Abbreviations: **aax**, anal axonosts; **af**, anal fin; **bcls**, bifid cloacal scale; **co**, comma-shaped cloacal scales; **csc**, complete scales; **cv**, cloacal vestibule; **opv**, opening for pelvic fin; **pcb**, post-coelomic bone; **pcn**, post-cloacal notch; **r**, ribs; **rsc**, reduced scales; **vks**, ventral keel scales. Scale bars: A, 2 mm; B, 5 mm.

Among studied pycnodontiforms, the cloaca is apparently absent only in all observed specimens and figures of *Mesturus*, in which we have seen no modified scales in this area. This includes the cast of the holotype, NHML 49417, where there is a region of scales in rows of different direction (see state 1 of character 77) on the base of the anal fin, but the scales of the cloacal region seem unmodified, and all this area is bordered ventrally by continuous keel scales. We have therefore coded as 0 for *Mesturus* in all of our characters regarding the

cloaca. Cloacal scales are certainly modified, but their precise number and arrangement cannot be established, in *Iemanja*, *Neoproscinetes*, *Nursallia*, *Palaeobalistum orbiculatum*, and *Trewavasia*.

101 Number of post-cloacal ventral keel scales
Cloacal and contour scales not differentiated (0); 10 or more (1); seven or eight (2); five or six (3); three or four (4); two (5); one (6); none (7). This character is a re-elaboration of Nursall's (1996b) characters 13 *pro parte* (comments about the relevance of the position of the cloaca for taxonomic purposes), 37 ("cloacal aperture located at about the midpoint of the ventral contour, i.e. well in front of the origin of the anal fin"), and 50 ("six or fewer ventral keel scales [scutes] separate the cloacal aperture from the origin of the anal fin"), that we consider as different states of a single character that can be numerically accounted for. Up to six states have been used because we have found distinct characteristic accounts. The number of post-cloacal ventral keel scales is that of the keel scales placed between the cloaca and the insertion of the anal fin, and does not include the modified scales forming the cloaca (not forming part of the keeled ventral border and without spines; see characters 102-104 and Figs 40-42). The unlabelled specimen of *Arduafrons* at the Museum Bergér has at least 10 keel scales between the cloaca and the anal fin ("about eight" in Nursall 1999a: 168), so it has been coded as 1. A high number of post-cloacal ventral keel scales is also present in, for instance, *Gyrodus* (Fig. 40A). These scales are, nonetheless, scarcer in most other pycnodonts (e.g., Figs 41; 42). The exact number is hard to confirm in *Gibbodon*, although it can be estimated as 5-6 (state 3). The observation is also difficult in *Brembodus*, but the holotype seems to show only two large scales between the cloaca and the anal fin, the same number exhibited by specimen MNHN DTS 61 D of *Nursallia* ? *gutturosum* (state 5).

102 Number of anterior cloacal modified scales
Cloacal scales not modified (0); mosaic of little scales (1); two (2); one (3); cloacal scales absent (4). We have counted in this character the scales of

the ventral border of the body that are modified in shape and direction, do not have a corresponding keel scale, and are anterior to the anal notch. We have treated the number of anterior and of posterior cloacal scales separately because they are not linked (see the different combinations in the data matrix). We consider that a cloacal scale is modified whenever it forms part of the border of the cloacal vestibule, it shows remarkable differences in size and direction when compared with other scales, and it is not in the same row of any keel scale. Other cloacal scales are not considered modified when, even though they may be part of the border of the cloaca, they do not show significant modifications in shape or direction when compared with other scales of the ventral region, and belong to the same row as the corresponding ventral keel scale, usually in a one to one relationship (except for the mosaic states).

Anomoeodus exhibits a differentiated cloaca. Nonetheless, the scale that forms the anterior border of the cloacal vestibule is not specially modified, but is simply a keel scale that bears spines on its midline (Dixon 1850: pl. 33; Woodward 1909: pl. 34, fig. 3; Kriwet 1999: fig. 7; pers. obs. on NHML 25780), so we have coded this character as 0 for this taxon. There is a mosaic of little polygonal to irregular scales (state 1) in *Apomesodon surgens* n. gen., n. sp. (ML 15660, Fig. 40B), *A. gibbosus* n. comb. (Frickhinger 1994: fig. 431), *Arduafrons* (NMHL P8658), and in *Gyrodus* (JM 3710, Fig. 40A). The scales of the cloaca are not clearly observable in *Brembodus* and *Gibbodon*, but there is no trace of curved scales; all of them seem to be in mosaic (relatively smaller scales plus anal notch in the latter). So, the character has also been coded as 1. State 2 is for two modified scales, as, for instance, in *Macromesodon* aff. *M. bernissartensis* and *Proscinetes* (Fig. 41A). State 3 is for one modified scale, as, for instance, in *Ocloedus subdiscus* n. comb. (Fig. 41B), *Macromesodon macropterus*, *Stemmatodus* (Fig. 41C), and *Stenamara* (Poyato-Ariza & Wenz 2000; Fig. 41D).

103 Number of posterior cloacal modified scales

Cloacal scales not modified (0); mosaic of little scales (1); three (2); two (3); one (4); no scales, posterior part of anal notch supported by a rib (5); cloacal scales absent (6). We have counted in this character the scales of the ventral border of the body that are modified in shape and direction, do not have a corresponding keel scale, and are posterior to the anal notch. There is a mosaic of little polygonal-irregular scales (state 1), quite more abundant than in the anterior region of the cloaca, in *Apomesodon surgens* n. gen., n. sp. (ML 15660, Fig. 40B), *A. gibbosus* n. comb. (Frickhinger 1994: fig. 431), *Arduafrons* (NMHL P8658), and in *Gyrodus* (JM 3710, Fig. 40A). Three scales (state 2) were observed only in *Proscinetes* (Fig. 41A). State 3, two scales, is somewhat more common. It appears in, for instance, *Anomoeodus* (Dixon 1850: pl. 33; Woodward 1909: pl. 34, fig. 3; Kriwet 1999: fig. 7; pers. obs. on NHML 25780) and *Ocloedus subdiscus* n. comb. (Fig. 41B). There is one scale (state 4) in, for instance, *Macromesodon macropterus*, *Macromesodon* aff. *M. bernissartensis*, and *Stenamara* (Poyato-Ariza & Wenz 2000; Fig. 41D). Curiously, and unique among the observed pycnodontiforms, the dorso-posterior border of the anal notch is not bordered by any modified scale, but supported instead by the distal end of a rib, in *Stemmatodus*. The ventro-posterior part of the anal notch is formed by a scale that bears a keel scale (e.g., MNHN JRE 42; NHML P.9672 and 43451; Fig. 41C). This is coded as no posterior modified scale (state 5).

104 Bifid scale in cloaca

Absent (0); present (1); present plus several comma-shaped scales (2). *Pycnodus* shows a thin, long, bifid central scale whose bifurcation forms the dorsal border of the anal notch (Nursall 1996b: fig. 10; pers. obs.). Such a scale, without flanking scales, has also been observed in the juvenile specimen of *Nursallia veronae* (MCSNV T.830), which presents a cloaca that is very similar to the cloaca of a young *Pycnodus*, such as MCSNV T.309. When the region is well preserved (e.g., MNHN BOL 126; see also Blot 1987: pl. 22, fig. 2), two smaller, elongated scales flanking the bifid scale, one anteriorly and one posteriorly, are also visible, and are accounted for

in the two preceding characters. Unfortunately, this region is missing (broken, hole and crack filled with glue) in the holotype of *Nursallia veronae*, and it requires further confirmation in adult specimens (coded as 1). State 2 is present only in *Oropycnodus ponsorti* n. comb. It also exhibits a bifid central scale, but, differently from state 1, this scale is doubled ventrally by curved, comma shaped scales, which are the ones that actually form the dorsal border of the anal notch (Fig. 42).

105 Post-cloacal notch

Absent (0); present (1). Among observed pycnodontiforms, only *Oropycnodus* n. gen. presents a notch between the cloaca and the anal fin. This post-cloacal notch is formed by the two ventral post-cloacal keel scales, which form a large, oval notch between them. This character is better observable in the lectotype (Fig. 42), but it is not a feature of preservation in this specimen only, as, whenever there are remains of these scales, they have the morphology that corresponds to this post-cloacal notch (e.g., both paralectotypes).

RESULTS OF THE CLADISTIC ANALYSIS

An abbreviated list of characters is given in Appendix 1; the complete data matrix is presented in Appendix 3. The cladistic analysis using the stepwise (closest) addition method resulted in 36 equally most parsimonious trees (MPTs) of 634 steps. The strict consensus tree (SCT) is depicted in Fig. 43. The SCT shows a relatively low number of undeterminations, which are not solved with any other consensus method (Adams, 50% majority rule, semistrictus). The consistency index (CI) is 0.465, and the homoplasy index (HI), 0.563. The CI excluding uninformative characters is 0.431, and the HI, 0.586. Uninformative characters are, nonetheless, kept, as they are useful for the diagnosis of the terminal taxa (see Systematics section below). The Retention Index (RI) is 0.576, and the Rescaled Consistency Index (RC), 0.268. These low values are expectable for a matrix with such a high num-

ber of characters, taxa, and points of interrogation, but they also indicate a relatively high degree of homoplasy (see Conclusions section).

Our discussion of the nodes will proceed from the base to the top of the tree (Fig. 43). The characters that define every nodes are listed in Appendix 4; we refer to this appendix for all the details that are not fully presented in this section. The differences between the 36 MPTs lie in the indetermined nodes: these are signalled by correlative letters in the tree; respectively, indeterminations A, B, C, and D. Only B is a total undetermination; the other three present limited possibilities of configuration. The indeterminations concern: the position of the genus *Micropycnodon* (A); the relative position of ? *Eomesodon barnesi* and *Eomesodon liassicus* (B); the sister-group of *Anomoeodus* (C); and the sister-group of *Iemanja* (D). The characters that define them are taken from alternative trees (trees numbers 1, 2, 3, 9, 22, 27, and 36). The alternative nodes form the series 1 (that is, A1, B1, and so on), and the series 2 (A2, B2, etc.); all of them are listed in Appendix 4. All other nodes are identical for all MPTs, and are numbered correlatively from base to top of the tree; the characters that define them are, in most cases, the same in all MPTs. If there are differences, they only affect the nodes that are adjacent to alternative nodes, and only in the characters that are different in the definition of the alternative nodes. The characters listed for each node in Appendix 4 are taken from the strict consensus tree.

We tested to run the data matrix with all characters unordered. The result was 72 MPTs 50 steps shorter (584 steps), but the strict consensus tree is much less satisfactory. In this case, *Paramesturus* is the stem-group of a total indetermination where only the following clades are found:

– *Brembodus* + *Gibbodon*
– (*Apomesodon gibbosus* n. comb. + *A. surgens* n. gen., n. sp.) + ? *Eomesodon barnesi*
– (*Coccodus* + *Ichthyoceros*) + *Trewavasia*
– (*Pycnodus* + *Oropycnodus* n. gen.) + (*Nursallia veronae* + ? *N. gutturosum* + ? *N. goedeli*)
– (*Macromesodon macropterus* + *M. bernissartensis*) + *M.* cf. *M. bernissartensis*
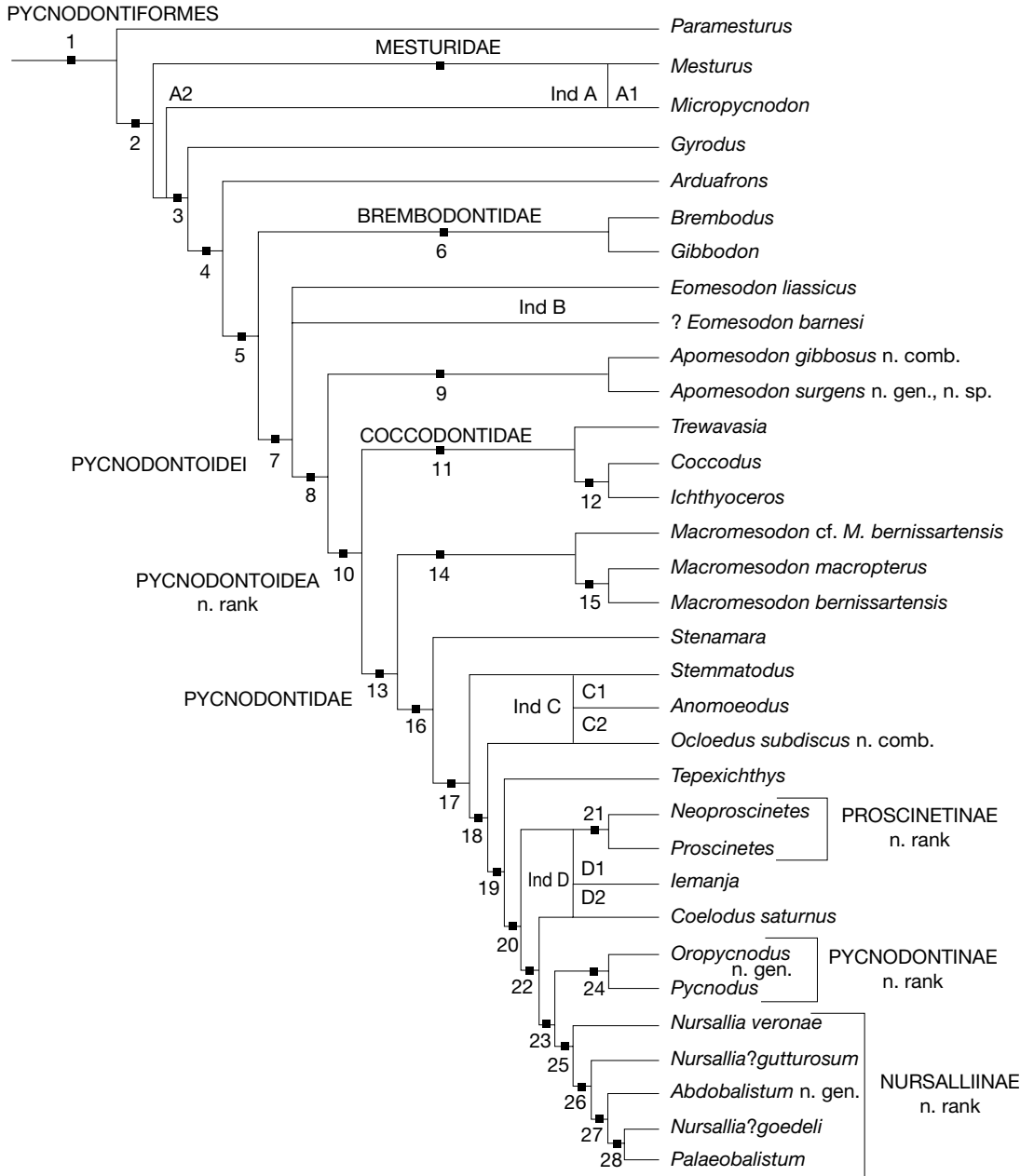
FIG. 43. — Cladogram showing the strict consensus tree. The nodes are numbered from base to top of the tree. The indetermina-tions are labelled Ind A, B, C, and D, also from base to top of the tree. Indeterminations A and C are depicted showing the only pos-sible nodes obtained in the alternative trees (A1, A2, C1, C2); B is a total indetermination, and the two alternatives for D cannot be graphically shown. For the characters defining each node, see Appendix 4.
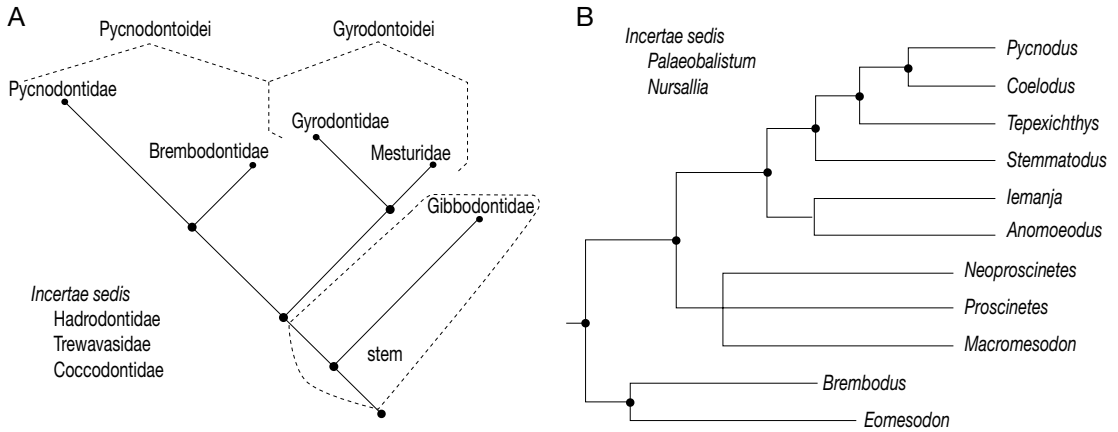
F_IG. 44. — Hypothesis of phylogenetic relationships of the Pycnodontiformes by Nursall (1996b: modified from figs 4 and 18); **A**, relationships of the basal groups; **B**, relationships of the Pycnodontoidei.

– *Stenamara* + {(*Anomoeodus* + *Ocloedus* n. gen. + *Stemmatodus*) + [*Tepexichthys* + (*Coelodus* + *Iemanja*) + (*Proscinetes* + *Neoproscinetes*)]}
In this case, it is obvious that ordering the characters results in a longer but much better resolved consensus tree.

Now we will compare our results (with some characters ordered, as listed in the Methods section) with Nursall's (1996b) hypothesis, the only phylogenetic arrangement previously available, presented in Fig. 44 herein.

Nodes 1-2: order Pycnodontiformes
The present analysis confirms that, as stated by Nursall (1996b), the order Pycnodontiformes is a strong monophyletic group. With the DELTRAN optimization, quite a number of the supposed auto- and synapomorphies of this order do appear in the present analysis defining node 2, that is, Pycnodontiformes minus *Paramesturus*. These are characters: 1(1), high body shape; 24(1), preopercular hypertrophied; 25(1), opercular process of hyomandibular reduced; 27(1), suboperculum and interoperculum absent; 28(1), opercular reduced; 36(1), crushing vomerine teeth, primitively circular in contour; 41(2), dentary small, primitively posteriorly bifid; 43(1), crushing prearticular teeth, primitively circular in

contour; 44(1), prearticular teeth forming rows; 85(1) and, dorsal and ventral contour scales differentiated. However, these and many other characters that define node 2, Pycnodontiformes minus *Paramesturus*, are actually unknown in *Paramesturus*. The program, with the DELTRAN optimization, extrapolates that they are absent in *Paramesturus*, but this needs confirmation when complete, well preserved specimens of this form are found. These characters are, nonetheless, present at the base of the Pycnodontiformes (node 1) with the ACCTRAN optimization. Actually, the Pycnodontiformes is an especially strong clade with this optimization, defined by 48 synapomorphies. On top of this, the analysis has not provided characters for *Paramesturus*, so it is obvious that the problem lies rather with this form than in the definition of the Pycnodontiformes. We consequently prefer to use all of the available autapomorphies to define the Pycnodontiformes. *Paramesturus* is in need of revision; Nursall (1999a: 170) notes two characters of this genus that are "contrary to the pycnodont condition". If some more pycnodontiform autapomorphies eventually turned out to be absent in this genus, then the order would need to be rediagnosed, or, more likely, the phylogenetic position of *Paramesturus* would need to be reconsidered out of the Pycnodontiformes.

Some of Nursall's (1996b) pycnodontiform characters are not interpreted as autapomorphic for this order by the present analysis because they are either unknown in many primitive forms (e.g., his number 16, anterior sagittal flanges present), or eventually absent in some pycnodonts. For instance, his character number 8 (presence of a high coronoid process) is not found in *Arduafrons* and *Ichthyoceros* (see presentation of character 47 above), and his character 13 (presence of a modified cloaca) seems to be absent in *Mesturus* (see introduction to characters 101-105 above). In turn, some of Nursall's synapomorphies, including the edentulous maxilla, do not appear in the analysis at the base of the Pycnodontiformes because we have made several derived states out of it; however, the presence of an edentulous maxilla, regardless of its morphology, is better regarded as an autapomorphy of the order. The same can be said about the morphology of the cleithrum. Character 9 of Nursall's (1996b: 131), vertical double mandibular articulation, does not appear in our diagnosis of the Pycnodontiformes. In our opinion, it is homologous to the articular-symplectic and angular-quadrate articulation of the Halecomorpha, because the bones that are involved in the double articulation and their topographic relationships are exactly the same. The fact that this articulation in pycnodontiformes is vertically arranged, instead of inclined as in *Amia* and other halecomorphs, is, in our opinion, a logical consequence of the vertical development of the pycnodont cranium.

Finally, some of Nursall's (1996b) synapomorphies have not been used in the present analysis because they are homogeneous among pycnodonts, and therefore of no use for the study of their interrelationships. But, since they are autapomorphic characters, they are also used for the diagnosis of the order in the Systematics section below: mesethmoid T-shaped in section; parasphenoid largely developed, edentulous, and inflected downwards; absence of supramaxilla; long and stout mandibular symphysis; ribs alate. The non-autapomorphic characters listed for the Pycnodontiformes in Appendix 4 have not been used for the diagnosis, but they provide additional information to characterize the order. They also provide some useful clues about which are the states that result primitive within this order for certain characters (e.g., number 9, the frontals are primitively curved and short for pycnodontiforms; numbers 36 and 43, the vomerine and prearticular teeth are primitively circular in contour for pycnodontiforms).

Indetermination I: family Mesturidae

Nursall (1999a) provided a revision and a diagnosis of the family Mesturidae. According to this author, it includes: *Mesturus*, the type genus; *Arduafrons*; *Micropycnodon*; and *Paramesturus*. However, *Arduafrons* and *Paramesturus* appear in the present analysis out of the Mesturidae because the mesturid characters provided by Nursall (1999a: 155) are interpreted by the present analysis either as primitive within Pycnodontiformes (e.g., our character 23, suborbital tesserae – cheeks covered by a mosaic in Nursall [1996b] – and our character 29, gular region covered by tesserae) or as autapomorphic of *Mesturus* (e.g., our character 13, parietal divided). Consequently, with the present evidence we interpret the family Mesturidae in a restricted sense, including only *Mesturus* (*M. verrucosus* and *M. leedsi*: Nursall 1999a) and *Micropycnodon* (*M. kansaensis* and *M. gaynaisensis*: Nursall 1999a), even though the latter is involved in indetermination A, node A1 being the one including it in the family Mesturidae. Pending further evidence, we prefer to keep *Micropycnodon* in the Mesturidae, which is consistent with the chararacter distribution that we have presented for the base of the Pycnodontiformes (alternative node A2 is based on a slightly different distribution of the characters present at the base). The present analysis could not find any autapomorphy to diagnose the family, but it provided a unique combination of derived characters: 49(2), strong crenulations in vomerine and prearticular teeth present in most teeth; 51(1), grooves in crushing teeth present; and 86(2), first dorsal ridge scale larger than subsequent scales. With ACCTRAN it presents two additional,
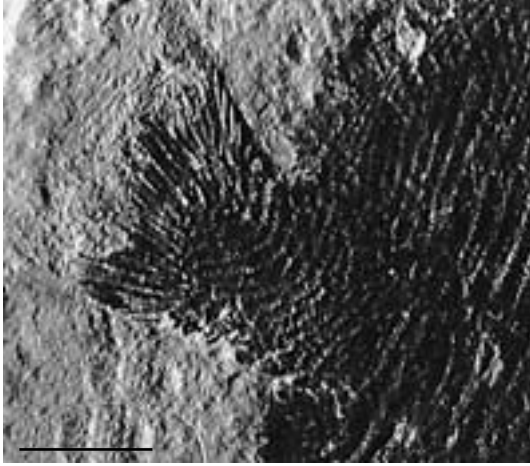
FIG. 45. — Caudal region of the holotype of *Gibbodon cenensis* Tintori, 1981, MCSNB 3317. Right side, lateral view. Photo courtesy F. Confortini, M. Malzanni, A. Paganoni. Scale bar: 5 mm.

useful characters, that have also been included in the diagnosis: 35(2), maxilla ornamented and elongated; and 69(2), anal fin at 60-69% of standard length.

Nodes 3-4: "suborder Gyrodontoidei"

Nursall (1996b) gathered the families Mesturidae and Gyrodontidae in the "suborder Gyrodontoidei" (Fig. 44A). According to the results of the present analysis, a "suborder Gyrodontoidei" *sensu* Nursall (1996b, 1999a) is a paraphyletic group. It is so because the characters used by this author (1996b: 133) are interpreted by the present analysis as primitive within Pycnodontiformes. For instance, his character 23, our 80(1), scale rows between dorsal and anal lepidotrichia present, appears, according to the present analysis, as a basal pycnodontiform character (node 1), to disappear in the Pycnodontoidei (node 7). In other words, the characters that could gather *Mesturus* and *Gyrodus* are insufficient to break up nodes 3 and 4, which separate *Gyrodus* and *Arduafrons* from the Mesturidae, making these two genera successive stem-groups to node 5. In the first place, the node 3, which separates *Gyrodus* from the Mesturidae, is a strong clade, defined by 14 synapomorphies, one

of which (15(1), dermal supraoccipital single) is an autapomorphy. Secondly, the node 4, which separates *Arduafrons*, is defined by seven synapomorphies. Finally, although *Paramesturus* is a problematic taxon (see comments above), the result is the same when the analysis is run with this form removed from the data matrix, although minor differences do occur in the character distribution. Therefore, none of the analyses makes any sister-group relationship of *Gyrodus* with *Mesturus*, *Micropycnodon*, *Arduafrons*, or any other genus.

We must bear in mind that it is possible that further findings may provide information to re-evaluate this hypothesis, as there are still large blanks in our current knowledge of the basal pycnodontiforms. For instance, the axial and caudal endoskeletons are not known in any of these forms but *Gyrodus*, and, at present, what we know of the cranial anatomy of *Arduafrons* and *Micropycnodon* is quite limited due to unsatisfactory preservational factors. With the present evidence, however, it is more parsimonious to consider the "suborder Gyrodontoidei" as a nonmonophyletic group, and therefore we do not use this taxon in the Systematics section below.

Family Gyrodontidae

As in Nursall (1996b), the Gyrodontidae appears in our analysis as a monogeneric family formed by the genus *Gyrodus* only. The familiar taxon is kept in the Systematics section below because it has become of common use. We consider that, at present, the 11 apomorphies that define the genus *Gyrodus* can be applied also to characterize the family Gyrodontidae. They include three autapomorphies: 48(1), central papilla in crushing teeth present; 55(4), anterior and posterior sagittal flanges with strengthened margins (unknown in Mesturidae); and 56(2), 10 or more anterior neural spines autogenous (unknown in all taxa between *Gyrodus* and the base of the tree).

Node 5: Pycnodontoidei plus Brembodontidae

This is a relatively strong clade, defined by 10 to 12 synapomorphies (depending on the alternative

node B chosen, characters 49(1) and 88 (2) may not be present in node 5). In any case, two of these characters (41(1), dentary small, posteriorly simple and 55(1), sagittal flanges anterior only) are autapomorphic. The genus *Gibbodon* appears within this node (see family Brembodontidae below), whereas it is the stem-group Pycnodontiformes after Nursall (Fig. 44A). It must be remarked, nonetheless, that the phylogenetic position assigned by Nursall (op. cit.) is based only on the presence of caudal homocercy in all pycnodontiforms but *Gibbodon*. However, we did not use this character in our analysis because the caudal skeleton of *Gibbodon* (Fig. 45) is quite difficult to interpret: the tail is twisted, the distal end of the fin rays is not preserved, and the scale covering obscures the endoskeleton. Although the scales seem to be slightly more numerous in the upper lobe, it is difficult to decide whether the tail is strictly heterocercal or homocercal, because the caudal pedicle is twisted, and the scales in the upper and lower lobe are somewhat distorted and not well preserved. Even though it may present some more scales in the upper caudal lobe, this could also be the case of *Mesturus* and *Arduafrons* (pers. obs.; Fig. 35). Externally, these tails, if not strictly homocercal, are on the verge of homocercy, so that the application of squamation criteria gives inconclusive results. In any case, the relief of the hypochordal elements under the scales of *Gibbodon* (pers. obs. on the holotype) suggests that they are somewhat enlarged, their number possibly being reduced. Their distal outline is shortened and curved, not long and sigmoid. These are all indications of possible internal homocercy. We did, nonetheless, test this character. We run the data matrix with the character "caudal fin heterocercal (0) or homocercal (1)" with several possible codifications for *Mesturus* and *Arduafrons*. Even when coded as heterocercal (0) for *Gibbodon* alone and as homocercal (1) for the rest of the taxa, the SCT and the MPTs were exactly the same ones that we are presenting herein (Fig. 43).

It is to be remarked, nonetheless, that even though the inclusion of *Gibbodon* within this node is the most parsimonious topology according to the present analysis, this genus presents numerous reversions (7 out of 13 characters), so that discovery of additional specimens, with the subsequent revision and re-description of this form, may eventually reassess its phylogenetic position.

Node 6: family Brembodontidae

Tintori (1981) erected this family to locate his new genera *Brembodus* and *Gibbodon*. Nursall (1996b) broke up the Brembodontidae by including *Brembodus* and *Eomesodon* in this family, as *Gibbodon* in his hypothesis is the stem-group Pycnodontiformes (see above). In the present analysis, *Brembodus* and *Gibbodon* appear as sister-groups, then restoring the original composition of the family. The only character used by Nursall to join *Brembodus* and *Eomesodon*, presence of "a dorsal prominence, formed by nuchal plates" (Nursall 1996b: number 43) is quite heterogeneous, since there are many different morphologies of this prominence. In addition, according to this analysis, the occurrence of a dorsal prominence and of nuchal plates (our number 83) is a character for node 4, therefore relatively primitive among pycnodontiforms, also present in *Arduafrons*, *Gibbodon*, and *Apomesodon* n. gen. The loss of nuchal plates is a reversion that occurs further up in the tree, at node 10. Among the characters used by Tintori (1981) to diagnose the Brembodontidae, only the presence of fringing fulcra remains in the revised diagnosis presented in the Systematics section below; this is so because all other characters are herein interpreted as primitive among pycnodonts and/or broadly present in other forms. In this analysis, node 6 is defined by six characters. Nonetheless, it is to be noticed that two of these characters are reversions, and that autapomorphies are lacking. As mentioned for *Gibbodon* above, it is possible that the discovery of new material of these forms, or the discovery of new basal forms, may reassess the definition and/or the position of the Brembodontidae. But at present it is more parsimonious to restore the original sense of the family (Tintori 1981) than to separate *Brembodus* and *Gibbodon*.

Node 7: suborder Pycnodontoidei
It is defined by five characters with DELTRAN, seven with ACCTRAN. There are no autapomorphies, but relevant synapomorphies include: 29(2), absence of ossifications in the gular region; 30(2), two branchiostegal rays, thin and separated; 56(3), number of anterior autogenous neural spines reduced to 10 or less; and 76(3), scales present only in the abdominal region (reverted in certain forms). A reversion that is common to all Pycnodontoidei is character 80(0), absence of scales between the bases of the dorsal, anal, and caudal lepidotrichia. The presence of these scales is therefore interpreted by the present analysis as a basal, general condition for Pycnodontiformes, being absent in Pycnodontoidei. Among the character defining this node in the present analysis, only our number 76 coincides with one of Nursall's (1996b: 135) synapomorphies for the Pycnodontoidei (his character 39, "body incompletely scaled"). The other three diagnostic characters of this author appear, according to the present analysis, in other nodes. One of them, the absence of opercular process (our 25, state 2), may alternatively appear at the base of node 10 (with DELTRAN) or at the base of node 4 (with ACCTRAN), since it is unknown in all of the taxa between these two nodes. In both cases it appears as an autapomorphic character. Therefore, it has been conservatively maintained in the diagnosis of the Pycnodontoidei, pending confirmation in *Arduafrons*, the Brembodontidae, *Eomesodon*, and *Abdobalistum* n. gen. Another pycnodontoid character of Nursall's (1996b), our 41(1), dentary posteriorly single, appears as an autapomorphy of nodes 4 (ACCTRAN) or 5 (DELTRAN), because the Brembodontidae, where the dentary is already posteriorly single, are herein out of the Pycnodontoidei (see next paragraph). Finally, the other synapomorphy of this suborder in Nursall (1996b), our character 32(3), dentary and premaxillary teeth incisiform *sensu stricto*, appears (and not as an autapomorphy) herein at the base of node 10, because these teeth in *Eomesodon* (pers. obs.) and *Apomesodon* n. gen. (Figs 14; 21B) are not considered as fully incisiform (see discussion of this character above).

According to Kriwet (1999: 235): "The presence of pharyngeal teeth is confirmed to be a synapomorphy of Pycnodontoidei". This is a conclusion from his revision of these teeth in pycnodont fishes. Pending study of their homologies, we follow Kriwet (1999) and use the term "branchial" for the teeth that occur in the branchial chamber of pycnodontiforms, in order to avoid confusion with the pharyngeal teeth of teleosts. The presence of branchial teeth was used to define only the crown-group in Nursall (1996b: character 122). According to Nursall (1999b: 196), "it is difficult to suggest a reason for the relatively late appearance of pharyngeal teeth (in pycnodontiforms)". Both authors suppose that branchial teeth are absent in primitive pycnodonts, although Kriwet (1999) regarded them as present in a broader number of genera (all pycnodontoids). We do not agree completely with the assumption that branchial teeth are absent in primitive pycnodontiforms. We initially intended to include a character on the branchial teeth of pycnodontiform fishes in our analysis. However, the morphologies of the teeth associated to the branchial chamber of both the outgroup and the ingroup are so variable, even at individual level, that polarization and coherent codification of this character were impossible to achieve. Within the outgroup, tiny, villiform teeth without pedicle are associated to the branchial arches of at least *Lepidotes* (Thies 1989) and *Amia* (Grande & Bemis 1998). This may be considered as the primitive state because it is the predominant state within the outgroup (Arnold 1981), so we attempted to have a character with this primitive state. However, several problems led us to disregard a character based on the branchial teeth of pycnodontiforms. All branchial teeth previously described from articulated remains of pycnodonts are larger than the standard villiform teeth of the outgroup, and pedicellate, but their size and morphology are quite variable. They may be small, conic, with a rounded section (e.g., *Gyrodus*, Lambers 1991: 520, fig. 17; *Iemanja*, Kriwet 1999: fig. 11; pers. obs.), or enlarged, hook-shaped, with an elliptical section (e.g., *Coccodus*, Kriwet 1999: fig. 10F-H; *Pycnodus*, Nursall

1996b: fig. 23; pers. obs.), although intermediate morphologies do occur (pers. obs.). Moreover, some of the teeth illustrated by Thies (1989: fig. 10C-G) for an articulated specimen of *Lepidotes* do present morphologies that vary from conic to hook-shaped, so that the presence of large, non-villiform branchial teeth may be a more primitive condition than that proposed by Nursall (1999b) and Kriwet (1999). As a consequence, a character based on branchial teeth cannot be polarized at present, and only a thorough revision of the detailed morphology and individual variation of the branchial teeth both in the outgroup and in the ingroup will allow such a character to be useful in the framework of a cladistic analysis. About the occurrence of this character within pycnodontiforms, it must be noticed that, according to Nursall (1999b), branchial teeth are absent in *Arduafrons*, *Brembodus*, *Eomesodon*, *Gibbodon*, *Gyrodus*, *Macromesodon*, *Mesturus*, *Micropycnodon*, *Neoproscinetes*, *Proscinetes*, and *Stemmatodus*. However, small branchial teeth are figured by Lambers (1991: fig. 17) for *Gyrodus*. In addition, we signal for the first time in the present paper the presence of branchial teeth in *Apomesodon surgens* n. gen., n. sp. (formerly *Eomesodon*; Fig. 21C), *Ichthyoceros* (Fig. 46A), *Macromesodon* (*M.* aff. *M. bernissartensis* from Las Hoyas; Poyato-Ariza & Wenz work in progress), *Oropycnodus* n. gen. (formerly *Palaeobalistum*; Fig. 46B), and *Proscinetes* (Fig. 46C1-3). In all cases, the branchial teeth are small, conic to comma-shaped, with the exception of *Oropycnodus ponsorti* n. comb., where there are remains of batteries of large, pedicellate, hook-shaped branchial teeth on type NMW 1854/XXXIX/39 (Fig. 46B), plus some smaller, sparse comma-shaped branchial teeth on paralectotype NMW 1854/XXXIX/40. That is, the presence of branchial teeth in pycnodonts is confirmed whenever the gill chamber is somewhat accessible, not only in derived forms, but also on relatively basal pycnodontiforms (*Gyrodus*, *Apomesodon* n. gen.). The different morphologies of these teeth are not necessarily a taxonomic difference, as they may appear in the same species
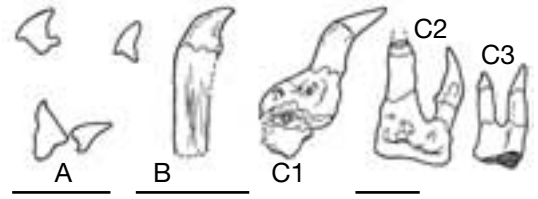
Fig. 46. — Camera lucida drawings of branchial teeth as seen in **A**, the gill chamber of specimen MNHN HAK 298 of *Ichthyoceros spinosus* Gayet, 1984; **B**, the gill chamber of paralectotype NMW 1854/XXXIX/39 of *Oropycnodus ponsorti* n. comb.; **C**, disarticulated from specimen FSL 400047 of *Proscinetes* sp. (**C1**, in gill chamber; **C2**, outside the body, anteroventral to left dentary; **C3**, same position, closer to left dentary). Scale bars: 1 mm.

(e.g., *Oropycnodus ponsorti* n. comb., as explained above). In addition, there is a continuous gradient of intermediate branchial teeth morphologies, so that the difference between small, comma-shaped ones and large, hook-shaped ones may eventually be not so clear (pers. obs.). Therefore, a careful study of the individual variations is necessary before assessing a taxonomic distribution to this character within Pycnodontiformes. In addition, the more specimens where at least remains of the branchial arches are observable, the more branchial teeth can be observed (Kriwet 1999; present paper). As a matter of fact, one cannnot be sure that these teeth are certainly absent in primitive pycnodonts; we would rather say that the gill chamber is simply not accessible, and therefore this character should be considered as unknown in those forms. In other words, in our opinion there is not certain absence of branchial teeth in the forms where the branchial arches are not accurately observable.

The genera included in the suborder Pycnodontoidei are the same than in Nursall (1996b), with the exception of *Brembodus*, which is the sister-group to *Gibbodon*, forming together the Brembodontidae. This family is excluded from the Pycnodontoidei by nodes 5 and 6, being the former especially strong (see above). We prefer to exclude the Brembodontidae from the Pycnodontoidei, rather than to include them, because they present many primitive features that do not seem to fit in this relatively derived clade.

Nodes 8-9 and alternative node B: Eomesodon *and* Apomesodon *n. gen.*

The three species traditionally assessed to the genus *Eomesodon* (*E. liassicus*, the type species, ? *E. barnesi*, and *Apomesodon gibbosus* n. comb.) do not appear as a monophyletic clade in any of the possible trees, as the third form is always separated from the other two by node 8, defined by six (DELTRAN) to five (ACCTRAN) synapomorphies. In addition, the relationships between *E. liassicus* and ? *E. barnesi* remain unsolved. They are involved in indetermination B; it presents all the possible combinations, and all alternative nodes are very weakly defined. It is probably due to the incompleteness and relatively poor preservation of the known material of both forms, which leads to quite a number of unknown character states in the data matrix. Therefore, it is not possible at present to know whether both species are sister-groups or not. We consequently keep ? *E. barnesi* within the genus with cautions. In turn, the former *Eomesodon gibbosus* is divided into two distinct species, since the specimens from the "Solnhofener Platenkalke" and those from Cerin present different combinations of characters. Both are sister-groups, forming a clade defined by node 9: the new genus *Apomesodon* n. gen. It is defined in the analysis by four characters, two of which are reversions. The diagnosis of *Apomesodon* n. gen. is based on these and on some other characters whose unique combination allows, by comparison, a revised diagnosis for *Eomesodon*. The present analysis interprets character 6(1), prognathism present, as a convergence of *Apomesodon* n. gen. and ? *E. barnesi* (unknown in *E. liassicus*), so it is not used in the diagnoses. Also some of the characters in node 8 are used in the diagnoses, as they are separating *Eomesodon* and *Apomesodon* n. gen. (number 7, differentiation of caudal pedicle; number 9, morphology of the frontals; number 21, presence of tubular infraorbitals; and 45, number of prearticular tooth rows). In turn, the characters defining *A. gibbosus* n. comb. are, by contrast, also included in the diagnosis of *A. surgens* n. gen., n. sp., and *vice versa*. It is to be remarked that four of the eight characters that define the former are, according to the present analysis, reversions. It is expected that the study of further specimens of *Eomesodon* and of transfer specimens of *Apomesodon* n. gen. will allow a better understanding of the character distribution.

Node 10: superfamily Pycnodontoidea n. rank

The family Coccodontidae, in its large sense (see node 11 below), appears as the sister-group of the family Pycnodontidae. Since the Coccodontidae is *incertae sedis* in Nursall's (1996b) hypothesis, two of the pycnodontid synapomorphies of this author, his numbers 49 and 50, appear at the base of (Coccodontidae + Pycnodontidae) in the present analysis. These are our numbers 24(3), presence of a dermohyomandibular, which is autapomorphic (it is unknown in *Coccodus* and *Ichthyoceros*, but present in *Trewavasia* and the Pycnodontidae), and 101(3), number of postcloacal scales reduced to six or less. The sister-group relationship of the Coccodontidae and the Pycnodontidae is very strong, supported by 15 characters (with ACCTRAN and DELTRAN), three of which are autapomorphies. Two of these autapomorphic characters concern the hyomandibular bone. They are the number 24, just mentioned; the number 25(2), absence of the opercular process in this bone; and the number 55(2), sagittal flanges on neural and haemal spines anterior only. Two reversions are common to (Coccodontidae + Pycnodontidae): number 3, absence of dorsal prominence, and number 83, absence of nuchal plates. The autapomorphies, together with an unique combination of other characters, allow to diagnose the new superfamily Pycnodontoidea n. rank, which includes the sister-families Coccodontidae and Pycnodontidae.

Nodes 11-12: family Coccodontidae

The node 11 gathers the genera *Coccodus*, *Ichthyoceros*, and *Trewavasia* in a single clade, the family Coccodontidae. The Coccodontidae are an *incertae sedis* monotypic family according to Nursall (1996b, 1999b), whereas the last two genera form the family Trewavasiidae, also *incertae sedis*. Gayet (1984), following Berg (1940) and Lehman (1966), included also the other two

genera in the Coccodontidae. Since *Coccodus* and *Ichthyoceros* appear as sister-groups in node 12, defined by nine characters (17 with ACC-TRAN), being one of them an uniquely derived state (36(4), vomerine teeth triangular in contour), the Trewavasiidae *sensu* Nursall (1996b) become a paraphyletic group, confirming the composition of the family proposed by Gayet (1984). The nine characters that define the Coccodontidae in the present paper (20 with ACCTRAN; the 10 additional characters are not used in the diagnosis) are completely different from those in Nursall (1996b: 140, 141). Since the family is not monotypic in the present paper, those characters coherently appear characterizing the genus *Coccodus* alone. The only exception is his character 63, "dermal bones of the skull form a single unit. Presumably this is a result of early ankylosis, for no traces of boundaries between units are seen" (Nursall 1996b: 141). Although this may be the appearance in unprepared individuals, transferred specimens of *Coccodus* clearly show the boundaries among the distinct elements of the dermal skull (Fig. 13; also MNHN HDJ 539 and 1299). There is no ankylosis in *Coccodus* except for midline fusion of the frontals (Fig. 13). The three coccodontid genera are quite derived, each of them being defined by a very high number of characters (see Appendix 4). This suggests that they are part of a long, separated evolutionary line. There is one remarkable reversion in *Ichthyoceros* and *Trewavasia*: the presence of scales in the caudal region; the complete absence of scales in *Coccodus* is an autapomorphy of this genus.

Node 13: family Pycnodontidae
The family Pycnodontidae has been interpreted in a restricted sense since Berg (1940), including only those forms with a dermocranial fenestra (e.g., Lehman 1966; Wenz 1989a, b). Nursall (1996b) enlarged the family to accommodate up to nine genera: *Macromesodon, Proscinetes, Neoproscinetes, Anomoeodus, Iemanja, Stemmatodus, Tepexichthys, Coelodus,* and *Pycnodus* (Fig. 44B). In the present paper, we follow Nursall in this interpretation of enlarged

Pycnodontidae. Firstly, because the dermocranial fenestra results to be a convergent character (see below), and secondly because all of the 15 grouped genera form a very strong clade, with a very characteristic and coherent derived anatomic pattern within the Pycnodontiformes. The Pycnodontidae herein include: the nine genera of Nursall (1996b), one of his *incertae sedis* genus, *Nursallia*, plus four new genera: *Abdobalistum* n. gen. (ex-*Palaeobalistum pro parte*), *Oropycnodus* n. gen. (ex-*Palaeobalistum pro parte*, ex-*Coelodus pro parte*), *Ocloedus* n. gen. (ex-*Coelodus pro parte*), *Stenamara* and *Palaeobalistum* (in strict sense). There are nine (DELTRAN) to six (ACCTRAN) characters defining this node. One of them, 14(1), is a relevant autapomorphy: presence of a parietal process. The presence of incompletely ossified scales, at least in the dorsal abdominal region of the body, is a relevant synapomorphy (number 75(2) herein; corresponds to the peltate and clathrate patterns). Three of Nursall's (1996b) characters are present only with the DELTRAN option: his numbers 45 and 47, corresponding to number 23 herein, suborbitals absent, and his number 46, corresponding to number 35 herein, maxilla reniform. Another significant character, number 24(3), dermohyomandibular present (his number 49), appears herein in node 10 as an autapomorphy of the Pycnodontoidea n. rank (since it is present in pycnodontids and at least in *Trewavasia* among coccodontids). The same applies to character 101(3), his character 50, six or less post-cloacal keel scales. The Pycnodontidae is therefore the most derived and by far the largest pycnodont family, including more than a half of the described pycnodont genera that are based on complete specimens.

Nodes 14-15: genus Macromesodon
It is a monophyletic group, although defined only by four characters. Only two of these characters are common with DELTRAN and ACC-TRAN: number 68(3), dorsal and anal fins rounded in the centre; and number 89(1), dorsal ridge scales in point contact with each other. The species from Las Hoyas, *M.* aff. *M. bernissartensis*, is

the sister-group to the other two, *M. bernissartensis* and *M. macropterus*, therefore suggesting that it actually is a distinct species. Nonetheless, node 15, *M. bernissartensis* + *M. macropterus*, is weak, defined by two reversions only (with one additional character with ACCTRAN). The *Macromesodon* from Las Hoyas is not essential for the monophyly of this genus, as, if removed from the analysis, *M. macropterus* and *M. bernissartensis* are still sister-groups, but there are important changes in other parts of the tree. We think that the relevant form from Las Hoyas requires further study; the diagnosis and the relationships of the genus *Macromesodon* and of its species are then provisionally postponed to the detailed description of *M.* aff. *M. bernissartensis* (Poyato-Ariza & Wenz work in progress). In any case, *Macromesodon* appears as the most basal pycnodontid, as in Nursall (1996b; Fig. 44B), although in his hypothesis it forms an undetermination with *Proscinetes* and *Neoproscinetes* (see node 21, Proscinetinae n. rank, below).

Nodes 16-19 and indetermination C: other basal Pycnodontidae

After *Macromesodon*, the genera *Stenamara*, *Stemmatodus*, and *Ocloedus* n. gen. are successively separated by nodes 16 to 19, with *Anomoeodus* involved in indetermination C. *Anomoeodus* appears as the sister-group of either *Stemmatodus* (C1) or *Ocloedus* n. gen. (C2). This indetermination is probably the result of the large number of unknown character states in *Anomoeodus*, a genus based on very incomplete material. The basal position is consistent for *Stenamara*, which was previously regarded as a primitive pycnodontid (Poyato-Ariza & Wenz 2000). In contrast, the relatively primitive position of *Stemmatodus* and *Ocloedus* n. gen. among pycnodontids is somewhat surprising. They are both considered as part of the crown-group Pycnodontidae by Nursall (1996b), and their position in the present analysis involves some convergences in relevant characters. For instance, 24(4), preopercular as large as the expanded ornamented portion of the dermohyomandibular, is interpreted by the analysis as a convergence of *Stemmatodus*, *Ocloedus* n. gen.,

and the Pycnodontinae n. rank. The superficial, ornamented portion of the dermohyomandibula is certainly less developed in the Proscinetinae n. rank and in *Iemanja*. Nonetheless, it would be very important to know the state of this character in *Anomoeodus*, *Coelodus saturnus*, and *Tepexichthys*, as they are currently coded as ? (see discussion of the character above). We expect that the knowledge of the state could result in a re-interpretation of the character distribution, and maybe of the relative phylogenetic position of these genera as well. In any case, *Ocloedus* n. gen. (= ex-*Coelodus*) *subdiscus* and *Coelodus saturnus* are separated by at least three nodes, so the genus *Coelodus* as previously interpreted is polyphyletic. In addition, their unique combination of characters and the autapomorphies of the type species of *Coelodus* allow clearly distinct genera to be diagnosed. *Coelodus* is restricted at present to the type species, and to eventual future species that would also present relatively low body, extremely elongated prearticular teeth, plus diastema and hypertrophied hypochordal elements in the caudal endoskeleton. In turn, the new genus *Ocloedus* n. gen. is erected for the specific name *subdiscus*, which is designed as the type species, and also for all other forms with high, rounded body; oval prearticular teeth; no diastema; plus enlarged hypochordal elements. We think that the specific name *costae* fits better in *Ocloedus* n. gen. than in the new, restricted diagnosis of *Coelodus*. Although *Ocloedus costae* n. comb. remains in need of revision, and that its body is less rounded than that of *O. subdiscus* n. comb., in *O. costae* n. comb. the teeth of the principal prearticular row are oval, not as elongated as those of *Coelodus saturnus*; the hypochordal elements in the caudal endoskeleton are only slightly enlarged, and there is absence of diastema, as in *Ocloedus* n. gen. (Woodward 1918: fig. 24; pers. obs. on NHML 1641, 1671a, and P.4394). Pending further revision of this form, we therefore remove the specific name *costae* to the genus *Ocloedus* n. gen. The same does not apply to *ponsorti*, which has also been considered as a species of *Coelodus* (see node 24 below).

Node 20: node 19 minus Tepexichthys
This genus appears in a position that is slightly more primitive than the one it presents in Nursall (1996b; see comments on the crown-group below). A detailed revision of this form may help enlighten its phylogenetic relationships within pycnodontids.

Indetermination D
The indetermination D involves the relative position of the genus *Iemanja* and the Proscinetinae n. rank. They appear as successive stem-groups to node 22, one or the other being the sister-group to that node. The possibility of a sister-group relationship between *Iemanja* and the Proscinetinae n. rank. does not appear in any tree. As one could expect, the two possible nodes are weakly defined, and they alter slightly the character distribution of the subsequent node (22). In addition, there are remarkable differences in the character distribution between DELTRAN and ACCTRAN in the alternative nodes. However, the character diagnosing *Iemanja* and the Proscinetinae n. rank. are the same with both alternatives. *Iemanja* occupies in this phylogeny a position comparable to that in Nursall (1996b), but is not herein the sister-group to *Anomoeodus* (no characters are provided by that author for that relationship).

Node 21: subfamily Proscinetinae n. rank
The genera *Proscinetes* and *Neoproscinetes* form an indetermination, together with *Macromesodon*, at the base of the Pycnodontidae in Nursall (1996b; Fig. 44B), although this author provides no characters at the base of that node (that is, joining the three genera). They are separated from the other pycnodontids by a single character, his number 109. In the present paper it corresponds to 24(4), preopercular as large as the expanded ornamented portion of the dermohyomandibular, which, as seen for nodes 16-19 above, is interpreted by this analysis as a convergence. The position of the first two genera is more advanced herein, as they are separated from *Macromesodon* by the four nodes just mentioned. In addition, *Proscinetes* and *Neoproscinetes* are sister-taxa, forming a rela-

tively strong clade (node 21) defined by seven synapomorphies, one of which, 40(1), alternation of one large and two small teeth on the main vomerine tooth row, is an autapomorphy. This sister-group relationship is reflected in the erection of the new subfamily Proscinetinae n. rank for these two closely related genera. A revised diagnosis for the type genus, *Proscinetes*, is also provided. It includes the terminal characters for this genus. Among these characters, some are different, and some are so far unknown in *Neoproscinetes*, therefore in need of confirmation in the latter (e.g., number of modified cloacal scales). The revised diagnosis of *Proscinetes* also includes one of Nursall's (1996b: number 106) terminal characters: falcate to acuminate dorsal and anal fin. The other character from this author (his 107, on the morphology of the caudal fin), is not used because it presents the same character state in *Neoproscinetes* (state 3 on character 73 herein).

Node 22: crown-group plus Coelodus saturnus
They are gathered by six characters (10 with ACCTRAN; this is the character distribution of the strict consensus tree). A remarkable synapomorphy that gathers *Coelodus* to the crown-group is character 59(2), hypochordal elements of the caudal endoskeleton hypertrophied. *Coelodus* occupies herein a position comparable to that in Nursall (1996b), although it is interpreted herein in a restricted sense, including only the type species (see comments on *Ocloedus* n. gen. in nodes 16-19 above). Since this node separates *Coelodus* in its new sense and *Ocloedus* n. gen., some of its characters have also been included in the revised diagnoses of both genera.

Node 23: crown-group Pycnodontidae
The crown-group Pycnodontidae appears herein formed by the subfamilies Pycnodontinae n. rank and Nursalliinae n. rank, which are sister-groups (see below). In Nursall (1996b), the crown-group Pycnodontidae included *Pycnodus*, as in the present analysis, but, differently, also *Coelodus* (former sense) and *Tepexichthys*. The last two genera appear in a relatively more basal position

in the present analysis. The main reason is probably that the most remarkable synapomorphy used by Nursall (1996b) to define advanced pycnodontids, presence of a dermocranial fenestra, as already noted in node 13 above, is interpreted by the present analysis as a convergent character. This is a rather unexpected result; it is convergent in the Pycnodontinae n. rank, *Ocloedus* n. gen., and *Tepexichthys*. It is possible that similar functional pressures on the cranial and mandibular musculature are better solved, with the elements available in the pycnodontid skull, by means of a similar, convergent fenestra. An alternative interpretation is the appearance of the fenestra at the base of node 19, to disappear independently in at least *Iemanja* and node 25 (Nursalliinae n. rank). This hypothesis is equally parsimonious (three steps), but maybe less understandable from a functional point of view. The other characters for the crown-group Pycnodontidae in Nursall (1996b) are: his 122, "pharyngeal teeth", but see comments on node 7 above; his 123, "notched maxilla", hardly observable in most other pycnodontids; and his 124, "postparietal bone" is equivalent to state 2 of character 86 herein. The "postparietal bone" seems to be the first ridge scale, incorporated to the skull roof, and larger than subsequent ridge scales, which is present in a large number of pycnodontids: the present crown-group and, at least, the Proscinetinae n. rank. In the present analysis, the crown-group is defined by six characters (also six, with differences, with ACCTRAN), two of them reversions, with one relevant autapomorphy: 104(1), presence of a bifid scale in the cloaca.

Node 24: subfamily Pycnodontinae n. rank

The subfamily Pycnodontinae n. rank is formed by the sister-genera *Pycnodus* and *Oropycnodus* n. gen. Both genera are joined by 10 synapomorphies (also seven, with some differences, with ACCTRAN), including two significant autapomorphies: 19(1), endocranium posteriorly exposed, with a postcephalic lacuna; and 87(1), scutellum-like contour scales present, dorsal only. The position of *Pycnodus* among the most derived pycnodontids agrees with

its position in Nursall (1999b). In turn, *Oropycnodus* n. gen. is erected for the specific name *ponsorti*, which had previously been assessed to the genera *Palaeobalistum* and *Coelodus*. In both cases, the genera would be polyphyletic if *ponsorti* was included, and, although in the same subfamily, it is quite different from *Pycnodus*, presenting three relevant autapomorphies. Therefore, it is considered a distinct genus. A revised diagnosis for *Pycnodus* is provided together with the diagnosis of the new genus.

Node 25-28: subfamily Nursalliinae n. rank

The genera *Abdobalistum* n. gen., *Palaeobalistum*, and the three nominal species of *Nursallia* included in the analysis are gathered together in the subfamily Nursalliinae n. rank, which is defined by at least eight synapomorphies, including: 32(2), premaxillary and dentary teeth robust, slightly flattened; they are the only Pycnodontidae where those teeth are not fully incisiform; and 76(2), body scales present in the abdominal region plus part of the caudal region; they are also the only Pycnodontidae with scales on the caudal region. At least two other relevant characters may also be defining this node (they appear with ACCTRAN): 10(1), prefrontal bone present; and 46(2), eight or nine teeth on main prearticular tooth row, but they are unknown in *Abdobalistum* n. gen. and *Nursallia* ? *goedeli*. The former could be a synapomorphy of the Nursalliinae n. rank or eventually of *Nursallia* (and it is, in any case, convergent with *Ichthyoceros* and *Trewavasia*), so it has been used with caution in the diagnosis of the Nursalliinae n. rank, pending confirmation of its presence in *Abdobalistum* n. gen. and in *Nursallia* ? *goedeli*.

Although this seems a strong node, the interrelationships of the nursalliin fishes are not fully satisfactory. Nodes 26 and 28 are ambiguously defined, since many of their characters are unknown in many of these fishes. There are numerous convergences and reversions, and the differences between the DELTRAN and ACCTRAN characters distributions are noticeable. This is due, in part, to the fact that *Palaeobalistum* and

Nursallia ? *goedeli* present a puzzling combination of highly derived and primitive characters, and also to the poor knowledge of the latter. As a matter of fact, *Nursallia* ? *goedeli* presents more than 80% of unknown characters, and is therefore a potential source of distortion. When this taxon is removed from the data matrix, the results are basically the same, but *Palaeobalistum* appears near the base of the tree, and *Nursallia* is a monophyletic genus consisting of *N. veronae* + *N. gutturosum*. For this reason, the latter has not been removed from the genus. In this case, several relevant characters that were defining the Nursalliinae n. rank appear now as autapomorphies of the genus *Nursallia*, and are used to proposed its revised diagnosis: 9(3), frontals curved, very broad; 54(3), neural and haemal adjacent arcocentra in hyper-complex contact; and 73(6), caudal fin vertical. The diagnoses provided herein for the Nursalliinae n. rank and for the genus *Nursallia* are to be taken with caution, as they intend to be only the base for their much needed revisions, notably for a detailed revision of *Nursallia* ? *goedeli* and of other putative species of this genus. At present, the type species, *Nursallia veronae*, presents one autapomorphy: 87(3), scutellum-like contour scales present, both dorsal and ventral. The distribution of the characters of the nominal species of *Nursallia* is very variable, changing considerably from DELTRAN to ACCTRAN. This indicates again that a detailed revision of the nominal species of *Nursallia* and of some invalid nominal species of *Palaeobalistum* is required. For instance, *N.* ? *goedeli* seems a distinct species, but its caudal scales are complete, and not reduced to scale bars, as in the type species and in *N.* ? *gutturosum*. This difference could be specific, or generic, so *N.* ? *goedeli* may not fit in *Nursallia*. In contrast, we consider that *N. flavellatum* ? (Cope, 1886) belongs to the genus; after the illustrations in Woodward (1907: pl. 7, fig. 3) and Martins (1959: pl. 12), it seems to be a crown-group pycnodontid, because of the hypertrophied hypochordal elements in the caudal endoskeleton (an autapomorphy of node 22, see above); a nursalliine, because there are scales present in the caudal region; and eventually

Nursallia, because of the apparently hyper-complex contact of the adjacent neural and haemal arches. But it might be indistinguishable from the type species or from *Nursallia* ? *gutturosum*, which would pose additional problems of synonymy. A revision of *flavellatum* is therefore indispensable to clarify the taxonomy and the relationships of the nursalliine fishes. One more example: the invalid name "*Palaeobalistum*" *bassanii* (D'Erasmo, 1914). As seen in D'Erasmo (1914: pl. 8), the scale pattern is peltate, and not imbricate as in *Palaeobalistum orbiculatum* (see characters 61 and 76 above), so it is not a species of *Palaeobalistum* in its new, restricted sense. As illustrated in D'Erasmo (1914: pl. 8), it does not fit in the Nursalliinae n. rank because it does not present hyper-complex contact between adjacent arcocentra, and because there are not scales on the caudal region, but only before the point of insertion of the dorsal and anal fins. Since the hypochordal elements of the caudal endoskeleton are not hypertrophied, it is not even a crown-group pycnodontid, and therefore not a pycnodontine. The latter feature, together with the lack of a diastema in the caudal endoskeleton and of a differentiated caudal pedicle, indicates that *bassanii* is not a *Coelodus*, as proposed by Blot (1987), at least in the new, restricted sense of this genus. However, it cannot be removed to *Ocloedus* n. gen. either, because *bassanii* apparently lacks a dermocranial fenestra. In this moment, it seems to fit better in *Proscinetes* because of the similar number of vertebrae of *bassanii* and most species of *Proscinetes*; the comparable relative development of the hypochordal elements of their caudal endoskeletons; the falcate shape of their anal fins; and the separation among their dorsal ridge scales. However, this assessment is to be taken with caution, pending detailed revision of the many nominal species of *Proscinetes* and of the original material of *bassanii*. In spite of all these problems with the nominal species of *Nursallia*, *Abdobalistum thyrsus* n. gen., n. sp., does not belong to the genus *Palaeobalistum*, now restricted to the type species, *P. orbiculatum* (see discussion of the nomenclatural problems in the list of pycnodontiform genera above). With or

without *Nursallia* ? *goedeli*, the genus *Palaeobalistum* sensu Blot (1987) is polyphyletic. In any case, *Abdobalistum* n. gen. presents a remarkable unique combination of characters that clearly indicates that is is a distinct genus. It includes two autapomorphies, characters number 87(2), scutellum-like contour scales present, ventral only, and 100(1), several scales attached to contour scales. These, together with an unique combination of reverted primitive and derived characters (which are different in all the nominal species of *Nursallia* and in *Palaeobalistum*), appear in all of the possible alternative nodes, and allow diagnosis of this new genus.

SYSTEMATICS

The following nomenclature is proposed according to the results of the cladistic analysis, mainly the phylogenetic tree (Fig. 43).

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Cope, 1887
Division HALECOSTOMI Regan, 1923
sensu Patterson 1973
Order PYCNODONTIFORMES Berg, 1937

REVISED DIAGNOSIS. — Halecostome fishes with the following autapomorphic characters: laterally compressed, high to rounded body shape; antorbital and ethmoid regions hypertrophied, with mesethmoid T-shaped in section; one or several unpaired dermal supraoccipital(s) present; parasphenoid largely developed, edentulous, inflected downwards; opercular process of hyomandibular vestigial or absent; suboperculum and interoperculum absent; operculum reduced; premaxillary process long and superficial; maxilla edentulous, loosely attached; supramaxilla absent; teeth on vomer and prearticular arranged in rows; dentary reduced; long, stout mandibular symphysis; cleithrum large, ventrally palaform; ribs alate; contour scales differentiated into dorsal ridge and ventral keel scales.

Genus *Paramesturus* Taverne, 1981

TYPE SPECIES. — *Paramesturus stuehmeri* Taverne, 1981.

INCLUDED SPECIES. — Monospecific genus.

Family MESTURIDAE Nursall, 1996

TYPE GENUS. — *Mesturus* Wagner, 1862.

INCLUDED GENERA. — The type genus, and *Micropycnodon* Hibbard & Graffham, 1945.

REVISED DIAGNOSIS. — Primitive pycnodontiform fishes with the following unique combination of derived characters: maxilla ornamented and elongated; grooves and strong crenulations present on most vomerine and prearticular teeth; anal fin at 60-69% of standard length; first dorsal ridge scale larger than subsequent dorsal ridge scales.

Family GYRODONTIDAE Berg, 1940

TYPE GENUS. — *Gyrodus* Agassiz, 1833.

INCLUDED GENERA. — Monotypic family.

REVISED DIAGNOSIS. — Primitive pycnodontiform fishes with the following autapomorphies: central papilla in vomerine and prearticular teeth present; sagittal flanges on neural and haemal spines both anterior and posterior, with strengthened margins; more than nine anterior neural spines autogenous.

Unamed clade

Genus *Arduafrons* Frickhinger, 1991

TYPE SPECIES. — *Arduafrons prominoris* Frickhinger, 1991.

INCLUDED SPECIES. — Monospecific genus.

Family BREMBODONTIDAE Tintori, 1981

TYPE GENUS. — *Brembodus* Tintori, 1981.

INCLUDED GENERA. — The type genus, and *Gibbodon* Tintori, 1981.

REVISED DIAGNOSIS. — Primitive pycnodontiform fishes with the following unique combination of primitive and derived characters: three premaxillary teeth; eight or nine teeth on main vomerine tooth row; pelvic fin placed at more than 55% of standard length; numerous fringing fulcra on paired and unpaired fins present; 10 to 14 dorsal ridge scales; six or less postcloacal ventral keel scales.

Suborder PYCNODONTOIDEI Nursall, 1996

REVISED DIAGNOSIS. — Pycnodontiform fishes with the following unique combination of primitive and derived characters: opercular process of hyomandibular absent (autapomorphy); ossifications in gular

region absent; two branchiostegal rays, thin and separated; crenulations on vomerine and prearticular teeth occasional and weak if present; scales not covering the whole body; and scales rows between bases of lepidotrichia of unpaired fins absent.

Unamed clade

Genus *Eomesodon* Woodward, 1918

TYPE SPECIES. — *Pycnodus liassicus* Egerton, 1855.

INCLUDED SPECIES. — The type species, ? *E. barnesi* (Woodward, 1906), and *E. depressus* ? Woodward, 1918.

REVISED DIAGNOSIS. — Primitive Pycnodontoid fishes with the following unique combination of primitive and derived characters: caudal pedicle differentiated; frontals curved and long; tubular infraorbitals absent; two dentary teeth; five prearticular tooth rows; 25 to 29 vertebrae; dorsal and anal fins rounded in the centre; 15 to 17 dorsal ridge scales.

Genus *Apomesodon* n. gen.

Gyrodus pro parte – Agassiz 1843: 236 (name only). — Winkler 1862: 86, tab. 1.

Mesodon pro parte – Wagner 1851: pl. 3, fig. 2. — Thiollière 1873: 13, pl. 2, fig. 2.

Eomesodon – Saint-Seine 1949: 130, figs 56-58, pl. 14, fig. A.

TYPE SPECIES. — *Mesodon gibbosus* Wagner, 1851.

INCLUDED SPECIES. — The type species, and *Apomesodon surgens* n. gen., n. sp.

ETYMOLOGY. — From the Greek prefix "Aπο-", "Apo-": from, separate; and the last part of its former genus "*Eomesodon*".

DIAGNOSIS. — Primitive pycnodontoid fishes with the following unique combination of primitive and derived characters: caudal pedicle not differentiated; frontals curved and short; tubular infraorbitals present; four dentary teeth; three prearticular tooth rows; more than 34 vertebrae; dorsal and anal fins rounded anteriorly; more than 17 dorsal ridge scales.

Apomesodon gibbosus (Wagner, 1851) n. comb.
(Figs 3C; 14B)

HOLOTYPE. — Specimen figured by Wagner (1851: pl. 3, fig. 2), currently housed at the Bayerischen Staatssammlung für Paläontologie und historische Geologie, München, Germany: AS VII 346.

TYPE HORIZON. — Early Tithonian.

TYPE LOCALITY. — "Solnhofener Plattenkalke", Bavaria, Germany.

REVISED DIAGNOSIS. — *Apomesodon* n. gen. with the following unique combination of primitive and derived characters: body depth less than 100% of standard length; dorsal prominence in obtuse angle, with anterior border inclined and posterior border horizontal, and consequently no dorsal apex; extrascapular not fused to parietal; all vomerine teeth (sub)circular; 12 to 13 hypochordal elements in caudal endoskeleton; less than 20 anal axonosts; caudal fin with straight distal border; five or more spines on dorsal ridge scales; more than 21 ventral keel scales; four to six spines on ventral keel scales.

Apomesodon surgens n. sp.
(Figs 3A, B; 14A; 21B, C; 28B; 39A, B; 40B)

Mesodon gibbosus – Thiollière 1858: 783 (name only); 1871: 33; 1873: 13, pl. 2, fig. 2.

Mesodon macropterus – Woodward 1895: 200 (infrapaginal note).

Eomesodon gibbosus – Saint-Seine 1949: 105, 129-132, 313; figs 56-58, pl. 14, fig. A.

HOLOTYPE. — ML 15443 (specimen figured by Thiollière 1873: pl. 2, fig. 2; Figs 14A; 21B, C).

PARATYPE. — ML 15660 / MNHN CRN-69 (part and counterpart of the same individual; Figs 3A, B; 28B; 39A, B; 40B). No other specimens are known.

ETYMOLOGY. — From the Latin verb "surgere": ascending, rising, in reference to the shape of the dorsal prominence.

TYPE HORIZON. — Kimmeridgian.

TYPE LOCALITY. — Cerin, Ain, France.

DIAGNOSIS. — *Apomesodon* n. gen. with the following unique combination of primitive and derived characters: body depth more than 100% of standard length; dorsal prominence pointed, with both anterior and posterior borders inclined; extrascapular fused to parietal; posterior teeth on main vomerine tooth row oval; 11 hypochordal elements on caudal endoskeleton; more than 20 anal axonosts; caudal fin with distal border convex; three or four spines on dorsal ridge scales; 18 to 21 ventral keel scales; seven or more spines on ventral keel scales.

Superfamily PYCNODONTOIDEA
Agassiz, 1833 new rank

TYPE FAMILY. — Pycnodontidae Agassiz, 1833 *sensu* Nursall 1996b.

DIAGNOSIS. — Pycnodontoid fishes with the following autapomorphies: dermohyomandibular present, with a small to enlarged ornamented superficial portion that articulates ventrally with the preoperculum; opercular process of dermohyomandibular absent; sagittal flanges on neural and haemal spines present only anteriorly. Unique combination of primitive and derived characters: dorsal prominence absent; premaxillary and dentary teeth fully incisiform; three or less dentary teeth; neural and haemal adjacent arcocentra in contact; two or less urodermals; nuchal plates absent; less than 18 dorsal ridge scales; spines on each dorsal ridge scale of increasing size in cephalocaudal sense; less than 18 ventral keel scales; less than seven post-cloacal ventral keel scales; anterior and posterior cloacal scales modified, not forming a mosaic.

Family COCCODONTIDAE Berg, 1940

TYPE GENUS. — *Coccodus* Pictet, 1850.

INCLUDED GENERA. — The type genus, *Ichthyoceros* Gayet, 1984, and *Trewavasia* White & Moy-Thomas, 1941.

REVISED DIAGNOSIS. — Pycnodontoid fishes with the following unique combination of primitive and derived characters: extrascapular not fused to parietal; neural and haemal corresponding arcocentra partially surrounding notochord; six to eight epichordal elements in caudal endoskeleton; hypochordal elements in caudal endoskeleton enlarged; less than 29 dorsal axonosts; if present, first dorsal ridge scale larger than subsequent dorsal ridge scales; two or less dorsal ridge scales; three or less ventral keel scales; at most one post-cloacal ventral keel scale.

Genus *Coccodus* Pictet, 1850

HOLOTYPE. — Specimen figured by Pictet (1850: pl. 9, fig. 9), currently housed at the Muséum de Genève: V-674 (unfigured counterpart: V-733).

TYPE SPECIES. — *Coccodus armatus* Pictet, 1850.

INCLUDED SPECIES. — Monotypic genus.

REVISED DIAGNOSIS. — Coccodontid fish with the following autapomorphies: supraoccipital spine present, single and robust; coronoid process low and straight, with strengthened dorsal border; large, four-limbed cleithrum, ornamented with strong parallel ridges and one hypertrophied spine; square, low and short anal fin; all scales absent, including body scales, dorsal and ventral contour scales, and cloacal scales. Unique combination of reverted primitive and derived characters: body shape fusiform, without dorsal apex; paired prefrontal bones absent; vomerine teeth triangular; eight or nine teeth on main vomerine tooth row; two prearticular tooth rows; less than 25 vertebrae.

Family PYCNODONTIDAE Agassiz, 1833
sensu Nursall 1996b

REVISED DIAGNOSIS. — Pycnodontoid fishes with one autapomorphic character, presence of a parietal, peniculus-like process, and with the following unique combination of derived characters: ornamentation of infraorbitals present only in the posteriormost, enlarged one; suborbitals absent, therefore cheeks naked; maxilla edentulous, oval to reniform; two or three dentary teeth; 10 or less autogenous anterior neural spines; scales incompletely ossified, at least in the dorsal abdominal region; spines on each ventral keel scale in contact with each other.

Genus *Macromesodon* Blake, 1905

TYPE SPECIES. — *Gyrodus macropterus* Agassiz, 1834.

INCLUDED SPECIES. — The type species, and *M. bernissartensis* Traquair, 1911; plus numerous nominal species based on isolated dentitions.

Genus *Stenamara* Poyato-Ariza & Wenz, 2000

TYPE SPECIES. — *Stenamara mia* Poyato-Ariza & Wenz, 2000.

INCLUDED SPECIES. — Monotypic genus.

Genus *Stemmatodus* Heckel, 1854

TYPE SPECIES. — *Pycnodus rhombus* Agassiz, 1839.

INCLUDED SPECIES. — Monotypic genus.

REVISED DIAGNOSIS. — Pycnodontid fishes with two autapomorphic characters: maxilla unornamented, with straight oral border; and no posterior modified cloacal scales, posterior part of anal notch supported by a rib. Unique combination of derived characters: body shape intermediate, maximum body height up to 70% of standard length; ventral apex absent; preoperculum of similar size to expanded ornamented region of the dermohyomandibular; vomerine teeth (sub)-circular in contour; eight or nine teeth in principal vomerine tooth row; 10 or more teeth in principal prearticular tooth row; six or less anterior autogenous neural spines; dorsal fin at 60%-69% of standard length (R); free dorsal axonost present; all body scales incompletely ossified, reduced to bar scales; and 10 to 14 ventral keel scales.

Genus *Anomoeodus* Forir, 1887

TYPE SPECIES. — *Pycnodus subclavatus* Agassiz, 1833.

INCLUDED SPECIES. — The type species, *A. angustus* (Agassiz, 1837), *A. willetti* Woodward, 1893, and *A. nursalli* Kriwet, 1999; plus numerous nominal species based on isolated dentitions.

Genus *Ocloedus* n. gen.

Microdon – Vidal 1902: 6. — Lacasa 1981: 70, 124, pl. 55.

Coelodus – Wenz 1968: 118. — Barale *et al.* 1984: table 2. — Wenz & Poyato-Ariza 1995: 50, fig. 22/1-2.

Proscinetes – Wenz & Poyato-Ariza 1995: 50.

TYPE SPECIES. — *Coelodus subdiscus* Wenz, 1989.

INCLUDED SPECIES. — The type species, *Ocloedus costae* (Heckel, 1856) n. comb., and cf. *Ocloedus* "*rosadoi*" (Silva Santos, 1963) n. comb.

ETYMOLOGY. — Anagram of *Coelodus*, the genus to which the *Ocleodus* species previously belonged to.

DIAGNOSIS. — Pycnodontid fish with the following unique combination of derived characters: mouth gape inclined; body discoid, maximum body height about 80% of standard length; caudal pedicle not differentiated; dermocranial fenestra present; preopercular of similar size to the expanded ornamented portion of the dermohyomandibula; larger prearticular teeth oval in contour; eight teeth on main prearticular tooth row; grooves on vomerine and prearticular teeth present; about 28 to 29 vertebrae; 12 or 13 hypochordal elements in caudal endoskeleton, some of them enlarged; diastema in caudal endoskeleton absent; pelvic fins at more than 55% of standard length; dorsal ridge scales in point contact with each other; three or four spines on dorsal ridge scales.

Ocloedus subdiscus (Wenz, 1989) n. comb.
(Figs 2B; 22B, C; 27B; 38A; 41B)

HOLOTYPE. — MNHN MSE-341 (Wenz 1989b: fig. 1, pl. 1; Kriwet *et al.* 1999: pl. 1, fig. 4).

PARATYPES. — MNHN MSE-442, MGSB 20.659 (Wenz 1989b: pl. 1, fig. 4; Fig. 22B).

REFERRED SPECIMENS. — IEI LP-084a-b; MNHN-MSE-290a-b, 291a-b, 292, 300a-b, 302a-b, 303a-b, 439a-b, 652a-b, 653a-b, 656, 965 (Figs 2B; 27B; 41B); MGB 536, 537-1, 29455a-b, 30345, 30377; MGSB 8.997, 13.376a-b, 20.658, 20.376 (Figs 22C; 38A), 27.298, 27.299, 56.216; NHML 10996a-b, 10997, 10999, 37497, 37500-1.

TYPE HORIZON. — Berriasian-Valanginian.

TYPE LOCALITY. — "La Pedrera de Meià", El Montsec, province of Lérida, Spain.

DIAGNOSIS. — See Kriwet *et al.* 1999.

Genus *Tepexichthys* Applegate, 1992

TYPE SPECIES. — *Tepexichthys aranguthyorum* Applegate, 1992.

INCLUDED SPECIES. — Monotypic genus.

Subfamily PROSCINETINAE Gistl, 1848
new rank

TYPE GENUS. — *Proscinetes* Gistl, 1848.

INCLUDED GENERA. — The type genus, and *Neoproscinetes* Figueiredo & Silva Santos, 1987.

DIAGNOSIS. — Pycnodontid fishes with the following autapomorphy: alternation of one large and two small teeth on main vomerine tooth row. Unique combination of derived characters: three vomerine tooth rows; eight or nine teeth on main vomerine tooth row (counting each couple of alternating small teeth as one tooth); about 30 to 34 vertebrae; dorsal ridge scales separated from each other; 18 to 21 ventral keel scales; spines on ventral keel scales placed in the posterior region of the midline.

Genus *Proscinetes* Gistl, 1848

TYPE SPECIES. — *Microdon elegans* Agassiz, 1833.

INCLUDED SPECIES. — The type species, ? *P. bassanii* (D'Erasmo, 1914), *P. bernardi* (Thiollière, 1852), *P. egertoni* (Thiollière, 1852), ? *P. itieri* (Saint-Seine, 1949), *P. ? radiatus* (Agassiz 1836), *P. sauvanasi* ? (Thiollière, 1852), *P. thiollieri* ? (Saint-Seine, 1949), *P. ? wagneri* (Thiollière, 1852).

REVISED DIAGNOSIS. — Proscinetine fish with the following unique combination of reverted primitive and derived characters: two large branchiostegal rays in contact; neural and haemal corresponding arcocentra not surrounding notochord, except individual exceptions in a few caudal vertebrae; pelvic fins at more than 55% of standard length; falcate to acuminate dorsal and anal fins; free dorsal axonost present; 40 to 49 anal axonosts; two urodermals; 15 to 17 dorsal ridge scales; and two anterior plus three posterior modified cloacal scales.

Unamed clade

Genus *Iemanja* Wenz, 1989

TYPE SPECIES. — *Iemanja palma* Wenz, 1989.

INCLUDED SPECIES. — Monotypic genus.

Unamed clade

Genus *Coelodus* Heckel, 1854 *sensu stricto*

TYPE SPECIES. — *Coelodus saturnus* Heckel, 1854.

INCLUDED SPECIES. — Monotypic genus.

REVISED DIAGNOSIS. — Derived pycnodontid fish with the following autapomorphies: prearticular teeth extremely elongated, up to five times longer perpendicularly to the longitudinal axis of the bone; diastema in caudal endoskeleton present, separating hypochordal elements 7 and 8. Unique combination of reverted primitive and derived characters: mouth gape subhorizontal; body ovoid in contour, maximum body height about 60% of standard length; caudal pedicle long, well differentiated; 11 teeth on main prearticular tooth row; grooves on vomerine and prearticular teeth present; about 31 vertebrae; 10 or 11 hypochordal elements in caudal endoskeleton, some of them hypertrophied; caudal fin double emarginated in distal contour; dorsal ridge scales separated from each other; no spines on dorsal ridge scales.

Coelodus saturnus Heckel, 1854

HOLOTYPE. — NMW 1857.XXXIII.2 (Heckel 1856: pl. 3, fig. 1; Figs 2A; 22A; 27A; 38B).

REVISED DIAGNOSIS. — As for genus (monotypic genus).

Subfamily PYCNODONTINAE Agassiz, 1833 new rank

DIAGNOSIS. — Derived pycnodontid fishes with the following autapomorphies: endocranium posteriorly exposed, with a postcephalic lacuna, and scutellum-like contour scales present, dorsal only. Unique combination of derived characters: dermocranial fenestra present; preopercular of similar size to the expanded ornamented portion of the dermohyomandibula; neural and haemal adjacent arcocentra in complex contact; six to eight epichordal elements in caudal endoskeleton, some hypochordal elements hypertrophied; scales in dorsal abdominal region of the body incompletely ossified, reduced to scale bars (except the ridge scales); seven to nine dorsal ridge scales; 10 to 14 ventral keel scales; and spines on ventral keel scales placed in the posterior region of the midline.

Genus *Pycnodus* Agassiz, 1833

TYPE SPECIES. — *Coryphaena apoda* Volta, 1809.

INCLUDED SPECIES. — The type species; plus numerous nominal species based on isolated dentitions.

TYPE HORIZON. — Early to middle Eocene.

TYPE LOCALITY. — Monte Bolca, Italy.

REVISED DIAGNOSIS. — Pycnodontine fish with the following unique combination of primitive and derived characters: body shape ovoid, maximum body height about 50-60% of standard length in adult specimens; dorsal apex placed before the point of insertion of the dorsal fin; ventral apex absent; caudal pedicle differentiated, well developed; extrascapular not fused to parietal; anterior infraorbital enlarged; vomerine teeth circular to subcircular in contour; eight or nine teeth on main vomerine tooth row; 10 or more teeth on main prearticular tooth row; crenulations on vomerine and prearticular teeth absent; last neural spine not supporting caudal fin rays vestigial; dorsal fin insertion at 40-49% of standard length; 50 to 59 dorsal axonosts; dorsal and anal fins strip-like to slightly acuminate; anal fin insertion at 50-59% of standard length; 40 to 49 anal axonosts; urodermals absent; seven or more spines on ventral keel scales; spines on each ventral keel scale separated from each other; one anterior modified cloacal scale; one post-cloacal ventral keel scale; cloaca with bifid scale and without comma-shaped scales; post-cloacal notch absent.

Genus *Oropycnodus* n. gen.

Palaeobalistum – Heckel 1856: 236, pl. 11, figs 1-15.

Coelodus – Blot 1987: 146, 147.

TYPE SPECIES. — *Palaeobalistum ponsortii* Heckel, 1854.

INCLUDED SPECIES. — Monotypic genus.

ETYMOLOGY. — From the Greek substantive "Ορο, ορεος", "Oro, oreos": mountain, in reference to Mont Aimé, the type and only locality; and "*Pycnodus*": the genus it is sister-group to.

DIAGNOSIS. — Pycnodontine fish with the following autapomorphies: opercular bone extremely reduced, almost bar-like; cloaca with bifid scale plus several comma-shaped scales; post-cloacal notch present. Unique combination of derived characters: body discoid, maximum body height about 70-80% of standard length in adult specimens; dorsal apex placed at the point of insertion of the dorsal fin; ventral apex present before the point of insertion of the anal fin; caudal pedicle not differentiated; all infraorbitals tubular; vomerine teeth oval in contour; seven or less teeth on main vomerine tooth row; seven or less teeth on main prearticular tooth row; crenulations on vomerine and prearticular teeth occasionally present, weak; last neural spine not supporting caudal fin rays reduced; dorsal fin insertion at 50-59% of standard length; 60 or more

dorsal axonosts; dorsal and anal fins rounded anteriorly; anal fin insertion at 60-69% of standard length; 50 or more anal axonosts; one urodermal present; four to six spines on ventral keel scales; spines on each ventral keel scale in contact with each other; two post-cloacal ventral keel scales; two anterior modified cloacal scales.

Oropycnodus ponsorti (Heckel, 1854) n. comb.
(Figs 4B; 11A, B; 17A, B; 29A, B; 42A, B; 46B)

LECTOTYPE. — NMW 1854/XXXIX/38 (Heckel 1856: pl. 11, fig. 1; Figs 4B; 17A, B; 42A, B).

PARALECTOTYPES. — NMW 1854/XXXIX/39 (Heckel 1856; Fig. 46B) and 1854/XXXIX/40 (Heckel 1856: pl. 11, fig. 2; Fig. 11A, B).

REFERRED SPECIMENS. — MNHN MTA 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 15, 16, 17, 38, 39, 40, 41, 42 (Fig. 29A), 43, 44, 45, 46, 47, 48, 49; NHML 30035, 30036, 30037, 30038, 30039, 30040, 30042, 30043, 30044, 30045, 30046, 30047, P1638.

TYPE HORIZON. — Paleocene (Montian).

TYPE LOCALITY. — Mont Aimé, Chalons-sur-Marne, France.

REVISED DIAGNOSIS. — As for genus (monotypic genus).

Subfamily NURSALLIINAE Blot, 1987
new rank

TYPE GENUS. — *Nursallia* Blot, 1987.

DIAGNOSIS. — Pycnodontid fishes with the following unique combination of primitive and derived characters: premaxillary and dentary teeth barely incisiform, not *sensu stricto*; neural and haemal corresponding arcocentra surrounding notochord partially to completely; neural and haemal adjacent arcocentra in complex to hyper-complex contact; hypochordal elements in caudal endoskeleton enlarged to hypertrophied; and scales present in abdominal and caudal regions of the body.

Genus *Nursallia* Blot, 1987

TYPE SPECIES. — *Nursallia veronae* Blot, 1987.

INCLUDED SPECIES. — The type species, *N. flavellatum* ? (Cope, 1886), *N.* ? *gutturosum* (Arambourg, 1954), *N.* ? *goedeli* (Heckel, 1854), *N. ventralis* ? (Davis, 1887).

REVISED DIAGNOSIS. — Nursalliine fish with the following autapomorphies: frontals strongly curved, very broad, giving the skull a hemispherical shape dorsally

and placing the orbit at about midway between the dorsal and the ventral borders of the head; neural and haemal adjacent arcocentra in hyper-complex contact; caudal fin vertical, very short, five to six times higher than long, with upper and lower lobes practically perpendicular to the axis of the body and defining a vertical axis in the fin, whose distal border is slightly convex. Unique combination of reverted primitive and derived characters: caudal pedicle differentiated; vomerine teeth (sub)circular in contour; neural and haemal corresponding arcocentra surrounding notochord completely; last neural spine not supporting precurrent caudal fin rays vestigial; six to eight hypochordal elements in caudal endoskeleton.

Genus *Abdobalistum* n. gen.

Palaeobalistum – Heckel 1856 *pro parte*: 204, 205, 229-233, pl. 1, fig. 11a-b, pl. 10.

TYPE SPECIES. — *Abdobalistum thyrsus* n. gen., n. sp.

INCLUDED SPECIES. — Monotypic genus.

ETYMOLOGY. — From the Latin adjective "Abdo, -itus": put away, removed, exiled; and the last part of its former genus "*Palaeobalistum*".

DIAGNOSIS. — Nursalliine fish with the following autapomorphies: scutellum-like contour scales present, ventral only; several reduced scales attached to most dorsal and ventral contour scales. Unique combination of reverted primitive and derived characters: body shape rounded, maximum body height about 85% of standard length; dorsal apex placed before the point of insertion of the dorsal fin; caudal pedicle not differentiated; crenulations on vomerine and prearticular teeth occasionally present, weak; grooves on vomerine and prearticular teeth present; 35 or more vertebrae; neural and haemal arcocentra surrounding notochord partially; dorsal and ventral adjacent arcocentra in complex contact; dorsal and anal fin strip-like; urodermals absent; caudal fin about twice higher than long, with distal border convex; all body scales incompletely ossified, reduced to bar scales; 15 to 17 dorsal ridge scales, in close contact with each other; 15 to 17 ventral keel scales.

Abdobalistum thyrsus n. sp.
(Fig. 4C, D)

Palaeobalistum orbiculatum – Heckel 1856 *pro parte*: 229-233, pl. 10.

Palaeobalistum orbiculatum – Blot 1987: "type = lectotype" 88-108, figs 42-48, pls 26-29.

HOLOTYPE. — MHML P 9830 (Fig. 4C, D; only known specimen).

ETYMOLOGY. — From the Latin substantive "thyrsus, -i", close-branched cluster, panicle; in reference to its autapomorphic multiple scales attached to most contour scales.

TYPE HORIZON. — Early to middle Eocene.

TYPE LOCALITY. — Monte Bolca, Italy.

DIAGNOSIS. — As for genus (monotypic genus).

Genus *Palaeobalistum* Blainville, 1818

Balistes – Faujas de Saint Fond 1803: 132, 133, pl. 6.

Diodon – Volta 1809 (1796): 168, 169, pl. 40.

Palaeobalistum – Blainville 1818: 338, 339. — Heckel 1856 *pro parte*: 204, 205, 229-233, pl. 1, fig. 11a-b.

Pycnodus – Agassiz II, pt. 1, 1833: 17, pt. II: 190, 191.

TYPE SPECIES. — *P. orbiculatum* Blainville, 1818.

INCLUDED SPECIES. — Monospecific genus.

REVISED DIAGNOSIS. — Nursalliine fish with the following unique combination of reverted primitive and derived characters: body shape intermediate, non-discoid, maximum body height less than 60% of standard length, with dorsal apex absent; caudal pedicle differentiated; crenulations and grooves on vomerine and prearticular teeth absent; infraorbitals as a mosaic of small plates; hypochordal elements of caudal endoskeleton enlarged; urodermals not differentiated; scales completely ossified, covering the whole body; scale rows in different directions; double scale rows present; scale rows between the bases of the lepidotrichia of unpaired fins absent; ornamentation made of tubercles; 15 to 17 dorsal ridge scales, in point contact with each other; 18 to 21 ventral keel scales; seven or more spines on ventral keel scales.

Palaeobalistum orbiculatum Blainville, 1818
(Fig. 4A)

Diodon orbicularis – Volta 1809 (1796): 168, 169, pl. 40.

Palaeobalistum orbiculatum – Blainville 1818: 338, 339. — Heckel 1856 *pro parte*: 204, 205, 229-233, pl. 1, fig. 11a-b.

Pycnodus orbicularis – Agassiz II, pt. 1, 1833: 17; pt. II; 1843: 190, 191.

Palaeobalistum zignoi – Blot 1987: 88-90, 108-117, fig. 49, tables 9, 10, pls 30-33.

HOLOTYPE. — MNHN BOL 0523 (Volta 1809: pl. 40; Fig. 4A; only known specimen).

REVISED DIAGNOSIS. — As for genus (monotypic genus).

CONCLUSION

The present paper presents a historic revision of the pycnodontiform genera that are known from articulated, more or less complete specimens, revealing the many nomenclatural problems that were still unsolved. Some revisions at specific level are also presented, when concerning the material from Spain and from the Lebanon that the authors are currently studying. Then, the first cladistic analysis for pycnodontiform fishes is carried out, focused on the interrelationships of the pycnodont genera and species revised.

In the present analysis, there are some differences in the character distribution when optimizing with DELTRAN or with ACCTRAN options. The differences are more abundant when involving taxa that have a high number of indeterminations in the data matrix (about 50% or more), and this is reflected in the difficulty of the character choice to diagnose certain high taxa. This is especially evident in the case of *Paramesturus* for the synapomorphic pycnodontiform characters that are unknown in this genus. We prefer to maintain all of the possible pycnodontiform synapomorphies while this genus is not better known.

Even in spite of this, the Pycnodontiformes are confirmed as a strong monophyletic group. This is also the case of the suborder Pycnodontoidei and of the family Pycnodontidae in enlarged sense (Nursall 1996b), but not of the "suborder Gyrodontoidei", which results as a paraphyletic group that should be avoided for taxonomic purposes. Another remarkable difference with the mentioned previous phylogenetic hypothesis lies in the position of *Gibbodon*, together with the restitution of the original composition of the Brembodontidae *sensu* Tintori (1981), although this involves a number of reversions in this family. Further studies on these intriguing forms are necessary to confirm it.

The present analysis has provided a hypothesis of phylogenetic relationships for forms that were

previously considered *incertae sedis*: *Palaeobalistum*, *Nursallia*, *Trewavasia*, *Ichthyoceros*, and *Coccodus*. The last three genera form the family Coccodontidae, restored to its original large sense (Berg 1940). This family is the sister-group to the Pycnodontidae, forming together a strong clade, the superfamily Pycnodontoidea n. rank. In turn, the subfamilies Proscinetinae n. rank, Pycnodontinae n. rank, and Nursalliinae n. rank are erected to locate genera with a well-defined sister-group relationship. The analysis, together with a historic revision of the nomenclatural problems, has revealed that a number of genera, as previously recognized, were not monophyletic: *Eomesodon*, *Coelodus*, and *Palaeobalistum*. These three genera are regarded now in a restricted sense. The new genera *Apomesodon* n. gen., *Ocloedus* n. gen., *Oropycnodus* n. gen., and *Abdobalistum* n. gen. have been erected to locate specific names that were previously in one (or two) of the other genera. The species *Apomesodon surgens* n. gen., n. sp. and *Abdobalistum thyrsu*s n. gen., n. sp. are also new.

There are still, however, many questions pending in the study of the Pycnodontiformes. Some of them concern the taxa that are based on incomplete, rare, and/or poorly preserved material: *Paramesturus*, *Palaeobalistum*, *Eomesodon*, *Anomoeodus*, and *Nursallia* ? *goedeli* are still poorly known, and this lack of information concerns not only those taxa themselves, but also the phylogenetic relationships of other, more or less related taxa. In turn, "*Coccodus*" *lindstroemi* and *Hadrodus* are not considered pycnodonts. All these taxa are in need of revision. Not to mention the very many nominal taxa that are based on isolated dentitions, many of which will eventually fall in synonymy after revision; there is an obvious problem of parataxonomy in pycnodontiforms that demands long, detailed studies of ontogenetic, sexual, and individual variation in complete specimens before being faced. In addition, the Pycnodontiformes are herein revealed as a highly homoplastic group (in the present analysis, the CI is 0.465, and the HI, 0.563). Reversions do occur, and these are just a few, relevant examples: presence of fringing fulcra in the Brembodontidae; complete squamation in two coccodontids; extension of the scales in the caudal region of the nursallines. There are puzzling combinations of primitive and derived characters (e.g., *Nursallia* ? *goedeli*, *Palaeobalistum*). Convergencies are especially abundant (e.g., in dental characters), and may eventually be as puzzling as the convergent presence of dermocranial fenestra in *Ocloedus* n. gen., *Tepexichthys*, and the Pycnodontinae n. rank, especially because this character has been broadly used to group advanced pycnodonts (Berg 1940; Lehman 1966; Wenz 1989a, b; Nursall 1996b). Although such a high homoplasy is somewhat unexpected in a supposedly anatomically uniform group, it confirms that mosaic evolution is far from uncommon in fishes, even within well defined monophyletic groups.

The present paper has, therefore, solved some issues, but it has also enhanced previous problems and revealed new ones. We still hope to provide a new insight to encouraging further studies on these fascinating fishes.

Acknowledgements

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APPENDIX 1

Abbreviated list of characters

1. Body shape (as measured by the ratio maximum body height/standard length)
fusiform, less than 40% (0); intermediate, 40-70% (1); discoid, 70-100% (2); deep, more than 100% (3).

2. Relative position of dorsal apex
apex absent (0); before the point of insertion of the dorsal fin (1); in the point of insertion of the dorsal fin (2).

3. Morphology of dorsal prominence
dorsal prominence absent (0); pointed, posterior border inclined (1); obtuse angle, posterior border (sub)horizontal (2); curved, anteriorly oriented (3); curved, dorsally oriented (4).

4. Relative position of ventral apex
apex absent (0); before the point of insertion of the anal fin (1); in the point of insertion of the anal fin (2).

5. Mouth gape
horizontal or subhorizontal (0); inclined (1); subvertical, opening downward (2).

6. Prognathism
absent (0); present (1).

7. Caudal pedicle
differentiated (0); not differentiated (1).

8. Antorbital and ethmoidal regions
normal (0); hypertrophied (1).

9. Morphology of frontal bones
rectangular, long (0); curved, long (1); curved, short (2); curved, very broad (3).

10. Prefrontal bones
absent (0); present (1).

11. Frontal spine
absent (0); present, simple (1); present, compound (2).

12. Dermocranial fenestra
absent (0); present (1).

13. Parietal
single (0); divided (1); absent (2).

14. Parietal process
absent (0); present (1).

15. Dermal supraoccipital
absent (0); single (1); divided into two or more unpaired plates (2).

16. Supraoccipital spine
absent (0); present, simple (1); present, compound (2).

17. Extrascapulars hypertrophied
no (0); yes (1).

18. Extrascapular(s) fused to parietal
no (0); yes (1).

19. Endocranium posteriorly exposed
no (0); yes (1).

20. Anterior portion of infraorbital sensory canal
closely surrounding the orbit (0); descending towards the ethmoid region (1).

21. Infraorbitals
row of plates around the ventral and posterior border of the orbit (0); mosaic of small plates partially covering the cheek (1); reduced to tubular ossifications around the infraorbital sensory canal (2); anterior infraorbital enlarged (3).

22. Infraorbital ornamentation
present in all infraorbitals (0); present only in the posteriormost one (1); absent in all infraorbitals (2).

23. Suborbitals
one or several rows (0); mosaic of small plates (1); absent as independent ossifications (2).

24. Preopercular and hyomandibular
preopercular single, smaller than opercular, hyomandibular deep, unornamented (0); preopercular single, hypertrophied, hyomandibular deep, unornamented (1); one large preopercular plus a small ornamented plate over the head of the hyomandibular (2); one large preopercular in close contact with a small ornamented portion of the hyomandibular, at the same superficial level (3); preopercular of similar size to expanded superficial ornamented portion of hyomandibular (4).

25. Opercular process of hyomandibular
present, well developed (0); present, reduced (1); absent (2).

26. Condyle in articular head of hyomandibular
absent (0); present (1).

27. Suboperculum and interoperculum
present (0); absent (1).

28. Opercular bone
well developed (0); reduced (1); extremely reduced (2).

29. Ossifications in gular region
large gular plate (0); small, numerous tesserae (1); no ossifications (2).

30. Branchiostegal rays
more than two (0); two, relatively large, in contact (1); two, thin, separated (2).

31. Premaxillary process
profound (0); anteriorly placed, long, superficial (1).

32. Morphology of premaxillary and dentary teeth
small, triangular to conic (0); robust, columnar to hook-shaped (1); robust, barely incisiform (2); very flattened, fully incisiform (3).

33. Crown of premaxillary and dentary teeth
simple (0); bifurcated (1).

34. Number of premaxillary teeth
more than three (0); three (1); two (2).

35. Maxilla
teeth-bearing, ornamented, elongated (0); edentulous, ornamented, ovoid (1); edentulous, ornamented, elongated (2); edentulous, unornamented, reniform (3); edentulous, unornamented, straight oral border (4); edentulous, unornamented, elongated oval (5).

36. Morphology of vomerine teeth
villiform to conic (0); circular to subcircular contour (1); oval contour (2); reniform contour (3); triangular contour (4).

37. Arrangement of vomerine teeth in regular rows
absent (0); present (1); absent anteriorly, present posteriorly (2).

38. Number of vomerine tooth rows
not arranged in rows (0); three (1); five (2).

39. Number of teeth in principal vomerine tooth row

teeth not arranged in rows (0); seven or less (1); eight or nine (2); 10 or more (3).

40. Alternation of teeth on main vomerine tooth row

absent (0); present (1).

41. Dentary

well developed, relatively broad (0); small, posteriorly elongated and simple (1); small, posteriorly bifid (2).

42. Number of dentary teeth

more than five (0); five (1); four (2); three (3); two (4).

43. Morphology of prearticular teeth

villiform to conic (0); circular contour (1); oval contour (2); sigmoid to drop-shaped contour (3); extremely elongated in contour (4).

44. Arrangement of prearticular teeth in regular rows

absent (0); present (1); absent anteriorly, present posteriorly (2).

45. Number of prearticular tooth rows

not arranged in rows (0); two (1); three (2); four (3); five or six (4).

46. Number of teeth on main prearticular tooth row

teeth not arranged in rows (0); seven or less (1); eight or nine (2); 10 or more (3).

47. Coronoid process

low, curved (0); high, straight dorsal border (1); high, club-shaped (2); low, straight dorsal border (3).

48. Central papilla in vomerine and prearticular teeth

absent (0); present (1).

49. Crenulations in vomerine and prearticular teeth

absent (0); occasionally present, weak (1); present in most teeth, strong (2).

50. Ridge on vomerine and prearticular teeth

absent (0); present (1).

51. Groove on vomerine and prearticular teeth

absent (0); present (1).

52. Number of vertebrae

35 or more (0); 30-34 (1); 25-29 (2); 24 or less (3).

53. Neural and haemal corresponding arcocentra

not surrounding notochord (0); surrounding notochord partially (1); surrounding notochord completely (2).

54. Neural and haemal adjacent arcocentra

separated from each other (0); simple contact (1); complex contact (2); hyper-complex contact (3); expanded and imbricate (4).

55. Sagittal flanges on neural and haemal spines

absent (0); anterior, small and short (1); anterior, large and long (2); anterior and posterior (3); anterior and posterior with strengthened margins (4).

56. Number of autogenous anterior neural spines

outgroup (?); most of them, including caudal ones (1); 10 or more (2); seven to 10 (3); six or less (4).

57. Relative length of last neural spine not supporting precurrent caudal fin rays

outgroup (?); reduced (1); less than half as long as preceding spines (2); vestigial (3).

58. Number of epichordal elements of caudal endoskeleton

nine or more (0); six to eight (1); four or five (2); three (3).

59. Relative development of hypochordal elements of caudal endoskeleton

only slightly enlarged (0); enlarged, plate-like (1); hypertrophied (2).

60. Number of hypochordal elements of caudal endoskeleton

14 or more (0); 12-13 (1); 9-11 (2); six to eight (3).

61. Diastema

absent (0); present (1).

62. Cleithrum

two limbs in angle, anteroventral limb subhorizontal (0); curved, anteroventral limb subhorizontal, slightly expanded (1); curved, anteroventral limb subvertical, expanded (2); cleithrum with three limbs (3); cleithrum with four limbs (4).

63. Spines on cleithrum

none (0); 1, hypertrophied (1); about 10 (2); about 50 (3).

64. Position of pelvic fins (ratio prepelvic distance/standard length)

45-55% (0); more than 55% (1); less than 45% (2).

65. Position of dorsal fin (predorsal length/standard length)

60%-69% (0); 40%-49% (1); 50%-59% (2); 70%-79% (3).

66. Number of dorsal axonosts

less than 20 (0); 20-29 (1); 30-39 (2); 40-49 (3); 50-59 (4); 60 or more (5).

67. Dorsal axonost not supporting lepidotrichium (free axonost)

absent (0); present (1).

68. Morphology of the dorsal and anal fins

strip-like (0); falcate to acuminate (1); sigmoid outline (2); rounded in the centre (3); rounded anteriorly (4); square (5).

69. Position of anal fin (preanal length/standard length)

70%-79% (0); 50%-59% (1); 60%-69% (2); 80%-89% (3).

70. Number of anal axonosts

10-19 (0); 20-29 (1); 30-39 (2); 40-49 (3); 50 or more (4); nine or less (5).

71. Urodermals

not differentiated (0); a series of three or more (1); two (2); one (3); absent (4).

72. Number of caudal principal fin rays

20-25 (0); nine or less (1); 10-19 (2); 26-35 (3); 36 or more (4).

73. Morphology of caudal fin

outgroup (?); stalked (1); distal border convex (2); distal border concave (3); distal border straight (4); double emarginated (5); vertical (6).

74. Fringing fulcra

present, numerous (0); present, scarce (1); absent (2).

75. Ossification of scales

complete in all scales (0); complete in abdominal scales, incomplete in caudal scales (1); complete in ventral scales, incomplete in dorsal scales (2); incomplete in all scales (3); scales absent (4).

76. Distribution of scales

whole body (0); whole body except caudal pedicle (1); abdominal region plus part of the caudal region (2); only abdominal region (3); body naked (4).

77. Arrangement of scales

rows in the same direction (0); rows in different directions (1); not forming rows (2); scales absent (3).

78. Suture between scales of the same row

not jagged (0); jagged (1).

79. Scale rows
simple (0); double (1).
80. Scale rows between the bases of the lepidotrichia of the dorsal and anal fins
absent (0); present (1).
81. Ornamentation
outgroup (?); ridges (1); reticulation (2); tubercles (3); small spines (4).
82. Large spines on scales
none (0); one (1); several (2).
83. Nuchal plates
absent (0); present (1).
84. Dorsal spine
absent (0); present (1).
85. Contour scales
not differentiated (0); differentiated (1); absent (2).
86. First dorsal ridge scale
not differentiated (0); about same size than subsequent ridge scales (1); larger than subsequent ridge scales (2); absent (3).
87. Scutellum-like contour scales
not differentiated (0); present, dorsal only (1); present, ventral only (2); present, dorsal and ventral (3); contour scales absent (4).
88. Number of differentiated dorsal ridge scales
dorsal contour scales not differentiated (0); 18 or more (1); 15 to 17 (2); 10 to 14 (3); seven to nine (4); one or two (5); dorsal contour scales absent (6).
89. Arrangement of dorsal ridge scales
dorsal contour scales in close contact with each other (0); point contact (1); separated from each other (2); dorsal contour scales absent (3).
90. Number of spines on dorsal ridge scales
no spines on dorsal contour scales (0); one or two (1); three or four (2); five or more (3); midline serrated (4); dorsal contour scales absent (5).
91. Distribution of spines on dorsal ridge scales
no spines on dorsal contour scales (0); all along the midline, or centered if only one spine present (1); posterior region (at most two thirds) of the midline (2); anterior region (at most two thirds) of the midline (3); dorsal contour scales absent (4).
92. Contact of spines on each dorsal ridge scale
no spines on dorsal contour scales (0); separated from each other (1); in contact with each other (2); dorsal contour scales absent (3).

93. Relative size of anterior and posterior spines on each dorsal ridge scale
no spines on dorsal contour scales (0); similar size (1); spines of increasing size in cephalocaudal sense (2); dorsal contour scales absent (3).
94. Number of ventral keel scales
not differentiated (0); 22 or more (1); 18 to 21 (2); 15 to 17 (3); 10 to 14 (4); two or three (5); ventral keel scales absent (6).
95. Arrangement of ventral keel scales
close contact with each other (0); point contact (1); ventral keel scales absent (2).
96. Number of spines on each ventral keel scale
no spines on ventral keel scales (0); one to three (1); four to six (2); seven or more (3); ventral keel scales absent (4).
97. Distribution of spines on ventral keel scales
no spines on ventral keel scales (0); all along the midline, or centered if only one spine present (1); posterior region (at most two thirds) of the midline (2); ventral keel scales absent (3).
98. Contact of spines on each ventral keel scale
no spines on ventral keel scales (0); separated from each other (1); in contact with each other (2); ventral keel scales absent (3).
99. Relative size of anterior and posterior spines on each ventral keel scale
no spines on ventral keel scales (0); all spines of similar size (1); spines of increasing size in cephalocaudal sense (2); ventral keel scales absent (3).
100. Several scales attached to the contour scales
no (0); yes (1); contour scales absent (2).
101. Number of post-cloacal ventral keel scales
cloacal and contour scales not differentiated (0); 10 or more (1); seven or eight (2); five or six (3); three or four (4); two (5); one (6); none (7).
102. Number of anterior cloacal modified scales
cloacal and contour scales not differentiated (0); mosaic of little scales (1); two (2); one (3); cloacal scales absent (4).
103. Number of posterior cloacal modified scales
cloacal scales not modified (0); mosaic of little scales (1); three (2); two (3); one (4); no scales, posterior part of anal notch supported by a rib (5); cloacal scales absent (6).
104. Bifid scale in cloaca
absent (0); present (1); present plus several comma-shaped scales (2).
105. Post-cloacal notch
absent (0); present (1).

APPENDIX 2

List of genera depicted in the figures

APPENDIX 3

Data matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abdobalistum	2	1	0	?	0	0	1	1	?	?	0	0	?	1	1	0	?	?	0	1	3	?	?	?	?	?	?	1	2	?
Anomoeodus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apomesodon gibbosus	2	1	2	0	1	1	1	1	2	0	0	0	0	0	1	0	0	0	0	?	1&2	?	?	1	?	?	1	1	2	2
A. surgens	3	1	1	1	1	1	1	1	2	0	0	0	0	0	1	0	0	1	0	1	2	?	?	1	?	0	1	1	2	2
Arduafrons	2	1	1	1	0	1	0	1	?	0	0	0	?	0	1	0	0	0	0	1	1	0	1	1	?	?	1	1	1	?
Brembodus	2	1	2	1	0	0	0	1	1	0	0	0	0	0	1	0	0	?	0	1	1	0	1	1	?	0	1	1	1	1
Coccodus	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
Coelodus saturnus	1	2	0	?	0	0	0	1	?	0	?	?	?	1	?	?	?	?	0	?	?	?	?	2	?	?	?	?	?	?
? Eomesodon barnesi	2	1	4	2	0	1	?	1	?	0	0	0	0	0	1	0	?	?	0	?	?	?	?	1	?	?	?	1	2	?
Eomesodon liassicus	2	1	3	1	0	?	0	1	1	0	0	0	0	0	1	0	0	1	0	?	0	0	?	1	?	?	1	1	?	2
Gibbodon	2	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	2	1	?	?	1	1	0	0	0
Gyrodus	2	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	1	1	1	2
Ichthyoceros	2	1	0	1	0	1	0	1	2	1	2	0	0	1	2	0	?	0	1	?	0	1	?	?	?	1	1	2	2	2
Iemanja	1	?	0	?	0	1	1	1	2	0	0	0	0	1	1	0	?	?	0	?	?	?	?	3	2	1	1	1	2	?
Macromesodon bernissartensis	2	1	0	1	1	0	1	1	2	0	0	0	0	1	1	0	?	?	0	?	?	?	?	?	?	?	?	1	?	?
M. cf. M. bernissartensis	2	1	0	1	1	0	1	1	2	0	0	0	0	1	1	0	0	1	0	1	2	1	2	3	2	?	1	1	2	?
M. macropterus	2	2	0	0	1	0	1	1	2	0	0	0	0	1	1	0	0	1	0	1	2	1	2	3	2	0	1	1	2	?
Mesturus	1	0	0	0	0	0	0	1	2	0	0	0	1	0	2	0	0	0	0	0	1	0	1	2	?	0	1	1	1	0
Micropycnodon	?	?	?	?	?	0	?	1	2	?	0	0	0	0	2	0	0	0	0	1	1	0	?	1	1	0	1	1	1	?
Neoproscinetes	2	1	0	1	1	0	0	1	2	0	0	0	0	1	1	0	0	?	0	1	2	1	2	3	2	1	1	1	2	2
Nursallia ? goedeli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nursallia gutturosum	2	2	0	0	0	0	0	1	3	1	0	0	0	?	1	0	0	0	0	0	3	0	2	3	?	0	1	1	2	?
N. veronae	2	2	0	0	0	0	0	1	3	?	0	0	0	?	1	0	0	?	0	0	?	?	?	?	?	1	?	1	?	?
Ocloedus subdiscus	2	2	0	2	1	0	1	1	2	0	0	0	1	0	1	1	0	0	1	0	1	2	1	2	4	?	0	1	1	2
Oropycnodus ponsorti	2	2	0	1	0	0	1	1	2	0	0	0	1	0	1	1	0	0	1	1	1	2	?	2	4	?	1	2	2	?
Palaeobalistum orbiculatum	1	0	0	0	0	0	0	1	?	?	0	?	0	?	?	0	0	1	0	?	1	0	?	?	?	?	?	1	?	?
Paramesturus	?	?	?	?	0	0	?	1	2	0	0	0	0	0	2	0	0	0	0	0	0	?	?	?	?	0	?	?	?	?
Proscinetes	2	2	0	2	1	0	1	1	2	0	0	0	0	1	1	0	0	1	0	1	2	1	2	3	2	0	1	1	2	1
Pycnodus	1	1	0	0	0	0	0	1	2	0	0	1	0	1	1	0	0	0	1	1	3	0	2	4	2	0	1	1	2	2
Stemmatodus	1	1	0	0	1	0	1	1	2	0	0	0	0	1	1	0	0	?	0	1	2	1	2	4	2	0	1	1	2	2
Stenamara	3	1	4	1	1	0	1	1	2	0	0	0	0	1	1	0	0	?	0	1	2	?	2	?	?	0	?	1	?	?
Tepexichthys	2	2	0	2	1	0	1	1	2	0	0	0	1	0	1	1	0	0	1	0	1	2	2	2	?	?	?	1	1	2
Trewavasia	2	1	0	0	2	0	1	1	2	1	1	0	2	0	1	0	1	0	0	0	2	0	2	3	2	?	1	1	2	1

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Abdobalistum	1	2	0	?	?	?	1	?	?	?	?	?	2	1	2	?	?	0	1	0	1	0	1	2	2	4	2	?	2	2	0	2
Anomoeodus	?	3	0	?	?	?	?	?	?	?	?	?	3	2	4	3	?	0	1	0	1	?	0	1	2	?	?	?	?	?	0	?
Apomesodon gibbosus	1	2	0	2	?	1	1	?	3	0	?	?	2	1	2	2	?	0	1	0	0	0	0	0	1	?	1	3	0	1	0	2
A. surgens	1	2	0	2	?	2	1	2	?	0	1	2	2	1	?	?	1	0	1	0	0	0	0	0	1	?	1	3	0	2	0	2
Arduafrons	1	1	0	2	1	2	1	?	3	0	?	2	2	?	?	3	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	1
Brembodus	1	2	0	1	?	2	1	2	2	0	1	2	2	1	4	2	1	0	0	0	0	2	2	1	1	1	1	2	0	3	0	2
Coccodus	1	3	0	2	?	4	1	1	2	0	?	4	2	1	1	2	3	0	1	0	1	3	1	1	2	?	1	1	1	2	0	4
Coelodus saturnus	1	3	0	?	?	2	1	2	3	0	?	?	4	1	2	3	?	0	0	0	1	1	1	1	2	3	1	?	2	2	1	2
? Eomesodon barnesi	?	?	?	?	?	?	?	?	?	?	?	?	2	1	4	2	1	0	1	0	0	?	0	0	1	?	?	?	0	?	0	2
Eomesodon liassicus	?	2	0	?	?	?	?	?	?	?	?	4	2	?	?	?	1	0	1	0	0	2	0	0	?	?	1	3	0	0	0	?
Gibbodon	0	2	1	1	?	2	1	1	2	0	1	1	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	2
Gyrodus	1	1	0	2	1	1	1	2	3	0	2	2	2	1	3	2	1	1	2	0	1	1	0	1	4	2	1	1	1	2	0	2
Ichthyoceros	?	3	0	?	?	4	1	1	3	0	?	4	3	1	2	3	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	3
Iemanja	1	?	?	?	5	3	2	2	?	0	?	?	1	0	?	?	1	0	0	0	0	2	1	4	3	3	1	2	1	3	0	2
Macromesodon bernissartensis	1	3	0	2	?	2	1	?	3	?	?	?	2	1	2	2	?	0	0	0	0	2	0	1	2	?	1	3	0	2	0	?
M. cf. M. bernissartensis	1	3	0	2	?	?	1	?	3	0	1	4	2	1	2	3	2	0	1	0	0	2	0	1	2	3	1	3	0	2	0	2
M. macropterus	1	3	0	2	3	?	1	?	2	0	1	4	2	1	2	2	1	0	0	0	0	2	0	1	2	3	1	3	0	2	0	2
Mesturus	1	1	0	1&2	2	1	1	2	3	0	2	1&2	1	1	4	3	1	0	2	1	1	1	0	?	?	?	?	?	?	?	?	1
Micropycnodon	?	?	?	?	?	2	1	2	1	0	?	?	2	1	3	1	2	0	2	0	1	?	?	?	?	?	?	?	?	?	?	?
Neoproscinetes	1	3	0	2	3	2	1	1	2	1	?	3	2	1	2	1	2	0	0	0	0	1	1	2	3	2	2	1	3	0	2
Nursallia ? goedeli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	3	2	?	2	2	2	3	?	?
Nursallia gutturosum	1	2	0	2	1	1	1	2	1	0	1	4	2	1	2	2	1	0	0	0	0	2	2	3	2	4	3	2	2	3	0	2
N. veronae	1	2	0	2	?	1	1	1	2	0	1	4	?	1	?	2	?	0	0	0	0	2	2	3	?	?	3	2	2	3	0	2
Ocloedus subdiscus	1	3	0	2	?	2	1	2	3	0	1	4	2	1	2	2	1	0	1	0	1	2	0	1	2	3	1	2	1	1	0	2
Oropycnodus ponsorti	1	3	0	2	?	2	1	?	1	0	1	4	2	1	2	1	1	0	1	0	0	2	2	2	2	4	1	1	2	2	0	2
Palaeobalistum orbiculatum	?	?	?	?	?	1	1	?	2	0	?	?	2	1	2	2	?	0	0	0	0	?	?	?	?	?	?	?	1	2	0	?
Paramesturus	1	1	0	?	?	?	1	?	3	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Proscinetes	1	3	0	2	?	2	1	1	2	1	1	4	2	1	2	2	1	0	0	0	0	1	0	1	2	3	1	2	1	2	0	2
Pycnodus	1	3	0	2	3	1	1	2	2	0	1	4	2	1	2	3	1	0	0	0	0	2	2	2	2	4	3	1	2	2	0	2
Stemmatodus	1	3	0	2	4	1	1	2	2	0	1	4	2	1	2	3	1	0	1	0	0	2	0	1	2	4	1	2	0	2	0	2
Stenamara	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	1	2	1	0	?	0	0	2	0	1	2	3	1	3	0	3	0	2
Tepexichthys	1	3	0	1	3	1	1	2	3	0	1	3	2	1	2	2	2	0	2	0	0	1	0	1	2	3	1	1	1	2	0	2
Trewavasia	1	1	0	1	?	1	1	?	3	0	1	3	1	1	?	3	1	0	0	0	0	2	1	1	2	?	1	1	1	1	0	2

	63	64	66	65	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
Outgroup	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
Abdobalistum	0	?	0	5	0	0	1	4	4	4	2	2	3	2	1	0	?	0	?	0	0	0	1	2	2	2	0	1	1	1	0	3
Anomoeodus	?	?	?	?	?	?	?	?	?	?	?	?	2	3	0	0	0	0	2	0	?	?	1	?	0	?	?	?	?	?	?	?
Apomesodon gibbosus	0	0	0	2	0	4	0	0	1	2	4	1	0	3	0	0	0	0	3&4	0	1	0	1	1	0	1	0	3	1	1	1	1
A. surgens	0	0	0	2	0&1	4	0	1	1	2	2	2	0	3	0	0	0	0	3	0	1	0	1	1	0	1	0	2	1	1	1	2
Arduafrons	0	0	3	3	0	0	0	2	0	3	4	2	0	0	0	0	1	1	3	0	1	0	1	1	0	1	0	3	1	1	1	1
Brembodus	0	1	1	2	1	1&4	0	1	1	2	2	0	0	0	0	0	0	1	3	0	1	1	1	1	0	3	0	3	1	1	1	2
Coccodus	1	1	?	0	0	5	?	5	2	2	?	2	4	4	3	?	?	0	1&3	?	0	0	2	3	4	6	3	5	4	3	3	6
Coelodus saturnus	0	?	?	5	0	1	?	3	?	0	5	2	2	3	0	0	0	0	?	3	?	0	1	?	?	3	2	0	0	0	0	?
? Eomesodon barnesi	0	2	3	2	0	3	2	1	?	?	?	2	0	3	0	0	0	0	3	0	1	0	1	1	0	2	0	?	?	?	?	?
Eomesodon liassicus	0	?	?	?	?	?	?	0	?	?	?	2	0	3	0	0	0	0	3	0	?	0	1	?	0	?	0	3	1	1	1	?
Gibbodon	0	1	0	0	0	0	0	5	0	2	?	0	0	0	0	0	0	1	3	0	1	0	1	1	0	3	0	2	1	1	1	2
Gyrodus	0	2	0	2	0	1	0	1	3	0	1	2	0	0	0	0	0	1	3	0	0	0	1	1	0	2	0	3	1	1	1	1
Ichthyoceros	3	1	2	0	?	0	3	5	0	1	2	2	0	0	2	0	0	0	4	2	0	1	2	0	5	0	1	1	1	?	?	5
Iemanja	0	?	0	3	?	?	2	3	3	0	?	2	2	3	0	0	0	0	1	0	?	0	1	?	0	?	0	?	?	?	?	?
Macromesodon bernissartensis	0	1	1	2	?	3	0	1	2	2	2	2	2	3	0	0	0	0	?	0	?	0	1	?	0	?	?	3	?	1	2	3
M. cf. M. bernissartensis	0	0	2	2	1	3	0	1	2	2	2	2	2	3	0	0	0	0	2	0	0	0	1	1	0	2	1	3	2	1	2	3
M. macropterus	0	0	2	2&3	1	2	0	2	3	2	5	2	2	3	0	0	0	0	1	0	0	0	1	1	0	2	1&2	3	2	1	2	2
Mesturus	0	?	0	2	0	0	2	1	0	3	2	1	0	0	1	1	1	1	3	0	0	0	1	2	0	1	0	2	1	1	1	1
Micropycnodon	0	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	0	?	3	0	?	?	1	2	0	?	?	?	?	1	?	?
Neoproscinetes	0	0	2	3	?	0	2	2	3	0	3	2	2	3	0	0	0	0	1	0	?	0	1	?	0	3	2	1	3	1	2	2
Nursallia ? goedeli	?	?	?	?	?	1	?	4	2	3	6	2	0	1	1	0	?	0	3	0	?	?	?	?	?	?	?	?	?	?	?	?
Nursallia gutturosum	0	0	2	5	0	1	2	4	?	4	6	2	2	2	0	0	0	0	1	0	0	0	1	2	0	2	1	?	?	?	?	3
N. veronae	0	0	2	5	0	1	2	4	4	3	6	2	1	2	0	0	0	0	1&3	0	?	0	1	2	3	3	1	0	0	0	?	4
Ocloedus subdiscus	0	1	2	2	0	1	2	2	2	2	5	2	2	3	0	0	0	0	3	0	0	0	1	1	0	3	1	2	2	2	2	3
Oropycnodus ponsorti	0	0	2	5	0	4	2	4	3	0	5	2	3	3	0	0	0	0	1&2&3	0	0	0	1	2	1	4	1	0	0	0	0	4
Palaeobalistum orbiculatum	0	0	0	?	?	?	1	?	?	3	?	2	0	0	1	0	1	0	3	0	?	0	1	?	0	2	1	1	1	1	0	2
Paramesturus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?
Proscinetes	0	1	2	3&4	1	1	2	3	2	0	3	2	2	3	0	0	0	0	1	0	0	0	1	2	0	2	2	0	0	0	0	2
Pycnodus	0	0	1	4	0	0	1	3	4	0	5	2	3	3	0	0	0	0	2&3	0	0	0	1	2	1	4	1	0	0	0	0	4
Stemmatodus	0	0	0	2	1	0	2	2	2	2	3	2	3	3	0	0	0	0	2	0	0	0	1	1	0	3	0	3	2	2	2	4
Stenamara	0	2	0	2	1	?	2	1	2	2	?	2	2	3	0	0	0	0	?	0	0	0	1	1	0	3	0	2	1	2	2	2
Tepexichthys	0	0	2	4	0	1	1	2	3	0	3	2	2	3	0	0	0	0	1	0	0	0	1	1	0	2	0	0	0	0	0	3
Trewavasia	2	0	2	1	0	4	0	0	4	2	2	2	0	2	0	0	0	0	3	1	0	0	1	2	0	5	0	4	1	1	2	5

	95	96	97	98	99	100	101	102	103	104	105
Outgroup	0	0	0	0	0	0	0	0	0	0	0
Abdobalistum	0	0	0	0	0	1	?	?	?	?	?
Anomoeodus	0	1	1	2	2	0	?	0	3	0	0
Apomesodon gibbosus	0	2	1	1	2	0	2	1	1	0	0
A. surgens	0	3	1	1	2	0	2	1	1	0	0
Arduafrons	0	3	1	1	2	0	1	1	1	0	0
Brembodus	0	?	?	?	?	0	5	1	1	0	0
Coccodus	2	4	3	3	3	2	7	4	6	0	0
Coelodus saturnus	?	?	?	?	?	0	?	?	?	?	?
? Eomesodon barnesi	0	?	?	?	?	?	2	?	?	?	?
Eomesodon liassicus	0	0	0	?	?	0	?	?	?	?	?
Gibbodon	0	3	1	1	?	0	3	1	1	0	0
Gyrodus	0	2	1	1	1	0	1	1	1	0	0
Ichthyoceros	0	1	1	?	2	0	6	3	4	0	0
Iemanja	?	?	?	?	?	0	?	?	?	?	0
Macromesodon bernissartensis	0	1	1	1	2	0	3	?	?	?	?
M. cf. M. bernissartensis	0	2	1	2	2	0	3	2	4	0	0
M. macropterus	0	1	1	2	2	0	3	3	4	0	0
Mesturus	0	3	1	1	1	0	0	0	0	0	0
Micropycnodon	0	2	1	1	1	?	?	?	?	?	?
Neoproscinetes	1	2	2	1	?	0	5	?	?	?	0
Nursallia ? goedeli	?	?	?	?	?	?	?	?	?	?	?
Nursallia gutturosum	0	?	?	1	2	0	5	?	?	?	0
N. veronae	1	?	?	?	?	0	4	?	?	1	0
Ocloedus subdiscus	0	3	2	2	2	0	5	3	3	0	0
Oropycnodus ponsorti	1	2	2	2	2	0	5	2	3	2	1
Palaeobalistum orbiculatum	0	3	1	1	?	0	?	?	?	?	?
Paramesturus	0	?	?	?	1	0	?	?	?	?	?
Proscinetes	1	2	2	1	2	0	5	2	2	0	0
Pycnodus	1	3	2	1	2	0	5	3	4	1	0
Stemmatodus	0	2	1	2	2	0	5	3	5	0	0
Stenamara	0	?	?	?	2	0	4	3	4	0	0
Tepexichthys	0	0&2	1	1	2	0	5	3	3	0	0
Trewavasia	?	3&4	1&2	1	2	0	6	?	?	0	0

APPENDIX 4

Complete list of apomorphies

In the following list, the characters defining each node are given for the first analysis, carried out with the complete data set. The number of each character is given, with the character state number in brackets, followed by the character state explanation; (AU), indicates autapomorphic character; (C), some relevant convergences; (R), reversion; numbers in brackets at the end of the explanation indicate the number of steps involved if more than one. The order of the nodes presented here is from base to top of the consensus tree in Fig. 43, including the alternative nodes. The present list ends with the generic and specific terminal taxa in alphabetical order. The distribution offered herein is the one obtained with the DELTRAN optimization option; changes when using the ACCTRAN option are also listed in each case.

NODES

Node 1: order Pycnodontiformes Berg, 1937
8(1), antorbital and ethmoid regions hypertrophied (AU);
9(2), frontals curved and short;
15(2), dermal supraoccipital present (AU), primitively as a series of two or more unpaired plates;
31(1), premaxillary process long and superficial;
32(1), premaxillary teeth columnar to hook-shaped;
37(1), vomerine teeth forming rows (AU);
39(3), 10 or more teeth in main vomerine row;
42(2), four dentary teeth (2);
99(1), spines on each dorsal ridge scale of similar size.
With ACCTRAN it also presents characters 1(1), 23(1), 24(1), 25(1)(AU), 27(1)(AU), 28(1)(AU), 29(1), 34(1), 35(1), 36(1), 38(2), 41(2)(AU), 43(2), 44(1), 45(3), 46(1), 47(1), 49(2), 51(1), 52(1), 57(1), 58(1), 60(2)(two steps), 62(1), 66(2)(two steps), 70(1), 72(3), 74(1), 80(1), 86(1), 88(1), 90(1), 91(1), 92(1), 93(1), 94(1), 96(3)(three steps), 97(1), and 98(1).

Node 2: Pycnodontiformes minus *Paramesturus* Taverne, 1981
1(1), body shape not-fusiform (AU), primitively intermediate;
21(1), infraorbitals as a mosaic of small plates;
23(1), suborbitals as a mosaic of small plates;
24(1), preopercular hypertrophied;
25(1), opercular process of hyomandibular reduced (AU);
27(1), subopercular and interoperculum absent (AU);
28(1), opercular reduced (AU);
29(1), tesserae in gular region;
34(1), three premaxillary teeth;
36(1), crushing vomerine teeth (AU), primitively circular in contour;
38(2), five vomerine tooth rows;
41(2), dentary small (AU), primitively posteriorly bifid;

43(2), crushing prearticular teeth (AU), primitively oval in contour;
44(1), prearticular teeth forming rows;
45(3), four prearticular tooth rows;
47(1), coronoid process high, with straight strengthened dorsal border;
52(1), 30 to 34 vertebrae;
66(2), 30 to 39 dorsal axonosts (2);
70(1), 20 to 29 anal axonosts;
74(1), fringing fulcra small and scarce;
80(1), scale rows between dorsal and anal lepidotrichia present;
85(1), dorsal and ventral contour scales differentiated (AU);
88(1), 18 or more dorsal ridge scales;
91(1), spines on dorsal ridge scales distributed all along the midline;
92(1), spines on each dorsal ridge scale separated among them;
93(1), spines on dorsal ridge scales of similar size;
94(1), 22 or more ventral keel scales;
96(2), four to six spines on ventral keel scales (2);
97(1), spines on ventral keel scales distributed all along the midline;
98(1), spines on each ventral keel scale separated among them.
With ACCTRAN it does not present characters 1, 23, 24, 25, 27, 28, 29, 34, 36, 38, 41, 43, 44, 45, 47, 52, 66, 70, 74, 88, 91, 92, 93, 94, 96, 97, and 98.

Alternative node A1: *Mesturus* Wagner, 1862 + *Micropycnodon* Hibbard & Graffham, 1945
49(2), strong crenulations in vomerine and prearticular teeth present in most teeth (C);
51(1), groove on vomerine and prearticular teeth present (C);
86(2), first dorsal ridge scale larger than subsequent scales (C).
With ACCTRAN it also presents characters 35(2), and 69(2), and lacks characters 49 and 51.

Alternative node A2: node 2 minus *Mesturus*
25(1), opercular process of hyomandibular reduced (AU);
36(1), vomerine teeth circular in contour;
43(2), prearticular teeth oval in contour;
45(3), four prearticular tooth rows.
With ACCTRAN it also presents characters 1(2), 4(1), 20(1), 30(2), 62(2), 71(1), 74(2), 88(2), 90(3), 101(1), 102(1), and 103(1), and lacks characters 25 and 45.

Node 3: node 4 plus *Gyrodus* Agassiz, 1833
1(2), body shape discoid;
4(1), ventral apex placed before the point of insertion of the anal fin;
9(1), frontals curved and long;

15(1), dermal supraoccipital single (AU);

34(2), two premaxillary teeth;

35(1), maxilla ovoid;

57(1), last neural spine not supporting precurrent caudal fin rays reduced;

58(1), six to eight epichordal elements in caudal endoskeleton;

62(2), cleithrum curved, anteroventral limb subvertical, expanded;

86(1), first dorsal ridge scale of about the same size than subsequent ridge scales;

90(3), five or more spines on dorsal ridge scales;

101(1), 10 or more post-cloacal ventral keel scales;

102(1), cloacal anterior scales modified, forming mosaic;

103(1), cloacal posterior scales modified, forming mosaic.

With ACCTRAN it lacks characters 34, 35, 57, 58, 80, and 93.

Node 4: node 5 plus *Arduafrons* Frickhinger, 1991

2(1), dorsal apex in the point of insertion of the dorsal fin;

3(1), dorsal prominence pointed, posterior border inclined;

20(1), anterior portion of infraorbitary sensory canal descending towards the orbit;

36(2), vomerine teeth oval in contour;

51(0), grooves on crushing teeth absent;

83(1), nuchal plates present;

99(2), spines on each ventral keel scale of increasing size in cephalocaudal sense.

With ACCTRAN it also presents characters 6(1), 25(2)(AU), 41(1)(AU), 45(4), and 58(2).

Node 5: Pycnodontoidei Nursall, 1996 plus Brembodontidae Tintori, 1981

18(1), extrascapular fused to parietal;

32(2), premaxillary and dentary teeth robust, barely incisiform (C);

41(1), dentary small, posteriorly elongated and simple (AU);

45(4), five or six prearticular tooth rows;

49(1), crenulations on vomerine and prearticular teeth occasionally present, weak;

52(2), 25 to 29 vertebrae;

55(1), sagittal flanges anterior only (AU), small and short;

58(2), four or five epichordal elements in caudal endoskeleton;

72(2), 10 to 19 caudal fin rays;

88(2), 15 to 17 dorsal ridge scales;

94(2), 18 to 21 ventral keel scales;

101(2), seven or eight post-cloacal ventral keel scales.

With ACCTRAN it presents characters 23(2) and 35(3), and lacks characters 45, 58 and 88.

Node 6: family Brembodontidae

34(1), three premaxillary teeth (R);

39(2), eight or nine teeth in main vomerine tooth row;

64(1), pelvic fin placed at more than 55% of standard length;

74(0), fringing fulcra present, numerous (2)(R);

88(3), 10 to 14 dorsal ridge scales;

101(3), five or six post-cloacal ventral keel scales.

With ACCTRAN it also presents characters 6(0)(R), 30(0)(R), 53(2)(2 steps), 54(1), and 60(3).

Node 7: suborder Pycnodontoidei

29(2), ossifications on gular region absent;

30(2), two branchiostegal rays, thin and separated;

58(3), three epichordal elements in caudal endoskeleton;

76(3), scales only in abdominal region (3);

80(0), scale rows between bases of lepidotrichia of unpaired fins absent (R).

With ACCTRAN it also presents characters 42(4)(two steps), 56(3), and 96(2), and it lacks character 30.

Alternative node B1: genus *Eomesodon* Woodward, 1918 (*E. liassicus* [Egerton, 1855] + ? *E. barnesi* [Woodward, 1906])

There are no characters defining this node with DELTRAN; with ACCTRAN it presents the following ones:

3(3), dorsal prominence curved, anteriorly oriented;

21(0), infraorbitals as a row of plates (R);

60(0), 14 or more hypochordal elements in caudal endoskeleton (2)(R);

64(2), pelvic fin at less than 45% of standard length;

65(3), dorsal fin at 70-79% of standard length;

68(3), dorsal and anal fins rounded in the centre;

69(2), anal fin at 60-69% of standard length;

96(0)(two steps) and 97(0), spines on ventral keel scales absent (R).

Alternative node B2: node 8 plus ? *Eomesodon barnesi*

29(2), no ossifications on gular region.

With ACCTRAN it presents characters 7(1), 9(2), and 21(2) instead of character 29.

Alternative node B3: node 8 plus *Eomesodon liassicus*

30(2), two thin, separated branchiostegal rays;

58(3), three epichordal elements in caudal endoskeleton.

With ACCTRAN it presents characters 45(2) and 70(0)(R) instead of characters 30 and 58.

Node 8: Pycnodontoidei minus *E. liassicus* and ? *E. barnesi*

5(1), mouth gape inclined;

7(1), caudal pedicle not differentiated;

9(2), frontals curved and short;

21(2), tubular infraorbitals present;

45(2), three prearticular tooth rows;

71(1), urodermals differentiated, primitively forming a series of three or more.

With ACCTRAN it lacks character 71.

Node 9: *Apomesodon* n. gen.

6(1), prognathism present;

52(0), 35 or more vertebrae (2)(R);

68(4), dorsal and anal fins rounded anteriorly;

88(1), 18 or more dorsal ridge scales (R).

With ACCTRAN it presents character 42(2)(two steps), and lacks characters 6 and 68.

Node 10: Pycnodontoidea n. rank
3(0), dorsal prominence absent (R);
24(3), dermohyomandibular present (AU), primitively with a small ornamented surface (2);
25(2), opercular process of hyomandibular absent (AU);
32(3), premaxillary and dentary teeth very flattened, fully incisiform;
42(3), three dentary teeth (2);
54(1), neural and haemal adjacent arcocentra in contact, primitively simple;
55(2), sagittal flanges anterior only, primitively large and long (AU);
65(2), dorsal fins at 50%-59% of standard length;
71(2), two urodermals;
83(0), nuchal plates absent (R);
93(2), spines on each dorsal ridge scale of increasing size in cephalocaudal sense;
94(3), 15 to 17 ventral keel scales;
101(3), five or six post-cloacal ventral keel scales;
102(3), one anterior modified cloacal scale;
103(4), one posterior modified cloacal scale.
With ACCTRAN it also presents characters 6(0)(R) and 88(3), lacks characters 25 and 42, and character 101 presents state 4 (two steps).

Node 11: family Coccodontidae Berg, 1940
18(0), extrascapular not fused to parietal (R);
53(1), arcocentra surrounding notochord partially (C);
58(1), six to eight epichordal elements in caudal endoskeleton (2) (C);
59(1), hypochordal elements in caudal endoskeleton enlarged (C);
66(1), 20 to 29 dorsal axonosts;
86(2), first dorsal ridge scale larger than subsequent dorsal ridge scales (C);
88(5), one or two dorsal ridge scales (3);
94(5), two or three ventral keel scales (2);
101(6), one post-cloacal ventral keel scale (3).
With ACCTRAN it also presents characters 4(0)(R), 10(1), 36(1), 38(1), 46(3), 63(1), 70(0)(R), 76(2), 82(1), 90(1), and 96(3), while characters 88 and 101 only involve two steps.

Node 12: *Coccodus* Pictet, 1850 + *Ichthyoceros* Gayet, 1984
5(0), mouth gape subhorizontal (R);
7(0), caudal pedicle differentiated (R);
36(4), vomerine teeth triangular in contour (AU);
38(1), three vomerine tooth rows (C);
42(4), two dentary teeth (C);
51(1), groove on vomerine and prearticular teeth present (C);
64(1), pelvic fins at more than 55% of standard length;
66(0), less than 20 dorsal axonosts (R);
70(5), nine or less anal axonosts.
With ACCTRAN it also presents characters 16(1), 47(0)(R), 52(3), 62(3), 69(3), 77(2), 82(2), 93(3), and 98(3), and lacks characters 38 and 42.

Node 13: family Pycnodontidae Agassiz, 1833 *sensu* Nursall 1996b
14(1), parietal process present (AU);
22(1), ornamentation of infraorbitals present only on the posteriormost one;
23(2), suborbitals absent;
35(3), maxilla edentulous, reniform;
42(4), two dentary teeth (C);
56(3), seven to 10 autogenous anterior neural spines;
75(2), ossification primitively complete in ventral scales and incomplete in dorsal scales;
81(2), ornamentation made of reticulation;
98(2), spines on each ventral keel scale in contact with each other.
With ACCTRAN it also presents character 91(2), and it lacks characters 23, 35, 42, and 56.

Node 14: genus *Macromesodon* Blake, 1905
67(1), dorsal axonost not supporting lepidotrichium (free axonost) present (C);
68(3), dorsal and anal fins rounded in the centre;
89(1), dorsal ridge scales in point contact;
91(2), spines placed on posterior region of midline of dorsal ridge scales.
With ACCTRAN it also presents characters 88(2) and 101(3), and it lacks characters 67 and 91.

Node 15: *Macromesodon macropterus* (Agassiz, 1834) + *M. bernissartensis* Traquair, 1911
49(0), crenulations on vomerine and prearticular teeth absent (R);
96(1), one to three spines on ventral keel scales.
With ACCTRAN it also presents character 81(1).

Node 16: Pycnodontidae minus *Macromesodon*
69(2), anal fin at 60-69% of standard length;
88(3), 10 to 14 dorsal ridge scales;
92(2), spines on each dorsal ridge scale in contact with each other;
101(4), three or four post-cloacal ventral keel scales.
With ACCTRAN it also presents characters 24(4), 73(3), and 90(2), and it lacks characters 88 and 101.

Node 17: node 16 minus *Stenamara* Poyato-Ariza & Wenz, 2000
58(2), four or five epichordal elements in caudal endoskeleton;
70(2), 30 to 39 anal axonosts;
73(3), caudal fin with distal border concave;
91(2), spines on dorsal ridge scales placed in the posterior region of the midline;
101(5), two post-cloacal ventral keel scales;
103(3), two modified posterior cloacal scales.
With ACCTRAN it also presents characters 2(2), 59(1), and 67(0)(R), and it lacks characters 73 and 91.

Alternative node C1: *Anomoeodus* Forir, 1887 + *Stemmatodus* Heckel, 1854
46(3), 10 or more teeth in main prearticular tooth row;
81(2), ornamentation made of strong reticulation.
With ACCTRAN it also presents characters 1(1)(R), 35(4), 36(1), 39(2), 56(4), 90(3), and 94(4).

Alternative node C2: *Anomoeodus + Ocloedus sub-discus* n. comb.

51(1), groove on vomerine and prearticular teeth present (C).

With ACCTRAN it also presents characters 60(1)(C)(R), 64(1), 73(5), and 89(1).

Node 18: node 17 minus *Stemmatodus*

2(2), dorsal apex in the point of insertion of the dorsal fin;

4(2), ventral apex in the point of insertion of the anal fin;

59(1), hypochordal elements in caudal endoskeleton enlarged (C);

65(2), dorsal fin at 50-59% of standard length;

67(0), free dorsal axonost absent (R);

68(1), dorsal and anal fins falcate to acuminate;

103(3), two post-cloacal scales (this character is present in this node only when *Anomoeodus* appears as the sister-group of *Ocloedus*).

With ACCTRAN it also presents character 12(1), and it lacks character 103.

Node 19: node 18 minus *Ocloedus* n. gen.

66(3), 40 to 49 dorsal axonosts;

71(3), one urodermal present;

72(0), 20 to 25 caudal fin rays (R);

81(1), ornamentation made of small ridges;

90(0), 91(0), 92(0), and 93(0), no spines on dorsal ridge scales (R);

98(1), spines on each ventral keel scale separated from each other.

With ACCTRAN it also presents characters 24(3), 49(0)(R), and 52(1).

Node 20: node 19 minus *Tepexichthys* Applegate, 1992

49(0), crenulations on vomerine and prearticular teeth absent (R);

86(2), first dorsal ridge scale larger than subsequent dorsal ridge scales;

95(1), ventral keel scales in point contact with each other (with alternative node D1).

With ACCTRAN it also presents characters 12(0)(R), 39(2), 53(1), 70(3), 95(1) (with alternative node D2), and 102(2), and it lacks character 49.

Alternative node D1: Node 20 minus Proscinetinae n. rank

5(0), mouth gap (sub)horizontal (R);

53(1), neural and haemal corresponding arcocentra constricting notochord partially;

70(3), 40-49 anal axonosts.

With ACCTRAN it also presents characters 1(1)(R), 4(0)(R), 21(3), 22(0)(R), 46(3), 52(2), 73(5), 94(4), and 104(1), and it lacks characters 53 and 70.

Character distribution of node 22 with this alternative

7(0), caudal pedicle present (R);

59(2), hypochordal elements in caudal endoskeleton hypertrophied;

66(5), 60 or more dorsal axonosts (2);

73(5), caudal fin double emarginated;

89(1), dorsal ridge scales in point contact with each other.

With ACCTRAN it also presents characters 71(4) and 81(3), and it lacks characters 73 and 89.

Alternative node D2: node 20 minus *Iemanja* Wenz, 1989

86(2), first dorsal ridge scale larger than subsequent ridge scales;

89(1), dorsal ridge scales in point contact with each other;

95(1), ventral keel scales in point contact with each other.

With ACCTRAN it also presents character 7(0)(R), and it lacks characters 86 and 95.

Character distribution of node 22 with this alternative

5(0), mouth gap (sub)horizontal (R);

7(0), caudal pedicle present (R);

59(2), hypochordal elements in caudal endoskeleton hypertrophied;

66(5), 60 or more dorsal axonosts (2);

73(5), caudal fin double emarginated.

With ACCTRAN it also presents characters 4(0)(R), 21(3), 22(0)(R), 46(3), 71(4), 81(3), 94(4), and 104(1), and it lacks characters 5 and 7.

Node 21: subfamily Proscinetinae n. rank

38(1), three vomerine tooth rows (C);

39(2), eight or nine teeth in main vomerine tooth row;

40(1), alternation on teeth of main vomerine tooth row present (AU);

52(1), 30 to 34 vertebrae (R);

89(2), dorsal ridge scales separated from each other (2);

94(2), 18 to 21 ventral keel scales;

95(1), ventral keel scales in point contact with each other;

97(2), spines on ventral keel scales in the posterior region of the midline (C).

With ACCTRAN it also presents characters 5(1), 67(1) and 103(2), and it lacks characters 39, 52, and 97.

Node 22: crown-group plus *Coelodus saturnus* Heckel, 1854 (character distribution in strict consensus tree)

5(0), mouth gape subhorizontal (R);

7(0), caudal pedicle differentiated (R);

59(2), hypochordal elements in caudal endoskeleton hypertrophied;

66(5), 60 or more dorsal axonosts (2);

73(5), double emarginated caudal fin;

89(1), dorsal ridge scales in point contact with each other.

With ACCTRAN it also presents charaters 4(0)(R), 21(3), 22(0)(R), 46(3), 71(4), 81(3), 94(4), and 104(1), and it lacks characters 5 and 89.

Node 23: crown-group Pycnodontiformes (Pycnodontinae n. rank + Nursalliinae n. rank)

4(0), ventral apex absent (R);

22(0), infraorbital ornamentation present in all infraorbitals (R);

39(1), seven or less teeth in main vomerine tooth row;

53(2), dorsal and haemal corresponding arcocentra surrounding the notochord completely;

56(4), six or less autogenous anterior neural spines;

104(1), bifid scale in cloaca present (AU).

With ACCTRAN it also presents characters 36(1), 52(2), 54(2), 57(3), and 70(4), and it lacks characters 4, 22, 39, and 104.

Node 24: subfamily Pycnodontinae n. rank

12(1), dermocranial fenestra present (C);

19(1), endocranium posteriorly exposed (AU);

24(4), preopercular of similar size to the expanded ornamented portion of the dermohyomandibula (C);

54(2), neural and haemal adjacent arcocentra in complex contact (C);

58(1), six to eight epichordal elements in caudal endoskeleton (C);

75(3), dorsal scales incompletely ossified, reduced to scale bars (C);

87(1), scutellum-like contour scales present, dorsal only (AU);

88(4), seven to nine dorsal ridge scales;

94(4), 10 to 14 ventral keel scales;

97(2), spines on ventral keel scales in the posterior region of the midline (C).

With ACCTRAN it also presents character 68(1)(R), and lacks characters 54 and 94.

Node 25: subfamily Nursalliinae n. rank

9(3), frontals curved, very broad;

32(2), premaxillary and dentary teeth robust, barely incisiform (C);

36(1), vomerine teeth (sub)circular in contour;

54(3), neural and haemal adjacent arcocentra in hypercomplex contact;

57(3), last neural spine not supporting precurrent caudal fin rays vestigial;

70(4), 50 or more anal axonosts (C);

73(6), caudal fin vertical;

76(2), body scales present in the abdominal region plus part of the caudal region.

With ACCTRAN it also presents characters 10(1)(C), 35(1), 46(2), 60(3), 72(3), and 97(0)(R), and it lacks characters 57, and 70.

Node 26: Nursalliinae minus *Nursallia veronae* Blot, 1987

72(4), 36 or more caudal principal fin rays;

88(2), 15-17 dorsal ridge scales (R);

95(0), ventral keel scales in close contact with each other (R).

With ACCTRAN it also presents characters 90(1), 91(1), 92(1), and 94(3).

Node 27: node 26 minus *Nursallia ? gutturosum* (Arambourg, 1954)

57(2), last neural spine not supporting caudal endoskeleton, less than half as long as preceding spines;

65(0), dorsal fin at 60%-69% of standard length (R);

69(1), anal fin at 50%-59% of standard length;

77(1), scales rows in different directions (C);

90(1), one to two spines on dorsal ridge scales;

91(1), spines on dorsal ridge scales distributed all along the border (centered if only one spine present);

92(1), spines on dorsal ridge scales separated from each other.

With ACCTRAN it also presents characters 2(0)(R), 52(2)(R)(2 steps), 60(2), 79, and 99(0)(R), and it lacks characters 90, 91, and 92.

Node 28: *Nursallia ? goedeli* (Heckel, 1854) + *Palaeobalistum* Blainville, 1818

72(3), 26-35 caudal principal fin rays (C);

75(0), ossification complete in all scales (R)(2);

76(1), scales distributed on all body except caudal pedicle (R);

81(3), ornamentation made of ridges.

With ACCTRAN it also presents characters 1(1)(R), 21(1)(R)(two steps), 71(2)(R)(two steps), 94 (2)(R), 96(3), and 97(1), and it lacks character 81.

Alternative node for the genus *Nursallia* Blot, 1987 (*N. veronae* + *N. gutturosum* when *N. ? goedeli* is removed)

7(0), caudal pedicle differentiated (R);

9(3), frontals curved, very broad (AU);

21(3), anterior infraorbital enlarged (C);

36(1), vomerine teeth (sub)circular in contour;

53(2), neural and haemal corresponding arcocentra surrounding notochord completely;

54(3), neural and haemal adjacent arcocentra in hypercomplex contact (AU);

57(3), last neural spine not supporting precurrent caudal fin rays vestigial;

60(3), six to eight hypochordal elements in caudal endoskeleton (C);

73(6), caudal fin vertical (AU).

TERMINAL TAXA

***Abdobalistum* n. gen.**

2(1), dorsal apex placed before the point of insertion of the dorsal fin;

7(1), caudal pedicle not differentiated;

21(3), anterior infraorbital enlarged (C);

49(1), crenulations on vomerine and prearticular teeth occasionally present, weak (C);

51(1), groove on vomerine and prearticular teeth present (C);

52(0), 35 or more vertebrae (R);

53(1), arcocentra surrounding notochord partially (C);

54(2), dorsal and ventral adjacent arcocentra in complex contact (C);

68(0), dorsal and anal fins strip-like (R);

71(4), urodermals absent (C);

73(2), caudal fin with distal border convex;
75(3), all body scales incompletely ossified, reduced to bar scales (C);
87(2), scutellum-like contour scales present, ventral only (AU);
89(0), dorsal ridge scales in close contact with each other (R);
96(0)(two steps)(R), 97(0), 98(0), 99(0), spines on ventral keel scales absent (R);
100(1), several scales attached to contour scales (AU).
With ACCTRAN it lacks characters 21, 52, 68, 71, 97, and 99.

Anomoeodus Forir, 1887
43(3), prearticular teeth sigmoid to drop-shaped, with tapering medial edge, obliquely set (C);
44(2), prearticular teeth anteriorly patchy, posteriorly arranged in rows (2);
45(4), five or six prearticular tooth rows;
46(3), 10 or more teeth in main prearticular tooth row;
51(1), groove on vomerine and prearticular teeth present (C);
96(1), one to three spines on ventral keel scales;
102(0), no modified anterior cloacal scales (R).
With ACCTRAN the characters are the same.

Apomesodon gibbosus n. comb.
3(2), dorsal prominence in obtuse angle, posterior border (sub)horizontal;
4(0), ventral apex absent (R);
18(0), extrascapular not fused to parietal (R);
36(1), vomerine teeth (sub)circular in contour;
60(1), 12 to 13 hypochordal elements in caudal endoskeleton (C);
70(0), 10 to 19 anal axonosts (R);
73(4), caudal fin with straight distal border;
74(1), fringing fulcra present, small and scarce;
94(1), 22 or more ventral keel scales.
With ACCTRAN the characters are the same.

Apomesodon surgens n. gen., n. sp.
1(3), body depth more than 100% of standard length;
90(2), three or four spines on dorsal ridge scales;
96(3), seven or more spines on ventral keel scales (C).
With ACCTRAN the characters are the same.

Arduafrons Frickhinger, 1991
6(1), prognathism present;
46(3), 10 or more teeth in main prearticular row;
47(0), coronoid process low, curved (R);
49(0), crenulations on vomerine and prearticular teeth absent (R);
52(0), 35 or more vertebrae (R);
62(1), cleithrum curved, anteroventral limb subhorizontal, slightly expanded;
65(3), dorsal fin at 70-79% of standard length;
66(3), 40 to 49 dorsal axonosts;
70(2), 30 to 39 anal axonosts;
72(3), 26 to 35 caudal principal fin rays (C);
73(4), caudal fin with straight distal border;
79(1), double scale rows present;
96(3), seven or more spines on ventral keel scales (C).

With ACCTRAN it also presents characters 71 (0)(R) and 88(1), and it lacks characters 6, 49, 72, and 96.

Brembodus Tintori, 1981
3(2), dorsal prominence in obtuse angle, with posterior border subhorizontal;
30(1), two relatively large branchiostegal rays, in contact with each other;
49(0), crenulations on vomerine and prearticular teeth absent (R);
53(2), arcocentra completely surrounding notochord (2);
54(1), neural and haemal adjacent arcocentra in simple contact;
60(3), six to eight hypochordal elements in caudal endoskeleton (C);
65(1), dorsal fin placed at 40-49% of standard length;
67(1), dorsal axonost not supporting lepidotrichium ("free axonost" present) (C);
68 (1&4), dorsal fin anteriorly rounded, anal falcate;
71(1), urodermals differentiated into a series of three or more of them;
84(1), dorsal spine present (AU);
101(5), two post-cloacal ventral keel scales (2).
With ACCTRAN it also presents character 23(1), and it lacks characters 53, 54, 60, 68, and 71.

Coccodus Pictet, 1850
1(0), body shape fusiform (R)(2);
2(0), dorsal apex absent (R);
4(0), ventral apex absent (R);
16(1), supraoccipital spine present, single and robust (AU);
39(2), eight or nine teeth in main vomerine tooth row;
45(1), two prearticular tooth rows;
47(3), coronoid process low with straight, strengthened dorsal border (AU);
52(3), 24 or less vertebrae;
62(4), cleithrum with four limbs (AU);
63(1), one hypertrophied spine on cleithrum present (AU);
68(5), anal fin square in shape (AU);
75(4)(four steps), 76(4), 77(3), body scales absent (AU);
85(2), 86(3), 87(4), 88(6), 89(3)(three steps), 90(5), 91(4), 92(3), 93(4), 94(6), 95(2)(two steps), 96(4)(two steps), 97(3), 98(3), 99(3), 100(2), 101(7), dorsal and ventral contour scales absent (AU);
102(4), 103(6), cloacal scales absent (AU).
With ACCTRAN it also presents characters 10(0)(R) and, 46(2), and it lacks characters 4, 16, 52, 63, 93, and 98; character 76 has two steps, and 96, one step.

Coelodus saturnus Heckel, 1854
1(1), body shape intermediate, maximum body height 40-70% of standard length (R);
43(4), prearticular teeth extremely elongated (AU);
46(3), 10 or more teeth on main prearticular tooth row;
51(1), groove on vomerine and prearticular teeth present (C);
52(1), 30 to 34 vertebrae;
61(1), diastema in caudal endoskeleton present (AU);
89(2), dorsal ridge scales separated from each other.

With ACCTRAN it also presents character 39(3), and it lacks characters 46 and 52.

? *Eomesodon barnesi* (Woodward, 1906)

3(4), dorsal prominence curved, dorsally oriented;
4(2), ventral apex in the point of insertion of the anal fin;
6(1), prognathism present;
64(2), pelvic fin at less than 45% of standard length;
65(3), dorsal fin at 70-79% of standard length;
68(3), dorsal and anal fins rounded in the centre;
69(2), anal fin at 60-69% of standard length.
With ACCTRAN it lacks character 6.

Eomesodon liassicus (Egerton, 1855)

3(3), dorsal prominence curved, anteriorly oriented (AU);
21(0), infraorbitals as a row of plates (R);
42(4), two dentary teeth (2);
60(0), 14 or more hypochordal elements in caudal endoskeleton (2)(R);
70(0), 10 to 19 anal axonosts (R);
96(0) and 97(0), no spines on ventral keel scales (R).
With ACCTRAN it lacks character 42.

Gibbodon Tintori, 1981

9(0), frontals rectangular and long (R);
20(0), anterior portion of infraorbitary sensory canal surrounding the orbit (R) (C);
21(0), infraorbitals as a row of plates (R);
23(2), suborbitals absent;
29(0), gular as a large plate (R);
31(0), premaxillary process profound (R);
33(1), crown of premaxillary tooth bifurcated (AU);
38(1), three vomerine tooth rows (C);
42(1), five dentary teeth;
66(0), less than 20 dorsal axonosts (2)(R);
70(5), nine or less anal axonosts;
90(2), three or four spines on dorsal ridge scales;
96(3), seven or more spines on ventral keel scales (C).
With ACCTRAN it also presents characters 68(0)(R) and 71(0)(R), and it lacks characters 23 and 96.

Gyrodus Agassiz, 1833

30(2), two branchiostegal rays, thin and separated;
48(1), central papilla on vomerine and prearticular teeth present (AU);
54(1), neural and haemal adjacent arcocentra in simple contact;
55(4), anterior and posterior sagittal flanges with strengthened margins (AU);
56(2), 10 or more anterior neural spines autogenous (AU);
59(1), hypochordal elements of caudal endoskeleton enlarged;
64(2), pelvic fin at less than 45% of standard length;
68(1), dorsal and anal fins falcate;
71(3), one urodermal (3);
73(1), caudal fin stalked;
88(2), 15 to 17 dorsal ridge scales.
With ACCTRAN it also presents character 72(0)(R), and it lacks characters 30 and 88, and character 71 has two steps.

Ichthyoceros Gayet, 1984

6(1), prognathism present;
10(1), paired prefrontal bone present (C);
11(2), compound frontal spine present (AU);
16(2), compound supraoccipital spine present (AU);
43(3), prearticular teeth sigmoid to drop-shaped, with tapering medial edge, obliquely set (C);
46(3), 10 or more teeth in main prearticular tooth row;
47(0), coronoid process low, curved (R);
62(3), cleithrum with three limbs (AU);
63(3), about 50 small spines on cleithrum present (AU);
69(3), anal fin at 80-89% of standard length;
71(0), urodermals not differentiated (R)(2);
72(1), less than 10 caudal fin rays (AU);
76(0), scales covering the whole body (R)(3);
77(2), scales not arranged in rows (AU);
81(4), ornamentation of small spines on dermal skull bones;
82(2), several spines present on body scales (AU);
90(1), one or two spines on dorsal ridge scales;
96(1), one to three spines on ventral keel scales.
With ACCTRAN it also presents character 4(1), and it lacks characters 10, 46, 47, 62, 69, 77, 82, and 90.

Iemanja Wenz, 1989

1(1), body shape intermediate, maximum body height 40-70% of standard length (R);
5(0), mouth gape subhorizontal (R);
6(1), prognathism present;
26(1), condyle in articular head of dermohyomandibular present (C);
35(5), maxilla unornamented, elongated oval (AU);
36(3), vomerine teeth reniform in contour (AU);
37(2), vomerine teeth anteriorly patchy, posteriorly arranged in rows (AU);
43(1), prearticular teeth circular in contour;
44(0), prearticular teeth completely patchy, not arranged in rows (R);
54(4), neural and haemal adjacent arcocentra expanded and imbricate (AU);
55(3), sagittal flanges anterior and posterior, without strenghtened margins (AU);
60(3), six to eight hypochordal elements in caudal endoskeleton (C);
65(0), dorsal fin at 60-69% of standard length (R).
With ACCTRAN it also presents characters 52(2) and 89(0)(R), and it lacks character 5.

Macromesodon bernissartensis Traquair, 1911

64(1), pelvic fin at more than 55% of standard length;
65(1), dorsal fin at 40-49% of standard length;
98(1), spines on each ventral keel scale separated from each other.
With ACCTRAN the characters are the same.

Macromesodon cf. *M. bernissartensis*

46(3), 10 or more teeth in main prearticular tooth row;
47(2), coronoid process high, club-shaped (C);
102(2), two anterior modified cloacal scales.
With ACCTRAN the characters are the same.

Macromesodon macropterus (Agassiz, 1834)

2(2), dorsal apex in the point of insertion of dorsal fin;
4(0), ventral apex absent (R);
39(2), eight or nine teeth in principal vomerine tooth row;
68(2), dorsal and anal fins of sigmoid outline;
70(2), 30 to 39 anal axonosts;
71(3), one urodermal;
73(5), caudal fin double emarginated;
81(1), ornamentation by ridges;
94(2), 18 to 21 ventral keel scales.
With ACCTRAN it lacks character 81.

Mesturus Wagner, 1862

13(1), parietal divided (AU);
24(2), one large preopercular plus one small ornamented plate;
35(2), maxilla ornamented and elongated;
43(1), prearticular teeth circular;
45(4), four prearticular tooth rows;
46(3), 10 or more teeth on main prearticular tooth row;
50(1), central, conspicuous ridge on vomerine and prearticular teeth present (AU);
62(1), cleithrum with anteroventral lim subhorizontal and slightly expanded;
69(2), anal fin at 60-69% of standard length;
72(3), 26 to 35 caudal principal fin rays (C);
77(1), scale rows in different directions (C);
78(1), jagged suture between scales of the same row (AU);
79(1), double scale rows present;
90(2), three or four spines on dorsal ridge scales;
96(3), seven or more spines on ventral keel scales (C).
With ACCTRAN it lacks characters 51, 62, and 90.

Micropycnodon Hibbard & Graffham, 1945

20(1), anterior portion of infraorbital sensory canal descending towards the ethmoid region;
36(2), vomerine teeth oval in contour;
39(1), seven or less teeth in principal vomerine tooth row;
46(1), seven or less teeth on principal prearticular tooth row;
47(2), coronoid process high, club-shaped (C);
With ACCTRAN it lacks character 46.

Neoproscinetes Figueiredo & Silva Santos, 1987

2(1), dorsal apex placed before the point of insertion of the dorsal fin;
4(1), ventral apex placed before the point of insertion of the anal fin;
7(0), caudal pedicle differentiated (R);
26(1), condyle in articular head of hyomandibular present (C);
42(3), three dentary teeth (R);
46(1), seven or less teeth on main prearticular tooth row;
47(2), coronoid process high, club-shaped (C);
53(1), neural and haemal corresponding arcocentra surrounding notochord partially;
54(2), dorsal and ventral adjacent arcocentra in complex contact (C);
57(2), last neural spine not supporting precurrent caudal fin rays less than half as long as preceding ones;

60(3), six to eight hypochordal elements in caudal endoskeleton (C);
68(0), dorsal and anal fins strip-like (R);
70(2), 30 to 39 anal axonosts;
90(1), one or two spines on dorsal ridge scales;
91(3), spines on dorsal ridge scales placed on anterior region of the midline of the scale;
92(1), spines on each dorsal ridge scale separated from each other;
93(2), spines on each dorsal ridge scale of increasing size in cephalocaudal sense.
With ACCTRAN the characters are the same.

Nursallia ? goedeli (Heckel, 1854)

60(3), six to eight hypochordal elements in caudal endoskeleton (C);
71(2), two urodermals.
With ACCTRAN it lacks character 71.

Nursallia ? gutturosum (Arambourg, 1954),

10(1), paired prefrontal bone present (C);
18(0), extrascapular not fused to parietal (R);
20(0), anterior portion of the infraorbital sensory canal surrounding the orbit (R)(C);
21(3), anterior infraorbital enlarged (C);
35(1), maxilla ornamented, ovoid;
39(1), seven or less teeth in main vomerine tooth row;
60(3), six to eight hypochordal elements in caudal endoskeleton (C).
With ACCTRAN it presents character 81(1), and it lacks characters 10, 21, 35, and 60.

Nursallia veronae Blot, 1987

38(1), three vomerine tooth rows (C);
60(3), six to eight hypochordal elements in caudal endoskeleton (C);
71(4), urodermals absent (C);
72(3), 26 to 35 principal caudal fin rays (C);
75(1), ossification of scales complete in abdominal scales, incomplete in caudal scales (R);
87(3), scutellum-like contour scales present, dorsal and ventral (AU);
94(4), 10 to 14 ventral keel scales;
101(4), three or four post-cloacal ventral keel scales.
With ACCTRAN it lacks characters 60, 71, 72, and 94.

Ocloedus subdiscus n. comb.

2(2), dorsal apex in the point of insertion of the dorsal fin;
12(1), dermocranial fenestra present (C);
24(4), preopercular of similar size to expanded ornamented portion of the dermohyomandibular (C);
51(1), groove on vomerine and prearticular teeth present (C);
59(1), hypochordal elements of caudal endoskeleton enlarged;
60(1), 12 or 13 hypochordal elements in caudal endoskeleton (C);
64(1), pelvic fins at more than 55% of standard length;
68(1), dorsal and anal fins falcate to acuminate;
73(5), caudal fin double emarginated;
81(3), ornamentation made of tubercles;

89(1), dorsal ridge scales in point contact with each other;

90(2), three or four spines on dorsal ridge scales;

96(3), seven or more spines on ventral keel scales;

97(2), spines on ventral keel scales placed in the posterior region of the midline.

With ACCTRAN it lacks characters 2, 24, 59, 68, and 90.

Oropycnodus n. gen.

4(1), ventral apex present before the point of insertion of the anal fin;

7(1), caudal pedicle not differentiated;

28(2), opercular bone extremely reduced (AU);

39(1), seven or less teeth in main vomerine tooth row;

46(1), seven or less teeth in main prearticular tooth row;

49(1), crenulations on vomerine and prearticular teeth occasionally present, weak (C);

68(4), dorsal and anal fins rounded anteriorly;

70(4), 50 or more anal axonosts (C);

98(2), spines on each ventral keel scale in contact with each other;

102(2), two anterior modified cloacal scales;

104(2), bifid scale in cloaca present, plus several comma-shaped scales (AU);

105(1), post-cloacal notch present (AU).

With ACCTRAN it also presents characters 21(2), 36(2), 57(1), and 71(3), and it lacks characters 70 and 102.

Palaeobalistum Blainville, 1818

1(1), body shape intermediate, maximum body height 40-70% of standard length (R);

2(0), dorsal apex absent (R);

21(1), infraorbitals as a mosaic of small plates;

59(1), hypochordal elements of caudal endoskeleton enlarged;

76(0), scales covering the whole body (R)(3);

79(1), double scale rows present;

94(2), 18 to 21 ventral keel scales;

96(3), seven or more spines on ventral keel scales (C).

With ACCTRAN it only presents characters 59 and 76.

Paramesturus Taverne, 1981

No characters have been found with DELTRAN or with ACCTRAN.

Proscinetes Gistl, 1848

30(1), two large branchiostegal rays in contact;

53(0), neural and haemal corresponding arcocentra not surrounding notochord (R);

64(1), pelvic fins at more than 55% of standard length;

67(1), free dorsal axonost present (C);

71(2), two urodermals (R);

88(2), 15 to 17 dorsal ridge scales (R);

102(2), two modified anterior cloacal scales;

103(2), three modified posterior cloacal scales.

With ACCTRAN it also presents character 53(0)(R), and it lacks characters 67, 102, and 103.

Pycnodus Agassiz, 1833

1(1), body shape intermediate, maximum body height 40-70% of standard length (R);

2(1), dorsal apex placed before the point of insertion of the dorsal fin;

18(0), extrascapular not fused to parietal (R);

21(3), anterior infraorbital enlarged (C);

36(1), vomerine teeth circular in contour;

46(3), 10 or more teeth in main prearticular tooth row;

57(3), last neural spine not supporting precurrent caudal fin rays vestigial (2) (C);

65(1), dorsal fin insertion at 40-49% of standard length;

66(4), 50 to 59 dorsal axonosts;

68(0), dorsal and anal fins strip-like (R);

69(1), anal fin insertion at 50-59% of standard length;

71(4), urodermals absent (C);

81(2 & 3), ornamentation made of reticulation and tubercles;

96(3), seven or more spines on ventral keel scales;

103(4), one post-cloacal ventral keel scale.

With ACCTRAN it also presents characters 70(3) and 102(3), and it does not present characters 21, 36, 46, 57, 68, 71, and 81.

Stemmatodus Heckel, 1854

1(1), body shape intermediate, maximum body height 40-70% of standard length (R);

4(0), ventral apex absent (R);

24(4), preoperculum of similar size to expanded ornamented region of the dermohyomandibular (C);

35(4), maxilla unornamented, straight oral border (AU);

36(1), vomerine teeth (sub)circular in contour;

39(2), eight or nine teeth in principal vomerine tooth row;

46(3), 10 or more teeth in principal prearticular tooth row;

56(4), six or less anterior autogenous neural spines;

65(0), dorsal fin at 60%-69% of standard length (R);

67(1), free dorsal axonost present (C);

75(3), all body scales incompletely ossified, reduced to bar scales (C);

94(4), 10 to 14 ventral keel scales;

103(5), no posterior modified cloacal scales, posterior part of anal notch supported by a rib (AU).

With ACCTRAN it also presents characters 2(1), 59(0)(R), 68(0)(R), 90(3), and it lacks character 24.

Stenamara Poyato-Ariza & Wenz, 2000

1(3), body deep, maximum body height more than 100% of standard length;

3(4), dorsal prominence curved, dorsally oriented;

45(1), two prearticular tooth rows;

60(3), six to eight hypochordal elements in caudal endoskeleton (C);

64(2), pelvic fins insertion at less than 45% of standard length;

65(0), dorsal fin at 60%-69% of standard length (R);

67(1), free dorsal axonost present (C);

90(2), three or four spines on dorsal ridge scales;

94(2), 18 to 21 ventral keel scales.

With ACCTRAN it also presents character 91(1), and it lacks characters 67 and 90.

Tepexichthys Applegate, 1992

12(1), dermocranial fenestra present (C);

22(2), ornamentation absent in all infraorbitals;

34(1), three premaxillary teeth (R);
36(1), vomerine teeth (sub)circular in contour;
42(3), three dentary teeth (R);
47(2), coronoid process high, club-shaped (C);
49(2), strong crenulations present in most vomerine and prearticular teeth (C);
52(1), 30 to 34 vertebrae (R);
58(1), six to eight epichordal elements in caudal endoskeleton (R);
66(4), 50 to 59 dorsal axonosts;
69(1), anal fin inserted at 50 to 59% of standard length;
88(2), 15 to 17 dorsal ridge scales (R).
With ACCTRAN it lacks character 52.

Trewavasia White & Moy-Thomas, 1941
4(0), ventral apex absent (R);
5(2), mouth gape subvertical, opening downward (AU);
10(1); paired prefrontal bone present (C);
11(1), front spine present, simple (AU);
13(2), parietal absent (AU);
17(1), extrascapular hypertrophied (AU);
20(0), anterior portion of infraorbital sensory canal surrounding the orbit (R)(C);
23(2), suborbitals absent as independent ossifications;

30(1), two branchiostegal rays, large, in contact with each other;
32(1), columnar to hook-shaped premaxillary and dentary teeth;
34(1), three premaxillary teeth;
36(1), vomerine teeth circular in contour;
43(1), prearticular teeth circular in contour;
46(3), 10 or more teeth in main prearticular tooth row;
49(0), crenulations on vomerine and prearticular teeth absent (R);
60(1), 12 or 13 hypochordal elements in caudal endoskeleton (C);
63(2), about 10 spines on cleithrum (AU);
68(4), dorsal and anal fins rounded anteriorly;
70(0), 10 to 19 anal axonosts (R);
71(4), urodermals absent (C)(2);
76(2), scales on abdominal region plus part of the caudal region;
82(1), one large spine on every scale present (AU);
90(4), dorsal ridge spines with serrated midline (AU);
96(1), two or three large spines on ventral keel scales.
With ACCTRAN it also presents character 42(3), and lacks characters 4, 10, 23, 36, 46, 68, 70, 76, 82, and 96.