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45

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CONTENTS/INHALT

Zitteliana	A 45	218 Seiten	München, 30.12.2005	ISSN 1612-412X

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Cover illustration: Ostracod *Callistocythere intricatoides* (Ruggieri, 1953) from the Thyrrenian of Altinova (Turkey). Left: Right valve, external view, BSPG 1980 X 1313 (length 0.640 mm). Right: Left valve, external view, BSPG 1980 X 1314 (length 0.646 mm). SEM Photograph: R. Matzke-Karasz (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

Umschlagbild: Ostrakode *Callistocythere intricatoides* (Ruggieri, 1953) aus dem Thyrrenium von Altinova (Türkei). Links: Rechte Klappe, Außenansicht, BSPG 1980 X 1313 (Länge 0,640 mm). Rechts: Linke Klappe, Außenansicht, BSPG 1980 X 1314 (Länge 0,646 mm). REM-Foto: R. Matzke-Karasz (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

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A comprehensive study of the skull and dentition of pycnodont fishes

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Abstract

The Pycnodontiformes is a monophyletic group of predominantly Mesozoic fishes with mostly deep and laterally compressed bodies. They are highly specialised with regard to their prey. This paper summarises the current knowledge of pycnodontiform head morphology and provides a detailed account of their dermato- and endocranial and visceral skeletal anatomy and dental morphology based on articulated and isolated material. The histology of pycnodontiform crushing teeth is considered. The differences in the ultrastructure of teeth between pycnodontiforms and teleosts support the interpretation that no closer relationships exist between both groups. The dentition of pycnodontiforms is characterized by considerable intrageneric and even intraspecific variation. Biometric characters, generally assumed to be independent of other characters, are applied to pycnodontiform dentitions and teeth. However, the biometric data and the corresponding aw/l-indices show that this method has great potential but that more data is necessary. These data also help separating plesiomorphic and advanced groups. Stomach contents, the presence of incisiform grasping teeth, and a specialised branchial armature in several pycnodontiforms indicate that the guild of grazers and browsers (herbivorous morphospace) might already have been realised in the Mesozoic conversely to recently published hypotheses. The phylogenetic relationships of pycnodontiforms are explored based on cranial characters. The most noticeable result is that there are drastic differences when different data sets are utilized. The current analysis implies that skull morphology of pycnodontiform fishes alone cannot at present provide deeper insights into the phylogenetic interrelationships of pycnodontiforms. The differences between this and previous studies also indicate that there is still the need to search for more characters and employ different outgroups. The cranial anatomy of pycnodonts exemplifies general evolutionary trends such as reduction of dermal skull covering, increasing upper jaw mobility, and certain improvements in food gathering and processing. These changes, however, are not entirely in accordance with the phylogenetic hypothesis presented here.

Key words: Neopterygii, Pycnodontiformes, dermatocranium, endocranium, visceral skeleton, dentitions, tooth histology, phylogeny

Zusammenfassung

Die Pycnodontiformes sind eine monophyletische Gruppe überwiegend mesozoischer Fische mit hohem und seitlich komprimiertem Körper. Die vorliegende Arbeit fasst den gegenwärtigen Kenntnisstand ihrer Schädelanatomie zusammen. Darüber hinaus wird eine umfassende Darstellung mit neuen Informationen zur kranialen und dentalen Morphologie auf Grundlage artikulierter und isolierter Exemplare gegeben. Die Histologie der molariformen Zähne wird erstmals detailliert dargestellt und diskutiert. Unterschiede in der Anordnung der einzelnen Akrodinlagen zwischen Pyknodontiern und Teleosteern mit ähnlichen Zahnmorphologien sowie das Fehlen einer äußeren Glanzschicht belegen, dass beide Gruppen nicht näher verwandt sind. Die Bezahnung und die Anordnung der Zähne können innerhalb einer Gattung und Art sehr stark variieren. Diese Unterschiede bzw. Ähnlichkeiten lassen sich mit Hilfe biometrischer Merkmale darstellen. Diese biometrischen Daten und der aw/l-Index der preartikularen Bezahnungen haben großes Potential und zeigen allgemeine Trends auf. Mehr Daten müssen aber zukünftig gesammelt werden, um den Wert solcher Merkmale besser abschätzen zu können. Pyknodontiforme Fische sind selektive Beutegreifer. Magen/Darminhalte sowie der Besitz inzisiformer Greifzähne und spezialisierter Branchialzähne verschiedener Pyknodontier zeigen, dass die Gilde der Graser und Weider innerhalb von Fischvergesellschaftungen (herbivorer Morphospace) bereits im Mesozoikum verwirklicht war. Eine Hypothese phylogenetischer Beziehungen pyknodonter Fische basierend auf kranialen und dentalen Merkmalen wird erstmals vorgestellt und diskutiert. Allgemeine Trends in der Evolution der Schädelanatomie sind Reduzierungen von Schädelelementen, zunehmende Mobilität des Oberkiefers sowie Verbesserungen des Nahrungsaufnahmeapparates zur Verwertung von Nahrung.

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Schlüsselwörter: Neopterygii, Pycnodontiformes, Dermatocranium, Endocranium, Visceralskelett, Dentition, Zahnhistologie, Phylogenese

1. Introduction

Pycnodont fishes ("the pycnodontiforms") are a morphologically and ecologically distinctive group of actinopterygians. Some 650 nominal species have been described to date belonging to 38 genera (Kriwet 2001a). Ten genera are based entirely on isolated dentitions and only 78 species are known from skeletal remains. The evolutionary history of pycnodontiforms encompasses a period of approximately 175 million years (Delsate & Kriwet 2004; Kriwet & Schmitz 2005). They first appear in the Late Triassic (Norian) of the northern margins of the Tethys (what is now northern Italy and Austria) (Tintori 1981) and persist into the Palaeogene (Eocene) (e.g., Longbottom 1984). During the Jurassic they rapidly diversified and pycnodont remains are common in sediments of Late Jurassic and Cretaceous age. They had a nearly world-wide distribution in the Mesozoic and Palaeogene and are considered major components of marine fossil fish assemblages (Kriwet 2001b). The distribution and ecology of pycnodont fishes has been described in general terms only to date by Schaeffer (1970), Nursall (1996a), and Poyato-Ariza et al. (1998).

Pycnodonts are characterized by a deep, rounded, and laterally compressed body, a frontal flexure of the skull in profile view, a more or less prognathous snout, and elongated dorsal and anal fins, which together with the caudal fin form an effective ruder (Fig. 1). In their body shape they superficially resemble Recent coral reef fishes like butterfly fishes (Chaetodontidae), doctor fishes (Acanthuridae), and parrot fishes (Balistidae) (Kriwet 2001b).

Most pycnodonts are small to medium sized fishes with a standard body length of some 25 cm or less. Only a few large forms with a standard body length of more than 50 cm are known. *Gyrodus circularis* is the largest pycnodont with a standard body length up to 200 cm (Kriwet & Schmitz 2005). Since their first monographic description by Agassiz (1833-1844) pycnodont fishes have been distinguished as a monophyletic taxon ("la famille des Pycnodontes").

Up to now, hundreds of papers concerning pycnodonts have been published and their monophyly and interrelationships are well-established (e.g., Nursall 1996b; Poyato-Ariza & Wenz 2002, 2005). Nevertheless, no detailed comparative morphological account of the skull morphology is available. In addition, the homology and terminology of skull elements are still debated and consequently different names are applied to the same elements.

The main objectives of this study are to (1) summarize the current knowledge of pycnodontiform skull anatomy, (2) provide a detailed comparative description and new information of skull and dental morphologies applying homology criteria, (3) depict extensive illustrations of pycnodont dentitions and tooth morphologies, (4) discuss the value of biometric data of dentitions and teeth, and (5) propose a phylogenetic hypothesis of pycnodont interrelationships based on cranial features.

2. Material and Methods

More than 1000 specimens of pycnodonts belonging to about 144 species were examined. Most specimens were mechanically prepared, only few acid-prepared fossils using the transfer technique of Toombs & Rixon (1959) were available. Peels of dermal skull bones were prepared following the technique of Schultze (1966) to elucidate the surface structures of bones and scales without destroying the material. Several vertical and thin sections of vomerine and prearticular dentition and isolated teeth of "*Coelodus*", *Macromesodon*, and *Proscinetes* were prepared to gather information on the nature of tooth replacement modes and the microstructure of teeth. Sectioned teeth were etched five to ten seconds with 2N HCl and subsequently analysed with a scanning electron microscope.

Illustrations were prepared by the author unless otherwise indicated. Drawings of nearly all studied specimens were executed by viewing under dissection microscopes (mainly Wild FM5 and Wild MZ8) equipped with a camera lucida. Most specimens were dusted with NH_4Cl or MgO_2 prior to drawing or photography. Restorations are based on these drawings and photographs, and oriented so that anterior is to the left.

I follow here the systematic arrangement presented by Poyato-Ariza & Wenz (2002) although discrepancies to yet unpublished results exist (Kriwet 2001a).

3. Terminology and Abbreviations

To avoid any misunderstanding, the terminology used in this study is explained. The terms "pycnodont" and "pycnodontiform" are used interchangeable for Pycnodontidae and Pycnodontiformes respectively. The term occlusal surface for teeth is not used in the sense of a "facies masticatoria" as in mammals, but rather only characterises the apical surface of the tooth crown, which is in direct contact with the food.

The nomenclature used for dermal skull bones in actinopterygians by many authors follows the traditional ("orthodox") terminology for actinopterygians and is not based on homology criteria. The difficulties in establishing the homology and the sometimes great variability of dermal elements in the head of actinopterygian fishes (e.g., Gregory 1933) led to the publication of different names for the same bone and is rather unintelligible (see also Schultze & Arsenault 1985). Recently, Kriwet (2004) and Poyato-Ariza & Wenz (2005) applied different names for for the same elements in pycnodontiform fishes. The terminology for the dermal head used in this study follows that of Jollie (1962) and Schultze (1993), who established homology criteria for skull bones in fishes.

Other abbreviations are: **ac**, aortic canal; **adso**, anterior dermosupraoccipital; **ai**, articulation with infrapharyngobranchial; **ang**, angular bone; **ar1**, anterior articular element; **ar2**, posterior articular element; **arc**, arcocentrum; **art**, articular bone; **asc**, modified scales flanking the cloakal opening; **aut**, anterior autogenous neural spines; **bpr**, processus basipterygoideus of the parasphenoid; **br**, branchial teeth; **bra**, branchial arches; **cha**, anterior ceratohyal; **chp**, posterior ceratohyal; **cde**, circumpulpar dentine; **cl**, cleithrum; **cs**, canal through symplectic; **den**, dentary; **dent**, dentary teeth; **detl**, prefrontal; **df**, dorsal

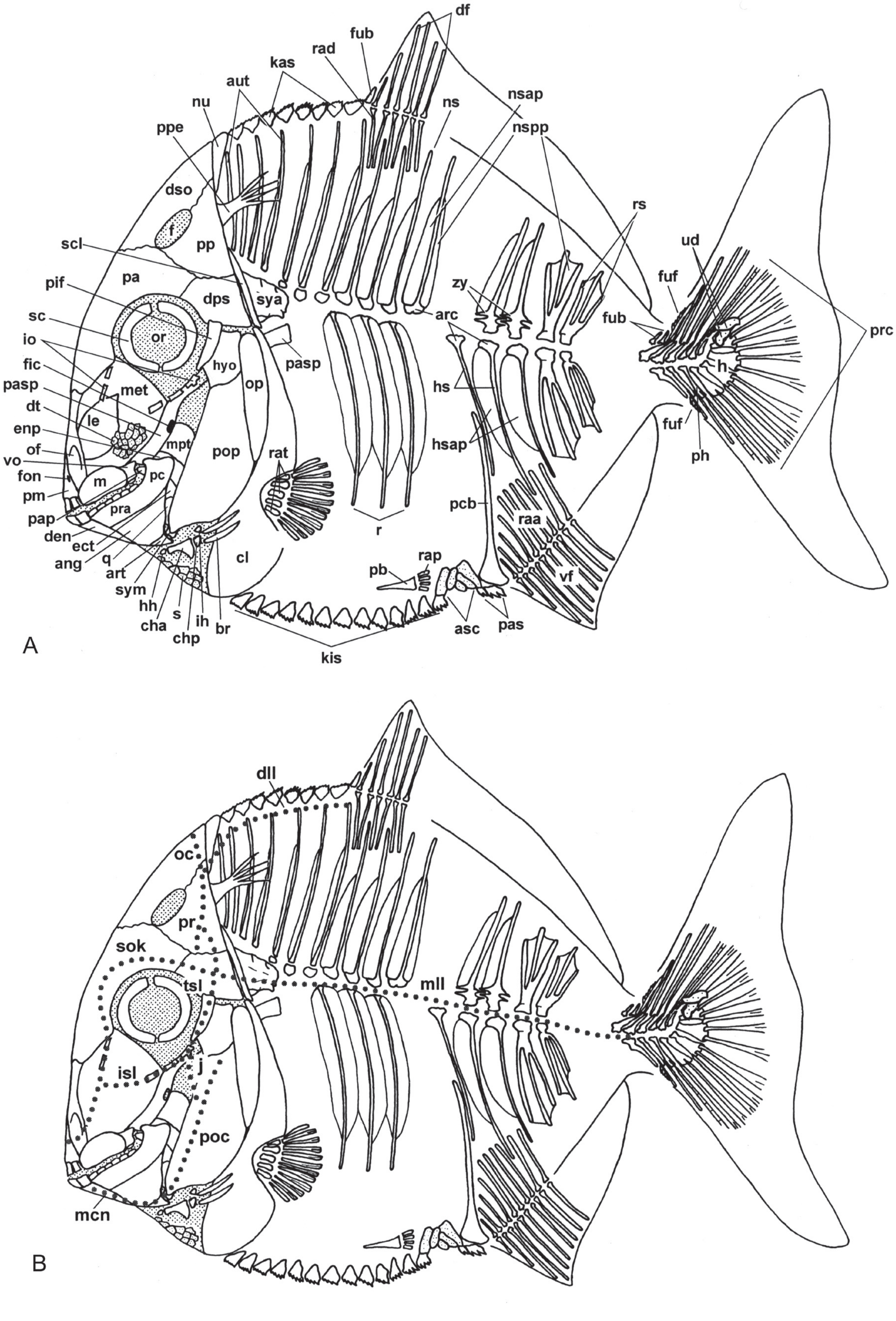


Figure 1: Composite pycnodont displaying the general pycnodont characters. **A:** Bony elements. **B:** Sensory lines. Not to scale. For explanation see text.

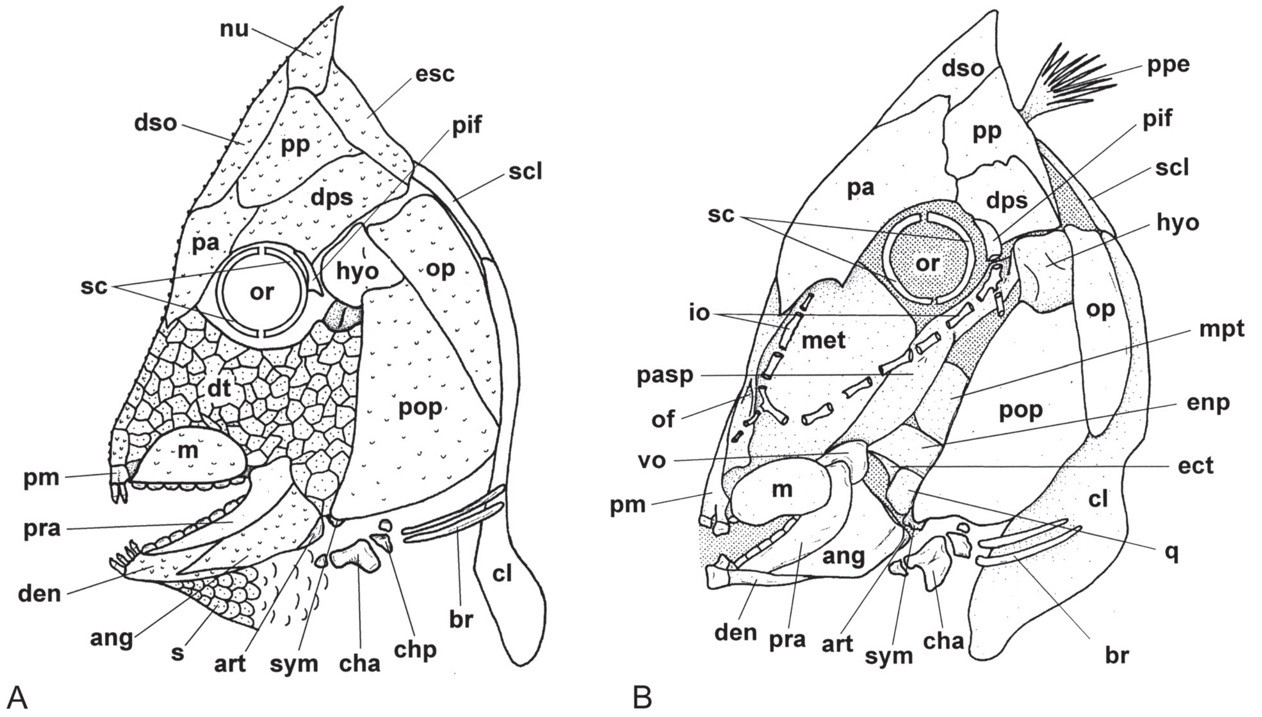


Figure 2: Restoration of pycnodont heads in lateral view. **A:** *Gyrodus hexagonus*. **B:** *Proscinetes elegans*. Not to scale. For explanation see text.

fin rays; **dll**, dorsal lateral line; **dpf**, compound bone consisting of parietal, postparietal, and dermopterotic; **dps**, dermopterosphenotic, **dpt**, dermopterotic; **dso**, dermosupraoccipital; **dsp**, dermosphenotic; **dt**, dermal tesserae; **ect**, ectopterygoid; **end**, endocranium; **enp**, endopterygoid; **eo**, exoccipital bone; **esc**, extrascapular bone; **f**, opening in the temporal region of the dermal skull; **fepa**, foramen for the efferent pseudobranchial artery; **fic**, foramen for internal carotid artery; **fon**, foramen for passage of the olfactoric nerve in the premaxillary process; **fub**, basal fulcra; **fuf**, fringing fulcra; **h**, hypural bones; **hh**, hypohyal; **hmc**, hyomandibular condyle, **hs**, haemal spine; **hsap**, anterior flange-like expansion of haemal spines; **hyo**, hyomandibula; **ic**, intercalar; **ih**, interhyal bone; **io**, infraorbital; **iop**, interoperculum; **isl**, infraorbital sensory canal; **kas**, dorsal ridge scales; **kis**, ventral ridge scales; **le**, lateral lamina of mesethmoid; **mcn**, mandibular sensory canal; **met**, mesethmoid bone; **mll**, main lateral line; **mpt**, metapterygoid; **m**, maxilla; **n.VIIh**, foramen for the passage of the cranial nerve VII plus the nerve for the anteroventral lateral line; **ns**, neural spine; **nsap**, anterior, flange-like expansion of the neural spine; **nspp**, posterior flange-like expansion of neural spine; **nu**, nuchal; **oc**, occipital commissure of sensory line system; **of**, olfactory fossa; **or**, orbit; **op**, operculum; **pa**, parietal bone; **pap**, palatinal process of the endopterygoid; **pas**, postanal scales; **pasp**, parasphenoid; **pb**, pelvic bone; **pc**, processus coronoideus; **pcb**, post-coelomic bone; **peb**, pectoral bar; **ph**, parhypural; **pif**, posterior infraorbital; **pm**, premaxilla; **poc**, preopercular sensory canal, **pop**, preoperculum; **pp**, postparietal bone; **ppe**, postparietal process; **ppt**, pterotic; **pr**, parietal sensory line; **pra**, prearticular bone; **prc**, principal caudal rays; **pro**, prootic; **ps**, pectoral spine; **psl**, postparietal branch of sensory line; **psa**, anterior ramus of pectoral spine; **psp**, posterior ramus of pectoral spine; **pt**, posttemporal bone; **pts**, pterosphenoid; **q**, quadrate; **qang**, articulation facet of the quadrate with the aticular; **qart**, articulation facet of the symplectic with the quadrate; **r**, ribs; **rad**, pterygiophores of dorsal fin; **raa,** pterygiophores of the anal fin; **rap**, radials of the pelvic fin; **rar**, retroarticular bone; **rat**, radials of the pectoral fin; **rs**, ridges reinforcing the anterior and posterior sagittal expansions on haemal and neural spines; **s**, scale, **sc**, sclerotic ring elements; **scl**, supracleithrum; **so**, supraotic; **sok**, supraorbital sensory canal; **sp**, sphenotic bone; **st**, supratemporals bone; **stpp**, supratemporals portion of the postparietal bone; **sya**, synarcual [fusion of exoccipitals and anteriormost vertebral elements to a solid compound structure.]; **sym**, symplectic; **sys**, symphysis of the prearticular bones; **tsl**, temporal (otic) portion of the sensory line; **ud**, urodermals; **vf**, fin rays of anal fin; **vo**, vomer; **zy,** zygapophyses.

Institutional abbreviations: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, U.S.A.; BMNH, The Natural History Museum, London, UK; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; DGC, Departamento de Geología, Universidad de Chile, Santiago, Chile; FMNH, Department of Geology, Field Museum of Natural History, Chicago, Illinois, U.S.A.; GPIT, Institut und Museum für Geologie und Paläontologie, Tübingen, Germany; IPFUB, Paläontologisches Institut der Freien Universität, Berlin, Germany; IPUM, Istituto di Paleontologia dell'Università degli Studi di Milani, Mailand, Italy; JME, Jura Museum, Naturwissenschaftliche Sammlungen Eichstätt, Germany (JME SOS: specimens from the Solnhofen quarries); MB. f., Museum für Naturkunde, Berlin, Germany, Fossil Fish Collection; MCSNB, Museo Civico di Scienze Naturali "E. Caffi", Bergamo, Italy; MGSB, Museo Geológico del Seminario, Barcelona, Spain; MNHN, Museum national d'Histoire

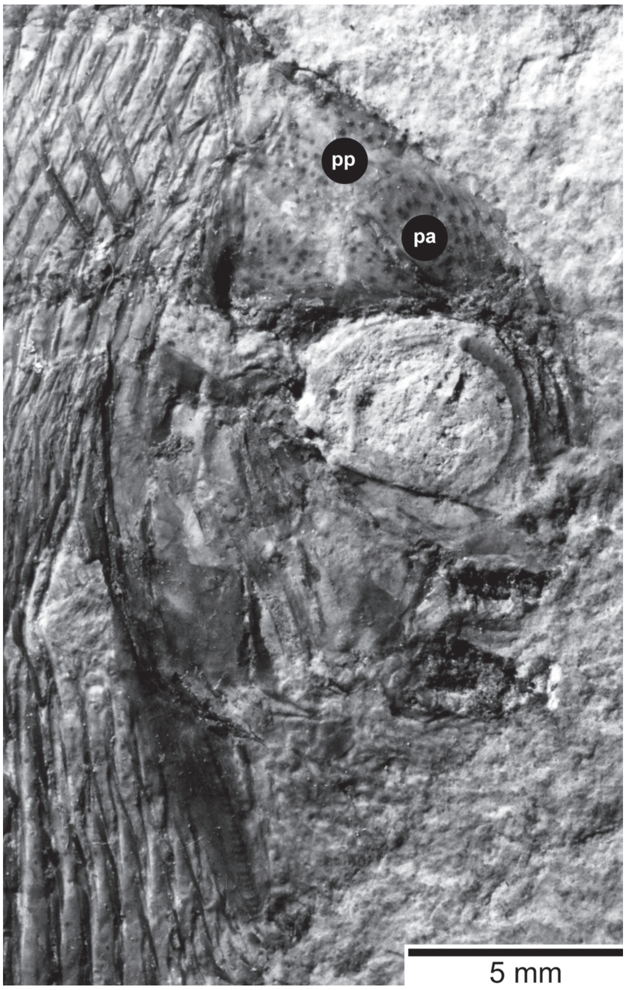


Figure 3: Head and anterior body of a juvenile specimen of *Gyrodus hexagonus* (MB. f 1336) from the Tithonian (Upper Jurassic) of Solnhofen area, southern Germany, displaying weakly ossified dermal skull bones.

naturelle, Paris, France; SGO, Museo Nacional de Historia Natural de Santiago, Chile; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

4. Cranial Morphology of Pycnodonts

The cranium of pycnodonts is considerably reduced in comparison to that seen in Ginglymodi, Halecomorphi, and teleosts. The standard pattern of the dermal skull of adults includes an unpaired dermosupraoccipital, paired postparietals, parietals, dermopterosphenotics (compound bones, see below), and posterior infraorbitals (Fig. 2). The dermatocranium of juvenile specimens is less ossified, and it is difficult to identify the sutures between bones (Fig. 3).

In contrast to other neopterygians, pycnodonts lack supra- and suborbitals, rostrals, supramaxillae, suboperculum, interoperculum, gular bones, and posttemporals. The endocranial elements of pycnodonts are less ossified than those of other neopterygians. The preservation of the endocranium is magre in most specimens; and only a few elements seem to be consistent throughout the order. The generalised pattern includes a large median mesethmoid, an unpaired supraotic and orbitopterosphenoid, and exoccipitals, prootics, pterotics, sphenotics, and epioccipitals. Dermal elements of the endocranium include the unpaired parasphenoid and vomer. Visceral elements are the paired hyomandibulas, symplectics, quadrates, metapterygoids, the suspensorium apparatus (including hyomandibula, preoperculum, ectopterygoids, entopterygoids, and metapterygoid, symplectic, and quadrate), the jaw apparatus, the branchial apparatus, and the hyoid apparatus. In the following, the dermatocranium, the endocranium (including the parasphenoid and vomer), and the visceral skeleton is described and discussed.

4.1 Dermatocranium

The head of pycnodonts is deep and fore-shortened. The snout protrudes more or less forwardly and the mouth opening is located terminally. Pycnodonts with exceptional prognathous snouts are *Arduafrons*, *Anomoeodus*, and *Iemanja*. The prognathism found in *Akromystax* differs from that of most other taxa because it is formed by the expansion of the premaxillae and the mandibular bones alone (Poyato-Ariza & Wenz 2005). All pycnodonts are characterized by a hypertrophy of the region between the orbit and snout, which results in enlargements of the mesethmoid and parasphenoid (Nursall 1996b). The mouth cleft is more or less oblique to the course of the notochord and turns downwards in most pycnodonts. In contrast to all other pycnodonts, the skull of *Coccodus* is relatively compressed ventro-dorsally. The pycnodont head is narrow and slightly triangular with a pointed anterior edge in basal view. Nursall (1996b) assumed that the head is tropibasic in development like that in most teleosts. In lateral aspect, the pycnodont head is also triangular and displays a more or less pronounced frontal flexure, which mirrors the flexure of the parasphenoid.

The dermatocranium forms a more or less rigid box for the endocranium. There is some variability of dermal bones found in pycnodonts that is mainly confined to the posterior margin of the skull (Fig. 2). However, pycnodonts possess a rather simple skull pattern with a small number of dermal bones. Therefore, it is possible to establish a basic pattern and

Figure 4: Holotype of *Coccodus lindstroemi* (AMNH 3698) in lateral view displaying the well-ossified dermatocranium and the strong occipital spine.

Figure 5: Disarticulated specimen of *Gyrodus hexagonus* (MB. f 1361) from the Tithonian (Upper Jurassic) of Solnhofen area, southern Germany displaying the dermosupraoccipital bone in dorsal view (arrow).

discuss the variations in this context. The pycnodont *Coccodus* is characterised by largely fused dermal bones, which form rigid unit without traces of sutures between bony elements visible. This results in a quite immobile head and its characteristic triangular appearance in lateral view (Fig. 4). Nursall (1996b) suggests that the fusion of dermal elements to a single, solid unit is the result of early ankylosis. This assumption is supported by the absence of sutures even in small (juvenile?) specimens (pers. observ.).

The generalised skull roof pattern is comprised of an unpaired median dermosupraoccipital, paired postparietals and parietals (Figs 2, 5). The dermosupraoccipital (Nursall 1996b, 1999a, 1999b) is a dermal bone, which is not homologous to the chondral supraoccipital bone of most teleosts (Maisey 1999). It roofs the post-temporal fossae and overlies the supraotic crest of the endocranium. Lambers (1991) interpreted the presence of a single dermosupraoccipital as an autapomorphic character for pycnodonts. Most pycnodonts posses a single median dermosupraoccipital. An anterior dermosupraoccipital is reported for *Micropycnodon* (e.g., Dunkle & Hibbard 1946; Nursall 1999a) (Fig. 6). However, Lambers (1991) doubted the identification of an additional dermosupraoccipital. Woodward (1895) mentioned a median ethmoid anterior to the dermosupraoccipital and the parietals. This bony element is interpreted as fused anterior dermosupraoccipital and posterior dermethmoid by Nursall (1999a) but represents in fact an additional dermosupraoccipital similar to the condition found in *Paramesturus*. *Mesturus verrucosus* does not exhibit this pattern (pers. observ.). The presence of a single or several dermosupraoccipital bones is assumed to be an autapomorphic character for pycnodonts (Nursall 1996b, 1999a).

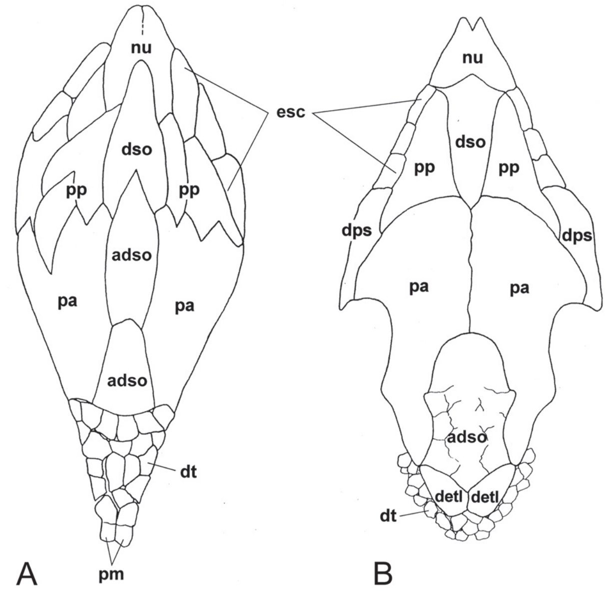


Figure 6: Reconstruction of the dermatocranium of pycnodonts in dorsal view. **A:** *Mesturus leedsi* displaying the variable number of marginal bones and the presence of median dermethmoids. **B:** *Micropycnodon gaynaisensis*, displaying lateral dermethmoids. Not to scale. Redrawn from Nursall (1999a).

There are unpaired, median bones posterior to the dermosupraoccipital, which were termed nuchals by Nursall (1999a) (Figs 2, 6). Nuchal plates (nu) are the anteriormost, elongated and imbricated ridge scales, which are obliquely orientated compared to the anterior scale rows (Poyato-Ariza & Wenz 2002). The number of nuchal plates may vary among pycnodonts. A nuchal plate is present in basal members of pycnodontiforms sensu Kriwet (2001a): *Arduafrons*, *Brembodus*, *Eomesodon*, and *Gibbodon*. *Macromesodon*, a member of advanced pycnodonts, however, also displays a nuchal plate. This inconsistent character distribution requires further examination.

Nuchal plates are positioned saddle-like on the dorsal ridge of the posterior region of the skull and the anterior part of the dorsal body and form a graded series from the dermosupraoccipital bone to the ridge scales. They form the anterior margin of the dorsal apical prominence where this character is present and are continuous posterior with the dorsal ridge scales. It is obvious that nuchal plates are a plesiomorphic character that was lost later but retained in few taxa (e.g., *Macromesodon*).

Nursall (1999a) interpreted the nuchal plates as part of the marginal series, which extends latero-ventral at the posterior margin of the skull in some pycnodonts (Figs 2A, 6). This marginal series represents extrascapular bones based on topographic position (Poyato-Ariza & Wenz 2002) and consists of one or several bones. It is continuous anteriorly with the postparietals, and ventrally reaches the level of the supracleithrum. Extrascapular bones are present in different actinopterygians

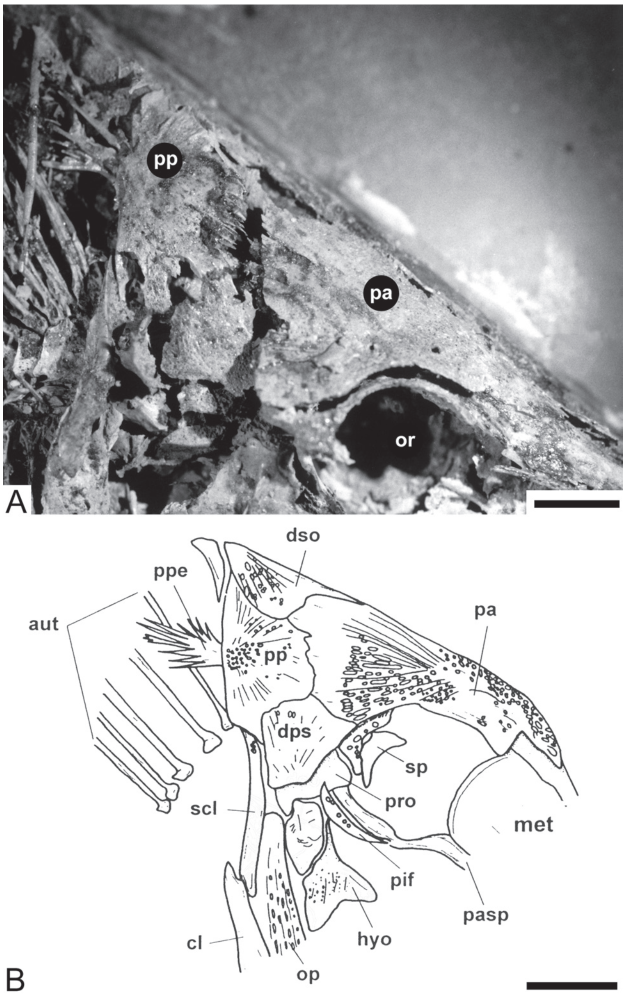


Figure 7: Dermatocranium of *Proscinetes elegans* (JME 1941.12a). Scale bar = 10 mm.

and have been differently named (e.g., tubulars, supratemporals, posttemporals, scale-bones, and supratemporo-tabulars). The number and presence/absence of extrascapulars exhibits significant intraspecific variation. For instance, the number of extrascapulars varies from one to several in *Mesturus leedsi* and *Gyrodus* spp. However, in some *Gyrodus* specimens even the extrascapular bones are absent (pers. obser.). Large pairs of extrascapulars are present in *Macromesodon*, *Mesturus*, *Micropycnodon*, and *Paramesturus* (Poyato-Ariza & Wenz 2002). In all other pycnodonts, the extrascapulars are reduced in size or missing (Kriwet 2001a). In *Trewavasia*, the extrascapulars are hypertrophied (Gayet 1984).

A large and unpaired spine, which is directed caudally, is fixed to the occipital region in *Coccodus* species (Fig. 4). It is compressed laterally, bilaterally symmetrical, and acuminate. The lateral sides are ornamented with regular ridges running from the base to the apex. The anterior and posterior margins are delicately denticulated. The morphology and sculpture of the occipital spine is the most important character to distinguish the three species in *Coccodus*. In *C. armatus*, this spine is delicately denticulated along the anterior and posterior margin whereas the spine is denticulated only along the posterior edge in *C. insignis*. In *C. lindstroemi*, the denticles are restricted to the posterior margin of the occipital spine as in *C. insignis*. However, the denticles are coarser in *C. lindstroemi* (about 14) and the spine itself is wider but shorter in *C. insignis*. Lamaud (1984) erroneously mentioned denticles on both margins of the occipital spine in *C. lindstroemi*. *Ichthyoceras* is similar in possessing a spine that arises from the postparietals and is directed posteriorly. The spine exhibits irregularly arranged spiny tubercles.

In the skull roof, the dermosupraoccipital bone borders the paired parietals antero-medially and is bordered by the paired postparietals ventro-laterally (Figs 1, 2, 6, 7). The parietals meet in the midline of the skull and are the largest of the dermal bones. They form the dorsal and antero-dorsal bony margin of the orbits and suture posteriorly the postparietals. Parietal spines in front or above the orbit are present in *Trewavasia* (1 spine), *Ichthyoceras* (3 spines) and *Hensodon* (3 spines) (Fig. 10). The spines are prominently ornamented. Poyato-Ariza & Wenz (2002) combined all head spines of pycnodonts in a single character and termed this structure supraoccipital spine. The topology of the spines, however, differs between *Coccodus* and the other three pycnodonts, and I suggest that these structures be separated, because the spine of *Coccodus* is large and positioned at the posteriormost edge of the occipital region conversely to the condition found in the other taxa.

The postparietals form most of the posterior margin of the dermal skull and do not reach the orbits (Fig. 7). Each postparietal bone carries the connection between the dorsal lateral line and the supraorbital canal (Fig. 1B).

There is a brush-like, internal extension of each postparietal (postparietal peniculus) that is directed posteriorly in advanced pycnodonts (Figs 1A, 2B, 7). The postparietal peniculus represents osseous extensions of occipital tendons for attachment of epaxial myosepta and is present in *Abdobalistum*, *Akromystax*, *Coelodus*, *Iemanja*, *Macromesodon*, *Neoproscinetes*, *Nursallia*,

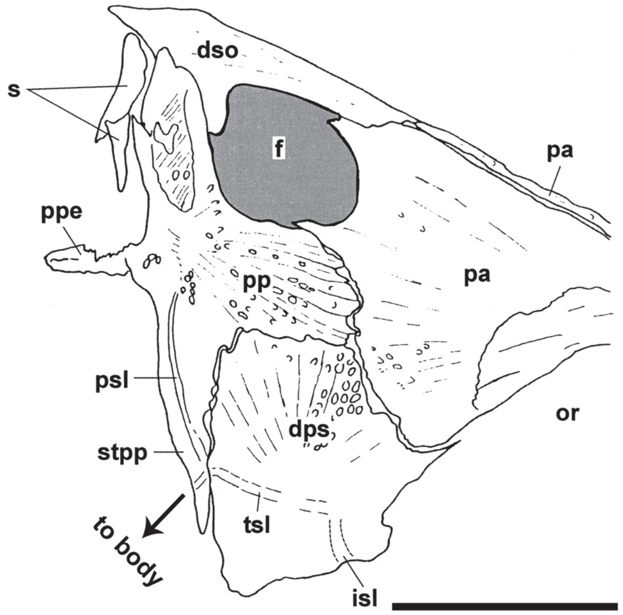


Figure 8: Camera lucida drawing of the occipital region of *Ocloedus subdiscus* (Wenz, 1989) (MGSB 13.376B) displaying parts of the sensory canals and the temporal opening. Scale bar = 5.0 mm. Modified from Kriwet et al. (1999).

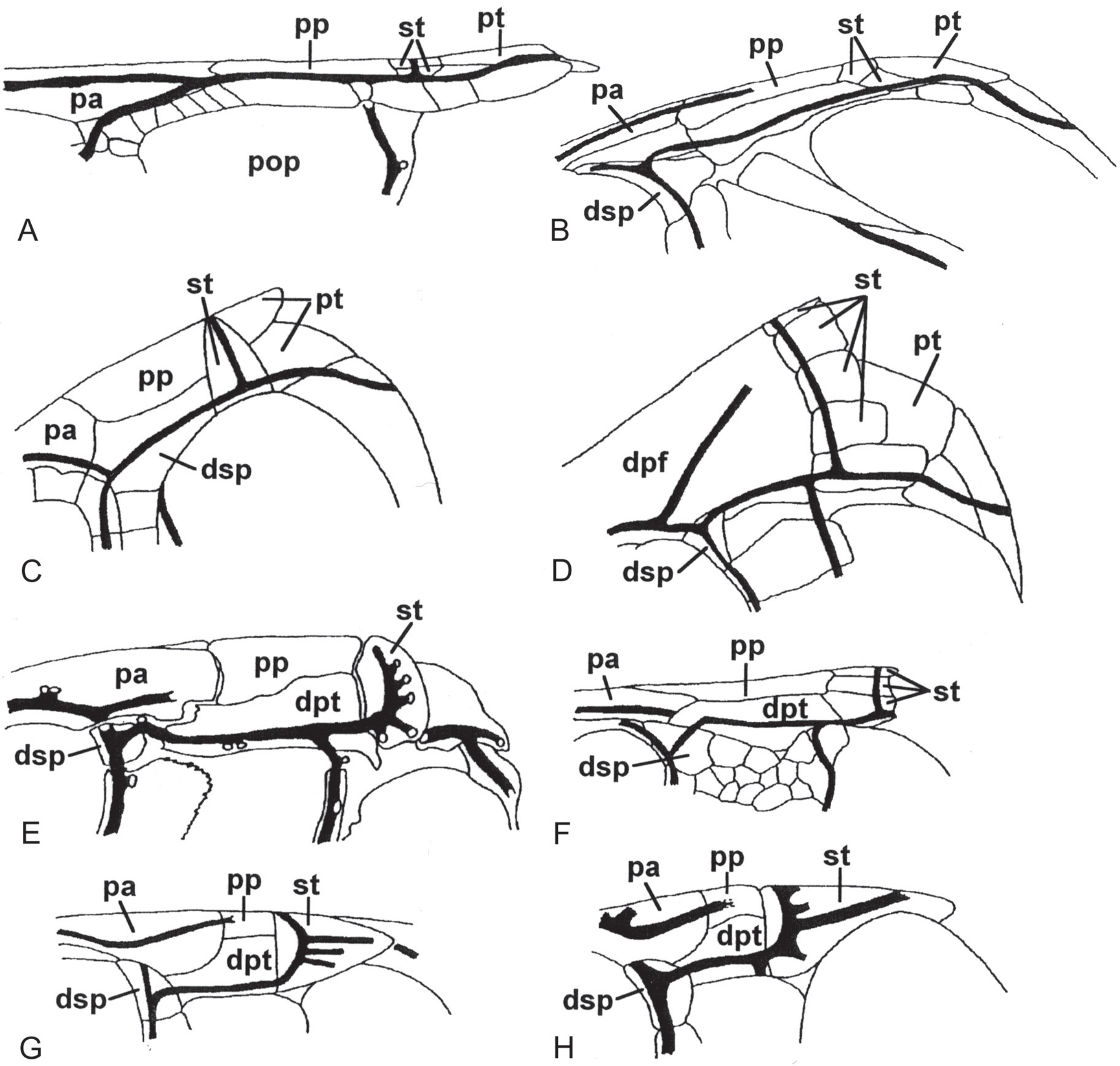


Figure 9: Patterns of cephalic sensory canals of the occipital region of some fossil and extant actinopterygians. **A:** *Polypterus bichir*. **B:** *Moythomasia durgaringa*. **C:** *Acentrophorus* sp. **D:** *Dapedium pholidotum*. **E:** *Amia calva*. **F:** *Lepisosteus oculatus*. **G:** *Pholidophorus bechei*. **H:** *Leptolepis coryphaenoides*. Not to scale. All left side, lateral view. Modified from Nybelin (1966), Lehman (1966), Moy-Thomas & Miles (1971), Wiley (1976), Gardiner (1984), Thies (1988), and Grande & Bemis (1998).

Ocloedus, *Oropycnodus*, *Proscinetes*, *Pycnodus*, *Stemmatodus*, *Stenamara*, and *Tepexichthys*.

In some pycnodonts, the dermosupraoccipital, parietals, and postparietals form the bony margin of an opening in the temporal region of the dermatocranium. This opening or fenestra is oval to subcircular in outline, with its long axis generally directed antero-ventrally (Figs 1A, 8). The presence of a fenestra is a derived character for pycnodontiforms (Nursall 1996b; Poyato-Ariza & Wenz 2002), and is shared by *Akromystax*, *Ocloedus*, *Oropycnodus*, *Pycnodus*, *Tepexichthys*. Basal pycnodonts, including the Mesturidae and Gyrodontidae lack the post-parietal brush-like extension and the temporal fenestra.

The postero-dorsal margin of the orbit is formed by a rectangular bone, which sutures the postero-ventral part of the parietal (Figs 1A, 8). Nursall (1999a) interpreted this compound bone as dermopterotic. It is named dermosphenotic in the skull reconstruction of *Ocloedus subdiscus* by Wenz (1989: fig. 1). This bone posteriorly borders a smaller bone labelled as dermopterotic in *Ocloedus subdiscus* (Wenz 1989). In most other pycnodont reconstructions, this bone is identified as dermopterotic. It overlies the dorsal parts of the endochondral sphenotic and posteriorly the pterotic. The dermopterotic of Wenz (1989) is in fact the ventral extension of the postparietal bone. Many pycnodonts have postparietal bones with more or less developed postero-ventral extensions. This extension probably corresponds to fused bony structures, since this portion carries parts of the sensory canal and might support the interpretation of fusion with the dermopterotic (Figs 1B, 8).

According to its articulation to the postparietal and parietal bones, the rectangular bone in front of the ventral extension of the postparietal can be regarded as the dermosphenotic bone. The post-orbital junction of the orbital and temporal portions of the sensory canal is located in the dermosphenotic

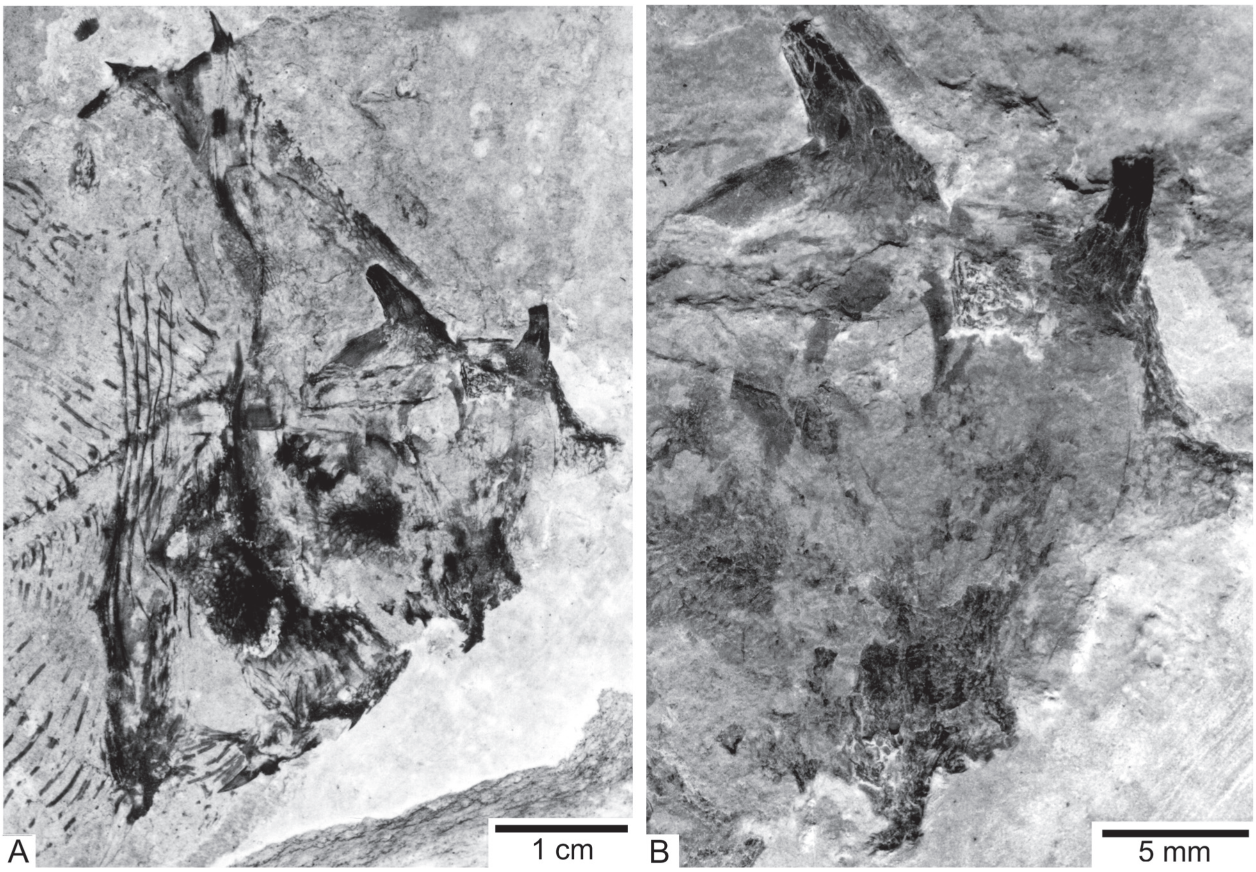


Figure 10: Holotype of *Hensodon spinosum* Kriwet, 2004 from the Upper Cretaceous of Lebanon. **A:** Anterior body and skull displaying the strong parietal spines. **B:** Close up of skull.

in actinopterygians (see above; Fig. 9). In pycnodonts, the supraorbital sensory canal divides into temporal and parietal branches in the bone in the posterior corner of the orbit and the infraorbital canal, which arises in this bone, marks the junction of the temporal canal with the main lateral line indicating parts of the dermosphenotic (see also below). Therefore, this bone is interpreted generally as a compound bone that consists of dermosphenotic and dermopterotic (Kriwet et al. 1999: 51). A similar fusion of dermopterotic and dermosphenotic bones is also evident in *Turbomesodon* (Poyato-Ariza & Wenz 2004). However, there is another small bone located at the posterior margin of the orbit that represents an additional independent dermosphenotic structure in this taxon, which is a rather unusual condition for pycnodonts. In other pycnodonts (e.g., *Stemmatodus*) the dermopterotic and dermosphenotics are independent bones based on the occurrence of sensory lines. Unfortunately, growth series, which permit reconstruction of the development of these bones and their fusion, do not exist.

There is a paired bone lying in the posterior margin of the orbit above the orbital process of the sphenotic in all pycnodonts. This bony element is loosely attached to the dermal skull and easily lost after death. This posterior infraorbital is generally identified as dermosphenotic (e.g., Lambers 1991); it carries the infraorbital sensory canal to the cheek bones.

The cheeks, and to varying degree also the snout and gular region, are covered with dermal tesserae in *Brembodus*, *Mesturus*, *Arduafrons*, *Micropycnodon*, *Paramesturus*, and *Gyrodus* (Figs 2A, 6). These tesserae are small, polygonal, non-imbricating dermal plates of varying size and form. They are irregularly arranged and the homologisation with dermal bones of other actinopterygians is not easy. However, similarities exist to *Lepisosteus*.

The cheeks are naked and the sensory canal bearing cheek bones are reduced to infraorbital ossicles in more advanced pycnodonts (Pycnodontoidei sensu Poyato-Ariza & Wenz 2002) (Fig. 2B). Ornamentation on infraorbital ossicles varies but is generally restricted to the posterior-most one.

Supra- and suborbital bones are absent in all pycnodonts. Poyato-Ariza & Wenz (2002) interpreted the presence of small plate-like tesserae in *Arduafrons*, *Brembodus*, *Gyrodus*, *Ichthyoceras*, and *Mesturus* as suborbital bones. However, this interpretation lacks any homological evidence.

The sclerotic ring of all pycnodonts consists of a complete ring of two bones, which are oriented anterior and posterior to the eyeball where preserved (Figs 1, 2).

The snout is supported by the transversal part of the T section of the mesethmoid in most pycnodonts and additionally by the premaxillary process in advanced pycnodonts. The presence of nasal bones was discussed in the past, and Nursall (1999b) suggested that nasal bones are absent in all pycnodonts. However, Poyato-Ariza & Wenz (2005) demonstrated the presence of nasal bones in *Turbomesodon praeclarus*.

The dermatocranium of some pycnodonts displays additional bones. A median compound bone (= interfrontal of Nursall 1999a), which interdigitates with the parietals and the dermosupraoccipital, is reported from *Mesturus leedsi*, e.g., as median ethmoid plate by Woodward (1895) and figured for *Hadrodus hewletti* by Bell (1986). An unpaired median bone anterior to the parietal and overlaying the mesethmoid was called dermethmoid by Nursall (1999a). It is present in *Mesturus leedsi* (Fig. 6A), *Brembodus*, *Trewavasia*, and probably in *Ichthyoceras* (pers. observ.). Lambers (1991) assumed the mosaic-like dermethmoid to be homologous with dermal tesserae and identified this bony structure in *Gyrodus*, *Mesturus*, *Paramesturus*, and *Micropycnodon*. Similar structure in *Coccodus* and *Pycnodus* (Gayet 1984) are undivided dermethmoids. However, I agree with Poyato-Ariza & Wenz (2002) in considering this structure a true dermal structure, which should be called preparietal (not prefrontal). No dermethmoid was found in *Coccodus* and *Pycnodus* by me. The subdivided dermethmoid of *Gyrodus* and allied forms represent dermal tesserae (Fig. 2A). Taverne (1981) identified a median dermethmoid in *Paramesturus stuehmeri* that rather represents the superficial, transversal part of the T section of the mesethmoid (Poyato-Ariza & Wenz 2002). Lateral dermethmoids (sensu Nursall 1999a) were reported from *Micropycnodon gaynaisensis*. The homologisation of the median compound bone, dermethmoid, and lateral dermethmoid with bony structures found in other neopterygians is obscure and not always possible. True preparietal bones are only present in *Akromystax*, *Ichthyoceras*, *Nursallia*, and *Trewavasia* according to Kriwet (2001a) and Poyato-Ariza & Wenz (2002, 2005).

The dermal cover of the skull displays a more or less pronounced ornamentation consisting of tubercles, ridges, rugae, and pits. A combination of some of these sculptures may occur and ontogenetic variation of the dermal skull ornamentation is found in some pycnodonts where growth series exist (e.g., *Gyrodus*, *Macromesodon*). The ornamentation is faint in juvenile specimens, often only consisting of small tubercles (Fig. 3). The ornamentation becomes coarser and the tubercles sometimes fuse to ridges during growth of the fish. Ganoin is absent on the dermal skull elements of all pycnodonts (Fig. 11). Peculiar is the presence of rather large, star-fish like structures, which

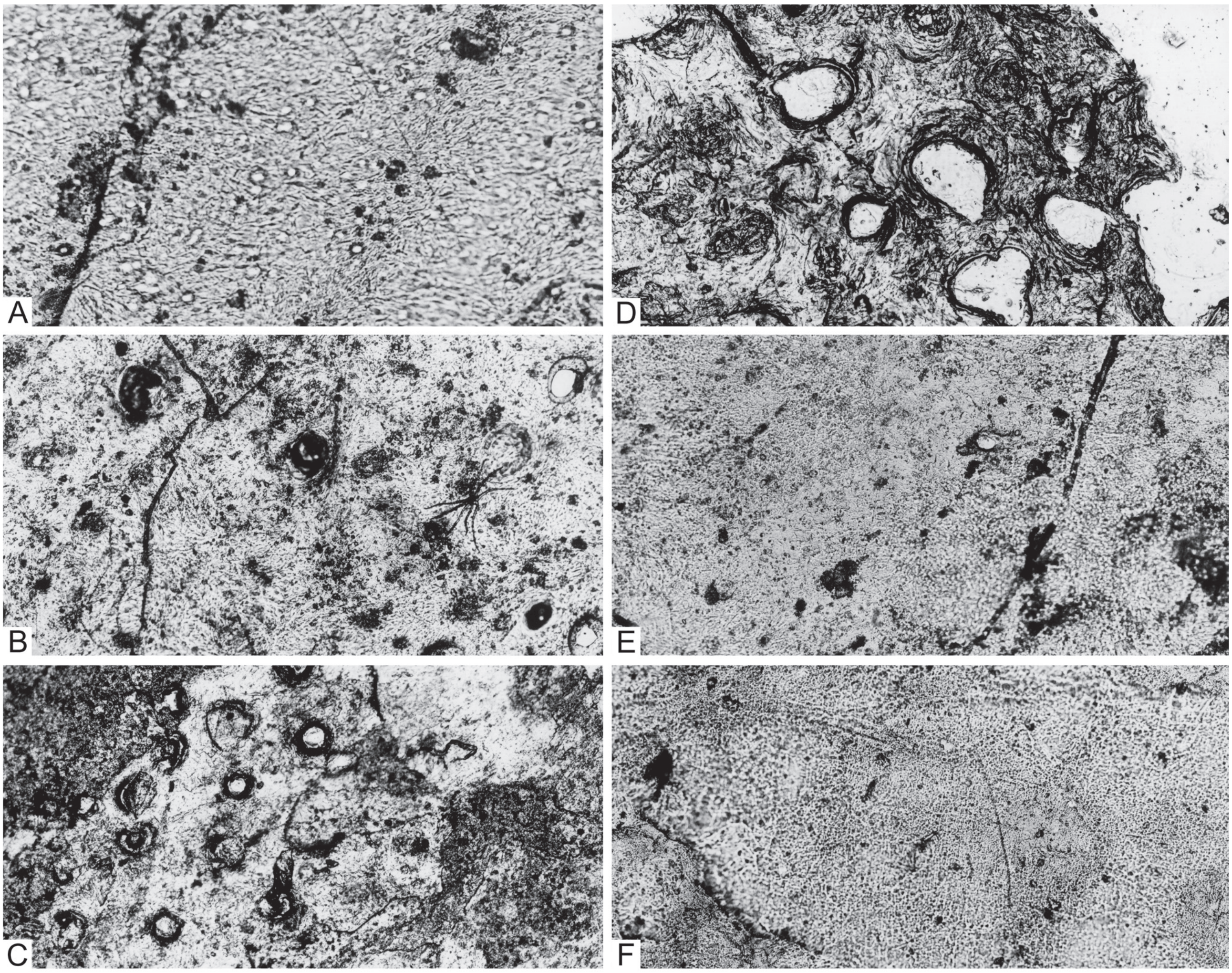


Figure 11: Micrographs of peels from dermal skull bones. **A:** Parietal bone of *Gyrodus hexagonus* (MB. f.1340). Magnification = x 32. **B:** Same displaying rather large bony cell. Magnification = x 64. **C:** Postparietal bone of *Gyrodus hexagonus* (MB. f.1336), juvenile specimen. Magnification = x 32. **D:** Postparietal bone of *Stemmatodus rhombus* (MB. f.7234). Magnification = x 64. **E:** Parietal bone of *Anomoeodus nursalli* (IPFUB Uña Pyc 1). Magnification = x 32. **F:** Preoperculum of *Gyrodus hexagonus* (MB. f.1340). Magnification = x 64.

are similar to structures that were identified as bony cells in *Lepidotes elvensis* by Malzahn (1963).

The pycnodont skull lacks several dermal elements that are typical for most actinopterygians, including the nasals, rostrals, supraorbitals, suborbitals, supramaxilla, intertemporal, posttemporals connecting the skull to the shoulder girdle, gular, suboperculum, and interoperculum. Differences in the number of dermal skull bones found in pycnodonts can be placed within an evolutionary line (Kriwet 1999a). Plesiomorphic pycnodonts such as *Arduafrons*, *Gyrodus*, and *Mesturus* display more ossifications compared to the more derived taxa such as *Coelodus*, *Iemanja*, *Ocloedus*, *Oropycnodus*, and *Pycnodus*. Reduction of bones includes the number of premaxillary and dentary teeth, the upper part of the preoperculum, and especially the marginal skull elements. *Pycnodus*, one of the last pycnodonts in the fossil record, completely lacks the operculum. Parallel to the reduction of bony elements new structures were established, e.g., a brush-like, internal extension of the postparietals (postparietal peniculus) for attachment of epaxial muscles and a dermic fenestra in the lateral wall of the dermatocranium that is related to enlargements of jaw muscle mass. The opening in the temporal side of the dermatocranium is analogous to the temporal fenestra in several teleosts.

4.2 Sensory Canals

There are two lateral sensory lines on the body (Fig. 1B). The main lateral line is positioned more or less parallel to the notochord and runs from the skull to the caudal peduncle. The dorsal lateral line, which branches off from the occipital commissure, is situated just below the dorsal ridge scales and ends before the insertion of the dorsal fin.

The occipital commissure is located in the dermosupraoccipital bone (Fig. 1B) and supports the interpretation that the nuchal is an additional element.

Traces of the lateral line sensory canal system of the skull are generally recognised only in part due to the massiveness and mode of preservation of dermal bones. Traces of the supraorbital sensory canal are recognised in the parietals. The branching of the temporal sensory canal into supraorbital and infraorbital sections is situated in the compound bone consisting of dermopterotic and dermosphenotic (dermopterosphenotic, see above). The position of the branching is a feature of the dermosphenotic bone. The post-orbital junction was considered a teleostean character by Schaeffer & Patterson (1984) and Johnson & Patterson (1996). However, this junction is also found in plesiomorphic actinopterygians and sarcopterygians. The infraorbital canal is carried by cheek tesserae in pycnodonts without reduced dermal head skeleton or by infraorbital ossicles tesserae in advanced forms. Nursall (1999b) compared the number of infraorbital ossicles of pycnodont to that of the infraorbitals seen in teleosts. The numbers provided regarding the canal-bearing infraorbitals of plesiomorphic teleosts varies from author to author, and depend on whether or not the lacrimal, antorbital, and posterior infraorbital (="dermosphenotic") are included. While Johnson & Patterson (1996), following Nelson (1969), gave seven as the plesiomorphic number for teleosts, Arratia (1997) stated that the generalised pattern included five or six, because the antorbital and posterior infraorbital (dermosphenotic) have to be excluded from the series. The number of infraorbital ossicles varies from five to seven in pycnodonts. However, I suggest that comparison of these structures directly to the infraorbital bones of teleosts should be abstained because the infraorbital ossicles represent remainders of the reduced dermal tesserae and homology of these structures is difficult to establish. There is no distinct lacrimal or antorbital bone in pycnodonts. The sole identifiable element, which is consistent throughout pycnodonts, is the posterior infraorbital, which carries the sensory canal to the cheeks. The rooting of the jugal branch of the preopercular sensory canal is situated directly postero-ventrally to the orbit.

The mandibular sensory canal is not well exposed due to the massiveness of the mandibular elements. However, some specimens exhibit some parts of it, and hence permit at least some general statements. It seems that the mandibular canal is running along the entire length of the jaw. This corresponds to the generalised condition in teleosts and other actinopterygians (Arratia 1997). The posterior opening is positioned medially, a condition also seen in other actinopterygians.

4.3 Endocranium

The snout is supported by a single, unpaired mesethmoid bone that is T-shaped in cross section (Fig. 12). The median plate envelops the anterior crest of the parasphenoid and the dorsal crest of the vomer. This structure is consistent in all pycnodonts. In transverse section, it is also T-shaped (Fig. 12). The narrow cross-piece supports the antero-dorsal surface

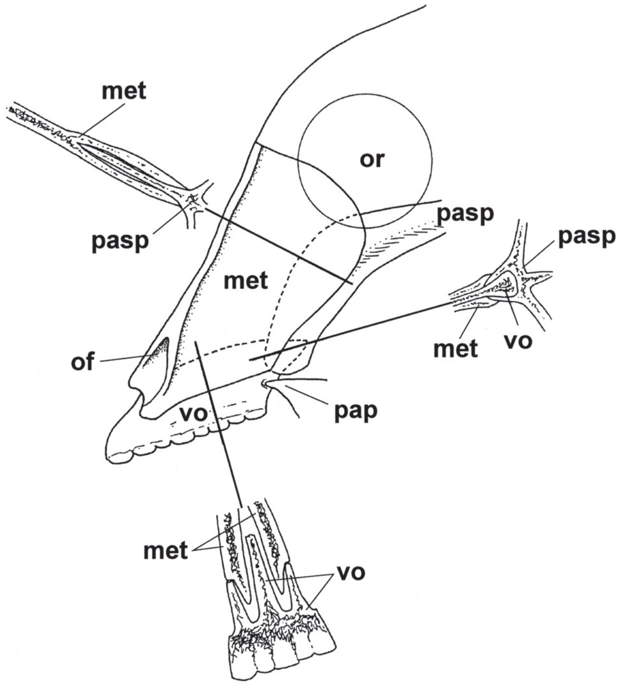


Figure 12: Schematic description of the relationships of the mesethmoid, parasphenoid, and vomer in pycnodont fishes. Modified from Nursall (1999b).

of the snout, the upright, plate-like septum with a compact bony surface, and a cancellous interior (Nursall 1999b). The cross-piece expands ventrally and bears lateral fossae for the olfactory sacs (Fig. 12). The mesethmoid is relatively thick antero-ventrally, bilaminar at its ventral edge, and envelops the dorsal crest of the vomer and widely overlaps a prolongation of the parasphenoid crest. Anteriorly, the vomerine crest rises to the level of the olfactory fossa on the mesethmoid. The parasphenoid itself fits in a shallow sagittal groove on the crest of the vomer. In this way, the parasphenoid and the vomer are firmly fixed and kept in place. The mesethmoid terminates in a straight, obliquely placed margin beneath the parietal bones directly in front of the orbital lamina of the parietals.

The braincase of pycnodonts is hardly known, because it is generally sheeted in a rigid dermal cover or not preserved at all, probably due to the fact that it is largely cartilaginous in most pycnodonts. Although endocranial remains are visible in many specimens, their identification is not always possible, because these elements display great variability in arrangement, number, and ossification pattern. Nursall (1999a) described the endocranium of a specimen in detail that he identified as *Mesturus* sp. Endocranial structures have also been reported from acid-prepared specimens of *Neoproscinetes penalvai* (Nursall & Maisey 1991; Nursall 1996b) and *Pseudopycnodus nardoensis* (Taverne 1997, 2003). Maisey (1999) described a few features of the endocranium of *Neoproscinetes penalvai* in a review of the supraotic bone in neopterygian fishes (see below).

The bones of the endocranium in *Neoproscinetes, Iemanja, Ocloedus,* and *Pycnodus* are separated from each other by extensive unossified spaces. Therefore, the endocranium is presented as osseous framework, and its interpretation and reconstruction are difficult. Consequently, there exists some controversy in identifying the various endocranial elements. In contrast, the plesiomorphic pycnodonts, represented by *Mesturus*, exhibit a well-ankylosed endocranium (Nursall 1999a). The unossified spaces between the individual endocranial elements found in more advanced pycnodonts may have been filled with cartilage, or there were cranial fenestra similar to the condition found in several teleosts (e.g., Forey 1977; Arratia 1982).

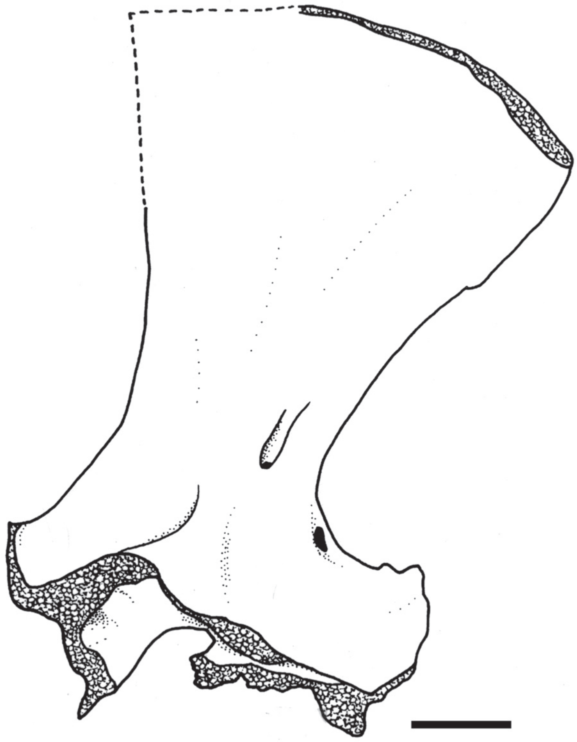


Figure 13: The supraotic bone of *Neoproscinetes penalvai* (AMNH 11990). Scale bar = 1.0 mm. Redrawn from Nursall (1999b).

The braincase is dorsally covered by a median chondral bone, which is located within the otico-occipital region. This bone is rather large and consists of a slightly expanded base and a large ascending plate, which ends just beneath the dermal skull covering (Fig. 13). The narrow process forms the posterior margin of the skull. This bone was recognised as posttemporal bone by several authors (e.g., Blot 1987), “median endochondral bone” by Gardiner et al. (1996), or supraoccipital bone (e.g., Nursall 1996b, 1999a; Taverne 1997). According to Nursall (1996b), the supraoccipital bone represents a synapomorphic character of pycnodonts and teleosts, its specialised morphology being a synapomorphy for pycnodonts. The bone under question lies in the otico-occipital region of the braincase and Nursall (1996b) assumed that this bone is fused anteriorly to the prootics. However, Maisey (1999) was unable to find a connection of the median bone to any other endocranial element in acid prepared specimens of *Neoproscinetes penalvai.* It is anteriorly separated from the prootics and from the ventral occipital complex by extensive unossified, presumably cartilage-filled spaces. In contrast, Maisey (1999) found that this bone is fused to a small posterior expansion of the pterosphenoid in some specimens of *Neoproscinetes*. As a result, he concluded that the supraoccipital bone of Nursall (1996b, 1999b) is actually the supraotic sensu Patterson (1975) based on its supposed position in front of the occipital fissure, position above the anterior semicircular canals, and fusion with the pterosphenoid. This assumption corresponds to the phylogenetic hypotheses proposed by Arratia (1999) and Kriwet (2001a), which show that the supposed supraoccipital bone of pycnodonts is not homologous with that of *Leptolepis coryphaenoides* and more advanced teleosts. According to Arratia (1999), a supraoccipital bone is absent in *Dapedium*, *Tetragonolepis*, pycnodontiforms, pachycormyforms, *Aspidorhynchus*, and *Pholidophorus bechei*. Thus, a supraoccipital is a synapomorphy of teleosts (Arratia 1999). The supraotic bone in pycnodonts separates the two cavernous posttemporal fossae in pycnodonts. The supraotic was to date found only in some Mesozoic non-teleostean neopterygians (Maisey 1999).

The proposed presence of a pterotic bone positioned posteriorly to the supraotic in *Neoproscinetes* (Nursall 1996b, 1999b), was not observed by Maisey (1999). However, there is a chondral element positioned between the exoccipital and the prootic in the holotype of *Iemanja* (Fig. 14). This element shows a spongious structure. Based on the position postero-dorsal to the prootic and slightly postero-ventral to the supraotic it may actually represent a pterotic bone as proposed by Nursall (1999b) for pycnodonts.

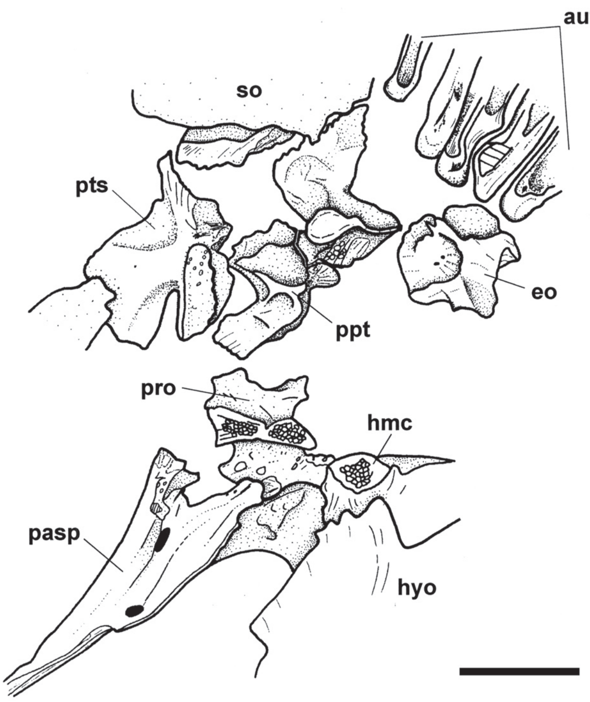


Figure 14: Endocranial elements of *Iemanja palma* (MNHN BCE 166a, holotype). Scale bar = 10 mm.

Cracked, endochondral structures antero-ventrally to the posterior infraorbitals and sclerotic bones, which are visible in some acid prepared specimens, may represent parts of the sphenotic.

The paired exoccipitals are fused with the two or three anterior-most dorsal neural arch elements in *Neoproscinetes* and most other pycnodonts. This bony block (= synarcual of Nursall & Maisey 1991) is relatively massive and well ossified. It surrounds the neural canal and may be effective as a element protecting the notochord during cranial elevation. The exoccipitals are either sutured in small specimens or fused to the posteriorly directed processes of the parasphenoid in large specimens. They are located postero-dorsal to the posterior processes of the parasphenoid. This may indicate that they were located at least partly behind the occipital fissure in life (Figs 14, 16). The anterior margin of the exoccipital is concavely indented for the vagus nerve. There is no basioccipital bone in *Neoproscinetes* and *Iemanja*, although a basioccipital was reconstructed for *Pseudopycnodus nardoensis* by Taverne (1997).

The paired prootic bones are located ventrally to the base of the supraotic and anteriorly to the exoccipitals (Fig. 14). They are separated from the latter by wide gaps. The prootics are in contact with the parasphenoid. In combination with the sphenotic bone they form a groove for the articulation of the hyomandibula with the neurocranium (the hyomandibular facet). The dorsal portion of the hyomandibula is broad without a distinct condylar process and fits in an elongate and rather narrow hyomandibular facet in most plesiomorphic pycnodonts. Several pycnodonts such as *Iemanja* possess a distinct condylar process at the antero-dorsal margin of the hyomandibular head that fits in a circular facet formed by the prootics and the sphenotics.

A distinct and comparably large bone is situated antero-dorsally to the prootic (Fig. 14). It has a thickened and rather straight posterior margin with a dorsally directed extension and a plate-like expanded and thin anterior portion. It is partly covered by the parietal bone and may represent the pterosphenoid bone.

The reconstruction of the labyrinth and the foramina for the cranial nerves is not possible in *Iemanja*. In the Recent *Amia calva*, the prootic bone borders ventro-laterally most of the labyrinth. In comparison, the prootic bone of pycnodonts is rather small (Nursall 1999a; pers. observ.). It may have covered only small portions of the labyrinth, and the pterotic bone and cartilage may have covered the labyrinth laterally and posteriorly. Dorsally it was probably bordered by endocranial cartilage as in *Amia*.

The labyrinth of actinopterygians is characterised by the presence of otoliths. Although many skulls of pycnodonts have been examined for this study no associated otoliths were found and no otolith in situ has been described to date in the literature and the attribution of isolated otoliths to pycnodonts is barely justified. Nevertheless, Stinton & Torrens (1968) assigned isolated otoliths to pycnodonts. They erected the new pycnodont genus *Sphaeronchus* based on isolated sagittae from the Bathonian of South England and identified two species, *S. dorsetensis* and *S. circularis* (Fig. 15). Similar otoliths occur in Mid-Jurassic deposits of northern Germany and Poland

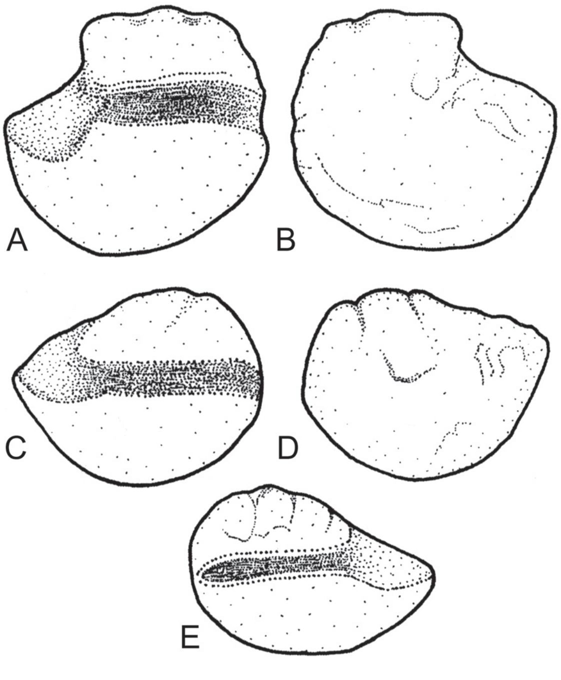


Figure 15: Otoliths assigned to pycnodonts. **A-B:** *Sphaeronchus dorsetensis* (BMNH P. 47394, holotype), left sacculith, inner (**A**) and outer faces (**B**). Antero-posterior length = 4.5 mm. **C – D:** *Sphaeronchus circularis*. Antero-posterior length = 2.6 mm. **C:** BMNH P. 47396, holotype, right sacculith, inner face. **D:** BMNH P. 47397, left sacculith, outer face. **E:** *Sphaeronchus circularis* (BMNH P. 47397), left sacculith, inner face. Antero-posterior length = 2.5 mm. From Stinton & Torrens (1968).

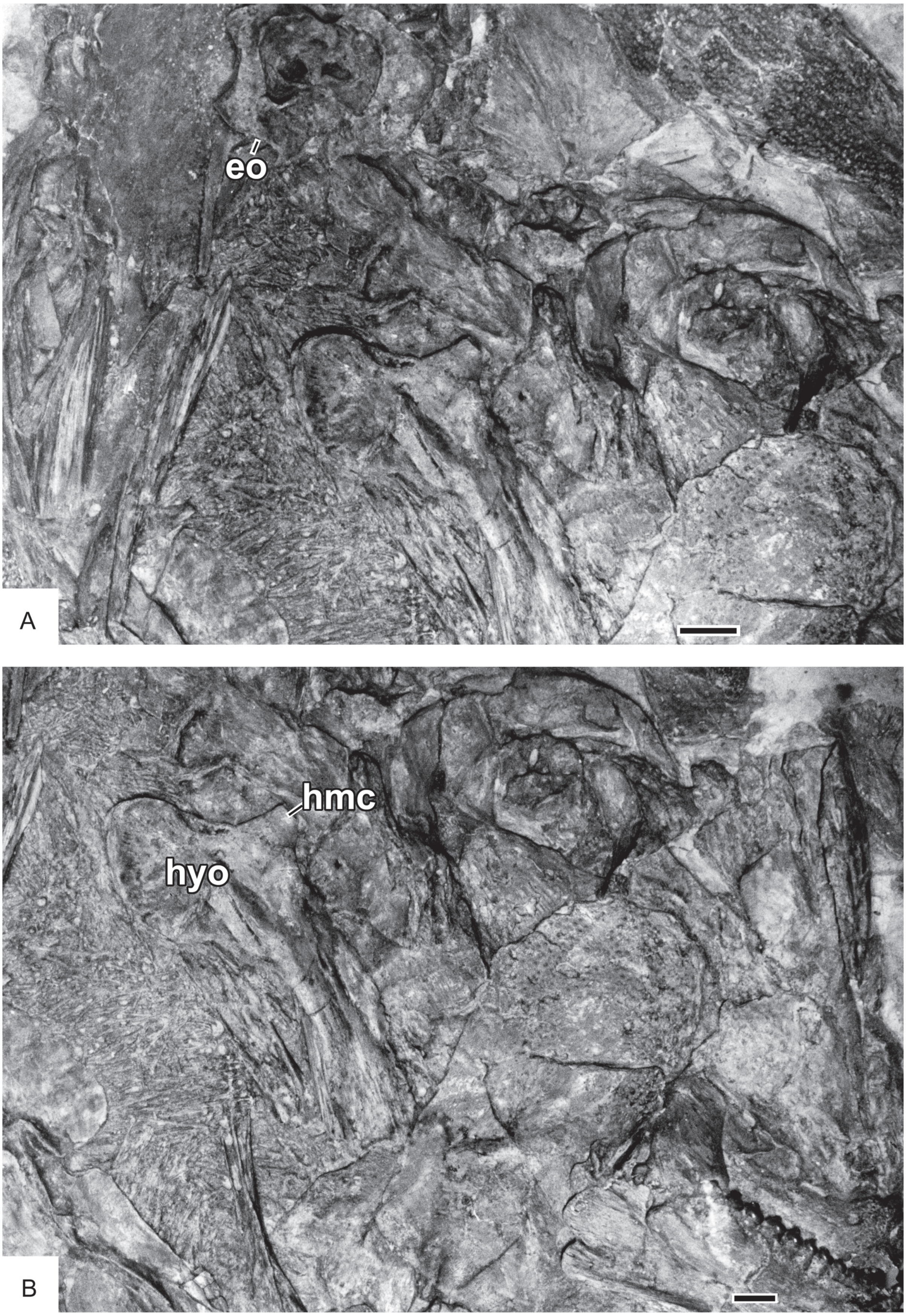


Figure 16: Skull of *Gyrodus circularis* (GPIT 0233) displaying endocranial elements. **A:** Posterior portion, displaying the sclerotic occular bones, the fused exoccipitals, and the upper part of the hyomandibula with the distinct neurocranial process. **B:** Same, displaying the hyomandibula and the pterygoquadrate arcade. Scale bars = 10 mm.

(pers. observ.). However, Nolf (1985) ascertained that these otoliths are indeterminable and identified them as "genus *Acanthopterygiorum*".

The morphology and size of the posterior myodome is not well-understood. It seems to be relatively large and extends far anteriorly. The floor of the myodome is formed by the parasphenoid and prootic ossifications with a large amount of cartilage form the lateral and dorsal walls.

The epioccipital, opisthotic, basisphenoid, and intercalar have not been observed from the examined specimens. Nursall & Maisey (1991) noted the presence of a small bone between the posterior parasphenoid processes in *Neoproscinetes penalvai* and interpreted it as small basisphenoid.

A peculiar feature of *Iemanja* is the presence of large lateral laminae in the mesethmoid (Fig. 17). They are half-egg shaped in outline with a curved ventral and a straight dorsal margin. *Akromystax* also displays hypertrophied lateral laminae, which are densely reticulated, and regarded as autapomorphic character for this taxon (Poyato-Ariza & Wenz 2005).

The base of the endocranium is covered by two dermal bones, the parasphenoid and the vomer. The parasphenoid is edentulous, long and inflected downward below the orbit. It reaches posteriorly behind the occipital margin of the skull below the level of the notochord and buttresses the vomer postero-dorsally (Figs 1A, 12, 17). It is single and median anterior to the orbits and bears a median dorsal crest, which is enveloped by the vertical lamina of the mesethmoid bone. There is a rather complex ventral keel, which separates the branchial chambers. A large fontanel is present about the midpoint of the ventral keel. The opening of the aortic canal is located within this fontanel, which can be closed forming an oval fenestra (e.g., *Anomoeodus*, *Iemanja*, *Neoproscinetes*,

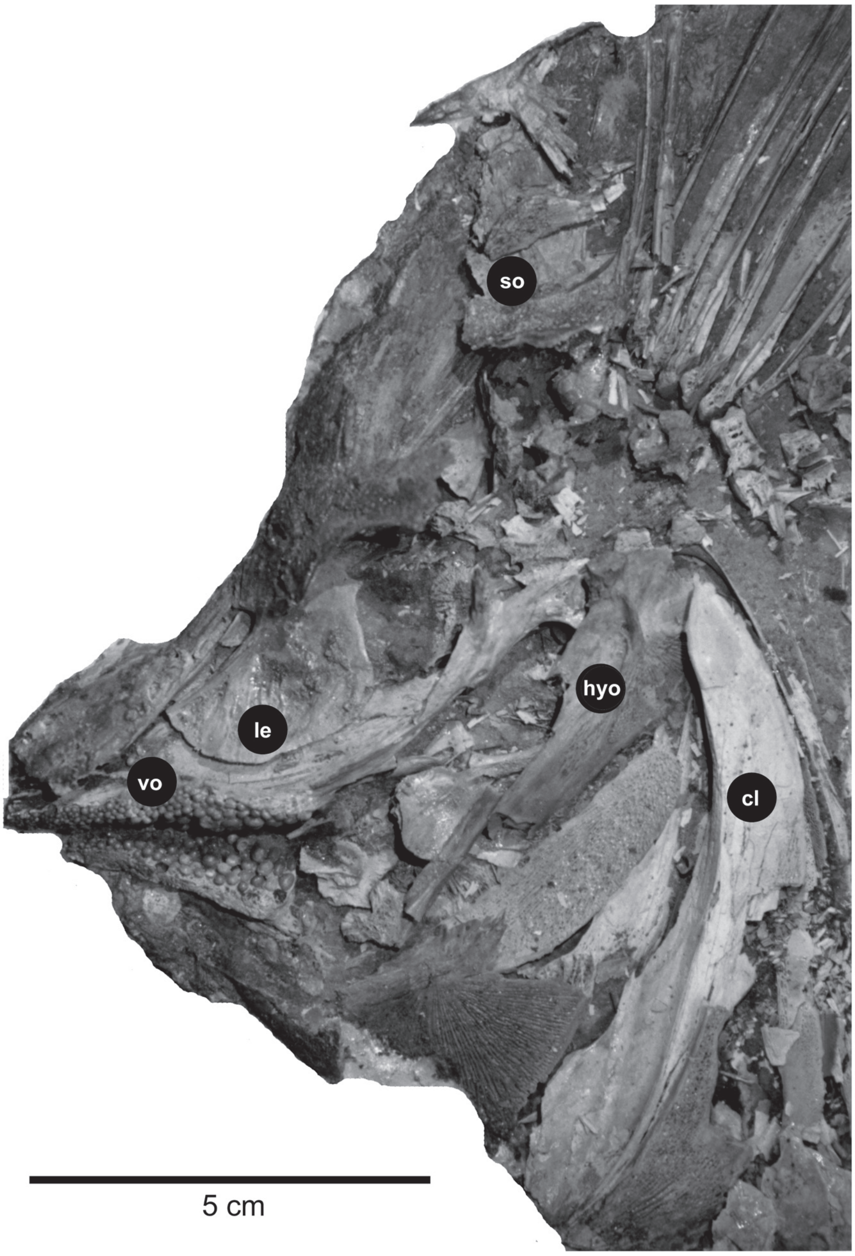


Figure 17: Acid prepared skull of *Iemanja palma* (MNHN BCE 166a, holotype) in lateral view displaying the lateral lamina of the emsethmoid, the parasphenoid/vomer-complex, and endocranial elements.

Palaeobalistum s.l., *Pycnodus*, *Trewavasia*) or be open forming a distinct notch (e.g., *Brembodus*, *Gyrodus*, *Macromesodon*, *Paramesturus*, *Proscinetes*; Fig. 18).

The basipterygoid process, which is located at the posterior end of the ventral keel, is short and stout (Fig. 18). The ascending processes are large and stout. The parasphenoid divides into a pair of posteriorly directed wings just behind the ascending process that pass ventro-lateral to the base of the skull up to the posterior ends of the exoccipitals.

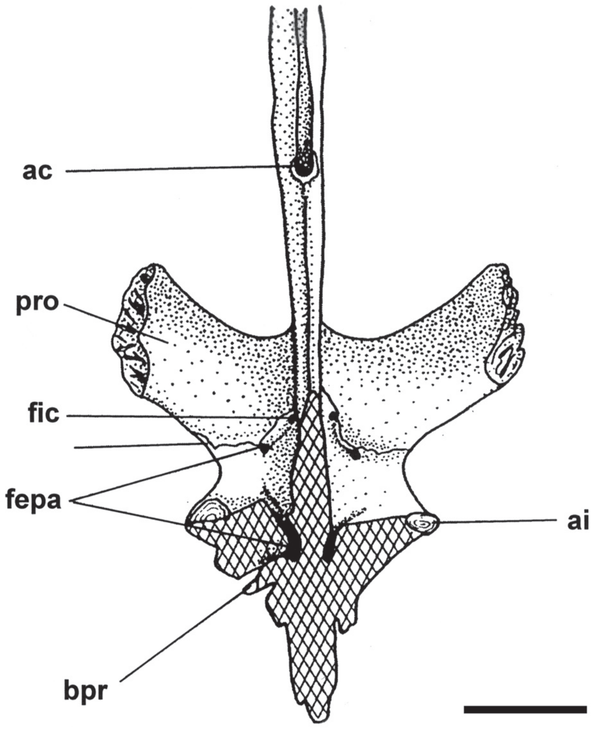


Figure 18: Reconstruction of the parasphenoid of *Mesturus* sp. (GPIT Pi 1261), ventral view. Scale bar = 10 mm. Redrawn from Nursall (1999a).

The vomer is a median element in the roof of the mouth (Figs 12, 17). It is a paired structure in plesiomorphic osteichthyans (e.g., Gardiner 1984). In *Lepidotes*, the vomer is unpaired or paired probably indicating an unnatural grouping. The dentition of the pycnodont vomer is comprised of rather large, molariform teeth, which are arranged in more or less regular tooth rows. Nursall (1996b) assumed that the character 'median vomer' relates *Dapedium* and pycnodonts to teleosts. However, this seems more likely to represent a parallelism occurring in several not closely related forms and may be the result of similar feeding habits (e.g., *Dapedium*, *Lepidotes*, and *Sargodon*).

5. Visceral Skeleton

5.1 Suspensorium

The suspensorium of actinopterygians consists of the palatoquadrate and hyomandibula, preoperculum, and symplectic. A single-unit bony palatoquadrate, which is not fused to the neurocranium, is a synapomorphy for acanthodians, actinopterygians, and sarcopterygians (Arratia & Schultze 1991). Separate elements are present in all three teleostome lineages. Separate endochondral elements of actinopterygians include an autopalatine (e.g., *Polypterus*, *Amia*, *Watsonulus*, most advanced teleosts), metapterygoid (e.g., advanced acanthodians, *Polypterus*, *Lepisosteus*, *Amia*, most teleosts), and quadrate (e.g., advanced acanthodians, *Polypterus*, *Lepisosteus*, *Amia*, teleosts). These bony elements originate from the cartilaginous palatoquadrate and thus ossify perichondrally. Timing of the ossification of the autopalatine varies among extant actinopterygians (Arratia 1997). For instance, the ossification begins late in ontogeny in *Amia* and plesiomorphic extant teleosts

Figure 19: Mandibular articulation of *Pycnodus platessus* (BMNH P. 1634) from the Eocene of Monte Bolca, Northern Italy displaying the two articulation pairs. The symplectic abuts the quadrate and there is an additional articulation surface between both (arrow). Acid prepared specimen.

(Arratia & Schultze 1991). Arratia (1997) assumed that the autopalatine ossifies late in ontogeny in fossil pholidophorids since a bony autopalatine is absent in juvenile specimens. Dermal elements associated with the palatoquadrate in actinopterygians are dermopalatine(s) (tooth plates), ectopterygoid, entopterygoid, dermal tooth plates (not present in all actinopterygians), and quadratojugal.

The preoperculum is included in the opercular series by most authors. However, the preoperculum of actinopterygians functionally belongs to the suspensorium apparatus because it serves as the origin of the adductor mandibulae muscles (Jollie 1962). Anatomically, the hyomandibula and symplectic bones are derived from the hyoid arch of the branchial skeleton. The symplectic develops at the same time as the hyomandibula from the cartilaginous preformed interhyal in actinopterygians (Véran 1988).

The suspensorium of pycnodonts is almost vertical as it is in teleosts. It consists of seven bony elements (Fig. 1A): ectopterygoid, entopterygoid, metapterygoid, hyomandibula, quadrate, symplectic, and preoperculum. In pycnodonts, there is no bony autopalatine in juvenile and adult specimens, and I assume that there was only a chondral pars autopalatina. The paired metapterygoids are relatively large and cover the dorsal portions of the entopterygoid. The ectopterygoid bone is a very delicate structure, which is not preserved in most examined specimens. The placement above each other of the pterygoid bones has been interpreted as a synapomorphy for pycnodonts (Lambers 1991; Nursall 1996b, 1999b). The quadrate is massive, situated ventrally to the entopterygoid and abuts the symplectic. An additional articulation surface is developed between both elements in some pycnodonts (e.g., in *Pycnodus*; Fig. 19). In contrast to teleosts, the quadrate does not possess the posteroventral process; a quadratojugal is not present contrary to the assumptions made by Nursall & Maisey (1991).

The preoperculum is hypertrophied. It is larger than the operculum and is separated from the neurocranium by a lacuna. Its form varies in pycnodonts. It is sort of triangular in pycnodonts where the upper edge is only partially reduced (e.g., *Gibbodon*) to roughly rectangular in advanced pycnodonts with largely reduced preoperculum (e.g., *Pycnodus*; Figs 1A, 2B). The sculpture of the preoperculum corresponds to the general skull ornamentation in most pycnodonts. In *Ichthyoceras*, it is spinose. Striking is the reduction of the upper margin of the preoperculum. The degree of reduction is not consistent within the group but rather varies from genus to genus. The preoperculum is strongly reduced in advanced pycnodonts such as *Pycnodus*.

The hyomandibula of pycnodonts is elongated and placed obliquely with respect to the braincase (Fig. 17). It is tightly fixed to the medial surface of the preoperculum supporting it . Rotation of the preoperculum during mouth opening was mainly initiated and augmented by ligaments, which were fixed to the hyomandibula (Fig. 20). It is more or less exposed above the preoperculum depending on the degree of reduction of the upper part of the preoperculum. The exposed portion of the hyomandibula is almost as large as or even larger than the remaining preoperculum in advanced pycnodonts such as *Coelodus*, *Stemmatodus*, *Tepexichthys*, and *Pycnodus*. The upper part of the hyomandibula of plesiomorphic pycnodonts such as *Mesturus* and *Brembodus* (Fig. 20C) is broad and flattened in lateral view. It articulates with an elongated and narrow facet on the neurocranium. This morphology resulted in limited rotation of the hyomandibula in more plesiomorphic pycnodonts. An articulation process was developed at the antero-dorsal edge of the hyomandibular head in *Gyrodus* and and *Neoproscinetes* mediating rotation mainly around it (Figs 16B, 20A, B). In *Iemanja*, this articulatory process is strong (Fig. 21). Thus, rotation of the suspensorium was more efficient in the advanced pycnodonts. The opercular process is reduced or absent in almost all other pycnodonts. Lambers (1991, 1992) indicated a vestigial opercular process in *Gyrodus* spp., which I did not observe.

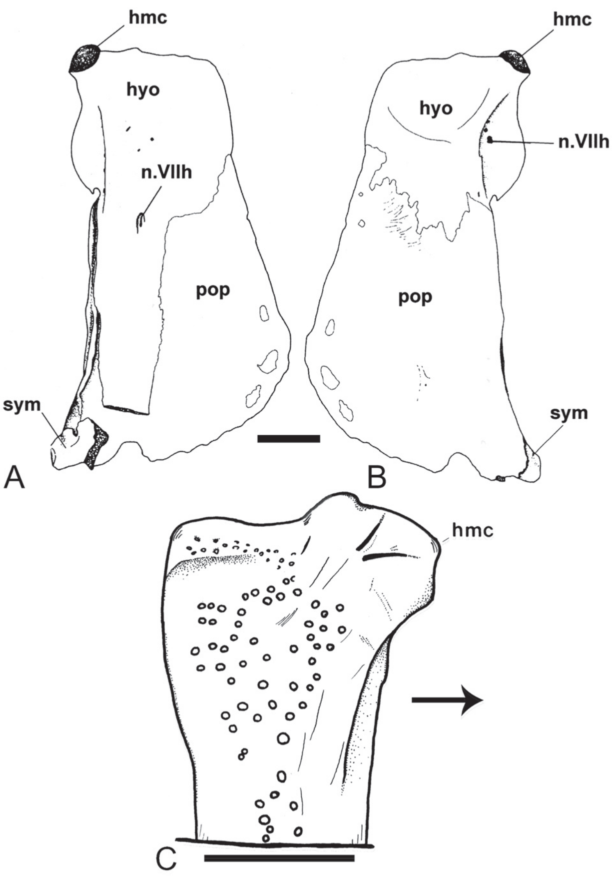


Figure 20: Hyomandibula/preoperculum relationship in pycnodontiforms. A-B: *Neoproscinetes penalvai* (AMNH 11990). Modified from Nursall (1999b). **A:** Medial view. **B:** Lateral view. Scale bar = 5.0 mm. **C:** Upper part of hyomandibula of *Brembodus ridens* displaying the broad articulation surface of the hyomandibula with the neurocranium. Based on IPUM uncat. Scale bar = 10 mm.

The exposed upper part of the hyomandibula is either more or less smooth (e.g., *Iemanja*) or exhibits irregularly arranged tubercles or ridges similar to the sculpture of the dermal bones (e.g., *Akromystax*, *Mesturus*, and *Oropycnodus*). This dermal-like pattern of the hyomandibula was suggested to present some kind of dermalisation by Nursall (1996b, 1999a, 1999b), who consequently called this part of the hyomandibula a dermohyomandibula. However, this sculpture is only

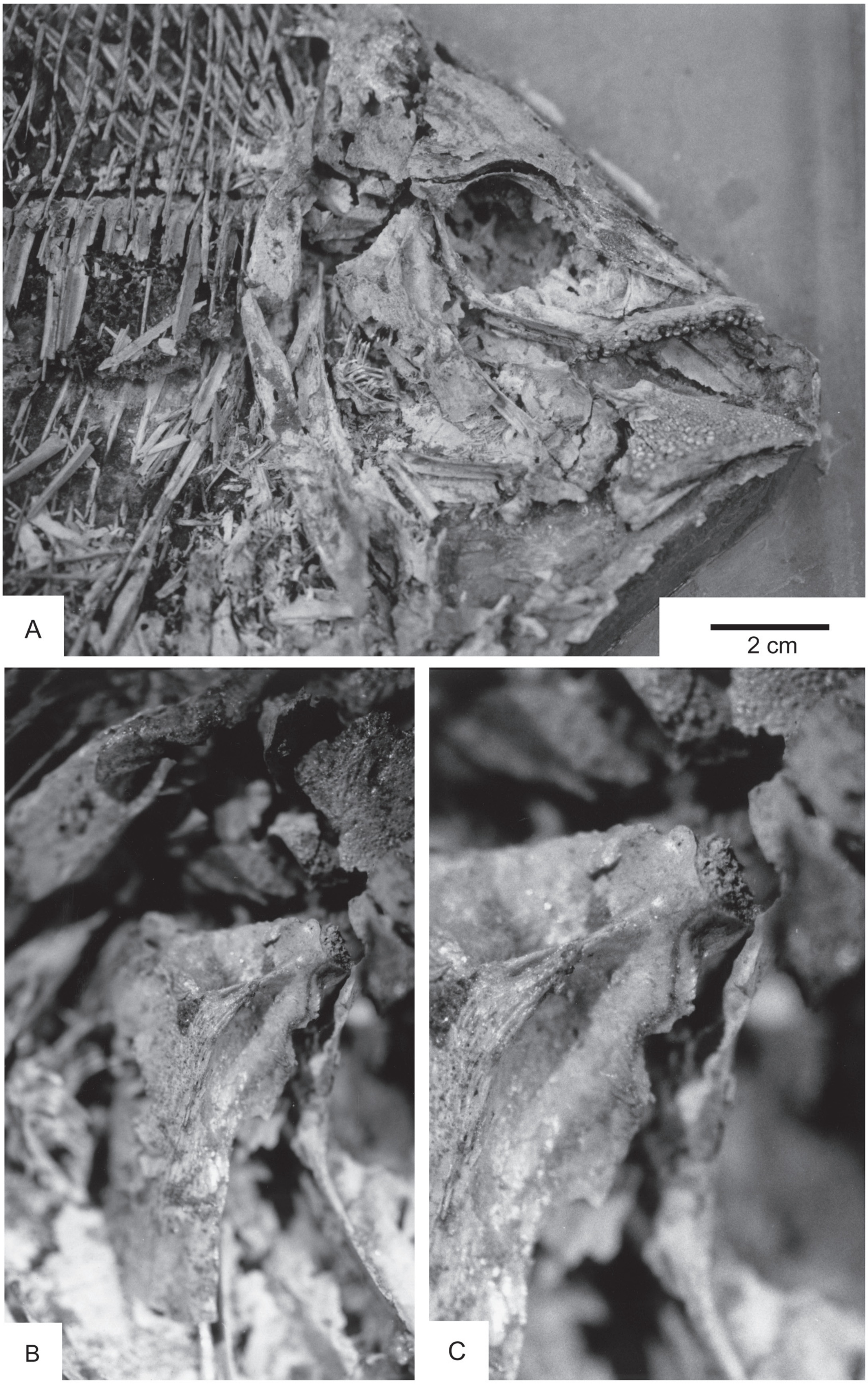


Figure 21: Acid prepared specimen of *Iemanja palma* (AMNH 13963) **A:** Skull and anterior trunk. **B:** Upper part of hyomandibula in antero-lateral view. **C:** Close up of hyomandibular head displaying the distinct neurocranial process.

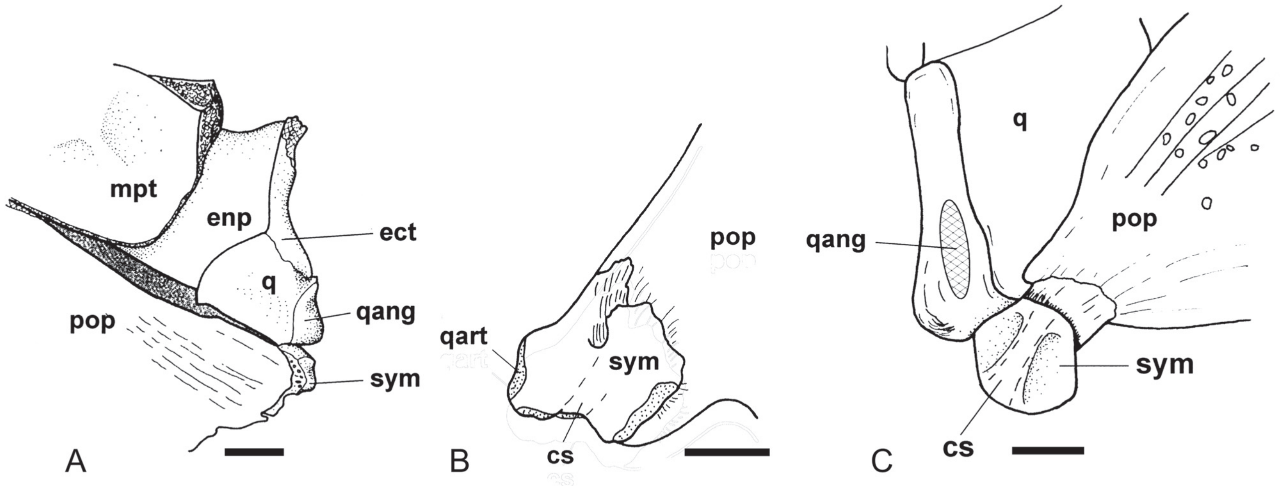


Figure 22: Symplectic-quadrate-preoperculum relationships in pycnodonts. **A:** *Neoproscinetes penalvai*, lateral view (AMNH 11852). Modified from Nursall (1999b). **B:** Symplectic of *Neoproscinetes penalvai* (AMNH 11843), medial view. Redrawn from Gardiner et al. (1996). **C:** Symplectic of *Proscinetes radiatus* (BMNH P.1627). Scale bar = 10 mm.

superficial and the hyomandibula is an endochondral bone. The development of a membranous outgrowth reflects a change in an existing structure rather than the development of a new bone with any implied homology. Consequently, the dermal-like pattern rather corresponds to a membranous outgrowth than to a true dermalisation and the term dermohyomandibula implies wrong homologies. A membranous outgrowth on the anterior or posterior region of the hyomandibula is found in many advanced actinopterygians (G. Arratia, pers. comm.). Nevertheless, Poyato-Ariza & Wenz (2002) suggest retaining this name as a descriptive term. The development of the membranous outgrowth of the upper part of the hyomandibula in pycnodonts is related to the reduction of the preoperculum since only the exposed hyomandibular parts show the dermal-like structure. The sculptured part of the hyomandibula was occasionally misinterpreted as operculum (e.g., Blot 1987) or dorsal preoperculum (Wenz 1989).

A small bone at the antero-ventral border of the preoperculum corresponds to the symplectic bone in pycnodontiforms (Fig. 22). It is rather massive, robust, and articulates with the antero-ventral edge of the medial surface of the preoperculum. The symplectic was probably fixed to the preoperculum by connective tissue. This condition differs from that seen in many other neopterygians, in which the symplectic does not contact with the preoperculum. The lack of contact between symplectic and preoperculum was considered a teleostean synapomorphy (e.g., Véran 1988; Pinna 1996). The symplectic of *Elops*, *Lepisosteus*, *Semionotus*, *Lepidotes*, *Dapedium*, and *Pachycormus* is placed medially to the quadrate (Gardiner et al. 1996; Arratia 1999). However, the situation in the plesiomorphic teleosts *Leptolepis coryphaenoides* and more advanced teleosts (e.g., *Elops*) is different from that found in other plesiomorphic teleosts, because the symplectic is separated from the preoperculum by the postero-dorsal process of the quadrate. The symplectic and quadrate are slightly inclined antero-ventrally to the hyomandibula in pycnodonts.

In pycnodonts, the quadrate is vertically oriented and lies dorsal to the symplectic. Generally, both elements are closely arranged with the symplectic being in contact with the quadrate, and even supporting it in some pycnodonts (e.g., *Pycnodus*). The articulation facet of these bones is convex. The symplectic condyle is more or less circular in outline and fits into the glenoid facet on the articular bone of the lower jaw.

The elongation of the suspensorium of pycnodonts is related to the shortening of the lower jaw and placement of the quadrate-mandibular articulation below the orbit, but not posteriorly to it as seen in plesiomorphic actinopterygians.

5.2 Opercular Apparatus

The opercular series of actinopterygians usually consists of preoperculum, operculum, suboperculum, and interoperculum. The size and shape of the bones have been used in generic and specific diagnosis of many actinopterygian taxa. The opercular apparatus of pycnodonts is reduced compared to that of other neopterygians (Figs 1A, 2). It is composed of a large and more or less triangular preoperculum (see above), an operculum that is attached to the postero-dorsal border of the preoperculum, and generally two short acinaciform (slender) branchiostegal rays (there are three broad rays in *Gibbodon*), which articulate with the ceratohyal elements. Sub- and interoperculum are missing. In addition, Poyato-Ariza & Wenz (2002) report more than two branchiostegal rays in a single specimen of *Mesturus*. However, this find needs to be confirmed.

The operculum is small, narrow, and dagger-shaped in almost all pycnodonts. *Pycnodus* completely lacks the operculum. The functional significance of the reduction of the operculum is unclear because the operculum is involved in the rotation of the hyomandibulo-preoperculum system in other pycnodonts and helps expanding the branchial chamber.

The reduced number of branchiostegal rays in pycnodonts is striking. A reduced number is also found in some plesiomorphic actinopterygians such as haplolepids, redfieldiiforms, saurichthyids, and lepisosteiforms (Lambers 1991) and some teleosts (McAllister 1968; Lambers 1991). However, the

Figure 23: Vertical section through an isolated and fragmentary skull of *Gyrodus* sp. from the Oxfordian (Upper Jurassic) of Chile displaying internal characters and articulation between vomer and premaxilla (arrow). For further explanations see text. Scale bar = 20 mm.

lowest number found in other actinopterygians is generally three. Acinaciform rays are also present in *Macrosemius* and *Propterus* (Bartram 1977) and advanced teleosts (McAllister 1968). The reduction of the branchiostegal rays to three and two short elements respectively in pycnodonts indicates a small branchiostegal membrane and suggests a relative small potential for opercular chamber expansion, which would affect the feeding habits.

No gular plate, suboperculum, and interoperculum are present in pycnodonts. The enlargement of the preoperculum

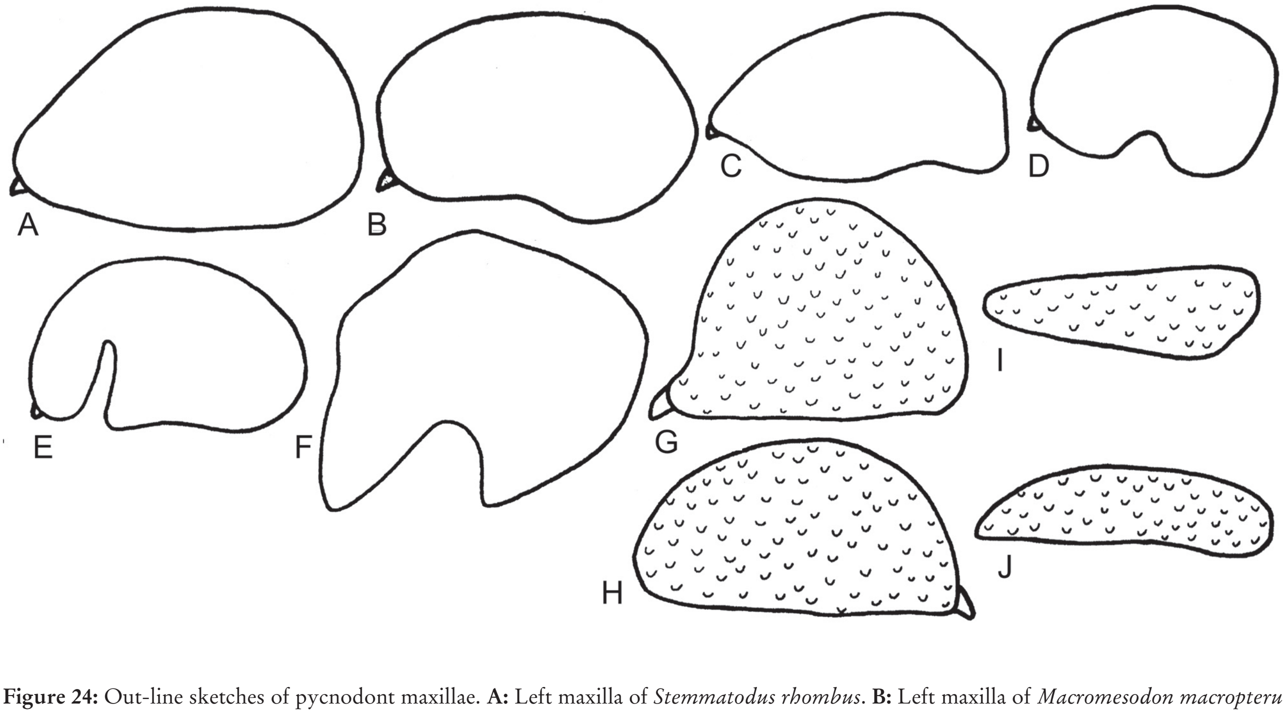


Figure 24: Out-line sketches of pycnodont maxillae. **A:** Left maxilla of *Stemmatodus rhombus*. **B:** Left maxilla of *Macromesodon macropterus*. **C:** Left maxilla of *Neoproscinetes penalvai*. **D:** Left maxilla of *Coelodus* sp. **E:** Left maxilla of *Tepexichthys aranguthyorum*. **F:** Left maxilla of *Oropycnodus ponsorti* (BMNH P.3003). **G:** Left maxilla of *Gyrodus hexagonus*. **H:** Right maxilla of *Gyrodus circularis*. **I:** Left maxilla of *Arduafrons prominoris*. **J:** Left maxilla of *Mesturus verrucosus*. All lateral view. Not to scale.

above the branchiostegals may be regarded as replacement of the suboperculum. The interoperculum developed in association with a mobile maxilla and a forwardly directed jaw articulation in the evolution of actinopterygians towards the characteristic halecostome suction feeding (Schaeffer & Rosen 1961; Lauder 1980, 1982). Thus, the interopercular bone is a key element in the chain of elements transmitting contraction of the levator operculi muscle to the mandible (Lauder 1983). The absence of the interoperculum and the associated interoperculo-mandibular ligament in pycnodonts indicates that there must have been an alternative way to transmit the forces from the opercular apparatus to the mandible (Kriwet 2001b). The branchial opening of pycnodonts was high but rather narrow due probably to the fore-shortened skull and the reduced operculum.

5.3 Jaw Apparatus

The upper jaw of lower actinopterygians usually includes a quite large and dentated maxilla that is fixed to the cheek and a dentated premaxilla. The lower jaw consists of a large and dentated dentary, angular, and articular, and ventrally a surangular posterior to the dentary, a prearticular, and the coronoids medial to the dentary. The jaw apparatus of neopterygians is characterised by several morphological innovations. For instance, the maxilla becomes free from the cheek region and a new dermal bone, the supramaxilla, develops dorsally to the maxilla. Most basal neopterygians possess only a single supramaxilla, whereas the more advanced forms possess two. The premaxilla-maxilla relation is very complex in teleosts. However, there are some problems concerning the interpretation of the length of the premaxillary and maxillary processes in fossil plesiomorphic teleosts (Arratia 1997). Thus, the joint and relation of these bones remain elusive to date. In advanced teleosts, premaxilla and maxilla form a functionally important structure for upper jaw protrusion.

The jaw apparatus of pycnodonts is unique. The upper jaw consists of paired premaxillae and maxillae as in other actinopterygians. However, the premaxillae bear a single row of styliform or chisel-shaped grasping teeth while the maxillae are edentulous. The lower jaw is composed of dentaries, prearticulars, angulars, and articulars. The dentaries bear a single row of styliform or chisel-shaped teeth as the premaxilla while the prearticular teeth are molariform and generally arranged in several rows (except in *Iemanja*).

The premaxilla is composed of a tooth-bearing portion and the ascending premaxillary process (Figs 1A, 2B). The ascending premaxillary process anteriorly roofs the snout and covers one third of the length of the anterior mesethmoid edge in advanced pycnodonts. In some plesiomorphic pycnodonts, it is relatively short and covered by dermal elements (e.g., *Arduafrons* and *Mesturus*). There is some confusion about the homology of the nasal process of the premaxilla within neopterygians, e.g., in *Amia* (Grande & Bemis 1998).

The nasal process of *Amia* forms the most profound part of the nasal cavity. But in pycnodonts, this process is completely superficial and actually like the superficial position of the ascending process of teleosts. There is no articular process of the premaxilla in pycnodonts. In advanced teleosts, the articular process of the premaxilla is well developed and articulates with the premaxillary process of the maxilla forming the protruable upper jaw. Nursall (1999b) reported that the connection between premaxilla and mesethmoid was not tight in *Macromesodon macropterus*. This assessment was based on X-ray photographs. In addition to this, a vertical section through an isolated skull of *Gyrodus* sp. from the Oxfordian of Chile also shows that the ascending process of the premaxillary bone is loosely attached to the anterior surface of the mesethmoid bone with some kind of articulation or attachment between the premaxilla and the anterior edge of the vomer (Kriwet 2000; Fig. 23). No nasal depression like that occurring in several advanced teleosts (e.g., Nanididae) is found on the snout to fix the premaxillary process. The morphology of the premaxilla of plesiomorphic teleosts differs from that of pycnodonts. The premaxilla of "pholidophorids" and *Leptolepis* is small, and the ascending process is rather short but massive similar to the condition seen in *Mesturus*. Nevertheless, it is assumed that the

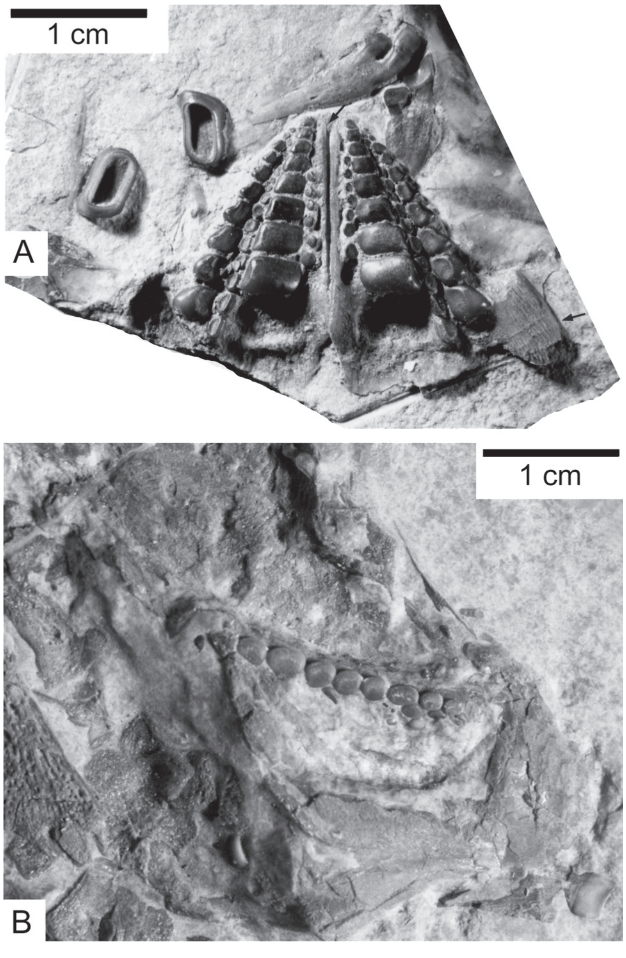


Figure 25: Jaw apparatus of pycnodonts. **A:** Associated prearticulars of *Proscinetes elegans* (BSP 1885 IX 60) displaying the long symphysis and displaced right dentary. **B:** Jaw apparatus of *Coelodus costae* displaying rather large right angular bone in lateral view and outer vomerine tooth row. Remark: Poyato-Ariza & Wenz (2002) consider *Coelodus* to be monogeneric including only the species *C. saturnus*. The species *C. elegans* is only tentatively assigned to *Coelodus* here pending further systematic analyses. Scale bar = 20 mm.

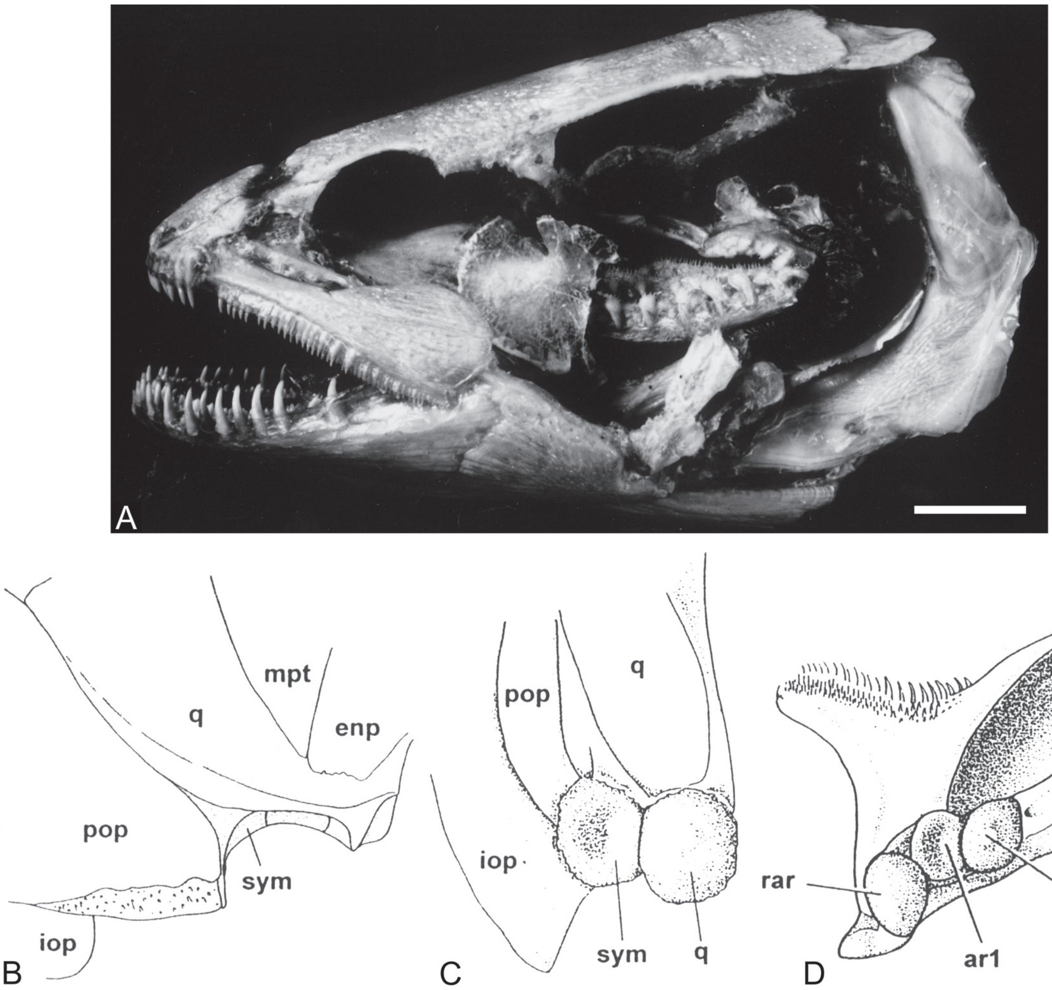


Figure 26: Skull of the extant *Amia calva*. **A:** Skull in lateral view with removed cheek and opercular bones. Scale bar = 10 mm. **B:** Quadrate-symplectic complex, medial view. **C:** Same in anterior view displaying the condylar quadrate and the glenoid symplectic. **D:** Mandible, posterior view, displaying the two articular elements and the retroarticular. For further explanations see text. Figures **B-D** provided by J. R. Nursall (Whaletown, Canada).

premaxilla of these teleosts was already mobile (e.g., Patterson 1977; Lauder 1982). The premaxilla has become secondarily fixed firmly to the neurocranium in several predaceous teleosts including *Hoplias* and *Salmon* (Lauder 1982).

The maxillae of pycnodonts are easily lost after death due to their loose attachment on the lateral surface of the head. In some pycnodonts the ventral margin of the maxillae is concave or deeply notched (Fig. 24D-F). Generally, the maxillae were anchored anteriorly by an articular peg (Fig. 24A-E, G, H). The articular peg fits into a shallow posteriorly indentation of the premaxillary bone in most pycnodonts, with the exception of *Mesturus* spp. where the maxillary bone is rather narrow and long without any anterior articulatory peg (Fig. 24J). Comparison with extant teleosts with similar dentitions (e.g., sparids, acanthurids) indicates the possibility that the maxilla was fixed posteriorly to the mandibular arch by a ligamentum maxillo-mandibulare.

The lower jaw is suspended from the suspensory apparatus by the quadrato-symplectic-mandibular joint. The mandible is short compared to that of plesiomorphic actinopterygians. The prearticular makes up most of the lower jaw. It was called "splenial" in the past (e.g., Lambers 1991). The prearticular bones form a more or less pronounced basin, in which the flat or convex oral surface of the vomerine dentition accurately fits during mandibular abduction. Both prearticulars meet medially along a long and vertically oriented symphysis, which is either rather short (e.g., *Hadrodus*) or very long (e.g., *Anomoeodus* and *Iemanja*) (Fig. 25). Thurmond (1974) assumed that both prearticulars were not tightly fixed and proposed a lateral adductive/abductive mandibular action. Nursall (1999b), conversely, suggested that the prearticulars were tightly fixed and rejected the interpretation of Thurmond (1974). In contrast, the surfaces of the symphysis show a rugose pattern indicating the presence of limited kind of connective tissue allowing some lateral movements during mouth closure.

Distinct coronoid ossifications are not present in pycnodonts. A distinct and stout process is tightly fused postero-laterally to the prearticular bone (Fig. 25). This process is usually called coronoid process although the bones included in the coronoid process are different in actinopterygians. Consequently, the coronoid process of pycnodonts is not homologous to that of palaeoniscoids or teleosts. The presence of a coronoid process was considered a neopterygian synapomorphy by Gardiner (1984). However, a well developed "coronoid process" was demonstrated for plesiomorphic palaeoniscoids by Gardiner (1967) and Gottfried (1993). This contradicts the assumption that a direct correlation exists between the presence of a "coronoid process" and a free maxilla in "subholosteans" as proposed by Schaeffer (1956).

5.4 Mandibular Articulation

The articulation of the lower jaw of pycnodonts is unique with similarities to the mandibular articulation of halecomorphs. Lower jaw articulation at the halecomorph level involves the quadrate and symplectic bones associated with different mandibular elements. Patterson (1973) suggested that the symplectic of "holosteans" and teleosts developed as a brace for the quadrate and described the articular relationships of the lower jaws of several "holostean" forms. The lower jaw of *Dapedium* articulates exclusively with the quadrate, the symplectic does not participate in the mandibular articulation. In *Furo*, the quadrate and symplectic are positioned next to one another. *Caturus* has a similar articular association. The main difference is that the symplectic is slightly postero-lateral to the quadrate, which is closer to the condition found in *Amia*. Patterson (1973) described the jaw joint of an unidentified parasemionotid as being rudimentarily similar to that seen in amiids, in that the symplectic, placed somewhat laterally, shares the articular articulation with the quadrate, which extends mediad. Consequently, Patterson (1973) placed the parasemionotids at the base of the Halecomorphi. Olsen (1984) reported similar articular associations from the parasemionotid *Watsonulus*, in which the symplectic is somewhat postero-lateral to the quadrate similar to the condition found in *Caturus* and *Amia*. Based on these discoveries, Olsen (1984) concluded that *Watsonulus* must be the plesiomorphic sister-group of the clade containing amiids, gars, and teleosts.

The quadrate articulates with an anterior articular element (Bridges's ossicle "c") in *Amia* (Grande & Bemis 1998; Fig. 26). Laterally to the quadrate, in a horizontal plane, the symplectic articulates with a posterior articular element (Bridges's ossicle "d"). A well-developed, synovial articular capsule binds the two points of conjunction. The quadrate is convex (condylar) and the symplectic concave (glenoid). The same condition is present in caturids (Patterson 1973; pers. observ.). The posteriormost element in the lower jaw of *Amia* is the retroarticular.

The articular association in pycnodonts is similar, but quite peculiar (Fig. 19). Both quadrate and symplectic participate in

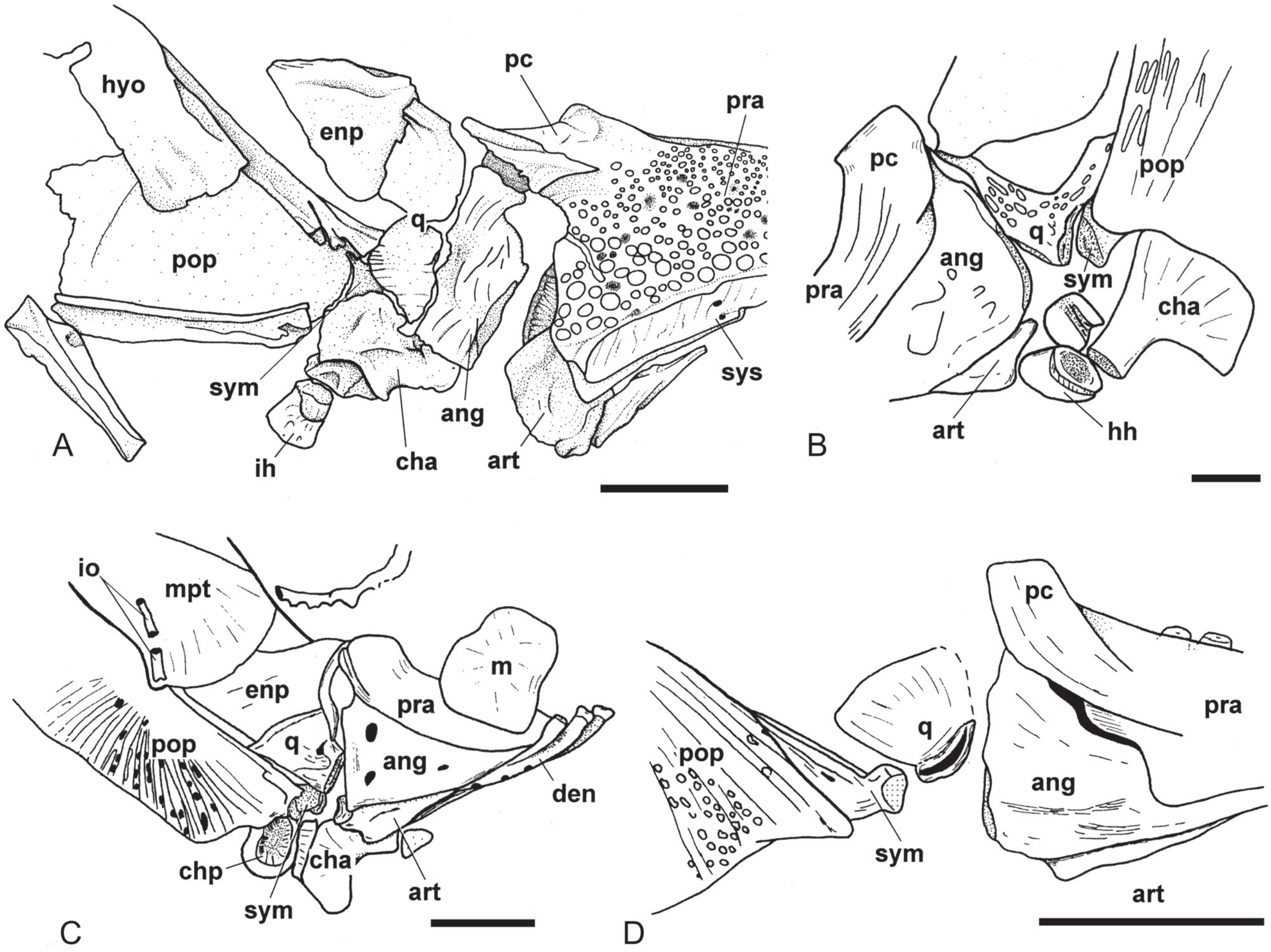


Figure 27: Mandibular articulations in pycnodont fishes. **A:** Pterygoquadrate arcade and mandibular articulation of *Iemanja palma* (AMNH 13963). Scale bar = 10 mm. **B:** *Macromesodon* sp. (BMNH P.11774), left side. Scale bars = 5.0 mm. **C:** *Macromesodon* sp. (BMNH 37109), right side. Scale bars = 5.0 mm. **D:** *Coelodus subdiscus* (MNHN MSE 442), right side. Scale bar = 5.0 mm.

the mandibular articulation. The quadrate lies vertical and dorsal to the symplectic and both are generally closely arranged. The articulation facet of each bone is convex. The quadrate condyle is more or less elliptical in outline, with a vertically oriented long axis. Laterally, the mandibular facet is comprised of a thickened, bevelled margin, whereas the medial part of the quadrate condyle is rarely preserved suggesting that the glenoid cavity originally may have been cartilaginous. The symplectic condyle is rather circular and fits into a glenoid facet on the articular of the lower jaw.

The similarity between *Amia* and pycnodonts in mandibular articulation is that both quadrate and symplectic are involved more or less independently. Their relationships with pterygoids and hyomandibula-preoperculum, respectively, are also similar (Fig. 27). Nevertheless, the relationships between symplectic and quadrate on the one hand and the mandible on the other hand differ between amiids and pycnodonts. In pycnodonts, the quadrate and symplectic articulate with the articular bone. However, a specimen of *Pycnodus platessus* shows that most of the symplectic articulates with the quadrate supporting it (Fig. 19). The surfaces of the quadrate and symplectic are oriented almost vertically in most pycnodonts with the symplectic in ventral position, whereas the surfaces of the quadrate and symplectic are almost horizontal in relation to one another in amiids and caturids, the symplectic medial to the quadrate. Moreover, both quadrate and symplectic articulatory surfaces are convex in pycnodonts, fitting concave facets on the mandible. Conversely, the quadrate articulatory surface is convex, while that of the symplectic is concave in amiids and caturids. The symplectic abuts the quadrate in pycnodonts and in some species an additional articulation surface is developed between both (e.g., *Pycnodus*). In amiids, the quadrate articulates with the anterior articular element (Bridge's ossicle "c") and the symplectic with the posterior articular element (Bridge's ossicle "d"), the whole complex being invested with a well developed articular capsule. This articular capsule may also have been developed in pycnodonts.

The dentaries are rather slender and are firmly sutured antero-ventrally to the prearticulars in pycnodonts during life but got easily disarticulated and lost after death (Fig. 25A). The angulars cover the postero-lateral portion of the mandible (Fig. 25B). The articulars are positioned medially to the angulars. There is no retroarticular ossification.

5.5 Dentitions

Pycnodonts have been defined by their unique tooth mor-

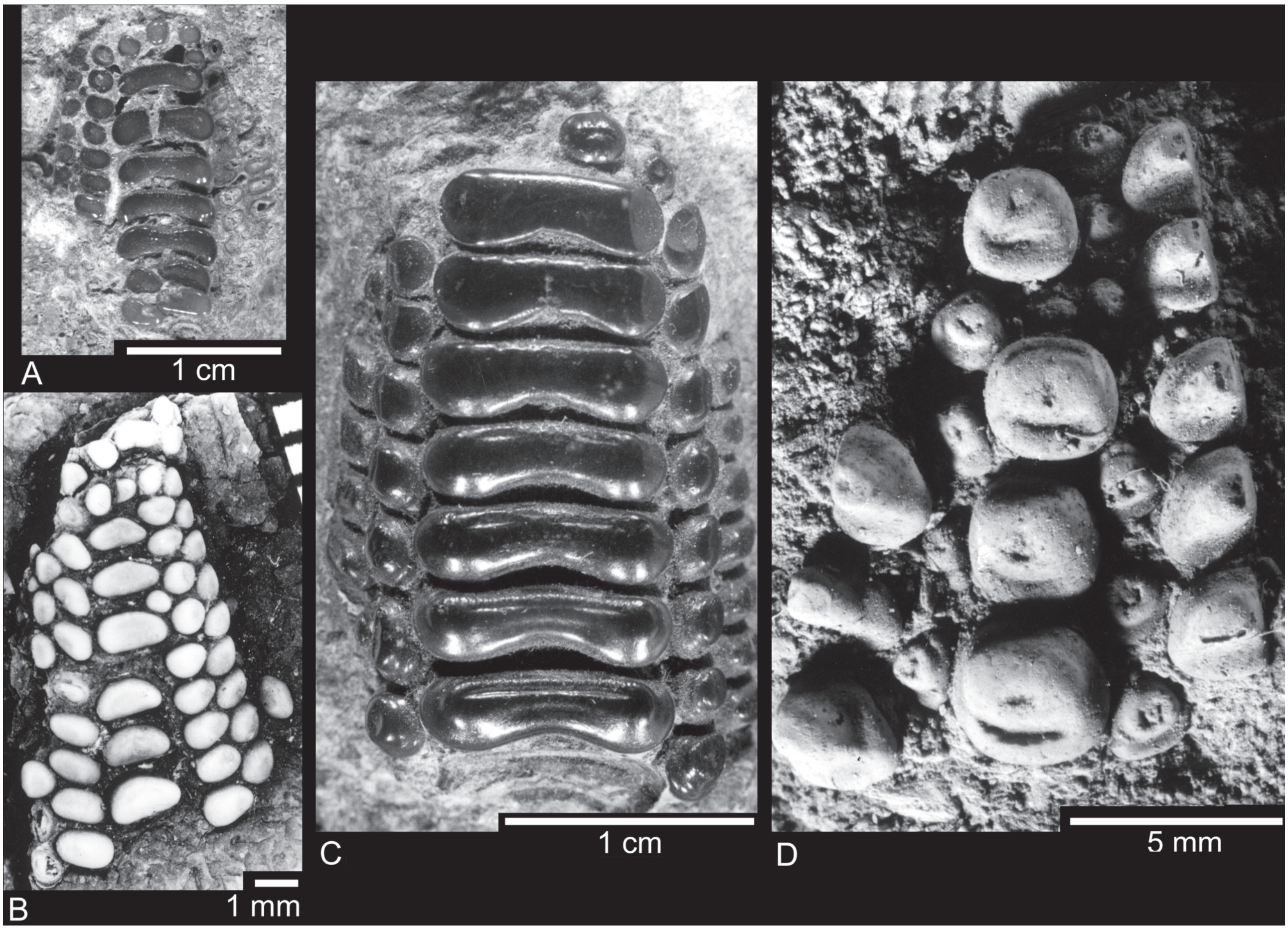


Figure 28: Isolated vomerine dentitions of pycnodonts. **A:** '*Coelodus*' sp. (IPFUB uncat.), Late Jurassic (Malm), Thüster Berg (northern Germany). **B:** '*Coelodus*' sp. (IPFUB Uña Pyc 15), late Barremian (Early Cretaceous), Uña (eastern Spain). **C:** '*Coelodus*' sp. (IPFUB uncat.), Wealden (Early Cretaceous), northern Germany (precise locality unknown). **D:** Pycnodont indet. (cf. *Gyrodus* sp.) (MB. f. 7133), Hauterivian (Early Cretaceous), Langenberg near Oker (northern Germany).

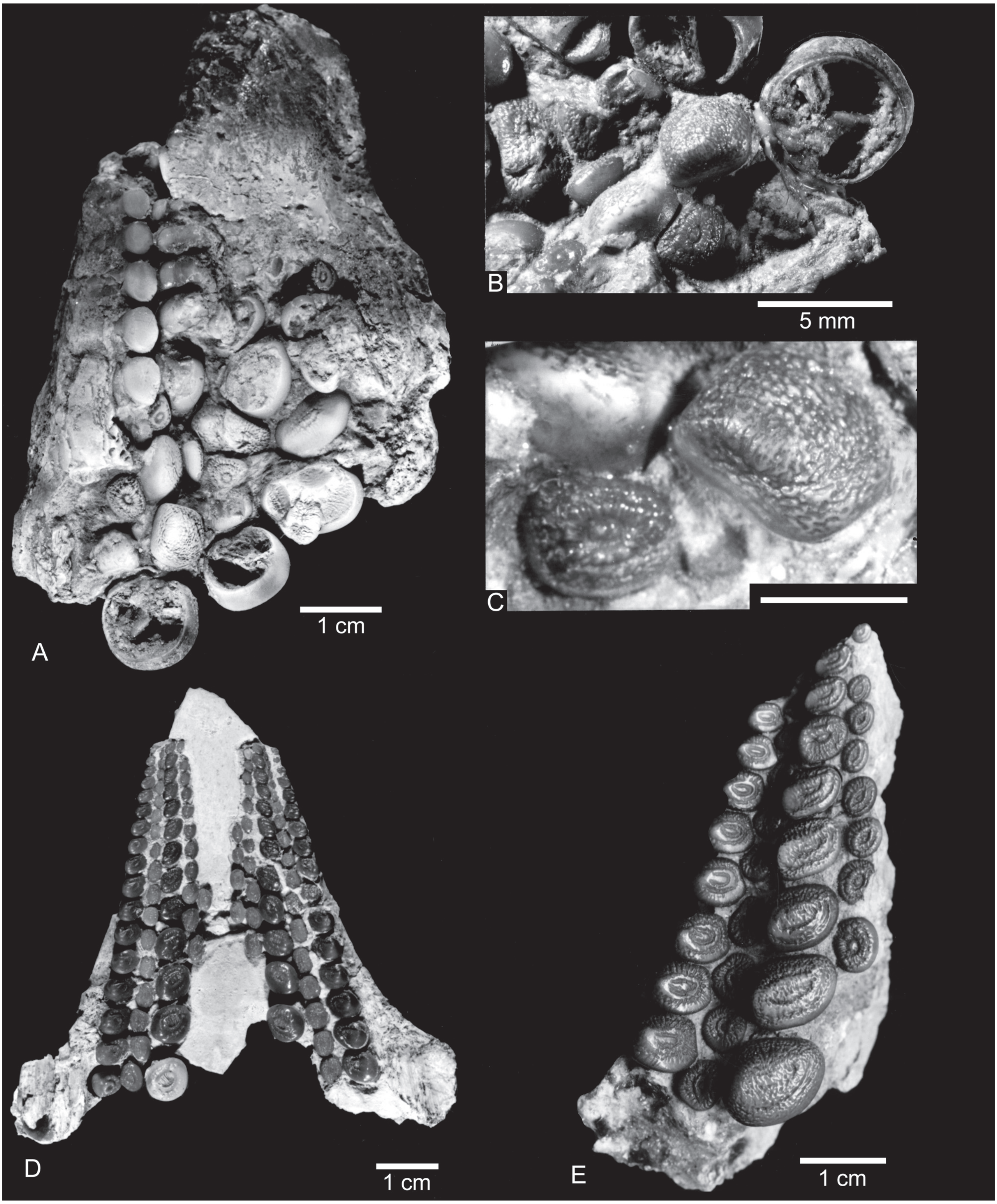


Figure 29: Dentitions and teeth of *Gyrodus circularis* from the Upper Jurassic of southern Germany. **A-C:** Holotype (BSP AS I 507). **A:** Associated vomerine and prearticulars. **B:** Posterior prearticular portion. **C:** Close up of B showing the two types of teeth occuring in *Gyrodus circularis*. **D:** Associated prearticular dentitions of specimen BSP 1972 XX 137. **E:** Left prearticular dentition of specimen JME SOS 3130 from Winterhof.

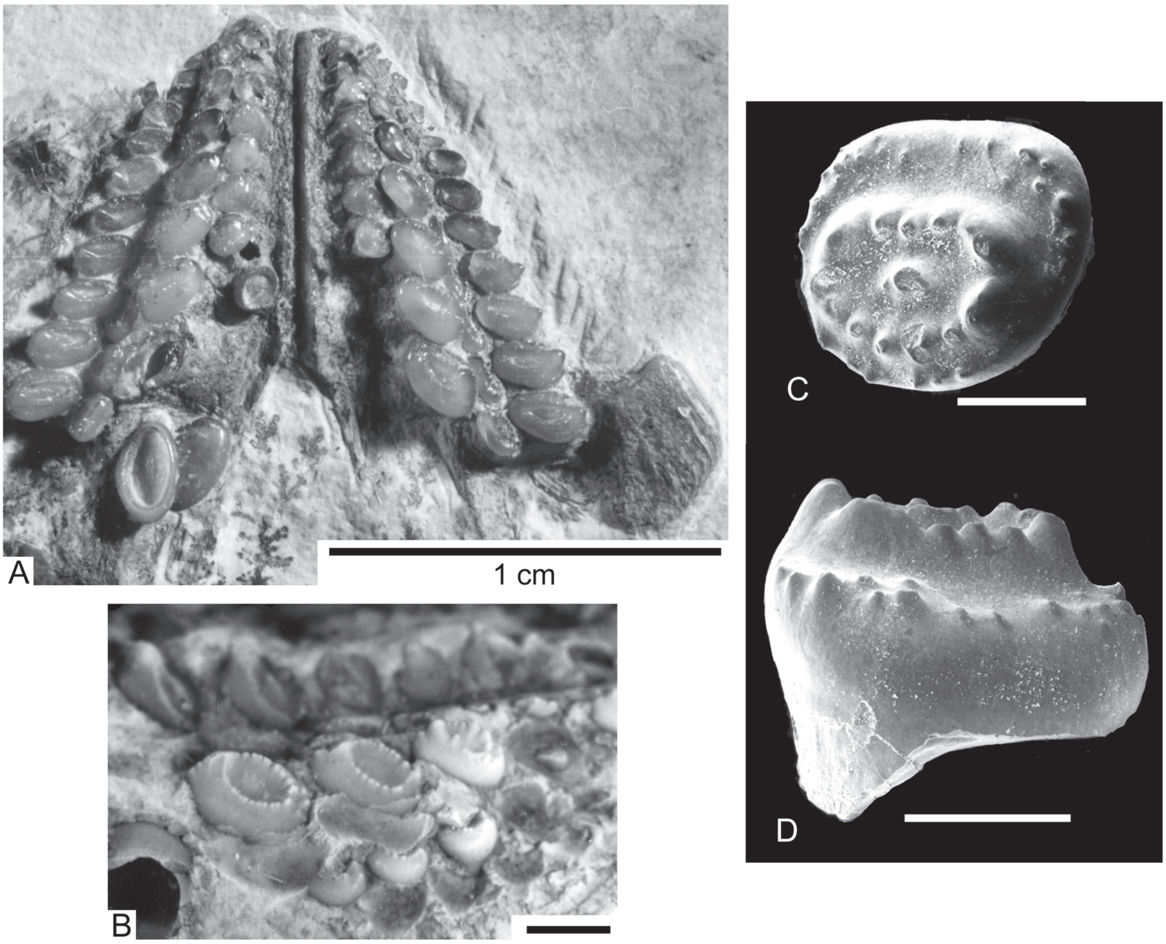


Figure 30: Dentitions and teeth of *Gyrodus hexagonus* from the Upper Jurassic of southern Germany. **A:** Associated prearticulars of MB.f. 1345. **B:** Posterior main prearticular teeth of BSP AS VII 1073. Scale bar = 10 mm. **C:** Isolated tooth of IPFUB (uncat.), occlusal view. Scale bar = 0.5 mm. **D:** Same as in C, posterior view. Scale bar = 0.5 mm.

phology and arrangement. The Greek word pycnos means "dense". Isolated teeth and dentitions are by far the most common remains preserved in the fossil record. For the last 150 years, the highly developed and specialised crushing heterodont dentition has long been regarded a main character in identification and most pycnodont species are based entirely on characteristics of the prearticular or vomerine dentitions. However, Poyato-Ariza (2003: 938-939) proposed a phylogenetic hypothesis based exclusively on dental characters and concluded that "the taxonomic assessment of isolated dentitions falls within the domain of parataxonomy ….. and cannot provide a hypothesis of phylogenetic relationships for pycnodontiform fishes". This is certainly a disappointing statement and I disagree with ascertaining dental taxonomy to be parataxonomic. Dentitional characters and their variation are still inadequately understood and it is, of course, possible to identify species and genera with the help of isolated dentitions (as correctly stated by Poyato-Ariza 2003). More data and better understanding of dentitional character traits will provide additional insights into phylogenetic interrelationships of pycnodontiform fishes. At present, they are useful and essential tools for identifying taxa in fossil assemblages where no articulated remains are preserved. More important, these remains are crucial for a more complete understanding of the diversity patterns of pycnodontiforms. Therefore, as many pycnodont dentitions and teeth as possible are figured in this study to provide additional information for further phylogenetic analyses (Figs 28-44).

Teeth are restricted to the unpaired vomer in the roof of the mouth and the paired prearticulars, premaxillae, and dentaries in pycnodonts. The teeth are arranged in longitudinal rows on the vomers and prearticulars with small teeth anteriorly, which increase in size posteriorly in most pycnodontiforms. In addition, there are styliform or prehensile grasping teeth confined to the premaxillae and dentaries. All teeth are rigidly fixed to the jaw elements and embedded in shallow depressions or sit on small bony elevations. Replacement of teeth was discussed controversially in the last few years. Nursall (1996b), for instance, assumed that there was a single generation of teeth and teeth were added from behind to the dentition. Similarly, Woodward (1895) and Thurmond (1974) suggested that new teeth were added to the dentition from behind, whereas Longbottom (1984) proposed that worn teeth were replaced by small irregularly disposed teeth. Hennig (1907) described an apparent replacement tooth beneath a broken tooth in the vomer of *Nursallia goedeli,* but considered this an exceptional

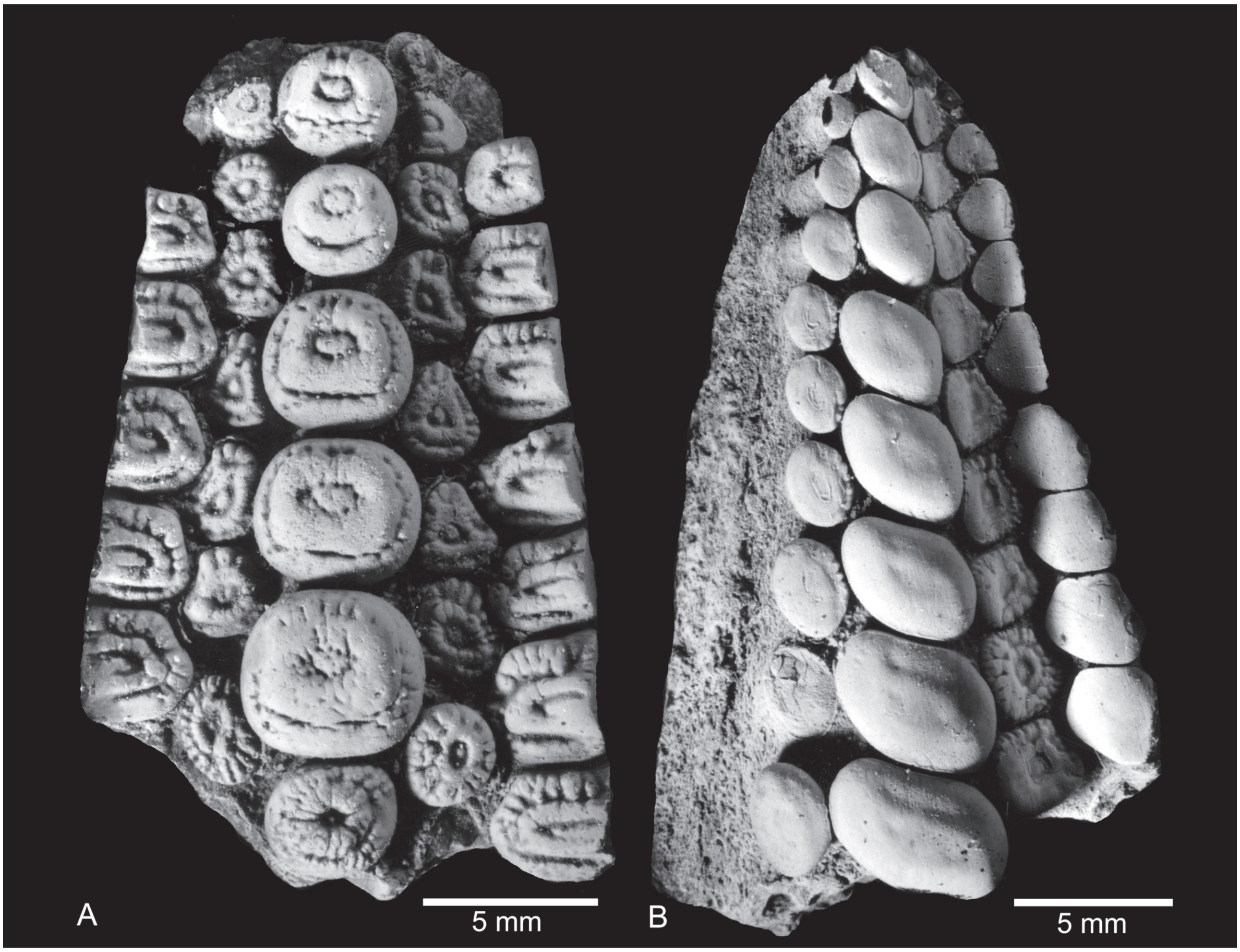


Figure 31: Isolated dentitions of *Gyrodus planidens* (MB. f. 7173) from the Upper Jurassic (Tithonian) of Weymouth, UK. **A:** Vomerine dentition. **B:** Right prearticular dentition.

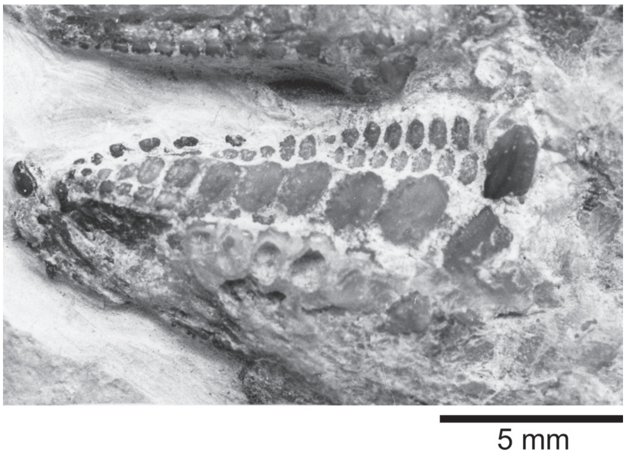


Figure 32: Left prearticular of *Mesturus verrucosus* from the Upper Jurassic of Wintershof West, southern Germany (JME SOS.2343a) displaying the arrangement and morphology of left prearticular teeth.

circumstance. Several specimens examined for this study occasionally exhibit an open depression with a newly formed tooth at its bottom posterior to the last teeth, similar to the condition mentioned by Hennig (1907). Thin and vertical sections through dentitional remains show additional replacement teeth (Fig. 45). Replacement of teeth is, however, occasional and not a consistent feature and probably occurred mainly in the posterior part of the dentition (Kriwet 2001a; Poyat-Ariza & Wenz 2005).

Wear patterns first occur on anterior teeth and then move posteriorly to the larger posterior teeth with age. Consequently, anterior teeth are mostly smooth, whereas posterior teeth exhibit their original ornamentation. The tooth ornamentation is generally well preserved in juvenile specimens; the ornamentation on teeth is completely lost in senile species (Fig. 46). In addition, wear patterns first occur laterally on teeth where the oral surfaces of the prearticulars are oblique or vertical.

Each premaxillary and dentary bone bears a single series of a few styliform or incisiform teeth. *Gibbodon* is extraordinary in that it possesses five bifid dentary teeth (Fig. 47). The vomerine and prearticular teeth are molariform and generally

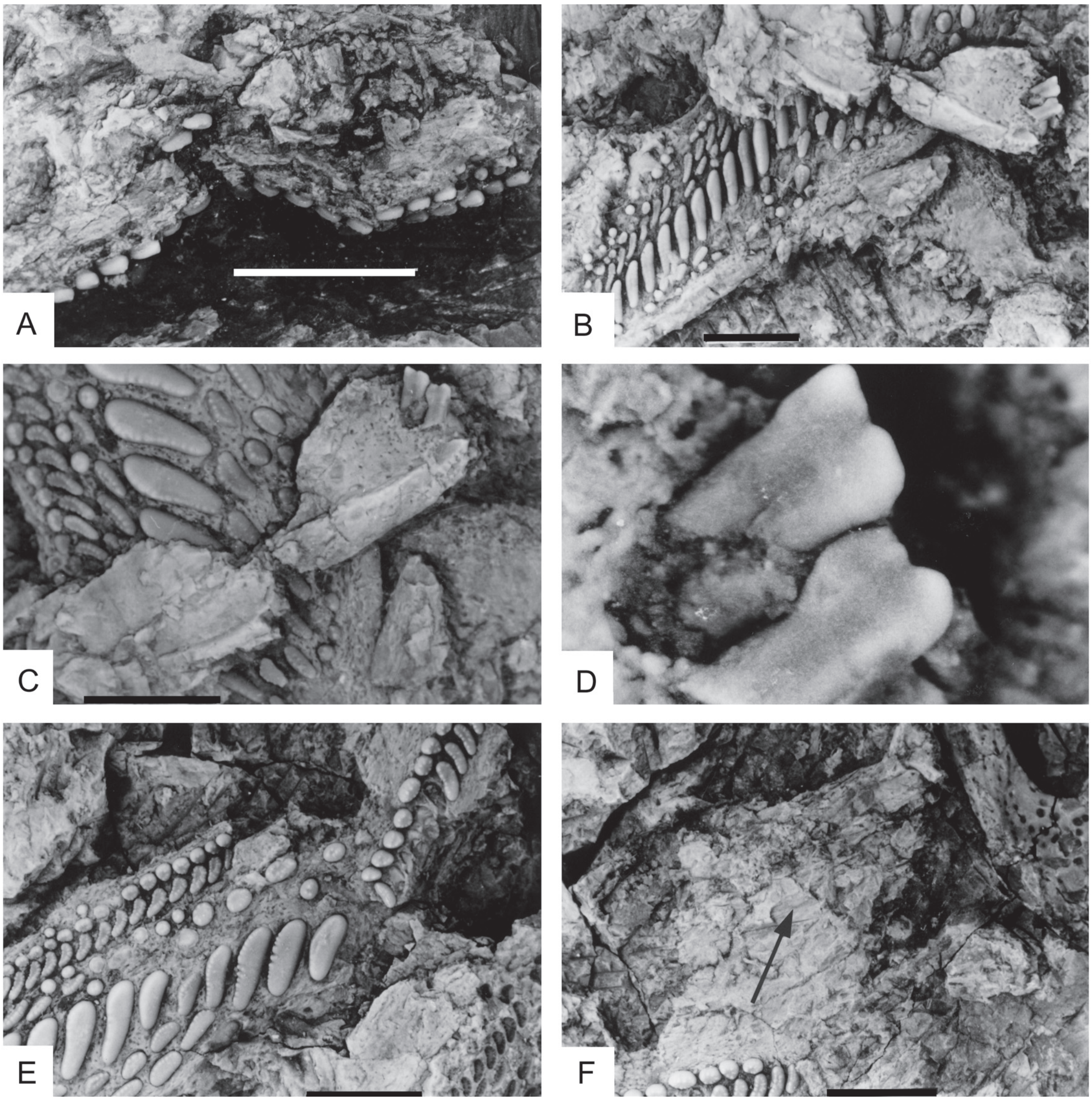


Figure 33: Holotype of *Anomoeodus nursalli* (IPFUB Uña Pyc 1). **A:** Vomer and vomerine dentition in lateral view. Scale bar = 2.5 mm. **B:** Right prearticular dentition and left dentary. Scale bar = 2.5 mm. **C:** Left dentary. Scale bar = 2.5 mm. **D:** Close up of left dentary teeth. **E:** Posterior portion of right prearticular dentition. Scale bar = 2.5 mm. **F:** Posterior portion of right prearticular dentition showing a well developed 'coronoid process' (aarow). Scale bar = 2.5 mm. Modified from Kriwet (1999b).

arranged in longitudinal rows forming a more or less dense pavement. Usually, there is a distinct main tooth row, which is characterised by the largest teeth and a varying number of medial and lateral tooth rows. The arrangement and number of tooth rows may be indicative of several pycnodonts at least on generic level. For instance, the prearticular dentition of *Ocloedus* is characterised by a main and two lateral tooth rows without any medial tooth row (see Kriwet et al. 1999: pl. 3). In contrast to that, the very similar prearticular dentition of *Proscinetes* differs since it exhibits a more or less developed medial tooth row (Fig. 48). *Anomoeodus* has very characteristic prearticular dentitions with the teeth arranged obliquely and the main teeth being generally trop-shaped (Fig. 33). The number of prearticular tooth rows varies considerably in *Anomoeodus* (Fig. 50). The prearticular and vomerine teeth of *Iemanja* are rounded without a distinct main row and irregularly arranged (Figs 27, 49). Kriwet (2003: tab. 1) presented a summary of the characteristic number of tooth rows for the different pycnodont genera.

The dentitional complex displays several important character sets such as the arrangement of teeth, number of tooth rows, presence of accessory teeth between the tooth rows, arrangement of medial and lateral tooth rows in comparison to the principal series, and the morphology of the teeth. The sculpture and ornamentation of teeth is only of minor value because the presence or absence of any sculpture depends on the degree of wear. The grade of wear increases during life and a tooth with distinct ornamentation patterns ultimately becomes smooth and rounded (Fig. 51). Thus, the character 'smooth teeth' can only be used when the teeth lack any ornamentation

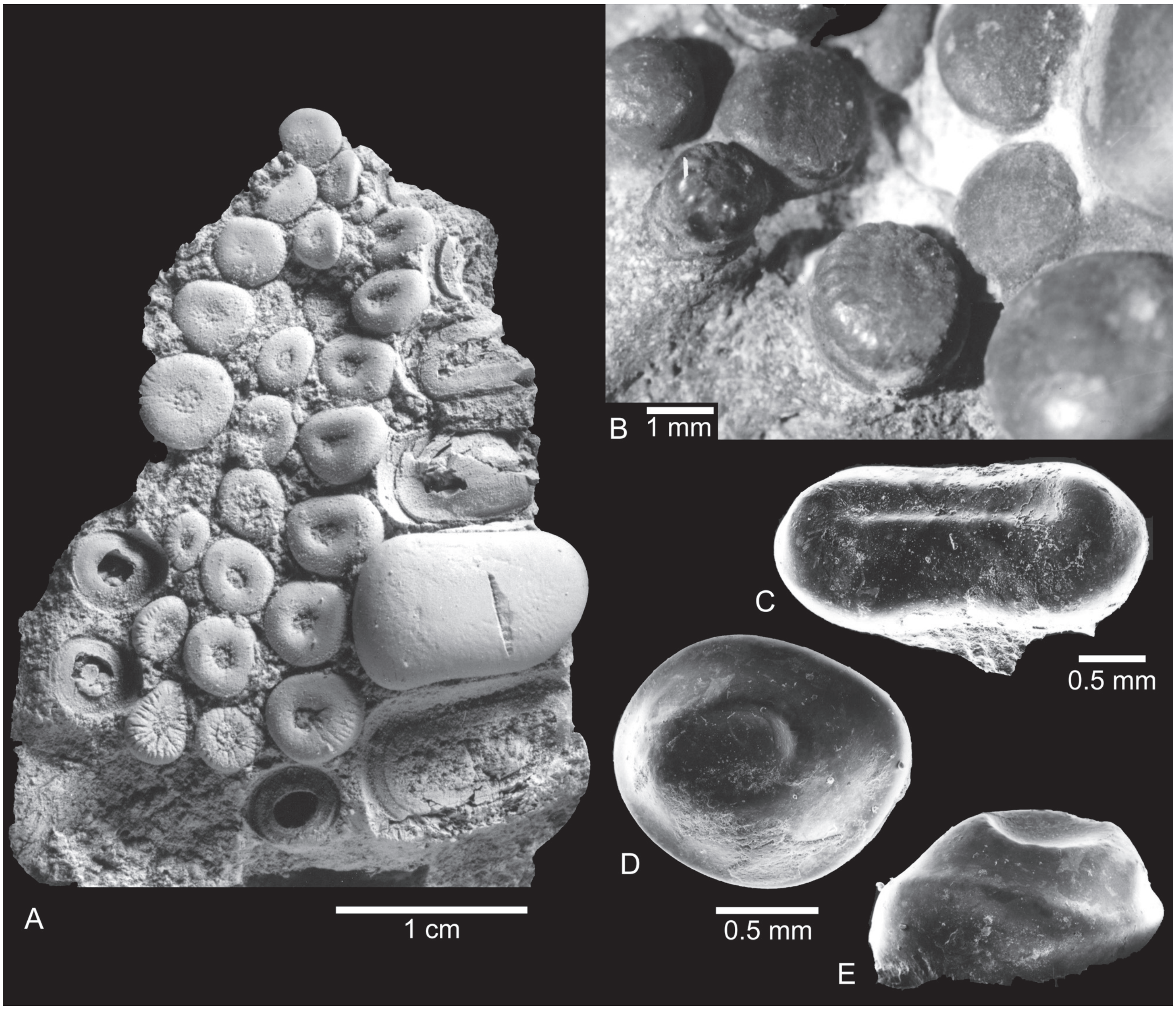


Figure 34: Prearticular dentition and teeth of *Macromesodon* spp. **A:** Left prearticular of *Macromesodon* sp. (IPFUB uncat.) from the Kimmeridgian of northwestern Germany. **B:** Close up of posterior prearticular lateral teeth of specimen BSP 1885 IX 66, occlusal view. **C:** Isolated prearticular main tooth of *Macromesodon macropterus* (MB. f.7279), occlusal view. **D-E:** Isolated prearticular lateral tooth of *Macromesodon macropterus*. **D:** Occlusal view. **E:** Lateral view.

throughout ontogeny, which requires ontogenetic series.

5.6 Histology of Teeth

Only little information on the histology of pycnodont teeth has been made available to date, e.g., Hennig (1906), Beaumont (1963), Peyer (1968), Ørvig (1973), and Goto & Inoue (1979). Generally, three hard tissues, which exhibit optical differences, can be distinguished in actinopterygian teeth. There is a dental layer (orthodentine) surrounding a pulp cavity, which is covered by a hypermineralised layer on its upper, and attachment bone on its lower portion. The orthodentine surrounds an undivided pulp cavity in pycnodonts (Fig. 52A-B). The tooth cap of actinopterygians is composed of a hard, hypermineralised tissue. This layer in actinopterygians has been referred to as enamel in zoological literature. The enamel is ectodermal in origin and formed by ameloblasts in mammals and reptiles; production does not start until a layer of mesodermal dentine is present (Poole 1967). It has been assumed that the hypermineralised layer in actinopterygians is secreted by the inner dental epithelium, the ectoderm, and by odontoblasts, the mesenchyme (Reif 1979). The true enamel of tetrapods is secreted entirely by the inner dental epithelium. Thus, the highly mineralised layer of actinopterygians represents a mixed matrix contains high amounts of collagen and was called acrodin (Ørvig 1973, 1978) or enameloid (Poole 1967). The definitive dentine differentiates only when the hypermineralised layer is fully differentiated in actinopterygians. Generally, two types of hypermineralised tissue co-occur on the same tooth in actinopterygians, i.e. acrodin (tegmental acrodin, cap enameloid) and collariform ganoin (Ørvig 1973,

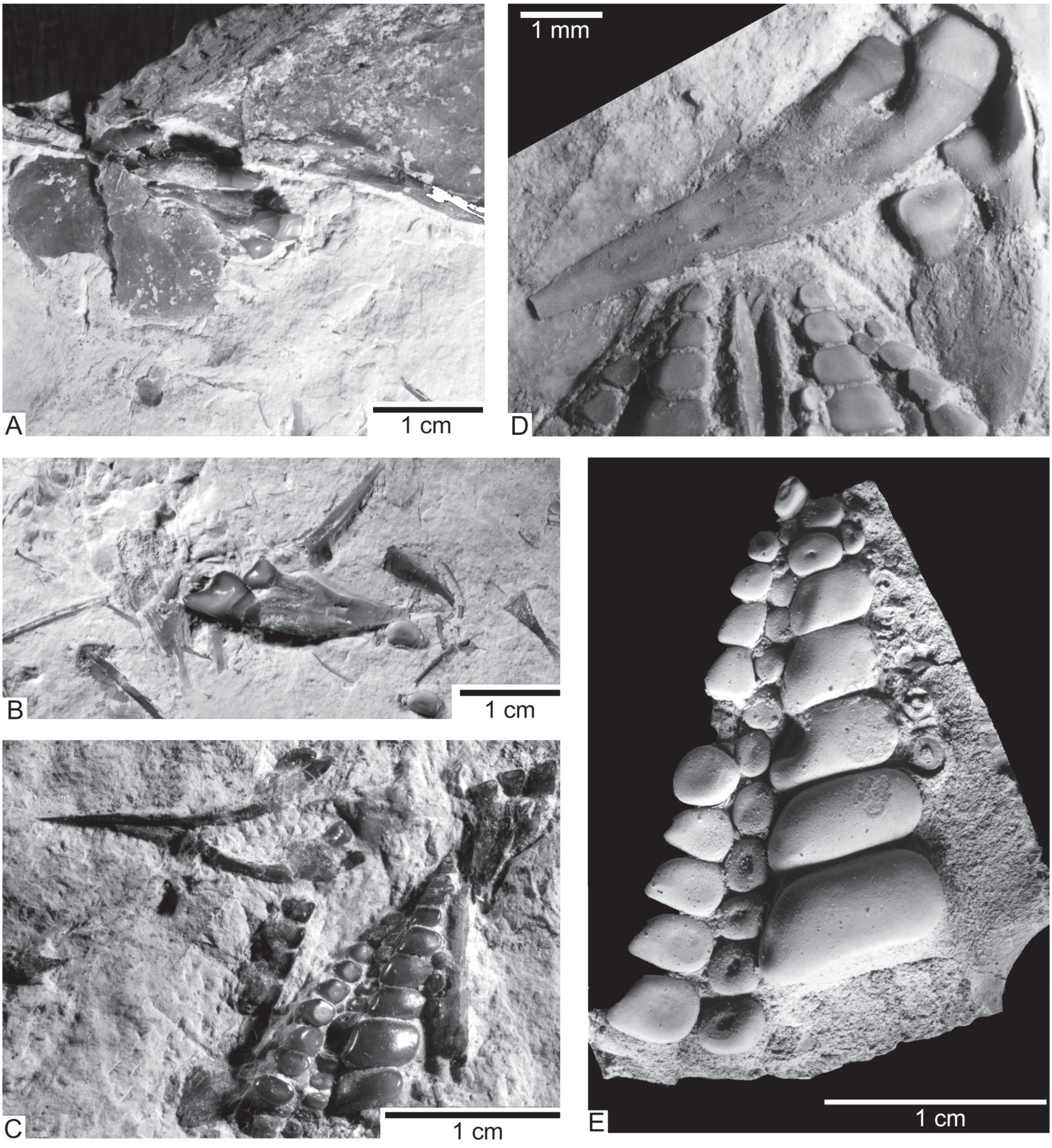


Figure 35: Jaw elements of *Proscinetes elegans* (A-C) and *P. hugii* (E). **A:** Both left and right maxillae and associated premaxillae of BSP 1885 IX 61. **B:** Right dentary of BSP 1885 IX 61. **C:** Associated premaxillae, dentaries, and prearticular dentition of MB. f.7278. **D:** Right dentary of BSP-1885 IX 60. **E:** Left prearticular dentition of MB. f.7138 from the Kimmeridgian of Langenberg near Oker, northern Germany.

1978). Although Hennig (1906) proposed the name tecodentine for the highly calcified outer tooth tissue in '*Pycnodus*' the term acrodin is used herein following Ørvig (1978). The collar ganoin basally adjoins the tegmental acrodin and occupies a position at the neck portion of the tooth. It is strongly reduced in thickness or even completely absent in extant teleosts with crushing dentition such as *Diodon* and *Labrodon*. The collar ganoin is relatively thin and restricted to the notch between tooth crown and tooth base in pycnodonts (Fig. 52C). Reif (1979) demonstrated that the tegmental acrodin displays a woven structure in most fossil and extant actinopterygians. In pycnodonts, the enameloid cap of blunt crushing teeth is rather thick and consists of aprismatic fibre bundles. The tegmental acrodin of pycnodonts is differentiated into two layers like in extant teleosts (Figs 53, 54). The inner one, which is rather narrow and into which dentine tubules penetrate, displays a relatively low degree of structural order with the fibre bundles being oriented more or less parallel to each other

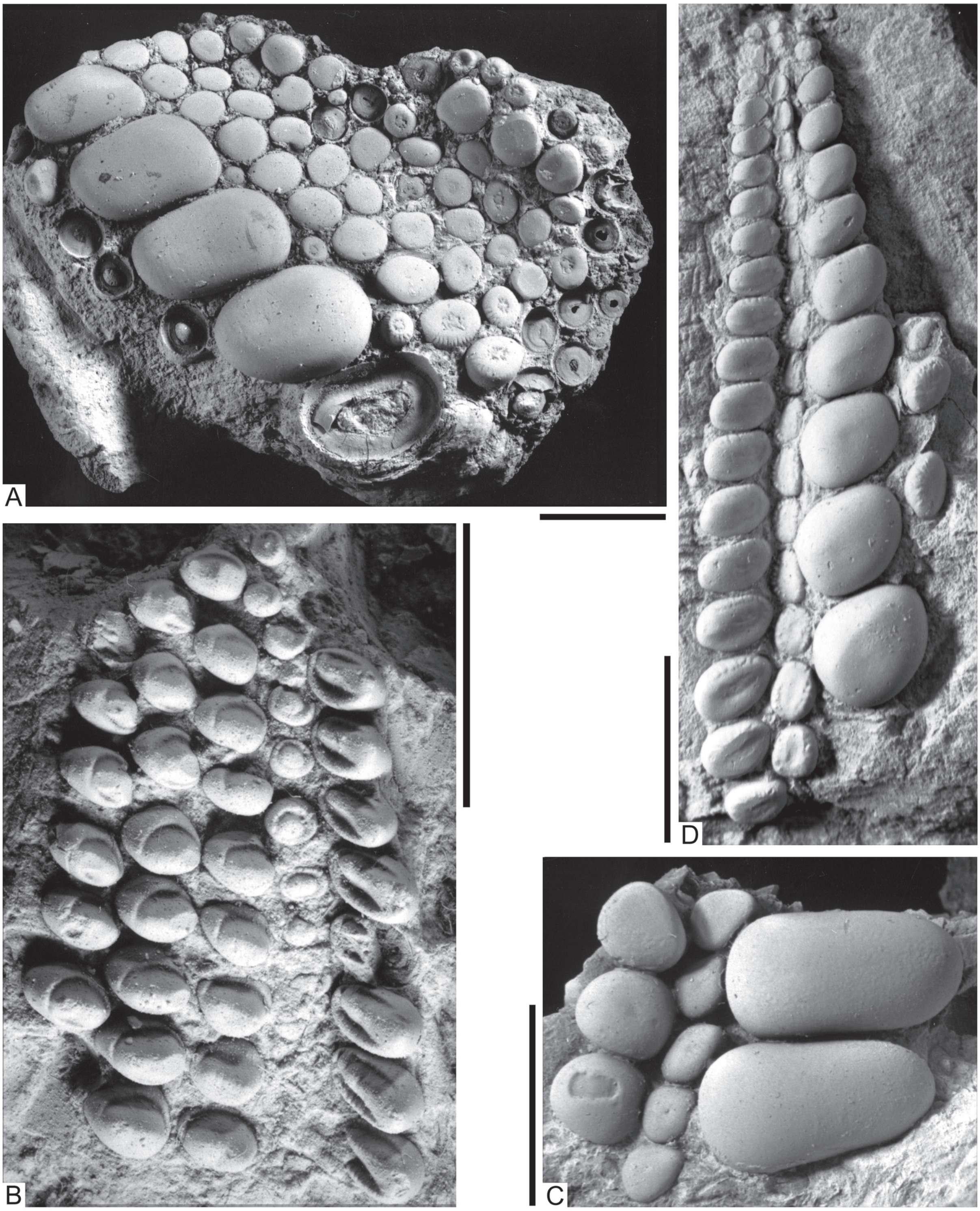


Figure 36: Dentitions of pycnodonts. **A:** Right prearticular of *Eomesodon granulatus* (MB. f. 7134) from the Tithonian (Upper Jurassic) of Holzen, northern Germany. **B:** Left prearticular dentition of a still undescribed pycnodont (MB. f.7233) from a Cretaceous erratic of the Baltic Sea. **C:** Fragmentary left prearticular of *Paramicrodon volcanensis* (DGC T 160, holotype) from the Lower Cretaceous of Chile. **D:** Left prearticular of *Paramicrodon chilensis* (SGO 516, holotype) from the Aptian (Lower Cretaceous) of Chile. Scale bars = 10 mm.

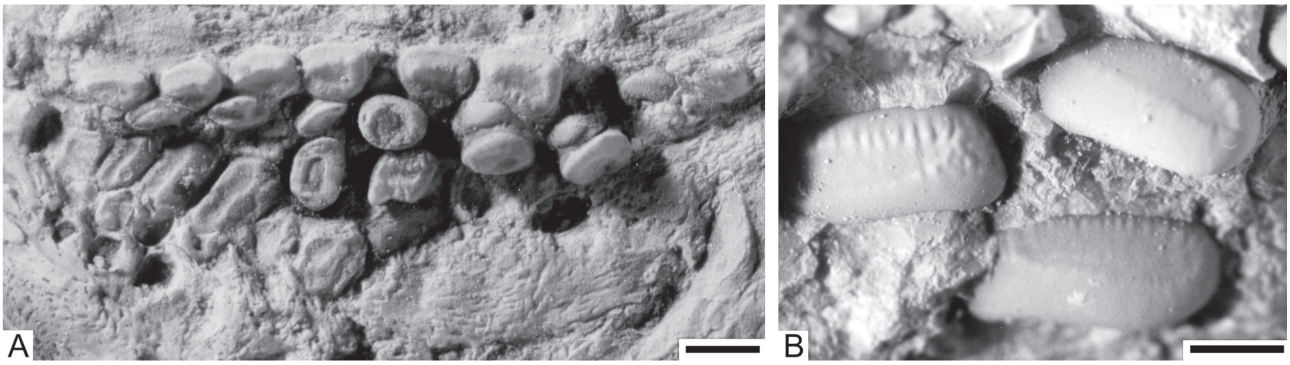


Figure 37: Dentitions of pycnodonts. **A:** Vomerine and prearticular teeth of an undescribed pycnodontid (FMNH PF 14919) from the Albian (Lower Cretaceous) of Puebla, Mexico. **B:** Prearticular teeth of *Macromesodon gibbosus*. (BSP 1955 I 82) from the Tithonian (?) (Upper Jurassic) of southern Germany. Scale bars = 1.0 mm.

and perpendicular to the dentin-acrodin boundary. The outer layer shows a very high degree of structural organisation with the fibre bundles being strongly woven. Hennig (1906: pl. 13, fig. 3b) figures a similar condition found in an isolated tooth from the Upper Jurassic. However, the tegmental acrodin of crushing teeth in extant and fossil teleosts such as *Pseudoscarus*, *Pagrus*, and *Sargus* exhibits a different separation and arrangement of the two layers (e.g., Ørvig 1978: fig. 62; Reif 1979: fig. 4). Here, the inner layer consists of woven fibres whereas the outer layer consists of pallial acrodin (Fig. 55). The woven acrodin certainly has higher compression strength rather than a high bending strength (Reif 1979). The differences found in the arrangement of woven and parallel acrodin layers between pycnodonts and teleosts also indicate that no closer relationships exist between these two groups. There is no outer shiny layer consisting of small crystallites in actinopterygians and selachians on the surface of the tooth crown but a mineralised or unmineralised acid resistant cuticule (Shellis & Berkowitz 1976) (= "Terminaldentin" of Schmidt & Keil 1958).

5.7 Biometric characteristics of Teeth and Dentitions

Most characters used in pycnodont taxonomy are morphological characters and hence descriptive. In contrast to the morphological, not measurable characters, biometric features are assumed to have definable reference points, which are independent of other characters but are always reproducible. Teeth are epigenetically prefixed, and thus one can assume that teeth of highly specialised organisms such as pycnodonts exhibit similar forms and size proportions for the same genus, if not the same species. Nevertheless, a first look at the pycnodont dentition shows that there is also variation in form and proportions among the teeth of different rows and even in the same row. These variations primarily concern the outer form (e.g., rounded, rectangular) or presence of ornamentations (present – absent, strong – feeble). Biometric data are generally used to describe the morphology independent of ornamentation and outer form. This method is also used herein to test the significance of such data. The characters used in this study are the length (**l**) and width (**w**) of teeth of different pycnodont species. Width (**w**) refers to the greatest, length (**l**) to the shortest measurement, regardless of tooth orientation because the results should be attributable to isolated teeth. The width as a percentage of the length (**w/l**) and the average of w/l (**aw/l**) for each tooth row has been calculated. This kind of measurement was selected for better comparison with isolated teeth and because similar measurements have been used by Schultze (1981) for *Paramicrodon*, Schultze (1991) for *Coelodus toncoensis*, Schultz & Paunovic (1997) for *Coelodus* and *Pycnodus* spp., and Kriwet (1999b) for *Anomoeodus* spp. The aim of this section is to present additional data on the metric characteristics of pycnodont teeth.

The arithmetic mean (**x**) indicates the average of the divergence of the data. It was calculated as the total of the individual measurements divided by the number of measurements. The variation (**range**) of measurements depends on the maximal and minimal values (**R = Max – Min**). The statistical standard tolerance (**s**) indicates the average of the distribution of the data and was calculated using Microsoft Excel program version 4.0. The variation coefficient (**V**) shows whether the variability of the data is strong or not and allows comparison of different data sets regardless of their dimensions. **V** is given in % and calculation was done using the formula: **V** = **s** x 100 / **x** [%].

For better comparison, only the main teeth of the vomerine and/or prearticular dentitions have been measured because these are the only teeth, which can be identified with confidence when isolated. As many species as possible of *Anomoeodus*, *Brembodus*, *Coelodus*, *Eomesodon*, *Macromesodon*, *Phacodus*, and *Pycnodus* have been examined. Most of the analysed specimens are isolated vomerine and prearticular dentitions. Unfortunately, there were not sufficient data for all species and genera. Therefore, the spot check for some species is not representative, because the data sets are restricted to small samples (two to five teeth of a single dentition).

The pycnodonts *Anomoeodus* and *Coelodus* have similar tooth morphologies and thus similar biometric characters. The aw/l-indices of *Anomoeodus* vary from 2.30 in *A. superbus* to 3.37 in *A. fraiponti*. The range is 1.46 with a relatively low standard tolerance of 0.32. The aw/l-indices of *Coelodus* show the greatest variation among pycnodonts with a range from

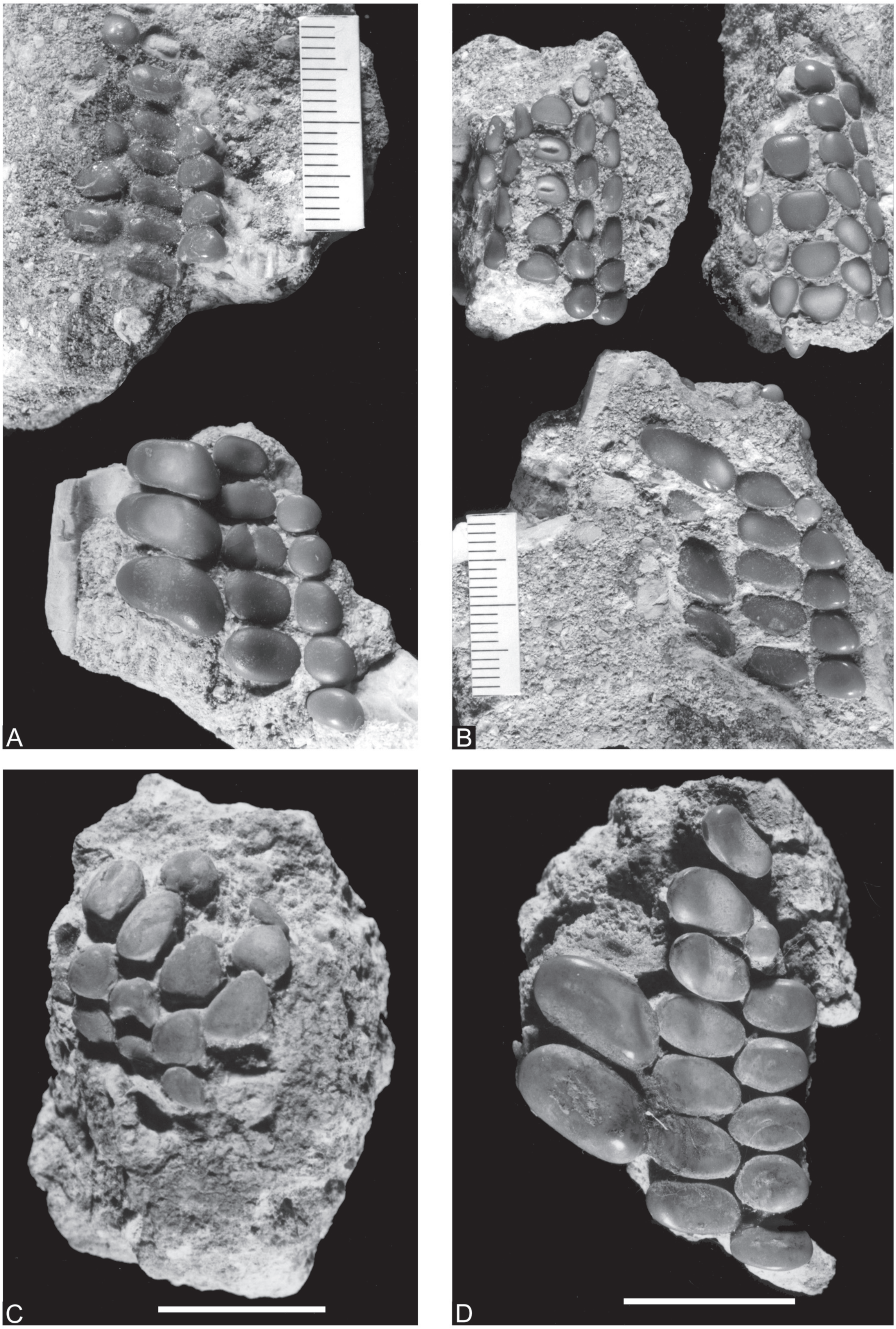


Figure 38: Dentitions of *Pycnodus* spp. **A:** Right prearticular dentitions of *Pycnodus pellei* from the Eocene of Morocco (private collection). Scale bar in mm. **B:** Two fragmentary vomerine (top) and a fragmentary right prearticular dentition of *Pycnodus pellei* from the Eocene of Morocco (private collection). Scale bar in mm. **C:** Fragmentary vomerine dentition of *Pycnodus variabilis* (BSP 1904 XII 81) from the Lutetian of Egypt. Scale bar = 10 mm. **D:** Fragmentary right prearticular dentition of *Pycnodus variabilis* (BSP 1904 XII 80) from the Lutetian of Egypt. Scale bar = 10 mm.

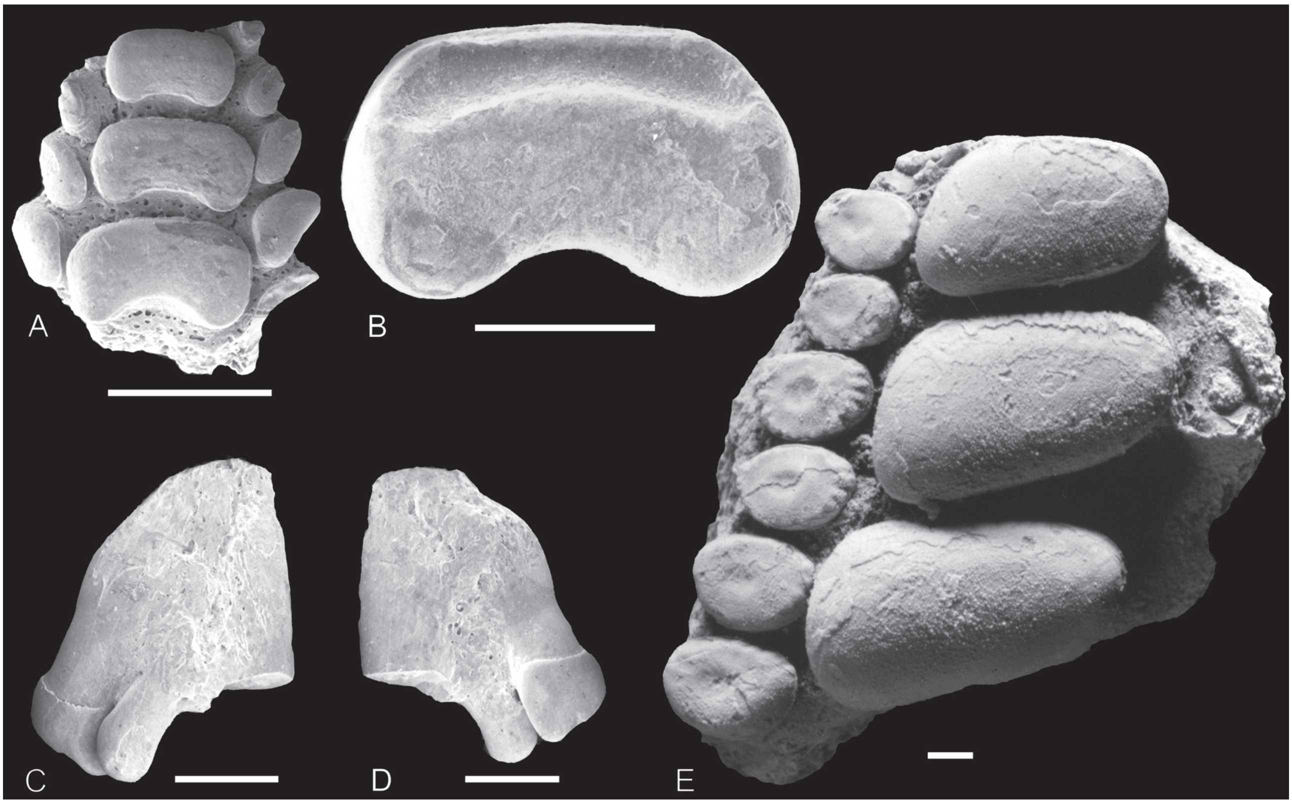


Figure 39: Isolated dentitions and teeth of new pycnodonts from the Iberian Peninsula (IPFUB uncat.). **A-D:** Specimens from the Barremian (Lower Cretaceous) of Galve, eastern Spain. **A:** Fragmentary vomerine dentition. Scale bar = 1.0 mm. **B:** Isolated main tooth. Scale bar = 5.0 mm. **C-D:** Fragmentary premaxilla. Scale bar = 1.0 mm. **C:** Lateral view. **D:** Mesial view. **E:** Fragmentary left prearticular dentition from the Berriasian (Lower Cretaceous) of Porto das Barcas, central Portugal. Scale bar = 1.0 mm.

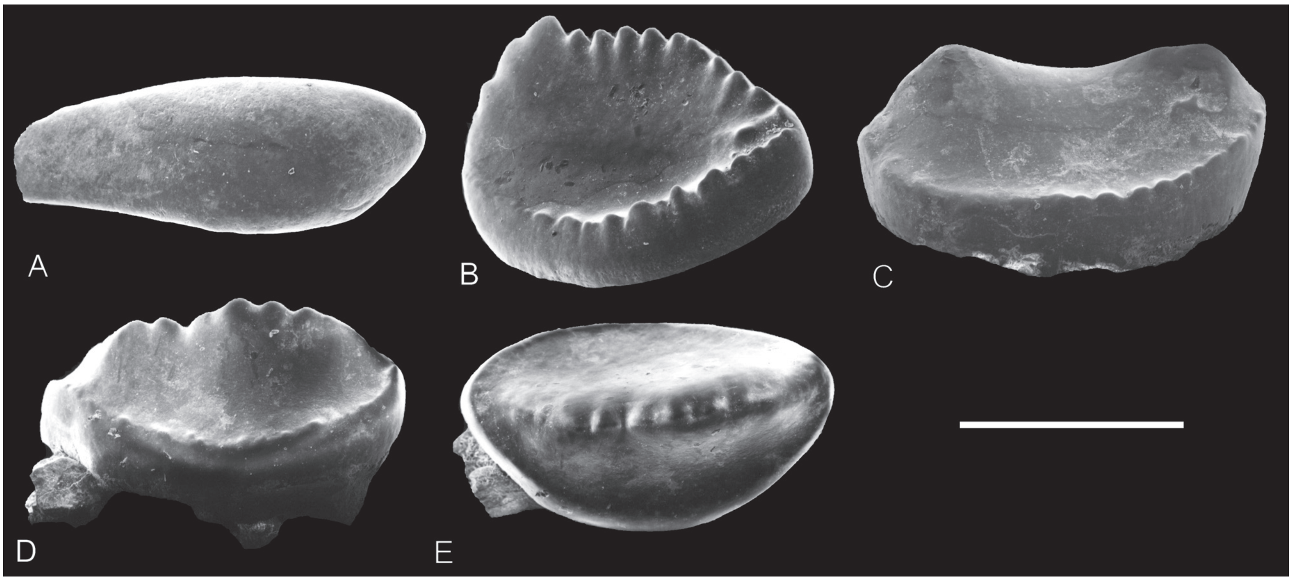


Figure 40: Isolated teeth of pycnodonts. **A:** Main prearticular tooth of *Anomoeodus* sp. from the Mosquerella Formation (Cenomanian, Upper Cretaceous) of Aliaga, Province of Teruel, eastern Spain. **B-E,** *Nursallia* sp. (MB. f. 7235) from a Turonian bone-bed of Delta County, Colorado, U.S.A. **B:** Specimen 1, anterior view. **C:** Specimen 2, anterior? view. **D:** Specimen 3, anterior view. **E:** Specimen 3, occlusal view. Scale bars = 0.5 mm.

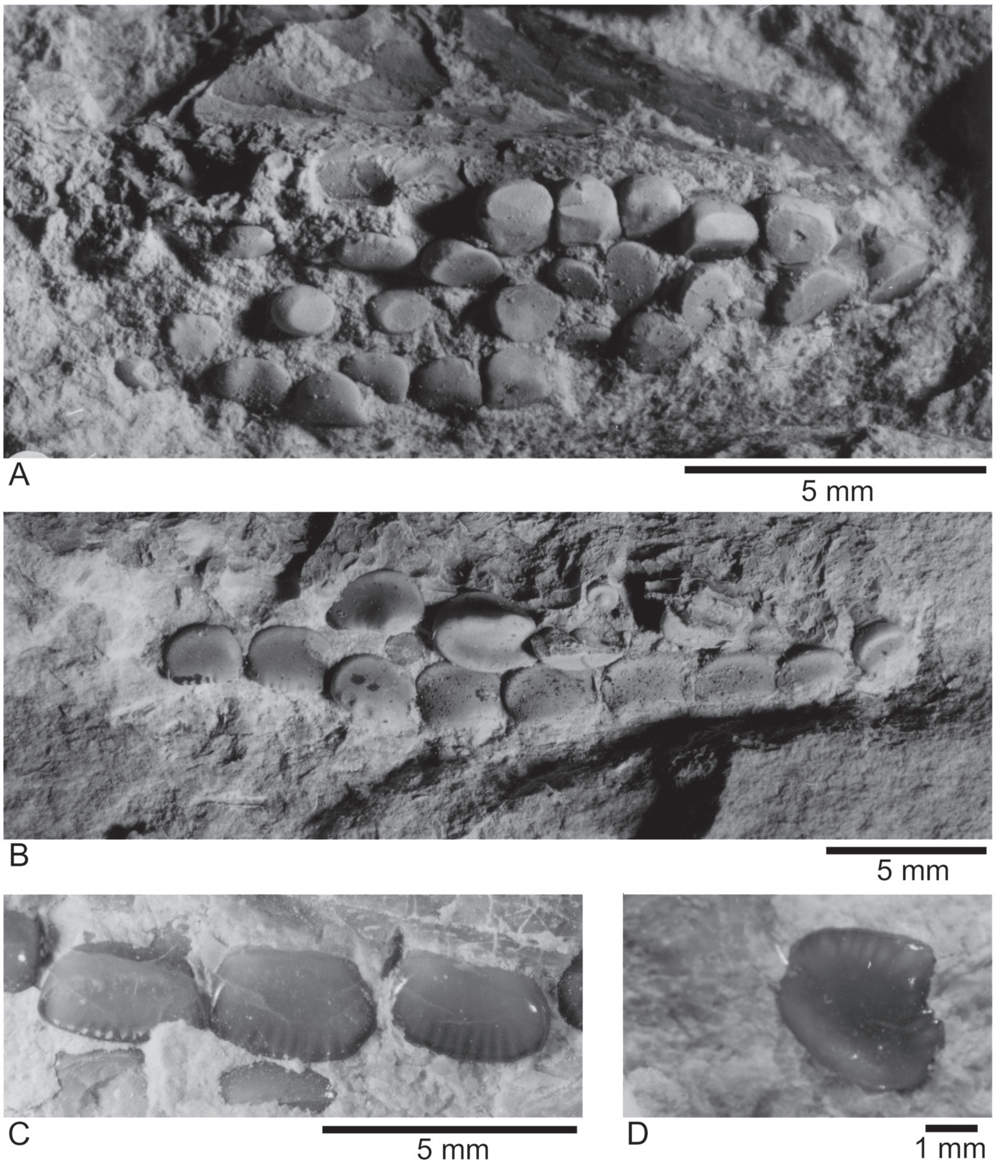


Figure 41. *Nursallia*? *goedeli*. **A:** Vomerine dentition with abraded teeth (MB. f. 7231). **B:** Vomerine dentition (MB. f. 7230). **C:** Vomerine teeth (BSP 1966 XXV 13). **D:** Close up of posterior vomerine tooth (BSP 1966 XXV). **Remark:** The species included in *Nursallia* (apart from *N. veronae*) and related forms are displaying rather great morphological variations and a revision of these taxa probably will lead to splitting of *Nursallia* as currently understood.

1.36 to 3.88 (range = 2.52). Consequently, *Coelodus* exhibits the greatest standard tolerance (s = 0.55). This is certainly related to the fact that dentitions with similar numbers of tooth rows and tooth morphologies, but which actually represent different genera (e.g. *Ocloedus* Poyato-Ariza & Wenz, 2002) were lumped together.

The biometric data of the other investigated pycnodonts differ significantly from those of *Anomoeodus* and *Coelodus*. In *Eomesodon*, the aw/l-indices range from 1.67 to 1.91 (R = 0.24). The standard tolerance is the smallest for pycnodonts (s = 0.09). The variation of aw/l-indices of *Macromesodon* ranges from 1.08 to 1.91 (R = 0.83) and the standard tolerance is 0.31, which is similar to that found in *Anomoeodus*. The variation of the aw/l-indices of *Pycnodus* is 2.01 to 2.67 (R = 0.66) and the standard tolerance are small (s = 0.21). The measurements show that there is a direct correlation between the range and the standard tolerance. It is also obvious that the mean aw/l-index is quite similar for several genera, e.g., *Pycnodus* (2.29) and *Coelodus* (2.38) on the one hand and *Brembodus* (1.54), *Macromesodon* (1.66), and *Eomesodon* (1.78) on the other hand. The most distinctive pycnodont is *Anomoeodus* with a mean aw/l-index of 2.95 followed by *Coelodus* with a mean aw/l-index of 2.38. This corresponds well to the transversally strongly elongate teeth. The range of *Coelodus* is with 2.52 larger than the arithmetic mean. Although the mean aw/l-index and consequently the arithmetic mean of *Pycnodus* (arithmetic mean x = 2.29) is similar to that of *Coelodus* (arithmetic mean x = 2.28), the range and standard tolerance of *Pycnodus* differs

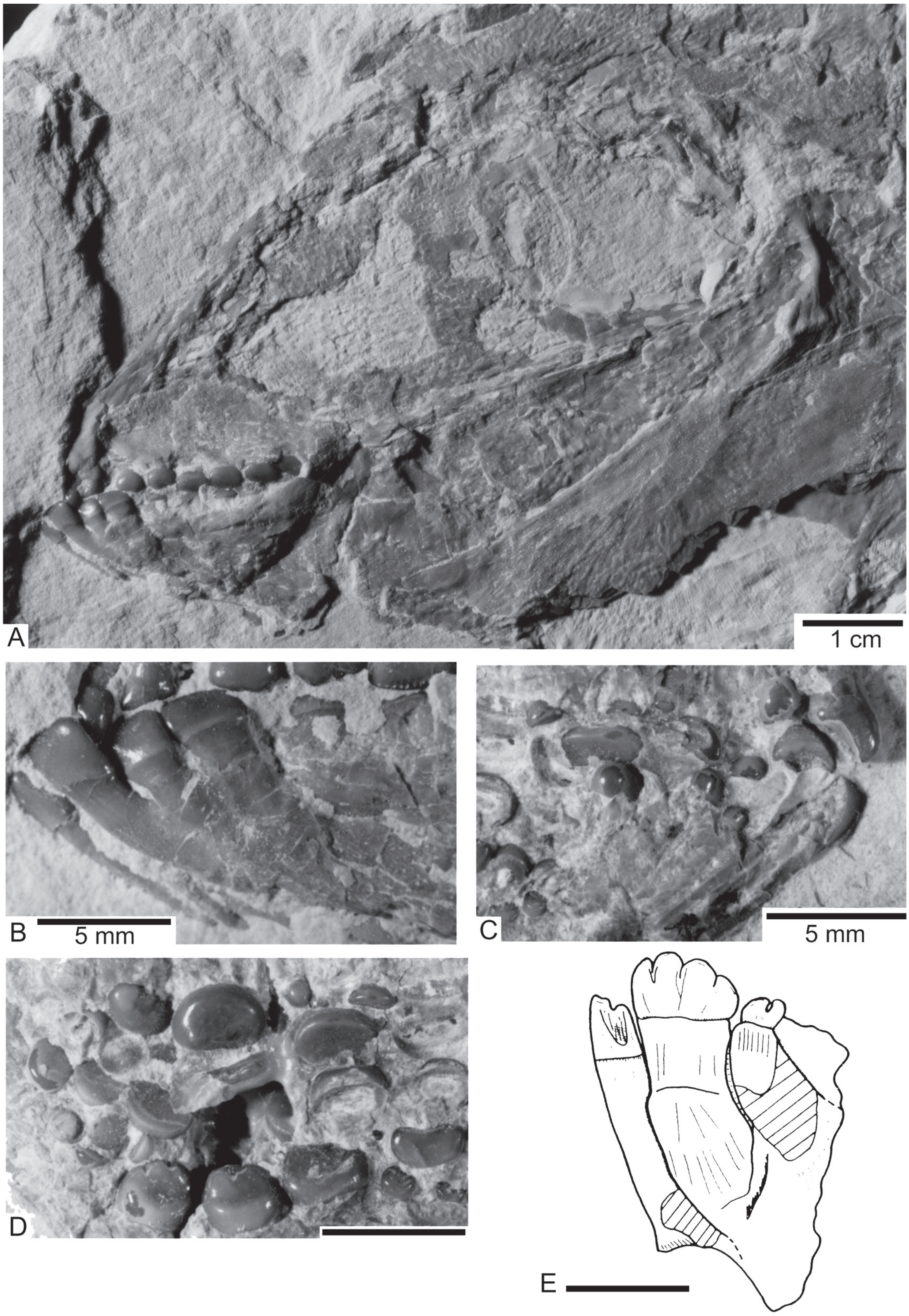


Figure 42: *Nursallia*? *goedeli*. **A:** Head of specimen BSP 10966 XXV 13 in lateral view with jaw apparatus. **B:** Close up of left dentary displaying the three grasping teeth. **C:** Anterior dentition of specimen BSP AS XXV 18. **D:** Posterior prearticular teeth of specimen BSP-AS XXV 18. **E:** Left dentary of specimen FMNH PF 14476 displaying incised tooth crowns.

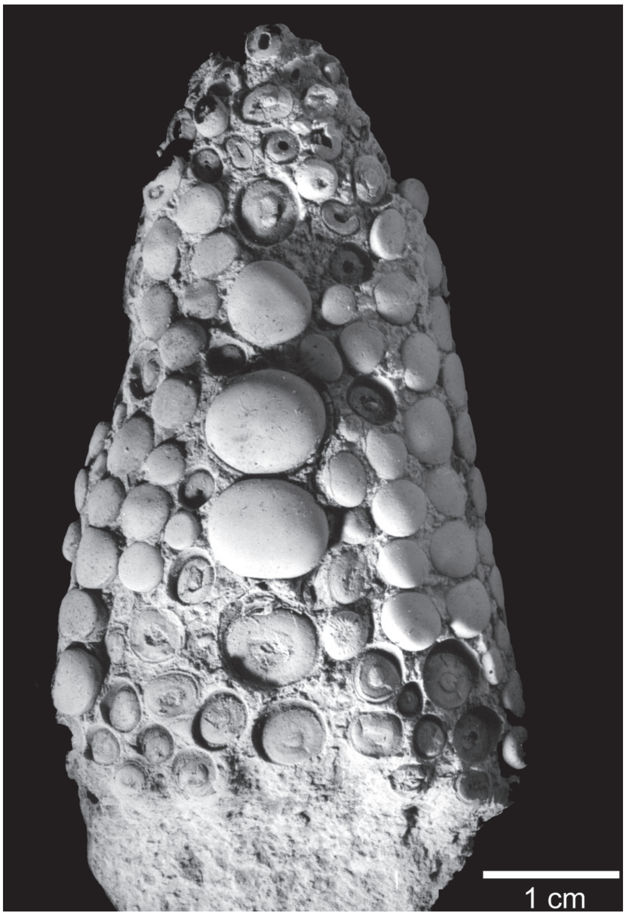


Figure 43: Isolated vomerine dentition of *Athrodon wittei* from the Kimmeridgian (Upper Jurassic) of northwestern Germany, occlusal view.

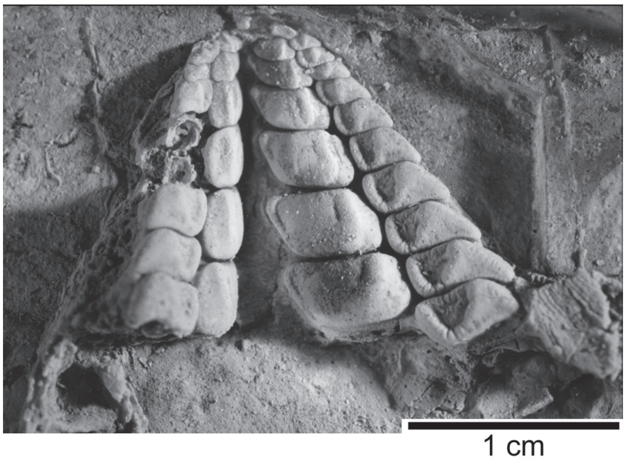


Figure 44: Associated prearticular dentitions of *Coccodus armatus* (IPFUB Leb 1).

significantly from that of *Coelodus*. *Eomesodon* is characterised by the smallest range (0.24). The range of the other examined genera is similar and amounts to 1/3 of the arithmetic mean. The variation coefficient correlates to the range and standard tolerance. It is 11.14% for *Anomoeodus*, 19% for *Macromesodon*, 23.61% for *Coelodus*, and 9.17% for *Pycnodus*. *Eomesodon*, again, is characterised by a low variation coefficient of 5.06%. The rather uniform biometric data of *Eomesodon* may be the result of the small spot check and further investigations may show that the range and variation of *Eomesodon* is by far greater than indicated in this study.

For comparison, the teeth of some vomerine dentitions from north-eastern Spain have been calculated in addition to the teeth of the prearticular dentitions. The material comes from the Lower Cretaceous of Uña and Galve (Province of Teruel) and the Upper Cretaceous of Albaina (southern Pyrenees). The specimen from Albaina has been identified as *Paramicrodon* by Poyato-Ariza et al. (1999). *Paramicrodon* is a pycnodont reported only from the Lower Cretaceous of North and South America. The presence of three tooth rows with rounded main teeth, which exhibit a pitted ornamentation, attributes the specimen from Albaina to *Phacodus* rather than to *Paramicrodon* in which the main teeth are elongate and do not possess pitted ornamentation. *Anomoeodus nursalli* has the greatest aw/l-indices of all Spanish pycnodonts. The three species of *Coelodus* exhibit similar aw/l-indices although the aw/l-index for the first left lateral tooth row of the Galve

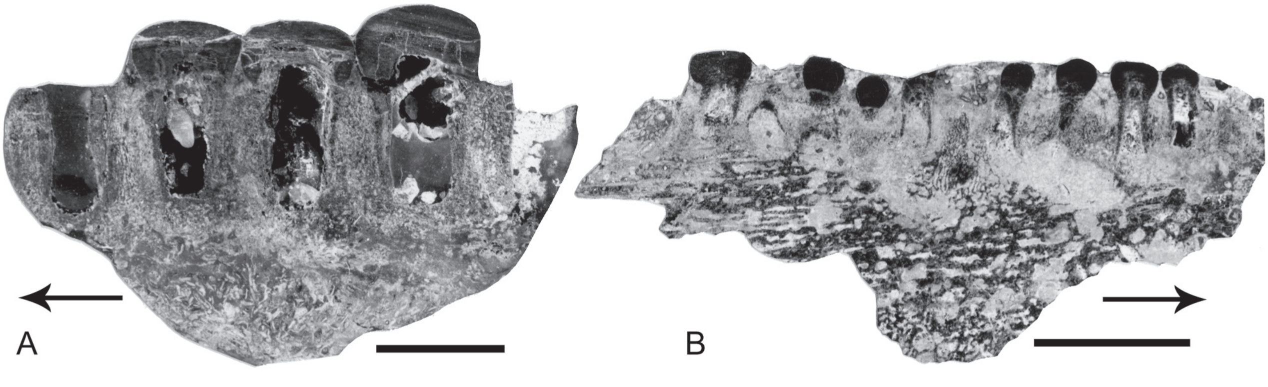


Figure 45: Vertical sections of pycnodont vomers from the Kimmeridgian (Upper Jurassic) of northwestern Germany. Arrows point anteriorly. Scale bars = 10 mm. **A:** *Macromesodon* sp. (IPFUB uncat.). **B:** *Proscinetes* sp. (IPFUB without number). There are two teeth well below the occlusal level with rather thin crown cusps. These teeth, although not directly below functional teeth, are interpreted here as replacement teeth similar to the condition seen in *Akromystax* (Poyato-Ariza & Wenz 2005).

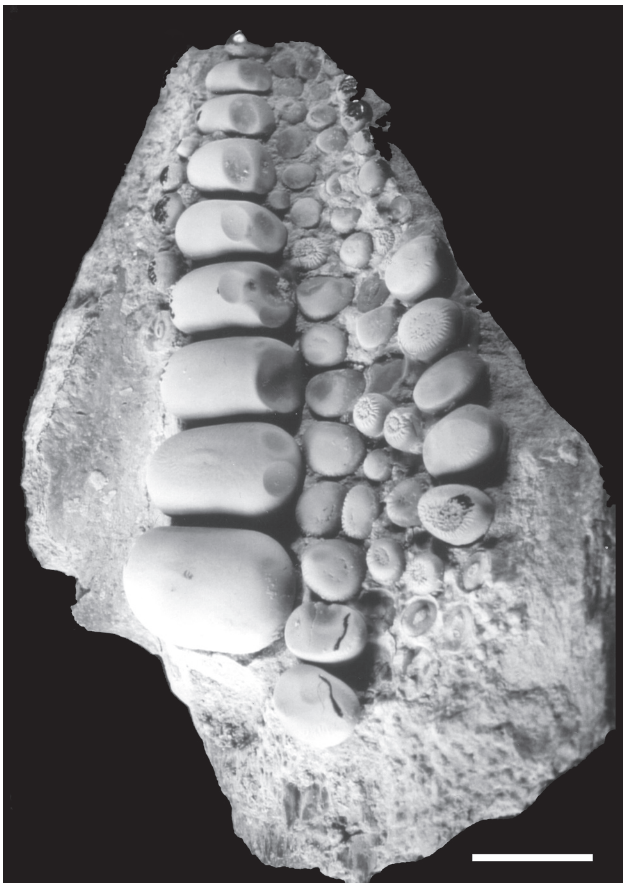


Figure 46: Right prearticular dentition of *Proscinetes hugii* (SMNS 4130) displaying wear patterns of teeth. These indicate that the occlusal surfaces of articulated prearticulars were more or less vertical resulting in strong wear of the lateral edges of main teeth. Scale bar = 5.0 mm.

species differs significantly from those obtained from the two Uña species. The values obtained for *Phacodus* are generally lower than those of the *Coelodus* spp. and *Anomoeodus* spp. However, the differences are not significant. At the moment, it is not easy to distinguish *Anomoeodus* from other pycnodonts in the Spanish localities. The data for pycnodonts with similar tooth morphology overlap one another and a differentiation is not possible.

Schultz & Paunovic (1997) calculated the arithmetic mean of the width and length indices of prearticular dentitions for several *Coelodus* spp. following the formula (w 1.lr / w mr) – (l 1.lr / l mr) (changed to the terminology of this study: w = width, l = length, 1.lr = first lateral row, mr = main row). The metric data show great variations and ranges and are not useful in correctly identifying species generally assigned to *Coelodus* (Figs 56, 57). Moreover, the error also supports that *Coelodus* as currently understood is polyphyletic.

The biometric data, which have been calculated for this study and which characterise the data sets, already point to rather great variations of the length and width found in pycnodont teeth (Fig. 56). In addition, the statistical parameters are not significantly different between the examined pycnodonts. The only exception is *Eomesodon* where the values are oriented along a line (Fig. 56). However, the data set for *Eomesodon* is too small to propose low ranges and standard tolerances. All other graphs display the variation of the mean aw/l-indices (Figs 56, 57).

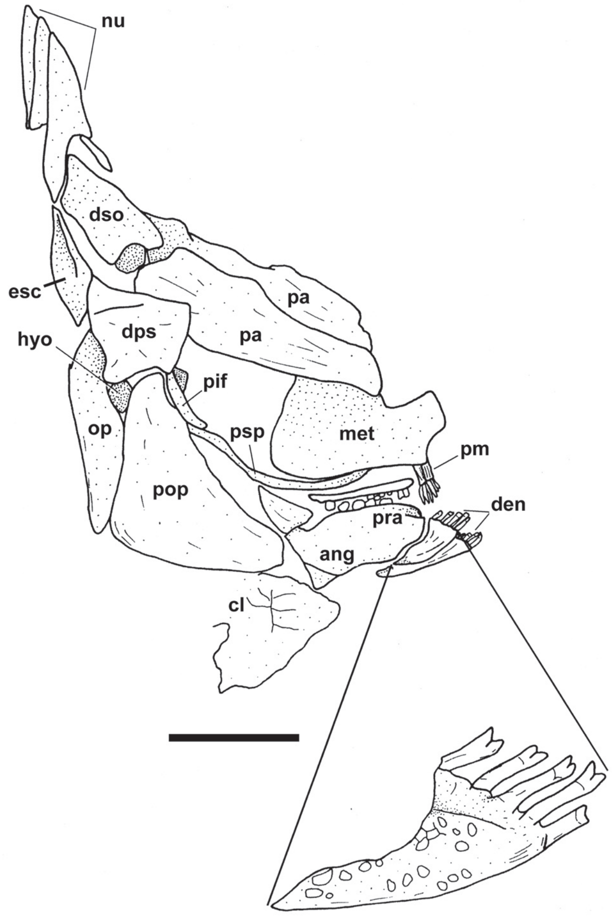


Figure 47: Camera lucida drawing of the skull of *Gibbodon cenensis* (MCSNB 3317, holotype) with left dentary showing the five bifid grasping teeth enlarged. Scale bar = 5.0 mm. **Remark:** This drawing differs slightly from the one provided by Poyato-Ariza & Wenz (2002).

The biometric data and corresponding aw/l-indices show that this method has immense potential but cannot at present be used for identifying all pycnodontiform genera and species. In addition, many species of different genera have similar values. The graphs (Figs 52, 53) also show that the data sets are limited and additional material is needed to enlarge the data sets. The available data display a general trend in grouping plesiomorphic (*Macromesodon*, *Brembodus*, and *Eomesodon*) and advanced taxa (*Coelodus* s.l. (including *Ocloedus*), *Pycnodus*, and *Anomoeodus*) together (Fig. 57).

5.8 Branchial apparatus and branchial teeth

The branchial skeleton and its associated elements vary among fossil and extant actinopterygians. The branchial

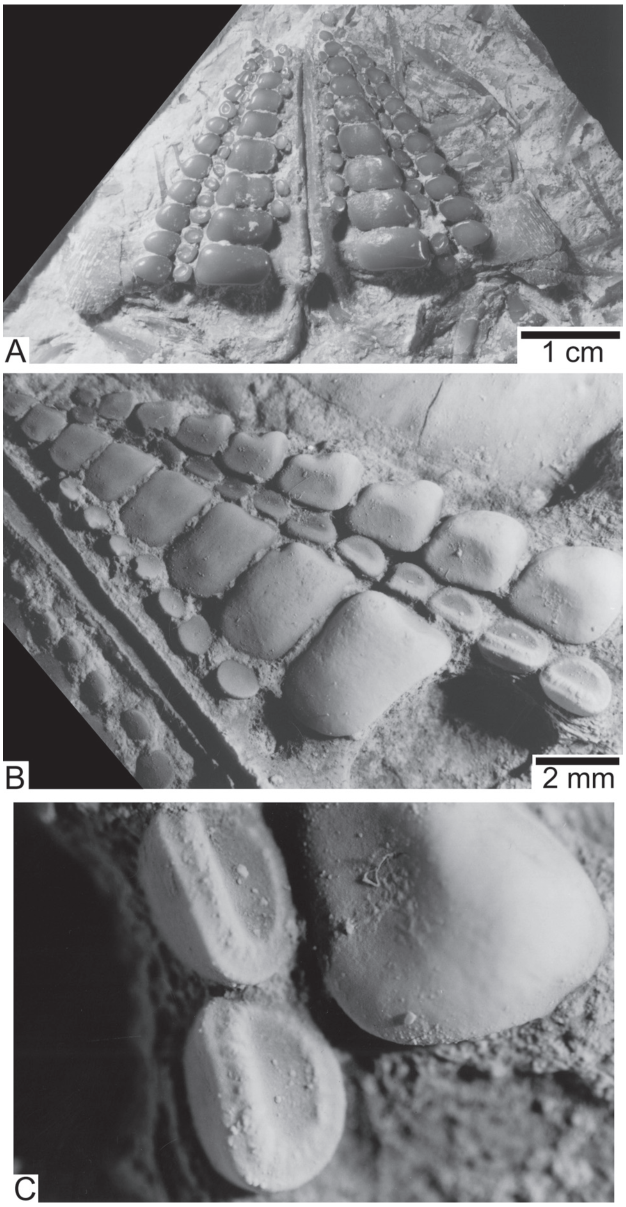


Figure 48: Prearticular dentitions of *Proscinetes elegans* from the Tithonian (Upper Jurassic) of southern Germany. **A:** Associated prearticulars of specimen BSP 1885 IX 61. **B:** Right prearticular of specimen BSP-1885 IX 60. Scale bar in mm. **C:** Close up of the two last teeth of the first lateral row and the last one of the second lateral row to show variation.

chamber is closely associated with respiration and feeding. The associated muscles are critical during deglutition.

Unfortunately, the branchial arches of pycnodonts are not well-preserved due to disarticulation and other taphonomic processes including chemical solution. Therefore, information is limited and it is impossible to reconstruct the branchial skeleton of pycnodonts. The best preserved structures found in the branchial chamber of pycnodonts are branchial teeth, which will be the main object of this section.

Traces of gill filaments and branchial arches are found in many pycnodont specimens, both mechanically and acid prepared (Fig. 58). The ceratobranchials are easily discernible. They are U-shaped in cross section, the U opens posteriorly. Gill filaments arise from the hollow of the U. There are five ceratobranchials present. Other structures and elements may correspond to the pharyngo-, epi-, and hypobranchials. However, they are scattered and do not permit accurate identification.

Tooth-like structures occur in the branchial chamber of several pycnodonts. Isolated hook- or claw-shaped teeth have been known in the fossil record since a long time. Such teeth were called *Ancistrodon* by Debey (1849). Roemer (1841, 1852) figured teeth of *Ancistrodon* and finally, Debey (in Schlüter 1881) presented a diagnosis together with three figures of *Ancistrodon*. Roemer and Debey considered *Ancistrodon* to be a shark. Dames (1883) has been the first to show that the teeth described as *Ancistrodon* are in fact pharyngeal teeth of actinopterygians but referred them to sparid teleosts. Leriche (1911) included teeth of *Ancistrodon* morphology in the

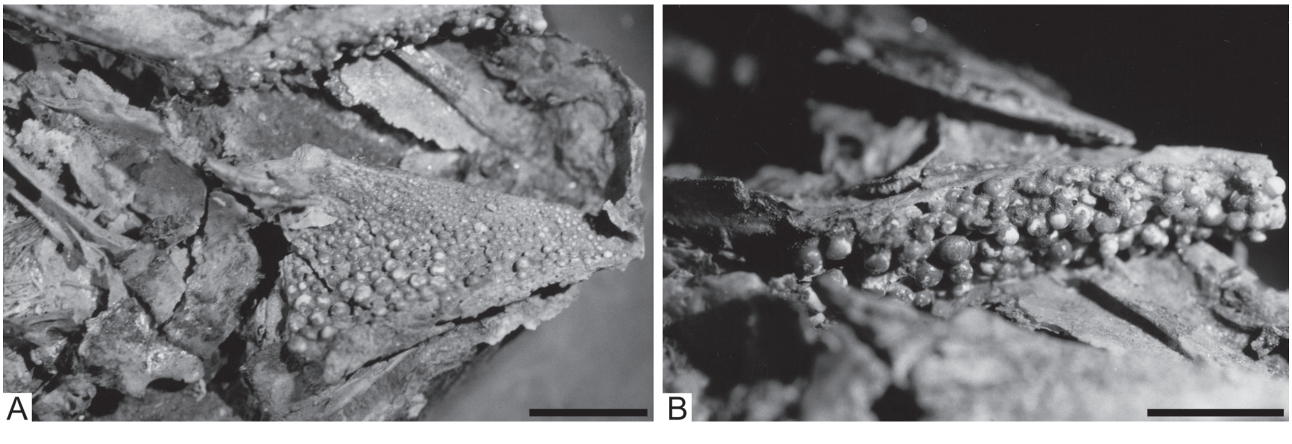


Figure 49: Dentition of *Iemanja palma* (AMNH 13963). **A:** Left prearticular dentition displaying the randomly and densely arranged grinding teeth that are all more or less rounded. **B:** Vomerine dentition displaying the irregularly arranged and rounded grinding teeth. Scale bars = 10 mm.

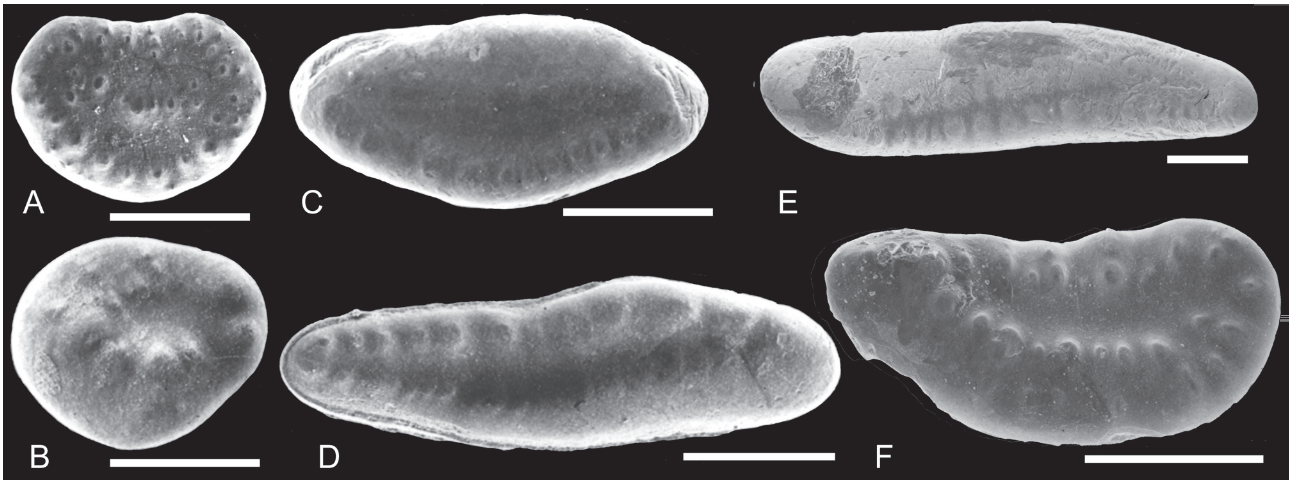


Figure 50: Prearticular teeth of *Anomoeodus nursalli* (IPFUB Uña Pyc 17) exemplifying the variation in tooth morphology. **A-C:** Lateral teeth. Scale bars = 0.5 mm. **D-E:** Principal teeth. Scale bars = 0.5 mm. **F:** Medial tooth. Scale bar = 0.5 mm.

pycnodont *Acrotemnus*. Nevertheless, Weiler (1929), based on histology, transferred them to *Stephanodus* (Fig. 59A-B) a genus created by Zittel (1887-90) and included both in his new genus *Eotrigonodon*, which was assigned to the extant Tetraodontiformes. Later, these assumptions were strengthened by Stromer & Weiler (1930).

However, Hay (1899: 790) assumed that the name *Ancistrodon* is preoccupied by the snake *Agkistrodon* Palisot De Beauvois because of the similar spelling. Consequently, he introduced the name *Grypodon* with the type-species *G. texanus* (Dames). White (1934) and Arambourg (1952) rejected the name *Ancistrodon* because of its insufficient definition, too. Nevertheless, according to the ICZN, *Grypodon* and *Eotrigonodon* must be regarded as junior synonyms of *Stephanodus*, and the name *Ancistrodon* takes consequently priority.

The variations in pharyngeal tooth morphology of *Stephanodus* indicate that different forms are grouped together. Bell (1986) described claw-shaped branchial teeth in the pycnodont genus *Hadrodus*, which are very similar to the teeth called *Ancistrodon*. He placed the genera *Ancistrodon* Roemer (= *Gryptodon* Hay), *Propenser*, and *Hadrodus* in the synonymy. Species to be included in *Hadrodus* sensu Bell (1986) are *Hadrodus hewletti* (Applegate, 1970), *Hadrodus marshi* Gregory, 1950, and *Hadrodus priscus* Leidy, 1857.

Tooth-like structures on gill rakers of *Gyrodus hexagonus* have been figured by Lambers (1991). This author pointed out that these structures are not branchial teeth sensu stricto. Poyato-Ariza & Wenz (2002) suggest, however, that these structures are branchial teeth. In the course of this study, similar structures have been observed in many specimens of *Gyrodus* and some other pycnodonts. These structures form small, accentuated spines or denticles that are similar to those present in the extant herring *Clupea harengus*. They are located on the lateral sides of the gill rakers in opposite position and form a passive-mechanical sieve. Small particles can pass this sieve, whereas larger particles are retained.

Isolated branchial teeth of *Stephanodus* morphology and isolated teeth or dentitions of *Anomoeodus* occur together in many Cretaceous localities, e.g., the Cenomanian of Egypt (Weiler 1935), Campanian of northern Germany (Albers & Weiler 1964), Campanian of the U.S.A. (Case & Schwimmer 1988; Robb 1989), Maastrichtian of Congo (Dartevelle & Casier 1949), Maastrichtian of the U.S.A. (Krause & Baird 1979), and Maastrichtian of Belgium (pers. observ.).

Several authors (e.g., Leriche 1911; Estes & Sanchíz 1982; Patterson 1993; de la Peña & Soler-Gijon 1996; de la Peña 1997) assumed that isolated teeth with *Stephanodus* morphology may not belong to teleosts but rather pycnodonts. Woodward (1917) already noted that some pycnodonts corresponds to extant *Balistes* in possessing clusters of small claw-shaped teeth and demonstrated the presence of hook-shaped teeth in the branchial chamber of articulated specimens of *Coelodus* from the Lower Cretaceous of Montsec, Spain. Similar tooth-like structures occur in other pycnodonts (Fig. 59C-M) such as *Ichthyoceras*, *Oropycnodus* (Poyato-Ariza & Wenz 2002), *Hadrodus* (Thurmond & Jones 1981; Bell 1986), *Tepexichthys* (Nursall 1996b), *Anomoeodus*, *Coccodus*, *Iemanja* (Kriwet 1999b), *Macromesodon*, *Palaeobalistum*, *Pycnodus*, and *Trewavasia*. However, pharyngeal teeth of the *Stephanodus* type also occur in the halecostome *Amia* (Grande & Bemis 1998; pers. observ.), the extant teleost *Blennius* (Goldschmid 1982: fig. 9), and the fossil semionotid *Lepidotes* (Thies 1989). To be consistent, Mudroch & Thies (1996) and Kriwet et al. (1997) attributed isolated hook-shaped pharyngeal teeth from the Jurassic of northern Germany and southern France to the semionotid *Lepidotes*, though isolated pycnodont teeth are common in both investigated localities. If *Lepidotes* and pycnodonts co-occur it is best to attribute isolated branchial teeth to Neopterygii indet.

Branchial teeth of pycnodonts are pedicellate and more or less hooked. Two different morphotypes can be distinguished (Fig. 59). The first type is styliform, sometimes blade-like and laterally compressed. The ventral prominence is slender and an oral surface is only poorly developed. The second type

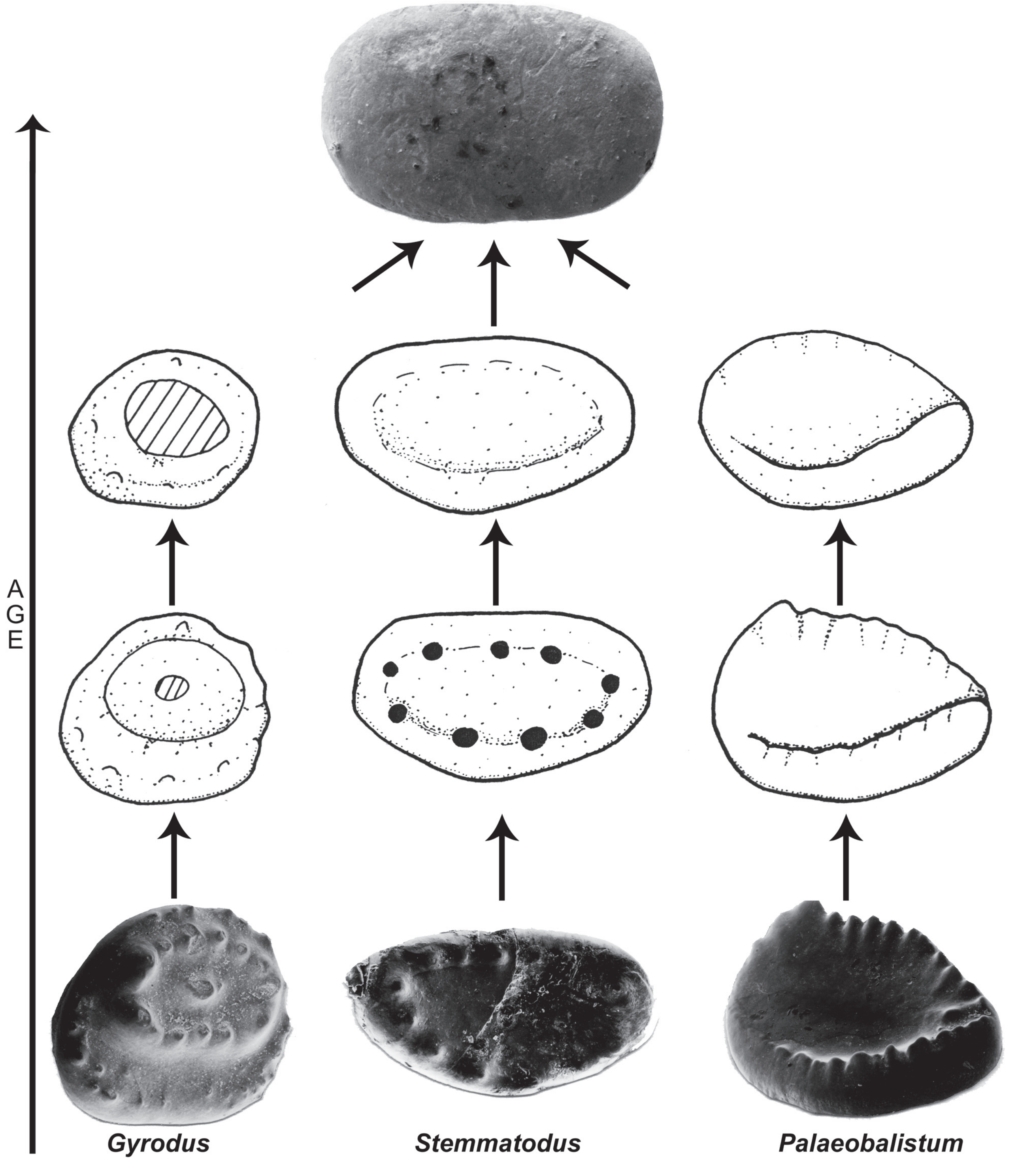


Figure 51: Schematic sketch of increasing abrasion of characteristic tooth ornamentations leading to smooth tooth crowns. The continuous abrasion of teeth makes it difficult to indetify isolated teeth when the occlusal surface is more or less smooth and indicates that only teeth with preserved sculpture may assist in taxonomic classifications. Figures not to scale.

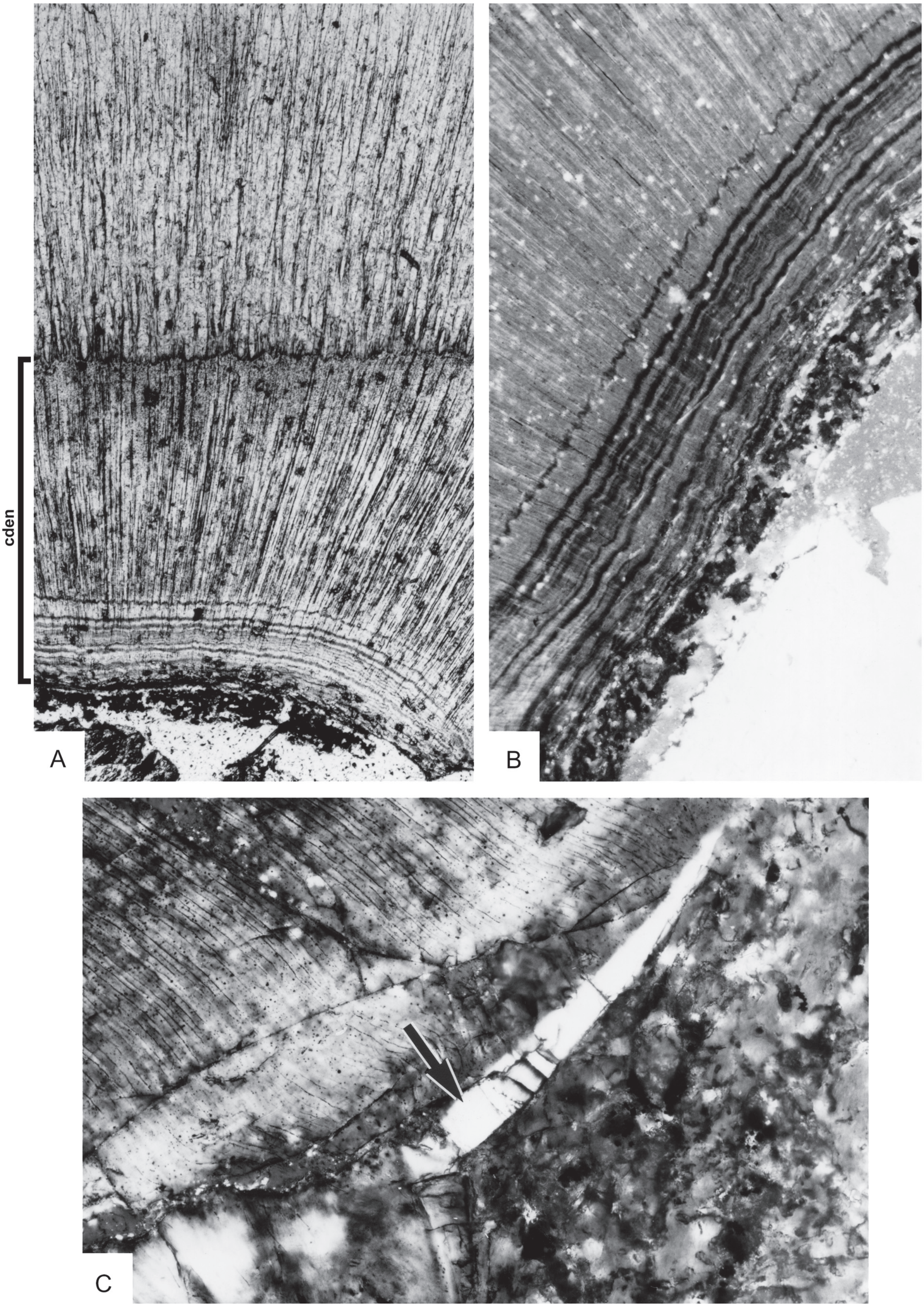


Figure 52: Transversal ground section of a principal tooth of *Macromesodon* sp. (IPFUB without number) from the Kimmeridgian (Upper Jurassic) of northwestern Germany. **A:** Acrodin-dentin boundary (black line in the middle). The circumpulpar dentine (cden) is rather narrow and shows growth lines at its base. Magnification x 25. **B:** Close up of growth lines in the circumpulpar dentine. Magnification x 50, x Nichols. **C:** Collar ganoin (arrow). Magnification x 200. x Nichols.

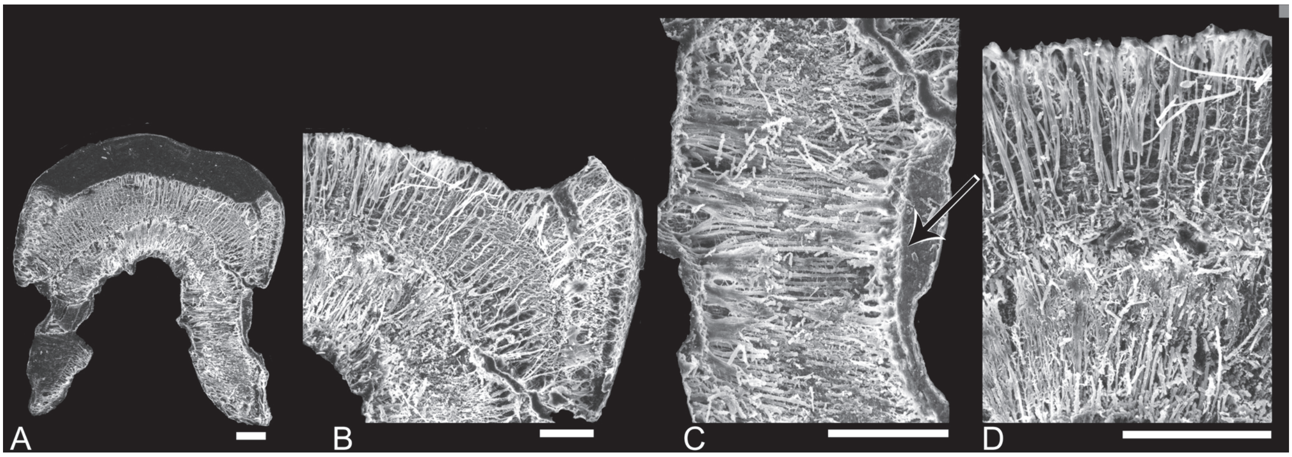


Figure 53: SEM pictures of a tooth of a new, undescribed pycnodont from the Lower Cretaceous of Galve, eastern Spain. Transversal section. Scale bars = 0.1 mm. **A:** Fragmentary specimen with parts of the occlusal acrodin cap lacking. **B:** Close up showing the circumpulpar dentine, pallial dentine, and remains of the acrodin cap. **C:** Circumpulpar dentine with remains of the collar ganoin (arrow). **D:** Circumpulpar dentine layer.

possesses an enlarged ventral prominence with a more or less wide and concave occlusal surface. The lateral margins of the occlusal surface may be notched.

However, hook-shaped teeth do not exclusively occur in the branchial chamber. In several extant species of balistids (e.g., *Balistes aculeatus* from the Pacific) hook-shaped teeth are positioned at the margins of the upper and lower jaws (Fig. 59L-N). These balistids are omnivorous but also grazers feeding on algae.

Generally, the pharyngeal teeth of pycnodonts are arranged in rather small groups without basal plates. Thus, the branchial dentition differs from the tooth plates of teleosts. The branchial

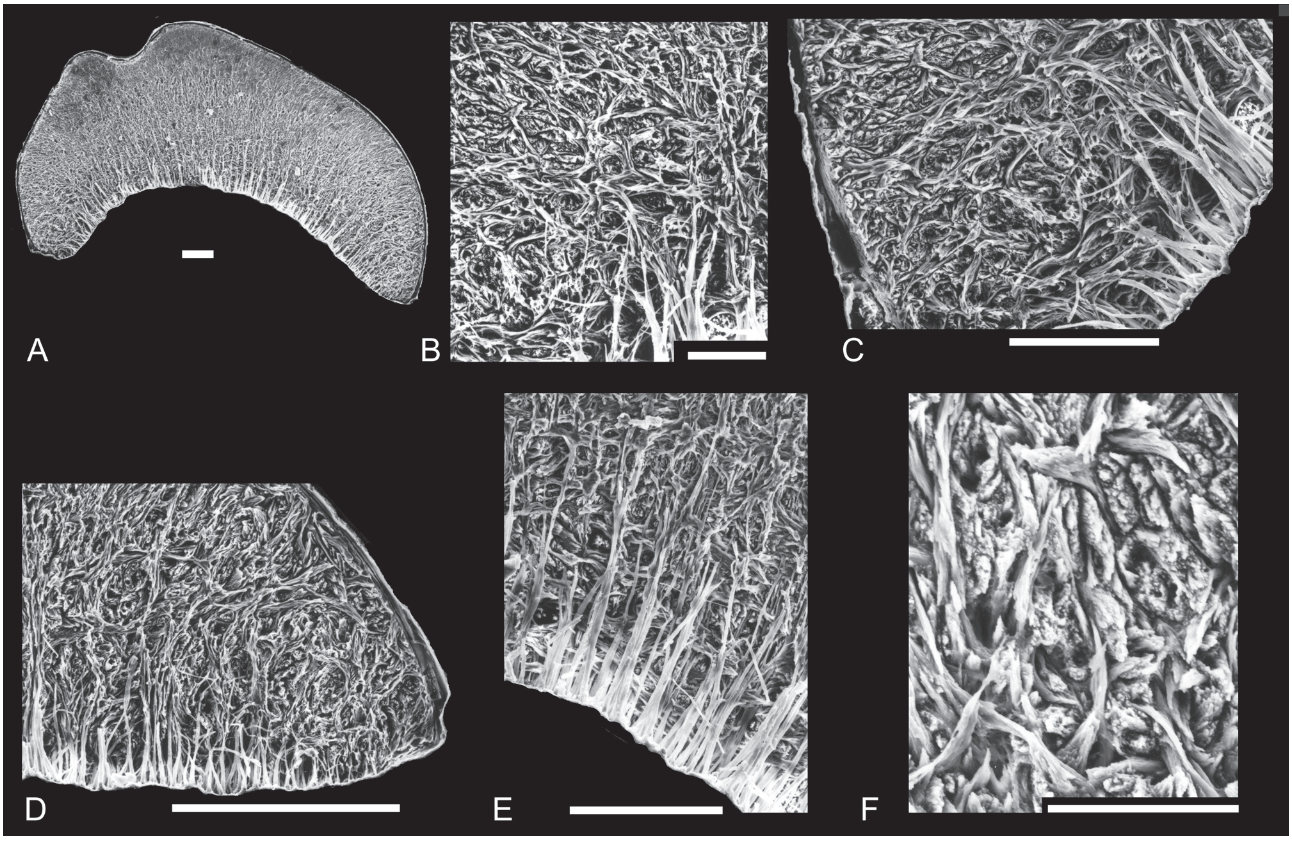


Figure 54: SEM pictures of transversal section of an isolated tooth of *Proscinetes* sp. from the Kimmeridgian (Upper Jurassic) of northwestern Germany. Scale bars = 0.5 mm when not state otherwise. **A:** Tooth crown. **B:** Close up of left side, displaying the woven acrodin. **C:** Close up of right side, displaying the woven acrodin. **D:** Close up of woven acrodin. **E:** Close up of inner acrodin layer with more or less perpendicular fibres. **F:** Close up of strongly woven fibres at crown surface. Scale bar = 0.05 mm.

Figure 55. Transversal ground sections of teeth of extant *Pseudoscarus* sp. (IPFUB without number) for comparison. East Pacific. **A:** Tooth base and bone of attachment. Magnification x 50. **B:** Abraded anterior tooth. Magnification x 50. **C:** Close up of acrodin (left) and acrodin-dentin boundary (middle). Magnification x 200. **D:** Posterior tooth. Magnification x 50. **E:** Close up of acrodin displaying the two acrodin layers.

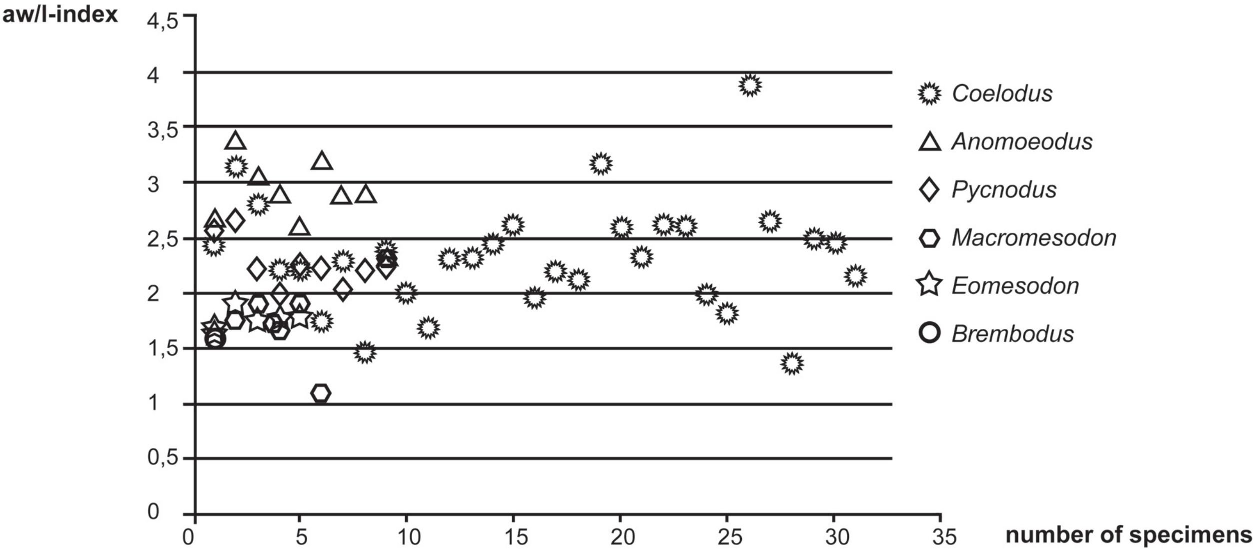


Figure 56: Comparison of aw/l-indices of the examined species and genera displaying the variation of biometric data. For further explanations see text. X-achsis gives number of specimens, y-achsis the aw/l-index. Remark: It should be noted that *Coelodus* as currently understood represents a polyphyletic grouping (Kriwet 2001a Poyato-Ariza 2002).

teeth occur high in the branchial chamber in pycnodonts. In extant teleosts with pharyngeal apparatus, pharyngeal teeth occur on the fourth pharyngo-branchials in the upper, and on the fifth ceratobranchials (e.g., the omnivorous roach *Rutilus*), or on the lower branchial arches. The modified bones are called "os pharyngeus inferior" (Goodrich 1930) or 'pharyngeal jaw' in cyprinids. The teeth in the branchial chamber of pycnodonts are certainly not homologous with the pharyngeal teeth of extant teleosts such as cyprinids. To distinguish the pharyngeal teeth of pycnodonts from pharyngeal teeth of teleosts, the tooth-like structures in the branchial chamber of pycnodonts are called branchial teeth instead of pharyngeal teeth (Kriwet 1999b); for a description of extant and fossil pharyngeal teeth of freshwater teleosts see Rutte (1962). The non-teleostean extant actinopterygians *Lepisosteus*, *Amia*, and *Elops* are unique in having many small tooth plates, which are grouped into a large posterior patch (Nelson 1969; Arratia 1999: fig. 9). No individual tooth plates can be related to a particular branchial arch. Unfortunately, the branchial skeleton of pycnodonts examined for this study is generally too poorly preserved for reconstruction. Therefore, it is not clear at present, whether the branchial dentition consists of dermal tooth plates, which are aligned with the pharyngobranchial and epibranchial gill arch elements as in plesiomorphic actinopterygians, or the dentition is similarly to that of *Lepisosteus* and *Amia* or to that found in teleosts with pharyngeal dental apparatus.

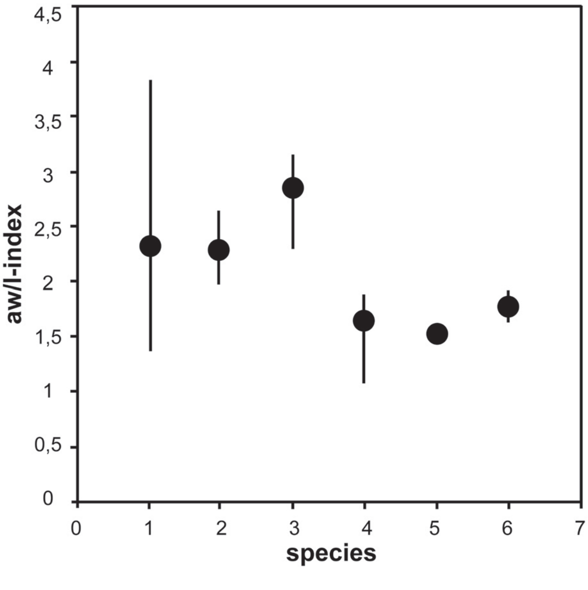


Figure 57: Comparison of the mean of aw/l-indices showing the tolerance and variation. Numbers are: 1 = *Coelodus*, 2 = *Pycnodus*, 3 = *Anomoeodus*, 4 = *Macromesodon*, 5 = *Brembodus*, 6 = *Eomesodon*. The high tolerance of aw/l-indices for *Coelodus* supports the assumption that this taxon represents a grouping of not necessarily closely related taxa. The small tolerance for *Eomesodon* is due to the small sample size.

The branchial teeth of pycnodonts are interpreted as protection for the gills like in extant herrings (e.g., Gibson 1988). Nursall (1996b) stated that there was no pharyngeal mill in pycnodonts. However, the particular morphology and location of branchial teeth high in the branchial chamber indicates that they actively participated in feeding in some way and do not correspond to the gill raker denticles in the passive mechanical sieve model of extant teleosts (Gerking 1994). This suggestion is supported by rare wear facets on the hook apices and the occlusal surfaces, which indicates that the branchial teeth assisted in the breaking down of hard shelled food and not only in protecting the gill rakers. However, the abrasion pattern is less pronounced than in extant cyprinids suggesting that food

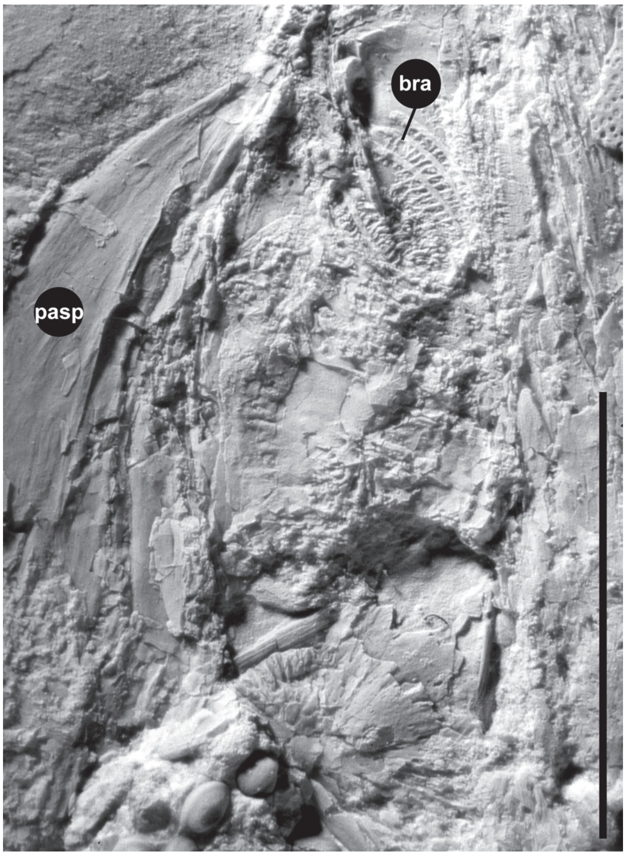


Figure 58: Branchial chamber of *Gyrodus hexagonus* (JME SOS 3140) from the Upper Jurassic of Blumberg, Bavaria displaying branchial arches and gill filaments. Left is anterior. Scale bar = 10 mm.

break-down by the action of branchial teeth was less important. Another possibility is that the branchial teeth were used to remove food particles suspended in the water and ingested during feeding. Indigestible shell fragments were sieved out and regurgitated like in extant durophageous teleosts.

The uniserial arrangement of branchial teeth in pycnodonts corresponds to the type of extant omnivore fishes. A horny plate benaeth the occipital region of the head in the dorsal wall of the oesophagus consisting of thickened epithelial cells like in several extant fishes with pharyngeal dental apparatus as support for pharyngeal teeth is absent in pycnodonts. There is also no specialised mastication process on the basioccipital that supports horny plates as in the extant *Rutilus*. The parasphenoid is complex in its posterior portion in pycnodonts. It is expanded laterally below the basioccipital forming ventroposteriorly directed wings. These wings may have served as some sort of support for the branchial teeth.

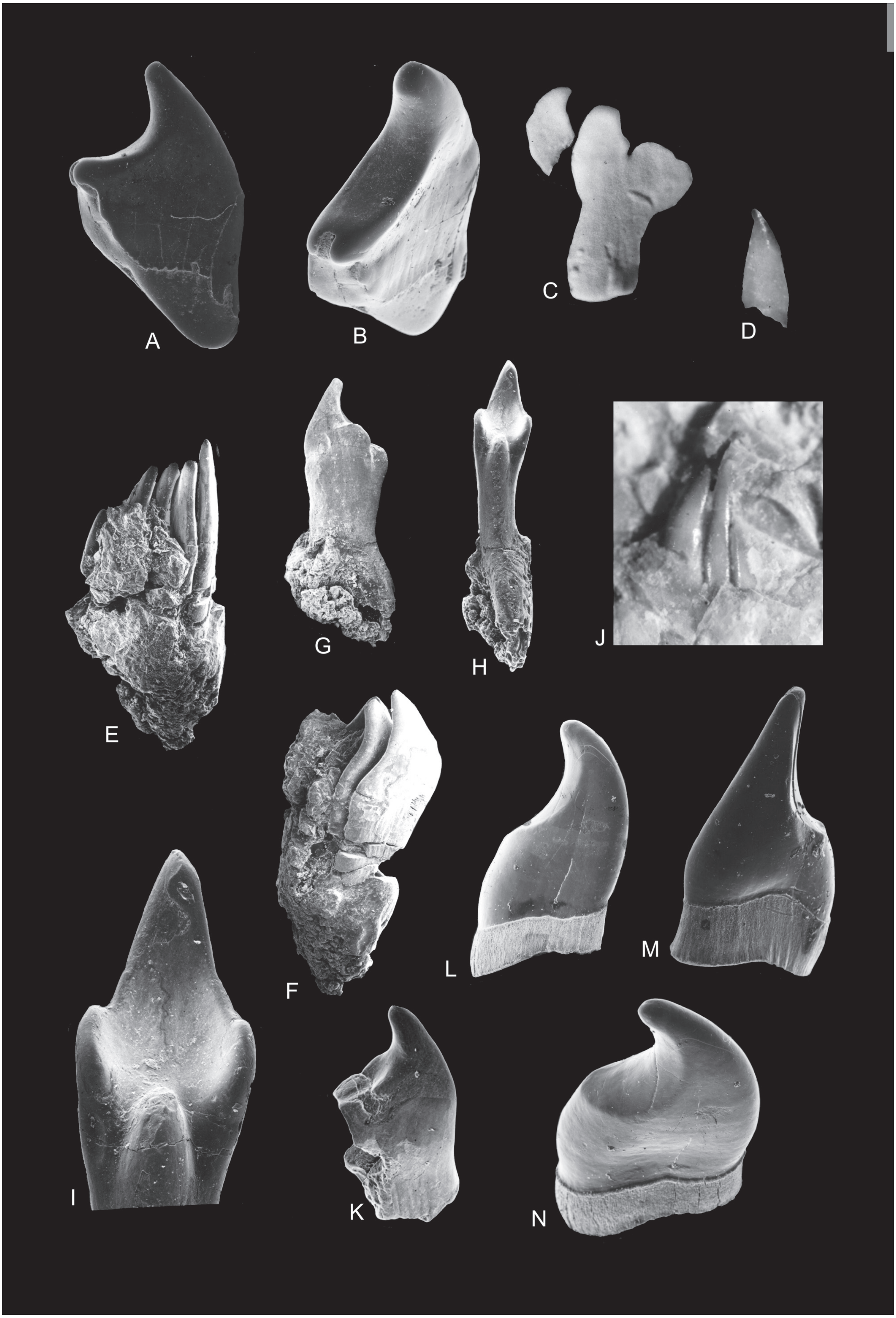
Bellwood (2003) and Bellwood & Hoey (2004) assumed that the "herbivorous morphospace" that is occupied by grazers and browsers today was not present in the Mesozoic. This suggestion is based on analyses of lower jaw closing lever ratios. However, pycnodonts are characteristic crushers with specialised jaw teeth and branchial armature for crushing ingested food similar to modern triggerfishes (Balistidae) and others. The diet of these fishes (e.g., Balistidae) consists not only of fish but also of prominent amounts of plants which are obtained by biting off the plants from the substrate (e.g., Gerking 1994). Kriwet (2001b) interprets pycnodonts as highly specialised fishes concerning their prey but also as grazers picking and biting off vagile and invagile prey from any substrate based on stomach analyses. These gut/intestine contents (e.g., corals in *Neoproscinetes*) in combination with the presence of incisiform grasping teeth and a specialised branchial armature in several pycnodonts also supports the hypothesis that the guild of grazers and browsers in coral reefs ("herbivorous morphospace") was already realised in the Mesozoic, probably as early as the Early Cretaceous.

5.9 Hyoid Arch

The hyoid arch of actinopterygians consists of an unpaired basihyal, and paired hypohyal, anterior and posterior ceratohyals, interhyal, and epihyal. There is a single bony element in the hypohyal region in amiiforms (Grande & Bemis 1998), lepisosteiforms (Wiley 1976), pachycormiforms (Wenz 1968), aspidorhynchiforms (Brito 1997), and in *Pholidophorus bechei* (Arratia 1999). Most teleosts with the exception of a few extant forms have two dorsally and ventrally arranged hypohyal ossifications (Arratia 1999; Arratia & Schultze 1990). According to Arratia (1999) the presence of two hypohyals is a synapomorphy for *Leptolepis coryphaenoides* and more advanced teleosts.

The morphology of the hyoid arch of pycnodonts corresponds to the general pattern found in non-teleostean actinopterygians. It consists of a single hypohyal, an anterior and a posterior ceratohyal and an interhyal (Figs 1, 60). The form of the interhyal varies considerably withinthe pycnodontiforms (Figs 60, 61). The anterior ceratohyal supports the two branchiostegal rays on each side of the head. It is generally short with a notched ventral margin and a plate-like posterior portion in lateral aspect. The anterior ceratohyal of pycnodonts is similar to that found in several teleosts and macrosemiids (Bartram 1977; Lambers 1991), but the pycnodont one is smaller in respect to the skull and more irregular. The hypohyal and the

Figure 59: Branchial and pharyngeal teeth of fossil and extant actinopterygians. **A-B:** Branchial tooth of *Ancistrodon* sp. (MB. f. without number). **A:** Lateral view. x 13. **B:** Occlusal view. x 18. **C:** branchial tooth of *Pycnodus platessus* (BSP-AS I 1208, holotype), lateral view. x 29. **D:** Branchial tooth of *Nursallia*? *goedeli* (BSP-AS XXV 20), lateral view. x 29. **E-I:** Branchial teeth of *Coccodus armatus*. *Coccodus* is one of the few pycnodonts with two different morphotypes. **E-F:** Branchial teeth of morphotype 1. **E:** Occlusal view. x 19. **F:** Lateral view. x 18. **G-I:** Branchial teeth of morphotype 2. **G:** Lateral view. x 17. **H:** Occlusal view. x 20. **I:** Close up of H displaying occlusal surface. x 65. **J:** Associated branchial teeth of *Nursallia*? *goedeli* (BSP AS XXV 20), lateral view. x 20. **L-N:** Pharyngeal teeth of extant *Balistes aculeatus* (MB. f. without number). **L:** lateral view. x 40. **M:** Lateral view. x 40. **N:** Occlusal view. x 60.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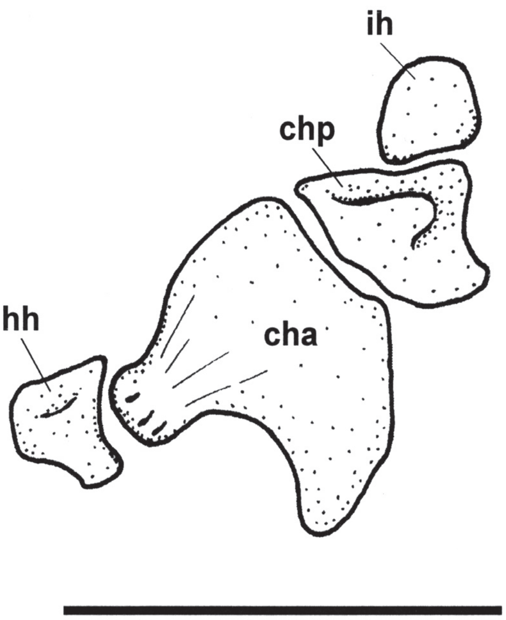

Figure 60: Hyoid apparatus of *Neoproscinetes penalvai* based on specimen AMNH 11893 showing the hypohyal, the anterior and posterior ceratohyal, and the interhyal. Scale bar = 5.0 mm.

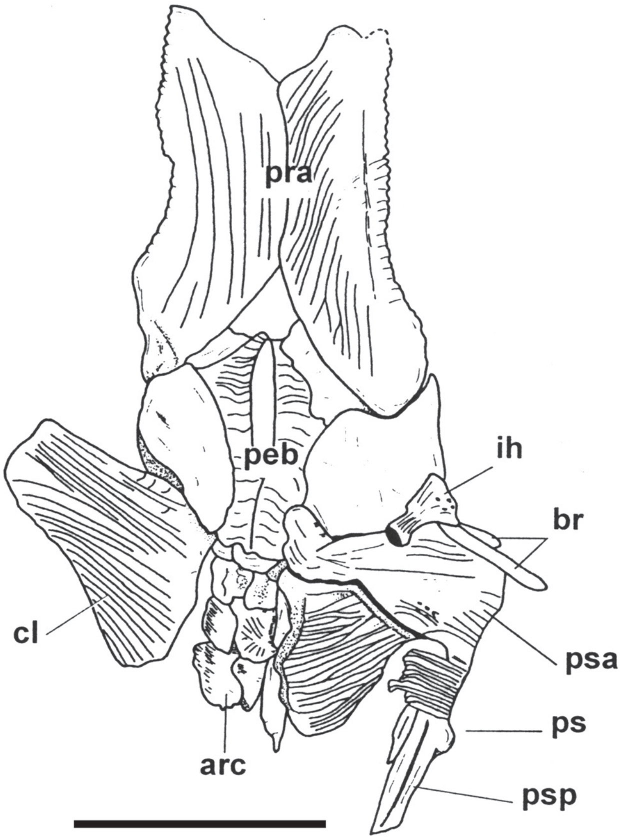

Figure 61: Ventral view of *Coocodus armatus* (MNHN HAK 319) exemplifying morphological variation of the interhyal bone and articulation of the pectoral spine.

rod-like interhyal are also small, but generally well-ossified. The attachment of these bones to one another or to any part of the suspensorium and/or opercular apparatus is unclear but may have been articulated via broad cartilaginous surfaces with each other as found in many extant actinopterygians. There may have been ligamentous connections between the hyoid arch and the mandible, the suspensorium, and/or pectoral girdle (see below). There is no basihyal in pycnodonts.

6. Phylogenetic analysis

The interrelationships of pycnodontiform fishes were recently analysed by Nursall (1996b) and Poyato-Ariza & Wenz (2002, 2005). In addition, Poyato-Ariza (2003) presented an analysis exclusively applying dental characters. Nursall's (1996b) hypothesis is based on proposed synapomorphies but does not present a cladistic analysis *sensu stricto*. The analysis of Poyato-Ariza & Wenz (2002), on the contrary, employed cladistic principles and used a data matrix including 33 taxa and 105 characters, 34 of which were processed as ordered.

The focus of the phylogenetic analysis presented in this study is on the cranial morphology using the original data matrix of Poyato-Ariza & Wenz (2002). The outgroup composition of Poyato-Ariza & Wenz (2002) was used to polarise characters. Only characters referring to the skull were employed in the analysis. Conversely to Poyato-Ariza & Wenz (2002) all characters are treated as unordered (Fitch parsimony) and unweighted. The new data matrix consists of 47 characters and was run with the WinClada program, version 1.00.08, on a PC.

Analyzing the original data matrix containing all characters with the WinClada program did not result in marked changes to the results obtained from employing the PAUP program on a Macintosh computer by Poyato-Ariza & Wenz (2002). I therefore assume that the results obtained in this study are similar to results that could be achieved if PAUP would have been used.

The following settings were employed herein: heuristic search, multiple TBR + TBR algorithm that searches for trees using tree bisection-recombination method of branch swapping with 1000 replications, DELTRAN optimization that puts changes on the tree as late as possible and initial MaxTrees setting was 33000. Bootstrap option with 1000 replications was used to calculate the support of nodes. Characters followed by an asterisk indicate autapomorphic features.

Figure 62 corresponds to the strict consensus tree of 50 equally parsimonious trees (MPTs) at 171 evolutionary steps. The consistency index (CI) is 0.52; the retention index (RI) is 0.57. The consistency index of the analysis excluding postcranial characters is slightly better than the one of Poyato-Ariza & Wenz (2002: 204). Cranial characters defining the terminal characters are given in the appendix.

The resolution of the phylogenetic relationships is rather good if cranial characters are exclusively analysed. Pycnodontiformes (node A) are characterized by hypertrophied antorbital and ethmoidal regions [8(1)*], a dermosupraoccipital [15(2)*], and vomerine teeth that are arranged in rows [37(1)]. This

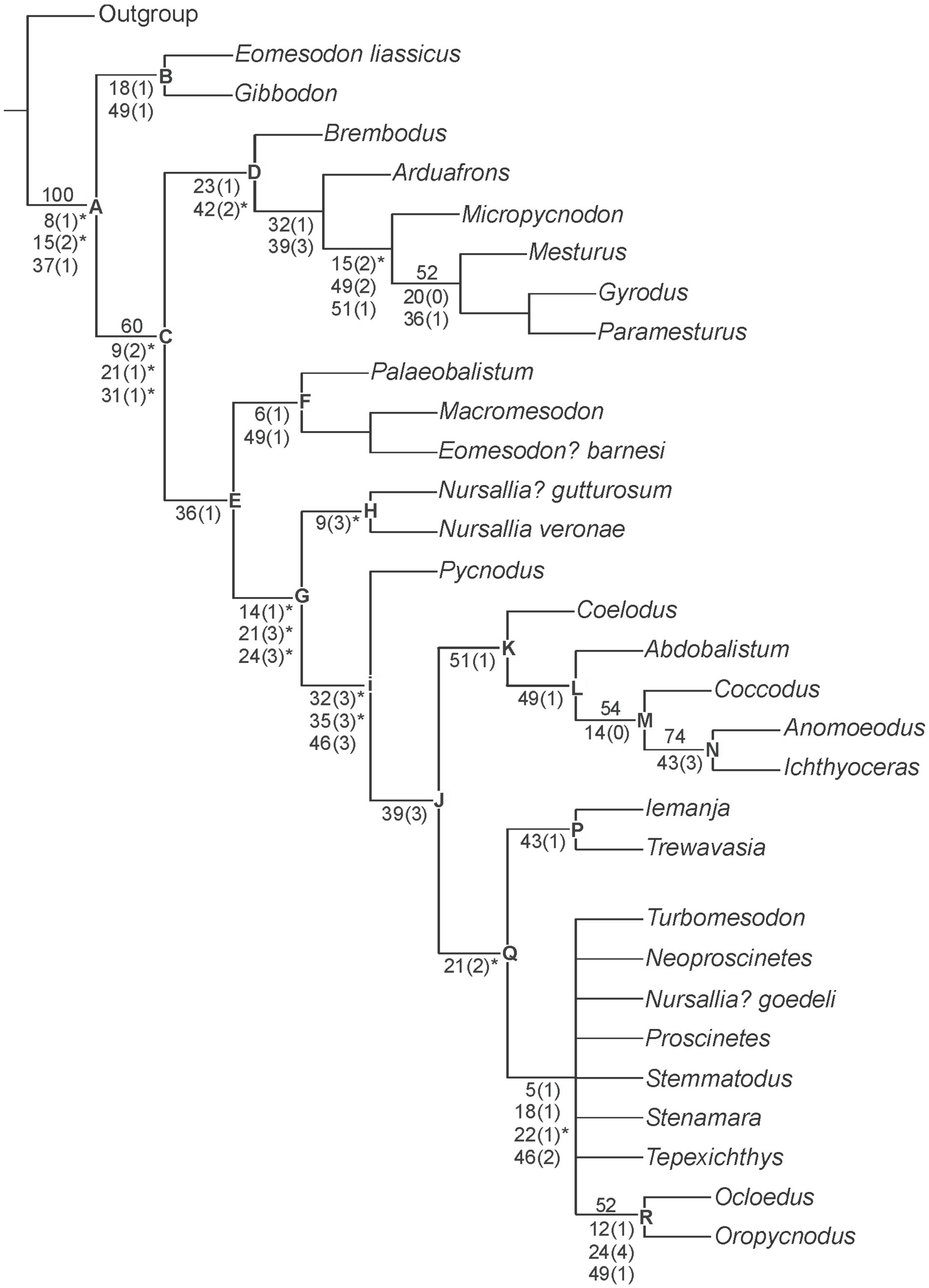

Figure 62: Phylogenetic relationships of pycnodontiform fishes based on cranial characters alon. Strict consensus tree of 50 MPTs at 171 evolutionary steps. CI = 0.52, RI = 0.57. Characters are from Poyato-Ariza & Wenz (2002, 2004). Numbers above branches are bootstrap values (only those over 50% are shown), number s below branches are characters and character states. Characters followed by an asterisk indicate autapomorphic features. Letters correspond to nodes discussed in the text.

confers with the phylogenetic hypothesis of Poyato-Ariza & Wenz (2002).

However, major changes in the arrangement of taxa are also evident. In the present analysis, *Gibbodon* and *Eomesodon liassicus* form a monophyletic group (node B), which is the most plesiomorphic member of the pycnodontiforms. This grouping is supported by two homoplastic characters [18(1) and 49(1)] and contradicts the arrangement found by Poyato-Ariza & Wenz (2002), where both are member of a clade comprising the Pycnodontoidei Nursall, 1996b plus Brembodontidae Tintori, 1981.

Pycnodontiformes minus *Gibbodon* and *Eomesodon liassicus* (Pycnodontoidei, node C) is supported by three autapomorphic cranial characters and consists of two sister groups. Character 31(1) (superficial premaxillary process) is one of the autapomorphic characters defining Pycnodontiformes in the analysis by Poyato-Ariza & Wenz (2002). Conversely, this character defines all pycnodonts above node C minus *Gibbodon* and *Eomesodon liassicus* in the present study.

A monophyletic group above node D includes *Brembodus*, *Arduafrons*, *Gyrodus*, *Mesturus*, *Micropycnodon*, and *Paramesturus* (Brembodontidae in part + Mesturidae + *Arduafrons* + *Gyrodus* + *Paramesturus* of Poyato-Ariza & Wenz 2002). *Paramesturus* is sister of *Gyrodus* in the present analysis, whereas it is the most basal pycnodont in the analysis of Poyato-Ariza & Wenz (2002). However, the authors did not find any character defining this taxon. Here, *Paramesturus* is defined by a single cranial character [infraorbitals as row of plates around the ventral and posterior border of the orbit; 21(0)]. The grouping of *Gyrodus* plus *Paramesturus* is, however, not supported by any cranial character.

Palaeobalistum plus *Macromesodon* plus *Eomesodon*? *barnesi* (node F) is sister to a group including all remaining pycnodonts above node G. This group is supported by two homoplastic characters alone.

The genus *Nursallia* (node H) is characterized by curved and very broad parietal bones. This character defines the subfamily Nursalliinae including *Nursallia*, *Abdobalistum*, and *Palaeobalistum*, and alternatively the grouping of *N. veronae* plus *N. gutturosum* when *N.*? *goedeli* is removed in the study of Poyato-Ariza & Wenz (2002).

Pycnodus is the basal member of a monophyletic group consisting of all pycnodonts above node J, which is supported by a single homoplastic character [39(3)]. This contradicts previous analyses where *Pycnodus* is always regarded as one of the most advanced pycnodonts.

Other differences include the arrangement of taxa formerly recognized as Coccodontidae by Poyato-Ariza & Wenz (2002). In the study presented here, *Coccodus* is member of a group including *Coelodus*, *Abdobalistum*, and *Anomoeodus* (node K). *Trewavasia* is sister to *Iemanja* (node P).

Poor resolution only occurs in the crown group with the relationships of *Turbomesodon*, *Neoproscinetes*, *Nursallia*? *goedeli*, *Proscinetes*, *Stemmatodus*, *Stenamara*, and *Tepexichthys* being unresolved (node Q). *Oropycnodus* and *Ocloedus* form a monophyletic grouping in the present study conversely to the hypothesis presented by Poyato-Ariza & Wenz (2002), where *Oropycnodus* and *Pycnodus* are sister to each other.

The most obvious result of this study is that there occur considerable differences if different data sets are employed, i.e. Poyato-Ariza (2003): dental characters; Poyato-Ariza & Wenz (2002): cranial and postcranial characters; this study: cranial and dental characters. Employing only limited data sets results in different degrees of poor resolution. The results of the present analysis imply that the skull morphology of pycnodontiform fishes provides significant insights into the phylogenetic interrelationships of pycnodontiforms. However, the discrepancies to other analyses using different data sets have to be explored and explained. The differences between this and previous studies also indicate that there is still the need to search for more characters and employ different outgroups. Kriwet (1999a, 2001b) and this study assume that the cranial anatomy of pycnodonts exemplifies general evolutionary trends such as reduction of dermal skull covering, increasing upper jaw mobility, and improvements in food gathering and processing. These changes, however, are not completely consistent with the hypothesis presented here and indicate that further research in the cranial anatomy is required.

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Appendix

The following characters of Poyato-Ariza & Wenz (2002) were used for the cladistic analysis presented herein: 5, 6, 8, 9-51, 83. In the following list, the cranial characters defining each terminal taxon are given. Character states are in brackets following the character numbers. Autapomorphic characters are indicated by an asterisk. Arrangement of taxa follows the phylogenetic hypothesis presented in Figure 62.

Eomesodon liassicus: 9(1)
Gibbodon: 33(1)*, 42(1)*
Brembodus: 9(1), 30(1)
Arduafrons: 6(1), 47(0)
Micropycnodon: 39(1), 46(1), 47(2)
Mesturus: 13(1)*, 24(2)*, 35(2)*, 43(1), 50(1)*
Gyrodus: 9(1), 15(1)
Paramesturus: 21(0)
Palaeobalistum: 18(1)
Macromesodon: 5(1)
Eomesodon? barnesi: 45(1)
Nursallia? gutturosum: 39(1)
Nursallia veronae: 38(1)
Pycnodus: 12(1), 19(1), 24(4)
Coelodus: 43(4)
Abdobalistum: 32(2)
Coccodus: 39(2), 45(1), 46(2)
Anomoeodus: 44(2)*, 45(4)
Ichthyoceras: 10(1), 11(2)*
Iemanja: 6(1), 37(2)*, 44(0)
Trewavasia: 5(2)*, 10(1), 11(1)*, 13(2)*, 14(0)
Turbomesodon: 39(22), 47(2), 49(1)
Neoproscinetes: 26(1), 38(1), 39(2), 40(1), 42(3), 46(1), 47(2)
Nursallia? goedeli: 14(0), 42(3), 47(2), 49(1)
Proscinetes: 30(1), 38(1), 39(2), 40(1)
Stemmatodus: 24(4), 35(4)*, 36(1), 39(2), 46(3), 49(1)
Stenamara: 45(1)
Tepexichthys: 12(1), 22(2)*, 34(1), 42(3), 47(2), 49(2)
Ocloedus: 51(1)
Oropycnodus: 5(0), 19(1), 28(2)*, 39(1)*, 46(1)