

The phylogeny of pycnodont fishes

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Abstract

†Pycnodontiformes is a monophyletic group with two suborders, Gyrodontoidei and Pycnodontoidei, each with two families. Another family is proposed to represent a stem group to the order. Five families remain incertae sedis. The order is the sister group to teleosts, within Halecostomi. Amiiformes is the sister group to pycnodonts + teleosts. The outgroup to Halecostomi is represented by *Dapedium* spp.

Introduction

This paper provides a list of annotated synapomorphies which define the order, suborders, families and genera of pycnodont fishes and which provide the basis for establishing phylogenetic relationships within Halecostomi.

The term “pycnodont” as used herein refers to members of the order †Pycnodontiformes. Informal reference to the suborder Pycnodontoidei is by the term “pycnodontoid”. Informal reference to the family Pycnodontidae is by the term “pycnodontid”.

The pycnodont fishes have been distinguished as a taxon since their description by AGASSIZ (1833-44) – “la famille des pycnodontes”. They clearly form a monophyletic group, which, at this stage of our understanding, we call an order – †Pycnodontiformes – following BERG (1940). Taxonomically, the order will be shown to be a plesion within Halecostomi [Halecomorphi + Teleostei].

Pycnodonts appeared in the Late Triassic (Norian) (TINTORI 1981) and persisted into the Eocene (Lutetian) (LONGBOTTOM 1984, BLOT 1987), a period of about 175 million years. They colonized the margins of western Tethys and spread across the opening Atlantic into the Americas during the Jurassic and Cretaceous Periods (NURSALL this volume).

Ten families are identified in the order, of which five are incertae sedis. These five families comprise six genera. I believe that two of the monotypic families (Palaeobalistidae BLOT 1987, and Nursalliidae BLOT 1987) will prove to be invalid and the genera they contain will be placed among the Pycnodontidae when more material has been studied. The families Hadrodontidae (*Hadrodus*), Trewavasiidae (*Trewavasia*, *Ichthyoceros*) and Coccodontidae (*Coccodus*) will possibly be placed within the suborder Pycnodontoidei, as discussed below (see p. 139).

Eighteen genera are identified in the remaining five families.

Gibbodontidae comprises the most primitive pycnodonts, known at present only from two specimens (*Gibbodon cenensis* TINTORI 1981 [Fig. 1], and a second, *Gibbodon* sp., in the Museo Friulano di Storia Naturale, Udine). The genus is marked chiefly by plesiomorphic characteristics (e.g., heterocercy; well-developed fin fulcra; full squamation; bifid prehensile teeth). Moreover, it is difficult to interpret in detail because of the state of preservation and its heavy covering of scales. Much more will have to be learnt from further specimens before *Gibbodon* can be placed more accurately in the pycnodont sequence. With current understanding, Gibbodontidae is hypothesized to represent a stem group (sensu JEFFERIES 1979, 1986) to a bipartite crown group encompassing the remainder of the pycnodonts (see Fig. 4).

The crown group of pycnodonts is proposed to have two major subdivisions, or suborders. The first of these, which I name Gyrodontoidei, comprises the families Mesturidae (*Mesturus*, *Micropycnodon*, and an undescribed genus) and Gyrodontidae (*Gyrodus* [Fig. 2]). The second suborder, which I call Pycnodontoidei, includes the families Brembodontidae (*Brembodus*, *Eomesodon*) and Pycnodontidae (*Macromesodon*

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