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## INTERRELATIONSHIPS OF PYCNODONTIFORM FISHES : PRELIMINARY REPORT ON THE FIRST CLADISTIC ANALYSIS OF THE ORDER

**Introduction : historic background.-** The pycnodontiform fishes is a group of actinopterygians, spread world-wide, and present in many Fossil-Lagerstätten, some of them described long ago from "classic" outcrops like, for instance, *Gyrodus*, *Macromesodon*, *Mesturus*, and *Proscinetes* from the Tithonian of Solnhofen (Blainville, 1818 ; Agassiz, 1833-1844 ; Wagner, 1862), or *Palaeobalistum* and *Pycnodus* from the Eocene of the Monte Bolca (Volta, 1796 ; Blainville, 1818 ). They are also present in many recently discovered Lagerstätten, such as *Brembodus* and *Gibbodon* from the Norian of the Zorzino limestones (Tintori, 1981), *Coelodus* from the Berriasian/Valanginian of Montsec (Wenz, 1989), *Tepexichthys* from the Albian of Tepexi de Rodríguez (Applegate, 1992), and *Macromesodon* from the Barremian of Las Hoyas (Wenz & Poyato-Ariza, 1995). Despite their broad distribution and their being known for centuries, active research on their common anatomical features and on their phylogenetic relationships is relatively recent. The first comprehensive compilation of pycnodonts is that of Lehman (1966), where they are described and listed as known at the time, being given the category of Order ; their phylogenetic relationships, however, are not addressed. Only Nursall's work in recent years has permitted to define the pycnodontiforms as a monophyletic group, with a phylogenetic hypothesis (Nursall, 1996a) and to apprehend their ecology and distribution (Nursall, 1996b). Our interest on the phylogenetic interrelationships of this group started when studying the pycnodonts from Montsec and Las Hoyas mentioned above, and some new forms from the Lebanon currently under study. We tried to include these forms in the phylogenetic context provided by Nursall (1996a), but found some problems on the interpretation, polarization, and distribution of certain characters. The mentioned paper presents, for the first time, phylogenetic trees, with distribution of 135 characters (a number of them being actually different states of a same given character). This author proposes a hypothesis of interrelationships of pycnodontiforms, but it does not present a cladistic analysis *sensu stricto*, and, consequently, no data matrix. As acknowledged by Nursall (1996a), the relationships that he proposed "should provide directions for further analysis" (op.cit. : 149). We intend to go one step forward and to provide, for the first time, a cladistic analysis of the interrelationships of the Pycnodontiformes.

**Material and methods.-** At the time of preparing this paper, it is our estimation that we have accomplished about 80% of the work necessary for the definitive analysis. At

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present, however, it is already possible to present some significant results. We have included 22 genera. The information on 6 of them comes, at this moment, from bibliographic sources only ; well preserved specimens of the other genera have been observed. Only forms known from at least partially complete, articulate specimens are included in the study ; taxa defined on dentition only are specifically avoided. The genera are *Arduafrons* (=“*Mesturoides*”), *Brembodus*, *Coccodus*, *Coelodus*, *Eomesodon* (up to 5 nominal forms), *Gibbodon*, *Gyrodus*, *Ichthyoceros*, *Iemanja*, *Macromesodon* (3 forms), *Mesturus*, *Micropycnodon*, *Neoproscinetes*, *Nursallia* (2 species), *Palaeobalistum* (3 species), *Paramesturus*, *Proscinetes*, *Pycnodus*, *Stemmatodus*, *Tepexichthys*, *Trewavasia*, and a new form from the Lebanon currently under study by the authors. Character polarization is based on Maddison et al’s (1984) compound outgroup comparison ; the outgroup included *Pteronisculus*, *Dapedium*, *Amia*, and *Semionotus*, with partially unresolved relationships among them. Eighty characters have been coded so, forming the data matrix that we ran with the PAUP program version 3.1.1 (Swofford 1993) for Macintosh computer. We are not presenting herein the data matrix in its current state or the cladograms that we have obtained so far, because they are still preliminary. We want, nonetheless, to indicate the main results obtained so far, that are present in all of the trees we have analysed ; they are presented below from bottom to top of the cladogram and compared with Nursall’s (1996a) phylogenetic hypothesis.

### Results and comparison.-

- 1.- The monophyly of the order Pycnodontiformes sensu Nursall 1996a, is confirmed, although the detailed distribution of some characters may be conflictive.
- 2.- *Gibbodon* is not the basalmost pycnodontiform, but the sister-group of *Brembodus* (see point 5).
- 3.- The “Suborder Gyrodontoidei” is not a monophyletic group, but a paraphyletic array of the basalmost pycnodontiforms : *Mesturus* (+ *Micropycnodon* + *Paramesturus*), *Arduafrons* (=“*Mesturoides*”), *Gyrodus*, and *Palaeobalistum zignoi*.
- 4.- The Suborder Pycnodontoidei sensu Nursall 1996a is a well defined monophyletic group, consisted of the monophyletic sister-families Brembodontidae as defined in point 5 + Pycnodontidae sensu Nursall 1996a.
- 5.- The Brembodontidae is formed by [(*Brembodus* + *Gibbodon*) + *Eomesodon*].
- 6.- The family Pycnodontidae sensu Nursall 1996a include the pycnodontiforms that are not mentioned previously in this section. The interrelationships among them need to be re-evaluated before a definitive study is achieved.
- 7.- The genus *Palaeobalistum* is polyphyletic, and will be redefined.
- 8.- The most derived pycnodontids are (*Coccodus* + *Ichthyoceros*). *Trewavasia* appears as a most basal pycnodont, relatively far from these genera.

We wish to emphasise that the results presented above are merely preliminar ; further homology tests, character polarisation checking, and homoplasy analyses are to be carried out prior to a deeper discussion of pycnodontiform interrelationships. Our detailed results will probably change when we add the new characters that we are presently analysing, and when we observe directly specimens of the taxa whose information is, in this moment, only bibliographical. We are confident, however, that the overall results briefly presented

in this paper will be maintained, and will constitute the base of a finest cladistic analysis (Poyato-Ariza & Wenz, work in progress). In addition, it is our intention to evaluate the relevance of the meristic and of the dental characters in the cladistically analysed interrelationships of pycnodontiforms, a group where the dentition is of particular interest, but presents serious problems in many taxonomic assessments.

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