Journal of Vertebrate Paleontology 23(4):937–940, December 2003

NOTE

DENTAL CHARACTERS AND PHYLOGENY OF PYCNODONTIFORM FISHES

FRANCISCO JOSÉ POYATO-ARIZA, Unidad de Paleontología, Departamento de Biología, Universidad Autónoma de Madrid, Cantoblanco, 28049-Madrid, francisco.poyato@uam.es

Pycnodontiforms are remarkable fishes that have been known for over two centuries. Complete specimens are present in Triassic to Eocene Lagerstätten, mostly from Europe and America, including, in chronological order, Zorzino in Italy, the Solnhofen area in Germany, Cerin in France, El Montsec and Las Hoyas in Spain, the Santana Formation in Brazil, Tepexi de Rodríguez in Mexico, and Monte Bolca in Italy (e.g., Saint-Seine, 1949; Tintori, 1981; Blot, 1987; Wenz, 1989a, b, 1991; Lambers, 1991; Maisey, 1991; Applegate, 1992, 1996; Frickhinger, 1994, 1999; Poyato-Ariza and Wenz, 1995, 2000, in press; Nursall, 1996a; Kriwet et al., 1999). Pycnodonts (Fig. 1A) are easily recognizable by their high, rounded body and well-developed dorsal and anal fins, which make them superficially resemble Recent butterflyfishes. Pycnodonts are also characterized by their conspicuous durophagous dentition on the vomer and the prearticulars (Fig. 1B–D). These dentitions are found as isolated remains at a very large number of localities and are often the only elements of these fishes that are preserved (Fig. 1C). Numerous taxa have been created solely on the basis of vomerine and/or prearticular dentitions (e.g., Agassiz, 1833–1843; Woodward, 1895; Thurmond, 1974; Longbottom, 1984).

Pycnodonts figure importantly in many classic paleoichthyological works, including those of Agassiz (1833–1843), Woodward (1895), and Lehman (1966). Nevertheless, the first comprehensive hypothesis on their phylogenetic relationships was that of Nursall (1996b), and the first cladistic analysis of their interrelationships was more recently put forward by Poyato-Ariza and Wenz (2002). To avoid problems of parataxonomy, these phylogenetic hypotheses were based on articulated material only.

The present paper analyzes the role of isolated dentitions in the study of the Pycnodontiformes. Dentitions are the only pycnodont remains at many localities and for many taxa (e.g., Fig. 1C), but the accuracy of their taxonomic assignments has never been tested. Their relevance for interpreting the diversity, phylogeny, and taxonomy of this group, including their parataxonomic implications, has occasionally been discussed (e.g., Poyato-Ariza et al., 1999a), but never seriously addressed. The intent here is to assess the effect of dental characters on interpreting the phylogenetic interrelationships of these fishes. This is a relevant issue because we need to know whether it is reliable to include those taxa that are known only from dentitions in future phylogenetic analyses.

With this purpose, data from Poyato-Ariza and Wenz (2002) are restudied. These data consist of 105 characters coded for 33 taxa; in addition to the published printed version, they are available online at <http://www.mnhn.fr/publication/geodiv/g02n1som.html>.

The phylogenetic hypothesis of Poyato-Ariza and Wenz (2002) is depicted on the left side of Figure 2. In order to test the role of dental characters in these relationships, the subset of dental characters was separated; they are listed in Appendix 1. Note that these characters concern not only the vomerine (Fig. 1C) and the prearticular (Fig. 1D) dentitions, but also those of the premaxilla and the dentary, which are rare as isolated bones. After separating out the subset of dental characters, two new cladistic analyses were carried out, the first with dental characters alone, and the second with non-dental characters only.

RESULTS

First Analysis: Dental Characters Alone

When only dental characters are used, without the rest of the original data set, the analysis (conducted using PAUP, version 3.1.1, run on an iMac computer, with the closest stepwise addition option of heuristic search) recovered 23,900 equally most parsimonious trees, each 75 steps

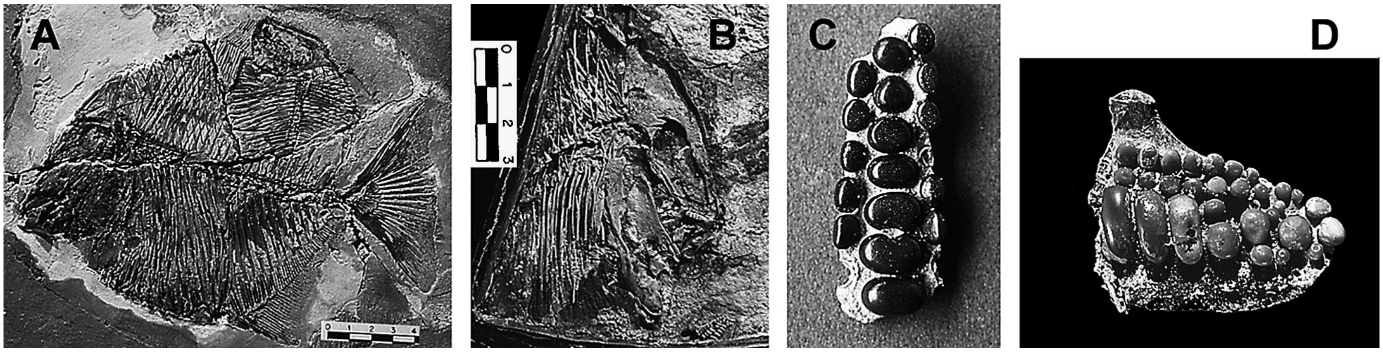

FIGURE 1. Examples of pycnodontiform fishes. **A**, *Oropycnodus* Poyato-Ariza and Wenz, 2002, from the Montian (Paleocene) of Mont Aimé, France. Specimens MNHN MTA 42 (Muséum national d'Histoire naturelle de Paris), adult individual plus subadult individual juxtaposed on dorsal caudal region. **B**, *Macromesodon* Blake, 1905, from the Barremian (Early Cretaceous) of Las Hoyas, Spain. Specimen MCCM LH-16363 (Museo de Ciencias de Castilla-La Mancha, Cuenca, Spain, provisionally housed at the Universidad Autónoma de Madrid), skull showing dentition plus anterior part of body, transfer preparation. Notice the toothed vomer and premaxillae in situ, and the detached left prearticular on bottom right corner. **C**, cf. *Paramicrodon* Thurmond, 1974, from the Maastrichtian (Late Cretaceous) of Albaina, Spain (see Poyato-Ariza et al., 1999b). Specimen JISL 91 (private collection of J. I. Sáez Laria, Vitoria, Spain; cast available at MCNA, Museo de Ciencias Naturales de Álava), isolated vomer in occlusal view, anterior end at top of photograph. Total length of bone as preserved: 35 mm. **D**, *Neoproscinetes* Figueiredo and Silva Santos, 1987, from the Aptian-Albian (Early Cretaceous) of the Santana Formation, Brazil (see Nursall and Maisey, 1991). Specimen MNHN BCE-104, left prearticular in occlusal view, detached from a 3-D acid-prepared skull. Total length of bone as preserved: 33 mm. **A**, **B**, **D**, photographs by D. Serrette, MNHN. **C**, photograph J. C. Corral, MCNA.

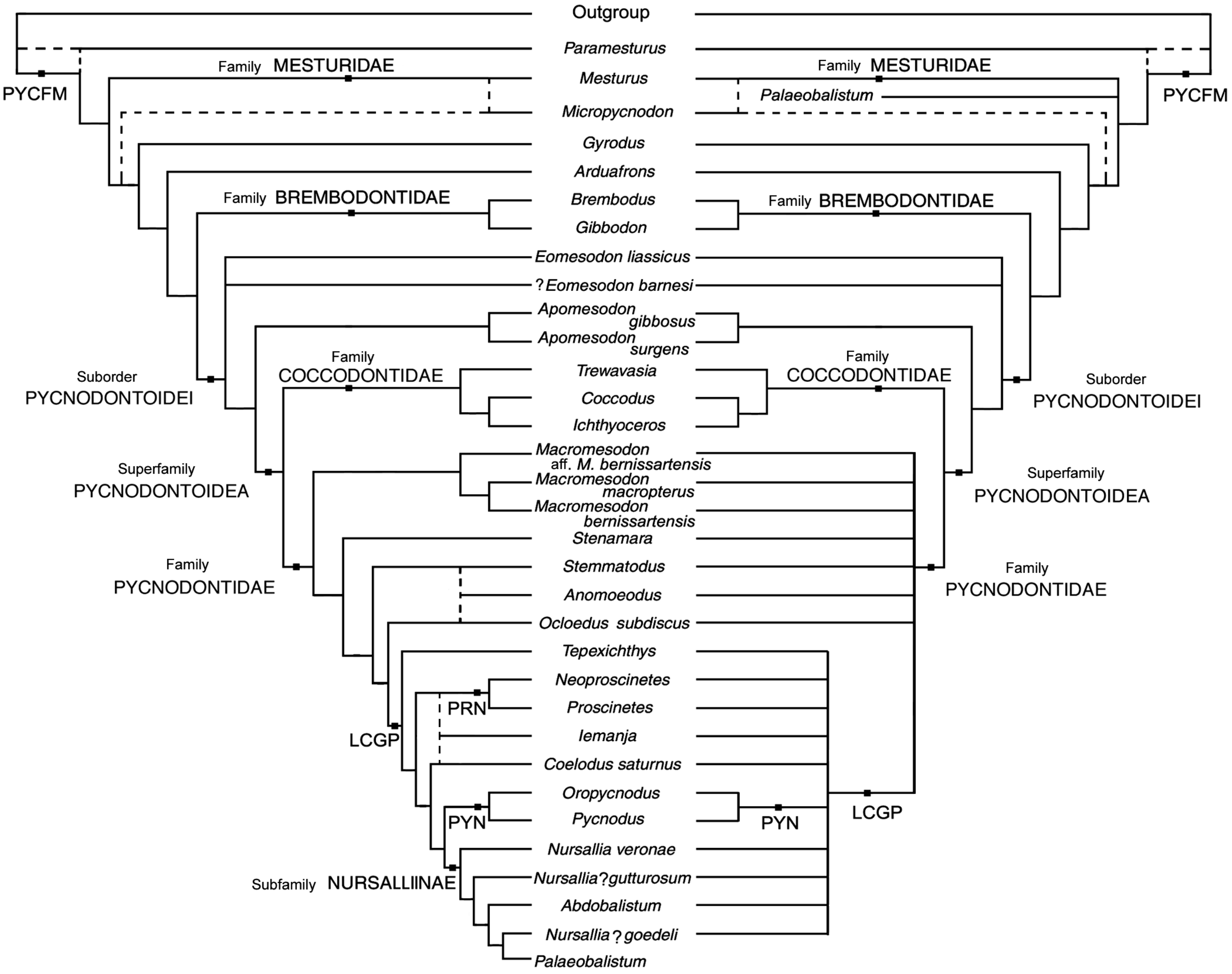

FIGURE 2. Comparison between the phylogenetic relationships of the Pycnodontiformes with and without dental characters. On the left: strict consensus tree obtained with the complete data set (slightly modified from Poyato-Ariza and Wenz, 2002). On the right: strict consensus tree obtained when dental characters are removed from the data matrix, i.e., a hypothesis of phylogenetic relationships without dental characters. LCGP, large 'crown-group' Pycnodontidae (this clade corresponds to node 19 in Poyato-Ariza and Wenz, 2002); PRN, subfamily Proscinetinae; PYCFM, order Pycnodontiformes; PYN, subfamily Pycnodontinae. Dotted lines represent possible sister-group relationships. As explained in the text, the analysis with dental characters alone results in a polytomy involving all taxa, and is therefore not depicted.

long, before running out of memory. The strict consensus tree from these is an unresolved polytomy of all 33 taxa in the analysis. A certain degree of poor resolution could be expected from this data subset, which has more taxa than characters, but the complete lack of resolution is both discouraging and interesting. It implies that the phylogenetic relationships of pycnodont taxa known only from isolated dentitions cannot be resolved, even when dental characters from the premaxilla, the vomer, the dentary, and the prearticular are all included.

There is one obvious question that arises from this result. If the phylogenetic relationships of a taxon known only from isolated dentitions cannot be resolved, might they be resolved if that taxon (e.g., a new species) could be assigned to a higher taxon (e.g., a previous genus) known from articulated remains? The answer is yes, they could, but the problem in the case of pycnodonts is precisely the taxonomic assessment of the isolated dentitions. Thus, it is a taxonomic, not a phylogenetic, issue. The taxonomic assessment of isolated pycnodont dentitions falls within the domains of parataxonomy, and clearly out of the scope of this short communication.

Second Analysis: Non-dental Characters

When the subset of dental characters listed in Appendix 1 is removed, and the remaining original data matrix from Poyato-Ariza and Wenz (2002) is run, the results are also quite interesting, especially when compared with the phylogenetic hypothesis that arises from the complete data matrix (Fig. 2). The PAUP program, run as described above, found 7,190 most parsimonious trees (MPTs) of 533 evolutionary steps. The strict consensus tree without dental characters (Fig. 2, right) is much less resolved than the original consensus tree with the complete data set (Fig. 2, left). This can be expected taking into account that the number of MPTs in the former case is considerably higher. However, the homoplasy is barely lower without the dental characters (homoplasy index of 0.555 versus 0.563 with the complete data set). This indicates that dental characters scarcely affect the overall homoplasy.

The new hypothesis without the dental characters (Fig. 2, right) involves only one major difference from the original analysis in the phylogenetic position of any pycnodont taxon, but this difference is quite striking. The taxon is the genus *Palaeobalistum*, a monotypic form known from a single, imperfect specimen (Blot, 1987:fig. 49, tabs. 9–10, pls. 30–33; Poyato-Ariza and Wenz, 2002:fig. 4a). It moves from the most derived group (subfamily Nursalliinae), to one of the most basal genera. This can be explained by the puzzling combination of primitive and derived characters exhibited by this genus. This change of position indicates that (what is known of) the dentition is very derived, whereas the non-dental characters are very primitive, especially the heavy squamation all over its body, formed by complete scales, similar to the squamation of *Mesturus*. In contrast, other body structures, such as the contour scales (similar to those of *Pycnodus*, *Abdobalistum*, or *Nursallia*), are very derived. The most parsimonious position of this genus using the complete data set is highly derived, but with only non-dental characters it is placed near the base of the tree. Therefore, the dental characters ''push'' *Palaeobalistum* from the base to the top of the tree, where it is better kept according to the total evidence until additional information is available on this genus.

Other than the position of *Palaeobalistum*, the phylogenetic relationships of non-pycnodontid pycnodontiforms are the same with the complete data set as they are without the dental characters (Fig. 2), including: the possible position of *Paramesturus* outside of the Pycnodontiformes; the indeterminate position of *Micropycnodon*, which may or may not be the sister-group of *Mesturus*; the paraphyly of a ''suborder Gyrodontoidei'' that would combine Mesturidae and Gyrodontidae; the sister-group relationship of *Brembodus* and *Gibbodon*, forming the Family Brembodontidae sensu Tintori (1981); the paraphyly of the genus *Eomesodon* as used prior to Poyato-Ariza and Wenz (2002); the monophyly and composition of the suborder Pycnodontoidei; the sister-group relationship of the monophyletic families Coccodontidae and Pycnodontidae, forming together the superfamily Pycnodontoidea; and the composition and interrelationships of the Coccodontidae. In brief, the dental characters do not affect the interrelationships of the non-pycnodontid Pycnodontiformes (except *Palaeobalistum*).

In contrast, the interrelationships of the taxa that form the family Pycnodontidae are very poorly resolved if dental characters are removed from the data matrix. In this case, only the subfamily Pycnodontinae, and the large 'crown-group' Pycnodontidae (LCGP on Fig. 2) including the 11 terminal taxa in Poyato-Ariza and Wenz (2002), are clades that can be defined without the dental characters. This indicates that: (1) the subfamily Pycnodontinae can be defined without dental characters, the subfamilies Proscinetinae and Nursalliinae cannot; (2) the seven basal pycnodontids of the complete data set are still basal pycnodontids without the dental characters, but their interrelationships cannot be resolved, including the status of the genus *Macromesodon* and its species; (3) the same applies to the 11 taxa forming the large, derived group Pycnodontidae.

CONCLUSIONS

The analyses presented above show that dental characters alone cannot provide a hypothesis of phylogenetic relationships for pycnodontiform fishes. Therefore, the phylogenetic position of those taxa known only from dental remains cannot be confidently assessed, and it is strongly discouraged here to include them in future phylogenetic analyses. A rigorous quantitative geometric morphometric approach could help solve this problem. However, it should be initially done only on the basis of accurately identified material; a large number of articulated specimens with well-exposed dentitions would be necessary for this purpose. At present, there is not enough of this type of material for most pycnodont taxa, but this approach should be seriously considered when more individuals with well-preserved dentitions are available.

Dental characters do not affect the interrelationships of the non-pycnodontid pycnodontiforms, but are indispensable for an assessment of the interrelationships of the Family Pycnodontidae. In this sense, the phylogenetic interrelationships of the Pycnodontidae are not, at present, as strongly resolved as are those of the basal Pycnodontiformes, and should be tested by further analyses.

It should not be concluded that dental characters are not phylogenetically informative. They are, but they should be considered only as part of the total morphological evidence, and not in isolation.

Acknowledgments—I thank Lionel Cavin, Alison Longbottom, and Michael Gottfried for improving the paper with their constructive revisions. I particularly thank Sylvie Wenz for her suggestions on the original manuscript, and especially for all the years working together. This is a contribution to projects BOS2001-0173, BTE2001-0185-C02-01, and ''Paleobiología y análisis del registro fósil de peces actinopterigios y condrictios del Mesozoico español'' (Contrato Ramón y Cajal), Ministerio de Ciencia y Tecnología de España.

LITERATURE CITED

Agassiz, L. 1833–1843. Recherches sur les Poissons fossils. Petitpierre, Neuchâtel, Suisse Vol. 2, pt. 1:310 pp., pt 2:336 pp.

Applegate, S. P. 1992. A new genus and species of pycnodont from the Cretaceous (Albian) of central Mexico, Tepexi de Rodríguez, Puebla. Revista del Instituto de Geología, Universidad Nacional Autónoma de México 10:164–178.

——— 1996. An overview of the Cretaceous fishes of the quarries near Tepexi de Rodríguez, Puebla, México; pp. 529–538 *in* G. Arratia and G. Viohl (eds.), Mesozoic Fishes 2: Systematics and Fossil Record. Verlag Dr. F. Pfeil, München.

Blake, J. F. 1905. A monograph of the fauna of the Cornbrash. Palaeontographical Society Monograph for 1907:1–106.

Blot, J. 1987. L'ordre des Pycnodontiformes. Studi e Ricerche sui Giacimenti Terziari di Bolca, Museo Civico di Storia Naturale, Verona 5:1–211.

Figueiredo, F. J., and R. da Silva Santos. 1987. Considerações taxinômicas dos picnodontidos da Formaçaõ Gramame (camada de Fostato), Pe. Anais X Congresso Brasileiro de Paleontologia, Rio de Janeiro:25–31.

Frickhinger, K. A. 1994. The Fossils of Solnhofen. Goldschneck-Verlag, Korb, Germany, 336 pp.

——— 1999. Die Fossilen von/The fossils from/ Solnhofen. Goldschneck-Verlag, Korb, Germany, 192 pp.

Kriwet, J., F. J. Poyato-Ariza, and S. Wenz. 1999. A revision of the pycnodontid fish *Coelodus subdiscus* Wenz 1989, from the Early Cretaceous of Montsec (Lleida, Spain). Treballs del Museu de Geologia de Barcelona 8:33–65.

Lambers, P. H. 1991. The Upper Jurassic actinopterygian fish *Gyrodus dichactinus* WINKLER 1862 (*Gyrodus hexagonus* [BLAINVILLE 1818]) from Solnhofen, Bavaria and anatomy of the *Gyrodus* AGASSIZ. Proceedings of the Koninklijke Nederlandse Akademie von Wetenschappen 94:489–544.

Lehman, J. P. 1966. Actinopterygii; pp. 1–242 *in* J. Piveteau (ed.), Traité de Paléontologie, Vol. IV (3). Masson et Cie., Paris.

Longbottom, A. E. 1984. New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali. Bulletin of the British Museum Natural History (Geology) 38:1–26.

Nursall, J. R. 1996a. Distribution and ecology of pycnodont fishes; pp. 115–125 *in* G. Arratia and G. Viohl (eds.), Mesozoic Fishes—Systematics and Paleoecology. Verlag Dr. F. Pfeil, München.

——— 1996b. The phylogeny of the pycnodont fishes; pp. 125–152 *in* G. Arratia and G. Viohl (eds.), Mesozoic Fishes—Systematics and Paleoecology. Verlag Dr. F. Pfeil, München.

———, and J. G. Maisey. 1991. *Neoproscinetes* Figueiredo and Silva Santos, 1987; pp. 125–137 *in* J. Maisey (ed.), Santana Fossils: An Illustrated Atlas. T.F.H. Publications, Inc., Neptune City, New Jersey.

Poyato-Ariza, F. J., A. D. Buscalioni, and J. Cartanyà. 1999a. The Mesozoic record of osteichthyan fishes from Spain; pp. 505–533 *in* G. Arratia and G. Viohl (eds.), Mesozoic Fishes 2: Systematics and Fossil Record. Verlag Dr. F. Pfeil, München.

———, C. Fielitz, and S. Wenz. 1999b. Marine actinopterygian fauna from the Late Cretaceous of Albaina, Spain; pp. 325–338 *in* H. Astibia, J. C. Corral, X. Murelaga, X. Orue-Etxebarría, and X. Pereda-Suberbiola (eds.), Geology and Palaeontology of the Upper Cretaceous Vertebrate-Bearing Beds of the Laño Quarry (Basque-Cantabrian Region, Iberian Peninsula). Estudios del Museo de Ciencias Naturales de Álava, Vol. 14, Núm. Espec. 1.

———, and S. Wenz. 2000. A new pycnodontiform fish from the Early Cretaceous of Las Hoyas (Cuenca, Spain). Bulletin de la Société Géologique de France 171:251–258.

———, and ——— In press. The new pycnodontid fish genus *Turbomesodon*, and a revision of *Macromesodon* based on new material from the Early Cretaceous of Las Hoyas, Cuenca, Spain. *in* G. Arratia and A. Tintori (eds.), Mesozoic Fishes 3: Systematics, Palaeoenvironments, and Diversity. Verlag Dr. F. Pfeil, München.

Poyato-Ariza, F. J., and S. Wenz. 2002. A new insight into pycnodontiform fishes. Geodiversitas 24:139–248.

Saint-Seine, P. de. 1949. Les poissons des calcaires lithographiques de Cerin (Ain). Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 2:1–357.

Thurmond, J. T. 1974. Lower vertebrate faunas of the Trinity Division in north-central Texas. Geoscience and Man 8:103–129.

Tintori, A. 1981. Two new pycnodonts (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). Rivista Italiana di Paleontologia e Stratigrafia 86:795–824.

Wenz, S. 1989a. *Iemanja palma* n. g., n. sp., Gyrodontidae nouveau (Pisces, Actinopterygii) du Crétacé inférieur de la Chapada do Araripe (N-E du Brésil). Comptes Rendus des Séances de l'Académie des Sciences de Paris, sér. 2a, 308:975–980.

——— 1989b. Une nouvelle espèce de *Coelodus* (Pisces, Pycnodontiformes) du Crétacé inférieur du Montsech (Province de Lérida, Espagne): *Coelodus subdiscus* n. sp. Geobios 22:515–520.

——— 1991. *Iemanja* Wenz, 1989; pp. 138–140 *in* J. Maisey (ed.), Santana Fossils: An Illustrated Atlas. T.F.H. publications, Inc., Neptune City, New Jersey.

Woodward, A. S. 1895. Catalogue of the Fossil Fishes in the British Museum (Natural History). Part III. London (Trustees of British Museum), London, 544 pp.

Received 8 April 2002; accepted 22 January 2003.

APPENDIX 1

Subset of dental characters from the data set by Poyato-Ariza and Wenz (2002), with their original numbering in that paper.

32. Morphology of premaxillary and dentary teeth: small, triangular to conic (0); robust, columnar to hook-shaped (1); robust, barely incisiform (2); very flattened, fully incisiform (3).
33. Crown of premaxillary and dentary teeth: simple (0); bifurcated (1).
34. Number of premaxillary teeth: more than 3 (0); 3 (1); 2 (2).
36. Morphology of vomerine teeth: villiform to conic (0); circular to subcircular contour (1); oval contour (2); reniform contour (3); triangular contour (4).
37. Arrangement of vomerine teeth in regular rows: absent (0); present (1); absent anteriorly, present posteriorly (2).
38. Number of vomerine tooth rows: not arranged in rows (0); 3 (1); 5 (2).
39. Number of teeth in principal vomerine tooth row: teeth not arranged in rows (0); 7 or less (1); 8 or 9 (2); 10 or more (3).
40. Alternation of teeth on main vomerine tooth row: absent (0); present (1).
42. Number of dentary teeth: more than 5 (0); 5 (1); 4 (2); 3 (3); 2 (4).
43. Morphology of prearticular teeth: villiform to conic (0); circular contour (1); oval contour (2); sigmoid to drop-shaped contour (3); extremely elongated in contour (4).
44. Arrangement of prearticular teeth in regular rows: absent (0); present (1); absent anteriorly, present posteriorly (2).
45. Number of prearticular tooth rows: not arranged in rows (0); 2 (1); 3 (2); 4 (3); 5 or 6 (4).
46. Number of teeth on main prearticular tooth row: teeth not arranged in rows (0); 7 or less (1); 8 or 9 (2); 10 or more (3).
48. Central papilla in vomerine and prearticular teeth: absent (0); present (1).
49. Crenulations in vomerine and prearticular teeth: absent (0); occasionally present, weak (1); present in most teeth, strong (2).
50. Ridge on vomerine and prearticular teeth: absent (0); present (1).
51. Groove on vomerine and prearticular teeth: absent (0); present (1).