Anais da Academia Brasileira de Ciências (2011) 83(2): 483-511
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
www.scielo.br/aabc

Taxonomic review and phylogenetic analysis of Enchodontoidei (Teleostei: Aulopiformes)

HILDA M.A. SILVA and VALÉRIA GALLO

Laboratório de Sistemática e Biogeografia, Departamento de Zoologia, Instituto de Biologia,
Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier, 524, Maracanã,
20550-013 Rio de Janeiro, RJ, Brasil

Manuscript received on September 24, 2010; accepted for publication on December 22, 2010

ABSTRACT

Enchodontoidei are extinct marine teleost fishes with a long temporal range and a wide geographic distribution. As there has been no comprehensive phylogenetic study of this taxon, we performed a parsimony analysis using a data matrix with 87 characters, 31 terminal taxa for ingroup, and three taxa for outgroup. The analysis produced 93 equally parsimonious trees (L = 437 steps; CI = 0.24; RI = 0.49). The topology of the majority rule consensus tree was: (*Sardinioides* + *Hemisaurida* + (*Nardorex* + (*Atolvorator* + (*Protostomias* + *Yabrudichthys*) + (*Apateopholis* + (*Serrilepis* + (*Halec* + *Phylactocephalus*) + (*Cimolichthys* + (*Prionolepis* + ((*Eurypholis* + *Saurorhamphus*) + (*Enchodus* + (*Paleolycus* + *Parenchodus*))))))) + ((*Ichthyotringa* + *Apateodus*) + (*Rharbichthys* + (*Trachinocephalus* + ((*Apuliadercetis* + *Brazilodercetis*) + (*Benthesikyme* + (*Cyranichthys* + *Robertichthys*) + (*Dercetis* + *Ophidercetis*)) + (*Caudadercetis* + (*Pelargorhynchus* + (*Nardodercetis* + (*Rhynchodercetis* + (*Dercetoides* + *Hastichthys*)))))). The group Enchodontoidei is not monophyletic. Dercetidae form a clade supported by the presence of very reduced neural spines and possess a new composition. Enchodontidae are monophyletic by the presence of middorsal scutes, and *Rharbichthys* was excluded. Halecidae possess a new composition, with the exclusion of *Hemisaurida*. This taxon and *Nardorex* are Aulopiformes *incertae sedis*.

Key words: Aulopiformes, Enchodontoidei, phylogeny, taxonomy.

INTRODUCTION

Enchodontoidei are extinct marine teleosts generally with an elongate body and long and narrow rod-like maxilla included in the mouth gape (Nelson 1994). They possess a long temporal range, extending from the Early Cretaceous to the Early Eocene, and a wide geographic distribution in sedimentary deposits of South America (e.g., Bolivia and Brazil), Africa (e.g., Democratic Republic of Congo, Egypt, and Morocco), Asia (e.g., Arabian Peninsula, India, Israel, Japan, and Lebanon), Europe (e.g., Belgium, England, Germany, Holland, Italy, and Sweden), and North America (Canada, Mexico, and United States) (e.g., Goody 1969, Chalifa 1996, Fielitz 2004, Figueiredo and Gallo 2006, Gallo et al. 2006).

The taxon was erected by Berg (1937) as a suborder, which included only the family Enchodontidae. According to this author, enchodontid fishes were similar to the members of the suborder Stomiatoidei also created by him, but the enchodontids bear a median row of dorsal scutes and their vertebrae do not possess parapophyses. Goody (1969) accomplished a comprehensive review of certain Late Cretaceous teleosteans, considering Enchodontoidei as part of the order Salmoniformes, together with three other suborders, Ichthyotringoidei, Cimolichthyoidei, and Halecoidei.

Rosen (1973) erected the order Aulopiformes comprising 15 living families, and the suborder Alepisau-

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Correspondence to: Hilda Maria Andrade da Silva
E-mail: hmasilva@yahoo.com.br

roidei with 15 fossil genera, without dividing them systematically (i.e., *Ichthyotringa, Apateodus, Apateopholis, Cimolichthys, Dercetis, Rhynchodercetis, Pelargorhynchus, Prionolepis, Enchodus, Palaeolycus, Eurypholis, Saurorhamphus, Halec, Phylactocephalus*, and *Hemisaurida*), as well as the fossil genera *incertae sedis* of the superfamily Synodontoidea, *Sardinius* and *Volcichthys*.

Nelson (1994) recognized the order Aulopiformes by Rosen (1973), as well as the suborders proposed by Goody (1969) as superfamilies, putting them in a single suborder, Enchodontoidei, composed of four superfamilies: Enchodontoidea (*Enchodus, Parenchodus, Palaeolycus, Eurypholis*, and *Saurorhamphus*), Cimolichthyoidea (*Cimolichthys, Prionolepis, Benthesikyme, Cyranichthys, Dercetis, Dercetoides, Pelargorhynchus, Rhynchodercetis*, and *Stratodus*), Halecoidea (*Halec, Hemisaurida*, and *Phylactocephalus*) and Ichthyotringoidea (*Ichthyotringa* and *Apateodus*). However, this classification was not developed in a phylogenetic framework.

Baldwin and Johnson (1996) accomplished a cladistic analysis of Aulopiformes, including only extant taxa. The authors maintained the monophyly of the taxon and added synapomorphies to those proposed by Rosen (1973), which are mainly related to the morphology of the dorsal portion of the gill arches. Their new synapomorphies are from the intermuscular system, internal soft anatomy, pigmentation pattern of larvae, and morphology of the pelvic girdle. Most of these features are very difficult to assess in fossil specimens.

Sato and Nakabo (2002) accomplished a phylogenetic analysis of living Aulopiformes based on morphological and molecular data. They divided it into the suborders Synodontoidei, Chlorophthalmoidei, Alepisauroidei, and Giganturoidei. Moreover, the authors proposed a new family of Aulopiformes (i.e., Paraulopidae).

Fielitz (2004) and Gallo et al. (2005) proposed hypotheses of the phylogenetic relationships of some fossil Aulopiformes (Enchodontoidea and Dercetidae, respectively).

Nelson (2006) placed the extinct aulopiforms in three suborders: Ichthyotringoidei, comprising the families Ichthyotringidae, Dercetidae, and Prionolepidae; Halecoidei, with a single family, Halecidae; and Alepisauroidei, with two families, Cimolichthyidae and Enchodontidae. The extant aulopiforms were classified in Synodontoidei (with four families), Chlorophthalmoidei (with six families), and Giganturoidei (with two families). Additionally, four living families were placed in the suborder Alepisauroidei.

In fact, the assemblage of extinct aulopiforms defined by Nelson (2006) corresponds to Enchodontoidei *sensu* Nelson (1994). However, Nelson (2006) did not discuss his reasons for disregarding the name Enchodontoidei and put its members in Alepisauroidei, Ichthyotringoidei, and Halecoidei. Moreover, Enchodontoidei were considered in the cladistic analysis of Dercetidae (Gallo et al. 2005), as well as in a preliminary approach by Silva and Gallo (2007). As there has not been a recent comprehensive phylogenetic study of Enchodontoidei, we review their classification history and provide a new cladistic analysis.

SYSTEMATIC HISTORY OF ENCHODONTOIDEI

In this paper we use the general classification of Nelson (1994), except for the family Enchodontidae (*sensu* Fielitz 2004).

Superfamily Ichthyotringoidea

According to Goody (1969), Ichthyotringoidea comprises two closely related families, Ichthyotringidae and Apateopholidae. The author considered mainly primitive features of the body and caudal skeleton, as well as a derived feature related to the rostral region. He stated that, despite the similarities shared by the taxa, Apateopholidae should be the more advanced taxon.

Family Ichthyotringidae. The family Ichthyotringidae (Table I) was created by Jordan (1905) to contain a single genus (i.e., *Ichthyotringa*). Goody (1969) positioned the family in the suborder Ichthyotringoidei. Later, Nelson (1994) included the taxon in the suborder Enchodontoidei together with other fossil aulopiforms. The generic epithet *Ichthyotringa* was created by Cope (1878) to replace the genus *Rhinellus* of Agassiz (1844), which was pre-occupied. The genus *Ichthyotringa* includes the following species: *Ichthyotringa furcata* (Agassiz, 1844), *I. tenuirostris* Cope, 1878, *I. damoni* (Davis, 1887), *I. ferox* (Davis, 1887), *I. delicata* (Hay, 1903), and *I. africana* (Arambourg, 1954). Forey et al. (2003), in the general list of fossil fishes from Lebanon, placed *Apateopholis* in the family Ichthyotringidae, but remarked that at least one species of *Apateopholis* is often misinterpreted as a species of the closely related *Ichthyotringa*. Only more recently a new ichthyotringoidei was reported to the El Doctor Formation in the Albian-Cenomanian of Mexico, *I. mexicana* Fielitz and González Rodríguez, 2008.

Goody (1969) ranked *Apateodus* as an addendum (*incertae sedis*) to the Ichthyotringidae with a single species (*A. striatus* Woodward, 1901). Nelson (1994, 2006) placed *Apateodus* in Apateopholidae, but he did not report the taxonomic status of *Apateopholis*. In Frickhinger (1995), the latter was considered an ichthyotringid and the former was not mentioned. Forey et al. (2003) positioned *Apateopholis* in the family Ichthyotringidae. Taverne (2004) maintained *Apateodus* and two other genera of Cretaceous alepisauroids (*Yabrudichthys* and *Rharbichthys*) as family *incertae sedis*. However, the same author (Taverne 2006c) suggested to exclude *Apateodus* from Ichthyotringidae. Fielitz and González Rodríguez (2008) accomplished a cladistic analysis of Ichthyotringoidea and placed *Apateodus* tentatively among the species of *Ichthyotringa*. More recently, Fielitz and Shimada (2009) described a new species of *Apateodus* (*A. busseni*) suggesting that the genus needs revision, but ranking it in Ichthyotringidae.

Family Apateopholidae. The family Apateopholidae (Table I) was erected by Goody (1969) to include only the genus *Apateopholis*, with two species [*A. laniatus* (Davis, 1887); *A. lanceolatus* Woodward, 1901]. The genus *Apateopholis* was erected by Woodward (1891) to substitute *Rhinellus* by Davis (1887), which was posteriorly allocated in *Belonostomus* by Woodward (1888). Ten years after the creation of the genus, Woodward (1901) put *Apateopholis* in synonymy with *Prionolepis*. Goody (1969) revalidated the generic epithet *Apateopholis* with the single species *Apateopholis laniatus*.

SUPERFAMILY CIMOLICHTHYOIDEA

This superfamily includes three families (i.e., Cimolichthyidae, Dercetidae, and Prionolepididae). According to Goody (1969), Cimolichthyidae and Dercetidae show a great similarity regarding the structures of the skull and body, especially in the rostral region. Moreover, general body squamation is lacking and two or three rows of isolated scutes are present on the flanks. Regarding the family Prionolepididae, the author pointed out some problems concerning its taxonomic placement. Unlike Woodward (1901), who assigned the genus *Prionolepis* to the Enchodontidae, Goody (1969) considered it closely related to dercetids and cimolichthyids.

Family Cimolichthyidae. The family (Table II) was erected by Goody (1969) to include the single genus *Cimolichthys*, which was designated by Leidy (1857) with the species *C. levesiensis*. Cope (1872), studying specimens from Niobrara (USA), recognized five species of *Cimolichthys*: *C. nepaholica, C. sulcatus, C. semianceps, C. contracta*, and *C. merrillii*. Later, Hay (1903) recognized only the species *C. nepaholica*, as other species were based mainly on isolated teeth and fragments of the jaws.

Family Dercetidae. Traditionally the creation of this family is attributed to Pictet (1850). However, he did not use the name Dercetidae, defining only a *Dercetis* group with *D. tenuis*, *D. triqueter*, and *D. linguifer*. As far as we know, the name Dercetidae was used for the first time by Woodward (1901).

The following taxa are regarded as valid in the most recent revisions of the Dercetidae (e.g., Taverne 1987, 1991, 2005a, b, 2006b, Chalifa 1989a, Gallo et al. 2005, Blanco et al. 2008) and in general fossil fish lists (e.g., Frickhinger 1995, Forey et al. 2003): *Apuliadercetis tyleri* Taverne, 2006a; *Benthesikyme armatus* (von der Marck, 1863); *B. rostralis* (Davis, 1887); *B. gracilis* (Signeux, 1954); *Brazilodercetis longirostris* Figueiredo and Gallo, 2006; *Caudadercetis bannikovi* Taverne, 2006b; *Cyranichthys ornatissimus* (Casier, 1965); *Dercetis elongatus* (Agassiz, 1837); *D. triqueter* Pictet, 1850; *Dercetoides venator* Chalifa, 1989a; *Hastichthys gracilis* (Chalifa, 1989a); *Leccedercetis longirostris* Taverne, 2008; *Nardodercetis vandewallei* Taverne, 2005a; *Ophidercetis italiensis* Taverne, 2005b; *Pelargorhynchus dercetiformis* von der Marck, 1858; *Rhynchodercetis hakelensis* (Pictet and Humbert, 1866); *R. yovanovitchi* Arambourg, 1943; *R. gortanii* (d'Erasmo, 1946); *R. regio* Blanco and Alvarado-Ortega, 2006;

TABLE I
Occurrences of the Superfamily Ichthyotringoidea (Fm = Formation; NDA = no data available).

Taxon	Provenance	Age	Selected References
Ichthyotringa africana	Jebel Tselfat	Cenomanian	Murray (2000), Forey et al. (2003), Taverne (2006c)
I. africana	Cinto Euganeo	Cenomanian-Turonian	Taverne (2006c)
I. damoni	Sahel Alma	Santonian	Forey et al. (2003), Taverne (2006c)
I. delicata	Hakel and Hajula	Cenomanian	Goody (1969), Forey et al. (2003), Taverne (2006c)
I. ferox	Sahel Alma	Santonian	Forey et al. (2003), Taverne (2006c)
I. furcata	Sahel Alma	Santonian	Goody (1969), Forey et al. (2003), Taverne (2006c)
I. furcata	Sendenhorst	Santonian	Goody (1969)
I. furcata	Niedersachsen	Santonian	Kriwet and Gloy (1995)
I. tenuirostris	Dakota and Nebraska	Upper Cretaceous	Taverne (2006c)
I. mexicana	El Doctor Fm.	Albian-Cenomanian	Fielitz and González Rodríguez (2008)
Apateopholis laniatus	Hakel	Middle Cenomanian	Goody (1969)
A. laniatus	Namoura	Middle Cenomanian	Forey et al. (2003)
A. lanceolatus	English Chalk	Turonian	Forey et al. (2003)
Apateodus striatus	Lewes	Turonian	Goody (1969)
A. striatus	NDA	Maastrichtian	Kruizinga (1924)
Apateodus sp.	Kaskapau Fm.	Turonian	Wilson and Chalifa (1989)
Apateodus sp.	Mumbay Fm.	Cretaceous-Tertiary	Cripps et al. (2005)
Apateodus sp.	Akli Fm.	Paleocene-Eocene	Rana et al. (2005)
Apateodus sp.	El Molino Fm.	Upper Campanian-Lower Paleocene	Gayet (1991), Jaillard et al. (1993)

R. serpentinus (Hay, 1903); *Robertichthys riograndensis* Blanco-Piñon and Alvarado-Ortega, 2005; and *Scandiadercetis limhamnensis* (Davis, 1890) (Table II).

Chalifa (1989a) stated that Dercetidae are a "relatively primitive" group, considering the presence of few apomorphies. She carried out a phylogenetic analysis of this taxon and recognized it as a monophyletic group, comprising the following clades: (*Dercetis*, (*Pelargorhynchus*, (*Dercetoides*, *Rhynchodercetis*))).

Taverne (1987, 1991) considered Dercetidae to be a clade of Stomiiformes. In reviewing the material studied by Chalifa (1989a) and discussing the relationships of genera, Taverne (1991) assumed a monophyletic condition for this family and used 33 characters to define it. He placed *Benthesikyme* as the most primitive genus, possessing most of (or all) these 33 "generalized conditions". Taverne (1991) also "distributed" 40 "apomorphies" to genera and groups of genera in the family.

Gallo et al. (2005) accomplished a cladistic analysis of the family Dercetidae, using an outgroup composed of Enchodontoidei taxa. The authors obtained only one tree supporting the monophyly of Dercetidae, based on two synapomorphies: absence of a longitudinal opercular crest and reduced neural spine. They also

TABLE II
Occurrences of the Superfamily Cimolichthyoidea (Fm = Formation; NDA = no data available).

Taxon	Provenance	Age	Selected References
Cimolichthys levesiensis	Chalk of Sussex	Turonian-Senonian	Goody (1969)
C. levesiensis	NDA	Cretaceous	Leriche (1902, 1906)
C. cf. *levesiensis*	Kaskapau Fm.	Turonian	Wilson and Chalifa (1989)
C. nepaholica	Niobrara Fm.	Coniacian-Santonian	Goody (1969, 1970)
C. nepaholica	Pierre Shale	Campanian	Goody (1969, 1970)
Cimolichthys sp.	Lac des Bois	Turonian	Fielitz (1996)
Apuliadercetis tyleri	Nardò	Campanian-Maastrichtian	Taverne (2006a)
Benthesikyme armatus	Westphalia	Campanian	Taverne (2005b)
B. gracilis	NDA	Santonian	Taverne (2005b)
B. rostralis	NDA	Santonian	Taverne (2005b)
Brazilodercetis longirostris	Atlântida Fm.	Turonian	Figueiredo and Gallo (2006)
Caudadercetis bannikovi	Nardò	Campanian-Maastrichtian	Taverne (2006b)
Cyranichthys ornatissimus	Kipala	Cenomanian	Taverne (1987)
Dercetis elongatus	NDA	Turonian-Senonian	Taverne (2005b)
D. triqueter	Sahel Alma	Santonian	Goody (1969), Taverne (2005b)
Dercetis sp.	Harrana	Maastrichtian	Kaddumi (2006)
Dercetoides venator	Amminadav Fm.	Lower Cenomanian	Chalifa (1989a)
Dercetoides sp.	Kaskapau Fm.	Turonian	Wilson and Chalifa (1989)
Hastichthys gracilis	Amminadav Fm.	Lower Cenomanian	Chalifa (1989a)
H. cf. *gracilis*	Namoura	Middle Cenomanian	Forey et al. (2003)
Leccedercetis longirostris	Nardò	Campanian-Maastrichtian	Taverne (2008)
Nardodercetis vandewallei	Nardò	Campanian-Maastrichtian	Taverne (2005a)
Ophidercetis italiensis	Nardò	Campanian-Maastrichtian	Taverne (2005b)
Pelargorhynchus dercetiformis	Sedenhorst	Upper Senonian	Goody (1969)
Rhynchodercetis hakelensis	Hakel	Middle Cenomanian	Goody (1969), Forey et al. (2003)
R. yovanovitchi	Jebel Tselfat	Lower Cenomanian	Arambourg (1954), Goody (1969), Taverne (1987)
R. yovanovitchi	Messina	Cenomanian	Leonardi (1966)
R. cf. *yovanovitchi*	Namoura	Middle Cenomanian	Forey et al. (2003)
R. gortanii	Trieste-Komen	Lower Cenomanian	Goody (1969), Forey et al. (2003)
R. regio	Agua Nueva Fm.	Turonian	Blanco and Alvarado-Ortega (2006)
R. serpentinus	Hakel and Hajula	Middle Cenomanian	Forey et al. (2003)

TABLE II (continuation)

Taxon	Provenance	Age	Selected References
Rhynchodercetis sp.	Trieste-Komen	Campanian	Cavin et al. (2000)
Rhynchodercetis sp.	Cinto Euganeo	Coniacian-Santonian	Sorbini (1976)
Rhynchodercetis sp.	Polazzo	Lower Senonian	Rigo (1999)
Rhynchodercetis sp.	Daoura	Cenomanian	Cavin and Dutheil (1999)
Robertichthys riograndensis	Agua Nueva	Lower Turonian	Blanco-Piñon and Alvarado-Ortega (2005)
Scandiadercetis limhamnensis	Saltholm Limestone	Danian	Taverne (2005b)
Prionolepis angustus	Tormarp	Upper Albian-Lower Cenomanian	Lundgren (1889)
P. angustus	English Chalk	Cenomanian-Turonian	Forey et al. (2003)
P. cataphractus	Hakel and Hajula	Middle Cenomanian	Forey et al. (2003)

verified that some of the superfamilies proposed by Nelson (1994) are not monophyletic. Taking into account the description of four new genera of Dercetidae from Nardò, Italy (Taverne 2005a, b, 2006a, b), as well as the new diagnoses of *Dercetis* and *Benthesikyme* (Taverne 2005b), Taverne (2006b) proposed a phylogenetic review of the Dercetidae, in which he provided a list of 43 plesiomorphies to this family. In the phylogenetic hypothesis furnished by Blanco et al. (2008), the monophyly of Dercetidae was confirmed and it was supported by the same synapomorphies shown in Gallo et al. (2005).

Dercetis was the first described genus of Dercetidae. It was created by Agassiz (1834) to accommodate the species *D. scutatus*. The taxon was briefly described on the basis of a single and almost complete specimen. The holotype was lost or destroyed, without being figured (Siegfried 1954, Goody 1969, Taverne 2005b). Pictet (1850) erected *Dercetis triqueter* and *D. linguifer*. Later, von der Marck (1863) identified a new genus within Dercetidae to include two new species, *Leptotrachelus armatus* and *L. sagittatus*. Pictet and Humbert (1866) synonymized *D. triqueter* and *D. linguifer* with *Leptotrachelus triqueter*. Siegfried (1966) redescribed the material by von der Marck (1863) and transferred the *Leptotrachelus* spp. for the genus *Dercetis* (*D. armatus* and *D. sagittatus*). Goody (1969) redescribed *D. triqueter* and claimed that *D. linguifer* was clearly *D. triqueter*.

Pelargorhynchus dercetiformis was erected by von der Marck (1858) based on several but poorly preserved specimens from Germany. There is no record of this genus in any other locality.

The genus *Benthesikyme* was created by White and Moy-Thomas (1940), including new species of *Leptotrachelus* described by several authors at the end of the nineteenth century and during the twentieth century. Taverne (2005b) furnished a comprehensive review of the genera *Dercetis*, *Leptotrachelus*, and *Benthesikyme*, in which *L. sagittatus* is probably a synonym of *D. elongatus*, *L. virgulatus* of *D. triqueter*, and *L. longipinnis* of *Benthesikyme gracilis*. The taxonomic status of *D. reussi*, *D. latiscutatus*, *D. maximus,* and *L. serpentinus* was also discussed but not in a conclusive way. Yet, Taverne (2005a, b) erected three new monotypic genera within the family Dercetidae, *Ophidercetis* (*O. italiensis*), *Nardodercetis* (*N. vandewallei*), and *Scandiadercetis* (*S. limhamnensis*). The latter had been proposed originally by Davis (1890) as *Dercetis limhamnensis*.

The genus *Rhynchodercetis* was erected by Arambourg (1943), comprising a single species, *R. yovanovitchi*, which is very abundant in deposits from the Lower Cenomanian of Morocco. Later, other *Rhynchodercetis* spp. were described: *R. hakelensis* (Pictet and Humbert, 1866); *R. gortanii* (d'Erasmo, 1946); and *R. regio* Blanco and Alvarado-Ortega, 2006. Chalifa (1989a) described *Dercetoides venator* and *Rhynchodercetis gracilis*. The latter was renamed as *Hastichthys gracilis* by Taverne (1991).

Blanco-Piñon and Alvarado-Ortega (2005) briefly described *Robertichthys riograndensis*, which is the second record of Dercetidae in the Turonian of Mexico. Blanco et al. (2008) provided a redescription of this taxon, as well as a discussion on its relationships.

Figueiredo and Gallo (2006) described *Braziloldercetis longirostris*, which is the first record of the family in South America.

Family Prionolepididae. The genus *Prionolepis* was created by Egerton (in Dixon 1850) with only one species, *P. angustus*. Later, Pictet and Humbert (1866) included one more species in the genus, *P. cataphractus*. Goody (1969) reviewed *P. cataphractus* and proposed the family Prionolepididae (Table II).

SUPERFAMILY ENCHODONTOIDEA

Family Enchodontidae. Previously to Woodward (1901), the genera assigned to Enchodontoidea were allocated in different families (Agassiz 1835, Pictet 1850, Cope 1872, 1874). The first attempt to classify the enchodontoids in a separate group was proposed by Woodward (1901), in which the author erected the family Enchodontidae and put it in the Isospondyli. He divided the family into two main groups based on the presence or the absence of a single tooth in palatine. In the first group, the author included the genera *Enchodus, Palaeolycus, Eurypholis*, and *Saurorhamphus*; the second consisted of the genera *Halec, Cimolichthys, Prionolepis, Leptecodon*, and *Pantopholis*. However, Woodward (1901) stated that the living families more closely related to the Enchodontidae were Alepisauridae and Odontostomidae, which possess the border of the upper jaw formed exclusively by the premaxilla, the maxilla being untoothed and excluded from the mouth gape.

After Woodward (1901), there was a long debate about the relationships of enchodontids and living fish families. Jordan (1905), Gregory (1933), and Arambourg (1954) agreed with the hypothesis of Woodward (1901) regarding the relationships of enchodontids and alepisaurids, but they positioned Enchodontidae in the suborder Iniomi. On the other hand, Regan (1911) and Romer (1945) rejected the hypothesis of Woodward (1901) and allocated the family into the Stomiatoidei, belonging to the suborder Isospondyli. Berg (1940) also rejected the enchodontids plus alepisaurids hypothesis and put enchodontids in the suborder Enchodontoidei into the Clupeiformes, as synonym of Isospondyli. The generic composition of Enchodontidae remained stable for some time, except for *Halec*, which was moved to the family Halecidae by Goody (1969), and for the inclusion of *Rharbichthys* by Arambourg (1954).

Goody (1969) accomplished a comprehensive review of the Enchodontidae, including the genera *Enchodus* and *Palaeolycus*. Also, he created the family Eurypholidae into Enchodontoidei to comprise the genera *Eurypholis* and *Saurorhamphus*.

Sorbini (1976) proposed a relationship between *Rharbichthys* and *Cimolichthys*. Taverne (1985) studied *Rharbichthys* and stated that it probably possessed close affinity with the halecids regarding the general proportions and the head shape.

Although the monophyly of Enchodontidae seems to be widely accepted, the previous diagnoses (e.g., Goody 1969, Rosen 1973, Chalifa 1989b) were not deduced from cladistic analyses.

Recently, Fielitz (2004) tested the monophyly of the family Enchodontidae, including living and extinct aulopiforms. The clade is supported by three synapomorphies: single dermopalatine tooth, dermopalatine bone with same length or shorter than the tooth, and interopercle absent. Alepisauridae appear in the analysis as the sister group of the clade formed by the extinct Aulopiformes. Enchodontidae were divided into four subfamilies: Rharbichthinae (with *Rharbichthys*), Palaeolycinae (with *Palaeolycus*), Eurypholinae (with *Eurypholis* and *Saurorhamphus*) and Enchodontinae (with *Enchodus*). The genus *Parenchodus* was put in synonymy with *Enchodus*.

The subfamily Rharbichthinae (Table III) is monotypic, being represented only by *Rharbichthys ferox* Arambourg, 1954. This species was considered by several authors as belonging to the Enchodontidae (e.g., Bertin and Arambourg 1958, Leonardi 1966, Goody, 1969), whereas Sorbini (1976) classified it in the family Cimolichthyidae. Yet, Taverne (1985) claimed that *R. ferox* is an alepisauroid.

The subfamily Palaeolycinae (Table III) is monotypic, comprising only *Palaeolycus dreginensis* described by von der Marck (1863). Later, it was reviewed by Siegfried (1954), who pointed out morphological similarities and putative relationships with the

TABLE III
Occurrences of the Superfamily Enchodontoidea (Fm = Formation; NDA = no data available).

Taxon	Provenance	Age	Selected References
Rharbichthys ferox	Jebel Tselfat	Upper Senonian	Arambourg (1954), Murray (2000)
R. ferox	Messina	Cenomanian	Leonardi (1966), Figueiredo et al. (2001)
R. ferox	Cinto Euganeo	Cenomanian-Turonian	Sorbini (1976), Figueiredo et al. (2001)
R. cf. *ferox*	Atlântida Fm.	Turonian	Figueiredo et al. (2001)
Palaeolycus dreginensis	Sedenhorst	Upper Senonian	Goody (1969), Siegfried (1954)
eurypholid	Harrana	Maastrichtian	Kaddumi (2006)
Eurypholis boissieri	Hakel and Hajula	Middle Cenomanian	Goody (1969)
E. boissieri	Namoura	Middle Cenomanian	Forey et al. (2003)
E. pulchellus	English Chalk	Cenomanian-Turonian	Goody (1969), Forey et al. (2003)
E. japonicus	Izumi	Campanian	Yabumoto and Uyeno (1994)
Saurorhamphus freyeri	Trieste-Komen	Lower Cenomanian	Goody (1969)
S. judeaensis	Amminadav Fm.	Lower Cenomanian	Chalifa (1985)
Enchodus sp.	El Molino Fm.	Maastrichtian-Danian	Gayet (1991)
Enchodus sp.	Trieste-Komen	Turonian-Campanian	Cavin et al. (2000)
Enchodus sp.	Polazzo	Lower Senonian	Rigo (1999)
Enchodus sp.	Atlântida Fm.	Lower Turonian	Gallo et al. (2006)
Enchodus sp.	Coqueiro Seco Fm.	Barremian	Coelho (2004)
Enchodus sp.	Lac des Bois	Turonian	Fielitz (1996)
Enchodus sp.	Ghareb	Campanian-Maastrichtian	Chalifa (1996)
Enchodus sp.	Niedersachsen	Lower Turonian	Kriwet and Gloy (1995)
Enchodus sp.	Goulmima	Lower Turonian	Cavin (1999)
Enchodus sp.	Iwaki	Cretaceous	Yabumoto and Uyeno (1994)
E. brevis	Amminadav Fm.	Lower Cenomanian	Chalifa (1989b)
E. bursauxi	Ouled Abdoun	Maastrichtian- Danian	Arambourg (1952)
E. bursauxi	West Desert	Upper Campanian	Chalifa (1996)
E. bursauxi	NDA	Maastrichtian	Chalifa (1996)
E. bursauxi	Ghareb	Campanian	Chalifa (1996)
E. bursauxi	Bentiaba	Upper Cretaceous	Jacobs et al. (2006)
E. dentex	Trieste-Komen	Cenomanian	Chalifa (1996), Forey et al. (2003)
E. dirus	several localities	Maastrichtian	Goody (1976)
E. elegans	Ouled Abdoun	Maastrichtian- Danian	Arambourg (1952)
E. elegans	Gramame Fm.	Maastrichtian	Rebouças and Silva Santos (1956), Coelho (2004)

TABLE III (continuation)

Taxon	Provenance	Age	Selected References
E. elegans	NDA	Maastrichtian	Chalifa (1996)
E. elegans	Bentiaba	Upper Cretaceous	Jacobs et al. (2006)
E. elegans	Palmyrides	Lower Maastrichtian	Bardet et al. (2000)
E. elegans	Ruseifa	Maastrichtian	Bardet and Pereda Superbiola (2002)
E. cf. *elegans*	Iembe	Upper Cretaceous	Jacobs et al. (2006)
E. faujasi	NDA	Maastrichtian	Goody (1968)
E. faujasi	Jadet	Maastrichtian	Breton et al. (1995)
E. faujasi	Bentiaba	Upper Cretaceous	Jacobs et al. (2006)
E. ferox	several localities	Campanian-Maastrichtian	Goody (1976)
E. gladiolus	several localities	Coniacian-Santonian	Goody (1976)
E. gracilis	Sedenhorst	Senonian	Chalifa (1996)
E. lewesiensis	Lewes	Turonian-Senonian	Chalifa (1996)
E. libycus	West Desert	Upper Campanian	Chalifa (1996)
E. libycus	Ghareb	Campanian	Chalifa (1996)
E. libycus	Gramame Fm.	Maastrichtian	Rebouças and Silva Santos (1956)
E. libycus	Cotinguiba Fm.	Cenomanian-Coniacian	Silva Santos and Salgado (1969), Coelho (2004)
E. libycus	Ouled Abdoun	Maastrichtian-Danian	Arambourg (1952)
E. libycus	NDA	Maastrichtian	Chalifa (1996)
E. longidens	Sahel Alma	Senonian	Forey et al. (2003)
E. cf. *longidens*	Akli Fm.	Paleocene-Eocene	Rana et al. (2005)
E. longipectoralis	Cotinguiba Fm.	Cenomanian-Coniacian	Silva Santos and Salgado (1969), Coelho (2004)
E. lycodon	Trieste-Komen	Cenomanian	Chalifa (1996), Forey et al. (2003)
E. macropterus	Sedenhorst	Upper Senonian	Siegfried (1954)
E. major	Sahel Alma	Senonian	Chalifa (1996)
E. cf. *major*	Trieste-Komen	Cenomanian	Chalifa (1996), Forey et al. (2003)
E. marchesettii	Hakel and Hajula	Middle Cenomanian	Goody (1969), Chalifa (1996)
E. mecoanalis	Namoura	Middle Cenomanian	Forey et al. (2003)
E. oliverai	Gramame Fm.	Maastrichtian	Rebouças and Silva Santos (1956), Coelho (2004)
E. oliverai	Cotinguiba Fm.	Cenomanian-Coniacian	Coelho (2004)
E. petrosus	several localities	Coniacian-Santonian	Goody (1976)
E. shumardi	several localities	Cenomanian-Maastrichtian	Goody (1976)

TABLE III (continuation)

Taxon	Provenance	Age	Selected References
E. cf. *shumardi*	Kaskapau Fm.	Turonian	Wilson and Chalifa (1989)
E. subaequilateralis	Gramame Fm.	Maastrichtian	Gallo-da-Silva (1993), Coelho (2004)
E. venator	Jebel Tselfat	Lower Cenomanian	Arambourg (1954), Chalifa (1996)
E. venator	Messina	Cenomanian	Leonardi (1966)
E. cf. *venator*	Cinto Euganeo	Cenomanian-Turonian	Sorbini (1976)
E. zinensis	Ghareb	Upper Campanian-Lower Maastrichtian	Chalifa (1996)
Parenchodus longipterygius	Kefar Shaul	Upper Cenomanian	Raab and Chalifa (1987)

extant genus *Odontostomus*. This genus is in synonymy with *Evermanella*, which is in the family Evermannellidae of the suborder Alepisauroidei.

The subfamily Eurypholinae (Table III) was originally proposed as a family (Eurypholidae) by Goody (1969) to encompass the genus *Eurypholis* by Pictet (1850). This genus comprises only the type-species (*E. boissieri* Pictet, 1850) and another one initially proposed as *Enchodus pulchellus* by Woodward (1901), but later redefined by Goody (1969) as *Eurypholis pulchellus*.

Nelson (1994) placed the family Eurypholidae in the superfamily Enchodontoidea in the suborder Enchodontoidei.

Fielitz (2004) suggested the arrangement of the genera *Eurypholis* and *Saurorhamphus* in the subfamily Eurypholinae.

Saurorhamphus freyeri was originally described by Heckel (1850), and transferred to the genus *Eurypholis* by Woodward (1901). However, d'Erasmo (1912) claimed that *Saurorhamphus* was actually a distinct genus, closely related to *Eurypholis*. Another species, *S. judeaensis*, was described by Chalifa (1985).

The subfamily Enchodontinae (Table III) includes only the genus *Enchodus* Agassiz, 1835, containing, however, about 24 valid species, most of them erected on the basis of fragmentary material (isolated teeth or pieces of jaws), as follows: *Enchodus brevis* Chalifa, 1989b; *E. bursauxi* (Arambourg, 1952); *E. dentex* (Heckel, 1856); *E. dirus* (Leidy, 1857); *E. faujasi* Goody, 1968; *E. ferox* Leidy, 1855; *E. gladiolus* (Cope, 1872); *E. gracilis* (von der Marck, 1858); *E. lewesiensis* (Mantell, 1822); *E. libycus* (Quaas, 1902); *E. longidens* (Pictet, 1850); *E. longipectoralis* (Schaeffer, 1947); *E. longipterygius* (Raab and Chalifa, 1987); *E. lycodon* Kner, 1867; *E. macropterus* (von der Marck, 1863); *E. major* Davis, 1887; *E. marchesettii* (Kramberger, 1895); *E. mecoanalis* Forey, Yi, Patterson and Davies, 2003; *E. oliverai* Maury, 1930; *E. petrosus* Cope, 1874; *E. shumardi* Leidy, 1856; *E. subaequilateralis* Cope, 1886 (= *E. elegans*); *E. venator* Arambourg, 1954; *E. zinensis* Chalifa, 1996 (e.g., Goody 1976, Chalifa 1996, Forey et al. 2003, Fielitz 2004).

Parenchodus longipterygius was described by Raab and Chalifa (1987) as belonging to the family Enchodontidae. The authors suggested a relationship with the genus *Enchodus*, due to similarities in some structures of the head, the absence of scales, and the fusion of the elements of the caudal fin. Fielitz (2004) put the genus in synonymy with *Enchodus*.

SUPERFAMILY HALECOIDEA

Family Halecidae. The family Halecidae (Table IV) was originally proposed by Agassiz (1834) including forms similar to the clupeoids and salmonoids. The grouping and its name were used only by Pictet (1850) and Davis (1887), being disused later. The family was re-erected by Goody (1969) into the suborder Halecoidei containing three genera: *Halec, Phylactocephalus*, and *Hemisaurida*. Nelson (1994) put Halecidae in the superfamily Halecoidea in the suborder Enchodontoidei. Later, Nelson (2006) opted to use the suborder Halecoidei by Goody (1969).

TABLE IV
Occurrences of the Superfamily Halecoidea.

Taxon	Provenance	Age	Selected References
Halec sternbergi	Bohemia	Middle and Upper Turonian	Goody (1969)
H. eupterygius	English Chalk	Turonian	Goody (1969), Forey et al. (2003)
H. haueri	Lesina	Lower Cenomanian	Goody (1969), Forey et al. (2003)
Phylactocephalus microlepis	Hakel and Hajula	Middle Cenomanian	Goody (1969), Forey et al. (2003)
Hemisaurida hakelensis	Hakel	Middle Cenomanian	Goody (1969), Forey et al. (2003)
H. neocomiensis	Trieste-Komen	Lower Cenomanian	Goody (1969), Forey et al. (2003)

TABLE V
Occurrence of *incertae sedis* taxa (Fm = Formation).

Taxon	Provenance	Age	Selected References
Nardorex zorzini	Nardò	Campanian-Maastrichtian	Taverne (2004)
Serrilepis longidens	Amminadav Fm.	Middle Cenomanian	Chalifa (1989c)
S. prymnostrigos	Namoura	Middle Cenomanian	Forey et al. (2003)
S. minor	Namoura	Middle Cenomanian	Forey et al. (2003)
Yabrudichthys	Amminadav Fm.	Lower Cenomanian	Chalifa (1989c)
Atolvorator longipectoralis	Coqueiro Seco Fm.	Barremian	Gallo and Coelho (2008)

Regarding the genus *Halec*, there are three valid species: *H. sternbergi* Agassiz, 1844 (type-species), *H. eupterygius* (Dixon, 1850), and *H. haueri* (Bassani, 1879).

The genus *Phylactocephalus* was erected by Davis (1887) and put in synonymy with *Halec* by Woodward (1901). Goody (1969) verified marked differences between the genera and separated them. He re-erected *Phylactocephalus* with a single species, *P. microlepis* Davis, 1887.

Kner (1867) created the genus *Hemisaurida* containing a single species, *H. neocomiensis*. Woodward (1901) and Romer (1966) suggested that this genus could belong to the family Myctophidae. Goody (1969) rejected this hypothesis based mainly on two features present in halecoids: maxilla partially excluded from the mouth gape and premaxilla without ascending and articular processes. Yet, Goody (1969) created the species *H. hakelensis*.

TAXA INCERTAE SEDIS

Family Nardorexidae. The monotypic family Nardorexidae (Table V) was proposed by Taverne (2004) with the species *Nardorex zorzini*. He placed the family in the suborder Alepisauroidei based on putative relationships with Enchodontoidei.

Family Serrilepidae. The taxon was proposed by Chalifa (1989c) with the single species *Serrilepis longidens*. Forey et al. (2003) added two new species to the genus, *S. prymnostrigos* and *S. minor*. According to these authors, among the aulopiforms, *Serrilepis* is more closely related to *Halec, Hemisaurida*, and *Phylactocephalus* and, therefore, it should be classified into the Halecidae. This relationship is based on two synapomorphies: fusion of dorsal hypohyal and anterior ceratohyal; fusion of first and second hypurals and third and fourth hypurals. However, this latter synapomorphy is present in *Atolvorator longipectoralis*

(Gallo and Coelho 2008), and we opted to use Chalifa's classification with *Serrilepis* in the family Serrilepidae (Table V).

Additionally, two other taxa, *Yabrudichthys striatus* Chalifa, 1989c, and *Atolvorator longipectoralis* Gallo and Coelho, 2008, are considered Enchodontoidei *incertae sedis* and Cimolichthyoidei *incertae sedis*, respectively (Table V).

MATERIALS AND METHODS

Material

The specimens of Enchodontoidei herein studied belong to several paleontological collections (see Appendix I). Extant aulopiform, stomiiform, and myctophiform fishes were used as comparative specimens represented by dry skeletons, alcohol-preserved, and cleared and stained specimens. They belong to the AO.UERJ, O.UERJ, and MZUSP (see Appendix I). Moreover, for the taxa of difficult access, as for instance, those deposited in Hebrew University of Jerusalem and Museo Civico di Storia Naturale di Verona, we selected information from available literature (e.g., Chalifa 1985, 1989 a, b, c, 1996, Raab and Chalifa 1987, Taverne 2005a, b, 2006a, b).

Institutional Abbreviations

AO.UERJ, Ichthyological Collection, Instituto de Biologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil; **DGM**, Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil; **FPH**, Fundação Paleontológica Phoenix, Aracaju, Brazil; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MZUSP,** Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; **NHM**, The Natural History Museum, London, England; **O.UERJ**, Ichthyological Collection, Instituto de Biologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil; **Pz.UERJ**, Paleozoological Collection, Instituto de Biologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil.

Cladistic Methododology

A data matrix was built with 87 characters, unordered and unweighted, 31 terminal taxa for ingroup, and three taxa for outgroup. The parsimony analysis was carried out using the computer program PAUP* version 4.0b10 (Swofford 2001), with the heuristic algorithm HSearch. We tried to apply the exact branch-and-bound algorithm, but due to the length and complexity of the data matrix, we failed to obtain a result even running the analysis for a few days.

The character states that could not be verified mainly due to poor preservation were coded in the matrix as "?" (missing data). All characters previously proposed in the literature have been reviewed: the character 54 was adapted from Goody (1969); the characters 1, 2, 21, 23, 26, 41, 63, 70, 71, 83, and 84 were from Chalifa (1989a); the characters 3, 10, 11, 16, 19, 24, 25, 29, 30, 33, 38, 42, 64, 65, 77, and 86 were from Taverne (1991); the characters 75, 76, and 81 were from Baldwin and Johnson (1996); the characters 5, 6, 7, 17, 31, 48, 49, 50, 52, 57, 62, 66, and 79 were from Fielitz (2004); the characters 4, 12, 14, 15, 18, 34, 39, 40, 43, 44, 45, 46, 47, 51, 56, 59, 60, 61, 67, 78, 85, and 87 were from Gallo et al. (2005). The new characters are 8, 9, 13, 20, 22, 27, 28, 32, 35, 36, 37, 53, 55, 58, 68, 69, 72, 73, 74, 80, and 82. The terminal taxa for the ingroup were: Ichthyotringidae (*Ichthyotringa*), Apateopholidae (*Apateodus*, *Apateopholis*), Cimolichthyidae (*Cimolichthys*), Dercetidae (*Apuliadercetis*, *Bentheskyme*, *Brazilodercetis*, *Caudadercetis*, *Cyranichthys*, *Dercetis*, *Dercetoides*, *Hastichthys*, *Nardodercetis*, *Ophidercetis*, *Pelargorhynchus*, *Robertichthys*, *Rhynchodercetis*), Prionolepididae (*Prionolepis*), Enchodontidae (*Rharbichthys*, *Palaeolycus*, *Eurypholis*, *Saurorhamphus*, *Enchodus*, *Parenchodus*), Halecidae (*Halec*, *Hemisaurida*, *Phylactocephalus*), Serrilepidae (*Serrilepis*), as well as the *incertae sedis* genera *Nardorex*, *Yabrudichthys*, and *Atolvorator*. Outgroup is based on *Protostomias* (Stomiiformes), *Trachinocephalus* (Aulopiformes), and *Sardinioides* (Myctophiformes).

Appendix II includes the coded data matrix, which was built based on the list of characters presented in the Results. Only character states that resulted in apomorphies were illustrated. Although the strict consensus is the real consensus that shows all possible topologies, we opted to present the majority rule consensus (MRC) because, in general, it possesses a better resolution. The MRC is a form of consensus that pre-

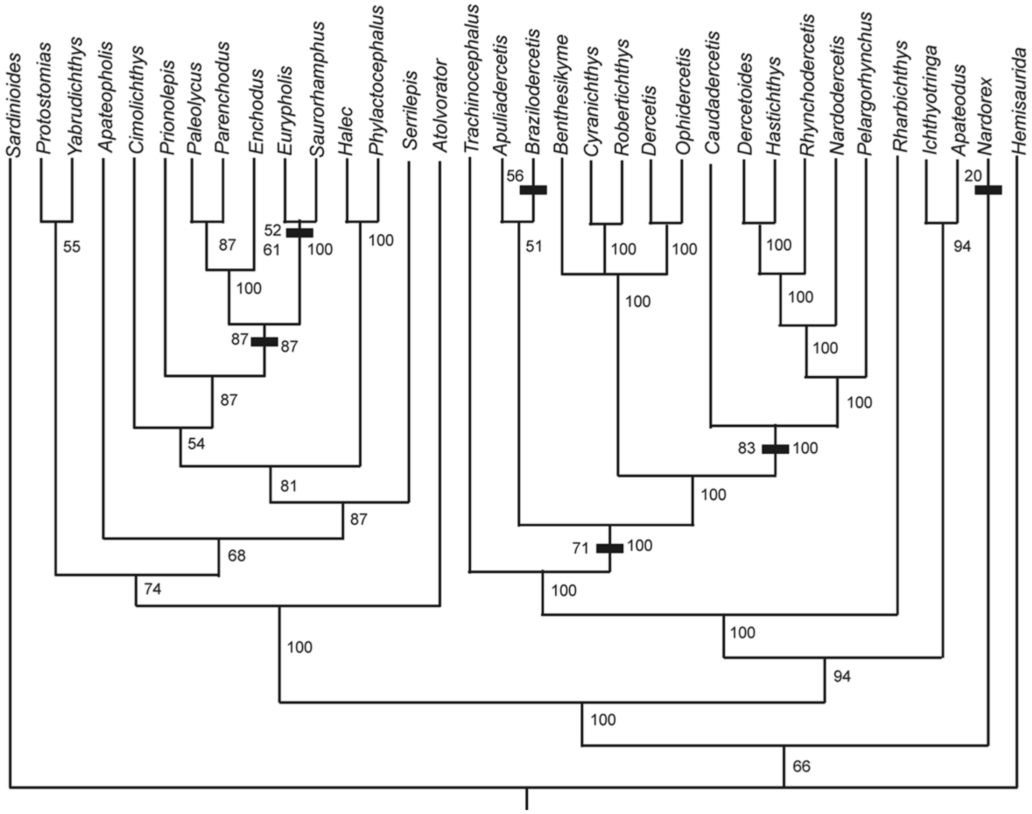

Fig. 1 – Majority rule consensus. Values represented at the right side in each branch indicate the percentage of the trees in which each clade is present. Numbers at the left side associated with a black bar indicate the characters that resulted in synapomorphies or autapomorphies.

serves all clades present in the majority (i.e., in more than 50%) of the obtained set of equally parsimonious cladograms (Margush and McMorris 1981). The 50% rule ensures that all included clades are compatible (Sharkey and Leathers 2001). In spite of some criticism (e.g., Sharkey and Leathers 2001), several authors are using MRC as a method of weighting clades to solve ambiguous strict consensus trees (e.g., Swofford 1991, Candall and Fritzpatrick 1996, Titus and Larson 1996, Lutzoni 1997).

RESULTS

Eighty-seven characters were analyzed in this study (see Appendix III). The cladistic analysis produced 93 equally parsimonious trees, with a tree length of 437 steps, consistency index (CI) of 0.24, and retention index (RI) of 0.49. The majority rule consensus tree is shown in Figure 1. The majority rule consensus tree is represented by the following topology: (*Sardinioides* + *Hemisaurida* + (*Nardorex* + (*Atolvorator* + (*Protostomias* + *Yabrudichthys*) + (*Apateopholis* + (*Serrilepis* + (*Halec* + *Phylactocephalus*) + (*Cimolichthys* + (*Prionolepis* + ((*Eurypholis* + *Saurorhamphus*) + (*Enchodus* + (*Paleolycus* + *Parenchodus*))))))) + ((*Ichthyotringa* + *Apateodus*) + (*Rharbichthys* + (*Trachinocephalus* + ((*Apuliadercetis* + *Brazilodercetis*) + (*Benthesikyme* + (*Cyranichthys* + *Robertichthys*) + (*Dercetis* + *Ophidercetis*)) + (*Caudadercetis* + (*Pelargorhynchus* + (*Nardodercetis* + (*Rhynchodercetis* + (*Dercetoides* + *Hastichthys*)))))).

DISCUSSION

Before discussing the cladistic analysis *per se*, we will furnish a brief comment on certain characters.

According to Chalifa (1989a) and Taverne (1991), the presence of a low head is a synapomorphy of Dercetidae. In this study, it is shared with two other genera outside the group, showing a homoplastic distribution.

In fossil aulopiform fishes, particularly in most of Cimolichthyoidei and Enchodontoidei (*sensu* Goody 1969), the snout length is equivalent to the diameter of the orbit (e.g., *Cimolichthys* and *Eurypholis*, respectively). All dercetids possess an elongate snout and the extreme condition is verified in *Hastichthys*, in which the snout length reaches more than 12 times the diameter of the orbit.

Fielitz (2004) considered the presence of vomerine teeth as a synapomorphy of the group formed by *Cimolichthys* and members of the family Enchodontidae. In the present study, this state of character has a homoplastic distribution, due to it is present in *Nardorex* and *Prionolepis*.

Gallo et al. (2005) interpreted the presence of a mesethmoid with a bifid anterior extremity as an autapomorphy of *Dercetis*, but herein this condition was also verified in *Nardorex* and *Sardinioides*. Yet, Gallo et al. (2005) pointed out a mesethmoid with a bifid posterior extremity in *Dercetis*. However, Taverne (2005b) described this bone with an acute posterior extremity, and we confirmed this feature in *Dercetis elongatus* (NHM P. 49793) and *D. triqueter* (MNHN SHA 523). Yet, Taverne (2006c) described *Ichthyotringa africana* as possessing a mesethmoid with acute posterior extremity, mainly based on specimens MNHN DTS 225-228. However, observing the specimen MNHN DTS 228, we verify a mesethmoid with bifid posterior extremity.

In Gallo et al. (2005), the autosphenotic spine posteriorly curved is a synapomorphy of the clade (*Rhynchodercetis*, *Hastichthys*). However, in this study, the character shows a slightly wide distribution, being also present in *Atolvorator* and *Trachinocephalus*. Taverne (2006b) stated that the autosphenotic of *Caudadercetis* is hidden by the frontals. For this reason, we opted to code it as missing data.

Accordig to Taverne (1991), *Pelargorhynchus* is characterized by four derived features, among them the loss of the supraoccipital crest. Gallo et al. (2005) considered the absence of the supraoccipital crest as an autapomorphy of *Pelargorhynchus*. In the present study, the character was differently interpreted, because its absence and/or loss were verified in other two taxa (*Benthesikyme* and *Rharbichthys*).

Gallo et al. (2005) pointed out the presence of a pterotic not projecting beyond the occiput in *Dercetis* based on available descriptions. However, we pointed out another condition (projecting beyond the occiput), following the redescription of the genus furnished by Taverne (2005b), as well as by direct observation of specimens of *Dercetis triqueter* and *D. elongatus*.

The presence of an unroofed post-temporal fossa in *Palaeolycus* followed Goody (1969), in contrast with Fielitz (2004) who pointed out a roofed condition. We verify a roofed condition in *Eurypholis* and *Saurorhamphus* in disagreement with Fielitz (2004). Gallo et al. (2005) pointed out a partially roofed post-temporal fossa in the genus *Dercetis*. However, following the redescription of the genus furnished by Taverne (2005b), as well as the direct observation of specimens of *Dercetis triqueter* and *D. elongatus*, we indicate herein a roofed post-temporal fossa to *Dercetis*.

Rosen (1973) pointed out the absence of orbitosphenoid in enchodontids. Additionally, Taverne (1991) stated that its absence would be a primitive condition of dercetids. Gallo et al. (2005) proposed the presence of orbitosphenoid as an autapomorphy of *Ichthyotringa*. Generally, the common absence of an orbitosphenoid in the specimens observed directly or indirectly is probably due to its fragility, which impedes a good preservation.

Gallo et al. (2005) suggested the presence of the basisphenoid as an autapomorphy of *Ichthyotringa*, but other taxa (i.e., *Apuliadercetis tyleri*, *Atolvorator longipectoralis* and *Robertichthys riograndensis*) bearing this bone were described after this study.

Taverne (1985) pointed out three conditions for the presence of teeth on the ectopterygoid: bone toothless or bearing some small conic teeth in a small portion of it as in *Rharbichthys ferox*, from the Cenomanian of Morocco; and well-developed teeth on the ectopterygoid similar to those found in the dentary of *Rharbichthys* cf. *ferox* from the Cenomanian-Turonian of Italy (see also Sorbini 1976). For this reason, the character was regarded as polymorphic.

In the cladistic analysis herein performed (Fig. 1), we demonstrate that the suborder Enchodontoidei is not a monophyletic group, as two genera of the outgroup belonging to another suborder and even to another order

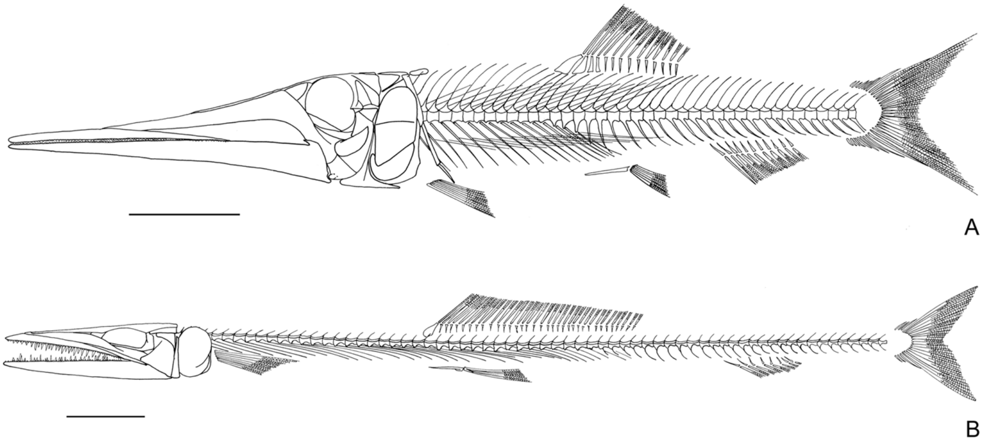

Fig. 2 – Neural spines. **A**, well-developed in *Apateopholis laniatus* (Davis, 1887), modified from Goody (1969); **B**, very reduced in *Dercetis triqueter* Pictet, 1850, modified from Goody (1969). Scale bars equal 20 mm.

(*Trachinocephalus* and *Protostomias*, respectively) went to the ingroup. Although *Trachinocephalus* belongs to the same order of the taxa herein studied (Aulopiformes), it is allocated into the suborder Synodontoidei, together with other extant members of Aulopiformes (Baldwin and Johnson 1996, Sato and Nakabo 2002). Arambourg (1954) and Taverne (1991) included *Protostomias* in the order Stomiifomes, based on generalized anatomical features, such as general shape of the body and a massive and tooth-bearing dentary, as well as the position of the median fins. Taverne (1992), in his comprehensive review of *Protostomias*, retained its placement in Stomiiformes.

Yet, the paraphyly of Enchodontoidei not allowed their taxonomic classification in the cladistic context.

The family Apateopholidae is not a monophyletic group, as *Apateopholis* is the sister-taxon of the clade including the family Enchodontidae (new usage) and the genera *Cimolichthys*, *Prionolepis*, *Halec*, *Phylactocephalus*, and *Serrilepis*. *Apateodus,* often placed with the Apateopholidae, is the sister-group of *Ichthyotringa*.

The monophyly of Dercetidae proposed by Gallo et al. (2005) and Blanco et al. (2008) was corroborated and supported by a single synapomorphy (very reduced neural spine; character 71) (Fig. 2), but the inclusion of new taxa changed the interrelationships of the family. The genus *Apuliadercetis* is the sister-group of *Brazilodercetis* and they are the basal clade of Dercetidae. *Cyranichthys* is the sister-taxon of *Robertichthys*, and *Dercetis* is the sister-taxon of *Ophidercetis*. These two clades plus *Benthesikyme* form a new clade, which is an intermediary group between the basal and crown groups. However, the relationships within this intermediary group are uncertain. *Caudadercetis* appears as the most basal taxon in the major clade of Dercetidae (*Caudadercetis*, (*Pelargorhynchus*, (*Nardodercetis*, (*Rhynchodercetis*, (*Hastichthys*, *Dercetoides*)))). This clade is sustained by the unique presence of a convoluted suture marking the contact between second and third hypurals (character 83; Fig. 3B), although this character in *Pelargorhynchus* was coded as missing data, as its caudal skeleton is unknown. A pipe-shaped preopercle is an autapomorphy of *Brazilodercetis* (character 56; Fig. 4B).

Gallo et al. (2005) and Blanco et al. (2008) pointed out two synapomorphies of Dercetidae: the absence of a longitudinal opercular crest and a reduced neural spine. However, the absence of an opercular crest was also verified in other taxa. Yet, according to Gallo et al. (2005), *Dercetoides* is the sister-taxon of the clade formed by *Rhynchodercetis* and *Hastichthys*, but in Blanco et al. (2008) *Dercetoides* is the sister-taxon of *Hastichthys*, and both are sister-taxa of *Rhynchodercetis*. On the other hand, Taverne (2006b) stated that *Dercetoides* is the sister-taxon of *Rhynchodercetis*, and *Hastichthys* is the sister-taxon of the clade (*Caudadercetis*, (*Pelargorhynchus*, (*Rhynchodercetis*, *Dercetoides*))). Herein,

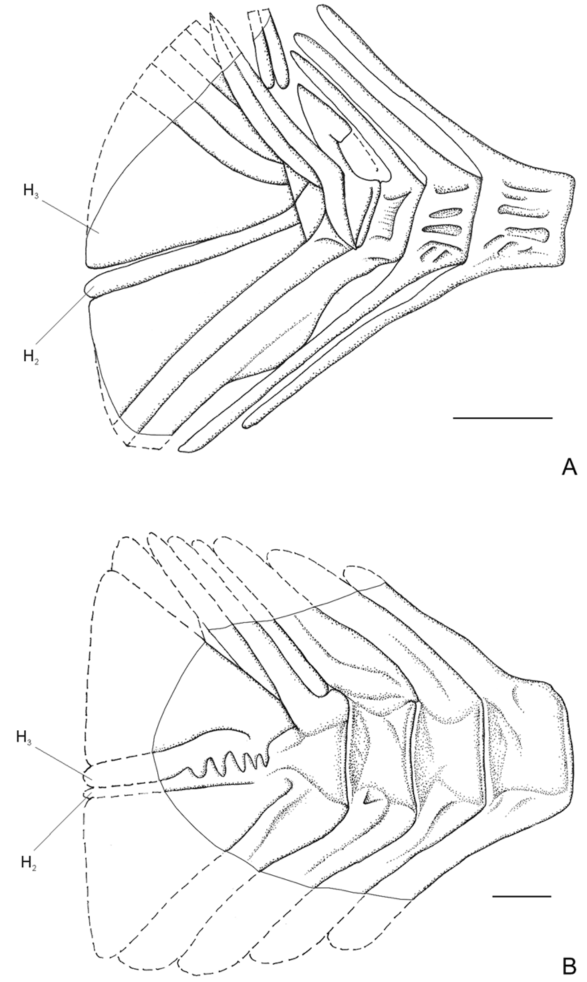

Fig. 3 – Contact between hypurals 2-3. **A**, free in *Ichthyotringa furcata* (Agassiz, 1844), modified from Goody (1969); **B**, convoluted suture in *Hastichthys gracilis* (Chalifa, 1989a), modified from Taverne (1991). **Abbreviation**: **H**, hypural. Scale bars equal 1 mm.

Hastichthys appears as the sister-taxon of *Dercetoides*. Taverne (2006b) suggested *Dercetis* as the most basal dercetids, and *Ophidercetis* as the sister-taxon of *Cyranichthys*. However, we obtained different results: *Dercetis* forms a clade with *Ophidercetis*, and *Cyranichthys* is related to *Robertichthys*.

The family Enchodontidae is confirmed as monophyletic, as has already been proposed by Fielitz (2004), but herein it possesses a new composition. *Parenchodus* forms a clade with *Palaeolycus*, and *Enchodus* is the sister-group of this clade; the clade formed by (*Eurypholis*, *Saurorhamphus*) is the basal sister-group. *Rharbichthys* was excluded from the Enchodontidae, being recognized in this analysis as the sister-group of the clade formed by the Dercetidae plus the genus *Trachinocephalus*. Fielitz (2004) proposed three synapomorphies of Enchodontidae: the presence of a single dermopalatine tooth, dermopalatine bone with same length or shorter than the tooth, and the absence of an interopercle. In this analysis, these features were not corroborated as synapomorphies. For instance, a single tooth on the dermopalatine is also present in *Ophidercetis*, a genus of Dercetidae (Taverne 2005b). The remaining synapomorphy of this family is the presence of middorsal scutes (character 87; Fig. 5). In addition, the clade (*Eurypholis*, *Saurorhamphus*) is supported by two synapomorphies: quadrate-mandibular articulation hidden (character 52; Fig. 6) and the presence of a spine on posterior border of the opercle (character 61; Fig. 7).

Halecidae possess a new composition: *Halec* is the sister-group of *Phylactocephalus*; and *Hemisaurida* was excluded from the family, being considered Aulopiformes *incertae sedis*, like *Nardorex*.

The presence of a well-developed supraoccipital divided into two distinct regions is an autapomorphy of *Nardorex* (character 20; Fig. 8B). These two regions are separated by a slight transverse ridge: the anterior region is reduced and contacts the parietals, whereas the posterior one is large, contacts the epioccipitals and bears a high median crest (Fig. 8B).

ACKNOWLEDGMENTS

We are most grateful to R.C.T. Cassab (Departamento Nacional de Produção Mineral, Rio de Janeiro), D.D.R. Henriques (Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro), O.T. Oyakawa (Museu de Zoologia/Universidade de São Paulo, São Paulo), M. Richter (The Natural History Museum, London), H.R.S. Santos (Universidade do Estado do Rio de Janeiro, Rio de Janeiro), W. Souza-Lima (Fundação Paleontológica Phoenix, Aracaju), and M. Véran (Muséum National d'Histoire Naturelle, Paris), for access to specimens in their care. We thank S.A. Azevedo, M.J. Cavalcanti, F.J. de Figueiredo, and J. Alvarado Ortega for critical comments to the M.S. thesis of the H.M.A.S advised by V.G., on which this paper is based. We are particularly grateful to T. Moulton for his help with the

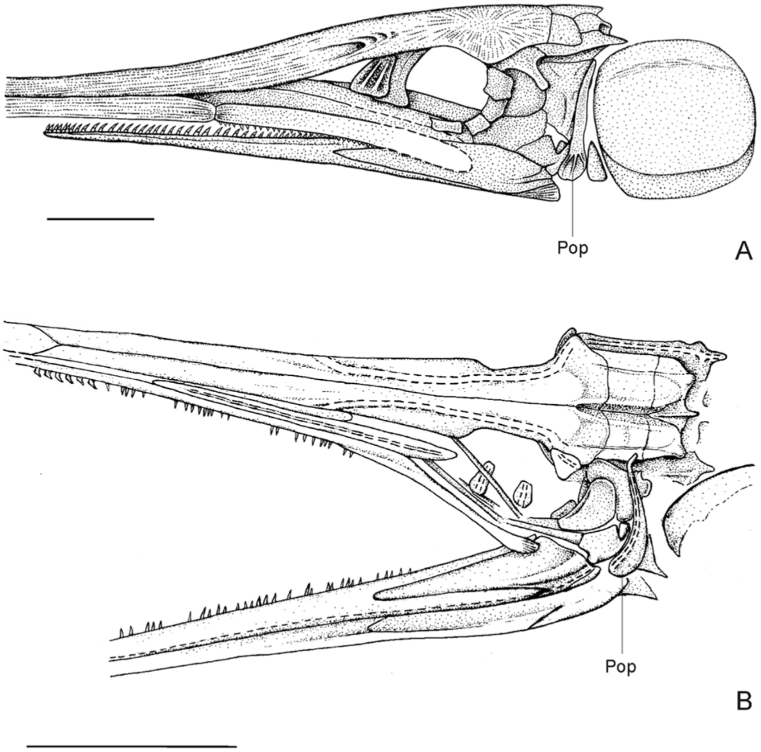

Fig. 4 – Preopercle shape. **A**, triangular in *Hastichthys gracilis* (Chalifa, 1989a), modified from Taverne (1991); **B**, pipe-shaped in *Brazilodercetis longirostris* Figueiredo and Gallo, 2006, modified from Figueiredo and Gallo (2006). **Abbreviation**: **Pop**, preopercle. Scale bars equal 10 mm.

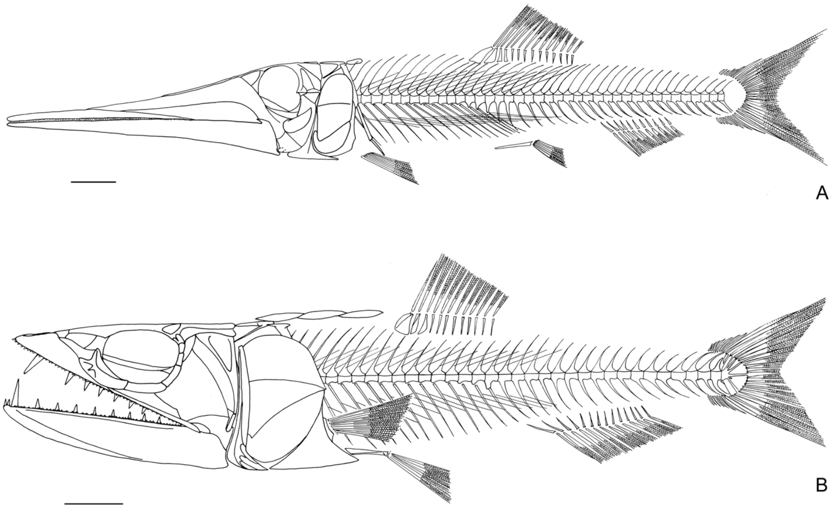

Fig. 5 – Middorsal scutes. **A**, absent in *Apateopholis laniatus* (Davis, 1887), modified from Goody (1969); **B**, present in *Eurypholis boissieri* Pictet, 1850, modified from Goody (1969). Scale bars equal 10 mm.

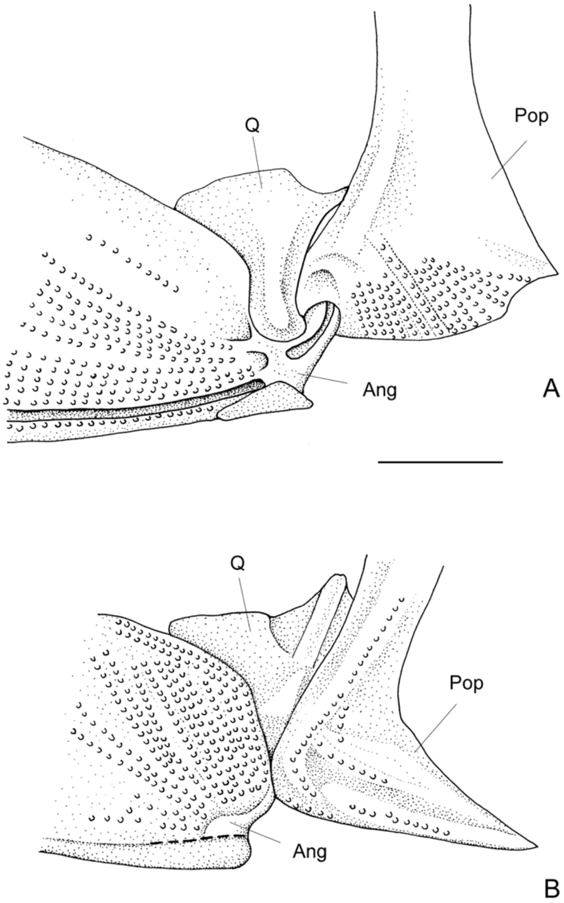

Fig. 6 – Quadrate-mandibular articulation. **A**, exposed in *Enchodus marchesettii*, modified from Fielitz (2004); **B**, hidden in *Eurypholis boissieri* Pictet, 1850, modified from Fielitz (2004). **Abbreviations**: **Ang**, angular; **Pop**, preopercle; **Q**, quadrate. Scale bars equal 3 mm.

English revision. This research was part of a Project supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 476708/2004-4) and the Fundação Carlos Chagas de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ E-26/171.215/2004). HMAS holds a fellowship from the FAPERJ and VG has research fellowship grants from the CNPq (Brazilian Federal Government), from the FAPERJ (Jovem Cientista do Nosso Estado), and from the PROCIÊNCIA (Rio de Janeiro State Government).

RESUMO

Os Enchodontoidei são peixes teleósteos marinhos extintos, com uma longa amplitude temporal e uma ampla distribuição geográfica. Tendo em vista que não há nenhuma proposta ampla para a filogenia deste táxon, foi realizada uma análise de parcimônia com base numa matriz de dados de 87 caracteres, 31 táxons terminais no grupo interno, e três táxons no grupo externo. Como resultado da análise, foram obtidas 93 árvores igualmente parcimoniosas (L = 437 passos; CI = 0,24; RI = 0,49). O consenso de maioria é representado pela seguinte topologia: (*Sardinioides* + *Hemisaurida* + (*Nardorex* + (*Atolvorator* + (*Protostomias* + *Yabrudichthys*) + (*Apateopholis* + (*Serrilepis* + (*Halec* + *Phylactocephalus*) + (*Cimolichthys* + (*Prionolepis* + ((*Eurypholis* + *Saurorhamphus*) + (*Enchodus* + (*Paleolycus* + *Parenchodus*))))))) + ((*Ichthyotringa* + *Apateodus*) + (*Rharbichthys* + (*Trachinocephalus* + ((*Apuliadercetis* + *Brazilodercetis*) + (*Benthesikyme* + (*Cyranichthys* + *Robertichthys*) + (*Dercetis* + *Ophidercetis*)) + (*Caudadercetis* + (*Pelargorhynchus* + (*Nardodercetis* + (*Rhynchodercetis* + (*Dercetoides* + *Hastichthys*)))))). O grupo

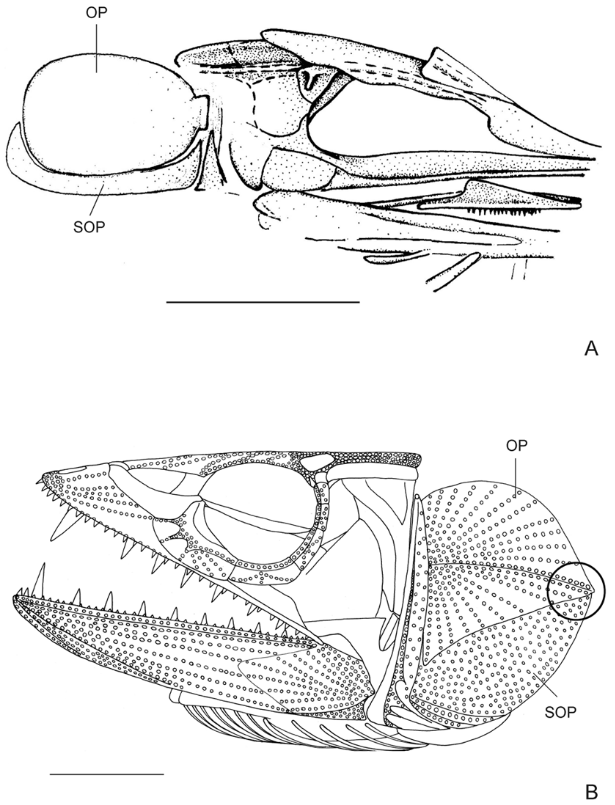

Fig. 7 – Spine on posterior border of the opercle. **A**, absent in *Brazilodercetis longirostris* Figueiredo and Gallo, 2006, modified from Figueiredo and Gallo (2006); **B**, present in *Eurypholis boissieri* Pictet, 1850, modified from Goody (1969), delimited by a circle. **Abbreviations**: **Op**, opercle; **Sop**, subopercle. Scale bars equal 10 mm.

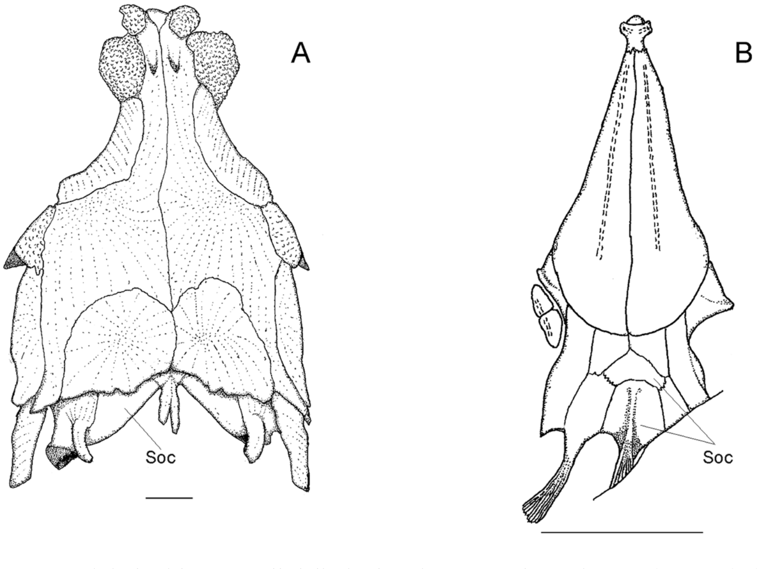

Fig. 8 – Supraoccipital with two well-delimited regions. **A**, absent in *Trachinocephalus myops* (Forster, 1801) (based on the specimen AO.UERJ 17); **B**, present in *Nardorex zorzini* Taverne, 2004 (modified from Taverne 2004). **Abbreviation**: **Soc**, supraoccipital. Scale bars equal 30 mm.

Enchodontoidei não é monofilético. Os Dercetidae formam um clado suportado pela presença de espinhos neurais muito reduzidos e possuem uma nova composição. Os Enchodontidae são um grupo monofilético, devido à presença de escudos no dorso, e *Rharbichthys* foi excluído do clado. Os Halecidae possuem uma nova composição, com a exclusão de *Hemisaurida*. Este táxon e *Nardorex* são Aulopiformes *incertae sedis*.

Palavras-chave: Aulopiformes, Enchodontoidei, filogenia, taxonomia.

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APPENDIX I
List of the analyzed material

RECENT MATERIAL

Synodontidae – *Trachinocephalus myops*: AO.UERJ 17; AO.UERJ 123; AO.UERJ 127; AO.UERJ 128; O.UERJ 471; O.UERJ 1334; O.UERJ 2073.

Evermannellidae – *Coccorella atlantica*: MZUSP 78-193.

Paralepididae – *Lestidium atlanticum*: MZUSP 60327; *Lestrolepis intermedia*: MZUSP 80717.

FOSSIL MATERIAL

Enchodontidae – *Enchodus* sp. 1: Pz.UERJ 489; Pz.UERJ 490; Pz.UERJ 491; *Enchodus* sp. 2: Pz.UERJ 485; Pz.UERJ 492; *Enchodus libycus*: FPH-01-82; FPH-02-12; FPH-01 679; FPH-01 742; FPH-01 677; FPH-01 810; FPH-01 808; FPH-01 809; DGM 642-P; *Enchodus oliveirai*: DGM 643-P; *Enchodus subaequilatelaris*: DGM 644-P; MN 4329-V; *Enchodus longipectoralis*: DGM 501-P; *Enchodus venator*: MNHN DTS 156, MNHN DTS 157 d g; MNHN DTS 158 d g; MNHN DTS 160; MNHN DTS 148; MNHN DTS 138 d g; MNHN DTS 149; MNHN DTS 141 d g; MNHN DTS 159 d g; MNHN DTS 155; MNHN DTS 190 d g; MNHN DTS 143; *Eurypholis boisseiri*: Pz.UERJ 493; NHM P. 48; NHM P. 63323; *Eurypholis longidens*: NHM P. 48084; NHM P. 409507; *Eurypholis pulchellus*: NHM P. 1703; *Eurypholis* sp.: NHM P. 47317; *Rharbichthys* cf. *ferox*: Pz.UERJ 448 a b; Pz.UERJ 451; Pz.UERJ 452; *Rharbichthys ferox*: MNHN DTS 118 d g; MNHN DTS 162 d g; MNHN DTS 130 d g; MNHN DTS 81 d g; MNHN DTS 86 d g; MNHN DTS 164 d g; MNHN DTS 97 d g; MNHN DTS 119 g d; MNHN DTS 163 g d; MNHN DTS 165; MNHN DTS 166; MNHN DTS 167; MNHN DTS 71; MNHN DTS 161; MNHN DTS 72 d g; MNHN DTS 126 d g.

Dercetidae – *Benthesikyme armatus*: NHM P. 2109; *Benthesikyme gracilis*: NHM P. 48085; NHM P. 49539; NHM P. 48087; NHM P. 1902; NHM P. 47359; NHM P. 49538; NHM P. 9170; NHM P. 47360; NHM P. 4738; NHM P. 46553; NHM P. 48088; NHM P. 46533; NHM P. 48086; *Benthesikyme rostralis*: MNHN SHA 499; MNHN SHA 501; MNHN SHA 505; MNHN SHA 513; MNHN SHA 578; MNHN SHA 2840; MNHN SHA 2849; *Benthesikyme* sp.: NHM P. 4019; *Brazilodercetis longirostris* Pz.UERJ 447; Pz.UERJ 471; Pz.UERJ 472; Pz.UERJ 473; Pz.UERJ 474; Pz.UERJ 475; Pz.UERJ 476; Pz.UERJ 477; Pz.UERJ 478; Pz.UERJ 495.; *Dercetis elongatus* 4018; 49536; NHM P. 15513; NHM P. 43098; NHM P. 4134; NHM P. 4132-33; NHM P. 41198; NHM P. 49793; NHM P. 12895; NHM P. 43512; NHM P. 31075-82.; *Dercetis* sp. NHM P. 49740; NHM P. 48155; *Dercetis triqueter* NHM P. 4852; NHM P. 49541; NHM P. 49535; NHM P. 4007; NHM P. 46524; NHM P. 4963; NHM P. 49537; NHM P. 47362; NHM P. 47361, MNHN SHA 520; MNHN SHA 523; MNHN SHA 572; MNHN SHA 2192 d g; MNHN SHA 2317; MNHN SHA 2444; MNHN SHA 3107; *Rhynchodercetis* cf. *gracilis* NHM P. 63235 a/b; NHM P. 63332; NHM P. 63246 a/b; NHM P. 62677 a/b; *Rhynchodercetis* cf. *yovanovitchi* NHM P. 62678; NHM P. 63236 a/b; NHM P. 63599; NHM P. 63261; NHM P. 62690; NHM P. 63262; *Rhynchodercetis gortanii* NHM P. 10913; *Rhynchodercetis hakelensis* NHM P. 6001; NHM P. 4739; NHM P. 4683; NHM P. 4866; *Rhynchodercetis serpentinus* NHM P. 51939; *Rhynchodercetis yovano-*

vitchi MNHN DTS 8; MNHN DTS 9 d g; MNHN DTS 10 d g; MNHN DTS 14; MNHN DTS 15; MNHN DTS 20; MNHN DTS 21; MNHN DTS 22; MNHN DTS 23; MNHN DTS 123; MNHN DTS 47; MNHN DTS 175; MNHN DTS 174; MNHN DTS 186; MNHN DTS 40; MNHN DTS 302; MNHN DTS 303; MNHN DTS 304; MNHN DTS 306; MNHN DTS 307; MNHN DTS 308; MNHN DTS 309; MNHN DTS 261 d g; MNHN DTS 96 d g; MNHN DTS 43 d g; MNHN DTS 310; MNHN DTS 189; MNHN DTS 176 d g; MNHN DTS177 d g; MNHN DTS 2; MNHN DTS 7; MNHN DTS 41; MNHN DTS 262; MNHN DTS 6 d g; MNHN DTS 263 a b.

Apateopholidae – *Apateodus striatus* NHM P. 61919; NHM P. 49799; NHM P. 4090-1; NHM P. 49821; NHM P. 12899; NHM P. 12898; NHM P. 33309; NHM P. 49067; NHM P. 479224; NHM P. 10058; NHM P. 49070; *Apateopholis laniatus* NHM P. 4745; NHM P. 4026; NHM P. 4870; NHM P. 63263; NHM P. 4869.

Cimolichthyidae – *Cimolichthys levesiensis* NHM P. 4039; NHM P. 4026; NHM P. 1810a; NHM P. 1811; NHM P. 38113; NHM P. 5491.

Prionolepididae – *Prionolepis cataphhractus* NHM P. 4864; NHM P. 9966; NHM P. 9967; NHM P. 9968; NHM P. 9970; NHM P. 47516; NHM P. 4871; NHM P. 47332; NHM P. 4006; *Prionolepis laniatus* NHM P. 39234.

Ichthyotringidae – *Ichthyotringa* sp. NHM P. 6015; NHM P. 14204; NHM P. 9996; NHM P. 48089 a/b; NHM P. 1882; NHM P. 49544; NHM P. 48092; NHM P. 48155; *Ichthyotringa africana* MNHN DTS 225; MNHN DTS 226; MNHN DTS 227 g d; MNHN DTS 228 d g.; *Ichthyotringa damoni* NHM P. 47367; NHM P. 4849; *Ichthyotringa furcata* NHM P. 49523; NHM P. 49525; NHM P. 48090; NHM P. 49545; NHM P. 48091; NHM P. 47363; NHM P. 48144; NHM P. 47364.

Halecidae – *Halec sternbergi* NHM P. 9004; NHM P. 9004; NHM P. 5732; *Halec eupterygius* NHM P. 11102; NHM P. 43388; NHM P. 32336; NHM P. 4289; NHM P. 43392; NHM P. 10920; NHM P. 32237; *Halec rugosus* NHM P. 13899; *Phylactocephalus microlepis* NHM P. 4757; NHM P. 105; NHM P. 47318; NHM P. 9151; *Hemisaurida hakelensis* NHM P. 48779; NHM P. 48780.

Atolvorator longipectoralis Pz.UERJ 486; Pz.UERJ 487; Pz.UERJ 496 a e b; Pz.UERJ 508 a e b; Pz.UERJ 509; Pz.UERJ 510.

Sardinioides minimus NHM P. 52513; NHM P. 52511; NHM P. 52512; NHM P. 52504 a.

Protostomias maroccanus MNHN DTS 18 d g; MNHN DTS 122 d g; MNHN DTS 172 d g; MNHN DTS 178; MNHN DTS 179 d g; MNHN DTS 184; MNHN DTS 77; MNHN DTS 381.

APPENDIX II
Data matrix of the cladistic analysis of Enchodontoidei.

Taxa / Characters	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45
Sardinioides	00000	000?1	00?00	100??	00000	1?0?1	10000	01000	10001
Protostomias	00000	10000	00?00	00100	1?1?0	01000	00110	00001	00100
Trachinocephalus	00030	00000	11000	00000	01000	00100	010?0	001?2	00210
Ichthyotringa	11100	001?0	?0001	0?000	0?000	??111	?0010	00100	?0200
Apateopholis	0011?	00??0	?0000	1?1?0	00111	??011	00010	00100	00001
Apateodus	?0000	00??0	10100	00000	1000?	0??11	10010	00000	00200
Cimolichthys	00021	00?10	00000	10000	00011	0?111	01001	00000	10200
Apuliadercetis	21101	00??0	00011	00000	1?0?0	13100	10010	01112	00010
Benthesikyme	2?10?	00??0	1?000	0?010	1?0??	1??11	??010	00113	0??1?
Brazilodercetis	?112?	00?00	10000	00000	1?1??	13000	10110	00112	01111
Caudadercetis	2110?	00??0	0???0	001??	1?1??	??1?0	100?0	0???2	?0210
Cyranichthys	1112?	????0	10000	00000	1?0??	1????	??010	0?010	0??10
Dercetis	21110	00??1	10000	00000	1?0??	12111	?0010	01112	00111
Dercetoides	2111?	???10	00?10	10100	101??	1?000	10010	0?113	00101
Hastichthys	2110?	???10	01010	10000	1?0??	12111	10111	00110	01001
Nardodercetis	21100	00??0	0?000	101?0	0????	1?000	?0110	0?100	01001
Ophidercetis	2110?	21?00	10000	00000	1?0??	12111	?0010	01112	00210
Pelargorhynchus	1113?	????0	00000	10110	1?1??	1?11?	??001	00110	00201
Rhynchodercetis	21100	00?00	01001	10100	1?1??	1?010	10110	00110	01001
Robertichthys	211?0	10???	?0??0	?????	1???0	1??1?	10010	00012	01210
Prionolepis	00031	00??0	10000	12000	00011	1?110	11000	00110	00111
Rharbichthys	0002?	21?00	10?00	0?110	0?0??	??1?1	10010	01100	00210
Palaeolycus	1002?	21?1?	?0?10	??1??	1?1??	??110	??000	10010	?0010
Eurypholis	00011	21?10	10000	12100	00011	12110	11001	11110	00200
Saurorhamphus	1111?	?0?10	10000	12100	1?011	1211?	10001	1?013	00000
Enchodus	0003?	?????	????0	????0	0????	??11?	10???	??000	10010
Parenchodus	0003?	2?1?0	10110	12100	1010?	1?011	?1001	01003	00210
Halec	00010	00?10	10000	10100	001??	0?111	11001	00102	10110
Hemisaurida	00000	00?1?	10?10	????0	00???	1?011	11000	00103	10111
Phylactocephalus	00010	00010	00000	????0	011??	??11?	01001	00102	10111
Nardorex	?0021	00111	10001	00001	0?01?	1311?	??000	01013	00000
Serrilepis	00030	000?0	10100	10000	1?111	00111	?0011	0?103	10101
Atolvorator	00000	??0??	?1100	01100	10100	02011	00010	?0100	10000
Yabrudichthys	00110	101??	?0000	????0	1010?	??000	?1010	0?1?0	00000

APPENDIX II (continuation)

Taxa / Characters	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-87
Sardinioides	00000	00000	00000	00000	01100	01001	01010	0000000
Protostomias	00001	10000	00000	001?0	1000?	00000	00?01	0001000
Trachinocephalus	11000	00000	20000	00000	00011	00000	10000	0000000
Ichthyotringa	010?0	1001?	10001	00010	01110	01001	00000	0000000
Apateopholis	00020	1001?	11101	01110	01000	01101	11000	0?01000
Apateodus	00020	00100	30001	00010	?????	?????	???0?	???????
Cimolichthys	01021	0001?	10001	011??	000?0	010?1	?10?0	?101220
Apuliadercetis	00020	00001	10010	000?0	00011	11001	21000	0101310
Benthesikyme	0???0	?????	?????	?????	???1?	?100?	???0?	01?13?0
Brazilodercetis	00000	00000	40010	0000?	????1	11???	?????	???132?
Caudadercetis	00020	0000?	10?00	00??0	?0011	11?00	01?01	1111000
Cyranichthys	0????	?????	10010	00?0?	????0	1????	?11??	???1120
Dercetis	01020	1001?	10000	00000	?0010	11000	01100	0101320
Dercetoides	01021	0000?	30000	01001	00011	11000	01000	0111310
Hastichthys	01020	00000	10010	0000?	00011	1100?	01001	0111310
Nardodercetis	00020	00000	???1?	00?00	00011	11001	10??0	0011310
Ophidercetis	01010	00000	30000	00000	0001?	11000	20101	0??1120
Pelargorhynchus	000?1	?00??	1?000	?010?	?0??0	11??1	?11?0	???0220
Rhynchodercetis	00000	0001?	10000	00000	00011	1?000	21100	0111310
Robertichthys	010?0	?????	10010	001??	000??	11??1	2????	???0310
Prionolepis	11000	000??	11001	001?1	01010	01111	21000	0000000
Rharbichthys	00000	10100	10000	01000	0110?	00001	21000	1001410
Palaeolycus	01011	1010?	?1001	0110?	0001?	01001	20001	0??1001
Eurypholis	00001	011?1	11101	11100	01110	01000	00000	0001111
Saurorhamphus	01001	11111	11101	11100	01010	01000	20001	0000111
Enchodus	?1110	?01??	11000	01100	0111?	01001	21??1	00?1001
Parenchodus	01121	10101	11001	01101	11001	00101	01101	0101001
Halec	01001	000??	11001	01010	01110	01001	01000	0000000
Hemisaurida	00020	0001?	20100	00000	01110	01001	21000	0001000
Phylactocephalus	00021	0000?	11001	01000	01110	01111	01000	0000000
Nardorex	00010	10000	00110	00100	01?10	00001	00001	???1000
Serrilepis	010?1	10101	11001	01111	01110	01001	01010	0100000
Atolvorator	01020	00100	10000	00100	10110	01001	1000?	?001000
Yabrudichthys	000?1	1010?	1111?	00110	0100?	01001	21110	0101000

APPENDIX III
List of characters used in the phylogenetic analysis of †Enchodontoidei.

1. Body length: slightly elongate [lesser than or equal to 1:10] (0);
   elongate [from 1:11 to 1:15] (1); very elongate [higher than 1:15] (2).
2. Head height: deep (0); low (1).
3. Snout length: short (0); long (1).
4. Dermal pattern on skull roof: smooth (0); only with tubercles (1); only with ridges (2);
   tubercles + ridges (3).
5. Vomerine teeth: absent (0); present (1).
6. Number of teeth on dermopalatine: two or more (0); none (1); single (2).
7. Dermopalatine length: twice or more times longer than its tooth (0);
   equal-sized or shorter than its tooth (1).
8. Antorbital: present (0); absent (1).
9. Nasal: present (0); absent (1).
10. Anterior extremity of mesethmoid: acute (0); bifid (1).
11. Posterior extremity of mesethmoid: bifid (0); acute (1); straight (2).
12. Autosphenotic spine: straight (0); posteriorly curved (1).
13. Suture between frontals: slightly sinuous (0); markedly sinuous (1).
14. Posterior border of frontal: behind the autosphenotic spine (0);
    at the level of the autosphenotic spine (1).
15. Shape of the post-orbital border: concave (0); convex (1).
16. Parietal length: long [length equal or larger than its height (0)];
    short [length smaller than its height (1)].
17. Supraorbital sensory canal in the skull roof: covered (0); exposed (1).
18. Extension of the supraoccipital: not separating parietals (0); separating parietals (1).
19. Supraoccipital crest: present (0); absent (1).
20. Supraoccipital with two well-delimited regions: absent (0); present (1).
21. Extension of pterotic: not projecting backwards beyond the level of occiput;
    (0) projecting beyond the occiput (1).
22. Dilatator fossa: unroofed (0); roofed (1).
23. Exposition of the post-temporal fossa: roofed (0); unroofed (1).
24. Orbitosphenoid: present (0); absent (1).
25. Basisphenoid: present (0); absent (1).
26. Supraorbital: present (0); absent (1).
27. Lachrymal shape: subtriangular (0); suboval (1); trapezoidal (2); rod-shaped (3).
28. Position of the mandibular suspensorium: inclined (0); vertical (1).
29. Ectopterygoid: toothless (0); toothed (1).
30. Endopterygoid: toothless (0); toothed (1).
31. Placement of articular facet for the hyomandibula: posteroventral (0); ventral (1).
32. Number of articular facet for the hyomandibula: a continuous facet (0); two facets (1).
33. Premaxilla: toothed (0); toothless (1).
34. Posterior extension of the premaxilla: reaching the orbit (0); not reaching the orbit (1).
35. Dermal pattern on premaxilla: smooth (0), ornamented (1).
36. Fenestra in the premaxilla: absent (0); present (1).
37. Ascending process of the premaxilla: absent (0); present (1).
38. Maxilla: toothless (0); toothed (1).
39. Placement of the maxilla: over the premaxilla (0); behind the premaxilla (1).
40. Teeth on upper jaw: only straight (0); absent (1); curved + straight (2); only curved (3).
41. Supramaxilla: absent (0); present (1).
42. Mandible length: equal to the snout (0); shorter than the snout (1).

43. Teeth on mandible: only straight (0); only curved (1); curved + straight (2).
44. Teeth size on upper jaw: absent or with same height (0); with different height (1).
45. Teeth size on mandible: different height (0); equal height (1).
46. Rows of teeth on upper jaw: single (0); two or more (1).
47. Rows of teeth on mandible: single (0); two or more (1).
48. Anteroventral prongs on dentary: absent (0); present (1).
49. Mandibular sensory canal: enclosed by bone (0); partially open (1); open (2).
50. Mandibular dermal pattern: smooth (0), ornamented (1).
51. Flange on anguloarticular: present (0); absent (1).
52. Quadrate-mandibular articulation: exposed (0); hidden (1).
53. Articular facet for the quadrate: shallow (0); deep (1).
54. Retroarticular process: present (0), absent (1).
55. Ornamentation in the infraorbital bones: smooth (0), ornamented (1).
56. Preopercle shape: L-shaped (0); triangular (1); crescent-shaped (2); rod-shaped (3); pipe-shaped (4).
57. Preopercular dermal pattern: smooth (0); ornamented (1).
58. Posteroventral spine in the preopercle: absent or reduced (0), well-developed (1).
59. Dimension of the opercle: deeper than long (0); longer than deep (1).
60. Opercle crest: absent (0); (1) present.
61. Spine on posterior border of the opercle: absent (0); present (1).
62. Opercular and subopercular dermal pattern: smooth (0); ornamented (1).
63. Interopercle: present (0); absent (1).
64. Mesocoracoid: absent (0); present (1).
65. Scapula and coracoid: individualized (0); co-ossified (1).
66. Supraneurals: present (0); absent (1).
67. Total number of vertebrae: more than 50 (0); equal or minus than 50 (1).
68. Number of caudal vertebrae: more than 20 (0); equal or minus than 20 (1).
69. Ribs: extending to the pelvic fin origin (0); surpassing the pelvic fin origin (1).
70. Transverse processes: one pair (0); two pairs (1).
71. Neural spines: well-developed [their length surpassing the length of the vertebral centrum] (0); very reduced [their length equal or minus than half of the length of the vertebral centrum] (1).
72. Neural spines bifid in the abdominal region: present (0); absent (1).
73. Distribution of epipleurals: extending to more than a half of the body (0); up to half of the body (1).
74. Distribution of epineurals: extending to more than a half of the body (0); up to half of the body (1).
75. Position of the pectoral fin: high [last fin-ray placed at the level of the ventral border of the opercle or a little above (0)]; low [last fin-ray placed below the level of the ventral border of the opercle (1)].
76. Orientation of the pectoral fin base: vertical (0), horizontal (1), inclined (2).
77. Origin of the pelvic fin: anterior to the dorsal fin (0); opposite or posterior to the dorsal fin (1).
78. Dorsal fin length: short [lesser than 20 rays (0]; long [more than 20 rays] (1).
79. Shape of the first proximal pterygiophore of the dorsal fin: different from the remnants (0); all equal in shape (1).
80. Anal fin length: short [up to 15 rays (0)]; long [more than 15 rays (1)].
81. Anal fin edge: not serrated (0); serrated (1).
82. Fusion of hypurals: free (0); fused (1).
83. Contact between hypurals 2-3: free (0); with convoluted suture (1).
84. Body scales: present (0); absent (1).
85. Flank scutes: absent (0); triangular (1); cordiform (2); tripartite (3); retangular (4).
86. Number of rows of scutes on flanks: absent (0); single (1); two or more (2).
87. Middorsal scutes: absent (0); present (1).