Anais da Academia Brasileira de Ciências
ISSN: 0001-3765
aabc@abc.org.br
Academia Brasileira de Ciências
Brasil

DE FIGUEIREDO, FRANCISCO J.; RIBEIRO, DOUGLAS R.M.
Relationships of †Codoichthys carnavalii Santos, 1994 (Teleostei, Clupeomorpha, †Ellimmichthyiformes) from the Late Aptian of São Luís-Grajaú Basin, NE Brazil
Anais da Academia Brasileira de Ciências, vol. 88, núm. 3, septiembre, 2016, pp. 1277-1307
Academia Brasileira de Ciências
Rio de Janeiro, Brasil

Anais da Academia Brasileira de Ciências (2016) 88(3): 1277-1307
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
http://dx.doi.org/10.1590/0001-3765201620150495
www.scielo.br/aabc

Relationships of †*Codoichthys carnavalii* Santos, 1994 (Teleostei, Clupeomorpha, †Ellimmichthyiformes) from the Late Aptian of São Luís-Grajaú Basin, NE Brazil

FRANCISCO J. DE FIGUEIREDO[1] **and DOUGLAS R.M. RIBEIRO**[1]

[1]Laboratório de Ictiologia, Departamento de Zoologia, Universidade do Estado do Rio de Janeiro,
Rua São Francisco Xavier, 524, Maracanã, 20550-013 Rio de Janeiro, RJ, Brasil

Manuscript received on July 29, 2015; accepted for publication on March 18, 2016

ABSTRACT

†*Codoichthys carnavalii* is a clupeomorph fish only found in calcareous concretions of Codó Formation, State of Maranhão. It is known based on three specimens housed in the paleontological collection of the Museu de Ciências da Terra of Departamento Nacional da Produção Mineral, Rio de Janeiro. It was omitted in most of recent cladistic analyses about clupeomorphs. We revisited its anatomy furnishing new data and additional restorations. Furthermore we explored the relationships of †*Codoichthys* with the computer program TNT based on a matrix with 30 taxa and 60 unordered and unweight characters. *Elops* was used to root the tree. The strict consensus was obtained from three shortest trees (L=181; CI=0.387; RI=0.632). The monophyly of †Ellimmichthyiformes is supported by a sigmoid cleithrum and an uniquely derived predorsal scute series. Most of subgroups showed low support indices. †Sorbinichthyidae and †*Horseshoeichthys* appear in the most basal position, and not closely related to †*Armigatus* or †*Diplomystus*. A †*Diplomystus* clade is more advanced than †*Armigatus* and sister-group of remaining †ellimmichthyiforms. Within †Paraclupeidae, †*Codoichthys* is sister-group of remaining †paraclupeids (including †thorectichthyines and †paraclupeines). Within †Paraclupeinae, †Triplomystini includes a †*Triplomystus* clade, a sister group of †*Rhombichthys* plus †*Tycheroichthys*, and †Paraclupeini with †*S. itapagipensis* and all other †ellimmichthyiform taxa.

Key words: †*Codoichthys*, São Luis-Grajaú Basin, Lower Cretaceous, systematics, Northeastern Brazil.

INTRODUCTION

Clupeomorpha is a great radiation of teleostean fishes that produced two major lineages: Clupeiformes and †Ellimmichthyiformes (Grande 1985). The former consists of 84 genera (Nelson 2006) and 397 living species (Lavoué et al. 2014) of fishes popularly known as herrings, sardines and anchovies together with many fossil taxa known since the Barremian (Figueiredo 2009). The latter is an archaic group of double-armored herring-like fishes including about 13 genera and at least 35 species found in many marine, estuarine, and freshwater deposits around the world ranging from the Hauterivian-Barremian (Santos and Corrêa 1985) to Middle Eocene (Patterson 1993).

Grande (1982, 1985) was the first to perceive the existence of †Ellimmichthyiformes. He intuitively indicated monophyly of the group on

---

Correspondence to: Francisco José de Figueiredo
E-mail: fjfig@globo.com

the basis of derived presence of subrectangular predorsal scutes. Unlike ordinary scales, he noted that these unpaired scutes are positioned at the dorsal midline and they are heavily ossified, often covered with cycloid scales. He also pointed out that many taxa of distant lineages of teleosts bear some type of dorsal scutes (e.g., many aulopiforms) and these scutes are commonly preserved in fossil fishes unlike true scales.

At first only †*Diplomystus* and †*Ellimmichthys* were placed within †Ellimmichthyiformes (Grande 1982) that also originally contained a single family (i.e.,†Ellimmichthyidae). Afterwards, due to nomenclatural priority, †Paraclupeidae was indicated by Chang and Grande (1997) as replacement name for this family. Since then new diagnoses, definitions and compositions of putative monophyletic subunits were proposed, and new non-clupeiform taxa coming from many fossil localities throughout the world were assigned to †Ellimmichthyiformes. Many phylogenetic analyses were carried out (e.g., Chang and Maisey 2003, Zaragueta-Bagils 2004, Alvarado-Ortega et al. 2008, Murray and Wilson 2013) but until now the monophyly of the group remains uncertain as well as its content.

The following nominal species of †Ellimmichthyiformes are known from Brazilian strata: †*Ellimmichthys longicostatus* from Hauterivian-Barremian non-marine deposits of Bahia (Longbottom 1988, Silva 1993, Carvalho and Figueiredo Souto 2005), †*Ellimmichthys maceioensis* from Aptian-Albian shales of Maceio Formation in Sergipe-Alagoas basin (Malabarba et al. 2004), †*Ellimma branneri* from Hauterivian to Aptian deposits of northeastern Brazil (Maisey 2000, Chang and Maisey 2003), †*Ellimma cruzae* from Albian-Aptian calcareous concretions of Cabo Formation (Santos 1990), †*Codoichthys carnavalli* from the Late Aptian of Codó Formation (Santos 1994), and †*Scutatuspinosus itapagipensis* from Hauterivian-Barremian shales of Marfim Formation of the Reconcavo Basin (Santos and Corrêa 1985). But the number must increase since undescribed material of †*Ellimmichthys*-like and †*Ellimma*-like fishes coming from the Lower Cretaceous of Bahia (e.g., Marizal and Candeias formations, Gallo and Figueiredo 2002), Upper Cretaceous (Turonian) of Pelotas Basin (Gallo et al. 2006), and Upper Cretaceous of the Santos Basin (salt beds of so-called Brazilian pre sal) are pending for description.

The fish fauna from Reconcavo Basin is mainly distributed in outcrops of Santo Amaro Group, particularly in the Itaparica, Candeias and Maracangalha formations (Carvalho and Figueiredo Souto 2005). †*E. longicostatus* was studied by Cope (1886) after material collected by the geologist Joseph Mawson in localities near Salvador and Simões Filho (Carvalho and Figueiredo Souto 2005). Santos (1949) stated that †*Ellimmichthys longicostatus* was collected together with remains of †*Lepidotes*, †*Cladocyclus*, †*Calamopleurus* and †*Mawsonia* by the paleontologist Lewellyn Ivor Price and Abel Oliveira, in Ilha de Itaparica. More recently, †*E. longicostatus* was collected in shales of Maracangalha Formation (Carvalho and Figueiredo Souto 2005).

Chang and Maisey (2003) while revisiting †*Ellimma branneri* considered only †*E. branneri* and †*E. cruzae* (=*E. cruzi*) as valid species for this genus. They indicated that †*Ellimma branneri* only partially agree with the diagnosis of †Paraclupeidae because anterior dorsal scutes are longer than broad unlike the posterior ones, broader than long. Thus they suggested a reassessment of characters supporting the monophyly of this family.

At first †*E. cruzae* (=*E. cruzi*) was identified as †*Ellimmichthys longicostatus* (Costa et al. 1979) but Santos (1990) assigned it to †*Ellimma* and named †*Ellimma cruzi* in honor of the paleontologist Norma Maria da Costa Cruz, from the staff of DNPM, Rio de Janeiro. We note the ending of the specific epithet is an incorrect original spelling based on an inadvertent mistake (ICZN 1999: art.

32.5.1), and should be corrected to the feminine †*E. cruzae*.

Murray and Wilson (2013) based on 24 taxa and 62 characters furnished the most recent phylogenetic review on †Ellimmichthyiformes. They divided the group in two major clades: †Armigatoidei (for †*Armigatus* and †*Diplomystus*) and †Ellimmichthyoidei (for remaining taxa). They tentatively named many subunits excluding or adding taxa. Thus †Paraclupeidae was divided in five subfamilies: †Scutatuspinosinae, †Thorectichthyinae, †Elliminae, †Ellimmichthyinae, and †Paraclupeinae. Notwithstanding the relevance to the knowledge of the relationships of †ellimmichthyiform fishes, many problems still remain particularly regarding the phylogenetic status of the Brazilian taxa †*Ellimma cruzae*, †*Scutatuspinosus itapagipensis* and †*Codoichthys carnavalii*.

Certainly †*Codoichthys carnavalli* is one of the most puzzling clupeomorph taxa described from Brazil. At first Santos, in 1945, considered it a species of †*Knightia*. Afterwards the same author (Santos 1994), based on comprehensive revisions by Grande (1982, 1985), classified it as Clupeomorpha *incertae sedis* although recognizing putative affinities with non-clupeiform clupeomorphs as †*Armigatus*, †*Ellimmichthys*, and †*Diplomystus*. Since then no rigorous attempt to decipher its relationships was undertaken.

Our goal in this paper is to describe in detail the morphology of †*Codoichthys carnavalii* as soon as the material permits and exploring its relationships within Clupeomorpha using cladistic methodology.

MATERIALS AND METHODS

MATERIAL

The specimens of †*Codoichthys carnavalli* herein studied belong to the paleontological collection of the Museu de Ciências da Terra of the Departamento Nacional de Produção Mineral, Rio de Janeiro, and consists of the type-series (see details in Santos 1994). They are referred with the abbreviation DGM followed by the institutional register number.

According to Santos (1994) the fishes were collected by the late geologists Odorico Albuquerque and Victor Dequech, even belonging to the Divisão de Geologia e Mineralogia of DNPM, in 1945, in the locality of Morro de Umburanas, State of Maranhão, northeastern Brazil (Fig. 1). All specimens examined are poorly preserved and laterally compressed. They are preserved in yellowish calcareous concretions and were previously mechanically prepared with steel needles of different sizes under dissecting microscope by Rubens da Silva Santos. We produced painted silicone peels from the type-series specimens to enhance anatomical features. Camera lucida drawings were made using a Motic-Quimis stereomicroscope with a drawing-tube attachment. Digital photographs of high resolution were obtained with a USB Camera under MIAS® Software and photograph camera Nikon D7100. For enhancing anatomical details and reducing bright during photograph sessions fossils were coated with a sublimate of magnesium oxide. Anteriormost vertebrae hidden by opercle were counted as three according to Grande (1985). Measurements and meristic counts follow Forey et al. (2003). Proportions are presented as a percentage of the standard length (SL). A “dagger” (†) preciding taxon indicates that it is known only by fossils.

GEOLOGICAL SETTING

The São Luís - Grajaú Basin is included in the Gurupe Graben System and encompasses an extensive area of about 250,000 km^2 in the center-north part of the State of Maranhão. It is a typical marginal rift basin, with predominantly Cretaceous filling. Codó Formation is in the lowermost sequence of Cretaceous deposits reaching of about 4,000m thick in the depocenters (Rossetti et al. 2004). This formation was deposited in a pre-rift phase and forms a bedding sequence of about 180 m through an area extending from Araguatins, Tocantins State, to Brejo Municipality, northeastern Maranhão. It is interspersed by Grajaú (below) and Itapecurú (above) formations and constituted mainly of lacustrine dark shales, evaporites and calciferous shales which include calcareous concretions and gypsum lenticular bedding (Santos 1994). There are two facies (Santos and Carvalho 2009): one lacustrine (lower unit), with †*Dastilbe elongatus* and other fossils also found in the Crato Formation of the Araripe Basin, and other estuarine (upper unit), represented by calcareous concretions from which Santos (1994) pointed out the occurrence of †*Codoichthys carnavalii* in association to fishes commonly found in Romualdo Member of Araripe Basin, for instance, †*Tharrias araripis*, †*Calamopleurus cylindricus*, †*Brannerion latum*, †*Vinctifer comptoni*, †*Santanichthys diasii*, †*Rhacolepis buccalis*, †*Cladocyclus gardneri*, and †*Araripelepidotes temnurus*.

The localities in the State of Maranhão from which Cretaceous fossil fishes were found are plotted in map (Fig. 1). According to Santos (1994) these localities are Morro de Umburanas in Brejo, Codó and Barra do Corda.

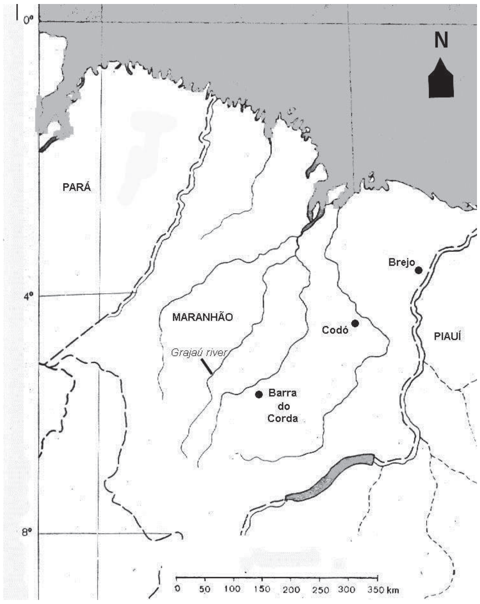

Figure 1 - Location map of Cretaceous fish-bearing beds cropping out in southeastern Maranhão (i.e., Barra do Corda, Codó e Brejo) after Santos (1994).

CLADISTIC ANALYSIS

We used cladistic principles (e.g., Wiley and Lieberman 2011, Wheeler 2012) and underlying computational technology to explore the phylogenetic relationships of †*Codoichthys carnavalii* together with other clupeomorphs. The analysis was performed with TNT computer program version 1.1 (Goloboff et al. 2003) to generate the shortest trees based on a polarized data matrix (Table I) composed of 30 taxa and 60 unordered and unweight selected characters taken from foregoing cladistics analyses of the †ellimmichthyiforms (i.e., Chang and Maisey 2003, Forey 2004, Zaragueta-Bagils 2004, Alvarado-Ortega et al. 2008, Murray and Wilson 2013). Only characters suggestive of immediate common ancestry (synapomorphic) are accepted as criteria for the recognition of monophyletic groups(=clades). We excluded some numerical characters of Alvarado-Ortega et al (2008) and Murray and Wilson (2013) because they introduce subjective procedure of cut a continuum when data of new taxa are added to the matrix, always producing new arrangements to accomodate them. Missing characters or unclear states owing to the quality of preservation (including ambiguous data) were coded as "?" in the matrix. ACCTRAN was the optimization choice due to the preservation of primary homology (de Pinna 1991). The tree-building routine was *traditional search* with random stepwise addition, ten trees held at each iterative step, and TBR (*tree bisection and reconnection*) branch swapping routine. Branches without support were collapsed.

TABLE I
Data Matrix

Taxon	**1-5**	**6-10**	**11-15**	**16-20**	**21-25**	**26-30**	**31-35**	**36-40**	**41-45**	**46-50**	**51-55**	**56-60**
†*Armigatus alticorpus*	00010	??00?	1????	??00?	10?1?	??00?	00000	???10	0000?	?1?00	01???	000?0
†*Armigatus brevissimus*	00010	12001	1001?	1000?	10110	?0001	00000	10010	00000	?1200	01010	000?0
†*Armigatus namourensis*	00010	12001	11?10	10000	10110	?0001	00000	11010	00001	11200	011?1	000?0
Chirocentrus dorab	01000	01100	21000	01101	01111	10101	10100	0100-	- - - --	-12--	0 -??0	00000
†*Codoichthys carnavalii*	00110	??00?	2?0??	01?0?	00110	00001	00001	?1010	00000	01100	000?0	01101
Denticeps clupeoides	01000	00110	20001	11201	00210	?1021	01010	0010-	- - - --	-100-	00100	00000
†*Diplomystus birdi*	00110	?2001	1?0??	???00	11110	0?001	0000?	??111	11000	21?00	011?1	000??
†*Diplomystus dentatus*	00110	?2001	11?10	11200	11110	10001	00000	?1111	11000	21100	02011	000?1
†*Diplomystus dubertreti*	00110	?200?	?????	?1?0?	11110	0000?	0?00?	???11	11000	21100	0?1??	000??
†*Diplomystus shengliensis*	00110	??001	11???	1?10?	10010	00000	00001	10?11	11100	211?0	0?110	000??
†*Diplomystus solignaci*	101??	??001	?????	1111?	10110	?000?	01000	???11	1?1??	?11??	02???	0?0??
†*Ellimma branneri*	10011	?0001	20?1?	01110	11110	00000	00000	10010	10111	01110	01110	011??
†*Ellimmichthys goodi*	1?011	??00?	2????	11111	11110	00000	0000?	1??10	10111	01110	0211?	0?000
†*Ellimmichthys longicostatus*	10011	?000?	2??1?	11111	11110	00001	00000	10110	10111	?1110	02111	010?0
Elops saurus	00000	00000	00000	10000	00000	00000	00000	1010-	- - - --	-00- -	0-000	00000
†*Ezkutuberezi carmenae*	10??0	??00?	2????	0?200	1?110	00100	00010	?0010	10111	?1010	011?1	0??0?
†*Horseshoeichthys armaserratus*	00000	?000?	2?0??	?0?01	10???	?????	??0??	???1?	?0???	?1???	0?0??	?0???
Odaxothrissa vittata	01000	01110	20000	01001	00111	10101	11100	0100-	- - - --	-1000	00010	00000
†*Ornategulum sardinoides*	00010	?0000	2001?	10000	00010	00000	00000	0100-	- - - --	-00- -	00000	00000
†*Paraclupea chetungensis*	10011	??001	2??1?	1?11?	10110	10000	01001	00111	01111	11111	02111	00000
†*Rhombichthys intoccabilis*	100??	??001	2??1?	011?0	10210	00011	00100	0001?	?0111	01121	02111	1000?
†*Scutatuspinosus itapagipensis*	00010	??00?	20010	01100	11?10	00001	0?000	10010	10111	01112	011?1	10001
†*Sorbinichthys africanus*	0?00?	?00?1	20???	1010?	01200	0?101	010??	?0010	?110?	21000	00??0	0000?
†*Sorbinichthys elusivo*	0010?	??001	??110	00100	11200	00000	000??	0?010	?110?	21000	000?0	00001
†*Thorectichthys marocensis*	10011	??001	2?110	11100	10100	00000	01000	11110	00010	01200	01011	00?0?
†*Thorectichthys rhadinus*	100?0	??0?1	2??10	11100	10100	00000	01000	1?110	00010	01210	01011	0000?
†*Triplomystus applegatei*	1?010	??0?1	2????	011??	11?1?	10011	00000	1111?	10111	01211	10010	?000?
†*Triplomystus noorae*	10010	12001	211??	1110?	10110	10010	00000	10010	10111	01201	12010	00011
†*Triplomystus oligoscutatus*	10010	12001	211??	?110?	1?110	1001?	00000	1??10	1011?	?1??1	1101?	0001?
†*Tycheiroichthys dunveganensis*	10000	??001	2?1??	01100	1111?	?00??	0?0?1	00010	0011?	11121	020?0	0011?
Missing data(?), Inapplicable (-)												

Selected †Ellimmichthyiformes used in analysis are listed below together with literature review from which anatomical data are better known and discussed. Characters have been taken mainly from literature and checked (if possible), and in the case of changes they are indicated in our list (see Appendix 1). Additional fossil specimens housed in institutional collections from which we made original observations or confirmed previous data are also indicated.

The fossil material is the following: †*Armigatus alticorpus* – all data are from Forey et al. (2003); †*Armigatus brevissimus* – n= 5, uncatalogued Pz. UERJ, data from Patterson (1967) and Grande (1982); †*Armigatus namourensis* – all data are from Forey et al. (2003); †*Diplomystus birdi* – all data from Grande (1982); †*Diplomystus dentatus* – n= 2, uncatalogued Pz.UERJ from Green River Formation, Wyoming; complementary data are taken from Cavender (1966) and Grande (1982); †*Diplomystus shengliensis* – all data taken from Chang and Maisey (2003); †*Diplomystus solignaci* – all data taken from Gaudant and Gaudant (1971) and Grande (1982); †*Diplomystus dubertreti* – data are from Signeux (1951) and Grande (1982); †*Ellimma branneri* – data are from Chang and Maisey (2003) and Pz.UERJ 77 and 95;†*Ellimmichthys longicostatus* – data are from Grande (1982), Chang and Grande (1997), Chang and Maisey (2003), and BMNH P. 7109; †*Ellimmichthys goodi* – data are taken from Eastman (1912) and Chang and Grande (1997); †*Ezkutuberezi carmenae* – all data are from Poyato-Ariza et al. (2000); †*Horseshoeichthys armiserratus* – all data are from Newbrey et al. (2010); †*Paraclupea chetungensis* – all data are from Chang and Grande (1997); †*Rhombichthys intoccabilis* – all data are from Khalloufi et al. (2010); †*Scutatuspinosus itapagipensis*: n=72, DGM 1164-P (holotype) to 1176-P, DGM 1207-P to 1264-P, complementary data are from Santos and Corrêa (1985) and Alvarado-Ortega et al. (2008); †*Sorbinichthys elusivo* – all data taken from Bannikov and Bacchia (2000); †*Sorbinichthys africanus* – all data taken from Murray and Wilson (2011);†*Tycheiroichthys dunveganensis* – all data are from Hay et al. (2007); †*Thorectichthys marocensis* – all data are from Murray and Wilson (2013); †*Thorectichthys rhadinus* – all data taken Murray and Wilson (2013); †*Tryplomystus noorae* – all data taken from Forey et al. (2003); †*Tryplomystus oligoscutatus* (all data taken from Forey et al. (2003); and †*Tryplomystus applegatei* – all data are from Alvarado-Ortega and Ovalles-Damián (2008).

We have not included in this analysis data of †*Ellimma cruzae*, †*Kwangoclupea dartevellei*, and †*Ellimmichthys maceioensis* because we think that their anatomy demands more study so that they will be reassessed elsewhere (work in progress). We include the living clupeiforms *Chirocentrus dorab* (data taken of Cavender 1966, Fujita 1990, Di Dario 2009), *Denticeps clupeoides* (data taken of Greenwood 1968, Di Dario and de Pinna 2006), *Odaxothrissa vittata* (data taken of Grande 1985), and the primitive clupeomorph †*Ornategulum sardinoides* (all data from Forey 1973a) as near outgroups together with the elopomorph *Elops saurus* (D. UERJ 190, n=15, 150-550 mm SL). To maximize applicable states of characters, *Elops saurus* was choiced as remote outgroup. This species was used for rooting the tree because this taxon is considered a morphologically generalized teleost whose anatomy is relatively well-known (see Ridewood 1904, Vrba 1968, Nybelin 1967, 1968, 1971, Forey 1973b, Taverne 1974).

MORPHOMETRIC ABBREVIATIONS

BD, body depth; HD, head depth; HL, head length; PANL, preanal length; PDL, predorsal length; SL, standard length.

ANATOMICAL ABBREVIATIONS

AA, anguloarticular; abd. sc, abdominal scute; an. PTG, pterygiophores of anal fin; ANT, antorbital; APAL, autopalatine; ASMX, anterior supramaxilla; c.sc; caudal scute; CL, cleithrum; CO, coracoid; D, dentary; EP, epural; EPL, epipleural intermuscular bone; EPM, epimeral intermuscular bones; EPN, epineural intermuscular bone; fac. MX APA, autopalatine facet for articulation with maxillary; f.r, fin ray; FR, frontal; H, hypural; h.sp, hemal spine; IO, infraorbital; io.c, infraorbital sensory canal; LA, lachrymal; lat.pr, lateral process of mesethmoid; LET, lateral ethmoid; md.c, mandibular sensory canal; MES, mesethmoid; MX, maxilla; n. sp, neural spine; n. sp. PU2; neural spine of the second preural centrum; n.a, neural arch; n.a. PU1, neural arch of the first preural centrum; OP, opercle; PA, parietal; pap, parapophysis; PAS, parasphenoid; PH, parhypural; pl.r, pleural rib; PMX, premaxilla; POP, preopercle; PSMX, posterior supramaxilla; PTM, posttemporal; PU1, first preural centrum; RAR, retroarticular; S, symplectic; SCL, supracleithrum; scl.b, sclerotic bone; SOC, supraoccipital; SOP, subopercle; stt. com, commissural supratemporal sensory canal; U1+H2, first ural centrum fused to second hypural; UN, uroneural; VC, vertebral centrum.

INSTITUTIONAL ABBREVIATIONS

BMNH P, formerly British Museum of Natural History, London; **DGM**, formerly Divisão de Geologia e Mineralogia do Departamento Nacional de Produção Mineral, nowadays Museu de Ciências da Terra; **D. UERJ**, a collection of cleared and stained fishes in Departamento de Zoologia of Universidade do Estado do Rio de Janeiro; **Pz.UERJ**, paleozoological collection of the Universidade do Estado do Rio de Janeiro.

SYSTEMATIC PALEONTOLOGY

Subdivision TELEOSTEI Müller, 1845

Cohort CLUPEOCEPHALA Patterson and Rosen, 1977

Subcohort OTOCEPHALA Johnson and Patterson, 1996

Superorder CLUPEOMORPHA Greenwood et al., 1966

Order †ELLIMMICHTHYIFORMES Grande, 1982

Family †PARACLUPEIDAE Chang and Chou, 1977

Diagnosis (amended from Santos 1994). Fusiform fish reaching 62 mm SL showing the following combination of features: HL equals 31% SL; predorsal dorsal profile slightly convex; anamestic antorbital present; medially united parietals; rugose ornamentation on frontal and parietal; well-developed supraoccipital crest; upper jaw and parasphenoid toothless; dentary bearing a patch of minute conical teeth on oral border and prominent coronoid process; two supramaxillae; quadrate-mandibular articulation placed below in the middle of the orbit; dorsal preopercle limb longer than ventral one, two recumbent tubules of preopercular sensory canal on ventral limb of preopercle; opercle equals 33% HL and ornamented with parallel striae on the lower half; L-like cleithrum with expanded posterior lamina; two postcleithra; predorsal scute series complete and composed of at least eight equal-sized keeled elements, all smooth and ovoid; at least seven curved and slender supraneurals; 33 preural vertebrae from which 11 caudal; epineurals fused to abdominal vertebrae; dorsal fin with at least 10 pterygiophores; at least 15 pterygiophores on anal fin; pelvic fin placed in opposition to dorsal fin; 10 prepelvic and nine postpelvic scutes; postpelvic scutes without pungent posterior process; vertebral column blending gradually upwards in the caudal region; three epurals; long neural spine of second preural centrum; parhypural fused to first preural centrum; large leaf-like neural arch of first preural centrum; the first uroneural reaching first preural centrum; six hypurals, the first one slender and with proximal condylar end contacting first ural centrum; second hypural slender and fused to first ural centrum; third hypural large and triangular;

caudal diastema present; first ural centra almost equal-sized to preural centra; equal-lobed caudal fin.

TYPE AND ONLY SPECIES: †*Codoichthys carnavalii* Santos, 1994.

†*Codoichthys carnavalii* Santos, 1994
(Figs. 2- 8)

Selected Synonymy:

1945. †*Knightia carnavalii* Santos [*nomen nudum* in a draft sent to II Congresso Pan-Americano de Engenharia de Minas e Geologia, Petrópolis].
1994. †*Codoichthys carnavalii* Santos, *An. Acad. Bras. Cienc.* 62(3), p. 133, Text-figure 2, Pl. 1, Figs. 1-3 [original description; type-locality: Morro de Umburanas].
2000. †*Codoichthys carnavalii* Santos: Maisey, *Cretaceous Res.* 21, p. 295 [only reference].
2000. †*Codoichthys carnavalii* Santos: Poyato-Ariza, López-Horgue and García-Garmilla: *Cretaceous Res.* 21, p.581 [only reference].
2009. †*Codoichthys carnavalii* Santos: Santos and Carvalho, *Serv. Geol. Bras.*, fig. 13.4 [data about taphonomy and paleoenvironment].

Diagnosis. – as for genus, monotypic genus.

Material examined. – Holotype: DGM 435-P; Paratypes: DGM 436-P; DGM 966-P.

Locality and geological time. – Morro de Umburanas, Brejo Municipality, State of Maranhão, Lower Cretaceous (Aptian) of São Luís – Grajaú Basin (see Rossetti et al. 2004, and particularly, Santos 1994).

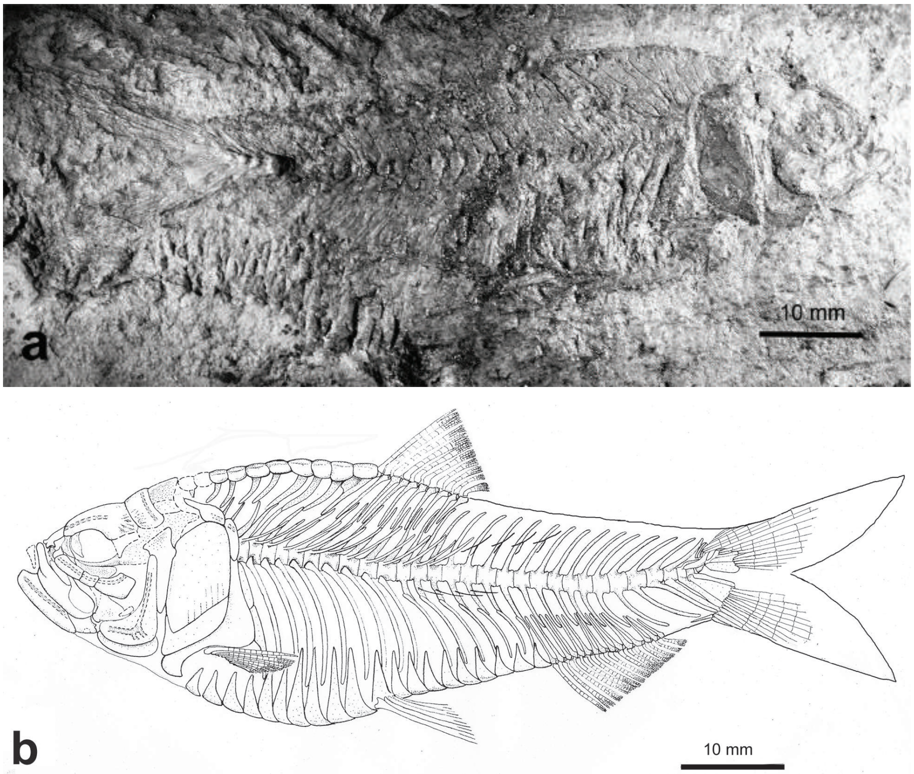

Figure 2 - a. †*Codoichthys carnavalli* Santos, 1994, DGM 435-P (Holotype), 62 mm SL, from marine deposit of the Late Aptian of Codó Formation, São Luís-Grajaú Basin, Northeastern Brazil. **b.** Restoration of entire fish based on holotype and complemented with data of DGM 436-P.

DESCRIPTIVE MORPHOLOGY

General Body Form

†*Codoichthys carnavalii* shows fusiform body, with predorsal profile rather arched (Figs. 2a, b). All specimens are preserved in lateral view suggesting that this fish was laterally compressed in life. HL corresponds to 28% of SL and almost equal to HD. Snout is short and upper jaw not extending behind the orbit. Both dorsal and ventral profile are slightly convex. BD corresponds to 27% SL. PDL is of about half (54%) of SL. Dorsal fin is placed at the middle point of the body, in opposition to the insertion of pelvic fin. PANL is 72% of SL and the base of anal fin length is about 16% of SL. The caudal fin is forked, with deep notch, showing equal-sized dorsal and ventral lobes.

Cranial bones. – Most of skull bones (Fig. 3a, b) are badly or incompletely preserved; hence interpretative restorations are furnished as far as the material permits. In the ethmoid region there is a short and robust **mesethmoid** (Figs. 3b, 4, MES) with prominent cup-like **lateral process** for palatine (Fig.4, lat.pr). Its length is almost equal the underlying lachrymal bone. Anteriorly mesethmoid shows a short recess to house the anteriormost end of maxilla.

The **lateral ethmoid** (Figs. 3b, 4, LET) is represented by two incomplete and imperfect separated portions. One corresponds to a fragment of the main body of left ethmoid lateral which was slightly displaced to occupy the center of a broad gape (a probable condriferous space of nasal pit in life) covered by mesethmoid. Other portion corresponds to a well-developed fan-like shield of perichondral bone associated to a cup-like upper edge (for meeting frontal bone dorsally) of the right ethmoid lateral compounding the anterior limit of the orbit. Ventrally, this bone produces a wing-like outgrowth to touch the shaft of the parasphenoid.

The **parasphenoid** (Fig. 3b, PAS) is a long, low, and slightly curved bone. Only its orbital portion is visible. It is toothless. Due to state of preservation, we are unable to determine presence of a dermal basipterygoid process.

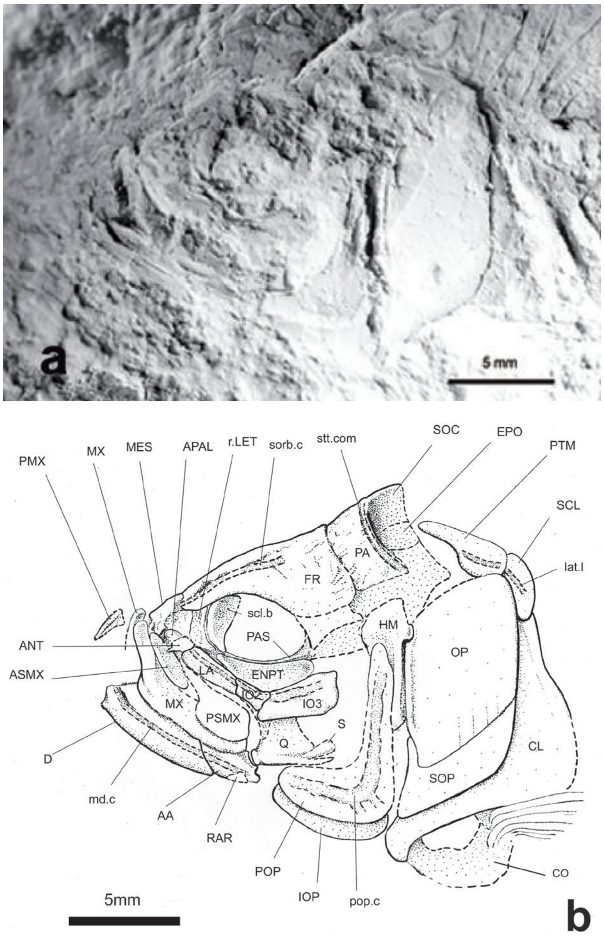

Figure 3 - a. Cranial bones and pectoral girdle †*Codoichthys carnavalii* Santos, 1994, from the Late Aptian of Codó Formation, São Luís-Grajaú basin, State of Maranhão, Northeastern Brazil; DGM 435-P (Holotype); reversed. **b.** Line drawing of the same and interpretative reconstruction.

The **frontal** (Figs. 3b, 5, FR) is the largest bone of the cranial roof covering completely the orbit and finishing a little behind it. It is narrower at the level of the ethmoid region and broadens considerably at the posterodorsal orbital corner. Close to the contact zone with parietal this bone is ornamented with coarse rugae. Due to preservation it is difficult to determine presence of fontanels or fossae. The supraorbital sensory canal run bone enclosed so that its presence on surface is hardly noted through a faint tubular relief. Pores are not observed.

The meeting between frontal and parietal is through a long transverse suture. There is an ascending profile anterior to the well-developed supraoccipital crest as in the skull of the unnamed †*Diplomystus* from the Cenomanian of the English Chalk (see Forey 2004) in contrast with †*Ellimma branneri* and †*Paraclupea*. Deep grooves for supraorbital sensory canal separated by a medial bony bridge as seen in the unnamed †*Diplomystus* from the English Chalk and Scutatuspinosus itapagipensis are lacking.

The **parietal** (Figs. 3b, 5, PA) is a large and subrectangular bone in lateral view. In the skull roof, judged by its placement and position of supraoccipital it meets its partner in the midline as commonly found in well-preserved †ellimmichthyiforms. As for frontal bone, there are rugose ornamentation near lateral border.

The **commissural supratemporal sensory canal** (Figs. 3b, 5, stt.com) is entirely bone-enclosed, running within a curved tubular relief on parietal. The supraoccipital is placed outside this commissure. Pores are not visible on surface.

Like many clupeomorphs, the otico-occipital region is almost equal in size to orbital and ethmoid regions. Unfortunately, autosphenotic, prootic and pterotic bones are not preserved. There are any evidence of *recessus lateralis* and temporal fossa. Noteworthy the temporal fossa seems to be lacking in all †ellimmichthyiforms, as for the *recessus lateralis*, so that dermosphenotic are not reduced and openings for preopercular and infraorbital branches of sensory canal are distantly positioned in otic neurocranium of certain well-preserved specimens (see Patterson 1970, Grande 1982, Forey 2004).

The **epioccipital** (Fig. 3b, EPO) is almost trapezoid and placed among parietal, supraoccipital, and an uninformative portion of pterotic. Its position in the skull resembles that found in †*Triplomystus noorae* (see Forey et al. 2003, p. 271, fig. 41). Posteriorly this bone shows a reduced smooth process to receive the upper arm of the posttemporal bone.

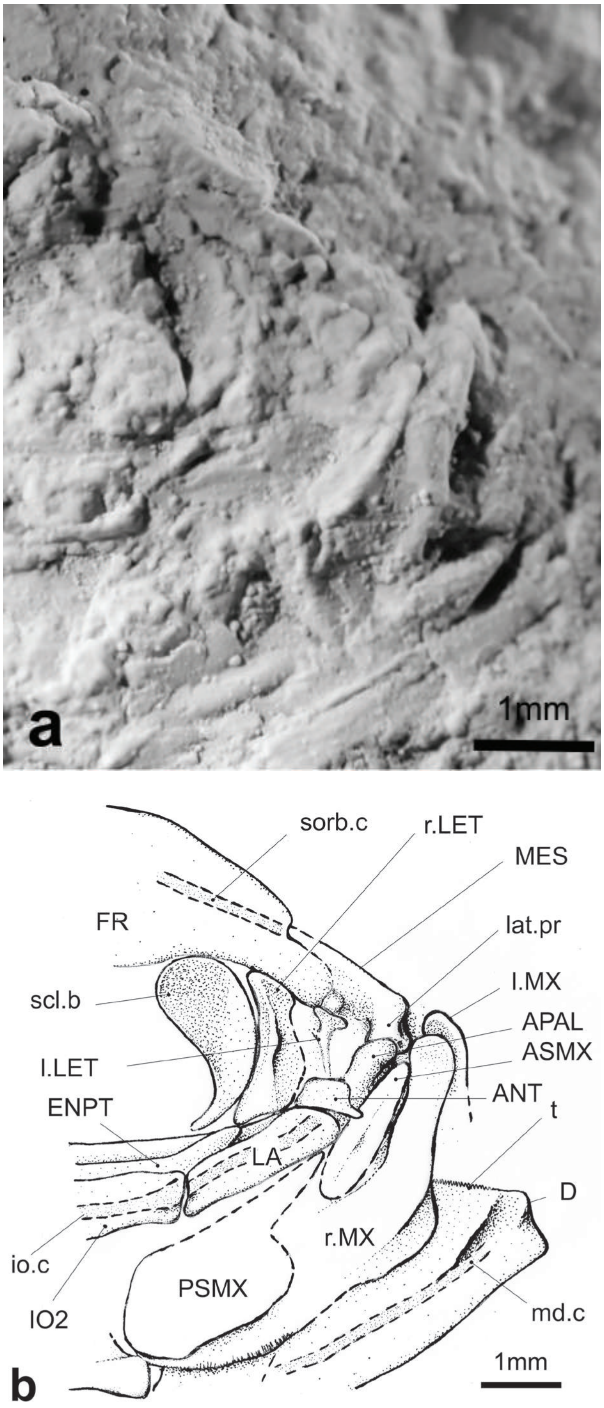

Figure 4 - **a**. Ethmoid region and associated structures of †*Codoichthys carnavalii*, DGM 435-P (Holotype); **b**. Line drawing and interpretative restoration of ethmoid region.

Behind parietals, there is a smooth **supraoccipital** (Fig. 3b, SOC) bearing a well-developed median crest resembling that of †*Diplomystus*. This bone does not separate the parietals as usual in clupeiforms. Due to the state of preservation it is not possible to determine presence of pre-epioccipital fenestra and posttemporal fossa. But a so-called **parietal excavation** as described by Forey (2004) in a three-dimensional skull of †*Diplomystus* from the Upper Cretaceous of the English Chalk is very probable (Fig. 5). Such excavation is considered by Forey (2004, Fig. 13, Node E) derived featured shared by †*Triplomystus*, †*Sorbinichthys*, and †*Diplomystus*. The same author stated it is absent in †*Ellimmichthys longicostatus*, †*Ellimma branneri* and †*Paraclupea*. Otherwise we also noted its presence in †*Scutatuspinosus* and †*Ellimma cruzae.*

The orbit of †*C. carnavalii* is large. Its diameter is contained of about 3 1⁄2 in HL. The eyeball were supported by two large shields of **sclerotic bones** from which only one (anterior) is preserved (Figs. 3 and 4, scl. b) in the holotype.

CIRCUMORBITAL BONES

Only anterior elements from this series remain. We interpreted a triangular bone displaced, lying on the anterior border of the **lachrymal** (=first infraorbital), as an anamestic **antorbital** (Figs. 3b, 4, ANT). It is very similar in shape to that of †*Leptolepides haerteisi*, an early euteleostean fish known form the Tithonian of Germany (see Arratia 1997, p. 71, Fig. 47). Besides the absence of antorbital has been claimed as a derived feature for †ellimmichthyiform fishes (Alvarado-Ortega et al. 2008) this bone is seen in †*Horseshoeichthys* (see Newbrey et al. 2010, fig. 2, identified as the first infraorbital bone, a mistake) in the same position and association of this bone as in *Denticeps clupeoides* (see Di Dario and de Pinna 2006).

Behind antorbital three infraorbital bones are preserved in a row. The **lachrymal** (=first infraorbital bone, Figs. 3b, 4, LA) is an elongate and rectangular bone lying on beneath the anterior half of the orbit. It shows an anterior border slightly

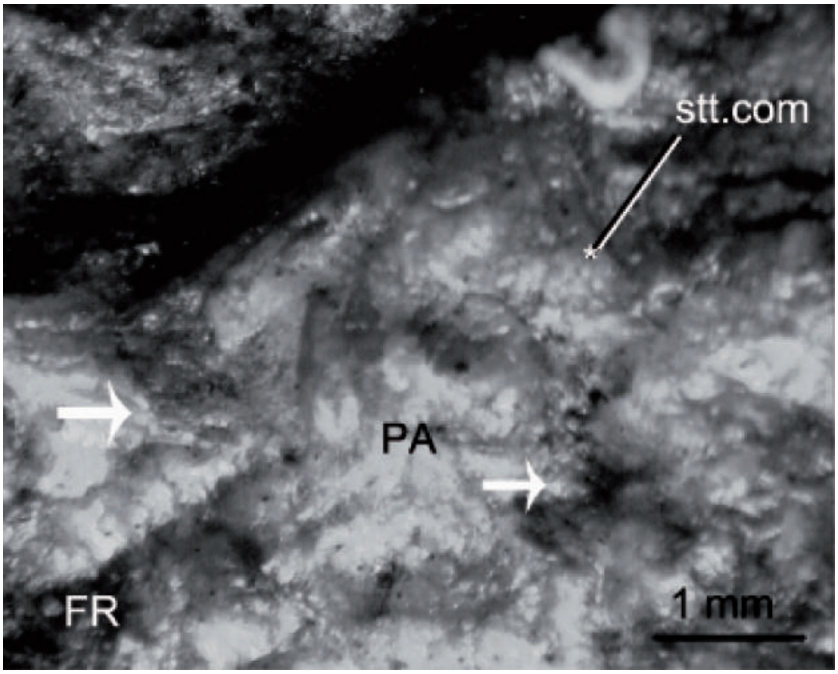

Figure 5 - Photograph of skull roof of †*Codoichthys carnavalii*, DGM 435-P (Holotype) showing vestiges of ornamentation (indicated with white arrows).

rounded. It covers only the anteriormost edge of the *suspensorium*, extending from the facet of articulation to maxilla of autopalatine to the level of the posterior border of ethmoid lateral. The infraorbital sensory canal is consistently present running within the bone close to the dorsal border in a slender bony tube.

The **second infraorbital bone** (Figs. 3b, 4, IO2) is short and low, almost rectangular. It is placed below the middle point of the orbit. The infraorbital sensory canal pierces the bone at the midline taking into account the presence of a conspicuous tubular relief.

The **third infraorbital bone** (Fig. 3b, IO3) is the largest of the set. It is subrectangular as in †*Diplomystus dentatus* (see Grande 1982, p. 10, Fig. 7) and show an anterior flange below the contact zone with second infraorbital. This bone forms most of the ventral rim of orbit extending from the level of the quadrate-mandibular joint to the posterior extremity of the symplectic, but not entirely recovering the cheek. The infraorbital sensory canal is bone-enclosed near the orbital rim. Its membranodermal component is very expanded.

The fourth and fifth infraorbital bones, although not preserved, judging by a great gap above third infraorbital, mighty be tubular flimsy bones as observed in †*Diplomystus dentatus* (see Grande 1982).

Jaws and suspensorium. – The **premaxilla** is partially preserved and displaced from the anteriormost region of skull (Fig. 3b, PMX). It is low, triangular and toothless. The **maxilla** (Figs. 3b, 4, MX) exhibits an elongate anterior process finishing in a dilated articular head. There is a short and blunt autopalatine condyle upon this bone. The main body of the bone produces a slightly convex dentigerous lamina (as in †*Diplomystus dentatus*) on oral edge and extends backwardly to end at the level of the middle point of orbit. True teeth are lacking.

There are two smooth supramaxillae incompletely preserved. The first one, the **anterior supramaxilla** (Figs. 3b, 4, ASMX), is an elongate and elliptical bone lying on the anterodorsal border of the maxilla. The **posterior supramaxilla** (Fig. 3b, PSMX) shows a large and ovoid main body, very fragmented in DGM 435-P, but its anterodorsal process is lost.

The lower jaw is relatively short, deep and well-ossified. Laterally it consists of **dentary**, **anguloarticular** and **retroarticular** (Fig. 3).

Most of the lower jaw is formed by the **dentary** (Fig. 3b, D) which contributes with at least 80% of length. This bone has a deep symphysis and the oral border ascends abruptly producing a high coronoid process. There is a short row of at least 20 minute conical teeth on oral border. The path of the mandibular sensory canal (Fig. 3b, md.c) is evident on surface through a slight and straight tubular relief. Pores are not visible.

The **anguloarticular** (Fig. 3b, AA) is a relatively short and deep bone. It contributes to form part of the coronoid process. Its articular facet for quadrate is well-developed. Posteriorly it shows a short and slightly rounded postarticular process. Its median portion is crossed by a extension of the mandibular sensory canal.

As for dentary, the anguloarticular is only a little incurved suggesting the presence of a low meckelian fossa and consequently few volume of adductor muscle in life. The posterior opening for the mandibular sensory canal is not observed laterally so that we interpreted it was placed medially. A small **retroarticular** (Fig. 3b, RAR) is visible at the posteroventral corner of the lower jaw upon anguloarticular.

The quadrate-mandibular articulation is placed below the middle point of the orbit. The triangular **quadrate** (Fig. 3b, Q) is well-ossified and slightly curved forwards. Its articular condyle for lower jaw is well-developed and the posteroventral process is short, sharp, and vertically oriented. The anterior border of preopercle is tightly attached to the posterior margin of posteroventral process. The dorsal margin of quadrate seems to be truncate.

A metapterygoid is not preserved but judged by a great gap on suspensorium this was of moderate size. The **symplectic** (Fig. 3b, S) is a short, narrow, and club-like bone inserted in a notch of posterodorsal margin of quadrate, between the main body of this bone and its posteroventral process.

The shape of the **hyomandibula** (Fig. 3b, HM) is inferred mainly from the imprint of this bone on the rock. It is vertically oriented in respect to braincase and shows an obliquely positioned articular head for otic neurocranium. The vertical process is elongate and the opercular process is very short and stout.

Anterior to quadrate there are a badly preserved **ectopterygoid** and an elliptical and a shield-like **endopterygoid** (Figs. 3b, 4, ENPT) closely associated. The latter is visible in the inner orbit and above the second and third infraorbitals. Both bones are toothless.

From the **autopalatine** remains only a prominent and robust facet for maxilla (Fig. 3b, APAL) placed anterior to lachrymal bone.

OPERCULAR SERIES

The usual complement of teleostean opercular bones is present in †*Codoichthys*. The **preopercle** (Fig. 3b, POP) is a L-shaped bone, with dorsal limb longer than the ventral one. The ventral limb has ventral margin slightly convex. The **preopercular sensory canal** (Fig. 3b, pop. c) runs into a bony tube in the midline of dorsal limb of the bone. We are unable to determine the presence of tubules in dorsal limb, but in the ventral limb the main canal gives off two conspicuous recumbent tubules (better seen in DGM 436-P) as in †*Ellimma branneri* (see Chang and Maisey 2003, p. 10, Fig. 5).

The **interopercle** (Fig. 3b, IOP) is a triangular and elongate bone underlying the entire length of the ventral limb of the preopercle. Its ventral edge is a slightly convex.

The **opercle** (Fig. 3b, OP) is a well-developed bone, deeper than long, with dorsal margin rounded and an oblique contact zone for subopercle ending in a protruding anteroventral corner. This bone is contained of about three times in the head length. The ventral half shows on surface fading ornamentation under form of parallel striations (better seen in DGM 436-P), a pattern shared with †*Ellimma* and †*Tycheroichthys*.

The **subopercle** (Fig. 3b, SOP) is a large and falcate bone. It shows digit-like anterior ascending process and smooth posteroventral margin. Its major depth is contained of about three times in the opercle depth.

PAIRED FINS AND GIRDLES

The pectoral girdle includes the posttemporal, supracleithrum, cleithrum, postcleithra, scapula, and coracoid. The **posttemporal** (Fig. 3b, PTM) exhibits a rounded and smooth-bordered main body and an elongate and sharp anterodorsal limb for contacting epioccipital. The ventral limb for intercalar is club-like, very slender and long. An oblique tubular relief for lateral line is seen along the main body of the bone. The **supracleithrum** (Fig. 3b, SCL) is an elliptical bone lying on the dorsal process of cleithrum. A short tubular relief for lateral line (Fig. 3b, lat.l) is visible on surface.

The **cleithrum** (Fig. 3b, CL) is a well-ossified L-shaped bone with expanded laminar posterior margin. Therefore it is not sigmoid as in most of †ellimmichthyiform fishes (see Forey 2004). The overall shape is similar to that of the clupeiform †*Santanaclupea silvasantosi* from the Araripe Basin, Northeastern Brazil (see Maisey 1993). The anteroventral process is elongate and projected forwards along all extension of the margin of subopercle. Regarding this aspect it is very similar to that of †*Diplomystus dentatus*.

There are two distinct **postcleithra** crossing over pectoral-fin rays in DGM 436-P. Grande (1985) indicated absence of postcleithra in †Ellimmichthyiformes. But since then postcleithra were registered in †*Horseshoeichthys* (Newbrey et al. 2010) and †*Triplomystus applegatei* (Alvarado-Ortega and Ovales-Damian 2008).

Unfortunately endosteal bones of pectoral girdle are badly preserved and uninformative. An imprint of a small and quadrangular scapula is seen in DGM 435-P. The coracoid (Fig. 3b, CO) is large, laminate and L-shaped. We counted at least 15 pectoral fin-rays and the uppermost fin-ray is the thickest of the set.

The pelvic bone is apparently hidden by abdominal scutes so that nothing is visible externally. The pelvic fin is in opposition to dorsal fin and remains in a middle point between insertions of pectoral and anal fins. There are five or six branched pelvic fin-rays.

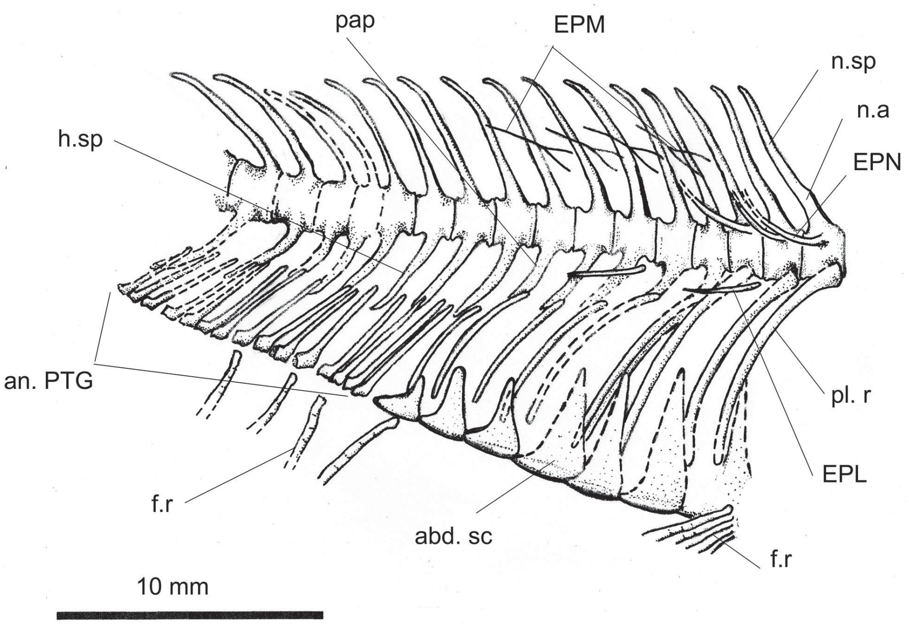

Figure 6 - Line drawing of posteriormost abdominal vertebrae, anal fin support, and associated structures of †*Codoichthys carnavalii*, DGM 435-P (Holotype).

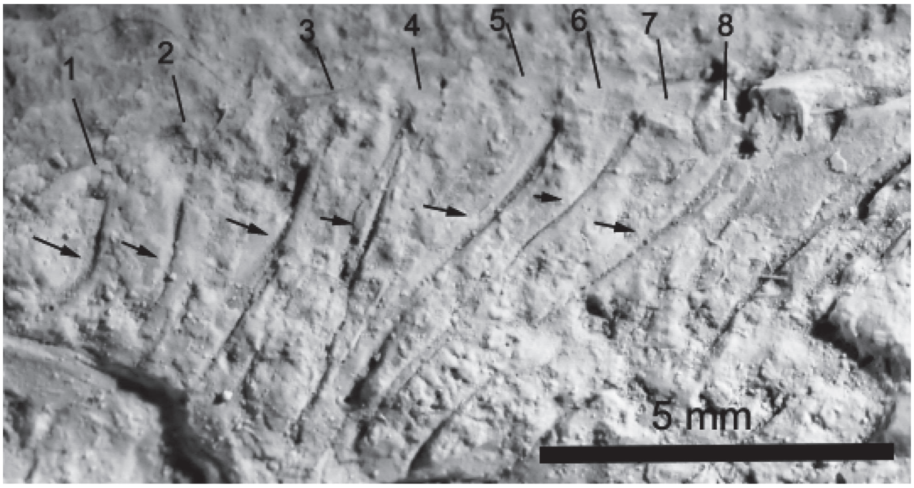

Figure 7 - Detail of dorsal scutes and supraneural bones of †*Codoichthys carnavalii*, DGM 435-P (Holotype). Arrows indicate supraneurals; scutes are numbered.

DORSAL AND ANAL FINS

The dorsal fin origins in a vertical line spanning abdominal vertebrae 10 and 11 (Fig. 2B). There are two rudimentary fin-rays followed of at least 10 fin-rays in association with at least 10 pipe-like proximal pterygiophores. The first pterygiophore shows an anterior lamina with a notch between dorsal and ventral branches, forming an acute angle. It supports the three anteriormost fin-rays. The number of anal-fin rays is inferred of 15 preserved pterygiophores. There are one rudimentary followed of at least 15 fin-rays.

VERTEBRAL COLUMN, PLEURAL RIBS AND INTERMUSCULAR BONES ASSOCIATED

There are, at least, 33 preural vertebrae, 11 in caudal region. All **vertebral centra** are hour-glass shaped in lateral view. Each **vertebral centrum** is smooth, except for weak longitudinal ridge separating grooves (Fig. 8B). The precaudal abdominal centra are mostly deeper than long. From the origin of dorsal fin backwards they became gradually longer than deep.

The **neural arches** (Fig. 6, n.a) are co-ossified to centra and the **parapophyses** (Fig. 6, pap). **Neural spines** (Fig. 6, n.sp) are long and touch proximal end of the dorsal pterygiophores. We are unable to determine the presence or not of bifid neural spines in the abdominal region due to the state of preservation. But in the caudal region, only a single neural spine fused to arch is seen.

Hemal spines (Fig.6, h.sp) are as fine and long as the neural spines. There are any consistent differences in size or thickness among spines contributing to sustain the caudal fin.

The **supraneural** (=predorsal) bones form a series of eight slender, long, and almost sigmoid elements closely associated to predorsal scutes (Fig. 7). The space among supraneurals are unequal. The first supraneural is very short and positioned far from the other ones. The posteriormost one is the longest and closely associated to anterior lamina of the first pterygiophores of the dorsal fin. Apparently all supraneurals reach the level of the tips of abdominal neural spines.

The **epineurals** (Fig. 6, EPN) are long, thin, and laterally arched. The anteriormost ones are proximally fused to the base of abdominal neural arches. They are symmetrically aligned along the vertebral column spanning an area corresponding to five to six vertebrae. In the transition between abdominal to caudal regions there are high on the flank detached epineurals forming **epimeral hypsiloid intermuscular bones** (Fig. 6, EPM), in a framework backwards spanning an area spanning eight vertebrae. They continue backwardly on caudal region in opposition to some detached **epipleurals** (Fig. 6, EPL).

There are at least 17 **pleural ribs**. They are long and slightly curved and reach the tip of abdominal scutes (Fig. 8). Each one shows a deep groove along most of its extension. The anteriormost pleural ribs are lodged in a groove of the abdominal vertebra whereas the remaining ones on short parapophyses.

PREDORSAL AND ABDOMINAL SCUTES

There are slight imprints of eight elliptical predorsal scutes bearing a median keel (Fig. 7). All scutes are smooth, subequal-sized and lack posterior spine. They touch the distal end of the supraneurals.

A row of pre-pelvic scutes composed of 10 elements originates closely to pectoral fin at the level of the last fin-ray (Fig. 2). Each scute is ventrally keeled and bears long and sharp triangular lateral processes. The abdominal postpelvic series shows nine scutes. They are triangular, ventrally keeled and show short posterior spine-like process unlike erected and pungent of the most of †ellimmichthyiform fishes. The series finishes at the origin of the anal fin.

CAUDAL ENDOSKELETON AND FIN

The caudal fin is forked and shows equal-sized lobes. It is supported by two preural and two ural

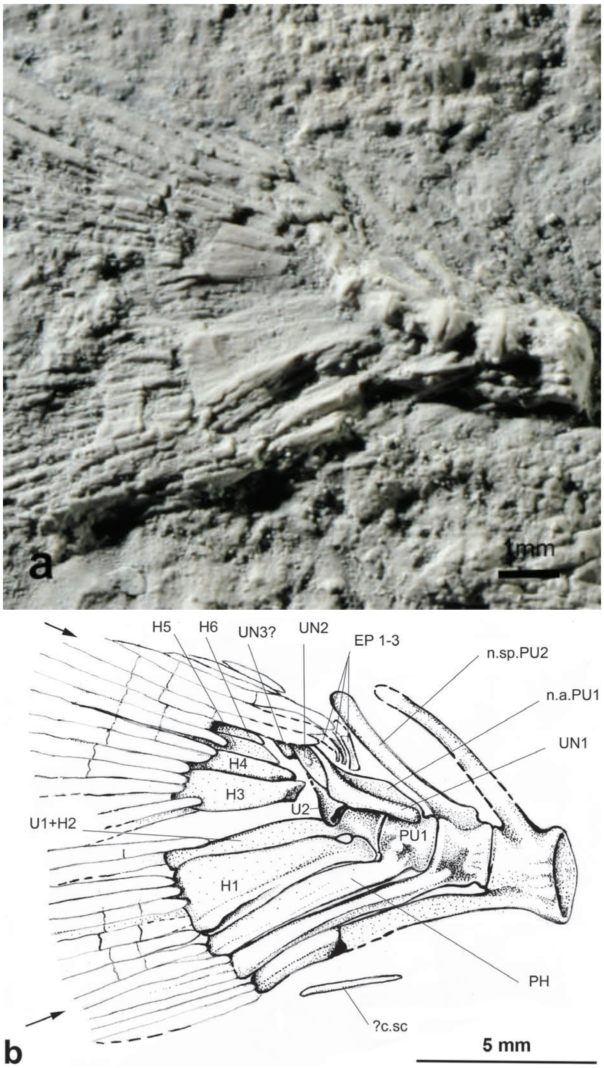

Figure 8 - †*Codoichthys carnavalli*. **a**. Caudal endoskeleton of DGM 435-P (holotype); **b**. Line drawing of caudal endoskeleton of holotype. Arrows indicate position of outer principal fin-rays.

centra. As usual in many basal teleosteans, there are 10 principal fin rays in the upper lobe and 9 in the lower lobe. The region of dorsal procurrent rays is very damaged but there are at least four preserved in DGM 435-P. There are at least seven ventral procurrent rays and a probable **ventral caudal scute** (Fig. 8b, c.sc). The vertebral axis bends gradually upwards as usually found in non-clupeiform clupeomorphs. The neural spine of the second preural centrum is slender and elongate. Most of endoskeletal structures are preserved (Figs. 8a, b).

The proximal end of **parhypural** (Fig. 8b, PH) is fused to the first preural centrum. The neural arch of first preural centrum is enlarged and leaf-like extending backwardly to cover the dorsal margin of the first ural centrum and to contact laterally the first uroneural. This condition differs from that of †*Diplomystus dentatus* in which only the neural arch of the first ural centrum is enlarged and backwardly expanded.

The first **ural centrum** (Fig. 8b, U1) is almost hour-glass shaped and equal-sized to preural centra. is hour-glass shaped and almost equal-sized to preural centra. However the second ural centrum (Fig. 8b, U2) is more reduced, cone-shaped with tubular posterior end.

We counted six **hypurals** (Fig. 8b). The **first one** (Fig. 8b, H1) is a large triangular plate, long and enlarged distally. Proximally it attaches the first ural centrum and contributes for the hypural foramen. The **second hypural** is slender and elongate, and fused to **first ural centrum** (Fig. 8b, U1+H2). The remaining four hypurals are associated to second ural centrum. The **third hypural** (Fig. 8b, H3) is triangular and large; its expanded spatulate portion invades ventrally space of lowermost hypurals. Probably it was attached to second ural centrum in life. There is a large diastema between third and second hypurals. This pattern differs from that of †*Scutatuspinosus* and †*Rhombichthys* whose third hypural has an upward process constraining the fourth hypural to project forwardly. This condition seems to be shared uniquely for these taxa. The other three hypurals are elongate and gradually decrease in size towards the dorsal margin of the upper lobe.

Our observations are in contrast with the original description. Santos (1994) pointed out the occurrence of four uroneurals. We consistently observed **two uroneurals** (Fig. 8b), all free from the centra. The existence of a third **uppermost**

uroneural (Fig. 8b, ?UN3) is probable taking into account by a clear space in the region anterior to the tips of invading fin rays and the presence of a strut of bone in this place. The **first uroneural** (Fig. 8b, UN1) extends forwards for reaching the first preural centrum laterally. It is placed laterally to the neural arch from the first preural centrum. The **second uroneural** (Fig. 8b, UN2) is short and fusiform, and lies on the dorsal margin of the second ural centrum close to the origin of the second ural centrum.

There are three thin, elongate and curved **epurals** (Fig. 8b, EP, numbered) occupying a space between neural spine of the second preural centrum and dorsal border of neural arch from the first preural centrum.

RESULTS OF THE PHYLOGENETIC ANALYSIS

The hypothesis generated by the present phylogenetic analysis corresponds to a strict consensus of three equally parsimonious trees (Fig. 9). The majority consensus tree shows the same topology. The tree has 181 evolutionary steps, Consistency Index (CI)=0,387, Retention Index (RI)=0,632.

It is not possible to confirm if †*Ornategulum* belongs with clupeomorphs. In this analysis this taxon is excluded of Clupeiformes and †Ellimmichthyiformes and placed outside as the sister group of all clupeomorphs used in this analysis.

†Sorbinichthyidae appears in a basal polytomy together with the enigmatic †*Horseshoeichthys* and all other †ellimmichthyiforms. But we think that the position of †*Horseshoeichthys* is doubtful because it shows many missing data in the matrix and herein confirmed as a "wild-card" (*sensu* Murray and Wilson 2013). Thus its position among †Ellimmichthyiformes still depends on the collection of well-preserved specimens. If so, excluding †*Horseshoeichthys*, †Sorbinichthyidae becames the putative sister group of all other †ellimmichthyiforms.

We have found no diagnostic character for †*Armigatus* so that species of this genus appear in a basal polytomy below more advanced taxa.

Species of †*Diplomystus* (excluding † *"D". solignaci*) form a group supported by the second higher value of Bremer index (3). We obtained a different placement for this group so that it is separated of †*Armigatus* and †Sorbinichthyidae, dismantling †Armigatoidei (†*Diplomystus in part* plus †*Armigatus sensu* Murray and Wilson 2013). †*Diplomystus* is placed in a more advanced position in the tree in comparison with †*Sorbinichthys* and †*Armigatus*. †*"Diplomystus" solignaci* is positioned within an advanced †Paraclupeidae but, in contrast with previous analyses, it appears as sister group of †*Paraclupea chetunguensis*.

Node 1 (=†Ellimmichthyiformes) is diagnosed by the uniquely derived *presence of predorsal scute series* (C=39) and *S-shaped cleithrum* (C= 21), this latter reversed in †*Codoichthys* and †*Horseshoeichthys*.

Node 2, linking species of †Sorbinichthyidae, are characterized by homoplastic features of pleural ribs insertion (C=18), subrectangular dorsal arm of posttemporal (C=22), a reversed condition to autogenous hypural (C=24), and spines on predorsal scutes (C=42). The latter is also shared with †*Diplomystus*.

Node 3, linking species of †*Armigatus* (in polytomy) and all †ellimmichthyiforms above †Sorbinichthyidae, is characterized by one striking ornamentation of skull roof (C=4), initial presence of teeth in a patch on parasphenoid (C=11), and certain number (22 to 30) of abdominal scutes (C=52).

A **Node 4**, linking †*Diplomystus* clade and †Paraclupeidae, is diagnosed by a special relation of pleural ribs and grooves of vertebral centra on abdominal region (C=18) and a conspicuous parietal excavation (C=60).

The **Node 5** (Bremer index =3) corresponds to the †*Diplomystus* clade and is diagnosed by the presence of sub-rectangular scutes in the anterior (C=40) and posterior (C=41) portion of predorsal series, spines on posterior edge of predorsal scutes (C=42, homoplastic feature shared with †*Sorbinichthys*).

Node 6, †Paraclupeidae *new usage* is diagnosed by another transformation of the character 11 (state 1 to 2), resulting in loss of teeth on parasphenoid (homoplasy shared with clupeiforms), and a derived number of predorsal scutes (C=46, state 2

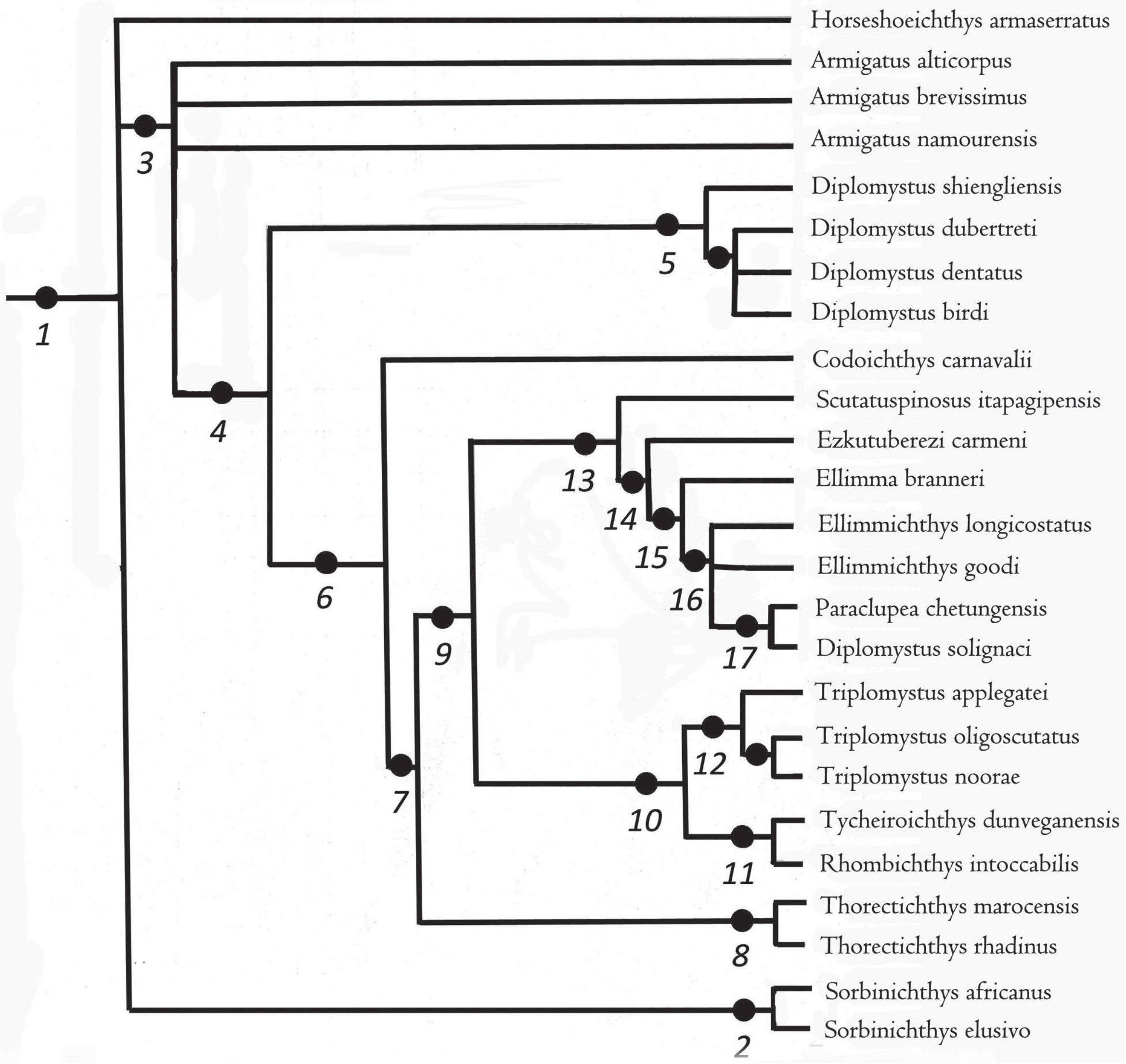

Figure 9 - The strict consensus of the three shortest trees obtained. Uniquely derived characters are indicated with an asterisk symbol (*). Synapomorphies supporting nodes are: **Node 1** (†Ellimmichthyiformes): 21[0►1],39*[0►1]; **Node 2** (†Sorbinichthyidae): 18[0►1], 22[0►1], 24[1►0], 42[0►1]; **Node 3** (unnamed): 4[0►1], 11[2►1], 52[0►1]; **Node 4** (unnamed): 18[0►1], 60[0►1]; **Node 5** (†*Diplomystus* clade): 40[0►1], 41[►1], 42[►1]; **Node 6** (†Paraclupeidae): 11[1►2], 46[2►0]; **Node 7**(unnamed): 1[0►1], 44[0►1]; **Node 8** (†Thorectichthyinae): 24[1►0], 30[1►], 32[0►1], 38[0►1], 48[1►2]; **Node 9** (†Paraclupeinae): 37[1►0], 43[0►1], 45[0►1]; **Node 10** (†Triplomystini): 29[0►1], 50[0►1]; **Node 11** (unnamed): 36[1►0], 49[01►2]; **Node 12** (unnamed): 26[0►1], 48[1►2], 51*[0►1]; **Node 13** (†Paraclupeini): 12[1►0], 53[0►1]; **Node 14** (unnamed): 30[1►0]; **Node 15** (unnamed): 5[0►1], 19[0►1]; **Node 16** (unnamed): 16[0►1], 20[0►1], 52 [1►2]; **Node 17** (unnamed): 22[1►0], 32[0►1], 40[0►1].

to 0). It contains †*Codoichthys* and all remaining †ellimmichthyiforms.

A **Node 7** (unnamed) includes †ellimmichthyiforms more advanced than †*Codoichthys*. It is divided in two subfamilies †Thorectichthyinae (**Node 8**, new name) and †Paraclupeinae (**Node 9**, new use). They share marked angle in front of the insertion of dorsal fin (C=1, secondarily lost is †*Codoichthys* and †*Scutatuspinosus*), and the size of scutes increasing backwards (C=44).

A **Node 8** (†Thorectichthyinae), linking species of †*Thorectichthys* is recognized by five apomorphies (C=24, 30, 32, 38, and 48, see Fig. 10) in addition to that proposed by Murray and Wilson (2013). This node shows the highest value of bootstrap (i.e., 75) in our analysis.

For **Node 9**, †Paraclupeinae, includes two sister tribes: †Triplomystini and †Paraclupeini. The latter includes tribes †Triplomystini (**Node 10**, *new usage*) and †Paraclupeini (**Node 13**, *new usage*). This node is characterized by reduction of neural spine of first preural centrum (C=37, state 1 to 0) and derived presence of ornamentation (C=43) and strong spine (C=45) in predorsal scutes.

†Triplomystini (**Node 10**) contains all species of †*Triplomystus* clade (**Node 12**, diagnosed by the homoplastic features *sharp end of first hypural* and *quantity of predorsal scutes*, and an uniquely derived C=51, i.e., *postdorsal scutes*) that is sister group (**Node 11**) of †*Tycheroichthys* plus †*Rhombichthys.*

This arrangement of **Node 11** is new and shows the highest value of decay (i.e., Bremer index equals 4). **Node 10** is characterized by two homoplastic features: derived number of uroneurals (C=29) and spatulate abdominal scutes (C=50).

†Paraclupeini (**Node 13**) is linking †*Scutatuspinosus* and advanced taxa by sharing homoplastic condition of characters 12 (absence of supraorbital, state 1 to 0) and 53 (loss of postcleithra). We think these characters used to diagnosed both groups demands more study. Noteworthy †*Scutatuspinosus* shows reversions (characters 1 and 50), and a independent acquisition (character 56).

Within †Paraclupeini, a **Node 14** is linking †*Ezkutuberei* and more advanced taxa (Node 15, †*Ellimma*, †*Ellimmichthys*, †*Paraclupea* and †*"Diplomystus" solignaci*). Only a reversion of character 30 (state 1 to 0) supported it. Better is the case of **Node 15** characterized *sculptured skull roof* (C=5, state 0 to 1) and *extension of epineurals and epipleurals on caudal region* (C=19, state 0 to 1). Assuming the condition found in †*Rhombichthys* and †*Triplomystus applegatei* not ambiguous (as interpreted by the TNT program), it is a putative uniquely derived feature for the clade.

Alignement between †*Ellimmichthys* and †*Paraclupea* was yet detected in early efforts to decipherrelationshipswithin†Ellimmichthyiformes (e.g., Chang and Grande 1997, Chang and Maisey 2003, Forey 2004). It is confirmed in **Node16** although species of †*Ellimmichthys* appear in a polytomy reflecting still bad knowledge of their structures. The node also includes the enigmatic †*"Diplomystus" solignaci* and is supported by three homoplastic features (characters 16, 20, and 52). In this we noted a well-supported clade (**Node 17**) formed by †*Paraclupea* and †*"Diplomystus"solignaci*. This node is the second highest value of bootstrap (i.e., 50) in our analysis although supported by homoplasies (characters 22, 32, and 40). Thus †*"Diplomystus"solignaci* is confirmed outside that genus.

We made an experimental analysis excluding the so-called 'wild-cards' or "swing taxa" (i.e., †*Ornategulum*, †*Ellimmichthys longicostatus*, †*Ezkutuberezi carmenae*, and †*Horseshoeichthys*, together with †*Ellimmichthys goodi*) and using command *traditional search*, we obtained seven trees (168 steps, CI 0,417, RI 0,611). Besides higher CI and lower steps, applying *strict consensus* we obtained a paraphyletic group for species of †*Sorbinichthys* and a great basal polytomy with remaining †Ellimmichthyiformes. In sum, in this step we have found a paradoxical result with Murray and Wilson (2013).

DISCUSSION AND CONCLUSIONS

After Grande (1985), the classification of Ellimmichthyiformes, in a historical perspective, become a continuous effort to add or exclude taxa. It was obviously associated with many attempts of tie the name of the taxon to at least one character that is necessary for membership. In this context Grande's approach was based on drawing-by-hand analysis, with a monophyly accepted *a priori* with selected characters and omitting homoplasies.

Since then †Ellimmichthyiformes seems to be generally accepted, besides strikingly short of characters. Particularly, we think that the reality of the group is better supported mainly because any member demonstrates close affinities with taxa outside (e.g., clupeiforms, ostariophysans, and elopomorphs).

Chang and Maisey (2003) were the first to use parsimony analysis performed in a computer program (i.e., PAUP version 4.0) to test monophyly of †Ellimmichthyiformes. Their results were obtained on the basis of a data matrix including 30 characters and 11 taxa. The characters used were all taken of Grande (1982, 1985) but they included new taxa too. As a result, they found a clade containing †*Armigatus*, †*Diplomystus*, †*Ellimma*, †*Ellimmichthys*, and †*Paraclupea*. This group was subdivided is two subclades, one for †*Armigatus* plus †*Diplomystus* and other containing †*Ellimma*, †*Ellimmichthys* and †*Paraclupea*. Noteworthy, these authors were the first to pointed out †*Scutatuspinosus* as showing some features indicating close affinities with †paraclupeines.

In an approach to known if Ellimmichthyiformes is a clade or a convenience group, Zaragueta-Bagils (2004) used a data matrix including 56 characters and 15 terminal taxa. He indicated that †*Armigatus brevissimus*, †*Diplomystus birdi*, and †*D. dentatus* form a group outside clupeiforms and †ellimmichthyiforms. His results dismantled †Ellimmichthyiformes.

Forey (2004) furnished a drawing-by-hand phylogenetic scheme for †Ellimmichthyiformes diagnosing the clade by a S-shaped cleithrum. Even he recognized two great subclades: a node D (for †*Armigatus*, †*Triplomystus*, †*Diplomystus*) and node C (for †*Paraclupea* and †*Ellimmichthys*). He stated Node D diagnosed by enlarged endopterygoid teeth, elongate anal fin, and deep and narrow opercle. His node C was characterized by characters taken of Grande (1982, 1985). Unfortunately, he omitted informative taxa as †*Ellimma*, †*Scutatuspinosus*, †*Codoichthys*, all yet known in that time.

Alvarado-Ortega et al. (2008) using a data matrix of 28 clupemorphs and 58 characters excluded †*Armigatus* from the †Ellimmichthyiformes. They used mainly characters taken of Grande (1982, 1985) and Zaragueta-Bagils (2004) and divided the group in two clades: †Sorbinichthyidae and †Paraclupeidae. According to them, †*Sorbinichthys* is a member of a †*Diplomystus* clade and †Paraclupeidae containing all other †ellimmichthyiforms. But certain taxa were omitted in the analysis of Alvarado-Ortega et al. (2008) as the case of †*Codoichthys* but other (e.g., †*Tycheroichthys*, †*Rhombichthys*, †*Torectichthys*) were only described in recent years. Other problem detected was about definition of characters and codification of states so that they were critically reassessed by Murray and Wilson (2013).

Murray and Wilson (2013) used 28 taxa and 62 characters in the most recent and complete cladistics analyses. Their results were condensed in a consensus tree of three shortest trees (176 steps, CI=0,44, RI=0,57) . It follows that†Armigatoidei (†*Armigatus* plus †*Diplomystus*) was found as sister of all other †ellimmichthyiforms. The strict and majority-role consensus trees were as our results, identical. As in our analysis neither decay (Bremer support) nor bootstrap analyses indicated strong support for any branch except for certain pair of species. †Ellimmichthyoidei contained †Sorbinichthyidae and †Paraclupeidae (including †scutatuspinosines, †thorectichthyines, and †paraclupeines). During their analyses some taxa were excluded because introduce many problems (i.e., many missing data), for instance, †*Ornategulum*, †*Ellimmichthys longicostatus*, †*Ezkutuberezi*, and †*Horseshoeichthys*. Even, they indicated † *Ellimmichthys* could be paraphyletic.

Recently some preliminary approaches to decipher relationships of †ellimmichthyiforms were carried out by F.J. de Figueiredo (unpublished data, Ph.D dissertation, Museu Nacional-UFRJ, Rio de Janeiro, 2006), F.J. de Figueiredo and D. Barros (unpublished data, abstracts of the 14th Congresso Latino Americano de Paleontologia de Vertebrados, p. 172, San Juan, Argentina, 2011), D.R.M. Ribeiro and F.J. de Figueiredo (unpublished data, abstracts of the 23th Congresso Brasileiro de Paleontologia, p. 270, Gramado, Rio Grande do Sul, 2013) and A. Nunes and F.J. de Figueiredo (unpublished data, abstracts of the 23th Congresso Brasileiro de Paleontologia, p.255, Gramado, Rio Grande do Sul, 2013).

F.J. de Figueiredo (unpublished data, Ph.D dissertation, Museu Nacional-UFRJ, Rio de Janeiro, 2006) furnished a review of articulated and complete clupeomorphs found in Lower Cretaceous and Tertiary deposits outcropping in many localities from the Northeastern Brazil. At first a data matrix containing 61 characters and 19 taxa were used in that analysis. The anatomy of many taxa were revisited in detail and a phylogenetic scheme was obtained. As a result †Ellimmichthyiformes appears as a weakly supported clade. Only a S-shaped cleithrum was indicated as uniquely derived feature, confirming hypothesis by Forey (2004). In addition, †Paraclupeidae only contained †*Ellimmichthys longicostatus*, †*Ellimma cruzae*, †*Triplomytus noorae*, †*Paraclupea* and a unnamed †*Ellimmichthys*-like taxon from the Lower Cretaceous of Reconcavo Basin, State of Bahia. †*Codoichthys*, †*Scutatuspinosus*, †*Ezkutuberezi*, and †*Ellimma branneri* appeared in a basal polytomy, and †*Diplomystus* (i.e., †*D. shengliensis* and †*D. dentatus*) plus †*Armigatus* formed a clade. Like Alvarado-Ortega et al. (2008) this analysis become dated because did not include many taxa only described recently.

F.J. de Figueiredo and D. Barros (unpublished data, abstracts of the 14th Congresso Latino Americano de Paleontologia de Vertebrados, p. 172, San Juan, Argentina, 2011) while revisiting the anatomy of †*Scutatuspinosus* preliminarly proposed a new hypothesis on phylogeny. They obtained eight trees with 128steps based on a data matrix including 15 putative ellimmichthyiforms, two basal clupeiforms (i.e., †*Santanaclupea silvasantosi* and †*Pseudoellimma gallae*, see Maisey 1993, Figueiredo 2009). And as for previous analyses, low index (CI=0.5; RI=0.6) indicating many missing data as the main problem. †Ellimmichthyiformes and †Paraclupeidae were confirmed. In addition Figueiredo and Barros suggested the exclusion of †*Ellimma cruzae* from the genus †*Ellimma* and put formally †*Codoichthys* within †Ellimmichthyiformes. But the inclusion of †*Santanaclupea silvasantosi* and †*Pseudoellimma gallae* as near outgroup in that analysis introduced many missing data and a doubtful result.

A. Nunes and F.J. de Figueiredo (unpublished data, abstracts of the 23th Congresso Brasileiro de Paleontologia, p.255, Gramado, Rio Grande do Sul, 2013) while describing new data about † *Ellimmichthys*-like taxon from the Lower Cretaceous of Reconcavo Basin, State of Bahia, once more worked on phylogeny. They used 22 taxa and 39 characters and obtained 102 trees, with 132 steps, CI=0.6; RI=0.79. It follows † Ellimmichthyiformes was diagnosed by a S-shaped cleithrum (one more time agreeing with Forey 2004) and †Paraclupeidae forming a clade including

†*Rhombichthys*, †*Tycheroichthys*, new taxon and †*Paraclupea*. But this analysis did not included recently described taxa and many characters of Murray and Wilson (2013).

D.R.M. Ribeiro and F.J. de Figueiredo (unpublished data, abstracts of the 23th Congresso Brasileiro de Paleontologia, p. 270, Gramado, Rio Grande do Sul, 2013) using unchanged data from literature (i.e., Santos 1994, Santos and Correa 1985, Chang and Maisey 2003, Alvarado-Ortega et al. 2008) and taxa recently described (i.e., †*Tycheroichthys dunveganensis*, †*Rhombichthys intoccabilis*) performed a preliminary cladistics analysis of † Ellimmichthyiformes. Their analysis was based on a data matrix containing 26 taxa and 57 characters. They obtained 10 shortest trees (L=177 passos, CI=0.463 e RI=0.652).

As a result, †*Codoichthys* appeared in basal position in a tree as sister group of remaining †Ellimichthyiformes. Once more †*Diplomystus* is indicated as paraphyletic taxon. †*Rhombichthys* revealed to be sister group of †*Ezkutuberezi* and appeared with†*Tycheroichthys* in a great polytomy together with †*Ellimma branneri*, †*Diplomystus solignaci*, †*Ellimmichthys*, and †*Paraclupea* plus †*Triplomystus*. They confirmed †Paraclupeidae with †*Scutatuspinosus* as sister group of the *deep-bodied* †Ellimmichthyiformes.

Noteworthy the unpublished results of Ribeiro and Figueiredo and Murray and Wilson (2013) appeared independently in the same year. Both works have not included or discussed data and results from each other.

Unlike results of D.R.M. Ribeiro and F.J. de Figueiredo (unpublished data, abstracts of the 23th Congresso Brasileiro de Paleontologia, p. 270, Gramado, Rio Grande do Sul, 2013) we took into account the corrections furnished by Murray and Wilson (2013), using new insights on characters and states (see Appendix 1, commented list of characters and states), and including new taxa. Thus we furnished an ultimate character list. Although highlighting character conflict we feel again the urgency of revisiting characters and reassessing taxa. Clearly the situation with regard to relationships of taxa within ellimmichthyiforms is unresolved and most of lineages are supported only by homoplasies. Many problems remain. For instance, although †*Horseshoeichthys* has an *incertae sedis* position at the base of the group in polytomy with †Sorbinichthyidae and all other †ellimmichtyiforms, we think that more informative specimens are need to decipher its relationships. Thus the most basal group of †Ellimmichtyiformes is probably †Sorbinichthyidae.

In sum, unlike Zaragueta-Bagils (2004) but agreeing with Alvarado-Ortega at al. (2008) and Murray and Wilson (2013) we confirm the existence of a †Ellimmichthyiformes group, though weakly supported. There are major differences between the topology of trees of Chang and Maisey (2003), Zaragueta-Bagils (2004), Forey (2004), Alvarado-Ortega et al. (2008), and Murray and Wilson (2013) and the hypothesis herein proposed. It confirms the impact of new described taxa in the phylogenetic analysis of a problematic group whose definition, diagnose, and composition wait for better results.

Particularly we noted that the main divergence among most of the analyses is about the position of †*Sorbinichthys*, †*Armigatus* and †*Diplomystus* in relation to the remaining taxa, difficulting linking. They are "swing" groups, sliding from the base of tree to near †Paraclupeidae. This latter includes mostly deep-bodied taxa, but its composition until now remains unresolved.

†*Codoichthys* is a basal and primitive †Paraclupeidae. In our analysis this taxon appears as sister group of remaining †paraclupeids.

As far as we known most recent phylogenetic analyses were prejudiced by many homoplasies and missing data. All phylogenetic schemes after Chang and Maisey (2003) produced trees with weakly supported branches.Thus, as claimed by Murray and Wilson (2013) we need more complete and informative specimens as well as revisiting old material in a search for new characters.

ACKNOWLEDGMENTS

We are indebted to Drs. Valéria Gallo and Hugo Ricardo S. Santos for reading a draft of this paper and for offering many helpful criticism and suggestions. We also thank Dr. Lionel Cavin and an anonymous reviewer for constructive critique and valuable comments. We are greatful to Maria Regina Salgado de Melo for producing high resolution photographs. Acknowledgement is also made to Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) for a grant-in-aid that enabled the junior author to work with fish fossil material in 2012. We thank the staff of the Departamento Nacional de Produção Mineral for hospitality during visits and loan of specimens.

REFERENCES

ALVARADO-ORTEGA J AND OVALLES-DAMIÁN E. 2008. *Triplomystus applegatei*, sp. nov. (Teleostei: Ellimmichthyiformes), a rare triple armored herring from Espinal quarry (Early Cretaceous), Chiapas, Southeastern Mexico. J Vert Paleontol 28(1): 53-60.

ALVARADO-ORTEGA J, OVALLES-DAMIÁN E AND ARRATIA G. 2008. A review of the interrelationships of the order Ellimmichthyiformes (Teleostei: Clupeomorpha). In: ARRATIA G ET AL. (Eds), Mesozoic Fishes 4 – Homology and Phylogeny, München: Verlag Dr. Friedrich Pfeil, Germany, p. 257-278.

ARRATIA G. 1997. Basal teleosts and teleostean phylogeny. Paleo Ichthyologica 7: 5-168.

BANNIKOV AF AND BACCHIA F. 2000. A remarkable clupeomorph fish (Pisces, Teleostei) from Upper Cretaceous marine locality in Lebanon. Senckenb Lethaea, Stuttgart, 80: 3-11.

CARVALHO MS AND de FIGUEIREDO SOUTO PR. 2005. Ocorrência de *Ellimmichthys longicostatus* (Cope, 1886) na Formação Maracangalha, Bacia do Recôncavo, Cretáceo Inferior. Paleontologia em Destaque, Rio de Janeiro 49: 49.

CAVENDER T. 1966. The caudal skeleton of the Cretaceous teleosts *Xiphactinus*, *Ichthyodectes*, and *Gillicus*, its bearing on their relationship with *Chirocentrus*. Occas Pap Mus Zool Univ Mich 650(29): 1-14.

CHANG MM AND GRANDE L. 1997. Redescription of *Paraclupea chetungensis*, an Early Clupeomorph from the Lower Cretaceous of Southeastern China. Fieldiana Geol New Series (37)1489: 1-19.

CHANG MM AND MAISEY JG. 2003. Redescription of *Ellimma branneri* and *Diplomystus shengliensis*, and relationships of some Basal clupeomorphs. Am Mus Novit 3404: 1-35.

COPE ED. 1886. A contribution to the vertebrate paleontology of Brazil. Proc Am Philos Soc 23(121): 3-4.

COSTA AC, MENDES VA AND ROCHA DEG. 1979. Síntese preliminar da Geologia do Projeto Extremo Nordeste do Brasil. Bol Núcleo NE da Soc Bras Geol 7: 421-440.

DE PINNA MCC. 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics 7: 367-94.

DI DARIO F. 2009. Chirocentrids as engrauloids: evidence from suspensorium, branchial arches, and infraorbital bones (Clupeomorpha, Teleostei). Zool J Linn Soc Lond 156: 363-383.

DI DARIO F AND de PINNA MCC. 2006. The supratemporal system and the pattern of ramification of cephalic sensory canals in *Denticeps clupeoides* (Denticipitoidei, Teleostei): additional evidence for monophyly of Clupeiformes and Clupeoidei. Pap. Avulsos Zool 46(10):107-123.

FIGUEIREDO FJ. 2009. A new clupeiform fish from the Lower Cretaceous (Barremian) of Sergipe-Alagoas Basin, Northeastearn Brazil. J Vert Paleontol 29(4): 1-13.

FOREY PL. 1973a. A primitive clupeomorph fish from the Middle Cenomanian of Hakel, Lebanon. Can J Earth Sci 10(8): 1302-1318.

FOREY PL. 1973b. A revision of the elopiform fishes, fossil and Recent. Bull Br Mus Nat Hist Geol Suppl 10: 1-222.

FOREY PL. 2004. A tree-dimensional skull of a clupeomorph of English Chalk. In: ARRATIA G AND TINTORI A (Eds), Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity, München: Verlag Dr. Friedrich Pfeil, Germany, p. 405-427.

FOREY PL, YI L, PATTERSON C AND DAVIES CE. 2003. Fossil Fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. J Syst Palaeontol 1(4): 227-330.

FUJITA K. 1990. The caudal skeleton of teleostean fishes, Tokyo: Tokay University Press, 897 p.

GALLO V AND FIGUEIREDO FJ. 2002. Clupeomorph fishes from the Lower Cretaceous of the Reconcavo Basin, Northeastern Brazil. J Vert Paleontol 22(3): 55A.

GALLO V, FIGUEIREDO FJ AND COELHO P. 2006. Paleoictiofauna da Formação Atlântida, Cretáceo Superior da Bacia de PelotasIn: GALLO V ET AL. (Eds), Paleontologia de Vertebrados: Grandes Temas e Contribuições Científicas. Rio de Janeiro: Livraria Editora Interciência, Brasil, p. 109-126.

GAUDANT M. AND GAUDANT J. 1971. Une nouvelle espéce de *Diplomystus* (Poisson, téléostéen) dans le

Crétacé supérieur du Sud Tunisien. Bul Soc Geol France 13: 156-159.

GOLOBOFF P, FARRIS J AND NIXON K. 2003. T.N.T: Tree Analysis Using New Technology. Program and documentation, available at http://www.lillo.org.ar/phylogeny/tnt.

GRANDE L. 1982. A revision the fossil genus *Diplomystus*, with comments on the interrelationships of clupeomorph fishes. Am Mus Novit 2728: 1-34.

GRANDE L. 1985. Recent and fossil Clupeomorph fishes with material for revision of the subgroups of Clupeoids. Bull Am Mus Nat Hist 181: 231-372.

GREENWOOD PH. 1968. The osteology and relationships of the Denticipitidae, a family of clupeomorph fishes. Bull Br Mus Nat Hist Zool 16: 215-273.

HAY MJ, CUMBAA SL, MURRAY AM AND PLINT AG. 2007. A new paraclupeid fish (Clupeomorpha, Ellimmichthyiformes) from a muddy marine prodelta environment: middle Cenomanian Dunvegan Formation, Alberta, Canada. Canad J Earth Sci 44(6): 775-790.

ICZN. 1999. International Code of Zoological Nomenclature, 4th ed., London: International Trust for Zoological Nomenclature, 306 p.

KHALLOUFI B, ZARAGÜETA-BAGILS R AND LELIÈVRE H. 2010. *Rhombichthys intoccabilis*, gen. et sp. nov. (Ellimmichthyiformes, Clupeomorpha, Teleostei), from the Cenomanian (Upper Cretaceous) of Ein Yabrud, Middle East: anatomical description and phylogenetic implications. J Vert Paleontol 30: 57-67.

LAVOUÉ S, KONSTANTINIDS P AND CHEN W-J. 2014. Progress in clupeiform systematics. In: GANIAS K (Ed), Biology and Ecology of Sardines and Anchovies. Boca Raton: CRC Press, Florida, USA, p. 3-40.

LONGBOTTOM AE. 1988. A note on the location of the type specimens of vertebrates from Brazil described by Cope in 1886. J Paleontol 62(5): 828-832.

MALABARBA MC, Do CARMO DA, GÓMEZ-PÉREZ I AND de QUEIROZ-NETO JV. 2004. A new clupeomorph fish from the Cretaceous Maceió Formation, Alagoas Basin, NE Brasil. Neues Jahrb Geol Paläont 233(2): 255-274.

MAISEY JG. 1993. A new clupeomorph fish from the Santana Formation (Albian) of NE Brazil. Am Mus Novit 3076: 1-15.

MAISEY JG. 2000. Continental break up and the distribution of fishes of Western Gondwana during the Early Cretaceous. Cretaceous Res 21: 281-314.

MURRAY AM AND WILSON MVH. 2011. A new species of *Sorbinichthys* (Teleostei: Clupeomorpha: Ellimmichthyiformes) from the Late Cretaceous of Morocco. Can J Earth Sci 48: 1-9.

MURRAY AM AND WILSON MVH. 2013. Two new paraclupeid fishes (Clupeomorpha: Ellimmichthyiformes) from the Upper Cretaceous of Morocco. In: ARRATIA G ET AL (Eds), Mesozoic Fishes 5 – Global Diversity and Evolution, München: Verlag Dr. Pfeil, Germany, p. 267-290.

NELSON JS. 2006. Fishes of the World. 4th ed., Hoboken: J Wiley and Sons, 601 p.

NEWBREY MG, MURRAY AM, BRINKMAN DB, WILSON MVH AND NEWMAN AG. 2010. A new articulated freshwater fish (Clupeomorpha, Ellimmichthyiformes) from the Late Cretaceous Horseshoe Canyon Formation, Alberta, Canada. Can J Earth Sci 47: 1183-1196.

NYBELIN O. 1967. Notes on the reduction of the sensory canal system and of the canal-bearing bones in the snout of higher Actinopterygian fishes. Ark Zool 19: 235-246.

NYBELIN O. 1968. The dentition in the mouth cavity of *Elops*. In: ORVIG T (Ed), Current problems of Lower Vertebrate Phylogeny, Stockholm: Nobel Symposium 4*,* p. 439-443.

NYBELIN O. 1971. On the caudal skeleton in *Elops* with remarks on the other teleostean fishes. Acta R Soc Sci Litt Gothobg Zool 7: 1-52.

PATTERSON C. 1967. Are the teleosts a polyphyletic group? In: Problémes actuales de paleontology (evolution des vertébrès). Colloques int CNRS, Paris, 163: 93-109.

PATTERSON C. 1970. A clupeomorph form the Gault (Lower Cretaceous). Zool J Linn Soc 49: 161-182.

PATTERSON C. 1993. Osteichthyes: Teleostei. In: BENTON M (Ed), The Fossil Record 2, London: Chapman and Hall, p. 621-656.

PATTERSON C AND ROSEN DE. 1977. Review of Ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bull Am Mus Nat Hist 158: 81-172.

POYATO-ARIZA FJ, LOPEZ-HORGUE MA AND GARCIA-GARMILLA F. 2000. A new early Cretaceous clupeomorph fish from the Arratia Valley, Basque Country, Spain. Cretaceous Res 21: 571-585.

RIDEWOOD WG. 1904. On the cranial osteology of the fishes of the families Elopidae and Albulidae, with remarks on the morphology of the skull in the lower teleostean fishes generally. Proc Zool Soc Lond 2: 35-81.

ROSSETTI DF, PAZ JDS AND GÓES AM. 2004. Facies analysis of the Codó Formation (Late Aptian) in the Grajaú Area, Southern São Luís-Grajaú Basin. An Acad Bras Cienc 76: 791-806.

SANTOS MECM AND CARVALHO MSS. 2009. Paleontologia das Bacias do Parnaíba, Grajaú e São Luís. Rio de Janeiro: Serviço Geológico do Brasil, CPRM, 211 p.

SANTOS RS. 1949. Sobre alguns peixes fósseis do gênero *Chiromystus* da Ilha de Itaparica, Bahia, Brasil. Divisão de Geologia e Mineralogia, Notas preliminares e Estudos 50, 12 p.

SANTOS RS. 1990. Clupeiformes e Gonorhychiformes do Cretáceo Inferior (Aptiano) da Formação Cabo, NE do Brasil. An Acad Bras Cienc 62: 261-268.

SANTOS RS. 1994. Ictiofáunula da Formação Codó, Cretáceo Inferior, com a descrição de um novo táxon – Codoichthys carnavalii (Pisces-Teleostei). An Acad Bras Cienc 66: 131-143.

SANTOS RS AND CORRÊA VLS. 1985. Contribuição ao conhecimento da paleoictiofaúnula do Cretáceo do Brasil. In: CAMPOS DA ET AL (Orgs), Coletânea de Trabalhos Paleontológicos, Brasília: Ministério das Minas e Energia e Departamento Nacional da Produção Mineral, p. 169-174.

SIGNEUX J. 1951. Notes paléoichthyologiques. V. *Diplomystus dubertreti*, une nouvelle espèce du Sénonien du Liban. Bul Mus Natl Hist Nat 23(2): 692-693.

SILVA VG. 1993. Taxonômica e posicionamento estratigráfico de paleovertebrados da Bacia do Recôncavo. Acta Geol Leopold 16(38): 41-58.

TAVERNE L. 1974. L'ostéologie d'*Elops* Linné, C., 1766 (Pisces: Elopiformes) et son intérêt phylogénétique. Acad R Belg Mém Cl Sci 41: 1-96.

VRBA ES. 1968. Contributions to the functional Morphology of fishes. Part V. The feeding mechanism of *Elops saurus* Linnaeus. Zool Afr 3: 211-236.

WHEELER W. 2012. Systematics: A Course of Lectures. New York: Wiley-Blackwell, 426p.

WILEY EO AND LIEBERMAN B. 2011. Phylogenetics: The Theory and practice of phylogenetic systematics, 2nd ed., New York: J Wiley and Sons, 432 p.

ZARAGUETA BAGILS R. 2004. Basal clupeomorphs and ellimmichthyiform phylogeny. In: ARRATIA G AND TINTORI A (Eds), Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity. München: Verlag Dr. Friedrich Pfeil, Germany, p. 391-404.

APPENDIX 1

LIST OF CHARACTERS AND STATES USED IN THE PHYLOGENETIC ANALYSIS

The present cladistic analysis of †Ellimmichthyiformes is based on the characters below. [0] at first represents the assumed plesiomorphic state and [1], and [2], and [3] the apomorphic states. They are present according to anatomical region, in logical flow, from the head to tail, except for four last additional characters from the list. The outgroup used to polarize characters and rooting tree is *Elops saurus*. Additional taxa used in this analysis are the clupeomorphs †*Ornategulum sardinioides*, *Chirocentrus dorab*, *Denticeps clupeoides*, and *Odaxothrissa vittata*. Further explanation of the characters and their coding see publications of Chang and Maisey (2003), Zaragueta-Bagils (2004), Alvarado-Ortega et al. (2008), and Murray and Wilson (2013). These publications followed of character number are referred by abbreviations CM#, Z#, AO# and MW# respectively. Additional relevant authors are included in parenthesis. Comments in brackets detail changes we made or add explanation.

(1) *Dorsal margin of the body with a marked angle at the insertion of the dorsal fin* (modified from AO1, Z56, Chang and Grande 1997, MW1): [0] absent; [1] present [Due to enlargement and grade of ossification of predorsal scutes there is among so-called paraclupeids an almost straight ascending profile in advance of the origin of the dorsal fin. Noteworthy Khalloufi et al. (2010) pointed out this character may be affected by the growth and size of an individual.]

(2) *Parietal bones* (AO2, CM4, Z1): [0] meeting in the midline; [1] completely separated by supraoccipital. [Early lineages of teleosts have parietals meeting in the midline, as in *Elops*. It is very difficult to check the states among different taxa due to lateral compressing of most available specimens. But we agree with Chang and Maisey (2003) *contra* Chang and Grande (1997) about coding primitive state of this character for †*Ellimmichthys longicostatus* and †*E. goodi*.]

(3) *Supraoccipital crest* (AO3, Z2): [0] low and small; [1] high. [A deep crest, with large laminar structure abruptly projected upward, is verified in †*Diplomystus shengliensis*, †*Ezkutuberezi carmenae*, and †*Codoichthys carnavalii* unlike most of †ellimmichthyiforms. It is found in †*Diplomystus dentatus*, †*D. dubertreti* and †*Rhombichthys*. Forey (2004) described it in the well-preserved skull of an unnamed †*Diplomystus* from the English Chalk. Due to poor definition it has been differently and subjectively interpreted by different researchers. Therefore this character was modified after the matrix by Murray and Wilson (2013) as lateral profile of skull roof, enhancing a distinct angle between anterior and posterior regions.]

(4) *Ornamentation of skull roof* (Z3, AO4, MW4): [0] Absent; [1] Present. [Murray and Wilson

(2013) simplified and joined characters 4 and 52 of Alvarado-Ortega et al. (2008) in a single character, and we used it here.]

(5) *Dermal roof sculptured with coarse irregular and radiating ridges or grooves*: [0] absent; [1] present. [The grade and topographic site of ornamentation on skull roof varies among taxa and according to age of individuals. Most of non-clupeiform clupeomorphs shows ornamentation under form of radiating ridges and grooves. It is particularly observed in †*Spratticeps* (Patterson 1970) and †*Ornategulum* (Forey 1973a). But the skull roof becomes strongly sculptured in †*Ellimmichthys*, †*Paraclupea*, and †*Ellimma*. The state is unknown in †*Diplomystus solignaci* and †*Rhombichthys* whereas †*Horseshoeichthys* exhibits a skull roof smooth. Many advanced clupeiforms commonly show parallel striae on border of the posterior part of frontal. Denticles or spines are homoplastically observed on dermal bones of *Denticeps clupeoides* and †*Sorbinichthys elusivo*. Noteworthy this character may be affected by age of the individual inasmuch as young individuals of †*Ellimma* lack ornamentation on dermal skull bones (Chang and Maisey 2003). Since the variety of ornamentation in frontal and parietal, we simplified the character Z4, AO5, and MW5.]

(6) *Posttemporal fossa* (AO6, Z6): [0] absent; [1] present. [Forey et al. (2003) described the presence of a posttemporal fossa in †*Armigatus namourensis* and †*Triplomystus noorae*. Even, Forey (2004) demonstrated its occurrence in a well-preserved skull of an unnamed †*Diplomystus* from the English Chalk. Apparently it is present in all other species of †*Diplomystus* except in the enigmatic †*D. solignaci* so that we used a question mark in the matrix. Unfortunately a posttemporal fossa is unknown in Brazilian taxa (i.e., †*Codoichthys*, †*Scutatuspinosus*, †*Ellimma*, †*Ellimmichthys*) and other taxa studied manly due to preservation.]

(7) *Cavity or fossa in the temporal region of the skull* (MW7, AO7, CM3, Z7, and modified from Forey 2004): [0] absence of cavity or fenestra; [1] pre-epioccipital fossa (i.e., between parietal, epioccipital and pterotic bones); [2] pre-epioccipital fenestra (i.e., between the parietal, epioccipital and supraoccipital bones). [Forey (2004) indicated originally differences between pre-epioccipital fenestra and fossa. It is not clear the state in †*Scutatuspinosus*, †*Codoichthys*, †*Ellimma* and †*Ellimmichthys* so that we coded as question mark.]

(8) *Recessus lateralis* (Grande 1985; CM1, Z8, MW8): [0] absent; [1] present. [The presence of a infraorbital canal merging with preopercular canal in the otic region in association with a reduction of dermosphenotic bone as far as we known is only found in clupeiform fishes (Grande 1985).]

(9) *Supramaxillae* (AO9, CM8, Z10, MW9): [0] two; [1] one or none. [According to Zaragueta-Bagils (2004) †ellimmichthyiform fishes show primitively two supramaxillae; it is the primitive state for teleosts (Arratia 1997, 1999). A reduction in number is assumed as secondary lost.]

(10) *Basipterygoid process of parasphenoid* (CM 11, AO10, Z11): [0] absent; [1] present.

[The dermal basipterygoid process is present in many †ellimmichthyiform fishes (Chang and Maisey 2003, Zaragueta-Bagils 2004, Forey et al. 2003, Forey 2004, Alvarado-Ortega et al. 2008). But due to poor preservation it is not possible to confirm if †*Scutatuspinosus*, †*Ezkutuberezi*, †*Ellimmichthys* and †*Codoichthys* show that state, therefore this character is coded as missing data for them.]

(11) *Teeth on parasphenoid* (modified from AO11, Z12, Grande 1982, 1985; MW11): (0) occupying most of the major extension of the orbital region; (1) only with a posterior osteoglossid-like tooth patch; (2) absent [All clupeiform fishes show toothless parasphenoid so far; the same for †*Scutatuspinosus*, †*Codoichthys*, †*Ellimma*, and †*Ellimmichthys*. A tooth patch backwardly placed on parasphenoid is only found in species of †*Armigatus* and †*Diplomystus*.]

(12) *Supraorbital* (AO12, Z13, MW12): (0) present; (1) absent. [This anamestic bone is commonly found in Clupeiformes and most of Elopiformes (e.g., *Elops* and *Albula*). But its putative presence is very difficult to confirm in many fossils due to flimsy nature and preservation. The situation is worse when few and badly preserved specimens are available. It is certainly found in †*Scutatuspinosus itapagipensis* (cf. DGM 1255-P and DGM 1253-P), †*Ellimma branneri*, †*Sorbinichthys africanus* (Murray and Wilson 2012) but doubtfully in †*Rhombichthys*. It is coded as missing data (question mark) in †*Codoichthys*. Furthermore we considered the presence of a supraorbital bone in †*Horseshoeichthys* uncertain so that it is herein coded ?]

(13) *Antorbital* (AO13, Z16, MW13): (0) present; (1) absent.[Although assumed as regularly present in many basal lineages of teleostean fishes (Arratia 1999), the presence or not this bone is very difficult to confirm in most of fossil fishes due to the flimsy condition. It commonly becomes easily lost or damaged. It is boomerang-like in †*Scutatuspinosus* (cf. DGM 1255-P) and quadrangular (and with canal) in †*Horseshoeichthys* (identified erroneously as a lachrymal by Newbrey et al. 2010) in which is very similar to *Denticeps clupeoides* (see Di Dario 2004). Gayet (1989) claimed the presence of an anamestic lachrymal as a synapomorphy of Clupeomorpha but as far is known it is not supported by any congruence of characters in foregoing analyses and, at worst, this bone clearly bears canal in *Denticeps* (see Di Dario and de Pinna 2006) and †*Horseshoeichthys* (see Newbrey et al. 2010).]

(14) *Beryciform foramen on anterior ceratohyal bone* (AO14, Z14, CM12, Grande 1985): (0) absent; (1) present. [It occurs in many taxa from early lineages of teleosts, many early euteleosteans, and early acanthomporhs. Otherwise it is absent in osteoglossomorphs, elopomorphs and advanced acanthopterygians. It is found in *Scutatuspinosus* (cf. DGM 1262-P). We coded this character mostly according to Zaragueta-Bagils (2004) assuming loss of this foramen in clupeiforms.]

(15) *Foramen on the posterior ceratohyal* (Z15, AO15): (0) absent; (1) present. [Although herein included in analysis, it is very difficult to verify this feature even in well-preserved specimens. It is a result of the enlargement of the groove for the hyoidean afferent artery. Apparently it is found in the hyoid apparatus of the unnamed †*Diplomystus* of the Cenomanian of English Chalk (Forey 2004). But as far as we known, among living clupeomorphs only *Denticeps clupeoides* possesses it. We found ceratohyal is widely covered by mandible and opercular bones in available specimens used in analysis. This feature contributes to increase the quantity of missing data in matrix.]

(16) *Teeth on endopterygoid* (CM9, AO16): (0) absent or minute; (1) present and well-developed. [many times it is only inferred of punctuated surface of this bone in association of isolated teeth.]

(17) *Halves of the neural arches of most abdominal vertebrae* (AO18, Z17): (0) independent; (1) fused medially. [see Arratia (1997) for explanation and discussion.]

(18) *Pleural ribs* (Z18, AO19): [0] all articulated with parapophyses along abdominal region; [1] the anteriormost ribs articulate with deep pits on the lateral side of the abdominal centra and those located posteriorly articulate with well-developed parapophyses; [2] all articulated with deep pits on the lateral side of abdominal centra. [Zaragueta-Bagils (2004) indicated states 0 and 1 as relevant and Alvarado-Ortega et al. (2008) modified it, including an additional state 2. We follow basically Murray and Wilson (2013) so that the state 1 occurs in †*Ellimmichthys* (Grande 1982), †*Paraclupea* (Chang and Grande 1997), †*Triplomystus* (Forey et al. 2003), †*Ellimma branneri* (Chang and Maisey 2003), and †*Diplomystus solignaci* (Gaudant and Gaudant 1971). †*Codoichthys* shares this last derived state.]

(19) *Epineurals and epipleurals in the caudal region* (Z19, AO20): (0) present, (1) absent. [According to Gaudant and Gaudant (1971) †*"Diplomystus" solignaci* does not show epineurals and epipleurals in the caudal region. We assumed epineurals and epipleurals occur in the caudal region of †*Diplomystus birdi*, †*D. dentatus*, †*D. dubertreti*, †*D. shiengliensis*, †*Sorbinichthys elusivo*, †*Sorbinichthys africanus*, †*Triplomystus noorae*, †*Triplomystus oligoscutatus*, *Chirocentrus dorab*, *Elops saurus*, *Odaxothrissa*, *Denticeps clupeoides*, and †*Ornategulum sardinioides*. Unlike Alvarado-Ortega et al. (2008), we clearly observed epineurals invading caudal region of †*Scutatuspinosus* (cf. DGM 1242-P).]

(20) *Epicentrals* (AO21, Z20, MW21): (0) absent; (1) present.

(21) *Shape of cleithrum* (modified of AO22, Forey 2004; MW22): (0) L-shaped; (1) sigmoid. [Forey (2004) claimed a sigmoid cleithrum is a synapomorphy of †Ellimmichthyiformes. Afterwards new non-clupeiform taxa were described bearing L-shaped cleithrum (e.g., †*Codoichthys* and †*Horseshoeichthys*).]

(22) *Dorsal process of posttemporal* (Z22, AO23): (0) slender and sharp; (1) sub-rectangular.

(23) *Hypurals* (AO26, CM20, Z23): (0) seven; (1) six; (2) five. [Alvarado-Ortega et al. (2008) counted six hypurals in †*Scutatuspinosus* probably assuming a common occurrence in †ellimmichthyiforms. We counted only five in our best preserved specimen examined (cf. DGM 1250-P). Therefore, we used question mark for this taxon.]

(24) *Second Hypural* (Z24, CM22, AO27): (0) autogenous; (1) fused to first ural centrum.

(25) *First hypural and first ural centrum* (Z25, AO28): (0) in contact; (1) without contact.

(26) *Shape of proximal end of first hypural* (Z26, AO29): (0) massive and forming an upward process; (1) sharp and straight.

(27) *Shape of second hypural* (AO30, Z27): (0) symmetrical to the fourth hypural; (1) very thin and stick-like. [Second and fourth hypurals are almost symmetrical in many clupeomorphs and most of †ellimmichthyiforms (Alvarado-Ortega et al. 2008). Apparently, only in *Denticeps clupeoides* it is stick-like.]

(28) *Size of the first ural centrum* (AO32, Z30): (0) roughly the same size as preural centra;
(1) smaller than the first preural centra.

(29) *Number of uroneurals* (Z29): (0) three; (1) two; (2) one. [Most of clupeomorphs (Grande 1985) and basal elopomorphs (Arratia 1997) exhibit three uroneurals. Unlike Alvarado-Ortega et al. (2008), we note the presence of three uroneurals in †*Scutatuspinosus* (cf. DGM 1250-P).]

(30) *Proximal extremity of the first uroneural* (Z31, AO34): (0) contacting second preural centrum; (1) not reaching or only contacting the first preural centrum. [In the basal and primitive teleostean fishes the first uroneural projects forwards anterior to second preural centrum (Patterson and Rosen 1977). In elopomorphs and basal clupeomorphs it reaches only the second preural centrum whereas in more advanced taxa, only first preural centrum is contacted. The coding of this character is based mainly on Zaragueta-Bagils (2004) but agreeing with Alvarado-Ortega et al. (2008) we considered the condition of †*Diplomystus birdi* and †*D. dentatus*, whose the first uroneural does not reach the second preural centrum. †*D. shengliensis* shows a first uroneural projecting forwardly to reach the second preural centrum (see Chang and Maisey 2003, fig. 12). Chang and Grande (1997) in contrast with Grande (1982) and Patterson and Rosen (1977) noted a first uroneural reaching the second preural centrum in †*Ellimmichthys longicostatus*. According to observations on BMNH P. 7109 we agree with older restorations. In †*Scutatuspinosus*, the first uroneural reach only the first preural centrum (cf. DGM 1250-P). Although Alvarado-Ortega et al. (2008) claimed an extension of the first uroneural to second preural centrum in †*Triplomystus applegatei*, it is not seen

in the figure and photo of the original description (Alvarado-Ortega and Ovalles-Damian 2008, fig. 5). It is present in †*Triplomystus noorae* according to Forey et al. (2003).]

(31) *Fusion of the first uroneural with the first ural centrum* (Z32, AO 35): (0) absent; (1) present. [The pleurostyle is certainly a homoplastic feature shared by clupeiforms and ostariophysans, but absent is all non-clupeiform clupeomorphs.]

(32) *Distal end of second uroneural* (Z34, AO37): (0) reaching the distal end of the first uroneural (or according Z34 – "ascending part of the hypural 2 as long as the first uroneural"); (1) not reaching the distal end of the first uroneural (According Z34 – "shorter"). [The coding is based mainly on Zaragueta-Bagils (2004) except for modifications presented by Alvarado-Ortega et al. (2008) in which †*Sorbinichthys* and †*Diplomystus solignaci* show second uroneural not reaching the distal end of the first uroneural and in †*Triplomystus* the proximal end of the second uroneural extends as far as that of the first uroneural.]

(33) *Parhypural* (Z35, AO38): (0) fused with the first preural centrum; (1) autogenous. [Except for isolated and independent cases of secondary fusion, a separation of the parhypural from the first ural centrum is present in most of clupeiform clupeomorphs (Grande 1985). Among species examined, it is fused to preural centrum in †*Scutatuspinosus* (cf. DGM 1250-P) and †*Codoichthys* such as in remaining †ellimmichthyiforms.]

(34) *Number of epurals* (AO40, Z37, CM23): (0) Three; (1) Two. [Three epurals are usually found in living clupeoids and most of non-clupeiform clupeomorphs. †*Codoichthys* and †*Scutatuspinosus* have three epurals. Among species examined, only †*Ezkutuberezi*, and *Denticeps* exhibit two epural bones. The presence of epurals in †Sorbinichthys is uncertain according to Murray and Wilson (2011).]

(35) *Position of epurals* (Z38, AO41): (0) Filling space between the neural spines of the first and second preural centra and the first uroneural; (1) placed far from the spine of the second preural centrum, leaving an open space between them. [According to Alvarado-Ortega et al. (2008) we noted epurals filling space between neural arch and first uroneural in †*Scutatuspinosus* (cf. DGM 1250-P) unlike †*Codoichthys*. According to Murray and Wilson (2013) the state for †*D. birdi* is unknown.]

(36) *Caudal scutes* (Z39, AO42): (0) absent; (1) present. [We coded this character according to Murray and Wilson (2013). But we are unable to determine the occurrence of caudal scutes in †*Codoichthys*. In caudal skeleton of †*Sorbinichthy elusivo* (see Bannikov and Bacchia 2000, text-fig. 5) there are about five elements anterior to dorsal procurrent rays of difficult homology. They may be homologous to that two-three of †*Paraclupea chetungensis* which Chang and Grande (1997) interpreted as dorsal scutes.]

(37) *Neural spine of the first preural centrum* (modified of Z40, AO43): (0) first preural neural arch plus spine shorter or equal to half of the first uroneural; (1) first preural neural arch plus spine longer than half of the first uroneural [We noted problems with the original definition of this character as *large and lanceolate* (or even very slender) versus *short or sub-rectangular*. Poor preservation and deformation can produce subjective interpretation. Murray and Wilson (2011) described a long and fine neural spine in †*Sorbinichthys africanus*. †*Scutatuspinosus* (cf. DGM 1250-P) shows lanceolate neural spine and very elongate second neural spine as in †*Sorbinichthys*. The spine is large, elongate, and slender in †*Diplomystus shengliensis*, †*D. dentatus*, †*Ellimmichthys longicostatus*, and †*Triplomystus applegatei* (Alvarado-Ortega and Ovalles-Damián 2008, text-fig. 5). In †*Triplomystus noorae* it is short (see Forey et al. 2003, fig. 44). Also it is clearly short and sub-rectangular in †*Ellimma branneri* (see Chang and Maisey 2003, fig. 8). According to Cavender (1966, fig. 3A) *Chirocentrus dorab* shows large neural spine and arch complex disagreeing

of codification furnished by Alvarado-Ortega et al. (2008) and Zaragueta-Bagils (2004).]

(38) *Neural arch of the first ural centrum* (Z42, AO44): (0) absent; (1) present.

(39) *Predorsal scutes series* (A45, MW 46): (0) absent; (1) present. [We assumed codification of Murray and Wilson (2013) except for †*Ellimmichthys longicostatus* and †*Armigatus brevissimus* in which we noted such series present.]

(40) *Sub-rectangular scutes in the anterior part of predorsal series* (Z47, MW 48): (0) absent; (1) present. [It is common in many non-clupeiform clupeomorphs the presence of sub-rectangular scutes since occiput to the origin of the dorsal fin. In certain advanced deep-bodied †paraclupeids, the anteriormost scutes are elliptical.]

(41) *Sub-rectangular scutes in the posterior part of predorsal series* (AO 47): (0) absent; (1) present.

(42) *Spines on the posterior margin of predorsal scutes* (Z48, AO48, MW 50): (0) absent; (1) present. [This feature was originally described as uniquely derived for †*Diplomystus* (see GRANDE 1982a). After, Santos and Corrêa (1985), claiming close affinities between †*Diplomystus* and †*Scutatuspinosus* on the basis of the form of the predorsal scutes pointed out the presence of spines on posterior border of scutes of the holotype of †*Scutatuspinosus*. However, Alvarado-Ortega et al. (2008) and Barros and Figueiredo (unpublished data 2011) indicated the posterior border all smooth except for the strong median spine. Herein we assumed the scalloped posterior border of †*Horseshoeichthys* as state 0 contra Murray and Wilson (2013).]

(43) *Prominent median strong spine on posteriormost predorsal scutes* (AO49, Z49, MW 51): (0) absent; (1) present. [This character is coded mainly based on Zaragueta-Bagils (2004). A median strong spine is present on the posteriormost scutes of many †ellimmichthyiform taxa such as †*Ellimmichthys*, †*Ellimma*, †*Sorbinichthys*, †*Paraclupea*, †*Triplomystus*, and † "*Diplomystus" solignaci*. This feature is also present on †*Scutatuspinosus* (cf. DGM 1164) but lacking in †*Codoichthys*. Unlike Murray and Wilson (2013) we coded primitive state for †*Diplomystus birdi*.]

(44) *Size of scutes of predorsal series* (Chang and Grande 1997; AO50, Z50; MW 52): (0) all equal-sized; (1) irregular, the size of scutes increases backwards in the series.

(45) *Surface of predorsal scutes* (CM15; Z51; AO51; MW 53): (0) smooth; (1) ornamented .

[This character is coded based on Alvarado-Ortega et al. (2008) except for †*Scutatuspinosus* that show fading radiating ornamentation at least in the posteriormost scutes (cf. DGM 1164).]

(46) *Number of scutes in predorsal series* (Z52, MW 54): [0] 6-14; [1] 16 to 19; [2] 20-41. [We coded according to Murray and Wilson (2013).]

(47) *Abdominal scutes series* (AO53; Z52; CM16): (0) absent; (1) present. [It is considered a synapomorphy of Clupeomorpha (Arratia 1997) besides certain basal taxa lack it (e.g., †*Ornategulum*, *Chirocentrus*).]

(48) *Number of predorsal bones* (MW 62): [0]10 or more; [1] 7-9; [2] 6 or fewer.

(49) *Prepelvic and postpelvic scutes* (modified of AO55, Z54, MW 57): (0) similar ; (1) prepelvic normal and postpelvic scutes with strong posterior spine; (2) both prepelvic and post pelvic with strong spines.

(50) *Shape of lateral wings of abdominal scutes* (modified of MW 59): (0) triangular; (1) spatulate; (2) quadrangular. [Most of clupeomorphs show triangular lateral wing of abdominal scute (Whitehead et al. 1985). In †*Paraclupea*, †*Rhombichthys*, †*Tycheroichthys*, and other deep-bodied †ellimmichthyiforms the scutes are more specialized becoming spatulate.] (51) *Postdorsal scutes series* (AO 58): (0) absent; (1) present. [As far as we known only species of †*Tryplomystus* show this feature.]

(52) *Number of abdominal scutes* (MW61): [0] fewer than 20; [1] 22-30; [2] more than 32. [In fact, some taxa will not show a number equivalent to

vertebral counts. We coded according to Murray and Wilson (2013).]

(53) *Postcleithra*: (0) present; (1) absent. [†*Triplomystus applegatei*, †*Horseshoeichthys armaserratus*, †*Codoichthys carnavalii*, †*Armigatus namourensis*, †*Tycheroichthys* and †*Thorectichthys* show postcleithra. According to Murray and Wilson (2013) it is also found in †*Diplomystus dentatus*. This bone is usually present in living clupeiform fishes, commonly two in number. However, Greenwood (1968) stated occurrence of postcleithra in *Denticeps* uncertain.]

(54) *Basisphenoid:* (0) present; (1) absent. [Basisphenoid is found in Elopiformes and Clupeiformes (e.g., *Sardinops*, *Denticeps*, *Engraulis*, *Alosa*), †*Ornategulum*, and †*Spratticeps* (see Patterson 1970) but lack in †*Diplomystus*, †*Triplomystus*, †*Ellimma*, †*Ellimmichthys*, †*Rhombichthys*, and †*Paraclupea*. It is absent in the complete and well-preserved skull of a unnamed †*Diplomystus* from the English Chalk (Forey 2004). Its presence in †*Scutatuspinosus* and †*Codoichthys* is doubtful so that is coded with question mark on the matrix. Apparently its absence is a probable case of secondary loss for †Ellimmichthyiformes.]

(55) *Third hypural* (Poyato-Ariza et al. 2000): (0) smaller than or almost equal-sized the first hypural; (1) triangular, larger than others hypural bones. [Poyato-Ariza et al. (2000) pointed out that the third hypural is enlarged and triangular in most of non-clupeiform clupeomorphs and it penetrates diastema region projecting downwards unlike the condition found in clupeiforms. Thus the third hypural extends below occupying the diastema region.]

(56) *Third hypural with upward process constraining the fourth hypural to project forwardly*: (0) absent; (1) present. [It is only found in †*Scutatuspinosus* (cf. DGM 1250-P) and †*Rhombichthys*.]

(57) *Two long and recumbent tubules of preopercular sensory canal on ventral limb*: (0) absent; (1) present. [In †*Codoichthys*, †*Ellimmichthys longicostatus* and †*Ellimma branneri* there are two (rare three) distinct recumbent tubules emerging from the main preopercular sensory canal.]

(58) *Striations on ventral part of opercle:* (0) absent; (1) present. [It is found in adults of †*Ellimma*, †*Tycheroichthys*, †*Codoichthys* and possibly in †*Thorectichthys marocensis* (see Murray and Wilson, 2013, fig. 2).]

(59) *Head deeper than long:* (0) absent; (1) present. [Murray and Wilson (2013) commented (but not included in matrix) that †*Tycheiroichthys* and †*Triplomystus* shared a deep head unlike other †ellimmichthyiforms.].

(60) *Parietal excavation*: (0) absent; (1) present. [Forey (2004) recognized through a drawing-by-hand analysis a clade within †Ellimmichthyiformes composed of †*Triplomystus*, †*Sorbinichthys,* and †*Diplomystus*. One of the derived states of character used was the presence of a parietal excavation. According to him it is absent in †*Armigatus*, †*Paraclupea*, and †*Ellimmichthys*. We found it in †*Codoichthys* and †*Scutatuspinosus* (cf. DGM 1279-P). Its presence is very probable in †*Ellimma cruzae* but not in †*E. branneri*.]