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The Cenomanian short snout enchodontid fishes (Aulopifomes, Enchodontidae) from Sierra Madre Formation, Chiapas, southeastern Mexico

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ABSTRACT

In this paper the short snout Cenomanian enchodontids from the El Chango quarry, Chiapas, southeastern Mexico, are reviewed. *Unicachichthys multidentata* nov. gen. and sp. is named and identified as a new member of the Enchodontidae because it has the predorsal scute series that is the distinctive character of such family. This new genus resembles other short snout enchodontids, as *Enchodus* and *Eurypholis*; however, *Unicachichthys* differs from these and other members of the family because it shows characters ever observed, including a multitoothed dermopalatine, the presence of a basal sclerotic bone, and the serrations in the posterior edge of the preopercle vertical limb. The inclusion of *Unicachichthys* in two phylogenetic analyses, based on studies previously performed, suggests that this is a primitive representative of the family Enchodontidae. Additionally specimens of two different species of *Enchodus* from the El Chango quarry are also described; these specimens are so scarce and fragmentary that it is not possible to determine their specific taxonomic identity. The record of these Mexican fossils enrich the knowledge about the diversity of Cenomanian enchodontids in the North American domain of the Tethys Sea, which now contains new taxa that should be considered in future efforts to recognize the phylogenetic and biogeographic processes experienced by this fish group.

1. Introduction

The El Chango quarry is an outcrop of creamy-yellow laminated limestone strata, near Ocozocoautla de Espinosa and Tuxtla Gutiérrez, State of Chiapas, southeastern Mexico (Fig. 1). This has been revealed as a Konservat Lagerstätte paleontological site, where the fishes are the most abundant, diverse, and best preserved fossils. Other taxa collected here include mollusks, crustaceans, insects, and plants (Ovalles-Damián et al., 2006; Vega et al., 2006; Alvarado-Ortega et al., 2009; González-Ramírez et al., 2013; among others). Although the age of the El Chango was firstly suggested as Albian (Vega et al., 2007; Alvarado-Ortega and Ovalles-Damián, 2008); recently, the taxonomical affinities of ammonites and fishes collected in this locality, as well as its lithological composition and geographical position were considered to suggest its Cenomanian age and belonging to the Cintalapa Member of the Sierra Madre Formation (Alvarado-Ortega and Than-Marchese, 2012; Moreno-Bedmar et al., 2014). The Sierra Madre Formation is a 2590 m thick geological unit of Aptian-Santonian dolomites and limestones deposited under shallow marine tropical conditions near shore (Rosales-Domínguez et al., 1997).

Alvarado-Ortega et al. (2009) reported the occurrence of short snout predaceous fishes from the El Chango quarry, referred to *Enchodus* Agassiz, 1835, as well as some long snout fishes belonging to *Saurorhamphus* Heckel, 1850. These genera are part of the family Enchodontidae, firstly named by Woodward (1901) to include *Enchodus* and its relatives. Today, the composition and relationships of enchodontids are somewhat problematic. Besides *Enchodus* and *Saurorhamphus*, the composition of this family originally suggested also includes *Palaeolycus* von der Marck, 1863; *Eurypholis* Pictet, 1850, *Halec*, Agassiz, 1834; *Cimolichthys* Leidy, 1857; *Leptecodon* Williston, 1899; *Pantopholis* Davis, 1887, and *Aspidopleurus* Pictet and Humbert, 1866 [although Woodward (1901) considered *Aspidopleurus* as synonymous with *Prionolepis* Egerton, 1850 (in Dixon,

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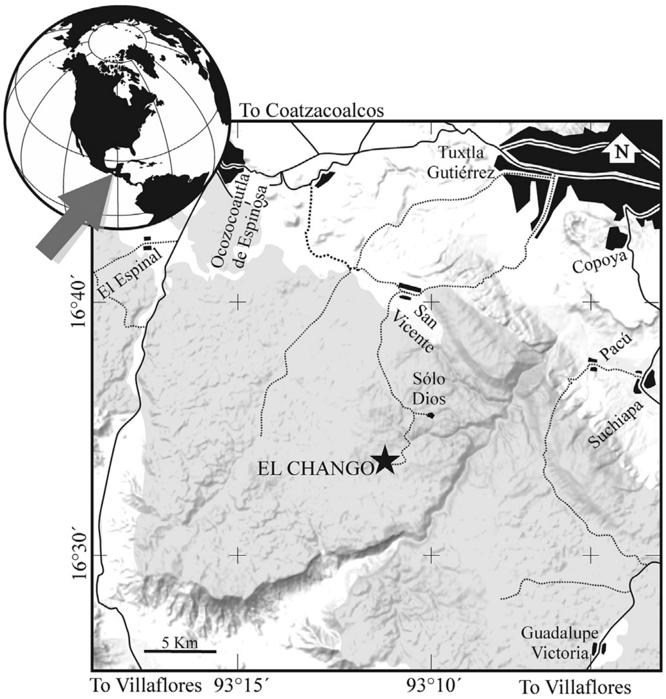

Fig. 1. Map of the Sierra Madre Formations outcrops near Tuxtla Gutiérrez, Chiapas, Mexico, showing the position of the El Chango quarry.

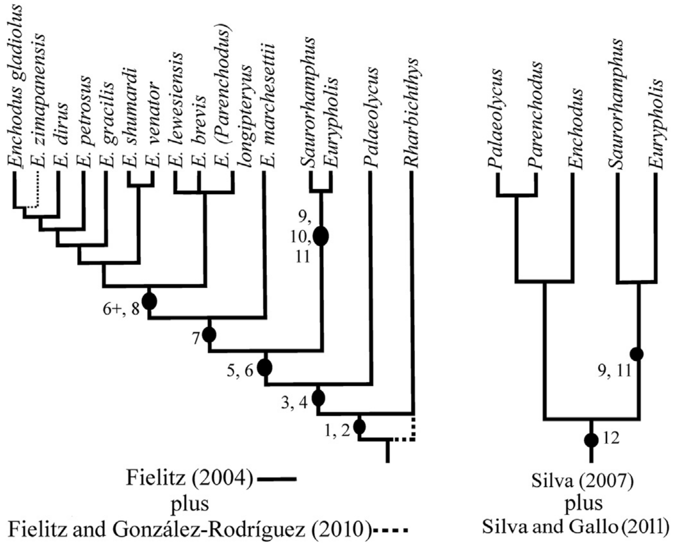

Fig. 2. Recent phylogenetic hypotheses of *Enchodus* and close relatives, the family Enchodontidae (based on Fielitz, 2004, fig. 2; Silva, 2007, fig. 9; Fielitz and González-Rodríguez, 2010, fig. 11; Silva, 2007; Silva and Gallo, 2011, fig. 1). Numbers represent synapomorphies: 1, Dermopalatine bearing a single terminal tooth; 2, interopercle absent; 3, supraorbital absent; 4, opercle with prominent middle horizontal strengthening or bar; 5, dentary prongs; 6, opercle and subopercle ornamented with numerous tubercles; 6+, opercle and subopercle ornamented with numerous ridges and tubercles; 7, ventral portion of the preopercle broadens anteriorly and posteriorly; 8, dermal surface of the frontal ornamented with radiating ridges with tubercles along each ridge; 9, articulation of lower jaw and quadrate covered. 10, Posterior ventral section of the preopercle forms a spine; 11, posterior edge of the opercle shows a middle acute angle or spine; 12, predorsal scute series.

1850); recently Alvarado-Ortega and Porras-Múzquiz (2012) claimed on the validity of *Aspidopleurus,* excluding *Prionolepis* from this family]. Woodward (1901) also thought that these extinct fishes are close related with the extant lancet and saber-tooth fishes. Eventually, other genera were added to this family, including *Apateodus* Woodward, 1901; *Volcichthys* D'Erasmo, 1946; *Rharbichthys* Arambourg, 1954; and *Parenchodus* Raab and Chalifa, 1987 (see Jordan, 1905; Gregory, 1933; Arambourg, 1954).

Otherwise, alternative ideas were suggested about the composition and relationships of the Enchodontidae (Regan, 1911; Berg, 1937; among others). Goody (1969) separated *Halec*, *Cimolichthys, Aspidopleurus, Leptecodon*, *Pantopholis,* and *Apateodus* from the Enchodontidae and placed this family into its own suborder, the Enchodontoidei; so the removed genera were included in three suborders (Ichthyotringoidei, Cimolichthyoidei, and Halecoidei) thought as basal representatives of the order Salmoniformes. Later, Rosen (1973) suggested these extinct fishes as part of different lineages of his suborder Aulepisauroidei, into the order Aulopiformes; however, this proposal was not reflected on a formal classification of these genera (Chalifa, 1989). After the discovery of *Parenchodus* in the upper Cenomanian of Israel, this monospecific genus has been considered repeatedly as synonymous with *Enchodus* (Fielitz, 2004; Cavin et al., 2012).

Recently, Nelson (1994) reranked and renamed the Goody's suborders as superfamilies of his suborder Enchodontoidei, in to the order Aulopiformes. Later, Nelson (2006) again reranked these taxa, breaking his own suborder, retaining two superfamilies into Enchodontoidea and raised the other two up to suborder level (Halecoidei and Ichthyotringoidei).

Up to now, at least three phylogenetic hypotheses on *Enchodus* and relatives are published (Fig. 2). Fielitz (2004) and Fielitz and González-Rodríguez (2010) examined the monophyly of the superfamily Enchodontoidea *sensu* Nelson (1994). Fielitz's (2004) data were also used by Cavin et al. (2012) to resolve the relationships of the *Enchodus* sp. from Gavdos, Greece. And the relationships of the suborder Enchodontoidei *sensu* Nelson (1994) were hypotethized by Silva (2007) and Silva and Gallo (2011).

After the review of the short snout enchodontid fossils from the El Chango quarry, including those referred to *Enchodus* by Alvarado-Ortega et al. (2009), we identified three species. One of these species represents a new genus and the other two are referred to *Enchodus*. Hence, the aim of the present work is to provide an accurate description of these short snout enchodontid fishes.

2. Materials and methods

Preparation methods. The acid technique of Toombs and Rixon (1959) was used to prepare part of the specimens described in this work. Pin vises and needles were used under a binocular microscope to clean remaining patches of limestone. As noted in the figures of this text, clean specimens were photographed under white light and when necessary they were coated with dust of magnesium to get black and white photos with high contrast.

Anatomical nomenclature. To facilitate comparison of the osteological details of fishes described here with other taxa already described, the anatomical nomenclature used in this paper follows Goody (1969), Fielitz (2004); Cavin et al. (2012).

Institutional abbreviations. CME, Colección de Material Extranjero, a sub-collection of the Colección Nacional de Paleontología (IGM), Instituto de Geología, Universidad Nacional Autónoma de Mexico. BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany. IHNFG, Instituto de Historia Natural –Fósil, Geográfico–, Museo de Paleontología “Eliseo Palacios Aguilera”, Chiapas, Mexico. MUZ, Museo de Paleontología de Múzquiz, Coahuila, Mexico.

Comparative materials examined. The following specimens were studied with comparative proposes. *Apateopholis laniatus* (Davis, 1887): BSPG 1966 XXV 436 (labeled as *Rhinellus laniatus*) and BSPG 1988 XXV 1329 (labeled as *Rhinellus longirostris*); both from

Hakel, Lebanon. *Aspidopleurus cataphractus* Pictet and Humbert, 1866: BSPG 1966 XXV 179, BSPG 1988 XXV 309 to 311, BSPG 1988 XXV 367 to 369, and BSPG 1988 XXV 1332; all from Hakel. *Aspidopleurus kickapoo* Alvarado-Ortega and Porras-Múzquiz, 2012: MUZ 343 from the La Mula quarry, Mexico. *Eurypholis* Pictet, 1850: CME 678, from Heckel. *Eurypholis boissieri* Pictet, 1850: BSPG 1988 XXV 374 and 376, both from Hakel. *Ichthyotringa furcata* (Agassiz, 1844): AS I 1155 1853 II 501 (in BSPG and labeled as *Rhinellus furcatus*), from Sahel Alma, Lebanon.

Phylogenetic analyses. The taxonomical position and relationships of the new genus described here are supported in two phylogenetic analysis performed with PAUP Version 4.0b10 (Swofford, 2002). Characters and data matrices of similar analyses previous published (Fielitz, 2004; Silva, 2007; Fielitz and González-Rodríguez, 2010; Silva and Gallo, 2011) were updated including this new genus and used in the present essay (Tables 1–4 in the Appendix I). All the analyses were performed under heuristic search, the trees were rooted using a specified out-group, gaps were treated as “missing”, and all characters are unordered and have equal weight. Multistate taxa are interpreted as uncertainty. All trees recovered in these analyses were optimized based on the accelerated transformation (ACCTRAN) criteria. In each analysis, the strict consensus trees were obtained when more than one tree (equally parsimonious) result from the heuristic research.

3. Systematic paleontology

Order Aulopiformes Rosen, 1973
Family Enchodontidae Woodward, 1901

Genus ***Unicachichthys*** nov. gen.
Type species: *Unicachichthys multidentata* nov. sp. described below

Diagnosis. As in the type species described below.

Etymology. The genus name honors the first and third author's *alma mater*, Universidad de Ciencias y Artes de Chiapas. The name is composed after the formal abbreviation of this institution, “UNICACH”, plus the Greek word “ichthys” or fish.

Unicachichthys multidentata nov. sp.

Holotype. IHNFG-2987, almost complete specimen (Figs. 3A; figs. 1 to 5 in Appendix II).

Paratypes. Specimen IHNFG-2988, almost complete fish only lacking the posterior part of both lobes of caudal fin (Fig. 3B; figs. 6 and 7 in Appendix II). Specimen IHNFG-4347, a fish lacking the posterior half of the body preserved in part and counterpart (Fig. 3C; figs. 8 to 12 in Appendix II).

Locality and horizon. El Chango quarry, Ocozocoautla de Espinosa Municipality, Chiapas, Mexico. Cenomanian limestones of the Cintalapa Member, Sierra Madre Formation.

Etymology. The species name is derived from the Latin words “*multum*” and “*dentata*” that mean “many” and “dentated” or “bearing of many teeth”. The combination of the specific and generic names means “the UNICACH's fish with many teeth”.

Diagnosis. Enchodontid fish with nude body except for three small predorsal scutes; lacking supraorbital bone; dermopalatine multitoothed; dentary bearing three rows of teeth and small prongs; articulation lower jaw–quadrate laterally exposed; basal sclerotic bone present; frontal, operclar bones, premaxilla, and dentary

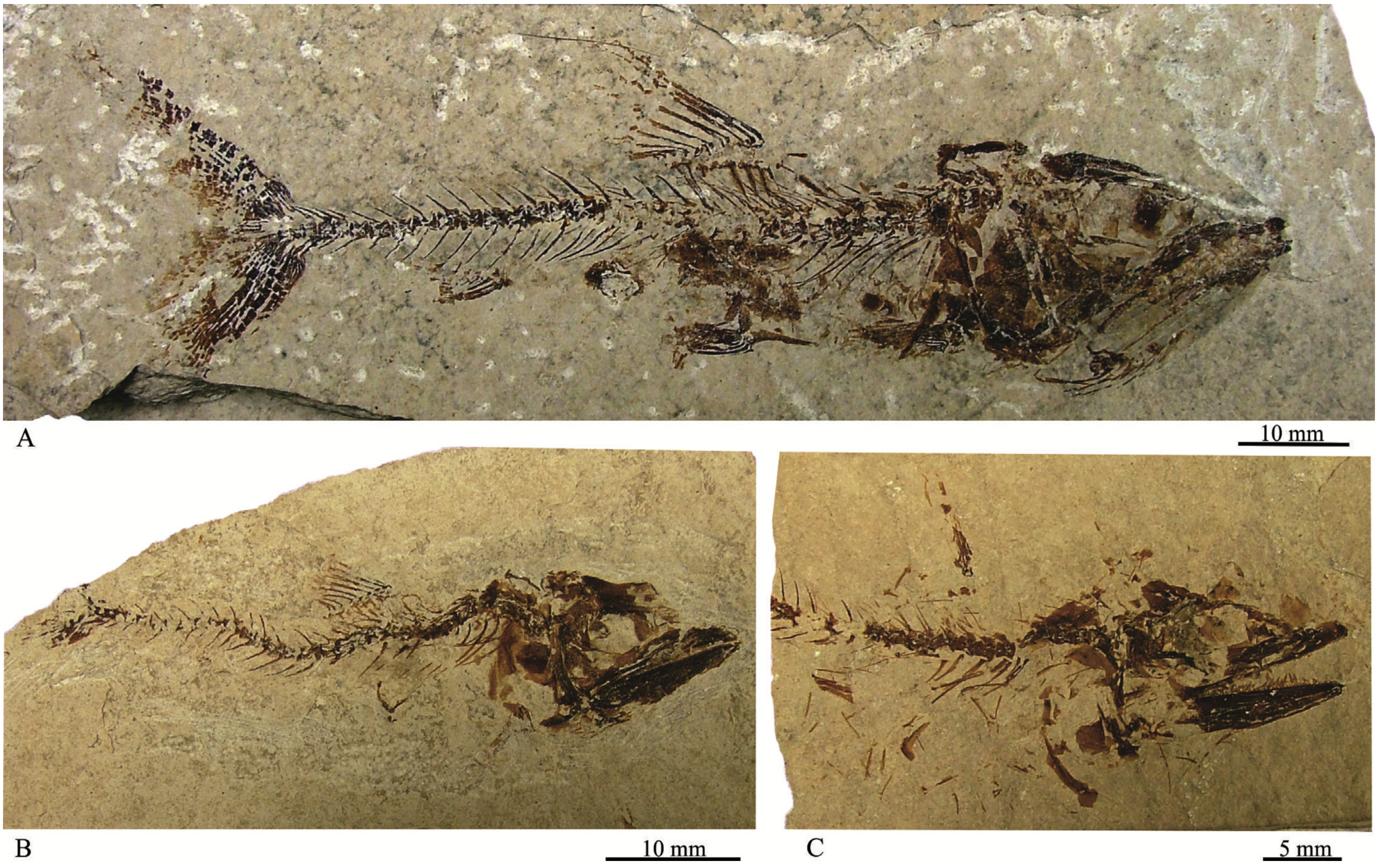

Fig. 3. *Unicachichthys multidentata* nov. gen. and sp.; A, specimen IHNFG-2987, holotype; B, specimen IHNFG-2988, paratype; C, part of the specimen IHNFG-4347, paratype. Appendix II show additional photographs of these specimens.

ornamented with a pattern of radiating ridges and tubercles; opercle with rounded posterior edge and a horizontal strengthening; horizontal posterior limb of the preopercle developed as a stout spine; posterior edge of preopercle vertical limb serrated; 34 vertebrae including 14 abdominal, 18 preural, and 2 ural centra; anterior abdominal neural arches are triangular, robust, and as long as the corresponding centra; abdominal neural arches halves and respective spines are no fused; hypurals fused forming two hypural plates.

3.1. *Description of* Unicachichthys multidentata *gen. and sp. nov.*

General proportions. In this pisciform and slender fish with robust head and shallow caudal peduncle, the fins and girdles are located on the body edge and the maximum body height is between the occiput and the dorsal fin. Table 1 summarizes the meristic data and body proportions of fossils described here. Since, IHNFG-2987 is the most complete specimen known and its vertebrae keep their life position (Fig. 4), the large part of the body proportions of the species are based on this specimen.

The maximum total length known in specimens of *Unicachichthys multidentata* nov. gen and sp. here studied is 108.4 mm, reaching a standard length (SL) of 86.4 mm. The triangular head, about 1.6 times longer than high, is slightly longer than one third of the SL (HL = 34.8–36.5% of SL). The maximum body height is about 21% of SL. The short dorsal fin is placed slightly behind of the middle of the body, from 53.4 to 65.0 % of SL. The small pelvic fin is opposed to the anterior half of dorsal fin, lying close to 56.7 % of SL. The anal fin is shorter than the dorsal fin and is placed far in the back of the trunk, between the 79.9 and 87.5% of SL. The pectoral fin is longer than the pelvic fin and covers one third of the abdominal length. The caudal fin is wide, deeply forked, and made up of two triangular symmetric lobes (Fig. 4).

Skull. The 90% of the skull roof is occupied by a couple of elongated and triangular frontals, which taper anteriorly (Figs. 4, 5). The supraorbital sensory canal is exposed in the frontals, in which it runs alongside and near to the outer edge. A couple of small parietal bones occupy the back of the skull roof; the posterior part of these bones overlap a rectangular supraoccipital bone, which is scarcely exposed by a small triangular flange. Radiating ridges covered with numerous small aligned tubercles strongly ornament all these bones.

The orbital region of the parasphenoid is a narrow, straight, and toothless bar that reaches the ethmoid region of the skull where probably it joins the vomers. Behind, the postorbital region of this bone widens and elevates forming the part of the lateral surface of the skull, in which is not possible to recognize the sutures between this and other bones.

In the ethmoid region of the skull, the mesethmoid articulates with the anterior borders of frontal bones and laterally it is covered by the premaxilla. The lateral ethmoid is a rectangular tilted bone located between the frontal and parasphenoid, which forms the anterior internal wall of the orbit. The specimen IHNFG-2988 seems to have a toothed vomer under the palatine bone.

Orbital bones. Although the circumorbitals are bad preserved in all the available specimens, probably these bones form an incomplete series with no elements above the orbital region. Flat osseous remains scattered around the orbit represent an undetermined number of circumorbital bones. The orbit is occupied by a flat basal sclerotic bone and two sclerotic bones enclosures (Figs. 4, 5, 6).

Hyopalatine series. The hyomandibular is an axe-shaped bone with an articular head somewhat rectangular, in which the articular surface is sinuous and tilted (Figs. 5, 6). The thin and slightly curved ventral process of the hyomandibular reaches the quadrate. The metapterygoid is rectangular and flat bone located between the hyomandibular, quadrate, ectopterygoid, and endopterygoid. The quadrate is triangular bone, about twice longer than high, in which the rounded and short articular head is tilted forward. The articulation between the lower jaw and quadrate is laterally exposed. The spiny symplectic does not exceed the dorsal edge of the quadrate. The ectopterygoid has an anterior thick long bar section toothed and a posterior flat and semicircular dorsal wing. The conical, stout, and acute ectopterygoid teeth have the same size and are evenly spaced along the ventral edge of this bone. The endopterygoid is a flat toothless bone.

The dermopalatine bone is a long semicircular structure with a straight and thick ventral edge, whose length is about the half of

Table 1

Body measurements and proportions, and structure accounts of the specimens named here *Unicachichthys multidentata*. nov. gen. and sp. All the measurements are expressed in millimeters; the proportions expressed as % of the standard length are enclosed between simple-brackets; the proportions expressed as % of the Head length are enclosed in double-brackets.

	IHNFG-2987	IHNFG-2988	IHNFG-4347
Standard length	86.4	51.6	—
Total length	108.4 (125.5)	59.6+ (115+)	—
Head length	31.6 (36.5)	18 (34.8)	19
Pre-dorsal length	46.2 (53.4)	27 (52.3)	24.1
Pre-pelvic length	49 (56.7)	—	—
Pre-anal length	69.1 (79.9)	—	—
Dorsal fin length	10 (11.6)	6 (11.6)	—
Anal fin length	6.6 (7.6)	—	—
Head height	19.6 ((62))	11.5 ((63.8))	≈10 ((≈52.6))
Maximum body height	17.5 (20.2)	≈11 (≈21.3)	≈9
Caudal peduncle height	≈2	1	—
Anal fin rays	9	—	—
Dorsal fin rays	10	9?	—
Pectoral fin rays	11	At least 6	—
Pelvic fin rays	8	—	—
Total vertebrae	34	34	—
Abdominal vertebrae	14	14	—
Caudal vertebrae	20	20	—

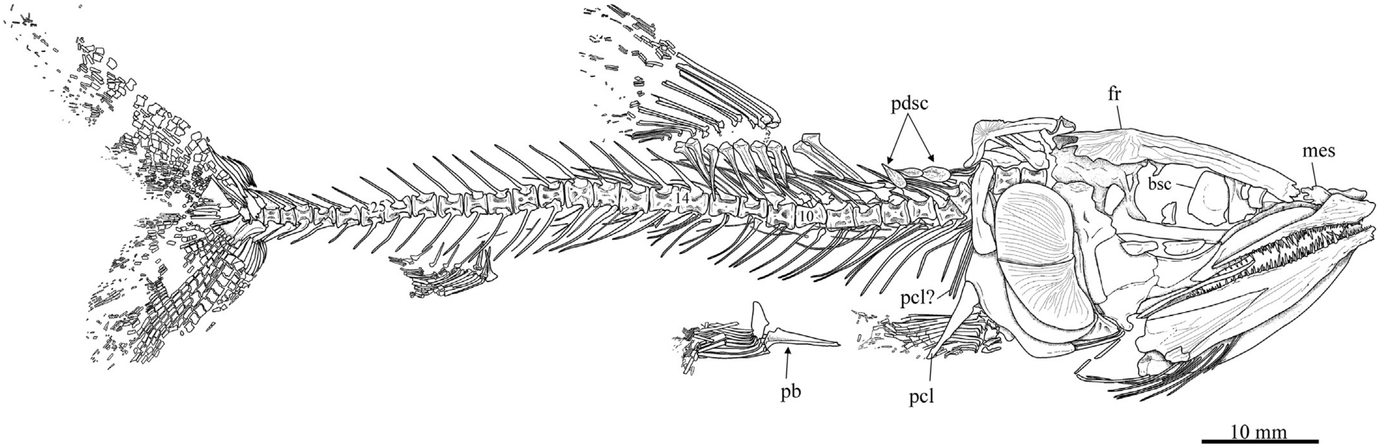

Fig. 4. Idealized drawings of the specimen IHNFG-2987, holotype of *Unicachichthys multidentata* nov. gen and sp., from the El Chango quarry (based on Fig. 3A). Abbreviations: fr, frontal; mes, mesethmoid; pb, pelvic bone; pcl, postcleitrum; pdsc, predorsal scutes (predorsal scute series); numbers on the centra show the position of these bones into the vertebral column.

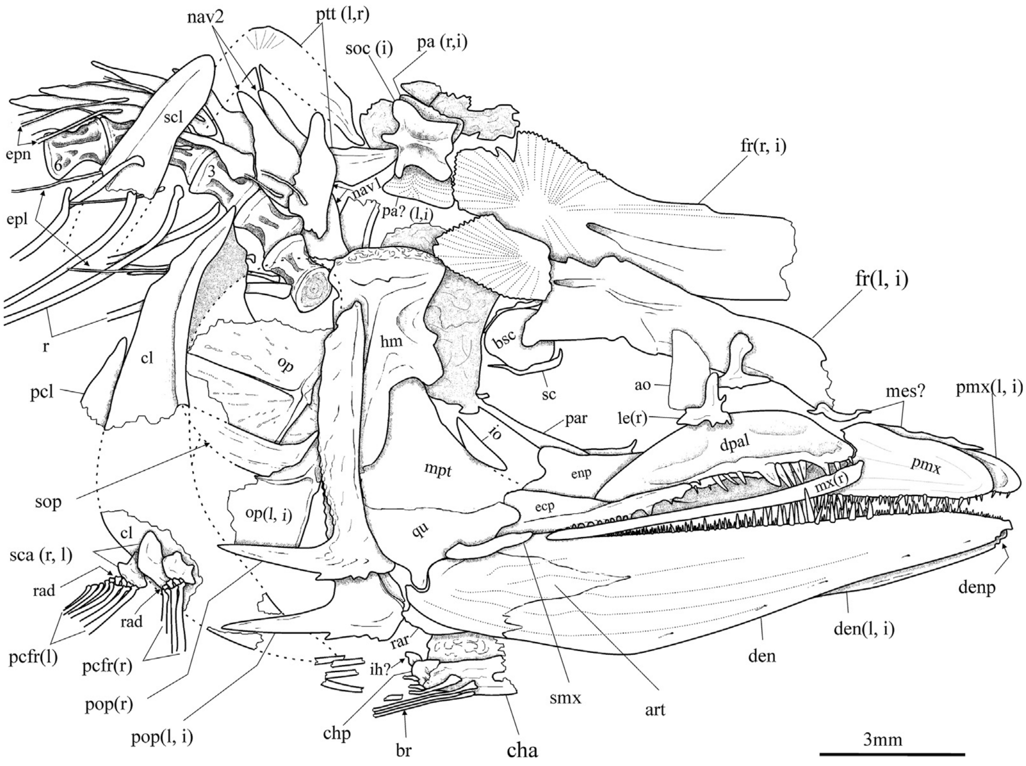

Fig. 5. Idealizedcha, ceratohyal anterior; chp, ceratohyal posterior; drawing of the head of *Unicachichthys multidentata* nov. gen and sp., specimen IHNFG-2988 (paratype), based on fig. 6 of Appendix II; A. Abbreviations: ao, antobital; art, articular; br, branchiostegal ray; bsc, basal sclerotic; cl, cleithrum; cha, ceratohyal anterior; chp, ceratohyal posterior; den, dentary; denp, dentary prongs; dpal, demopalatine; ecp, ectopterygoid; enp, endopterygoid; epl, epipleural; epn, epineural; fr, frontal; hm, hyomandibular; ih, interhyal; io, infraorbital; le, lateral ethmoid; mes, mesethmoid; mpt, metapterygoid; mx, maxilla; nav, naural arch; op, opercle; pa, parietal; par, parasphenoid; pcfr, pectoral fin ray; pcl, postcleitrum; pmx, premaxilla; pop, preopercle; ptt, posttemporal; qu, quadrate; r, rib; rad, radial; rar, retroarticular; sc, sclerotic; sca, scapula; scl, supracleithrum; smx, supramaxilla; soc, supraoccipital; sop, subopercle; letters r and l, arrows in C show the serration in the posterior edge of the preopercle vertical limb; enclosed in brakets indicate the right and left position of paired bones; numbers on the centra indicate their position in the vertebral column.

the lower jaw. Numerous sharp teeth, tightly spaced and irregular sized, are along the ventral edge of this bone. It is unclear if these teeth are arranged in rows or patches (Figs. 5, 6).

Upper jaws. The premaxilla, maxilla, and supramaxilla form the upper jaw (Figs. 5, 6). The large triangular premaxilla is four times longer than deep, where the anterior part rises forming an ascending process. Premaxilla occupies the anterior two thirds of the jaw and is projected backward beyond the anterior edge of the orbit. The premaxilla labial surface is ornamented with some tubercles and ridges projected backward. The alveolar border of premaxilla is straight and shows at least two rows of small, slender, and sharp teeth that are uniformly spaced and curved backward. The maxilla is an elongated, smooth, and toothless laminar bone of uniform height that occupies the posterior third of the jaw. In IHNFG-2988 there is a long, triangular, and flat supramaxilla overlapping the dorsal end of the maxilla.

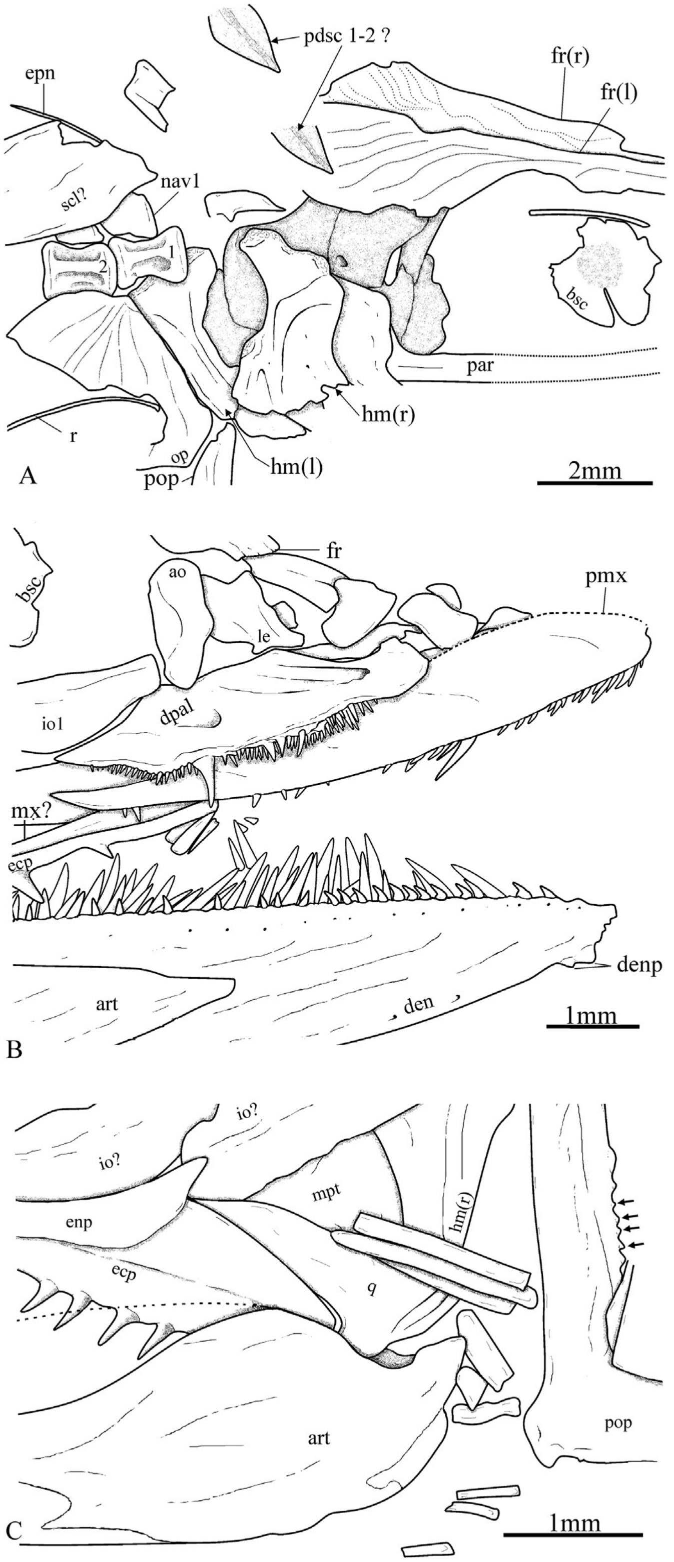

Fig. 6. Idealized drawings of details preserved in the specimen IHNFG-4347, paratype of *Unicachichthys multidentata* nov. gen and sp.; A, posterior part of the head and anterior vertebrae (based on fig. 8 in Appendix II); B, part of the jaws (based on fig. 9 in Appendix II); C, area the articulation of lower jaw and quadrate (based on fig. 12 in Appendix II). Abbreviations: ao, antobital; art, articular; bsc, basal sclerotic; den, dentary; denp, dentary prongs; dpal, demopalatine; ecp, ectopterygoid; enp, endopterygoid; epn, epineural; fr, frontal; hm, hyomandibular; io, infraorbital; le, lateral ethmoid; mpt, metapterygoid; mx, maxilla; nav, neural arch; op, opercle; par, parasphenoid; pdsc, predorsal scute; pmx, premaxilla; pop, preopercle; qu, quadrate; r, rib; scl, supracleithrum; left and right position of paired bines are respectively indicated by r and l within brakets; numbers on the centra indicate their position in the vertebral column.

Lower jaws. The lower jaw is a long and triangular structure in which the alveolar border is straight, the coronoid processes is poorly developed, and the mandibular sensory canal is enclosed. (Figs. 4, 5, 6). This jaw is formed by the dentary, articular, angular, and retroarticular bones, which externally are ornamented with longitudinal ridges. The articulation of this jaw with the quadrate is slightly behind the orbit. The dentary occupies about three quarters of the lower jaw length; near to the anterior end of its ventral border, there are two small and slightly rounded dentary prongs. The symphysial edge of this bone is shallow and sinuous. Dentary is armed with at least three rows of tightly spaced teeth, which include short conical teeth over the alveolar border and longer and sharper teeth placed internally.

Externally, the angular is triangular and projected forward (Fig. 5, 6). Its small articular process forms part of the small and concave facet for the quadrate that is almost horizontally oriented and laterally exposed; above this process, this bone has a thickening band. The lateral internal face of the mandible is preserved as impression in IHNFG-2987; here the articular participates in the facet for the quadrate. The retroarticular seems to be an autogenous bone in the posterior ventral border of the lower jaw.

Opercular bones. The opercular series comprises the opercle, preopercle, and subopercle bones; there is no skeletal remain suggesting the presence of the interopercle (Figs. 4, 5, 6). The opercle is kidney-shaped, about 1.5 times higher than long. Its anterior edge is straight and thicker while the rest of the borders are gently curved. The facet for the hyomandibular is near to the middle of the height of the anterior edge of this bone. Radiating ridges and tubercles originated in the area of this articular facet ornament the external surface of the opercle; in this facet also originates a notable thicker bar or crest that cross horizontally all the opercle length.

The preopercle is an inverted L-shaped bone; its vertical limb is stout and about uniformly wide whereas the horizontal limb forms a stout spine (Figs. 5, 6). The lower half of the posterior edge of the vertical limb is serrated; this condition is given by a series of small tubercles of similar size and equally spaced. The length of the ventral limb is about the half of the preopercle height. This bone has an inconspicuous, short, and rounded anterior ventral process. Irregular ridges cover the external surface of this bone. The subopercle is poorly preserved in the referred specimens; however, this semicircular flat bone that also is intensely ornamented with ridges and tubercles seems to have a short anterior process.

Branchiostegal rays and branchial arch. In IHNFG-2987 there are about 13 branchiostegal rays preserved beneath the lower jaw and subopercle (Fig. 5). These elongated bones attach the anterior and posterior ceratohyals. In IHNFG-2988, the anterior ceratohyal is an elongated flat bone devoid of any foramen and the posterior ceratohyal is a small triangular structure associated with some brachiostegal rays; in this same specimen, a stout rectangular interhyal bone is located above the posterior ceratohyal.

Vertebral column. Thirty four centra form the vertebral column including 14 abdominal and 20 caudal (18 preural and two ural) (Fig. 4). The centra are bobbin shaped, longer than high, and have strong central constrictions reinforced with longitudinal ridges. Those centra in the middle of the body are slightly longer than those located in front and behind. The opercle and pelvic girdle

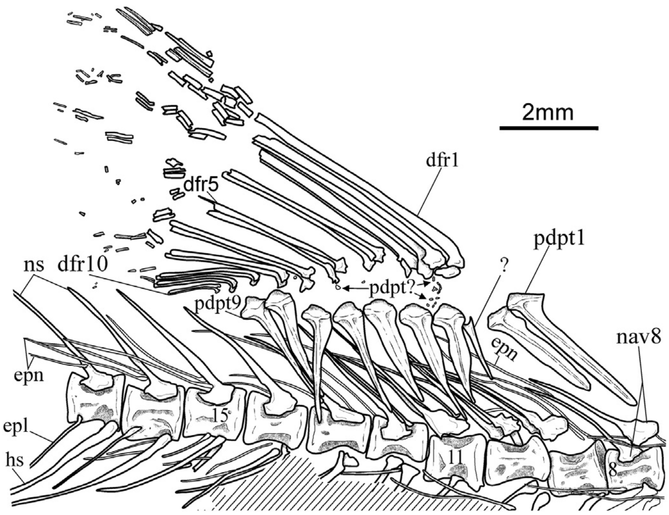

Fig. 7. Idealized linedrawing of dorsal fin preserved in IHNFG-2987, holotype of *Unicachichthys multidentata* gen and sp. nov. ((based on fig. 3 in Appendix II). Abbreviations: dfr, dorsal fin ray; epn, epineural; hs, hemal spine; nav, neural arch; ns, neural spine; pdpt, proximal dorsal pterygiophore; number on the centra show its position into the vertebral column.

cover three or four anterior abdominal centra. Two thirds of the abdominal area is enclosed by 10 pair of ribs, which are thin, slightly curved, and progressively shorter. The proximal end of each rib has a wide head to articulate with the lateral-ventral cavity of the respective abdominal centrum, except in the two posterior abdominal centra that have short stout parapophyses associated with small free ribs.

The abdominal centra are not fused with the large and high neural arches (Figs. 4 to 7); here the opposite halves of the neural arches and the associated neural spines are not fused to each other. The neural arches of the first seven abdominal centra are hypertrophied having a broad triangular shape. All the abdominal centra are associated to autogenous epineurals and epipleurals. Epineurals also are present in the five anterior caudal centra and epipleurals are associated to hemal spines of the seven anterior caudal centra. The epineurals arise on the neural arches. The epipleurals arise near to the articular head of the ribs and in the middle of the hemal spines. No supraneurals are present.

Pectoral girdle and fin. The pectoral girdle includes the posttemporal, supracleithrum, cleithrum, and probably one postcleithrum (Figs. 4, 5). The posttemporal is V-shaped bone with the horizontal limb two times longer than the vertical limb; its surface is ornamented with ridges and tubercles radiating from its vertex. The supracleithrum is a long, ovate, and flat bone with rounded dorsal head; its dorsal half is also ornamented with ridges and tubercles arranged parallel and vertically. The supracleithrum meets with the cleithrum at the level of the vertebral column. The external surface of the cleithrum is boomerang-shaped and weakly ornamented with few ridges. A single wide ovate postcleithrum is present behind the cleithrum, behind this remains of another long structure that probably represents an additional postcleithrum is preserved (Figs. 4, 5).

The pectoral fin is located on the ventral portion of the cleithrum near to the abdominal border of the trunk. Eleven segmented and distally ramified rays form the pectoral fin (Figs. 4, 5). The first and longest of these rays is nearly as long as five abdominal centra reaching the anterior extreme of the pelvic bone; the others rays are progressively shorter. At least four radials articulate with the base of the pectoral rays; these elements show the shape of a dog-bone-cookie (Fig. 5).

Pelvic girdle and fin. The pelvic is a long triangular bone anteriorly tapered, as long as three centra of the abdominal region. Probably both pelvic bones meet to each other along their middle edge. The lateral or ischial process well developed in the rear of the pelvic bone. The pelvic fin rises below abdominal centra 12, near to the middle of the body, and opposed to dorsal fin. Eight segmented and branched rays form the pelvic fin. The tips of pelvic rays are not preserved; however, it is possible to see that the pelvic fin is shorter than the pectoral (Fig. 4).

Dorsal fin. This is a triangular structure that consists of 10 dorsal rays supported on nine pterygiophores in the holotype and nine rays and nine pterygiophores in IHNFG-2988. The base of this fin is above the abdominal centra 11–15 (Figs. 4, 7). The terminal half of all dorsal fin rays is segmented and branched. The dorsal pterygiophores are like spines with anterior and posterior laminar wings; the first of these is as long as three abdominal centra located between the neural spines of abdominal centra 8 and 7; the remaining pterygiophores tend to be shorter. The holotype probably has distal dorsal pterygiophores.

Anal fin. This triangular fin is shorter than the dorsal fin; this consists of nine segmented and branched rays lying below vertebrae 21–24 (=preural centra 9–12) (Fig. 8). Eight long proximal anal pterygiophores support this fin; the first three have anterior and posterior laminar wings and are the longest in the series; the first is placed between the hemal spines of centra 20 and 21 (=preurals 13 and 14). Distal anal pterygiophores are small paired bones located between the anal proximal pterygiophores and rays. The holotype shows an anal fin stay; this wide, flat, and triangular structure is located at the end of the fin base.

Caudal fin. The triangular dorsal and ventral caudal fin lobes are so posteriorly separated from each other that the maximum height of the fin exceeds the trunk height. This fin consists of 19 principal rays into I+8–9+I order, which respectively are preceded by eight dorsal and seven ventral procurrent rays (Figs. 4, 9).

The caudal fin is supported on thick hemal and neural spines fused to the first three preural centra, which are strongly tilted backward. Among these neural spines that on the preural 2 is the thickest. The first pleural probably is fused with two uroneurals

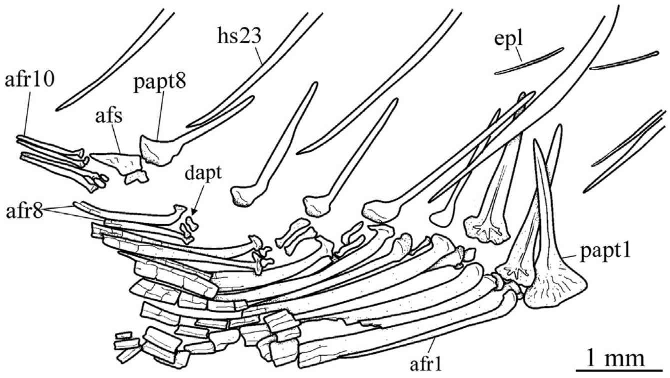

Fig. 8. Idealized linedrawing of anal fin preserved in IHNFG-2987, holotype of *Unicachichthys multidentata* nov. gen and sp. (based on fig. 4 in Appendix II). Abbreviations: afr, anal fin ray; afs, anal fin stay; dapt, distal anal pterygiophore; epl, epipleural; hs, hemal spine; papt, proximal anal pterygiophore.

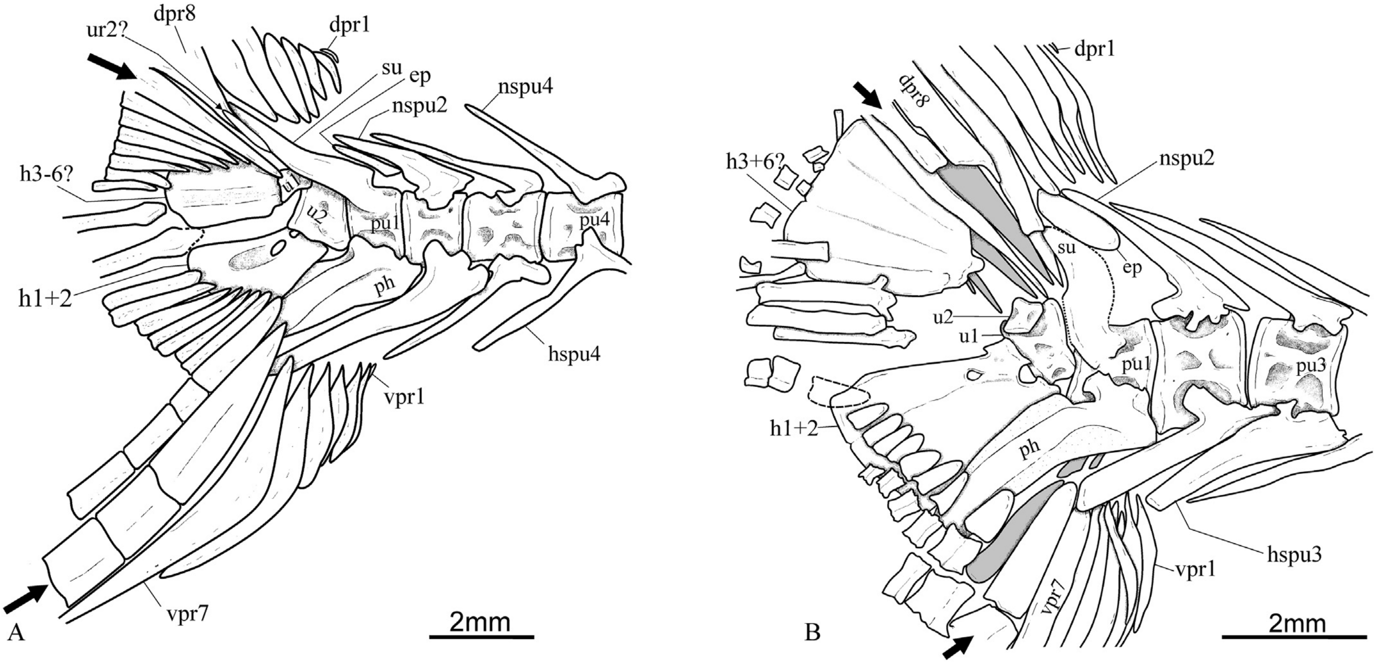

Fig. 9. Idealized linedrawings of caudal skeletons preserved in specimens of *Unicachichthys multidentata* nov. gen and sp.; A, IHNFG-2988, paratype (based on fig. 7 in Appendix II); B, IHNFG-2987, holotype (based on fig. 5 in Appendix II). Abbreviations: dpr, procurrent ray of dorsal caudal fin lobe; ep, epural; h1+2, hypural 1 and 2 fused to each other; h3+6, hypural plate formed by the fusion of hypurals 3 to 6; hspu, hemal spine of preural centrum; nspu, neural spine of preural centrum; ph, parhypural; pu, preural centrum; su, stegural; u, ural centrum; ur, uroneural; vpr, procurrent ray of ventral caudal fin lobe; arrows enclose the principal caudal fin rays in the upper and lower lobes.

forming a wide and long stegural. It is not clear if preural 1 has a neural arch because the stegural covers this part of the skeleton. Parhypural is a stout structure attached to preural 1 that has two laminar wings projected forward and back from its base. In IHNFG-2988, a free uroneural is present behind the stegural (Fig. 9). A wide epural is present between the stegural and the hemal spine of preural 2.

Two unfused ural centra are present; these are relatively smaller than the last preural centra. Hypurals are fused to each other forming two fan structures, in which the number hypurals involved is only suggested by some longitudinal thickenings. Hypurals 1 and 2 forms a ventral hypural plate that has two short articular heads for ural 1. Four hypurals probably are fused into the dorsal hypural plate, which joints with the small ural 2 (Fig. 9).

Scales and scutes. The body is naked except by a series of three small predorsal scutes placed between dorsal fin and occiput. These scutes are small, flat, and long ovoid; they are ornamented with inconspicuous and unordered ridges that produce a rough superficial appearance. The predorsal scutes are dislocated in all the specimens studied; therefore, it is not possible to conclude if these were in contact to each other nor the area that they cover on the predorsal edge (Figs. 4, 6, 10).

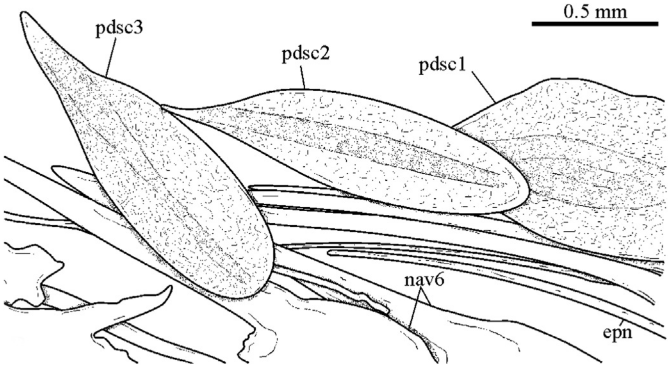

Fig.10. Idealizede linedrawing of predorsal scutes preserved in IHNFG-2987, holotype of *Unicachichthys multidentata* nov. gen and sp. (based on fig. 2 in Appendix II). Abbreviations: epn, epineural; nav, neural arch; pdsc, predorsal scute.

3.2. *Remarks on* Unicachichthys multidentata *gen and sp. nov.*

Unicachichthys multidentata nov. gen. and sp. is identified as a new member of the family Enchodontidae, previously analyzed by other authors (Fielitz, 2004; Silva, 2007; Fielitz and González-Rodríguez, 2010; Silva and Gallo, 2011; and Cavin et al., 2012). The monophyly of this family is a general agreement except for the problematic inclusion of some genera (e.g. *Rharbichthys*) and the composition of the in-groups (Fig. 2). *Unicachichthys multidentata* nov. gen. and sp. has some of the synapomorphies supporting the monophyly of this family and in-groups already published. The remarkable characteristics of this new Mexican fossil fish are the lack of interopercle and supraorbital, the presence of the horizontal strengthening or bar in the opercle, the radiating tubercles ornamenting the opercle and subopercle, the presence of anteroventral prongs on dentary, and the occurrence of a series of predorsal scutes between the occiput and the dorsal fin (2–6, and 12 respectively in Fig. 2); all these characters suggest that this new species belongs to the family Enchodontidae. Additionally, in this fish, horizontal limb of the preopercle forms a long stout spine (10 in Fig. 2) suggesting that it could be member of the subfamily Eurypholinae (*Eurypholis* plus *Saurorhamphus*); however, the presence of a dermopalatine bone bearing numerous teeth is a significant character of *Unicachichthys multidentata* gen. and sp. nov. that conflicts with a supposed diagnostic character (synapomorphy) of the family Enchodontidae previously accepted by other authors, in which the dermopalatine bears a single long tooth (1 in

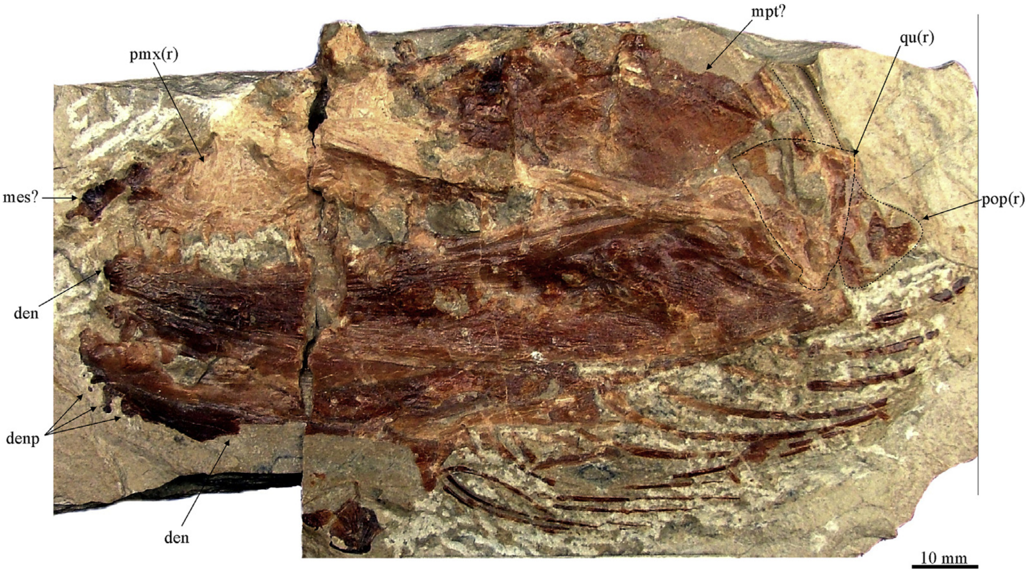

Fig. 11. *Enchodus* sp. 1 from the El Chango quarry, specimen IHNFG-2989. Abbreviations: den, dentary; denp, dentary prongs; mes, mesethmoid; mpt, metapterygoid; pmx, premaxilla; pop, preopercle; qu, quadrate; enclosed in brackets (r) and (l) indicate the right or left position of paired bones, respectively.

Fig. 2). This dermopalatine multi-tooth condition may represent a plesiomorphic condition that deserves further analyzes; therefore, the relationships of *Unicachicthys* beyond the family level suggested in this paper are based on our own phylogenetic analyses. Other primitive condition present in this new species is the presence of a basal sclerotic bone, which had not been previously documented in this family.

Genus ***Enchodus*** Agassiz, 1835
Type species: *Enchodus lewesiensis* (Mantell, 1822), Cenomanian-Campanian Chalk deposits of Sussex, southeastern England.

***Enchodus* sp1.**

Material referred. Specimen IHNFG-2989 (Fig. 11), specimen extremely fragmented showing complete lower jaw, part of the bones that form the upper jaw, and some elements of the hyomandibular and opercular series.
Locality and horizon. El Chango quarry, Ocozocoautla de Espinosa Municipality, Chiapas, Mexico. Cenomanian limestones of Cintalapa Member, Sierra Madre Formation.

3.3. *Description of* Enchodus *sp1. from the El Chango quarry*

The lower jaw of this specimen is 110 mm long, which suggest that the complete specimen probably had 60 cm of standard length (Fig. 11). This is the largest Enchodontidae specimen as far collected in the El Chango quarry. The lower jaw is triangular having a straight and long alveolar border and a gently curved ventral border; it shows a very shallow symphysis and an extremely reduced coronoid process. The dentary forms the two anterior thirds of the lower jaw, and the rest is occupied mainly by the angular. The articulation of lower jaw with the quadrate is laterally exposed. There are three stout processes or prongs in the anterior end of the ventral border of the dentary bone. Along the alveolar border there is a row of large and conical fang-like teeth, which are uniformly spaced in the posterior half of the jaw; additionally, smaller teeth constitute an additional row that is located on the lingual surface of the jaw. The external surface of this bone is intensely ornamented with longitudinal ridges on which there are tubercles. A small area alongside the posterior border of the angular, where the surface is smooth but the bone is thicker, stands as a vertical bar. The mandibular sensory canal is exposed at least in the anterior half of the lower jaw.

The ventral edge of the right premaxilla bone is preserved in this specimen; it shows a row of relative small teeth along its alveolar border. The ventral part of the preopercle shows the wide rounded shape of its anterior and posterior limbs. No interopercle remains are preserved.

3.4. *Remarks on* Enchodus *sp1. from the El Chango quarry*

Despite the extremely incomplete condition of IHNFG-2989; its inclusion into the genus *Enchodus* is supported because it shares some synapomorphies and diagnostic characters of the family Enchodontidae defined by Fielitz (2004: 627–632). This specimen lacks the interopercle as other enchodontids and it shows dental prongs as *Eurypholis*, *Saurorhamphus*, and *Enchodus* (including *Parenchodus*) (2 and 5 in Fig. 2, respectively). In *Eurypholis* and *Saurorhamphus* the articulation between the lower jaw and the quadrate is hidden (9 in Fig. 2) while in IHNFG-2989 this articulation is laterally exposed as in *Enchodus* and other enchodontds.

The inclusion of IHNFG-2989 within *Enchodus* is supported in two characters. As occurs in the other members of this genus, in this fossil the preopercle is triangular, broad anteriorly and posterioly (7 in Fig. 2). In this specimen the posterior border of the angular has a smooth and thicker vertical bar; Fielitz (2004) noted that this character is also present in *Cimolichthys* but among enchodontids this is only present in *Enchodus.* Currently, the specific allocation of this specimen is not possible.

***Enchodus* sp2.**

Material referred. Specimen IHNFG-2653, small fish lacking the anterior part of the head and the trunk behind the dorsal fin (Fig. 12).
Locality and horizon. El Chango quarry, Ocozocoautla de Espinosa Municipality, Chiapas, Mexico. Cenomanian limestones of Cintalapa Member, Sierra Madre Formation.

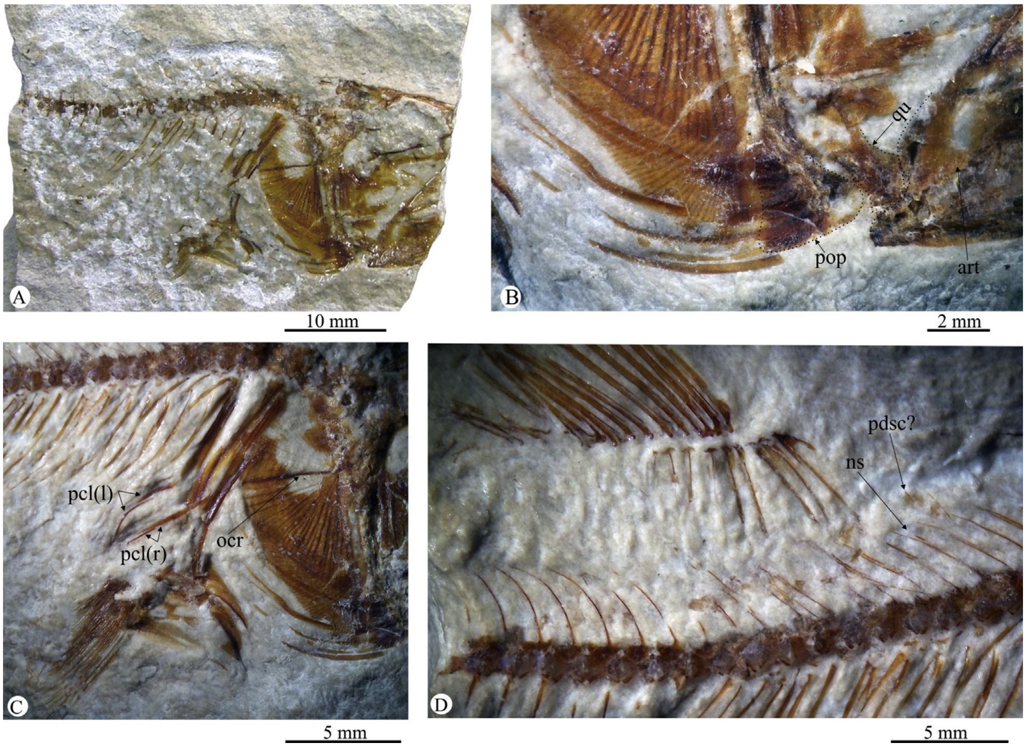

Fig. 12. *Enchodus* sp. 2 from the El Chango quarry, specimen IHNFG-2653; A, general view before the preparation; B, region of the articulation between the lower jaw and the quadrate; C, region of the pectoral girdle; D, region of the dorsal fin. Abbreviations: art, articular; ns, neural spine; ocr, opercular crest; pcl, postcleitrum; pdsc, predorsal scute; pop, preopercle; qu, quadrate.

3.5. *Description of* Enchodus *sp2. from the El Chango quarry*

The partial skeleton preserved in the specimen is 37 mm in length (Fig. 12). This suggests that the complete specimen may have 70 mm of standard length. The bones of the posterior part of the head are bad preserved that is hard to describe them. The orbital section in the parasphenoid is a narrow and toothless bar. Remains of two small and elongated circumorbital bones border the orbit ventrally. The hyomandibular is a t-shaped bone and the metapterygoid is somewhat flat and rectangular. Below of these bones, the quadrate is triangular with a rounded and short articular head projected anteroventrally. The articulation of lower jaw and quadrate is laterally exposed. The smooth posterior vertical thick area or bar alongside the posterior border of the articular bone is present. No ornaments are visible on the surface of the lower jaw.

Bones of the opercular series are well preserved (Figs. 12). The opercle is kidney-shaped, about 1.5 times higher than long; its anterior edge is straight and thicker with the articular facet for the hyomandibular located near the middle of its height. The external surface of this bone is intensely ornamented with ridges and tubercles that radiate from its articular process area. It is noticeable a middle horizontally crest or thicker ridge crossing all the opercle length.

The preopercle is a triangular bone, in which the vertical limb is uniformly narrow and the horizontal limb is expanded ventrally and posteriorly (Fig. 12B). The subopercle is a semicircular flat bone beneath the ventral edge of the opercle. The interopercle is not present. The preopercle and subopercle are ornamented with the same pattern of ridges and tubercles noted in the opercle. Seven elongated and curved branchiostegal rays are preserved and distributed beneath the preopercle and subopercle.

About 23 vertebrae are preserved, including 14 or 15 abdominal centra. All centra are bobbin shaped, slightly longer than high; the first three do not have ribs but the next 11 or 12 have long ribs that enclose two thirds of the abdominal area. The ribs are thin, slightly curved, and progressively shorter; in these the proximal end is slightly expanded forming a head that probably attach directly on the lateroventral surface of the respective vertebra. The neural and hemal arches are small and probably fused with the centra. The neural and hemal spines are long, uniformly thin, and undivided structures except for those in the abdominal region that are bifid from their join with the neural arches. Probably the neural arches of abdominal vertebrae are kept as unfused halves. In this specimen some epineurals and epipleurals are preserved.

The cleithrum and two postcleithra are exposed in the pectoral girdle (Fig. 12C). The external surface of the cleithrum is narrow and C-shaped; the height of its vertical limb is two times the length of its horizontal limb. There are two thread-like postcleithra. Eighteen branched and segmented rays form the pectoral fin. The dorsal fin is triangular and includes 16 branched and segmented rays supported by undefined number of dorsal pterygiophores (9 are preserved). The dorsal pterygiophores have anterior and posterior wings. The body is totally nude; no scales are present, except for the remains of a small flat and ovoid structure that could to be a predorsal scute (Fig. 12D).

3.6. *Remarks on* Enchodus *sp. 2. from the El Chango quarry*

Despite the scarce morphological data recovered from IHNFG-2653 (Fig. 12); it is possible to recognize this as a member of Enchodontidae and *Enchodus* because it shares some diagnostic and synapomorphies of this family identified by Fielitz (2004). IHNFG-2653 lacks of interopercle as other enchodontids (2 in Fig. 2); its opercle shows the central ridge or crest and lacks the supraorbital bone as in *Palaeolycus*, *Eurypholis*, *Saurorhamphus*, and *Enchodus* (including *Parenchodus*) (4 in Fig. 2); the preopercle is triangular, broad anteriorly and posterioly, as in the species of the genus *Enchodus* (7 in Fig. 2); and its opercle, preopercle, and subopercle are ornamented with the same pattern of ridges-plus-tubercles (6+ in Fig. 2) found in nominal species of *Enchodus* but *E. marchesettii* (Kramberger, 1895). The smooth and thicker vertical bar alongside the posterior border of the articular bone, noted in IHNFG-2653, also is diagnostic of *Enchodus*. Currently, the specific allocation of this specimen is not possible.

4. Phylogenetic analyses

The relationships of *Unicachichthys multidentata* nov. gen. and sp. into the family Enchodontidae documented here are supported on the results of two phylogenetic analyses, which involve the replication of previous studies (Figs. 2, 4, and Appendix I). Data matrices used in those previous studies (Fielitz, 2004; Silva, 2007; Fielitz and González-Rodríguez, 2010; Silva and Gallo, 2011) were updated in the present study including *Unicachichthys* and other considerations (Appendix I). The specimens here identified as *Enchodus* 1 and *Enchodus* 2 are not included in these analyses because their fragmentary condition provides poor morphological data.

The phylogenetic approach deployed in this work is not intended as an exhaustive effort to generate a new phylogenetic hypothesis of Enchodontidae. This does not attempt to support or reject any of the hypotheses previously described because: 1) the previous studies are partially incompatible given that they are built on different hierarchical taxonomical levels (genus *versus* species); 2) these try to resolve the relationships of different taxonomical groups (suborder *versus* family); and 3) these are supported on numerous different characters. The authors simply employ these hypotheses as frameworks to support the recognition of *Unicachichthys* as a new member of the family Enchodontidae. Figure 13 shows the simplified versions of the two phylogenetic studies widely documented in Appendix I; this figure is intended to facilitate comparison with previous phylogenetic hypothesis (Fig. 2).

4.1. Phylogenetic analysis 1: based on Silva (2007) and Silva and Gallo (2011)

This phylogenetic analysis includes the characters and data matrix considered by Silva (2007) and Silva and Gallo (2011) to resolve the relationships among genera of the suborder Enchodontoidei *sensu* Nelson (1994) (tables 1 and 2, Appendix I). The data matrix is updated considering the following observations: A) *Aspidopleurus* is a valid genus (see Alvarado-Ortega and Porras-Múzquiz, 2012) and is used rather than *Prionolepis*. B) Giersch (2014:65) noted that *Robertichthys* Blanco, Alvarado-Ortega, and Gallo, 2008, probably is not an enchodontoid (one of us (JAO) agrees with this observation) and so it was removed from the analysis. C) Character 6 (number of teeth on dermopalatine) are coded as 0 and 2 in *Saurorhamphus* and *Enchodus* respectively, instead "?" of Silva (2007) and Silva and Gallo (2011); these changes are based on the report of a sparse row of teeth on the dermopalatine in *Saurorhamphus* by Chalifa (1985, p. 186) and the occurrence of a single long tooth on the dermopalatine of all the species of *Enchodus* (Fielitz, 2004, p. 634). D) Although Silva and Gallo (2011:510 and appendix II) described only two states of character for their character 17 (supraorbital sensory canal in the skull roof covered (0) or exposed (1); their coded this as 2 in *Aspidopleurus*

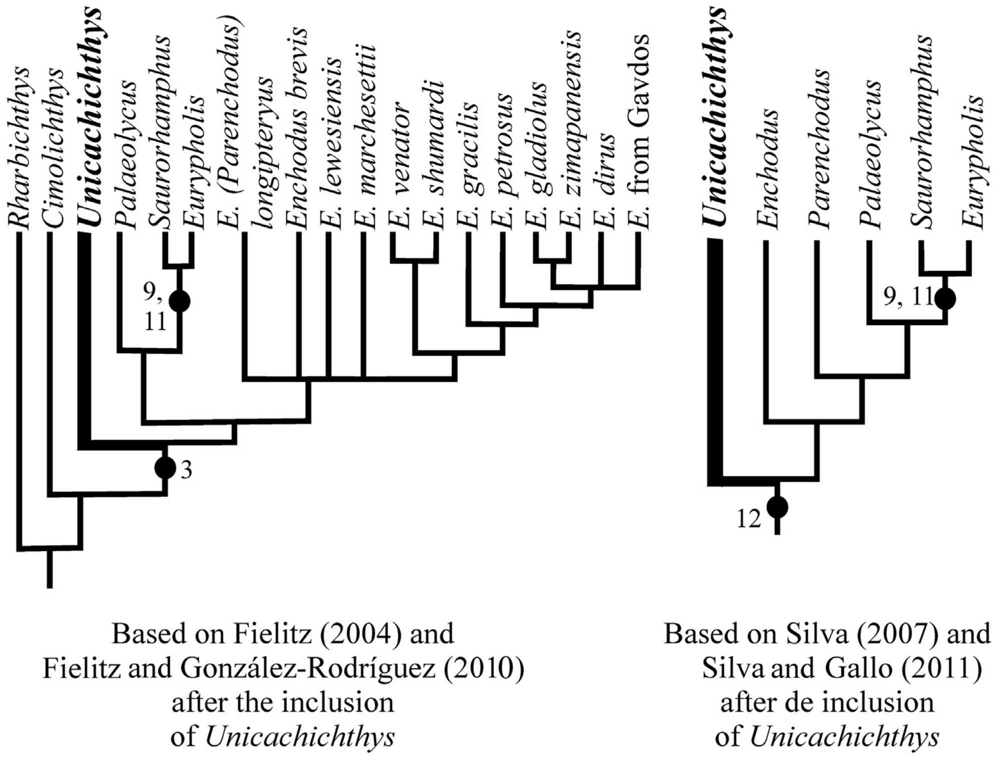

Fig. 13. Phylogenetic hypotheses of the family Enchodontidae including *Unicachichthys* gen. nov. from the El Chango quarry, based on previous phylogenetic hypothesis of this family (compare to Fig. 2 and Appendix I). Synapomorphies: 3, Supraorbital bone absent; 9, articulation of the lower jaw and quadrate is covered; 11, posterior edge of the opercle shows a middle acute angle or spine (at the end of the horizontal middle horizontal strengthening or bar of this bone); 12, predorsal scute series.

(=*Prionolepis*), *Eurypholis*, *Saurorhamphus*, and *Parenchodus*. We consider this situation as a simple stenographic mistake and we modify the state of character (to 1) in the updated data matrix. E) Contrary to Silva and Gallo (2011, state 0 of character 22), who considered the dilatator fossa of *Cimolichthys* as unroofed, Goody (1969: 36) describe this as roofed; hence, we coded 1 for this genus in the updated data matrix instead 0. F) *Enchodus* species have an opercular horizontal strengthening ridge or crest (see Goody, 1969; Fielitz, 2004; among others) (this character is unknown only in *E. lewesiensis*); hence, the character number 60 (opercle crest) in this genus is coded as 1(=present) for *Enchodus* rather than 0 (absent) as in Silva and Gallo (2011, appendix II). G) The characters 56 (shape of the preopercle) is coded as 1 in *Unicachychthys* because the shape of its preopercle is similar to those of *Eurypholis boissieri* and *Saurorhamphus*.

The updated data matrix used in the present analysis includes 34 taxa and 87 characters (table 2, Appendix I). The out-group taxa considered in this analysis are the same than in the previous analyses, *Protostomias* (Stomiiformes), *Trachinocephalus* (Aulopiformes), and *Sardinioides* (Myctophiformes). We obtained 138 equally parsimonious trees of 432 steps; all of them with consistency index (CI) equals to 0.2431. Figure 1 in Appendix I shows the strict consensus tree. This result contrasts with that obtained in the previous studies that produced 93 equally parsimonious trees of 437 steps, and similar CI of 0.24, (Silva and Gallo, 2011, p. 495). This result agrees with conclusions of previous works that show the suborder Enchodontoidei as unnatural clade because two members of the out-group, *Protostomias* and *Trachinocephalus*, are revealed as part of the in-group taxa (node D of Figure 1 in Appendix I).

The resulting low values of CI of the present and previous phylogenetic studies show the absence of synapomorphies among the morphological evidences included in the analyses. Our assay reveals the presence of only seven irreversible derived characters that result in six synapomorphies plus one autapomorphy (fig. 1, Appedix I). Among these synapomorphies, one is involved in unifying Enchodontidae as a monophyletic family and other three defining its internal taxa (3, 5, 9, and 11 in Fig. 13). Our result shows the Family Enchodontidae including *Unicachichthys* nov. gen. as a monophylectic group supported on a single synapomorphy, the occurrence of predorsal scutes (12 in Fig. 13 and 87-1 in fig. 1, Appendix I), and 12 homoplasic characters (node N, fig. 1 in Appendix I). These homoplasies include 4 characters not observed in *Unicachichthys* nov. gen. (vomerine teeth present; posterior edge of the frontal reaches the level of the autosphenotic spine; hyomandibular facet in ventral position; and lack of mesocoracoid); as well as other 8 characters documented here in this new genus, including the supraorbital sensory canal exposed in the skull roof; lack of supraorbital; premaxilla posterior tip reaches the orbit; premaxilla with an ascending process; toothless maxilla; upper jaw teeth of different size; dentary prongs present (absent in *Palaeolycus*, *Eurypholis*, and *Saurorhamphus*, see below); and 20 caudal vertebrae.

In the present analysis, monophyly of the family Enchodontidae minus *Unicachichthys* nov. gen. is based on a singular mixture of five homoplasic characters (Node P, fig. 1, Appendix I). These characters include the occurrence of one dermopalatine tooth; demopalatine length equals or shorter than its tooth; mandibular sensory canal partially open; long anal fin (with at least 15 rays); and hypurals not fused to each other. Contrary, *Unicachichthys* nov. gen. has a demopalatine bearing many teeth; this dermopalatine is at least two times longer than its teeth; the mandibular sensory canal is enclosed by bone; the anal fin is short (it consists of nine anal fin rays); and the hypurals are in two fan plates.

In the present analysis, *Palaeolycus* plus *Eurypholis* and *Saurorhamphus* constitute the most derived group within the family Enchodontidae (Node Q, fig. 1, Appendix I), which share a single synapomorphy, a fenestra in the premaxilla; as well as nine homoplasies including a slightly elongate body, the maxilla place behind the premaxilla; as these occur in *Unicachychthys*; bones of the skull roof ornamented only with tubercles; pterotic projected beyond the occiput; toothless endopterygoid; absence of supramaxilla; dentary without prongs; more than 20 caudal vertebrae, and the pelvic fin origin is anterior of the dorsal fin. Contrary, in *Unicachichthys* the skull roof bones are ornamented with tubercles and ridges; the pterotic bone and endopterygoid teeth are unknown; there is a supramaxilla, at least two dentary prongs, and only 20 caudal vertebrae; and the pelvic fin entirely is opposed to the dorsal fin base.

Finally, our result reveals *Saurorhamphus* and *Eurypholis* as the most derived and the best supported enchodontid in-group (Node R, fig. 1 in Appendix I). The monophyly of this group is supported in two synapomorphies including the quadrate-mandibular articulation hidden and the posterior edge of opercle forming a spine (9 and 11 in Figs. 2 and 13; and 52-1 and 61-1, fig. 1, Appendix I). Additionally, nine homoplasies also support this group; these include the occurrence of posttemporal fossa roofed and the posterior border of frontal located behind the autosphenotic spine, which are characters unknown in *Unicachichthys*. Others of these homoplasic characters are the upper jaw teeth absent or being of similar in size; the presence of flank scutes of triangular shape and ordered in a single row; these differ from *Unicachichthys nov. gen.* that has upper jaw teeth of different size and no flank scutes. The other five of these homoplasies are also present in *Unicachichthys nov. gen.* (mandibular sensory canal enclosed by bone, retroarticular process present, posteroventral spine in the preopercle well-developed, and the high position of pectoral fin (the last finray placed at the level of the ventral border of the opercle or a little above).

4.2. Phylogenetic analysis 2: based on Fielitz (2004) and Fielitz and González-Rodríguez (2010)

The present analysis includes all data built by Fielitz (2004) to resolve the relationships within Enchodontidae and later used by Fielitz and González-Rodríguez (2010) to recognize the position of the *E. zimapanensis* within this family (tables 3 and 4, Appendix I). Our updated of this data matrix incorporates data of two additional taxa, *Enchodus* from Gavdos described by Cavin et al. (2012), *Unicachichthys multidentata* nov, gen. and sp. described here in; as well as one additional character – the predorsal scute series- that was revealed as a synapomorphy of Enchodontidae by Silva (2007) and Silva and Gallo (2011) (character 88, tables 3 and 4, Appendix I). As in Fielitz's (2004) study the out-group considered in the analysis includes *Myctophus* and *Diplophos*. The resulting updated data matrix used in this analysis includes 28 taxa and 88 characters.

Figure 13 and figure 2 of Appendix I show the consensus of those analysis result in 24 equally parsimonious trees of 276 steps and CI = 0.504 obtained in the present phylogenetic analysis. This consensus tree slightly contrasts with those published by Fielitz (2004, p. 626) and Fielitz and González-Rodríguez (2010, p. 1348). In the first of these studies only three equally parsimonious trees of 247 steps and CI = 0.24 were recovered while the second generated nine equally parsimonious trees of 252 steps and CI = 0.55.

Our result suggests the integration of *Unicachichthys multidentata* nov. gen. and sp. within Enchodontidae is not opposed to the monophyletic nature of this family (Fig. 13); however, it shows different relationships among enchodontids (see Fig. 2). According Fielitz (2004), *Rharbichthys* and *Palaeolycus* are located in their own subfamily (Rharbichthinae and Palaeolycinae, respectively) and *Cimolichthys* is not a member of the family Enchodontidae. Our result suggests that the Fielitz's subfamilies could be artificial. In one side, *Rharbichthys* has a more remote position than *Cimolichthys* in relation to *Enchodus* and allies, and their integration into Enchodontidae are weakly supported only on a combination of homoplasic characters (Nodes G and H, fig. 2, Appendix I); the exclusion of *Rharbichthys* from this family was also noted by Fielitz and González-Rodríguez (2010, fig. 11), whose phylogenetic tree contains the non-discussed polytomy *Rharbichthys-Cimolichthys*-Enchodontidae. And in the other side, here in *Palaeolycus* is located far from the base tree and forms the most derived monophyletic enchodontid group with *Eurypholis* and *Saurorhamphus* (Node K, fig. 2, Appendix I).

Based on our resulting tree (Fig. 13), the Enchodontidae family is defined in the first node of the in-group supported with a synapomorphy (Node I, fig. 2, Appendix I). This node shows that *Unicachichthys* nov. gen. is the sister group of other enchodontid fishes [*Enchodus* [*Palaeolycus* [*Saurorhamphus, Eurypholis*,]]], (*Rharbichthys* and *Cimolichthys* are close related but not form part of this family). In this sense one synapomorphy defines this family Enchodontidae —the lack of supraorbital - (3 in Figs. 2 and 13; 43-1, fig. 2, Appendix I) documented in *Unicachichthys* nov. gen., as well as in seven homoplasic characters also documented in this new Mexican fish, which include skull roof bones ornamented with radiating ridges, presence of dentary prongs, mandibular sensory canal enclosed by bone, opercle bearing a horizontal strengthening ridge or bar, preopercle ornamented with ridges, and opercle and subopercle ornamented with ridges and tubercles, and cleithrum ornamented with ridges (fig. 2, Appendix I). Two additional homoplasic characters of Enchodontidae are unknown in *Unicachichthys* nov. gen., these are related with the exposition of the occipital sensory canal on parietal bones and the shape of the dermopalatine teeth (5 and 15 in tables 3 and 4, fig. 2, Appendix I)

In this phylogenetic analysis, *Unicachichthys multidentata* nov. gen. and sp. differs from the other enchodontids that form a monophyletic group in a mixture of homoplasic characters (Node J, fig. 1, Appendix I). These characters include an ectopterygoid with few teeth (between six to eight) with the second tooth being longest; a single dermopalatine tooth longest than this bone; lacking of supramaxilla; two tooth rows on dentary in which the first of the outer row is at least 33% longer than others; eight infraorbital bones; and one postcleithra. Contrary, in *Unicachichthys* the number of ectopterygoid teeth is unknown but all of them are of similar size; the dermopalatine bears multiple teeth that are smaller than the dermopalatine length; the number of postcleithra could be one or two; and there is one supramaxilla, probably five infarorbital bones; three tooth row without any anterior tooth especially elongated.

A complete description of characters supporting the relationships of the sister enchodontid group of *Unicachichthys nov. gen.* is presented in the Appendix I. It is remarkable, except for *Parenchodus*, that our two analyses have similar topologies in this [*Enchodus* [*Palaeolycus* [*Saurorhamphus*, *Eurypholis*,]]] group (Fig. 13).

5. Discussion

It is remarkable the few number of synapomorphies supporting our and the previous hypotheses on Enchodontid relationships (Figs 2, 13; figs. 1 and 2, Appendix I); therefore it is hard to support any nomenclatural proposal for *Enchodus* and allies. Based on our result, even the definition of the family Enchodontidae could be a matter of generality, in which different nodes are involved (e.g. M in fig. 1 and G to J in fig. 2 of Appendix I); however, in this paper we take in account the presence of synapomorphies to define the family Enchodontidae and confirm the inclusion of *Unicachichthys* within this clade.

Based on our results (Fig. 13) and the taxonomical considerations of previous work (Goody, 1968, 1969, 1976; Gayet, 1991; Fielitz, 1996; Forey et al., 2003; Gallo et al., 2006; Jacobs et al., 2006; Silva, 2007; Kaddumi, 2009; Friedman, 2012; among others), currently the family Enchodontidae encloses five or six genus and at least 33 nominal species, including: 1) *Unicachichthys multidentata* gen and sp. nov., describe here. 2) *Palaeolycus dreginensis* von der Marck 1863, from the upper Campanian of Sedenhorst, Westphalia, Germany (Siegfried, 1954; Goody, 1969). 3) Two species of *Eurypholis*, the type species *E. boissieri* Pictet, 1850, from the Lebanese middle Cenomanian deposits at Hakel, Hajula, and Namoura (also spelled as Nammoura); and *E. pulchellus* (Woodward, 1901), from the Cenomanian-Turonian deposits of the English Chalk, England [although a third nominal species of *Eurypholis* from Campanian marine deposits of Japan was named as *E. japonicus* Uyeno and Minakawa, 1983; Forey et al. (2003) considered that this may belong to *Enchodus*]. 4) At least three species of *Saurorhamphus*, counting the early Cenomanian species *S. freyeri* Heckel, 1850 (type species), from Comen Slovenia; *S. judeaensis* Chalifa, 1985, from the Amminadav Formation, Israel; and the middle Cenomanian *S. giorgiae* Bannikov and Bacchia, 2005, from Namoura, Lebanon [a potential new species of *Saurorhamphus* from the El Chango and El Espinal quarries was identified by Alvarado-Ortega et al. (2009)]. 5) The robust body species, *Parenchodus longipterygius* Raab and Chalifa, 1987, from the upper Cenomanian deposits of Kefar Shaul, Israel [Fielitz (2004) included this species into the genus *Enchodus*; however, Silva and Gallo (2011), and Cavin et al. (2012) suggests that it deserves to be placed in its own genus (Fig. 2). The ambiguous position of *P. longipterygius* persists in this work (Fig. 13)]. 6) *Enchodus* is certainly the most diverse enchodontid genus; also, it shows wider temporal and geographical distribution.

Although Woodward (1901, p. 190–205) listed 71 nominal species of *Enchodus*; many of them represent extremely fragmented, isolated, and poorly informative remains. Although it is desirable to undertake an exercise to recognize valid species and possible synonyms in this great cluster; many of these species have simply fallen into disuse. Despite this situation, *Enchodus* is by far the genus most diverse and best known; morphological details, distribution and phylogenetic relationships of 25 species have been published in the literature during the last 25 years (Yabumoto and Uyeno, 1994; Chalifa, 1996; Fielitz, 1996, 2004; Cavin, 1999; Rigo, 1999; Bardet et al, 2000; Cavin et al., 2000, 2007; Bardet and Pereda Superbiola, 2002; Gallo et al., 2006; Silva, 2007, tbl. 9; Friedman, 2012; Nagrodski et al., 2012; among others). The bulk of the reports about *Enchodus* show that this fish lived between the Cenomanian to Eocene along the marine areas of North America, South America, Europe, Africa, Middle East, Antarctica, and Asia (Green, 1913; Arambourg, 1952; Siegfried, 1954; Rebouças and Silva-Santos, 1956; Leonardi, 1966; Goody, 1969, 1976; Raab, 1967; Silva-Santos and Salgado, 1969; Applegate, 1970; Sorbini, 1976; Chalifa, 1989; Wilson and Chalifa, 1989; Gayet, 1991; Rana et al., 2005; Becker et al., 2010; Bogan and Agnolin, 2010; among others). The vague reports of *Enchodus* in pre-Cenomanian deposits of South America and Africa (Gayet, 1989; Coelho, 2004) have not been conclusively confirmed; therefore, *E. zimapanensis* from the Albian-Cenomanian strata of Muhi quarry still is the oldest enchodontid species as far known. Although the predorsal scutes series could be no longer a valid synapomorphy of this family (12 in Figs. 2 and 13) because *E. zimapanensis* lacks these scutes (Fielitz and González-Rodríguez, 2010); probably this absence is an artifact of the poor preservation that is common in this Mexican site.

Curiously our results show *Palaeolycus* as the sister group of the well supported *Saurorhamphus* plus *Eurypholis* clade (Fig. 13,

Appendix I). Although, there are no synapomorphies supporting such unexpected relationship, this hypothesis deserves additional study beyond this work. Also, our results suggest that *Rharbichthys*, and consequently the subfamily Rharbichthinae erected by Fielitz (2004), is not part of Enchodontidae. Our conclusions are not used here to create a new taxonomic scheme because it could be extremely weak due the lack of synapomorphies as far identified. These results should not be understood as a failure of the present or previous phylogenetic studies; these may be artifacts of several factors that deserve further study. The present authors are aware that the depth anatomical review of all named and potential new enchodontids taxa is now mandatory, particularly those from Mexican Cretaceous localities (Maldonado-Koerdell, 1956; González-Barba and Espinosa-Chávez, 2005; Giersch et al., 2008; Carbot-Chanona and Than-Marchese, 2013; among others).

Although the phylogenetic position of *Enchodus zimapanensis* seems suspicious in the present and previous hypotheses (Figs. 2, 4), in which this, the oldest *Enchodus* as far known (Albian-Cenomanian), appears as the sister species Coniacian-Maastrichthian *E. gladiolus* (Cope, 1872) forming the most derived group among *Enchodus* species. This apparent inconsistency shows that our phylogenies still fail to reproduce disparity (explosive diversification) of this group that took place near the Albian-Cenomanian boundary.

6. Conclusions

The El Chango quarry is a lower Cenomanian site in Chiapas, discovered less than a decade ago. Unexpectedly this has become the Mexican site with the greatest diversity of enchodontid fishes, which have potential important implications for the phylogenetic and biogeographic studies. At least three different short snout enchodontid species are represented in this marine deposit including the most primitive enchodontid so far known, described and named here as *Unicachichthys multidentata.* Two different species of *Enchodus,* a relative large is species named as *Enchodus* sp. 1, plus a tiny one identified as *Enchodus* sp. 2, from this site are also described here. Additionally Alvarado-Ortega et al. (2009, p. 12–15) report a potential new species of *Saurorhamphus* in this site, which is a Mexican long snout enchodontid fish still requires to be properly described.

These Mexican fossils constitute an interesting taxonomical set at the Western domain of the Tethys Sea, a region where these fishes were previously virtually unknown. This record is remarkable because it provides fresh data about the distribution of old enchodontids, which undoubtedly could lead us to understand the origin and diversification of this family and compels us to re-evaluate the results of those scarce previous biogeographic studies that involve this family (Silva and Gallo, 2007; Cavin et al., 2012; Carbot-Chanona and Than-Marchese, 2013). At this point, it is difficult to suggest a well-supported taxonomic arrangement of Enchodontidae because the low number synapomorphies as far identified; however, *Unicachichthys* nov. gen. together with *Enchodus*, *Perenchodus*, *Palaeolycus*, *Eurypholis*, and *Saurorhamphus* are part of this natural family.

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References

Agassiz, L., 1833–1844, 5 volumes plus supplement. Recherches sur les Poissons Fossiles. Imprimerie de Petitpierre, Neuchâtel, 1420 p.

Applegate, S.P., 1970. The Vertebrate Fauna of the Selma Formation of Alabama. Part VIII. The Fishes. Fieldiana 3, 383–433.

Alvarado-Ortega, J., Ovalles-Damián, E., 2008. *Triplomystus applegatei*, sp. nov. (Teleostei: Ellimmichthyiformes), a rare “triple armored herring” from El Espinal Quarry (Early Cretaceous), Chiapas, southeastern Mexico. Journal of Vertebrate Paleontology 28 (1), 53–60.

Alvarado-Ortega, J., Porras-Múzquiz, H.G., 2012. The first American record of *Aspidopleurus* (Teleostei, Aulopiformes), from La Mula quarry (Turonian), Coahuila State, Mexico. Revista Brasileira de Paleontologia 15 (3), 251–263.

Alvarado-Ortega, J., Than-Marchese, B.A., 2012. A Cenomanian aipichthyoid fish (Teleostei, Acanthomorpha) from America, *Zoqueichthys carolinae* gen. and sp. nov. from El Chango quarry (Cintalapa Member, Sierra Madre Formation), Chiapas, Mexico. Revista Mexicana de Ciencias Geológicas 29 (3), 735–748.

Alvarado-Ortega, J., Ovalles-Damián, E., Blanco-Piñón, A., 2009. The fossil fishes from the Sierra Madre Formation, Ocozocoautla, Chiapas, Southern Mexico. Palaeontologia Electronica 12 (2.4A), 1–22.

Arambourg, C., 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes et Mémoires, Service des Mines et de la Carte Géologique du Maroc 92, 1–372.

Arambourg, C., 1954. Les poissons crétacés du Jebel Tselfat (Maroc). Notes et Mémoires, Service des Mines et de la Carte Géologique du Maroc 118, 1–188.

Bannikov, A.F., Bacchia, F., 2005. New species of the Cenomanian Eurypterygii (Pisces, Teleostei) from Lebanon. Paleontological Journal 39 (5), 514–522. Translated from the Russian, original version published in Paleontologicheskii Zhurnal, 5, 53–61.

Bardet, N., Pereda Suberbiola, X., 2002. Marine reptiles from the Late Cretaceous Phosphates of Jordan: palaeobiogeographical implications. Geodiversitas 24, 831–839.

Bardet, N., Cappetta, H., Suberbiola, X.P., Mouty, M., Al Maleh, A.K., Ahmad, A.M., Khrata, O., Gannoum, N., 2000. The marine vertebrate faunas from the Late Cretaceous phosphates of Syria. Geological Magazine 137 (03), 269–290.

Becker, M.A., Mallery Jr., C.S., Chamberlain Jr., J.A., 2010. Osteichthyans from an Arkadelphia Formation–Midway Group lag deposit (Late Maastrichtian–Paleocene), Hot Spring County, Arkansas, USA. Journal of Vertebrate Paleontology 30 (4), 1019–1036.

Berg, L.S., 1937. A classification of fish-like vertebrates. Bulletin de l'Académie des Sciences de l'URSS 4, 1277–1280.

Blanco, A., Alvarado-Ortega, J., Gallo, V., 2008. *Robertichthys riograndensis* from the Lower Turonian (Upper Cretaceous) Vallecillo Lagerstätte, NE-Mexico: Description and relationships. In: Arratia, G., Shultze, H.-P., Wilson, M.V.H. (Eds.), Mesozoic Fishes IV –Homology and Phylogeny. Verlag Dr. Friedrich Pfiel, München, Germany, pp. 389–398.

Bogan, S., Agnolin, F.L., 2010. Primera ictiofauna marina del Cretácico Superior (Formación Jaguel, Maastrichtiano) de la Provincia de Río Negro, Argentina. Papéis Avulsos de Zoologia, Museu de Zoologia da Universidade de São Paulo 50, 175–188.

Carbot-Chanona, G., Than-Marchese, B.A., 2013. Presencia de *Enchodus* (Osteichthyes: Aulopiformes: Enchodontidae) en el Maastrichtiano (Cretácico tardío) de Chiapas, México. Paleontología Mexicana 6 (1), 8–16.

Cavin, L., 1999. Occurrence of a juvenile teleost, *Enchodus* sp., in a fish gut content from the Upper Cretaceous of Goulmima, Morocco. Special Papers in Palaeontology 60, 57–72.

Cavin, L., Jurkovšek, B., Kolar-Jurkovšek, T., 2000. Stratigraphic succession of the Upper Cretaceous fish assemblages of Kras (Slovenia). Geologija 43, 165–195.

Cavin, L., Alexopoulos, A., Piuz, A., 2012. Late Cretaceous (Maastrichtian) ray-finned fishes from the island of Gavdos, southern Greece, with comments on the evolutionary history of the aulopiform teleost *Enchodus*. Bulletin de la Société géologique de France 183 (6), 561–572.

Chalifa, Y., 1985. *Saurorhamphus judeaensis* (Salmoniformes: Enchodontidae), a new longirostrine fish from the Cenomanian of Ein-Yabrud, near Jerusalem. Journal of Vertebrate Paleontology 5 (3), 181–193.

Chalifa, Y., 1989. New species of *Enchodus* (Pisces: Enchodontoidei) from the Lower Cenomanian of Ein-Yabrud, Israel. Journal of Paleontology 63 (3), 356–364.

Chalifa, Y., 1996. New species of Enchodus (Aulopiformes: Enchodontidae) from the Northern Negev, Israel, with comments on evolutionary trends in the Enchodontoidei. In: Arratia, G., Schultze, H.-P. (Eds.), Mesozoic Fishes Systematics and Paleoecology. Verlag Dr. Friedrich Pfeil, München, Germany, pp. 349–367.

Coelho, P.M., 2004. Revisão sistemática dos †Enchodontidae (Euteleostei: Aulopiformes) do Brasil. Masters degree thesis. Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil, 83 p.

Cope, E.D., 1872. On the families of fishes of the Cretaceous formations of Kansas. Proceedings of the American Philosophical Society 12, 327–357.

Davis, J.W., 1887. The fossil fishes of the Chalk of Mount Lebanon in Syria. Royal Dublin Society, Scientific Transactions 3, 457–636.

D'Erasmo, G., 1946. L'ittiofauna cretacea dei dintorni di Comeno nel Carso Triestino. serie 3(8). Atti della Regia Accademia delle Scienze fisiche e matematiche della Società Reale di Napoli 11, 1–134.

Dixon, F., 1850. The Geology and Fossils of the Tertiary and Cretaceous Formations of Sussex. Longmans, Brown, Green, and Longmans, England, London.

Fielitz, C., 1996. A late Cretaceous (Turonian) ichthyofauna from Lac des Bois, Northwest Territories, Canada, with paleobiogeographic comparisons with Turonian ichthyofaunas of the Western Interior Seaway. Canadian Journal of Earth Sciences 33 (10), 1375–1389.

Fielitz, C., 2004. The phylogenetic relationships of the †Enchodontidae (Teleostei: Aulopiformes). In: Arratia, G., Wilson, M.V.H., Cloutier, R. (Eds.), Recent Advances in the Origin and Early Radiation of Vertebrates. Verlag Dr. Friedrich Pfeil, München, Germany, pp. 619–634.

Fielitz, C., González-Rodríguez, K.A., 2010. A new species of *Enchodus* (Aulopiformes: Enchodontidae) from the Cretaceous (Albian to Cenomanian) of Zimapán, Hidalgo, México. Journal of Vertebrate Paleontology 30 (5), 1343–1351.

Forey, P.L., Yi, L., Patterson, C., Davies, C.E., 2003. Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. Journal of Systematic Palaeontology 1 (4), 227–330.

Friedman,M.,2012.Ray-finnedfishes(Osteichthyes,Actinopterygii)fromthetypeMaastrichtian,theNetherlandsandBelgium.SpecialIssue,8ScriptaGeologica113–142.

Gallo, V., Figuereido, F.J., Coelho, P.M., 2006. Paleoictiofauna da Formação Atlântida, Cretáceo Superior da Bacia de Pelotas, sul do Brasil. In: Gallo, V., Brito, P.M., Silva, H.M., Figuereido, F.J. (Eds.), Paleontologia de Vertebrados: Grandes Temas e Contribuições Científicas. Interciência, Rio de Janeiro, pp. 13–131.

Gayet, M., 1989. Note préliminaire sur le matériel paléoichthyologique éocrétacique du Rio Benito (sud de Bata, Guinée Équatoriale). Bulletin du Muséum national d'histoire naturelle. Section C, Sciences de la terre, paléontologie, géologie, minéralogie 11 (1), 21–31.

Gayet, M., 1991. Holostean and teleostean fishes from Bolivia. I. Revista Tech, 12. In: Suárez-Soruco, R. (Ed.), Fósiles y Facies de Bolivia. YPFB, Cochabamba, pp. 453–494.

Giersch, S., 2014. Die Knochenfische der Oberkreidezeit in Nordostmexiko: Beschreibung, Systematik, Vergesellschaftung, Paläobiogeographie und Paläoökologie. PhD Thesis, Ruprecht-Karls-Universität Heidelberg, Germany, 275 pp.

Giersch, S., Frey, E., Stinnesbeck, W., González-González, A.H., 2008. Fossil fish assemblages of northeastern Mexico: new evidence of mid Cretaceous Actinopterygian radiation. In: Krempaská, Z. (Ed.), 6th Meeting of the European Associat ion of Vertebrate Paleontology, 30th June–5th July, Volume of Abstracts. Museum of Spiš, Spišská Nová Ves, Slovak Republic, pp. 43–45.

González-Barba, G., Espinosa-Chávez, B., 2005. Cenomanian-Turonian fish fauna from the Boquillas Formation at Jaboncillos, north-west Coahuila, Mexico. In: Poyato-Ariza, F.J. (Ed.), Fourth International Meeting on Mesozoic Fishes –Systematics, Homology, and Nomenclature–, Maraflores de la Sierra, Madrid, España, August 8th–14th, Extended Abstracts. Servicio de Publicaciones de la Universidad Autónoma de Madrid/UAM Ediciones, Spain, pp. 105–107.

González-Ramírez, I., Calvillo-Canadell, L., Cevallos-Ferriz, S.R.S., 2013. Coníferas Cupresáceas fósiles de “El Chango”, Chiapas (Aptiano). Paleontología Mexicana 63, 24–31.

Goody, P.C., 1968. Skull of *Enchodus Faujasi* from Maastricht of southern Holland. Proceedings of the Koninklije Nederlandse Akademie van Wetenschappen, Series B-Physical Sciences 71, 209–231.

Goody, P.C., 1969. The relationships of certain Upper Cretaceous teleosts with special reference to the myctophoids. Bulletin of the British Museum (Natural History) Geology Supplement 7, 1–225.

Goody, P.C., 1976. *Enchodus* (Teleostei: Enchodontidae) from the Upper Cretaceous Pierre Shale of Wyoming and South Dakota with an evaluation of the North American enchodontid species. Palaeontographica Abteilung A Band A152, 91–112. Lieferung, 4–6.

Green, W.R., 1913. A description of the specimens of the teleostean genus *Enchodus*, in the University of Kansas Museum. Kansas University Science Bulletin 7 (2), 71–107 p1. I–XVII.

Gregory, W.K., 1933. Fish Skulls: A Study of the Evolution of Natural Mechanisms. American Philosophical Society, Malabar, Florida, 481+vii p.

Heckel, J.J., 1850. Beitrage zur Kenntniss der fossilen Fische Osterreichs. Denkschriften der Kaiserlichen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche 1, 201–242. + 15 pls.

Jacobs, L.L., Mateus, O., Polcyn, M.J., Schulp, A.S., Antunes, M.T., Moraos, M.L., Tavares, T.S., 2006. The occurrence and geological setting of Cretaceous dinosaurs, mosasaurs, plesiosaurs, and turtles from Angola. Journal of the Paleontological Society of Korea 22 (1), 91–110.

Jordan, D.S., 1905. A Guide to the Study of Fishes, Vol. 1. H. Holt, New York.

Kaddumi, H.F., 2009. Fossils of the Harrana Fauna: And the Adjacent Areas. Eternal River Museum of Natural History, Amman, Jordan.

Kramberger, K.G., 1895. De piscibus fossilibus Comeni, Mrzleci, Lesine et M. Libanonis. Djela Jugoslavenske Akademije Znanosti i Umjetnosti 16, 1–67, 12 pls.

Leidy, J., 1857. Remarks on *Saurocephalus* and its allies. Transactions of the American Philosophical Society 11, 91–95.

Leonardi, A., 1966. L'ittiofauna Cenomaniana di Floresta-Messina. Palaeontographia Italica 60, 33–65.

Maldonado-Koerdell,M.,1956.PecesfósilesdeMéxico,III.NotapreliminarsobrelospecesdelTuronianoSuperiordeXilitla,SanLuisPotosi(México).Ciencia16,31–35.

Mantell, G., 1822. The Fossils of the South Downs; or Illustrations of the Geology of Sussex. Lupton Relfe, London, p. 320. +42 pls.

Marck, W. von der, 1863. Fossile Fische, Krebse und Pflanzen aus dem Plattenkalk der jüngsten Kreide in Westphalen. Palaeontographica 11, 1–83. + 14 pls.

Moreno-Bedmar, J.A., Latil, J.L., Villanueva-Amadoz, U., Calvillo-Canadell, L., Cevallos-Ferriz, S.R.S., 2014. Ammonite age-calibration of the EL Chango Fossil-Lagerstätte, Chiapas state (SE Mexico). Journal of South American Earth Sciences 56, 447–453.

Nagrodski, M., Shimada, K., Schumacher, B.A., 2012. Marine vertebrates from the Hartland Shale (Upper Cretaceous: Upper Cenomanian) in southeastern Colorado, USA. Cretaceous Research 37, 76–88.

Nelson, J.S., 1994. Fishes of the World, third ed. John Wiley and Sons, New York. 600 p.

Nelson, J.S., 2006. Fishes of the World, fourth ed. John Wiley and Sons, New York. 624 p.

Ovalles-Damián, E., Alvarado-Ortega, J., Blanco-Piñón, A., 2006. Los peces fósiles del Cretácico inferior de Ocozocoautla, Chiapas. In: Memoria X Congreso Nacional de Paleontología y libreto guía de la excursión a Tepexi de Rodríguez, Puebla. Publicación especial 5. Instituto de Geología, 61 pp.

Pictet, F.J., 1850. Description de quelque poissons fossiles du Mont Liban. Frick, J-G, Genève.

Pictet, F.J., Humbert, A., 1866. Nouvelles recherches sur les poissons fossiles du Mont Liban. Chez Georg.

Raab, M., 1967. *Enchodus elegans* dartevelle and casier from the senonian of Israel. Israel Journal Earth Sciences 16, 174–179.

Raab, M., Califa, Y., 1987. A new enchodontid fish genus from the upper Cenomanian of Jerusalem, Israel. Palaeontology 30, 717–731.

Rana, R.S., Kumar, K., Singh, H., Rose, K.D., 2005. Palaeocene–Earliest Eocene Akli Formation, Giral Lignite Mine, Barmer District, western India. Current Science 89 (9), 1606–1613.

Rebouças, J.C., Silva Santos, R., 1956. Fauna ictiológica do fosfato de Pernambuco. Ministério da Agricultura, Departamento Nacional da Produção Mineral, Divisão de Geologia e Mineralogia 162, 1–29.

Regan, C.T., 1911. The anatomy and classification of the teleostean fishes of the order Iniomi. Annals and Magazine of Natural History 7, 120–133.

Rigo, D., 1999. The fossils of the Cretaceous Lagerstätte of Polazzo (Fogliano-Redipuglia, Gorizia, NE Italy). Natura Nascosta 19, 10–19.

Rosales-Domínguez, M.C., Bermúdez-Santana, J.C., Aguilar-Piña, M., 1997. Mid and Upper Cretaceous foraminiferal assemblages from the Sierra de Chiapas, southeastern Mexico. Cretaceous Research 18, 697–712.

Rosen, D.E., 1973. Interrelationships of higher euteleosteans fishes. In: Greenwood, P.H., Miles, R.S., Patterson, C. (Eds.), Interrelation of Fishes. Zoological Journal of the Linnean Society. Academic Press, London, pp. 397–513. Supplemet 1.

Siegfried, P., 1954. Die Fisch-Fauna des Westfälischen Ober-Senons. Palaeontographica Abteilung A 106 (1-2), 1–36.

Silva, H.M.A., 2007. Revisão taxonômica e filogenética dos peixes Enchodontoidei (*sensu* Nelson, 1994) e considerações biogeográficas. Masters degree Thesis. Programa de Pós-graduação em Ecologia e Evolução, Universidade do Estado do Rio de Janeiro, Brazil, 142 p.

Silva, H.M.A., Gallo, V., 2007. Parsimony analysis of endemicity of enchodontoid fishes from the Cenomanian. Carnets de Géologie v. Letter 1–8. Carnets de Géologie, Letter, 2007/01, 1–8.

Silva, H.M.A., Gallo, V., 2011. Taxonomic review and phylogenetic analysis of Enchodontoidei (Teleostei: Aulopiformes). Anais da Academia Brasileira de Ciências 83 (2), 483–511.

Silva-Santos, R., Salgado, M.S., 1969. *Enchodus longipectoralis* (Schaffer) um Teleostei do Cretáceo de Sergipe. Rio de Janeiro. Anais da Academia Brasileira de Ciências 41 (3), 381–392.

Sorbini, L., 1976. L'ittiofauna cretacea di Cinto Euganeo (Padova- Nord Italia). Bolletino Museo Civico di Storia Naturale 3, 469–567.

Swofford, D.L., 2002. PAUP* version 4. Phylogenetic analysis using parsimony (and other methods). Sinauer Associates, Sunderland, Massachusetts, USA.

Toombs, H.A., Rixon, A.E., 1959. The use of acids in the preparation of vertebrate fossils. Curator 2, 304–312.

Uyeno,T.,Minakawa,T.,1983.Anewenchodontoidfishofthegenus*Eurypholis*fromCretaceousofJapon.BulletinoftheNationalScienceMuseum,SeriesC9(2),79–83.

Vega, F.J., Alvarez, F., Carbot-Chanona, G., 2007. Albian penaeoidea (Decapoda: Dendrobranchiata) from Chiapas, Southern Mexico. Memorie della Societá Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 35 (2), 6–8.

Vega, F.J., García-Barrera, P., Perrilliat, M., del, C., Coutiño, M.A., Mariño-Pére, R., 2006. El Espinal, a new plattenkalk facies locality from the Lower Cretaceous Sierra Madre Formation, Chiapas, southeastern Mexico. Revista Mexicana de Ciencias Geológicas 23 (3), 323–333.

Williston, S.W., 1899. A New Genus of Fishes from the Niobrara Cretaceous. Kansas University Quarterly 8 (3), 113–115. +XXVI pls.

Wilson, M.V.H., Chalifa, Y., 1989. Fossil marine actinopterygian fishes from the Kaskapau Formation (Upper Cretaceous: Turonian) near Watino, Alberta. Canadian Journal of Earth Sciences 26, 2604–2620.

Woodward, A.S., 1901. Catalogue of the Fossil Fishes in the British Museum (Natural History), Part IV. British Museum (Natural History), London, 636 p.

Yabumoto, Y., Uyeno, T., 1994. Late Mesozoic and Cenozoic fish faunas of Japan. Island Arc 3 (4), 255–269.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2015.12.026.

APPENDIX I

The Cenomanian short snout enchodontid fishes (Aulopifomes, Enchodontidae) from Sierra Madre Formation, Chiapas, southeastern Mexico

by

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Phylogenetic analysis 1: Based on Silva (2007) and Silva and Gallo (2011)

The present analysis includes the characters and data matrices created by Silva (2007) and Silva and Gallo (2011) (Table 1) to resolve the relationships among genera of the suborder Enchodontoidei *sensu* Nelson (1994), These data matrices are updated herein considering the observations described into the main text of this appendix (Table 2). Procedures and protocols considered to perform these analyses are described in the main text. The Figure 1 shows the strict consensus tree obtained in this analysis.

Table 1. List of characters of the "Phylogenetic analysis 1" performed in the present appendix and used to build up the data matrix of Table 3 (after Silva (2007) and Silva and Gallo (2011)).

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

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

Table 2. Data matrix for the “phylogenetic analysis 1” of this appendix, based on Silva (2007) and Silva and Gallo (2011), modifications from the original data matrices and described into the main text are highlighted (characters and state of characters are defined in Table 1).

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888
Taxon/Node	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
Sardinoides	00000000?1	00?00100??	000001?0?1	1000001000	1000100000	0000000000	0000001100	0100101010	0000000
Protostomias	0000010000	00?0000100	1?1?001000	0011000001	0010000001	1000000000	001?01000?	0000000?01	0001000
Trachinocephalus	0003000000	1100000000	0100000100	010?0001?2	0021011000	0000020000	0000000011	0000010000	0000000
Ichthyotringa	11100001?0	?00010?000	0?000??111	?001000100	?0200010?0	1001?10001	0001001110	0100100000	0000000
Apateopholis	0011?00??0	?00001?1?0	00111??011	0001000100	0000100020	1001?11101	0111001000	0110111000	0?01000
Apateodus	?000000??0	1010000000	1000?0??11	1001000000	0020000020	0010030001	00010?????	????????0?	???????
Cimolichthys	0002100?10	0000010000	010110?111	0100100000	1020001021	0001?10001	011??000?0	010?1?10?0	?101220
Apuliadecertis	2110100??0	0001100000	1?0?013100	1001001112	0001000020	0000110010	000?000011	1100121000	0101310
Benthesinkyme	2?10?00??0	1?0000?010	1?0??1??11	??01000113	0??1?0???0	??????????	????????1?	?100????0?	01?13?0
Brazilodecertis	?112?00?00	1000000000	1?1??13000	1011000112	0111100000	0000040010	0000?????1	11????????	???132?
Caudadecertis	2110?00??0	0???0001??	1?1????1?0	100?00???2	?021000020	0000?10?00	00??0?0011	11?0001?01	1111000
Cyranichthys	1112?????0	1000000000	1?0??1????	??0100?010	0??100????	?????10010	00?0?????0	1?????11??	???1120
Decertis	2111000??1	1000000000	1?0??12111	?001001112	0011101020	1001?10000	00000?0010	1100001100	0101320
Decertoides	2111????10	00?1010100	101??1?000	100100?113	0010101021	0000?30000	0100100011	1100001000	0111310
Hastichthys	2110????10	0101010000	1?0??12111	1011100110	0100101020	0000010010	0000?00011	1100?01001	0111310
Nardodecertis	2110000??0	0?000101?0	0????1?000	?01100?100	0100100020	00000???1?	00?0000011	1100110??0	0011310
Ophidecertis	2110?21?00	1000000000	1?0??12111	?001001112	0021001010	0000030000	000000001?	1100020101	0??1120
Pelargorhynchus	1113?????0	0000010110	1?1??1?11?	??00100110	00201000?1	?00??1?000	?010??0??0	11??1?11?0	???0220
Rhynchodecertis	2110000?00	0100110100	1?1??1?010	1011000110	0100100000	0001?10000	0000000011	1?00021100	0111310
Robertichthys	211?010???	?0??0?????	1???01??1?	1001000012	01210010?0	?????10010	001??000??	11??12????	???0310
Aspidopleurus	0003100??0	1000011000	000111?110	1100000110	0011111000	000??11001	001?101010	0111121000	0000000
Rharbichthys	0002?21?00	10?000?110	0?0????1?1	1001001100	0021000000	1010010000	010000110?	0000121000	1001410
Palaeolycus	1002??21?1?	?0?10??1??	1?1????110	??00010010	?001001011	1010??1001	0110?0001?	0100120001	0??1001
Eurypholis	0001121?10	1000011100	0001112110	1100111110	0020000001	011?111101	1110001110	0100000000	0001111
Saurorhamphus	1111?00?10	1000011100	1?0111211?	100011?013	0000001001	1111111101	1110001010	0100020001	0000111
Enchodus	0003?2????	????0????0	0??????11?	10?????000	10010?1110	?01??11001	011000111?	0100121??1	00?1001
Parenchodus	0003?2?1?0	1011011100	1010?1?011	?100101003	0021001121	1010111001	0110111001	0010101101	0101001
Halec	0001000?10	1000010100	001??0?111	1100100102	1011001001	000??11001	0101001110	0100101000	0000000
Hemisaurida	0000000?1?	10?10????0	00???1?011	1100000103	1011100020	0001?20100	0000001110	0100121000	0001000
Phylactocephalus	0001000010	00000????0	011????11?	0100100102	1011100021	0000?11001	0100001110	0111101000	0000000
Nardorex	?002100111	1000100001	0?01?1311?	??00001013	0000000010	1000000110	0010001?10	0000100001	???1000
Serrilepis	00030000?0	1010010000	1?11100111	?00110?103	10101010?1	1010111001	0111101110	0100101010	0100000
Atolvorator	00000??0??	?110001100	1010002011	00010?0100	1000001020	0010010000	0010010110	010011000?	?001000
Yabrudichthys	00110101??	?0000????0	1010???000	?10100?1?0	00000000?1	1010?1111?	001100100?	0100121110	0101000
Unicachichthys	0003100???	??0???1?1?	0????1?11?	??001?1012	1001001121	?010?11101	011??0111?	0000121000	0101001

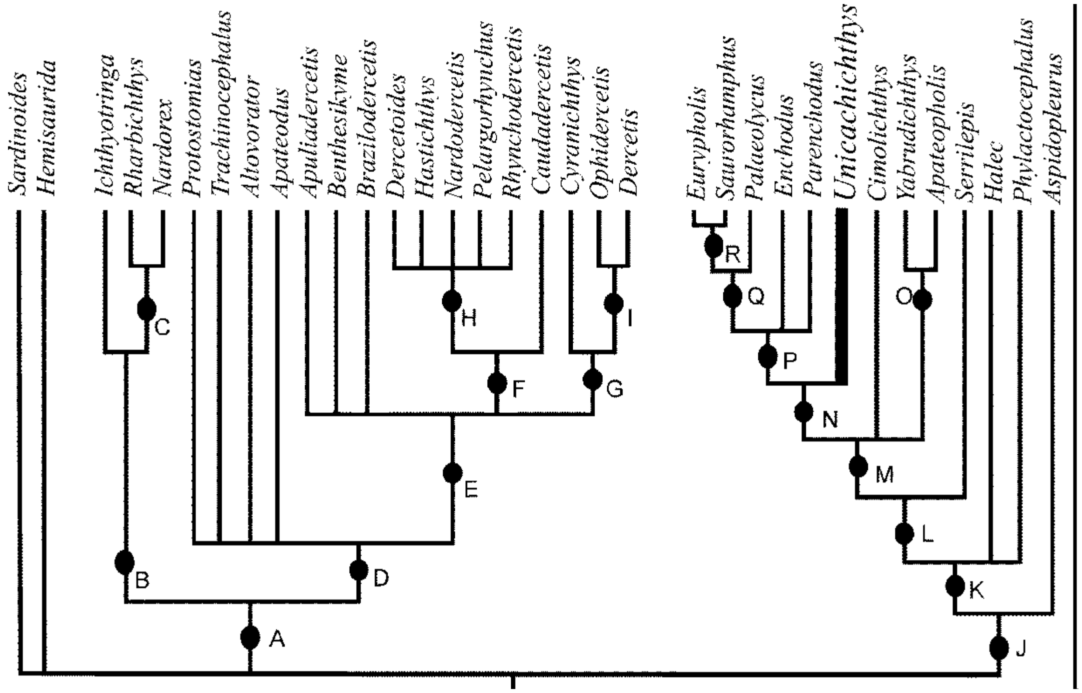

Figure 1.- Relationships of the suborder Enchodontoidei including *Unicachichthys*. Characters supporting nodes (synapomorphies are underlined) are these: **A:** 16-0, 28-1, 34-1, 41-0, 43-2, 45-0, 77-0, 84-1. **B:** 8-1, 15-1, 27-3, 52-1. **C:** 4-2, 5-5, 24-1, 37-1, 72-0, 81-1. **D:** 21-1, 26-0, 49-2, 67-0. **E:** 1-2, 2-1, 3-1, 26-1, 30-0, 39-1, 40-2, 44-1, 68-0, 70-1, 71-1, 75-0, 77-1, 82-1, 85-3. **F:** 9-1, 11-0, 18-1, 23-1, 83-1. **G:** 30-1, 37-1, 43-1, 47-1, 70-0, 76-2, 78-1, 86-2. **H:** 16-1, 28-0, 40-0, 44-0, 45-1, 86-1. **I:** 6-2, 7-1, 43-2, 49-1, 80-1, 85-1. **J:** 4-3, 9-1, 24-1, 25-1, 28-1, 32-1, 43-1, 44-1, 47-1, 49-2, 55-1, 57-1, 60-1, 63-1, 64-1, 76-2. **K:** 18-1, 23-1, 26-0, 31-0, 35-1, 50-1, 62-1, 76-0. **L:** 34-1, 44-0, 51-1, 53-1, 82-1. **M:** 8-1, 43-0, 45-0, 68-0, 76-2, 84-1. **N:** 5-1, 14-1, 17-1, 26-1, 31-1, 34-0, 37-1, 38-0, 44-1, 48-1, 64-0, 68-1, 87-1. **O:** 3-1, 4-1, 28-0, 35-0, 41-0, 47-0, 58-1, 69-0. **P:** 6-2, 7-1, 49-1, 80-1, 82-0. **Q:** 1-1, 4-1, 21-1, 30-0, 36-1, 39-1, 41-0, 48-0, 68-0, 77-0. **R:** 14-0, 23-0, 44-0, 49-0, 52-1, 54-1, 58-1, 61-1, 75-0, 85-1, 86-1. ***Apateodus*:** 38-0, 56-3, 60-1, 64-1. ***Apateopholis*:** 13-1, 28-0, 32-0, 45-1, 50-0, 53-0 54-1, 66-1, 73-1, 76-1. ***Apuliadecertis*:** 5-1, 11-0, 14-1, 15-1, 27-3, 29-0, 37-1, 43-0, 55-1, 59-1, 75-1, 76-2, 86-1. ***Aspidopleurus*:** 5-1, 17-1, 30-0, 39-1, 41-0, 46-1, 49-0, 65-1, 65-1, 68-0, 73-1, 74-1. ***Atolvorator*:** 12-1, 13-1, 17-1, 18-1, 23-1, 28-0, 31-0, 41-1, 47-1, 53-1, 63-1, 66-1, 76-1. ***Benthesikyme*:** 19-1, 30-1, 40-3, 43-1, 47-1, 70-0, 76-2, 78-1, 86-2. ***Brazilodecertis*:** 4-2, 5-1, 23-1, 27-3, 28-0, 29-0, 33-1, 42-1, 43-1, 45-1, 49-0, 56-4, 59-1, 75-1, 76-2, 86-2. ***Caudadecertis*:** 80-1, 81-1, 85-0. ***Cimolichthys*:** 4-2, 5-1, 11-0, 18-0, 22-1, 23-0, 34-0, 38-0, 43-2, 51-0, 53-0, 54-1, 57-0, 64-0, 67-0, 85-2, 86-2. ***Cyranichthys*:** 1-1, 4-2, 38-0, 40-0, 59-1. ***Decertis*:** 4-1, 10-1, 45-1, 51-1, 54-1, 76-0. ***Decertoides*:** 4-1, 14-1, 29-0, 40-3, 43-1, 47-1, 50-1, 56-3, 62-1, 65-1. ***Enchodus*:** 32-0, 50-0. ***Eurypholis*:** 1-0, 21-0, 38-1, 43-2, 47-0, 51-0, 68-1, 76-0, 80-0. ***Halec*:** 4-1, 31-1, 40-2, 45-0, 49-0, 63-0. ***Hastichthys*:** 12-1, 14-1, 18-0, 23-0, 28-1, 30-1, 33-1, 35-1, 42-1, 43-0, 47-1, 59-1, 75-1, 80-1. ***Hemisaurida*:** 9-1, 14-1, 24-1, 25-1, 32-1, 40-3, 43-1, 44-1, 49-2, 54-1, 55-1, 56-2, 58-1, 76-2, 84-1. ***Ichthyotringa*:** 1-1, 2-1, 3-1, 47-1, 54-1, 60-1, 64-1, 84-0. ***Nardodecertis*:** 12-1, 21-0, 23-0, 29-0, 33-1, 39-0, 42-1, 43-0, 59-1, 75-1, 76-1, 77-0, 82-0. ***Nardorex*:** 9-1, 10-1, 20-1, 34-0, 38-0, 30-1, 40-3, 43-0, 49-1, 56-0, 58-1, 59-1, 63-1, 80-1. ***Ophidecertis*:** 56-3, 7-0. ***Palaeolycus*:** 4-2, 35-0, 37-0, 67-0. ***Parenchodus*:** 13-1, 21-1, 24-0, 28-0, 40-3, 41-0, 43-2, 49-2, 65-1, 66-1, 68-0, 69-0, 70-1, 72-0, 73-1, 76-0, 78-1, 82-1. ***Pelargorhynchus*:** 1-1, 4-3, 19-1, 28-1, 34-0, 35-1, 50-1, 63-1, 65-1, 70-0, 75-1, 78-1, 84-0, 85-2, 86-2. ***Phylactocephalus*:** 4-1, 11-0, 22-1, 40-2, 47-0, 63-0, 64-0, 73-1, 74-1. ***Protostomia:*** 6-1, 11-0, 18-1, 23-1, 22-1, 27-1, 28-0, 29-0, 30-0, 31-0, 33-1, 38-0, 40-1, 43-1, 44-0, 49-0, 50-1, 51-1, 56-0, 63-1, 66-1, 68-0, 69-0, 70-1, 72-0, 75-0, 80-1. ***Rharbichthys*:** 6-2, 7-1, 15-0, 18-1, 19-1, 44-1, 53-1, 62-1, 69-0, 76-2, 77-1, 85-4, 86-1. ***Rhynchodecertis*:** 9-0, 12-1, 15-1, 33-1, 42-1, 43-0, 49-0, 54-1, 76-2, 78-1. ***Sardinoides*:** 10-1, 11-0, 37-1, 38-0, 56-0, 69-0, 79-1. ***Saurorhamphus*:** 2-1, 3-1, 6-0, 7-0, 32-0, 40-3, 84-0. ***Serrilepis*:** 13-1, 18-0, 21-1, 27-0, 32-0, 40-3, 65-1, 79-1. ***Trachinocephalus:*** 4-3, 12-1, 22-0, 27-0, 29-0, 30-0, 31-0, 32-1, 40-2, 44-1, 46-1, 47-1, 49-0, 56-2, 68-0, 70-1, 72-0, 75-0, 76 -1, 84-0. ***Unicachichthys*:** 19-1, 39-1, 40-2, 58-1, 72-0. ***Yabrudichthys*:** 6-1, 21-1, 24-0, 29-0, 30-0, 59-1, 62-0, 78-1, 79-1.

Phylogenetic analysis 2: Based on Fielitz (2004) and Fielitz and González-Rodriguez (2010)

The present analysis includes all data from Fielitz (2004) and Fielitz and González-Rodriguez (2010) (Table 3), used to resolve the relationships within Enchodontidae and the position of the *E. zimapanensis* in this family, respectively. The updated data matrix used here (Table 4) also incorporates data of two additional taxa, *Enchodus* from Gavdos described by Cavin et al. (2012) and *Unicachichthys multidentata* described in the main text of this appendix. Procedures and protocols considered to perform these analyses are described in the main text. The Figure 2 shows the strict consensus tree obtained in this analysis.

Table 3. List of characters of the used in the Phylogenetic analysis 2 of this appendix. This is an updated version of those matrices constructed by Fielitz (2004) and Fielitz and González-Rodríguez (2010).

1. Shape of the rostrodermethmoid: 0) narrow, with lateral wings; 1) wide with lateral wings; 2) narrow, without lateral wings.
2. Contact of rostrodermethmoid with frontal bones: 0) ventrally; 1) dorsally; 2) without overlap or underlap.
3. Dermal pattern on frontal bones: 0) absent; 1) present as radiating ridges; 2) present as ridges with tubercles along each ridge; 3) present as tubercles.
4. Parietal bones: 0) meet with each other medially; 1) separated by the supraoccipital.
5. Occipital sensory canal on parietal bones: 0) absent; 1) covered by a heavy ridge of bone; 2) in a trough.
6. Vomerine teeth: 0) present; 1) absent.
7. Facet for the articulation with the hyomandibula: 0) posteroventral to the dilatator fossa; 1) ventral to the dilatator fossa.
8. Posttemporal fossa: 0) unroofed; 1) roofed.
9. Parasphenoid: 0) narrow beneath the orbit; 1) wide beneath the orbit.
10. Ectopterygoid; 0) articulates flush with the quadrate’s anterior margin; 1) inserts into an anterior incisure of the quadrate.
11. Ectopterygoid teeth: 0) present; 1) absent.
12. Ectopterygoid teeth: 0) absent; 1) numerous [>8] and all of about the same size; 2) between six to eight teeth with the second tooth longest.
13. Dermopalatine teeth: 0) numerous and in several rows; 1) several in a single row; 2) a single tooth.
14. Dermopalatine bone: 0) at least twice as long relative to the longest dermopalatine tooth; 1) shorter than the longest dermopalatine tooth.
15. Dermopalatine teeth cross section: 0) conical; 1) laterally compressed with two cutting edges; 2) two offset cutting edges; 3) elliptical with one anterior cutting edge.
16. Lateral view of dermopalatine teeth: 0) curved; 1) straight; 2) sigmoidal.
17. Dermopalatine teeth apical barbs: 0) absent; 1) present.
18. Second epibranchial uncinate process: 0) absent; 1) present and enlarged; 2) present, not enlarged.
19. Cartilaginous condyle on dorsal surface of third pharyngobranchial: 0) articulates with second epibranchial; 1) absent.
20. Gill rakers: 0) long; 1) present as tooth plates.
21. Second pharyngobranchial tooth plate: 0) present; 1) absent.
22. Third pharyngobranchial: 0) does not extend anteriorly beyond tips of epibranchial 1 and pharyngobranchial 2; 1) extends beyond tips of epibranchial 1 and pharyngobranchial 2.
23. Third pharyngobranchial toothplate: 0) covers large area of pharyngobranchial 3; 1) restricted to lateral edge of pharyngobranchial 3.
24. Third pharyngobranchial teeth: 0) small; 1) large.

25. Fifth ceratobranchial teeth: 0) scattered over anterodorsal surface; 1) mostly restricted to medial edge of anterodorsal surface; 2) all restricted to medial edge of anterodorsal surface.
26. Gap between ceratobranchial 5 and basibranchial 4 cartilage: 0) absent; 1) present; 2) ceratobranchial separated from main body of basibranchial 4 by tail or small nubbins of cartilage extending posteriorly from basibranchial 4.
27. Basibranchial 3: 0) terminates beneath anterior of basibranchial 4 cartilage; 1) terminates beyond posterior of basibranchial 4 cartilage.
28. Third hypobranchial gill rakers or toothplates: 0) present; 1) absent.
29. Number of branquiostegal rays on anterior ceratohyal: 0) five or more; 1) four or less.
30. Maxilla: 0) excluded from gape of jaw; 1) included in gape and is toothed; 2) maxilla included in gape, but teeth absent.
31. Shape of premaxilla: 0) long and narrow; 1) deep anterior with long ascending process; 2) deep anterior with no ascending process; 3) large wedge-shaped bone.
32. Premaxillary teeth: 0) larger than palatine teeth; 1) of equal size with palatine teeth; 2) smaller than palatine teeth.
33. Supramaxilla: 0) absent; 1) two supramaxillae present; 2) single large supramaxilla; 3) single supramaxilla present but greatly reduced.
34. Mandible-quadrate articulation: 0) exposed on lateral side; 1) hidden.
35. Dentary symphysis: 0) tapers to a narrow point; 1) remains deep.
36. Anteroventral prongs on dentary: 0) absent; 1) present.
37. Number of dentary tooth rows: 0) three or more; 1) two; 2) one.
38. Dentary teeth: 0) most or several of equal size; 1) a single long tooth near the symphysis, at least 33% longer than the others posterior to it.
39. Dentary teeth posterior to longest tooth: 0) equal in size; 1) decreasing in size posteriorly.
40. Mandibular sensory canal: 0) open; 1) partially open; 2) enclosed by bone.
41. Mandibular dermal pattern: 0) absent; 1) present as ridges; 2) as ridges with tubercles along each ridge; 3) as tubercles.
42. Vertical bar on posterior portion of articular: 0) absent; 1) present.
43. Supraorbital bone: 0) present; 1) absent.
44. Number of infraorbital bones: 0) six; 1) eight; 2) five; 3) four.
45. Ventral portion of preopercle: 0) anteriorly-directed limb; 1) small posterior limb; 2) broadens anteriorly and posteriorly.
46. Posterior edge of ventral portion of preopercle: 0) rounded; 1) tapers to point; 2) tapers to point, with spine.
47. Opercular horizontal strengthening ridge or bar: 0) absent; 1) present; 2) continues past posterior edge to form a spine.
48. Interopercle: 0) present; 1) absent.
49. Preopercular dermal pattern: 0) absent; 1) present as ridges; 2) present as ridges with tubercles along each ridge; 3) present as tubercles.
50. Opercular and subopercular dermal pattern: 0) absent; 1) present as ridges; 2) present as ridges with tubercles along each ridge; 3) present as tubercles.
51. Pectoral fin position: 0) close to the lateral midline of the body; 1) low on body.
52. Position of the pelvic fin: 0) anterior to the dorsal fin; 1) at or posterior to the dorsal fin.
53. Ventral limb of posttemporal: 0) ossified; 1) ligamentous.
54. Supracleithrum dermal pattern: 0) absent; 1) present as ridges; 2) present as tubercles.
55. Shape of ventral portion of cleithrum: 0) narrow and maintaining a uniform width; 1) widening anteriorly; 2) widening anteriorly and posteriorly.
56. Cleithrum dermal pattern: 0) absent; 1) present as ridges; 2) present as tubercles.
57. Number of postcleithra: 0) two; 1) one; 2) none; 2) three.
58. Pectoral-fin base oriented: 0) vertically; 1) horizontally.
59. Medial process of pelvic girdle: 0) not joined medially; 1) joined medially by cartilage.
60. Posterior process of pelvic girdle: 0) present; 1) absent.
61. Autogenous pelvic cartilages: 0) absent; 1) present.
62. Shape of anterior-most proximal dorsal pterygiophore: 0) narrow blade; 1) triangular.
63. Anal-fin pterygiophores: 0) not fused; 1) fused.
64. Number of supraneurals: 0) three or more; 1) two; 2) one; 3) none.

65. Percentage of caudal vertebrae: 0) <25%: 1) 40-60%; 2) >60%.
66. Number of open neural arches: 0) more than four; 1) first four; 2) none.
67. First rib originates on: 0) third vertebra; 1) fourth vertebra; 2) fifth vertebra; 3) second vertebra; 4) first vertebra.
68. Ossification of ribs: 0) in cartilage; 1) some in membrane bone; 2) all in membrane bone.
69. Baudelot's ligament: 0) originates on first vertebra; 1) originates on more than one vertebra.
70. Epipleural bone origin: 0) third vertebra; 1) second vertebra; 2) first vertebra.
71. Position of epipleurals: 0) all beneath horizontal septum; 1) displaced dorsally into horizontal septum.
72. Epipleurals on first and second vertebrae: 0) autogenous; 1) fused to centra.
73. Origin of epipleurals: 0) all on the neural arch; 1) some on centrum or parapophysis; 2) all on the centrum.
74. Epineurals: 0) all attached to the axial skeleton; 1) most unattached; 2) all unattached.
75. Epicentrals: 0) ligamentous; 1) ossified; 2) absent.
76. Epicentral attachment: 0) all attached to either centrum or parapophyses; 1) anterior ones attached to distal end of epipleurals.
77. Body scales: 0) present; 1) lateral line scales only.
78. Dorsal bony scutes: 0) absent; 1) present but small and without ornamentation; 2) present but large and with ornamentation.
79. Margin of anal fin: 0) not indented; 1) indented.
80. Fleshy midlateral keel: 0) absent; 1) present.
81. Eyes: 0) round and laterally directed; 1) slightly flattened and laterally directed; 2) tubular and dorsally directed.
82. Mode of reproduction: 0) separate sexes; 1) synchronous hermaphrodites.
83. Stomach walls: 0) thick, unpigmented; 1) thin, pigmented.
84. Swim bladder: 0) present, 1) absent.
85. Larval eyes: 0) Round; 1) vertically elongated.
86. Larval head spines: 0) Absent; 1) present.
87. Larval peritoneal pigment: 0) Absent; 1) single or multiple unpaired peritoneal pigment sections.
88. Middle predorsal orsal scutes: 0) Absent; 1) present.

Table 4. Data matrix for the “phylogenetic analyses 2 and 3” based on data from Fielitz (2004) and Fielitz and González-Rodríguez (2010), modifications to the original data matrix are highlighted (characters are defined in Table 3 of this appendix).

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
Diplophos	0000010010	0000?0?000	0000000001	101010100?	0000000000	0100002100	0000101000	0000000000	0?00000
Myctophum	0?00000000	0000000000	0000010100	0000000000	0000000000	0000000000	1000020000	0000000000	000AA00
Synodus	1000110111	1000001111	0000020000	0020000002	0000000000	0000000010	0000002201	1000000000	0001002
Alepisaurus	2?000?0??0	1010111111	1111101010	02?0002001	1001110011	10000?0111	1013114212	1101101011	0111011
Omosudis	?1?001??00	1010111111	11111010?0	0220102001	1001110011	10000?0111	1012114212	1101101011	0111011
Paralepis	0?0?010?00	1010001111	1011100110	022000100?	0001000000	1000?00111	1001114212	1102201010	0101001
Coccorella	0100000?00	?010?01111	1111200010	022010210?	0001000000	1010103111	1101210102	1010311010	2101101
Evermannella	0100000?01	1010?01111	1011100010	022010101?	0001100000	1010103111	1101210102	1010311010	2101101
Chlorophthalmus	0000?10?00	101000?110	0000000010	0020002001	0000000000	000??03011	0001210101	100000?000	0101001
Bathysaurus	10110?0??0	??00001111	0001000110	011?00000?	0000000000	0000?03011	0000003102	1020201000	1101001
Cimolichthys	2111000000	1100000???	?????????2	3230000000	110?100001	110??0????	???31?????	??????12??	???????
Palaeolycus	1??1???1??	1221101???	?????????2	?2?0101101	101?111111	10?100????	?1031?????	??????11??	???????
Rharbichthys	?1?????1?0	1121310???	?????????1	0200002000	0003010101	0100003???	?1031?????	??????10??	???????
Eurypholis	1131201000	1221110???	?????????2	3201011102	3011122133	0002221???	?1031?????	??????12??	???????
Saurorhamphus	22312?10?0	?1?011????	?????????2	3201011002	301?122133	0002221???	?1031?????	??????12??	???????
Parenchodus	?0212???10	022?111???	?????????2	2200111100	201?211122	1100001???	??0020????	??????12??	???????
E. lewesiensis	1121210110	0221110???	?????????2	?2?0011110	11????????	??????????	??????????	??????11??	???????
E. venator	0121?10110	1221200???	?????????2	2230011110	211?211122	110112????	?1?3??????	??????11??	???????
E. marchessettii	1131110110	1221110???	?????????2	3230011100	3112211133	1100121???	?10120????	??????11??	???????
E. petrosus	1021110111	1221210???	?????????2	3200012100	211?211122	1100111???	?10310????	??????11??	???????
E. gladiolus	0021110111	0220321???	?????????2	3200011100	211?211122	???111????	???3?0????	??????11??	???????
E. shumardi	??21110?10	?221310???	?????????2	3200011110	211?211122	??0112????	??????????	??????1???	???????
E. dirus	????????10	?221321???	?????????2	3200012100	011?21?10?	??????????	??????????	??????1???	???????
E. gracilis	0?21?11110	1221310???	?????????2	3200012100	211?211122	1101121???	?1?320????	??????11??	???????
E. brevis	??21??0100	0221110???	?????????2	2200011100	2113211122	11021?????	?1012?????	??????11??	???????
E. zimapanensis	?12??1?000	022130????	????????02	3200011100	211?211122	1101112???	??131?????	??????10??	???????
E. sp. Gavdos	001???011?	?2?1321???	??????????	???00?2100	11??2?0?11	??????????	??????????	??????????	???????
Unicachichthys	??21?0??01	?100?10???	?????????2	3130010002	1113121112	110102?0??	?000100??1	0021??110?	???????

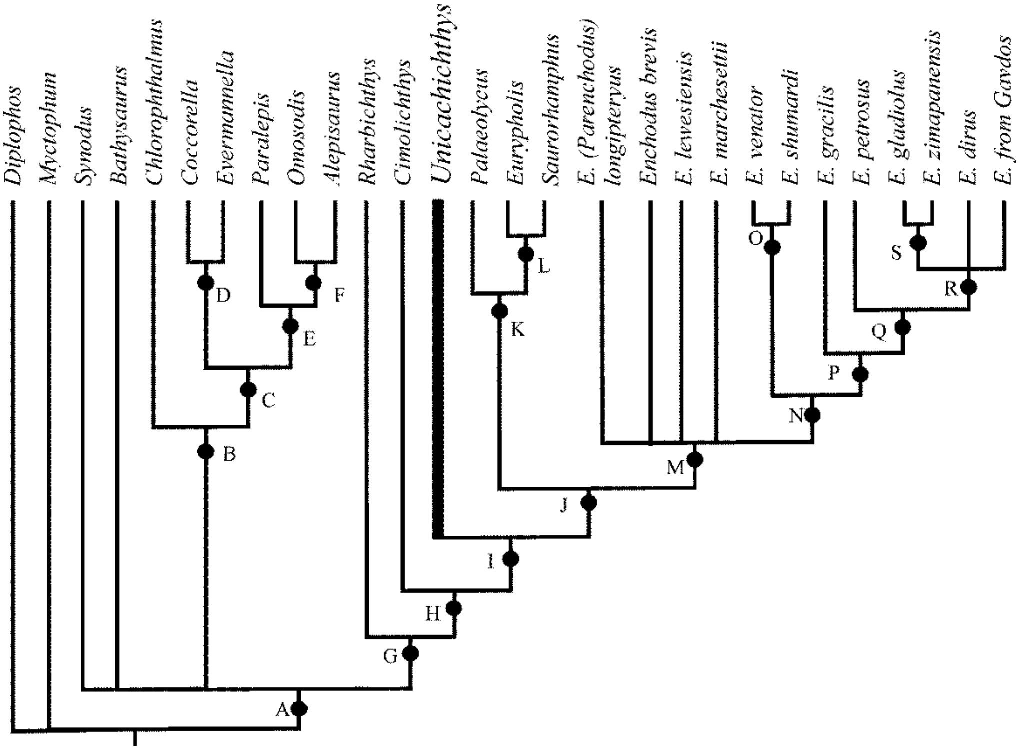

Figure 2. Relationships of the family Enchodontidae *sensu* Fielitz (2004) including *E. zimapanensis*, *Enchodus* from Gavdos (Cavin et al., 2012), and *Unicachichthys***.** Supporting Characters of nodes in this tree (synapomorphies are underlined) are these: **A**: 4-1, 29-1, 32-2, 57-3, 60-1, 75-2, 77-1, 82-1. **B:** 1-0, 13-1, 37-2, 40-1, 64-1, 65-2, 66-1. **C:** 2-1, 21-1, 23-1, 25-1, 44-1, 51-1, 58-1, 61-1, 70-2, 79-1. **D:** 6-0, 35-1, 53-1, 55-1, 62-1, 73-1, 75-3, 76-1, 81-2, 85-1. **E:** 30-0, 65-1, 67-4, 68-2, 69-1, 72-1, 74-1. **F:** 1-2, 15-1, 16-1, 22-1, 27-1, 41-1, 45-1, 46-1, 49-1, 50-1, 63-1, 64-2, 75-1, 80-1, 83-1, 86-1. **G:** 2-1, 3-1, 4-1, 12-1, 16-1, 17-0, 29-0, 28-1, 30-1, 33-0, 44-3, 46-1, 48-1, 50-1, 52-1, 62-1, 64-3, 65-1, 71-0, 73-2, 74-1, 81-1. **H:** 30-2, 31-3, 33-3, 41-1, 42-1, 45-1, 51-1, 54-1, 57-0, 78-1. **I:** 3-2, 5-1, 15-1, 36-1, 40-2, 43-1, 47-1, 49-1, 50-2, 56-2. **J:** 12-2, 13-2, 14-1, 33-0, 37-1, 38-1, 44-2, 57-1. **K:** 3-3, 5-2, 7-1, 42-0, 50-1, 52-0. **L:** 8-0, 34-1, 41-3, 46-2, 47-2, 49-3, 50-3, 51-0, 54-2, 55-2, 78-2. **M:** 6-1, 9-1, 40-0, 41-2, 45-2, 49-2, 55-1, 65-2. **N:** 1-0, 15-3. **O:** 39-1. **P:** 2-0, 37-2. **Q:** 56-1, 65-1. **R:** 11-0, 16-2, 17-1, 57-2, 63-1. **S:** 37-1. ***Alepisaurus***: 64-3. ***Bathysaurus***: 3-1, 4-1, 12-1, 28-1, 32-1, 33-1, 67-3, 70-2, 73-2, 81-1. ***Chlorophathalmus***: 20-0, 24-0, 32-0, 75-0. ***Cimolichthys***: 1-2, 8-0, 16-0, 46-0, 48-0, 78-2. ***Coccorella***: 22-1, 25-2, 38-1. ***Diplophos***: 9-1, 30-1, 31-1, 33-1, 35-1, 37-1, 52-1, 57-2, 58-1, 65-1, 67-1. ***Enchodus brevis***: 9-0, 54-2. ***E. dirus***: 3-1, 41-0, 47-0, 49-0. ***E.* from Gavdos**: 3-1, 41-1, 47-0, 49-1. ***E. gladiolus***: 10-1, 14-0. ***E. gracilis***: 7-1. ***E. lewesiensis***: 39-1, 41-1. ***E. marchesettii***: 3-3, 33-3, 41-3, 49-3, 50-3. ***E. petrosus***: 1-1, 10-1, 15-2, 54-0. ***E. venator***: 15-2, 16-0, 31-2, 33-3. ***E. zimapanensis***: 2-1, 8-0, 9-0, 16-0, 78-0. ***Evermannella***: 10-1, 37-1, 39-1, 45-1. ***Myctophum***: 6-0, 26-1, 28-1, 61-1,66-2. ***Omosudis***: 35-1. ***Palaeolycus***: 16-0, 17-1, 35-1, 36-0, 40-1, 56-0. ***Paralepis***: 28-1, 37-1, 74-2. ***Parenchodus***: 17-1, 35-1, 42-0, 55-0, 64-0, 78-2. ***Rharbichthys***: 13-2, 14-1, 15-3, 37-2. ***Saurorhamphus***: 1-2, 2-2, 12-1, 14-0, 38-0. ***Synodus***: 5-1, 9-1, 10-1, 26-2, 40-2, 67-2, 68-2, 87-2. ***Unicachichthys***: 10-1, 32-1, 46-2, 62-0, 64-0.

References

Cavin, L., Alexopoulos, A., Piuz, A., 2012. Late Cretaceous (Maastrichtian) ray-finned fishes from the island of Gavdos, southern Greece, with comments on the evolutionary history of the aulopiform teleost *Enchodus*. Bulletin de la Société géologique de France, 183(6), 561–572.

Fielitz, C., 2004. The phylogenetic relationships of the †Enchodontidae (Teleostei: Aulopiformes), in: Arratia, G., Wilson, M.V.H., Cloutier, R. (eds.), Recent Advances in the Origin and Early Radiation of Vertebrates. Verlag Dr. Friedrich Pfeil, München, Germany, p. 619–634.

Fielitz, C., González-Rodríguez, K. A., 2010. A new species of *Enchodus* (Aulopiformes: Enchodontidae) from the Cretaceous (Albian to Cenomanian) of Zimapán, Hidalgo, México. Journal of Vertebrate Paleontology, 30(5), 1343–1351.

Nelson, J.S., 1994. Fishes of the World. 3rd ed. John Wiley and Sons, New York, 600 p.

Silva, H.M.A., 2007. Revisão taxonômica e filogenética dos peixes Enchodontoidei (*sensu* Nelson, 1994) e considerações biogeográficas. Masters degree Thesis, Programa de Pós-graduação em Ecologia e Evolução, Universidade do Estado do Rio de Janeiro, Brazil, 142 p.

Silva, H.M.A., Gallo, V., 2011. Taxonomic review and phylogenetic analysis of Enchodontoidei (Teleostei: Aulopiformes). Anais da Academia Brasileira de Ciências, 83(2), 483–511.

APPENDIX II

The Cenomanian short snout enchodontid fishes (Aulopifomes, Enchodontidae) from Sierra Madre Formation, Chiapas, southeastern Mexico

by

Jesús Alberto Díaz-Cruz, Jesús Alvarado-Ortega, and Gerardo Carbot-Chanona

Additional photographs of *Unicachichthys ~~multivertebrata~~* nov. gen and sp.

This appendix provides additional photographs of *Unicachichthys ~~multivertebrata~~* nov. gen. and sp. described and phylogenetically analyzed in the main text and Appendix I of this manuscript . These images are intended to support the description of this species and also it provides the ability for readers to have access to details preserved in the specimens studied.

Fig. 1. *Unicachichthys multidentata* nov. gen. and sp., head of IHNFG-2987, holotype.

Fig. 2. *Unicachichthys multidentata* nov. gen. and sp., region behind the head of IHNFG-2987, holotype.

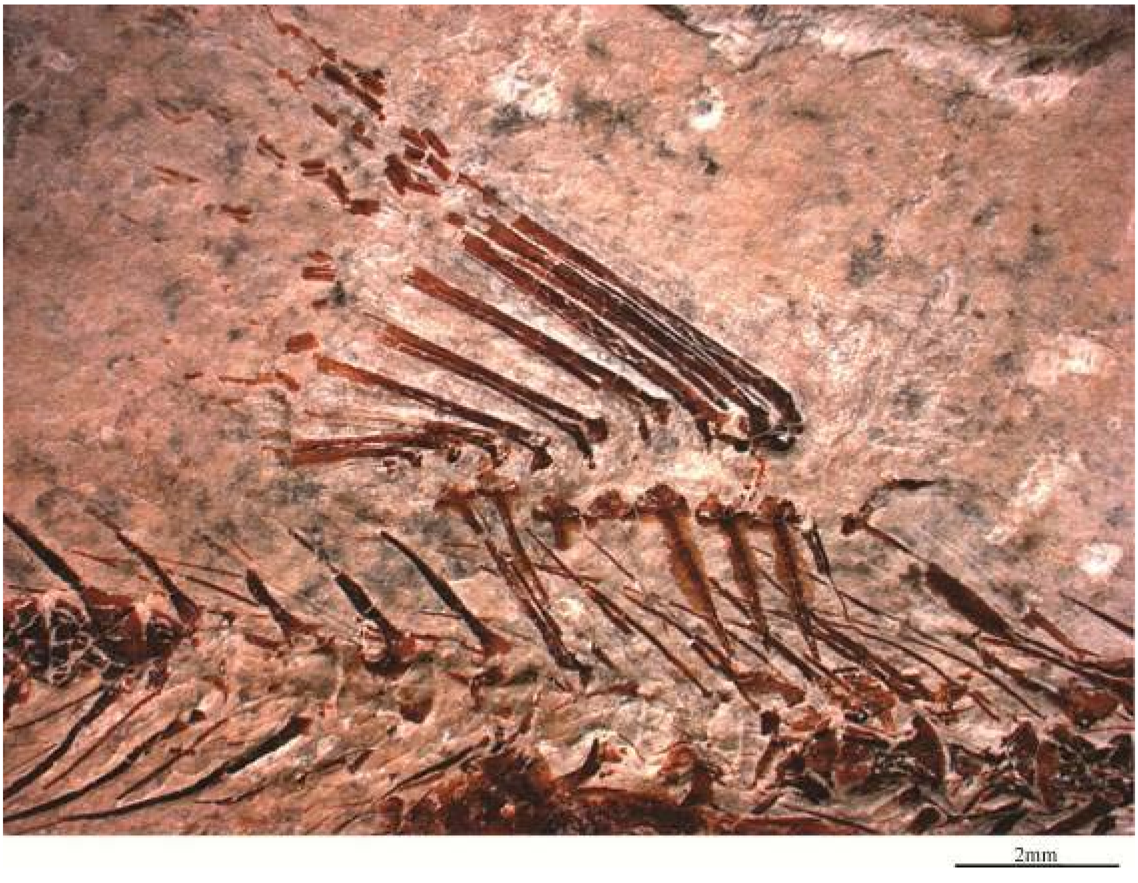

Fig.3. *Unicachichthys multidentata* nov. gen. and sp., anal fin of IHNFG-2987, holotype.

Fig. 4. *Unicachichthys multidentata* nov. gen. and sp., anal fin of IHNFG-2987, holotype.

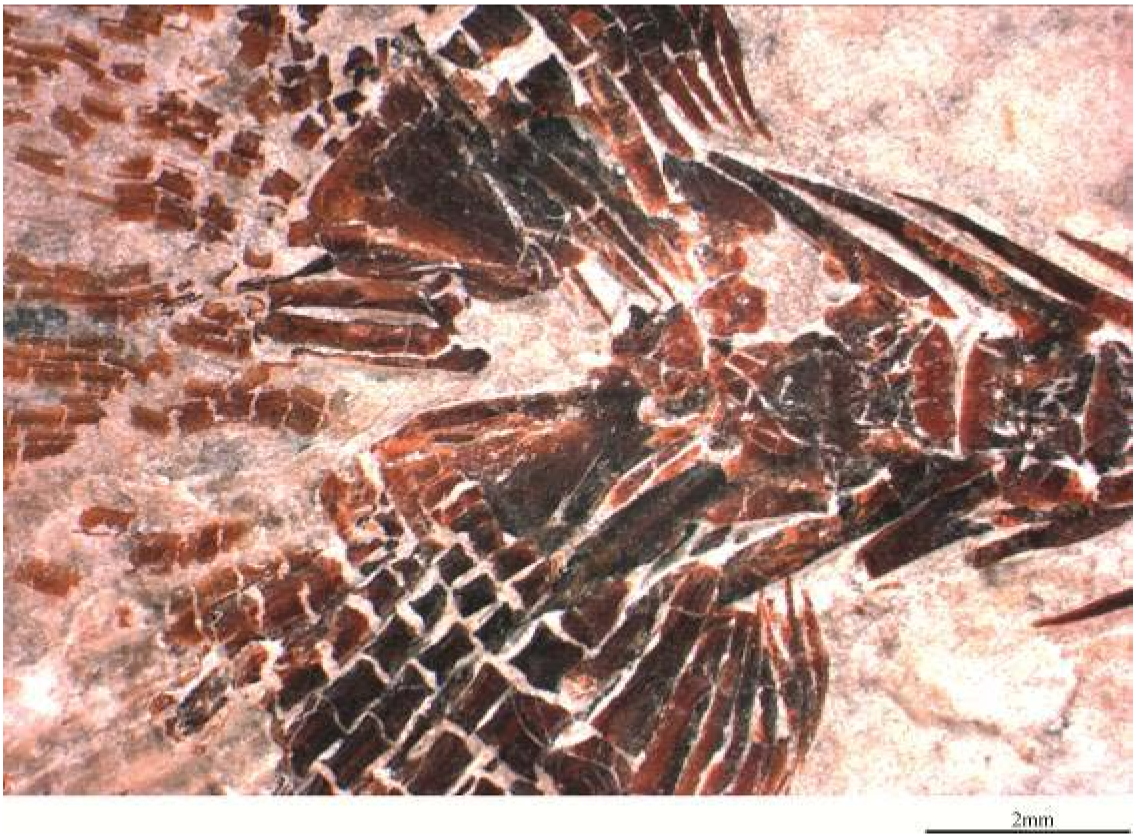

Fig. 5. *Unicachichthys multidentata* nov. gen. and sp., caudal skeleton of IHNFG-2987, holotype.

Fig. 6. *Unicachichthys multidentata* nov. gen. and sp., head of IHNFG-2988.

Fig. 7. *Unicachichthys multidentata* nov. gen. and sp., caudal skeleton of IHNFG-2988.

Fig. 8. *Unicachichthys multidentata* nov. gen. and sp., skull and first abdominal vertebrae in part of IHNFG-4347.

Fig. 9. *Unicachichthys multidentata* nov. gen. and sp., jaws and demopalatine in part of

IHNFG-4347.

Fig. 10. *Unicachichthys multidentata* nov. gen. and sp., region of the opercle and lower jaw-quadrate articulation in part of IHNFG-4347.

Fig. 11. *Unicachichthys multidentata* nov. gen. and sp., counter part of IHNFG-4347.

Fig. 12. *Unicachichthys multidentata* nov. gen. and sp., región of the articulation of lower jaw-quadrate in counter part of IHNFG-4347.