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New semionotiform (Neopterygii) from the Tlayúa Quarry (Early Cretaceous, Albian), Mexico

ADRIANA LÓPEZ-ARBARELLO[1] & JESÚS ALVARADO-ORTEGA[2]

[1] *Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Strasse 10, D-80333 München, Germany.*
E-mail: a.Lopez-Arbarello@lrz.uni-muenchen.de
[2] *Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, México, D. F., 04510, México.*
E-mail: alvarado@geologia.unam.mx

Abstract

We describe a new semionotiform fish, *Tlayuamichin itztli* **gen. et sp. nov.** from the Early Cretaceous (Albian) of Mexico, which constitutes one of the youngest semionotid articulated remains. The new taxon is represented by five well-preserved specimens from the Tlayúa Quarry near Tepexi de Rodríguez in Puebla State, central Mexico. A series of paraethmoid bones anterior to the supraorbital series, supraorbital bones extending beyond the anterior rim of the orbit, the presence of a large pentagonal supraorbital closing the anterior rim of the orbit, seven anterior infraorbitals, dorsally expanded infraorbitals at the ventral border of the orbit, and the most dorsal suborbital separating the preoperculum from the dermopterotic are potential autapomorphic features of the new taxon. The very long frontals, a dermopterotic that does not contact the anterodorsal corner of the operculum and the presence of a modified pectoral scale are additional features that help to diagnose the taxon. *Tlayuamichin itztli* **gen. et sp. nov.** resembles most closely "*Lepidotes*" *minor* from the Middle Purbeck Beds (early Berriasian), England. These two taxa share similarity with other species of *Semionotus* from the Early Jurassic of North America and the Triassic of Europe, suggesting interesting biogeographic relationships.

Key words: Semionotiformes, new taxon, anatomy

Introduction

The Semionotiformes represent a monophyletic group including the poorly defined semionotids, the macrosemiids and the lepisosteids (Brito 1997; Cavin & Sutheethorn 2006; López-Arbarello 2006). The fossil record of the group goes back to the Early Triassic (Deecke 1889) and semionotiforms are very well represented, with several taxa of semionotids and the first records of macrosemiids, through the Triassic of Central Europe, suggesting a rapid radiation during that time (López-Arbarello 2008a). The occurrence of Triassic semionotids outside Europe today is doubtful because *Semionotus kanabensis* (Schaeffer & Dunkle, 1950) originally described as a species from the Chinle Formation, Utah, USA, actually is being recovered from the lithologically superficially similar, Lower Jurassic Whitmore Point Member of the Moenave Formation (Milner & Kirkland 2006: 511). Possible semionotiforms from the Triassic of Gondwana has recently been revised and there is no certain evidence for the presence of the group in this supercontinent (López-Arbarello *et al*. 2010). In the Jurassic however, the group is already widely spread with several records in Asia (Su 1996; Cavin & Sutheethorn 2006), Europe (Agassiz 1833–1844; Wenz 1968; Wenz *et al*. 1994; Lambers 1999), North America (McCune 2004), and Gondwana (López-Arbarello *et al*. 2008). Except for the lepisosteids, the fossil record of which starts in the Early Cretaceous to the present, macrosemiids and semionotids have their last appearances during the middle Cretaceous. The youngest macrosemiids are known from the Coenomanian-Turonian of Morocco (Murray & Wilson 2009) and the Cenomanian of Mexico (Alvarado-Ortega *et al.* 2009), whereas the youngest articulated remains of semionotids are known from the Cenomanian of Africa (Forey *et al*. in press), and Aptian-Albian of South America (Gallo & Brito 2004; López-Arbarello & Codorniú 2007).

In 1996 Applegate reported the occurrence of the first semionotiform found in Mexico, in the Early Cretaceous of Puebla. The record was based on two specimens from the Tlayúa quarry, near Tepexi de Rodríguez, Puebla

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State, central Mexico (Fig. 1), which he identified as an indeterminate species of the genus *Lepidotes*. The semionotiforms are very rare in the Tlayúa Quarry and since Applegate´s report only three additional specimens have been collected in this locality. The material is very well preserved and its detailed study led us to the recognition of a new semionotiform genus and species. The aim of the present work is to provide a detailed description of this new taxon and to discuss its systematic relationships with other semionotiforms.

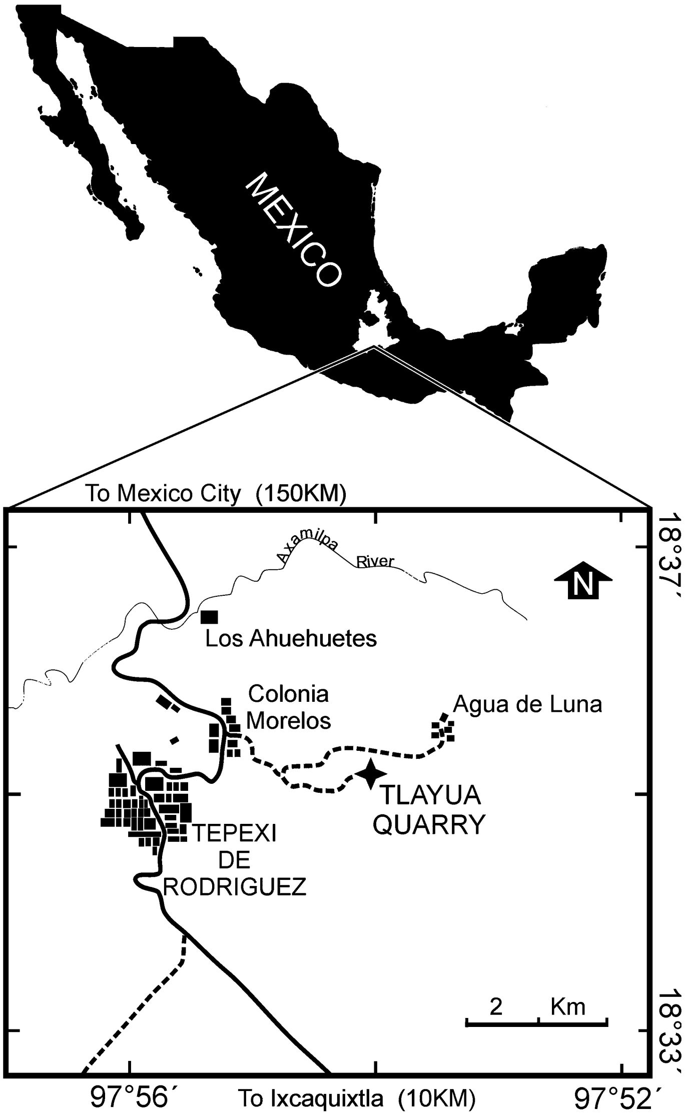

FIGURE 1. Location map of the Tlayúa Quarry near Tepexi de Rodríguez, Puebla State, central Mexico.

Geological and palaeontological setting

In the area of Tepexi the Rodríguez, the Late Paleozoic low-grade metamorphosed rocks of the Acatlán Complex are the oldest rocks known. This complex was an emergent area of land exposure during the Jurassic and possibly the Early Cretaceous (Applegate *et al.* 2006). The base of the Tlayúa Formation is unknown, but it probably deposited directly above this Paleozoic-Early Cretaceous strata.

Based on the limestones that crop out in the Tlayúa ravine Pantoja-Alor (1992) described the Tlayúa Formation with three carbonate members. It is characterized as a sequence of thick and massive bluish gray micritic (mudstone to wackestone) limestone strata that reaches at least 50 m of depth. The Lower Member is also characterized by its intraclasts, concretions and lenses of chert, biostromes, and miliolids, as well as by the occurrence of the rudist *Toucasia polygyra* and inoceramids of the genus *Chondrodonta*, which indicate a Lower Albian age for this member (Alencáster 1973). The Middle Member is a sequence of 35 m of thinly bedded to laminated yellow-brown micritic limestone strata intercalated with thinly yellow-reddish- purple clay hematitic layers. These hematitic clay layers are highly fossiliferous and bear a large array of well-preserved vertebrates and invertebrates (Applegate *et al*. 2006). Based on biostratigraphic (Seibertz & Buitrón 1987; Cantú-Chapa 1987; Seibertz & Spaeth 2002) and magnetostratigraphic analyses (Benammi *et al*. 2006) the age of the Middle Member of the Tlayúa Formation is considered as Middle-Upper Albian. The Upper Member is a sequence of dolomite and dolomitic limestone, truncated by overlying continental Tertiary deposits. The lithology of the Upper Member ranges from dolomite crystals with intraclasts and miliolids, to dolomite crystals in a micritic matrix (Pantoja-Alor 1992). The miliolid species *Dicyclina schlumbergeri* gives this member a Cenomanian age (Pantoja-Alor 1992). Continental Tertiary deposits overlay the truncated Upper Member of Tlayúa Formation.

A large fossil assemblage from the Tlayúa quarry including the specimens described in the present article is nowadays deposited in the Colección Nacional de Paleontología at the Museo María del Carmen Perrilliat M., housed in the Instituto de Geología of the Universidad Nacional Autónoma de México, which acronym is IGM. This fossil assemblage is very diverse and characterized by well-preserved vertebrates (see Alvarado-Ortega 2005; Alvarado-Ortega *et al*. 2006; Applegate *et al*. 2006; for a complete faunal and floral list). The invertebrate fauna includes foraminifera, sponges, corals, bivalves, gastropods, cephalopods, arthropods (including arachnids, insects, isopods, decapods, crabs, and ostracods), and echinoderms (see Applegate 1988, 1992; Applegate *et al.* 2009; Feldmann *et al.* 1998; Guerrero-Arenas 2004; Martín-Medrano *et al.* 2009; among others). The assemblage of the Tlayúa Quarry is dominated by fishes (70%) including a large amount of marine and some possible freshwater taxa (see Applegate *et al*. 2006; Alvarado-Ortega *et al*. 2006). Other vertebrate fossils include turtles, pterosaurs, crocodiles, and lizards (Reynoso 2000; Reynoso & Callison *et al*. 2000; among others). A few fossil plants and palynomorphs have also been recovered in Tlayúa (Martínez-Hernández & Ramírez-Arriaga 1996; Alvarado-Ortega 2005; Applegate *et al.* 2006).

Two radically different interpretations of depositional environments have been proposed for the strata at the Tlayúa Quarry. In one case the environment is interpreted as shallow marginal marine and/or a stagnant coastal lagoon with periodic freshwater influences and hypersaline and anaerobic conditions. This interpretation is based on the petrographical and mineralogical composition, isotopical analyses of C^{13} and O^{18}, algal mat structures, and the characteristic exotic fossil assemblage of Tlayúa, which includes a mixture of terrestrial, freshwater, and marine organisms (Applegate *et al*. 1982; Malpica-Cruz *et al*. 1989; Martill 1989; Pantoja-Alor 1992; Espinosa-Arrubarrena & Applegate 1996; Guerrero-Arenas 2004; Applegate *et al*. 2006; Alvarado-Ortega *et al*. 2007; Suarez *et al*. 2009). However, Kashiyama *et al*. (2004) provided another interpretation suggesting that the fossiliferous strata of Tlayúa were accumulated in an open marine basin with either anaerobic or dysaerobic conditions. In this case, the interpretation is based on a microfacies study and a detailed spectral analyses that shown evidences of Milankovitch cyclicity. The first of these two environmental interpretations of Tlayúa is currently found to be better supported from the so far available evidence (Suarez *et al*. 2009).

Material and methods

Apart from the semionotiform specimens from the Tlayúa quarry, which are listed in the Systematic Palaeontology section, several other taxa in different collections were examined for the sake of comparison.

Institutional abbreviations. BGS GSM, British Geological Survey; BSPG, Bayerische Staatsammlung für Paläeontologie, München, Germany; GZG.V, Geowissenschaftliches Zentrum der Georg-August-Universität, Göttingen, Germany; IGM, Instituto de Geología, Universidad Nacional Autónoma de México; JME, Jura Museum, Naturwissenschaftliche Sammlungen Eichstätt, Germany; MBf, Fossil Collection, Museum für Naturkunde der Humboldt Universität zu Berlin, Germany; MHIN-UNSL-GEO, Museo de Historia Natural de la Universidad Nacional de San Luis, San Luis, Argentina; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHM, Natural History Museum, London, UK; NMC, Naturkunde-Museum Coburg, Coburg, Germany; NMB, National Museum, Bloemfontein, South Africa.

Comparative material. *Araripelepidotes temnurus*: BSPG 1965-I-132; *Lepidotes elvensis*: BSPG AS-I-625, 1940-I-8, MBf 1372, 1495, 1591, MNHN-JRE 250–2, 254, 545 (holotype), MNHN-HLZ 32, NHM P. 14539; *L. laevis*: MNHN-CRN 61; *L. mantelli*: NHM P. 2401, 2456 (holotype), 3036–7, 3048–49, 3517–8, 6336, 6344–5, 6348c, 6362, 6933, 7333, 11832–3, 14451; *L. minor*: BGS GSM 27975 (lectotype); MBf 1617–9, NHM P. 8047, 1118, 29398–9, 41157; *L. semiserratus*: NHM P. 3828, 3528a, 7410, 35556, 62939; *Macrosemius rostratus*: BSPG 1986 XV 119; *M. fourneti*: BSPG AS I 768 (holotype); *Macrosemiocotzus americanus*: IGM 8163 (holotype); *Neosemionotus puntanus*: MMP 1114 (holotype); MHIN-UNSL-GEO-V8, V64, V68, V183–185, V187–191; *Notagogus denticulatus*: BSPG AS I 768 (holotype), 1967 I 303, 1986 XV 120; *Notagogus decoratus*: BSPG 1986 XV 119; *Notagogus novomundi*: IGM 8172 (holotype), IGM 8173 and IGM 8174; *Paralepidotus ornatus*: BSPG 2003 XXIX 218, 2003 XXIX 632, BSPG 2007 I 62; *Pliodetes nigeriensis*: MNHN-GDF 1198, 1274, 1275 (holotype), 1276–78, 1285, 1288, 1295, 1297, 1298, 1300; *Propterus microstomus*: AS VII 268 (holotype), AS I 637; BSPG 1986-XV-121, BSPG 1964-XXIII-145; Semionotidae **gen. et sp. nov.** (López-Arbarello & Sferco in press): JME Scha 80; *Semionotus bergeri*: BSPG AS-I-512, 1960-I-25, 1960-XVI-2; GZG.V.010.001 (lectotype), GZG.V.010.001 (lectotype), V.010002, MBf 15461, 15464, 15466, NMC 1264, 15128 (4 specimens), 15129; *S. capensis*: BSPG 1908-I-502, MBf 12240 (8 specimens), and photographs of several specimens in the NMB.

The semionotiforms from the Tlayúa quarry are preserved in hematitic clay and they were chemically and mechanically prepared at the IGM. The specimens were studied under binocular microscopes and all drawings were made with camera lucida.

Skull bones are named according to the use of most authors in actinopterygians. The bones carrying the infraorbital sensory canal anterior to the orbit are referred to as ‘anterior infraorbitals’ following Wenz (1999, 2003) and López-Arbarello and Codorniú (2007). The ossifications of the palatoquadrate are named after Arratia and Schultze (1991). Fringing fulcra are named according to Patterson (1982). Scutes, unpaired and paired basal fulcra are identified according to López-Arbarello and Codorniú (2007). The relative position of the fins and the scale counts is expressed in a pterygial formula where D, P, A, and C indicate the number of scale rows between the first complete row behind the pectoral girdle and the insertion of the dorsal, pelvic, anal, and caudal fins respectively, and T is the total number of scale rows between the pectoral girdle and the caudal inversion (Westoll 1944).

Anatomical abbreviations. a.ch, anterior ceratohial bone; a.io, anterior infraorbitals; ang, angular bone; b.fu, basal fulcrum; br, branchiostegal rays; cl, cleithrum; cor, coronoid bones; d, dentary; d.c.fu, unpaired basal caudal fulcra; d.cl, series of denticles on the cleithrum; dpal, dermopalatine bone; dpt, dermopterotic bone; ds, dermosphenotic bone; ecp, ectopterygoid bone; enp, endopterygoid bone; ex, extrascapular bone; fr, frontal bone; fr.fu, fringing fulcra; io, infraorbital bone; iop, interoperculum; mps, modified pectoral scale; mpt, metapterygoid bone; msc, main sensory canal; mx, maxilla; mx.p, articular anterior process of the maxilla; n, nasal bone; op, operculum: pa, parietal bone; p.ch, posterior ceratohial; pcl, postcleithrum; pmx, premaxilla; pet, paraethmoid bones; pop, preoperculum; psph, parasphenoid; pt, posttemporal bone; qu, quadrate; ra, radial; rar, retroarticular bone; sag, surangular bone; sc, scute; scl, supracleithrum; smx, supramaxilla; so, supraorbital bone; sop, suboperculum; sph, sphenotic; su, suborbital bone; u.b.fu, unpaired dorsal caudal fulcra; vo, vomer. The labels “(r)” or “(l)” after any of the abbreviations indicate right or left elements respectively.

Systematic palaeontology

Infraclass Neopterygii Regan, 1923

Order Semionotiformes Arambourg and Bertin, 1958 *sensu* Olsen & McCune 1991

Family Semionotidae *sensu* Wenz, 1999

Tlayuamichin new genus

Lepidotes Applegate, 1996: 531, fig. 1
Type species. *Tlayuamichin itztli* **gen. et sp. nov.** (Fig. 2)

Derivation of name. The generic name is written in the Náhuatl language, which is the language of the Mexica people. The Mexica people inhabited the area around the Tlayúa quarry in prehispanic times. The name *Tlayuamichin* is formed with the words “tlayúa” after the Náhuatl name of the fossil locality, and “michin” that means fish.

Diagnosis. As for the type and only species.

***Tlayuamichin itztli* gen. et sp. nov.**
(Figs 2–15)

Lepidotes sp. Applegate, 1996: 531, fig. 1

Holotype. IGM 6716; fairly complete specimen of 403 mm SL (Fig. 2). Although missing parts of the unpaired fins, the specimen is almost completely and excellently preserved.

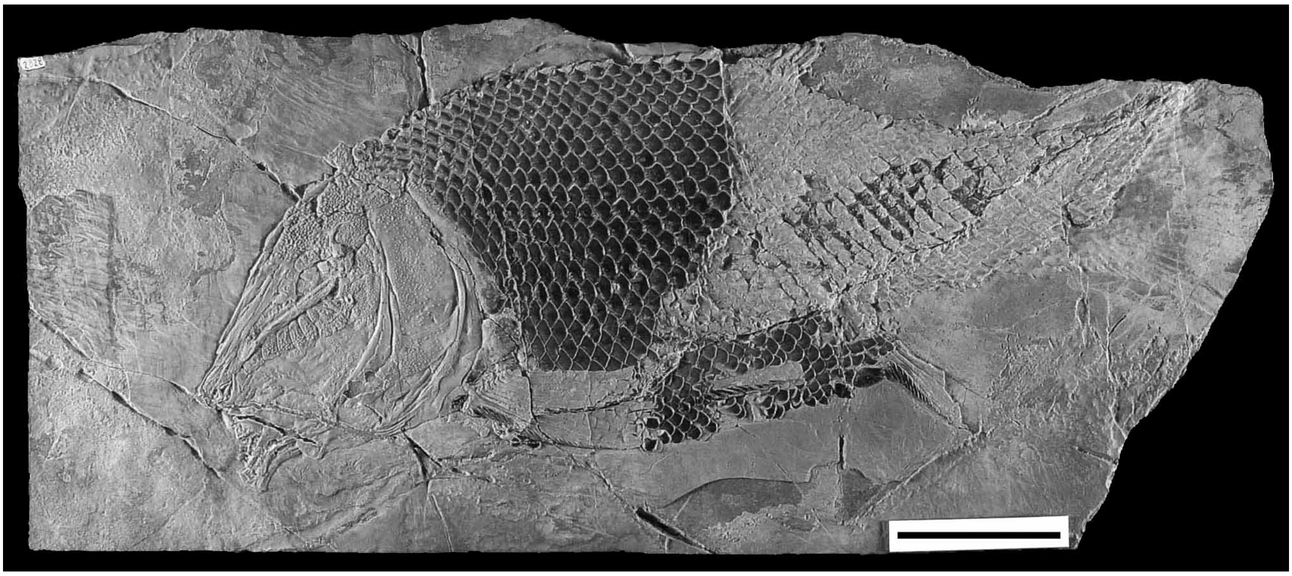

FIGURE 2. *Tlayuamichin itztli* **gen. et sp. nov.** Holotype (IGM 6716) preserved in left lateral view. Standard length of the specimen = 403 mm. Scale bar equals 70 mm.

Paratypes. IGM 6717–5 (Figs 3–5). IGM 6717 is an almost complete specimen, but preserved in lateroventral view and, although the bones are not largely displaced, the skull is disarticulated (Fig. 3A). IGM 6718 is missing the head and pectoral girdle, but the dorsal, anal, and caudal fins are very well preserved (Fig. 3B). IGM 6719 contains a very well preserved and articulated skull with the anterodorsal portion of the body without fins (Fig. 4). IGM 6720 is partially incomplete (the paired fins and part of the unpaired fins and squamation are missing) but, although some of the bones of the head are crushed, its general preservation is excellent displaying some important skull features not preserved in the holotype (Fig. 5).

Type locality. Tlayúa quarry, near Tepexi de Rodríguez, Puebla, Mexico (Fig. 1).

Type horizon. Middle Member of the Tlayúa Formation (Pantoja-Alor, 1992); Middle-Upper Albian (Early Cretaceous) (Seibertz & Buitrón 1987; Cantú-Chapa 1987; Seibertz & Spaeth 2002; Benammi *et al.* 2006).

Derivation of name. The name of the fish is also written in the Náhuatl language. The species epithet "itztli" means "obsidian" and it refers to the scale color in this fish. The complete generic and species name of this semionotid means "the fish of Tlayúa with obsidian color scales".

Diagnosis. Frontals very long, about 4,5 times longer than wide, and narrowing anteriorly up to 37% of their maximal width; antorbital process absent; dermopterotic with anteroventral process articulating with the sphenotic*; operculum does not contact the dermopterotic; a series of paraethmoids anterior to the supraorbital series*; supraorbital series extends beyond the anterior rim of the orbit*; large pentagonal supraorbital partially closing the anterior rim of the orbit*; seven anterior infraorbitals*; infraorbitals at the ventral border of the orbit expanded dorsally, acuminating anterodorsally*; dorsalmost suborbital separating the preoperculum from the dermopterotic; premaxillary teeth smaller than other jaw or palatal teeth*; modified pectoral scale present.

Pterygial formula: $\frac{\quad D23 \quad}{P7\ A18\ C28}T34$

Description. *Tlayuamichin itztli* is a fusiform fish with gently curved dorsal and ventral borders. Although the SL in IGM CT 1 and IGM CT 2, the most complete specimens available, is 42.2 and 27.6 cm respectively; *Tlayua-*

michin itztli could be larger as shown by IGM CT 2, in which the SL could be around 44.6 cm. The maximal depth of the body (MBD), measured midway between the insertion of the pectoral and pelvic fins, is 0.39–0.4 of the SL. The head is triangular and slightly deeper than long. The maximal depth of the head (MDH) enters about 3.6 times in the SL and is almost 1.7–1.9 times the depth of the caudal peduncle. The length of the head (HL) is 0.3 of the SL and 5–5.5 times the longitudinal diameter of the orbit. The paired fins are sub-abdominal, the pelvic fin being located just behind the middle of the body, at 0.52 of the SL. Both unpaired fins are short and located in the posterior half of the body. The dorsal fin inserts at the 24rd raw of scales, at 0.6 of the SL, and the anal fin at the 17th raw of scales, at 0.68–0.74 of the SL. Body proportions are based on the specimens IGM 6716, 6718 and 6720.

Skull roof. The bones of the skull roof are densely ornamented with tubercles. The ornamentation is more dense in the posterior part of the skull, on the extrascapulars, parietals, dermopterotics and posterior part of the frontals. Several tubercles in this area preserve a very thin layer of ganoin. There are two (left side of IGM 6716; Figs 6–7) or three (right side of IGM 6719 and 6720; Figs 4, 8–9) extrascapular bones on each side of the skull. When two extrascapulars are present, the medial extrascapulars are larger than the lateral ones, and are mediolaterally elongate, narrower medially than laterally. When three extrascapulars are present, the two most medial elements occupy an area equivalent to the single medial extrascapular described before. The lateral extrascapulars are trapezoidal, a little narrower dorsally than ventrally. The parietals are rectangular, twice as long as wide, and about a third of the length of the frontals. They form a sinuous inter-parietal suture. In the holotype, the inter-parietal suture has an indentation to the left, but in IGM 6719 there is no indentation in this suture (Fig. 4). The parietals articulate with the frontals anteriorly, laterally with the dermopterotic, and posteriorly they meet the median extrascapulars only. In IGM 6719 the lateralmost extrascapular apparently articulates with the parietal, but this is due to the post-mortem ventral displacement of the parietal and dermopterotic (Fig. 9). The frontals are very long, about 4,5 times longer than wide and articulate with each other through a sinuous suture. The frontals are widest at the posterodorsal corner of the orbit and the posterior border is rounded. Anteriorly, the frontal narrows gradually up to 37% of it maximal width and there is no antorbital process. The nasal bones are well preserved in the holotype (IGM 6716; Figs 6–7, 10) and in IGM 6719. They are delicate, longitudinally elongate bones with laterally curved anterior ends.

The exposed portion of the dermopterotic is rectangular, about 3 times longer than wide. This bone articulates with the frontal anterodorsally, with the lateral extrascapular posteriorly, with the parietal dorsally, and with a large suborbital anteroventrally. In *Tlayuamichin itztli* the dermopterotic does not contact the anterodorsal corner of the operculum, as it is the case in many other semionotiforms. The anterior portion of the ventral margin of the dermopterotic is distinctly concave and the bone is expanded in an anteroventral process that articulates medially with the sphenotic and is superficially overlapped by the dermosphenotic (Fig. 9A–B).

Braincase and parasphenoid. Although no isolated braincase is preserved, some braincase structures are exposed in the holotype mainly. The sphenotic forms a strong lateral process that is projected laterally and presents a dermal component, which is superficially exposed between the dermosphenotic, the last infraorbital bone, and the suborbital bones (Figs 6–7). This small tear-shape dermal component of the sphenotic is ornamented with tubercles covered with a very thin layer of ganoin.

The ethmoidal and orbital regions of the braincase are partially preserved. *Tlayuamichin itztli* peculiarly has a series of apparently endochondral bones aligned lateral to the very elongate ethmoidal region and above the parasphenoid. The series of paired bones extend from the first supraorbital to the tip of the snout dorsal to the antorbital, and these bones, six in total, show a serial correspondence with the anterior infraorbital bones (Figs 6–7, 10). The endochondral nature of these bones is indicated by the state of preservation, but it is not possible to certify this condition. Also, their actual origin is unknown and very difficult to interpret due to the lack of information. Such bones are so far unknown in other actinopterygians and, thus, comparisons are not possible. They might be ossifications originated from the ethmoidal cartilage, probably homologous with the lateral ethmoids. Since these bones are placed laterally along the elongate ethmoidal region, we propose to name them paraethmoids, indicating their topographic relationships. The paraethmoids are well preserved in the holotype (IGM 6716) only, where the paraethmoids 3 and 4 are very damaged due to the intrusion of two displaced anterior infraorbitals from the right side of the skull. In IGM 6720 (Fig. 8) the most posterior of these elements is probably laterally covered by the most anterior dermal supraorbital (this supraorbital is missing in the holotype).

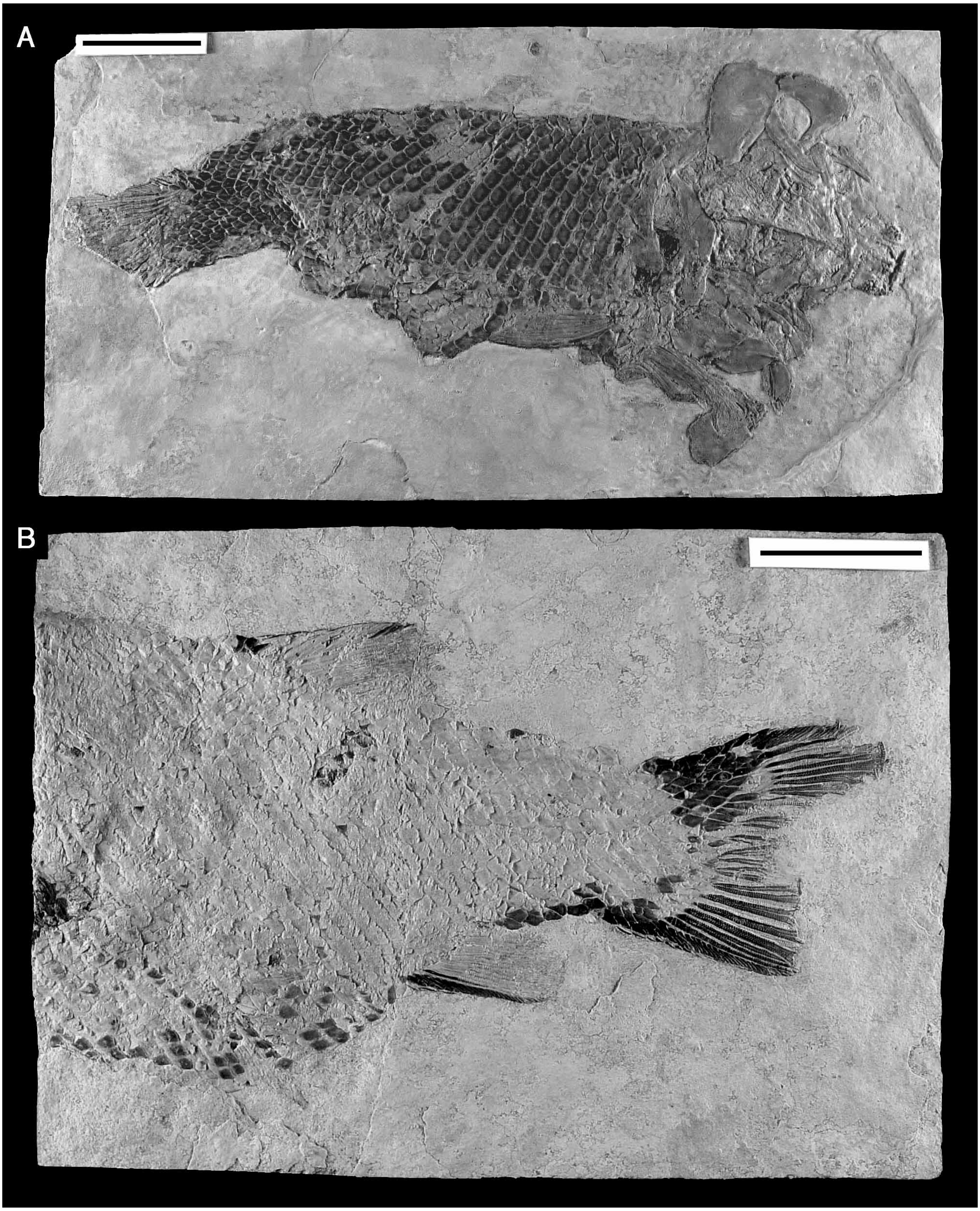

FIGURE 3. *Tlayuamichin itztli* **gen. et sp. nov.** A, Specimen IGM 6717 preserved in right lateroventral view. B, specimen IGM 6718 preserved in right lateral view. Scale bars equal 70 mm.

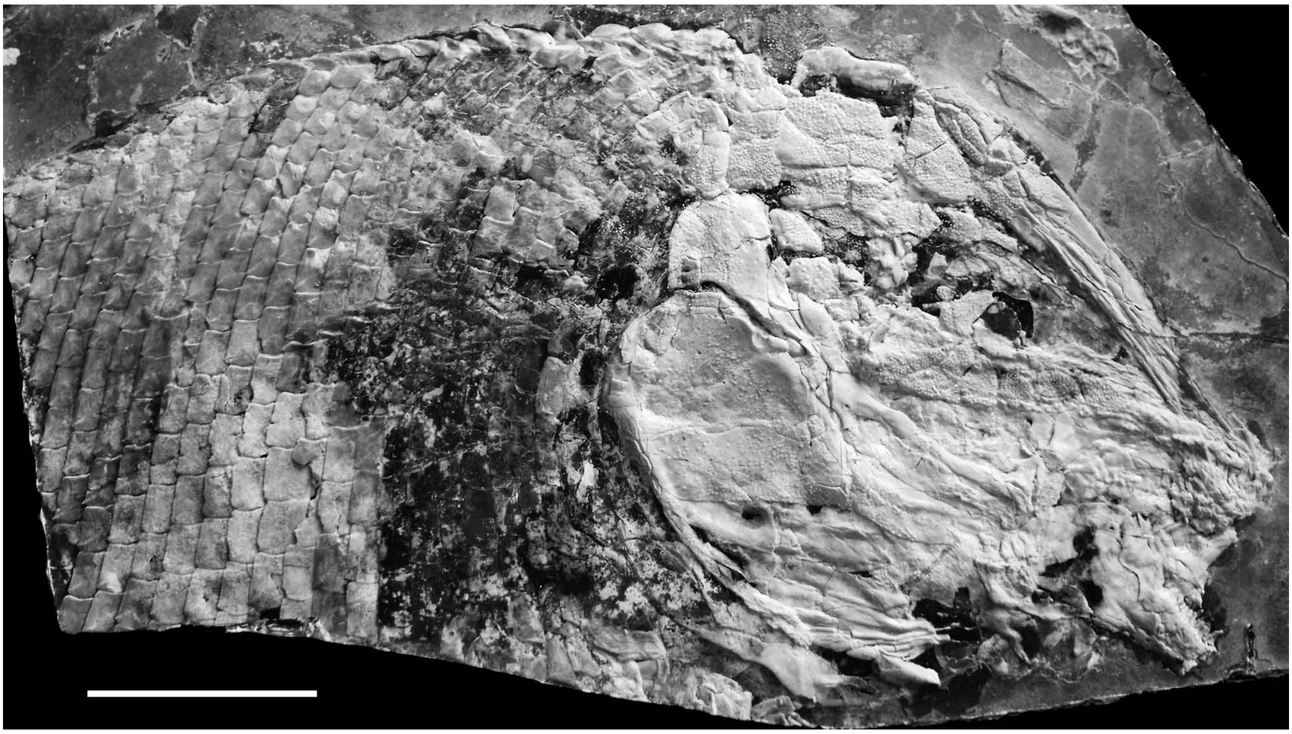

FIGURE 4. *Tlayuamichin itztli* **gen. et sp. nov.** Specimen IGM 6719 preserved in right lateral view. Scale bar equals 50 mm.

FIGURE 5. *Tlayuamichin itztli* **gen. et sp. nov.** Specimen IGM 6720 preserved in right lateral view. Scale bar equals = 50 mm.

Some partially preserved chondral elements within the orbit most probably represent remains of the orbitosphenoid. The orbital part of the parasphenoid is exposed in the holotype and in IGM 6719 and 6720 (Figs 4, 8). In IGM 6717 the parasphenoid is completely exposed, though poorly preserved in ventral view. The parasphenoid is edentulous and extends back throughout the area corresponding to the prootics and ends at the central portion of the basioccipital forming two posterior processes. There is a longitudinal deep median groove along the dorsal surface of the orbital section of the parasphenoid. Within the orbital region, the parasphenoid broadens posteriorly, reaching its maximal breadth at the posterior wall of the orbit, where there are two long and narrow basipterygoid processes. Dermal and possible chondral portions of the basipterygoid processes cannot be distinguished, but the processes are very large.

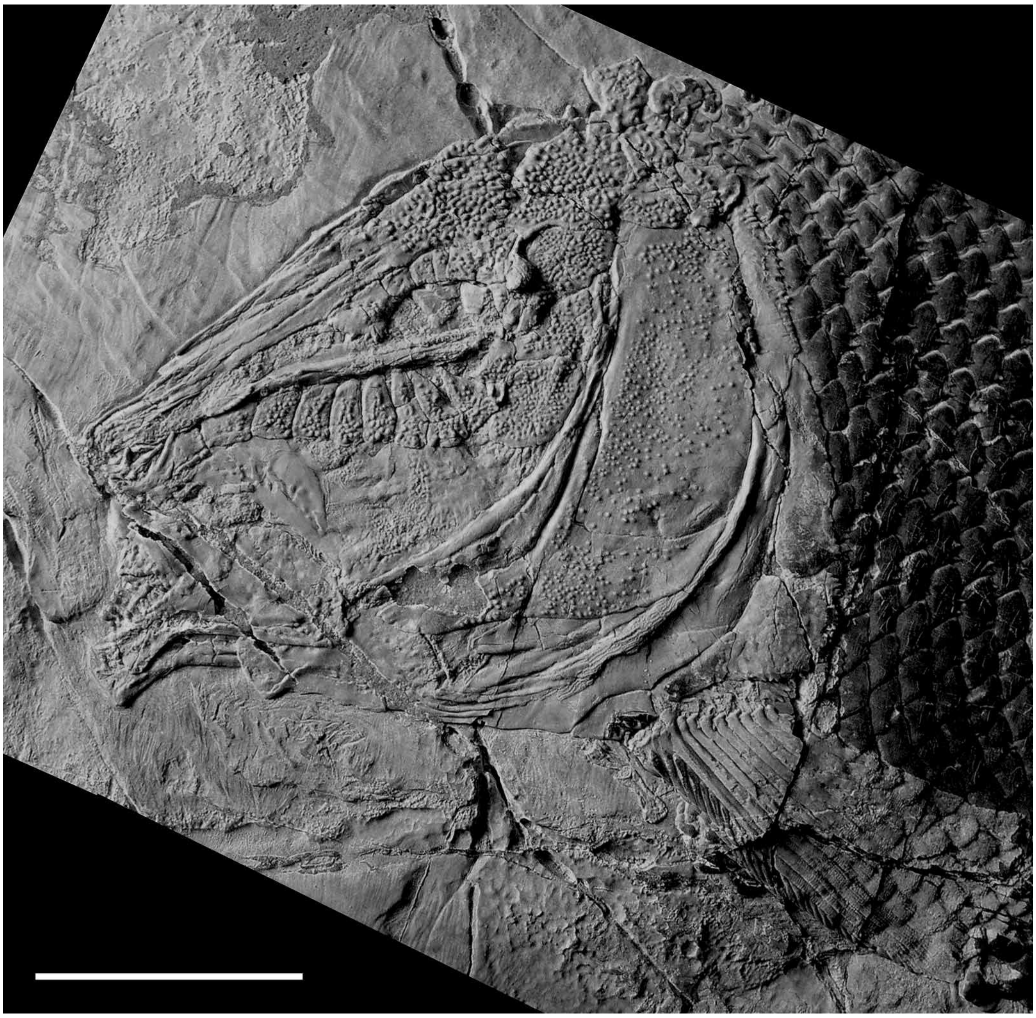

FIGURE 6. *Tlayuamichin itztli* **gen. et sp. nov.** Detailed photograph of the skull in IGM 6716 (holotype). Scale bar equals = 50 mm.

Circumborbital series. The circumorbital series, which is completely preserved in the holotype (IGM 6716; Figs 6–7) and IGM 6720 (Fig. 8), involves five supraorbitals, the dermosphenotic, six infraorbitals (io1—io6 in anterior to posterior direction), seven anterior infraorbitals (a.io1–a.io7 in anterior to posterior direction) and the antorbital. The circumborbital series is open (IGM 6716 and 6719; Figs 4, 6–7, 10), though it appears to be closed in IGM 6720 (Fig. 8) due to the anterodorsal displacement of the bones in the anteroventral portion of the skull. *Tlayuamichin itztli* is very peculiar in having the most anterior supraorbital element very large, placed exactly at the anterior rim of the orbit so that the bone, which has the shape of an inverted pentagon, has equally large orbital and anteorbital portions (it should be noticed that in IGM 6716 the bone is fractured right at the level of the anterior rim of the orbit, giving the appearance of two separate ossifications; Figs 6–7, 10). This pentagonal supraorbital forms a ventral wedge that faces a dorsal wedge formed by the last anterior infraorbital (a.io7) and the first infraorbital (io1) together, so that the two opposite wedges are partially closing the orbit anteriorly. In IGM 6720 there is another additional supraorbital anterior to this pentagonal bone (Fig. 8). There are no traces of such an additional supraorbital in the other specimens, but it might have been present and not preserved. In any case, *Tlayuamichin itztli* is very peculiar in having a long series of supraorbital bones, which extends beyond the orbit anteriorly. The remaining supraorbitals are rectangular and relatively small bones. The supraorbital bones are ornamented with tubercles, which are covered with a very thin layer of ganoin.

As usual in semionotiforms, the dermosphenotic is located at the posterodorsal corner of the orbit. This bone is rectangular, about twice as deep as long, and as long as the adjacent supraorbital (Figs 4, 6–8). The dermosphenotic is also ornamented with tubercles covered with a very thin layer of ganoin.

The infraorbital bones are best preserved in the holotype (IGM 6716; Figs 6–7). Among the six infraorbitals, three form the ventral margin of the orbit (infraorbitals io1–io3), the fourth infraorbital (io4) is placed at the posteroventral corner of the orbit and the last two infraorbitals (io5–io6) form the posterior margin of the orbit. The infraorbitals three to six (io3–io6) articulate with suborbital bones posteriorly. The infraorbitals five and six (io5–io6) are relatively small, deeper than long, rectangular bones. The infraorbital four (io4) is about twice the size of the infraorbital five (io5) and smaller than the infraorbital three (io3); it has a concave orbital border and is convex posteriorly. The infraorbitals one to three (io1–io3) are irregularly triangular, acuminated anterodorsally. In the holotype, the infraorbital three (io3) is slightly rotated clockwise and displaced dorsally because of the extrusion of the basipterygoid process of the parasphenoid. When moved back to its natural position, the infraorbital three (io3) alone forms most of the ventral margin of the orbit. The same happens in IGM 6720. The infraorbital two (io2) is the deepest bone of the whole series, followed by the infraorbital one (io1), which is only slightly shallower, and the infraorbital three (io3), which is about 20% shallower than the infraorbital two. Accordingly, the ventral margins of the infraorbitals 1–3 together describe a gently convex curve.

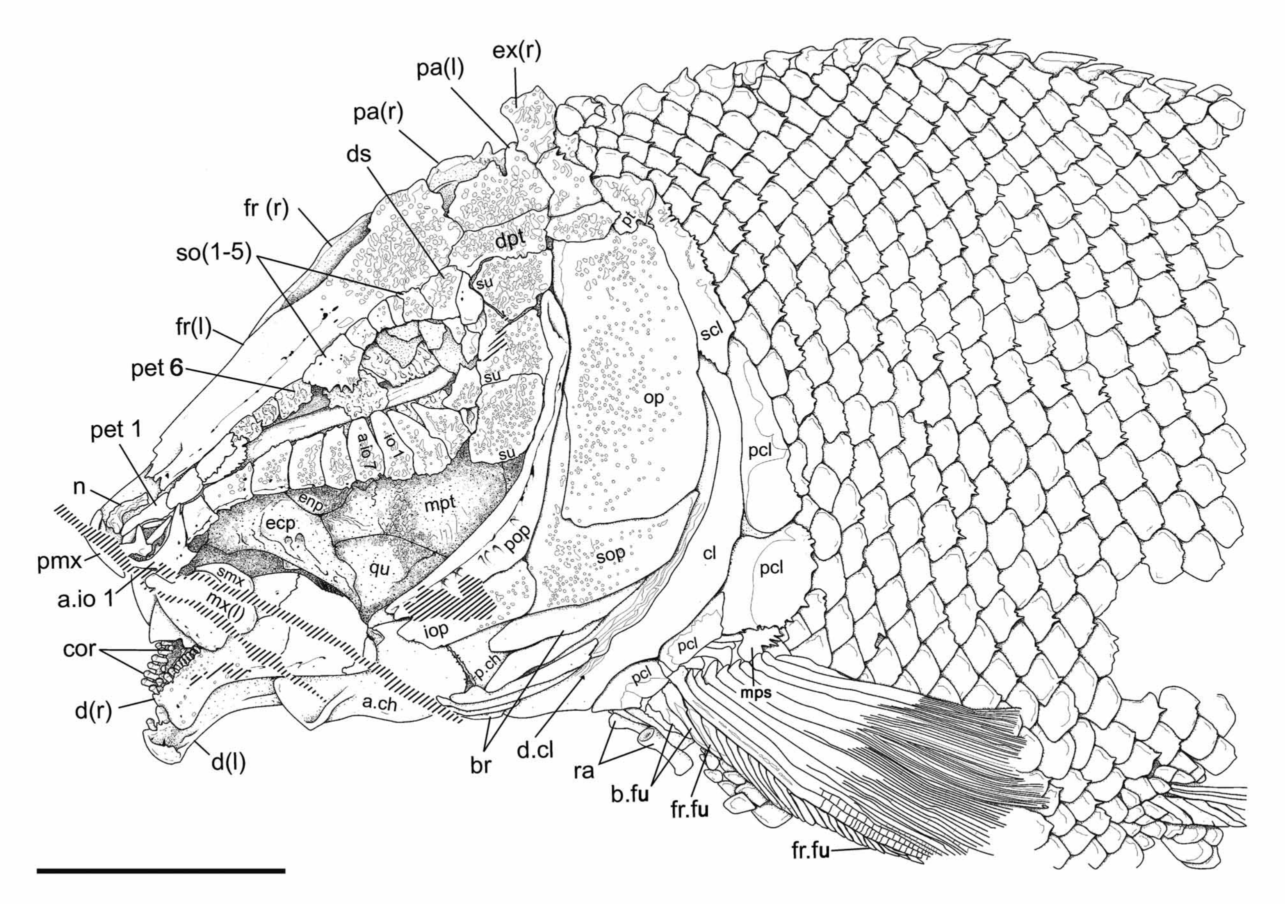

FIGURE 7. *Tlayuamichin itztli* **gen. et sp. nov.** Line drawing of the skull in IGM 6716 (holotype). Scale bar equals = 50 mm.

The seven anterior infraorbitals are aligned ventral to the level of the parasphenoid (Figs 6–7, 10). The anterior infraorbitals four to seven (a.io4–a.io7) are approximately rectangular, deeper than long, with their depths gradually decreasing anteriorly. The anterior infraorbital 7 is slightly acuminated dorsally, in the anterior infraorbital 6 the dorsal border is only slightly shorter than the ventral border, and the dorsal and ventral borders of the infraorbital 5 are approximately equal. The anterior infraorbital 4 is more irregular in shape, with the posterior border deeper than the anterior border and has, thus, anteroventrally inclined dorsal border. The anterior infraorbital 3 is approximately rectangular, about 1,5 times longer than deep, with the dorsal border a little longer than the ventral border. The anterior infraorbital 2 is smaller than its adjacent elements in the series. It is slightly narrower dorsally than ventrally and has a small laminar outgrowth ventral to the passage of the infraorbital sensory canal. Such an outgrowth is not present in the more posterior anterior infraorbitals. The first anterior infraorbital is somewhat boomerang-shaped and also has a well-ossified outgrowth ventral to the passage of the infraorbital sensory canal.

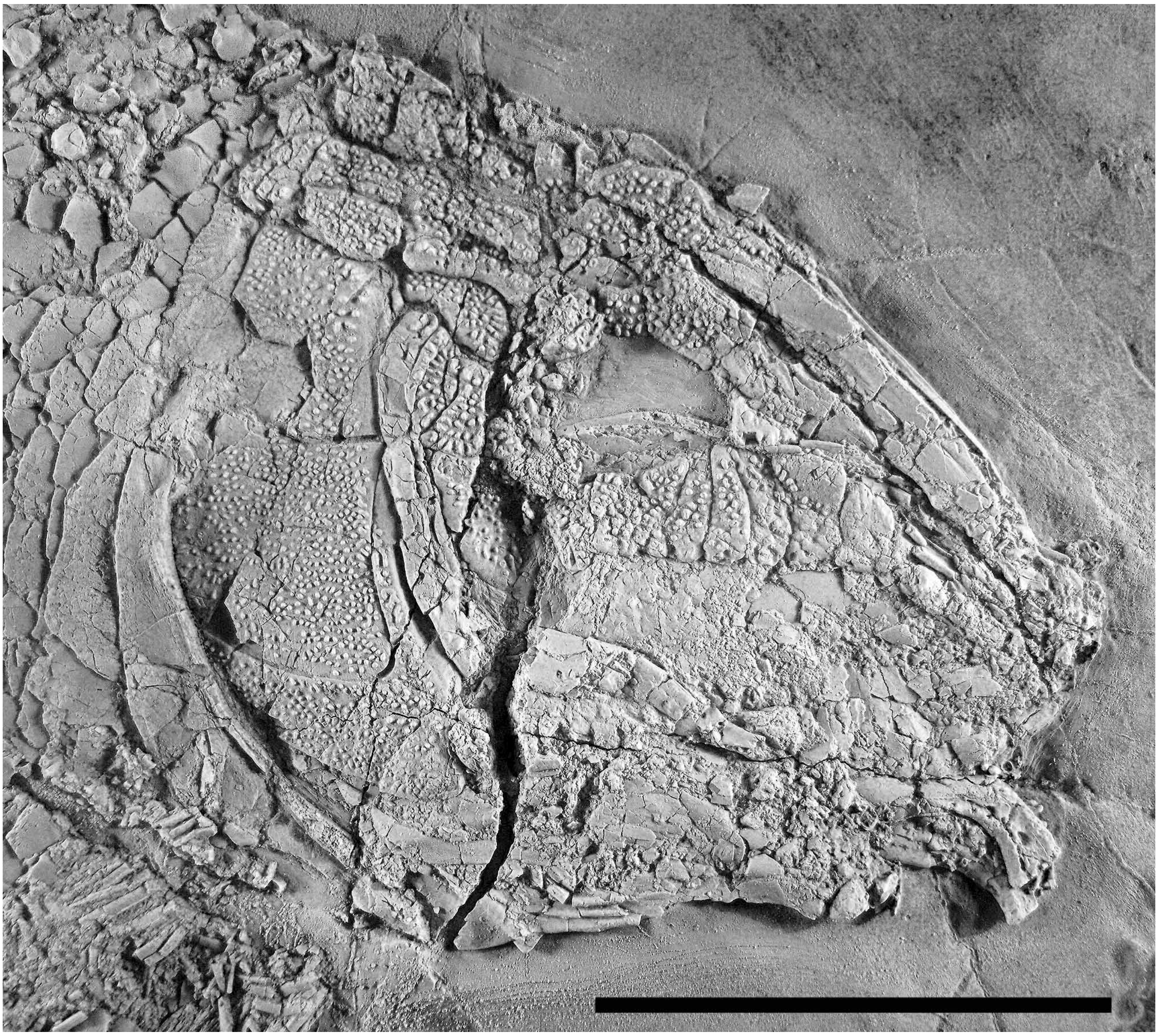

FIGURE 8. *Tlayuamichin itztli* **gen. et sp. nov.** Detailed photograph of the skull in IGM 6720. Scale bar equals = 45 mm.

All the infraorbital and anterior infraorbital bones are also ornamented with tubercles covered with a very thin layer of ganoin, which are denser towards the ventral and posteroventral border of the circumborbital ring.

The most anterior bone of the infraorbital series is usually interpreted as the antorbital. In *Tlayuamichin itztli* this most anterior element resembles the small, almost tubular antorbital in "*Lepidotes*" *minor* illustrated by Patterson (1975: fig. 135) (Figs 6–7). An irregularly shaped ossification preserved anterior to the antorbital and dorsal to the anterior end of the first anterior infraorbital might represent a displaced rostral.

Suborbital bones. There are three suborbital bones in *Tlayuamichin itztli*, and they are also densely ornamented with tubercles covered with a thin layer of ganoin. They are all of similar size and aligned in a single row completely covering the area between the circumborbital bones and the preoperculum, but do not extend anteriorly, ventral to the orbit. The most dorsal suborbital is expanded posteriorly and completely separates the preoperculum from the dermopterotic (Figs 6–8).

Opercular bones. The preoperculum is a crescent-shape bone, very narrow and gently curved, narrowing both dorsally and anteriorly (Figs 6–8). Anteriorly, the preoperculum extends beyond the anterior margin of the orbit. Dorsally, the preoperculum does not reach the dermopterotic; its dorsal tip being widely separated from that bone by the most dorsal suborbital. The operculum is large and subrectangular, a little narrower dorsally than ventrally. It is twice as deep as long in the holotype and in IGM 6720 (Figs 6–8), but only 1,6 times deeper than long in IGM 6717 (Fig. 3) and, thus, the shape of this bone is somewhat variable within the species. There are three irregularly shaped opercular ossifications in IGM 6719: a large dorsal operculum, an even larger ventral operculum, and a small rounded ossification at the anteroventral end of the ventral operculum (Fig. 9). The three bones occupy together an area about 1,5 times deeper than long, but the dorsal operculum is about 0,6 times narrower than the ventral operculum. The suboperculum has a very high ascending process, which is about 70% of the maximal length of the bone (completely exposed only in the holotype; Figs 6–7). The ascending process forms an interior angle of about 90° with the dorsal border of the suboperculum. In IGM 6716, 6717 and 6720 the suboperculum is deepest anteriorly, where it reaches about 30% of the depth of the operculum, and tapers posteriorly with curved dorsal and ventral borders (Figs 3, 6–8). In IGM 6719 the suboperculum is almost equally deep throughout its length and forms a sinuous articulation with the ventral operculum (Fig. 9). The ascending process of the suboperculum in this fish is hidden by the somewhat displaced preoperculum. Anteriorly, the suboperculum articulates with the interoperculum through an almost vertical suture. The interoperculum extends anteriorly up to the level of the anterior end of the preoperculum, thus extending medioventral to the whole ventral margin of that bone. The ventral border of the interoperculum is gently convex. All the opercular bones are ornamented with numerous tubercles covered with ganoin, except for the preoperculum where the tubercles are only very few and scattered. It is worthy to note that the peculiarities of the opercular bones in IGM 6719 described above are considered as abnormalities. IGM 6719 presents multiple ossification of the operculum and probably also de preoperculum and an abnormal shape of the suboperculum. Although it is important to report such cases, in the lack of ontogenetic information it is impossible to know the causes or processes that might led to such deviations in this fish.

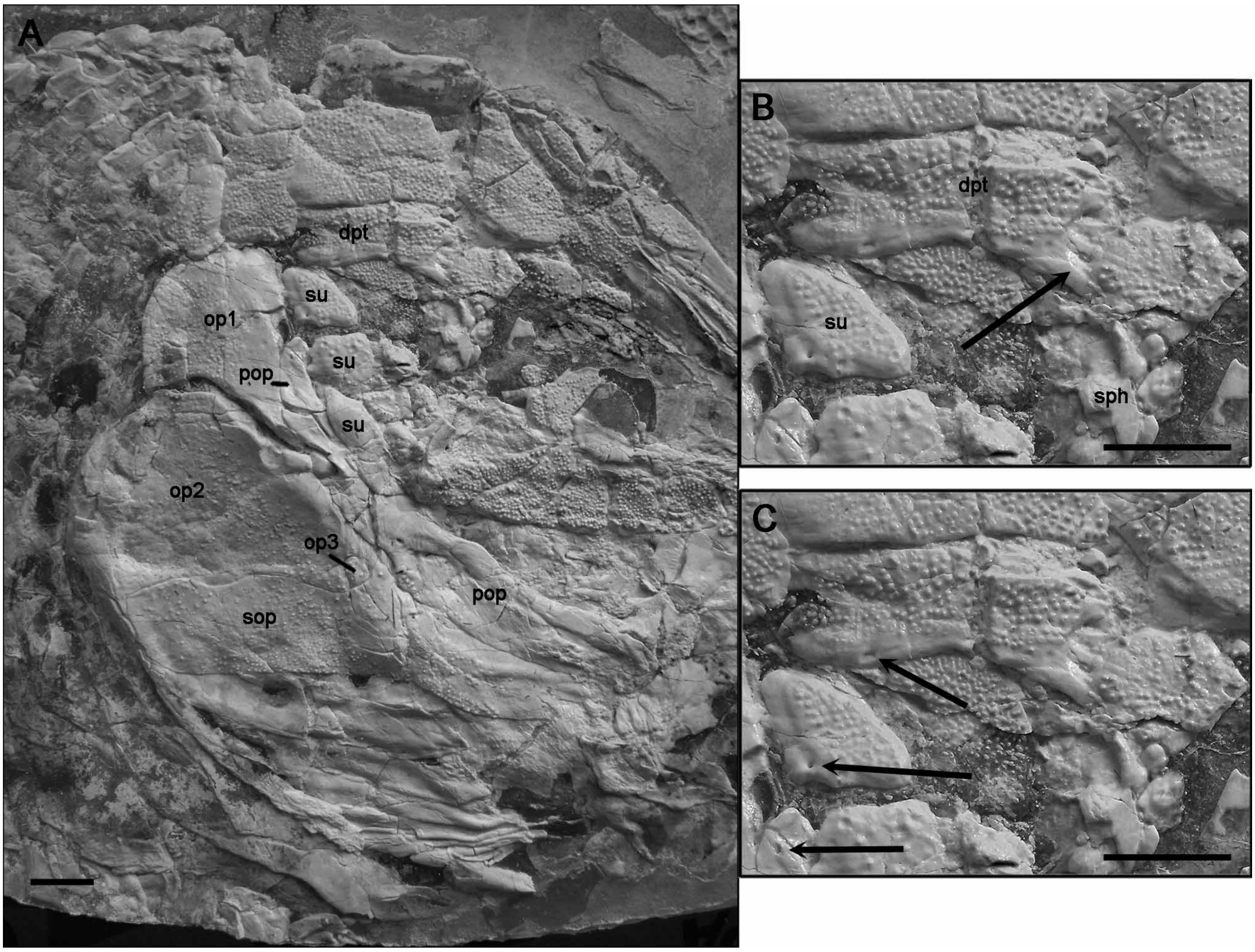

FIGURE 9. *Tlayuamichin itztli* **gen. et sp. nov.**, details of the skull in IGM 6719. A, posterior part of the skull showing multiple opercular ossifications and the peculiar shape of the suboperculum in this specimen. B, detailed photograph of the dermopterotic bone; the arrow points to the peculiar anteroventral process of this bone in the new taxon. C, same photograph as in B, but in this case the arrows point to the pores of the preopercular sensory canal in the preoperculum (below), suborbital (middle) and dermopterotic (above). Scale bars equal = 10 mm.

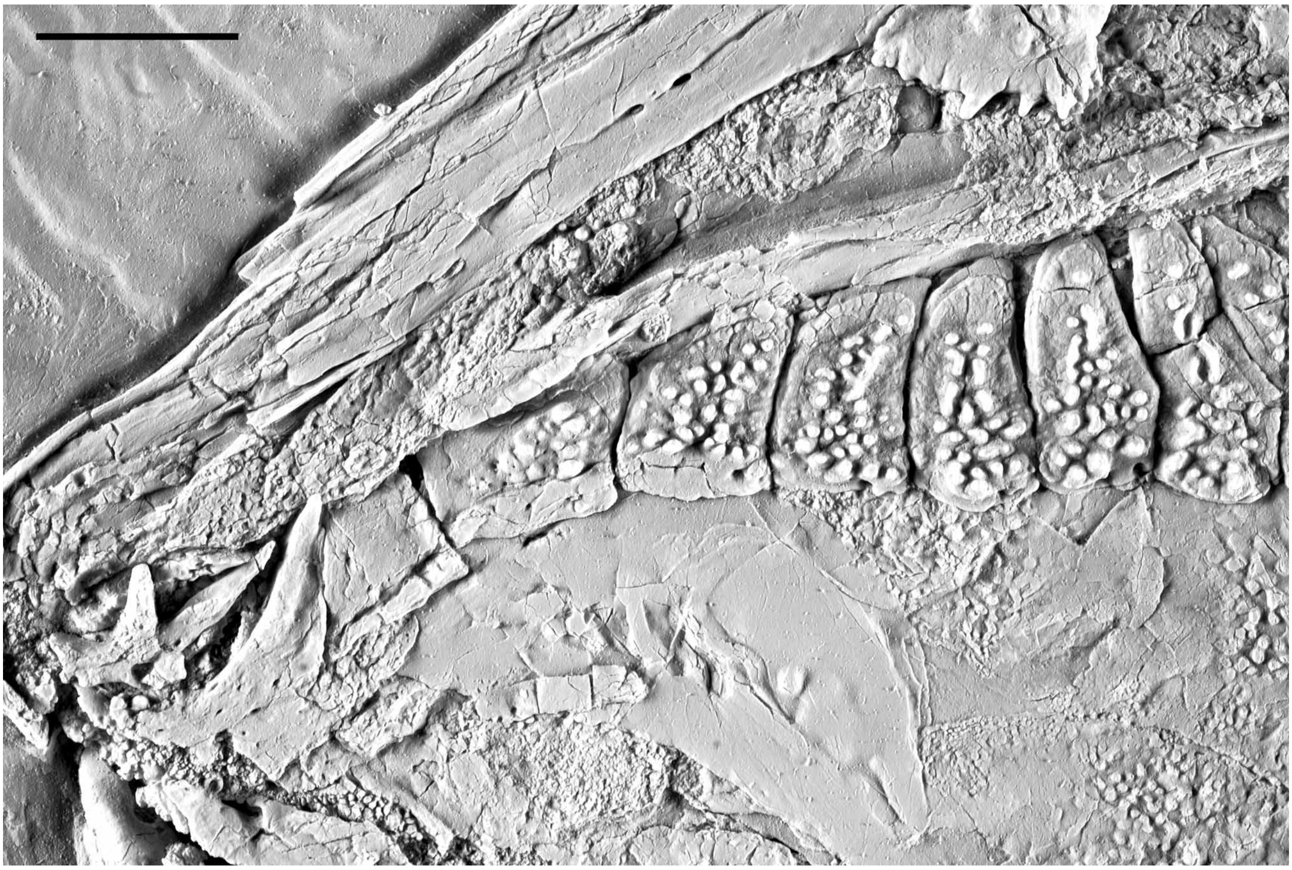

FIGURE 10. *Tlayuamichin itztli* **gen. et sp. nov.**, ethmoidal region of the skull in IGM 6716 (holotype) showing the paraethmoids as indicated in Figure 7 (labeled as "pet"). Scale bar equals = 10 mm.

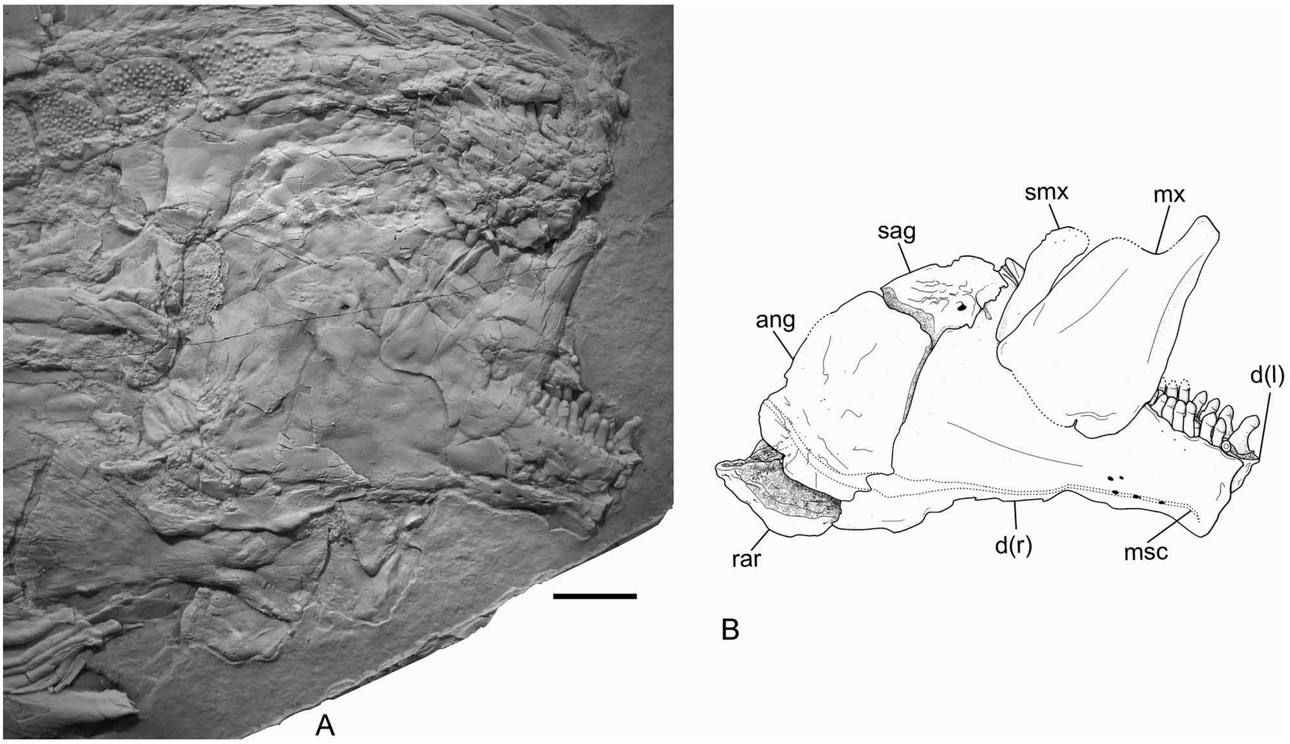

FIGURE 11. *Tlayuamichin itztli* **gen. et sp. nov.**, jaws in IGM 6719. A, photograph; B, line drawing. Note that the retroarticular bone is a little displaced posteriorly. Scale bar equals = 10 mm.

Jaws. The jaws are best preserved in IGM 6719 (Fig. 11), but they are also relatively well preserved in the holotype and IGM 6717 (Figs 3, 6–7, 12). The lower jaw joints the quadrate at the level of the anterior orbital margin. It is a triangular structure, about 2.5 times longer than deep. The posterior and dorsal borders of the lower jaw are convex, the ventral border bents ventrally at the alveolar portion, and the alveolar border is straight, inclined anteriorly. The dentary symphysis is straight, vertical, and is contained about 2.5 times in the maximum depth of the coronoid process and more than 5 times in the total length of the lower jaw. The lower jaw is only exposed in lateral view in the available specimens, and the dentary, angular, surangular and retroarticular bones are recognized. The dentary is large and elongate, with a short posteroventral process, which is only about 15 % of the total length of the lower jaw. The posterior border of the dentary, which articulates with the angular, forms an obtuse angle with the posteroventral process. Small tubercles ornament the external lateral surface of the anterior portion of the dentary below the alveolar border. There is a single row of dentary teeth, which have short pedicles and rounded crowns. Of the right side of the skull, two coronoid bones, anterior and posterior, are exposed in IGM 6716 (Figs 6–7). Only the posterior of these coronoid bones is exposed on the left side of this specimen. The coronoids bear only one raw of teeth, which are identical to the marginal teeth of the dentary. The angular articulates with the dentary between the coronoid process and the posteroventral process, with the retroarticular posteroventrally, and with the surangular anterodorsally (Fig. 11). The angular is excavated for the articulation of the quadrate posteriorly. This articular facet is concave and well distinct, but not deeply excavated. As usual in semionotiforms, the surangular places on top of the lower jaw articulating dorsal to the angular and dentary, and it is dorsally convex. The retroarticular is relatively large and well ossified, forming the posteroventral end of the lower jaw. It articulates with the posteroventral process of the dentary anteriorly, and with the angular anterodorsally.

The upper jaw is also shown in IGM 6716, 6717 and 6719 (Figs 6–7, 11, 12). The premaxillae are badly preserved; in IGM 6716, only the nasal processes of both premaxillae are exposed. In IGM 6717 the two premaxillae are preserved in ventral view (Fig. 12). The alveolar portion of the premaxilla is narrow. The exact number of premaxillary teeth is unknown; three alveoli are preserved in the right premaxilla and four in the left premaxilla, but in both cases the bone is broken and more alveoli might have been present. According to the size of the alveoli, the premaxillary teeth are notably smaller than the vomerine or dermopalatine teeth and even fairly smaller than the dentary teeth. Therefore, the premaxillary teeth are the smallest in the jaws and palate. The maxilla is best preserved in IGM 6719 and is an edentulous flat bone. The articular process is strong, rod-like and long (broken in IGM 6719, Fig. 11, but complete in IGM 6717, Fig. 12). Immediately posterior to this process, the maxilla expands abruptly dorsally forming a subrectangular plate with rounded corners, which is about 1.2 times longer than deep (Fig. 11). The posterior border of the maxilla is almost well preserved in IGM 6719 only. However, the border is broken and, thus, it was reconstructed in Figure 11B according to the imprint left on the dentary. The posterior border of the maxilla is therefore almost straight and immediately below the broken piece there is a sharp indentation close to the posteroventral corner of the bone, which is not due to any kind of fracture or brake. A long and slender supramaxilla lies along the whole dorsal border of the maxillar plate.

Palatoquadrate ossifications. In *Tlayuamichin itztli* the cheek is naked and the palatoquadrate ossifications are best exposed and well preserved in the holotype (IGM 6716), which shows large part of the quadrate, ectopterygoid, metapterygoid, and only some parts of the entopterygoid (Figs 6–7). The quadrate is fan shaped with convex dorsal border and the articular process directed ventrally. The articular process of the quadrate is small and short. Only the most anterior portion of the quadratojugal is visible in IGM 6716 attached to the ventral border of the quadrate and far back far from the articular facet for the lower jaw. The ectopterygoid articulates with the whole anterior border of the quadrate; its shape is crescent, with gently convex dorsal and concave ventral borders, and it is about two times longer than the quadrate. The anterior portion of the ectopterygoid is broken in the holotype and no teeth are preserved in this area. The two dermopalatines are well exposed in IGM 6717 (Fig. 12). The bones are broad, rounded, and bear 7–9 teeth irregularly ordered. IGM 6717 also shows the paired vomers, which are still articulated. Each vomer bears 4–5 irregularly arranged teeth. These palatine and vomerine teeth are similar to those on the jaws, also with relatively short pedicles and rounded crowns, though somewhat larger than them. The entopterygoid is also exposed in IGM 6717 and it is completely edentulous. Only the posterior portion of the entopterygoid is exposed in IGM 6716 suturing with the ectopterygoid and metapterygoid, but not with the quadrate (Figs 6–7). The metapterygoid is very broad, meeting the dorsal border of the entopterygoid anteriorly and the ectopterygoid and quadrate ventrally (Figs 6–7).

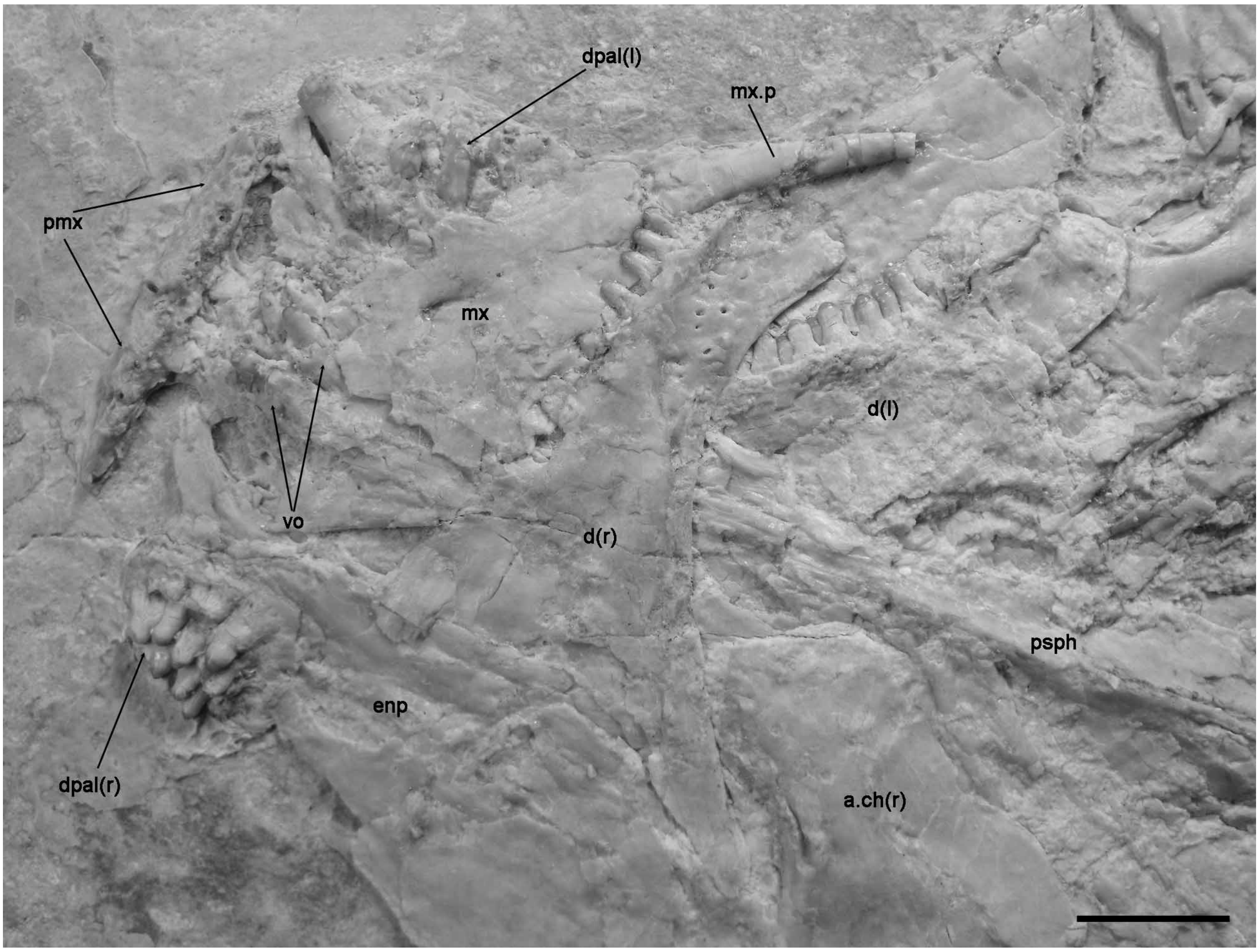

FIGURE 12. *Tlayuamichin itztli* **gen. et sp. nov.**, detailed photograph of the anterior part of the skull preserved in ventral view in IGM 6717. Scale bar equals = 10 mm.

Hyoid arch and branchiostegal rays. The hyoid arch is partially shown in IGM 6716, 6717, and 6719 (Figs 3A, 4, 6–7, 12). The hyomandibula is not shown in any of the available specimens. The anterior ceratohyal is relatively large and slightly waisted. Its posterior border is about two times deeper the anterior one. The constriction or waist divides the anterior ceratohyal in two portions, the posterior portion being twice as long as the anterior portion. The longitudinal axis and the anterior and posterior borders of the anterior ceratohyal are massively ossified, whereas the rest of the bone is laminar. The posterior ceratohyal is partially shown in the specimens mentioned above. The anterior and posterior ceratohyals articulate through cartilage and a superficial medial irregular suture. No hypohyal or basihyal is preserved, not even in IGM 6717, which preserves the skull in ventral view and, thus, these bones probably remain cartilaginous.

The branchiostegal rays are preserved partially articulated in IGM 6716 and 6719 (Figs 4, 6–7). Considering the two specimens, the following arrangement is interpreted: five slender branchiostegal rays articulate with the anterior ceratohyal, and two larger, plate-like branchiostegals articulate with the posterior ceratohyal. The most posterior branchiostegal ray is overlapped by the suboperculum and has approximately the same length as the ventral margin of that bone, and about three times the length of the most anterior and smallest branchiostegal ray.

Sensory canals of the head. The trajectories of the cephalic sensory canals are best preserved in IGM 6716 and 6719 (Figs 4, 6–7). The supraorbital sensory canal is represented by a groove that is perforated from time to time, throughout the central portion of the nasals, the lateral portion of the frontals and the central portion of the anterior halves of the parietals. In the parietals, the anterior, middle and posterior pit lines are also represented by perforated grooves.

The temporal sensory canal is represented by some relatively large pores on the anterior and ventral margins of the dermopterotic, and on the lateral margin of the most lateral extrascapular. In the extrascapulars, the supraoccipital commissure is also represented by pores, but it is not possible to know whether it was continuous from one to the other side of the skull.

The supraorbital bones are all pierced by foramina that are interpreted as the orbital sensory canal as described in López-Arbarello and Sferco (in press). The orbital canal meets the temporal and infraorbital canals in the dermosphenotic. The trajectory of the infraorbital sensory canal is represented by grooves in several infraorbital bones. In the small infraorbital bones placed at the posterior border of the orbit, the sensory canal probably traversed their thickened anterior margin. More anteriorly, the grooves representing the canal are shown in the ventral half of the infraorbital bones. From the posteroventral corner of the orbit forwards, the grooves are gradually closer to the ventral border of these bones. Additionally, a series of relatively large pores at the ventral margin of the infraorbital bones most probably represent the exits of branches of the infraorbital sensory canal. In the antorbital the infraorbital canal is only represented by two pores placed at its ventral margin. As mentioned above, a small bone traversed by a groove and placed anterior to the antorbital probably represents a rostral traversed by the ethmoidal commissure.

The preopercular sensory canal apparently traversed the thickened anterior margin of the preopercular bone. At least 8 pores distributed throughout the central portion of the preoperculum in IGM 6716 indicate the exits of branches from this sensory canal. In the most dorsal suborbital there is a pore at the ventral margin, placed directly opposite to the thickened anterior margin of the preoperculum, and followed by a superficial slight groove that ends opposite to a pore at the ventral margin of the dermopterotic (Fig. 9C). These structures indicate that the preopercular sensory canal traversed the posterior portion of the most dorsal suborbital, a bone that, as explained above, completely separates the preoperculum from the dermopterotic.

Anteriorly, the preopercular sensory canal continues as the mandibular sensory canal through the angular and the dentary. In these bones, the mandibular canal is represented by several fenestrae and a groove running close to the ventral border of the lower jaw. Additional pores in one or the other specimen are not constantly present and might represent branches of the main canal or might have a different origin (e.g. innervation or nutrition).

Pectoral girdle. The dermal bones of the pectoral girdle are best preserved in the holotype (IGM 6716; Figs 6–7), in which the left girdle is complete and articulated, including a posttemporal bone, a supracleithrum, a cleithrum, probably a serrated organ and four postcleithra. As usual in semionotiforms the posttemporal has an approximately triangular outline, narrowing dorsally. The bone is densely ornamented with ridges and/or tubercles covered with a thin layer of ganoin, and ends dorsally at the level of the dorsal border of the median extrascapular bone when three extrascapular bones are present. The anteroventral process of the posttemporal is short and broad, laterally compressed. The posteroventral border of the posttemporal is convex and articulates with a concave surface in the supracleithrum.

The supracleithrum is dorsoventrally elongate and the exposed portion is relatively narrow. The supracleithrum is overlapped by the posttemporal dorsally and the operculum anteriorly, and it ventrally overlaps the cleithrum and the most dorsal postcleithrum. The posterior border of the supracleithrum is straight through most of its length, until meeting the most dorsal postcleithrum, where it bents anteroventrally, so that the bone tapers in that direction. Only dorsal to the postcleithrum, the posterior margin of the supracleithrum is ornamented. In the holotype (IGM 6716) this area is garnished with a series of parallel and short ridges, which become gradually more tenuous in dorso-ventral direction (Figs 6–7). In the dorsal portion of the bone, these ridges project as spines beyond the border of the bone. However, the same area is ornamented with tubercles in IGM 6719 (Fig. 9) and with tubercles and ridges in IGM 6720 (Fig. 8).

In lateral view the cleithrum has a crescent shape, slightly deeper than long and anteriorly reaches a level around the posterior rim of the orbit. The cleithrum has up to seven sinuous and variably interrupted series of denticles along the edge between the branchial and lateral surfaces. The lateral surface of the cleithrum is notably narrow and its free border is smooth. The four postcleithra are aligned following the curved made by the posteroventral border of the cleithrum. Differing from the other dermal components of the pectoral girdle, the exposed portion of the postcleithra is covered with a layer of ganoin. The first, most dorsal postcleithrum is dorsoventrally elongate, narrowing dorsally. It is the deepest among the postcleithra, but it is narrower than the adjacent postcleithrum. This second postcleithrum is approximately as deep as long and has a very gently concave anterior border, and a convex posterior border. The two following postcleithra are much smaller than the elements described before. Both are elongate and their shape accommodate to the shape of the posterior border of the cleithrum. As is the case of the supracleithrum, the two most dorsal postcleithra are variably ornamented with tubercles and/or ridges, which are sometimes projected in spines. Ventral and medial to the second postcleithrum there is a modified scale with three strong spines projecting backwards (Figs 6–7). To facilitate comparisons (see discussion) we refer to this scale, which is well exposed in the holotype (IGM 6716), as the modified pectoral scale.

Of the endochondral components of the pectoral girdle, only five radials are exposed in the holotype (Figs 6–7). Three of these radials are only partially exposed because they are preserved in articulation. The other two radials are disarticulated and displaced ventral to the skull and anterior to the pectoral fin.

Paired fins. The pectoral fin is best and almost completely preserved (only the distal fin rays are missing) in the holotype (IGM 6716; Figs 6–7), comprising nine lepidotrichia. The proximal third to one half of each lepidotrichium is unsegmented, contrasting strongly with the distal portion, which is finely segmented and intensively branched. The first lepidotrichium does not branch and its terminal segment is elongate, covered with ganoin and completes the series of fringing fulcra, which are laying on this first ray. The proximal portion of the first pectoral ray forms a lateral ridge, which is also covered with ganoin. Scattered remains of a few small broken spines are preserved on the proximal portion of the second to fourth pectoral rays. From the second ray onwards, the lepidotrichia are asymmetrically branched, the medial portion being always more intensively branched than the lateral one. Also, the branching is gradually more intense towards the medial rays. Two short and paired basal fulcra are preceding the series of short fringing fulcra.

The pelvic fins are also best, though only partially preserved in the holotype (IGM 6716; Fig. 2), where the pelvic fin is located about 0.52 of the standard length, right behind the seventh vertical row of scales. The total number of rays is unknown, but at least two lepidotrichia are preserved. Resembling the case of the pectoral fin, the proximal segment of the first pelvic fin ray forms a lateral ridge, which is covered with a thin layer of ganoin. A series of fulcra garnish the pelvic fin, including one unpaired basal fulcrum, one paired basal fulcra, and at least eight fringing fulcra.

Unpaired fins. The unpaired fins are best preserved in IGM 6718 (Figs 3B, 13–14). The dorsal fin is short and originates right back of the level of the pelvic-fin insertion. The dorsal fin is incompletely preserved in IGM 6716 and 6720 (Figs 2, 5), but both specimens show that this fin originates at the 23rd vertical row of scales, at about 0.6 of the standard length. There are 13 lepidotrichia in the dorsal fin of IGM 6718 (Fig. 13A), the height of which decreases progressively posteriorly and, thus, the shape of the fin was probably triangular. All dorsal fin rays, including the first one, branch at least two times. There are five large paired basal fulcra, and at least 10 large fringing fulcra. Among these fulcra, the two posterior paired basal fulcra and two anterior fringing fulcra are the largest, being almost 1.5 times higher than the adjacent fulcra.

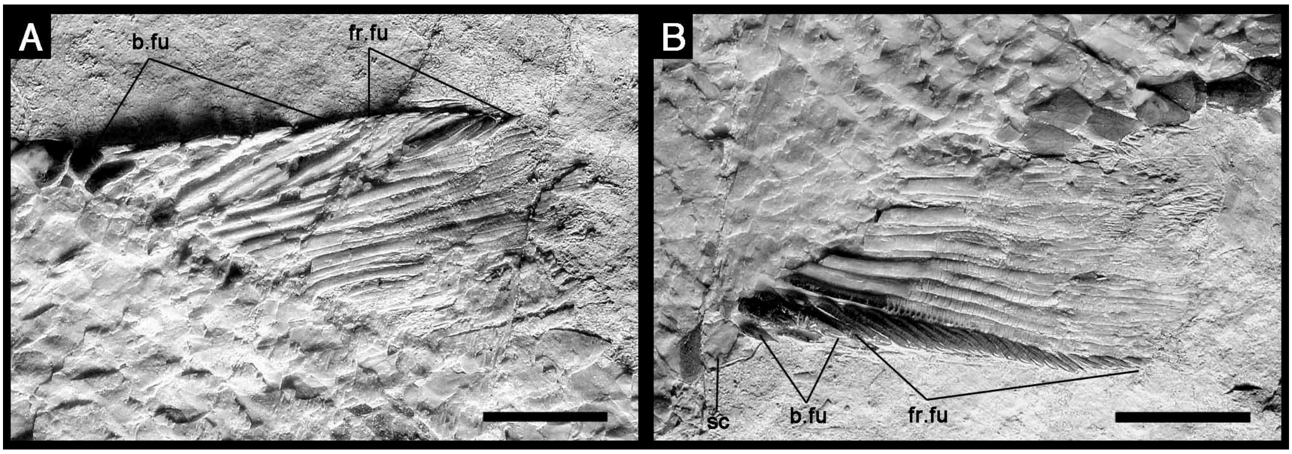

FIGURE 13. *Tlayuamichin itztli* **gen. et sp. nov.** Detailed photograph of: A, the dorsal fin in IGM 6718; B, the anal fin in IGM 6718. Scale bars equal = 20 mm.

The anal fin is also incompletely preserved in both IGM 6716 and 6720 (Figs 2, 5), but these specimens show its origin at the 18th vertical row of scales, at 0.72–0.74 of the standard length. The anal fin is almost complete and well preserved in IGM 6718 (Fig. 13B), comprising seven lepidotrichia, the two distal thirds of which are finely segmented and branched, including the first ray that branches at least once. The proximal half of the first lepidotrichium is covered with lateral patches of ganoin. The anal fin is garnished with three paired basal fulcra, and at least 19 small fringing fulcra. There is a single large preanal scute, which is about three times larger than the adjacent scales.

The caudal fin is also very well preserved in IGM 6718 (Fig. 14), but the distal portions of the fin rays are missing, so that the shape of the fin is unknown. Both in this specimen and in IGM 6720, there are nine and eight lepidotrichia forming the dorsal and ventral caudal lobes respectively. As shown in IGM 6716, all caudal fin rays are laterally covered with patches of ganoin. The caudal fin rays are intensively branched, with the exception of the two marginal rays, and finely segmented like the lepidotrichia in the other unpaired fins. In this case however, the proximal unsegmented portion is short and almost totally covered with scales. As far as preserved, the dorsal and ventral marginal rays are unbranched. The most posterior flank scales are relatively longer and oval. There are at least six unpaired dorsal caudal fulcra covering the body lobe of the tail, followed by three paired basal fulcra and at least 13 fringing fulcra laying on the dorsal marginal ray. Ventrally, the caudal fin is preceded by one short unpaired basal fulcrum and five paired basal fulcra, and there are at least 22 small fringing fulcra on the ventral marginal ray.

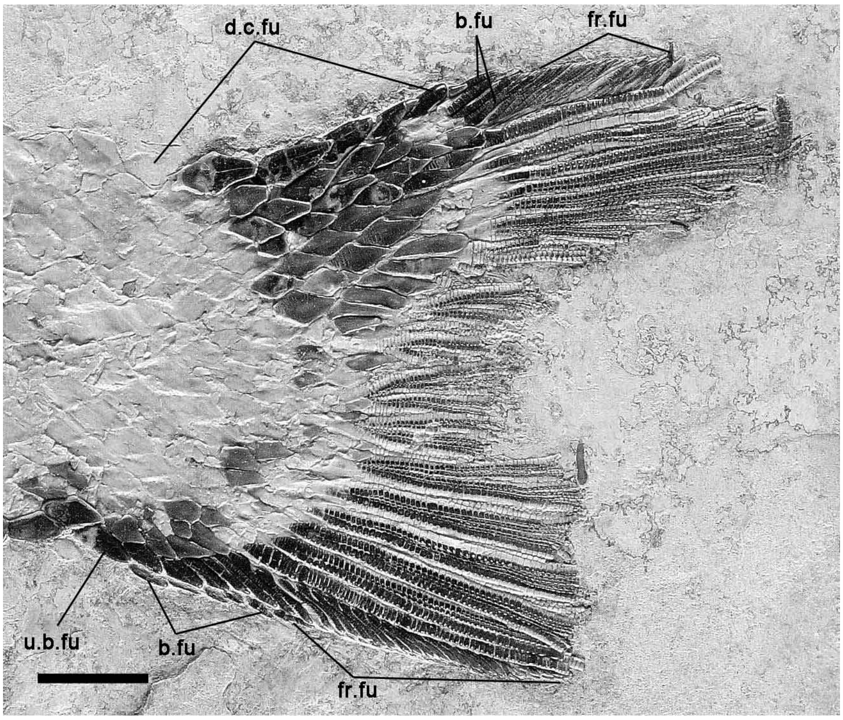

FIGURE 14. *Tlayuamichin itztli* **gen. et sp. nov.** Detailed photograph of the caudal fin in IGM 6718. Scale bar equals = 20 mm.

Squamation. The body is covered with large and thick rhomboid scales. The squamation pattern is best preserved in the holotype (IGM 6716; Fig. 2), in which are 34 vertical rows of scales from the operculum to the hinge line, and a complete ridge of scales along the dorsal midline between the skull and the dorsal fin. The scales are not ornamented and have smooth surfaces. Most of the scales on the flank in IGM 6716 form one or two spines at their posteroventral angle (Fig. 6). However, such spine is only insinuated in the scales of IGM 6719 (Fig. 4) and generally absent in IGM 6720 (Fig. 5), which shows that the feature is highly variable within the species. On the flank, the scales are generally rectangular, approximately as deep as long, only somewhat deeper than long immediately behind the operculum. The dorsal ridge scales are conspicuous, slightly longer than those adjacent scales and bears a short posterior spine directed backward (Fig. 15A). In the caudal peduncle, the scales are about 2 times longer than deep and have smooth borders in all the specimens. There are seven inverted rows of scales forming the body lobe of the tail. Among them, the scales of the marginal row are distinctively elongate and not diamond shape as the other scales in the caudal region. Six scales are preserved in this marginal row, but there is a fragment of a seventh scale and one scales is evidently missing both ventrally and dorsally and, thus, nine is the total number of scales in this row. Nevertheless, this marginal row does not reach the tip of the body lobe, which is formed by the two following rows of scales.

The articular processes of the scales are only shown in the middle flank region of IGM 6717. In this area, the scales show well-developed articular, anterodorsal and anteroventral processes (anterior pegs) (Fig. 15B). The articular process that serves in the peg-and-socket articulation (dorsal peg) is not very high and places right at the base of the anterodorsal process. The anterodorsal and anteroventral processes serve in the longitudinal articulation and are oriented in diverging directions, with the anterodorsal process being larger than the anteroventral process.

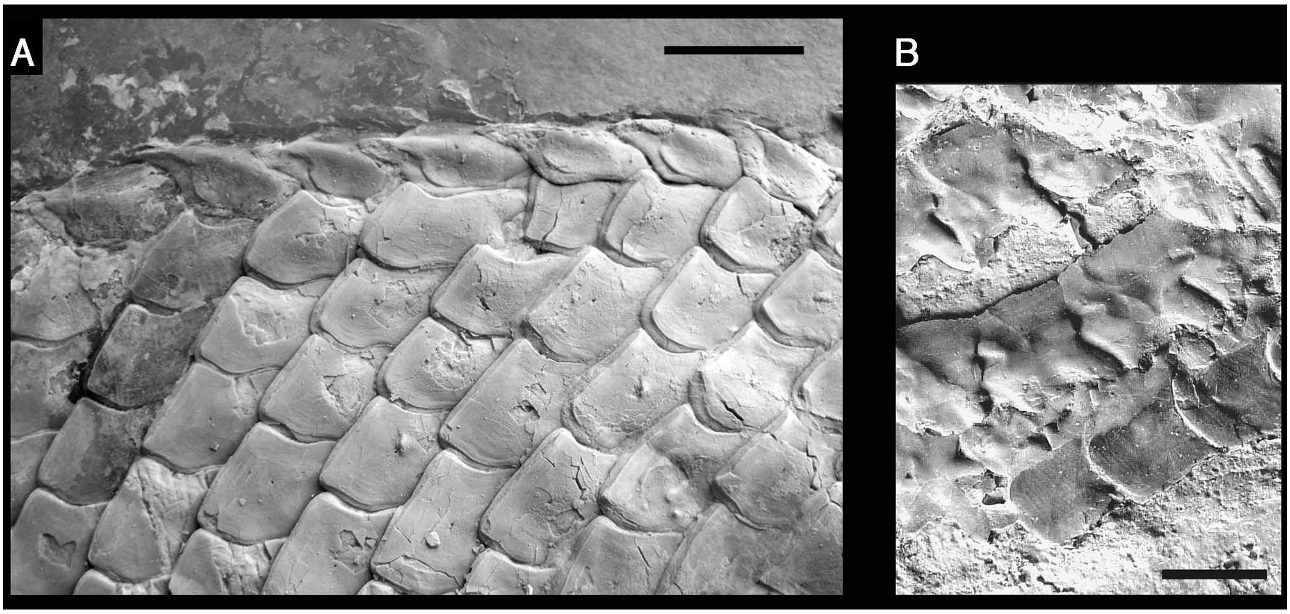

FIGURE 15. *Tlayuamichin itztli* **gen. et sp. nov.** Detailed photograph of: A, the dorsal ridge scales in IGM 6719; B, several partially articulated scales in IGM 6717 showing the well-developed articular, anterodorsal and anteroventral processes. Scale bars equal = 10 mm.

Discussion

Among the three groups that constitute the Semionotiformes, the monophyly of Macrosemiidae and Lepisosteidae has already been proofed (Bartram 1977, Wiley 1976, González-Rodríguez & Reynoso 2004, González-Rodríguez *et al*. 2004, Murray & Wilson 2009). Quite the opposite, the family Semionotidae currently includes a variety of genera that most probably represent a polyphyletic assemblage including, in alphabetic order, the genera *Araripelepidotes*, *Lepidotes*, *Neosemionotus*, *Neolepidotes*, *Paralepidotus*, *Pliodetes*, *Sangiorgioichthys*, *Semiolepis*, *Semionotus*, *Sinolepidotus*, and *Tianfuichthys*. Semionotids are however very important to understand the history of the Semionotiformes, because they include the oldest and the most basal forms. Semionotids and macrosemiids disappeared during the Late Cretaceous, while the fossil record of lepisosteids starts only in the Early Cretaceous. The youngest records of semionotids correspond to isolated remains (scales, teeth and isolated bones) from the Late Cretaceous (Senonian) of South America (Gallo & Brito 2004) and a very recently described new species of *Lepidotes* from the Cenomanian of the Kem Kem beds in Morocco (Forey *et al*. in press). With the exception of the later, represented by two three dimensionally preserved skulls, *Tlayuamichin itztli* represents one of the youngest articulated remains of semionotids. Other Early Cretaceous articulated and well-preserved semionotids are only known from the Lagarcito Formation in Argentina (*Neosemionotus puntanus*; López-Arbarello & Codorniú 2007), the Santana Formation in Brazil (*Araripelepidotes temnurus* and *Lepidotes wenzae*; Gallo & Brito 2004), the Aptian of Niger (*Pliodetes* Wenz 1999), Las Hoyas in Spain, Europe (*Lepidotes microrhis* and *Lepidotes tanyrhis*; Wenz 2003), Zhejiang Province, China (*Sinolepidotus* and *Neolepidotes*; Chang & Miao 2004) and the English Purbeck (“*Lepidotes*” *minor*; Woodward 1916).

Tlayuamichin itztli is most probably closely related to “*Lepidotes*” *minor*, shearing with this taxon several morphological features. “*Lepidotes*” *minor* (Agassiz, 1833) is a fish from the Middle Purbeck Beds at Swanage, Dorset, England (now known to be of earliest Cretaceous age; Cope 2008), which was first described as a species of *Lepidotes*. Although McCune (1986) discussed the possible affinities of this species with the genus *Semionotus*, transferring the species to this genus, her ideas have not been accepted and the species has been kept in *Lepidotes* and has even been used as one of the best examples representing *Lepidotes* in some comparative and cladistic analyses (e.g. Patterson 1975, Cavin & Suteethorn 2006). This is a very unfortunate situation because, as mentioned above, *Semionotus* and *Lepidotes* represent very different fishes (López-Arbarello 2008a, b). A thorough revision is needed to clarify the taxonomic status of “*Lepidotes*” *minor*, which most probably will have to be referred to a new genus.

Among the characters sheared by *Tlayuamichin itztli* and "*Lepidotes*" *minor*, a suboperculum with a very high ascending process, its depth being at least half of the length of the dorsal border of the bone, is so far only known in these two taxa. The ornamentation of the skull bones is also very similar and peculiar in the two taxa, which also shear a similar shape and arrangement of the bones in the snout (nasals, rostral and antorbitals; see description), an edentulous maxilla, semitritorial dentition, and scales with well-developed articular, anterodorsal and anteroventral processes, for both peg-and-socket and longitudinal articulation. However, "*Lepidotes*" *minor* does not have the diagnostic features of *Tlayuamichin itztli* and, thus, the fishes represent different taxa.

Other morphological features present in *Tlayuamichin itztli* and "*Lepidotes*" *minor* like a laterally compressed skull, very long frontals, large dorsal-fin fulcra are also found in the species of *Semionotus* (*S. bergeri*, *S. elegans*, *S. capensis*, and (*S. kanabensis*). Additionally, these taxa share with the macrosemiids a stable number of eight rays in the lower lobe of the caudal fin. However, the scales of *Tlayuamichin itztli* and "*Lepidotes*" *minor* resemble most closely the typical scales of *Lepidotes*, with well-developed dorsal and ventral anterior pegs and variably developed dorsal peg (López-Arbarello 2008b).

A very interesting feature found in *Tlayuamichin itztli* is the presence of a modified pectoral scale (Fig. 7). Such scale is not as elongate as the teleost axillary process, but it has the same topographic relationships and might represent an analogous structure. Further research is necessary to understand the distribution and evolution of this feature in neopterygians. Another interesting feature to further explore in other neopterygians is the dermal exposure of the sphenotic between the dermopterotic, dermosphenotic, infraorbital and suborbital bones. A dermal component of the sphenotic is also exposed in *Semionotus elegans* (Olsen & McCune 1991), *Heterolepidotus*, *Ophiopsis* and *Macrepistius* (Bartram 1975), and *Watsonulus* (Olsen 1984).

The relationships between *Tlayuamichin itztli* and "*Lepidotes*" *minor* will be explored in detail in a cladistic analysis (López-Arbarello & Alvarado-Ortega in prep.), but the morphological similarity between the two species is remarkable. Also these species seem to be closely related with the North American species of *Semionotus*, including the Hettangian (Early Jurassic) freshwater species *S. elegans* from the Boonton Formation (Newark Supergroup), New Jersey, Eastern USA (Olsen & McCune 1991) and *S. kanabensis* from the Kanab Area (Whitmore Point Member of the Moenave Formation), Utah, Western USA (see Lucas *et al*. 2005; Milner & Kirkland 2006; Milner *et al*. 2006). Therefore, if these systematic relationships are confirmed, the Early Cretaceous distribution of such potential clade shows an interesting biogeographic pattern that involves continental Early Jurassic North American species and marine Early Cretaceous circum-North American species. Additionally, within this paleobiogeographic scenario, the close relationship of *Tlayuamichin itztli* and "*Lepidotes*" *minor* might be reflecting a dispersal route through a connecting Early Cretaceous seaway along coastal shallow marine environments of Europe and North America, resembling the dispersion pattern drawn for the tribe Vidalamiini (Grande & Bemis 1998: 641) and the families Ionoscopidae (Alvarado-Ortega & Espinosa-Arrubarrena 2008) and Ophiopsidae (Brito & Alvarado-Ortega 2008: 151–152).

The biogeographic pattern shown by *Tlayuamichin itztli* and its relatives is linked to the Late Triassic-Jurassic breakup of the supercontinent of Pangaea that includes the assembling of Mexico and the opening of the Gulf of Mexico and the Atlantic Ocean. Although close to the end of the Triassic, the Raethian Sea Transgression marked the end of a long period of the characteristic continental red-bed sedimentation along North and Western Europe (Cope 2006, Lindström & Erlström 2006); the breakup of this supercontinent began in the Middle Triassic with the emergence of a continental rift zone at its centre. This rift zone was progressive and slowly active until the Sinemurian (Early Jurassic) when the fast deposit of the Central Atlantic Magmatic Province (CAMP) occurred (McHone 2003). The CAMP is one of the largest known flood basalt provinces formed in the Phanerozoic with an extending area along central Pangaea from modern central Brazil, western Africa, Iberia, north-western France, to south-eastern North America (McHone 2000), the activity of which during the posterior 60 My is associated with the split and spreading of Pangaea into northern and southern fragments (Laurasia and Gondwana) and the origin of the Central and Southern Atlantic oceans (McHone 2002, Knight *et al*. 2004).

The opening of the Gulf of Mexico from the Late Triassic to Early Cretaceous can be described as a process of three steps (Alaníz-Alavez *et al*., 1996; Ortega-Gutiérrez *et al*. 2000; Salvador 1991; Padilla y Sánchez 2007; Goldhammer & Johnson 2001; among others): 1) The appearance of Late Triassic–Sinemurian faults and deformation systems that generated grabens containing continental deposits around the proto-Gulf; 2) The southward movement of the Maya Block during the Bajocian-Callovian, at the same time that continental basalt and salt were deposited within the proto-Gulf area; 3) The spreading of the seafloor and deposit of oceanic crust within the Gulf of Mexico during the Oxfordian-Barresian.

The separation of North America and Europe is linked to the development of the North Atlantic Igneous Province (NAIP), the deposits of which are spread from Greenland to Norway (Jolley & Bell 2002). The evolution of NAIP is here described in four steps (Meyer *et al*. 2007, fig. 2): 1) The Permo-Jurassic no-breaking magnetic events along rift system of the Greenland-Norway area; 2) The Early Cretaceous extensive magmatic events that originate the first separation stage between Europe and North America; 3) The Late Cretaceous-Palaeocene spreading of the seafloor within the Labrador Sea and the separation of Greenland and Canada; 4) The continental separation between North-western Europe and Greenland during the Early Eocene after breakup and the early spreading of the seafloor immediately northeast of Iceland.

The Boonton, Chinle, and probably the Moenave formations are deposited within basins that are grabens originated during the Triassic rift activity associated to the CAMP and located far from the sea. Although the Tethys Sea covered Western Europe at that time (Rethian), there are no evidences supporting a Tethyan origin of the Early Jurassic North American *Semionotus* species, *S. kanabensis* and *S. elegans*. On the other hand, evidence from the ammonite fossil record shows different episodic sea transgressions from the Pacific covering the central part of Mexico and filling the Gulf of Mexico (Cantú-Chapa 2001:8) during the Early Jurassic (Bajocian Oxfordian). However, the same evidence also show that the sea route between the Tlayúa Quarry and the Purbeck, which are the localities of *Tlayuamichin itztli* and "*Lepidotes*" *minor* respectively, was available since the Early Oxfordian, when the Gulf of Mexico and the Tethys Sea were finally connected to each other.

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References

Agassiz, L. (1833–1844) *Recherches sur les Poissons Fossiles*. Petitpierre, Neuchâtel et Soleure, Suisse, 1420 pp.

Alaníz-Alvarez, S.A., van der Heyden, P., Nieto-Samaniego, A.F. & Ortega–Gutiérrez, F. (1996) Radiometric and kinematic evidence for Middle Jurassic strike-slip faulting in southern Mexico related to the opening of the Gulf of Mexico. *Geology*, 24, 443–446.

Alencaster, G. (1973) Una nueva especie de *Toucasia* en el Cretacico medio de los estados de Oaxaca y Puebla. *Paleontologia Mexicana*, 36, 1–20.

Alvarado-Ortega, J. (2005) *Sistemática de los peces Ichthyodectiformes de la cantera Tlayúa, Puebla, México.* Tesis de Doctorado. Posgrado en Ciencias Biológicas, Instituto de Geología, UNAM, México, 302 pp.

Alvarado-Ortega, J., González-Rodríguez, K.A., Blanco-Piñón, A., Espinosa-Arrubarrena, L. & Ovalles-Damián, E. (2006) Mesozoic Osteichthyans of Mexico. *In*: Vega, F.J., Nyborg, T.G., Perrilliat, M.C., Montellano-Ballesteros, M., Cevallos-Ferriz. S.R.S. & Quiroz-Barroso, S.A. (Eds), *Studies on Mexican Paleontology, Topics on Geobiology,* Volume 24. Springer, Dordrecht, The Netherlands, pp. 169–207.

Alvarado-Ortega, J., Espinosa-Arrubarrena, L., Blanco, A., Vega, F.J., Benammi, M. & Briggs, D.E.G. (2007) Exceptional preservation of soft tissues in Cretaceous fishes from the Tlayúa Quarry, Central Mexico. *PALAIOS*, 22, 682–685.

Alvarado-Ortega, J. & Espinosa-Arrubarrena, L. (2008) A new genus of Ionoscopiforms fish (Halecomorphi) from the Early Cretaceous (Albian) lithographic Limestone of the Tlayúa Quarry, Puebla, México. *Journal of Paleontology*, 82(1), 163–175.

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.

Applegate, S.P., Buitrón, B.E. & López-Neri, P. (1982) La Cantera Tlayúa en la región de Tepexi de Rodríguez, Puebla, El Solnhofen de México. *VI Congreso Nacional de Zoología, Universidad Autónoma de Sinaloa, Resúmenes*.

Applegate, S.P. (1988) A new genus and species of a holostean belonging to the family Ophiopsidae, *Teoichthys kallistos*, from the Cretaceous, near Tepexi de Rodríguez, Puebla. *Universidad Nacional Autónoma de México, Instituto de Geología, Revista*, 7(2), 200–205.

Applegate, S.P. (1992) A new genus and species of pycnodont, *Tepexichthys aranguthyorum* from the Cretaceous (Albian) of Central Mexico, Tepexi de Rodríguez, Puebla. *Universidad Nacional Autónoma de México, Instituto de Geología, Revista*, 10(2), 164–178.

Applegate, S.P. (1996) An overview of the Cretaceous fishes of the quarries near Tepexi de Rodriguez, Puebla, Mexico. *In*: Arratia, G. & Viohl, G. (Eds), *Mesozoic Fishes - Systematics and Paleoecology.* Verlag Dr. Friedrich Pfeil, Munich, pp. 529–538.

Applegate, S.P., Espinosa-Arrubarrena, L., Alvarado-Ortega, J. & Benammi, M. (2006) Revision of recent investigations in the Tlayúa Quarry. *In*: Vega, F.J., Nyborg, T.G., Perrilliat, M.C., Montellano-Ballesteros, M., Cevallos-Ferriz, S.R.S. & Quiroz-Barroso, S.A. (Eds), St*udies on Mexican Paleontology: Topics in Geobiology*, Volume 24. Springer, Dordrecht, The Netherlands, pp. 275–304.

Applegate, S.P., Buitrón-Sánchez, B.E., Solís-Marín, F.A. & Laguarda-Figueras, A. (2009) Two Lower Cretaceous (Albian) Fossil Holothurians (Echinodermata) from Tepexi De Rodriguez, Puebla, Mexico. *Proceedings of the Biological Society of Washington*, 122(1), 91–102.

Arambourg, C. & Bertin, L. (1958) On the fossil fishes found by Mr. Gardner in the Province of Ceará, in the North of Brazil. *Edinburgh New Philosophical Journal* 30, 82–84.

Arratia, G. & Schultze, H.-P. (1991) Palatoquadrate and its Ossifications: Development and Homology within Osteichthyans. *Journal of Morphology*, 208, 1–81.

Bartram, A.W.H. (1975) The holostean fish genus *Ophiopsis* Agassiz. *Zoological Journal of the Linnean Society*, 56, 183–205.

Bartram, A.W.H. (1977) The Macrosemiidae, a Mesozoic family of holostean fishes. *Bulletin of the British Museum (Natural History), Geology*, 29, 137–234.

Benammi, M., Alvarado-Ortega, J. & Urrutia-Fucugauchi, J. (2006) Magnetostratigraphy of the Lower Cretaceous strata in Tlayúa Quarry, Tepexi de Rodriguez, state of Puebla, Mexico. *Earth Planets Space*, 58, 1295–1302.

Brito, P.M. (1997) Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoïque: ostéologie, relations phylogénétiques, données environnmentales et biogéographiques. *Geodiversitas*, 19, 681–772.

Brito, P.M. & Alvarado-Ortega, J. (2008) A new species of *Placidichthys* (Halecomorphi: Ionoscopiformes) from the Lower Cretaceous Marizal Formation, northeastern Brazil, with a review of the biogeographical distribution of the Ophiopsidae. *In*: Cavin, L., Lingbottom, A. & Richter, M. (Eds), *Fishes and the break-up of Pangea*. Geological Society, London, Special Publications, pp. 145–154.

Cantú-Chapa, A. (1987) Las amonitas del Albiano Superior de Tepexi de Rodríguez, Puebla. *Sociedad Mexicana de Paleontología, Revista*, 1, 159–160.

Cantú-Chapa, A. (2001) Mexico as the western margin of Pangea based on biogeographic evidence from the Permian to the Lower Jurassic. *In*: Bartolini, C., Cantú-Chapa, A., & Buffler, R.T. (Eds.), *The western Gulf of Mexico Basin: Tectonics, sedimentary basins and petroleum systems*. American Association of Petroleum Geologists Memoir 75, Tulsa, Oklahoma, pp. 1–27.

Cavin, L. & Suteethorn, V. (2006) A new Semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic - Lower Cretaceous Deposits of North-East Thailand, with Comments on the Relationships of Semionotiforms. *Palaeontology*, 49, 339–353.

Chang, M.-M. & Miao, D. (2004) An overview of Mesozoic Fishes in Asia. *In:* Arratia, G. & Tintori, A. (Eds.) *Mesozoic Fishes 3 – Systematics, Paleoenvironment and Biodiversity.* Verlag Dr. Friedrich Pfeil, München, pp. 535–563.

Cope, J.C.W. (2006) Jurassic: the returning seas. *In*: Brencheley P.J. & Rawson, P.F. (Eds), *The geology of England and Wales*, 2nd Edition. The Geological Society, London, pp. 325–364.

Cope, J.C.W. (2008) Drawing the line: the history of the Jurassic-Cretaceous boundary. *Proceedings of the Geologists' Association*, 119, 105–117.

Deecke, W. (1889) Ueber Fishe aus verschiedenen Horizonten der Trias. *Palaeontographica*, 35, 97 138.

Espinosa-Arrubarena, L. & Applegate, S.P. (1996) A paleoecological model of the vertebrate bearing beds in the Tlayúa Quarries, near Tepexi de Rodriguez, Puebla, Mexico. *In*: Arratia, G. & Viohl, G. (Eds), *Mesozoic Fishes - Systematics and Paleoecology.* Verlag Dr. Friedrich Pfeil, Munich, pp. 539–550.

Feldman, R.M., Vega, F.J., Applegate, S.P. & Bishop, G.A. (1998) Early Cretaceous arthropods from the Tlayúa Formation at Tepexi de Rodriguez, Puebla, Mexico. *Journal of Paleontology*, 71(1), 79–90.

Forey, P.L., López-Arbarello, A. & Macleod, N. (in press) A new species of *Lepidotes* (Actinopterygii: Semionotiformes) from the Cenomanian (Upper Cretaceous) of Morocco. *Palaeontologia electronica*.

Gallo, V. & Brito, P.M. (2004) An overview of Brazilian semionotids. *In:* Arratia, G. & Tintori, A. (Eds.) *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity.* Verlag Dr. Friedrich Pfeil, München, Germany, pp. 253–264.

Goldhammer, R.K. & Johnson, C.A. (2001) Middle Jurassic – Upper Cretaceous paleogeographic evolution and sequence stratigraphic framework of the northwest Gulf of Mexico rim. *In*: Bartolini, C., Cantú-Chapa, A. & Buffler, R.T. (Eds) *The western Gulf of Mexico Basin: Tectonics, sedimentary basins and petroleum systems*. American Association of Petroleum Geologists Memoir 75, Tulsa, Oklahoma, pp. 45–81.

González-Rodríguez, K., Applegate, S.P. & Espinosa-Arrubarrena, L. (2004) A New World macrosemiid (Pisces: Neopterygii-Halecostomi) from the Albian of México. *Journal of Vertebrate Paleontology*, 24, 281–289.

González-Rodríguez, K. & Reynoso, V.-H. (2004) A new *Notagogus* (Macrosemiidae, Halecostomi) species from the Albian Tlayúa Quarry, Central Mexico. *In:* Arratia, G. & Tintori, A. (Eds.) *Mesozoic Fishes 3 – Systematics, Paleoenvironments* *and Bioidiversity*. Verlag Dr. Friedrich Pfeil, München, pp. 265–278.

Grande, L. & Bemis, W.E. (1998) A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Society of Vertebrate Paleontology Memoir*, 4, 1–690.

Guerrero-Arenas, R. (2004) *Icnofósiles de invertebrados de la Formación Tlayúa en Tepexi de Rodriguez, Puebla, México*. Facultad de Ciencias, Universidad Nacional Autónoma de México, unpublished Masters degree thesis, 49 pp.

Jolley, D.W. & Bell, B.R. (2002) The evolution of the North Atlantic Igneous Province and the opening of the NE Atlantic rift. *Geological Society, London, Special Publications*, 197, 1–13 p.

Kashiyama, Y., Fastovsky, D.E., Rutherford, S., King, J. & Montellano, M. (2004) Genesis of a locality of exceptional fossil preservation: paleoenvironments of Tepexi de Rodriquez (mid-Cretaceous, Puebla, Mexico). *Cretaceous Research*, 25, 153–177.

Knight, K.B., Nomade, S, Renne, P.R., Marzoli, A., Bertrand, H. & Youbi, N. (2004) The Central Atlantic Magmatic Province at the Triassic–Jurassic boundary: paleomagnetic and 40Ar/39Ar evidence from Morocco for brief, episodic volcanism. *Earth and Planetary Science Letters*, 228, 143–160.

Lambers, P.H. (1999) The actinopterygian fish fauna of the Late Kimmeridgian and Early Tithonian ‘Plattenkalke’ near Solnhofen (Bavaria, Germany): state of the art. *Geologie en Mijnbouw*, 78, 215–229.

Lindström, S. & Erlström, M. (2006) The late Rhaetian transgression in southern Sweden: Regional (and global) recognition and relation to the Triassic–Jurassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241, 339–372

López-Arbarello, A. (2006) Ordering the semionotids 1: incorporating the recently described and revised taxa in a cladistic study. *Journal of Vertebrate Paleontology*, 26, 91A.

López-Arbarello, A. (2008a) Revision of *Semionotus bergeri* Agassiz, 1833 (Uper Triassic, Germany), with comments on the taxonomic status of *Semionotus* (Actinopterygii, Semionotiformes). *Paläontologische Zeitschrift*, 82, 40–54.

López-Arbarello, A. (2008b) What, if anything, is *Lepidotes*? *Erlanger geologische Abhandlungen*, Sonderband 6, 41.

López-Arbarello, A. & Codorniú, L. (2007) Semionotids (Neopterygii, Semionotiformes) from the Lower Cretaceous Lagarcito Formation, San Luis Province, Argentina. *Journal of Vertebrate Paleontology*, 27, 811–826.

López-Arbarello, A. & Sferco, E. (in press) New semionotiform (Actinopterygii: Neopterygii) from the Late Jurassic of southern Germany. *Journal of Systematic Palaeontology.*

López-Arbarello, A., Rauhut, O.W.M. & Cerdeño, E. (2010) The Triassic fish fauna of the Cuyana Basin, Western Argentina. *Palaeontology*, 53, 249–276, DOI: 10.1111/j.1475-4983.2010.00931.x.

López-Arbarello, A., Rauhut, O.W.M. & Moser, K. (2008) Jurassic fishes of Gondwana. *Revista de la Asociación Geológica Argentina*, 63(4), 586–612.

Lucas, S.G., Tanner, L.H. & Heckert, A.B. (2005) Tetrapod biostratigraphy and biochronology across the Triassic-Jurassic boundary in northeastern Arizona. *New Mexico Museum of Natural History and Science, Bulletin*, 29, 84–94.

Malpica-Cruz, V.M., Pantoja-Alor, J. & Galguera-Rosa, G. (1989) Microfacies de la Cantera Tlayúa, Puebla, Mexico. *Simposio sobre Geologia Regional de Mexico*, 3, 53–56.

Martill, D. (1989) A new Solnhofen in Mexico. *Geology Today*, 5, 25–28.

Martín-Medrano, L., Thuey, B. & García-Barrera, P. (2009) New Albian (Early Cretaceous) Ophiuroids from Tlayúa quarry, Publa, Mexico. *Palaeontology*, 52(1), 83–94.

Martínez-Hernández, E. & Ramírez Arriaga, E. (1996) Palaeocorología de Angiospermas de la Flora Mexicana Durante el Mesozoico y Terciario: algunas evidencias palinológicas. *Sociedad Botánica de México, Boletín*, 58, 87–97.

McCune, A.R. (1986) A revision of *Semionotus* (Pisces: Semionotidae) from the Triassic and Jurassic of Europe. *Palaeontology*, 29, 213–233.

McCune, A.R. (2004) Diversity and speciation of semionotid fishes in Mesozoic Rift Lakes. *In:* Dieckmann, U., Doebeli, M., Metz, J.A.J. & Tautz, D. (Eds.) *Adaptive speciation*. Cambridge University Press, 362–379.

McHone, J.G. (2000) Non-plume magmatism and rifting during the opening of the central Atlantic Ocean. *Tectonophysics*, 316, 287–296

McHone, J.G. (2002) Volatile emissions of Central Atlantic Magmatic Province basalts: Mass assumptions and environmental consequences. *In*: Hames, W.E., McHone, J.G., Renne, P.R. & Ruppel, C. (Eds), *The Central Atlantic Magmatic Province*. American Geophysical Union, Geophysical Monograph, 136, pp. 241–254.

McHone, J.G. (2003) *Igneous Features and Geodynamic Models of Rifting and Magmatism Around the Central Atlantic Ocean*: invited website paper. MantlePlumes, 11 pp. Available form: http://www.mantleplumes.org/CAMP.html.

Meyer, R., Wijk, J. & Gernigon, L. (2007) The North Atlantic Igneous Province: a review of models for its formation. *In*: Foulger, G.R. & Jurdy, D.M. (Eds), *Plates, plumes, and planetary processes*. Geological Society of America Special Paper, 430, Boulder, Colorado, USA, pp. 525–552.

Milner, A.R. & Kirkland, J.I. (2006) Preliminary review of the Early Jurassic (Hettangian) freshwater Lake Dixie fish fauna in the Whitmore Point Member, Moenave Formation in Southwest Utha. *In:* Harris, J.D., Lucas, S., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. & Kirkland, J.I. (Eds) *The Triassic-Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin 37*, Albuquerque, pp. 607.

Milner, A.R., Kirkland, J.I. & Birthisel, T.A. (2006) The geographic distribution and biostratigraphy of Late Triassic-Early Jurassic freshwater fish faunas of the southwestern United States. *In:* Harris, J.D., Lucas, S., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. & Kirkland, J.I. (Eds) *The Triassic-Jurassic Terrestrial Transition. New Mexico Museum of Natural*

History and Science Bulletin 37, Albuquerque, pp. 607.

Murray, A.M. & Wilson, M.V.H. (2009) A new Late Cretaceous macrosemiid fish (Neopterygii, Halecostomi) from Morocco, with temporal and geographical range extensions for the family. *Palaeontology*, 52, 429–440.

Olsen, P.E. (1984) The skull and pectoral girdle of the parasemionotid fish *Watsonulus eugnathoides* from the Early Triassic Sakamena Group of Madagascar, with comments on the relationships of the holostean fishes. *Journal of Vertebrate Paleontology*, 4, 481–499.

Olsen, P.E. & McCune, A.R. (1991) Morphology of the *Semionotus elegans* species group from the Early Jurassic part of the Newark Supergroup of eastern North America with comments on the Family Semionotidae (Neopterygii). *Journal of Vertebrate Paleontology*, 11, 269–292.

Ortega-Gutiérrez, F., Sedlock, R.L. & Speed, R.C. (2000) Evolución tectónica de México durante el fanerozóico. *In*: Llorente-Bousquets, J., Gonzalez-Soriano, E. & Papavero, N. (Eds), *Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una sintesis de su conocimiento, Volumen II*. Universidad Nacional Autónoma de México, México D.F., pp. 3–59.

Padilla y Sánchez, R.J. (2007) Evolución geológica del sureste mexicano desde el Mesozoico al presente en el contexto regional del Golfo de México. *Boletín de la Soceidad Geológica Mexicana*, 59(1), 19–42.

Pantoja-Alor, J. (1992) Geología y paleoambientes de la Cantera Tlayúa, Tepexi de Rodriguez, estado de Puebla. *Revista - Instituto de Geologia*, 9, 156–169.

Patterson, C. (1975) The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London*, 269, 275–579.

Patterson, C. (1982) Morphology and interrelationships of primitive actinopterygian fishes. *American Zoology*, 22, 241–259.

Regan, C.T. (1923) 24. The Skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower Neopterygian Fishes. *Proceedings of the Zoological Society of London*, 1923, 445–461.

Reynoso, V.H. (2000) An unusual aquatic sphenodontian (Reptilia: Diapsida) from the Tlayúa Formation (Albian), Central México. *Journal of Paleontology*, 74(1), 133–148.

Reynoso, V.H. & Callison, G. (2000) A new scincomorph lizard from the Early Cretaceous of Puebla, México. *Zoological Journal of the Linnean Society*, 130, 183–212.

Salvador, A. (1991) Origin and development of the Gulf of Mexico Basin. *In*: Salvador, A. (Ed.), *The Gulf of Mexico Basin*. Geological Society of America, The Geology of North America, v. J, pp. 389–444.

Schaeffer, B. & Dunkle, D.H. (1950) A semionotid fish from the Chinle Formation, with consideration of its relationships. *American Museum Novitates*, 1457, 1–30.

Seibertz, E. & Buitrón, B.E. (1987) Paleontología y estratigrafía de los *Neohibolites* del Albiano de Tepexi de Rodrı´guez, Estado de Puebla (Cretácico Medio, México). *Sociedad Mexicana de Paleontología*, 1, 285–299.

Seibertz, E. & Spaeth, C. (2002) Cretaceous belemnites of México III: The Albian Neo- and Mesohibolites of the ‘‘Mexican Solnhofen’’ Tepexi de Rodríguez (state of Puebla) and their biostratinomy (Lower Cretaceous). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 225, 55–74.

Su, D.Z. (1996) A new semionotid fish from the Jurassic of Sichuan Basin and its biostratigraphic significance. *Vertebrata Palasiatica*, 34, 91–101.

Suarez, M., González, L., Ludvingson, G., Vega, F. & Alvarado-Ortega, J. (2009) Isotopic composition of tropical paleo-precipitación during the Early Cretaceous. *Geological Society of America Bulletin*, 121, 1584–1595.

Wenz, S. (1968) *Compléments à l'étude des poissons actinoptérygiens du Jurassique français*. Centre National de la Recherche Scientifique, Paris, France, 1–276 pp.

Wenz, S. (1999) *Pliodetes nigeriensis*, gen. nov. et. sp. nov., a new semionotid fish from the Lower Cretaceous of Gadoufaoua (Niger Republic): phylogenetic comments. In: Arratia, G. & Schultze, H.-P. (Eds.) Mesozoic Fishes 2 – Systematics and Fossil Record. Verlag Dr. Friederich Pfeil, München, Germany, pp. 107–120.

Wenz, S. (2003) Les *Lepidotes* (Actinopterygii, Semionotiformes) du Crétacé inférieur (Barrémien) de Las Hoyas (Province de Cuenca, Espagne). *Geodiversitas*, 25, 481–499.

Wenz, S., Bernier, P., Barale, G., Bourseau, J.P., Buffetaut, E., Gaillard, C. & Gall, J.C. (1994) L'ichthyofaune des clacaires lithographiques du Kimméridgien supérieur de Cerin (ain, France). *Geobios*, M.S. n° 16, 61–70.

Westoll, T.S. (1944) The Haplolepidae, a new family of Late Carboniferous bony fishes. A study in Taxonomy and Evolution. *Bulletin of the American Museum of Natural History*, 83, 1–121.

Wiley, E.O. (1976) The Phylogeny and Biogeography of Fossil and Recent Gars (Actinopterygii: Lepisosteidae). *University of Kansas, Miscellaneous Publications*, 64, 1–111.

Woodward, A.S. (1916–1919) The fossil fishes of the English Wealden and Purbeck formations. *Palaeontographical Society*, Part II, 49–104.