THE FIRST AMERICAN RECORD OF ASPIDOPLEURUS (TELEOSTEI, AULOPIFORMES), FROM LA MULA QUARRY (TURONIAN), COAHUILA STATE, MEXICO

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ABSTRACT – A new species of Aspidopleurus Pictet & Humbert is described based on a single and almost complete specimen from marine Turonian marl strata belonging to the Eagle Ford Formation, which is exploited in La Mula Quarry, Municipality of Acuña, Coahuila State, Mexico. The new species shows the most outstanding characteristic of this genus, namely, that the whole flank of the trunk is covered by a single row of scutes. The new species differs from the type species A. cataphractus Pictet & Humbert, because the former has only 42 lateral scutes, 22 abdominal vertebrae, and only 11 dorsal and anal fin rays, while the latter species has 45 lateral scutes, 24 abdominal vertebrae, and 18 dorsal and 14 anal fin rays. Additionally, these two species are separated from Prionolepis angustus Egerton, a species that for a long time was thought to be a close relative of A. cataphractus. In Aspidopleurus the scutes are comparatively shorter, strongly ornamented and not posteriorly serrated, whereas in Prionolepis Egerton the scutes are very high and smooth with a serrated posterior. Therefore, A. cataphractus, once included as a species of Prionolepis, is placed again in its own genus together with the new species here proposed. The present report of Aspidopleurus in Mexico is the first for America, and represents the westernmost distribution of this genus in the Tethys Sea Domain, revealing the wide geographical distribution of Aspidopleurus along the latitudinal extension of the Tethys Sea, from the Middle East (Hakel and Hadjula, Lebanon) to southern North America.

Key words: Aspidopleurus, Prionolepis, Aulopiformes, La Mula Quarry, Múzquiz, Turonian, Mexico.

RESUMO – Uma nova espécie de Aspidopleurus Pictet & Humbert é descrita com base em um único espécime quase completo, proveniente do estrato marinho margoso de idade Turoniano pertencente à Formação Eagle Ford, que é explorado na Pedreira La Mula, Município de Acuña, Estado de Coahuila, México. A nova espécie apresenta característica mais marcante desse gênero que é o flanco todo do tronco coberto por uma única fileira de escamas. A nova espécie difere da espécie tipo A. cataphractus Pictet & Humbert, porque a primeira tem apenas 42 escamas laterais, 22 vértebras abdominais, e apenas 11 raios na nadadeira dorsal e anal, enquanto a última tem 45 escamas laterais, 24 vértebras abdominais, 18 raios na nadadeira dorsal, e 14 raios na nadadeira anal. Além disso, estas duas espécies são separadas de Prionolepis angustus Egerton, uma espécie que durante muito tempo foi considerada ser relativamente próxima de A. cataphractus. Em Aspidopleurus as escamas são comparativamente mais curtas, fortemente ornamentadas, e não dentadas posterioriamente, enquanto em Prionolepis Egerton, estas são muito elevadas, lisas e serrilhadas posteriormente. Portanto, A. cataphractus, uma vez incluída como uma espécie de Prionolepis, é colocada novamente no seu próprio gênero juntamente com a nova espécie aqui proposta. O registro de Aspidopleurus no México é o primeiro na América, e representa a distribuição mais ocidental do gênero no domínio do Mar de Tétis, de modo que revela a ampla distribuição geográfica de Aspidopleurus ao longo da extensão latitudinal do Mar de Tétis do Oriente Médio (Hakel e Hadjula, Libano) ao sul da América do Norte.

Palavras-chave: Aspidopleurus, Prionolepis, Aulopiformes, Pedreira La Mula, Múzquiz, Turonian, México.

INTRODUCTION

Grey Egerton (in Dixon, 1850, p. 368) described Prionolepis angustus Egerton in Dixon, 1850 based on isolated scutes from Cenomanian deposits of the Lower Chalk at Burwell, near Newmarket, England, believing that this species was related to Aspidorhynchiformes. Those scutes are smooth, show pectinated or saw-like posterior borders, and probably form a single row that covers each of the body flanks. Later on, Pictet & Humbert (1866) described Aspidopleurus cataphractus Pictet & Humbert, 1866 based on almost complete and well preserved fossil specimens from the middle Cenomanian limestone strata of Hakel, Lebanon. After Woodward (1898, 1901) placed these two species within Prionolepis Egerton in Dixon, 1850, the composition of this genus has not been questioned.

Although other European poorly preserved scute remains of Prionolepis were found in the Upper Albian or Lower Cenomanian strata of Tormarp, near Örkelljunga, Sweden.
(Lundgren, 1889), and some other scarce and fragmentary scutes collected in the Cenomanian-Coniacian marine strata of the Lower and Upper Chalk, southern England, were identified as *P. angustus* by Woodward (1901, p. 230), additional remains have not been reported for Europe. The anatomy of *Prionolepis* is documented mainly based on *Prionolepis* [Aspidopleurus] cataphractus (see Goody, 1969; Forey et al., 2003), which has proved to be more abundant and well documented in large collections, including entire and exceptionally preserved specimens from the rich Cenomanian fossil strata of Hadjula and Hakel, Lebanon.

When Goody (1969) performed the accurate anatomical review of *Prionolepis*, entirely based on *P. [Aspidopleurus] cataphractus*, he assumed Woodward’s proposal (1898, 1901), retaining *P. angustus* and *P. cataphractus* in this genus. This author also erected the family Prionolepididae, which is entirely based on characters documented only in *P. [Aspidopleurus] cataphractus*. Recently, Bogan et al. (2011) described *Belonostomus lamarquensis* Bogan, Taverne & Agnolin, 2011, a Campanian-Maastrichtian aspidorhynchiform fish from deposits of the Allen Formation, Argentina, which has scutes with the features previously found in *P. angustus* (see discussion). This finding raises the possibility that *P. angustus* is a close relative of *B. lamarquensis* or may be related to Aspidorhynchiformes, as was suggested by Egerton (in Dixon, 1850). According to the illustration given by Goody (1969, fig. 85) for the scutes of *P. [Aspidopleurus] cataphractus*, these seem not to be like those described for *P. angustus*.

These reasons permit the suggestion that the material of *Prionolepis angustus* and *Aspidopleurus cataphractus* really belong to different genera. Because of this and the proposal of *A. cataphractus* as the type species of the genus, there is an implication of the taxonomic nomenclature of the genus *Prionolepis* and the family Prionolepididae, which, as noted before, are entirely diagnosed based on the anatomical characteristics of *A. cataphractus*. Hence, herein the names *Prionolepis* and Prionolepididae are proposed to be replaced by *Aspidopleurus* and Aspidopleuridae, respectively, retaining the same diagnoses provided by Goody (1969). The possible relationships of *Prionolepis angustus*, *Belonostomus lamarquensis* and other aspidorhynchiforms are beyond the scope of this work.

Recent paleontological surveys on the Upper Cretaceous marine deposits of Coahuila State, Mexico, revealed the first occurrence of *Aspidopleurus* (previously identified as *Prionolepis*) in America. Although Stinnesbeck et al. (2005, p. 406) reported a “Prionolepididae indeterminate” from El Rosario as part of the fishes “tentatively identified” and “apparently collected randomly at El Rosario and other quarries in the area”, these authors have not provided additional data. On the other hand, Alvarado-Ortega & Porras-Múzquiz (2009a) identified a specimen from La Mula Quarry as a possible new species of *Prionolepis*. The aim of the present paper is to describe this latter specimen as a new species for the genus *Aspidopleurus*.

**GEOLOGICAL SETTING**

Roemer (1852) and Shumard (1860) developed the first studies on the marine Cretaceous sequences of shales and limestones with fossil remains of fishes, reptiles and diverse invertebrates throughout different localities of central Texas, USA. Later, Hill (1887) named these strata as the Eagle Ford Formation based on those outcrops located in Eagle Ford, Dallas County. MacGown et al. (1967) described this formation as a sequence of platy dark-gray bituminous shales with selenite and calcareous concretions, which are interbedded rhythmically with thin sandstones and sandy limestones. According to these and other authors (e.g. Dutton et al., 1994), the thickness of this formation ranges between 91 and 130 m.

Today, well-documented Eagle Ford Formation strata throughout Texas and Dakota are often considered as a group. According to Moreman (1942), Barnes (1972) and Hsu & Nelson (2002), among others, this group involves two formations: the South Bosque at the top and the Lake Waco at the bottom. Alternatively, Sellards et al. (1966) suggested that the group includes the Tarrant, Britton, and Arcadia Park formations.

Since Petróleos Mexicanos (Pemex, 1998) began research on the Cretaceous rocks in the north of Mexico, several outcrops of the Eagle Ford Formation have been reported in the country. These rocks crop out in the Coahuila and Nuevo León states, within the Sabinas and Burgos basins, where they represent tracts of a transgressive system deposited under a middle-neritic environment near to the Tamaulipas or Burro-Peyotes paleo-peninsula (Eguíuluz, 2001; González-Sánchez et al., 2007). In Mexico, this formation conformably overlies the Buda Formation limestones, and its upper contact is transitional and conformable with the Austin Formation (Santamaria et al., 1991).

La Mula Quarry is located between the coordinates 29°09′24.5″N and 102°31′01.1″W, within the Municipality of Acuña, Coahuila, northeastern Mexico (Figure 1). This is a sequence of about 3 m thick with centimetric, parallel and finally laminated marls bearing small iron oxide nodules (about 3 cm in diameter), which are interbedded with fine and iron oxide-rich clay layers. These fossil-bearing strata, belonging to the Eagle Ford Formation, were discovered in 2002, when local people began the manual extraction of marl limestone slabs. Paleontological studies in La Mula Quarry (Blanco-Piñón et al., 2004; Blanco-Piñón & Alvarado-Ortega, 2005; Vega et al. 2007; Aguilar & Porras-Múzquiz, 2009) revealed the peculiar fossil assemblage of this paleontological site, which includes fishes (shark teeth, Pycnodontiformes (*Nursallia* Blot, 1987), Icthyodectiformes (*Saurodon* Hays, 1830 and other unidentified specimens), Tseltatiformes (*Tseltatia* Arambourg, 1943), Crossognathiformes (*Pachyrhizodus* Dixon, 1850), Enchodontidae (*Enchodus* Agassiz, 1835), *Laminospondylus* Springer, 1957, Clupeiformes and others non-identified teleostean remains), marine reptiles, raninid crabs, ammonites, bivalve inoceramids (*Inoceramus*...
Sowerby, 1814 and *Platycerammus* Seitz, 1932) and other invertebrates. Also in this locality there are levels with a lot of insolated scales and disarticulated fish bones, ichnofossils and coprolites. Vertebrate fossils from la Mula Quarry are highly compressed, and only occasionally have some 3D specimens been collected. The vertebrate skeletons are preserved by phosphate minerals embedded in calcite minerals, and the soft tissues are often preserved as phosphate patches seen below the scales and between the ribs and gills. According to Blanco-Piñón et al. (2004), the fossil preservation and fine matrix of the strata found in this locality suggest they were deposited in a neritic environment with oxygen-depleted bottom waters and low-energy conditions.

**SYSTEMATIC PALEONTOLOGY**

*Order Aulopiformes* Rosen, 1973

*Suborder Alepisaurioidei* sensu Nelson, 2006

**Aspidopleuridae fam. nov.**

**Diagnosis.** Fish with body elongated and relatively shallow; neurocranium shallow and acutely pointed anteriorly; posttemporal fossa roofed; mesethmoid with large wing-like structure directed ventrolaterally; supratemporal sensory canal on the parietals and supratemporals; maxilla stout with two prominent rows of teeth; supramaxilla absent; single row of deep scutes covering each trunk flank from the head to caudal peduncle; scutes strongly ornamented with tubercles and ridges; about 45 vertebrae in total of which at least 20 are caudal; dorsal fin short and in the middle of the standard length; and anal fin small and remote (emended after Goody, 1969, p. 178).

**Aspidopleurus** Pictet & Humbert, 1866

**Type species.** *Aspidopleurus cataphractus* Pictet & Humbert, 1866.

*Aspidopleurus kickapoo* sp. nov. (Figures 2-7)

**Holotype.** MUZ 343, specimen preserved in part and counterpart.

**Type locality.** Turonian marl strata, La Mula Quarry, Eagle Ford Formation, Municipality of Acuña, Coahuila State, northern Mexico (Figure 1).

**Etymology.** The species name honors the Kickapoo people (“the ones that go by the land”), an American native tribe that in 1849 immigrated to north of Coahuila, where they still live.

**Diagnosis.** *Aspidopleurus* species reaching 240 mm in standard length (SL); the head length is about 27% of its SL; both unpaired fins are short and have 11 rays on each one; dorsal fin length is about 14.1% of SL; anal fin length is about 6.25% of SL; 45 total vertebrae including 22 abdominal and 23 caudal vertebrae; a row of 42 ornamented scutes covering each flank of the body; ratio between the major and secondary axes of larger scales ranging from 5 to 6.

**Description.** General features: in the specimen MUZ 343 the head is turned up with respect to the axis of the trunk, and some vertebrae are disjointed and not aligned with each other. Although this condition may cause minor mistakes in measurements of the body, the scales and other bones of the specimen are not scattered. Although MUZ 343 lacks the caudal rear, its estimated total length (TL) is 263 mm. The Standard length (SL), measured from the tip of the head to caudal fin peduncle, is 240, including...
65 mm of head length (HL) and 175 mm of the trunk length (TKL). The dorsal and pelvic fins rise near to the middle of the SL, the first in the anterior half of the SL and the second in the posterior half; the pre-dorsal length (Pdl) and pre-pelvic length (PPl) are 112 mm and 148 mm, respectively. The anal fin is relatively short, remote and located near to the caudal peduncle; the pre-anal length is 202 mm. The dorsal fin length (DL) is about 34 mm and the anal fin length is about 15 mm. The maximum body depth (MBD) and caudal fin peduncle depth (CFPD) in this specimen are about 26 mm and 10 mm, respectively (Figure 2). Table 1 summarizes the body measurements and proportions of specimen MUZ 343.

Skull: unfortunately the head of MUZ 343 is fragmented and its osteological details are lost (Figure 3). The frontals are

![Figure 2](image1.png) **Figure 2.** Specimen MUZ 343, holotype and only known specimen of *Aspidopleurus kickapoo* sp. nov., from La Mula Quarry, Municipality of Acuña, Coahuila State, northern Mexico. **A-B**, part and counterpart (A is a mirror image of the original). **C**, reconstruction. Scale bar = 25 mm.

<table>
<thead>
<tr>
<th>Measurement (mm)</th>
<th>As proportions in % of SL</th>
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<tr>
<td>Standard length (SL)</td>
<td>240</td>
</tr>
<tr>
<td>Head length (HL)</td>
<td>65</td>
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<tr>
<td>Trunk length (TKL)</td>
<td>175</td>
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<tr>
<td>Maximum body depth (MBD)</td>
<td>26</td>
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<tr>
<td>Caudal fin peduncle depth (CFPD)</td>
<td>10</td>
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<tr>
<td>Predorsal length (PDL)</td>
<td>112</td>
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<tr>
<td>Dorsal fin length (DL)</td>
<td>34</td>
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<tr>
<td>Prepelvic length (PPL)</td>
<td>148</td>
</tr>
<tr>
<td>Preanal length (PAL)</td>
<td>202</td>
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<tr>
<td>Anal fin length (AL)</td>
<td>15</td>
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in contact with each other up to their middle edges, and are so large that they roof almost all the skull. The join between the frontal and parietal is visible in lateral view; but it is unclear if the supraoccipital joins the frontals. The sphenotic borders the orbital dorsoposterior portion, and joins the frontal dorsally and the pterotic posteriorly. Although the large hyomandibular head covers a large part of the lateral skull surface, a stout pterotic bone is visible in the back of the skull. It seems that the sphenotic and pterotic bones form the articular facet for the hyomandibular. The parasphenoid bone is visible only along its straight orbital section. A trapezoid-like lateroethmoid bone forms the anterior border of the orbit and joins the parasphenoid and frontal bones (Figure 3).

Hyopalatine bones: the hyopalatine is a C-like stout bone; its head has a larger anterior expansion covering a large part of the lateral skull surface, and its ventral limb is thin and slightly curved forwards (Figure 3). The quadrate is triangular, its wide dorsal and laminar section is projected forwards and its short massive ventral ends forms a stout articular head. The lower jaw articulation rests posteriorly to the orbit. The symplectic is not preserved. The palatine is covered by the remains of laminar bones that could be part of the circumorbital bone series. The ectopterygoid and endopterygoid are long, narrow, thin and probably non-toothed bones, projected in parallel to the parasphenoid orbital section and attached to the anterior edge of the quadrate (Figure 3).

Circumorbital bones: although it is impossible to determine the number and shape of the bones in the circumorbital series, MUZ 343 shows fragments of laminar infraorbital bones covering the hyomandibular series, below the ocular orbit (Figure 3), and over the skull postorbital area. Other remains of laminar bones in the ocular orbit may be fragments of the sclerotic bones.

Upper jaw: the upper jaw involves two smooth bones: a prominent triangular premaxilla with gently rounded ends, as well as a bar-like maxilla (Figure 3). The maxilla has a straight alveolar border forming the anterior half of the gape.

Figure 3. Head and anterior abdominal body region of MUZ 343, holotype of *Aspidopleurus kickapoo* sp. nov., from La Mula Quarry. A, close up of the head in the part of the specimen as a mirror image of the original (see Figure 1A); B, close up of the head in the counterpart (see Figure 1B); C, representative drawing of the head based on A and B. Abbreviations: art, articular; br, branchiostegal ray; cor, coracoid; cl, cleithrum; ecp, ectopterygoid; enp, endopterygoid; den, dentary; fr, frontal; hm, hyomandibula; io, infraorbital; le, lateral ethmoid; mes, mesethmoid; mpt, metapterygoid; mx, maxilla; op, opercle; pa, parietal; par, parasphenoid; pcf, pectoral fin ray; pmx, premaxilla; pop, preopercle; pt, posttemporal; pto, pterotic; r, rib; sc, scale; sca, scapula; soc, supraoccipital; sop, subopercle; spo, sphenotic; q, quadrate. Numbers on scales and vertebral centra show the position of each element in the respective series following an anterior posterior direction. Scale bar = 20 mm.
Both bones bear millimetric-sized acute teeth slightly inclined backwards, probably forming more than one row.

Lower jaw: the mandible is a long, triangular, unornamented structure with straight dorsal and ventral borders, lacking of coronoid process. The dentary is long, narrow and has a shallow symphysis. It bears numerous, small and backward-inclined acute teeth that probably form more than one row along the alveolar border. The teeth have irregular millimetric sizes and are similar to those found in the upper jaw. Some large teeth are located near to the anterior jaw end (Figure 3). The articular bone is triangular. A small articular process is projected backward on the posterior border of this bone; it shows a shallow articular facet for the quadrate. Below this process there is a small knob forming a retroarticular process. The mandibular sensory canal runs along the ventral portion of dentary and articular bones. Some pores or small openings of this canal are exposed along the lower jaw.

Opercular bones: the opercle is a large kidney-like laminar and smooth bone, about twice deeper than long with a straight anterior edge and a sinuous posterior border. The impression of this bone (Figure 3) reveals that its inner surface has a central straight ridge. The preopercle is a deep and thin triangular bone with a narrow dorsal tip lying behind the hyomandibula head; its ventral arm is rounded and very short. The preopercular sensory canal runs near anterior edge, opening ventrally in three pores located near to posterior edge (Figure 3). The subopercle is a long and narrow curved, laminar bone that lies below the opercle (Figure 3). At least four overlapping branchiostegals are observed below the subopercle. No trace of an interopercle is observed, and probably this bone is not present in *Aspidopleurus kickapoo* sp. nov. as in *A. cataphractus* (Silva & Gallo, 2011).

Vertebral column: the vertebrae are preserved in both the part and counterpart of MUZ 343 (Figure 2). Although the surfaces of all the vertebrae are lost and they appear as impressions or molds of the vertebrae, they are evident due to the crystallized inter-vertebral spaces. The vertebral column consists of 45 vertebrae with 22 abdominal and 23 caudal vertebrae, including ural 2 and the possible fusion of preural vertebra 1 and ural 1 (all vertebrae are numbered in Figures 3-6). The vertebrae are biconcave and the inter-vertebral spaces are connected through the medial pores of the centra.

![Figure 4](image_url) Figure 4. Middle region of the body in MUZ 343, holotype of *Aspidopleurus kickapoo* sp. nov., from La Mula Quarry. Coahuila, northern Mexico. **A**, close up of the anal fin area preserved in the part of the specimen (see Figure 1 A); **B**, representative drawing of the middle region of the body shown in A. **Abbreviations:** dfr, dorsal fin ray; ep, epipleural bone; pvb, pelvic bone; pvfr, pelvic fin ray; sc, scutes; nspu, neural spine of preural centra; r, rib; ?, unknown bone, probably belonging to other fish; number on scales and vertebral centra show the position of each element in the respective series following an anterior-posterior direction. Scale bar = 10 mm.

![Figure 5](image_url) Figure 5. Anal fin ray skeleton of MUZ 343, holotype of *Aspidopleurus kickapoo* sp. nov., from La Mula Quarry. **A**, close up of the anal fin area preserved in the part of the specimen (see Figure 1 A); **B**, representative drawing of anal fin shown in A. **Abbreviations:** afr, anal fin ray; apt, anterior pterygiophore; hspu, hemal spine of preural centra; sc, scutes; numbers on scales and vertebral centra show the position of each element in the respective series following an anterior-posterior direction. Scale bar = 10 mm.
**Figure 6.** Caudal skeleton of MUZ 343, holotype of *Aspidopleurus kickapoo* sp. nov., from La Mula Quarry. A, close up of the caudal fin as it is preserved in the part of the specimen (see Figure 1 A); B, representative drawing of caudal skeleton shown in A. Abbreviations: h, hypural; hspu, hemal spine of preural centra; na+ns, neural arch and neural spine fused; ph, parhypural; pu, preural centra; sc, scutes; napu, neural arch of preural centra; u, ural centra. Numbers on scales and vertebral centra show the position of each element in the respective series following an anterior-posterior direction; rows show the first and last principal caudal fin rays. Scale bar = 10 mm.

**Figure 7.** Scutes of MUZ 343, holotype of *Aspidopleurus kickapoo* sp. nov., from La Mula Quarry. A, close up of the scutes located behind the dorsal fin; B, representative drawing of the scutes shown in A (arrows show the lateral canal trajectory). Scale bar = 4 mm.
The vertebrae are about twice longer than high along the anterior half of the body, but they become progressively shorter, and those near to the tail are almost as long as high. Unfortunately, the bony elements associated with the vertebra centra (i.e. neural arches, neural spines and possible epineurals and supraneurals) are not preserved, or obscured except a couple of neural arches near to the tail (Figure 6). It is possible to recognize 17 ribs and six or seven epipleural intermuscular bones along the abdominal area. These ribs are long, slender and inclined posteriorly. The ribs placed in front of the pelvic girdle embrace the whole abdominal area and the posterior ones are progressively shorter.

Pectoral girdle and fins: girdle bones of MUZ 343 include the posttemporal, supracleithrum, cleithrum, scapula, and coracoids (Figures 2-3). The forked posttemporal bone, ornamented with tubercles and ridges, includes a long dorsal oval limb and a short ventral limb. The supracleithrum, also ornamented, is an ovoid laminar bone attached to the posttemporal posterior ventral end and the cleithrum dorsal tip. The cleithrum is a large curved bone, with a narrow dorsal limb adjoinning. The coracoid is a laminar structure located below the cleithrum. Part of the scapula is exposed between the cleithrum and coracoids, at the back of the girdle. The pectoral fin includes 13 segmented and branched rays. The larger pectoral rays are as long as a series of five abdominal vertebrae (Figure 2). The pelvic girdle is preserved in dorsal view, and the right pelvic bone is close to the vertebral column and partially covered by the scutes (Figure 4). Each pelvic bone is a triangular structure, about five times longer than wide, which involves two anterior laminar sections or flanges that arise from a thickened medial support. The lateral middle sections of both pelvic bones are joined to each other at their anterior and posterior ends. Nine branched and segmented rays form a triangular pelvic fin and articulate with the posterior facet of each pelvic bone. The dorsal fin is acuminate and includes 11 fin rays, which originate above the level of abdominal vertebrae 15-22 (Figure 4). The first dorsal ray seems to be unbranched and shorter than the following rays, which are deeply branched and segmented. The anal fin shape is unknown because its anterior rays are broken.

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<th>Aspidopleurus kickapoo</th>
<th>Aspidopleurus cataphractus</th>
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<tr>
<td>Head length (HL)</td>
<td>27</td>
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<td>Trunk length (TKL)</td>
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<tr>
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<tr>
<td>Vertebrae</td>
<td>(22 abd + 23 ca)</td>
<td>(24 abd + 21 ca)</td>
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Table 2. Comparison of measurements and counts of fin rays, scales, and vertebrae of Aspidopleurus kickapoo sp. nov. and A. cataphractus [based on data from Goody (1969) and the BSPG specimens of the Otto Haas Collection listed in the present manuscript].
Eleven anal pterygiophores are preserved suggesting that the fin could be composed of the same number of rays. All the anal fin rays are segmented and branched. The articulation of the pterygiophores and anal fin rays extends below vertebrae 34-38. The anterior pterygiophore extends near to the end of the hemal spine tip of vertebra 30 (Figure 5). Most of the caudal fin bones of MUZ 343 are crushed and it is not possible to recognize their shape (Figure 6). The caudal fin is forked and involves two small rounded lobes of similar size. The caudal fin support is composed of three or four vertebrae, preurals 2 and 3, ural 2 and probably preural 1 that is fused to ural 1 as it occurs in A. cataphractus (Goody, 1969, p. 187). The ventral lobe of the caudal fin is supported by hemal spines of the preurals 2 and 3, the parhypural and two hypurals. The anterior elements of the dorsal caudal fin lobe are not preserved, and there are no recognizable remains of the uroneurals or epurals.

The preural 3 bears thin long hemal and neural spines, the preural 2 has an expanded hemal spine without a neural spine, and the preural 1 probably lacks both structures.
(Figure 6). The compound centra resulting from the fusion between the preural 1 andural 1 bears a wide parhypural anteriorly and two hypurals. The hypural 1 is triangular and the largest whereas the hypural 2 is spatiform; these two hypurals support are slightly projected downward and support the rays of the ventral lobe of the caudal fin. They are separated from the other hypurals by a small gap or hiatus. Ural 2 joins at least two additional hypurals. Hypurals 3 and 4 are also rectangular; the former is slightly larger than hypural 2. At least 19 principal fin rays are present; in the dorsal lobe, the most dorsal is unbranched and the rest are branched whereas in the ventral lobe there are nine branched and one unbranched rays. There are two and at least five anterior procurent fin rays in the dorsal and ventral caudal fin lobes, respectively.

Scutes: there is a continuous row of 42 scutes placed along the flank of the body, from the back of the posttemporal bone to the caudal fin peduncle (Figure 2). Apparently there were no other scales or scutes covering other areas of the body. The scutes are rectangular structures with rounded edges, deeper than long, having a slight inflection forward in the middle and in their dorsal portions. The lateral line canal runs along the whole body throughout the middle inflections of the scutes (Figure 7). In the most complete and larger scutes, the ratio between their major and secondary axes varies between 5 and 6 (Figure 8). These axes are defined here as perpendicular lines along the scute body; the major axis is projected along the top and bottom midpoints, whereas the secondary axis is a line projected over the lateral canal path (Figure 7). Although the scutes are of a regular size throughout the anterior two-thirds of the trunk, between the occiput and anal fin, beyond this region they get gradually smaller (Figure 2). The scutes overlap each other, the thin rear of one covering the thickened anterior edge of the subsequent one. These scutes are completely ornamented with tubercles and ridges resembling those of the posttemporal and supracleithrum bones. The ridges and tubercles are aligned downward, along the thickened anterior edge and in the lower third of the scutes. Behind and above these regions, they are arranged horizontally (Figure 7).

DISCUSSION AND CONCLUDING REMARKS

Goody (1969, p. 178) considered the family Prionolepididae and the genus Prionolepis to involve two species: the type species Prionolepis angustus and P. cataphractus. In the present paper, the second species is located in its own genus Aspidopleurus together with the new species A. kickapoo sp. nov. Therefore, since P. angustus is known by only some scutes (Figure 9) and the genus Prionolepis and family Prionolepididae were entirely diagnosed based on the anatomical characters of A. cataphractus, such diagnoses are applicable to Aspidopleurus, and the new family name, Aspidopleuridae, replacing Prionolepididae. Actually, the phylogenetic position of P. angustus is uncertain because its scarce fossil record does not present enough anatomical features to support its undoubted inclusion as a member of the Aspidorhynchiformes or Aulopiformes.

The inclusion of Aspidopleurus kickapoo sp. nov. in the genus Aspidopleurus, together with the type species A. cataphractus, is strongly justified. These two species share common anatomical details except for some meristic features of unpaired fins, scales, and vertebrae (see Table 2). The dorsal fin of A. cataphractus involves 18 rays and represents about 16.7% of the SL; its anal fin includes 14 rays and extends along 9.9% of the SL. In contrast, the unpaired fins of A. kickapoo sp. nov. are shorter and have less rays; the dorsal and anal fin lengths are 14.1% and 6.25% of the SL, respectively, and both only includes 11 rays (Figures 4-5). Additionally, A. cataphractus shows a scute series of 45 along the whole trunk flank whereas the new species has only 42. Although in both species there are a total of 45 vertebrae, the abdominal vertebrae are 24 in A. cataphractus and 22 in A. kickapoo sp. nov.

In Aspidopleurus cataphractus the trunk is deeper than in A. kickapoo sp. nov. The MBd of A. cataphractus is 13.2% of SL whereas in A. kickapoo it is just 10.8% (Table 2). Although the measurements of A. kickapoo sp. nov., could be slightly altered by the body compression, as is evident by the disarticulation of some vertebrae (Figure 2), the specific variation in the body proportion is correlated with the presence of deeper scales in A. cataphractus (Figure 8).

In Aspidopleurus and Prionolepis the scutes are rectangular structures with rounded edges, always deeper than long. In Aspidopleurus the size of the scutes varies along the body (Figures 2-7), and those of the first two-thirds of the trunk are the deepest (a complete scute series is unknown in Prionolepis). In Aspidopleurus the scutes are inclined along the body, forming an angle with the longitudinal axis of the body (and the vertebral column); therefore, it is difficult to determine the height-length ratio when they are isolated, as is the case in the holotype of Prionolepis angustus (Figure 9), or displaced as occurs in A. cataphractus and A. kickapoo sp. nov. (Figure 2). This is probably the reason behind the size difference (expressed as depth-length ratios) of the scutes in A. cataphractus reported by other authors. Woodward (1901) and Goody (1969) reported this proportion as 5 and 3 respectively. Unfortunately none of these authors described the criteria used to determine the proportions of the scutes in Aspidopleurus and Prionolepis. Therefore, in this paper, the scute ratio (sr) is considered to be the proportion between its major and secondary axes (ma and sa), as is illustrated in Figure 8. In Prionolepis angustus, A. cataphractus and A. kickapoo sp. nov. the scute ratio of the larger scutes (located in the anterior two-thirds of the trunk) range from 10-10.5, 6-7 and 5-6, respectively, which means that the depth of the scutes decreases in these species following the same order.

When Woodward (1898, p. 411) reviewed the fossil fishes from Lebanon housed in the Edinburgh Museum of Science and Art, he identified some characteristics of Prionolepis angustus in a small specimen of Aspidopleurus cataphractus, previously referred to Engraulis tenuis by Davis (1887). This author recognized the possible synonymy of these fishes when he wrote that this small fish might represent “a small example of Prionolepis (or Aspidopleurus)”. Two years later,
Woodward (1901, p. 230-231) formally published this generic synonymy, keeping the name Prionolepis and keeping both species mainly because the proportions of their scutes are different (compare Figures 7-8). Although he also included the species Apatopelus laniatus (Davis, 1887) in Prionolepis, later Goody (1969, p. 30) reinstated it in its own genus.

Today, Prionolepis angustus is a valid species known only from a few and poorly preserved scutes. This fact imposes a taxonomic name that is subject to the rules of the ICZN (International Commission on Zoological Nomenclature, 1999), and also represents the morphological unit subject to the exercise of comparative anatomy required for the establishment of possible new species. As noted in the introduction of the present paper, the recent discovery of Belonostomus lamarquensis, which bears lateral scutes with the pattern described for P. angustus (Figure 9), raises the possibility that P. angustus could be a close relative to B. lamarquensis or may represent a member of the order Aspidorhynchiformes as firstly noted by Egerton (in Dixon, 1850).

The scales described as Prionolepis angustus and those found in Belonostomus lamarquensis are very similar (Figure 9). In both species the scales show a “pectinate general shape”, are subrectangular, dorsoventrally elongated, and have two sections: a posterior section with regular, closely spaced parallel ridges forming a deeply undulated or serrated rear; and a smooth, thicker anterior section, with a vertical groove. Although such a description matches with the illustration of the scutes in Aspidopleurus cataphractus published by Goody (1969, fig. 85), in fact A. cataphractus and A. kickapoo sp. nov. have scales with common characteristics (Figure 8), where the posterior border is not pectinated and the lateral external surface is totally covered with abundant tubercles, which in the posterior dorsal section are horizontally ordered. Besides, according to Egerton (in Dixon, 1850), the scutes of P. angustus have “the perforation of the lateral line…near to their upper extremities”; on the contrary, in A. cataphractus and A. kickapoo sp. nov., the canal (or perforation) for the lateral line is near and above the middle of the scales (Figure 7).

Today, it is currently impossible to develop a comparative analysis including Prionolepis angustus because this species is known only by a few scales. Since the present context shows that the scales of this species are significantly different from those observed in A. cataphractus and A. kickapoo sp. nov., it is proposed here to distinguish these genera, keeping both species of Aspidopleurus in the family Aspidopleuridae. Although the scutes of Prionolepis angustus are very similar to those found in Belonostomus lamarquensis, assessment of the taxonomic affinities of P. angustus requires additional and more complete material, as well as a more accurate description.

Aspidopleurus cataphractus has been considered as a member of different suprageneric taxa related to Enchodus Agassiz, 1835. Woodward (1901) believed that it was a member of the family Enchodontidae. Goody (1969, p. 240, fig. 100) placed this species (which at that time was considered to be in the genus Prionolepis) in the family Prionolepididae, as a group of the suborder Cimolichthyoidae, order Salmoniformes. Later Rosen (1973) erected the order Aulopiformes, including Prionolepididae into the suborder Alepisaurioidei. Although later the same author (Rosen, 1985) assumed the Aulopiformes to be a non-natural group, Baldwin & Johnson (1996), Sato & Nakabo (2002) and Davis (2010) found that the extant aulopiforms represent a natural group. Other authors have attempted to recognize the phylogenetic relationships of fossil Aulopiformes. Nelson (1994) placed all of them in the suborder Enchodontoidae, divided into four superfamilies: Enchodontidae, Halecoidea, Ichthyotringoidea and Cimolichthyoidae (comprising Prionolepididae and Aspidopleurus cataphractus). More recently, Fielitz (1999) suggested that the fossil and extant alepisaurioids constitute their own order, the Alepisauriformes, that includes three superfamilies: Scopalarchoidea, Paracephaloidea and Alepisaurioidae (including A. cataphractus). Nelson (2006) considered that these fishes are naturally organized into three suborders: Halecoidei, Ichthyotringoidei and Alepisaurioidae (including A. cataphractus in the family Enchodontidae). Based on a comprehensive analysis of the Enchodontoidei sensu Nelson (1994), Silva (2007, p. 82-87) suggested that Prionolepis (including P. angustus and A. cataphractus) is an incertae sedis aulopiform genus. More recently, Silva & Gallo (2011, fig. 1) recognized the non-natural phylogenetic condition of the suborder Enchodontoidae, but they found that this genus is part of the enchodontid lineage because it constitutes the sister group of the clade formed by their family Enchodontidae and Eurypholis+Surorhamphus.

In this work, Aspidopleurus is located in its own family. Since A. kickapoo sp. nov. is very similar to the best known and most complete species, A. cataphractus, this finding does not have implications for the systematics and relationships of this genus. Nevertheless, it complements the data concerning paleobiogeography and diversity of this genus. On the one hand and contrary to Goody (1969, p. 240), who thought that Prionolepis (including P. angustus and A. cataphractus) “continued into the Turonian without diversification”, A. kickapoo sp. nov. represents a Turonian species differentiable from the Cenomanian A. cataphractus. On the other hand, A. kickapoo sp. nov. expands longitudinal distribution known for this genus along the Tethys Sea Domain from Middle East and Europe to the east of Mexico in the western Tethys.

Aspidopleurus kickapoo sp. nov. is just another species added to other Cretaceous fishes from an increasing number of localities in Mexico, which today show an enhanced picture on fish diversity in the western Tethys Sea Domain and the opening of the North American Western Interior Seaway (e.g. Blanco-Piñón, 2003; Blanco-Piñón et al., 2004; Blanco & Alvarado-Ortega, 2005; Alvarado-Ortega et al., 2006a,b,c, 2009; Alvarado-Ortega & Porras-Múzquiz, 2009b; Giersch et al., 2008, 2010; Fielitz & González-Rodríguez, 2010).

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