On the occurrence of *Vinctifer ferrusquiai* sp. nov. (Actinopterygii, Aspidorhynchiformes) in the Kimmeridgian (Late Jurassic) deposits near Tlaxiaco, Oaxaca, southern Mexico

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ABSTRACT

Vinctifer ferrusquiai sp. nov. is described in this paper. This aspidorhynchid fish was found in Kimmeridgian marine deposits of the Sabinal Formation, exposed in the Llano Yosobé, near Tlaxiaco, Oaxaca, Mexico. The single specimen of this species shows enough diagnostic characters to be included in the order Aspidorhynchiformes, the family Aspidorhynchidae, and the genus *Vinctifer*. These characters include an elongate rostrum consisting of the premaxillae fused and anteriorly elongated, forming a tube-like, as well as an preopercular sensory canal located close to the posterior edge of the preopercle. Other features are the lack of premaxilla, the development of a wide posterior expansion of the maxilla, and a stout triangular preopercle. A unique combination of characters supports the erection of this new species, whose ganoine on dermal bones of the head are strongly ornamented with tubercles and ridges, and the flank scales are entirely smooth and not serrated. This Jurassic record is the first indubitable pre-Cretaceous finding of *Vinctifer,* the oldest into the Hispanic Corridor, and the oldest in North America.

Key words: Aspidorhynchiformes; Aspidorhynchidae; *Vinctifer*; Kimmeridgian; Mexico.

RESUMEN

El pez Vinctifer ferrusquiai sp. nov. se describe en este trabajo. Este aspidorrínquido proviene de los depósitos marinos de la Formación Sabinal del Kimmeridgiano, expuestos en el Llano Yosobé, cerca de Tlaxiaco, Oaxaca, México. El único ejemplar de esta especie muestra suficientes caracteres para ser incluido en el orden Aspidorhynchiformes, en la familia Aspidorhynchidae y en el género Vinctifer. Los rasgos más distintivos de esta especie son: un rostro alargado, formado por la fusión anterior de las premaxilas, que se extienden formando un tubo, así como el canal sensorial preopercular localizado cerca del borde posterior del preopérculo; otros rasgos importantes son la ausencia del hueso premaxilar, la expansión posterior del maxilar y un preopérculo triangular. Una combinación única de caracteres apoya la erección de esta nueva especie, cuya ganoína en los huesos dérmicos de la cabeza está fuertemente orna-mentada con tubérculos y crestas, mientras que sus escamas laterales son completamente lisas y no dentadas. Este primer hallazgo de Vinctifer del Jurásico, indudablemente, es el más antiguo dentro de los dominios del Corredor Hispano y el más antiguo de América del Norte.

Palabras clave: Aspidorhynchiformes; Aspidorhynchidae; Vinctifer; Kimmeridgiano, México.

INTRODUCTION

The Llano Yosobé is a recently discovered, paleontological locality near Tlaxiaco town, Oaxaca, southern Mexico (Alvarado-Ortega *et al*., 2014) (Figure 1). The fossil fish, objective of this, study was found in the Sabinal Formation. The bottom of this Kimmeridgian (Late Jurassic) unit consists of interbedded siltstones, dark bituminous shales bearing nodules, and limestones. This sequence rests above the Oxfordian-Early Kimmeridgian marly limestone informally named as the "*Caliza con Cidaris*" (*i.e.* Buitrón, 1970).

Both units are interpreted as shallow marine sequences deposited in the Tlaxiaco basin, which was a depocenter located in the mexican part of the Hispanic Corridor. Therefore, the Llano Yosobé fossil record is important for the understanding of the Jurassic marine biotic interchange between the Eastern-European Tethys Sea Domain and the Western-American Paleopacific Ocean, which had contact through the Hispanic Corridor.

Up to now, the fossil assemblage recovered in the Llano Yosobé includes carbonaceous plant remains, invertebrates, and vertebrates preserved within nodules and on the surfaces of the stratification planes. These vertebrates include hybodontid sharks (teeth and fin spines of *Planohybodus* Rees and Underwood, 2008) actinopterygian fishes (numerous remains of *Gyrodus* Agassiz, 1833; scales attributable to *Scheenstia* López-Arbarello and Sferco, 2011; *Pleuropholis cisnerosorum* Alvarado-Ortega and Brito, 2016; *Nhanulepisosteus mexicanus* Brito, Alvarado-Ortega, Meunier, 2017; and numerous remains of undetermined taxa), as well as many marine reptiles as ophthalmosaurid ichthyosaurs, pliosaurids, metriorhynchid crocodylomorphs, and turtles (also see Barrientos-Lara *et al*., 2015; Alvarado-Ortega and Brito, 2016; Brito *et al*., 2017; López-Conde *et*
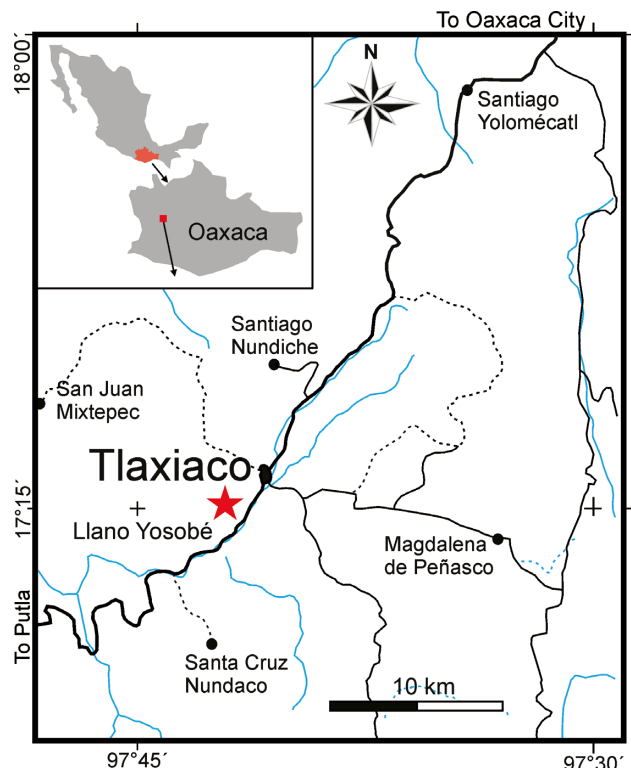
Figure 1. Map of Tlaxiaco showing the position of the Llano Yosobé (modified from Barrientos-Lara *et al.*, 2015, fig. 1).

al., 2017; among others). The rich record of invertebrates from this site includes three taxa previously described by Felix (1891): *Myophorella sologureni*, *Astarte microphyes*, and *Gryphaea mexicana*, as well as *Exogyra*-like ostreoids, undetermined bivalves, ostracods, diverse ammonites, and aptychi that today are the objectives of taxonomical and biostratigraphical studies in progress.

Vinctifer Jordan, 1919, is part of the order Aspidorhynchiformes and its single family, Aspidorhynchidae. This is an extinct, highly specialized, basal teleostean group known from the Middle Jurassic to Late Cretaceous in shallow epicontinental marine deposits throughout America, Europe, Australia, Africa, Antarctica, and Middle East (Arratia, 1999; Brito, 1997; Brito and Ebert, 2009; López-Arbarello and Schröder, 2013; Maisey, 1991; Patterson, 1973, 1977; Patterson y Rosen, 1977; among others). Apart from *Vinctifer*, other five nominal genera constitute the family Aspidorhynchidae; these are: *Aspidorhynchus* Agassiz, 1833, and *Belonostomus* Agassiz, 1843, that include numerous species, as well as three monospecific taxa: *Richmondichthys sweeti* (Etheridge and Woodward, 1892), *Pseudovinctifer chilensis* Arratia, 2015, and *Jonoichthys challwa* Gouiric-Cavalli, 2015. A first classification of *Richmondichthys sweeti* was thought as a representative of *Aspidorhynchus*, then as a *Vinctifer* and even as a *Belonostomus* (Brito, 1997; Etheridge, 1872; Etheridge y Woodward, 1892; Jack and Etheridge 1872; Maisey, 1993; and among others); recently, Bartholomai (2004) re-described this and allocated it into its own genus.

Previously, *Vinctifer* comprised two nominal species from Early Cretaceous deposits in northeastern Brazil (Brito, 1997). The type species, *V. comptoni* (Agassiz, 1841), is known from Aptian-Albian deposits of the Santana (Araripe Basin) and Muribeca (Sergipe Basin) formations. The second species, *V. longirostris* Santos, 1990, is from the Aptian Marizal Formation (Tucano Basin) and the lower levels of the Santana Formation (Araripe Basin). Additionally, this genus

has been collected in other Jurassic and Cretaceous sites, including numerous localities in Brazil belonging to the Barremian outcrops of the Missão Velha Formation, the Aptian-Albian Codó Formation (Parnaiba Basin), and the Aptian Riachuelo Formation. Specimens belonging to *Vinctifer* also came from the Tithonian Nordenskjöld Formation (= Ameghino Formation) in Antarctica (Graham Land, Antarctic Peninsula), the Aptian Paja Formation in Colombia (near Villa de Leiva), the Aptian Apon Formation in Venezuela, the Early Cretaceous deposits of western Africa (Equatorial Guinea), as well as the Albian Tlayúa Formation in Mexico (see Alvarado-Ortega *et al.*, 2006; Applegate 1996; Arratia *et al.*, 2004; Brito, 1988, 1992, 1997; Brito *et al.* 1994; Brito and Yabumoto, 2011; Maisey, 1991, 2000; Moody and Maisey, 1994; Richther and Thomson, 1989; Schultze and Stöhr, 1996; Taverne, 1969; among others).

The aim of this paper is to describe and determine the taxonomic identity of the specimen IGM 8873, recovered from a nodule of Kimmeridgian deposits of the Llano Yosobé locality. This fossil fish represents the first, unquestionable record of the genus *Vinctifer* in Jurassic deposits.

MATERIALS AND METHODS

Institutional abbreviations

IGM, Colección Nacional de Paleontología (Instituto de Geología, Universidad Nacional Autónoma de México). CME, Colección de Material Extranjero, a subcolecction into IGM. UERJ PMB, Coleção de Paleozoologia (Universidade do Estado do Rio de Janeiro, Brazil). DNPM. DGM, Departamento Nacional de Producao Mineral.

Preparation methods abbreviations

The specimen studied here was recovered within a nodule from the Llano Yosobé site. It was prepared following different mechanical procedures. An air-powered micro-chisel was used to remove the superficial rock of the nodule, away from the fossil. Different needles and scrapers allowed the removal of sediments from the surface and near the fossil. The fossil was hardened with a plexigum solution in ethyl acetate and, when necessary, cyanoacrylate was used to bond detached fossil elements.

Anatomical nomenclature and abbreviations

The preserved osteological elements of the fossil described here were named following the nomenclature used in recent works for Aspidorhynchiformes (*i.e.*, Brito, 1997; Moody and Maisey, 1994; Taverne, 1969; among others). In the same way, the abbreviations of these elements used in the figures of this work are based on similar works (Bartholomai, 2004; Brito, 1988, 1992; Gouiric-Cavalli 2015; Maisey, 1991, 2000).

Comparative materials

Aspidorhynchus acutirostris Blainville, 1818: CME 677, skull and fragments of the jaws from the Tithonian lithographic limestones of Solnhofen, Germany. V*inctifer* sp.: CME 902 and CME 903 (five parts), scales from Aptian sediments of the Romualdo Formation, Brazil. *Vinctifer comptoni* (Agassiz, 1841): UERJ PMB 1, 2, 3, 4, 5, 49, 52, 53, 54, 60, 61, 63, 64, 65, 66, and 80; as well as CME 872; these fossils include fragmentary and almost complete fishes 3-D preserved in nodules from the Aptian-Albian Santana Formation, Brazil. *Vinctifer longirostris* Santos, 1990: DNPN. DGM 538-P, 460-P, 461-P, 462-P, and 463-P; UERJ PMB 74, 75, 76, 77, 78, and 79; these fossils include fragmentary and almost complete fishes preserved as impressions from the Aptian sediments of the Marizal Formation, Brazil.

SYSTEMATIC PALEONTOLOGY

Order ASPIDORHYNCHIFORMES Bleeker, 1859
Family ASPIDORHYNCHIDAE Nicholson and Lydekker, 1889
Genus *VINCTIFER* Jordan, 1919
Vinctifer ferrusquiai sp. nov.
(Figures 2 and 3)

Nomenclatural Act. The new taxonomic name established in this article agrees with the requirements of the International Code of Zoological Nomenclature (ICZN); hence, this nomenclatural act is recorded in ZooBank, the online registration system of the ICZN. The Life Science Identifiers for this publication is also recorded in ZooBank as: urn:lsid:zoobank. org:pub:CD32D020-E5B7-4816-913C-EEE2E067A0D4

Holotype. IGM 8873, fish with part of the head and the anterior part of the trunk preserved and exposing the left and right sides (Figures 2 and 3).

Etymology. The specific name honors our colleague, Dr. Ismael Ferrusquía Villafranca, for his contributions to the knowledge of the geology and paleontology of Oaxaca.

Locality and Age. The Llano Yosobé site, near Tlaxiaco, Oaxaca, southern Mexico; Kimmeridgian marine deposits belonging to the Sabinal Formation (Alvarado-Ortega *et al.*, 2014).

Diagnosis. *Vinctifer* species with an estimated maximum standard length of 261 mm and exhibits a unique combination of characteristics including the enamel of dermal bone of the skull strongly ornamented with tubercles and ridges as in *V. comptoni*; and flank scales smooth and not serrated as in *V. longirostris*.

Description

The specimen was recovered from a nodule. This is somewhat laterally compressed. After the preparation, this exhibits bones of both sides of the orbital and postorbital sections of the head and the anterior part of the trunk (Figures 2 and 3).

According to Brito (1997, p. 688), the body proportions of *Vinctifer* show that the head plus the rostrum is one third of the standard length, and the head without the rostrum is two times longer than high. In IGM 8873, the part of the head (including the opercle) preserved is about 60 mm of length, from the ethmoid region to the posterior opercle rim; the terminal end of the preserved rostrum (maxillae) is 13 mm long; and the head height is close to 37 mm. These data suggest that the head length (without the rostrum) of IGM 8873 was, at least, 87 mm. Therefore, the estimated standard length of this specimen is 261 mm.

Skull. The anterior part of the skull of IGM 8873 is obscured or lost. The preserved part exhibits that the skull roof is almost flat, somewhat laterally compressed, and largely occupied by the frontals, parietals, and dermopterotic bones that are fused to each other (Figure 3). This forms a couple of fronto-parietal-dermopterotic bones that are asymmetrically extended in their middle edge; therefore, their suture is practically harmonic until passing the orbital region and deeply sinuous beyond. Both, fronto-parietals-demopterotic are almost three times longer than wide. Anteriorly, in front of the orbit these bones taper and form a slightly sinuous anterior edge. A small, displaced fragment of bone joint with the anterior edge of the right fronto-parietal-dermopterotic is here tentatively interpreted as a part of the rostral. Posteriorly, these composed bones are partially separated from the anterior edge of the extrascapular bones, which joint with fronto-parietals-dermopterotic just above the middle of the opercle. The supraorbital sensory canal runs all along the lateral edge of the fronto-parietal-demopterotic. The extrascapulars are rectangular, almost twice wider than long. Also, these are medially attached to each other throughout an asymmetrical sinuous suture. Behind these, the pair of postemporal bones are elongated bones with rounded posterior edges (Figure 3).

Bones of the skull roof are covered by ganoine and distinctly ornamented. The anterior third of the fronto-parietals are rather smooth while the posterior part is covered with tubercles as well as sinuous and somewhat reticular longitudinal grooves. The extrascapulars share the same ornamentation with ridges.

Jaws. Only the posterior portion of the bones that are part of both jaws are preserved. Among these, the posterior part of the maxilla is an ovoid, extended, flat, and smooth structure that displays a strongly curved dorsal edge and a slightly curved ventral edge. No teeth or alveoli are preserved in the maxillae. A possible posterior fragment of the right premaxilla is preserved. The anterior tip of the rostrum of this fish is preserved; this consists of the anterior ends of both maxillae that are strongly attached to each other and ornamented with fine longitudinal striae. Unfortunately, the premaxillar bones only show the dorsal surface; hence, the presence or absence of teeth or alveoli in this structure cannot be confirmed (Figure 3).

Below, covered by the maxillae, the terminal parts of the lower jaws are preserved. The angular bears a well-developed articular process that externally is almost totally covered by the retroarticular bone. The articular fossa for the quadrate and symplectic is located below the middle orbit. Although a small fragment of the dentary is observed below the maxilla, this and other lower jaw bones are obscured or lost.
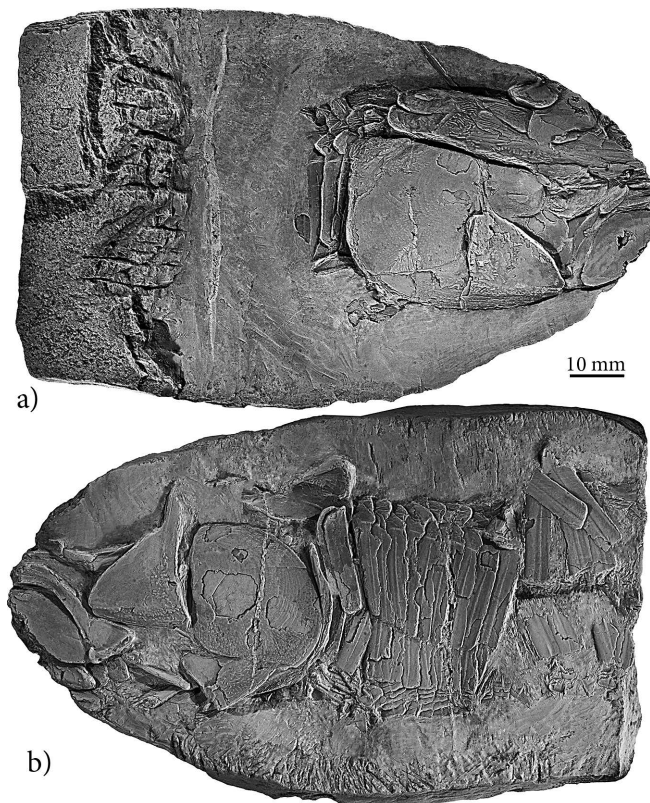

10 mm

a)

b)

Figure 2. IGM 8873, holotype of *Vinctifer ferrusquiai* sp. nov. from the Kimmeridgian deposits of the Llano Yosobé, near Tlaxiaco, Oaxaca, Mexico.

Suspensorium. Bones of this series are partially covered by the postorbital bones (Figures 2 and 3). The quadrate is a triangular structure that lacks the posterior process and bears a stout articular head leaned downwards and forwards. This bone meets the ectopterygoid anterodorsally and the metapterygoid dorsally. The joint between the quadrate and the hyomandibula is obscured. The symplectic bone is a thick-nail like bone, strongly attached to posterior edge of the quadrate. The symplectic is short; its height does not exceed the dorsal edge of the quadrate. Large part of the quadrate bone was lost during the preparation. Symplectic and quadrate bones form part of the articular head of lower jaw and these articulate directly with the articular facet of the lower jaw.

The ectopterygoid is a flat and smooth boomerang shaped bone (Figure 3). Although the anterior end of this bone is lost and both ectopterygoids expose their external surface; some small conical teeth of uniform size is observed below the ventral rim of the right ectopterygoid. The endopterygoid and hyomandibular bones are not exposed. Only part of the metapterygoid is visible below the postorbital bones and joined with the dorsal edge of the quadrate. A possible fragment of the right palatine bone is present in front of the orbit.

Circumorbital bones. Although the circumorbital bones are scattered in around the orbit of both side of IGM 8873; it seems that these bones constitute an enclosed ring of five infraorbitals plus the dermosphenotic, one supraorbital, and two large suborbitals (Figure 3).

The infraorbitals are slender, rectangular, and flat bones. The infraorbital 1, located anteriorly in the series, is the longest; it lies on the ethmoid region of the skull and is leaned upward; its main axis is about three times its minor one. The infraorbitals 2 and 3, located below the middle part of the orbit, are shorter but at least two times longer than high. The infraorbital 4 and 5 are rectangular flat bones bordering the posterior edge of the orbit.

There are two large suborbital bones located behind the posterior infraorbitals; these flat smooth bones cover part of the cheek and the entire postorbital lateral region of the skull. The ventral suborbital is trapezoidal and the dorsal suborbital is rectangular with rounded corners, about 1.2 times longer than high (Figure 3).

One supraorbital and a single dermosphenotic dorsally enclose the orbital ring. Both are long triangular bones directed downward, which are about equal in length, and have rounded corners. These flat smooth bones are approximately three times longer than high and meet to each other above the middle of the orbit. At least one right sclerotic bone is preserved (Figure 3); however, in life this fish must have a couple of symmetric sclerotic bones occupying both eyeballs as it occurs in well preserved specimens of *Vinctifer*.

The infraorbital sensory canal runs near the orbital edge of the infraorbital bones, where it is intensely branched. It seems that this canal also penetrates the dermosphenotic before to meet with the supraorbital canal.

Opercular bones. The opercular series consists of three laminar bones and lacks interopercle (Figure 3). The opercle is the largest element in the series; it is kidney shaped, higher than long, with a straight anterior edge, sinuous ventral edge, and posterior and dorsal edges curved. The ventral region of the opercle is more extended backwards than the dorsal one. Below, the subopercle is present as an inverted isosceles triangle, about two times longer than deep, in which the dorsal edge is equally extended than the opercle.

The preopercle is a roughly triangular bone, equally high as the opercle. Whereas its upper quarter forms a sharp projection, the rest of the bone is shaped like an equilateral triangle in which the anterior edge is convex while the ventral and posterior ones are straight and somewhat sinuous, respectively. The preopercular sensory canal runs along this bone, near to its ventral and posterior edges, forming a posteroventral acute angle. This sensory canal is strongly branched all along its horizontal section and in the ventral half of its vertical section; each of these branches opens in a pore (Figure 3).

Bones of the opercular series are covered with ganoine that is well ornamented with tubercles and ridges (Figures 2 and 3). In the opercle, the surface is almost entirely ornamented with tubercles aligned in concentric lines. The focus of these lines is located just at the beginning of the last quarter of the height of its anterior edge, apparently opposite to the articular facet exposed on the inner surface of this bone. The tubercles are progressively greater toward the edges of this bone; they are ankylosed near to the ventral edge forming short and sinuous ridges. The subopercle is covered with sinuous ridges of variable size and randomly arranged. Although, most of the preopercle surface is smooth; relative few small tubercles are between the preopercular sensory canal and ventral and posterior edges. Also, a small surface located in front of the ventral half of horizontal section of preopercular sensory canal is ornamented with large tubercles and sinuous short ridges.

Branchial arch. Disarticulated and scattered elements of the branchial arch on the left are preserved in the left side of the specimen. These bear numerous, elongated thread-like gill filaments and robust, elongated gill rakers are also visible (Figure 3).

Pectoral and pelvic fins. Only the cleithrum and supracleithrum elements are perseverved in the pectoral girdle. Other bones of this girdle are not exposed. The pectoral fin of this fish comprises at least five rays, whose bases are flat and wide. The terminal ends of these rays are obscured (Figure 3).

In lateral view, the cleithrum seems an inverted "L" structure, almost uniformly thin throughout (Figure 3). The horizontal limb of this bone is almost as long as the vertical limb height and the joint of its limbs form rounded posterior corner. The terminal third of the vertical limb of this bone is thinner than the rest of the bone. The entire surface of the horizontal limb and the lower half of the vertical limb are strongly ornamented with long sinuous crests that in some cases are fused forming a net.

The supracleithrum is a high triangular bone, noticeably wider than the dorsal end of the cleithrum (Figure 3); it covers the laterally surface of the body behind the opercle and slopes dorsally covering the occiput. In IGM 8873 the left supracleithrum bone is dislocated, rotated, and exhibit its internal surface where it is clear that this bone encloses the sensitive canal of the lateral line. The right supracleithrum is in life position in this fish; the ganoine on the surface of this bone is entirely ornamented with tubercles and sinuous ridges.

Scales. The part of the trunk preserved in IGM 8873 is entirely covered of thick ganoine scales arranged in longitudinal rows (Figures 2 and 3). The dorsal region of the trunk is covered with a row of middle dorsal scales associated with two rows of dorsal scales placed laterally on each side of the trunk. Additionally, there are two rows of flank scales covering the lateral sides of the trunk and at least five rows of ventral scales on the abdominal region. At least the flank and ventral scales have a dorsal middle large spine-like articular process and a small central depression in the ventral one; therefore, the dorsal process of one scale inserts within the ventral depression of the immediate superior scale.

The general shape of scales of the middle dorsal row is not clear because they are amply overlapping; however, these seems to be elongated and ovoid. Contrary, the shape of scales of the associated dorsal rows is elongated and rectangular. The ganoine of dorsal scales is strongly ornamented with remarkable tubercles and sinuous longitudinal ridges (Figure 3).
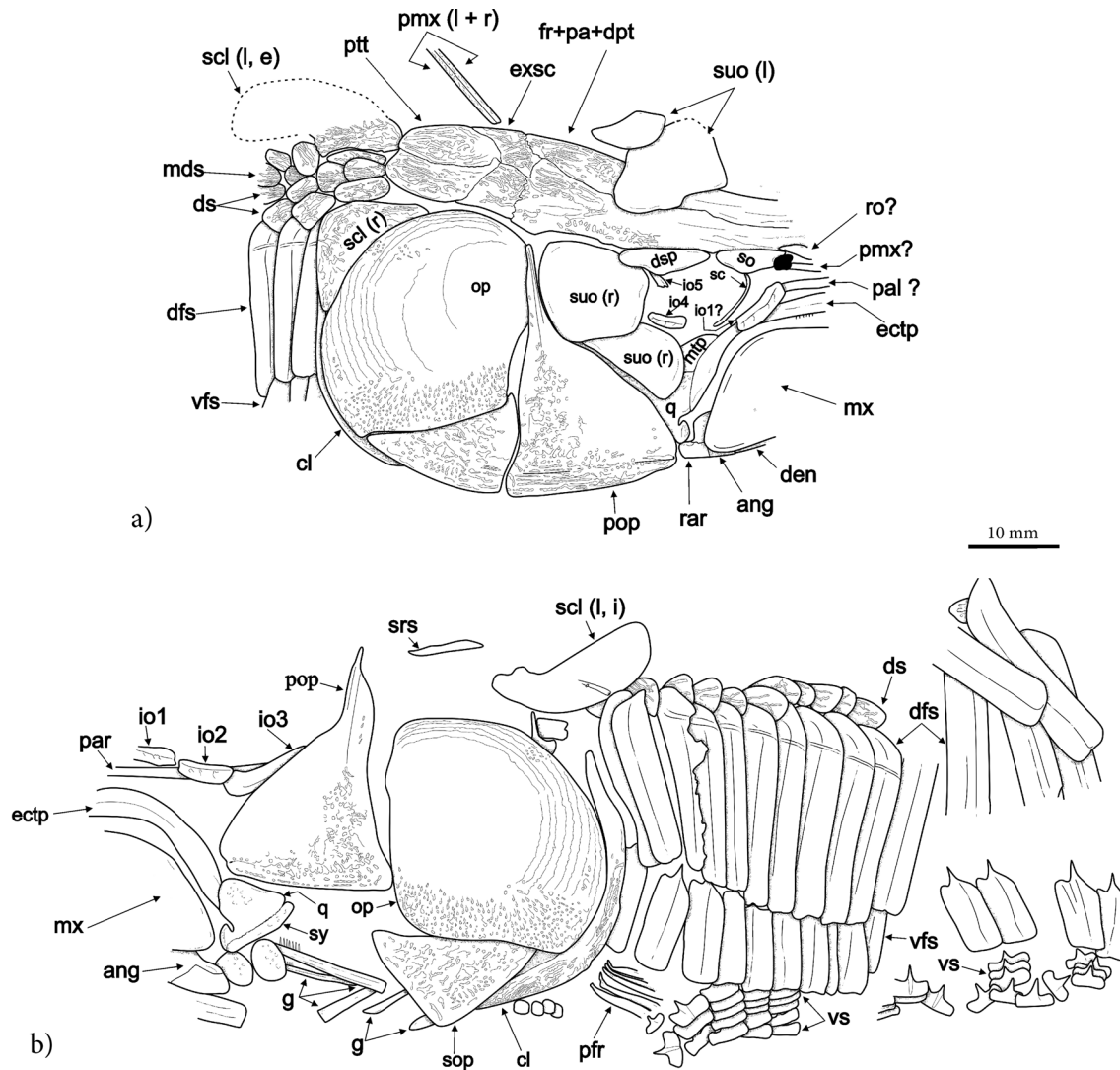
Figure 3. Idealized line drawing of IGM 8873, holotype of *Vinctifer ferrusquiai* sp. nov. from the Kimmeridgian deposits of the Llano Yosobé, near Tlaxiaco, Oaxaca, Mexico (based on Figure 2). Abbreviations: ang, angular; cl, cleithrum; den, dentary; dfs, dorsal flank scale; dms, dorsal middle scale; ds, dorsal scale; dsp, dermosphenotic; ectp, ectopterygoid; exsc, extrascapular; fr+pa+dpt, fronto-parietal-dermopterotic (fusion of frontal, parietal, and demopterotic bones); g, gill elements; io 1-5, infraorbital; mtp, metapterygoid; mx, maxilla; op, opercle; pal, palatine; par, parasphenoid; pfr, pectoral fin ray; pmx, premaxilla; pmx (l + r), rostrum (including the terminal ends of both maxillae); pop, preopercle; ptt, posttemporal; q, quadrate; sc, sclerotic; scl, supracleitrum; sop, subopercle; so, supraorbital; suo, suborbital; rar, retroarticular; ro, rostral; srs, skull roof section; sy, symplectic; vfs, ventral flank scale; vs, ventral scale. Abbreviations enclosed in parentheses: e, external surface; i, internal surface; l, left side; r, right side.

The scales of both flank rows are flat, rectangular plates, higher than long. The scales on the dorsal flank row are hypertrophied; in these, the height is between four and five times the length. The upper sixth part of each dorsal flank scale tapers dorsally forming a triangular wing tilted forward, which is also leaned inward participating in the covering of the dorsal trunk region. Contrary, the scales on the ventral flank row are also remarkable: these are equally long but about almost half high than those placed immediately above (Figures 2 and 3).

In both flank scales, the edges are practically harmonious, straight, and without serration. In these scales, the ganoine is practically smooth except for some inconspicuous tubercles present in the posterior half on the inward wing of the dorsal flank scales, as well as, for the middle straight ridge that runs from top to bottom in dorsal and ventral flank scales. This middle straight ridge represents the posterior limit of the overlapping of the flank scales. In opposite position to this middle straight ridge, the internal surface of flank scales, shows a shallow and wide groove, in which the little thickened anterior edge of the subsequent posterior scale is accommodated (Figures 2 and 3).

In IGM 8873, at least five rows of ventral scales are covering the abdominal region of the trunk (Figure 3). Overall, these are rectangular, about two times longer than high, and its dorsal edge bears a prominent spiny dorsal process. These scales are almost entirely smooth, except for a small keel at the base of the dorsal process.

DISCUSSION

Since the family Aspidorhynchidae is the single member of the order Aspidorhynchiformes, the diagnosis of this family published by Brito (1997, p. 686) is transferable to this order. This author pointed out that the members of the family share four unambiguous synapomorphies, including: 1) the premaxillae are fused and anteriorly

elongated forming a tube-like rostrum; 2) the lower jaw has a predentary as an accessory bone attached to symphysial edge of both dentaries; 3) the neurocranium occipital process is formed by the intercalar and autopterotic bones; and 4) the propercle sensory canal is located close to the posterior edge of the preopercle. Brito (1997) also recognized a peculiar combination of other characteristics (homoplasies) that support the monophyly of this family, including (continuing with the numbering): 5) absence of the interopercle bone; 6) the remote back position of the dorsal and anal fins; 7) the small size of caudal fin; 8) the presence of at least four hypurals (two below of the caudal diastema); 9) three pairs of uroneurals in caudal skeleton; 10) the skull bones covered with ganoine; and 11) the presence of rows of rectangular high hypertrophied flank scales covering the lateral sides of the trunk. Despite the fragmentary and incomplete condition, *Vinctifer ferrusquiai* sp. nov. from the Jurassic of Mexico undoubtedly represents an aspidorhynchid fish because it has the synapomorphies 1 and 4, was well as the homoplasies 5, 10, and 11 (Figures 3 and 4).

The genera currently located within Aspidorhynchidae are more than those considered in the last comprehensive study of this family, performed by Brito (1997). Table 1 was constructed based on data published by different authors (Arratia, 1999, 2015; Bartholomai, 2004; Brito, 1988, 1992, 1997; Brito *et al*. 1994; Brito and Ebert, 2009; Brito and Yabumoto, 2011; Gouiric-Cavalli 2015; Maisey, 1991; Moody and Maisey, 1994; Richter and Thomson, 1989; Patterson, 1973, 1977; Patterson and Rosen,1977; Shultze and Störh, 1996; and Taverne, 1969); this table summarizes and highlights the characteristics shared by *Vinctifer ferrusquiai* sp. nov. and different aspidorhynchid genera. Unfortunately, *V. ferrusquiai* does not show large part of skull bones considered in this comparative table; particularly, bones of the anterior region of the head are unknown in this fish. Therefore, it is not possible to analyze the possible affinities of this new species based on the peculiarities of the maxilla, premaxilla, predentary, and parasphenoid bones (including their size and whether they bear teeth), even when these bones have valuable taxonomic information to recognize the different aspidorhynchid genera.

Pseudovinctifer is the most poorly known aspidorhynchid fish; two isolated and extremely fragmented specimens represent this genus (one consists of a lower jaw and the other exhibits the opercle and the cleithra (Arratia, 2015). *Vinctifer ferrusquiai* sp. nov. displays a kidney-like opercle that is equally long than high, a condition shared by other aspidorhynchid except *Pseudovinctifer,* whose opercle is higher than long. *Aspidorhynchus* differs from other aspidorhynchids, including *V. ferrusquiai*, because the bones of its head are not fused; in other aspidorinchids there are fusions between different skull bones. *Vinctifer ferrusquiai* shows the fusion between the parietals, frontals and dermopterotic bones.

Considering the rest of aspidorhynchids (Table 1), *Richmondichthys* and *Vinctifer* belong to a set that differ from other aspidorhynchids because the maxilla is posteriorly expanded, the premaxilla is absent, and the preopercle is triangular shaped. *Vinctifer ferrusquiai* sp. nov. exhibits all these characteristics supporting its inclusion into this set. In an opposite way, *Aspidorhynchus, Belonostomus*, and *Jonoichthys* have a thin elongated maxilla associated to a single supramaxilla as well as an preopercle showing the typical inverted-L shape.

Regarding the Richmondichthys-Vinctifer group, *Vinctifer ferrusquiai* is considered as a new species of *Vinctifer* because it shears at least two characteristics with the other nominal species of this genus. The dorsal flank scales are five to six times higher than long and the infraorbital bones are elongated rectangular bones. Infraorbital bones of *Richmondichthys* are unusually expanded being higher than long and its dorsal flank scales are considerably higher (6 to 8 times higher than long) (see Bartholomai, 2004, figs. 2 and 3; Gouiric-Cavalli, 2015, fig. 8).

According to data published by Brito (1997), the differences between the two valid nominal species of *Vinctifer* previously known, *V. comptoni* and *V. longirostris*, are minimal but significant (Figure 4). On the one hand, in *V. comptoni* the anterior portion of its premaxilla that forms the rostrum, placed in front of the lower jaw, approximately represents one third of the total length of the skull while the predentary bears very small teeth, is slightly longer than high, and represents one-fifth of the length of the lower jaw (= dentalosplenial in Brito, 1997). Also, in *V. comptoni* the enamel on dermal bones of head and scales is ornamented with sinuous ridges and tubercles visible to the naked eye. Particularly, on the flank scales these ornaments form longitudinal lines ending in the tip of the serration throughout the posterior edge. In a different way, *V. longirostris* exhibits comparative long predentary and maxilla bones as well as dermal bones of the head and scales without ornaments. In *V. longirostris,* the anterior portion of the premaxilla corresponds to half of the total length of the skull; its predentary bears comparative stout teeth; it is two and a half times longer than high, and is one third of the lower jaw length; the enamel on dermal bones and
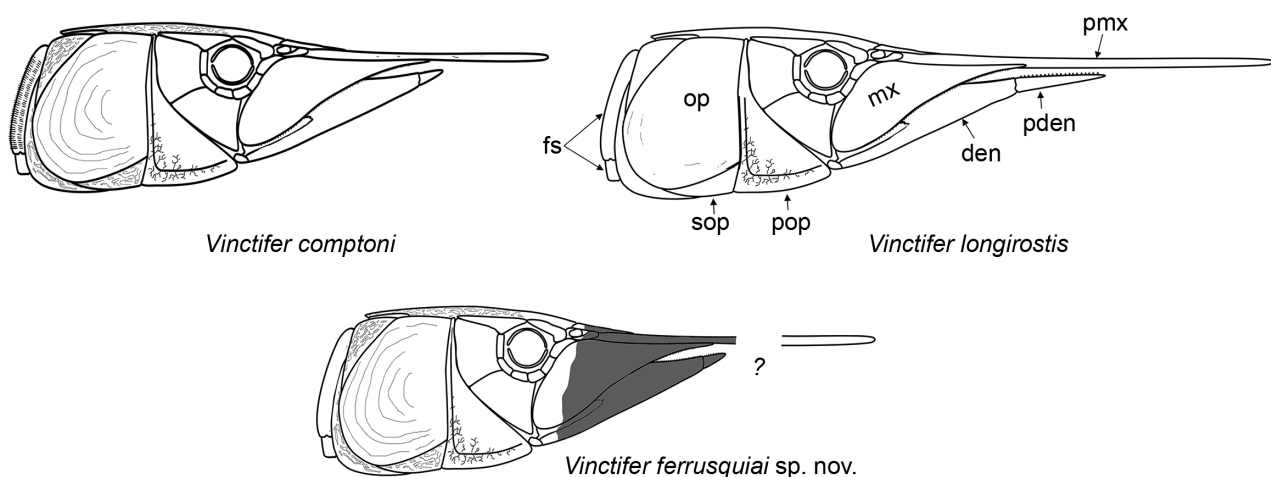

Figure 4. Heads of the three species of *Vinctifer* highlighting the differences in the proportions of predentary and premaxillae bones, as well as in the ganoine ornaments on flank scales and dermal head bones. Abbreviations: den, dentary; fs, flank scale; mx, maxilla; op, opercle; pden, predentary; pmx, premaxilla; pop, preopercle; sop, subopercle. Gray area covers that part of the head of *Vinctifer ferrusquiai* that is unknown.

Table 1. Comparative characteristics of genera of the family Aspidorhynchidae contrasted with the specimen IGM 8873 (shared characters within the gay box).

Characteristics	*Richmondichthys*	*Vinctifer*	IGM 8873	*Jonoichthys*	*Belonostomus*	*Aspidorhynchus*	*Pseudovictifer*
Predentary teeth		Yes					No
Premaxillary teeth	No		?			Yes	
Parasphenoid teeth							
Maxillary teeth	No	Yes					?
Premaxilla	Short	Long				Long	
Predentary							
Flank scales	Ornamented		Smooth			Ornamented	
Infraorbital bones	Expanded	Rectangular, longer than high					
Opercle	As longer than high						Higher
Neurocraneoum	Fused					Unfused	?
Maxilla	Expanded			Thin			
Preopercle	Triangular			Inverted L-shaped			
Supramaxilla	No			?		Yes	
Height/length of dorsal flak scales	6-8	5-6		≈ 4	2-3	4-5	?

scales has no ornaments; and finally, the flank scales are not serrated.

Although the only specimen of *Vinctifer ferrusquiai* sp. nov. lacks a significant portion of the head, between the nasal region and the terminal end of the rostrum (= anterior extension of maxillae), so neither predentary bone nor the real size of the rostrum are known (Figure 4); this fish presents a unique combination of characteristics that support its inclusion in a new species. The ganoine on dermal bones of the head is intensely ornamented with ridges and tubercles as in *V. comptoni* whereas that on the flank scales is smooth and so its posterior edge is harmonious, straight, and not serrated as occurs in *V. longirostris*.

In *Vinctifer comptoni*, the ganoine on the dermal bones of the head is always well ornamented being an invariable character independent of the body size of the organisms. The same happens with the smooth appearance of the ganoine observed in the same bones of individuals of *V. longirostris*. This observation suggests that the presence or absence of these ornamentations in the head is a persistent character throughout the ontogeny of *Vinctifer*; hence, the ornamentation of the head of *V. ferrusquiai* is a significant character that separates this Mexican species from *V. longirostris*.

To verify the validity of the smooth and non-serrated condition of the flank scales of *V. ferrusquiai*, we compared this feature with the ornamentation of the flank scales of smaller and larger specimens of *V. comptoni* and *V. longirostris*. We noted that in *V. longirostris* the scales are smooth and not serrated, independently of the size of individuals. As for *V. comptoni*, both ornamentations became more conspicuous in larger organisms. Even in specimens of *V. comptoni* smaller than IGM 8873 (holotype of *V. ferrusquiai* with an estimated standard length of 261 mm), the flank scales have weak longitudinal ridges; such ornamentations result notorious and significantly different from those smooth flank scales observed in *V. longirostris* and *V. ferrusquiai*.

Summarizing, *Vinctifer ferrusquiai* sp. nov. is a new species distinguishable from the other two nominal species of this genus because it

is the only one that combines three characters: the dermal bones of the head are intensely ornamented and the flank scales are smooth and not serrated. It should be noted that a good number of nodules from the Llano Yosobé locality, are currently deposited in the Colección Nacional de Paleontología (UNAM), where they are constantly being prepared to recover the fossils encapsulated there. Therefore, it is expected to have more material of this species in the future.

CONCLUSIONS

The knowledge of the fossil record of aspidorhynchids has grown significantly in the last years (Gouiric-Cavalli, 2015); however, the full understanding on their phylogenetic and biogeographical processes has faced a wide bias in their record out of Europe. Apart from the case of *Vinctifer*, in and around the Gondwanan domains, these fossils are rather scarce, poorly preserved, or have not been studied in detail. As noted by Brito (1997), the family Aspidorhynchidae originated during the Middle Jurassic in the Eastern Domain of the Tethys Sea, which then bathed the Paleoarchipelago of Europe. From there, they had a fast dispersion reaching the Caribbean, South America, and Antarctica probably in the Late Jurassic.

Certainly, the early diversification of Aspidorhynchidae occurred in the European area of Laurasia (Brito, 1997), where *Aspidorhynchus* and *Belonostomus* have been intensely recovered. The discovery of these two genera plus *Vinctifer*, *Richmondichthys*, *Pseudovinctifer*, and *Jonoichthys* in and around the Gondwana domains, which includes the southern end of North America (México, Cuba), South America (Brazil, Colombia, Chile, Venezuela, and Argentina), Australia, Africa, and Antarctica, suggest that Aspidorhynchids also experienced an important diversification pulse within the domains of Gondwana since the Late Jurassic.

As a matter of fact, *Vinctifer* represents a peri-Gondwanan group, whose origin has, so far, been a mystery due to the poor preservation

of recovered fossils outside Brazil. The discovery of *V. ferrusquiai* sp. nov. in the Jurassic deposits of Mexico, in a site that forms part of the northern rim of the ancient Hispanic Corridor, provides important data to understand the evolution of these fishes. This allows us to definitively recognize the existence of this genus in the Late Jurassic, extending its temporal range about 50 million years, from the Kimmeridgian (Late Jurassic) to the Early Cretaceous. On the other hand, this shows that the ancestors of this group were able to reach the central part of America through an alternative path that would have opened westward from Europe, the Hispanic Corridor, which turns out to be more natural to that other possible routes (*i.e.* across the eastern and southern margins of Gondwana).

The integral recognition of the natural history of the Aspidorhynchiformes is still an unfinished task. After the complete study of the aspidorhynchids elaborated by Brito (1977) and after the addition of three new genera, all of them from Gondawana, it is desirable to perform the comprehensive morphological and phylogenetical review of this group. This effort goes beyond the scope of this work; however, the authors of this paper are currently preparing the description of Early Cretaceous aspidorhynchids from Tlayúa quarry, Mexico.

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