



Scale morphology and specialized dorsal scales of a new teleosteomorph fish from the Aptian of West Gondwana

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Abstract. Scales of a new species of Teleosteomorpha from the continental Aptian of the south of South America are studied. These neopterygians are from the La Cantera Formation in central Argentina, and were previously identified as Pholidophoriformes. They present ganoid scales; most of them are rhombic with well-developed peg-and-socket articulations and possessing a smooth surface. They have a straight posterior margin, but occasionally, some scales of the flank have a sinuous posterior margin with one or two serrations. The shape of the scales varies along the body from large, rectangular and deeper than long scales behind the head to the preanal region to smaller and rhomboidal scales in the caudal region. There are a few horizontal rows along the flank and about 32 lateral line scales. Thick, round ganoid scales are present in the prepelvic region close to the ventral margin. The round and rhombic scales present growth lines, which form concentric ridges on the external side. A characteristic row of deep scales forms the dorsal margin on each side of the body; a row of median ridge scales is not present. This is a unique feature of the studied fishes. Scutes covered with unornamented ganoine precede the pelvic, dorsal, and anal fins, as well as the dorsal and ventral margins of the caudal fin. The posterior margin of the dorsal lobe of the caudal fin is formed by a single line of scales, which continues and covers the base of the first principal caudal ray. Histological studies reveal a lepisosteoid-scale type with multiple ganoine layers, lack of dentine, and the presence of canaliculi of Williamson. The macro- and micromorphology of the scales shows features that are found in other teleosteomorphs, but also in other neopterygians.

1 Introduction

Cretaceous continental actinopterygian faunas from southern South America are scarce compared to marine ones. Records from the Southern Hemisphere have been less studied than those of the Northern Hemisphere (Arratia and Cione, 1996; Arratia, 2004; López-Arbarello, 2004). The La Cantera Formation represents upper Aptian continental deposits from western central Argentina. Among its biodiversity is a group of ganoid neopterygians (López-Arbarello et al., 2002; Arcucci et al., 2009, 2015). After more than 30 years of collecting, fishes are the only vertebrates recorded, but they have never been studied in detail (Castillo-Elías, 2011; Castillo-Elías et al., 2012; Giordano and Arratia, 2011, 2013).

Neopterygians from La Cantera Formation have been assigned to the order Pholidophoriformes (Berg, 1937) since 1969 (Flores, 1969). However, such assignment was based on unreliable generalized characters found in many actinopterygians (Arratia, 2000, 2013), such as specimen size, the presence of bones covered by ganoine, and ganoid scales. These were the common traits for identifying “pholidophoriforms”, a group now interpreted as non-monophyletic (Arratia, 2000, 2013). Our current studies suggest that the fishes from the La Cantera Formation are not “pholidophoriforms”. Their cranial and postcranial features represent a new combination of characters that indicates new species of neopterygians. At least two of the species from the La Cantera Formation are within the Teleosteomorpha (Giordano, 2015), and one of them is the subject of study here.

Scales of fishes can provide valid taxonomic and phylogenetic information for different taxa (e.g., Schultze, 1966, 1996, 2015; Sire and Meunier, 1994; Richter and Smith, 1995; Meunier and Brito, 2004; Vullo et al., 2009; Arra-

tia and Schultze, 2012). Detailed descriptions (micro- and macromorphology) of these structures could be a tool for helping to clarify taxonomic assignments and possible relationships of fishes from the La Cantera Formation.

2 Geological setting

The material examined in this study originates from the type locality of the La Cantera Formation in western central Argentina (32°49', 33°06' S and 66°59', 66°46' W; Fig. 1). The formation outcrops in the San Luis Basin is part of the Del Gigante Group that corresponds to a continental filling of an extensive system related to the break-up of Gondwana (Rivarola and Spalletti, 2006). The La Cantera Formation has been interpreted as a lacustrine environment based on its lithological characteristics, as well as the presence of freshwater algae and ostracods. It has a measured thickness of 31 m at its type locality (Prámparo, 1999a) and is composed of papery, laminated green-grey mudstones interbedded with siliciclastic siltstones (Criado-Roque et al., 1981) and layers of primary gypsum. The gypsum layers go from 1 mm to decimeters in thickness, most of them with laminar, massive, and granular textures (G. Castillo-Elías, personal communication, 2013). The La Cantera Formation could represent ephemeral lakes related to a fluvial environment with some periods of a quiet lacustrine system (Criado-Roque et al., 1981), which allowed the preservation of delicate structures, such as leaves, stems, flowers, frail fish remains, and insect exuviae. The actinopterygian fishes occur within a rich paleobiological association including plant remains and palynomorphs belonging to angiosperms, gymnosperms, bryophytes (*Tallithes* sp., *Muscites* sp., among others) and pteridophytes, freshwater ostracods, and different insect groups – for example, Orthoptera, Coleoptera, Diptera, among others, and *Notonecta mazzoniae*, a fresh water heteropteran (Arcucci et al., 2009, 2015; López-Arbarello et al., 2002; Petrulvičius et al., 2010; Puebla, 2009; Puebla et al., 2012). The microphytoplankton is dominated by freshwater algae (*Scenedesmus*, *Tetrastrum*, *Crucigeniella*, *Tetraedron*, *Botryococcus*, *Leiosphaeridia*). At some levels of the section, this microphytoplankton constitutes more than 80 % of the total assemblage (Prámparo, 1999b). The angiosperm palynomorphs are present at low percentages, but they become more frequent at the top of the studied sections. They are useful in determining the age of the formation. The taxa identified are *Afropollis* (*A. operculatus*, *A. zonatus*, and *A. aff. jardinus*), *Retimonocolpites* sp., *Stellatopollis* sp., *Clavatipollenites* sp., *Tucanopollis*, *Pennipollis* (ex. *Brenneripollis*) *peroreticulatus*, and *Asteropollis* complex (*Stephanocolpites mastandreaei/Huitrinipollenites transitorius*). *Afropollis* and the *Astereopollis* complex appear in Argentina in the Aptian, indicating a Cretaceous age for the formation. Finally, the lack of tricolpate pollen in the

microflora places the La Cantera Formation in the late Aptian (Prámparo, 1990, 1994, 1999a, 2012; Prámparo et al., 2007).

3 Material and methods

3.1 Material

Specimens studied in this work are small, approximately 5.5 cm in total length. Their body flanks are totally covered by ganoid scales, and they have a hemiheterocercal caudal fin (Fig. 2). Fishes studied herein have characters that place them within the clade Teleostemorpha (Arratia, 2001). They share with other Teleostemorpha the presence of a unique supramaxillary bone lying on the last dorsal third of the maxilla, two suborbital bones, a complex pectoral ray (for complex ray definition see Arratia, 2008, 88–91), two principal rays forming the dorsal and ventral margins of the caudal fin, and the main leading ray (the longest segmented-and-branched ray) corresponding to the second principal ray in the dorsal and ventral margins of the caudal fin, as well as in the dorsal and anal fins, besides other characters (Arratia, 2008, 2013; Giordano, 2015).

Detailed observations of the macro- and microstructure of the scales have been made mostly on complete or almost complete specimens, but also on disarticulated ones, as well as on isolated scales from different regions of the body (see list of samples below).

The material revised for this research is held in the following Argentinian institutions: MIC, Museo Interactivo de Ciencias in Universidad Nacional de San Luis (UNSL), San Luis; CORD, Museo de Paleontología in Universidad Nacional de Córdoba, Córdoba; and MLP, Museo de La Plata in Universidad Nacional de La Plata, Buenos Aires.

Specimens of Teleostemorpha n. sp. 1 (after Giordano, 2015) are listed below:

Complete or almost complete specimens: MIC-V46 b; MIC-V52; MIC-V519 a; MIC-V523; MIC-V535 a, b; MIC-V568; MIC-V621 a, b; MIC-V635; MIC-V560; MIC-V568; MIC-V644; MIC-V659 a, b; MIC-V660 a, b; MIC-V661 a, b; MIC-V662; MIC-V695 a; MIC-V701 a, b; MIC-V702; MIC-V703 a, b; CORD-PZ 2027, 2029; CORD-PZ 2028, 2033; CORD-PZ 2087; CORD-PZ 2088; CORD-PZ 2092; CORD-PZ 2030; MLP 85-IV-15-1; MLP 85-IV-15-2 -4; and MLP 85-IV-15-6 -7.

Isolated scales and disarticulated-fragmented specimens (most of them not catalogued and bearing the field name): MIC-V634; MIC-V699; MIC-V700; MIC-V706 a, b; “T-5.5”, “T-99”; “T-123”; and “8”, “C1”, “C3”, “P2008”, and “5.5-AM”.

3.2 Methods

The senior author mechanically prepared the material, and some specimens were also prepared for histological and

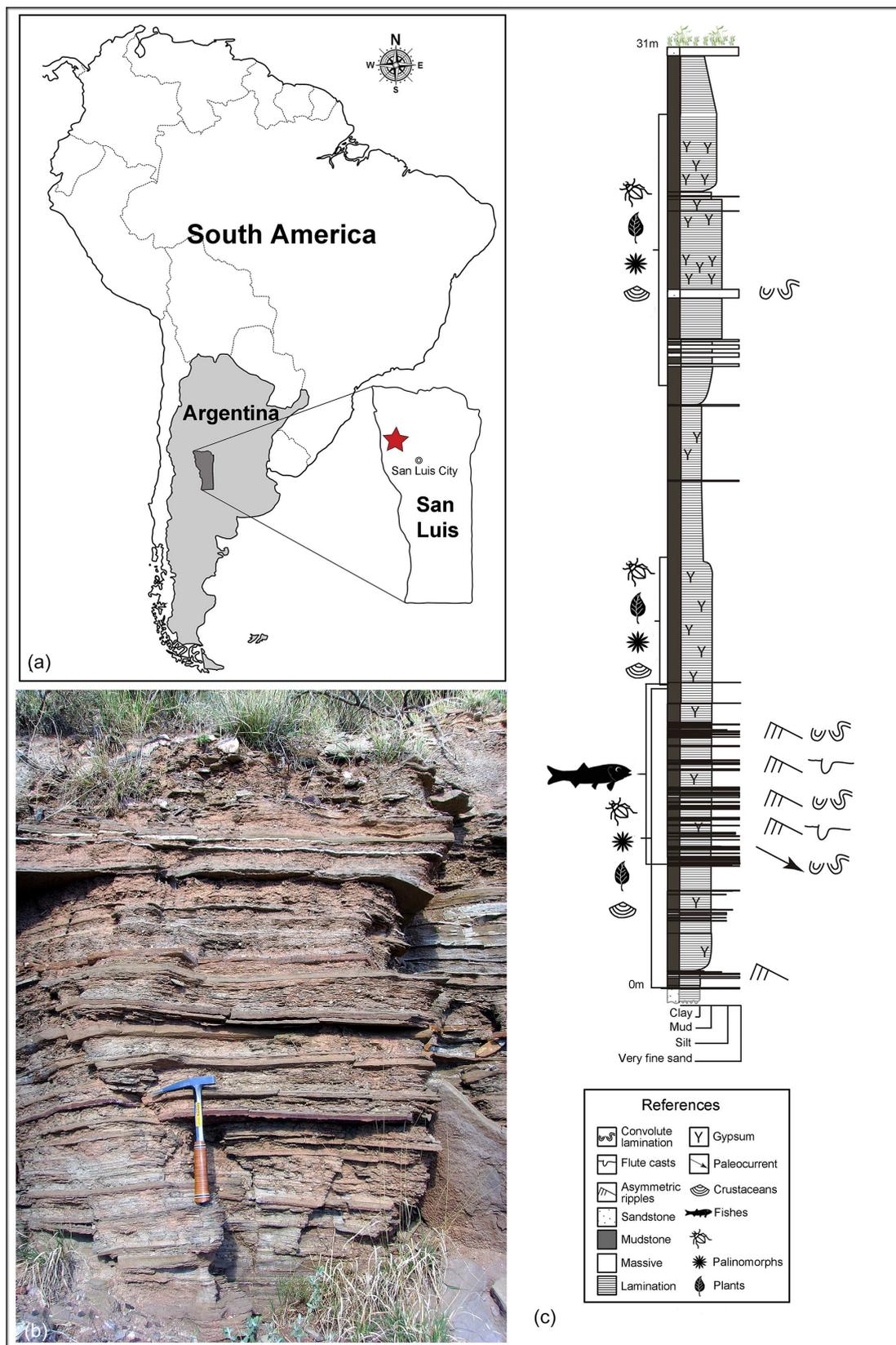


Figure 1. (a) Geographic provenance of specimens from the La Cantera Formation, San Luis, Argentina. Star indicates the type locality. (b) Stratigraphic section in the type locality. (c) Interpretative stratigraphic sequence of La Cantera Formation at the type locality. Courtesy of Gabriela Castillo-Elías.

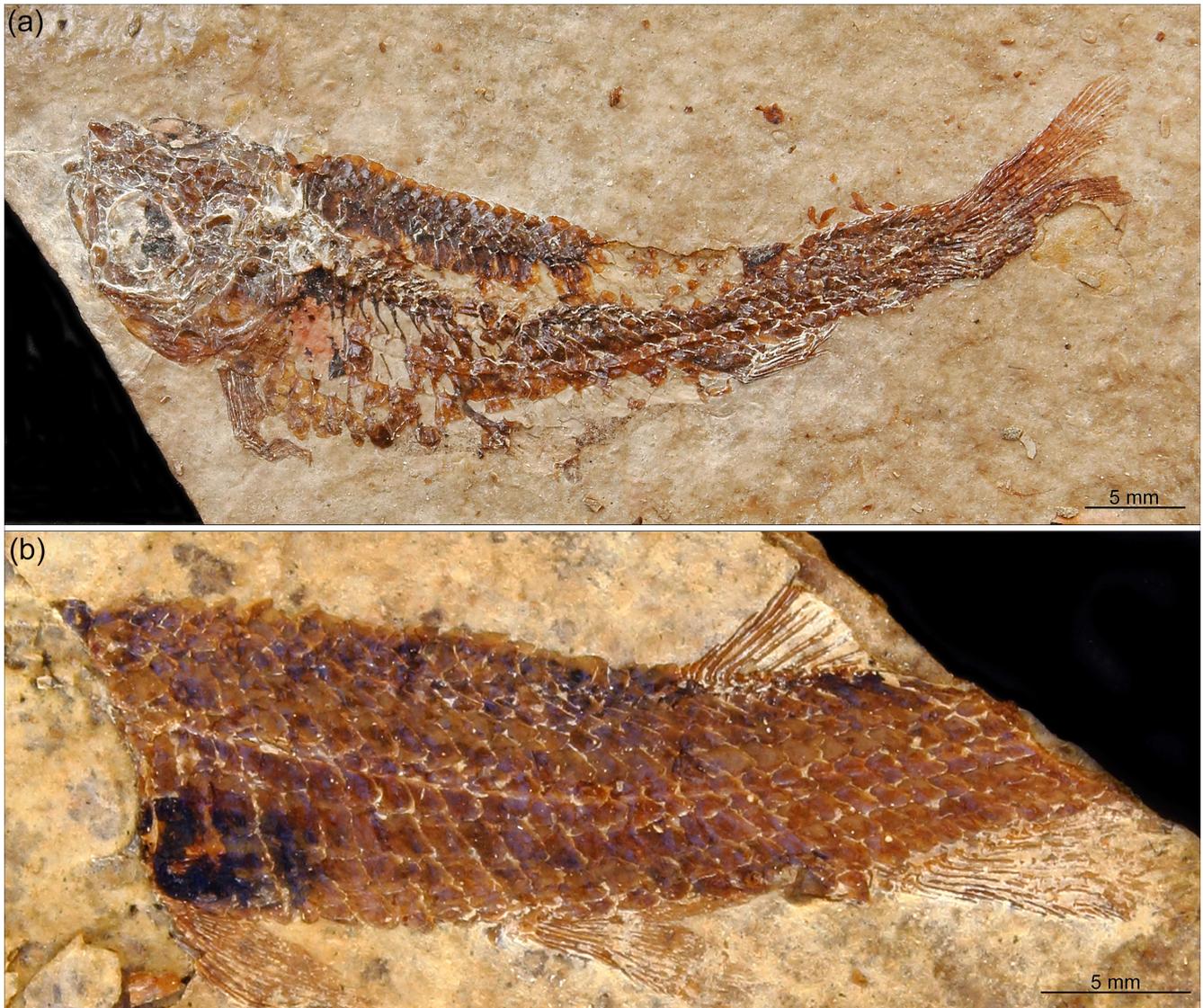


Figure 2. Teleosteomorpha n. sp. 1. (a) MIC-V701a one of the most complete specimens from the La Cantera Formation. (b) Specimen MIC-V703a, showing body completely covered by ganoid scales.

scanning electron microscopy (SEM) studies in the laboratories of the UNSL.

Specimens were studied by direct observation and interpretative drawings were made using a binocular microscope with an attached camera lucida (Leica M80) at UNSL, following Schultze (1966, 1996) for interpretation of scales. The surfaces of scales were observed under SEM, and histological sections were analyzed under a petrographic microscope (Leica DM750P) using regular and polarized light, following Gayet and Meunier (1986). Photographs were taken with digital cameras (Sony Cyber-shot DSC-HX1 and Canon EOS T3i).

4 Description of scales

4.1 Macromorphology

The whole body flank, including the bases of the unpaired fins, is covered by ganoid scales (Fig. 2b). Most scales have a well-developed peg-and-socket articulation (Figs. 3 and 4), except the postanal ones. The anterior margin of all scales is devoid of anterodorsal or anteroventral processes. The posterior margin of most scales is straight; nevertheless, some flank scales have one serration (Fig. 3a–c). The ventral border is sinuous (Fig. 3b and c). The inner surface of each scale bears the typical keel of ganoid scales that serves as attachment for Sharpey’s fibers, which connect with the keel of adjacent scales in the next vertical row (Figs. 3c and 5a).

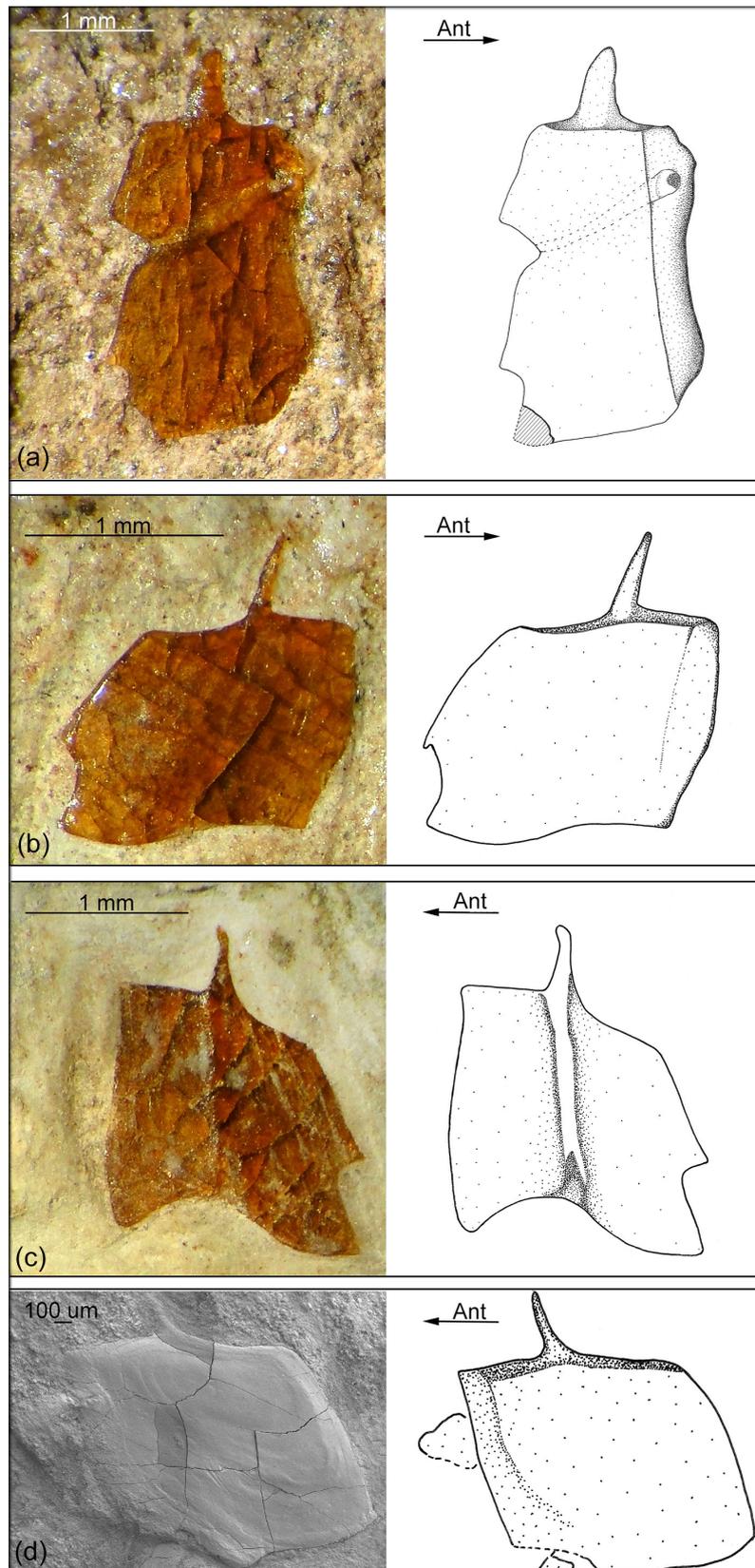


Figure 3. Sample of pre-anal ganoid scales with well-developed peg-and-socket articulation of *Teleosteomorpha* n. sp. 1. (a) MIC-V634, an isolated mid-flank scale, which carries the lateral line. (b) A ventral flank scale of specimen MIC-V631, showing a serrated posteroventral margin. (c) Specimen MIC-V706b, inner surface of another ventral flank scale, with serrated posteroventral margin and the typical keel and groove for peg-and-socket articulation. (d) SEM photograph ($\times 50$) of specimen MIC-V706a; ant, antierad.

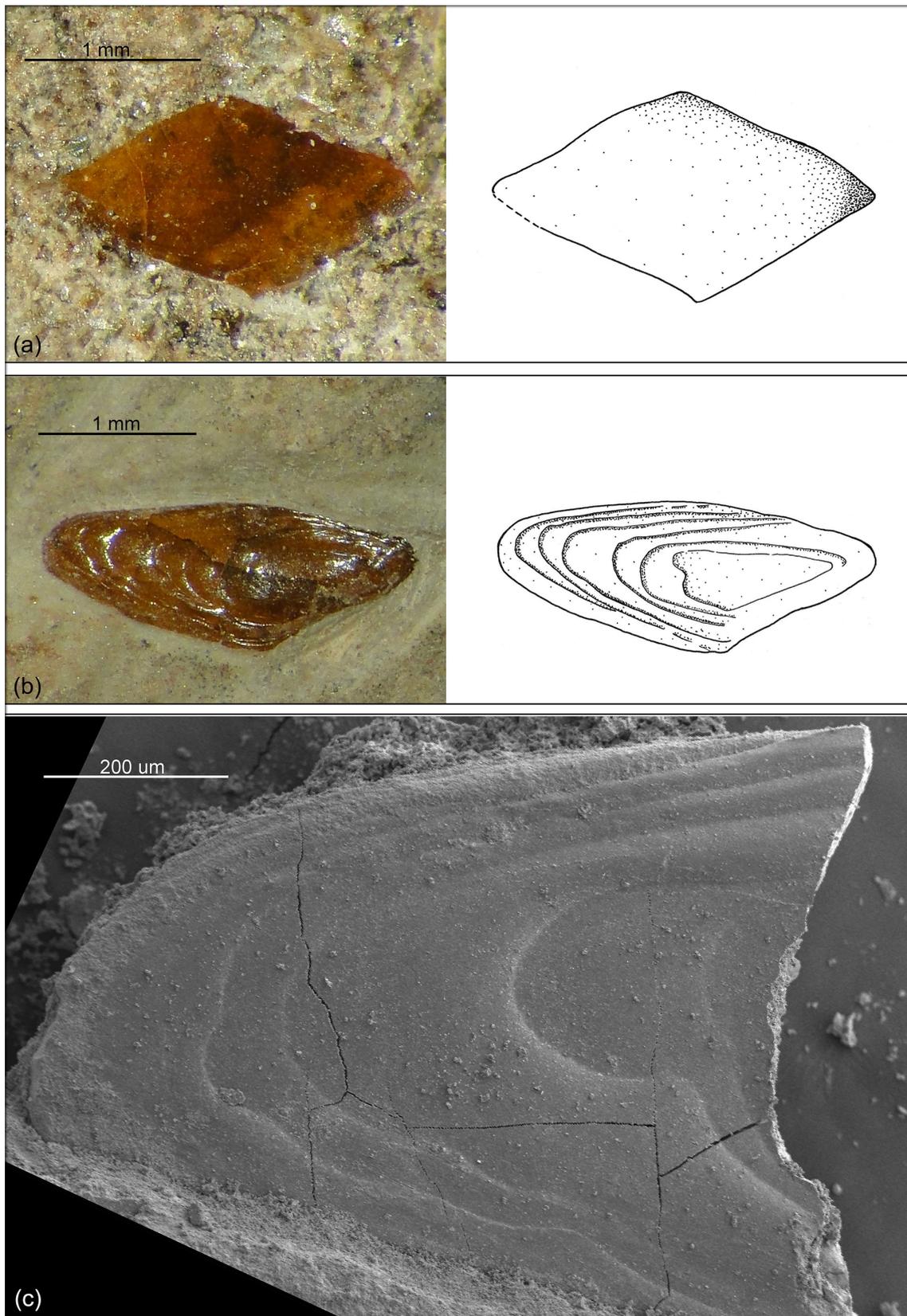


Figure 4. Post-anal rhombic scales of *Teleosteomorpha* n. sp. 1. from the La Cantera Formation. (a) MIC-V699, an isolated scale. (b) Sample MIC-V706b, showing concentric pattern of growth lines in external view. (c) Other sample of MIC-V706b under SEM; growth lines on external surface.

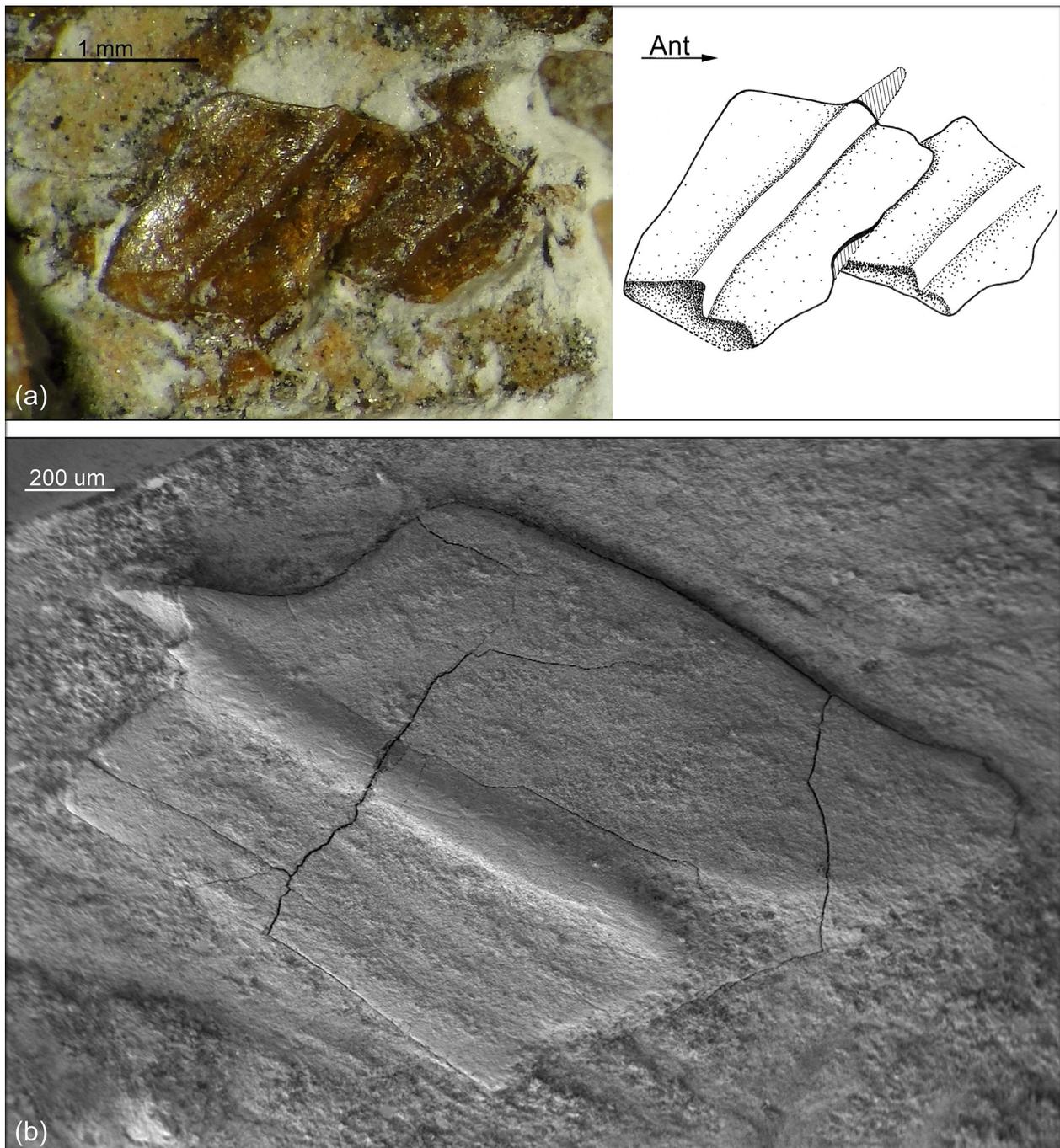


Figure 5. Inner view of middle flank scales of *Teleosteomorpha* n. sp. 1, showing main elements of peg-and-socket articulation, the keel, the groove, and the peg. **(a)** Picture and camera lucida drawing of some scales of specimen MIC-V523. **(b)** SEM photograph of one of the scales of sample MIC-V706a; ant, antieriad.

Most scales, as well as the surfaces of head bones, have a smooth ganoine surface. The scales of the most ventral scale row present a subtle concentric pattern of growth lines in the prepelvic margin (Fig. 6). The same concentric pattern can be seen in a few caudal scales (Fig. 4b and c). At the level of the dorsal fin, scales are arranged in five to seven (in exceptional

cases eight) horizontal rows along the flank, demarcating a shallow body, which is about 23 % of standard length.

Shapes and sizes of the scales vary according to body regions. The scales are rectangular and deeper than long between the head and pre-anal region, and they become smaller and rhomboidal with no peg caudally, conferring more flex-

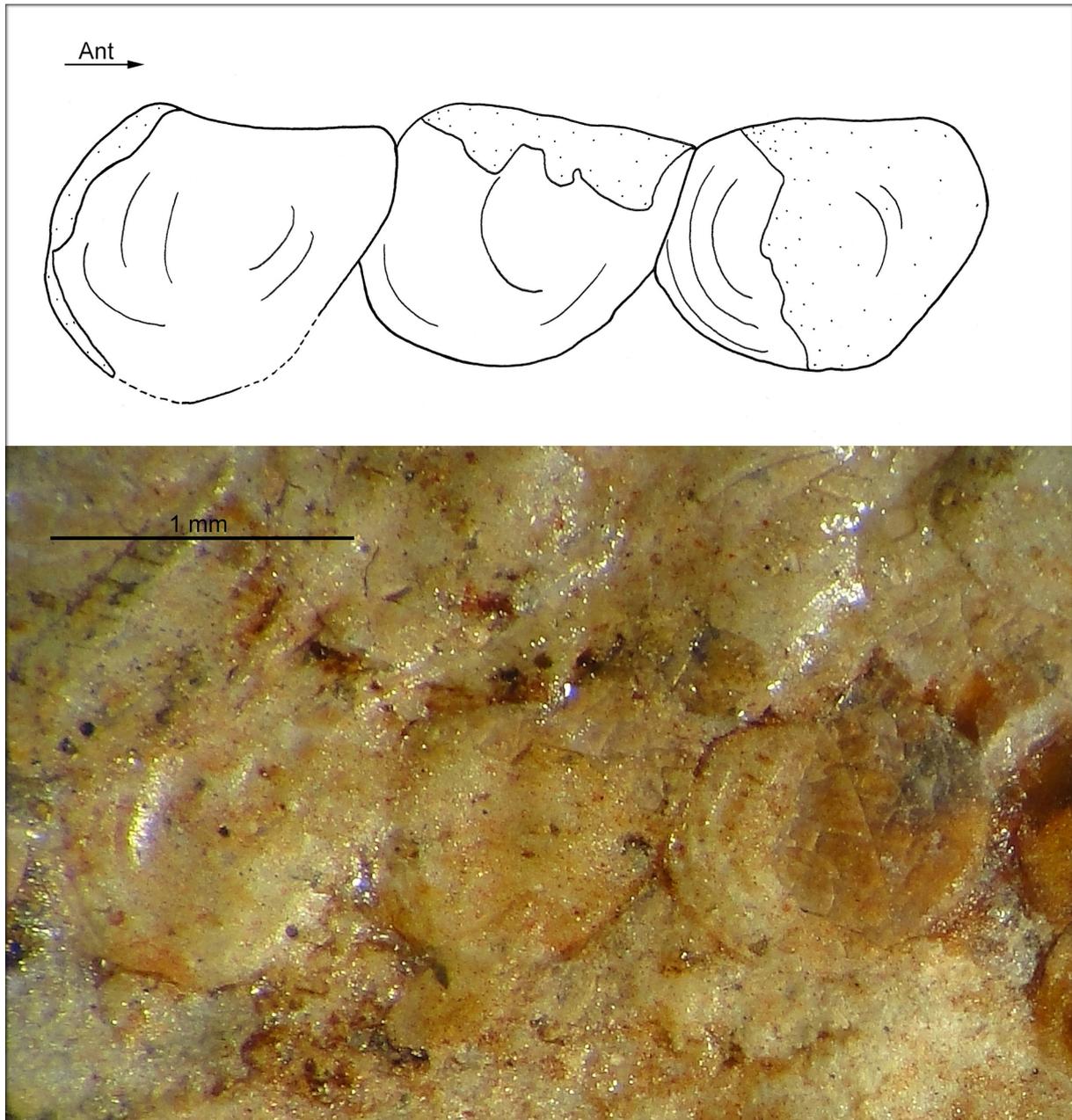


Figure 6. Teleosteomorpha n. sp. 1. Rounded ventral pre-anal scales in specimen MIC-V621b. Note the growth lines; ant, anterior.

ibility to this region (Fig. 7). The scales of each horizontal scale row, especially those in the pre-anal region, are different in shape.

The most dorsal scale row consists of a series of deep scales devoid of spines or processes. Such a scale row forms the dorsal margin of the body on each side (Figs. 8 and 9). These scales are peculiar, forming the dorsal margin in pairs; there is a row on the left side and another on the right side at the dorsal margin (Figs. 9 and 10). This pattern begins behind the skull in some specimens (Figs. 9 and 10), but it starts in about the 10th vertical scale row in others (Fig. 8a). In spec-

imen MIC-V701, the dorsal scales have a caudad-directed point in the opposite direction to the rest of the flank scales (Figs. 2a and 10).

The second to fourth horizontal scale rows (from dorsal to ventral) carry the lateral line so that the lateral line has a middle to dorsal position on the flank. There are some exceptions where the lateral line is placed in the fifth horizontal scale row. The lateral line extends over 32 or 33 scales along the body. The lateral line scales change their shape and size, depending on the regions of the flank, as in the other scales of the body. Changes in the scales along the lateral line are grad-

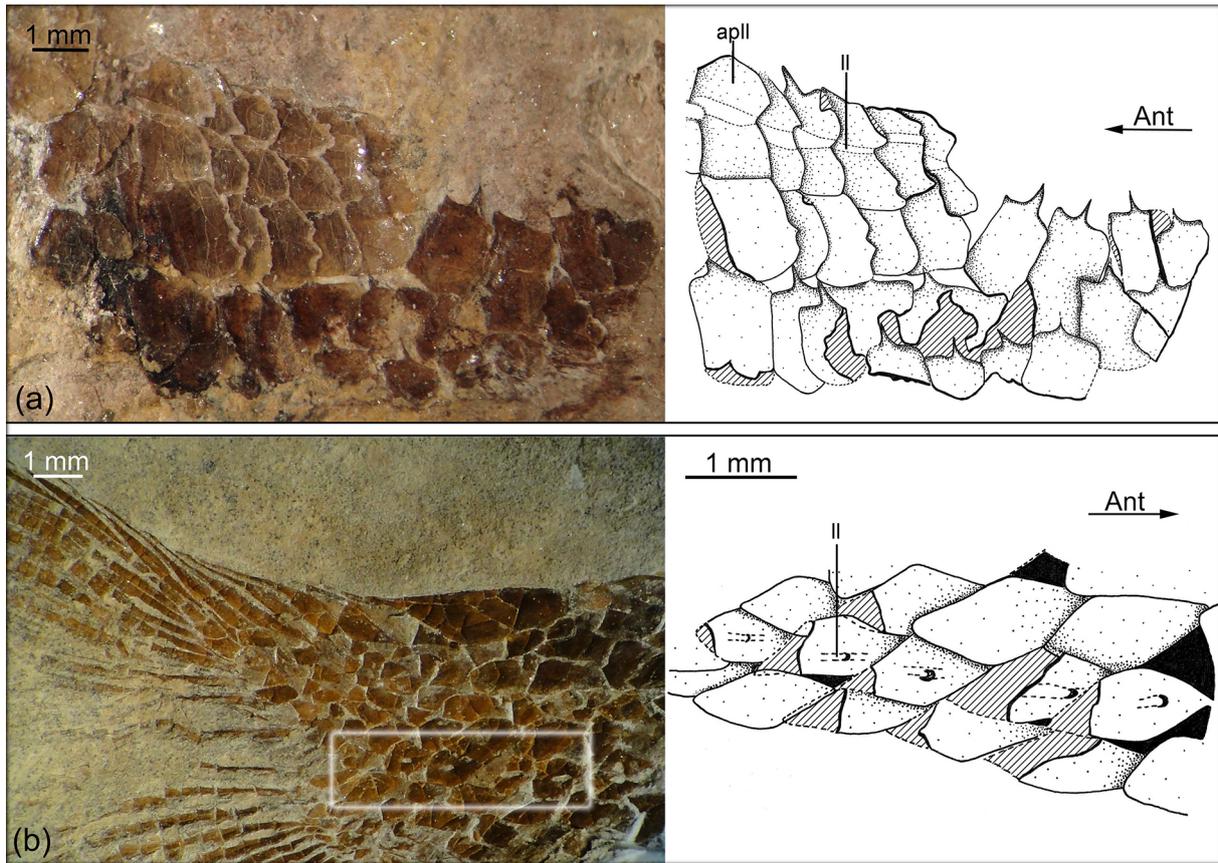


Figure 7. Squamation of the flank of *Teleosteomorpha* n. sp. 1 from the La Cantera Formation. (a) Pre-anal scale patch in MIC-V635. (b) Scales from caudal peduncle of MIC-V523. Note that the lateral line passes through them; asll, additional pore of lateral line or pitline; ll, main lateral line; ant, anterior.

ual, but it is possible to differentiate between four morphologies: (1) the lateral line scales of the pre-pelvic region are deeper than long and present a notch on their posterior margin (Figs. 3a and 7a). (2) The scales decrease in depth in the pelvic fin region, becoming almost square, and are marked by a small notch at their posterior margin. (3) Lateral line scales above the anal fin are square (Fig. 11). (4) The lateral line scales of the caudal peduncle are rhombic, and in some cases have, in addition to the posterior opening, a pore in a nearly central position (Fig. 7b).

The lateral line ends in the last scale of the basal axial lobe of the caudal fin with the inversion of the scale rows (Fig. 12). No accessory lateral line has been observed in any specimen; however, there are some scales with additional pores in branches of the lateral line canal (Fig. 11b).

Vertical scale rows above the lateral line have the same pattern as vertical rows below it, so there is no intercalation of scale rows into the dorsal vertical rows. Three or four horizontal scales rows are arranged below the lateral line. Those of the pre-anal region are deeper than long, except the scales of the most ventral horizontal row, which are rounded to square and show concentric growth pattern (Fig. 6). All ven-

tral scales become rhomboidal in the caudal region (Figs. 4 and 7).

In the upper lobe of the caudal fin, there are four or five scale rows with reversed direction to that of the body (Fig. 12). The most posterior scale row forms the posterior margin of the dorsal lobe with three to five scales that start just above the last lateral line scale. The row continues with a line of two to five scales that cover the base of the first principal caudal ray (Fig. 12). Both dorsal and ventral margins of the caudal fin are preceded by elongate, oval scutes. The dorsal scute is slightly broader than the ventral one; nevertheless, both scutes are almost of the same size (Figs. 12 and 13a–b). Also, large, slightly oval or round scutes precede the pelvic, dorsal, and anal fins. All mentioned scutes are covered by unornamented ganoine. Specimen MIC-V519a shows three anal scutes of different shapes and size just in front of the anal fin (Fig. 13c).

4.2 Micromorphology and histology

SEM studies reveal that even though flank scales seem to have a smooth surface, at a magnification of 3000×, they

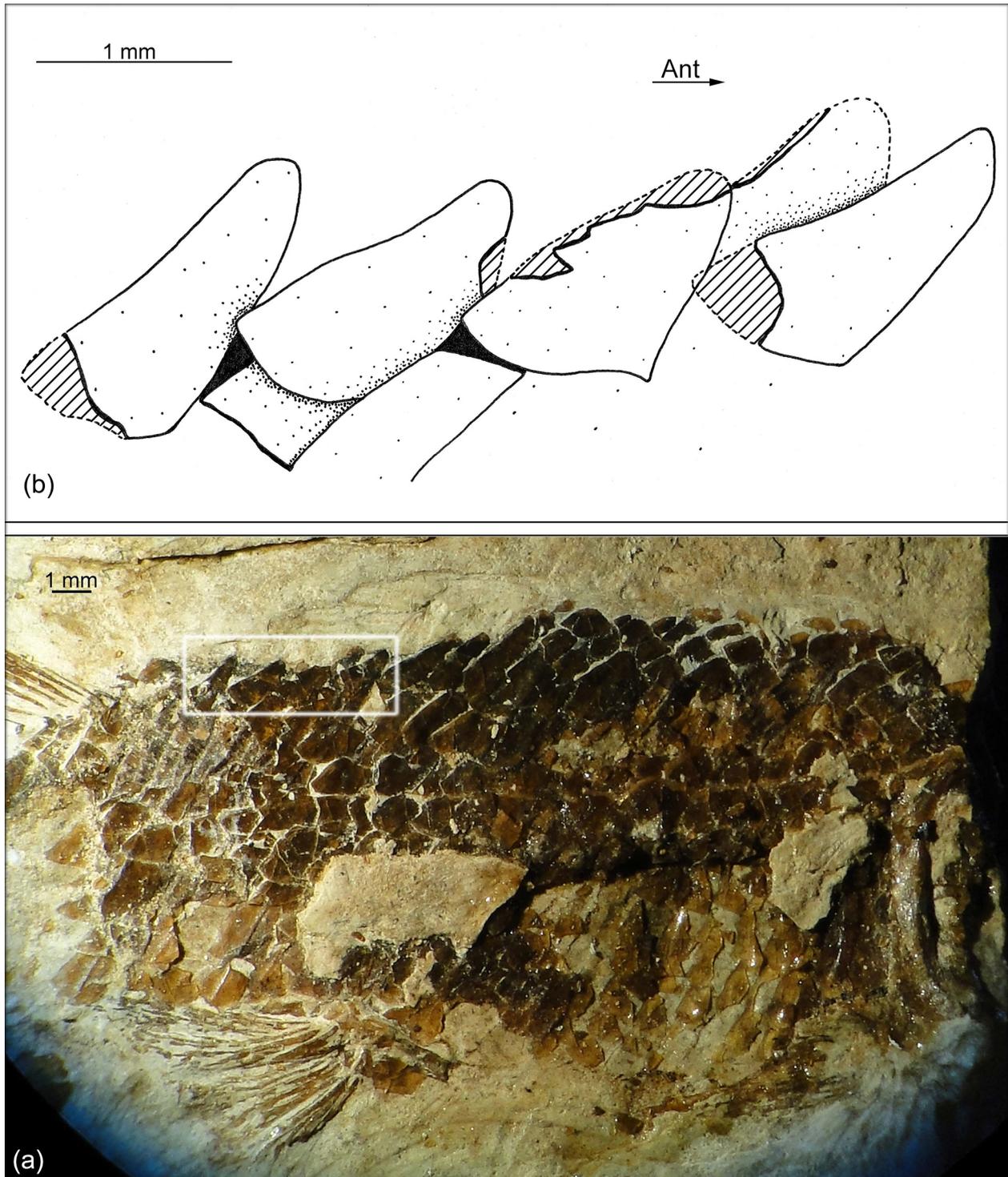


Figure 8. (a) Flank of *Teleosteomorpha* n. sp. 1 (MIC-V662). (b) Detail of the uppermost dorsal scale row in the pre-anal region; ant, anterior.

actually present striae (Fig. 14). The striae cover the surface of the scales and are arranged in an anterodorsal-to-posteroventral pattern. We cannot decide whether these striae are original structures of the surface or scratches caused af-

ter death of the fish. Microtubercles described for the surface of ganoine by Schultze (1966), Ørvig (1967), and Gayet and Meunier (1986) are not present.

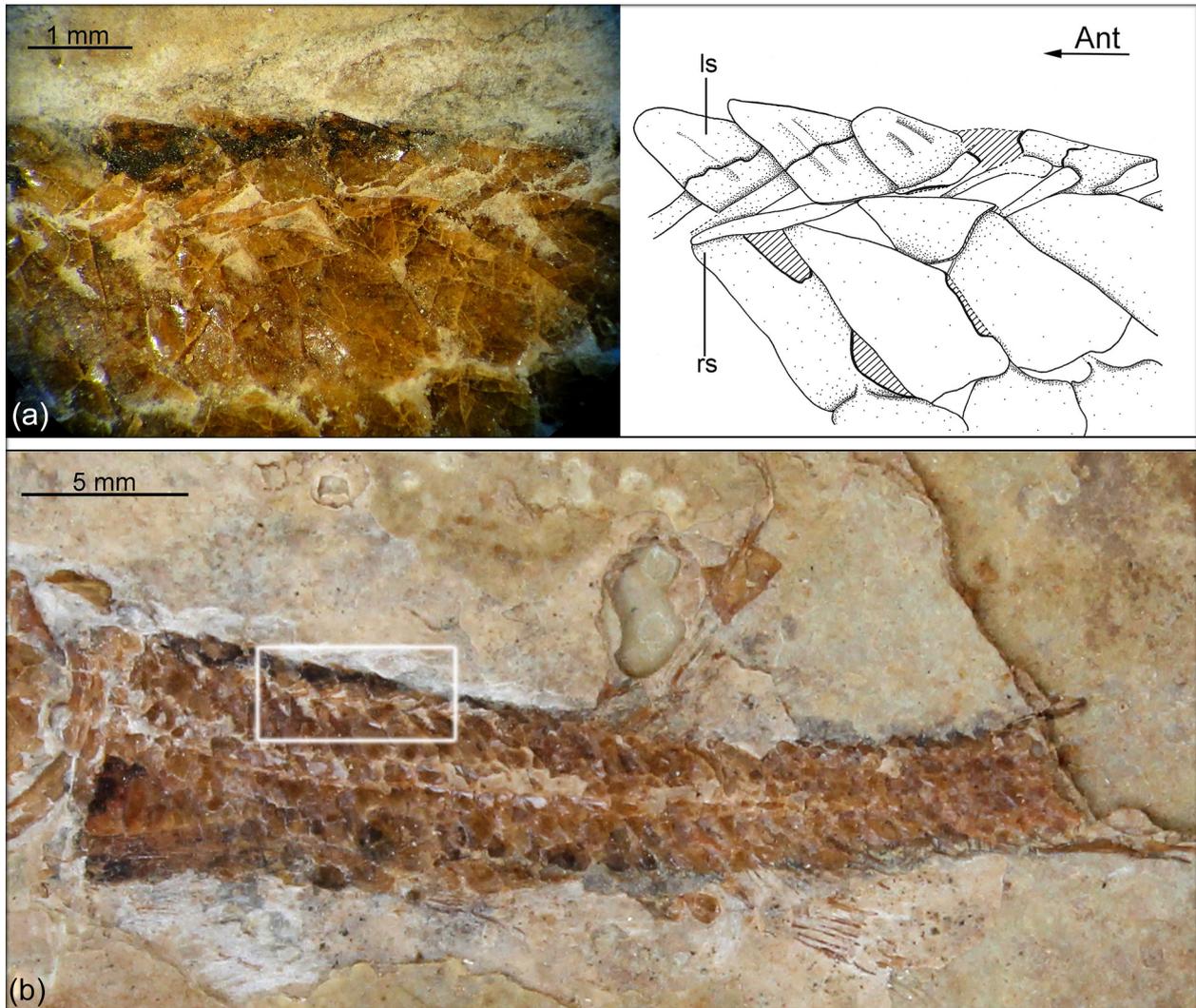


Figure 9. (a) Postcranial region of *Teleosteomorpha* n. sp. 1 (MIC-V660); white rectangle marks detail in (b). (b) Picture and camera lucida drawing showing the particular pattern of missing median dorsal row, but a series of scales on each side of dorsal margin; ant, anterior; ls, left side scales; rs, right side scales.

Histological slides show a lepisosteoid-type scale where ganoine layers directly overlie the surface of the basal bony plate, and dentine is lacking between both tissues (Fig. 15a). Ganoine, as in most actinopterygians, is composed of multiple layers (Sire et al., 2009), as can be seen in photographs under normal and polarized light (Fig. 15b and c). Besides the ganoine layers, the histological microstructure shows the basal bony plate with all the lepisosteoid features (Schultze, 1966; Fig. 15d herein): stratified lamellar bone, osteocyte spaces, canaliculi of Williamson, Sharpey's fibers, and vascular canals. Sharpey's fibers are connective fibers that attach keels horizontally in neighboring vertical scale rows. Vertically, scales are connected by peg-and-socket articulation (Schultze, 1996).

5 Comparison with scales of other Teleosteomorpha and other Neopterygii

The macromorphology of the scales described shows features found in other neopterygians, including most Teleosteomorpha or stem-group teleosts, with particular characters unique to *Teleosteomorpha* n. sp. 1.

The clade Teleosteomorpha comprises the large group of Teleostei plus their stem groups (Arratia, 2001: Fig. 3). According to Arratia's (2013) phylogenetic hypothesis, the Aspidorhynchiformes, the Pachycormiformes, and the Middle Triassic fish *Prohalecites porroi* stand as stem teleosts. These taxa are more closely related to crown-group teleosts than to their closest extant relatives (e.g., *Amia* and *Lepisosteus*).

Two principal types of scales are present in the clade Teleosteomorpha. Elasmoid scales of cycloid type are the

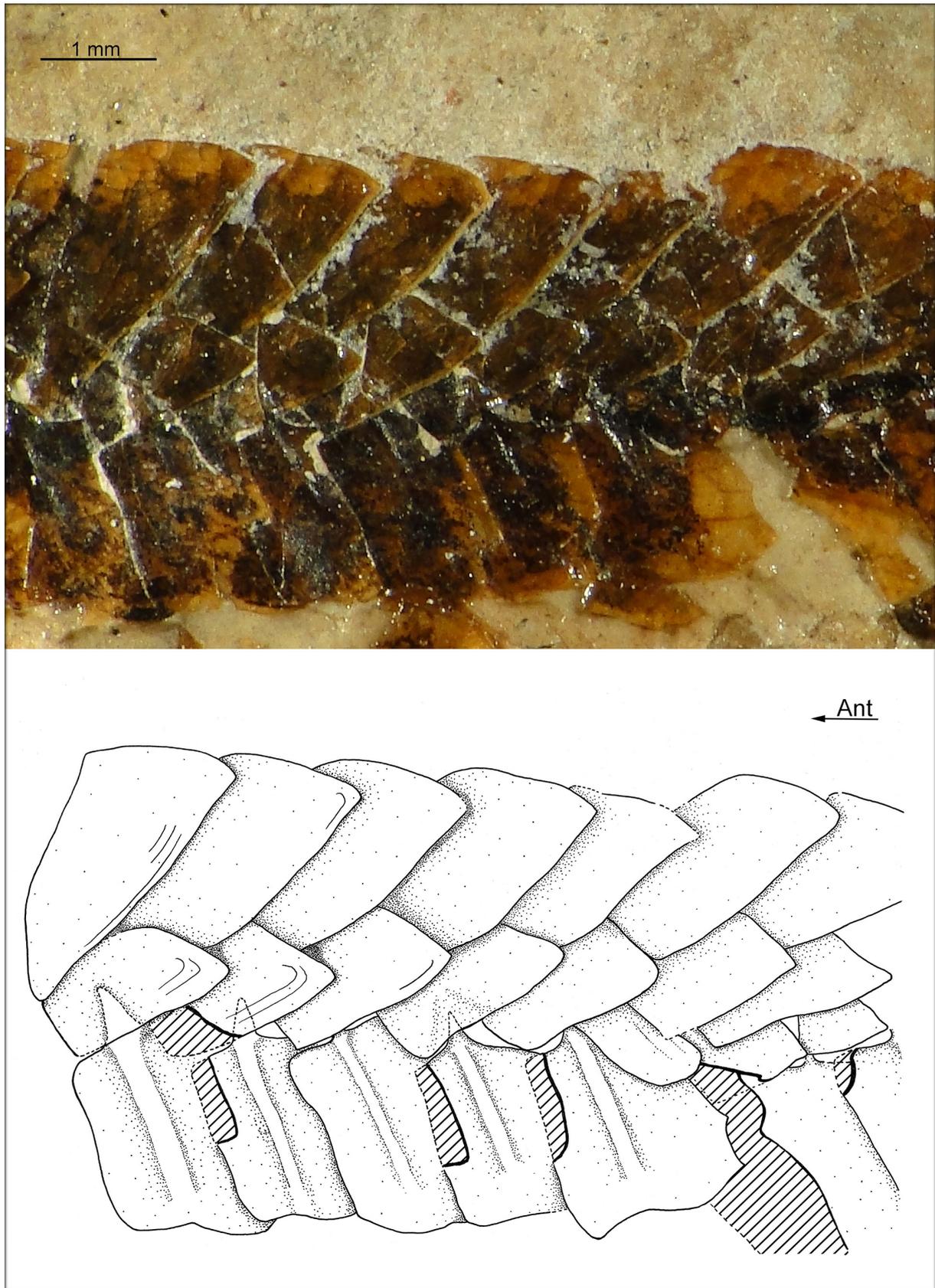


Figure 10. Postcranial region of *Teleosteomorpha* n. sp. 1 (MIC-V701a). Detail in photograph and drawing of uppermost scale row in lateral view. It shows the second row also, as well as the first row scale from the left side of the specimen; ant, anterior.

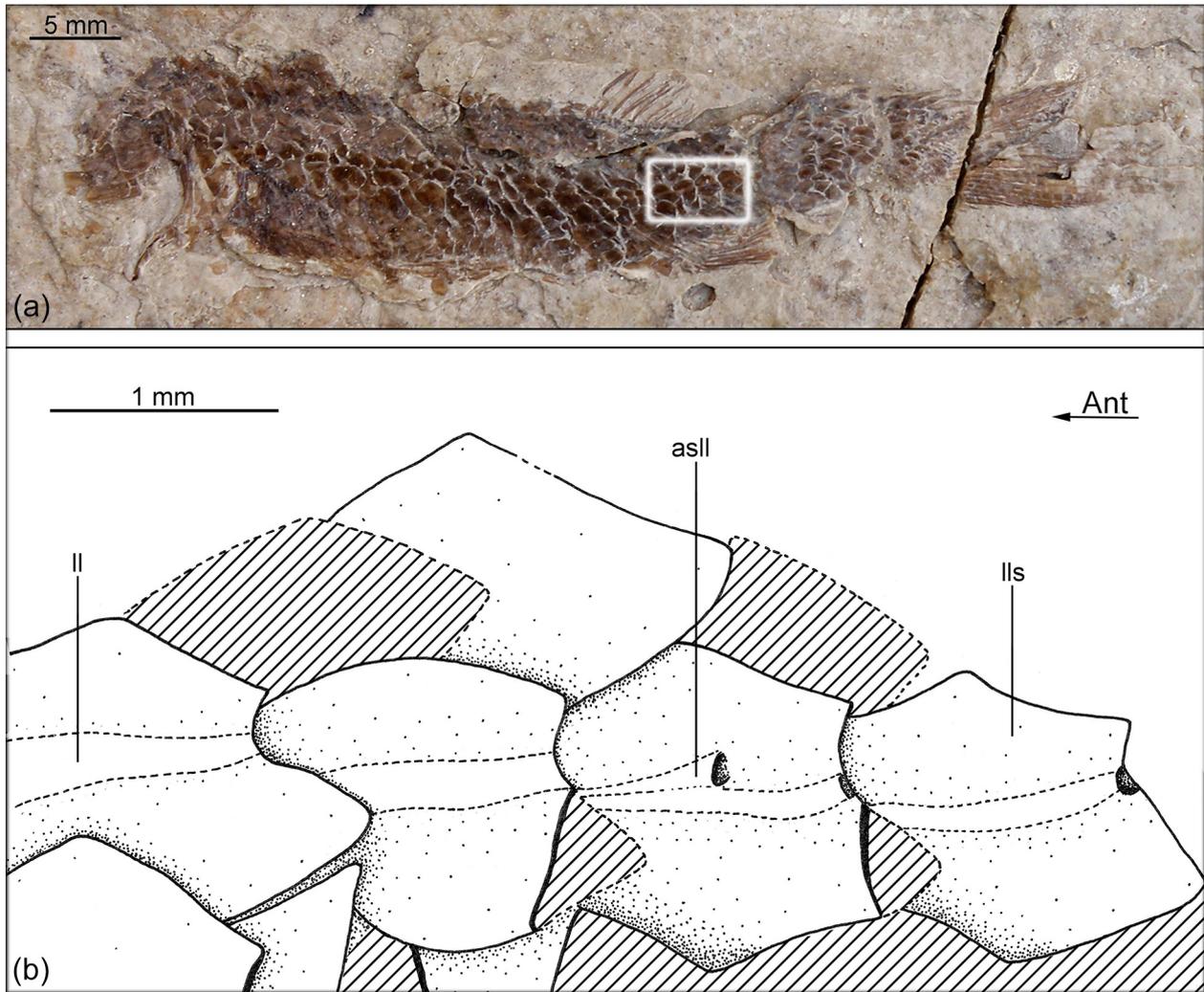


Figure 11. Scales of *Teleosteomorpha* n. sp. 1. (a) Specimen MIC-V46a. (b) Detail of camera lucida drawing of scales carrying the main lateral line; ant, anteriad; asll, branch from lateral line with opening at surface; ll, main lateral line with opening at posterior margin; lls, lateral line scales.

most common. These are restricted to most Teleostei from *Leptolepis corhyphaenoides* and all more derived ones (Schultze, 1966, 2015; Meunier and Brito, 2004; Arratia and Schultze, 2007; Arratia, 2015). Ganoïd scales of lepisosteoid type are present among most basal forms, for example, in members of the family Aspidorhynchidae (Schultze, 1966; Brito, 1997; Brito and Meunier, 2000), in the teleost family Pholidophoridae (Nybelin, 1966; Arratia, 2013, 2015), in *Catervariolus hornemani* (Taverne, 2011), in species of *Siemensichthys* (Arratia, 2000), and in *Dorsetichthys bechei* (Nybelin, 1966; Arratia, 2013). Amioid-type scales are also present among teleosts, but only in species of *Eurycormus* (Schultze, 1966, 2015; Arratia and Schultze, 2007; Schultze and Arratia, 2015).

Scales of *Teleosteomorpha* n. sp. 1 from the La Cantera Formation are of the lepisosteoid type with multiple ganoïne layers, canaliculi of Williamson (Schultze, 1966,

2015; Sire et al., 2009) in the basal bony layer, and no dentine. The surface of the flank scales is smooth, and microscopically it is bare of tubercles or denticles. This condition is shared with certain teleosts, such as *Pholidophorus latiusculus* and *Pholidoctenus serianus* (Arratia, 2013). Contrarily, aspidorhynchids in general present flank scales with macroscopic ganoïne ridges and microscopic ornamentations of ganoïne tubercles. The genus *Aspidorhynchus* is the exception, having scales devoid of ganoïne (Schultze, 1966; Brito, 1997; Brito and Meunier, 2000; Bartholami, 2004; Gouiric-Cavalli, 2015; Schultze and Arratia, 2015). Pachycormiformes have generally tiny flank scales with very thin ganoïne, which may even be missing (Schultze, 1966; Arratia and Schultze, 2013; Gouiric-Cavalli and Cione, 2015). Body scales are absent in the Triassic teleosteomorph *Prohalecites porroi* (Tintori, 1990).

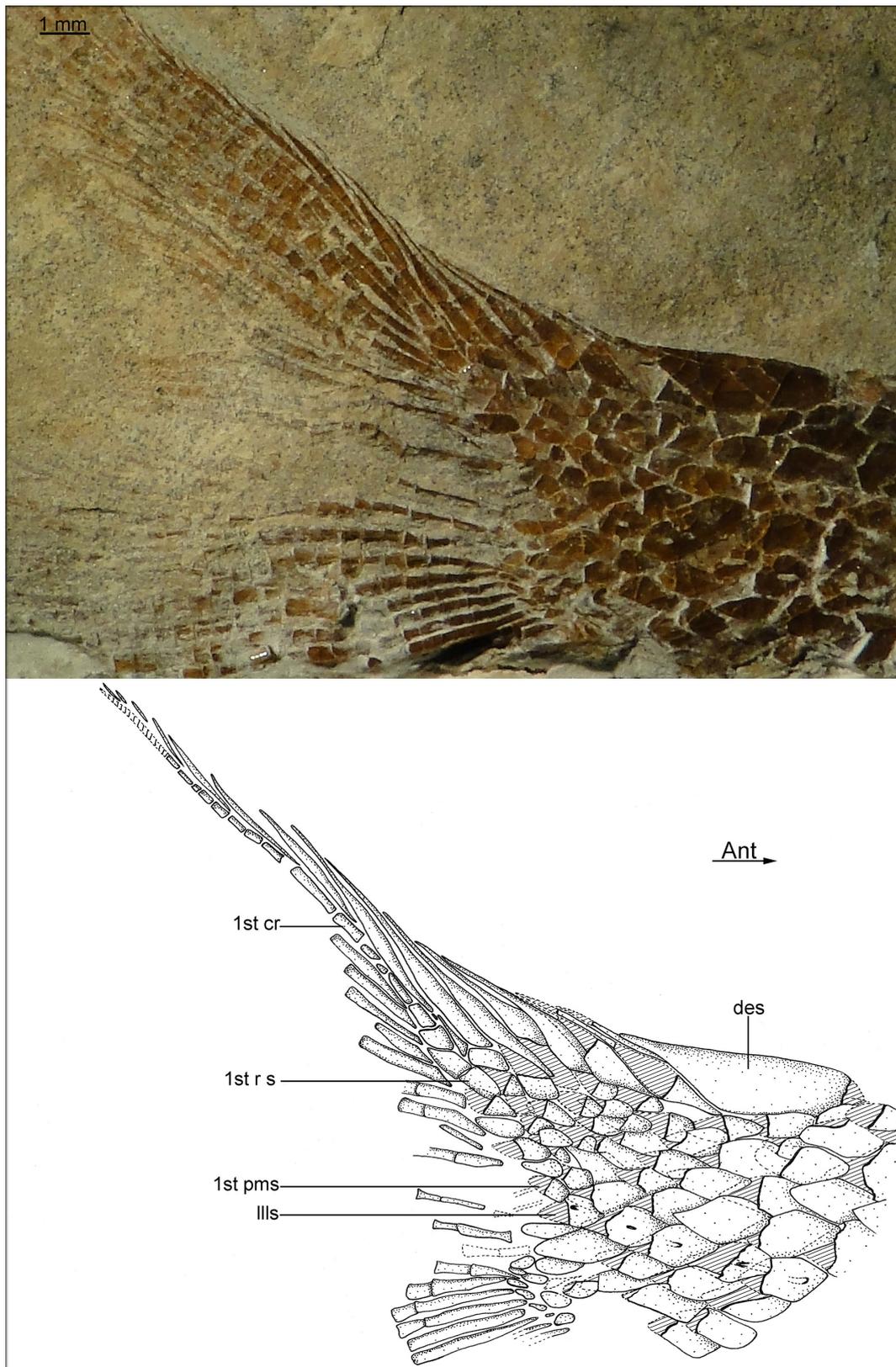


Figure 12. Picture and camera lucida drawing of caudal fin squamation of *Teleosteomorpha* n. sp. 1 (MIC V523). Dorsal lobe shows the base of the first principal ray covered by scales. Note the dorsal scute preceding caudal fin; ant, anteriad; des, dorsal caudal scute; Ills, last lateral line scale; 1st cr, first caudal ray; 1st r s, first ray scales; 1st pms, first posterior margin scale.

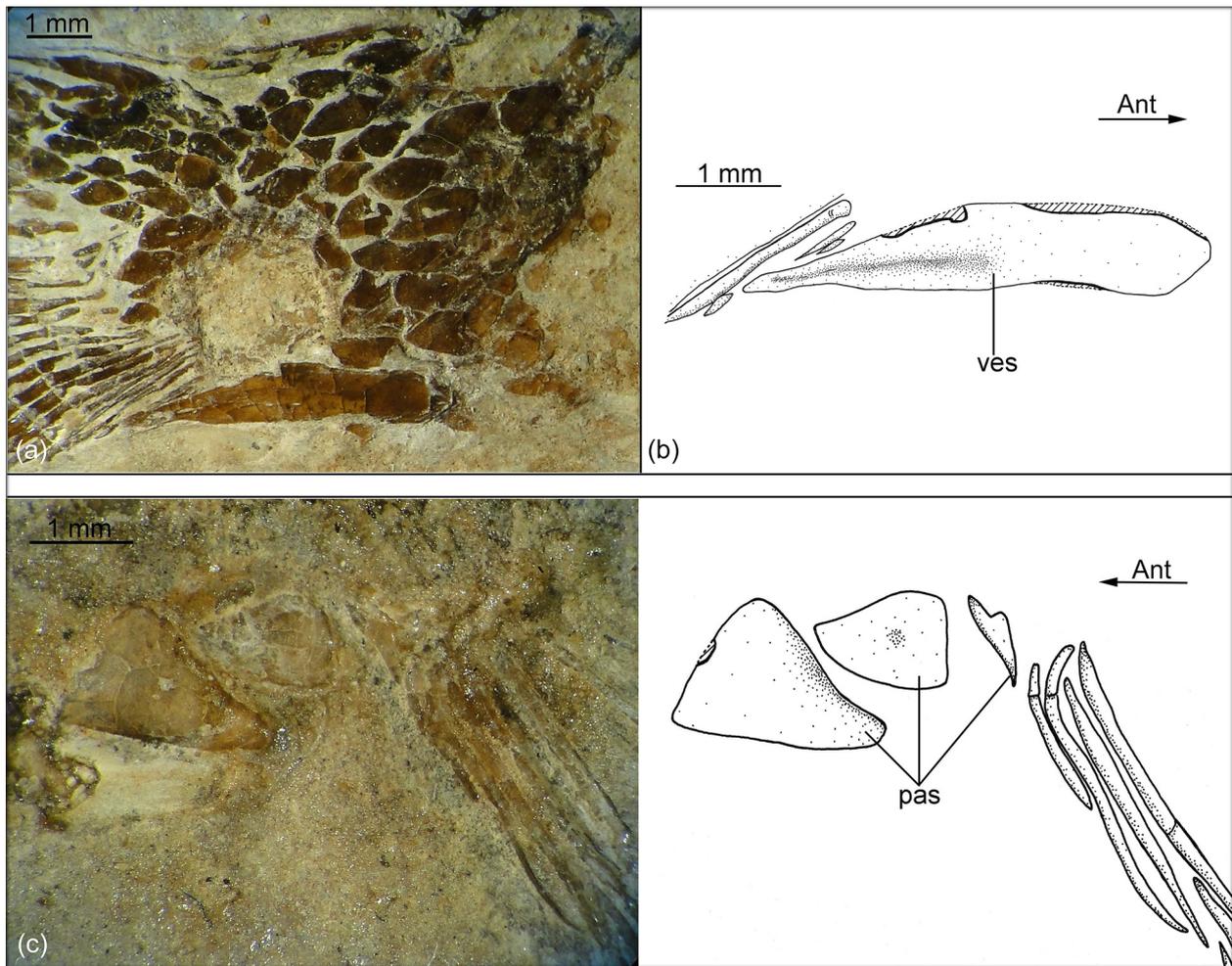


Figure 13. Scutes of *Teleosteomorpha* n. sp. 1. (a) Ventral scute preceding caudal fin in specimen MIC-V662. (b) Camera lucida drawing of scute in detail. (c) Pre-anal scutes in specimen MIC-V519a; ant, antierid; pas, preanal scutes; ves, ventral caudal scute.

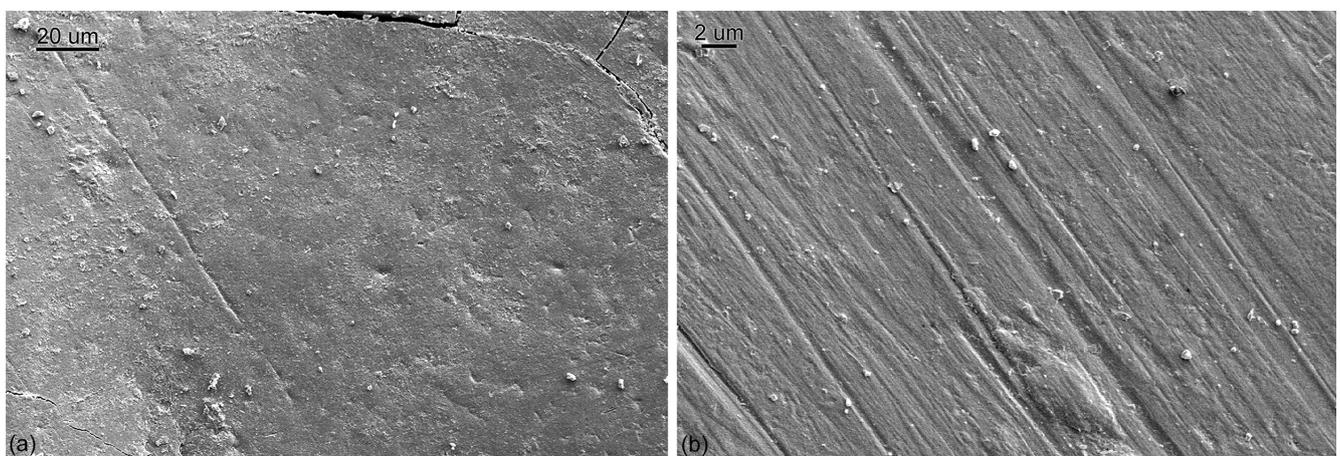


Figure 14. (a) SEM photograph of flank scale of *Teleosteomorpha* n. sp. 1 (sample "T-5.5"). (b) SEM photograph of flank scale of *Teleosteomorpha* n. sp. 1 (MIC-V706).

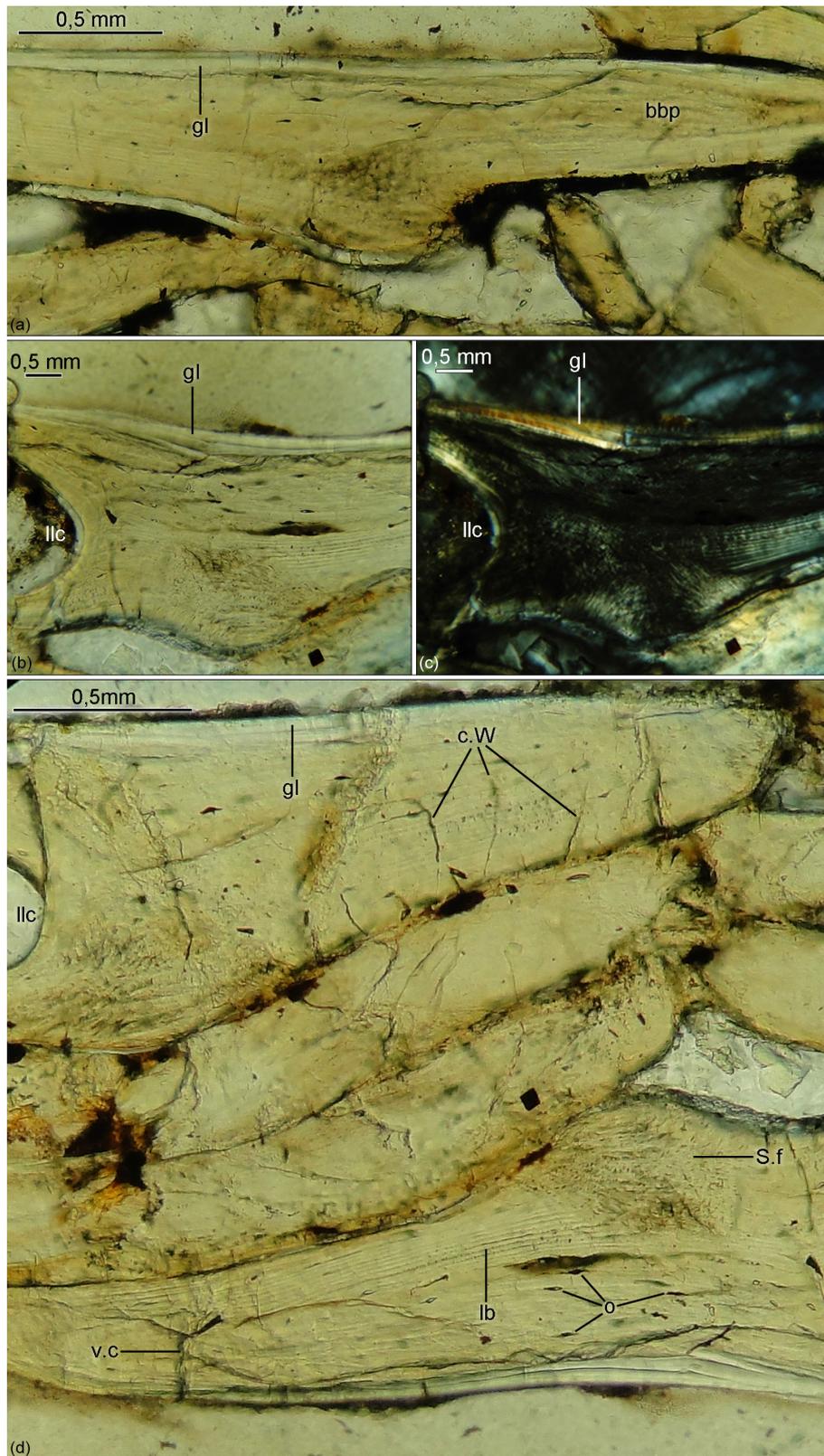


Figure 15. Histological slides of *Teleosteomorpha* n. sp. 1 (specimen MIC-V523) observed under petrographic microscope. (a) Lepisosteoid-scale type. (b) Multiple ganoine layers under normal light. (c) Multiple ganoine layers under polarized light. (d) Ganoine and basal bony plate with all the lepisosteoid features; bbp, basal bony plate; c.W, canaliculi of Williamson; gl, ganoine layers; lb, laminar bone; llc, lateral line canal; o, lacunae (osteocyte spaces); sv.c, vascular canal; S.f, Sharpey's fiber.

The presence of ganoid scales with peg-and-socket articulation is also a common feature of holostean neopterygians, such as semionotiforms, lepisosteiforms, and macrosemiiforms (Schultze, 1966, 1996, 2015). Ganoid scales of *Teleosteomorpha n. sp. 1* of the La Cantera Formation present a well-developed dorsal peg, but they lack an anterodorsal process. The same pattern occurs, for example, in the Macrosemiiformes (e.g., *Macrosemius*, *Propterus*, and *Legnonotus*; Schultze, 1966; Vullo et al., 2009); however, this pattern differs from lepisosteiforms and most semionotiforms (e.g., Cavin et al., 2009; López-Arbarello, 2012; Gibson, 2013), which possess anterodorsal or anteroventral processes. Stem teleosts and a few more advanced ones with ganoid scales also present a peg for articulation in a dorsal position (e.g., *Vinctifer comptoni*, *Jonoichthys challwa*, *Pholidophorus latiusculus*, *Knerichthys bronni*, *Pholidoctenus serianus*, *Catervariollus hornemani*, *Siemensichthys macrocephalus*, and *Dorsetichthys bechei*; Schultze, 1966; Brito, 1997; Arratia, 2000, 2013; Taverne, 2011; Gouiric-Cavalli, 2015).

Teleosteomorpha n. sp. 1 presents deeper than long flank scales in their preanal region, as in other *Teleosteomorpha* with ganoid scales (see Schultze, 1966; Brito, 1997; Brito and Ebert, 2009; Bartholomai, 2004; Arratia, 2000, 2013; Gouiric-Cavalli, 2015). Even though most of the scales studied have straight margins, some have a sinuous posterior margin on the same specimen. In this sense, these scales resemble the scales of some species of the Triassic family Pholidophoridae (Zambelli, 1977; Arratia, 2013). Unique to the fishes from the La Cantera Formation is the undulating ventral margin of the scales (Fig. 3).

The thick, round scales in the ventral margin of the preanal region are ganoid scales and not elasmoid scales, in contrast to the round amioid scales in the anteroventral part of the body of Macrosemiiformes. There are amioid scales in the gular region of some species of macrosemiiforms and, furthermore, there are ganoid scales on the flanks of the same individual (e.g., *Macrosemius rostratus*, *Propterus microstomus*, and *Notagogus denticulatus*; Schultze, 1966; Bartram, 1977; Arratia and Schultze, 2012).

The most dorsal scales of the flank are unique to *Teleosteomorpha n. sp. 1* from the La Cantera Formation in being paired structures. Most basal neopterygians have a row of unpaired, bilaterally symmetrical ridge scales in the dorsal midline. For example, these dorsal ridge scales are characteristically elongated into a spine in the family Semionotidae (Olsen and McCune, 1991; López-Arbarello, 2012; Gibson, 2013). Paired scales like those present in *Teleosteomorpha n. sp. 1* from the La Cantera Formation have not been reported in any other neopterygian. Indeed, this structure could be considered an autapomorphic character of this South American species.

Ganoine-covered scutes around the anus are not known among stem-group teleosts such as pachycormiforms, aspidorhynchiforms, *Prohalecites*, and more derived teleosts

including Pholidophoridae and other related groups. However, these structures are common among holosteans, such as Semionotiformes, Lepisosteiformes (Bürgin, 2004; Lombardo and Tintori, 2008; Grande, 2010; Cavin et al., 2013), and Macrosemiiformes (Schultze, 1966; Bartram, 1977; Bravi, 1994; González-Rodríguez and Reynoso, 2004; González-Rodríguez et al., 2004; Arratia and Schultze, 2012). In this character, *Teleosteomorpha n. sp. 1* from the La Cantera Formation resembles non-teleosteomorph neopterygians.

Ganoine-covered scutes preceding the caudal fin are known within Halecomorpha in general, for example *Watsonulus eugnathoides*, *Ophiopsiella attenuata* (= *Ophiopsis attenuata*), *Cipaclichthys scutatus*, and *Teoichthys brevipina* (Grande and Bemis, 1998; Arratia, 2008; Brito and Alvarado-Ortega, 2013; Machado et al., 2013; Lane and Ebert, 2015). These scutes occur in numbers of two to four and generally on both dorsal and ventral margins of the caudal fin. There are also some examples of halecomorphs with a unique dorsal and ventral scute associated with the caudal fin, such as *Ophiopsis muensteri* (= *Furo muensteri*), *Ophiopsiella procera* (= *Ophiopsis procera*), "*Furo*" *longiserratus*, and *Eurypoma grande* (Schultze, 1966; Arratia and Schultze, 2007; Arratia, 2008; Lane and Ebert, 2012, 2015). In stem-group teleosts and most derived teleosts, it is more common to find one scute associated with the dorsal, ventral, or both margins of the caudal fin. Such scutes in *Teleosteomorpha* are proportionally much larger than those found in Halecomorpha. Some examples among *Teleosteomorpha* are the Triassic fish *Prohalecites porroi* (Tintori, 1990; Arratia and Tintori, 1999), the Cretaceous species herein studied, and aspidorhynchids and pachycormids, with certain species even presenting more than one scute (Arratia and Lambers, 1996; Arratia, 2008; Arratia and Schultze, 2013). Other examples of the presence of caudal scutes among Teleostei at basal nodes are some species of the family Pholidophoridae (e.g., *Pholidophorus gervasuttii*, *Knerichthys bronni*, and *Parapholidophorus nybelini*), the Jurassic fish *Dorsetichthys bechei*, members of the Siemensichthys group, and *Catervariolus hornemani* (Arratia, 2000, 2013; Arratia and Schultze, 2007; Taverne, 2011). The caudal fin of these fishes is preceded by a prominent epaxial scute and a large hypaxial scute – that is, large in comparison to the size of dorsal or ventral basal fulcra. The scutes are covered by ganoine in all these groups. As a rule, the dorsal caudal scute is larger than the ventral one (Arratia, 2008). In contrast, *Teleosteomorpha n. sp. 1* from the La Cantera Formation presents both scutes of almost the same size.

Rhombic, modified ganoid scales covering parts of the bases of the upper epaxial caudal rays were defined as urodermals by Patterson (1968) and Arratia and Schultze (1992). The base of the uppermost caudal principal fin ray in specimens of *Teleosteomorpha n. sp. 1* from the La Cantera Formation is covered by a row of scales that cannot be considered as urodermal-like elements. Urodermals have

been described among teleosteomorphs for *Prohalecites porroi* (Tintori, 1990; Arratia and Tintori, 1999) and certain Pachycormiformes, for example *Euthynotus* and *Sauropsis* (Arratia and Lambers, 1996; Arratia and Schultze, 2013), but not for Aspidorhynchiformes. The presence of urodermals is also shared with other groups of Neopterygii, such as certain species of Macrosemiiformes, Lepisosteiformes, and Semionotiformes (Bartram, 1977; Arratia, 2008; López-Arbarello, 2012).

The analysis of the morphological diversity of scales within Neopterygii could provide a set of characters to be used for interspecific differentiation and to show patterns of separation at higher taxonomic levels.

6 Conclusions

As in most other basal neopterygians, the fishes described herein show ganoid scales of the lepisosteoid type. The scales of *Teleosteomorpha* n. sp. 1 from the La Cantera Formation share many common features with other teleosteomorphs in their shape and arrangement. One of the most significant characters is the presence of a prominent scute preceding the dorsal margin of the caudal fin. Unique to the fishes studied here are deep paired dorsal scales with rounded dorsal margins and the lack of median dorsal ridge scales. Among features that *Teleosteomorpha* n. sp. 1 shares with holosteans are ganoine-covered scutes related to the anal fin.

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