
Volume 30, issue 3, June 2009 ISSN 0195-6671
ELSEVIER
CRETACEOUS
RESEARCH

Cretaceous Research 30 (2009) 727–748

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Description of *Aetostreon pilmatuegrossum* sp. nov. from the Lower Cretaceous of Argentina (Neuquén Basin), and significance of the conservative left valve morphology in oysters of the genus *Aetostreon* Bayle

A.E. Rubilar [a], D.G. Lazo [b,*]

[a] *Sección Paleontología y Estratigrafía, Servicio Nacional de Geología y Minería, casilla 10465, Santiago, Chile*
[b] *Departamento de Ciencias Geológicas, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, 1428 Buenos Aires, Argentina*

ARTICLE INFO

Article history:
Received 3 June 2008
Accepted in revised form 26 December 2008
Available online 6 January 2009

Keywords:
Ostreoidea
Aetostreon
Taxonomy
Lower Cretaceous
Neuquén Basin
Argentina

ABSTRACT

Aetostreon pilmatuegrossum sp. nov., a large and very convex ostreid from the Pilmatué Member of the Agrio Formation (Neuquén Basin, Argentina), is described based on specimens recovered from upper Valanginian beds of the *Pseudofavrella angulatiformis* and *Neocomites* sp. ammonite subzones. This work also includes a general morphologic discussion of the well-known Lower Cretaceous oysters from Europe, Asia and Africa, most of them considered synonymous of *Aetostreon latissimum* (Lamarck) in the last decades. The left valves of these oysters share a set of morphological characters that seems to respond to a very distinct but conservative anatomical pattern inherited from their direct ancestor, instead of evidence for their taxonomic uniformity at the species level. Specifically, they show differences in several characters and/or their degree of development and co-occurrence in a particular growth stage, which probably have systematic value, as in the species here described. *Aetostreon pilmatuegrossum* sp. nov. is probable closely related to an undescribed lower Valanginian species recorded in the Chachao Formation of the Neuquén Basin, and also has affinities with an association of Barremian oysters from South Africa that seems to be its direct descendant.

1. Introduction

Ostreids of the genus *Aetostreon* Bayle are frequently recorded from the Lower Cretaceous of Argentina and Chile and were studied mainly during the end of the nineteenth and middle of the twentieth centuries. Generally, they have been assigned to European species (*e.g. A. latissimum* (Lamarck), the updated classical identification) or even to new taxa, based on rare and poorly preserved specimens (*e.g.* Bayle and Coquand, 1851; Hupé, 1854; Behrendsen, 1891, 1922; Philippi, 1899; Burckhardt, 1900a,b; Stanton, 1901; Haupt, 1907; Weaver, 1931; Leanza and Castellaro, 1955).

Several authors have suggested relative taxonomic uniformity for many of the Cretaceous oysters of the genus *Aetostreon*, recorded primarily from the Tethyan regions of Europe, Asia and Africa, lumping them under the species *A. latissimum* (Lamarck) (e.g. Newton, 1924; Cox, 1954; Pugaczewska, 1975; Dhondt and Dieni, 1988; Cooper, 1995). As a result, this species has a long stratigraphic record and an extensive geographic distribution, restricting its chrono-stratigraphic utility.

Nevertheless, recent mainly unpublished studies of the abundant and well-preserved Upper Jurassic and Lower Cretaceous specimens of *Aetostreon* recorded in Argentina (Rubilar *et al.*, 2000a,b; Rubilar and Lazo, 2003) and Chile (Rubilar, 2003) have allowed the recognition of persistent differences in the development of several characters of the left valve in many assemblages, obtained through an accurate stratigraphic sampling. These features probably have taxonomic significance beyond similarity of the shells and the broad morphological plasticity of these oysters.

The objective of this work is to describe a large species of *Aetostreon* recorded in west-central Argentina (Fig. 1). Considering its close morphological affinities with *Aetostreon latissimum* (Lamarck) and its putative synonyms, the taxonomic discussion starts with a general analysis of their common morphological pattern (based on a literature review), pointing out morphological differences and probable taxonomic and phylogenetic significances.

The classification and type of the ligament area are based on Malchus (1990). The hinge axis was taken as the reference for shell orientation and measurements (Stenzel, 1971). The most prominent or projected structure of the left valve in many Nanogyrini has been named as keel, carina or ridge (*e.g.* Stenzel, 1971; Malchus and

* Corresponding author.
E-mail address: dlazo@gl.fcen.uba.ar (D.G. Lazo).

0195-6671/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.cretres.2008.12.013

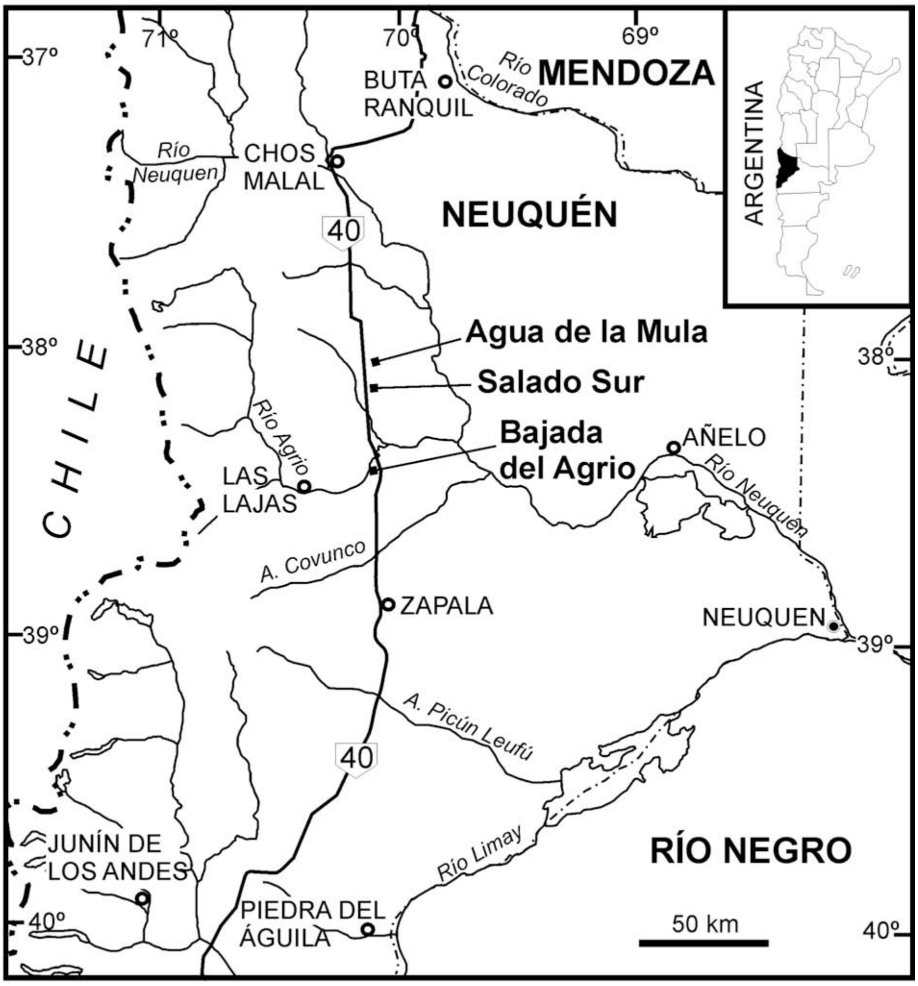


Fig. 1. Map of the Neuquén Basin showing the location of fossil localities.

Aberhan, 1998). In order to precise the morphological changes that occur along the growth in several representatives of *Aetostreon*, including the new species, we refer as the main convexity the strongly convex zone or keel developed in a particular growth-stage (*e.g.* Rubilar, 2005), which forms the 'most convex zone' in the adult stage.

The described and figured specimens are deposited in the Paleontology Collection of the Area de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (CPBA). Each catalogue number and suffix refers to a sample and a particular specimen, respectively, obtained from a particular stratigraphic section and level.

1.1. Location, geological setting, and age

The studied oysters were collected from the Pilmatué Member of the Agrio Formation, which crops out extensively in the Neuquén Basin, with variations in thickness, lithology, and fossil content (Marchese, 1971). The basin is a stratigraphically and economically important latest Triassic to early Cenozoic depocentre, located in west-central Argentina (32°–40° S), that comprises more than 4000 m of continental and marine siliciclastic, carbonate, and evaporitic deposits (Legarreta and Gulisano, 1989).

The stratotype of the Agrio Formation, which consists of three members, has a maximum thickness of 1600 m. The Pilmatué (lower) and Agua de la Mula (upper) members consist of marine shales, sandstones, and limestones, whereas the Avilé (middle) Member is a fluvial to aeolian sandstone deposited during a major regression in the middle Hauterivian. The marine members of the Agrio Formation represent mixed siliciclastic-carbonate sedimentation and have been interpreted as storm influenced shoreface to offshore settings (Lazo, 2006a). A refined ammonoid biostratigraphy indicates a range from the lower Valanginian to Lower Barremian for the whole unit (Aguirre-Urreta *et al.*, 2007). This zonation is easily followed from the north to south ends of the basin and has allowed biostratigraphic constraints of the recorded oysters.

Weaver (1931) described the abundant fauna of the Agrio Formation, composed principally of marine invertebrates (bivalves, gastropods, nautiloids, ammonoids, corals, crustaceans, echinoderms and serpulids), diverse trace-fossil, and scarce vertebrate remains. Studies on the bivalve fauna had been focused solely on trigonioid taxonomy (see Leanza, 1993), although recent analyses encompasses the taxonomy, taphonomy and palaeoecology of a number of bivalve groups such as bakevelliids, inoceramids and pholadomyids (Lazo 2003a,b, 2006b, 2007a). A list of the bivalves collected in the Pilmatué Member and their palaeoecological significance can be found in Lazo (2007b).

Remarkably, oysters from the Agrio Formation have never been described in detail. The studied specimens were collected from the Pilmatué Member, at three localities in central Neuquén: Agua de la Mula, Salado Sur, and Bajada del Agrio (Fig. 2). They represent

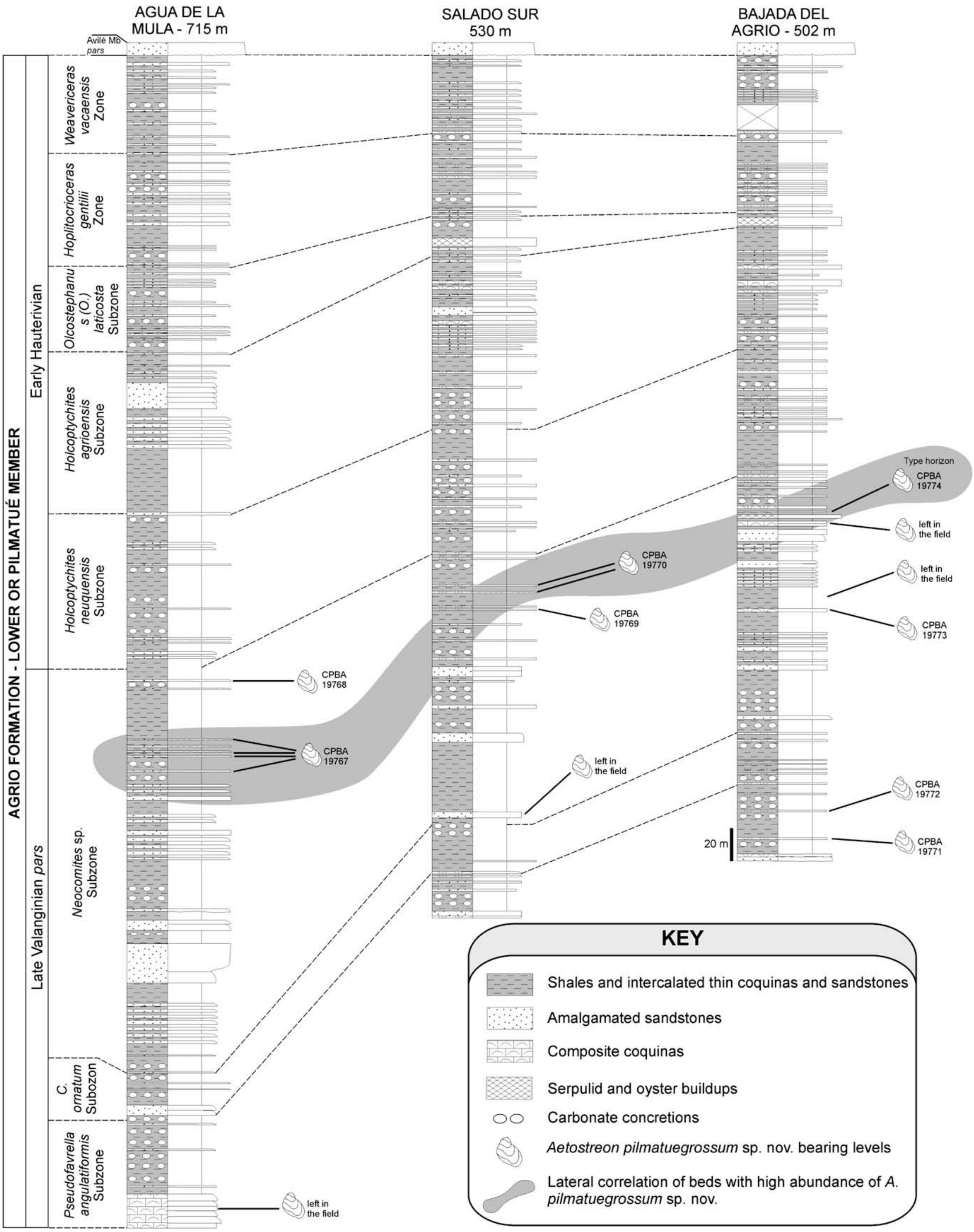


Fig. 2. Stratigraphic sections of the Pilmatué Member of the Agrio Formation in Agua de la Mula, Salado Sur and Bajada del Agrio (Neuquén Basin, Argentina), showing the occurrence of *Aetostreon pilmatuegrossum* sp. nov. Shaded zone indicates highest abundance of this species in the measured logs. Ammonite zonation and age from Aguirre-Urreta et al. (2007).

a 44.2 km km north-south transect (Fig. 1), and comprise mixed siliciclastic carbonate deposition on a gently, northward dipping marine shelf. The studied specimens of *Aetostreon pilmatuegrossum* sp. nov. were obtained in levels biostratigraphically assigned to the upper Valanginian *Pseudofavrella angulatiformis* and *Neocomites* sp. ammonite subzones (Fig. 2).

The entire Agrio Formation is well exposed in the northern and southern Salado range (Agua de la Mula and Salado Sur, respectively). Agua de la Mula (S38° 04.070′, W70° 0.1032′) can be accessed from national road 40 along a gravel road that leads to a dry oil well. It is the type locality of the upper member. Salado Sur (S38° 12.913′, W70° 0.3227′) can be accessed from road 40 along a gravel road that leads to Pampa Amarga. Finally, Bajada del Agrio (S38° 27.262′, W70° 04.844′) is located some 5 km south-west from Bajada del Agrio village. The Agrio Formation is well-exposed in the slopes adjacent to gravel road 10.

2. Summary of *Aetostreon* bearing facies, taphonomy, and paleoenvironments

Aetostreon pilmatuegrossum sp. nov. is a scarcely recorded species in the Pilmatué Member of the Agrio Formation in comparison to other epifaunal bivalves. For instance, *Mimachlamys robinaldina* (d'Orbigny) and small sized oysters belonging to *Amphidonte* (Ceratostreon) Bayle are usually abundant in many levels. The studied specimens were collected from a variety of shell beds ranging from thin pavements to thick amalgamated shell beds in the scale of tens of meters. Accordingly, the shell condition varied from pristine articulated shells to fragments. The best specimens were recorded in pavements embedded in dark-grey shales of the *Neocomites* sp. subzone, where *A. pilmatuegrossum* sp. nov. peaks in abundance (shaded zone in Fig. 2). These pavements are tabular and readily recognized in the field. They can be laterally followed from Agua de la Mula to Bajada del Agrio. Specimens were recorded out of life position in different shell orientations. Shell condition is pristine, but articulated and disarticulated specimens were recorded. They show low degrees of fragmentation, dissolution and abrasion, contrary to significant encrustation and bioerosion. Cyclostomes colonies, serpulids, small oysters and plicatuloids were found encrusting the external surfaces. The associated fauna also include nautiloids and a diverse bivalve assemblage (see Lazo, 2007b).

Sedimentologic and taphonomic data suggest an autochtonous to slightly parautochtonous origin of the pavements, corresponding to within-habitat time averaged assemblages. *Aetostreon pilmatuegrossum* sp. nov. lived in muds in an inner shelf environment frequently disturbed by distal storm processes. Pavements probably represent small scale transgressive surfaces occurring in the transgressive system tract (see Lazo, 2006a).

In particular, pavements of A. *pilmatuegrossum* sp. nov. were recorded in association with serpulid mass aggregations from the *Neocomites* sp. subzone in Bajada del Agrio (Lazo, 2007c). These aggregations are lenses mainly composed of *Parsimonia antiquata* (Sowerby) in a gregarious life habit, reaching 2 m of maximum thickness. They were used as surface for attachment by some specimens of *A. pilmatuegrossum* sp. nov. (Fig. 11D). Recent mass aggregations of serpulids occur in stressed aquatic settings as for example lagoons, bays, and fiords. They can acquire a gregarious life habit under a range of salinities, from brachyhaline to hyperhaline waters (Ten Hove and van den Hurk, 1993). However, oxygen isotopic data analyzed from oyster shells were used to calculate paleosalinities. Results indicated that euhaline waters prevailed through the deposition of the *Neocomites* sp. subzone (see Lazo *et al.*, 2008).

3. Systematic Paleontology

Superfamily Ostreoidea Rafinesque, 1815

Family Gryphaeidae Vialov, 1936

Subfamily Exogyrinae Vialov, 1936

Tribe Nanogyrini Malchus, 1990

Genus *Aetostreon* Bayle, 1878

Type species: *Gryphaea latissima* Lamarck, 1801, p. 399; 1819, p. 199.

Aetostreon pilmatuegrossum sp. nov.
Figs. 3–14
1899 *Exogyra Couloni* ? Defr. Philippi, p. 16, Pl. 7, figs. 1a–c.
2007b *Aetostreon* sp. Lazo, Fig. 4H, I.
2008 *Aetostreon* sp. Lazo et al., Fig. 2A-C.

Etymology: the specific name is a combination of 'Pilmatué' (the stratigraphic unit where the material is present) and *grossus* (Latin): big.

Age: Late Valanginian, *Pseudofavrella angulatiformis* and *Neocomites* sp. ammonite subzones (Aguirre-Urreta *et al.*, 2007).

Type locality and horizon: Bajada del Agrio (Neuquén, Argentina); 212 m above the base of the Pilmatué Member, *Neocomites* sp. Subzone (Fig. 2).

Holotype: CPBA 19774.25 (Fig. 3, Fig. 12B, D–E). Adult specimen collected by D. Lazo (measurements in Table 1).

Paratypes: 28 specimens (Figs. 4–11, 12A, C); 8 from Agua de la Mula (CPBA 19767, 19767.1, 5, 8, 13, 26, 28, 30), 7 from Salado Sur (19769; 19770.1–2, 5–7,13), and 13 from Bajada del Agrio (19771.2, 7; 19772.3, 5; 19774.0, 4–5, 8, 20, 23, 26, 31–32).

Additional material: more than 69 specimens. Catalogue numbers: CPBA 19767 and 19768 (Agua de la Mula); CPBA 19770 (Salado Sur); CPBA 19771–19774 (Bajada del Agrio).

Diagnosis. Large oysters (maximum height *ca.* 138 mm). The left valve is very prominent and tends to have a subtrigonal outline, with a very wide and truncated posteroventral margin. The anterior flank is formed by a high and globoid convexity next to the anterior margin, followed by a deep sulcus. A primary keel with well defined tubercles is restricted to the umbonal region. In later growth stages, the most convex zone of the valve is formed by a very wide, irregular and elevated secondary keel, limited in the ventral third by a narrow anterior margin.

Description. The studied specimens are very large to medium sized, with a maximum height of at least 138 mm (Table 1). The left valve is very prominent and is more robust in its mid and ventral thirds. It is wide to very wide (H/L *ca.* 1,0–1,4) and has mainly a subtrigonal outline; subovoidal in some specimens.

The dorsoanterior margin is little convex or almost straight, with a small concavity. Its length is variable, depending on the development of a well-defined anterior geniculation. The posteroventral margin is wide and truncated, with a slightly convex to almost straight outline (Fig. 3, Fig. 4F, G, Fig. 5F, G Fig. 6E, G, Fig. 7C, E, Fig. 8C, H, Fig. 11D, Fig. 12A, B).

The shell convexity near the anterior margin tends to be very high in the dorsal half of the valve, or inclusive up to its ventral third. It is formed by a very wide and rounded anterior globoid convexity (Fig. 3, Fig. 4A, D, G, Fig. 6A, D, Fig. 7B, E, Fig. 8A, E, Fig. 9A, C, D, Fig. 10B, C, D, Fig. 11A, C, Fig. 12A, B, C, D), which is linked with a well-defined anterior geniculation. In very few specimens this zone is slightly convex (Fig. 8G). In the rest of the anterior flank of the valve there is a wide and deep sulcus, well defined in the ventral third (Fig. 3).

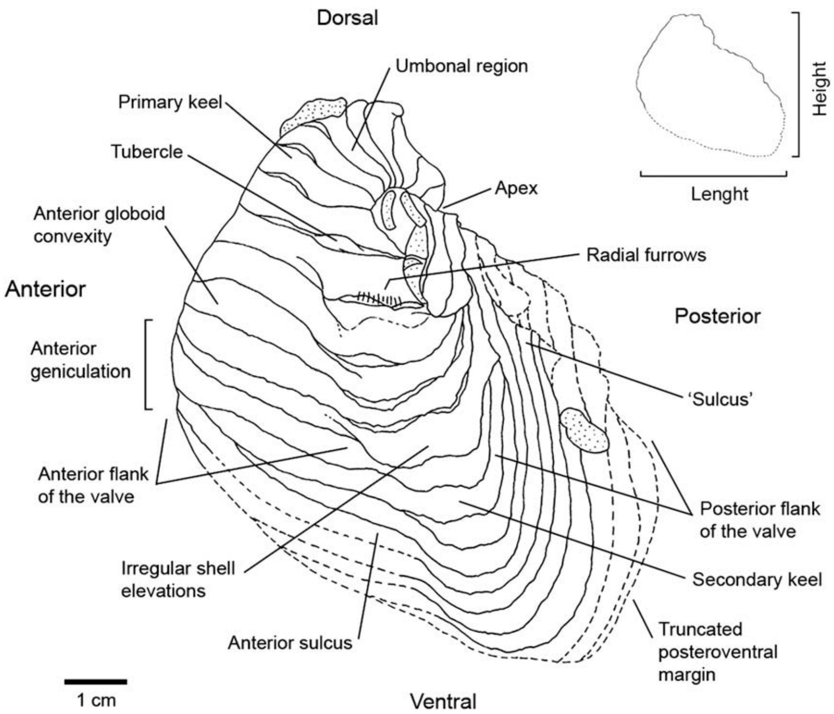


Fig. 3. Shell morphology of *Aetostreon pilmatuegrossum* sp. nov., and terminology of the left valve used throughout the text. External view based on the holotype, CPBA 19774.25, with a subtrigonal outline.

In the initial growth stages, the main convexity of the valve is relatively narrow and is located near of the dorsoanterior margin. This primary (umbonal) keel has a discontinuous and irregular growth, with abrupt shell elevations (Fig. 3, Fig. 4B, Fig. 5D, 6B, D, Fig. 7B, Fig. 8E, Fig. 9C, Fig. 10B, E, Fig. 11C, Fig. 12E). In few specimens it is linked with a prominent and almost flat surface that covers the umbonal region (Fig. 3, Fig. 12B).

The primary keel is replaced, more or less abruptly, by a very wide and prominent secondary keel, at the same height where the anterior globoid convexity starts its development (Fig. 3). In most specimens it is located nearer to the posterior margin, has a straight or slightly curved trajectory, and its width increases very slightly with growth. The secondary keel is well delimited by a narrow anterior margin and a subvertical surface (Fig. 3, Fig. 4D, Fig. 6A, G, I, Fig. 7C, D, E, Fig. 8H, Fig. 12A, B) in the ventral third of the valve, and they may produce a curvature of the shell (or notch) in the ventral commissure (Fig. 7A). In most of the specimens the external surface has wide and irregular shell elevations (Fig. 3), which vary in shape, size and prominence (Fig. 4A, G, Fig. 5C, Fig. 6C, Fig. 12B); nevertheless, this surface may be uniform and almost flattened (Fig. 7E). The posterior flank of the secondary keel tends to be very wide and smooth and cover the posterior flank of the valve (Fig. 3); in some specimens this structure has a well defined posterior margin (*e.g.* Fig. 6A). The external surface and the posterior flank of the secondary keel form the truncated posteroventral margin in the commissure.

The sulcus and posterior flange are not well-developed. The sulcus may be represented by a narrow or wide groove (Fig. 4G, Fig. 6A, E), and the posterior flange by a lobe (Fig. 8A).

The umbonal region is generally narrow and little prominent. It has a variable convexity in different specimens, although it tends to be smaller than the rest of the valve. The coiling ranges from strongly to slightly opisthogyrate (Fig. 3).

The attachment area is very small or imperceptible in most of the studied specimens; in some it is very large and is located on the posterior surface of the umbonal region (Fig. 5G, Fig. 10D, Fig. 11D), or even on the dorsal external surface of the valve (Fig. 8C, G). The shell is thick (about 35 mm in larger specimens; *e.g.* CPBA 19770.1, Fig. 7E) or very thick (almost 63 mm in CPBA 19774.23, Fig. 10D) in the dorsal half.

The external surface is very irregular. Growth lamellae are well defined on the most convex surface and the dorsal part of the posterior flank of the valve. Some specimens have a narrow or wide "auricle" or "wing" near the apex (Fig. 4C, Fig. 6G, Fig. 7C, E, Fig. 8C, Fig. 12B). Several growth lines form almost rounded tubercles or small concentrations of shell on the primary keel (Fig. 4B, Fig. 6B, Fig. 10B, Fig. 12E) but also on the anterior margin of the secondary keel (Fig. 4D, G, Fig. 5A, G, Fig. 6A, G, Fig. 12B). Small and low relief radial furrows are restricted to the surface of the imbricating lamellae (Fig. 4D, Fig. 5A, Fig. 7E, Fig. 12B, Fig. 13A).

The ligament area is elongated or very elongated in different specimens, and is running out of the commissure plane (exogyroid type). The initial coiled region is restricted to the first stage of growth of the valve, and the later uncoiling growth is posteriorly curved or straight (similar to the gryphaeoid type) (Fig. 4E, Fig, 5B, Fig. 6F, Fig. 7A, Fig. 8D, F, Fig. 9B, Fig. 10F, Fig. 12E). The anterior and posterior bourrelets are well defined.

The adductor muscle scar is big, ovate or subcircular (higher than long), with a truncated anterodorsal margin (Fig. 7A, Fig. 12E). It lacks a buttress and is located closer to the dorsoposterior margin, in the mid third or in the dorsal half of the valve. The umbonal cavity is absent. The paradontal depression (Fig. 8D, Fig. 12E) and recess are only well defined in some specimens. The commissural shelf is smooth, wider adjacent to the dorsoposterior margin (Fig. 5B, Fig. 6F).

The microstructure of the shell is dominated by chambers, and the solid part is composed by branching cross foliation (Fig. 14).

The right valve is slightly concave or flattened, thicker in the dorsoanterior region. One specimen shows narrow and raised radial striae in several part of the external surface (Fig. 8B; Fig. 13B).

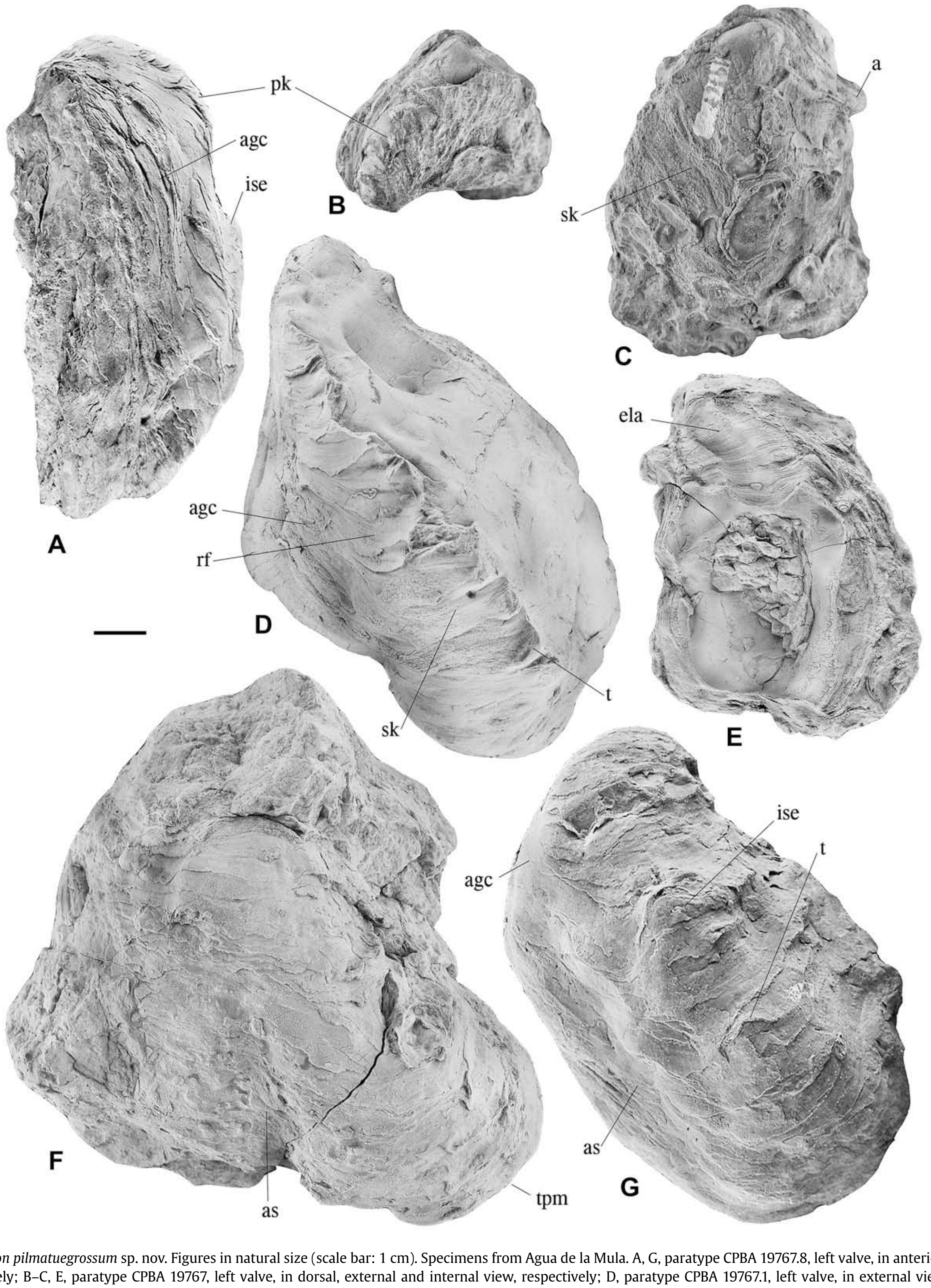


Fig. 4. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Agua de la Mula. A, G, paratype CPBA 19767.8, left valve, in anterior and external view, respectively; B–C, E, paratype CPBA 19767, left valve, in dorsal, external and internal view, respectively; D, paratype CPBA 19767.1, left valve, in external view; F, paratype 19767.13, left valve, in external view. a: 'auricle'; agc: anterior globoid convexity; as: anterior sulcus; ela: exogyroid ligament area; ise: irregular shell elevation; pk: primary keel; rf: radial furrows; sk: secondary keel; t: tubercle; tpm: truncated posteroventral margin.

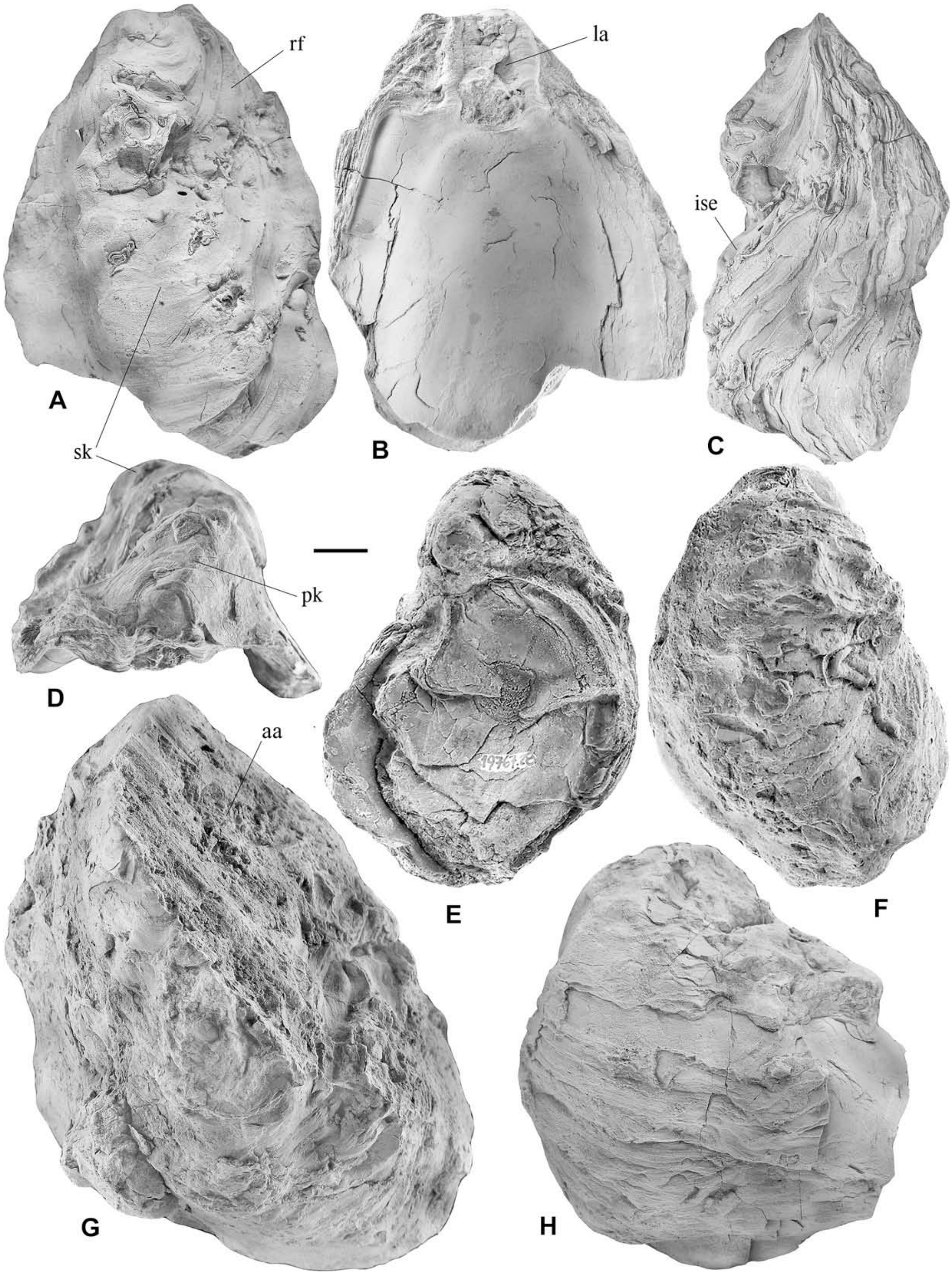


Fig. 5. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Agua de la Mula. A–D, paratype CPBA 19767.26, left valve, in external, internal, posterior and dorsal view, respectively; E-F, paratype CPBA 19767.28, E right valve, in external view, F left valve, in external view; G, paratype CPBA 19767.5, left valve, in external view; H, paratype CPBA 19767.30, left valve, in external view. aa: attachment area; ise: irregular shell elevation; la: ligament area; pk: primary keel; rf: radial furrows; sk: secondary keel.

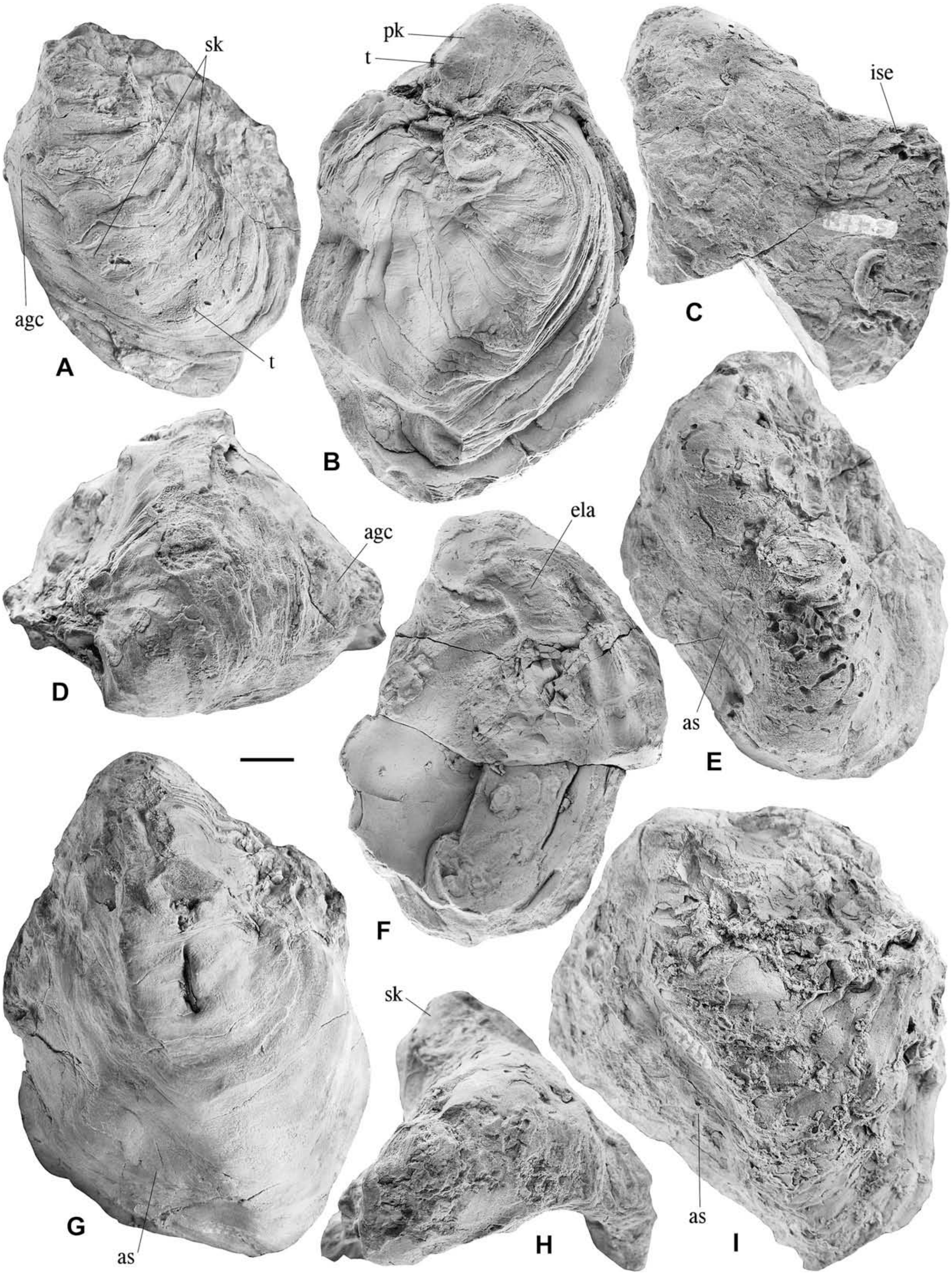


Fig. 6. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Salado Sur. A, paratype CPBA 19770.13, left valve, in external view; B, D, G, paratype CPBA 19770.6, B, right valve, in external view, D, G, left valve, in dorsal and external view, respectively; C, E-F, H, paratype CPBA 19770.5, left valve, in anterior, external, internal and dorsal view, respectively; I, paratype CPBA 19770.2, left valve, in external view. agc: anterior globoid convexity; as: anterior sulcus; ela: exogyroid ligament area; ise: irregular shell elevation; pk: primary keel; sk: secondary keel; t: tubercle.

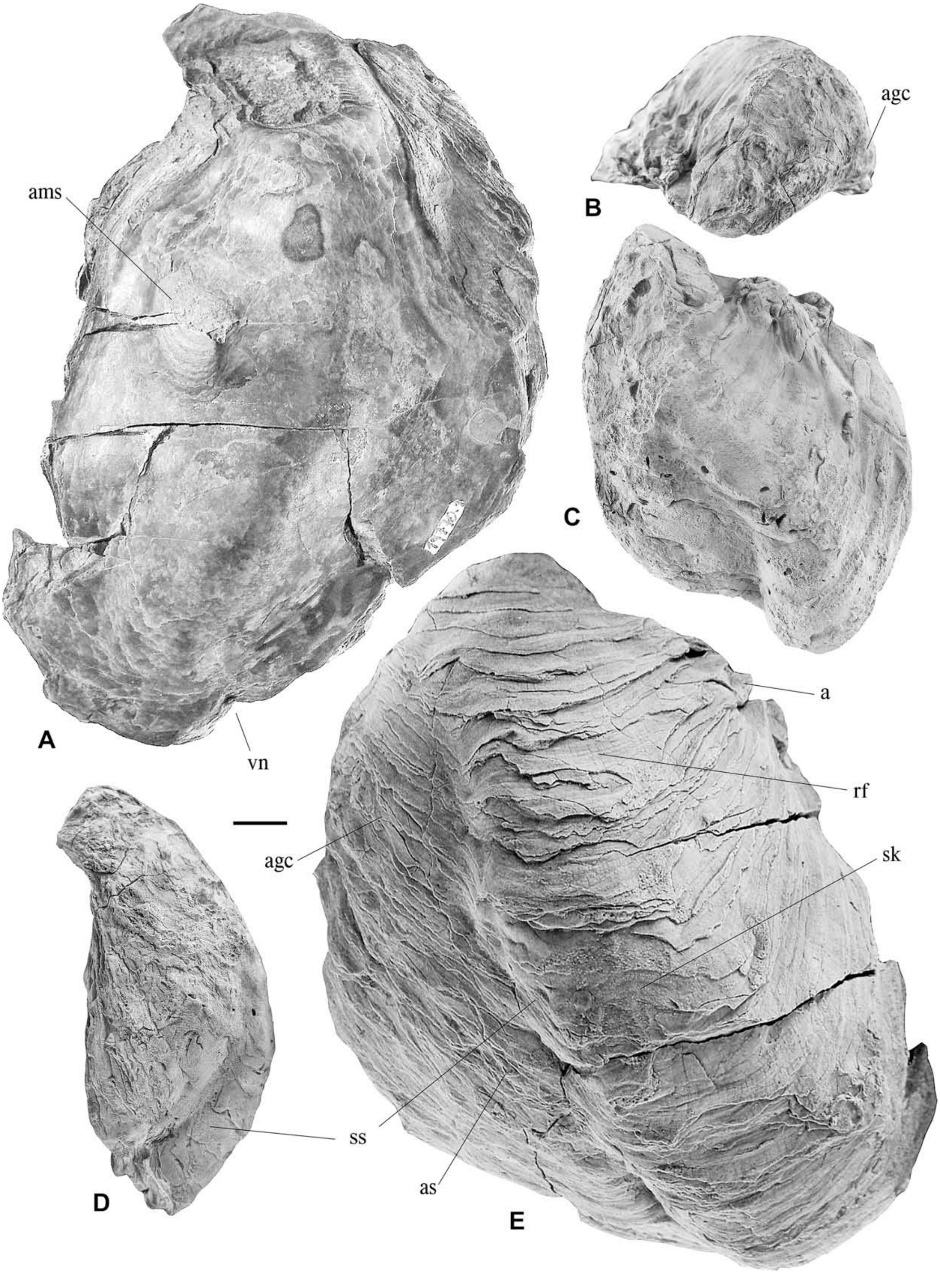


Fig. 7. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Salado Sur. A, E, paratype CPBA 19770.1, left valve, in internal and external view, respectively; B–D, paratype CPBA 19769, left valve, in dorsal, external and anterior view, respectively. a: 'auricle'; agc: anterior globoid convexity; ams: adductor muscle scar; as: anterior sulcus; rf: radial furrows; sk: secondary keel; ss: subvertical surface; vn: ventral notch.

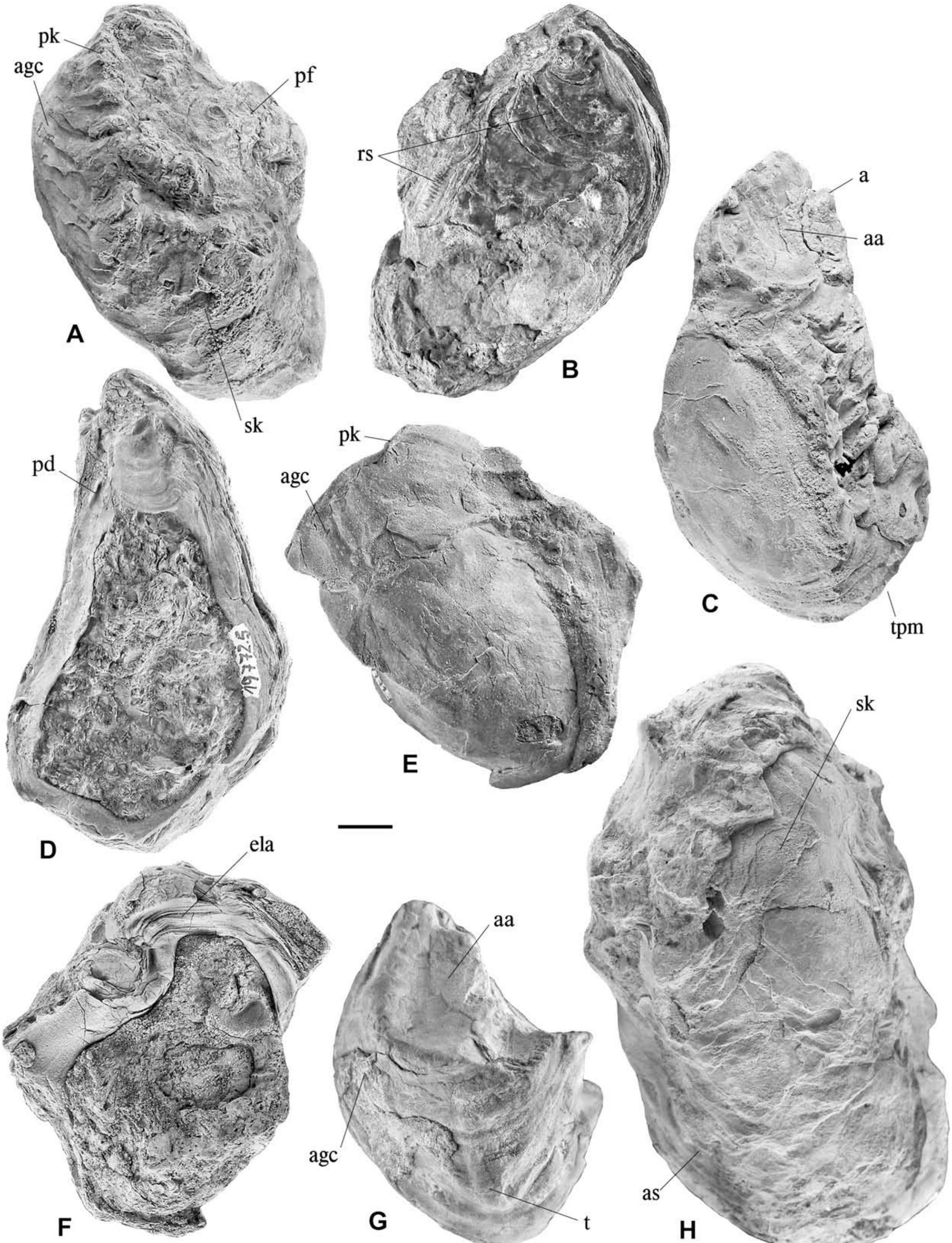


Fig. 8. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Salado Sur (A–B) and Bajada del Agrio (C–H). A–B, paratype CPBA 19770.7, A, left valve, in external view, B, right valve, in external view; C–D, paratype CPBA 19772.5, left valve, in external and internal view, respectively; E-F, paratype CPBA 19771.7, left valve, in external and internal view, respectively; G, paratype CPBA 19771.2, left valve, in external view; H, paratype CPBA 19772.3, left valve, in external view. a: 'auricle'; aa: attachment area; agc: anterior globoid convexity; as: anterior sulcus; ela: exogyroid ligament area; pd: paradontal depression; pf: posterior flange; pk: primary keel; rs: radial striae; sk: secondary keel; t: tubercle; tpm: truncated posteroventral margin.

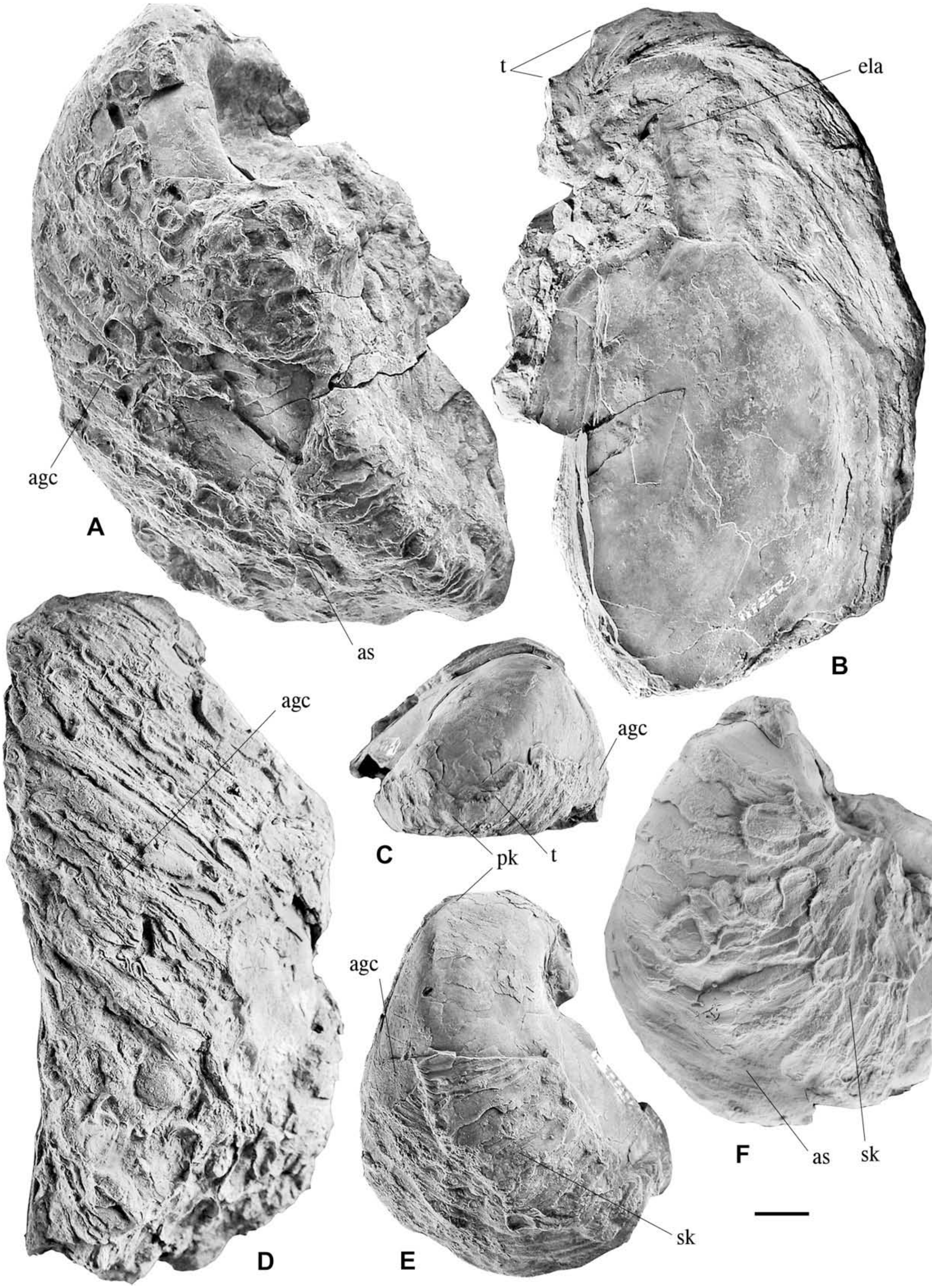


Fig. 9. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Bajada del Agrio. A–B, D, paratype CPBA 19774.8, left valve, in external, internal and anterior view, respectively; C, E, paratype CPBA 19774.4, left valve, in dorsal and external view, respectively; F, paratype CPBA 19774.20, left valve, in external view. agc: anterior globoid convexity; as: anterior sulcus; ela: exogyroid ligament area; pk: primary keel; sk: secondary keel; tubercle.

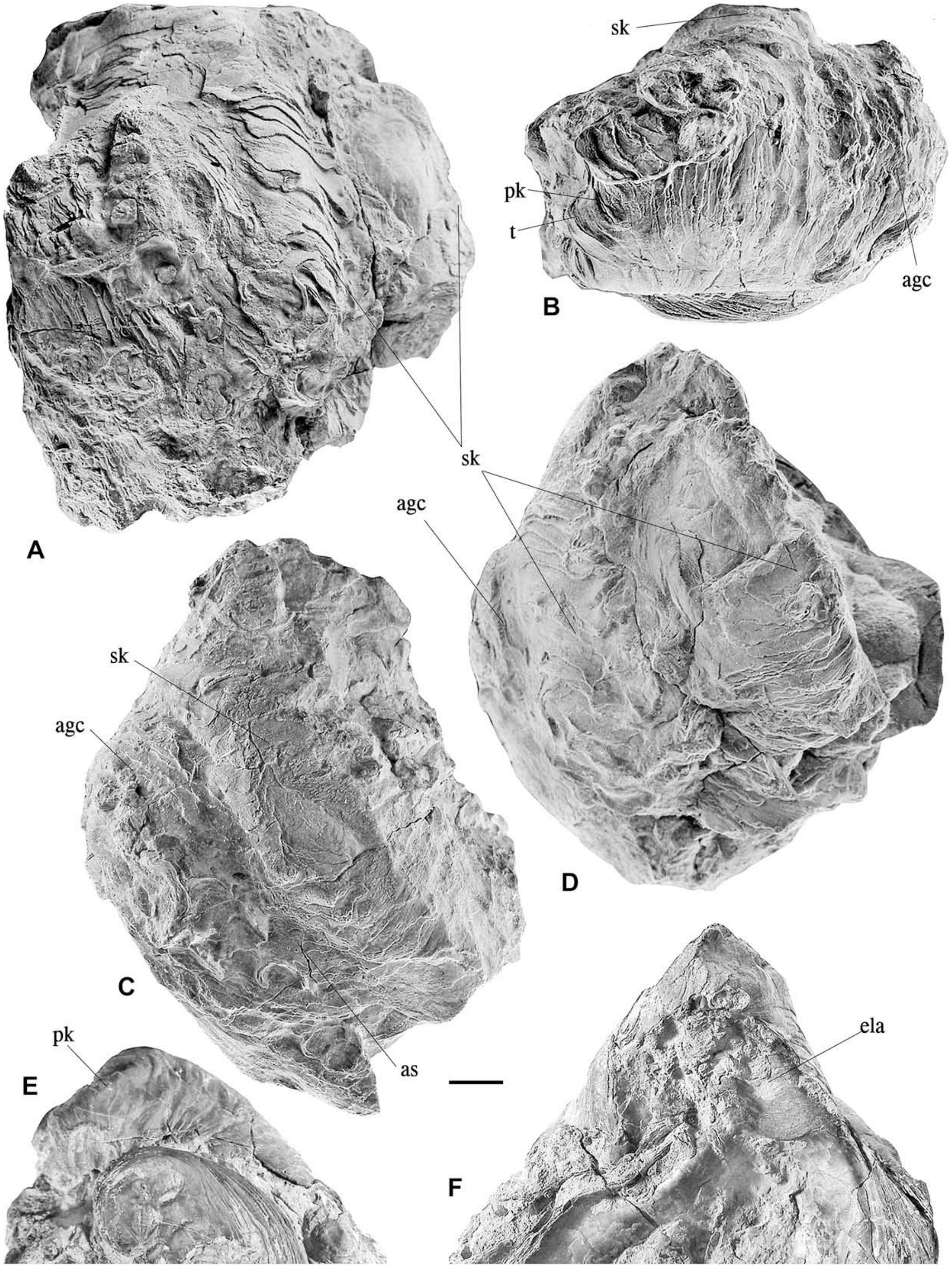


Fig. 10. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Bajada del Agrio. A, D, F, paratype CPBA 19774.23, left valve, in anterior, external and internal view (partial), respectively; B-C, E, paratype CPBA 19774.31, B-C, left valve, in dorsal and external view, respectively, E, right valve, in external view (partial). agc: anterior globoid convexity; as: anterior sulcus; ela: exogyroid ligament area; pk: primary keel; sk: secondary keel; t: tubercle.

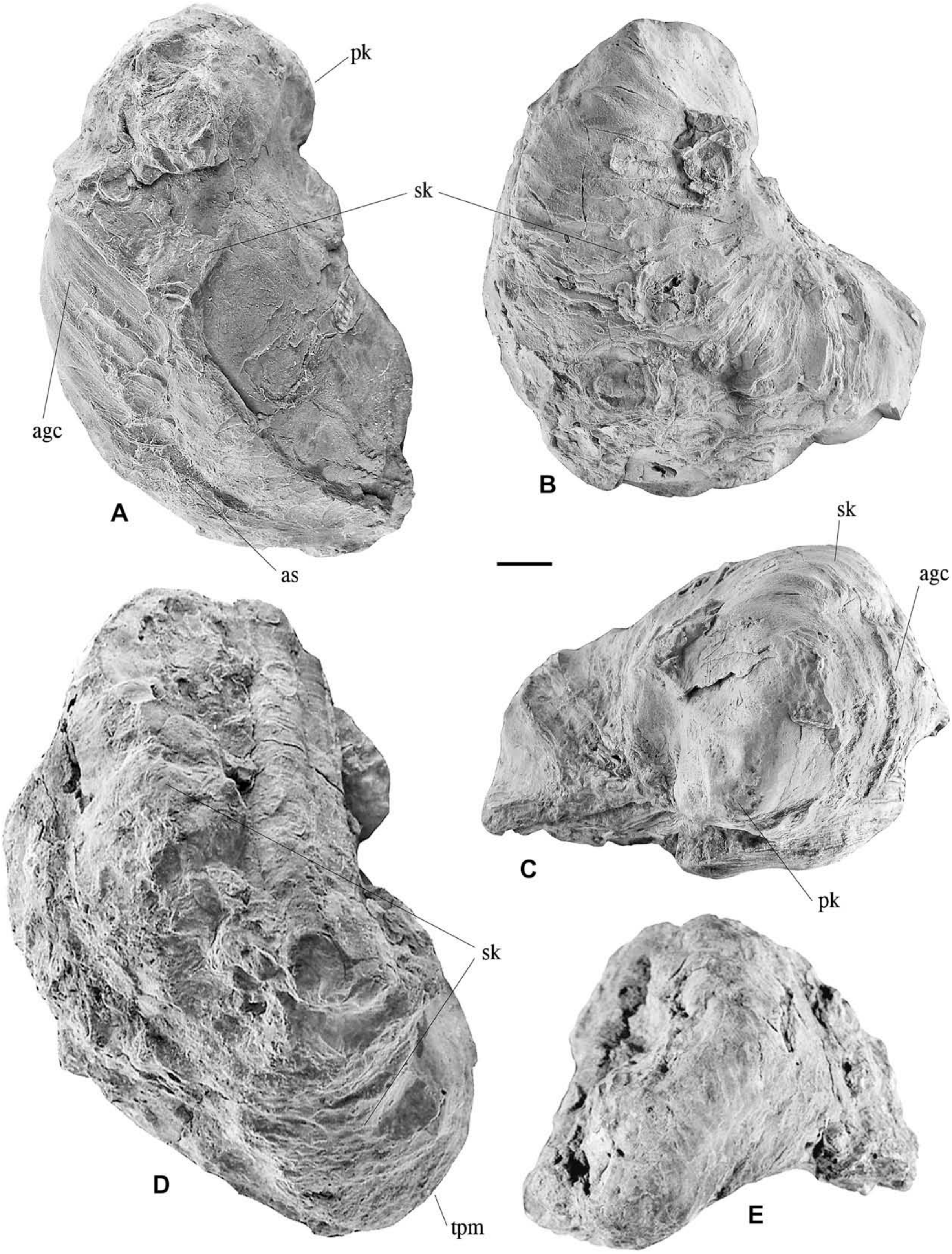


Fig. 11. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Bajada del Agrio. A, paratype CPBA 19774.5, left valve, in external view; B-C, paratype CPBA 19774.0, left valve, in external and dorsal view, respectively; D–E, paratype CPBA 19774.32, left valve, in external and dorsal view, respectively. agc: anterior globoid convexity; as: anterior sulcus; pk: primary keel; sk: secondary keel; tpm: truncated posteroventral margin.

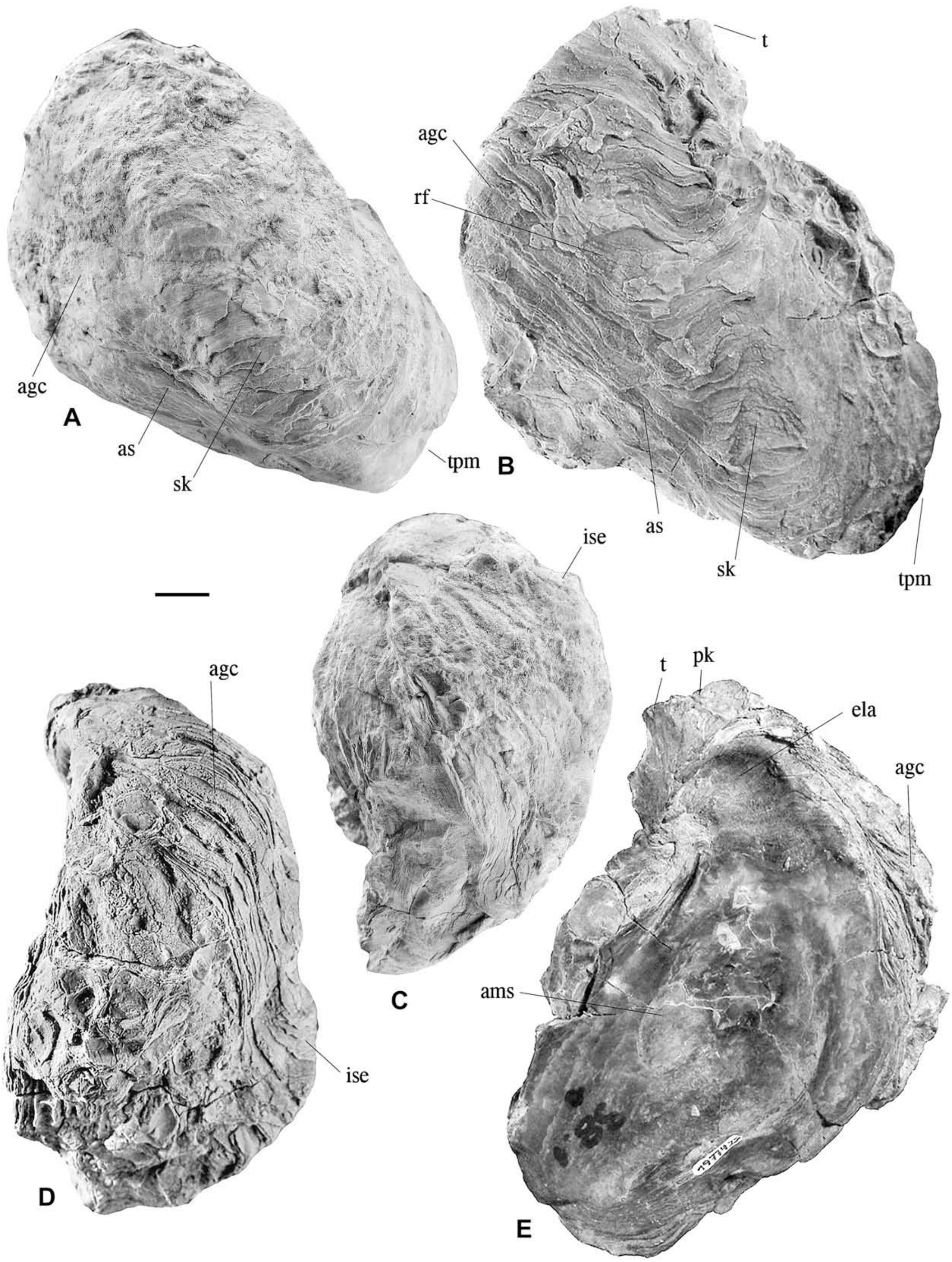


Fig. 12. *Aetostreon pilmatuegrossum* sp. nov. Figures in natural size (scale bar: 1 cm). Specimens from Bajada del Agrio. A, C, paratype CPBA 19774.26, left valve, in external and anterior view, respectively; B, D–E, holotype CPBA 19774.25, left valve, in external, anterior and internal view, respectively. agc: anterior globoid convexity; ams: adductor muscle scar; as: anterior sulcus; ela: exogyroid ligament area; ise: irregular shell elevation; pk: primary keel; rf: radial furrows; sk: secondary keel; t: tubercle; tpm: truncated posteroventral margin.

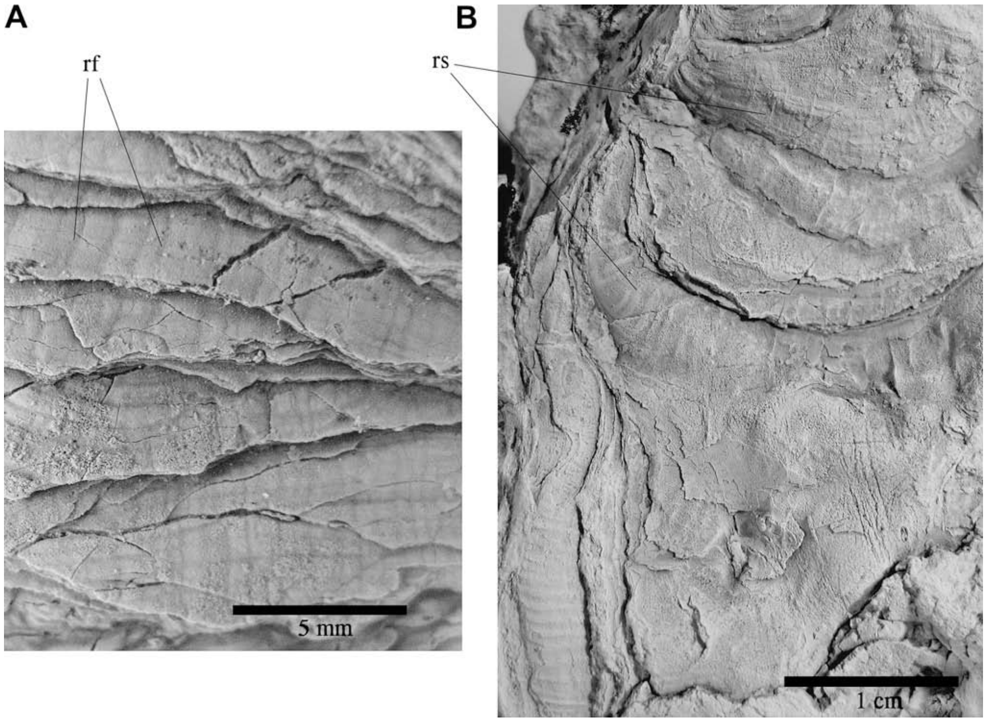


Fig. 13. Details of the radial ornamentation in *Aetostreon pilmatuegrossum* sp. nov. A, CPBA 19770.1 (Fig. 7E), radial furrows (rf) on the secondary keel, left valve, ventral third. B, CPBA 19770.7 (Fig. 8B), radial striae (rs) on the right valve.

3.1. Morphological discussion

Although the diagnostic features of *Aetostreon pilmatuegrossum* sp. nov. can be readily observed in the studied material, very few specimens are morphologically similar due to a high degree of variability in the development and co-occurrence of the primary shell features through ontogeny.

The main morphological features of this species, such as the high globoid convexity next to the anterior margin and the greater prominence and width of the secondary keel, start to develop at the same time during an early growth-stage (Fig. 3). In addition, from this growth stage the left valve tends to be wider dorsoanteriorly, forming a small concavity on the respective margin. This apparent correlation of the mentioned structures suggests a marked morphological change in ontogeny that probably is involved in the origin of *Aetostreon pilmatuegrossum* sp. nov. from its probable ancestor (see below). The size differences among the irregular shell elevations present on the primary and secondary keels may also be linked with the mentioned change, although the tubercles are not well defined in the secondary keel.

The very prominent and wide secondary keel is the most important component in defining the general organization of the valve. It tends to cover the posterior flank of the valve (Fig. 3), producing not only a marked subtrigonal outline but probably also the absence of a well defined sulcus and posterior flange. However, the secondary keel is the structure with the highest degree of variability in the new species, due especially to the differences in shape, size, and prominence of the shell elevations and tubercles.

Some specimens recorded in the *Pseudofavrella angulatiformis* Subzone in Bajada del Agrio (*e.g.* CPBA 19771.2) represent the most extreme morphotype within the present species. They appear convergent with Jurassic *Liostrea* Douvillé, based on its relative low convexity adjacent to the anterior margin, the almost straight ligament, and with its site of attachment located in the dorsal external surface of the left valve (Fig. 8G).

The ligament area is considered exogyroid (Malchus, 1990) because it is very elongated, coiled, and running out of the commissure plane. Nevertheless, it differs from the standard type because the coiled region is restricted to the first stage of growth of the valve. In addition, the later uncoiling growth is only posteriorly curved or straight, and the posterior bourrelet is well defined from the growth stage where this area becomes uncoiled. Similar morphology has been observed in Barremian *Aetostreon* collected in Zululand (Cooper, 1995), which are closely related with the new species here described (see below).

The radial striae present in the external surface of a right valve (Fig. 8B, Fig. 13B) seems to be very similar to those observed in Jurassic species of *Gryphaea* in Europe (*e.g. G. bilobata* Sowerby) and South America (Rubilar, 2006). It is necessary to establish the occurrence of this ornamentation in other species of *Aetostreon* to determine its taxonomic significance.

4. Taxonomic discussion

4.1. Common morphological pattern and differences between Aetostreon pilmatuegrossum sp. nov.*,* Aetostreon latissimum (Lamarck)*, and other related taxa*

Aetostreon pilmatuegrossum sp. nov. has close morphological affinities with Lower Cretaceous oysters identified in the literature as '*Gryphaea*' *latissima* Lamarck (1801), '*G.*' *couloni* Defrance (1821), '*G.*' *sinuata* Sowerby and Sowerby (1822), '*G.*' *aquila* Brongniart (*in* Cuvier and Brongniart, 1822) and '*Exogyra*' *aquila* Goldfuss (1833). These and other related taxa are recorded in different regions of North America (Texas, New Mexico), South America (Colombia, Chile, Argentina), Europe (England, Spain, France, Switzerland, Germany, Sardinia, Bulgaria), Asia (Turkey, Crimea, Caucasus) and Africa (Morocco, Algeria, Egypt, Somalia, Tanzania, South Africa, Madagascar), ranging from the Valanginian to the Aptian (*e.g.* Dhondt and Dieni, 1988) or even the upper Albian (Cooper, 1995).

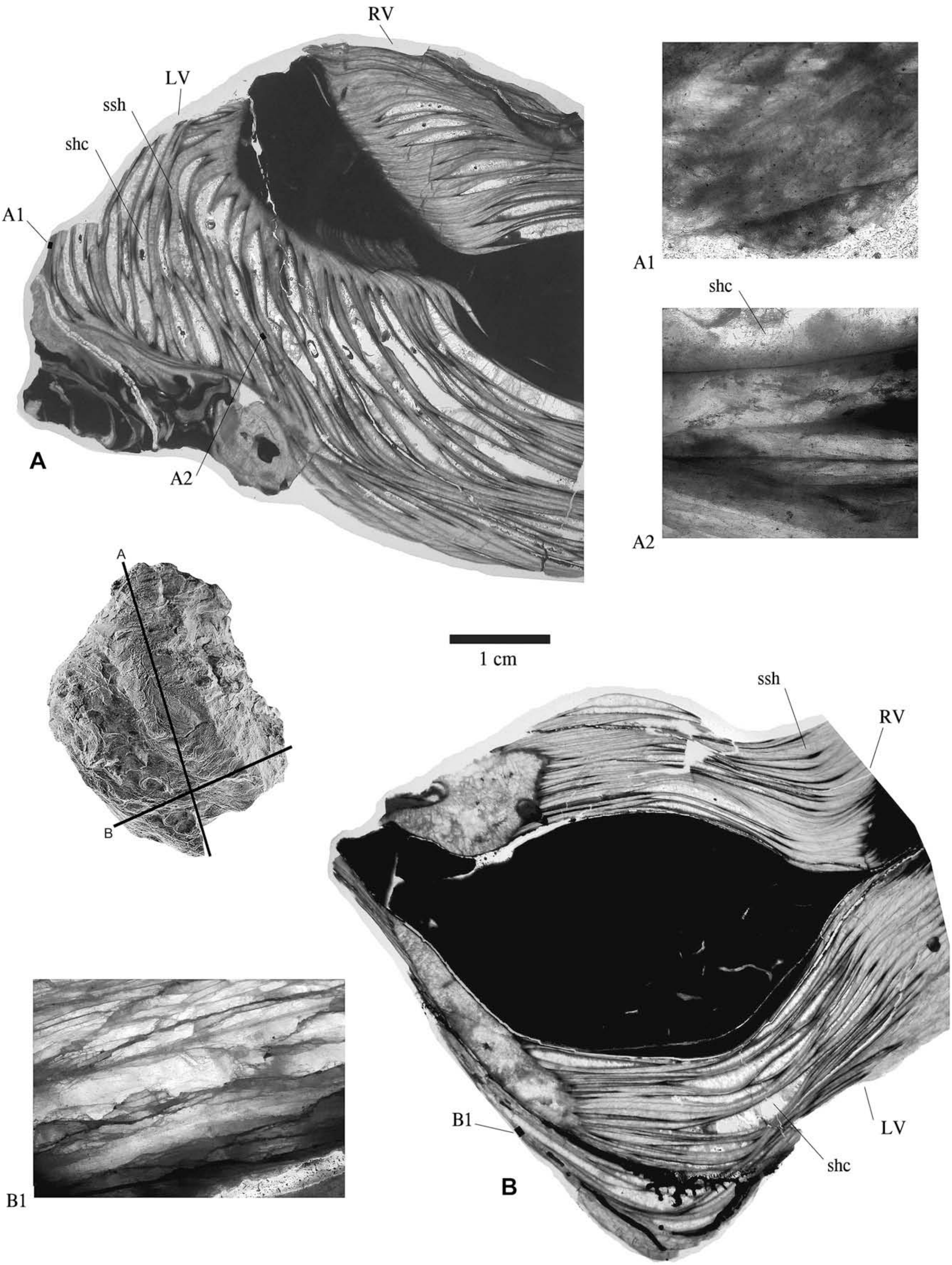


Fig. 14. Microstructure of the shell in a complete specimen of *Aetostreon pilmatuegrossum* sp. nov. CPBA 19774.31, A, dorso-ventral cross section, umbo to the left; A1, left valve, close up of the outer shell layers, ×40; A2, left valve, close up of solid shell layers, ×40. B, antero-posterior cross section, showing a marked thickening of the secondary keel; B1, left valve, close-up of the outer shell layers, ×40. LV: left valve; RV: right valve; shc: shell chamber; ssh: solid shell.

Table 1
Measurements (mm) of the almost complete and incomplete (?) left valves of *Aetostreon pilmatuegrossum* sp. nov.

Specimen No.	Height (H)	Length (L)	H/L	Width (W)	W/H
19767	71	52	1.37	41	0.58
19767.1	?101	?69	?1.46	64	?0.63
19767.5	104	93	1.12	77	0.74
19767.8	?95	79	?1.20	?47	?0.49
19767.13	94	107	0.88	58	0.62
19767.28	?78	58	?1.34	45	?0.58
19767.30	?76	?73	?1.04	?48	?0.63
19769	73	62	1.18	40	0.55
19770.1	?138	107	?1.29	?77	?0.56
19770.2	80	72	1.11	?47	?0.59
19770.5	76	?66	?1.15	51	0.67
19770.6	86	?73	?1.18	52	0.60
19770.7	76	52	1.46	39	0.51
19770.8	67	52	1.29	49	0.73
19770.13	?64	?61	?1.05	?43	?0.67
19771.2	?65	?50	?1.30	35	?0.54
19772.1	?84	?59	?1.42	57	?0.68
19772.3	105	?75	?1.40	71	0.68
19772.5	85	50	1.7	38	0.45
19774.0	80	?85	?0.94	46	0.58
19774.4	70	?58	?1.21	41	0.59
19774.5	?100	?68	?1.47	?51	?0.51
19774.8	?130	?80	?1.63	?58	?0.45
19774.20	80	?60	?1.33	41	0.51
19774.25	?102	?80	?1.28	?54	?0.53
19774.26	75	89	0.84	56	0.75
19774.29	105	105	1.00	56	0.53
19774.32	120	77	1.56	56	0.47

The remarkable morphological affinity between most of these oysters (with very similar structures and/or a degree of variability in the left valve) has led to extensive discussions concerning their taxonomic validity (*e.g.* Woods, 1913). Recently they have been included in a very long synonymy list of *Aetostreon latissimum* (Lamarck, 1801) (Dhondt and Dieni, 1988). The most representative specimens of this species were illustrated by Bayle (1878, Pl. 139, figs. 1–3; reproduced by Stenzel, 1971, figs. J92 1a–c) and Pervinquière (1910, figs. H., H.[a], H.[b], H.[c]) (see Stenzel, 1971, p. N1117-N1119 for discussion).

Thus, *Aetostreon latissimum* (Lamarck) has been considered a morphologically very variable or plastic species. The morphological differences observed in specimens coming from various assemblages or localities were interpreted as morphotypes developed in response to environmental factors such as substrate or space availability for growth (Dhondt and Dieni, 1988; Cooper, 1995). However, the lack of more detailed comparisons among the mentioned assemblages or taxa (*e.g.* considering local developments of the convexity in different zones of the left valve) has limited the recognition of morphological differences that might be taxonomically useful.

The left valves of these oysters, including *A. pilmatuegrossum* sp. nov., certainly have a very similar morphological configuration or pattern, which can be described as follows:

1. There are two main morphotypes readily identified by the valve's outline: subtrigonal or subovoidal to subtrapezoidal. In specimens with a subtrigonal outline, the main convexity or keel is well-defined in all growth-stages, and the growth of the shell is oriented in a ventroposterior direction. In specimens with a subovoidal outline, the keel is poorly defined in the adult stage (*e.g.* ventral third); in some cases it is replaced by a rather uniform external surface, and the growth of the shell tends to be oriented in a ventral direction.
2. The dorsoanterior flank, in the umbonal region, is steeply raised. Later in ontogeny, frequently after a small concavity on this margin of the shell (produced by a moderate to large increase in width), the convexity adjacent to the anterior margin can be still high (with at least one anterior fold; see point 8 below) or progressively lower as long as the shell grows.
3. The main convexity of the shell is narrow, like a keel, especially in the umbonal region. This morphology can be present or absent on the ventral third of the valve (see point 1). It is curved in the umbonal region, followed by a rather straight segment in the middle zone (or third) of the shell. The most convex zone or keel, in the adult growth stage, is generally closer to the posterior margin and tends to be uniform throughout its length; nevertheless, it may have local variations in width or convexity.
4. The posterior flank of the valve tends to spread in a posterior direction after the umbonal region, and has a slightly convex to almost straight posterior margin. Nevertheless, it can be replaced by a surface which is more or less subvertical to the commissure (like in some Jurassic *Gryphaea*; Rubilar, 2005).
5. The sulcus and posterior flange can be present or are not well defined on the posterior flank. The sulcus may be wide and deep or narrow and very shallow. Where it is present, the posterior flange has in general a moderate to low convexity, which tends to be increased during growth.
6. The umbo is generally narrow and little prominent. The coiling is well or slightly opisthogyrate, and the attachment area is very small in most of the representatives.
7. The ornamentation includes growth-lamellae, folds and grooves, and tubercles. The growth-lamellae are very frequent on the most convex zone and posterior flange. Approximately radial folds and grooves may be present on the anterior flank of the valve, and particularly near the anterior margin. The tubercles are common on the main convexity of the shell from the umbonal region, except in the ventral third of the valve; they can be short or wide and rounded or elongated even in the same specimen.
8. The ligament area is exogyroid, although the top can be just slightly curved posteriorly. The height is elongated or very elongated.

Despite these pronounced similarities, the oysters assigned to *Aetostreon latissimum* (Lamarck) by Tavani (1948), Prozorovskii *et al.* (1961), Pugaczewska (1975), Dhondt and Dieni (1988) and Cooper (1995) probably represent different taxa. Each assemblage shows morphological differences in terms of the general form and convexity of the left valve, particularly considering the degree of development of the above mentioned characters during ontogeny, and their co-occurrence in a particular growth stage (see Table 1).

The same observations are valid for many of the specimens originally assigned to different taxa (*e.g.* Defrance, 1821; Sowerby and Sowerby (1822); Cuvier and Brongniart, 1822; Goldfuss, 1833; Coquand, 1869; Woods, 1913; Newton, 1924) and later considered as synonyms of *Aetostreon latissimum* by several authors (*e.g.* Dhondt and Dieni, 1988).

In contrast, the specimens identified as '*Ostrea*' *couloni* Defrance by Pictet and Campiche (1871, Pl. 187, figs. 1–3; Pl. 188, figs. 1–2) show a close morphological affinity with the representative material of *A. latissimum* (Lamarck) (Bayle, 1878; Pervinquière, 1910; Stenzel, 1971; see Table 1). In effect, the left valves figured by Pictet and Campiche (more than 100 mm in height) are wide (especially in the mid and ventral thirds), the outline varies from subrectangular to subovoidal or subtrigonal, and the general convexity is moderate. The convexity adjacent to the dorsoanterior margin tends to be low from the proximity of the umbo. The keel is located in the center of the valve or nearer to the posterior margin. It is poorly defined near the posteroventral margin or even in the ventral third, is oriented in a ventroposterior or ventral direction, and is wider and tends to have a straight trajectory from the mid third of the shell. The sulcus is very wide and the posterior flange tends to show a low convexity, although they can be undifferentiated.

'*Exogyra*' *potosina* Castillo and Aguilera (1895; Cragin, 1905) appears to be an *Aetostreon* from the Upper Jurassic of Texas, U.S.A. and Durango, Mexico, that may reach a large size (height *ca.* 80 mm). Nevertheless, the best known large-sized oysters that closely resemble *Aetostreon latissimum* (Lamarck) are especially prevalent in the Lower Valanginian of the Neuquén Basin (*e.g.* Burckhardt, 1900a,b; Weaver, 1931; Biró Bagóczky, 1964, 1980; Rubilar, 2003), predating *Aetostreon pilmatuegrossum* sp. nov. In addition, these large-sized oysters comprise a lineage dating back to the Tithonian Vaca Muerta Formation (Rubilar *et al.* 2000a, b; see below), where at least four close-related species have been recorded. These Tithonian species are smaller (height < 50 mm) and have a unique subtrigonal outline. Some of them are also present in equivalent units cropping out in Chile (Covacevich *et al.*, 1976).

According to unpublished data (fossil collections of S. Damborenea and M. Manceñido, Museo de La Plata), the morphological changes observed in this Tithonian Valanginian lineage elucidate the origin, morphology, and variability of characteristic Lower Cretaceous oysters such as *Aetostreon imbricatum* (Krauss) and *A. latissimum* (see below). Thus, the pronounced similarity in left valves of Aetostreon species (discussed above) delineates the close evolutionary relationships between these oysters over the specific level, and the retention of morphologic development inherited from their most direct ancestor, which is probably represented in the mentioned Tithonian–Valanginian lineage from South America.

4.2. *Systematic relationships of* Aetostreon pilmatuegrossum *sp. nov.*

Philippi (1899, p. 16, Pl. 7, figs. 1a–c) sketched an oyster specimen identified as '*Exogyra Couloni*? Defr.' from a locality southeast of Santiago. Unfortunately, this specimen is lost in the Museo Nacional de Historia Natural of Chile, and it seems to have been collected south-eastern Santiago, near the borderline with Argentina. Philippi's specimen is particularly similar to one of the *Aetostreon pilmatuegrossum* sp. nov. (CPBA 19770.1; Fig. 7E). The similarities include the large size (maximum height of 115 mm), the presence of an anterior globoid convexity, and the nature of the keel in the adult growth stage (very prominent, with a narrow anterior margin and a subvertical surface).

Aetostreon pilmatuegrossum sp. nov. and *Aetostreon latissimum* (Lamarck) share the presence of several characters as figured in Aptian specimens illustrated by Bayle (1878, Pl. 139, figs. 1–3) and Pervinquière (1910, figs. H., H.[a], H.[b], H.[c]), which are especially concerned with the very similar (and phylogenetically conservative) morphological pattern of the left valve, previously discussed (see Section 4.1).

They differ because in *Aetostreon latissimum* (Lamarck) the left valve tends to be very wide, with a well-defined posterior flank. The specimens with typical subtrigonal outline tends to be poorly defined; instead, they consist in transitional morphologies ranging between subtrigonal and subovoidal. As a whole, the shell is less prominent and has a low convexity in the ventral third. The convexity of the shell next to the anterior margin seems to vary between high or low. The most convex zone is located in the middle of the valve. It is narrow and uniform in width and prominence along the growth of the shell. It does not have a narrow anterior margin, and is less developed in the ventral third. The posterior flank of the valve is wide, where the sulcus and posterior flange are well defined. The external surface is more uniform (with a low development of growth lamellae), and the tubercles on the keel are smaller.

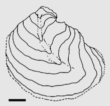
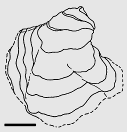
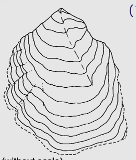
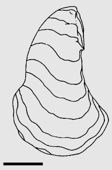
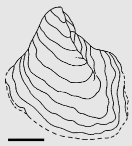
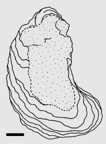
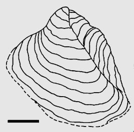
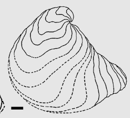
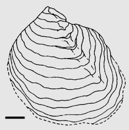
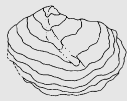
In contrast, *Aetostreon pilmatuegrossum* sp. nov. has a narrower left valve and a well-defined subtrigonal outline. The shell is very prominent, especially in the mid and ventral thirds. In addition, the valve has a very high and globoid convexity next to the anterior margin, followed by a sulcus. The most convex zone is located near to the posterior margin, and is abruptly more wide and prominent in comparison with the main convexity of the shell in the umbonal region. It tends to be delimited by a narrow anterior margin, to have irregular shell elevations, and to maintain or even accentuate its development in the ventral third (Fig. 3). The posterior flank of the valve is narrow and smooth, and the sulcus and posterior flange are very poorly differentiated. The external surface is more irregular, with frequent growth-lamellae and bigger tubercles located mostly next to the anterior margin of the most convex zone (secondary keel).

The species described here can be distinguished from others associations or taxa assigned to *Aetostreon latissimum* (Lamarck) (Table 1) by its frequent sub-trigonal outline, marked by a wide and truncated posteroventral margin. The convexity of the shell is high (rounded or globoid) adjacent to the anterior geniculation's zone (Fig. 3), followed posteriorly by a wide sulcus. In this part of the anterior flank the folds or flanges are absent. The main convexity of the shell shows a relatively abrupt change in width and prominence at the end of the umbonal region (primary and secondary keel), a feature partially shared only by the *Aetostreon* specimens described by Cooper (1995) (discussed below). The posterior flank of the valve is narrow and mainly formed by the posterior flank of the secondary keel; the sulcus and posterior flange tends to be not well defined. Finally, the umbo's convexity varies from low to very high. These characters also permit the differentiation of *Aetostreon pilmatuegrossum* sp. nov. from other North and South American and Caribbean Cretaceous oysters (e.g. Böse, 1910; Newton, 1924; Imlay, 1937, 1940; Anderson, 1938; Dietrich, 1938; Royo y Gómez, 1953; Leanza and Castellaro, 1955; Bürgl, 1957; Guzmán, 1985; Hallam *et al.*, 1986; Rubilar, 2000, 2003).

In the Neuquén Basin, the large Lower Valanginian oysters from the Chachao Formation appear to represent the direct ancestor of *Aetostreon pilmatuegrossum* sp. nov. They were assigned to '*Exogyra*' *couloni* (Defrance) or *Aetostreon latissimum* (Lamarck) (Burckhardt, 1900a,b; Weaver, 1931; Damborenea *et al.*, 1979), as well as to the variety '*Exogyra couloni* var. *leufuensis*' Weaver (1931), although they correspond to an undescribed species. In these oysters, the subtrigonal outline is especially obvious in the lower levels of the succession (Rubilar *et al.*, 2000a,b), with relatively narrow shells displaying a well developed keel extending into the adult growth-stage (*e.g.* ventral third; Burckhardt, 1900b, Pl. 21, figs. 7–8; Damborenea *et al.*, 1979, Pl. 6, figs. 5–10). In contrast, the specimens with more or less subovoidal outlines are only found in the upper levels. They are very wide, with an extensive posterior flank, and the keel is commonly restricted to the umbonal region (Burckhardt, 1900a, Pl. 28, fig. 2; 1900b, Pl. 22, fig. 3; Weaver, 1931, Pl. 19, figs. 88–91, 93a,b; Damborenea *et al.*, 1979, Pl. 7).

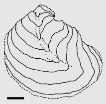
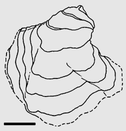
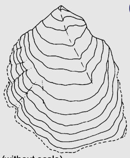
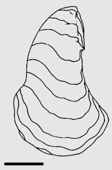
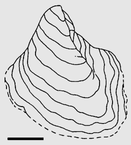
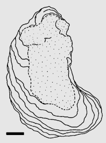
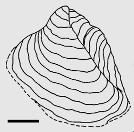
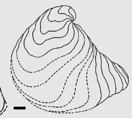
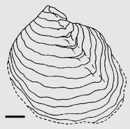
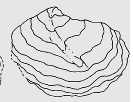
Aetostreon pilmatuegrossum sp. nov. is closely related to these subovoidal specimens, which have a relatively large size (they can surpass a height of 100 mm), several show an elevated and rounded dorsoanterior convexity near the anterior margin, the most convex zone has a width increase from the mid third of the valve, and the sulcus and posterior flange are poorly developed or even absent. They differ because in the Chachao specimens the outline is subovoidal, the shell is less prominent and its convexity is lower in the ventral third. In addition, the most convex zone tends to be poorly defined in the adult stage of growth, and is oriented towards the ventral margin.

Table2
Main morphological features observed in ten assemblages or taxa described in the literature, most of them lumped under the first species, A. latissimum (Lamarck). The figures (scale bar: 1 cm) are based on a selected specimen.

Assembla ges or taxa	*Aetostreon latissimum* (Lamarck), in Bayle (1878) and Pervinquière (1910)	'*Exogyra latissima* Lamarck', in Tavani (1948)	'*Exogyra latissima* (Lamarck)', in Prozorovskii *et al.* (1961)	*Aetostreon latissimum* (Lamarck), in Pugaczewska (1975)	*Aetostreon latissimum* (Lamarck), in Dhondt and Dieni (1988)	*Aetostreon latissimum* (Lamarck), in Cooper (1995)	'*Gryphaea couloni*' Defrance, in Pervinquière (1910)	'*Gryphaea sinuata*' Sowerby, in Sowerby (1822)	'*Exogyra sinuata*' (Sowerby), in Woods (1913)	'*Gryphaea aquila*' Brongniart, in Cuvier and Brongniart (1822)
Characters in the left valves	 (Based on Pervinquière, 1910, Fig. H.)	 (Based on Tavani, 1948, pl. 15, Fig. 7)	 (without scale) (Based on Prozorovskii *et al.*, 1961, Pl. 12, Fig. 1)	 (Based on Pugaczewska, 1975, Pl. 7; Fig. 1b)	 (Based on Dhondt and Dieni, 1988, Pl. 8, Figs. 1a)	 Based on Cooper, 1995, Fig. 14A)	 (Based on Pervinquière, 1910, Fig. T.[a])	 Based on Sowerby, 1822, Pl. 336)	 Based on Woods 1913, Text-fig. 195)	 (without scale) Based on Cuvier and Brongniart, 1822, Pl. 9, Fig. 11B)
Maximum height	*ca.* 120 mm	*ca.* 97 mm	*ca.* 120 mm (?)	*ca.* 83 mm	*ca.* 150 mm	*ca.* 170 mm	*ca.* 80 mm	*ca.* 67 mm (?)	*ca.* 100 mm	(?)
1. General width. 2. The widest zone	1. Wide to very wide. 2. Mid and ventral thirds	1. Wide. 2. Ventral third or half	1. Wide. 2. Mid and ventral thirds	1. Narrow. 2. Ventral third	1. Wide to very wide. 2. Mid and ventral thirds	1. Wide. 2. Mid and ventral thirds	1. Wide. 2. Mid third	1. Very wide. 2. Ventral half	1. Wide. 2. Ventral third or half	1. Very wide. 2. Mid third
Outline (morphotypes)	Subtrigonal to slightly subovoidal	Subtrapezoidal to subtrigonal	Subtrigonal	Subtrigonal to slightly subovoidal	Subtrapezoidal to subtrigonal	Subtrigonal to slightly subovoidal	Subtrigonal	Subtrigonal	Subtrigonal to slightly subovoidal	Subrectangular to subtrigonal
Anterior geniculation	Very rounded (wide, uniform)	Generally very rounded (wide)	Very rounded (wide)	Acute and few prominent (ventral third) or rounded	Very acute and prominent (ventral third; it seems to represent a wide fold)	Very rounded (wide, generally uniform)	Very acute and prominent (mid third; it seems to represent a wide anterior fold)	Very rounded (wide)	Generally very rounded (wide)	Relatively acute and prominent (mid third)
General convexity	Moderate to high	High (globoid), especially in mid and ventral thirds	Very high	Very high, especially in the dorsal and mid thirds	High	Moderate to high, especially in the ventral half or third	Moderate	Moderate (?)	Moderate to high (globoid) in the mid and ventral thirds	Moderate to low
Shell next to the anterior margin: 1. Convexity following the umbonal zone. 2. Anterior fold(s)	1. High and rounded (in the dorsal half) or very low and almost flattened. 2. Absent or very little differentiated (dorsal third)	1. High and rounded (in the dorsal third) or moderate to low. 2. Especially one, very or few convex (mid and ventral thirds)	1. High and rounded (dorsal third). 2. More than one, convex and with different width (mid third)	1. Very high and rounded (up to the mid third). 2. Generally more than one, few convex (ventral third)	1. High or very high and rounded (up to the mid third). 2. Absent (?) or more than one, with similar width (ventral third)	1. Moderate to high (dorsal and mid thirds).2. Probably absent	1. Moderate to low (mid third).2. Absent (?)	1. Moderate to low (dorsal half).2. Absent	1. Moderate to high (dorsal third or half), or low.2. Absent or generally more than one, variable in width and convexity (ventral half)	1. Very low and flattened.2. Absent (?)
Main convexity: 1. General location. 2. Spread of the narrower part (keel). 3. Tubercles.4. Final development	1. Nearer to the posterior margin or in the Mid zone of the valve. 2. Dorsal and mid thirds. 3. Small and elongated. 4. Near or in the posteroventral margin	1. Nearer to the anterior margin. 2. Especially in the dorsal third. 3. Small, rounded or elongated. 4. Next or in the ventroanterior (or ventral) margin	1. Nearer to the posterior margin. 2. Dorsal and mid thirds. 3. Small and elongated. 4. Next to the posteroventral margin	1. Close or nearer to the posterior margin. 2. Especially in the dorsal half. 3. Generally small and elongated. 4. In the posteroventral margin	1. Nearer to the posterior margin or in the Mid zone of the valve. 2. Especially in the dorsal and mid thirds. 3. Big but not well developed, or small and elongated. 4. In the posteroventral margin	1. Mid zone of the valve or close to the anterior margin. 2. Dorsal third (?). 3. Very big and prominent but with irregular outline. 4. Next to the posteroventral (or ventral) margin	1. Nearer to the posterior margin.2. Dorsal, mid and ventral thirds.3. Generally big and almost rounded.4. In the posteroventral margin	1. Nearer to the anterior margin. 2. At least in the dorsal half (?). 3. Not well developed (?). 4. In the posteroventral margin (?)	1. Nearer to the posterior margin or in the Mid zone of the valve. 2. Especially in the dorsal and mid thirds. 3. Generally big and elongated. 4. Next or in the posteroventral margin	1. Mid zone of the valve. 2. Dorsal and mid thirds. 3. Big and elongated. 4. Far from the posteroventral margin

(*continued on next page*)

Table2 (*continued*)

Assembla ges or taxa **Characters in the left valves**	*Aetostreon latissimum* (Lamarck), in Bayle (1878) and Pervinquière (1910)  (Based on Pervinquière, 1910, Fig. H.)	'*Exogyra latissima* Lamarck', in Tavani (1948)  (Based on Tavani, 1948, pl. 15, Fig. 7)	'*Exogyra latissima* (Lamarck)', in Prozorovskii *et al.* (1961)  (without scale) (Based on Prozorovskii *et al.*, 1961, Pl. 12, Fig. 1)	*Aetostreon latissimum* (Lamarck), in Pugaczewska (1975)  (Based on Pugaczewska, 1975, Pl. 7; Fig. 1b)	*Aetostreon latissimum* (Lamarck), in Dhondt and Dieni (1988)  (Based on Dhondt and Dieni, 1988, Pl. 8, Figs. 1a)	*Aetostreon latissimum* (Lamarck), in Cooper (1995)  Based on Cooper, 1995, Fig. 14A)	'*Gryphaea couloni*' Defrance, in Pervinquière (1910)  (Based on Pervinquière, 1910, Fig. T.[a])	'*Gryphaea sinuata*' Sowerby, in Sowerby (1822)  Based on Sowerby, 1822, Pl. 336)	'*Exogyra sinuata*' (Sowerby), in Woods (1913)  Based on Woods 1913, Text-fig. 195)	'*Gryphaea aquila*' Brongniart, in Cuvier and Brongniart (1822)  (without scale) Based on Cuvier and Brongniart, 1822, Pl. 9, Fig. 11B)
Sulcus	Uniform. Wide and generally deep	Irregular, well defined only in the ventral half. Generally wide and shallow	Irregular. Wide and shallow	Irregular. Narrow and shallow	Generally uniform. Wide and deep	Generally absent (?)	Uniform. Narrow and deep	Uniform (?). Very wide and shallow (?)	Generally irregular. Wide (or narrow), deep or shallow	Uniform. Very wide, shallow
Posterior flange: 1. Origin. 2. Beginning of a marked posterior spreading. 3. Width. 4. Convexity	1. From the umbonal zone. 2. Next to the umbonal zone. 3. Wide or very wide. 4. Moderate to high	1-2. Mid or ventral thirds. 3. Wide. 4. Low or moderate	1. From the umbonal zone. 2. Mid third. 3. Wide. 4. Low	1. Not well defined. 2. Ventral third. 3. Narrow (?). 4. Very low	1. From the umbonal zone. 2. End of the dorsal and especially in the mid thirds. 3. Wide or very wide (posterior lobe). 4. Generally moderate	Not well defined	1. From the umbonal zone. 2. From the dorsal third (?). 3. Narrow. 4. Moderate to high	1. From the umbonal zone. 2. Dorsal third (?). 3. Wide. 4. High (?)	1. From the umbonal zone or not well defined. 2. Generally in the dorsal third. 3. Generally wide. 4. Moderate to low	1. From the umbonal zone. 2. In the dorsal third. 3. Very wide. 4. Very low
Umbonal zone: 1. Width. 2. Attachment area	1. Narrow or wide. 2. Very small	1. Relatively narrow. 2. Very small	1. Narrow. 2. Very small	1. Wide. 2. Very small	1. Narrow. 2. Very small	1. Wide or narrow. 2. Very big or small (in the dorsal external surface of the valve)	1. Narrow. 2. Very small	1. Narrow. 2. Medium to small (?)	1. Very narrow. 2. Variable (very small to large)	1. Narrow. 2. Very small

Aetostreon pilmatuegrossum sp. nov. is also closely related to Barremian oysters from Zululand, assigned by Cooper (1995, figs. 10–14) to *Aetostreon latissimum* (Lamarck). In these specimens (height *ca.* 170 mm), as in the species here described, the left valve has very high convexity in the mid or ventral third as well as near to the anterior margin, where the surface of the shell tends to be convex or even globoid and very inclined towards the commissure. They have a narrow keel only in the dorsal third of the valve (umbonal region), whereas particularly in the mid and ventral thirds the most convex zone is wide as well as prominent, and tends to be separated from the anterior flank of the valve especially by an inclined surface. It is discontinuous, with big and irregular elevations of the shell, and in some specimens the keel reaches the border of the shell and constitutes a wide and almost truncated posteroventral margin. Furthermore, the sulcus and posterior flange are undifferentiated, the exogyroid ligament area combine characters with the gryphaeoid types, and the depression and paradontal recess are present.

They differ because in the Zululand specimens the subtrigonal outline is less differentiated from the subovoidal one, probably due to the lower degree of differentiation between the most convex zone and the rest of the valve. The left valve is less prominent and the convexity next to the anterior margin is less marked. The most convex zone is located in the middle of the valve or closer to the anterior margin. It has a curved trajectory that follows the growth orientation of the valve, is commonly oriented in a ventral direction, and is less prominent and uniform (in the absence of a well-defined anterior margin). The attachment area is large, and the exogyroid ligament area can be more curved and lower. Nevertheless, the mentioned great morphological affinity between both associations and their ages suggest that the Zululand ostreids are probable descendants of the Neuquén species.

5. Conclusions

The large upper Valanginian oysters from the Pilmatué Member of the Agrio Formation (Neuquén Basin) belong to a new species, *Aetostreon pilmatuegrossum*. It is likely that the direct ancestor of this species occurs in the upper levels of the Chachao Formation, of early Valanginian age. Barremian specimens from Zululand, assigned to *Aetostreon latissimum* (Lamarck) by Cooper (1995), probably represent its direct descendants.

According to the new data from southern South America and a preliminary morphological analysis based on the literature of several Lower Cretaceous *Aetostreon* from Europe, Asia and Africa, which are considered to be *Aetostreon latissimum* (Lamarck), it is possible to recognize two main groups of characters in the left valve in these oysters.

The most general or integral of them consists of characters and/or a organization of the left valve, which correspond to a very conservative morphological pattern. Probably inherited from their most direct ancestor, this pattern reflects the close relationships of these oysters at least at the genus level. In *Aetostreon* these characters covers, for example (apart from the umbonal coiling and absence of chomata), a significant level of variability centralized in the subtrigonal and subovoidal morphotypes. In addition, the convexity adjacent to the anterior margin and its changes through ontogeny tends to be complex (like in Jurassic oysters; Rubilar, 2005), including the presence of folds. The conservative umbonal keel (with tubercles) tends to be wide and irregular in the adult growth stage, where it is less differentiated particularly in the subovoidal morphotype. In addition, the typical exogyroid coiling of the ligament area may be restricted to the first stage of growth of the valve.

Other more variable characters are represented by morphological structures and/or changes in the convexity, present in a particular zone or growth stage of the shell in specimens from the same or taxonomically equivalent populations. They are excluded as possible ecophenotypic variability and may affect the features of the more conservative morphological pattern above discussed. They appear to reflect interspecific differences. For example, in *Aetostreon pilmatuegrossum* sp. nov. they include an almost invariable abrupt increase in left-valve convexity at the end of the umbonal region, expressed by a high and globoid anterior convexity and a persistent, very wide, prominent, and irregular most convex zone in the adult growth-stage (secondary keel). The taxonomical significance of these characters is remarked considering that very few specimens of *Aetostreon pilmatuegrossum* sp. nov. are morphologically similar; they display a high degree of variability in the main shell features during growth.

A similar specific value probable have the morphological differences observed in the assemblages or taxa included in Table 2, considered generally as synonyms of *A. latissimum* (Lamarck). This makes necessary to carry out a systematic revision of this species and its supposed synonyms, oriented to precise their diagnostic characters and the degree of variability.

Acknowledgements

The authors are indebted to Susana Damborenea and Miguel Manceñido (Museo de La Plata) for their permission to include some unpublished data concerning the succession of *Aetostreon* present in the Tithonian – Valanginian of the Neuquén Basin. M. Beatriz Aguirre-Urreta (Universidad de Buenos Aires) is especially thanked for her continued support and encouragement. Nikolaus Malchus (Universidad Autonoma de Barcelona) and Peter Harries (University of South Florida) are thanked for their careful revision of the manuscript. D. Lazo expresses his gratitude to Silvia Lanés, Andrea Concheyro, Peter and Sue Rawson, Marcela Cichowolski, Romina Sanci, Cecilia Rodríguez and Gaston Iovine for their help during field work in the Neuquén Basin. Nikolaus Malchus and the late Annie Dhondt kindly provided many valuable papers. This work was supported by PICT 14143 and UBACYT X084 grants to María Beatriz Aguirre Urreta and PICT 32985 grant to D. Lazo. A. Rubilar is indebted to Eugenia Fonseca, Raúl Berríos (SERNAGEOMIN) and Teresa Torres (University of Chile) for their support in obtaining the thin sections and photographs included in Fig. 14. Rodrigo Otero (University of Chile) gave technical assistance with the figures design.

References

Aguirre-Urreta, M.B., Mourgues, F.A., Rawson, P.F., Bulot, L.G., Jaillard, E., 2007. The Lower Cretaceous Chañarcillo and Neuquén Andean basins: ammonoid biostratigraphy and correlations. Geological Journal 42, 143–173.

Anderson, F., 1938. Lower Cretaceous Deposits in California and Oregon. Geological Society of America, Special Paper 16, 339 pp., 84 pls.

Bayle, E., 1878. Fossiles principaux des terrains, 4. Explication de la Carte Géologique de la France, France Service carte géologique, Paris, atlas. 158 pls.

Bayle, E., Coquand, H., 1851. Mémoire sur les Fossiles secondaires recueillis dans le Chili par M. Ignace Domeyko et sur les terrains auxquels ils appartiennent. Mémoires de la Société Géologique de France 2, 4 (1), 1–47.

Behrendsen, O., 1891. Zur Geologie des Ostabhanges der argentinischen Cordillere. Zeitschrift der Deutsche Geologischen Gesellschaft 43 (1), 369–420.

Behrendsen, O., 1922. Contribución a la geología de la pendiente oriental de la Cordillera Argentina. Actas de la Academia Nacional de Ciencias 7, 161–227.

Biró-Bagóczky, L., 1964. Estudio sobre el límite entre el Titoniano y el Neocomiano en la Formación Lo Valdés, Provincia de Santiago, principalmente en base a ammonoideos. Memoria de título inédita, Universidad de Chile, Departamento de Geología, 118 pp.

Biró-Bagóczky, L., 1980. Estudio sobre el límite entre el Titoniano y el Neocomiano en la Formación Lo Valdés, Provincia de Santiago (33°50′ Lat. Sur) Chile, principalmente sobre la base de ammonoideos. Segundo Congreso Argentino de

Paleontología y Bioestratigrafía y Primer Congreso Latinoamericano de Paleontología, Buenos Aires, Actas 5, pp. 137–52.

Böse, E., 1910. Monografía Geológica y Paleontológica del Cerro de Muleros. Instituto Geológico de México, 193 pp., 48 pls.

Burckhardt, C., 1900a. Profils géologiques transversaux de la Cordillere Argentino–Chilienne. Stratigraphie et tectonique. Anales del Museo de La Plata, Sección Geológica y Mineralógica 2, 1–136.

Burckhardt, C., 1900b. Coupe géologique de la Cordillere entre Las Lajas et Curacautin. Anales del Museo de La Plata, Sección Geológica y Mineralógica 3, 1–100.

Bürgl, H., 1957. Bioestratigrafía de la sabana de Bogotá y alrededores. Boletín Geológico 5 (2), 113–185.

Castillo, A., del, Aguilera, J., 1895. Fauna fósil de la Sierra de Catorce, San Luís Potosí. Comisión Geológica de México. Instituto Geológico de México, Boletín 1, 55.

Cooper, M., 1995. Exogyrid oysters (Bivalvia: Gryphaeoidea) from the Cretaceous of southeast Africa. Part 1. Durban Museum Novitates 20, 1–48.

Coquand, H., 1869. Monographie du genre *Ostrea*. Terrain Crétacé. H. Seren, Marseille, 215 pp., Atlas, Baillière and Fils, Paris, 75 pls.

Covacevich, V., Varela, J., Vergara, M., 1976. Estratigrafía y sedimentación de la Formación Baños del Flaco al sur del Río Tinguiririca, Cordillera de Los Andes, Provincia de Curicó, Chile. Primer Congreso Geológico Chileno, Santiago, Actas 1, pp. A191–211.

Cox, L., 1954. Lower Cretaceous Mollusca from Pointe-a-Pierre, Trinidad. Journal of Paleontology 28 (5), 622–636.

Cragin, F., 1905. Paleontology of the Malone Jurassic formations of Texas. U.S. Geological Survey, Bulletin 266, 172.

Cuvier, G., Brongniart, A., 1822. Description géologique des environs de Paris. Paris, pp. 428 17 pls.

Damborenea, S., Manceñido, M., Riccardi, A., 1979. Estudio paleontológico de la Formación Chachao. Informe Final inédito. Yacimientos Petrolíferos Fiscales O1-31, 152 pp.

Defrance, M., 1821. Dictionnaire des Sciences Naturelles. XIX ed., Strasbourg, pp. 540.

Dhondt, A., Dieni, I., 1988. Early Cretaceous bivalves of Eastern Sardinia. Memorie Di Scienze Geologiche, Padova, 40, 97 pp.

Dietrich, W., 1938. Lamelibranquios cretácicos de la Cordillera Oriental. In: Ministerio de Industrias y Trabajo, Bogotá. Estudios Geológicos y Paleontológicos sobre la Cordillera Oriental de Colombia, 3, pp. 81–108.

Goldfuss, A., 1833–1841. Petrefacta Germaniae. Düsseldorf, 2, 312 pp. 94 pls.

Guzmán, G., 1985. Los Grifeidos Infracretácicos *Aetostreon couloni* y *Ceratostreon boussingaulti*, de la Formación Rosablanca, como indicadores de oscilaciones marinas. In: Publicaciones Geológicas Especiales, Proyecto Cretácico, Ingeominas, Bogotá, Contribuciones, 16, pp. XII(1)–XII(16).

Hallam, A., Biró-Bagóczky, L., Pérez, E., 1986. Facies analysis of the Lo Valdés Formation (Tithonian – Hauterivian) of the high cordillera of central Chile, and the palaeogeographic evolution of the Andean Basin. Geological Magazine 123 (4), 425–435.

Haupt, O., 1907. Beiträge zur Fauna des Oberen Malm und der unteren Kreide in der argentinischen Cordillere. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 23, 187–236.

Hupé, L., 1854. Fauna Chilena. Moluscos. In: Gay, C. (Ed.), Historia Física y Política de Chile, Zoología, 8. Maulde y Renou, Paris, pp. 407.

Imlay, R., 1937. Lower Neocomian fossils from the Miquihuana region, Mexico. Journal of Paleontology 11 (7), 552–574. pls. 70–83.

Imlay, R., 1940. Neocomian faunas of northern Mexico. Bulletin of the Geological Society of America 51 (1), 117–190.

Lamarck, J., 1801. Système des animaux sans vertèbres. Paris, pp. 432.

Lamarck, J., 1819. Histoire naturelle des animaux sans vertèbres. Paris, 6, 1, pp. 343.

Lazo, D.G., 2003a. The genus *Steinmanella* (Bivalvia, Trigonioida) in the Agrio Formation (Lower Cretaceous), Neuquén Basin, Argentina. Journal of Paleontology 77, 1069–1085.

Lazo, D.G., 2003b. Taxonomy, facies relationships and palaeobiology of bakevelliid bivalves from the Lower Cretaceous of west-central Argentina. Cretaceous Research 24, 765–788.

Lazo, D.G., 2006a. Análisis tafonómico e inferencia del grado de mezcla temporal y espacial de la macrofauna del Miembro Pilmatué de la Formacion Agrio, Cretácico Inferior de cuenca Neuquina. Ameghiniana 43, 311–326.

Lazo, D.G., 2006b. The occurrence of *Neocomiceramus curacoensis* (Weaver) in the Agrio Formation, Neuquén Basin, Argentina. Journal of Paleontology 80, 1113–1124.

Lazo, D.G., 2007a. The bivalve *Pholadomya gigantea* in the Early Cretaceous of Argentina: Taxonomy, taphonomy, and paleogeographic implications. Acta Palaeontologica Polonica 52, 375–390.

Lazo, D.G., 2007b. Early Cretaceous bivalves of the Neuquén Basin, west-central Argentina: notes on taxonomy, palaeobiogeography and palaeoecology. Geological Journal 42, 127–142.

Lazo, D.G., 2007c. Análisis de biofacies y cambios relativos del nivel del mar en el Miembro Pilmatué de la Formación Agrio, Cretácico Inferior de cuenca Neuquina, Argentina. Ameghiniana 44, 73–89.

Lazo, D.G., Aguirre-Urreta, M.B., Price, G.D., Rawson, P.F., Ruffell, A.H., Ogle, N., 2008. Palaeosalinity variations in the Early Cretaceous of the Neuquén Basin, Argentina: Evidence from oxygen isotopes and palaeoecological analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 260, 477–493.

Leanza, A., Castellaro, H., 1955. Algunos fósiles cretácicos de Chile. Revista de la Asociación Geológica Argentina 10 (3), 179–213.

Leanza, H.A., 1993. Jurassic and Cretaceous Trigoniid bivalves from west-central Argentina. Bulletins of American Paleontology 105, 1–95.

Legarreta, L., Gulisano, C.A., 1989. Análisis estratigráfico secuencial de la cuenca Neuquina (Triásico Superior-Terciario Inferior). In: Chebli, G., Spalletti, L. (Eds.), Cuencas Sedimentarias Argentinas. Serie Correlación Geológica 6, 221–243.

Malchus, N., 1990. Revision der Kreide-Austern (Bivalvia: Pteriomorphia) Ägyptens (Biostratigraphie, Systematik). Berliner Geowissenschaftliche Abhandlungen A 125, 231, 688 pp.

Malchus, N., Aberhan, M., 1998. Transitional Gryphaeate/Exogyrate oysters (Bivalvia: Gryphaeidae) from the Lower Jurassic of northern Chile. Journal of Paleontology 72 (4), 619–631.

Marchese, H.G., 1971. Litoestratigrafía y variaciones faciales de las sedimentitas mesozoicas de la cuenca Neuquina, Provincia del Neuquén, República Argentina. Revista de la Asociación Geológica Argentina 24 (3), 343–410.

Newton, R., 1924. On some marine Cretaceous mollusca from Trinidad. Proceedings of the Malacological Society of London 16, 140–148. pls. 6–7.

Pervinquière, L., 1910. *Gryphaea latissima* Lamarck, 1801, 194. Palaeontologia Universalis, Paris, fiche, 4 pp., 8 pls.

Philippi, R., 1899. Los fósiles secundarios de Chile. Santiago-Leipzig, 104 pp.

Pictet, F., Campiche, G. 1864–1871. Description des fossiles du terrain Crétacé des environs de Ste. Croix. Matér. Paléont. Suisse, Genève, III–IV, pp. 558–352, 41 + 55 pls.

Prozorovskii, V., Korotkov, V., Mamontova, E., Poretskaja, E., Prozorovskaja, E., 1961. Neocomian of western Turkmenia. In: Trudy Vsegei, Leningrad, new serie, 51, 234 pp., 20 pls. (in Russian).

Pugaczewska, H., 1975. Neocomian oysters from central Poland. Acta Palaeontologica Polonica 20 (1), 47–72.

Rafinesque, C., 1815. Analyse de la nature ou tableau de l'Univers et des corps organisés. Palermo, pp. 224.

Royo y Gómez, J., 1953. Fósiles del Cretácico Inferior de Venezuela. Acta Científica Venezolana 4 (4), 135–153.

Rubilar, A., 2000. *Aetostreon* sp. nov. del Neocomiano, sur de Chile y Argentina, y su afinidad morfológica con *Gryphaea* Lamarck. Noveno Congreso Geológico Chileno, Puerto Varas, Actas 2, pp. 249–253.

Rubilar, A., 2003. Nuevos estudios acerca de las ostras del Cretácico Inferior de Chile. Décimo Congreso Geológico Chileno, Concepción, pp. 10.

Rubilar, A., 2005. Heterochrony in Middle Jurassic species of *Gryphaea* (Ostreoidea, Gryphaeidae) from southern South America. Geologica Acta 3 (2), 185–203.

Rubilar, A., 2006. Gryphaeate oysters with radial ornamentation in the Middle Jurassic of Chile and Argentina: supraspecific affinities and possible taxonomic implications. Undécimo Congreso Geológico Chileno, Antofagasta, Actas II, pp. 121–24.

Rubilar, A., Damborenea, S., Manceñido, M., 2000a. Ostras del Tithoniano–Valanginiano en el sur de Mendoza (Argentina). Noveno Congreso Geológico Chileno, Puerto Varas, Actas 1, p. 549.

Rubilar, A., Damborenea, S., Manceñido, M., 2000b. Cambios heterocrónicos en *Aetostreon* (Ostreoidea, Gryphaeidae) del Tithoniano – Valanginiano, en el sur de Mendoza (Argentina). Ameghiniana 37 (4), 78R–79R.

Rubilar, A., Lazo, D.G., 2003. Avances en el estudio de las ostras presentes en el Miembro Pilmatué de la Formación Agrio (Valanginiano Superior – Hauteriviano Inferior) en Neuquén, Argentina. Ameghiniana 40 (4), 91R.

Sowerby, J., Sowerby, J. de C., 1812–1846. The Mineral Conchology of Great Britain. London, 1–7, 648 pls.

Stanton, T., 1901. The Marine Cretaceous Invertebrates. In: Scott, W. (Ed.), Reports of the Princeton University Expeditions to Patagonia, 1896–1899 Princeton and Stuttgart, 4. Paleontology 1, 43. 9 pls.

Stenzel, H., 1971. Oysters. In: Moore, R. (Ed.), Treatise on Invertebrate Paleontology. N, Mollusca, 6. University of Kansas Press and Geological Society of America, 3, pp. 953–1224.

Tavani, G., 1948. Fauna malacologica cretacea della Somalia e dell' Ogaden. Parte Prima–Lamellibranchiata. Palaeontographia Italica. Memorie di Paleontología 43, 83–154. pls. 10–20.

Ten Hove, H.A., van den Hurk, P., 1993. A review of recent and fossil serpulid "reefs"; actuopalaeontology and the "Upper Malm" serpulid limestones in NW Germany. Geologie en Mijnbouw 72, 23–67.

Vialov, O., 1936. Sur la classification des huitres. Academy of Scienses URSS, Comptes rendus (Doklady). new series 4, 13, 17–20.

Weaver, C., 1931. Paleontology of the Jurassic and Cretaceous of West Central Argentina. Memoirs of the University of Washington 1, pp. 595.

Woods, H., 1913. A monograph of the Cretaceous Lamellibranchia of England. Ostreidae, Radiolitidae, additions, distribution, bibliography, Index, 2. Palaeontographical Society, London, 9, pp. 341–473, pls. 55–62.