

THE GENUS *STEINMANELLA* CRICKMAY (BIVALVIA) IN THE TRANSITION BETWEEN THE VACA MUERTA AND MULICHINCO FORMATIONS, EARLY VALANGINIAN, NEUQUÉN BASIN, ARGENTINA



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Abstract. The genus *Steinmanella* Crickmay is recorded in several Lower Cretaceous marine units of the Neuquén Basin. It is particularly abundant at the transition between the Vaca Muerta and Mulichinco formations. This paper presents a taxonomic revision of this fauna, discusses the stratigraphic range of each species, and describes and interprets the associated lithofacies based on detailed field sections, newly collected specimens and revision of previous fossil collections. Four sections were measured in northern Neuquén comprising the upper beds of the Vaca Muerta Formation and the lower ones of the Mulichinco Formation. The *Steinmanella* fauna was dated accurately on the basis of a precise ammonoid zonation. The species were found in the *Neocomites wichmanni* and *Lissonia riveroi* zones of early Valanginian age. Specimens were collected *in situ* from dark grey shales, alternating siltstones, wackestones and mudstones, and rudstones. Three species were identified: *Steinmanella curacoensis* (Weaver), *S. quintucoensis* (Weaver), and *S. subquadrata* sp. nov. *Steinmanella curacoensis* has an oval outline, poor demarcation of carinae, flank and corselet ribs partially intercalated at the median part of the valve, and oval escutcheon. *Steinmanella quintucoensis* has a furrow below the marginal carina, subrectangular outline, robustly tuberculated flank ribs, and lanceolate escutcheon. *Steinmanella subquadrata* sp. nov. has a subquadrated outline, well-marked carinae, and oval escutcheon ornamented with thin ribs and small elongated tubercles.

Key words. Trigonioidea. Valanginian. *Steinmanella*. Neuquén Province. Vaca Muerta Formation. Mulichinco Formation.

Resumen. EL GÉNERO *STEINMANELLA* CRICKMAY (BIVALVIA) EN LA TRANSICIÓN ENTRE LAS FORMACIONES VACA MUERTA Y MULICHINCO, VALANGINIANO TEMPRANO, CUENCA NEUQUINA, ARGENTINA. El género *Steinmanella* Crickmay se registra en distintas unidades marinas del Cretácico Inferior en la Cuenca Neuquina. En particular, es muy abundante en la transición entre las formaciones Vaca Muerta y Mulichinco. Este trabajo presenta una revisión taxonómica de esta fauna, con una discusión del rango estratigráfico de cada una de las especies halladas y la descripción e interpretación de las litofacies asociadas, sobre la base de nueva información de campo disponible y revisión de colecciones previas. Se midieron cuatro perfiles en el norte de Neuquén, abarcando los últimos metros de la Formación Vaca Muerta y los primeros de la Formación Mulichinco. La fauna de *Steinmanella* fue datada con precisión mediante una zonación de amonoides. La fauna fue hallada en facies de lutitas grises oscuras, limolitas, wackestones y mudstones alternantes, y rudstones. Se identificaron tres especies: *Steinmanella curacoensis* (Weaver), *S. quintucoensis* (Weaver), y *S. subquadrata* sp. nov. Las mismas fueron registradas en las zonas de *Lissonia riveroi* y *Neocomites wichmanni*, correspondientes al Valanginiano temprano. *Steinmanella curacoensis* presenta un contorno oval, carenas pobremente marcadas, costillas del flanco intercaladas con las del área y un escudete oval. *Steinmanella quintucoensis* presenta un surco bajo la carena marginal característico, contorno subrectangular, costillas del flanco con tubérculos robustos y un escudete lanceolado. *Steinmanella subquadrata* sp. nov. presenta un contorno subcuadrado, carenas bien demarcadas y un escudete oval con costillas delgadas y tubérculos elongados y pequeños.

Palabras clave. Trigonioidea. Valanginiano. *Steinmanella*. Provincia de Neuquén. Formación Vaca Muerta. Formación Mulichinco.

THE Order Trigonioidea was one of the most important groups of bivalves during the Mesozoic, found in a variety of shallow water settings and widely distributed across the globe (Darragh, 1986). The main morphological features of Mesozoic trigonioids are (1) thick aragonitic shell, (2) prominent ornamentation, (3) valves usually divided in corselet, escutcheon and flank, and (4) large cardinal teeth with characteristic secondary dentition (see Newell and Boyd, 1975). Trigonioidea are presently restricted to the small-sized genus

Neotrigonia Cossman which comprises six species and occurs in the epicontinental seas of Australia (Darragh, 1986). Observation of many features of the soft parts and behaviour of the living species allowed paleobiological interpretations of the fossil ones (e.g., Tevesz, 1975).

In Argentina, the Early Cretaceous was a time of diversification and expansion of trigonoid faunas, and numerous studies have been carried out on the taxonomy, paleoecology, and life habits of this group (e.g., Weaver, 1931;

Camacho and Olivero, 1985; Leanza, 1993; Villamil *et al.*, 1998; Lazo, 2003; Luci, 2010). In particular, the genus *Steinmanella* Crickmay, 1930, has been abundantly recorded from different Tithonian to Barremian lithological units in the Neuquén and Austral Basins (*e.g.*, Camacho and Olivero, 1985; Leanza, 1993; Lazo, 2003). The genus belongs to the Myophorellidae (see Cooper, 1991) and is characterized by robust forms with subquadrate to subrectangular valves ornamented with coarsely tubercled ribs on the flank and rugose ribs in the corselet; the escutcheon is lanceolate to oval, and carinae are represented by rows of small tubercles. Related forms were reported from several localities around the world. A number of Early Cretaceous species are known from the Neuquén Basin (Weaver, 1931; Lambert, 1944; Camacho and Olivero, 1985; Leanza and Garate Zubillaga, 1987; Leanza, 1993), but only recently some of them were properly revised on the basis of extensive collections, detailed stratigraphic sections, and precise dating based on associated ammonoids (Leanza, 1993, 1998; Lazo, 2003). Despite the abundance of studies on *Steinmanella* there are still important issues to be clarified concerning their life habit, stratigraphic range, and facies distribution. Very little is known

about the lithofacies in which specimens are found, and stratigraphic ranges are often very vaguely determined. In addition, the introduction of new specific names based on scarce or poorly preserved specimens is also problematic because a critical factor that has not been adequately addressed is the intraspecific variation occurring in this group.

In this sense, this contribution aims to (1) describe the *Steinmanella* fauna recorded in the upper part of the Vaca Muerta Formation and the basal part of the Mulichinco Formation in the Neuquén Basin, based on new material and revision of former collections; (2) describe the *Steinmanella*-bearing lithofacies and interpret the paleoenvironment inhabited by the fauna; and (3) date the *Steinmanella*-bearing beds based on the associated ammonoids.

GEOLOGICAL SETTING

The Neuquén Basin is an important back-arc depocenter located in west-central Argentina and covering an area of over 120,000 km² (Fig. 1). It holds a thick sedimentary record of marine and continental facies containing abundant fossils. The age ranges from the latest Triassic to Paleogene (Legarreta and Gulisano, 1989; Vergani *et al.*, 1995;

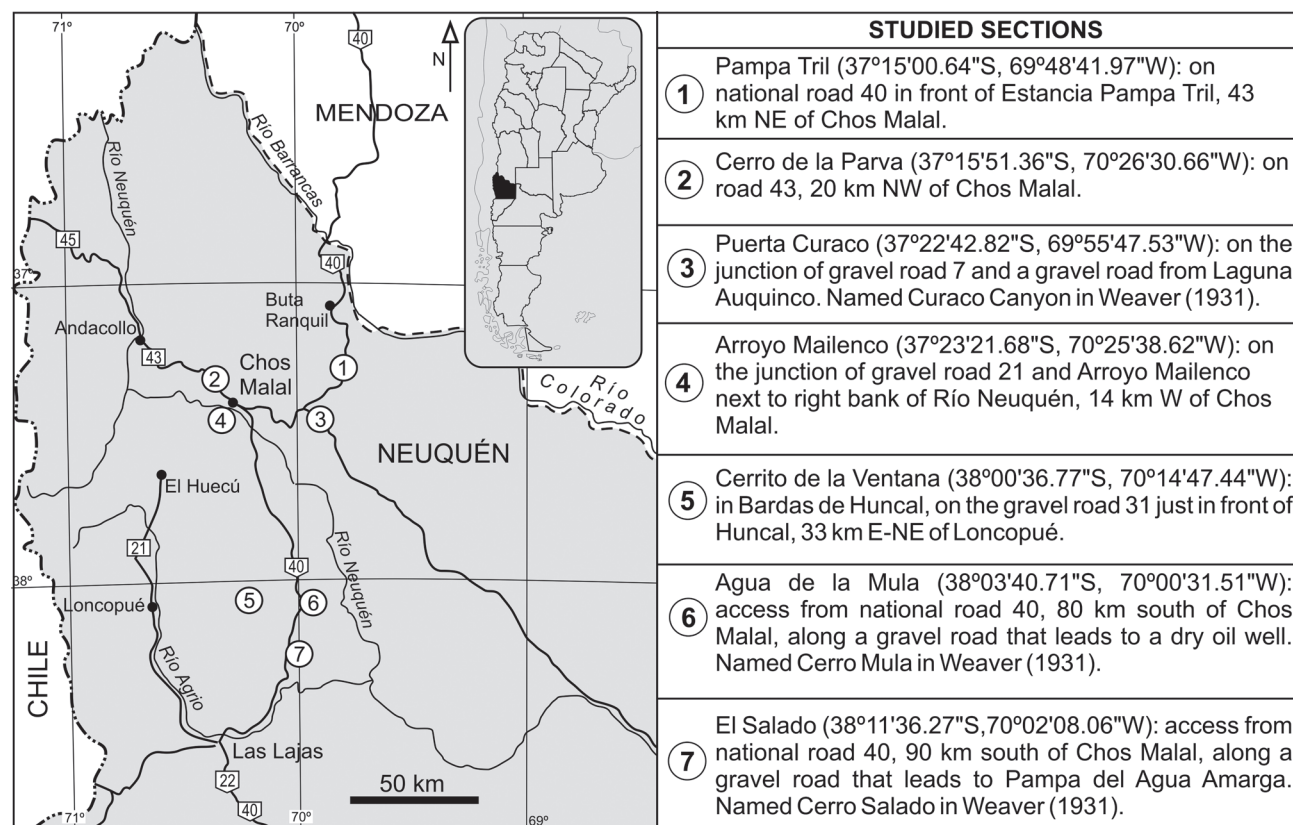


Figure 1. Map showing studied localities/ Mapa mostrando las localidades estudiadas.

Howell *et al.*, 2005). The studied bivalve assemblage was recorded from the transitional beds between the Vaca Muerta and Mulichinco formations exposed in northern Neuquén. These units belong to the Mendoza Group—which is best represented in Neuquén Province—with thickness exceeding 3000 m and spanning the early Tithonian to the earliest Barremian. The Mendoza Group includes the Tordillo, Vaca Muerta, Mulichinco and Agrio formations, and represents a major transgressive unit with two important retreats of the seashore represented by the Mulichinco Formation and the Avilé Member of the Agrio Formation (Vergani *et al.*, 1995).

The Vaca Muerta Formation, originally described by Weaver (1931), is a thick transgressive unit dominated by bituminous black shales and is renowned for its high abundance of early Tithonian–early Valanginian ammonoids and marine reptiles (*e.g.*, Weaver, 1931; Leanza, 1973; Leanza *et al.*, 1977; Riccardi, 1988; Aguirre-Urreta and Rawson, 1999; Fernández and De la Fuente, 1988; Spalletti *et al.*, 1999). In the study area it overlies the Tordillo Formation and is overlain by the Mulichinco Formation. It has been interpreted as a distal low-energy marine ramp deposited under quiet-water conditions, but interrupted by occasional turbidites (see Leanza *et al.*, 2002; Spalletti *et al.*, 2008). Towards the top of the unit, a shallower environment is envisaged, above the storm wave base, on a distal mid-ramp to proximal outer-ramp setting influenced by storms (Spalletti *et al.*, 2000; Kietzmann *et al.*, 2008). The unit has been extensively studied because of its importance as oil source rock; many contributions have focused on its geochemistry, sedimentology and sequence stratigraphy (*e.g.*, Leanza *et al.*, 1977, 2003; Gulisano *et al.*, 1984; Spalletti *et al.*, 2000, 2008; Doyle *et al.*, 2005; Kietzmann *et al.*, 2008). Abundant organic matter suggests a poorly oxygenated seafloor (Doyle *et al.*, 2005). A detailed ammonoid zonation of the Vaca Muerta Formation may be found in Leanza (1981a,b), Riccardi (1988) and Aguirre-Urreta and Rawson (1999). The genus *Steinmanella* can be traced back to the Tithonian beds of the unit, but this study will focus only on the early Valanginian records. For Tithonian and Berriasian records see Leanza (1993).

The Mulichinco Formation—also defined by Weaver (1931)—represents a major retreat of marine facies and its basal contact is considered a Type I sequence boundary that marks an abrupt to gradual shift from marine to estuarine and fluvial facies in different parts of the basin (Schwarz and Howell, 2005). In the study area it is overlain by the Agrio Formation. The age of the unit is early Valanginian to early late Valanginian, and comprises part of the *Lissonia riveroi*

and *Olcostephanus (O.) atherstoni* zones (Aguirre-Urreta and Rawson, 1999). Numerous studies have focused on its lithofacies, paleoenvironments, and sequence stratigraphy (*e.g.*, Weaver, 1931; Marchese, 1971; Leanza and Hugo, 1977; Gulisano *et al.*, 1984; Schwarz, 2003; Schwarz and Howell, 2005). Previous records of *Steinmanella* from the Mulichinco Formation may be found in Weaver (1931) and Leanza (1993).

MATERIALS AND METHODS

The study area is located in northern Neuquén Province. Fossil localities are, from north to south: Pampa Tril, Cerro de la Parva, Puerta Curaco, Arroyo Mailenco, Cerrito de la Ventana, Agua de la Mula, and El Salado (Fig. 1). Fossil material was collected at each locality and studied in the laboratory for taxonomic purposes and comparisons with previous fossil collections including types of Burckhardt (1903), Weaver (1931), and Leanza (1993).

Detailed sections of the transition between the Vaca Muerta and Mulichinco formations were measured at Pampa Tril, Cerro de la Parva, Puerta Curaco, and Cerrito de la Ventana (Fig. 2). Lithofacies were described in the field on a bed-by-bed basis taking into account geometry, lithology, and sedimentary structures. Qualitative taphonomic observations were made on each collected specimen of *Steinmanella* including articulation, fragmentation, dissolution, corrosion, and encrustation; these were ranked as low, medium, and high.

At Cerrito de la Ventana the studied interval comprises the uppermost Vaca Muerta Formation, sharply overlain by fluvial conglomerates and sandstones of the Mulichinco Formation. The contact between the two units is a very distinctive erosive surface, which marks a sudden facies shift (Fig. 3.1). Because of this, the interval measured at Cerrito de la Ventana involves only the topmost meters of the Vaca Muerta Formation, up to the first continental facies of the Mulichinco Formation. The scenario is quite different in the other studied localities, given that the contact between the Vaca Muerta and Mulichinco formations is transitional; black and dark grey shales are progressively intercalated with thin beds of sandy siltstones and thin sandstones with wave ripples (Fig. 3.2). Ammonoid faunas belonging to the *Neocomites wichmanni* and *Lissonia riveroi* zones were identified in the field; they are indicative of an early Valanginian age for the measured interval (Fig. 2; Aguirre-Urreta and Rawson, 1999).

Repositories are as follows: (1) **BMNHC**, Burke Museum of Natural History and Culture, Seattle; (2) **BSPG**,

TRANSITION BETWEEN THE VACA MUERTA AND MULICHINCO FORMATIONS

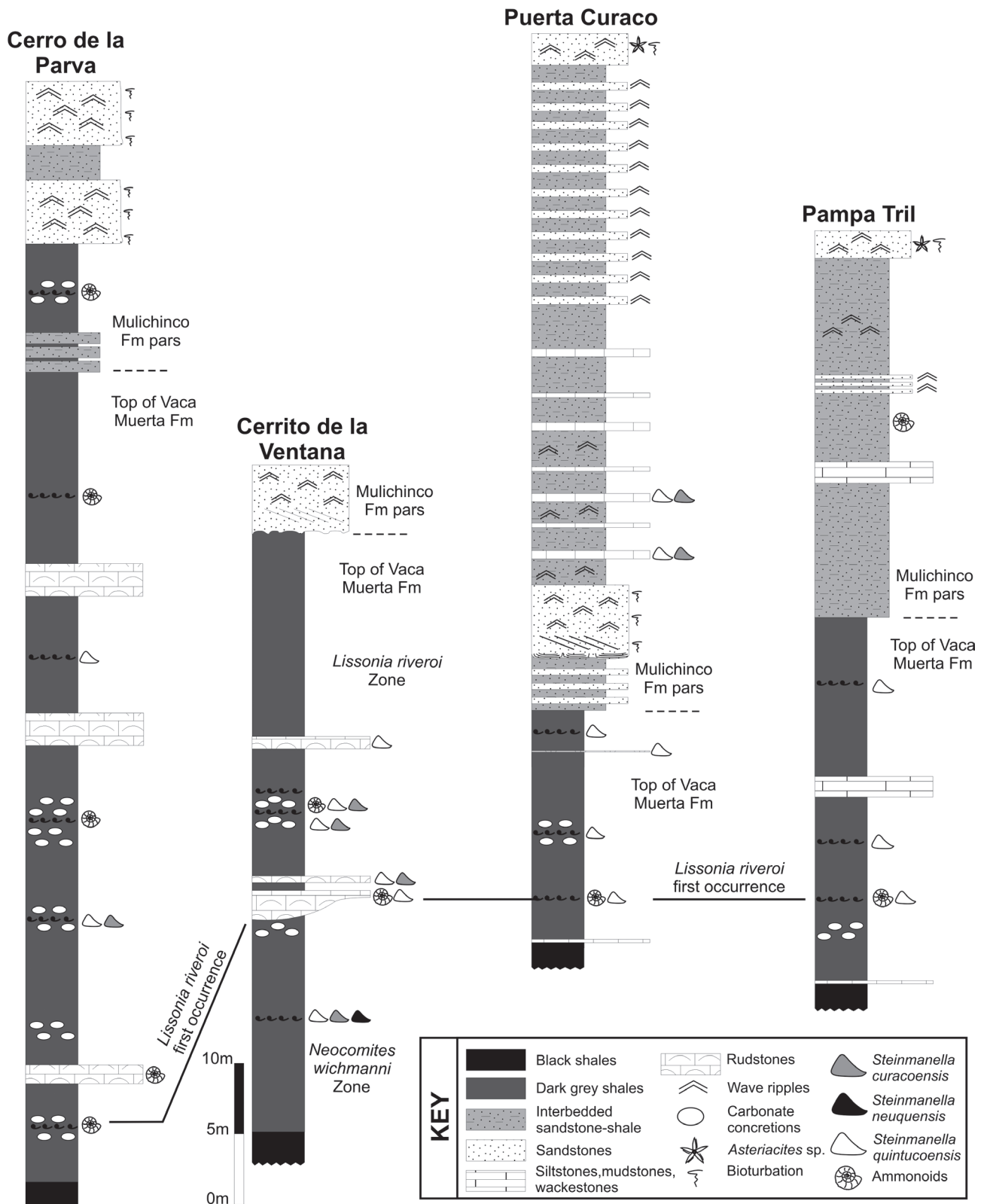


Figure 2. Measured *Steinmanella*-bearing sections in Northern Neuquén/ Perfiles portadores de *Steinmanella* medidos en el norte de Neuquén.

Bayerische Staatssammlung für Paläontologie und Geologie, München; (3) **CPBA**, Colección de Paleontología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires; (4) **MOZ**, Museo Olsacher, Zapala.

Besides the authors' collections, the following specimens were revised: (1) Holotype of *Steinmanella neuquensis* Burckhardt BSPG AS XXXV 11 from the Early Cretaceous of a section located on the left bank of the Río Agrio just in front of Las Lajas in Neuquén, collected by C. Burckhardt; (2) *S. transitoria* (Steinmann) MOZ P0916 figured in Leanza (1993, pl. 10, fig. 1–2); (3) *S. splendida* (Leanza) MOZ P2553 figured in Leanza (1993, pl. 11, fig. 5–8); (4) *S. neuquensis* (Burckhardt) MOZ P2767 figured in Leanza (1993, pl. 12, fig. 6–7); (5) *S. steinmanni* (Philippi) MOZ P0917 figured in Leanza (1993, pl. 13, fig. 1, 10).

STEINMANELLA-BEARING LITHOFACIES

Dark grey shales (Fig. 3.6–7)

Description. Finely laminated dark grey shales, alternating with thin, tabular layers of massive calcareous black shales and mudstones. Levels of calcareous nodules commonly intercalated. Nodules spherical to ellipsoidal with rounded margins, 5–30 cm long and 5–10 cm thick, they can eventually reach up to 1.5 m in length. Frequently with uncrushed specimens of bivalves and ammonoids. Lamination deflected around nodule's margins. Ammonoids and diverse bivalve assemblages commonly recorded. *Steinmanella* shells occur abundantly *in situ*.

Taphonomic observations. *Steinmanella* specimens with pristine preservation. Infilling generally calcareous shale, but some shells partially empty and crushed. Disarticulation, fragmentation, corrosion and chipped margins generally low. Dissolution occurs in umbonal and hinge region of specimens of *S. curacoensis* from Cerrito de la Ventana. Encrustation variable, some specimens heavily covered and others without infestation. Epibionts include oysters, mytilids, and serpulids.

Interpretation. This facies resulted from decantation processes in a low-energy setting below fairweather wave base. Seafloor was oxygen-controlled, but the presence of diverse bivalve assemblages, including shallow and deep infaunal ones—some of them with thick, well-calcified shells—points to normal oxygen conditions, at least temporarily. Accordingly, Doyle *et al.* (2005) proposed anoxic/dysoxic conditions for the Vaca Muerta Formation, with increasing oxygen levels towards the top of the unit. Carbonate nodules are interpreted as symsedimentary and related to pauses in sedimentation (Brett and Baird, 1986). The sedimentary environment is thus interpreted as a distal mid-ramp to proximal outer-ramp.

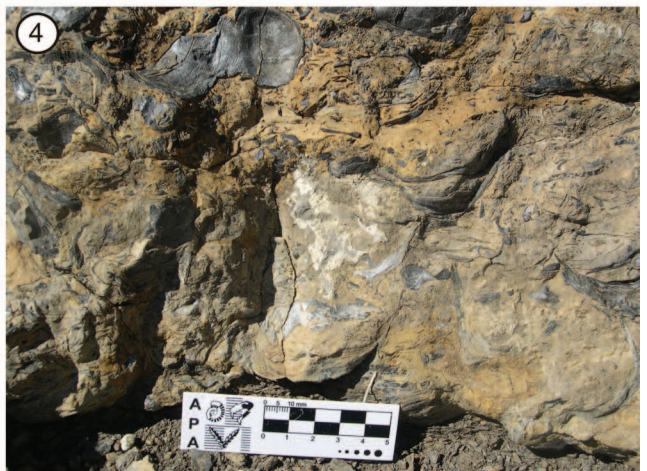
Alternating siltstones, wackestones and mudstones (Fig. 3.5)

Description. Thin, tabular, grey to yellowish-brown coloured shaly siltstones alternating with thin wackestones and mudstones. Beds with distinct lower and upper contacts, reaching a thickness of up to 10 cm. Shell pavements frequently intercalated, most with convex-down valves. Some beds with wave ripples on top. Fossils subparallel to bedding, including *Steinmanella* specimens along with other infaunal, semiinfaunal and epifaunal bivalves, and few gastropods. Some infaunal specimens in life position. This lithofacies was found in the middle part of the measured section at Puerta Curaco (Fig. 2).

Taphonomic observations. Infillings are shaly and calcareous. Preservation of *Steinmanella* is similar to that of the previous lithofacies (overall well-preserved: high articulation, low fragmentation, moderate corrosion, and low number of specimens with chipped margins). Encrustation by oysters and serpulids is moderate. Deep infaunal forms usually in life position.

Interpretation. The unstable orientation of valves (convex side down), presence of wave ripples and abundance and diversity of benthic elements point to a shallower environment in comparison to the previously described lithofacies,

Figure 3. Field pictures/ *Fotos de campo*. **1**, Outcrops of the measured section at Cerrito de la Ventana; notice the sharp contact between the Vaca Muerta and Mulichinco formations/Afloramientos del perfil medido en Cerrito de la Ventana, mostrando el marcado contacto entre las formaciones Vaca Muerta y Mulichinco; **2**, outcrops of the measured section at Pampa Tril/ afloramientos del perfil medido en Pampa Tril; **3**, rudstone lithofacies, showing the size of the oysters and bioclast packing, and amalgamated beds (arrow points to contact between two beds), Cerrito de la Ventana section/ litofacies de rudstones, mostrando el tamaño de las ostras y el empaquetamiento de los bioclastos, y el amalgamamiento de los bancos (la flecha señala el contacto entre dos bancos); perfil de Cerrito de la Ventana; **4**, detail of rudstones showing the fine, calcareous matrix, and variation in bioclast size, Cerrito de la Ventana section/ detalle de rudstones mostrando la matriz calcárea, fina, y la variación en el tamaño de los bioclastos; perfil de Cerrito de la Ventana; **5**, Alternating siltstones, wackestones and mudstones lithofacies, showing the one valve thick pavements intercalated in the laminated siltstones, Puerta Curaco section/ litofacies de alternancia de pelitas, wackestones y mudstones, mostrando los pavimentos de una valva de grosor intercalados en pelitas; perfil de Puerta Curaco; **6**, detail of an *in situ* specimen of *Steinmanella*, in dark grey shales lithofacies; Pampa Tril section/ detalle de un ejemplar *in situ* de *Steinmanella*, en la litofacies de lutitas gris oscuro; perfil de Pampa Tril; **7**, same as 6, from Puerta Curaco section/ igual que 6, perfil de Puerta Curaco.



possibly a mid-ramp setting with influence of storm currents and waves. Accordingly, Schwarz *et al.* (2006) interpreted an open marine, storm and wave influenced setting for the basal section of the Mulichinco Formation at Puerta Curaco, and Rodríguez *et al.* (2007) described for their Facies Association B—which resembles this lithofacies—a similar setting in the nearby locality of Vega de Escalone. The pavements with unstable orientation of valves could result from overturning of valves by the activity of burrowers or some other kind of bioturbators, or by the action of turbulent flows, more likely storm currents and waves.

Rudstones (Fig. 3.3–4)

Description. Simple to amalgamated, grey, tabular rudstones with erosive to gradational base; fine, shale calcareous matrix. Beds 30 cm thick, but reaching 3 m of maximum thickness conforming channelled structures a few meters wide. Shells subparallel or oblique to bedding. Large oysters and trigonioids dominate in abundance over unidentified shell debris. Size selection is poor, with bioclasts ranging from millimetres to nearly entire oysters of over 10 cm in length. Frequent nesting, stacking, and convex-down oriented shells. This facies is recorded in Cerrito de la Ventana and Cerro de la Parva.

Taphonomic observations. Shells are empty or have a fined-grained calcareous infilling. Articulation is high, fragmentation and chipped margins are moderate, and corrosion is low. Encrustation is moderate, mostly by oysters and sepulids.

Interpretation. This lithofacies is interpreted as calcareous storm deposits. Abundance of bioclasts and structures such as nesting and stacking, as well as unstable position of the valves suggest that deposition took place under turbulent conditions. Size of most of the bioclasts is considerable, requiring high water-energy to be mobilised. Low taphonomic modification could result from the nature of the matrix, since mud is significantly less abrasive than sand, and these beds carry a shaly matrix. Amalgamated rudstones may be considered more proximal than simple rudstones, and may result by stacking of several storm-events or by successive reworking of these banks. Channelled rudstones are possibly related to the infilling of previous structures. These amalgamated rudstones are sedimentologic in origin, with a complex inner structure (Kidwell *et al.*, 1986).

OVERALL PALEOENVIRONMENTAL INTERPRETATION

The dark grey shales lithofacies is the most similar to the type section of the Vaca Muerta Formation, which exposes

dark, bituminous shales accumulated in a basinal to outer-ramp environment. In the measured sections, the lighter colour and presence of a quite diverse benthic association, including shallow and deep infaunal bivalves, along with robust, thick-shelled ones, suggest a slightly shallower environment than that usually envisaged for the Tithonian part of the Vaca Muerta Formation, a distal mid-ramp to proximal outer-ramp (Aigner, 1982). This interpretation is reinforced by the intercalation of some distal tempestites (rudstones lithofacies) interrupting the finer background sedimentation. In this setting, trigonioids preserved in shales are represented by autochthonous to slightly parautochthonous specimens, and those preserved in rudstones correspond to specimens reworked from a shallower environment.

At Puerta Curaco, Pampa Tril and Cerro de la Parva the environment gradually shifts from an outer-ramp (dark grey shales lithofacies of the upper part of the Vaca Muerta Formation) to a mid-ramp with storm influence (represented by the alternating siltstones, mudstones and wackestones lithofacies belonging to the Mulichinco Formation), and benthic associations become more diverse and abundant. Preservation of trigonoid remains is quite good. Although reworking was probably more intense than in the dark grey shales lithofacies, it is still likely that fossil assemblages are autochthonous to parautochthonous, as suggested by the quite low taphonomic modification observed.

It is likely that, even in the dark grey lithofacies, oxygen levels were good enough to allow the development of an abundant and diverse benthic fauna, which is in contrast to what is commonly observed in older beds of the Vaca Muerta Formation. The presence of deep burrowers—as well as *Steinmanella* specimens with thick valves and abundant epibiont faunas towards its top—provide evidence of normal oxygen conditions at least temporarily. This is in agreement with findings by Doyle *et al.* (2005), who reported a relative increase in oxygen levels towards the top of the Vaca Muerta Formation. Oxygen levels are likely to have been normal in the shallower Mulichinco Formation since the organic content of the shales is reduced and benthic associations increase in diversity.

SYSTEMATIC PALEONTOLOGY

Supraorder classification follows Cooper (1991) and the style of synonymy list follows Matthews (1973). Only those references with new and figured specimens of *Steinmanella* are included in the synonymy list. Comparisons are made considering only the Early Cretaceous species of the Neuquén Basin, since Tithonian species with bundled ribs and

tubercled corselets can be easily separated [*i.e.*, *S. splendida* (Leanza, 1941), *S. erycina* (Phillipi, 1899), and *S. haupti* (Lambert, 1944)]. Likewise, *Steinmanella vacaensis* (Weaver, 1931) and related forms from the Austral Basin (*i.e.*, *S. katterfeldensis*, *S. posadensis*, *S. maxima* Camacho and Olivero, 1985) are large and highly elongated species that can be easily differentiated from the study material. Most of the African and Indian species will be excluded from the comparison since *S. holubi* (Kitchin, 1908), *S. herzogi* (Goldfuss, 1837) and *S. kensleyi* Cooper, 1979 are very different from the spe-

cies described herein; on the other hand, *S. hennigi* (Lange, 1914) is a very poorly preserved specimen that does not allow much comparison. The Indian *S. mamillata* (Kitchin, 1903) is similar to the material studied and thus included in discussions.

Geographic and stratigraphic provenances are based on authors' data and repository information of specimens listed under synonymy.

Terminology and measurements

The complex sculpture of trigoniods has given rise to

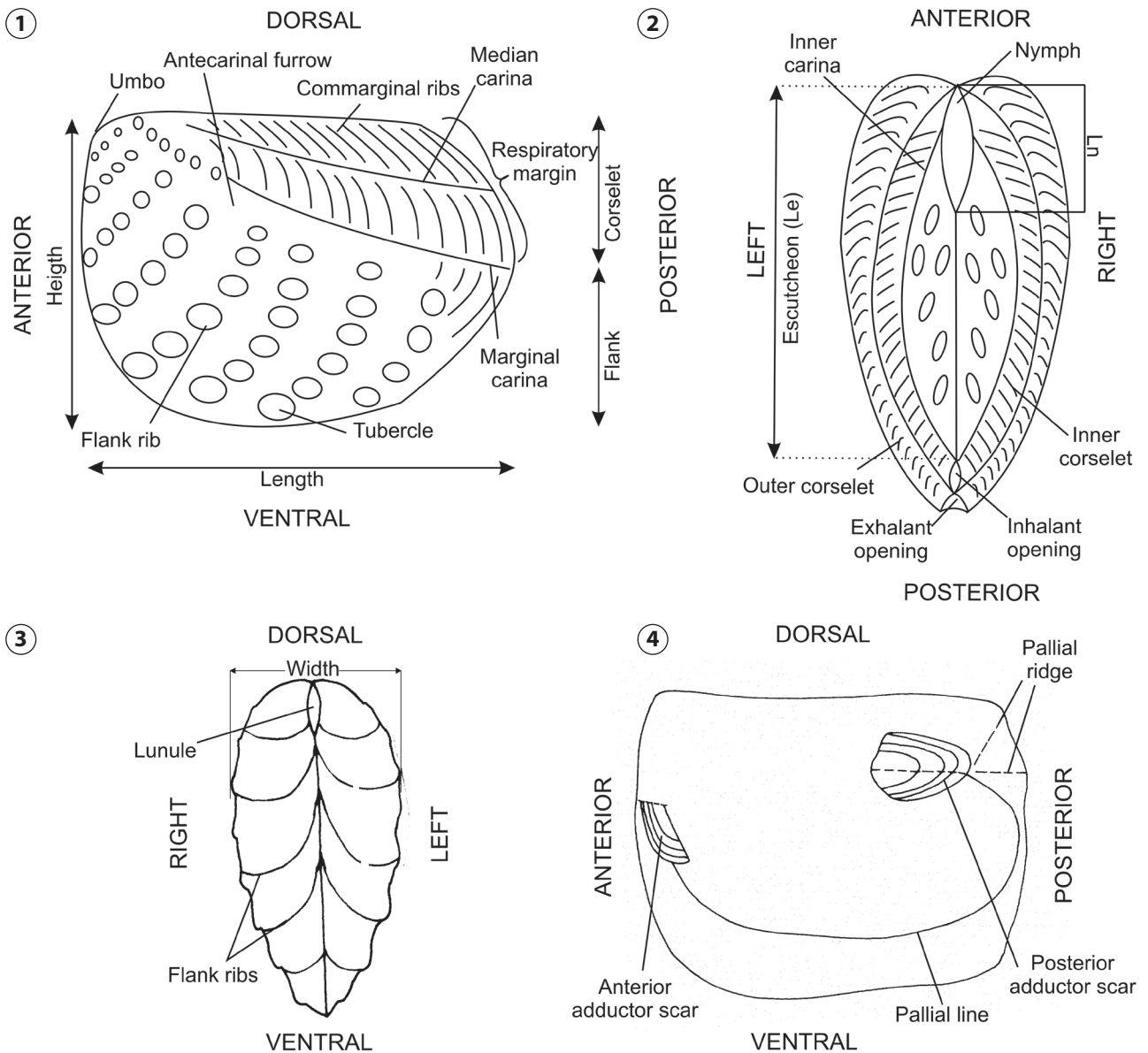


Figure 4. Morphological characters used in the description of *Steinmanella* species/ Caracteres morfológicos utilizados en la descripción de las especies de *Steinmanella*. **1.** Lateral external view of left valve/ vista lateral externa de la valva izquierda. **2.** Dorsal view of shell/ vista dorsal de la conchilla. **3.** Anterior view of shell/ vista anterior de la conchilla. **4.** Internal view of right valve/ vista interna de la valva derecha. **References/ Referencias.** Le, length of escutcheon/ largo del escudete; Ln, length of nymph/ largo de la ninfa.

an abundance of morphological terms. Descriptive terms used are those listed and defined by Cox (1969a,b), Fleming (1964) and Saul (1978). They are illustrated in Figure 4. In addition, the following term is used: pedal elevator muscle scar is a scar located beneath the beaks.

For details in terminology and measured characters see Figure 4, and for measurements see supplementary files online Tables 1–3. Shell size is said to be small, medium or large as compared with other specimens of the same genus, for example those from Camacho and Olivero (1985) and Lazo (2003). Measurements were taken using a digital calliper (accurate to 0.2 mm) and recorded in millimetres. Abbreviations are as follows: (1) L/H = elongation; (2) H/W = inflation; (3) Le = length of escutcheon; (4) Ln = length of nymph. Angular measurements are accurate to the nearest degree: (1) Av = angle between the anterior and ventral margins; (2) Pv = angle between the posterior and ventral margins.

Order TRIGONIOIDA Dall, 1889

Suborder MYOPHORELLINA Cooper, 1991

Superfamily MYOPHORELLOIDEA Kobayashi, 1954

Family MYOPHORELLIDAE Kobayashi, 1954

Subfamily STEINMANELLINAE Cooper, 1991

Genus *Steinmanella* Crickmay, 1930

Type species. *Trigonia holubi* Kitchin, 1908; by original designation (Crickmay, 1930).

Emended diagnosis (modified from Camacho and Olivero, 1985; Cooper, 1991; Leanza, 1998). Robust shell, medium to large-sized; subquadrate to subrectangular or ovate outline; flank ornamented with arched ribs, prominently tuberculated (or nodate); corselet with rugose ribs, transversally oriented; lanceolate escutcheon, decorated with radial rows of tubercles and thin radial ribs; marginal carina delineated by tubercles.

Geographic and stratigraphic provenance. Tithonian-Barremian, Aptian? from Argentina, Chile, Perú, Tanzania, South Africa, and India (Camacho and Olivero, 1985; Lazo, 2003).

Discussion. Although the genus was introduced by Crickmay (1930), the origin of the group can be traced back to Steinmann (1881), who recognized the Section Pseudoquadratae typified by '*Trigonia*' *transitoria* n. sp. to include those trigonioids with intermediate morphology between two groups defined by Agassiz (1841), the Clavellatae and Quadratae. The genus is considered to have a Gondwanic distribution (see Camacho and Olivero, 1985). According to Kobayashi and Amano (1955) and Nakano (1968) the genus *Steinmanella* probably derived from *Myophorella* Bayle, which is also a Gondwanic group (Camacho and Olivero, 1985). The genus *Yaadia* Saul is regarded as derived from *Steinmanella*, restricted to the Valanginian-Maastrichtian of the North Pacific Ocean (Saul, 1978; Cooper, 1991).

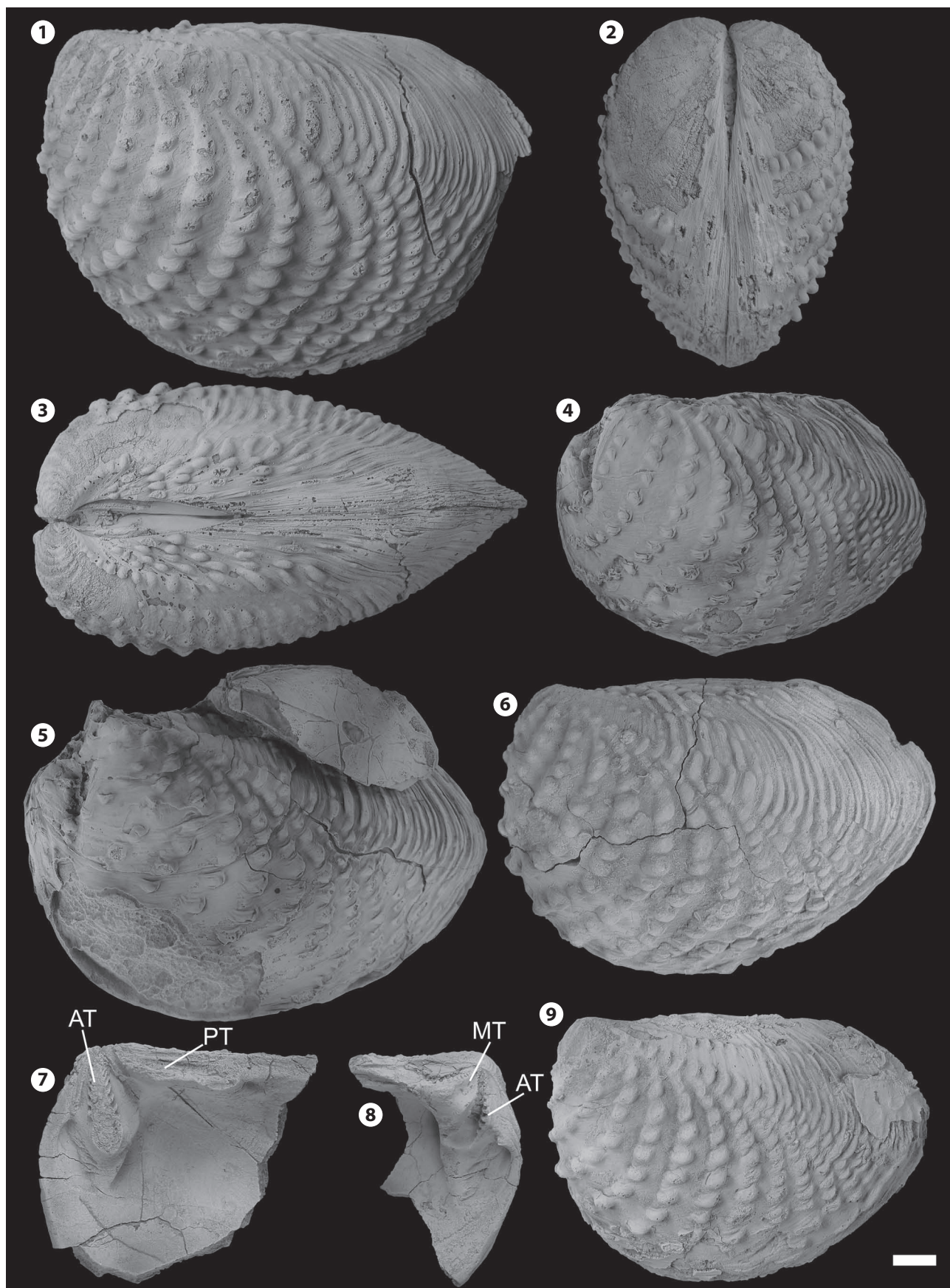
Species of the genus *Steinmanella* show significant intraspecific variability and thus a large number of specimens is necessary in order to assert the extent of morphological variation, adult shells being more informative than juvenile ones. The genus had a complex taxonomic treatment (for a detailed summary see Camacho and Olivero, 1985). In Argentina it was subdivided in a number of rather poorly defined subgenera (see Leanza, 1993). Thus, subgenera are not used in this paper until a thorough revision of the genus is carried out and proper diagnoses of subgenera are achieved.

***Steinmanella curacoensis* (Weaver, 1931)**

Figures 5–6, Table 1

- v. 1931 *Trigonia transitoria* var. *curacoensis* Weaver, pl. 22, figs. 115–118
- v. 1944 *Trigonia steinmanni* Philippi; Lambert, pl. 9, figs. 3–4. [*non Trigonia steinmanni* Philippi, 1889]
- v. 1987 *Steinmanella steinmanni* (Philippi); Leanza and Garate Zubillaga, pl. 13, figs. 1–2 [*non Trigonia steinmanni* Philippi, 1889]
- v. 1993 *Steinmanella* (*Transitrigonia*) *steinmanni* (Philippi); Leanza, pl. 13, figs. 1, 10 [*non Trigonia steinmanni* Philippi, 1889]
- v. 2008 *Steinmanella curacoensis* (Weaver); Luci, p. 70–76, Fig. 29.

Figure 5. *Steinmanella curacoensis* (Weaver, 1931). 1–3, CPBA 20545 in left, anterior and dorsal views, Puerta Curaco, Mulichinco Formation/ en vista izquierda, anterior y dorsal, Puerta Curaco, Formación Mulichinco; 4, CPBA 20306, juvenile in left view, showing a sunken aspect of umbonal area due to dissolution, Cerrito de la Ventana, top of Vaca Muerta Formation/ juvenil en vista izquierda, mostrando un aspecto hundido del área umbonal por efecto de la disolución, Cerrito de la Ventana, tope de la Formación Vaca Muerta; 5, CPBA 20307, left view of adult with attached mytilid, showing the same kind of dissolution as the former specimen, Cerrito de la Ventana, top of Vaca Muerta Formation/ vista izquierda de un ejemplar adulto con un mytilido epibionte, con el mismo tipo de disolución que el ejemplar anterior, Cerrito de la Ventana, tope de la Formación Vaca Muerta; 6, CPBA 20545 in left valve view, Puerta Curaco, Mulichinco Formation/ en vista de la valva izquierda, Puerta Curaco, Formación Mulichinco; 7, CPBA 20545, right valve hinge, Puerta Curaco, Mulichinco Formation/ charnela de la valva derecha, Puerta Curaco, Formación Mulichinco; 8, CPBA 20545, left valve hinge, posterior tooth missing/ charnela de la valva izquierda, falta el diente posterior; 9, CPBA 20545: left valve view, Puerta Curaco, Mulichinco Formation/ vista de la valva izquierda, Puerta Curaco, Formación Mulichinco. **References/ Referencias.** AT: anterior tooth/ diente anterior; MT: mid tooth/ diente medio; PT: posterior tooth/ diente posterior. Scale bar / escala gráfica= 1 cm.



Diagnosis. Suboval outline, flank with small tubercles, corselet with thin rugose ribs partially intercalated with flank ribs in the median part of the valve, carinae poorly marked, elongated oval escutcheon.

Type material. Syntypes of *Steinmanella curacoensis*, BMNH 115, 116, 117 (see Fig. 6) from the Early Cretaceous of Cerro Mula, Cerro Salado, and Loma Tilhué in Neuquén collected by C. E. Weaver.

Additional material. From authors' collection: 115 specimens from Puerta Curaco (CPBA 20543, 20544, 20545); seven from Cerrito de la Ventana (CPBA 20306-20307); one from El Salado (CPBA 20322), one specimen (CPBA 18007) collected by Aguirre-Urreta from the Vaca Muerta Formation in Cerrito de la Ventana, two specimens (CPBA 7547) collected by Lambert (1944; pl. 9, fig. 3-4).

Geographic and stratigraphic provenance. The material studied was collected from the top of the Vaca Muerta Formation and the base of the Mulichinco Formation, from the early Valanginian *Neocomites wichmanni* and *Lissonia riveroi* zones (Aguirre-Urreta and Rawson, 1999). Weaver (1931) recorded *S. curacoensis* from the top of the Vaca Muerta Formation and the Mulichinco Formation at Puerta Curaco and Cerro Mula. Leanza and Garate Zubillaga (1987) and Leanza (1993) collected one specimen in the Valanginian of the Mulichinco Formation at Puerta Curaco (Weaver's type locality); the latter reported the finding of one specimen in the *Olcostephanus atherstoni* Zone. Lambert (1944) collected one specimen from the Early Cretaceous of Chacay Melehue. It has also been reported from Chile, but these records need revision (e.g., Reyes *et al.*, 1981).

Description. Ovate outline with rounded, curved margins. Shell inflated. Dorsal margin straight, anterior margin convex, ventral margin ample convex, continuous with the posterior margin. Respiratory margin with narrow openings. Shell thin. Beaks slightly protruding over dorsal margin. Anterior view heart shaped.

Flank ornamented with finely tuberculated ribs, attaining their maximum curvature towards venter. Fifteen ribs maximum. Ribs close together and thinner near marginal carina. Twelve to fifteen tubercles on each rib, rounded to oval, small, slightly elongated transversely to the ribs. Marginal

carina poorly demarcated, with small tubercles in its anterior portion. Middle and posterior parts of the shell without clear separation of flank and corselet.

Corselet triangular in shape, ornamented with commarginal ribs reaching the dorsal flank. Median carina with small tubercles on its anterior portion. Inner carina with small tubercles.

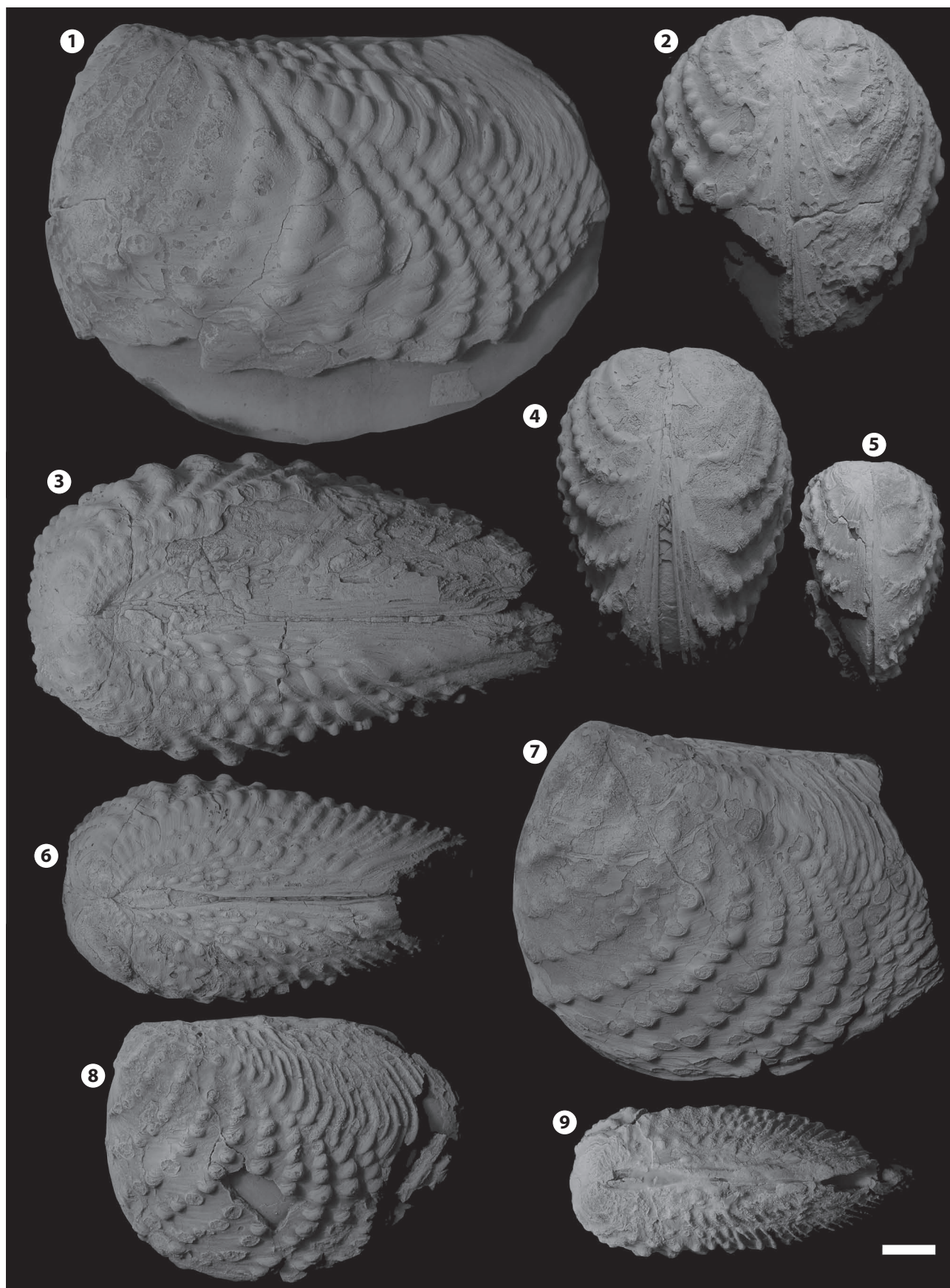
Escutcheon oval and elongated, with rows of small, elongated tubercles densely disposed. Nymph deep, narrow and elongated. Lunule narrow and elongated.

Pallial line continuous, well-defined. Anterior adductor scar situated below the hinge, subcircular, slightly elongated dorsoventrally; posterior adductor scar subcircular, elongated anteroposteriorly, tapering posteriorly; situated dorsally anterior to the respiratory openings. Left valve hinge with three cardinal teeth: one middle bifid striated tooth, and an anterior, small, striated tooth. Posterior tooth reduced or absent. Right valve with two cardinal teeth: one wide posterior striated tooth, and an anterior striated buttressed tooth. Left valve with conical scar of pedal elevator muscle beneath hinge. Pallial ridge conspicuous.

Discussion. A number of authors have placed *S. curacoensis* (Weaver, 1931) in the synonymy of *S. steinmanni* (Philippi, 1899). Lambert (1944) was the first to adopt this criterion and his opinion was followed by Lo Forte (1988), Leanza and Garate Zubillaga (1987), and Leanza (1993).

The holotype of *S. steinmanni* (Philippi, 1899, p. 64, pl. 30, figs. 1-2) from Chile is considered to be lost (Pérez and Reyes, 1989) and thus all information available for identification of the species are Philippi's sketches and a brief, cryptic description. In addition, the stratigraphic position and age of the species are also unknown. The illustration of the dorsal view of the holotype is strongly schematic, while the left lateral view is somewhat clearer and shows the presence of a furrow below the marginal carina that is not mentioned in the original description. Flank ribs have small tubercles that seem to be elevated from the shell surface by a slight basal buttress. There seems to be a complete absence of carinae separating corselet and flank and the outer and inner corselets. The dorsal sketch shows an escutcheon demarcated by tuberculated carinae, and ornamented with very thin radial ribs. In our opinion *S. steinmanni* is morphologically different from *S. cu-*

Figure 6. *Steinmanella curacoensis* (Weaver, 1931). 1-3, Syntype BMNH 116 in left lateral, anterior and dorsal views, Locality 1594 Cerro Salado, top of the Vaca Muerta Formation/ *sintipo, en vistas lateral izquierda, anterior y dorsal, Localidad 1594 Cerro Salado, tope de la Formación Vaca Muerta*; 4, 6-7. Syntype BMNH 115 in anterior, dorsal and left lateral views, Locality 1740 Cerro Mula, top of the Vaca Muerta Formation/ *sintipo, en vistas anterior, dorsal y lateral izquierda, Localidad 1740 Cerro Mula, tope de la Formación Vaca Muerta*; 5, 8-9, Syntype BMNH 117 in anterior, left lateral and dorsal views, Locality 100 Loma Tilhué, Mulichinco Formation/ *sintipo, en vistas anterior, lateral izquierda y dorsal, Localidad 100 Loma Tilhué, Formación Mulichinco*. Scale bar/ *escala gráfica* = 1 cm.



racoensis and thus they should be considered as two separate, valid species. *Steinmanella curacoensis* does not have a furrow below the marginal carina; though poorly marked, carinae are recognizable, especially in the anterior third of the shell; the escutcheon is more elongated and is ornamented by rows of small tubercles; and the posterior half of the shell shows an interdigitation of the flank and corselet ribs. In contrast, and in addition to all differences already mentioned, *S. steinmanni* has no intercalated ribs between the flank and corselet.

Lo Forte (1988) reported a specimen of *S. steinmanni* (CPBA 15393) from the Tithonian-Early Cretaceous of Quebrada de Agua Blanca, Mendoza. Luci (2008) revised this specimen and found that the corselet is ornamented with small nodules, therefore placing this specimen in the group of *Steinmanella* with nodose corselets, proposed by Leanza (1993) as the subgenus *S. (Splenditrigonia)*.

Steinmanella mammillata (Kitchin, 1903, p. 100–103, pl. 9, figs. 8–9) has a more subrectangular outline, a straight anterior margin and is weakly inflated; the anterior portion shows a furrow below the marginal carina; the corselet's anterior portion is ornamented with tubercles and its ribs are thicker. *Steinmanella neuquensis* (Burckhardt, 1903, p. 74–75, pl. 14, figs. 4–6, from Agrio River near Las Lajas) can be differentiated from *S. curacoensis* because it has a more subquadrate outline, better delineated carinae, and more prominent tubercles on the flank. *Steinmanella pehuenmapuensis* (Leanza, 1998, p. 60, pl. 1, figs. 1–4) is clearly distinguished from *S. curacoensis* by its triangular shape, blunt anterior margin, prominent carinae, furrow below the marginal carina, medial corselet furrow and larger flank tubercles. *Steinmanella quintucoensis* (Weaver, 1931, p. 248, l. 21, fig. 111, pl. 23, figs. 119–125) differs by having a prominent furrow below the marginal carina and large tubercles on the flank. *Steinmanella subquadrate* sp. nov. is more subquadrate and has better marked carinae, a corselet divided into upper and lower parts, and a different disposition of the flank's ribs. *Steinmanella transitoria* (Steinmann, 1881, p. 260, pl. 13, fig. 3) is different from *S. curacoensis* because it shows a furrow below the marginal carina, more robust ribs on the flank, a well-defined corselet and more conspicuous carinae.

Steinmanella quintucoensis (Weaver, 1931)

Figures 7–8, Table 2

- v. 1931 *Trigonia transitoria* var. *quintucoensis* Weaver, p. 248–250; pl. 21, fig. 111, pl. 23, fig. 119–125.
- 1944 *Trigonia transitoria* Steinmann; Lambert, pl. 6, fig. 1. [*non Steinmanella transitoria* (Steinmann, 1881)]
- 1987 *Steinmanella quintucoensis* (Weaver); Leanza and Garate Zubillaga, pl. 12, figs. 5–6.
- 1993 *Steinmanella quintucoensis* (Weaver); Leanza, pl. 14, fig. 1, 2, 4, 10.
- v. 2008 *Steinmanella quintucoensis* (Weaver); Luci, pls. 25–26.
- v. 2010 *Steinmanella quintucoensis* (Weaver); Luci, pls. 3–4.

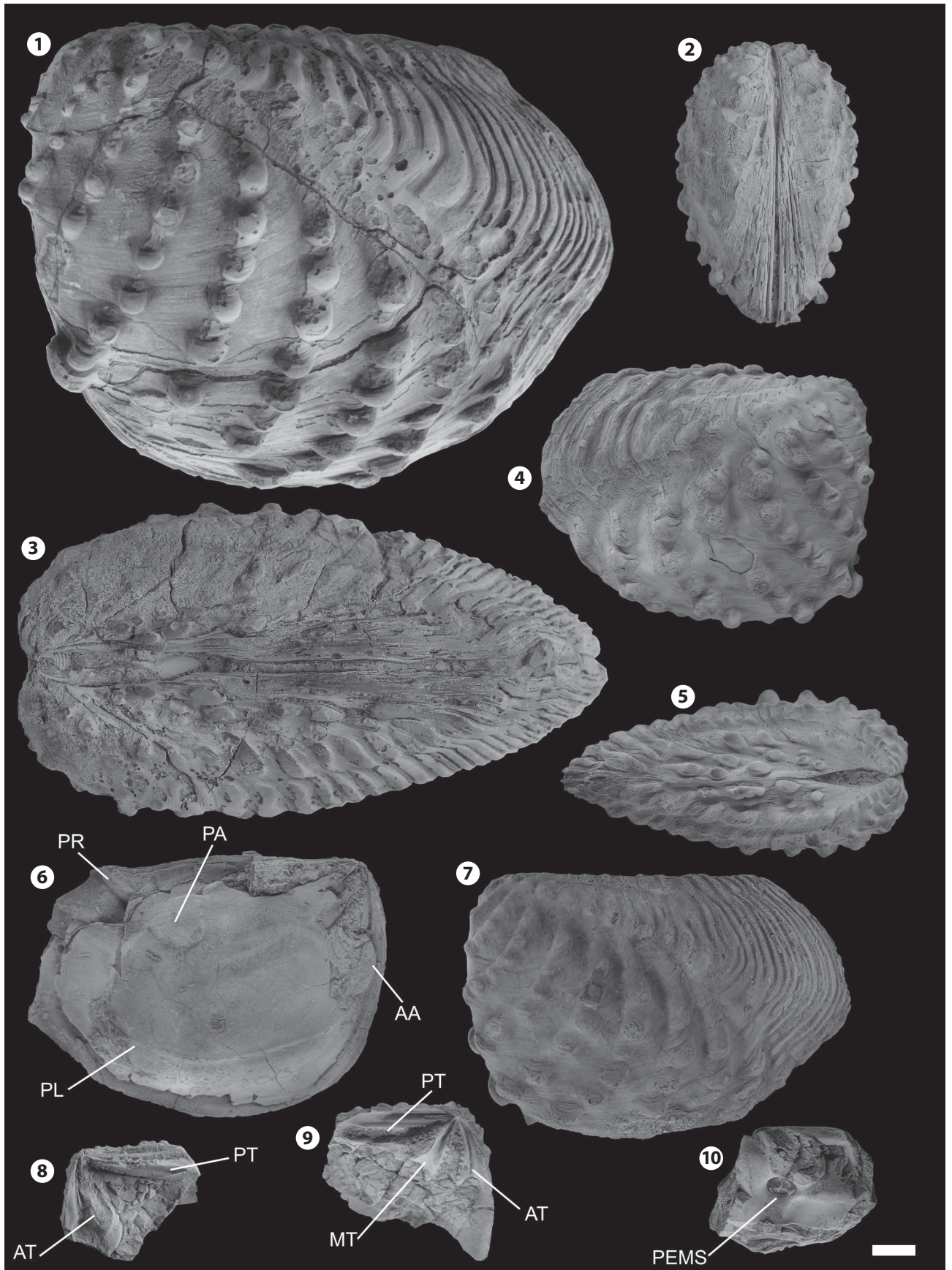
Diagnosis. Shell subrectangular, flank with coarsely tuberculated ribs, prominent furrow below the marginal carina expanded posteriorly, corselet with rugose ribs, carinae well-marked on the anterior third of the shell, lanceolate escutcheon with small tubercles and fine radial ribs.

Type material. Syntypes of *Steinmanella quintucoensis* BMNHC 118, 119, 122 (see Fig. 8) from the Early Cretaceous of Cerro Salado in Neuquén collected by C. E. Weaver.

Additional material. From authors' collection: 176 specimens from Cerrito de la Ventana (CPBA 20300–20302); nine topotypes from El Salado (CPBA 20303); five from Cerro La Parva (CPBA 20548); 38 from Pampa Tril (CPBA 20549, 20550); 10 from Puerta Curaco (CPBA 20542, 20541) and two from Arroyo Mailenco (CPBA 20540), one specimen collected by Aguirre-Urreta, Rawson and Espona (CPBA 18007) from Cerrito de la Ventana, and three collected by Dásquez from the top of the Vaca Muerta Formation in Agua de la Mula.

Geographic and stratigraphic provenance. In the present study, this species was recorded near the top of the Vaca Muerta Formation and the base of the Mulichinco Formation, in the *Neocomites wichmanni* and *Lissonia riveroi* Zones, early Valanginian. Weaver (1931) recorded this species in the Quintuco and Mulichinco formations; Lambert (1944) described a specimen from Covunco without age data. Leanza and Garate Zubillaga (1987) reported the finding of their specimens at Cerrito de la Ventana, in the Vaca Muerta Formation in beds containing *Lissonia riveroi* of early Valanginian age. Leanza (1993) described new specimens from the

Figure 7. *Steinmanella quintucoensis* (Weaver, 1931), from Cerrito de la Ventana, top of the Vaca Muerta Formation / *provenientes de Cerrito de la Ventana, tope de la Formación Vaca Muerta*. **1, 3**, CPBA 20301, left lateral and dorsal views/ *vistas lateral izquierda y dorsal*; **2**, CPBA 20300, anterior view/ *vista anterior*; **4–5**, CPBA 20301, right lateral and dorsal views/ *vistas lateral derecha y dorsal*; **6**, CPBA 20300, internal mould in right lateral view/ *molde interno en vista lateral derecha*; **7**, CPBA 20301, left valve view/ *vista de la valva izquierda*; **8**, CPBA 20300, right valve hinge/ *charnela de la valva derecha*; **9**, CPBA 20301, left valve hinge/ *charnela de la valva izquierda*; **10**, CPBA 20302, left valve hinge from ventral view/ *charnela de la valva izquierda en vista ventral*. **References / Referencias.** **AA:** anterior adductor scar/ *cicatriz del aductor anterior*; **AT:** anterior tooth/ *diente anterior*; **MT:** mid tooth/ *diente medio*; **PA:** posterior adductor scar/ *cicatriz del aductor posterior*; **PEMS:** pedal elevator muscle scar/ *cicatriz del músculo elevador pedal*; **PL:** pallial line/ *línea palial*; **PR:** pallial ridge/ *cresta palial*; **PT:** posterior tooth/ *diente posterior*. Scale bar/ *escala gráfica*= 1 cm.



same locality, but of late Berriasian to early Valanginian age. It has also been found in Chile, but records need revision (e.g., Corvalán and Pérez, 1958).

Description. Large, robust shell, subrectangular outline; equivalve and inequilateral. Dorsal margin slightly convex, anterior and ventral margins convex, posterior margin v-shaped. Beaks slightly opisthogyrous, small. Narrow, elongated lunule. Inhalant and exhalant openings conspicuous.

Flank and corselet well-differentiated by a furrow below the marginal carina. Flank with tuberculated ribs. Conspicuous smooth furrow below the marginal carina dividing flank from corselet, widening posteriorly. Flank with nine to thirteen oblique ribs. Anteriormost four ribs near beaks, strongly curved; middle and posterior ribs nearly straight, curved pronouncedly towards the ventral margin and the furrow below the marginal carina, meeting at an angle of 45°. Ribs widely spaced, with usually six to seven large, rounded tubercles. Marginal carina with small nodules in the anterior third of the shell and commarginal ribs in the posterior portion.

Corselet triangular, ornamented with concentric, rugose ribs. Median groove and carina between the lower and upper corselet. Escutcheon lanceolate, spanning two thirds of shell length, ornamented with radial ribs and small tubercles. Nymph deep and lanceolate, extending up to the first third of the escutcheon.

Anterior adductor scar rounded, placed under the beaks on the anterior margin of the shell. Posterior adductor scar slightly elongated along the anteroposterior axis, deep and conspicuous, divided by a longitudinal ridge. Pallial line continuous and conspicuous. Left hinge with three cardinal teeth. Anterior cardinal tooth elongate, median tooth wide and bifid, and posterior tooth elongate. Teeth transversely striated. Right hinge with two elongate, striated teeth. Anterior cardinal oriented dorso-ventrally and posterior cardinal oriented antero-posteriorly. Conspicuous pallial ridge. Juvenile shells (L < 5 cm) more rounded in outline.

Discussion. Weaver (1931) acknowledged the morphologic variability shown by *Steinmanella transitoria* Steinmann and nominated three new varieties: *S. transitoria* var. *quintucoensis*, *S. transitoria* var. *curacoensis*, and *S. transitoria* var. *vacaensis*. The latter was soon accepted, but the first two were regarded by Lambert (1944) as junior synonyms of *S. transitoria*. Later, other authors revalidated *S. transitoria* var. *quintucoensis* (Saul, 1978; Reyes Bianchi *et al.*, 1981; Camacho and Olivero, 1985; among others). Finally, Leanza and Garate Zubillaga (1987) were the first to raise the variety to specific rank, highlighting that it features a unique, very

wide and smooth furrow below the marginal carina, a criterion shared herein.

Steinmanella curacoensis (Weaver, 1931, p. 251–254, pl. 24, fig. 115–118) differs from *S. quintucoensis* by its oval outline, lack of carinae and furrow below the marginal carina, and smaller and more closely spaced ribs, with smaller, closely spaced tubercles. *Steinmanella mammillata* (Kitchin, 1903, p. 100–103, pl. 9, figs. 8–9) presents a furrow below the marginal carina only on the anterior part of the shell, a poorly defined escutcheon and a corselet ornamented with nodes on its anterior portion. *Steinmanella neuquensis* (Burckhardt, 1903, p. 74–75, pl. 14, figs. 4–6) lacks a furrow below the marginal carina, and has smaller flank tubercles and different ornamentation on the escutcheon. *Steinmanella pehuenmapuensis* (Leanza, 1998, p. 60, pl. 1, figs. 1–4) has a narrower furrow below the marginal carina and is subtriangular in outline. It has a more acuminate posteroventral margin, a blunt anterior margin and prominent umbos. *Steinmanella steinmanni* (Philippi, 1899, p. 64, pl. 30, fig. 1–2) differs from *S. quintucoensis* because it shows a suboval outline, greater number of ribs on the flank, and smaller and more closely spaced tubercles. *Steinmanella subquadrata* sp. nov. has a subquadrate outline, oval escutcheon and well-marked carinae. *Steinmanella transitoria* (Steinmann, 1881, p. 260, pl. 13, fig. 3) has a poorly defined furrow below the marginal carina, a more conspicuous separation of the upper and lower corselet, better developed carinae and smaller flank tubercles. The shell is more acute posteriorly, and the anterior margin is straighter.

***Steinmanella subquadrata* sp. nov.**

Figures 9–10, Table 3

- v. 1931 *Trigonia neuquensis* Burckhardt; Weaver, pl. 22, figs. 112–114 [*non Trigonia neuquensis*, Burckhardt, 1903, p. 74–75, pl. 14, figs 4–5].
- v. 1993 *Steinmanella neuquensis* (Burckhardt); Leanza, pl. 12, figs. 6, 7 [*non Trigonia neuquensis*, Burckhardt, 1903, p. 74–75, pl. 14, figs 4–5].
- v. 1993 *Steinmanella (Splenditrigonia) splendida* (Leanza); Leanza, pl. 11, figs. 5–8 [*non S. splendida*, (Leanza, 1941), p. 225, pl. 1, figs. 1–2].
- v. 2008 *Steinmanella neuquensis* (Burckhardt); Luci, pl. 28.

Derivation of name. The specific name refers to the subquadrate outline of the shell.

Diagnosis. Subquadrate shell, flank with tuberculate ribs, corselet with thin rugose ribs, well marked carinae, corselet

with conspicuous mid furrow, oval escutcheon with rows of tubercles and delicate radial ribs.

Type material. The specimen designated to be the holotype of *S. subquadrata* is CPBA 20547.1 from Puerta Curaco, collected by the authors near the *Steinmanella* bearing alternating siltstones, wackestones and mudstones in the *Lissonia riveroi* Zone.

Additional material. From authors' collection: six specimens from Cerrito de la Ventana (CPBA 20304, 20321); three from El Salado (CPBA 20305); two from Puerta Curaco (CPBA 20547), one specimen collected from Cerrito de la Ventana by Aguirre-Urreta, Rawson and Espona (CPBA 18007).

Geographic and stratigraphic provenance. The material studied here was recorded near the top of the Vaca Muerta Formation, in the *Neocomites wichmanni* and *Lissonia riveroi* zones, of early Valanginian age (Aguirre-Urreta and Rawson, 1999). The occurrence of the synonymised specimens is as follows: Leanza's (1993) specimens were found in the late Berriasian and Valanginian of the Vaca Muerta Formation at Cerrito de la Ventana; Weaver (1931) reported the finding of his specimens from Cerro Salado and Cerro Vaca Muerta, in association with *S. quintucoensis*, in the upper part of the Quintuco Formation.

Description. Subquadrate, equivalved and inequilateral shell, inflated, with thick valves (5.8 mm), tapering posteriorly. Dorsal margin straight, anterior margin straight to convex, ventral margin ample convex. Posterior margin straight, forming an obtuse angle with the dorsal and ventral margins. Inhalant and exhalant openings conspicuous. Dorsal and anterior margin meeting at a nearly right angle. Beaks small, opisthogyrous; lunule narrow. Valves divided into corselet and flank by a well-developed marginal carina; absence of furrow below the marginal carina. Marginal carina tuberculate for the first half of valve length. Anterior view of the shell heart-shaped, with flank ribs reaching the anterior commissure.

Flank ornamented with tuberculate ribs; anterior ribs at right angle with the marginal carina, middle ribs at acute angle; posterior almost subparallel to marginal carina. Tubercles small- to medium-sized.

Corselet triangular in shape, ornamented with concentric rugose ribs, and divided by a conspicuous furrow into upper narrow corselet, and lower posteriorly expanded triangular corselet.

Escutcheon oval, up to half of valve length, ornamented with thin concentric ribs, and small, elongated tubercles. Nymph deep and lanceolate.

All specimens preserved articulated; no internal characters could be observed.

Discussion. Inconsistencies between Burckhardt's (1903) description and illustrations of *S. neuquensis* may have led

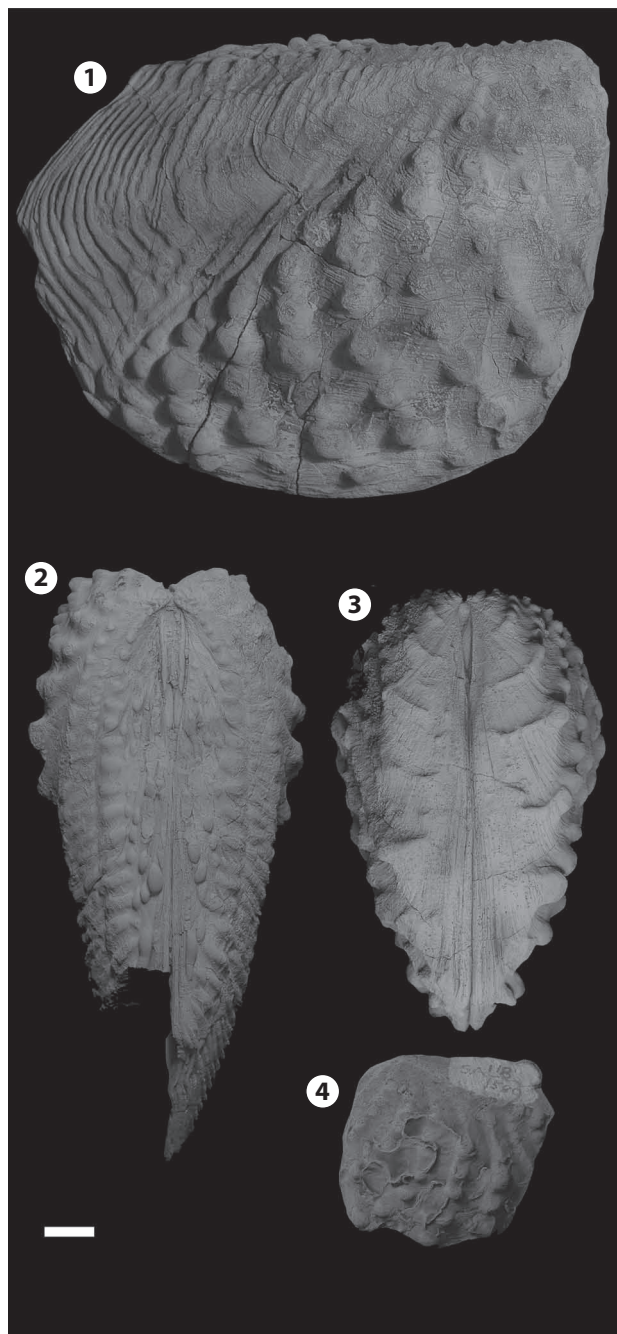
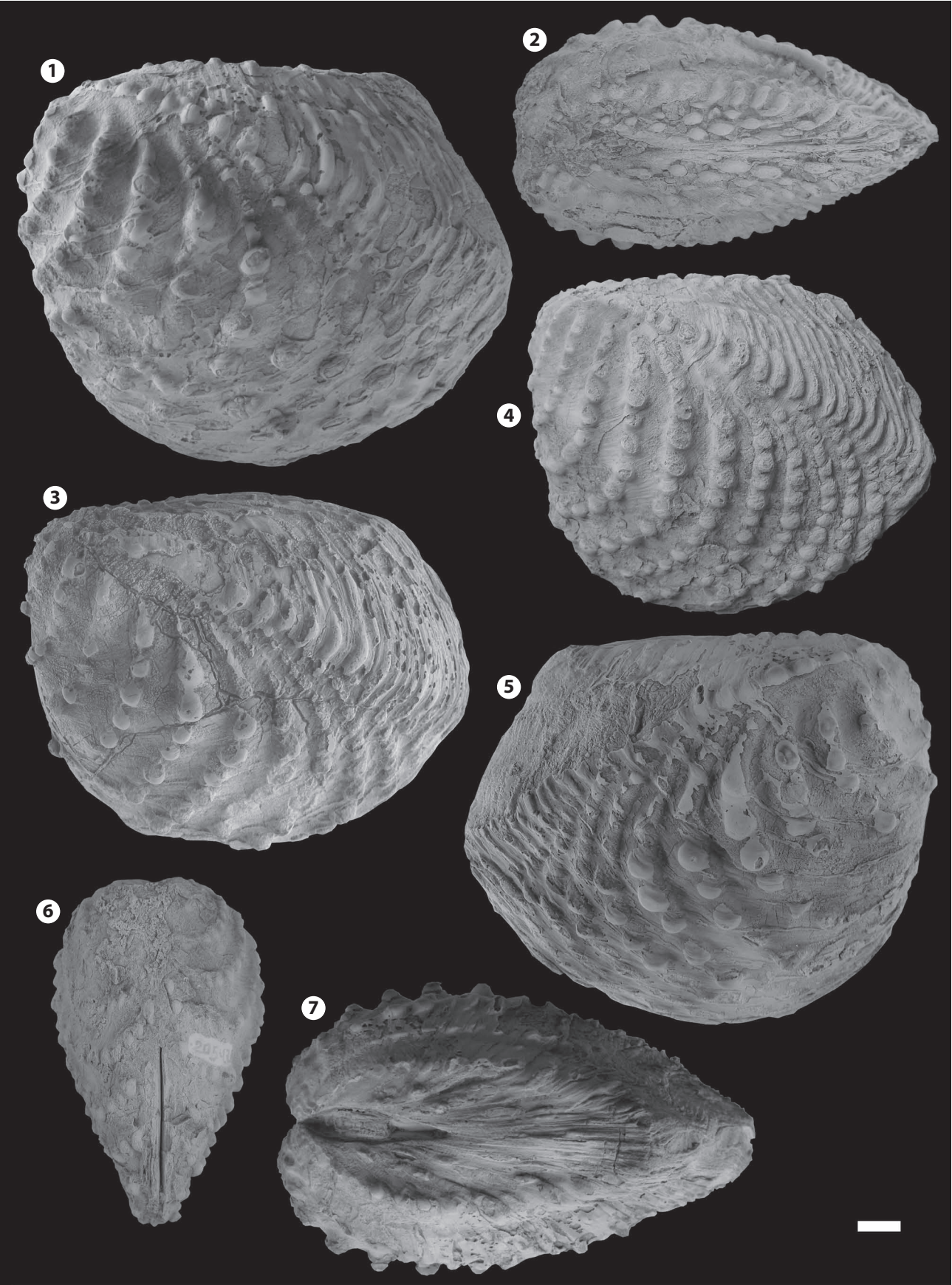


Figure 8. *Steinmanella quintucoensis* (Weaver, 1931), from Locality 1589 Cerro Salado, top of the Vaca Muerta Formation/ *provenientes de la Localidad 1589 Cerro Salado, tope de la Formación Vaca Muerta Formation*. **1, 3–4**, Syntype BMNHC 119 in right lateral, dorsal and anterior views/ *sintipo, en vistas lateral derecha, dorsal y anterior*; **2**, Syntype BMNHC 118 in left lateral view/ *sintipo, en vista lateral izquierda*. Scale bar/escala gráfica= 1 cm.



later authors to misinterpret the true identity of the species. Several authors (e.g., Weaver, 1931; Lambert, 1944; Camacho and Olivero, 1985; Leanza and Garate Zubillaga, 1987; Leanza, 1993) identified different specimens from several localities as *S. neuquensis*, but they did not agree with the original description and pictures of the holotype. Some of those specimens are here regarded as synonyms of *S. subquadrata* sp.nov..

The holotype of *Steinmanella neuquensis* (Burckhardt, 1903, p. 74–75, pl. 14, fig. 4–6) is a worn anterior fragment of a left valve (see Fig. 11). In lateral view the flank ribs are curved pronouncedly towards the ventral margin. Marginal and inner carinae are not demarcated. Ribs are continuous between flank and corselet and the boundary is given mostly by a change in ornamentation and curvature of the shell. The dorsal margin is straight and the anterior margin is incomplete. The escutcheon is poorly preserved. Shell inflation is low for the genus.

Burckhardt (1903) described some of the mentioned features, such as the weak inflation of the valve, straight dorsal margin, flank ribs curving strongly towards the ventral margin, wide and flat corselet, and poor demarcation of carinae. He referred, however, to some features of the escutcheon that are not readily recognisable in the photograph of the specimen. The illustration shows a poorly marked escutcheon carina and a few thin, radially elongated tubercles that would correspond to the escutcheon. In his description he referred to the outline of the valve as quadrangular, but the specimen is incomplete. He also described a longitudinal furrow that separates the corselet in an upper and lower portion, but this could not be observed neither in the original illustration nor in the photograph of the holotype. In addition, corselet ribs are illustrated as bifurcating and originating in the uppermost end of the flank ribs.

The holotype of *S. neuquensis* was collected by Burckhardt near Las Lajas, on the left bank of Río Agrio. Beds outcropping in this section have been mapped as belonging to the Mulichinco Formation (Leanza and Hugo, 2005). We revisited the section and found a succession of tens of meters of fine sandstones intercalated with coquinas. There are at least five *Steinmanella* bearing levels associated with poorly

preserved ammonoids that seem to indicate a Berriasian to earliest Valanginian age. These beds are older than the studied interval and thus the holotype of *S. neuquensis* should be older than the *Steinmanella* species studied here.

Steinmanella curacoensis (Weaver, 1931, p. 245, pl. 22, fig. 115–118; see Figs. 5–6 here) differs from *S. subquadrata* because it is more elongated, has poorly demarcated carinae and more closely-arranged tubercles in the flank. *Steinmanella mammillata* (Kitchin, 1903, p. 100–103, pl. 9, figs. 8–9) presents a poor demarcation of carinae, a greater anteropos-

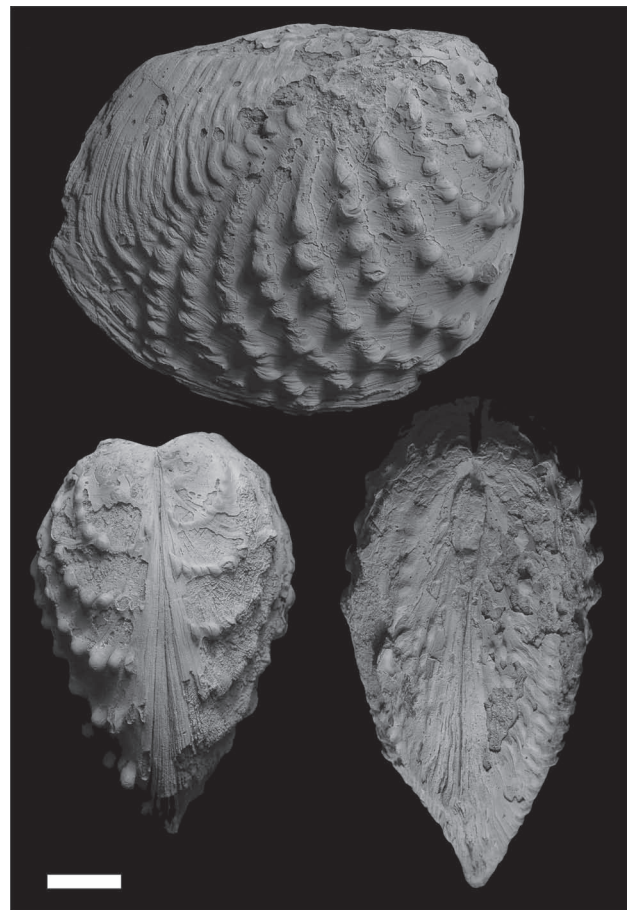


Figure 10. *Steinmanella subquadrata* sp.nov. **1–3**, BMNHC 126 in right lateral, anterior and dorsal views, Locality 1590 Cerro Salado in label (Locality 1705, 7 km SE of Cerro Mocho, on specimen), top of the Vaca Muerta Formation/ en vistas lateral derecha, anterior y dorsal, Localidad 1590 Cerro Salado en etiqueta (Localidad 1705, 7 km SE de Cerro Mocho, en el ejemplar), tope de la Formación Vaca Muerta. Scale bar/ escala gráfica= 1 cm.

Figure 9. *Steinmanella subquadrata* sp.nov. **1, 7**, CPBA 20305 in left lateral and dorsal views, El Salado, top of the Vaca Muerta Formation/ en vistas lateral izquierda y dorsal, El Salado, tope de la Formación Vaca Muerta; **2, 4, 6**, Holotype CPBA 20547.1 in dorsal, left lateral and anterior views, Puerta Curaco, Mulichinco Formation/ Holotipo, en vistas dorsal, lateral izquierda y anterior, Puerta Curaco, Formación Mulichinco; **3**, CPBA 20304 in left valve view, Cerrito de la Ventana, top of Vaca Muerta Formation/ en vista de la valva izquierda, Cerrito de la Ventana, tope de la Formación Vaca Muerta; **5**, CPBA 20305 in right valve view, El Salado, top of Vaca Muerta Formation/ en vista de la valva derecha, El Salado, tope de la Formación Vaca Muerta. Scale bar/ escala gráfica= 1 cm.

terior elongation, a corselet ornamented with nodes on its anterior part, and an elongate, poorly defined escutcheon. *Steinmanella pehuenmapuensis* (Leanza, 1998, p. 60, pl. 1, fig. 1–4) has a distinctive triangular outline, a pointed posterior margin, a blunt anterior margin, and a prominent marginal carina. *Steinmanella quintucoensis* (Weaver, 1931, p. 248, pl. 21, fig. 111; pl. 23, fig. 119–125; see also Figures 7–8 here) is more elongated than *S. subquadrata* and has a very conspicuous furrow below the marginal carina that is absent in the latter species. *Steinmanella steinmanni* (Philippi, 1899, p. 64, pl. 30, fig. 1–2) is different from *S. subquadrata* because it has an oval outline, more conspicuous beaks, smaller tubercles, and poorly defined carinae. *Steinmanella transitoria* (Steinmann, 1881, p. 260–261, pl. 13, fig. 3) is more elongated than *S. subquadrata* and has a well-demarcated marginal carina, a narrower angle between respiratory and posterior margin and a wider nymph. Also, the flank ribs of *Steinmanella transitoria* are less arched and carry larger tubercles.

DISCUSSION

Despite the abundance and diversity displayed by the genus *Steinmanella*, little is known about the environment inhabited by its species. Lazo (2003) pointed out that species of *Steinmanella* were abundant in both dark-grey shales and storm-deposited sandstones of the Agrio Formation. We also report *Steinmanella* specimens in dark grey shales, rudstones and alternating siltstones, wackestones and mudstones, the first two belonging to a proximal outer ramp, and the latter to a mid-ramp. Therefore, these trigonioids were able to survive under both quiet and agitated water conditions, and both in sandy and muddy substrates.

This observation is in agreement with other studies on trigonioid paleoecology. Stanley (1977) found that many trigonioids were capable of withstanding high water energy and also shifting substrata; but he also referred to some of these bivalves which inhabited more stable muddy bottoms. In a more recent survey of European trigonioids, Francis and Hallam (2003) corroborated Stanley's (1977) observations, and reported trigonioids from a dysoxic argillaceous bottom of a quiet-water environment much like the dark grey shales of the Vaca Muerta Formation described herein. In this respect, extant *Neotrigonia* is often found on the continental shelf, but can also be found in tidal channels filled with poorly sorted sand (Stanley, 1977). Stanley (1977, 1978) concluded that most trigonioid occurrences take place in shallow water settings (10–15 m), the extant *Neotrigonia* being unrepresentative of the family since they inhabit depths of 70 to 100 m.

Although trigonioids were greatly varied in shape and ornamentation, the same characteristic features (thick valves, strong, striated dentition, coarse ornamentation) seem to signal them as quite efficient burrowers (Stanley, 1978). The abundance of *Steinmanella* in both sand and shale beds, and in both quiet and wave dominated settings indicates that this genus was well-adjusted to inhabiting these environments with equal success, and it is quite common to find them in great abundance in both scenarios. This allowed *Steinmanella* to become a conspicuous faunal element of shallow settings. The finding of these trigonioids at the top of the Vaca Muerta Formation reinforces the postulated shallower environment proposed for that interval, as compared to the Tithonian laminated black shales of the unit. This is due to the apparent preference of these bivalves for shallow settings.

Another issue concerning the genus *Steinmanella* in the

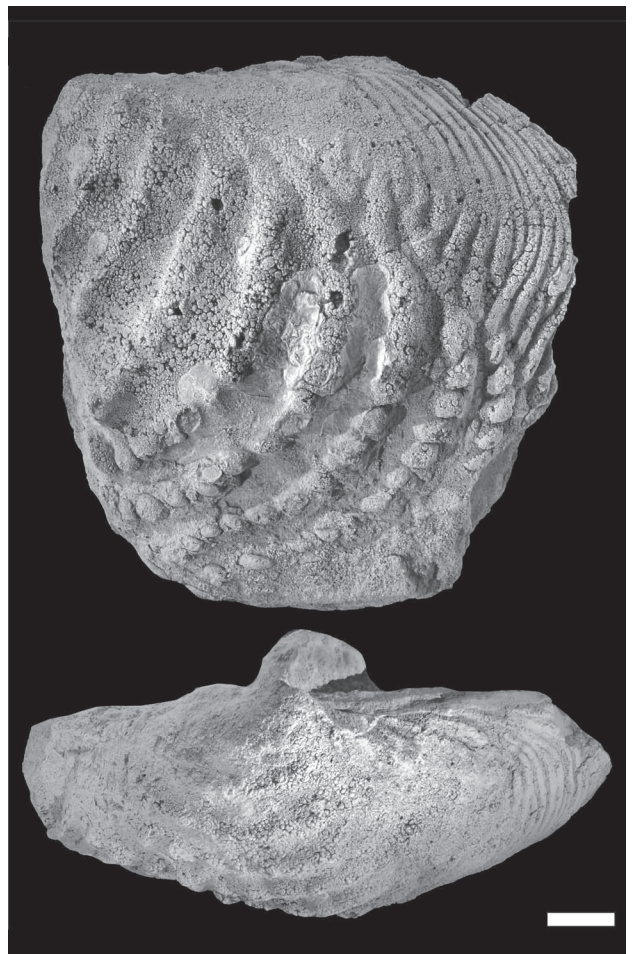


Figure 11. *Steinmanella neuquensis* (Burckhardt, 1903). 1–2, Holotype BSPG AS XXXV 11 in left lateral and anterodorsal views, left bank of Río Agrio just in front of Las Lajas/ Holotipo, en vistas lateral izquierda y anterodorsal, margen izquierda del Río Agrio frente a Las Lajas. Scale bar/ escala gráfica= 1 cm.

Early Cretaceous of the Neuquén Basin is the overall absence of precise stratigraphic ranges at the species level. Occurrences are generally reported from repository specimens without reliable provenance or age information, or on the finding of unique specimens. The problem dates back to the very establishment of some of the species, since many of them were defined in the beginning of the twentieth century when ammonoid zonations and lithostratigraphy were poorly known. Figure 12 shows the stratigraphic range of Early Cretaceous species based on our data and previously published data. It is interesting to note that the early Valanginian was a moment of origination and coexistence of three species of *Steinmanella* that co-occur in the same beds. This is in contrast to the late Valanginian–Hauterivian of the Agrio Formation where monospecific associations have been recorded (see Lazo, 2003; Lazo *et al.*, 2009). Species described in this paper were found at the top of the *Neocomites wichmanni* Zone, and along the *Lissonia riveroi* Zone.

Age	Zone	Early Cretaceous <i>Steinmanella</i> ranges (Neuquén Basin)	
Barr.	<i>Parasitoceras groeberi</i>		
	<i>Crioceratites diamantensis</i>		
	<i>Crioceratites schlagintweiti</i>		
	<i>Spitidiscus ricardii</i>		
Late Hauterivian	<i>Weavericeras vacuensis</i>		
	<i>Hoplitocrioceras gentili</i>		
	<i>Holcoptychites neuquensis</i>		
Early Hauterivian	<i>Weavericeras vacuensis</i>		
	<i>Hoplitocrioceras gentili</i>		
	<i>Holcoptychites neuquensis</i>		
Late Val.	<i>Pseudofavrella angulatiformis</i>		
	<i>Olcostephanus atherstoni</i>		
Early Val.	<i>Lissonia riveroi</i>		
	<i>Neocomites wichmanni</i>		
Berriasian	<i>Spitoceras damesi</i>		
	<i>Argentiniceras noduliferum</i>		

Figure 12. Stratigraphic range of known *Steinmanella* species for the Early Cretaceous of the Neuquén Basin. Data from this research, Leanza (1993), and Lazo (2003). Zonation based on Riccardi (1988) and Aguirre-Urreta *et al.* (2007). *Rango estratigráfico de las especies conocidas de Steinmanella para el Cretácico temprano de la Cuenca Neuquina. Información extraída del presente trabajo, Leanza (1993), y Lazo (2003). Zonación basada en Riccardi (1988) y Aguirre-Urreta et al. (2007).*

The interval spanning the *Olcostephanus atherstoni* Zone is known to contain *Steinmanella* specimens, but a revision based on detailed field work is needed to elucidate such occurrences. This interval is included in the Mulichinco Formation, but it can also belong to the base of the overlying Agrio Formation in different areas of the basin (Schwarz *et al.*, 2006).

Future work will focus on collecting more specimens from the *Olcostephanus atherstoni* Zone and from Tithonian–Berriasian beds to complete the Early Cretaceous record of the genus *Steinmanella* in the Basin.

CONCLUSIONS

The genus *Steinmanella* is abundantly recorded in the upper beds of the Vaca Muerta Formation and the lower marine beds of the Mulichinco Formation. It is represented by three species: *S. quintucoensis*, *S. subquadrata*, sp. nov. and *S. curacoensis*.

Recorded species can be recognised by external features. These are: small flank tubercles, poor carinae demarcation and flank and corselet intermingling ribs in *S. curacoensis*, a furrow below the marginal carina and large flank tubercles in *S. quintucoensis*; the square outline, oval escutcheon, and strong demarcation of carinae in *S. subquadrata*.

Specimens were found in alternating siltstones, wackestones and mudstones, dark grey shales, and rudstones with low to moderate taphonomomic alteration.

Associated lithofacies point to a mid-ramp to a proximal outer-ramp setting.

The age assigned to *S. quintucoensis*, *S. subquadrata* and *S. curacoensis* is early Valanginian, as indicated by their association with ammonites of the *Neocomites wichmanni* and *Lissonia riveroi* ammonoid zones.

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