Intraspecific variability and systematics in South American Syrotrigoniinae (Trigoniida, Bivalvia)

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A B S T R A C T

The systematics of the genus *Syrotrigonia* is revised in the light of the intraspecific variability of a large sample of *Syrotrigonia sigeli* from the Valanginian from Neuquén Basin, Argentina. The genus can be recognized by the presence of concentric or subconcentric costae surrounding the umbo, later on developing an inflection and finally resulting in a set of anterior horizontal to commarginal costae and another set of posterior sub-vertical costae. The anterior part of the area bears transverse, usually anteriorly concave, costae which direct towards the umbo on the escutcheon; initially they are continuous with those on the flank, but later on they usually alternate. General shell shape, the presence of an antecarinal sulcus, the junction pattern between both sets of costae and the number of horizontal costae relative to vertical costae are variable among species, while costae width or density and the development of horizontal vs. commarginal costae may vary highly within species. The presence of commarginal rugae developed on the whole surface of the shell is interpreted as a result of environmental perturbations. A brief biogeographical interpretation of the family Buchotrigoniidae is also outlined. *Syrotrigonia* probably originated in North America in the Tithonian, being widespread in the Pacific coast of South America by Early Cretaceous times; at least six (probably seven) South American species could be recognized. By Aptian times the taxon reached the Tethyan realm, its last record being Aptian or Albian in age. The frequent presence of different species in marginal marine deposits suggests a euryhaline lineage adapted to salinity variations, this may also be the cause of the frequent presence of commarginal rugae. Considering the high variability displayed in the analyzed material, large samples are needed to characterize new species within the group.

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1. Introduction

The Trigoniida is generally accepted as a group with frequent episodes of convergent evolution of shell ornamentation. However, such feature is generally used for taxa characterization within it. When adequately known, ornamentation details have proven to be highly variable, and thus a better appreciation of such variability, either at an interspecific or intraspecific level, is needed in order to improve the understanding of the systematics and phylogeny of the group.

The family Buchotrigoniidae Leanza, 1993 (Trigoniida, Bivalvia) was proposed for a group of genera of controversial systematic position, mostly from South America, but some species were also recorded in North America, Europe and the Middle East. The family is characterized by the ornamentation pattern of the flank, which initially bears oblique ribs surrounding the umbo, but later on develops two sets of costae: an anterior one of subhorizontal, sometimes commarginal, costae, and a posterior one of subvertical costae or rugae. The dominance of the commarginal ornamentation on some shells is not unusual, especially on older individuals, and a high systematic value has been frequently attributed to this character. Nevertheless, the presence of commarginal disturbances appears to be a phenotypic trait that may usually be associated to the environmental conditions where the individuals developed. Insufficient knowledge of intraspecific variability of these and other shell features resulted in the proliferation of ill characterized or poorly delimited nominal taxa, which has so far hindered the analysis of possible phylogenetic relationships within the group. As highlighted by Allmon (2013), the matter of how palaeontologists define species is of utmost importance, especially for evolutionary

studies, so *Syrotrigonia* shell ornamentation, together with other features, is analyzed in this paper aiming at attaining definitions that conform better to biological species.

A detailed analysis was performed on a large sample of shells assignable to the species *Syrotrigonia sigeli* (Leanza and Garate-Zubillaga, 1987) from Lower Cretaceous beds in Neuquén Basin. The ornamentation pattern, including the development of strong commarginal rugae, was characterized throughout the sample, trying to establish the variation range within the species. From this

starting point, other South American species within the genus *Syrotrigonia* Cox, 1952 were reviewed in order to get a better systematic framework for the group. Finally a brief biogeographical interpretation of the family is outlined.

2. Geological setting

The studied samples were recovered by the authors in a section logged at a site South of Barda Negra, Neuquén Province, Argentina
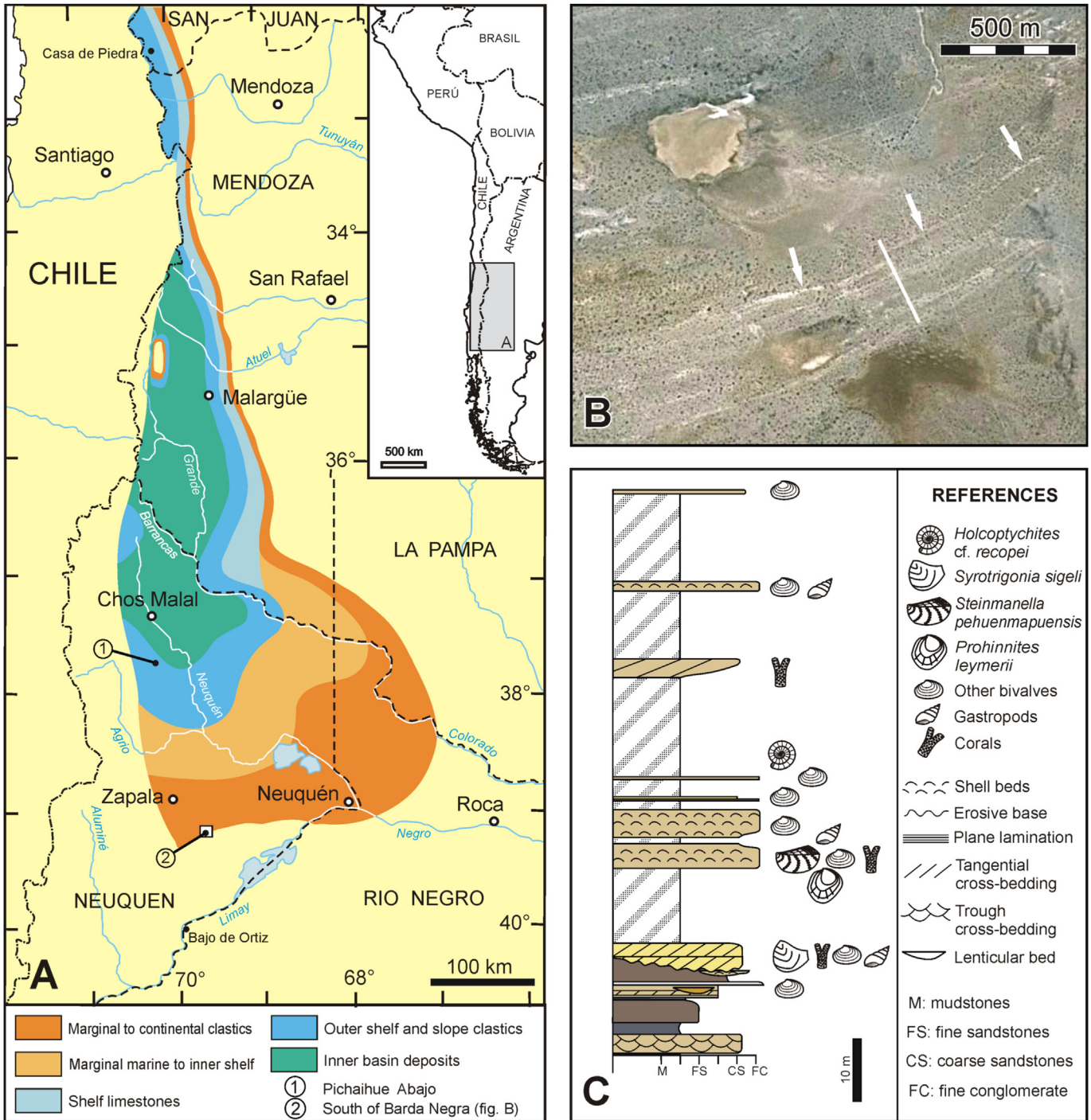

Fig. 1. Location and stratigraphic information of the outcrops with remains of *Syrotrigonia sigeli* (Leanza and Garate-Zubillaga, 1987). A, palaeogeographic sketch of Neuquén Basin for late Valanginian times, modified from Legarreta and Uliana (1991, 2000). B, detail of South of Barda Negra outcrops (locality 2) and location of logged section (white line), arrows point to large scale coarse sandstone bars (Base image from Google Earth). C, South of Barda Negra logged section.
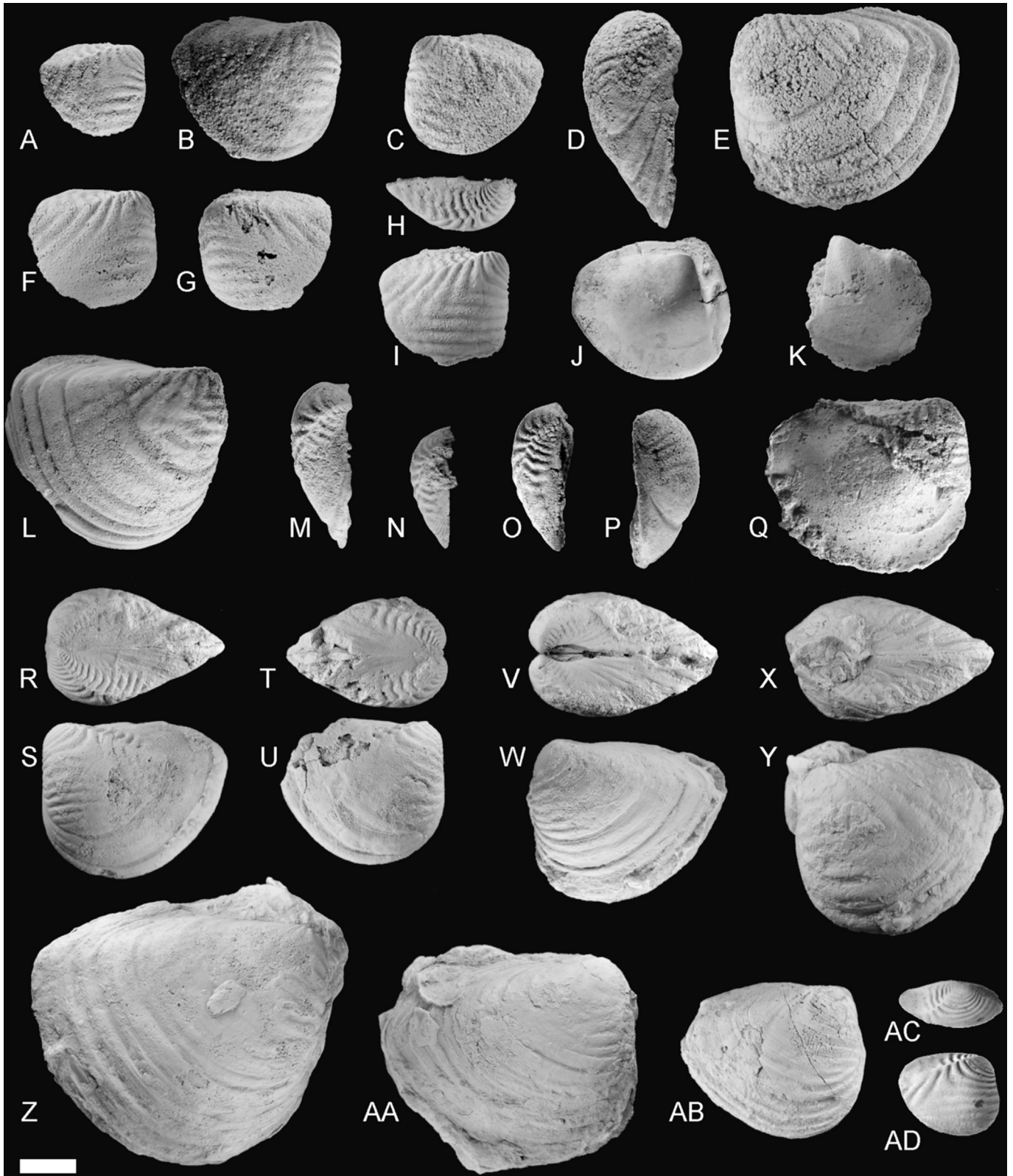
Fig. 2. Studied samples of *Syrotrigonia sigeli* (Leanza and Garate-Zubillaga, 1987). A–Q, sample from South of Barda Negra: A–I, L, N–Q MCF-PIPH 679. A–B, MCF-PIPH 679/1, right lateral view. A, first stage identified by a growth check. B, final stage. C, MCF-PIPH 679/2, left lateral view, first stage identified by a growth check. D–E, MCF-PIPH 679/3. D, dorsal view. E, left lateral view. F, MCF-PIPH 679/4, right lateral view. G, MCF-PIPH 679/5, left lateral view, first stage identified by a growth check. H–I, MCF-PIPH 679/6. H, dorsal view. I, right lateral view. L, MCF-PIPH 679/7, right lateral view. N, MCF-PIPH 679/8, dorsal view. O, MCF-PIPH 679/9, dorsal view. P, MCF-PIPH 679/10, anterior view. Q, MCF-PIPH 679/11, internal mould and umbonal region of right valve. J–K, M MCF-PIPH 536. J–K, MCF-PIPH 536/1; J, left valve, internal view. K, internal mould of the left valve. M, MCF-PIPH 536/2, dorsal view. R–AB, sample from Pichaihue Abajo: R–S, holotype for *Syrotrigonia brocardoi* Leanza, 1993 MOZ-PI 5319. R, dorsal view. S, left lateral view. T–U, paratype for *S. brocardoi* MOZ-PI 5318. T, dorsal view. U, right lateral view. V–W, holotype for *S. sigeli* MOZ-PI 1610/1. V, dorsal view. W, left lateral view. X–AB, paratypes for *S. sigeli*. X–Y, MOZ-PI 1610/6. X, dorsal view. Y, left lateral view. Z, MOZ-PI 1610/10, right lateral view. AA, MOZ-PI 1610/9, right lateral view. AB, MOZ-PI 1610/2, right lateral view. AC–AD, sample from Bajo de Ortiz, MLP 17881. AC, dorso-lateral view. AD, right lateral view. Scale bar represents 10 mm.

(Fig. 1), from strata assignable to the Mendoza Group (cf. Gulisano et al. 1984), which were mapped as "Hauteriviano (incl. Barremiano)" by Suero (1951). Calcarenites and limestones are dominant in the study area, with fine-grained lithologies subordinated to them. These beds were considered by Leanza and Hugo (1997) as a coastal marine facies of the Agrio Formation (Weaver, 1931). In this area, they rest on non-marine strata that were referred to "Valanginiano (incl. Berriasiano)" by Suero (1951) and to "Formación Bajada Colorada" by Leanza and Hugo (1997). Further south-west they are overlain by deposits of La Amarga Formation, also continental (Leanza and Hugo, 1997).

Towards the middle of the section (Fig. 1C), the species *Steinmanella pehuenmapuensis* Leanza and *Prohinnites leymerii* (Deshayes) were found, indicating a late Valanginian age (Lazo et al. 2009; Aguirre-Urreta et al. 2011; Lazo and Luci, 2013), and a few meters above them the occurrence of *Holcoptychites* cf. *recopei* (Douvillé) documents the earliest Hauterivian local ammonite Subzone. From these evidences, the underlying layers that yielded *S. sigeli* are here regarded as (probably late) Valanginian in age. This is consistent with data from nearby localities, like Cerro Birrete, where marine facies of the Agrio Formation from the late Valanginian *Decliveites crassicostatus* Subzone crop out, overlying continental strata attributed to Bajada Colorada Formation (Aguirre-Urreta and Rawson, 2010; Cataldo and Lazo, 2012).

The studied samples (Fig. 2A–Q) were collected from the base of the logged section (Fig. 1C). These beds, which are also reminiscent of the calcareous deposits of the Ortiz Formation at Bajo de Ortiz in Río Negro province (cf. Rolleri et al. 1984a, b) where the same species also occurs (Manceñido and Damborenea, 1984), have a lenticular geometry (at least two large scale lenses were recognized), with a lateral extension of about 0.6 km (Fig. 1B). Other beds of this kind could be laterally identified (Fig. 1B), although probably at somewhat different stratigraphic positions. They are dominated by very coarse sandstone/calcarenite to small-pebble concentrations, with subordinated rudstones packed with evidently re-sedimented corals (fragmented, concordant branches) and frequent shells of *Syrotrigonia*, together with other bivalves; degree of fossil concentration and packing are variable laterally, with some of the beds containing isolated shells. Trough cross-bedding is common, often with coarser grains in the foresets; some

herringbone structures are also present. Small scale lenses are frequent and are interpreted as channel infillings. Such evidence is compatible with a scenario involving lateral transport and mixing among various local environmental settings.

The analyzed lenticular beds contain a varied marine fauna, composed of scleractinians, serpulids, gastropods, mytilids, pectinids, trigonids, astartids, etc. Some thin to medium-thick beds are dominated by scleractinian coral remains, and some of them can be amalgamated; a bed locally dominated by mytilids was also found. Most shells are silicified, many of them showing a reddish colour. Although some shells are well preserved (Fig. 2F–I) most of them show different degrees of superficial wear and rounding, most probably as a result of corrosion, yet the concordant arrangement, disarticulation and good size sorting of the bioclasts hint to significant remobilization (though fragmentation is low), hence, such wear is better regarded as a product of corrasion. The marginal palaeogeographic position of the locality near the Huincul High, together with the reduced thickness, plus sedimentary and architectural features of the deposits involved, suggest a condensed deposit with resultant time-averaging.

On the grounds of the sedimentologic evidence these beds are here interpreted as representing large bar structures that could occasionally separate a lagoon or a protected bay from the open sea. Despite the clear marine nature of the fauna, the possibility of salinity variations should be taken into account. Either by freshwater inflow or by evaporation, such restricted environments favour the development of abnormal and/or fluctuating salinity levels. Incidentally, periodic dilution from normal marine salinity occurred during the Valanginian in the Neuquén Basin, especially southwards, according to Lazo et al. (2008). Besides, the development of the Huincul High may have contributed to the isolation of this portion of the basin.

3. Material and methods

A large sample of *S. sigeli* (MCF-PIPH 454, 455, 457, 534, 536 and 679) was recovered and was described and compared to previous collections (MOZ-PI 1033, 1610, 4196, 5318 and 5319 and MLP 17881) paying particular attention to intraspecific variability; descriptive terminology follows Carter et al. (2012). Length, height and width were measured, as shown in Fig. 3, with callipers on about 55 well preserved shells; whenever possible, various ontogenetic stages were considered. Statistical analyses were performed using PAST 2.10 (Hammer et al. 2001).

4. Systematic palaeontology

Specimens housed in the collections of the following institutions were examined CPBA, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; MCF, Museo Municipal Carmen Funes, Plaza Huincul, Argentina; MLP, Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MOZ, Museo Provincial de Ciencias Naturales Prof. Dr. Juan A. Olsacher, Zapala, Argentina; MUSM, Museo de Historia Natural Javier Prado, Lima, Peru; SNGM, Servicio Nacional de Geología y Minería (SERNAGEOMIN), Santiago, Chile and USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

4.1. Systematic background for the Buchotrigoniidae

Despite the questions concerning its relationships, the group has been recognized long time ago, and many species have been variably included and/or excluded from it (Table 1). In 1838 von Buch, based on some shells from Colombia, described the species
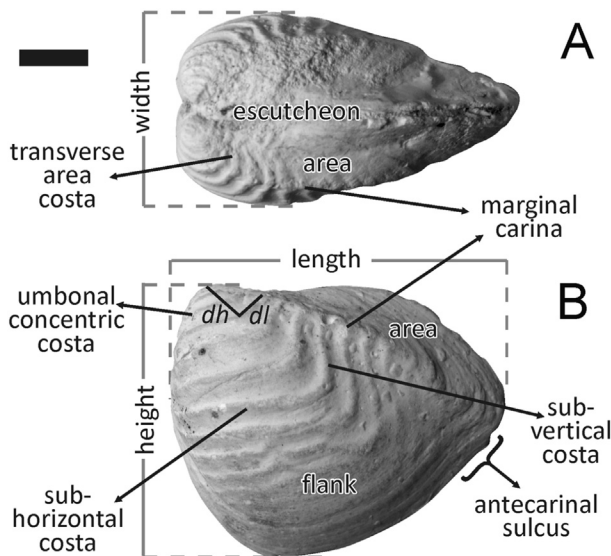

Fig. 3. Plastoholotype of *Syrotrigonia libanotica* (Vokes, 1946), SNGM 7462, from the Aptian of Abeih valley (Lebannon), showing the main features of Syrotrigoniinae shells, and the measurements taken. A, dorsal view. B, left lateral view. Scale bar: 10 mm.

Table 1

Summary of the systematic interpretation of the species included within the Buchotrigoniidae (rows) according to different authors (columns). Species are grouped by subfamily and ordered chronologically by year of first description; grey cells indicate that the species name was not yet available. B.: *Buchotrigonia*, N.: *Neobuchotrigonia*, S: *Syrotrigonia*.

	Nominal species, original reference	Dietrich (1938)	Cox (1952, in Cox et al. 1969)	Rivera and Alleman (1974), Alleman (1986)	Pérez and Reyes (1980, 1986)	Pérez and Reyes (1994, 1996, 1997)	This paper
Syrotrigoniinae	*Trigonia lorentii* Dana, 1849	*Trigonia (B.) lorentii*		*B. lorentii*			*Syrotrigonia? lorentii*
	Trigonia syriaca Fraas, 1878 non Conrad, 1852		*B. (S.) fraasi* Cox, 1952 / *B. (S.) libanotica* (Vokes, 1946)		*B. (S.) fraasi*	*S. fraasi*	*Syrotrigonia libanotica*
	Trigonia distans Conrad, 1852		*B. (Syrotrigonia) distans*		*B. (S.) distans*		*Syrotrigonia distans*
	Trigonia collombi Vilanova y Piera, 1863		*B. (B.) collombi*				*Syrotrigonia collombi*
	Trigonia deshayesi Vilanova y Piera, 1863		*B. (B.) deshayesi*				*Syrotrigonia?* sp.
	Trigonia goodelli Cragin, 1897						*Syrotrigonia goodelli*
	Trigonia paradisensis Lisson, 1907			*B. paradisensis*	*B. (S.) paradisensis*	*S. paradisensis*	*Syrotrigonia paradisensis*
	Trigonia flexicostata Fritzsche, 1924	synonym of *B. abrupta*	*B. (B.) flexicostata*				possible synonym of *S. paradisensis*
	Trigonia inca Fritzsche, 1924	synonym of *B. abrupta*	*B. (B.) inca*			*S. inca*	synonym of *S. paradisensis*
	Trigonia forti Lisson, 1930	*Trigonia (B.) forti*		*B. forti*			*Syrotrigonia forti*
	Trigonia gerthi Lisson, 1930			*B. gerthi*	*B. (S.) gerthi*	*S. gerthi*	synonym of *S. paradisensis*
	Trigonia steinmanni Lisson, 1930 (non Philippi, 1899)			*B. steinmanni*	*B. (S.) steinmanni*	*S. steinmanni*	synonym of *S. paradisensis*
	Trigonia mathewsi Richards, 1947					*S. mathewsi*	synonym of *S. paradisensis*
	Vaugonia niranohamensis santa-mariae Geyer, 1973					*Buchotrigonia* sp.	*Syrotrigonia* sp.
	Vaugonia yokoyamai batafluviae Geyer, 1973					*Syrotrigonia* sp.	*Syrotrigonia* sp.
	Buchotrigonia (S.) biroi Pérez and Reyes, 1986				*B. (S.) biroi*	*S. biroi*	*Syrotrigonia biroi*
	Buchotrigonia (S.) chilensis Pérez and Reyes, 1986				*B. (S.) chilensis*	*S. chilensis*	*Syrotrigonia chilensis*
	Quoiecchia sigeli Leanza and Garate-Zubillaga, 1987						*Syrotrigonia sigeli*
	Syrotrigonia brocardoi Leanza, 1993					*S. brocardoi*	synonym of *S. sigeli*
	Syrotrigonia obesa Pérez and Reyes, 1997					*S. obesa*	*Syrotrigonia obesa*
Buchotrigoniinae	*Trigonia abrupta* von Buch, 1838	*Trigonia (B.) abrupta*	*B. (B.) abrupta*	*B. abrupta*	*B. (B.) abrupta*	*B. abrupta*	*Buchotrigonia abrupta*
	Trigonia humboldtii de Buch, 1839	synonym of *B. abrupta*	*B. (B.) humboldtii*				*Buchotrigonia?* sp.
	Trigonia disparilis d'Orbigny, 1844						
	Trigonia pizcuetana Vilanova y Piera, 1863	synonym of *B. abrupta*	*B. (B.) pizcuetana*				
	Trigonia orbignana Lisson, 1930	synonym of *B. abrupta*					
	Trigonia coquandi Lisson, 1930	synonym of *B. abrupta*					
	Trigonia hopkinsi Olsson, 1944					*N. hopkinsi*	
	Trigonia reesidei Stoyanow, 1949				*B. (B.) residei*	*B. residei*	
	Buchotrigonia (B.) topocalmensis Pérez and Reyes, 1980				*B. (B.) topocalmensis*	*N. topocalmensis*	
	Neobuchotrigonia (?) *jaillardi* Pérez and Reyes, 1996					*N.* (?) *jaillardi*	
	Buchotrigonia perezi Villamil, 1992					*B. perezi*	
	Buchotrigonia etayoi Villamil, 1992					*B. etayoi*	*Buchotrigonia etayoi*
	Buchotrigonia kauffmani Villamil, 1992					*B. kauffmani*	
	Trigonia cazadoriana Wilckens, 1905		*B. (B.) cazadoriana*		*Pterotrigonia cazadoriana*		*Steinmanella* sp.
	Trigonia transitoria Steinmann var. *raimondii* Lisson, 1930			*B. transitoria* var. *raimondii*		*Steinmanella raimondi*	*Trigonia* sp.
	Trigonia oyamensis Welter, 1933			*B. oyamensis*			
	Trigonia (Laevitrigonia) scheibei Dietrich, 1938	*Trigonia (Laevitrigonia) scheibei*	*B. (B.) scheibei*		*Laevitrigonia scheibei*		

Trigonia abrupta associated to *Ammonites galeatus* von Buch, 1838 (later known as *Pulchellia galeata* and of Barremian age according to Arkell et al. 1957; Wright et al. 1996). The species was figured by de Buch (1839, pl. 2, fig. 21–22), and characterized as having a triangular shell, with the earlier flank ribs surrounding the umbo; later during ontogeny, two sets of ribs were developed: a posterior one of vertical and straight ribs or rugae, and an anterior one of horizontal ribs, initially in contact with the posterior set, but later on separated from it. A century later, Dietrich (1938) defined the subgenus *Trigonia (Buchotrigonia)* designating *T. abrupta* as its type species, and considered the species *Trigonia humboldtii* de Buch, 1839, *Trigonia pizcuetana* Vilanova y Piera, 1863, *Trigonia orbignyana* Lisson, 1930 and *Trigonia coquandi* Lisson, 1930 as junior synonyms of *T. abrupta*. *Trigonia lorentii* Dana, 1849 and *Trigonia forti* Lisson, 1930 were accepted as different species within the subgenus, while *Trigonia flexicostata* Fritzsche, 1924 and *Trigonia inca* Fritzsche, 1924 were regarded as "variations within *Buchotrigonia*" (Dietrich, 1938, p. 99). In 1949 Stoyanow defined the species *Trigonia reesidei* from Arizona as closely related to *T. abrupta* and *T. humboldtii* within his "group of *Trigonia abrupta*" or "Abruptae".

In 1952 Cox made a synthesis of the systematics for the order Trigoniida, listing all the available genera; he raised *Buchotrigonia* to a generic status, adding to its diagnosis the presence of transverse ribs on the area and the absence of tubercles on the flank ribs (in 1839 de Buch had described some knobs at the intersection of flank ribs with growth lines, and also Dietrich, in 1938, described some pustules on umbonal ribs). Cox also considered two subgenera: *Buchotrigonia* s. str. and *Syrotrigonia* Cox, 1952. In the first one, having ill-defined marginal and escutcheon carinae, except in early growth stages, he included several species (Table 1). The subgenus *Buchotrigonia (Syrotrigonia)* was characterized as having prominent marginal carina, with a broad antecarinal depression, and flank costae oblique to growth lines and bending up steeply at the edge of the depression. The species *Trigonia libanotica* Vokes, 1946 (=*B. (S.) fraasi* Cox, 1952) and *Trigonia distans* Conrad, 1852 from Lebanon region were included within this subgenus.

During the last decades of the twentieth century the group was extensively revised. When describing the species *Buchotrigonia (Buchotrigonia) topocalmensis* Pérez and Reyes, 1980, those authors made a revision of the subgenus, and they only accepted the species *B. (B.) abrupta*, *B. (B.) reesidei* and *B. (B.) topocalmensis*. In 1986 the same authors revised the subgenus *Syrotrigonia* and they accepted within it the species *B. (S.) fraasi*, *B. (S.) distans*, *B. (S.) paradisensis* (Lisson, 1907), *B. (S.) gerthi* (Lisson, 1930), *B. (S.) steinmanni* (Lisson, 1930), *Buchotrigonia (S.)* sp. in Manceñido and Damborenea 1984, *B. (S.) chilensis* Pérez and Reyes, 1986 and *B. (S.) biroi* Pérez and Reyes, 1986. Later on, Leanza (1993) described the new species *Syrotrigonia brocardoi*.

In 1993 Leanza proposed to accommodate both *Buchotrigonia* and *Syrotrigonia* as full genera in a new subfamily Buchotrigoniinae, easy to recognize by the flank ornamentation together with the presence of an antecarinal depression (in *Syrotrigonia*) or with transverse ornamentation on the area (in *Buchotrigonia*). Finally, Pérez and Reyes (1996, 1997) made a new revision of the group, now ranked as a family (Buchotrigoniidae) with two subfamilies: Buchotrigoniinae (genera *Buchotrigonia* and *Neobuchotrigonia*) and Syrotrigoniinae (genus *Syrotrigonia*). The family was included in the Myophorellacea (*sensu* Cooper, 1991) because of the development and ornamentation of the area (at least on its initial stages), and the presence of a marginal carina fully or partially developed. The subfamily Buchotrigoniinae comprises species with eccentric oblique flank ribs surrounding the umbo on the initial stages, later on developing the previously described two sets, with the two kinds of ribs either drawing an 'L' when they meet, or crossing each other; the meeting of area and flank ribs results in a *chevron* pattern. The subfamily Syrotrigoniinae was characterized as having a medium-sized area, bearing transverse ribs on its initial stages; the flank has an antecarinal depression and is ornamented by smooth ribs, oblique and concentric on the umbonal region, and subconcentric and subvertical later on, joining in a 'V' or more complex patterns. Fig. 3 shows these main features of the shell on the type species of the genus.

For the purposes of this paper, the overall systematic framework of family level taxa provided by Pérez and Reyes (1997) is used, with the proviso that presence of an antecarinal depression is not considered as diagnostic of the Syrotrigoniinae. Further discussion about the species included in each group, and reference to the possibly related genus *Quoiecchia* Crickmay, are given below.

4.2. Description of the studied material and systematic reappraisal of the Syrotrigoniinae

Order: Trigoniida Dall, 1889
Superfamily: Myophorelloidea Kobayashi, 1954
Family: Buchotrigoniidae Leanza, 1993
Subfamily: Syrotrigoniinae Pérez and Reyes, 1997
Genus: *Syrotrigonia* Cox, 1952

Type species − *Buchotrigonia (Syrotrigonia) fraasi* Cox, 1952 = *Trigonia libanotica* Vokes, 1946.

Emended diagnosis − Short, subtrigonal shell. Flank with concentric or subconcentric costae surrounding the umbo, later on developing an inflection and finally resulting in a set of anterior horizontal to commarginal costae and another set of posterior subvertical costae; both sets usually join in V-shaped or more complex patterns. Anterior part of the area with transverse ribs, sometimes slightly curved anteriorwards (modified from Pérez and Reyes (1986) and Leanza (1993)).

Discussion − The presence of a wide ante-carinal depression as described by Cox (1952) seems to be a late acquisition within the group, since in early species it is poorly developed or even absent. Usually, only one or two anterior costae are related to one subvertical costa; when there are two anterior costae, they join the posterior one at the same point, resulting in a bifurcated pattern.

One of the main differences with the Buchotrigoniinae is that area costae in the latter tend to generate a chevron pattern which is never found in *Syrotrigonia*.

S. sigeli (Leanza and Garate-Zubillaga, 1987)
          (Fig. 2A−AD)

v 1984 *Buchotrigonia (Buchotrigonia)* sp. nov.; Manceñido and Damborenea, p. 430, pl. 3, Figs. 7 and 8.

v *1984b Buchotrigonia (B.)* sp. nov.; Rolleri et al., p. 512, 513.

v 1986 *Buchotrigonia (Syrotrigonia)* sp.; Pérez and Reyes, p. 79, Fig. 6.

*v 1987 *Quoiecchia sigeli* n. sp.; Leanza and Garate-Zubillaga, p. 226, pl. 8, Figs. 4−7.

v 1993 *Syrotrigonia brocardoi*, new species; Leanza, p. 57, pl. 16, Figs. 4, 7, 10 and 12.

v 1993 *Quoiecchia sigeli* Leanza and Garate; Leanza, p. 63, pl. 17, Fig. 3.

1997 Syrotrigonia sp.; Pérez and Reyes, p. 252.

1997 *S. brocardoi*; Pérez and Reyes, p. 252.

Material — The studied material is housed under catalogue numbers MCF-PIPH 454, 455, 457, 534, 536 and 679 (South of Barda Negra). Also the specimens MOZ-PI 1033, 1610, 4196, 5318 and 5319 (Pichaihue Abajo) and MLP 17881 (Bajo de Ortiz) were examined.

Geographical range — Argentina — Río Negro (Manceñido and Damborenea, 1984) and Neuquén (Leanza and Garate-Zubillaga, 1987; Leanza, 1993 and this paper) Provinces.

Age — Tithonian-Berriasian? (Bajo de Ortiz material, Rolleri et al. 1984b, p. 516; Manceñido in Riccardi and Damborenea, 1993, p. 286—289), late Valanginian (Pichaihue Abajo material, formerly as Hauterivian, Leanza and Garate-Zubillaga, 1987, p. 226—227; Leanza, 1993, p. 63 and 57—58: *i.e. Lyticoceras pseudoregale* Zone = *Pseudofavrella angulatiformis* Zone *sensu* Aguirre-Urreta and Rawson, 1995; Aguirre-Urreta et al. 2005) and late Valanginian (South of Barda Negra material).

Dimensions — (in mm, max/mean/min) Length: 51.7/30.0/17.2; Height: 46.2/27.1/15.0; Width (1 valve): 15.2/10.5/5.2.

Emended diagnosis — Small to medium subtrigonal shell, moderately inflated. Orthogyrate to slightly opisthogyrate umbos, anteriorly located. Escutcheon carina absent; marginal carina well developed on early stages, turning into a broad angulation on later stages. Without antecarinal depression. Escutcheon ill-defined, smooth except near the area, where area-costae bend forward and fade out. Area ornamented by transverse costae in the umbonal region, then becoming smooth. Flank ornamentation developed in different degrees and, when developed, consisting of oblique ribs surrounding the umbo on early stages, later on differentiating into sets of subhorizontal and subvertical costae meeting in a down-pointing V-shaped inflection; the V usually fades out on later growth stages (modified from Leanza and Garate-Zubillaga (1987) and Leanza (1993)).

Description — The shell of this species is of medium to large size (up to 5 cm long), subtrigonal and equivalve, with a straight dorsal margin almost continuous with the posterior margin. Ventral margin is convex, gradually leading into a nearly straight anterior margin (in some shells such transition can be somewhat more abrupt, *e.g.* Fig. 2L, Z). Valves are inequilateral, with the umbos

anteriorly located, and the shell is thick, moderately to highly globose (Fig. 2D, H, M—O, R, T, V, X), with maximum width anteriorly displaced; posteriorly it is somewhat compressed. The escutcheon is more developed on relatively wider shells, and it is smooth, except near the area. The area is ornamented anteriorly by transverse costae, slightly concave towards the umbo (Fig. 2H, M, O); these same costae bend anteriorly on the escutcheon, at least in some shells (Fig. 2H, R, T). The ornamentation of the area and the escutcheon fades out when the shell reaches about 2 cm long. On early stages the area is clearly differentiated from the escutcheon by its ornamentation and by certain depression on the latter, but on later stages both regions become hard to distinguish. The relationship between area costae and flank ribs is variable, usually being continuous at the beginning and becoming alternate at either side of the carina later on (Fig. 2H, T, AC), though in some shells they remain continuous throughout (Fig. 2R). Early flank ribs are oblique, surrounding the umbo, while later on the ribs start to deflect, generating an inflection pointing ventrally on the central to posterior flank (Fig. 2A—C, F—G, I, AD). As new ribs are added, the inflection becomes more conspicuous, but at the same time, the ribs are less prominent on that part, resulting in two sets of ribs on later stages: one subvertical and one subhorizontal (Fig. 2B, C, E, G, L). Anteriorly the subhorizontal ribs tend to bend sligtly downwards (Fig. 2A—C, F—G, P). Strong commarginal growth-rugae tend to appear in most of the larger shells (Fig. 2B, E, L); these are variably present in samples from Pichaihue Abajo, some of them having very closely disposed rugae (Fig. 2W, Z—AB).

Inner features could be seen only in a few shells, usually badly preserved. The posterior adductor muscle scar could be identified below the area-escutcheon region in a middle position (Fig. 2J—K); dorsal to it and closer to the dorsal margin is the much smaller posterior pedal retractor muscle scar. Pallial line is continuous and very conspicuous, without a sinus (Fig. 2J—K, Q). Marginal crenulations are developed along the ventral margin (Fig. 2Q), but since outer shell surface is not well preserved, the correspondence between those crenulations and vertical ribs cannot be ascertained. As seen on other trigoniides, a short ridge is developed on the posterior inner surface of the shell (Fig. 2J), which probably helped to separate water currents. Hinge is poorly preserved, but seems to be the usual schizodont type (trigonian-grade of Newell and Boyd, 1975) found in trigoniides (Fig. 2O).

Discussion — *Syrotrigonia sigeli* was originally described as *Q. sigeli* due to the presence of subconcentric rugae on the flank (see below, section 4.3), which are crossed on the posterior part by radial folds; the area bears seven to eight transverse costellae near the umbo, being ornamented on the remaining surface by oblique striae arising from the flank rugae (Leanza and Garate-Zubillaga, 1987; Leanza, 1993). *Syrotrigonia brocardoi* on the other hand, was characterized as having subvertical and subconcentric costae meeting in a down-pointing V-shaped inflection in the posterior flank, being replaced in a mid-late growth stage by conspicuous concentric rugae; the area is ornamented by transverse costae in the umbonal region, then smooth (Leanza, 1993). As can be seen both characterizations are very similar, but a strong emphasis was given to subconcentric rugae in *Q. sigeli*. Nevertheless, rugae are truly subconcentric only on initial stages; later on the whole shell is affected by commarginal elements (Fig. 2W, Y, Z—AB), which anteriorly coincide with costae, and posteriorly reach the area, generating the "oblique striae"; further, the subconcentric initial costae go across these commarginal rugae, a disposition already noticed by Leanza and Garate-Zubillaga (1987). So the general ornamentation pattern of the flank is the same in both nominal species: subvertical posterior folds or costae contacting subconcentric anterior costae, and being interrupted at older stages by commarginal rugae. Considering that shell shape and size is the
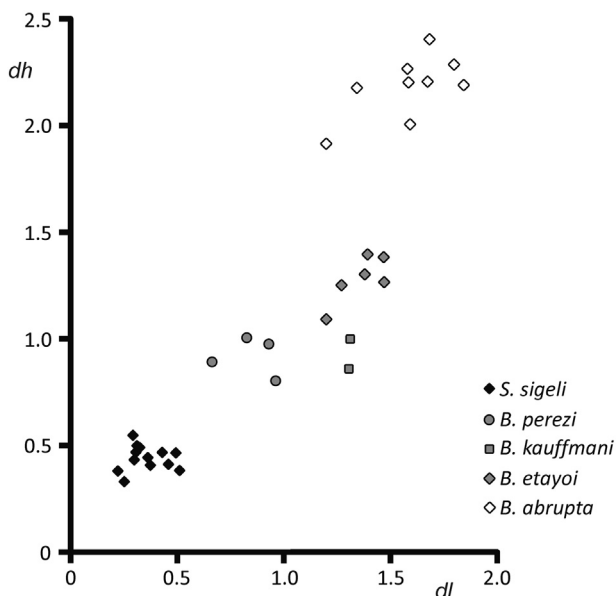

Fig. 4. Relationship between the distance from the umbo to the first costa-inflection (dh) and the distance perpendicular to dh from the first costa-inflection to the marginal carina (dl) as measured by Villamil (1992); data for *Buchotrigonia* species as figured in Villamil (1992).
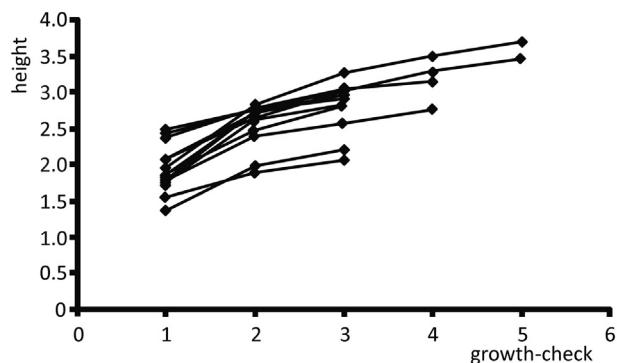
Fig. 5. Shell height for *Syrotrigonia sigeli* against growth stages marked by commarginal rugae for individuals with more than two growth checks within the sample from South of Barda Negra, Neuquén, Valanginian.

same in both samples (compare Fig. 2R—U with Fig. 2V—AB), there is no reason to keep them as separate species. The samples from South of Barda Negra (Fig. 2A—Q) and those from Bajo de Ortiz (Fig. 2AC—AD) clearly show the diagnostic features of the species.

Despite the overall characterization given above, and the basic similitude among samples, there is also a great amount of morphological variability within the species. General shell shape in lateral view remains relatively constant (Fig. 2); although elongation of the shell shows some variability (Fig. 2Z—AA), no allometric relationship could be found between height and length during ontogeny, at least for the measured stages (allometry coefficient — a.c. — = 1.00, $p_{(ac=1)}$ = 0.99, r = 0.99) and the relationship height/length ranges between 0.80 and 0.99. Width, on the other hand, is more variable (width/length ratio between 0.50 and 0.83), and it shows positive allometry with respect to length (allometry coefficient — a.c. — = 1. 23, $p_{(ac=1)}$ = 0.0006, r = 0.91).

Ornamentation is a character difficult to quantify. Villamil (1992), when describing three *Buchotrigonia* species from Colombia, proposed some measurements for the particular flank ornamentation of the buchotrigoniids. The distance from the umbo to the first costa-inflection (*dh*, Fig. 3B), the distance perpendicular to *dh* from the first costa-inflection to the marginal carina (*dl*, Fig. 3B) and the number of costae per centimetre on the anterior flank were measured on the analyzed sample. The first two variables showed relatively constant values (Fig. 4), with less dispersion than that obtained by Villamil (1992). Costae density on the anterior flank was measured as integer values; since costae disposition may vary with development and early formed costae may be obscured by superficial corrasion, it was simply measured as the number of costae (from the younger one reaching the anterior margin) that fall within a centimeter, instead of dividing the total number of costae by the length of the anterior margin. In all the measured shells the number of costae per centimeter was 6. Although some shells seem to differ in density and width of costae (specially the vertical ones, see Fig. 2F, I, Y), this may also be due to differences in preservation.

The ornamentation pattern is variable within the sample. Despite not common, at least one shell has a duplicated horizontal costa (Fig. 2L), and another shell was found with a zig-zag pattern on its ribs. While some shells show the ornamentation well developed (Fig. 2I), on others it is attenuated on late stages (Fig. 2L, Z—AA), although in many cases that could be due to (or enhanced by) superficial corrasion (Fig. 2E). The mentioned commarginal growth-rugae are a very common feature on the sample (Fig. 2B, E, L). Usually, after the first of these rugae, the previous ornamentation is lost, indicating some major perturbation to the morphogenetic mechanism responsible for shell secretion. As already mentioned, these rugae are present —and usually more densely arranged (Fig. 2W, Y—AB)— on the type material of the species. On

the new material from South of Barda Negra, they are quite conspicuous, and despite their frequency in the fossil assemblage, they seem to be the result of environmental perturbations rather than traits of the regular ornamentation of the shell. This was concluded from two main features:

1 — Commarginal ornamentation usually has a regular arrangement, with ribs secreted by periodic extrusions of the mantle margin above the normal shell profile (Checa, 2002). While some progressive wider separation of the ribs is to be expected as shell grows, the material from South of Barda Negra shows the opposite: *i.e.*, commarginal rugae are progressively closer as shell grows (Fig. 2B, E, L, Fig. 5). This may bear some important ecological implications (see below).

2 — After prolonged halts of shell secretion, usually a new shell is produced below the old one, and the abandoned margin remains raised (Checa, 2002). In most specimens of the studied material, the commarginal rugae look more like a raised shell margin than like a true rib, *i.e.* an elevation on the shell surface (Fig. 2D, M, P).

According to Boshoff (1968), these rugae should be considered as a consequence of a decremental phenomenon; strongly developed growth-cessation lines (stronger than the normal ones caused by seasonal variation) suggest an unusually long stoppage of growth or at least its retarded progression over a more extended time period. Considering the frequency of these perturbations on the population, an ecological trigger cannot be ruled out. Long standing ecological factors may cause regular variations on certain habitats, and thus the 'variant' may even be regarded as a norm, but a taxonomist should attempt to identify and isolate physiopatological effects when recognizing species (Boshoff, 1968). The interruption of regular ornamentation on trigoniid shells after some perturbation has already been reported in other species (see Echevarría, 2012). Hence, these growth-rugae are here regarded as growth-checks. Boshoff (1968, p. 215) pointed out that, due to unpredictable salinity variations, estuarine bivalve shells usually develop a large number of concentric cessation lines. As mentioned before, the environment where this assemblage developed was probably subject to abnormal or fluctuating salinity levels. These variations are usually associated with lower growth rates (*e.g.* Gunter, 1961; Marsden, 2004; Tarnowska et al. 2009 and references therein) and even negative scopes for growth (*i.e.*, energy available for production of somatic and/or reproductive tissue; *e.g.* Navarro, 1988; Navarro and Gonzalez, 1998), since when a non-motile organism is exposed to salinities which differ from its optimum, more energy is expended in osmoregulation. Probably, a sudden change in water salinity may cause a halt in growth, resulting in the pattern of growth-rugae or growth-checks observed. Shell growth curve on molluscs is commonly sigmoid (Wilbur and Owen, 1964), and is usually adjusted to a von Bertalanffy model. Despite the fact that the first commarginal ruga appears at variable sizes on the shells (from 1.5 to 3.1 cm long), it was found that the subsequent ones follow this pattern (Fig. 5). This seems to indicate that the commarginal growth-rugae were produced cyclically, as if they were induced by some periodic environmental disturbance.

Syrotrigonia biroi (Pérez and Reyes, 1986)
(Fig. 6A—H)

1973 *Buchotrigonia steinmanni* (Lisson); von Hillebrandt, p. 179.

1985 *Buchotrigonia(?) sp. nov. cf. B.(?) steinmanni* (Lisson); Pérez and Reyes, p. 96.

*v 1986 *Buchotrigonia (Syrotrigonia) biroi* sp. nov.; Pérez and Reyes, p. 85, pl. 2: Figs. 1—20.

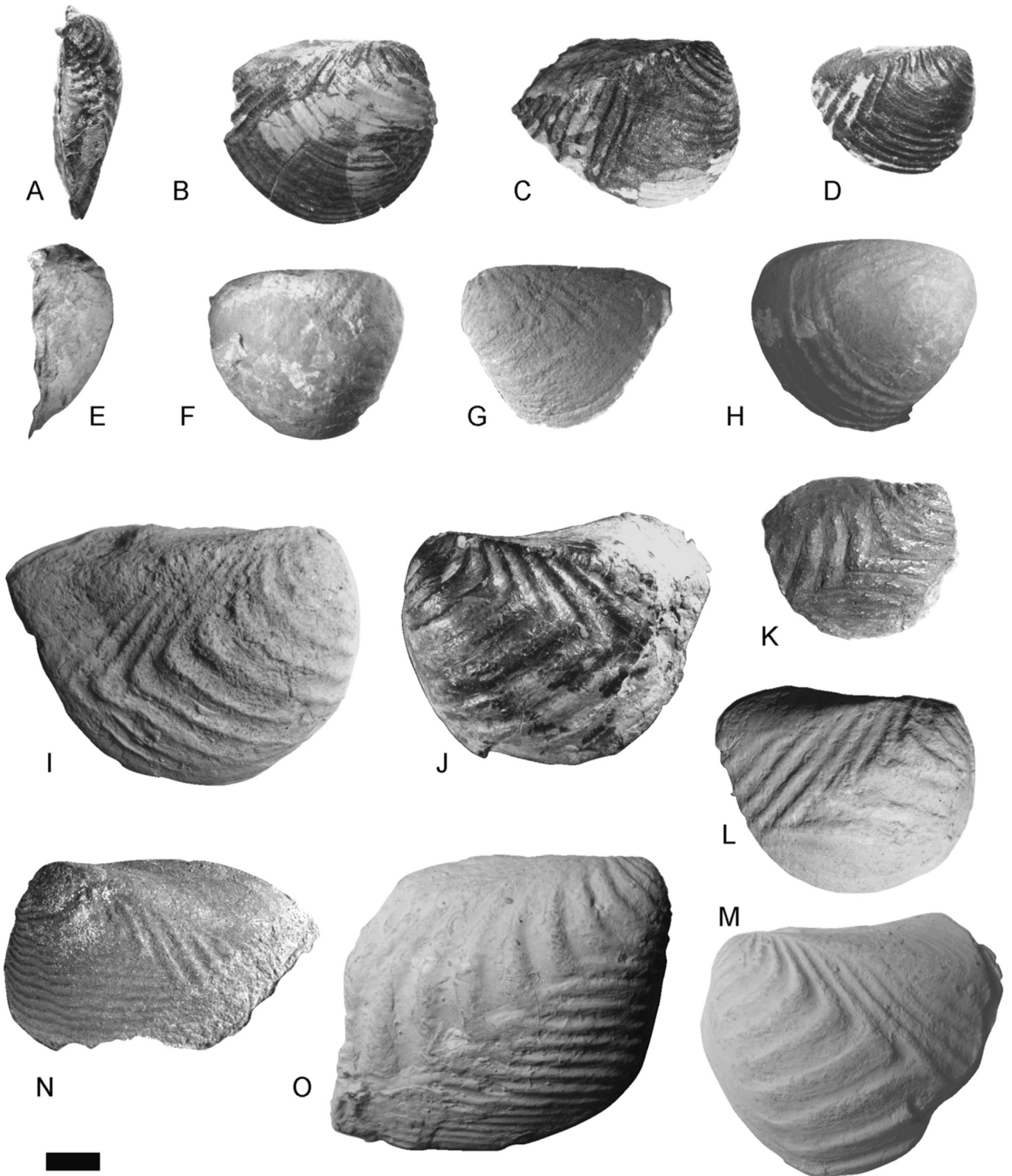v 1991 *Buchotrigonia (Syrotrigonia) biroi* Pérez y Reyes; Lo Forte, p. 791., pl. 1: Figs. 1—8.

Fig. 6. Comparative material of other *Syrotrigonia* species discussed here. A–H, studied material of *Syrotrigonia biroi* (Pérez and Reyes, 1986). A–D, Neocomian of Quebrada Vicuñita, Atacama, Chile. A–B, holotype SNGM 7115. A, dorsal view. B, right lateral view. C, paratype SNGM 7116, right lateral view. D, paratype SNGM 7117, right lateral view. E-H, Neocomian of Cordillera Casa de Piedra, San Juan, Argentina. E–F, CPBA 16315. E, dorsal view. F, right lateral view. G, CPBA 16318, left lateral view. H, CPBA 16310, right lateral view. I–M, studied material of *Syrotrigonia paradisensis* (Lisson, 1907). I, SNGM 7481, plastohypotype of *Trigonia paradisensis* Lisson, 1907, Valanginian of Aspitia, Lima Department, Peru, right lateral view. J, USNM 153037, syntype of *Trigonia mathewsi* Richards, 1947, Valanginian of Huayla, Ancash Department, Peru, left lateral view. K, SNGM 7453, plastosyntype of *Trigonia inca* Fritzsche, 1924, Valanginian of Quebrada de Baños, Santa valley, Ancash Department, Peru, right lateral view. L, SNGM 7446, plastosyntype of *Trigonia gerthi* Lisson, 1930, Valanginian of Huaylas, Ancash Department, Peru, right lateral view. M, SNGM 7492, plastosyntype of *Trigonia steinmanni* Lisson, 1930 (non Philippi, 1899) Valanginian of Huaylas, Ancash Department, Peru, left lateral view. N, left lateral view of *Syrotrigonia? lorentii* (Dana, 1849), USNM 3581, syntype, Isla San Lorenzo, Lima, Peru. O, right lateral view of *Syrotrigonia forti* (Lisson, 1930), SNGM 7444, plastoholotype, Valanginian of Huaylas, Ancash Department, Peru. Scale bar represents 10 mm.

v 1996 *Buchotrigonia (Syrotrigonia) biroi* Pérez y Reyes; Aguirre-Urreta and Lo Forte, p. 207, Fig. 12a.

Studied material — CPBA 16310—16323 (Casa de Piedra Cordillera, San Juan Province, Argentina, Fig. 1A), SNGM 7115—7129 (Atacama Region, Chile).

Geographical range — Chile — Atacama Region (Pérez and Reyes, 1986) — and Argentina — southwest San Juan Province (Lo Forte, 1991; Aguirre-Urreta and Lo Forte 1996).

Age — Neocomian (Pérez and Reyes, 1986; Lo Forte, 1991).

Dimensions — (in mm, max/mean/min) Atacama material: Length: 48.5/36.8/23.7; Height: 44.6/31.9/21.5; Width (1 valve): 12.4/8.6/5.4; San Juan material: Length: 37.6/33.2/27.5; Height: 39.3/34.7/29.2; Width (1 valve): 17.7/15.8/15.3.

Description — The shell is medium-sized to large (up to 5 cm), short, subtrapezoidal to subtriangular (Fig. 6A—H); it is moderately elongated (height/length ratio ranging between 0.73 and 0.92) and compressed (width/length ratio ranging from 0.35 to 0.52). Dorsal margin is straight. While the postero-dorsal angle is very obtuse, the postero-ventral angle is about 90°. Posterior margin is wide and antero-ventral margin is almost semicircular (the ventral portion may be less convex than the anterior one, especially in more elongated shells, Fig. 6C). Escutcheon is poorly developed, with anteriorly directed thin transverse ribs entering from the area. Escutcheon carina is obsolescent, while marginal carina is well developed anteriorly, becoming broad and rounded distally; with a wide and shallow antecarinal depression (not developed on initial stages). Area is well developed, ornamented with transverse ribs (slightly concave anteriorly) on the umbonal region, then smooth; it bears a submedian sulcus. Flank costae alternate with those on the area (in some shells the earliest costae are continuous between the flank and the area). Oblique ribs, initially concentric, quickly shift into two sets of vertical and horizontal (at the beginning) to commarginal (at the end) costae (Fig. 6C—D); both sets usually (though not always, *e.g.* Fig. 6D) separated by a smooth surface. The surface occupied by vertical ribs may be variably developed and is associated to a shallow antecarinal sulcus, so vertical ribs are levelled with the flank anterior surface. One of the shells (SNGM 7122) shows a zig-zag pattern at the terminal end of one vertical rib.

Discussion — The description provided above was based on the type series, housed at the SERNAGEOMIN. The shells recovered from San Juan (Argentina), examined at the University of Buenos Aires collections (Fig. 6E—H), bear several differences with those from Atacama (Chile) and in some aspects the type material of *S. biroi* seems closer to *S. sigeli* than to the shells from San Juan. Nevertheless, given the close affinities between both species, we prefer to maintain the current identification.

Syrotrigonia biroi from San Juan seems to be taller (height/length ratio between 0.98 and 1.16) and wider (width/height ratio between 0.67 and 1.11) than the type series (compare the holotype, Fig. 6A and B, with the shell in Fig. 6E and F). Also, it is more triangular in lateral view (Fig. 6F—H) with a straighter anterior margin in most specimens, and the angle between the area and the flank surfaces being smaller. Ornamentation is usually attenuated due to corrasion, but, when preserved (commonly on the flank and less frequently on the area), it is similar to that of the shells from Atacama; escutcheon ornamentation could not be observed.

It is noteworthy that when defining the species, Pérez and Reyes considered it as a highly variable taxon. As can be clearly seen, elongation may differ among shells (Fig. 6B and C), the vertical set of ribs may be more developed on some individuals (Fig. 6C), and both sets may be in contact in some cases (Fig. 6D).

The main differences between *S. biroi* and *S. sigeli* are the smaller size (although the paratypes include some large shells) and the absence of antecarinal depression in the latter. The junction between the early vertical and horizontal costae is more clear on *S. sigeli* and the horizontal ribs tend to bend downward at that point, resulting in a V shaped inflection; both samples of *S. biroi*, on the other hand, are dominated by true commarginal ribs instead of subhorizontal ones, hence the junction between both sets (when developed) tends to form an L-shaped inflection (Fig. 6D, F—H).

Both Chilean and Argentinian records of *S. biroi* come from marginal condensed successions, without reliable biostratigraphic indicators, making it difficult to provide a precise age for them. The species seems to be restricted to southern South America, like *S. sigeli*. Given the low degree of biostratigraphic precision for many of the records, the detailed evolutionary relationships among these taxa cannot be accurately established.

Syrotrigonia paradisensis (Lisson, 1907)
(Fig. 6I—M)

*v 1907 *Trigonia Paradisensis* nov. sp.; Lisson, p. 34, pl. 4: Figs. 1—2.

v 1924 *Trigonia inca* n. sp.; Fritzsche, p. 49, pl. 3: Figs. 1—3.

? 1924 *Trigonia flexicostata* n. sp.; Fritzsche, p. 50, pl. 3: Fig. 4a, b.

v 1930 *Trigonia Steinmanni* nov. sp.; Lisson, p. 6, pl. 2: Fig. 1—3. [*non Trigonia Steinmanni* Philippi, 1899, p. 64, pl. 30, Figs. 1—2; although both are primary homonyms, no replacement name is needed for the junior, invalid one, under ICZN, 1999, Art. 60.2].

v 1930 *Trigonia Gerthi* nov. sp.; Lisson, p. 8, pl. 3: Figs. 1—5.

v 1930 *Trigonia paradisensis* Lisson; Lisson, p. 18, pl. 9: Figs. 1—5.

v 1947 *Trigonia mathewsi* n. sp.; Richards, p. 55, pl. 8: Figs. 9 and 10.

1956 *Buchotrigonia gerthi* Lissón; Benavides-Cáceres, p. 368—369, 392, 425—426, 429.

1956 *Buchotrigonia flexicostata* Fritzsche; Benavides-Cáceres, p. 368—369, 392.

1956 *Buchotrigonia inca* Fritzsche; Benavides-Cáceres, p. 368—369, 392.

1978 *Buchotrigonia steinmanni* (Lisson, 1930); Reyes and Pérez, p. 26, pl. 3: Fig. 5 (reproduced from Lisson, 1930).

1985 *Buchotrigonia?* aff. *inca* (Fritzsche); Etayo-Serna, p. 18, pl. 1: Figs. 9 and 26.

1985 *Buchotrigonia?* aff. *paradisensis* (Lisson); Etayo-Serna, p. 18.

1991 *Buchotrigonia (Syrotrigonia) gerthi* (Lisson); Prado-Velazco, p. 446.

1991 *Buchotrigonia (Syrotrigonia) steinmanni* (Lisson); Prado-Velazco, p. 446.

1991 *Buchotrigonia (Syrotrigonia) paradisensis* (Lisson); Prado-Velazco, p. 446.

Studied material — Plastohypotypes of *T. paradisensis*, SNGM 7481—7482; plastosyntype of *T. inca*, SNGM 7453; plastoholotype of *Trigonia steinmanni*, SNGM 7492; plastosyntypes of *Trigonia gerthi*, SNGM 7446—7448; syntypes of *T. mathewsi*, USNM 153037; paratypes of *T. mathewsi*, USNM 153036; material identified as *Buchotrigonia gerthi*, MUSM.

Geographical range − Colombia − Boyacá Department (Etayo-Serna, 1985) − and Peru − Callao Province (Lisson, 1907, 1930), and Lima (Lisson, 1930), Áncash (Fritzsche, 1924, Lisson, 1930; Richards, 1947; Benavides-Cáceres, 1956; Prado-Velazco, 1991), La Libertad (Benavides-Cáceres, 1956) and Cajamarca (Benavides-Cáceres, 1956) Departments.

Age − Valanginian (Benavides-Cáceres, 1956; Rivera and Alleman de D'Ans, 1974, Etayo-Serna, 1985; Alleman, 1986; Prado-Velazco, 1991) and maybe Hauterivian (Etayo-Serna, 1985).

Dimensions − (in mm, max/mean/min) Length: 64.5/52.6/34.9; Height: 45.9/38.3/29.3; Width (1 valve): 22.1/16.8/10.4.

Description − Shell is large (up to 6.5 cm), short and subtrapezoidal (Fig. 6I–M); dorsal margin is slightly concave. Postero-dorsal angle is obtuse, while postero-ventral corner is almost at right angle. Ventral margin is slightly curved, gradually merging to the anterior convex margin. Escutcheon is distinguishable from the area, being slightly excavated and nearly smooth. Area bears transverse anterior ribs crossing to the escutcheon, but fading quickly; it is smooth posteriorly, and it has a submedian sulcus. Area ribs, where developed, are continuous with those of the flank, although in some shells they can alternate posteriorly. Escutcheon carina is absent, while marginal carina is well developed anteriorly, becoming wider and more rounded posteriorly. Flank has a wide and shallow antecarinal depression. Flank ribs are oblique and concentric on the initial stages; later on the inflection develops producing the typical subvertical and subhorizontal rib sets; the inflection projects posteriorly as growth goes on. Ventral margin is crenulated as a result of the development of the posterior vertical ribs. The ribs are almost as wide as the intercostal spaces, and they fade out towards the anterior margin, resulting in a smooth, wide, tapering surface (although in the plastohypotype for *T. paradisensis* it is narrow). In some shells, the last few horizontal costae are thinner and appear duplicated with respect to the vertical ones (Fig. 6I); this ornamentation pattern is not as much developed as in *Syrotrigonia? lorentii* or *Syrotrigonia forti*, although reminiscent of it.

Discussion − There is little doubt that all these variously named shells belong to closely related taxa. When defining *T. steinmanni* (Fig. 6M), Lisson (1930) already recognized the strong similarity with *T. paradisensis* (Fig. 6I); he also compared it with *T. inca* (Fig. 6K), but considered both as separate species because of the different robustness of flank costae. *Trigonia gerthi* (Fig. 6L) was regarded by the author also as very similar to *T. steinmanni*, but even though both groups of shells were found together, he defined two different species based on the intercostal space, identically developed in both sets of ribs in the first taxon. *Trigonia paradisensis* was defined by Lisson (1907) on the basis of the nodes developed on the costae angulations and on the carina; these appear on the plastohypotype as thickenings of the rib (at least on the inflection point, Fig. 6I). Lisson (1907) considered *T. paradisensis* as related to *T. lorentii*, but based on the differences in adult sculpture and on the fact that they were found in different strata, he considered them as separate species, even though they were found at the same locality. When describing *T. mathewsi* (Fig. 6J), Richards (1947) did not compare it with any of Lisson's species, probably being unaware of them; later on, Benavides-Cáceres (1956) regarded this species as a junior synonym of *T. gerthi*. Considering the strong similarities among these nominal taxa, they are here regarded as belonging to the same species. Although there are some differences in shell shape (the plastohypotype of *Trigonia paradisiensis* appears somewhat more elongated than the other shells, Fig. 6I), this variability does not exceed the variability seen in other species of the genus (see Figs. 6B−C). Ornamentation is also very conservative within the group; costae density may vary within the taxon, but considering the overall similarity in shell shape and ornamentation, these variations are here regarded as intraspecific. It is noteworthy that the anterior set of costae is clearly subhorizontal, like in *S. sigeli*, and not commarginal, and also that at the meeting point the subhorizontal costae tend to bend downwards, as in the Argentinean species.

This taxon developed in northern South America; it seems to have been related to the group of *Syrotrigonia? lorentii* and *S. forti*, being the main difference the ornamentation pattern of the flank. On the other hand, this species may be strongly related to the Tethyan species (*Syrotrigonia libanotica* and *Syrotrigonia distans*, and possibly *Syrotrigonia collombi*), differing mainly in the kind of shell growth, slightly opisthogyrate in the South American species (producing a concave dorsal margin and a dorsally curved area) versus orthogyrate in the others (at least in *S. libanotica*, with a straight dorsal margin and a flat area).

There are also some shells probably related to *S. paradisensis*, from the Batá Formation (Boyacá Department, Colombia), which were described by Bürgl (1960) as *Trigonia* aff. *literata* Young and Bird, 1828; later on, Geyer (1973) defined the subspecies *Vaugonia niranohamensis santa-mariae* and *Vaugonia yokoyamai batafluviae* based on material from the same unit. According to Etayo-Serna in Pérez and Reyes (1986) and Etayo-Serna et al. (2003) these shells belong to the genus *Syrotrigonia*. The description and photographs provided by Bürgl (1960) clearly allow for such determination; although the available data are insufficient to assign them to any particular species, they could possibly belong to the lineage discussed here, considering the age of the Batá Formation (now regarded as late Valanginian-Hauterivian according to the palynological information provided by Etayo-Serna et al. 2003). Regarding the subspecies defined by Geyer (1973), Pérez and Reyes (1997) considered *V. niranohamensis santa-mariae* as close to *Buchotrigonia etayoi*, due to the ornamentation pattern shown on the photograph by Geyer (1973, pl. 5, Fig. 5); nevertheless, the description provided by Geyer (1973, p. 78) together with the scarcity of material and the presence of other shells assignable to *Syrotrigonia* in the same formation, suggest that this taxon should be included within the latter genus. *Vaugonia yokoyamai batafluviae* was accepted by Pérez and Reyes (1997) as a *Syrotrigonia*.

Syrotrigonia? lorentii (Dana, 1849) − **S. forti** (Lisson, 1930) plexus (Fig. 6N−O)

v 1849 *Trigonia lorentii* (Dana); Dana, p. 721, pl. 15: Fig. 2.

1907 *Trigonia Lorentii* Dana; Lisson, p.32−33, pl. 3: Figs. 2−3.

1921 *Trigonia lorentii* Dana; Douglas p.253, pl. 15: Fig. 7.

1929 *Trigonia Lorentii* Dana; Steinmann, p. 92, Fig. 103.

v 1930 *Trigonia Forti* nov. sp.; Lisson, p. 4, Fig. 4.

1987 *Anditrigonia lorentii* Dana; Villavicencio de Dávila and Rangel-Zavala, p. 12−13, pl. 3: Figs. 3 and 5.

1991 Anditrigonia (Anditrigonia) lorentii (Dana); Prado-Velazco, p. 446.

Studied material − Syntypes of *T. lorentii*, USNM 3581; plasto-topotypes of *T. lorentii*, SNGM7467−7468; plastoholotype of *T. forti*, SNGM 7444.

Geographical range − Peru − Callao Province (Lisson, 1907) and Lambayeque Department (Villavicencio de Dávila and Rangel-Zavala, 1987) for *S.? lorentii* and Áncash Department (Lisson, 1930) for *S. forti*.

Age −Valanginian for *S.? lorentii* (Rivera and Alleman de D'Ans, 1974, Prado-Velazco, 1991) and for *S. forti* (Lisson, 1930; Rivera and Alleman de D'Ans, 1974).

Dimensions − *S. forti*, plastoholotype: Length: >59.4 mm; Height: 53.0 mm; Width (1 valve): 17.8 mm; *S.? lorentii*, best

preserved syntype: Length: 58.0 mm; Height: 36.8 mm; Width: 14.1 mm.

Description — Shell is large (about 6–7 cm long) somewhat elongated, subtrigonal to subquadrangular and orthogyrate. Dorsal margin is straight, while the anterior margin is straight to slightly curved and the ventral margin is convex. Escutcheon and area are poorly preserved, apparently smooth, although *T. forti* seems to bear transverse ribs on the anterior region of the area and one of the studied shells of *T. lorentii* appears to have transverse ribs preserved anteriorly. Marginal carina is indistinguishable and the antecarinal depression is incipient in *S.? lorentii*. Umbonal flank ribs are oblique and concentric, and as ontogeny goes on they develop an inflection, differentiating subvertical and subhorizontal sets of ribs always meeting on the mid-flank. Later on, subhorizontal ribs duplicate, causing a bifurcation at the meeting point.

Discussion — Despite sharing the ornamentation pattern, these two species also bear some differences which suggest that they are two different species. The shell of *Syrotrigonia? lorentii* is subtriangular (Fig. 6N), while in *S. forti* seems to be subquadrangular (although the posterior part of the shell is missing, Fig. 6O) and more obese. Also, *S.? lorentii* bears thinner ribs, more densely arranged and straighter than *S. forti*. Although here considered as two related species, given their strong resemblance (which was already recognized by Lisson, 1930), the possibility of being separate species with convergent morphology cannot be ruled out; as mentioned before, some shells of *S. paradisensis* and *S. sigeli* may occasionally bear some bifurcating horizontal ribs. Even when describing *S. paradisensis*, Lisson (1907) mentioned the similitude of this last species with young *S.? lorentii* (although such similarity was subsequently disregarded by the same author, Lisson, 1930). *Syrotrigonia? lorentii* was found on San Lorenzo Island (Callao Province, Peru), in beds lying below *S. paradisensis*; this stratigraphic relation may be a hint to the origin of this last taxon.

Various authors considered *Trigonia lorentii* as related to the buchotrigoniids (Table 1). Unfortunately, no material with well preserved area could be analyzed; despite the mention by Villavicencio de Dávila and Rangel-Zavala (1987) of numerous thin transverse striae, Lisson (1907) described some oblique striae developed on the dorsal and ventral halves of the area, meeting in the middle in a *chevron*-like pattern. Considering the strong similarity of flank ornamentation pattern with other species within the genus, this taxon is here regarded as *Syrotrigonia? lorentii*, pending analysis of better preserved area ornamentation.

The type series of *S.? lorentii* was studied (USNM 3581), showing once again high sculptural variability. Vertical costae width differs between individuals, as well as the angle between both sets (from almost right to acute angles); this is particularly important considering the significance traditionally given to this kind of character for defining species within the genus. Anterior-set costae are usually horizontal (Fig. 6N), but at least in one shell are commarginal and separated by wide smooth spaces; sometimes there are some horizontal costae not joining vertical ones. Some of these variations were already recognized by Douglas (1921) when studying the species.

Non-South American species of Syrotrigonia. The first species to be included in the genus were recorded from the Tethys realm (Lebanon Mountains, Middle East) and their systematic history is not simple (Table 1). In 1852 Conrad, based on fossils from the Lebanon region (p. 214 and 232, pl. 3: Figs. 19, 20, 21, 23 and pl. 4: Fig. 26) described the species *Trigonia syriaca* providing a meagre description and some puzzling drawings, some of which may even not represent trigoniids at all. Fraas (1878) assigned some shells, also from Lebanon, to *T. syriaca* Conrad, 1852, providing a more detailed description and better figures (p. 299, pl. 6: Figs. 2–4 [*sic*,

recte pl. 5: Figs. 2–5]) and subsequently, Noetling (1886, p. 856, pl 24: Figs. 1–4, pl 25: Figs. 1–3), considered that the taxa described by Conrad and by Fraas may not represent the same species, but, given that the characterization done by Fraas was widespread in the literature, he proposed to maintain the name *T. syriaca* but considering Fraas as author. Nevertheless, since this is not allowed under the International Code of Zoological Nomenclature rules, Vokes (1946, p. 168) renamed Fraas' (1878) species as *Trigonia libanotica* Vokes, 1946 (pl. 4: Figs. 8–12; Fig. 3 herein), based on the description by Noetling (1886) and assigning new type material (probably topotypes of those illustrated by Fraas since the original ones were lost). When Cox (1952) proposed the subgenus *Syrotrigonia*, he was unaware of Vokes' proposal, and so he called the species *Buchotrigonia (Syrotrigonia) fraasi* Cox, 1952 and chose it as type species for the subgenus, but later on he recognized the priority of Vokes' name (Cox in Cox et al. 1969, p. N480). *Trigonia distans* Conrad, 1852 (p. 232, pl. 4: Fig. 27) was also re-described by Fraas (1867, p. 93, pl. 1: Fig. 14), but Noetling (1886, p. 860, pl. 25: Fig. 4) considered that there was no doubt about the identity of both forms, and so the original author was maintained. Nevertheless, Cox (1952) included the species in the subgenus as "*T. distans* Noetling, 1886 (*non* Conrad)" without further explanation. If the species described by Conrad and Noetling are truly different, then a new name should be given to the second one, but since no sound evidence has been provided for that interpretation, the species is here accepted as *Trigonia distans* Conrad, 1852.

Syrotrigonia libanotica resembles *S. paradisensis* in many aspects, but also bears some differences. The most notorious ones are the presence of a straight dorsal margin and an orthogyrate shell; also, subhorizontal costae seldom show the downwards bending on the meeting point with the subvertical ones, and flank ornamentation fades away as the shell grows (although the analyzed material — Plastoholotype: SNGM 7462 — has a prominent growth line, after which shell ornamentation disappears, probably reflecting some environmental disturbance). As in *S. paradisensis*, a couple of subhorizontal ribs are duplicated. *Syrotrigonia distans* is similar to *S. libanotica*, differing mostly on the absence of the set of subvertical costae; Noetling (1886) considered these species so similar that he suggested that the former may have evolved from the latter by loss of the vertical costae.

Another possible mention of a Tethyan *Syrotrigonia* can be found in Vilanova y Piera (1863); he described three species from the Aptian of Spain which were considered as buchotrigoniids by subsequent authors: *Trigonia collombi*, *Trigonia deshayesi* and *T. pizcuetana*. Dietrich (1938) considered *T. pizcuetana* as a synonym of *Buchotrigonia abrupta*; later on, Cox (1952) treated the three of them as valid species within the subgenus *Buchotrigonia (Buchotrigonia)*, while Royo y Gómez (1953) considered both *T. collombi* and *T. pizcuetana* as synonyms of *T. abrupta*. Vilanova y Piera (1863) provided only short descriptions of the three species, accompanied by very detailed drawings; if these drawings are to be trusted, it appears that *Trigonia collombi* and *T. pizcuetana* would be different species, since the former shows characters of *Syrotrigonia* (concentric oblique ribs around the umbo, vertical and horizontal sets meeting on a V-pattern, transverse ribs on the area), while the latter is probably a *Buchotrigonia* (eccentric ribs in a tight bundle around the umbo, flank and area costae meeting in an anteriorly-pointing chevron pattern) and may truly be a synonym of *B. abrupta*. *Trigonia deshayesi* also shows close affinites with *Syrotrigonia*, although it may represent an individual with anomalous development. *Syrotrigonia collombi* has duplicated horizontal costae, like *S.? lorentii* and *S. forti* from Peru.

In 1897, Cragin named the species *Trigonia goodelli* based on some shells from the Malone Formation, Texas, and considered it as belonging to the section Undulatae; based on the presence of this

species together with *Trigonia vyschetzkii* Cragin, 1893, which he regarded among the Clavellatae, he interpreted the whole formation as Jurassic. Later on he described the species as having straight antecarinal ribs which turn abruptly forward at an elbow-like angle, reducing in size but increasing in number, and becoming "partially resolved each into a series of small tubercles" (Cragin, 1905, p. 58). The analysis of the material described by Cragin (USNM 29042) clearly enables to include the species within the genus *Syrotrigonia*, based on area ornamentation (transverse costae) and initial concentric ribs on the flank (although they are somewhat elongated dorso-ventrally); no distinctive antecarinal depression has been observed. Despite the presence of tubercles may seem unusual, it appears as a late ontogenetic development, together with some irregularities on the ribs; even more, after a growth-check on one of the shells, the tubercles appear disordered and horizontal ribs cannot be recognized. This suggests that some environmental perturbation may have favoured the development of the tubercles, or at least may be responsible for the irregularity of their arrangement. Although Kitchin (1926) questioned the Jurassic age of the Malone Formation, based on the trigoniid faunas, it is now accepted that *S. goodelli* is indeed Tithonian (Albritton and Smith, 1965). Hence, leaving aside the dubious age for the shell of *S. sigeli* from Río Negro Province (Argentina), *S. goodelli* is the oldest *Syrotrigonia* species recorded (and also the earliest Buchotrigoniidae), thus pointing to a North American origin for the family, which apparently spread and diversified in South America during the Cretaceous. Also worth noticing, bifurcated horizontal ribs seem to be a primitive character, later lost in the most widespread species.

Other species of Syrotrigonia. There are two other species of *Syrotrigonia* which raised no major controversy since their original description (Table 1): *Syrotrigonia chilensis* (Pérez and Reyes, 1986) and *Syrotrigonia obesa* Pérez and Reyes, 1997. *Syrotrigonia chilensis* was recovered from the Neocomian of Atacama (Chile) from older strata than those bearing *S. biroi*. The area and flank on the umbonal region is very similar to other species within *Syrotrigonia*, with concentric ribs on the flank and transverse costae on the area; as the shell grows the subvertical and subhorizontal sets of costae become differentiated, but at the contact between both sets, complex patterns (W-shaped and √-shaped) develop. According to the authors, this is the main difference with *S. biroi*; it is possible then that the younger species had evolved from the older one by effacing of the ornamentation of the flank, especially at the meeting point between both sets of costae.

Syrotrigonia obesa comes from beds of uncertain age (within the interval late Hauterivian to Aptian) from Coquimbo Region, Chile (Pérez and Reyes, 1997). It has a large (up to 8 cm) relatively wide and elongated shell; one of its conspicuous features is the development of commarginal costae or rugae on the ventral half of the shell. Nevertheless, on the first half, the typical ornamentation of *Syrotrigonia* can be recognized; in this species the anterior costae are commarginal and meet the vertical costae with a simple L-shaped or V-shaped pattern, similar to what is found in *S. biroi*. Shell shape, on the other hand, is reminiscent of that of *S. paradisensis*, being only larger and more elongated.

4.3. Systematic reappraisal of the family

The widely assumed close systematic relationship between *Buchotrigonia* and *Syrotrigonia* stems from the original proposal by Cox (1952) of *Syrotrigonia* as a subgenus within *Buchotrigonia*. As already said, their differences were emphasized and used as bases for successive rises in rank up to the level of subfamilies, still united under a single family (Leanza, 1993; Pérez and Reyes, 1997).

However, Nakano (1968) had challenged such close relationship, suggesting that *Syrotrigonia* and *Buchotrigonia* could be descendants from different stocks. Although the possibility of independent derivation(s) may be worth pursuing further, it is beyond the aims of the present contribution and therefore the most generally applied systematic scheme (Bouchet and Rocroi, 2010; Carter et al. 2011) is currently followed here.

The general characterization of the subfamilies Buchotrigoniinae and Syrotrigoniinae provided by Pérez and Reyes (1997) is used here. The presence of eccentric umbonal costae in a tight bundle and a *chevron* pattern at the meeting of area and flank ornamentation were considered as diagnostic features of the subfamily Buchotrigoniinae; also, the contact of many subconcentric ribs with only one subvertical rib is a common feature of species included within the subfamily. The anterior set of ribs may follow a growth line along its posterior part (hence it is commarginal on this portion), developing an L-shaped design when meeting the subvertical costae, although this ornamentation pattern may appear in some *Syrotrigonia* species too.

The subfamily Syrotrigoniinae was characterized by concentric or subconcentric costae surrounding the umbo and transverse ribs on the anterior part of the area, sometimes slightly curved anteriorwards, but never generating the chevron pattern found in *Buchotrigonia* and related forms. Usually, only one or two anterior costae are related to one subvertical costa; when there are two anterior costae, they join to the posterior one at the same point, resulting in a bifurcated pattern. The anterior set of costae tends to be subhorizontal, joining with the subvertical set in V-shape or more complex patterns, but in some species the meeting of both sets is similar to that of *Buchotrigonia*. The presence of a wide antecarinal depression as described by Cox (1952) seems to be a late acquisition within the group, since in early species it is poorly developed or even absent.

Judging from the literature, there are also certain additional, insufficiently known taxa which can be considered as Buchotrigoniidae, or at least as closely related to the family, but they could not yet be confidently included in either subfamily. The species *Trigonia heterosculpta* Stanton, 1901, from the Barremian of Santa Cruz province (Argentina), was regarded by Tashiro (1979) as an Apiotrigoniinae; nevertheless, both area and flank show an ornamentation pattern typical of the Buchotrigoniidae. While in the Apiotrigoniinae the L-shaped costae appear suddenly on early growth stages, due to the appearance of the subvertical costae (Tashiro, 1979), *T. heterosculpta* develops a bending of the subconcentric costae, becoming progressively more V-shaped and finally developing the subvertical and subhorizontal set of costae (Stanton, 1901); this kind of development is more typical of the Buchotrigoniidae. Casts of the three illustrated syntypes could be examined (MLP 23423-23425), corroborating the detailed description offered by Stanton (1901). Early ornamentation on the area is similar to that observed in *Syrotrigonia*, although umbonal costae seem to be more diagonal than transverse; on later growth stages the area is smooth (except for growth lines) and bears a wide furrow (another difference with the Apiotrigoniinae according to Tashiro, 1979). Flank umbonal costae are concentric, surrounding the umbo, and in a dense disposition. Adult sculpture seems closer to that of *Buchotrigonia*, particularly to the species defined by Villamil (1992), although it is worth mentioning that the anterior set of costae (usually oblique on the adult) do not contact the first subvertical rib, which usually reaches the ventral margin. From these evidences, it is here concluded that, in spite of its uncertain generic assignment, the species most likely represents the southernmost record for the Buchotrigoniidae rather than an outlandish Apiotrigoniinae.

The genus *Quoiecchia* Crickmay, 1930 was proposed to include the single species *Quoiecchia aliciae* Crickmay, 1930 from Hauterivian or Barremian strata from British Columbia, Canada (Poulton, 1977). It was originally characterized mostly by its ornamentation with two sets of furrows: a radial set, strong near the umbo and becoming obsolete near the middle of the flank, and a commarginal set, appearing at 1 cm from the umbo and becoming increasingly stronger towards the basal margin (Crickmay 1930). Cox (1952) disregarded the genus, considering that it was based on immature specimens of unknown affinities, but Poulton (1977) considered it a valid genus and described the presence on the flank of anteroventrally sloping oblique costae near the umbo which extended also to the area. Its systematic position was variously treated: Crickmay (1930) regarded it as related to the genus *Haidaia* Crickmay, 1930 (a synonym of *Myophorella* Bayle, 1878 according to Cox, 1952 or a subgenus within the latter according to Kobayashi and Tamura, 1955); Saveliev (1958) included *Quoiecchia* in the Laevitrigoniinae; Poulton (1977) referred it to the Myophorellinae, while Tashiro (1979) doubtfully included it in the Apiotrigoniinae. The commarginal flank costae, the lack of pustules and the absence of an antecarinal sulcus, preclude the inclusion of *Quoiecchia* in the Laevitrigoniinae. The similarity with the rostrate Apiotrigoniinae is only superficial: as mentioned before the L-shaped costae appear suddenly in that subfamily, and, further, concentric costae tend to be subhorizontal, while in *Quoiecchia* the early costae surround the umbo, becoming subradial as shell grows (Poulton, 1977, p. 11, pl. 2 Fig. 9). This development of flank ornamentation seems closer to that found in the Buchotrigoniidae within the myophorelloid lineage. Such a strong resemblance of the Canadian genus with the Buchotrigoniidae may help to explain why the original specimens of *S. sigeli* were formerly referred to *Quoiecchia*.

4.3.1. The Buchotrigoniinae

The record for *Buchotrigonia* and its allies is discontinuous, apparently punctuated by many gaps. The three stratigraphically oldest nominal species were defined by Villamil (1992) for the late Berriasian of Cundinamarca (Colombia). *Buchotrigonia etayoi* Villamil, 1992 description was based on a large sample, while the other two associated species (*Buchotrigonia perezi* Villamil, 1992; *Buchotrigonia kauffmani* Villamil, 1992) were defined on few shells each. The material from the Batá Formation of Boyacá (Colombia) described by Geyer (1973) as *V. niranohamensis santamariae* and

thought to be Early Jurassic, is in fact late Valanginian-Hauterivian (Etayo-Serna et al., 2003) and should be considered a *Buchotrigonia* close to *B. etayoi* according to Pérez and Reyes (1997), but the scarcity and fragmentary nature of the material makes this assignation dubious, and it may also belong to *Syrotrigonia* (see section 4.2 on *S. paradisensis*).

The next record for the genus is the type species, *B. abrupta* (von Buch, 1838) from the Barremian of Colombia; this species has the eccentric costae of the flank more developed, with the change on ornamentation starting later (Villamil, 1992). This species (together with the closely related, and probably synonyms, *T. pizcuetana* Vilanova y Piera, 1863 and *T. reesidei* Stoyanow, 1949) had a wide distribution during the Aptian, being found in Spain (Vilanova y Piera, 1863, Coquand, 1865), Colombia (Dietrich, 1938; Villamil, 1992), and SE Arizona, USA (Stoyanow, 1949), although Colombian records may be as young as Albian (Bürgl, 1954); during the Albian it was present in Peru (Benavides-Cáceres, 1956; Villavicencio de Dávila and Rangel-Zavala, 1987).

Although Benavides-Cáceres (1956) mentioned a "*Buchotrigonia robinaldina* d'Orbigny (=*B. lissoni* Sommermeier)" (p. 392) from the *Parahoplites nicholsoni* Zone (early Albian of Peru), this is probably a typographical error meant for "*Ptychomya robinaldina* d'Orbigny (=*P. lissoni* Sommermeier)", as he did for the Inca Formation (p. 380).

Probably related to the previous group of species is the French Coniacian species *Trigonia disparilis* d'Orbigny, 1844 (p. 157, Pl. 299 Figs. 3—4), which already Lycett (1872—1879, p. 126 see errata on p. 240) recognized as related to *T. humboldtii* (=*B. abrupta*) and is here tentatively assigned to the genus *Buchotrigonia*.

A group of probably related species appeared between the Santonian and the Maastrichtian on the northern Pacific margin of South America (Olsson, 1944; Pérez and Reyes, 1980, 1996; Dhondt and Jaillard, 2005) and most of them were included in the genus *Neobuchotrigonia* Pérez and Reyes, 1996. This genus was considered by those authors as related to *Buchotrigonia*, but with the development of a larger, thicker and proportionally wider shell, a change of the posterior margin from short and rounded to long and straight, and the extension of the surface of the flank occupied by eccentric costae (what seems to be a general evolutionary trend within the group — Villamil, 1992).

5. Biogeography

5.1. Historical biogeography

From the present systematic revision it is concluded that, though having probably originated in the Late Jurassic of North America, *Syrotrigonia* is a characteristic genus of the Early Cretaceous of South America, as already discussed by Pérez and Reyes (1986). The history of the taxon in southern South America is not clear, since most of the records lack accurate biostratigraphic markers associated; it may start during the Tithonian-Berriasian (Manceñido and Damborenea, 1984; Rolleri et al. 1984b) with the presence of *S. sigeli* (Fig. 7), but its age is not certain. During the Early Cretaceous it diversified, and the species *S. chilensis* and *S. biroi* appeared, while *S. sigeli* thrived in the Valanginian. *Syrotrigonia obesa* also occurred in southern South America, during the Hauterivian-Aptian time span. In northern South America the genus is recorded since the Valanginian (Fig. 7), with the species *S.? lorentii*, *S. forti* and *S. paradisensis*; this last species represent a relatively common and widespread taxon which was found in Colombia and Peru. During the Aptian the species *S. collombi*, *S. libanotica* and *S. distans* are recorded in the Tethyan realm. The youngest records for the genus may be *S. libanotica* and *S. distans*,
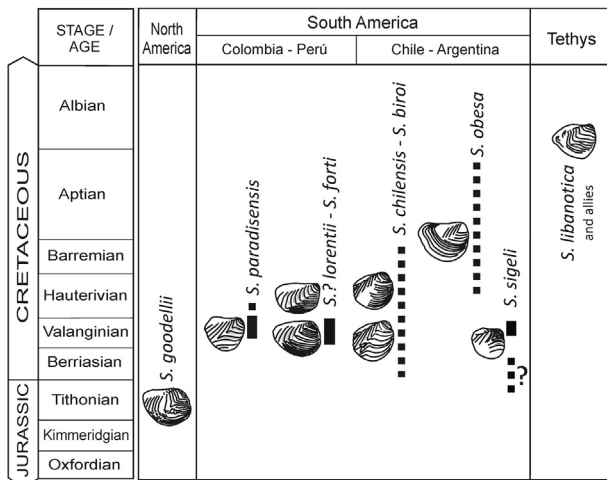

Fig. 7. Stratigraphic and geographic range of the South American species of *Syrotrigonia*.

which were found in strata of Aptian or Albian age in the Middle East.

The Buchotrigoniinae are more common in northern South America; they appeared on the record during Berriasian times in Colombia; the next occurrence was from Barremian to Albian times, with the type species, and by the Aptian they attained their major expansion, reaching North America and Western Europe. There is also a probable record from the Coniacian from France and after that they reappeared in the South American record by the Santonian from Ecuador, then expanded their geographic range to northern Chile during the Campanian, and had a last record from the Peruvian Maastrichtian.

As mentioned above, other taxa likely belonging to the family seemingly spread farther north up to southwestern Canada (*Q. aliciae*) and southwards to southern Patagonia (*"T." heterosculpta*) during Hauterivian-Barremian times.

There are two other unconfirmed mentions of possible Buchotrigoniidae outside South America. In 1959, Wellman (p. 151, Table 2) listed a ?*Buchotrigonia* sp. on a table prepared by Dr. C.A. Fleming for a locality in New Zealand; unfortunately, no description or picture was included. Moreover, according to Pérez and Reyes (1980), Fleming himself later considered that *Buchotrigonia* was not present in New Zealand, and no Buchotrigoniidae is mentioned in his monograph on New Zealand trigoniids (Fleming, 1987), therefore this record should better be disregarded. Concerning *Syrotrigonia picteti* (Coquand) from the upper Hauterivian-Aptian of Yemen (as listed by Howarth and Morris, 1998, p. 31), once again there is no description or photograph associated, but even if the material could be assigned to *Trigonia picteti* Coquand, 1865, this species has not yet been confirmed as a Buchotrigoniidae.

5.2. Ecological biogeography

It is noteworthy the frequency of references to marginal environments for the records of the different species of Buchotrigoniidae. When describing the species *Trigonia inca* and *Trigonia flexicostata* (=*S. paradisensis*), Fritzsche (1924, p. 35) considered the depositional environment as hyposaline, a fact that was confirmed by Benavides-Cáceres (1956, p. 368) and Romero et al. (1995, p. 138); Dietrich (1938) even proposed that the irregularities on the costae of these species were due to the incoming of fresh water to their living habitat. The records for *S. biroi* and *S. chilensis* stand out by the lack of biostratigraphic markers; although Pérez and Reyes (1986) did not specify the provenance environment, they mentioned that both species come from the upper-most part of the Pedernales Formation, which was interpreted by García (1967) as deposited in a transitional environment, gradually changing to the Agua Helada Formation, strictly continental. Also, the shells of *S. biroi* described by Lo Forte (1991) were found in a condensed succession, attributable to a basin margin (Aguirre-Urreta and Lo Forte 1996). For *S. sigeli* in Río Negro, both the fossil content and sedimentologic information (Manceñido and Damborenea, 1984; Rolleri et al. 1984b), point to a shoreline environment with salinity variations. This seems also to be the case for the samples from the south of Barda Negra as discussed in section 2. On the other hand, any detailed environmental interpretations concerning the specimens from Pichaihue Abajo are hindered due to uncertainties as to the precise provenance levels of those particular shells. There are also references of marginal environments for the genus *Buchotrigonia*; when describing *Buchotrigonia reesidei*, Stoyanow (1949, p. 14–15) mentioned shallow-water deposits for most of the bearing strata, with dolomite beds and silicified wood. This recurrent association of species within the family, and particularly within the genus *Syrotrigonia*, with marginal environments, subject to salinity variations, suggests a euryhaline lineage.

This raises the need to reconsider certain characters of the group which are usually regarded as of systematic value. It may be apposite to recall that changes in salinity have long been blamed as a likely source of shell-secreting alterations of non-traumatic origin in palaeopathology literature (Moodie, 1923; Tasnádi-Kubacska, 1962), as well as certain anomalous effects noticed on shells of extant marine bivalves (Boshoff, 1968). The present study suggests that strong commarginal growth-rugae accompanying the entire shell margin, as well as development of pustules and zig-zag patterns on costae may be reinterpreted as examples of disrupted ornamentation in responses to episodes of environmental stress.

In this context, it is remarkable that members of the family were best represented (considering frequency and geographical extension of the records) during the Valanginian and the Aptian, *i.e.* moments of global sea-level fall (Haq et al. 1987; Haq, 2014). In a sequence-stratigraphy framework, if the rate of sea-level fall is slow, shelf margin facies prograde over the shelf edge (Haq et al. 1987) thus having higher chances of being preserved. So the major expansions of the family may not actually represent periods of evolutionary success but rather time intervals with higher chances of fossilization.

6. Conclusions

- *Quoiecchia sigeli* should be referred to the genus *Syrotrigonia* due to its ornamentation pattern (particularly the area sculpture); the nominal species *S. brocardoi* is a junior subjective synonym of it. Shell shape and flank ornamentation is variable within the species, but the presence of commarginal rugae is interpreted as a result of environmental perturbation.

- In southern South America the species *S. sigeli*, *S. chilensis*, *S. biroi* and *S. obesa* are recorded; in these species the anterior set of costae sometimes can be commarginal and the presence of duplicated costae is rare; both sets are united by a 'V' or more complex patterns, or can be separated by a smooth surface.

- In northern South America the species *S.? lorentii*, *S. paradisensis* and *S. forti* were found; in this group costae junction is in an 'L' or 'V' pattern, with the anterior set subhorizontal. The presence of duplicated anterior costae is common, with some species characterized by this kind of sculpture. Tethyan species (*S. collombi*, *S. libanotica*, *S. distans*) may be related to these taxa.

- Earliest representatives of *Syrotrigonia* are recorded in the Tithonian of North America (*S. goodelli*), and by the Valanginian occurred along most of the Pacific coast of South America. During the Aptian the genus reached the Tethyan realm. Its youngest record is Aptian or Albian. The taxon was adapted to marginal marine environments, being able to withstand certain salinity variations.

- *Syrotrigonia* is well defined on the basis of the flank ornamentation pattern together with the anteriorly curved (straight in some species) costae on the anteriormost portion of the area, persisting, though attenuated and anteriorly directed, into the escutcheon. Area ornamentation is probably the main difference with the related genus *Quoiecchia*, while area and flank ornamentation separate them from the Buchotrigoniinae. Certain characters, like general shell shape, presence of antecarinal sulcus, junction pattern between anterior and posterior sets of costae and number of horizontal costae per vertical costae may be useful for species discrimination, but in any case, species definition requires relatively large samples, in order to adequately encompass the intraspecific variability. Characters like costae width or density, growing pattern of the anterior set of costae (horizontal or commarginal), or tubercle development, have proven to be highly variable within some species, so extreme caution should be taken when defining species

based only on those characters. The presence of commarginal rugae, frequent among members of the subfamily, is most probably the result of environmental perturbations due to habitat instability.

Acknowledgements

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