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New late Tremadoc-early Arenig silicified brachiopods from the lower part of the San Juan Formation, Argentine Precordillera

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Abstract. The lowermost part of the San Juan Formation (*Archaeorthis* Zone) contains a more diverse brachiopod fauna than has previously been reported. The age of the sampled interval ranges from the late Tremadoc (*P. deltifer* Zone) to the early Arenig (*P. elegans* Zone). The basal patch-reefs have yielded the oldest Ordovician brachiopods of the Precordilleran carbonate platform, represented by an undetermined syntrophiidine. The overlying burrowed wackestones and bioclastic grainstones contain the following taxa: *Tritoechia (Parvitritoechia) preandina* n. subgen. et sp., *Tritoechia (Tritoechia) prima* n. sp., *Orthidium prominens* n. sp., *Nothorthis marginata* n. sp. (with two subspecies, *N. m. marginata* and *N. m. crassicosta* n. subsp.), *Syntrophia sanjuanina* n. sp. and *Parallelostrophia septata* n. gen. et sp. The low-diversity pentamerid-dominated assemblages recovered from the channel and intermound facies, as well as the *Archaeorthis*-dominated communities from the overlying whole-fossil wackestones, flourished in the high-energy, shallow-water environments prevailing at the beginning of the late Tremadoc-early Arenig transgressive event. The increase in brachiopod abundance and diversity upwards in the section appears to be related to the increasing environmental stability resulting from the gradual deepening of the basin.

Resumen. NUEVOS BRAQUIÓPODOS SILICIFICADOS DEL TREMADOCIANO TARDÍO- ARENIGIANO TEMPRANO DE LA PARTE INFERIOR DE LA FORMACIÓN SAN JUAN, PRECORDILLERA ARGENTINA. La parte inferior de la Formación San Juan (Zona de *Archaeorthis*) contiene una fauna de braquiópodos más diversa de lo que se había previamente reportado. La edad del intervalo muestreado se extiende desde el Tremadociano Tardío (Zona de *P. deltifer)* al Arenigiano Temprano (zonas de *P. proteus* y de *P. elegans*). Los biohermos basales contienen los braquiópodos ordovícicos más antiguos de la plataforma carbonática de la Precordillera argentina, representados por un Syntrophiidina indeterminado. Los wackestones bioturbados y los grainstones bioclásticos suprayacentes contienen los siguientes braquiópodos: *Tritoechia* (*Parvitritoechia) preandina* n. subgen. et sp., *Tritoechia (Tritoechia) prima* n. sp., *Orthidium prominens* n. sp., *Nothorthis marginata* n. sp. (con dos subespecies, *N. m. marginata* y *N. m. crassicosta* n. subsp.), *Syntrophia sanjuanina* n. sp. y *Parallelostrophia septata* n. gen. et sp. Las comunidades de baja diversidad dominadas por pentaméridos asociadas a los biohermos y las comunidades dominadas por *Archaeorthis* presentes en los wackestones suprayacentes, que incluyen la mayor parte de la fauna silicificada aquí descripta, florecieron en ambientes someros de alta energía prevalecientes en los comienzos de la transgresión del Tremadociano Tardío-Arenigiano Temprano. El subsequente incremento en la diversidad y riqueza de los braquiópodos podría estar relacionado con la condiciones más estables resultantes de la gradual profundización de la cuenca.

Key words. Brachiopods. Early Ordovician. Argentine Precordillera. Paleoecology.

Palabras clave. Braquiópodos. Ordovícico Temprano. Precordillera argentina. Paleoecología.

Introduction

This paper is the second of a series on the silicified brachiopods of the San Juan Formation, and is concerned with the fauna recovered from the lowermost part of this unit. The fauna reported previously (Benedetto, 2001a) was mainly collected from the second and third silicified intervals encompassing the *Niquivilia* and *Monorthis* brachiopod biozones (Herrera and Benedetto, 1991) respectively, which range in age from the upper part of the *Oepikodus evae/O. intermedius* Zone to the *M. parva* Zone (lowermost Whiterock, middle Arenig).

The *Archaeorthis* Zone is characterized by low-diversity assemblages dominated by *Archaeorthis sanroquensis* Benedetto. Previously described brachiopods from this zone are *Nothorthis termalis* (Herrera and Benedetto), *Ranorthis niquivilensis* Benedetto, *Syntrophia* sp., and an unidentified pentamerid (Benedetto, 2001a, 2002). New detailed field sampling of

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the silicified beds distributed through the lowest 30 m of the San Juan Formation showed that brachiopods from the *Archaeorthis* Zone are not only abundant but also are more diverse than had been supposed. The main purpose of this work is to describe the well-preserved late Tremadoc-early Arenig brachiopods obtained by acid etching of samples from the silicified interval overlying the sponge-receptaculitid reef-mounds which, according to Cañas and Carrera (1993), constitute the base of the San Juan Formation.

On the basis of better preserved specimens than those available at the time in the first publication (Benedetto, 2001a), we described and illustrated the new syntrophidine genus *Parallelostrophia*, the oldest known tritoechiid from the Precordillera basin, represented by the new subgenus *Tritoechia* (*Parvitritoechia*) and a new species of *Tritoechia* (*Tritoechia*), together with new species of *Orthidium*, *Nothorthis*, and *Syntrophia*. In addition, we report the first brachiopods recovered from the basal patch-reefs of the San Juan Formation. Although the material is still scarce and fragmentary, its discovery is significant as it constitutes the oldest record (late Tremadoc) of brachiopods in the Ordovician carbonate platform of the Argentine Precordillera.

Stratigraphic setting and age

Sampled sections are located on the western slope of the Cerro Cumillango, Cerro La Silla and Cerro San Roque (figure 1). The Cerro Cumillango section starts with two main banks of mound-shaped bioherms. In the Cerro La Silla section, located northward along the same thrust (Niquivil thrust, Jordan *et al.*, 1993) the reef-mound association is composed of *Girvanella*-rich calcimicrobial biolithites, lithistid sponges and *Calathium* (Cañas, 1999). In both the Cerro Cumillango and San Roque sections, the reef-mound facies is succeeded by a 8-10 m thick interval of non-fossiliferous cherty limestones. The overlying succession, which has furnished most of the brachiopods included in this study, consists of 25-30 m of medium- to thick-bedded burrowed, whole fossil wackestones interbedded with lithoclastic and bioclastic grainstones and packestones. Fossils include brachiopods, pelmatozoans, gastropods, nautiloids, trilobites, bivalves and calcareous algae (Cañas and Carrera, 1993; Vaccari, 1995; Carrera, 1997; Sánchez, 2001). The diverse marine fauna along with the lithofacial evidence indicate a low-energy, shallow open platform punctuated by storm events (Cañas, 1999).

The age of the bioherms, according to the associated conodonts, is mid-late Tremadoc (*P. deltifer* Zone), while the overlying wackestones and bioclastic packestones yielding the silicified fauna described herein (figure 2) encompass the late Tremadoc-early Arenig *P. proteus* Zone and probably range into the lowermost part of the *P. elegans* Zone (Lehnert, 1995; Albanesi *et al.*, 1995, 1998).

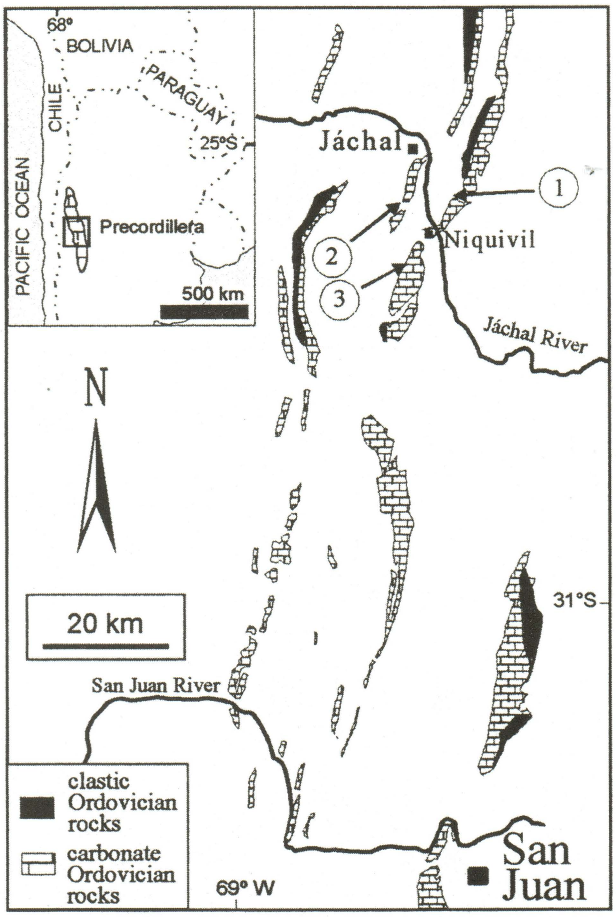


Figure 1. Location map of the studied area showing Ordovician outcrops and sampled fossiliferous localities (encircled numbers). 1, Cerro La Silla section; 2, Cerro San Roque section; 3, Cerro Cumillango section / *Mapa de ubicación del área de estudio mostrando los afloramientos ordovícicos y las localidades fosilíferas muestreadas (números en círculos).*

Brachiopod biostratigraphy

Herrera and Benedetto (1991) recognized five assemblage zones in the Early Ordovician carbonate succession of the Precordillera. They are, in ascending order, the *Archaeorthis*, *Huacoella*, *Niquivilia*, *Monorthis* and *Ahtiella* zones, ranging in age from the Tremadoc to Llanvirn. Detailed sampling of the lower part of the San Juan Formation carried out in the last three years (Cech, 2000; Esbry, 2001; Benedetto, 2001a, 2002) has substantially increased our knowledge on the taxonomic composition and stratigraphic ranges of brachiopods from the *Archaeorthis* Zone. This zone, about 80-90 m thick, can be divided in several "assemblages", each characterized by a distinctive brachiopod association. Such assemblages appear to be controlled by environmental fluctuations and hence they may represent ecological rather than biostratigraphic units. However, since they are not recurrent through the biozone they may confidently be used to make intra-basinal correlations. The following assemblages have been recognized: (1) A lowermost assemblage, ranging from 6.5 to 15.5 m above the top of reef-mounds in the San Roque section and from 8 to 11.5 m in the Cerro Cumillango section, characterized by the extreme abundance of pentamerids (*Syntrophia sanjuanina* n. sp., *Parallelostrophia septata* n. gen. et sp.). (2) A very low diversity assemblage in which pentamerids are nearly absent and *Orthidium prominens* n. sp. is the dominant form associated with *A. sanroquensis*. (3) A third assemblage, containing a relatively more diverse fauna, starts with the first appearance of tritoechiids (*Tritoechia* (*Parvitritoechia*) *preandina* n. subgen. et sp., *Tritoechia* (*Tritoechia*) *prima* n. sp.), *Nothorthis marginata* n. sp., and *Nothorthis marginata crassicosta* n. subsp.; the latter is confined to the higher part of the silicified horizon. (4) The faunal composition of the succeeding 25-30 m of the *Archaeorthis sanroquensis* Zone is still poorly known because most of brachiopods are entirely calcified. This assemblage is characterized by the widespread occurrence of *Ranorthis niquivilensis* (Benedetto, 2002) which persists approximately 10 m above the last appearance of *Archaeorthis sanroquensis*. (5) Finally, a slightly more diversified association formed by *Leptella* cf. *alata* Benedetto and Herrera, *Hesperonomia* sp. and *Hesperonomiella* sp. appears immediately above the last record of *Archaeorthis*, with-

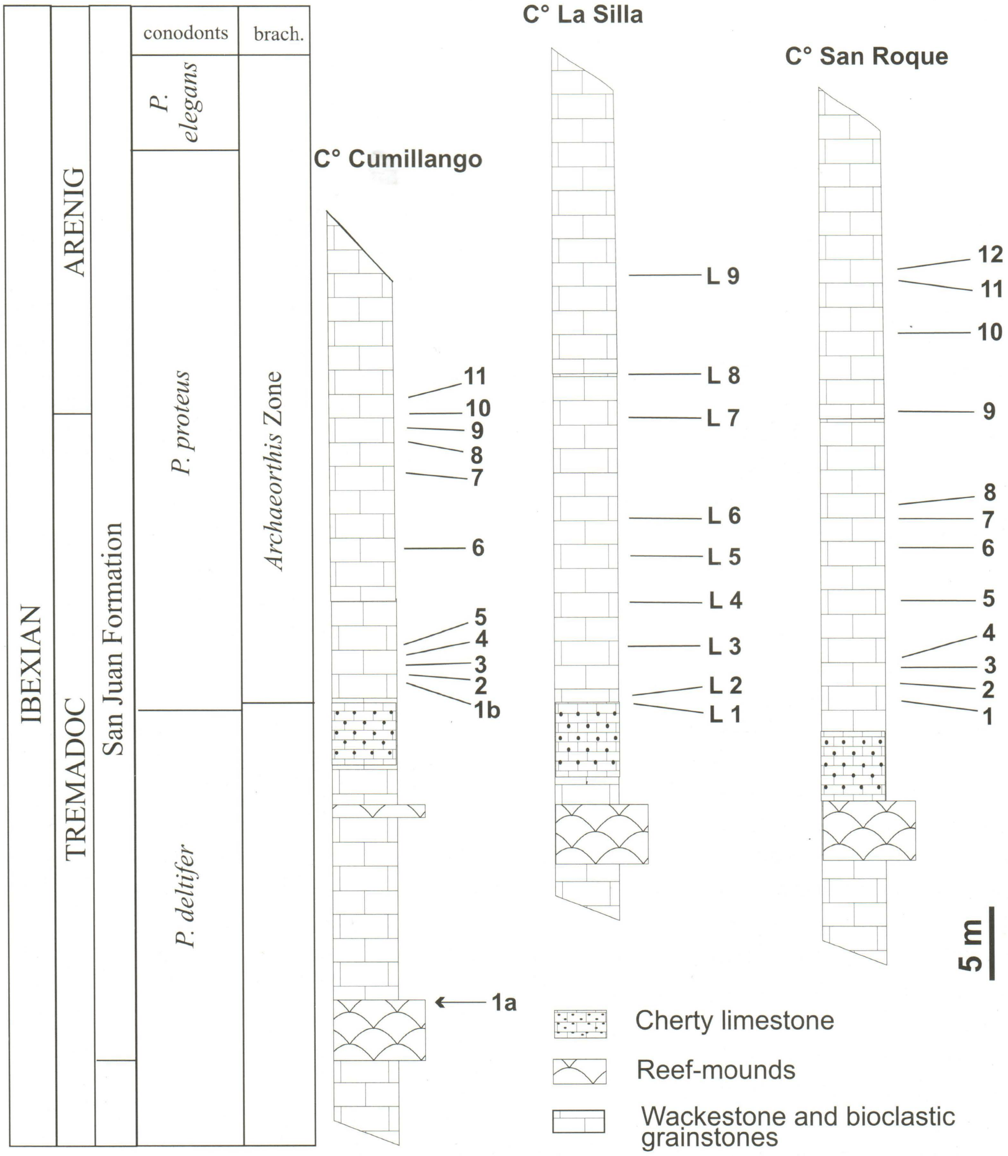


Figure 2. Stratigraphic columns of the San Juan Formation in the studied sections showing fossiliferous levels / *Columnas estratigráficas de la Formación San Juan en las secciones estudiadas, mostrando los niveles fosilíferos.*

in the "transition interval" between the *Archaeorthis* and the succeeding *Huacoella* Zone.

Palaeoecology

The stratigraphic interval encompassed by the *Archaeorthis* Zone is characterized by lithoclastic-bioclastic grainstones alternating with bioturbated wackestones. This facies association has been interpreted as representing storm-dominated, inner ramp deposits (Cañas, 1999). Fossil concentrations are typically bidimensional, reflecting a high-energy environment and successive events of cementation (hardgrounds). Benthic communities developed under such conditions were typically of low diversity and low abundance (Carrera 2001). Sponges are virtually absent in this interval becoming very abundant in the overlying communities (Cech and Carrera, 2002).

On the basis of biovolume percentages (see Sánchez *et al.*, 1993, 1996 and references therein for methodological details) and multivariate analysis, Cech and Carrera (2002) recognized at least ten communities, all of which dominated by epifaunal suspension-feeders. In the lowermost part of the *Archaeorthis* interval, corresponding to 'assemblage 1' defined above, two macluritacean-dominated communities have been recognized: the macluritacean-pentamerid community and the macluritacean-*Archaeorthis* community. The former is constituted by similar percentages of planospiral gastropods and the new pentamerid *Parallelostrophia*, whereas the latter is dominated by macluritacean gastropods with *Archaeorthis* as a subordinate form. 'Assemblage 2' includes the macluritacean-*Archaeorthis*-*Orthidium* community, which is essentially similar to those from 'assemblage 1' but differs in the addition of low percentages of *Orthidium prominens* n. sp. A rather different set of communities occurs in 'assemblage 3', which is characterized by the sudden addition of several new brachiopod taxa. All of these communities are broadly dominated by planospiral gastropods but differ from each another in the relative dominance of *Nothorthis marginata crassicosta* n. subsp., *Archaeorthis sanroquensis* (Herrera and Benedetto), *T.* (*Tritoechia*) *prima* n. sp., *T.* (*Parvitritoechia*) *preandina* n. subgen. et sp., and *Orthidium prominens* n. sp. 'Assemblage 4', as stated above, includes only calcified fossils. Cech and Carrera (2002), in their study of the benthic communities from the upper *Archaeorthis* Zone at the Niquivil section, showed that this interval is dominated by *Ranorthis niquivilensis* Benedetto, and distinguished the *Fisherites*-*Ranorthis* and *Ranorthis* communities. 'Assemblage 5' is marked by a significant change in taxonomic composition and community structure (Sánchez *et al.*, 1999; Cech and Carrera, 2002). At these levels, illaenid trilobites become gradually dominant, and sponges and brachiopods attain higher values of diversity and abundance than in the underlying communities. The two communities recognized within the assemblage 5, the *Illaenus-Psarodictyum* community and the *Illaenus-Fisherites-Rhopalocoelia* community, include illaenomorph trilobites (supposedly temporary filter-feeders, Brenchley and Harper, 1998), a variety of demosponges (e.g. *Allosacus*, *Psarodictyum*, *Rhopalocoelia*, *Archaeoscyphia*, anthaspidellids, streptosolenids) and brachiopods (*Ranorthis niquivilensis*, *Paralenorthis* sp., *Tritoechia* sp., *Leptella* cf. *alata* Benedetto and Herrera, *Orthidium* sp., *Hesperonomia* sp., *Hesperonomiella* sp., and other forms not yet determined).

In summary, the *Archaeorthis* Zone starts with low-diversity and low-abundance communities, often dominated by one species, and ended with more diverse, biologically-accommodated communities. The basal communities were disrupted by storm events and typical opportunistic species such as *Archaeorthis sanroquensis* became dominant. The pentamerid-dominated communities recovered from the channel and intermound facies, as well as the *Archaeorthis*-dominated assemblages from the overlying whole-fossil wackestones, flourished in the high-energy shallow water settings prevailing at the beginning of the late Tremadoc-early Arenig transgressive event (Benedetto, 2000). The subsequent increase in number of guilds, and hence ecospace occupation, upwards in the succession seems to be correlated with the more stable environmental conditions resulting from the gradual deepening of the basin through the *Archaeorthis* Zone. The maximum flooding was attained at the transition between the *Archaeorthis* and the *Huacoella* zones (Cañas, 1999; Carrera *et al.*, 1999).

Systematic palaeontology

(by J. L. Benedetto)

Type and figured specimens examined in this study are deposited in the Palaeontologic Collection of the Cátedra de Estratigrafía y Geología Histórica / Cátedra de Paleontología (Escuela de Biología), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, prefix CEGH-UNC.

Order ORTHIDA Schuchert and Cooper, 1932
Suborder ORTHIDINA Schuchert and Cooper, 1932
Superfamily ORTHOIDEA Woodward, 1852
Family ORTHIDIELLIDAE Ulrich and Cooper, 1936

Genus ***Orthidium*** Hall and Clarke, 1892

Type species. *Orthis gemmicula* Billings, 1862.

Orthidium prominens n. sp.

Figures 3.A-I

Holotype. A dorsal valve, CEGH-UNC 20776.

Paratypes. 13 ventral valves and 10 dorsal valves, CEGH-UNC 20777-20799.

Derivation of name. Refers to the prominent cardinal process.

Type locality and type stratum. Cerro Cumillango section, base of the San Juan Formation, level 7.

Occurrence. Cerro Cumillango section, levels 4, 6, 7; Cerro San Roque section, levels 5, 7, 8, 11, 12. Cerro La Silla, level L4.

Diagnosis. Small, dorsibiconvex shells of *Orthidium* with 7-8 costellae per mm crossed by impersistent, regularly-spaced concentric lamellae; ventral interarea proportionally high, curved; high, triangular median plate bearing a very high, blade-like cardinal process flanked by low ridges; dorsal muscle field large, subpentagonal divided by a prominent median ridge.

Description. Shell small, ventribiconvex, semielliptical in outline, average width 4.4 mm, average length 4.1 mm (ventral valves) and 3.65 mm (dorsal valves); length/width ratio of ventral valves 0.97, dorsal valves 0.86. Hinge line straight, slightly shorter than maximum width. Cardinal extremities perpendicular or slightly obtuse. Ventral valve moderately to strongly convex, 40-45 % as deep as wide, often with a shallow sulcus on the anterior third of valve. Ventral interarea curved, relatively high, 15-18 % as high as wide, apsacline. Delthyrium large, nearly equidimensional, unmodified. Dorsal valve gently convex, with well-defined median sulcus extending from beak to anterior margin; lateral areas swollen and convex. Dorsal interarea very low, parallel-sided, anacline. Ornament multicostellate with 7-8 costellae per mm, crossed by impersistent, regularly-spaced concentric lamellae.

Ventral interior with relatively large, suboval, dorsoventrally flattened teeth bearing small crural fossettes on their inner faces. Dental plates short, strongly receeding, continuous anteriorly with low ridges outlining subtriangular muscle field, extending anteriorly for about 1/3 of valve length; anterior margin nearly straight, variably raised on valve floor. Diductor muscle scars narrow, parallel-sided, flanking broad, weakly concave median adductor area. Vascula media straight, narrow, widely separated each another, diverging from anterior ends of diductor scars.

Dorsal interior with high, triangular, postero-ventrally directed, median plate located between brachiophores, fused laterally with inner sides of sockets; cardinal process arising on the top of plate as a very high, slender blade flanked by low ridges simulating a trilobate structure. Sockets deep, semiconical, posteriorly excavated beneath hinge line. Brachiophores long, blade-like, ventrally directed. Dorsal muscle field large, subpentagonal, occupying about 60 % of valve length, divided longitudinally by a prominent median ridge. Adductor muscle scars deeply impressed, anterior pair elongate, much larger than the suboval posterior pair.

Remarks. The new species resembles the type species *O. gemmiculum* (Billings) in its small size, number of costellae and slightly marked growth lamellae, but its outline is less transverse, the maximum shell width is located anterior to hingeline and the ventral valve frequently bears a median sulcus, absent in the type species. Internally *O. prominens* n. sp. differs in its much higher and slender cardinal process. In shell proportions the Precordilleran species is similar to *O.* cf. *gemmiculum* from the Irish Tourmakeady Limestone, although in the latter the growth lamellae tend to be more prominent and the cardinal process is a massive, tongue-shaped structure. *Orthidium bellulum* Ulrich and Cooper, from Canadian rocks of Nevada, differs from *O. prominens* n. sp. in its greater size, more transverse shell outline and stronger and more spaced growth lamellae. In its narrower shell outline, strong ventral valve convexity and ornament, the new species *O. prominens* is very similar to *O. barnesi* Ross, from the Whiterock *Orthidiella* Zone of Nevada (Ross, 1970), from which it differs in having a less convex dorsal valve and higher, blade-like cardinal process. *Orthidium fimbriatum* Cooper resembles *O. prominens* in its sulcate ventral valve but differs in being more transverse and in having stronger growth lamellae. However, as internal features have not been illustrated in Cooper's monograph, both species cannot be compared in detail. The specimens referred to *Orthidium* sp. (Benedetto, 2001a) from late Arenig (*Monorthis* Zone) levels of the San Juan Formation are often longer than wide and have an unusually high ventral interarea. The Llanvirn species *O. geniculatum* Herrera and Benedetto can be distinguished from *O. prominens* by having more transverse outline and well-defined, ventrally directed geniculation.

Superfamily PLECTORTHOIDEA Schuchert and LeVene, 1929

Family RANORTHIDAE Havlíček, 1949

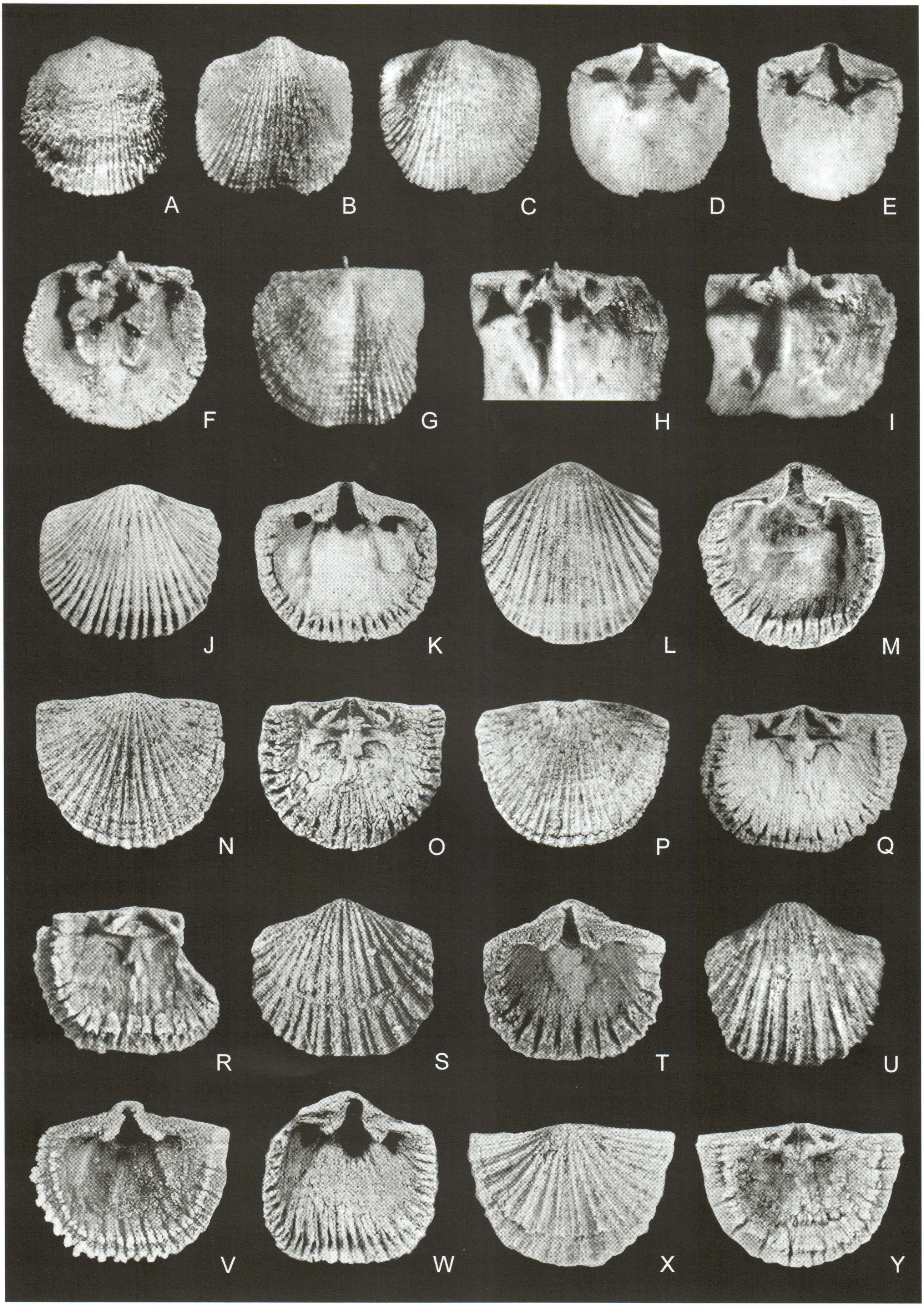
Genus *Nothorthis* Ulrich and Cooper, 1938

Type species. *Nothorthis delicatula* Ulrich and Cooper, 1938, p. 106, pl. 17c, figs. 6-14.

Nothorthis marginata n. sp.

Figures 3.J-Q

2001a. *Nothorthis* sp. Benedetto, figs. 4A-D.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Holotype. A dorsal valve, CEGH-UNC 20744, from the Cerro San Roque section, level 11.

Paratypes. 11 ventral valves and 13 dorsal valves, CEGH-UNC 20745-20748 and 20851-20860, from the Cerro San Roque section.

Derivation of name. Refers to the dorsal marginal thickening.

Type locality and type stratum. Cerrro San Roque section, base of the San Juan Formation, level 11.

Diagnosis. Planoconvex, semielliptical species of *Nothorthis* with 8-9 subangular costellae per 3 mm and well-defined dorsal sulcus; median ridge short, extending anteriorly 30-40 % of valve length; cardinal process generally absent, occasionally represented by a faint low ridge; dorsal muscle field strongly impressed; interior of dorsal valve with well-defined subperipheral ridge.

Description. Shell planoconvex, small, up to 6.3 mm wide, generally 5.5-6.0 mm wide, with average length/width ratio 0.74 in dorsal valves and 0.94 in ventral ones. Outline semielliptical. Cardinal extremities right-angled to slightly acute. Ventral valve strongly and evenly convex, averaging 45 % as deep as wide. Ventral interarea approximately 20 % as high as wide, slightly curved below the umbo, orthocline to weakly apsacline; delthyrium narrow, higher than wide, completely open. Dorsal valve posteriorly gently convex; broad sulcus originating near the umbo becoming wider and deeper anteriorly. Anterior commissure broadly uniplicate. Dorsal interarea very low, planar, steeply anacline to catacline. Notothyrium small, open. Ornament ramicostellate, formed by angular costellae subequal in size, in number of 8-9 per 2 mm measured at valve midlength.

Ventral interior with teeth plate-like, subtriangular, bearing well-developed crural fossettes; dental plates poorly defined. Muscle field short, rounded anteriorly, confined to the deep delthyrial cavity, slightly raised on valve floor, extending anteriorly 20-25 % valve length. Individual muscle scars undifferentiated. Vascula media narrow, widely separated from each another, diverging forward slightly.

Dorsal interior with brachiophores proportionally long, flattened distally, diverging anteriorly at about 100º-110º, bounding deep, semiconical sockets floored in their anterior portions by well-developed fulcral plates. Notothyrial platform low, triangular in outline, gently concave, merged with a median ridge initially broad and flat narrowing rapidly forward to disappear at about 30-40 % of valve length. Cardinal process generally absent; only 2 of 26 valves possess a faint, low ridge occupying the entire length of the notothyrial platform (figure 3.N). Dorsal muscle field large, extending anteriorly to midlength or slightly beyond; posterior adductor pair strongly impressed, ovate, buttressed posteriorly by thick shell deposits; anterior pair roundly triangular, their posterior portions wedged between the median ridge and the inner side of the posterior impressions, a short oblique ridge dividing the two pairs. Internal surface of valve with well-defined subperipheral ridge.

Remarks. The genus *Nothorthis* was erected by Ulrich and Cooper (1938) to include small transverse orthids with a premuscular thickening in the ventral valve, long brachiophores and incipient ridge-like cardinal process. Although the presence of fulcral plates was not mentioned in the original diagnosis, they were described by Rubel (1961) in the Estonian species *Nothorthis penetrabilis* and, as Havlíček (1977) noted, they also are evident in some specimens illustrated by Cooper (1956) in his Chazy brachiopods monograph. On the basis of this and other features (i.e. dorsal muscle pattern) Havlíček (1977) considered that *Nothorthis* and *Ranorthis* are closely related genera, which essentially differ by the absence of a cardinal process in the former. In the North American species *N. delicatula* Ulrich and Cooper and *N. transversa* Cooper, however, a thin cardinal process is often present. The new Precordilleran species *N. marginata* is referred to *Nothorthis* rather than to *Ranorthis* on basis of its relatively transverse shell outline and the nearly complete absence of the cardinal process.

Nothorthis is a common brachiopod in the lower part of the San Juan Formation. The Cerro San Roque specimens share some features with *Nothorthis termalis* (Herrera and Benedetto, 1989; Benedetto, 2001a), in particular the shell size and

Figure 3. A-I. ***Orthidium prominens*** n. sp., **A,** exterior of ventral valve / *exterior de valva ventral*, CEGH-UNC 20782, X7; **B,** exterior of ventral valve / *exterior de valva ventral,* CEGH-UNC 20778, X7; **C, D,** exterior and interior of ventral valve / *exterior e interior de valva ventral*, CEGH-UNC 20780, X7; **E,** interior of ventral valve / *interior de valva ventral*, CEGH-UNC 20779, X7; **F,** interior of dorsal valve / *interior de valva dorsal,* CEGH-UNC 2077, X8; **G, H, I,** dorsal valve, holotype / *valva dorsal, holotipo* CEGH-UNC 20776, exterior / *exterior* (X7), interior / *interior* (X9) and interior oblique view / *y vista interior oblicua* (X9). **J-Q.** ***Nothorthis marginata*** n. sp. **J, K**, exterior and interior of ventral valve / *exterior e interior de valva ventral*, CEGH-UNC 20745, X5; **L, M,** exterior and interior of ventral valve / *exterior e interior de valva ventral*, CEGH-UNC 20747, X5; **N, O,** exterior and interior of dorsal valve, holotype / *exterior e interior de valva dorsal, holotipo* CEGH-UNC 20744, X5; **P,** exterior of dorsal valve / *exterior de valva dorsal*, CEGH-UNC 29748, X5; **Q,** interior of dorsal valve / *interior de valva dorsal*, CEGH-UNC 20745. **R-Y,** ***Nothorthis marginata crassicosta*** n. subsp. **R,** interior of dorsal valve / *interior de valva dorsal*, CEGH-UNC 20752, X 7; **S, T,** exterior and interior of ventral valve / *exterior e interior de valva ventral,* CEGH-UNC 20751, X5,5; **U,** exterior of ventral valve / *exterior de valva ventral*, CEGH-UNC 20753, X6; **V,** interior of ventral valve / *interior de valva ventral*, CEGH-UNC 20757, X5,5;**W,** interior of ventral valve / *interior de valva ventral*, CEGH-UNC 20754, X5; **X, Y,** exterior and interior of dorsal valve, holotype / *exterior e interior de valva dorsal, holotipo* CEGH-UNC 20749, X6,5.

outline, number of costellae, cardinalia morphology and dorsal muscle scars pattern. The new species, however, differs in having less well-defined fasciculate ornament, stronger subperipheral thickening, and especially shorter dorsal median ridge, which in *N. termalis* is more prominent and reaches the peripheral thickening. Furthermore, the sporadic development of a low, ridge-like cardinal process in *N. marginata* also serves to distinguish the two species. *Nothorthis marginata* differs from the type species *N. delicatula* Ulrich and Cooper, from the Lévis Formation boulders of Quebec, in its less transverse outline, slightly coarser and somewhat fasciculate ornament, deeply impressed dorsal muscle field, and well-developed subperipheral thickening in the dorsal valve. The Caradoc species *N. tarda* Cooper shares with the Precordilleran species a strongly impressed dorsal muscle field, but differs in that it has a more convex dorsal valve and a more prominent dorsal median ridge, and it lacks a submarginal thickening. *Nothorthis transversa* Cooper, like other North American species, clearly differs from *N. marginata* in lacking submarginal rim and, in addition, in having much longer dorsal median ridge. The Estonian species *N. penetrabilis* Rubel has in common with *N. marginata* a similar dorsal muscle field and an incipient thickening along the periphery of dorsal valve (*cf.* Rubel, 1961, pl. 12, fig. 5), but the latter is less prominent and closer to the valve margin than in *N. marginata*. Additionally, in the Precordilleran species the dorsal sulcus is wider and deeper and the dorsal median ridge is relatively longer than in *N. penetrabilis*.

Nothorthis marginata crassicosta n. subsp.

Figures 3.R-Y, 4.A-D

2001b. *Nothorthis termalis* (Herrera and Benedetto), pl. 1, figs. 40-42 (non figs. 32-39) .

Holotype. A dorsal valve, CEGH-UNC 20749.

Paratypes. 12 ventral valves and 14 dorsal valves, from the Cerro Cumillango section, levels 5, 6 and 7, CEGH-UNC 20750-20775; 1 ventral valve and 2 dorsal valves from the Cerro La Silla section, level 3c-2 (equivalent to L2), CEGH-UNC 17849-17851.

Derivation of name. From the Latin *crassus*, coarse and costae, ribs.

Type locality and type stratum. Cerro Cumillango section, base of the San Juan Formation, level 7.

Occurrence. Lower part of the San Juan Formation, Cerro Cumillango section, levels 5, 6 and 7; Cerro La Silla, level L2.

Diagnosis. Small, semielliptical shells; ornament ramicostellate with tendency to fasciculation, formed by 14-16 primary angular costellae enlarged distally; ventral valve often with subperipheral thickening; dorsal valve with short and broad dorsal median ridge and sharp subperipheral rim; cardinal process variably developed, present in approximately one third of specimens.

Description. Shell semielliptical, planoconvex, small, up to 7.1 wide, with average length / width ratio 0.70 in dorsal valves and 0.97 in ventral valves. Cardinal extremities generally perpendicular, slightly acute in small valves. Ventral valve strongly and evenly convex, averaging 50% as deep as wide in larger specimens. Ventral interarea approximately 20% as high as wide, normally orthocline; delthyrium narrow, slightly higher than wide, open. Dorsal valve gently convex in posterior one third, becoming shallowly concave anteriorly due to the development of a broad median sulcus originating near the umbo. Anterior commissure broadly uniplicate. Dorsal interarea very low, planar, steeply anacline to catacline. Ornament ramicostellate with tendency to fasciculation, formed by 14-16 primary angular costellae enlarged and dichotomized distally, numbering 5-6 in 2 mm measured at valve midlength.

Ventral interior with vestigial dental plates. Delthyrial cavity deep. Ventral muscle field moderately raised on valve floor, with roundly acute anterior margin, extending anteriorly for about 30-40 % valve length. Internal surface of larger specimens often bearing a submarginal thickening. Vascula media narrow, straight, widely separated and slightly diverging anteriorly.

Dorsal interior with brachiophores proportionally long, flattened distally, diverging anteriorly at about 100º-110º, bounding deep semiconical sockets floored in their anterior portions by well-developed fulcral plates. Notothyrial platform low, triangular in outline, slightly concave. Dorsal median ridge short and broad, generally masked by shell deposits in front of the notothyrial platform. ridge. Cardinal process variably developed, present in approximately 1/3 of sample (12 of 38 available specimens); when present varying from almost imperceptible to a low, acute ridge slightly expanded anteriorly. Dorsal muscle field large, generally poorly impressed, extending anteriorly slightly beyond the midlength; posterior adductor pair ovate, smaller than the subtriangular anterior ones; anterior and posterior adductor scars separated by a short oblique ridge. Submarginal thickening sharp, developed along the entire valve margin.

Remarks. At first sight, the Cerro Cumillango specimens appear relatively similar to *Nothorthis marginata* n. sp. in dimensions, proportions and internal features. However, the Cerro Cumillango sample, herein recognized as a different subspecies, differs externally in having, in average, coarser ornament and more defined fascicostellae, especially near the margins. Internally *N. marginata crassicosta* n. subsp. differs in having broader and weaker dorsal ridge and an incipient submarginal thickening in the ventral valve; the latter feature, however, may also occasionally be present in *N. m. marginata*. Moreover, in the new subspecies the proportion of specimens bearing cardinal process is higher than in *N. marginata*. When present, it varies from an almost imperceptible median ridge to a low, anteriorly thickened ridge, its development being independent of shell size. The presence of a cardinal process has been regarded as one of the diagnostic features that differentiate *Ranorthis* from *Nothorthis* (Havlícek, 1977), so that in this respect *N. m. crassicosta* appears to be intermediate between the two genera. Since in some North American species of *Nothorthis* (i.e. *N. transversa* Ulrich and Cooper) an incipient cardinal process may also be sporadically present, this feature itself is not conclusive for generic distinction. The shell outline, defined as elongate semi-oval in *Ranorthis* and transversely semioval in *Nothorthis*, also is somewhat variable in species of both genera, even though it tends to be more transverse in *Nothorthis*. It appears that ornament, fasciculate in *Ranorthis* and ramicostellate in *Nothorthis*, is a more stable feature to differentiate the two genera. In this respect, the Cumillango specimens are more similar to *Ranorthis*. The species *N. termalis* (Herrera and Benedetto), recently re-described by Benedetto (2001a), differs from *N. marginata crassicosta* n. subsp. in its finer ornament, much longer and prominent dorsal median ridge and in lacking a cardinal process. In a number of features (i.e. shell outline, number of costellae, degree of fasciculation, development of cardinal process) the Cumillango subspecies is intermediate between *N. m. marginata* and *Ranorthis cumillangoensis* Benedetto. The latter, recorded from slightly younger horizons of the San Juan Formation (Benedetto, 2002), is nearly identical to *N. marginata crassicosta* in size and ornament, but differs in the more elongate shell outline and especially in that the dorsal median ridge reaches the marginal thickening, which usually is strongly elevated medially simulating the platform of plectambonitoids. In the few available dorsal interiors of *R. cumillangoensis* the cardinal process is always well defined, but the sample is too small to assess its size variations and frequency of apparition.

As previously pointed out (Benedetto, 2002) it seems likely that *Ranorthis cumillangoensis* was derived from *N. termalis*, and that *N. marginata* (lacking fascicostellate ornament, short dorsal ridge) was the ancestral species of this lineage. However, in the pattern of ornamentation and frequency of presence of the cardinal process the new subspecies *N. m. crassicosta* is more closely allied to *R. cumillangoensis* than to *N. marginata*. The ambiguity in the phylogenetic relationships of the Argentine species of *Nothorthis* and *Ranorthis* may be due to mosaic evolution originated by the decoupling of the rate and time at which the cardinal process appears, as well as the degree of development of both the dorsal median ridge and peripheral thickening.

Order BILLINGSELLIDA Schuchert, 1893
Suborder CLITAMBONITIDINA Öpik, 1934
Superfamily POLYTOECHIOIDEA Öpik, 1934
Family TRITOECHIIDSE Ulrich and Cooper, 1936

Genus ***Tritoechia*** Ulrich and Cooper, 1936

Type species. *Deltatreta typica* Schuchert and Cooper, 1932.

Subgenus ***Tritoechia* (*Parvitritoechia*)** nov. subgen.

Type species. *Tritoechia* (*Parvitritoechia*) *preandina* n. subgen. et n. sp.

Etymology. Refers to the parvicostellate ornament.

Diagnosis. Subgenus of *Tritoechia* with well-defined parvicostellate ornament over entire shell surface formed by a few accentuated ribs separated by numerous weaker, subequal intercostal ribs. Hollow costellae and aditicules lacking. Internal features similar to *Tritoechia*.

Species assigned. *Antigonambonites pyramidalis* Bates (1968), pl. 6, figs. 12-18, Treiorwerth Formation, Arenig, Wales. This species was subsequently assigned to *Tritoechia* by Neuman and Bates (1978), pl. 64, figs. 39-49. *Tritoechia* sp. B (Benedetto, 2001b, figs. 3L-N) from the volcano-sedimentary rocks exposed at the Vega Pinato locality, western Puna region, Argentina.

Remarks. The external ornament was not mentioned in the original diagnosis of *Tritoechia* by Ulrich and Cooper (1936) (see also Ulrich and Cooper, 1938) but Williams and Wright (1965), in the first edition of the *Treatise*, stated that this genus possesses a multicostellate ornament with hollow costellae. In the revised edition, Rubel and Wright (2000) added to the diagnosis the presence of aditicules. In fact, in the about thirty five known species of *Tritoechia* the radial ornament varies from equally or subequally multicostellate to subequally parvicostellate. The ornament, in some species (i.e. *T. crassa* Popov *et al.*, 2001) has been described as unequally parvicostellate, but since addition of new costellae occurs by both intercalation and branching it appears as unequally multicostellate. We propose to erect the new subgenus *Tritoechia* (*Parvitritoechia*) to include tritoechiids with well-defined, unequally parvicostellate ornament over the entire shell consisting of a few prominent, widely spaced ribs separating intercostal sectors bearing numerous weaker, subequal costellae. Furthermore, *Tritoechia* (*Parvitritoechia*) differs from

Tritoechia (*Tritoechia*) in lacking aditicules and hollow costellae, both features being well developed in the type species *T. typica* (Schuchert and Cooper). Otherwise, the new subgenus *T.* (*Parvitritoechia*) is essentially similar to *T.* (*Tritoechia*), especially in the internal morphology. The markedly parvicostellate ornament of the Irish genus *Acanthotoechia* Williams and Curry (1985) is like that of *T.* (*Parvitritoechia*), but differs in having rows of cylindrical hollow spines on both accentuated and intermediary ribs.

Among described species of *Tritoechia*, only the Welsh *T. pyramidalis* (Bates) can be confidently ascribed to *T.* (*Parvitritoechia*). The specimens referred to *Tritoechia* sp. from the Arenig Vega Pinato volcaniclastic succession of northwestern Argentina, even though poorly preserved, are very similar in ornament to the Welsh species and therefore they are also re-assigned to the new genus. In the Tasmanian species *Tritoechia lewisi* Brown young specimens are initially unequally parvicostellate but with growth become definitely multicostellate (Brown, 1948; Laurie, 1980); its assignment to *Tritoechia* (*Tritoechia*) is supported here.

Tritoechia* (*Parvitritoechia*) *preandina n. sp.

Figures 4.N-X

Holotype. A silicified ventral valve, CEGH-UNC 20901.

Paratypes. 3 fragmentary ventral valves and 2 dorsal valves from the Cerro San Roque section, level 11, CEGH-UNC 20902-20906; 4 ventral exteriors and 2 dorsal exteriors from the Cerro la Silla section, level 3c2 (L2), CEGH-UNC 20907-20912: 2 incomplete exteriors of dorsal valve, Cerro Cumillango section, level 10, CEGH-UNC 20915-20916; 2 exteriors of ventral valve, Niquivil (north) section, CEGH-UNC 20913-20914.

Derivation of name. Refers to the pre-Andean location of the Precordillera mountain belt.

Type locality and type stratum. Lower part of the San Juan Formation (lower part of the *Archaeorthis* Zone), Cerro San Roque section, level 11.

Occurrence. Lower part of San Juan Formation. Cerro San Roque, levels 11 and 12; Cerro La Silla, levels L2 and L8, Niquivil, levels 1-3; Cerro Cumillango, level 10.

Diagnosis. Medium-sized, transversely semielliptical shells with moderately convex ventral valve and gently convex, shallowly sulcate dorsal valve. Ventral interarea about 15% as high as wide. Ornament markedly parvicostellate formed by 8-12 widely-spaced accentuated ribs separated by concave or V-shaped intercostal sectors bearing 5-10 subequal parvicostellae.

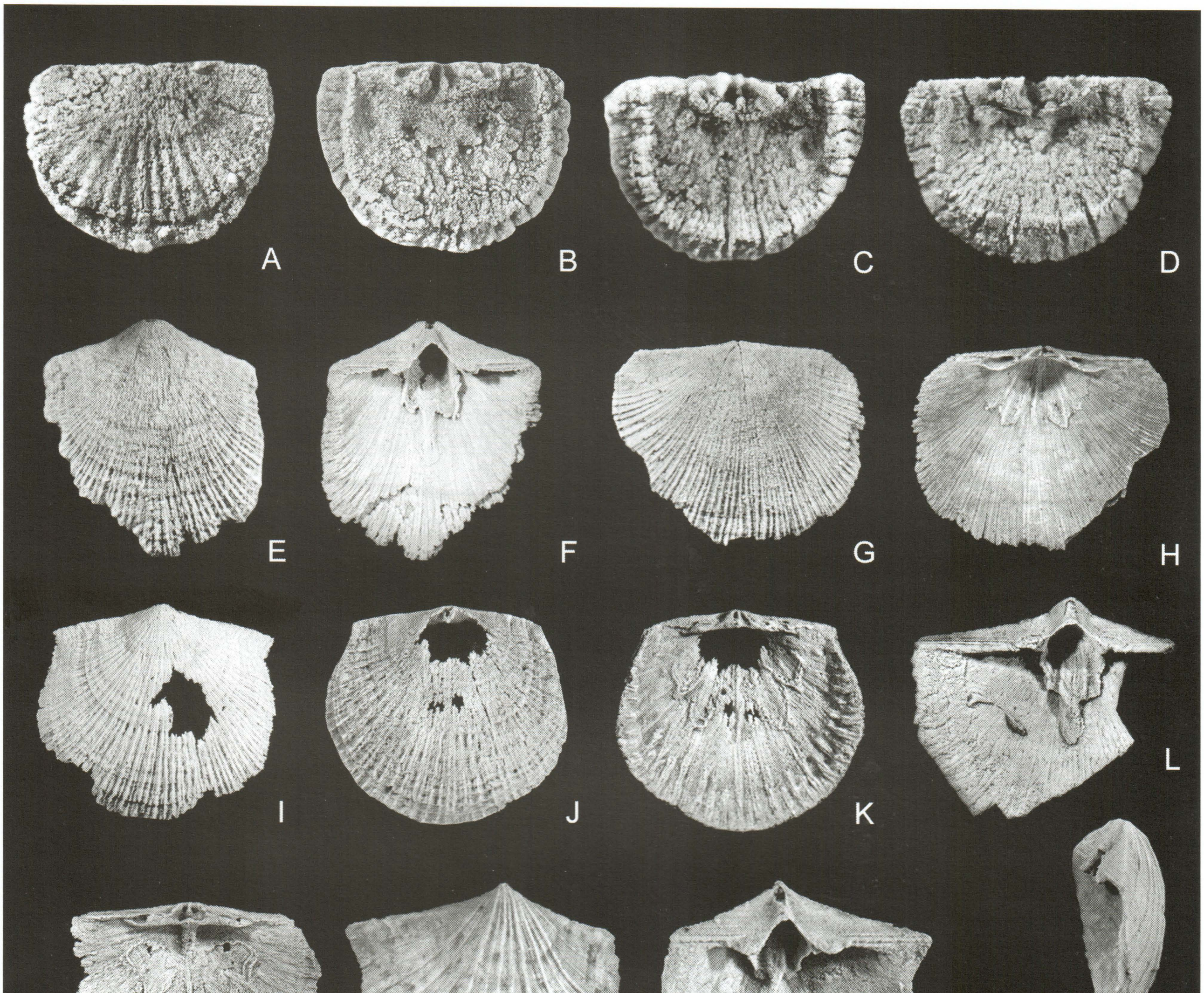
Description. Shell medium-sized, up to 21 mm wide, semielliptical, slightly wider than long (average length/width ratio 0.77), widest at hinge; cardinal extremities acute, slightly auriculate. Anterior commissure rectimarginate. Ventral valve moderately and evenly convex, maximum thickness at the posterior third. Beak pointed, weakly incurved. Ventral interarea apsacline, relatively low, planar, about 15% as high as wide, forming with the commissural plane an angle of about 40º. Delthyrium partially closed by semiconical, apically perforated pseudodeltidium. Dorsal valve gently convex, with shallow median sulcus. Dorsal interarea planar, about a half as high the ventral, strongly anacline to orthocline. Notothyrium bounded by high chilidial plates joined near the apex. Chilidium not preserved.

Parvicostellate ornament formed by 8-12 widely-spaced, prominent ribs; intercostal sectors concave, often V-shaped, bearing 5-10 weaker, rounded subequal parvicostellae; in some specimens one or rarely two of them may become somewhat more marked near the anterior margin. Hollow ribs lacking.

Ventral interior with broad, plate-like teeth bearing well-developed, subtriangular crural fossettes. Pedicle callist prominent. Dental plates thick, long, slightly converging toward the valve floor and prolonged anteriorly by low ridges bounding the muscle field which extends anteriorly up to 1/3 of valve length. Adductor track impressed on high, flat-topped median ridge, in some specimens prolonged a short distance beyond the muscle field; diductor scars narrow, parallel-sided, as long as the adductors, impressed on concave areas flanking the median ridge. Vascular system not impressed.

Dorsal interior with subtriangular, posteriorly inclined notothyrial platform. Cardinal process simple,

Figure 4. A-D. *Nothorthis marginata crassicosta* n. subsp. **A, B,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal*, CEGH-UNC 20750, X5,5; **C,** interior of dorsal valve / *interior de valva dorsal*, CEGH-UNC 20762, X6; **D,** interior of dorsal valve / *interior de valva dorsal,* CEGH-UNC 20763, X5,5. **E-M. *Tritoechia* (*Tritoechia*) *prima*** n. sp. **E, F,** exterior and interior of ventral valve / *exterior e interior de valva ventral*, CEGH-UNC 20919, X2; **G, H,** exterior and interior of dorsal valve, holotype / *exterior e interior de valva dorsal, holotipo* CEGH-UNC 20917, X2; **I,** exterior of ventral valve / *exterior de valva ventral,* CEGH-UNC 20918, X2; **J, K,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal,* CEGH-UNC 20921, X2,25; **L,** interior of ventral valve / *interior de valva ventral,* CEGH-UNC 20927, X2; **M,** interior of dorsal valve / *interior de valva dorsal,* CEGH-UNC 20922, X2,25. **N-X. *Tritoechia* (*Parvitritoechia*) *preandina*** n. subgen. et sp. **N, O, P, Q**, ventral valve, holotype / *valva ventral, holotipo* CEGH-UNC 20901, exterior, interior, lateral and posterior views / *vistas exterior, interior, lateral y posterior,* X3,5; **R,** latex cast of fragmentary exterior of ventral valve / *molde de latex de exterior fragmentario de valva ventral*, CEGH-UNC 20906, X2; **S,** exterior of ventral valve / *exterior de valva ventral*, CEGH-UNC 20908, X2; **T,** exterior of ventral valve / *exterior de valva ventral,* CEGH-UNC 20909, X2; **U, V**, exterior and interior of fragmentary dorsal valve / *exterior e interior de valva dorsal fragmentaria,* CEGH-UNC 20902, X5: **W, X,** exterior and interior of fragmentary dorsal valve / *exterior e interior de valva dorsal fragmentaria*, CEGH-UNC 20903, X4.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ridge-like, thickened anteriorly. Dental sockets deep, semiconical, bounded by high, blade-like, widely-divergent socket ridges. Median ridge very short and thick, merged with the base of the notothyrial plataform. Dorsal muscle field subcircular in outline, marked by a peripheral ridge. Adductor scars radially arranged. Vascular system not preserved.

Discussion. The new Precordilleran species *Tritoechia* (*Parvitritoechia*) *preandina* differs from *T.* (*P.*) *pyramidalis* Bates in having concave, V-shaped intercostal areas giving to the valve surface an undulating aspect. In addition, *T.* (*P.*) *pyramidalis* can be distinguished by its more inclined, steeply apsacline ventral interarea and shorter and less divergent socket ridges. The specimens referred to *Tritoechia* sp. B from the Vega Pinato volcaniclastic rocks (Benedetto, 2001b) seem to be more closely related to the Welsh *T.* (*P.*) *pyramidalis* than to *T.* (*P.*) *preandina*, but available material is too limited to make accurate comparisons.

Tritoechia* (*Tritoechia*) *prima n. sp.

Figures 4.E-M

Holotype. A dorsal valve CEGH-UNC 20917.

Paratypes. 3 ventral valves and 3 dorsal valves from the Cerro San Roque section, level 11, CEGH-UNC 20918-20923; 1 ventral valve, 2 dorsal valves and several fragmentary valves from the Cerro Cumillango section, levels 5, 6, 7 and 8, CEGH-UNC 20924-20926; 1 ventral valve, Cerro La Silla section, level L2, CEGH-UNC 20927.

Derivation of name. From the Latin *primus*, first, denoting that this species represents the first appearance of *Tritoechia* in the San Juan Formation.

Type locality and type stratum. Lower part of the San Juan Formation (lower *Archaeorthis* Zone), Cerro San Roque section, level 11.

Occurrence. Lower part of San Juan Formation. Cerro San Roque, levels 11 and 12; Cerro La Silla, level L2, Cerro Cumillango, levels 5-8; Niquivil, levels 1-3.

Diagnosis. Medium-sized, semielliptical, slightly auriculate shells of *Tritoechia* with a moderately convex ventral valve; ventral interarea about 28 % as high as wide, apsacline, forming with the commissural plane an angle of 30º-40º. Multicostellate ornament formed by 9-12 subequal costellae per 3 mm. Ventral muscle field subrectangular extending up to 1/3 of valve length. Notothyrial platform narrowly triangular flanked by strong chilidial plates, supported by short median septum confined to the depression beneath the notothyrial platform.

Description. Shell medium-sized, up to 16 mm wide, semielliptical, slightly wider than long (average length/width ratio 0.91). Maximum width located between 1/3 and 1/2 of valve length. Cardinal extremities slightly auriculate. Anterior commissure rectimarginate to gently uniplicate. Ventral valve moderately and evenly convex, the maximum height at about 1/3 of valve length. Interarea plane, apsacline, about 28% as high as wide, forming with the commissural plane an angle of 30º-40º. Delthyrium covered by a strongly arched semiconical pseudodeltidium bearing a relatively large apical foramen. Dorsal valve gently convex, often with a very shallow sulcus on the anterior third. Dorsal interarea very low, planar, anacline. Notothyrium flanked by a pair of strong ridge-like chilidial plates.

Ornament multicostellate with two or three generations of costellae added by intercalation, rarely by branching, varying in number from 9 to 11 per 3 mm on the anterior third of valve. Concentric growth lamellae well defined towards the anterior margin.

Ventral interior with small plate-like teeth supported by high, short dental plates subparallel or slightly convergent to each another. Muscle field subrectangular, bounded laterally by ridge-like prolongations of dental plates, extending anteriorly up to 1/3 of valve length; narrow diductor scars divided longitudinally by a flat-topped, moderately raised median adductor track. Rounded, variably developed median ridge, fading at mid-length of the valve.

Dorsal interior with simple blade-like cardinal process. Notothyrial platform narrowly triangular flanked by chilidial plates, overhanging anteriorly; short median septum confined to the depression beneath the notothyrial platform. Sockets transversely elongate, deeply excavated below the interarea, bounded by slender, gently arched socket ridges. Muscle field wider than long, strongly impressed in mature specimens, formed by radially arranged petaloid adductor scars of about equal size, occasionally bisected by faint transmuscle septa. Median ridge narrow, fading at the anterior end of muscle field or slightly beyond. Dorsal mantle canals not impressed.

Discussion. The new species is similar to *T.* (*T.*) *delicatula* Ulrich and Cooper (1936) in shell size, height and inclination of ventral interarea, and muscle field morphology. The North American species can be distinguished by its more transverse shell outline, nonauriculate cardinal extremities and finer ornament. *Tritoechia* (*T.*) *prima* differs from the *T.* (*T.*) *gigas* Benedetto (2001a), from slightly younger strata of the Precordillera (mid-Arenig, *Huacoella* Zone), in being much smaller and in having a lower ventral interarea. In addition, *T.* (*T.*) *gigas* possesses radially ridged vascula genitalia. The two Llanvirn species from the San Juan Formation, *T. azulensis* Benedetto and *T. inaequicostata* Benedetto (1987) can readily be distinguished by their higher and strongly inclined ventral interaeas.

Order PENTAMERIDA Schuchert and Cooper, 1931
Suborder SYNTROPHIIDINA Ulrich and Cooper, 1936
Superfamily PORAMBONITOIDEA Davidson, 1853
Family SYNTROPHIIDAE Schuchert, 1896

Genus ***Syntrophia*** Hall and Clarke, 1893

Type species. *Triplesia lateralis* Whitfield.

Syntrophia sanjuanina n. sp.
Figures 5.A-N

2001a. *Syntrophia* sp., Benedetto, p. 16, pl. 5, figs. 18-26.

Holotype. A dorsal valve, CEGH-UNC 20866.

Paratypes. 2 ventral valves and 2 dorsal valves from the Cerro San Roque, level 5, CEGH-UNC 20867-20870; a ventral valve from the Cerro San Roque, level 5, CEGH-UNC 20873; five conjoined valves, 3 ventral valves and 4 dorsal valves from the Cerro la Silla, level B, CEGH-UNC 18036-18047; 2 ventral valves and 5 dorsal valves from the Cerro La Silla, level L2, CEGH-UNC 20861-20865 and 20871-20872. 1 ventral valve and 4 dorsal valves from the Cerro Cumillango section, levels 1 and 2, CEGH-UNC 20874-20878.

Derivation of name. After the San Juan Province.

Type locality and type stratum. San Juan Fomation, Cerro San Roque section, level 4.

Occurrence. Lowermost part of the San Juan Formation (lower part of the *Archaeorthis sanroquensis* Zone), Cerro San Roque section, levels 1 to 5; Cerro La Silla section, level L2 (= level B, Benedetto, 2001a); Cerro Cumillango section, levels 1b and 2.

Diagnosis. Medium-sized, subequally biconvex *Syntrophia* lacking fold and sulcus. Spondylium strongly elevated, spatulate, anteriorly free, averaging 62% as wide as long. Thick brachiophore bases strongly convergent medially to form a narrow and deep septalium prolonged anteriorly by a median ridge fading at about the mid-valve lengtht.

Description. Medium-sized, largest specimens up to 20 mm wide, subequally biconvex shells. Outline semielliptical, approximately as wide as long, the maximum width slightly anterior to the hinge; cardinal extremities rounded, obtuse; lateral and anterior margins uniformly rounded. Ventral valve moderately to strongly convex, averaging 35% as deep as long; maximum convexity at about the posterior third, evenly convex in both lateral and transversal profiles, without evidence of sulcus; anterior commissure nearly straight. Ventral interarea low, gently curved, apsacline. Dorsal valve moderately convex, of approximately equal convexity than ventral, lacking fold; dorsal interarea very low, curved, anacline. Exterior smooth, except for weak growth lines near margin.

Ventral interior with small triangular teeth supported by thick, slightly convergent dental plates forming the posterolateral walls of spatulate, strongly elevated, anteriorly free spondylium. In dorsal view the spondylium is subrectangular in outline averaging 62% as wide as long, their lateral margins are subparallel or slightly divergent anteriorly and the anterior margin is uniformly rounded. Posteriorly is supported by a thick and short median ridge merged with the posterior wall of the valve. Mantle canal system not preserved.

Dorsal interior with knob-like brachiophores supported by thick bases strongly convergent to the valve floor to form a narrow and deep septalium prolonged anteriorly by a median ridge fading at about the mid-valve lengtht. Fulcral plates well defined, forming floors of narrow, transversely elongated sockets. Dorsal muscle field commonly weakly impressed, in some large specimens well-impressed subquadrangular posterior adductor scars separated from anterior pair by a slightly oblique ridge.

Discussion. Previously few, relatively incomplete specimens from the Cerro La Silla section were assigned to *Syntrophia* and left in open nomenclature because of the lack of well-preserved ventral valves (Benedetto, 2001a). The new available best preserved material obtained from the Cerro Cumillango samples allows recognition of a new species of *Syntrophia* relatively similar to *Syntrophia torynifera* Ulrich and Cooper (1938), from the roughly contemporaneous Black Rock and Smithville formations of Arkansas. As in the North American specimens, the spondylium simplex is tongue-shaped, posteriorly sessile and almost free anteriorly. The key feature that distinguish the Precordilleran species from *S. torynifera* n. sp. is the relative convexity of the dorsal valve, which is approximately as deep as the ventral in *S. sanjuanina* whereas in the Canadian species it is markedly less convex than the ventral one. Moreover, *S. sanjuanina* can be distinguished by the somewhat less divergent and thickened brachiophore bases. In spondylium morphology it is more similar to *S. arethusa* (Billings), from the Lévis boulders of Quebec (Canada), but in the latter the septalium seems to be shorter and thicker than in *S. sanjuanina*. However, available data on shape and shell convexity of the Canadian species are not satisfactory for precise comparison. The type species *S. lateralis* (Whitfield), from the Arenig Cassin Formation of Vermont, differs from the Precordilleran form in the more transverse shell outline, in the incipient fold and sulcus, and internally in the much shorter spondylium and the less prominent and shorter dorsal septum. The Canadian species *S. longaeva* Ulrich and Cooper clearly differs in having well-defined fold and sulcus anteriorly and a smaller and more delicate septalium.

Family SYNTROPHIIDAE? Schuchert, 1931
Gen. et sp. nov.
Figures 5. W-Z

Material and occurrence. 8 fragmentary ventral and dorsal valves, CEGH-UNC 20928- 20935, from the upper part of the reef-mounds near the base of the San Juan Formation, late Tremadoc.

Description. Shell medium-sized, maximum width (inferred) of about 13 mm; exterior apparently smooth. Ventral valve slightly more convex than dorsal. Ventral interarea gently curved, about twice as high as the dorsal, with open, triangular delthyrium. Teeth short, thickened; dental plates receding, convergent, forming lateral margins of anteriorly strongly elevated spondylium, about a half as wide as long, supported by stout median ridge. Lateral apical cavities filled by secondary deposits. Dorsal interior with flattened brachiophores diverging from each other at about 70-80º; brachiophore bases discrete, short, slightly convergent toward valve floor but not united medially. Sockets shallow, subtriangular; fulcral plates, if present, masked by secondary deposits.

Discussion. The available material consists of several fragments and a few incomplete, coarsely silicified ventral and dorsal valves. Most specimens have damaged cardinal extremities and margins, and their outline and nature of anterior commissure cannot be determined. The tongue-shaped, anteriorly elevated spondylium supported by short median septum is similar to that of *Syntrophia*, but dorsal interiors differ from this genus in lacking evidence of septalium. In the reef-mound specimens, the cardinalia are orthid-like, with proportionally long, somewhat compressed brachiophores supported by short and separated plates. If a rudimentary septalium was developed by convergence of brachiophore supporting plates, it probably is masked by the thick secondary deposits filling the cavities beneath the fulcral plates. Despite the fact that this form is still poorly known, available morphological evidence is enough to consider it as a new genus. The spondylium morphology suggests a relationship with syntrophiids. If septalium originated by convergence and further union of brachiophore plates, the absence of this structure in the new genus may be considered as an ancestral condition in the syntrophiid lineage. Additional similarities in the brachiophore morphology as well as in the overall shell aspect (size, convexity, apparent absence of fold and sulcus, interareas morphology) support the view that this form may be a possible ancestor of *Syntrophia sanjuanina.*

Family Uncertain

Genus ***Parallelostrophia*** nov.

Type species. *Parallelostrophia septata* n. sp., by monotypy.

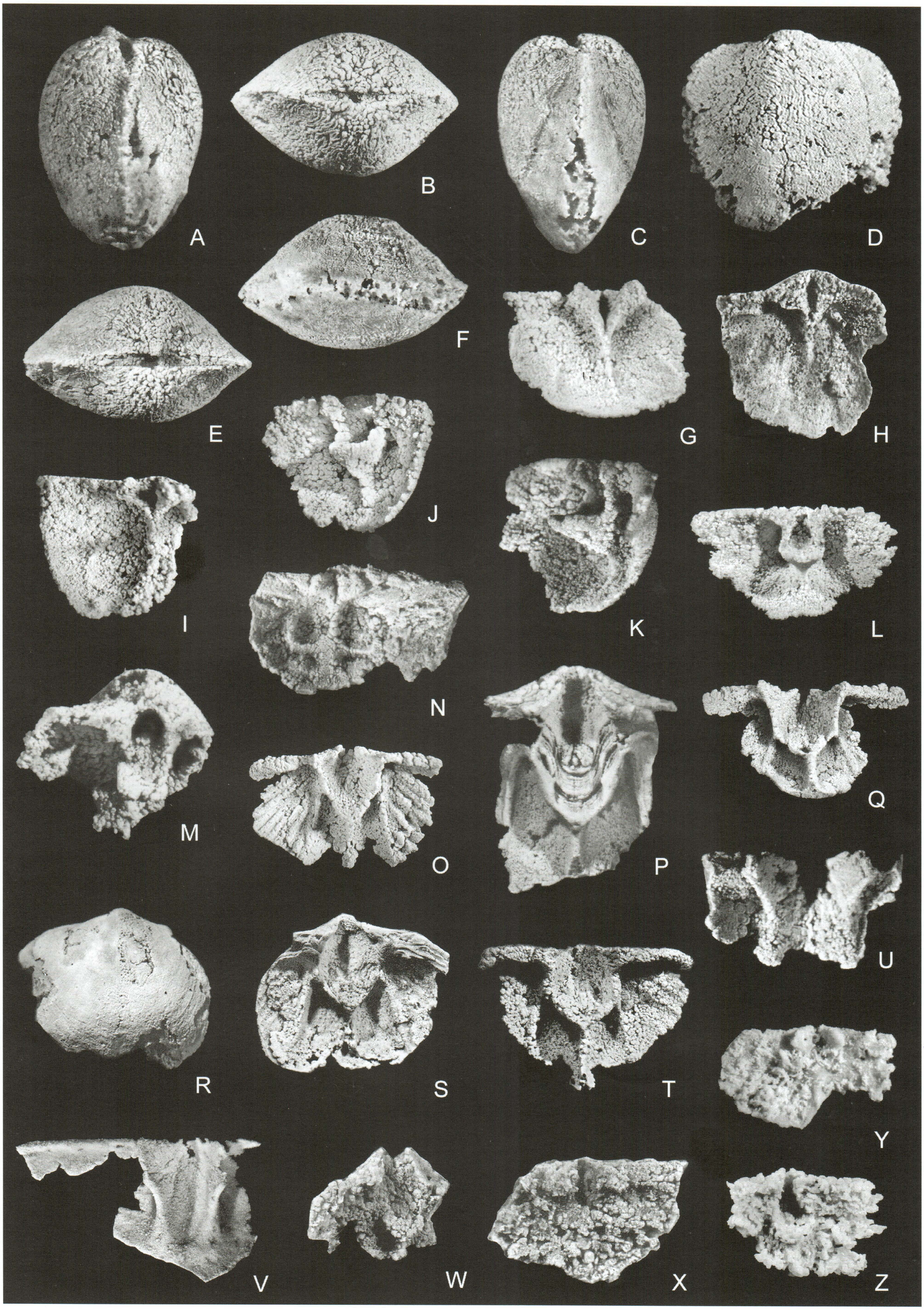
Etymology. Refers to the subparallel brachiophore plates.

Diagnosis. Medium-sized, ventribiconvex, externally smooth syntrophiidines lacking fold and sulcus. Ventral interarea proportionally high, strongly apsacline. Ventral interior with elevate spondylium supported by a high, long median septum and two shorter lateral septa; dorsal interior with long, initially convergent, then subparallel brachiophore bases.

Discussion. Although this pentamerid is very common through the lowermost part of the San Juan Formation, only a few fragmentary valves, most of them unsuitable for morphologic analysis, were obtained during the initial sampling along the Cerro la Silla section. This material was described as an unidentified genus tentatively referred to the family Syntrophopsidae (Benedetto, 2001a). With the new information available, based on more complete and better preserved ventral and dorsal valves, it is now evident that it represents a new genus characterized by a particular combination of features which has not been recorded previously in other syntrophidines.

The prominent spondylium supported by a high median septum is comparable to that of clarkellids and syntrophiids, but the presence of a pair of strong lateral septa simulating a spondylium triplex, and

Figure 5. A-N. ***Syntrophia sanjuanina*** n. sp. **A, B,** lateral and posterior views of conjoined valves / *vistas lateral y posterior de ejemplar articulado,* CEGH-UNC 18044, X2,5; **C, D, E, F,** lateral, ventral, posterior and anterior views of conjoined valves / *vistas lateral, ventral, posterior y anterior de ejemplar articulado,* CEGH-UNC 18045, X2,5; **G,** interior of dorsal valve, holotype / *interior de valva dorsal, holotipo* CEGH-UNC 20866, X2; **H,** interior of dorsal valve / *interior de valva dorsal* CEGH-UNC 20861, X2,25; **I,** interior of incomplete dorsal valve / *interior de valva dorsal incompleta* CEGH-UNC 18036, X3,25; **J, K, L**, anterior, lateral oblique and normal views of ventral interior / *vistas anterior, lateral oblicua y normal de interior de valva ventral*, CEGH-UNC 20867, X2; **M,** incomplete ventral valve, intenal view / *vista interna de una valva ventral incompleta,* CEGH-UNC 20868, X4; **N**, interior of dorsal valve / *interior de valva dorsal,* CEGH-UNC 18037, X3. **O-V.** *Parallelostrophia septata* n. gen et sp. **O,** interior of incomplete ventral valve / *interior de valva ventral incompleta,* CEGH-UNC 18510, X2; **P,** interior of incomplete ventral valve / *interior de valva ventral incompleta,* CEGH-UNC 20899, X2; **Q,** ventral valve, anterior oblique view / *vista anterior oblicua de valva ventral*, CEGH-UNC 20896, X2; **R, S,** exterior and interior of ventral valve, holotype / *exterior e interior de valva ventral, holotipo* CEGH-UNC 20899, X2; **T,** interior of ventral valve / *interior de valva ventral,* CEGH-UNC 20879, X2; **U,** interior of incomplete dorsal valve / *interior de valva dorsal incompleta,* CEGH-UNC 20880, X3; **V,** interior of dorsal valve / *interior de valva doral,* CEGH-UNC 20890, X4,5. **W-Z.** ***Syntrophiidae***? n. gen. et sp. **W,** interior of incomplete ventral valve /*interior de valval ventral incompleta*, CEGH-UNC 20928, X3; **X,** interior of dorsal valve / *interior de valva dorsal*, CEGH-UNC 20929, X3; **Y,** Interior of dorsal valve / *interior de valva dorsal,* CEGH-UNC 20930, X3; **Z,** interior of ventral valve / *interior de valva ventral*, CEGH-UNC 20932, X3.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the long and prominent dorsal septum constitute distinctive features of *Parallelostrophia*. The only genus possessing lateral septa is *Tetralobula* which clearly differs from *Parallelostrophia* in its radial ornament, well-developed fold and sulcus and short and strongly convergent brachiophore bases. The brachiophore plates in *Parallelostrophia* are initially convergent, becoming almost perpendicular to the valve floor and subparallel to each other. Such long, but not medially united brachiophore plates are only known in *Porambonites* and in members of the problematic family Parallelasmatidae. The new genus is immediately distinguishable from *Porambonites* in having a well-developed spondylium; externally it can be distinguished by its smooth surface and the absence of a fold and sulcus. The parallelasmatids *Paralleleasma* and *Didymelasma* differ in having subpentagonal or subtriangular shells with paucicostate to pauciplicate ornament and in lacking lateral septa supporting the spondylium.

The taxonomic affinities of the new genus *Parallelostrophia* are problematical. It shares some features with the tetralobulids (e.g. discrete brachiophore plates, spondylium supported on median septum butressed occasionally by a pair of lateral septa; fold and sulcus subdued), but its assignation to this family is not supported by the presence of long, subparallel brachiophore bases. The internal features of *Parallelostrophia* suggest affinities with the Parallelasmatidae, but members of this family are unique in having astrophic or short-hinged smooth shells becoming paucicostate or pauciplicate anteriorly.

Parallelostrophia septata n. sp.

Figures 5.O-V

2001a. Syntrophopsidae? gen. et sp. indet., Benedetto, p. 16, pl. 5, figs. 27-34.

Holotype. A ventral valve, CEGH-UNC 20900.

Paratypes. 7 ventral valves and 3 dorsal valves from the Cerro La Silla secion, level L2, CEGH-UNC 20880-20889; four ventral valves from the Cerro La Silla, level 2, CEGH-UNC 18510-18514 (some of these specimens were described and illustrated in Benedetto, 2001a), 5 ventral valves from the San Roque section, levels 4 and 5, CEGH-UNC 20896-20899; 5 ventral valves and 1 dorsal valve from the Cerro Cumillango section, levels 7 and 11, CEGH-UNC 20890-20895.

Derivation of name. Refers to the presence of prominent lateral septa.

Type locality and type stratum. San Juan Formation, Cerro San Roque section, level 4.

Occurrence. Restricted to the lowermost part of the San Juan Formation (lower part of the *Archaeorthis* Zone), Cerro San Roque section, levels 2, 4 and 5; Cerro La Silla section, level L2; Cerro Cumillango section, levels 1, 2 and 6.

Diagnosis. The same as for the genus.

Description. Shell medium-sized, up to 21 mm wide, subcircular in outline, unequally biconvex, with dorsal valve less convex than ventral. Hinge line straight, short, attaining about 2/3 of shell width (inferred, no complete valves available); anterior commissure not well preserved in available specimens, apparently rectimarginate. Ventral valve evenly and strongly convex, the maximum convexity at the posterior third, without evidence of sulcus. Ventral interarea relatively high, 30-40% as high as wide, curved, transversely striated, strongly apsacline; delthyrium very large, triangular. Dorsal valve uniformly curved; fold absent. Interarea half as high as the ventral, steeply anacline; notothyrium completely open, triangular. Shell surface smooth except for obscure fine radial striations observed on a single specimen.

Ventral interior with small, triangular teeth supported by thick plates slightly converging medially to form the lateral walls of a prominent, spoon-shaped spondylium, averaging 62% as wide as long; spondylium strongly elevated anteriorly, supported by a high, blade-like median septum flanked by a pair of well-defined lateral septa, commonly lower and shorter than the median one. The three septa extend beyond the front of spondylium, the median septum being the longest and more prominent, attaining at least the mid-valve length (no complete valves are available). Ventral muscle field with large diductor scars occupying most of spondylium and adductor field suboval or subtriangular located on the anterior end of spondylium. Areas between the lateral septa and the posterior margin radially ridged in some specimens.

Dorsal interior with plate-like, anteriorly divergent brachiophores with discrete supporting plates slightly convergent to the valve floor; brachiophore bases extend anteriorly as long, subparallel ridges. Sockets small, semiconical, erected on thin, small fulcral plates well elevated on valve floor. Adductor field not discernible.

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