An outer-ramp brachiopod assemblage from the uppermost San Juan Formation (middle Arenig), northern Argentine Precordillera: paleoecologic and biogeographic implications

Juan L. BENEDETTO[1] and Norma CECH[1]

Abstract. Rhynchonelliformean brachiopods from the Arenig outer-ramp carbonate facies exposed at the Guandacol-Gualcamayo depocenter (northern Precordillera basin) include the new species *Orthidium guandacolensis*, *Taffia* (*Chaloupskia*) *minima* and *Leptella* (*Petroria*) *ventrocristata*. Associated taxa are *Archaeorthis* sp., *Ffynnonia* sp. and *Tritoechia* (*Tritoechia*) sp. The overlying basinal black shales (Gualcamayo Formation) have yielded *Pelonomia*? sp. On the basis of the age of *Ffynnonia* occurrences in western Gondwana it is suggested that this genus migrated from the Famatina back-arc basin to the open platform waters of the northern Precordillera basin and then to shallower water settings of the carbonate ramp located to the south (in present coordinates). The studied assemblage is characterized by low values of richness, diversity and equitability. The nature of substrate is interpreted as the main controlling factor in the distribution of brachiopods through the carbonate ramp. The muddy substrates prevailing in the outer-ramp were colonized mainly by semi-infaunal (tritoechiids) and subsidiarily by liberosessile brachiopods (plectambonitoids), other suspension feeders are rare. In the ramp-to-basin and basinal black shales the decreasing oxygen level was probably the main barrier to permanent colonization of rhynchonelliformean brachiopods.

Resumen. UNA ASOCIACIÓN DE BRAQUIÓPODOS DE RAMPA EXTERNA DE LA PARTE SUPERIOR DE LA FORMACIÓN SAN JUAN (ARENIGIANO MEDIO), NORTE DE LA PRECORDILLERA ARGENTINA: IMPLICANCIAS PALEOECOLÓGICAS Y BIOGEOGRÁFICAS. La fauna de braquiópodos rinconelliformes arenigianos provenientes de facies carbonáticas de rampa externa expuestas en el depocentro de Guandacol-Gualcamayo (Precordillera norte) incluye las nuevas especies *Orthidium guandacolensis*, *Taffia* (*Chaloupskia*) *minima* y *Leptella* (*Petroria*) *ventrocristata*. Otros taxones asociados son *Archaeorthis* sp., *Ffynnonia* sp. y *Tritoechia* (*Tritoechia*) sp. Las lutitas negras suprayacentes (Formación Gualcamayo) son portadoras de *Pelonomia*? sp. La asociación estudiada está caracterizada por bajos valores de riqueza, diversidad y equitatividad. Se interpreta que la naturaleza del sustrato fue el principal factor de control en la distribución de los braquiópodos a través de la rampa carbonática. Los fondos fangosos desarrollados en la rampa externa fueron colonizados principalmente por braquiópodos semi-infaunales (tritoéchidos) y subsidiariamente por liberosésiles (plectambonitoideos), mientras que otros suspensívoros están prácticamente ausentes. En la transición entre la rampa distal y la cuenca profunda el decreciente nivel de oxígeno en el sustrato fue probablemente la barrera principal para la colonización de los braquiópodos rinconelliformes. Sobre la base de la edad de las ocurrencias de *Ffynnonia* en Gondwana occidental se sugiere que este género migró desde la cuenca de trasarco de Famatina a la rampa distal del norte de la Precordillera, y de allí a las aguas más someras de rampa media localizadas hacia el sur (en coordenadas actuales), en la región central de la cuenca precordillerana.

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

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

Introduction

The San Juan Formation is a widespread, ca. 350 m thick carbonate unit that characterizes the eastern belt of the Precordillera basin. In the central and southern parts of the basin it ranges in age from late Tremadoc to early Llanvirn (Lehnert, 1995; Albanesi

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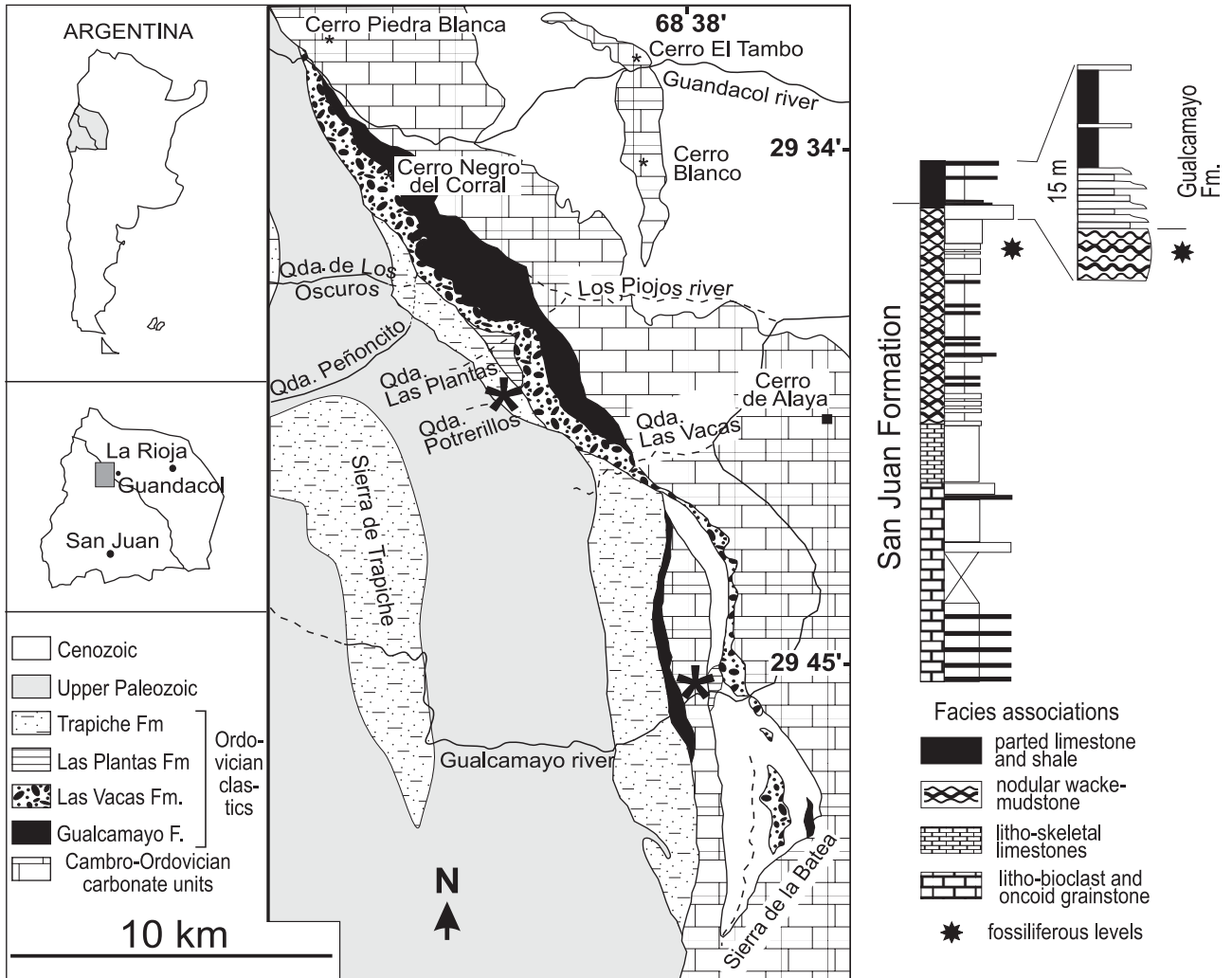
et al., 1998; Albanesi and Ortega, 2002, and references therein). It is overlain in transition by the Los Azules Formation black shales which bear a rich graptolite fauna referred to the Da2 *U. dentatus* Zone (Ortega and Rickards, 2003). Towards the northern part of the basin (Guandacol-Gualcamayo area) (figure 1) the transition to basinal facies -represented by black shales and dark limestones named Gualcamayo Formation- occurs earlier, in the middle Arenig, as conodonts and graptolites from the topmost levels of the San Juan Formation demonstrate, indicating that drowning of the carbonate ramp was diachronous

Figure 1. Geological map of the Guandacol-Gualcamayo region (from Astini, 1998) showing fossiliferous localities (asterisks) and colum-nar section of the upper part of the San Juan Formation and lower part of the Gualcamayo Formation (modified from Cañas, 1999) / *ma-pa geológico de la región de Guandacol-Gualcamayo (de Astini, 1998) indicando las localidades fosilíferas (asteriscos) y columna estratigráfica de la parte superior de la Formación San Juan e inferior de la Formación Gualcamayo (modificado de Cañas, 1999).*

from north to south (Hünicken, 1985; Albanesi *et al.*, 1998; Ortega and Albanesi, 1999).

Development of the carbonate ramp encompasses a varied array of lithofacies ranging from inner-ramp, wave-agitated shoal environments to deep-ramp settings (Cañas, 1995, 1999), including two reef horizons, the first near the base and the second to-wards the upper third of the unit (Cañas and Carrera, 2003). Skeletal and intraclastic wackestones and packestones bearing rich marine megafaunas are the most typical and widely distributed lithologies of the San Juan Formation. They have been interpreted as mid-ramp deposits developed between fair-weather and storm-wave base (Cañas, 1999, 2002). Most pre-viously described Arenig brachiopods from the San Juan Formation come from these settings (Benedetto,

2001a, 2002; Benedetto and Herrera, 1993; Benedetto *et al.*, 2003). The only published brachiopod from deep-water rocks of this age is *Nanorthis fragilis* Benedetto, which occurs in the parted limestones forming the transition between the San Juan and Gualcamayo formations (Benedetto *et al.*, 1986).

The purposes of this paper are, firstly, to describe the brachiopod fauna recovered from the outer-ramp deposits developed at the top of the San Juan Formation in the Guandacol depocenter. Secondly, the main paleocological traits of these deep-water as-semblages will be examined in order to compare them with the time-equivalent shallower assem-blages flourishing in the central portion of the basin. Much research has been completed on benthic com-munities from such inner- and mid-ramp settings, es-

pecially those spanning the Arenig *Huacoella radiata* and *Niquivilia extensa* brachiopod zones (Sánchez *et al.*, 1993, 2003; Carrera, 1997, 2000, 2001; Carrera *et al.*, 1999; Cech and Carrera, 2002; Carrera and Cech, 2003; Cech, 2004; Waisfeld *et al.*, 2003). These paleoecological works constitute an excellent data base for a comparative study of brachiopod assemblages developed along an inner- to outer-ramp gradient. This study provide an opportunity to examine the role of the physical factors in structuring communities and to assess the role of these deep-water assemblages in the origin and dispersion of the environmentally comparable early Llanvirn (*Ahtiella argentina* Zone) brachiopod faunas.

Stratigraphic occurrence, age and preservation

Most of brachiopods described below come from the uppermost part of the San Juan Formation cropping out at Quebrada Potrerillos, a tributary of the Los Piojos River. A few specimens were recovered from equivalent beds exposed at the Gualcamayo river (figure 1). In these sections, the upper 30 m of the San Juan Formation is characterized by thin-bedded limestones with nodular stratification interbedded with shale partitions. Limestones consist essentially of bioturbated bioclastic wackestones and nodular, often pyritic dark-gray mudstones. According to Cañas (1995, 1999) these nodular limestones were deposited in quiet-waters, below the storm wave base, in a distal ramp setting. The brachiopod assemblage described in this paper was recovered from these levels. They are overlain by a package ca. 15 m thick of parted limestones formed by couplets of dark mudstones and graptolitiferous black shales deposited in a deep ramp-to-basin transition (Cañas, 1995). This interval grades upward to the basinal black shales of the Gualcamayo Formation.

The age of brachiopods is well constrained by conodonts (Albanesi *et al.*, 1999) and graptolites (Ortega and Albanesi, 1999). The uppermost nodular limestones of the San Juan Formation and the overlying parted limestones have yielded abundant conodonts belonging to the *T. laevis* Zone, which correlates with the *Baltoniodus triangularis* Zone of Baltoscandia (Bergström, 1995). The FAD of *Tripodus laevis* has been proposed as the marker of the base of the Middle Ordovician Series (Webby, 1998), but currently the FAD of *Protoprioniodus aranda* was selected a the key horizon for the Lower/Middle Ordovician boundary owing to its wider geographic and environmental range (Albanesi and Carrera, 2001; Albanesi *et al.*, 2003). In the Potrerillos river section, *P. aranda* has been recorded from the top of the San Juan Formation and the base of the overlying

Gualcamayo Formation (Albanesi *et al.*, 1999). The basal levels of the latter contain a diverse graptolite assemblage referred to the *Isograptus victoriae maximus* Zone of Ca3 age (Ortega and Albanesi, 1999). Ecologically, it can be ascribed to the deep-water isograptid biofacies (*cf.* Cooper, 1998).

Outside the Guandacol depocenter, in the central Precordillera, coeval strata are represented by middle-ramp highly fossiliferous wackestones punctuated by thin intraclast lime conglomerates. Cañas (1995) interpreted this facies as deposited in low energy settings within the photic zone, with low sedimentation rates, affected sporadically by storm events. Megafossils include sponges, trilobites, bryozoans, brachiopods, echinoderms, gastropods, rostroconchs, cephalopods, receptaculitids and algae. The brachiopod assemblage encompassing the *T. laevis* Zone was referred to the *Niquivilia* Zone (Herrera and Benedetto, 1991), which was recently redefined and renamed as *Niquivilia extensa* Zone (Benedetto, 2002). The nominal species of this zone is present everywhere the mid-ramp facies are exposed. In the Gualcamayo area (Gualcamayo River section) it has been recorded about 40 m below the contact with the Gualcamayo Formation (Benedetto and Herrera, 1993), from shallower facies than those analyzed herein.
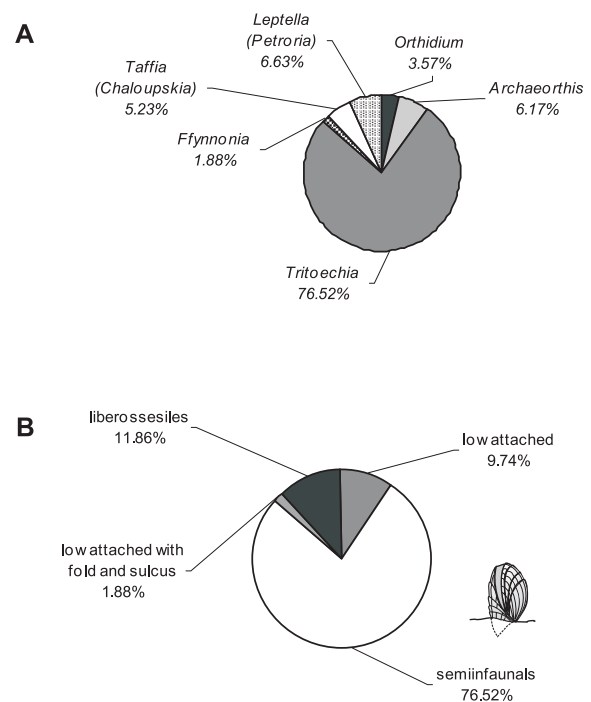

Figure 2. Pie diagrams showing percentages of outer-ramp assemblage from Quebrada Potrerillos section, northern Precordillera. **A,** genera; **B,** guilds / *diagrama en mosaico con los porcentajes relativos de la asociación de rampo externa en la Quebrada Potrerillos, Precordillera norte. **A,** composición de géneros; **B,** composición de los grupos funcionales.*

Skeletal remains in the nodular limestones are mostly silicified. Acid etching of a sample of ca. 7 kg yielded well preserved but relatively scarce brachiopod shells and abundant trilobite sclerites. Fragments of other megafossils are rare. Although less well preserved than the etched specimens, some calcified brachiopods have also been recovered directly from the outcrops. High-quality internal molds were obtained by dissolution of calcareous shells.

Paleoecology

As stated above, the studied brachiopod assemblage occurs in dark gray nodular wackestones-mudstones which are absent at the type section of Cerro La Silla (central Precordillera). This lithofacies is interpreted as having been deposited in an outer ramp environment, mostly below storm wave-base (Cañas, 1999). The fauna is dominated by trilobites and brachiopods, with hexactinellid spicules as minor components.

For paleoecologic analysis, the faunal content was estimated by counting identifiable silicified brachiopod remains in the etched residue as well as molds in the insoluble muddy matrix. The relative abundance of taxa in terms of biovolume was calculated for each species following the procedure proposed by Sánchez *et al*. (1993), which consists in estimating the biovolume by submerging in water a series of conjoined specimens of different size and measuring the volume displaced. On the basis of these measurements a curve representing the 'shell volume/shell width' ratio was constructed for each species. On the basis of shell morphology, which reflects particular life strategies, brachiopod taxa were ascribed to different guilds in order to evaluate the ecospace occupation. (Bambach, 1983; Thayer, 1983; Waisfeld *et al*., 2003) (table 1). Diversity was estimated according to the Shannon index ($D = - \sum pi \ln [pi]$), where $pi = ni /N$, where ni = biovolume of the i'th species, and N = total biovolume), and richness by counting the total number of species in the sampled level. The studied assemblage from Quebrada Potrerillos is characterized by low values of richness (6 taxa) and diversity (0.9). The latter is due to the dominance of *Tritoechia* sp. (76.52%) respect to the other components (figure 2.A). The six brachiopod taxa present in the assemblage were referred to four guilds, of which the semi-infaunal one is by far the more abundant in terms of percentage of total biovolume (76.52%). The low attached forms were divided in biconvex shells, umbo down (9.74%) and transverse shells with strong fold and sulcus (1.88%). The liberosessiles represent 11.86% of the total (figure 2.B).

A comparison of outer shelf assemblages with coeval communities developed in the shallower water facies of the central Precordillera basin studied by Cech and Carrera (2002) and Cech (2004) reveals that richness values are similar but diversity is higher in the central Precordillera assemblages (1.59). The latter value indicates high equitability, reflecting that none taxon clearly dominates respect to the others (figure 3.A). The most abundant taxon is *Niquivilia extensa* (36.5%) followed by *Leptella* (*Leptella*) spp. (22.86%), *Tritoechia* sp. (19.9%), *Huacoella radiata* (10.95%), *Hesperonomia* sp. (4.37%), *Paralenorthis* sp. (4.13%) and unidentified orthids (1.29%). On the other hand, the mid-ramp facies contains only three guilds, of which the liberosessiles are largely dominant, while the semi-infaunals and pedunculate low-attached are less represented in the communities (figure 3.B). Although a quantitative analysis of components other than the brachiopods is beyond the scope of this study, it should be noted that sponges and gastropods, which are among the main components of the central Precordillera communities, are nearly absent in the outer-ramp deposits.

Among physical parameters, substrate is considered a key factor controlling the brachiopod distribution, while other variables as temperature, salinity, light, current strength, seem to have played a secondary role in the bathymetric distribution, at least in the living rhynchonelliform brachiopods (Richardson, 1997). The dominance in the studied brachiopod association of the semi-infaunal life-style, followed in importance by the free-lying forms, is consistent with the expected reduction of the pedicle system in the low-energy muddy substrates prevailing in outer shelf environments. According to Sánchez *et al*. (1996) such a strategy became frequent in stable and relatively soft substrates. The semi-in-

Table 1. Genera and guilds in the studied assemblages / *géneros y grupos funcionales de las asociaciones estudiadas.*

	Northern Precordillera (Quebrada Potrerillos)	Central Precordillera (Niquivil and Cerro La Silla)
Guilds	Genera	
Low attached biconvex shells, umbo down	*Archaeorthis* *Orthidium*	*Hesperonomia* *Paralenorthis* orthids indet.
Low attached transverse shells strong fold and sulcus	*Ffynnonia*	——————
Liberosessiles	*Leptella (Petroria)* *Taffia (Chaloupskia)*	*Leptella (Leptella)* *Huacoella* *Niquivilia*
Semi-infaunals	*Tritoechia*	*Tritoechia*

faunal mode of life of *Tritoechia* has been inferred from the relatively small foramen piercing apically the pseudodeltidium. Sánchez and Tóffolo (1996) considered that such a reduced, probably rachet-like pedicle, played a secondary role in the attachment. In their reconstruction, *Tritoechia* is oriented with the apical region of its pyramidal ventral valve sunk in the bottom and the anterior commissure well above the sediment-water interface. For this reason it is considered as a semi-infaunal form.

The free-lying plectambonitoids (the liberosessile guild) are characterized by concavoconvex or planoconvex, transverse, often alate shells having small apical foramen or lacking them. This life strategy, as stated above, dominates the mid-ramp communities of the Central Precordillera. According to Sánchez and Tóffolo (1996) and Sánchez *et al.* (1996) the liberosessile brachiopods flourished in relatively stable carbonate substrates affected occasionally by storm waves, the stability on the substrate being achieved by mean of their reduced, probably functional pedicle. It is uncertain, however, to what extent such a pedicle was capable to elevate the shell above the substrate (*cf.* Rong and Cocks, 1989). It seems likely that adults of *Taffia* and *Leptella* (*Petroria*) reclinated on the bottom, with the thickened umbonal region of ventral valve slightly buried. In the Precodilleran mid-ramp deposits this guild was occupied by three genera (*Leptella*, *Huacoella* and *Niquivilia*) and six or more species. The fact that in the Precordillera basin the liberosessiles were more

diversified in shallower than in deeper water carbonates seems to be in contradiction with trends observed in other regions and ages where plectambonitoids attain higher biovolume values in deep water settings (Potter and Boucot, 1992; Patzkowsky, 1995; Sánchez *et al*, 1996; Benedetto, 2001b). The deviation from this general pattern is due to the great expansion, in terms of biomass, of *Tritoechia* (low value of equitability). It is interesting to note that in the lower Llanvirn limestone beds of the uppermost San Juan Formation exposed at Talacasto, plectambonitoideans also tend to be associated with tritoechiids, as cluster analysis (R-mode) of brachiopod taxa showed (Sánchez and Tóffolo, 1996), though biovolume values in the former are higher. Such a link suggests that both life strategies were equally advantageous for inhabiting muddy soft substrates. Tritoechiids, however, are absent in the overlying deeper water parted limestones (base of the Gualcamayo Formation) in which only monospecific populations of *Nanorthis fragilis* have been recovered. This small thin-shelled species may be interpreted as an opportunistic r-strategist able to tolerate lowered oxygen values. Associated forms are trilobites of the nileid biofacies and numerous linguliformean brachiopods, mainly acrotretids (Benedetto *et al.*, 1986). Because these assemblages are absent in the interbedded black shales, the brachiopod-bearing levels may be interpreted as periods of colonization triggered by brief oxygenation events (Wignall, 1990). The organic-rich graptolitic black shales forming the bulk of the Gualcamayo Formation have yielded only few valves of a plectambonitoid referred herein to *Pelonomia*? sp. Clearly, the dysaerobic conditions of the bottom inhibited the colonization not only of most suspension-feeding rhynchonelliformean brachiopods but also of deposit-feeders, as the absence of bioturbation indicates.

In summary, the nature of substrate is interpreted as the main controlling factor in the distribution of brachiopods within the carbonate ramp. The mid-ramp settings are characterized by low sedimentation rates sporadically affected by storm events, with recurrent development of firmgrounds and hardgrounds covered by bioclastic debris. Level bottom communities are dominated by encrusting organisms (receptaculitids), sponges, bryozoans, gastropods, crinoideans and brachiopods (Carrera, 2001), the latter forming relatively diverse and equitable assemblages. The muddy substrates developed in the outer-ramp areas were colonized mainly by semi-infaunal brachiopods (tritoechiids) and subsidiarily by liberosessile forms (plectambonitoids), other suspension feeders becoming almost absent. In the ramp-to-basin transition the decreasing of the oxygen level was probably the main barrier for a perma-
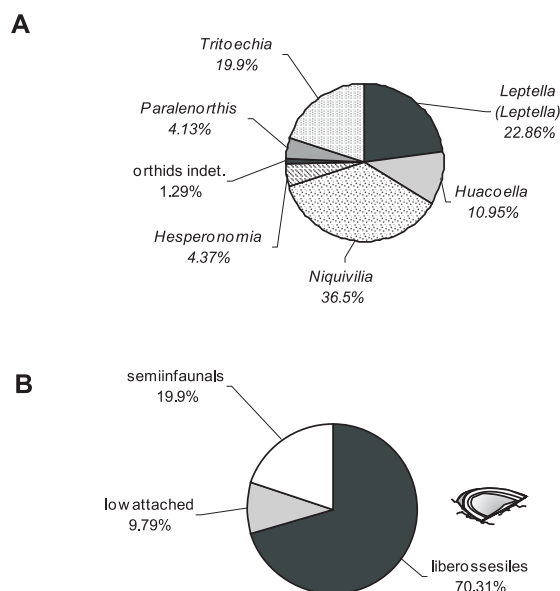

A

Tritoechia 19.9%
Paralenorthis 4.13%
orthids indet. 1.29%
Hesperonomia 4.37%
Niquivilia 36.5%
Leptella (Leptella) 22.86%
Huacoella 10.95%

B

semiinfaunals 19.9%
low attached 9.79%
liberossesiles 70.31%

Figure 3. Pie diagrams showing percentages of mid-ramp assemblages from the Niquivil section, central Precordillera, **A,** genera, **B,** guilds / *diagrama en mosaico con los porcentajes relativos de las asociaciones de rampa media del área de Niquivil (Precordillera central).* **A,** *composición de géneros,* **B,** *composición de los grupos funcionales.*
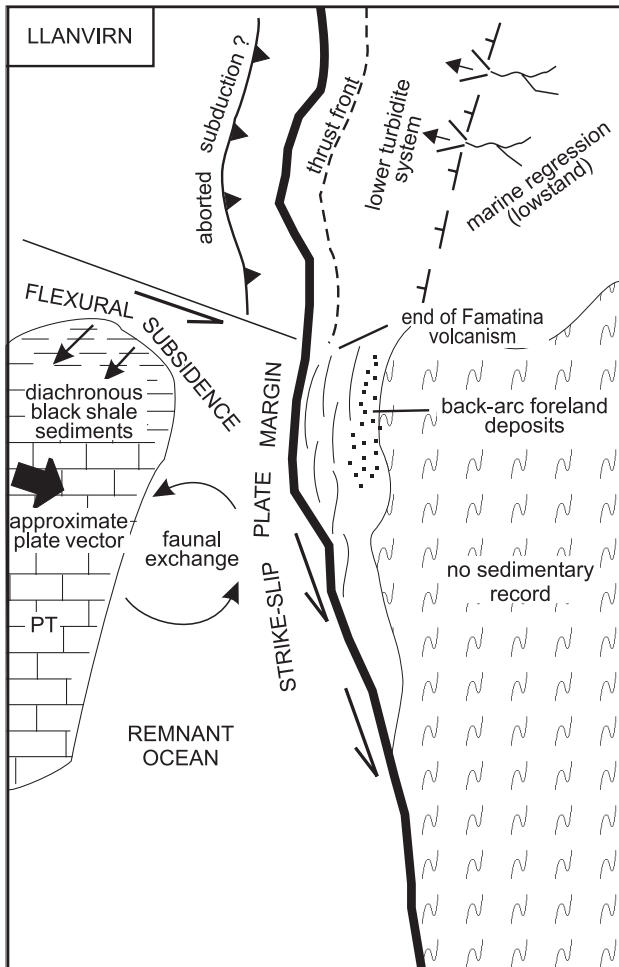
Figure 4. Schematic paleogeographic reconstrucction showing inferred relationships between the proto-Andean margin of Gondwana and the Precordillera terrane (PT) in the Llanvirn (from Benedetto, 2004) / *reconstrucción paleogeográfica esquemática mostrando las relaciones entre el margen proto-Andino de Gondwana y el terreno Precordillera (PT) en el Llanvirniano (de Benedetto, 2004).*

nent colonization of rhynchonelliformean brachiopods.

The diachronism of the genus *Ffynnonia*

The genus *Ffynnonia* Neuman and Bates is a distinctive brachiopod of the Celtic Province defined by Neuman (1976), which developed during the Arenig-early Llanvirn along the periphery of Gondwana, at mid- to high-latitudes. Celtic brachiopods have been recorded typically in high-latitude siliciclastic or volcaniclastic rocks deposited in peri-insular or continental margin settings (Neuman and Harper, 1992), and less frequently in warmer water carbonate platforms surrounding isolated terranes (e.g. Precordillera terrane; Benedetto, 1998 and references therein). They include a high proportion of endemic taxa,

most of them confined to a single or a few localities. *Ffynnonia* was first recorded in Wales, from the upper Arenig Treiorwerth Formation (Bates, 1968). It was subsequently discovered in upper Arenig-lower Llanvirn strata of the San Juan Formation, in the Argentine Precordillera (Benedetto, 2001a; Benedetto, 2003b) and in the Suri Formation of the Famatina Range, western Argentina (Benedetto, 2003a). According to the well-constrained mid Arenig age of the Suri Formation (*O. evae* Zone, Albanesi and Astini, 2000), the Famatina basin contains the earliest known representatives of *Ffynnonia*. This supports the contention that volcanic islands and volcanic chains peripheral to the Iapetus Ocean may have acted as 'centers of origin' of numerous Ordovician taxa (Neuman, 1976; Fortey, 1984) and may have played a key role in the early Ordovician radiation of brachiopods and bivalves (Benedetto and Sánchez, 2003; see also Harper and McNiocaill, 2002). In the Famatina Range *Ffynnonia* suddenly appears in the Suri Formation; no brachiopods have been found so far in the underlying laminated siltstones and black shales of lower Arenig age. The ancestor of *Ffynnonia*, as well as that of the closely related *Platystrophia* (Zyukov, 2001), remain uncertain. We believe that the best candidate, at the present state of knowledge, is the alimbellid *Astraborthis quebradensis* Benedetto, from upper Tremadoc beds of the Central Andean basin of northwestern Argentina and Bolivia, which possesses a number of features suggesting a link with the platystrophiids and, in particular, with *Ffynnonia* (Benedetto and Carrasco, 2002). If so, the latter originated in the Famatina basin and then migrated to other Celtic sites (e.g. Wales, Precordillera terrane).

It is noticeable that the age of the outer-shelf, *Ffynnonia*-bearing beds in the northern Precordillera is intermediate between those of Famatina Range and central-southern Precordillera basin. In the context of the hypothesis that the Precordillera is an allochthonous terrane -recently reassessed by one of us (Benedetto, 2004)-, the existence of a remnant basin ca. 300 km wide separating this microcontinent from the Gondwana margin has been inferred (figure 4). By the early Llanvirn the first stages of collision initiated and this seaway became much narrower. In turn, the back-arc basin developed behind the Famatina basin underwent a regressive event and finally emerged, as lithofacial analysis and increasing vulcano-tectonic activity indicates (Astini and Benedetto, 1996; Astini, 1999). As result of these phenomena, the high-gradient narrow shelves adjacent to the volcanic edifices became gradually unstable promoting the migration of a number of brachiopod taxa towards the open waters lying to the west (in present coordinates). Two main migration waves can be discerned. The first included some taxa recorded in the

Suri Formation, such as *Ffynnonia*, *Skenidioides* and *Hesperonomiella* of which only the former is present in the intermediate-age, deep-water deposits of the northern Precordillera. It seems, therefore, that *Ffynnonia* migrated from the Famatina back-arc basin to the open platform waters of the northern Precordillera basin and then to shallower settings of the central and southern parts of the carbonate ramp. The second migratory event involved a larger number of taxa present in the overlying Molles Formation of the Famatina Range (upper *O. evae-B. navis* Zones), including *Skenidioides*, *Monorthis*, *Hesperonomia*, *Productorthis*, *Ahtiella*, *Rugostrophia* and *Camerella*. All of them have been recorded in upper Arenig and/or lower Llanvirn carbonate beds of the San Juan Formation in inner or, more frequently, in mid-ramp settings. These genera appear to have an earlier history of expansion in volcanosedimentary rocks that continues on the carbonate ramp as they adapt to a new set of physical and biotic conditions. It should be noted, however, that the majority of these taxa become abundant only in the uppermost part of the San Juan Formation (lower Llanvirn, *L. variabilis* Zone), which deposited in deeper waters than the underlying mid-ramp Arenig carbonates (Cañas, 1999).

Up to now, *Taffia* (*Chaloupskia*) and *Leptella* (*Petroria*) have not been reported from the Famatina basin. Both taxa are known from younger (lower Llanvirn) beds of the Precordillera carbonate platform, in settings ranging from subtidal, demosponge-dominated biofacies (e.g. Talacasto-Villicum area) to outer-shelf brachiopod-dominated biofacies (topmost levels of the Cerro Viejo area) (Sánchez *et al.*, 1996). The occurrence of *T.* (*Chaloupskia*) *minima* in the outer-ramp deposits of the Guandacol area slightly predates that of the type species *T.* (*Chaloupskia*) *scabrella* Neuman in the Hølonda Limestone of Norway (upper Arenig-lower Llanvirn; Neuman and Bruton, 1989). The lower Llanvirn Precordilleran species *T.* (*Chaloupskia*) *anomala* Benedetto and Herrera, from Cerro Viejo, and *T.* (*Chaloupskia*) sp. nov., from Talacasto (not yet described) are thought to be direct descendants from the outer-shelf species *T.* (*C.*) *minima*. It should be noted that the two Llanvirn species are larger and thick-shelled compared to the deep water Arenig species, and comae are always strongly developed. All these features are interpreted as being advantageous for inhabiting shallower waters.

Systematic paleontology (by J.L. Benedetto)

All figured and cited specimens are deposited in the Centro de Investigaciones Paleobiológicas (CIPAL), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina (prefix CEGH-UNC).

Order ORTHIDA Schuchert and Cooper, 1932
Suborder ORTHIDINA Schuchert and Cooper, 1932
Superfamily ORTHOIDEA Woodward, 1852
Family NANORTHIDAE Havlíček, 1977

Genus *Archaeorthis* Schuchert and Cooper, 1931

Type species. *Orthis electra* Billings, 1865

Archaeorthis sp.
Figures 5.A-5.K

Material and occurrence. Three fragmentary ventral valves and two dorsal valves CEGH-UNC 21801-21805; two internal molds of dorsal valve, CEGH-UNC 21806 and 21832. Uppermost levels of the San Juan Formation, Quebrada Potrerillos.

Description. Medium size, largest specimen 11,6 mm wide, ventribiconvex, subelliptical shells (average length/width ratio 0,84). Cardinal extremities rounded, obtuse; maximum width at mid-length. Ventral valve moderately and evenly convex, maximum convexity in the posterior third. Ventral interarea planar, strongly apsacline (almost orthocline in one specimen), slightly higher than the dorsal interarea. Delthyrium open, large, unmodified. Dorsal valve gently convex with a shallow broad sulcus originating at umbo. Dorsal interarea narrow, planar, anacline. Ornament multicostellate with rounded primary costellae, finer second-order costellae originating at valve mid-length, and in some specimens third-order costellae developed incipiently at valve margin; number of costellae increases almost exclusively by intercalation; in mature specimens the count is of 6-7 costellae per 2 mm.

Ventral valve interior with strong teeth supported by very short dental plates extending anteriorly into medially convergent muscle-bounding ridges. Crural fossettes shallow, subcircular. Muscle field subrhomboidal buttressed anteriorly by a prominent, elongate oval premuscular callosity (the anterior extension of callosity and other proportions cannot be determined because of the incompleteness of available specimens).

Dorsal valve interior with subtriangular concave notothyrial platform strongly raised above the valve floor and continuous with a stout, rounded median dorsal ridge extending anteriorly to about one-half valve length. Cardinal process absent. Brachiophores thickened distally, widely divergent, bounding deep crenulated dental sockets excavated partially into the posterior wall of the valve; in a largest specimen they are floored by stout incipient fulcral plates (figure 5.F). Dorsal muscle field with subtriangular anterior

adductor scars and smaller, elongate oval posterior scars; anterior pair of adductor scars penetrates as a wedge between the median dorsal ridge and the inner side of the posterior pair.

Remarks. The Potrerillos specimens are assigned to the genus *Archaeorthis* rather than to the closely related *Nanorthis* on the basis of the prominent premuscular thickening in the ventral valve. In addition, both teeth and brachiophores are strong, like in the former genus. A distinctive feature of our specimens is the morphology of the dorsal muscle field, with the posterior portion of the anterior pair located between the median ridge and the posterior adductor scars, like in the genera *Nothorthis* and *Ranorthis*. The only other species of *Archaeorthis* recorded from the San Juan Formation is *A. sanroquensis* Benedetto, which comes from the lowermost part of the unit, of latest Tremadoc-earliest Arenig age (Benedetto, 2001a). It differs from the Potrerillos sample in that number of costellae increases mainly by bifurcation, the less prominent dorsal median ridge, and the dorsal adductor scars configuration, which are arranged in front each to another so that the contact between them is almost perpendicular to the dorsal ridge instead of oblique. *A. parviuscula* Ulrich and Cooper 1938, from the Sarbach Formation of North America, resembles *Archaeorthis* sp. in the strong dorsal median ridge but differs in its smaller size, finer ornament and less developed premuscular callosity.

Family ORTHIDIELLIDAE Ulrich and Cooper, 1936

Genus *Orthidium* Hall and Clarke, 1892

Type species. *Orthis gemmicula* Billings, 1862.

Orthidium guandacolensis sp. nov.
Figures 5.L-5.W

2001a. *Orthidium* sp. Benedetto, p. 6, pl. 1, figs. 22-31.

Holotype. A dorsal valve CEGH-UNC 21811.
Paratypes. Two conjoined specimens, three ventral valves, three dorsal valves, one external mold and one internal mold of ventral valve, and five internal molds of dorsal valves, CEGH-UNC 21812-21826, 21831.

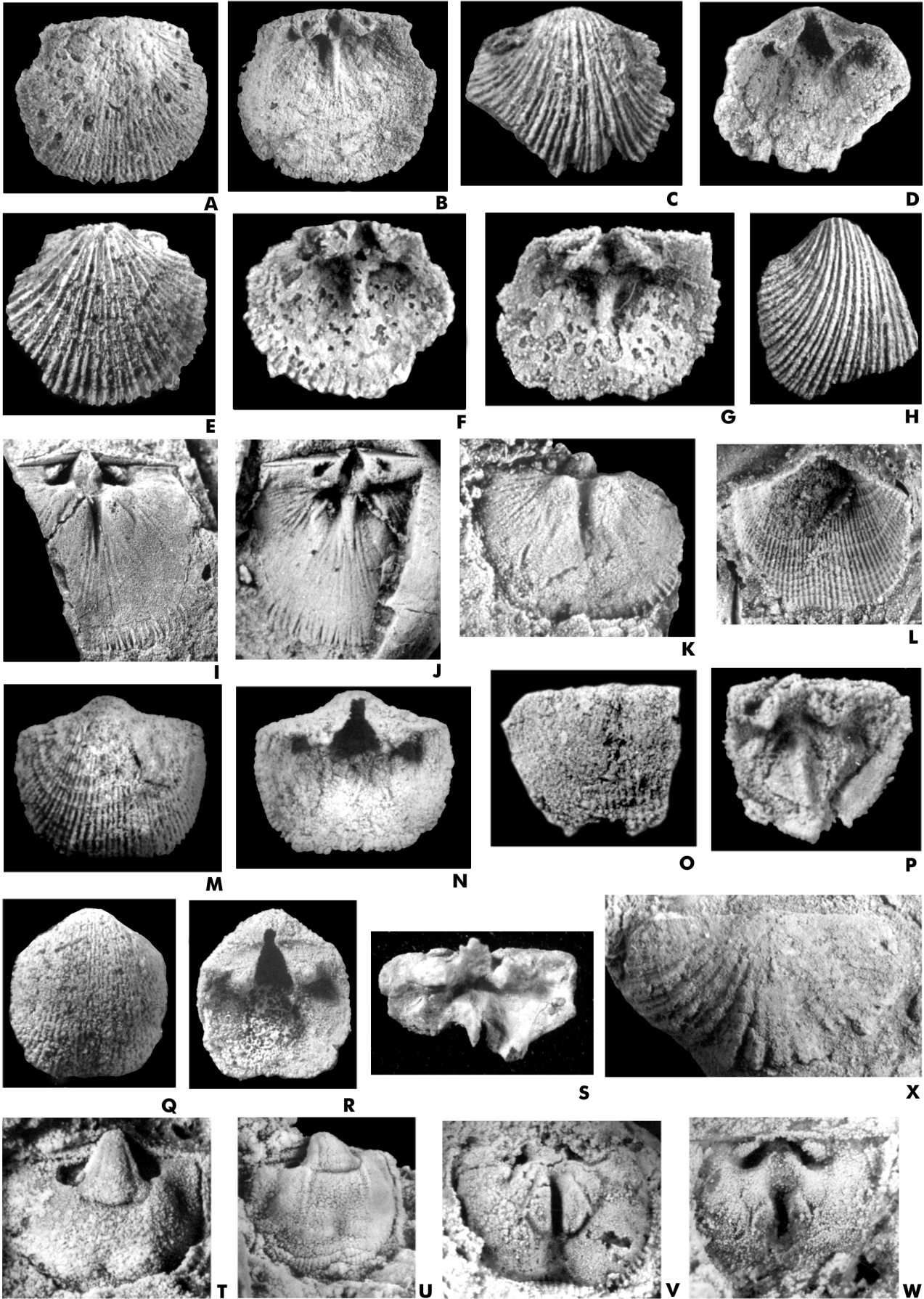**Derivation of name.** Refers to the Guandacol village.
Type locality and type stratum. San Juan Formation, uppermost levels exposed at Quebrada Potrerillos, Guandacol area.

Diagnosis. Small, up to 5,6 mm wide, strongly ventribiconvex *Orthidium* with proportionally high curved ventral interarea. Costellate radial ornament with 5-6 rounded costellae per mm; concentric growth lamellae irregularly distributed. Ventral interior with large massive teeth. Cardinal process large, plate-like, trilobed distally. Dorsal muscle field divided by a median ridge initially broad and rounded becoming higher and blade-like anteriorly.

Description. Shell minute, up to 5,6 mm wide, strongly ventribiconvex. Maximum width slightly beyond the hinge line; cardinal extremities almost orthogonal. Shell almost as long as wide, but in mature and ephebic specimens a ventral 'trail' is developed because of allometric growth, the valve becoming proportionally long and narrow (figures 5.Q, 5.R). Ventral valve strongly convex averaging 42% as deep as wide, non sulcate or with shallow, smoothly rounded sulcus on the anterior half. Ventral interarea proportionally high, curved, transversely striated, apsacline. Delthyrium broad, triangular. Dorsal valve gently convex, sulcate, with very low, anacline interarea. Ornament finely costellate, with 5-6 rounded costellae per mm and up to 50 costellae on the entire valve. Concentric lamellae irregularly distributed, impersistent, more numerous near the periphery of valve.

Ventral interior with large massive teeth supported by thick, receding dental plates almost completely masked by shell deposits filling the lateral apical cavities. Ventral muscle field confined to the deep delthyrial cavity, weakly elevated above the valve floor. Diductor scars very narrow, continued anteriorly by straight, slightly divergent vascula media; adductor field broad, triangular.

Dorsal interior with large subquadrangular, plate-like cardinal process directed posteriorly to occupy almost the entire delthyrial and notothyrial openings in conjoined valves; distally it is trilobate, with a small rounded median crest and smooth lateral lobes. Brachiophores thickened, fused with the

Figure 5. A-K. *Archaeorthis* sp. **A, B,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal* CEGH-UNC 21801, X3; **C, D,** exterior and interior of ventral valve / *exterior e interior de valva ventral* CEGH-UNC 21804, X4; **E, F,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal* CEGH-UNC 21803, X5,5; **G,** interior of dorsal valve / *interior de valva dorsal* CEGH-UNC 21805, X6; **H,** exterior of incomplete ventral valve / *exterior de una valva ventral incompleta* CEGH-UNC X3,5. **I, J,** internal mold and latex replica of dorsal valve / *molde interno y réplica de caucho de valva dorsal* CEGH-UNC 21806, x3,75; **K,** internal mold of dorsal valve / *molde interno de valva dorsal* CEGH-UNC 21832, x4,5. **L-W.** *Orthidium guandacolensis* n. sp. **L,** external mold of ventral valve / *molde externo de valva ventral*, CEGH-UNC 21820, X6,5; **M, N,** exterior and interior of ventral valve / *exterior e interior de valva ventral* CEGH-UNC 21812, X6,5; **O, P,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal* CEGH-UNC 21812, X8,5; **Q, R,** exterior and interior of ventral valve / *exterior e interior de valva ventral* CEGH-UNC 21813, X6; **S,** interior of dorsal valve, holotype / *interior de valva dorsal, holotipo* CEGH-UNC 21811, X6; **T,** internal mold of ventral valve / *molde interno de valva ventral* CEGH-UNC 21822, X5; **U,** internal mold of ventral valve / *molde interno de valva ventral* CEGH-UNC 21831, X4,5; **V,** internal mold of dorsal valve / *molde interno de valva dorsal* CEGH-UNC 21821, X7,5; **W,** internal mold of dorsal valve / *molde interno de valva dorsal* CEGH-UNC 21825, X10. **X,** *Ffynnonia* sp., exterior of dorsal valve / *exterior de valva dorsal* CEGH-UNC 21820, X4,5.

sides of the cardinal process forming a massive arched structure. Dental sockets deep, hemispherical. Dorsal muscle field strongly impressed, rhomboidal, extending anteriorly for one-half to two-third valve length, divided longitudinally by a median ridge initially broad and rounded becoming higher and blade-like anteriorly; anterior adductor scars large, subtriangular, located on either side of the median ridge, bounded laterally by low ridges; posterior pair pear-shaped, about of equal size of slightly smaller than the anterior ones, separated from them by a low, oblique ridge.

Remarks. The Potrerillos specimens clearly differ from type species *O. gemmiculum* (Billings) in its less transverse and strongly ventribiconvex shell and its much shallower dorsal sulcus. Internally both species are similar, although in the North American species the cardinal process seems to be smaller and less compressed anteroposteriorly. *Orthidium bellulum* Ulrich and Cooper (1938) from the Upper Pogonip Group of Nevada differs in its more transverse outline and stronger growth lamellae. The internal features of the closely related *O. fimbriatum* Cooper (1956), from the Table Head Group of Newfoundland, are unknown. *O. guandacolensis* sp. nov. has some features in common with *O. barnesi* Ross (1970), from the Antelope Valley Limestone (Arenig), especially the comparatively narrow outline and the strongly ventribiconvex lateral profile. However, *O. barnesi* can be differentiated by its coarser ornament and the slightly auriculate cardinal extremities which coincide with the maximum shell width. Internally, the plate-like cardinal process is similar in both species, even though in the Precordilleran species it is subrectangular instead of triangular in posterior view. In view that other internal features were not adequately described and illustrated in the 1970 Ross' paper, a more detailed comparison with this species is impracticable.

Among the San Juan Formation species, *O. guandacolensis* sp. nov. is very similar to the specimens referred to *Orthidium* sp., from the *Monorthis cumillangoensis* Zone (middle Arenig) at Cerro Cumillango (Benedetto, 2001a), in its external ornament, elongate shell outline, unusually high ventral interarea and strong teeth. The single fragmentary dorsal valve available from Cerro Cumillango is also somewhat similar. Thus it is probable that the Cumillango specimens are conspecific with *O. guandacolensis*. The late Tremadoc species *O. prominens* Benedetto, from the lower part of the San Juan Formation (Benedetto *et al.*, 2003) clearly differs in its smaller size (rarely exceeds 4 mm wide), lower ventral interarea and cardinal process with a highly developed median elevation. Perhaps the main feature distinguishing the two species is the morphology of the dorsal median ridge, which is uniformly narrow and high in *O. prominens*, whereas in *O. guandacolensis* it is initially broad and low becoming blade-like anteriorly. The early Llanvirn species *O. geniculatum* Herrera and Benedetto is readily distinguished by its more transverse outline, stronger and regularly-spaced concentric lamellae, geniculate shell, and slender and more divergent brachiophores.

Superfamily PLECTORTHOIDEA Schuchert and Le Vene, 1929

Family PLATYSTROPHIIDAE Schuchert and Le Vene, 1929

Genus *Ffynnonia* Neuman and Bates, 1978

Type species. *Pleurorthis costatus* Bates, 1968.

Ffynnonia sp.
Figure 5.X

Material and occurrence. One dorsal valve, CEGH-UNC 21810. Uppermost levels of the San Juan Formation, Quebrada Potrerillos.

Figure 6. A-J, *Taffia (Chaloupskia) minima* n. sp. **A,** ventral valve exterior / *exterior de valva ventral* CEGH-UNC 21775, X7; **B,** dorsal valve exterior / *exterior de valva dorsal* CEGH-UNC 21809, X12; **C,** internal mold of ventral valve / *molde interno de valva ventral* CEGH-UNC 21786, X6; **D, E,** exterior and interior of ventral valve / *exterior e interior de valva ventral* CEGH-UNC 21777, X4,5; **F, G,** exterior and interior of dorsal valve, holotype / *exterior e interior de valva dorsal, holotipo* CEGH-UNC 21774, X7; **H,** internal mold of dorsal valve / *molde interno de valva dorsal* CEGH-UNC 21787, X6; **I,** internal mold of ventral valve / *molde interno de valva ventral* CEGH-UNC 21808, X6; **J,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal* CEGH-UNC 21783, X7. **K-S,** *Leptella (Petroria) ventrocristata* n. sp., **K,** latex cast of ventral valve exterior / *molde del exterior de valva ventral* CEGH-UNC 21833, X4; **L,** interior of ventral valve, holotype / *interior de valva ventral, holotipo* CEGH-UNC 21798, X4; **M,** internal mold of dorsal valve / *molde interno de valva dorsal* CEGH-UNC 218830, X3; **N,** internal mold of ventral valve / *molde interno de valva ventral* CEGH-UNC 21807, X4,5; **O,** internal mold of ventral valve / *molde interno de valva ventral* CEGH-UNC 21797, X4; **P, Q,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal* CEGH-UNC 21791, X3,5; **R, S,** dorsal and ventral views of conjoined specimen / *vista dorsal y ventral de un ejemplar con valvas articuladas* CEGH-UNC 21795, X4. **T-Y,** *Tritoechia (Tritoechia)* sp., **T, U,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal* CEGH-UNC 21834, X2,5; **V, W,** exterior and interior of ventral valve / *exterior e interior de valva ventral* CEGH-UNC 21835, X2,5; **X,** internal mold of ventral valve / *molde interno de valva ventral* CEGH-UNC 21841, X4; **Y,** exterior and interior of dorsal valve / *exterior e interior de valva dorsal* CEGH-UNC 21837, X3. **Z-Z2,** *Pelonomia?* sp. **Z,** external mold of dorsal valve / *molde externo de valva dorsal* CEGH-UNC 21859, X4; **Z1, Z2,** internal mold of dorsal valve and latex cast / *molde interno de valva dorsal y réplica de caucho* CEGH-UNC 21860, X3,5.
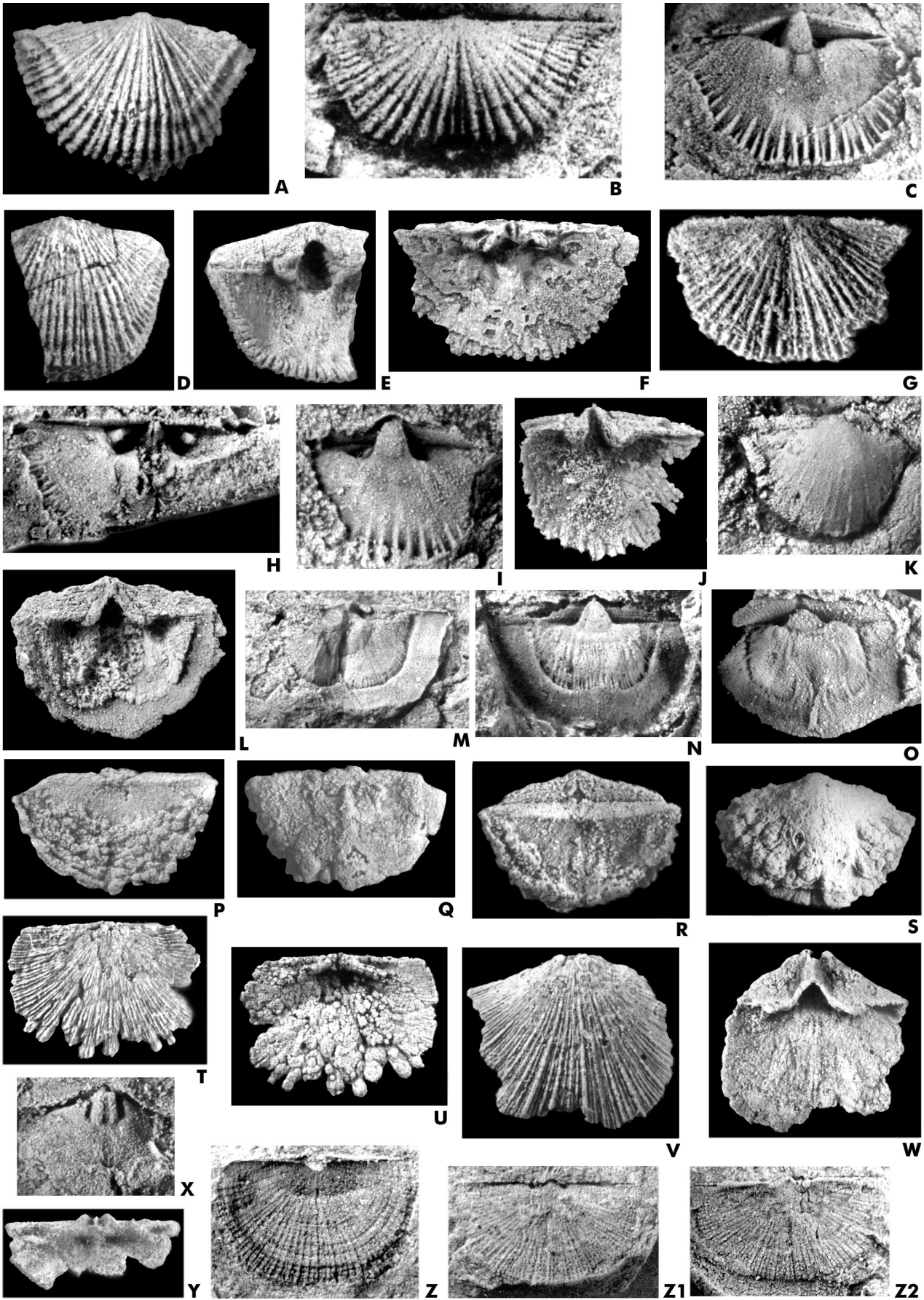
Description. Shell transverse, 12,2 mm wide and 7,1 mm long. Maximum width slightly beyond the straight hinge line. Cardinal extremities rounded. Dorsal valve moderately convex, with well-defined median fold. Ornament coarsely costellate, with six primary costellae on flanks and four on the fold; ribs bifurcate near the mid-valve length and close to the anterior margin. Internal features unknown.

Remarks. *Fynnonia* is a highly distinctive taxon of the upper part of the San Juan Formation (late Arenig-earliest Llanvirn) in the central part of the basin (Benedetto and Herrera, 1986; Benedetto, 2001a). It has also been recorded in the Famatina basin, from the Suri Formation (early Arenig) (Benedetto, 2003a). Externally, it can be recognized by its transverse shell bearing a well-defined dorsal fold and facicostellate radial ornament. On the basis of these features the single specimen recovered from the Potrerillos area is tentatively assigned to *Ffynnonia*, the available material being too limited for specific identification.

Order STROPHOMENIDA Öpik, 1934
Suborder STROPHOMENIDINA Öpik, 1934
Superfamily PLECTAMBONITOIDEA Jones, 1928
Family TAFFIIDAE Schuchert and Cooper, 1931
Subfamily TAFFIINAE Schuchert and Cooper, 1931

Genus *Taffia* Butts, 1926

Type species. *Taffia planoconvexa* Butts, 1926.

Subgenus *Taffia* (*Chaloupskia*) Neuman in Neuman and Bruton, 1989

Type species. *Chaloupskia scabrella* Neuman in Neuman and Bruton, 1989.

Taffia (*Chaloupskia*) *minima* sp. nov.
Figures 6.A-6.J

Holotype. A silicified dorsal valve, CEGH-UNC 21774.
Paratypes. Two conjoined valves, seven ventral valves and two dorsal valves, CEGH-UNC 21775-21785. Three external molds of dorsal valve, CEGH-UNC 21800, 21808 and 21809, two internal molds of ventral valve, CECG-UNC 21786 and 21799, and two of dorsal valve, CEGH-UINC 21787-21788.

Derivation of name. Refers to small size of shells.
Type locality and type stratum. San Juan Formation, uppermost levels exposed at Quebrada Potrerillos, Guandacol area.

Material assigned. Two ventral valves from the lower member (parted limestoners) of the Gualcamayo Formation, Quebrada Gualcamayo, CEGH-UNC 21789-21790.

Diagnosis. Minute, ventribiconvex species of *Taffia*

(*Chaloupskia*) with subequally multicostellate ornament formed by 26-35 narrow, subangular, mostly simple ribs. Pseudodeltidium confined to the posterior half of delthyrium. Comae absent. Ventral muscle field bounded anteriorly by a premuscular callosity. Notothyrial platform narrow merged anteriorly with a broad rounded median ridge. Simple, blade-like cardinal process always present.

Description. Shell minute, up to 9 mm wide (normally 5-6 mm wide), ventribiconvex; growth markedly allometric, so that juvenile specimens tend to be considerably more transverse than the largest ones (average length/width ratio in specimens up to 6 mm wide: 0,60). Hinge line long, straight, extending into small ears at cardinal extremities. Ventral valve moderately and evenly convex, slightly carinate; flanks nearly flat to slightly concave. At the front of largest specimens there is an angular, dorsally directed geniculation. Umbo minute, not raised beyond hinge line or barely protruding from them in larger specimens. Ventral interarea planar, large, apsacline. Delthyrium triangular, its posterior half closed by a gently arched pseudodeltidium. Dorsal valve gently convex, with well defined median sulcus narrow posteriorly but becoming broad and shallow anteriorly. Dorsal interarea low, planar, about 40 % as high as the ventral one, anacline to almost catacline. Chilidium not preserved in available material. Ornament multicostellate, with 26-35 narrow, subangular, mostly simple ribs (density 7-8 ribs per 2 mm), coarser and rounded anteriorly; a few costellae added on the anterior third by intercalation and bifurcation. Concentric ornament of fine, closely spaced growth lines, more marked on the anterior third of valve. Comae not developed.

Ventral interior with stout, bluntly triangular teeth supported by thick, strongly receding dental plates; inner face of teeth bearing shallow, elongate oval crural fossettes. Ventral muscle field subtriangular, confined to the delthyrial chamber, with arcuate anterior margin and bounded anteriorly by a subcircular thickening attaining one half of valve length. Vascula media narrow, straight, moderately divergent, originated at the anterolateral ends of muscle field.

Dorsal interior with robust, laterally compressed brachiophores diverging at about 90°, bounding deep, semiconical dental sockets. Notothyrial platform narrow, elevated, merged anteriorly with a broad rounded median ridge fading at valve midlength. Cardinal process simple, blade-like, slightly thickened anteriorly. Poorly impressed dorsal muscle field consisting of smaller elongate oval anterior pair of adductor scarsand larger subcircular posterior ones.

Remarks. In the revision by Ulrich and Cooper (1938), *Taffia* is characterized as a taffiid having planoconvex or concavoconvex profile, costellate or-

nament, well-developed chilidium and pseudodeltidium, and orthoid cardinalia lacking cardinal process. With respect to the latter feature, Neuman (1976) noted that in a few specimens of the type species *T. planoconvexa* Butts, from the Oddenville Formation (lower Arenig, Alabama) the cardinal process is variably developed, leading Cocks and Rong (1989, 2000) to introduce in the diagnosis of *Taffia* the statement "usually without simple cardinal process (but rarely present)". However, in our new species the cardinal process is a persistent character, like in those specimens attributed to *Taffia anomala* Benedetto and Herrera (1986), from the lower Llanvirn of the Precordillera, in which it varies from a low to thick ridge. Another feature that differentiates the Potrerillos specimens from the type material of *Taffia* is the biconvex lateral profile of shells, the dorsal valve being always gently convex. In both features our material approaches to the genus *Chaloupskia* erected by Neuman (in Neuman and Bruton, 1989) to include taffiids from the Arenig Lower Hovin Group (Hølonda, Norway) characterized by its planoconvex to vetribiconvex profile, persistent blade-like cardinal process and exteriors of largest specimens overgrown by comae, the latter being considered as the principal diagnostic feature. Although in the revised edition of the Treatise Cocks and Rong (2000) synonymized *Chaloupskia* with *Taffia* it seems adequate to retain it as a valid subgenus of *Taffia* to account for the above mentioned differences. Besides the type species *Taffia (Chaloupskia) scabrella* Neuman and *Taffia* sp. from the Summerford Group, Newfoundland (Neuman, 1976), the Precordilleran species *Taffia anomala* should also be included in this subgenus on the basis of its prominent comae and its well-developed cardinal process (*cf.* Benedetto and Herrera, 1986, pl. 3, figs. 1, 2, 6). *T. (Chalaoupskia) minima* sp. nov. differs from *T. (C.) scabrella* in its smaller size, equally costellate ornament and narrower dorsal ridge. Taking into account that in *T. (C.) scabrella* comae appear in specimens longer than 8 mm, their absence in our material can be attributed to the small size of specimens. The Precordilleran species *T. (C.) anomala* Benedetto and Herrera clearly differs from *T. (C.) minima* in its larger size, narrower sharp-crested and less numerous costellae (numbering 18-24 on the entire surface) and the presence of comae on the periphery of both valves. In addition, the pseudodeltidium in *T. (C.) anomala* covers almost entirely the delthyrium while in *T. (C.) minima* it is restricted to the posterior half.

Subfamily LEPTELLINAE Williams, 1965

Genus *Leptella* Hall and Clarke, 1892

Type species. *Leptaena sordida* Billings, 1862.

Subgenus *Leptella (Petroria)* Wilson, 1926

Type species. *Petroria rugosa* Wilson, 1926.

Diagnosis (Revised). Subgenus of *Leptella* with well developed comae on exteriors of both valves, especially on their anterior half ; external surface smooth or with fine, widely-spaced radial costellae.

Leptella (Petroria) ventrocristata sp. nov.
Figures 6.K-6.S

Holotype. A ventral valve CEGH-UNC 21798.
Paratypes. Two conjoined specimens, two ventral valves and one dorsal valve, CEGH-UNC 21791-21795; one external mold of ventral valve, CEGH-UNC 21833; one internal mold of dorsal valve and six internal molds of ventral valves, CEGH-UNC 21796, 21797, 21807, and 21827-21830.

Derivation of name. Refers to the presence of a ventral subperipheral rim.
Type locality and type stratum. San Juan Formation, uppermost levels exposed at Quebrada Potrerillos, Guandacol area.
Diagnosis. Small to medium-sized species of *Leptella (Petroria)* with prominent comae on the anterior half of both valves and fine, widely separated radial costellae. Ventral interior with stout, transversely elliptical, unsupported teeth. Interior of ventral valve with elevated, anteriorly bilobed subperipheral platform. Dorsal platform weakly elevated.
Description. Small to medium-sized, up to 13 mm wide (normally 8-10 mm wide), strongly concavo-convex, transversely semielliptical shells (average length/width ratio of ventral valve: 0,72). Cardinal extremities acute, mucronate in young specimens. Ventral valve strongly and evenly convex, maximum thickness at mid-length. Ventral interarea large, curved, transversely striated, orthocline. Delthyrium broad, triangular, almost entirely closed by a strongly arched pseudodeltidium enclosing apically a small rounded foramen. Dorsal valve strongly concave, deflected ventrally near the margin. Dorsal interarea planar, slightly narrower than ventral, transversely striated, hypercline. Notothyrium bounded laterally by thick chilidial plates and covered posteriorly by a small arched chilidium. Prominent shell overgrowths or 'comae' invariably present on the anterior half of both valves forming 3-7 roughly concentric rows. External surface free of comae bearing widely separated fine costellae visible on well-preserved external molds (figure 6 K).

Ventral interior with stout, transversely elliptical, unsupported teeth. Ventral muscle field short, confined to the deep delthyrial cavity, surrounded by

thick secondary deposits; adductor and diductor muscle scars indistinguishable from each other. Elevated, anteriorly bilobed, slightly undercut sub-peripheral platform extending anteriorly for about 3/4 valve length, its periphery radially striated and interrupted by several gaps corresponding to the passage of vascular trunks. Vascular system deeply impressed, saccate, with straight, slightly diverging vascula media which bifurcate near the margin.

Dorsal interior with rod-like, thin brachiophores projecting ventrally. Robust, widely divergent socket ridges merged posteriorly with thickened chilidial plates. Dental sockets shallow, semiconical. Dorsal platform weakly elevated medially, bilobed, radially striated, divided longitudinally by a narrow ridge which is initially broad and rounded becoming thinner and higher anteriorly, not continued beyond the platform. Dorsal muscle field poorly impressed, semielliptical, slightly elevated above the valve floor.

Remarks. Cooper (1956) provided a detailed description and discussion of the type material of *Petroria rugosa* Wilson. He stated that *Petroria* is closely related to *Leptella* Hall and Clarke from which differs in few characters, mainly the presence of 'prominent wavy lamellae' (comae) on the external surface, the presence of a callosity anterior to the ventral muscle field, and the median septum extending anteriorly to the 'visceral disk' (platform). Although the latter feature has been considered diagnostic of the subgenus *Leptella* (*Petroria*) by Cocks and Rong (1989, 2000), Benedetto and Herrera (1993) noted that in specimens of *Leptella* (*Leptella*) *variabilis* Benedetto and Herrera the anterior prolongation of the dorsal septum is highly variable, ranging from absent to fully developed. Such a variation has also been observed in populations of *Petroria* (*Petroria*) *rugosa acuta* Benedetto and Herrera (1986, pl. 2, figs. 8 and 11). Moreover, in some well-established species of *Leptella* (*Leptella*) such as *L.* (*L.*) *musculosa* Williams and Curry and *L.* (*L.*) *alata* Benedetto and Herrera, the median septum is often well developed outside the platform. The premuscular thickening in the ventral valve also is a variable feature. It is well developed in the type species *L.* (*L.*) *sordida* (Billings) as well as in the Precordilleran species *L.* (*L.*) *alata*, *L.* (*L.*) *variabilis* and *L.* (*L.*) *plana* (Benedetto and Herrera, 1993) but it is absent in the Irish species *L.* (*L.*) *musculosa*. On the other hand, a premuscular callus is present in *Leptella* (*Petroria*) *rugosa elevata* Benedetto and Herrera. The absence of dental plates was considered a distinguishing feature of *Petroria* by Williams and Curry (1985), but in both genera dental plates are usually very short and masked by secondary deposits. As Williams and Curry (1985) noted, *Petroria* and *Leptella* are very similar internally,

but they can readily be distinguished externally as *Petroria* has prominent shell overgrowths or comae. The same criterion was used by the author to separate the two subgenera (Benedetto, 2001a, p. 15).

The new species *L.* (*P.*) *ventrocristata* differs from the type species *L.* (*P.*) *rugosa* Wilson in having a conspicuous platform in the ventral valve. The closest species is *L.* (*P.*) *rugosa acuta* Benedetto and Herrera, from the top of the San Juan Formation at the Cerro Viejo area (latest Arenig/earliest Llanvirn), which shares the presence of a ventral platform, but usually it is weaker and confined to the sides of the valve. This is probably a synapomorphy that links phylogenetically the two species. In addition, *L.* (*P.*) *rugosa acuta* differs from *L.* (*P.*) *ventrocristata* sp. nov. in its larger shell size, more convex and less transverse ventral valve and strongly elevated dorsal platform. The internal features of *P. austrina* Ross are unknown in the type material from the Antelope Valley Limestone leading Ross (1972) to refer questionably this species to *Petroria*. The specimens assigned to L. (*P.*) cf. *austrina* Ross by Ross and James (1987), from a Cow Head Group boulder (Newfoundland; lower *Orthidiella* Zone, upper Arenig), differ in their strongly concavo-convex shell, sulcate dorsal valve, less prominent comae, and shorter dorsal platform.

Subfamily PELONOMIINAE Cocks and Rong, 1989

Genus *Pelonomia* Cooper, 1956

Type species. *Orthis delicatula* Billings, 1865.

Pelonomia? sp.
Figures 6.Z-6.Z2

Material and occurrence. One external mold of dorsal valve and one internal mold of dorsal valve; one fragmentary internal mold of ventral valve, CEGH-UNC 21859-21861. Lower part of the Gualcamayo Formation, Quebrada Los Sapitos.

Description. Subrectangular shell, 9,5 mm wide and 6,1 mm long. Cardinal extremities right-angled, coinciding with maximum width. Ventral valve gently convex, at least in the posterior third (the only region preserved in the available specimen). Dorsal valve gently concave posteriorly becoming flat in the anterior half. Ornament subequally parvicostellate, with 6-7 narrow rounded costellae in 2 mm separated by wide flat interespaces bearing one or rarely two finer costellae. Ventral interarea planar, catacline, with delthyrium covered apically by an incipient pseudodeltidium; dorsal interarea catacline, approximately one third as high as ventral. Chilidium not preserved in the available specimen.

Ventral interior too poorly preserved for description of internal features. Dorsal interior with widely

divergent, thin, blade-like socket ridges bounding narrow, slit-like dental sockets. Cardinal process very small located near the medial junction of socket ridges. A flat, slightly raised area is present in front of the cardinalia. Median ridge and platform absent. Dorsal muscle field not impressed.

Remarks. This small plectambonitoid is difficult to place sistematically because of the very limited available material. The absence of platform and ridges inside the dorsal valve, and the small cardinal process indicate closest affinities with the enigmatic Pelonomiinae, erected by Cocks and Rong (1989) to include the monotypic genus *Pelonomia* Cooper 1956. In size, outline, shell profile, ornament and cardinalia features, the Potrerillos specimens are comparable to *P. delicatula* (Billings), from the Cow Head Formation (Llanvirn). They differ from this species in lacking spine-like pseudopunctae along the dorsal internal sulcus, which is considered a diagnostic feature of this genus. In addition, our material lacks of dorsal sulcus and ventral fold, and for this reason the Potrerillos specimens are referred questionably to *Pelonomia*.

Order BILLINGSELLIDA Schuchert, 1893
Suborder CLITAMBONITTIDINA Öpik, 1934
Superfamily POLYTOECHIOIDEA Öpik, 1934
Family TRITOECHIIDAE Ulrich and Cooper, 1936

Genus *Tritoechia* Ulrich and Cooper, 1936

Subgenus *Tritoechia* (*Tritoechia*) Ulrich and Cooper, 1936

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

Tritoechia (*Tritoechia*) sp.
Figures 6.T-6.Y

Material and occurrence. One fragmentary conjoined specimen, two ventral valves and two dorsal valves, two internal molds of ventral valve and three internal molds of dorsal valve, CEGH-UNC 21834-21844. Uppermost levels of the San Juan Formation, Quebrada Potrerillos.

Description. Shell up to 19 mm wide, semielliptical (average length/width ratio 0,61). Cardinal extremities slightly obtuse. Ventral valve subpyramidal, gently convex in lateral view. Beak pointed, slightly curved. Ventral interarea planar, very high (averaging 45% as high as wide), radially striated, apsacline, forming with the commissural plane an angle of 45°-60°. Pseudodeltidium strongly arched, semiconical, bearing a circular apical foramen. Dorsal valve gently convex, non-sulcate or bearing a broad shallow sulcus on its anterior half. Dorsal interarea very low, planar, strongly anacline. Notothyrium entirely covered by an arched chilidium. Ornament subequally multicostellate, with 7-8 rounded costellae in 2 mm near the anterior margin. Interior of ventral valve with plate-like, semielliptical teeth supported by short receding dental plates subperpendicular to valve floor. Ventral muscle field subrectangular, with narrow elongate median adductor scars more elevated than the broader lateral diductor scars. A faint median ridge starts in front of the muscle field fading at about 3/4 valve length. Dorsal interior with triangular, posteriorly inclined, anteriorly free notothyrial platform bounded laterally by high chilidial plates. Cardinal process thick, posteriorly enlarged. Dental sockets slit-like, deep, open laterally, bounded by thick gently arched socket ridges running subparallel to the posterior margin. Dorsal median ridge very short, thick, merged with the front of notothyrial platform and confined to a depression below them. Dorsal muscle field poorly impressed, large, bisected by faint radial transmuscle septa.

Remarks. Although this form is relatively abundant in the etched residues, all available specimens are fragmentary. Their multicostellate ornament indicates that they are attributable to *Tritoechia* (*Tritoechia*) rather than to the recently erected subgenus *Tritoechia* (*Parvitritoechia*) Benedetto which possesses a distinctive markedly parvicostellate ornament. The Potrerillos species differs from *T.* (*T.*) *prima* Benedetto (in Benedetto *et al.*, 2003), from the lower part of the San Juan Formation (upper Tremadoc), among other features, in its higher and more inclined interarea. The lower Arenig species *T.* (*T.*) *gigas* Benedetto can be distinguished by its larger size, less inclined and shorter ventral interarea, and longer and strongly raised ventral muscle field. In size, ornament and interarea inclination our material approximates to *T.* (*T.*) *mollesensis* Benedetto (2003a), from approximately coeval volcanosedimentary beds of Famatina Range (Molles Formation). Available material, however, is too incomplete for more accurate comparisons.

Acknowledgements

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