



Taxonomic position and phylogenetic relationships of the bivalve *Goniophorina* Isberg, 1934, and related genera from the early Ordovician of northwestern Argentina

Teresa M. SÁNCHEZ¹

Abstract. On the basis of collections from Tremadoc and Arenig successions of northwestern Argentina, the affinities of *Goniophorina* Isberg, 1934, are reassessed. Studied material includes ucumariids, lipanellids, *Goniophorina*, and other specimens for which the new genus *Lossella* is proposed with the new species *L. juancruzi* sp. nov. as type species. *Goniophorina* and *Lossella* are grouped in the new family Goniophorinidae. Synapomorphies of goniophorinids, ucumariids, and lipanellids lead to the conclusion that *Goniophorina* integrates a major group of edentulous bivalves, a lineage of which -the ucumariids- probably gave rise to Anomalodesmata. This fauna represents a rapid, local diversification event that is part of the west-Gondwanan bivalve radiation during the early Ordovician.

Resumen. POSICIÓN TAXONÓMICA Y RELACIONES FILOGENÉTICAS DEL BIVALVO *GONIOPHORINA* ISBERG, 1934, Y GÉNEROS RELACIONADOS DEL ORDOVÍCIO TEMPRANO, NOROESTE DE ARGENTINA. Sobre la base de colecciones del Tremadociano y Arenigiano del noroeste Argentino se discuten las afinidades de *Goniophorina* Isberg, 1934. El material incluye ucumariidos, lipanellidos, *Goniophorina* y otros ejemplares para los cuales se propone el nuevo género *Lossella* cuya especie tipo es *L. juancruzi* sp. nov. *Goniophorina* y *Lossella* se incluyen en una nueva familia, Goniophorinidae. Las sinapomorfías de goniophorinidos, ucumariidos y lipanellidos permiten concluir que *Goniophorina* integró un grupo de bivalvos edéntulos, de los cuales los ucumariidos probablemente dieron origen a Anomalodesmata. Esta fauna representa un rápido evento local de diversificación que forma parte de la radiación de los bivalvos en el oeste de Gondwana durante el Ordovícico temprano.

Key words. Goniophorinids. Early Ordovician. Northwestern Argentina.

Palabras clave. Goniophorinidos. Ordovícico temprano. Noroeste de Argentina.

Introduction

The genus *Goniophorina* Isberg, 1934, is a common fossil in the fine-grained sandstones and shales of Early Ordovician age of western Argentina. Harrington (1938) first recognized the genus in Argentina and erected the species *G. tenuicostata* on the basis of material from beds of the *Kainella meridionalis* Zone (early Tremadoc) exposed near to Iruya village, in the Jujuy province of northwestern Argentina. Subsequent collections enlarged the spatial and temporal distribution of the genus, which are now recorded from middle Arenig strata of the Cordillera Oriental and the Famatina basin (figure 1) (Sánchez, 1997). A careful analysis of these collections, along with additional material from new localities, allows

the definition of the new genus *Lossella*, a taxon related to *Goniophorina*, but showing differences enough to separate it as a new genus. The aim of this contribution is to reassess previous assignments to *Goniophorina* and, on the basis of this revision, to discuss the taxonomic position and phylogenetic relationships of this genus and related forms in the context of the early radiation of Gondwanan bivalves.

Definition of the genus *Goniophorina* Isberg

Sánchez (2003, 2005), following Liljedahl (1994), considered that the presence or absence of radial ornament is a useful diagnostic feature at species level but not to separate the subgenera *G. (Goniophorina)* and *G. (Cosmogoniophorina)*. Consequently, the subgenus *Cosmogoniophorina* was rejected and the following revised diagnosis of the genus *Goniophorina* Isberg, 1934 was proposed: 'Shell equivalve, strongly inaequilateral, elongated, inflated; posterior margin obliquely truncated; anterior margin rounded; dorsal and ventral margins diverging posteriorly; strong umbonal ridge extending from beak to pos-

¹Centro de Investigaciones Paleobiológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba y Consejo Nacional de Investigaciones Científicas y Técnicas. Avenida Vélez Sarsfield 299, 5000 Córdoba, Argentina
tsanchez@com.uncor.edu

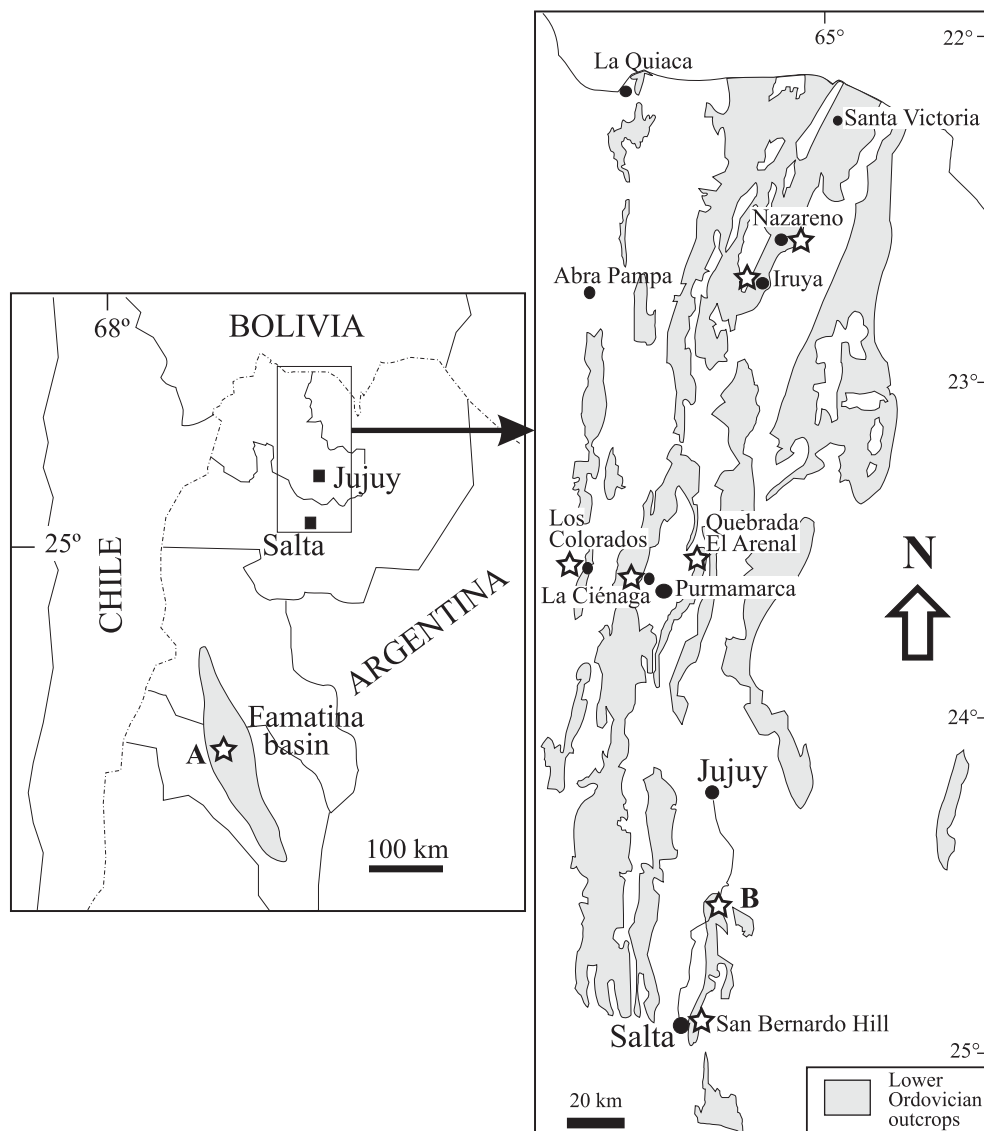


Figure 1. Location map of the described species from the Cordillera Oriental (part of the Northwestern Argentina basin) and the Famatina basin. **A**, Cachiuyo River, Famatina basin; **B**, Road 9 (Salta-Jujuy), km 1651.5 / *mapa de ubicación de las especies analizadas de la Cordillera Oriental (parte de la cuenca del Noroeste Argentino) y de la cuenca de Famatina. A*, Río Cachiuyo, cuenca de Famatina; **B**, Ruta 9 (Salta-Jujuy), km 1651,5.

terovertral angle, separating convex anteroventral area from convex posterior slope. Comarginal growth lines, sometimes with radial ornament. Anterior adductor muscle scar rounded, well-impressed, posterior adductor muscle scar ill-preserved. Edentulous' (Sánchez, 2005, p. 545).

Isberg (1934) considered *Goniophorina* as the ancestor of *Goniophora* Phillips, 1848. However, this author had doubts on their phylogenetic relationships due to the differences in the type of ligament, which is internal in *Goniophorina* and external in *Goniophora* (Isberg, 1934, p. 205), and in the presence of cardinal teeth in *Goniophora*. According to Isberg (1934, p. 205), the absence of teeth in *Goniophorina* may be due

to its Silurian record, older than that of *Goniophora* (Devonian). Therefore, he defined *Goniophorina* as a 'primitive' form from which *Goniophora* could have derived. This point of view was followed in the Treatise, where the two genera are differentiated only on the basis of the presence or absence of teeth (Newell, 1969, p. N396). This fact probably generated some confusion in subsequent works. Babin and Gutiérrez-Marco (1991) described and illustrated *Goniophora* (*Cosmogoniophora*) sp. from the middle Ordovician Hesperian Massif (Spain). However, in their material there is no evidence of a ventral sinus, a feature indicating *Goniophora* was a byssate form (Stanley, 1972). Rather, the shell outline of the illus-

trated specimens (Babin and Gutiérrez-Marco, 1991, pl. 5, figs. 3 and 4) is close to that of the Argentine *Goniophorina* material (e.g., from Iruya and Los Colorados localities of the Cordillera Oriental, and from the Famatina basin). Also, *Goniophora* (*Cosmogoniophora*) *extensa* Cope (1996) from the Arenig of Llangynog Inlier (South Wales), resembles *Goniophorina* rather than *Goniophora* Phillips. It lacks a well-developed ventral sinus, and the author stated that it is closest to the material assigned to *Goniophora* (*Cosmogoniophora*) sp. by Babin and Gutiérrez-Marco (1991) [Cope, 1996, p. 1006; pl. 4, figs. 3 and 5. Note that in the captions these figures are referred to *Goniophorina* (*Cosmogoniophorina*)].

Cope (2004) considered that *Goniophora* and *Goniophorina* are closely related genera. However, it becomes evident that similarities mostly concern to the presence of a subumbonal carina, and in a lesser degree to the shell outline. The detailed description of *Goniophora* by Johnston (1993; see also Babin, 1966, and Bradshaw, 1999) established the most important differences between this genus and *Goniophorina*, such as the presence of 2 or 3 cardinal teeth, a posterior internal ridge, an internal ligament, and the anterior adductor scar bounded internally by a strong myophoric buttress in *Goniophora*. Additionally, it is important to note that *Goniophora* was probably endobysate (Stanley, 1972, text-fig. 28F). By contrary, an analysis of the shell outline of *Goniophorina* indi-

cates that it was not byssate, but probably a free end-ofaunal (or semiendofaunal) form (figure 2).

Early Ordovician records of *Goniophorina* in Argentina

Until now, all species of *Goniophorina* recorded in Argentina have been assigned to or compared with *G. tenuicostata* Harrington.

So far, the records of *Goniophorina* in Argentina are the following (see localities in figure 1):

Goniophorina tenuicostata Harrington (figures 6.A-C). Early Tremadoc (*Kainella meridionalis*, *C. angulatus* zones), Santa Rosita Formation, Iruya, (Harrington, 1938).

G. cf. tenuicostata. Early Tremadoc (*Kainella meridionalis*, *C. angulatus* zones), Caldera Formation, and lower late Tremadoc, Floresta Formation, Sierra de Mojotoro (Sánchez and Vaccari, 2003) (but see below).

G. tenuicostata. Early Arenig. Cieneguillas Formation, La Ciénaga, west Purmamarca (Sánchez, 2005) (but see below).

G. tenuicostata (figure 6.D). Middle Arenig. Acoite Formation, Los Colorados (Sánchez, 1997).

G. tenuicostata (figure 6.E). Middle Arenig. Suri Formation, Famatina Basin (Sánchez, 1997).

Specimens of *G. tenuicostata* Harrington usually display variability in the ornament, even those re-

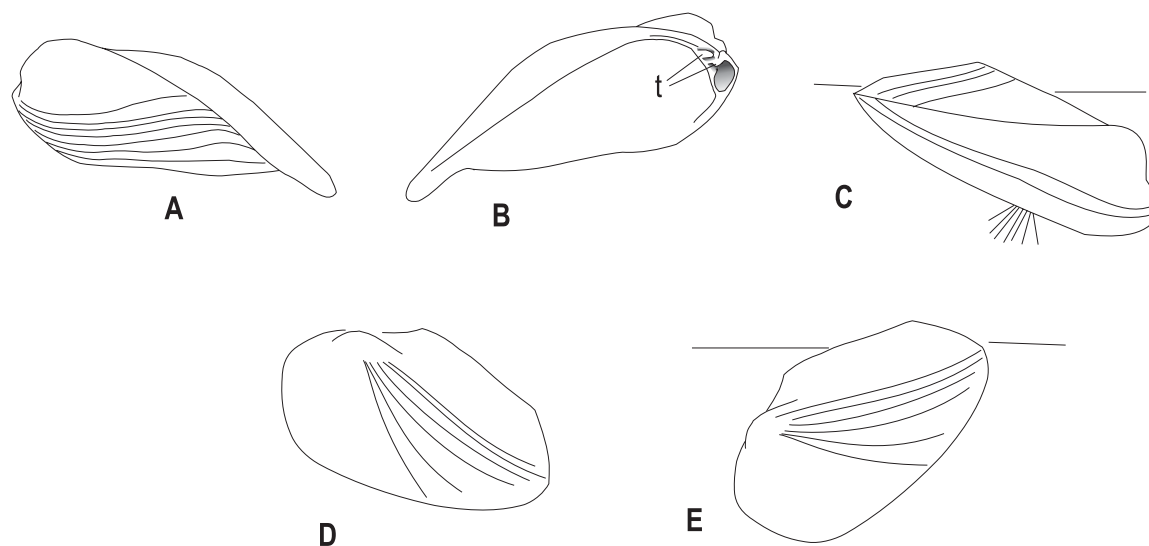


Figure 2. Schematic drawing of / dibujos esquemáticos de *Goniophora* and *Goniophorina*. **A, B**, *Goniophora pravinasuta* Johnston, 1993. **A**, external view of left valve showing outline shell and posteroumbonal carina / exterior de valva izquierda mostrando el contorno de la valva y la carina posumbonal; **B**, internal view of the same valve showing myophoric buttress limiting the anterior adductor muscle, and cardinal teeth (t), $\times 1.3$ (simplified from Johnston, 1993, fig. 53, A, B) / vista interna de la misma valva mostrando el septo miofórico que limita al músculo aductor anterior y dientes cardinales (t), $\times 1.3$ (simplificado de Johnston, 1993, fig. 53, A, B); **C**, Reconstruction of life habit of *Goniophora chemungensis* (Vanuxem) (simplified from Stanley, 1972, text-fig. 28 F) / reconstrucción del modo de vida de *Goniophora chemungensis* (Vanuxem) (simplificado de Stanley, 1972, text-fig. 28 F). **D-E**, *Goniophorina tenuicostata* Harrington, 1938 (drawn from Harrington, 1938, Lám. III, figs. 1 and 5) / (tomado de Harrington, 1938, Lám. III, figs. 1 y 5); **D**, left valve showing ornament / valva izquierda mostrando la ornamentación; **E**, reconstruction of life habits of *Goniophorina* / reconstrucción del modo de vida de *Goniophorina*.

covered from the same horizon. In some individuals a fine radial ornamentation covers the entire shell surface, while in others it is confined to the central region of the valve, being absent on the slopes. These changes in ornament were attributed either to within-population variations or to a preservational artifact (Sánchez and Vaccari, 2003). However, the lack of a subumbonal carina in specimens previously referred to *Goniophorina*, such as *Goniophorina* cf. *C. tenuicostata* (Sánchez and Vaccari, 2003) from the Floresta Formation and *G. tenuicostata* (Sánchez, 2005) from the lower Arenig Cieneguillas Formation, is considered a feature taxonomically significant enough to recognize the new genus *Lossella*, to which these two species are referred.

Taxonomic position and phylogenetic relationships of *Goniophorina*

Goniophora Phillips has been placed in the Family Mecynodontidae Haffer, 1959 (Babin, 1966; Johnston, 1993; Bradshaw, 1999); however most authors have referred *Goniophorina* Isberg to Modiomorphidae Miller, these placements attest to the significant differences between both genera. However, after the revision of modiomorphids by Fang and Morris (1997), *Goniophorina* cannot be placed in this group. Previous suggestions by Waller (1990) and Johnston (1993), as well as the cladistic analysis of Carter *et al.* (2000) agree with the new arrangement proposed by Fang and Morris (1997), which suggested that some genera related to *Modiomorpha* Hall, 1869, must be included in the Anomalodesmata. According to Fang and Morris (1997) modiomorphids are characterized by a broad hinge plate, an usually subordinate or absent radial ornament, and probably byssiferous habits.

On the other hand, genera such as *Modiolopsis* Hall, 1847, *Whiteavesia* Ulrich, 1893, and similar "early modioliform Paleozoic genera" should be removed from Modiomorphidae and placed in Modiolopsoidea Fisher (*nom. transl.* Modiolopsidae) (Fang and Morris, 1997). Therefore, *Goniophorina* cannot be included in the modiolopsids, which display modioliform byssate shells (Fang and Morris, 1997; Sánchez, 2005). In a previous paper (Sánchez, 2005) *Goniophorina* was tentatively placed in the Family Lipanellidae Sánchez due to the predominantly radial ornamentation, the edentulous condition of the hinge, and the absence of a byssal sinus. However, as Sánchez (2005) pointed out, the development of anterior and posterior slopes (see figure 4) suggest a relationship of *Goniophorina* to the Family Ucumariidae Sánchez.

Ucumariids are characterized by the development of pustules at the intersections of radial and comarginal costae. The simplest ucumariid, *Ucumaropsis*

Sánchez, displays a simple pattern of densely-packed, fine radial costae bearing small pustules (figures 6.K, L, O), whereas *Ucumaris* Sánchez shows prominent radial costae with a series of finer ones within the interspaces (figures 6.J, M). As a result, two different types of pustules developed, small pustules located on the intercalated costae, and larger ones on the prominent costae. In lipanellids there are two prominent subumbonal carinae and several folds, which developed behind the anterior carina (figure 6.N). Additionally, small radially arranged accessory subumbonal muscle scars are preserved in some specimens (Sánchez, 2005).

It becomes evident that the Argentine species of Goniophorinidae analyzed herein share a series of features such as an edentulous hinge, predominant radial ornament, and the development of slopes, all of which are synapomorphies when compared with other early Ordovician taxa from the same basin (e.g., *Intihuarella* Sánchez, in Sánchez and Vaccari, 2003) or other areas (e.g., *Babinka* Barrande, upper Tremadoc of the Montagne Noire, Babin, 1977).

The early radiation of bivalves in the Argentine Cordillera Oriental is documented beginning in the upper early Tremadoc (*Kainella meridionalis* Zone, *Cordylodus angulatus* Zone), with the first record of *Goniophorina tenuicostata* and *Lossella juancruzi* gen. et sp. nov. The basal stem of this cladogenetic event is unknown due to the lack of records from the lowermost Tremadoc-upper Cambrian strata of the basin. It is hypothesized that the ancestor was probably a simple *Lossella*-like form.

Figure 3 shows a phylogenetic tree constructed on the basis of the morphological features and age of the species considered. *Lossella* gen. nov. seems to be the simplest form of the ensemble. It possesses the above mentioned synapomorphies (hinge, ornament, and slopes) but lacks a well-defined subumbonal carina such as that of *Goniophorina*. Also, specimens of *Lossella* display fine radial and comarginal ornament, but pustules as those of ucumariids are not developed. *Lossella juancruzi* gen. et sp. nov. first appears in the early Tremadoc and persists until the early Arenig. The apomorphic feature of *Goniophorina* is its well-developed carina (figure 3, node 1). The species *G. tenuicostata* Harrington reached the middle Arenig without significant changes, and then dispersed throughout the Cordillera Oriental basin and into the Famatina Basin. At the base of the goniophorinid radiation arose the ucumariids, with their distinctive pustules at the intersection of radial and comarginal lines (figure 3, node 2). *Ucumaris conradoi* Sánchez (figure 6.J) is the oldest species of the family, but its derived characters make it difficult to establish the relationship with the younger *Ucumaropsis lermaensis* Sánchez (figure 6.K), recorded from upper Tremadoc

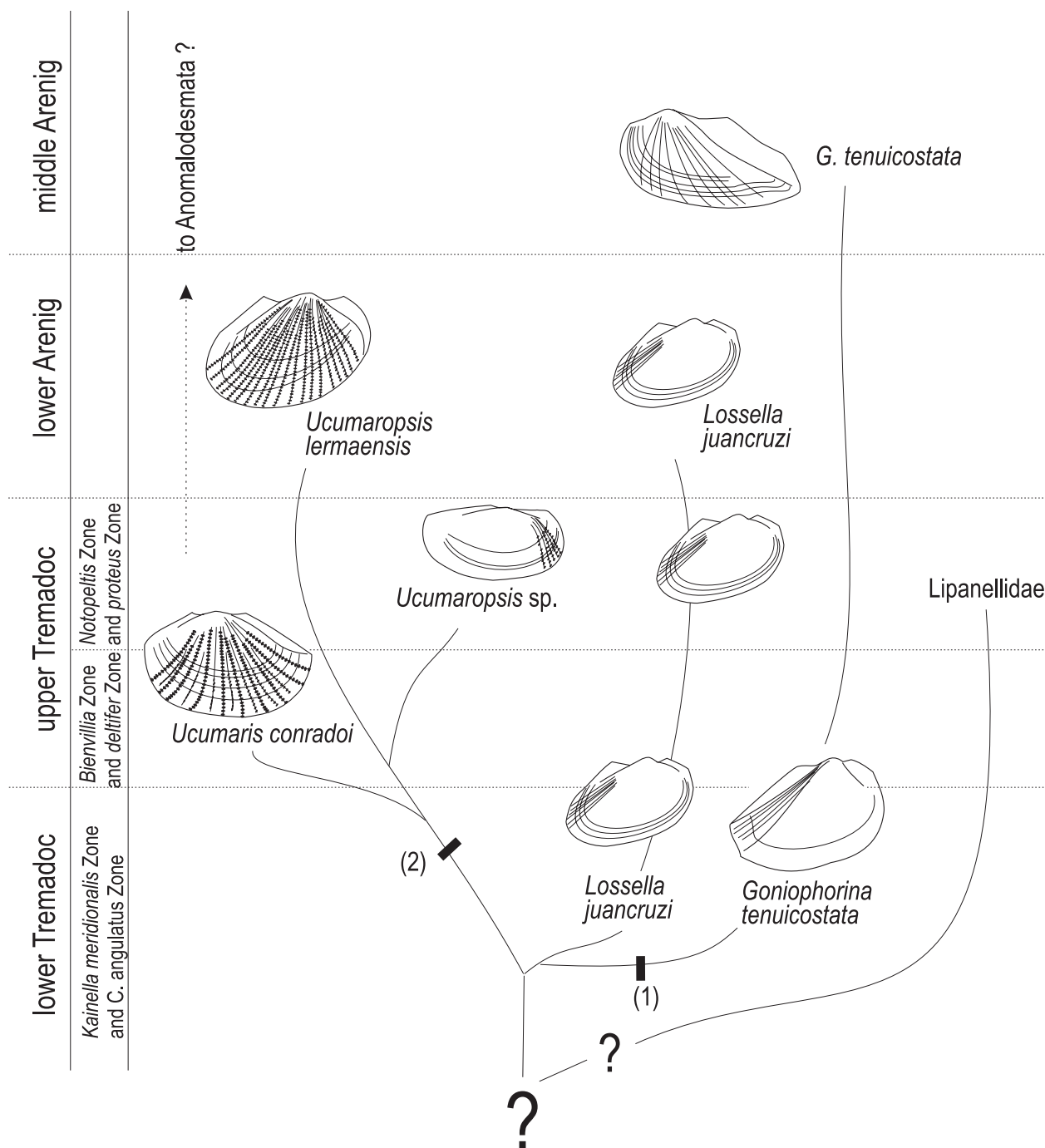


Figure 3. Proposed phylogenetic tree of the analyzed species. Apomorphies: 1, carina; 2, pustules (see age and stratigraphic provenance of species in the text) / árbol filogenético propuesto de las especies analizadas. Apomorfías: 1, carena; 2, pústulas (ver edad y procedencia estratigráfica de las especies en el texto).

and lower Arenig strata. It is postulated that *Ucumaris* and *Ucumaropsis* shared an unknown 'pustulate' ancestor. Despite its younger record, the shell surface of *Ucumaropsis* retains a simpler ornament pattern (a single order of radial lines and pustules) which was probably inherited from the ancestral form, whereas *Ucumaris*, with a more complex ornament (two orders of both radial lines and pustules) may have split off

from the lineage leading to *Ucumaropsis*. The lipanelid *Lipanelia* Sánchez (figure 6.N) also possesses the three synapomorphies that characterize the ensemble of species considered in the evolutionary tree. Although the ornamental pattern of *Lipanelia* is by far more complex (see below), it probably derived from a species having fine radial ornament typical of *Goniophorina*, *Lossella* and the ucumariids.

I conclude that *Goniophorina* integrates a major group of edentulous bivalves, a lineage of which -the ucumariids- probably gave rise to the Anomalodesmata (Sánchez, in Sánchez and Vaccari, 2003). In this scenario, the new Family Goniophorinidae is proposed here to include *Goniophorina* and *Lossella* n. gen. Goniophorinids show closest affinities with the ucumariids and possibly also with the lipanellids.

The placement of the families discussed in this paper is difficult because most of the higher taxa were defined on younger forms. The rapid initial stage of diversification is characterized by 'primitive' bivalves that lack derived characters used to erect orders and suborders. Ucumariids were classified into the Anomalodesmata by Sánchez (in Sánchez and Vaccari, 2003) due to their apparent phylogenetic links with this major group (presence of pustules). However, ucumariids do not display some of the typical features of anomalodesmatan (e.g. shell gapes).

Until a thorough revision of the classification of basal groups of bivalves has been made, the material described herein is not referred to categories higher than family.

Finally, it is important to remark that this event is part of the west-Gondwana bivalve radiation, which involves other groups such as the intihuellids, which are strongly related to the cycloconchids (Sánchez, in Sánchez and Vaccari, 2003). The importance of Gondwanan shelves in the earliest bivalve diversification was first recognized by Babin (1993, 1995). Additional evidence (e.g. intihuellids and ucumariids from the northwestern basin, and *Catamarcaia* from the middle Arenig of the Famatina basin, which is considered as the basal stem giving rise to arcoids, Sánchez, 1995; Carter *et al.*, 2000) confirmed this suggestion and reinforced the importance of the western basins of Argentina in the first stages of Ordovician bivalve diversification (Sánchez and Benedetto, 2004).

Systematic paleontology

The descriptions of specimens are based on features shown in figure 4. The anterior and posterior slopes (or corselets, Johnston, 1993) are the flattened surfaces of the shell immediately below the dorsal margin. A slope is always developed behind the umbo, but in most of the species it is present in both the anterior and posterior regions. Development of slopes defines the length of the cardinal margin.

Specimens are deposited in the paleontological collection of the Centro de Investigaciones Paleobiológicas, Universidad Nacional de Córdoba, under the prefix CEGH-UNC. Revision of previous assigne-

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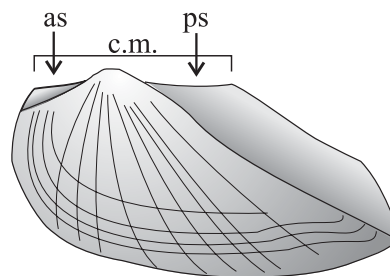


Figure 4. Schematic drawing of *Goniophorina* showing slopes and cardinal margin; **as**, anterior slope; **ps**, posterior slope; **c.m.**, cardinal margin / dibujo esquemático de *Goniophorina* mostrando los 'slopes' y el borde cardinal; **as**, 'slope' anterior; **ps**, 'slope' posterior; **c.m.**, margen cardinal.

ments includes material from collections of the Museo de Geología, Mineralogía y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy, prefix JUY-P.

Family GONIOPHORINIDAE nov.

Type genus. *Goniophorina* Isberg, 1934.

Diagnosis. Equivalve, inaequilateral shells with flattened areas (slopes) usually developed behind and anterior to umbo, sometimes only with posterior slope; non byssate; edentulous; fine radial ornament usually covering the shell surface.

Assigned genera. *Goniophorina* Isberg, *Lossella* gen. nov.

Goniophorina Isberg, 1934

Type species. *Goniophorina volvens* Isberg, 1934.

Goniophorina tenuicostata Harrington, 1938

Figures 6.A-E

Comments. Harrington (1938) erected the species *Goniophorina tenuicostata* on the basis of six specimens coming from the "Quebrada Colorada, Iruya. Black shales with *Kainella* (lower Tremadoc)" (Harrington, 1938, p. 135). No other information about the stratigraphic horizon was given. Specimens were housed as "Colección doctor J. Keidel" in the Dirección de Minas y Geología (Harrington, 1938, p. 135). Unfortunately, so far this collection has not been located and it is presumed lost. No other specimens from the Harrington's original sample are available in other repositories. The exact levels from which the original *Goniophorina tenuicostata* material was obtained remain unknown, so that it is unlikely new specimens will be found. However, the illustrations and de-

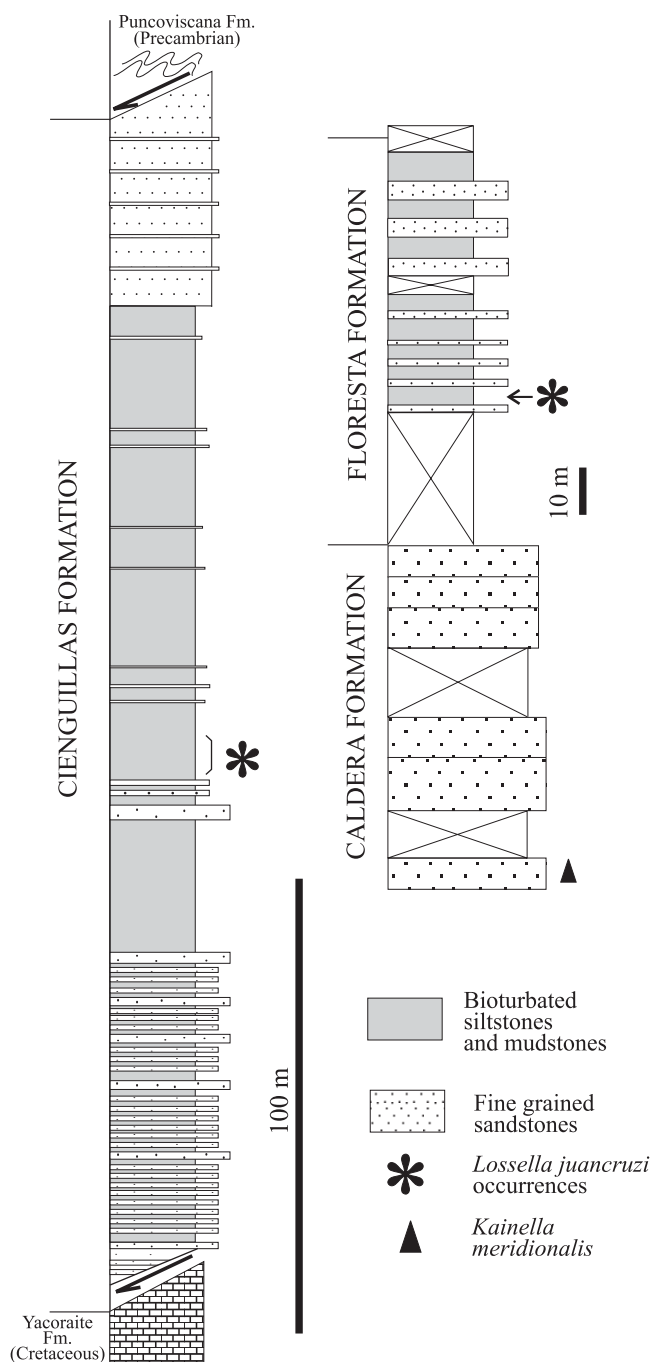


Figure 5. Stratigraphic columns of the Floresta (sierra de Mojotoro, Road 9, km 1651.5) and Cieneguillas (La Ciénaga) formations from which *Lossella juancruzi* gen. et sp. nov. was recovered. Occurrence of *Kainella meridionalis* is indicated to show its stratigraphic position respect to the levels bearing *Lossella juancruzi* gen. et sp. nov. / columnas estratigráficas de las formaciones Floresta (sierra de Mojotoro, Road 9, Km 1651.5) y Cieneguillas (La Ciénaga), de donde provienen los ejemplares de *Lossella juancruzi* gen. et sp. nov. La procedencia de *Kainella meridionalis* está indicada para mostrar su posición estratigráfica respecto a los niveles portadores de *Lossella juancruzi* gen. et sp. nov.

scription given by Harrington (1938) are enough to recognize the species *G. tenuicostata* as a valid taxon. Although no formal diagnosis of this species was

given, Harrington (1938, p. 134) gave a detailed description of the material. Some relevant features of the species are the following: "Small valves, size of the greater is 14.5 mm length and 10 mm height. Shell elongated-elliptical, with truncate posterior extremity ...Anterior area wide, posterior narrow... Posterior margin right, meeting the inferior margin at an acute-rounded angle, and the superior margin at an obtuse angle (about 130°). Articular line short ...Small, well-defined, not protruding umbos... Well defined subumbonal carina. Areas between the carina and both, the anterior and the posterior dorsal margins flat and depressed when compared with the general convexity of the valve. Shell ornamented by numerous and weak radial costae". Harrington (1938, Lám. III, figs. 1, 4, 5) figured three specimens but he did not designate a holotype. Cope (2002) designated the specimen of the Harrington's Lám. III, figure 1 as the lectotype of the species, reproduced herein as figure 6.A.

Pojeta (1971, p. 17) considered that the specimen figured by Harrington in lám. III, fig. 4 (here reproduced as figure 6.B) shows taxodont teeth, and then he suggested that this specimen is the oldest palaeotaxodont, an opinion followed by Cope (2002, p. 44). However, the photographs in the Harrington's paper are not conclusive to recognize the presence of teeth in the specimen of the figure 4. Therefore, it must be cautious with respect to the hinge nature of this specimen.

Lossella gen. nov.

Type species. *Lossella juancruzi* gen. et sp. nov.

Etymology. In honour of Renato Loss, paleontologist of the Instituto de Geología y Minería de Jujuy, who first collected the early Tremadoc specimens.

Diagnosis. Ovate to subquadrate, posteriorly elongated goniophorinids without subumbonal carina.

Discussion. Material from the Floresta and Caldera formations was assigned with doubts to the species *G. tenuicostata* Harrington on the basis of the absence of a well defined carina (Sánchez and Vaccari, 2003). Although development of anterior and posterior slopes, radial ornament, and edentulous hinge are similar to those of *Goniophorina* Isberg, the absence of the diagnostic subumbonal carina makes necessary the erection of the new genus *Lossella* to include this material.

Lossella juancruzi sp. nov.

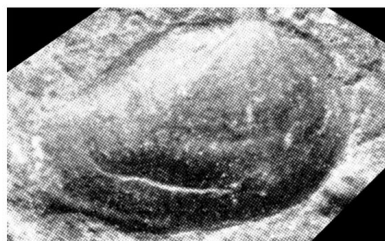
Figures 6.F-I

2003. *Goniophorina* (*Cosmogoniophorina*) cf. *tenuicostata* Harrington, Sánchez and Vaccari, p. 422, fig. 6.P, Q.

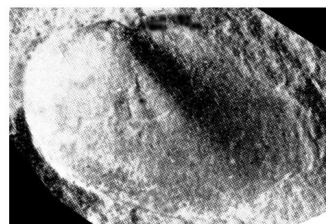
2005. *Goniophorina tenuicostata* Harrington, Sánchez, p. 545, fig. 4.18.



A



B



C



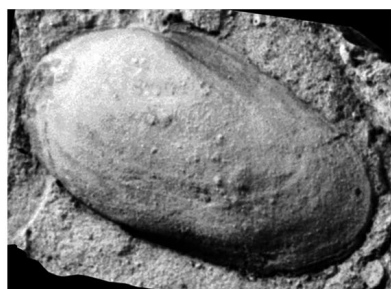
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E



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G



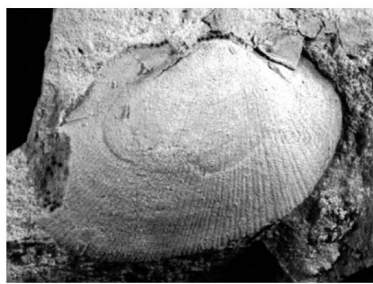
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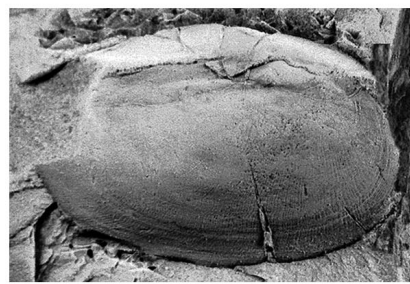
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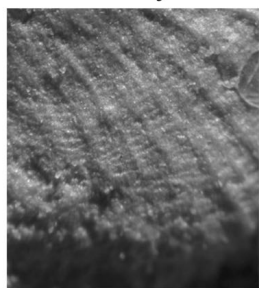
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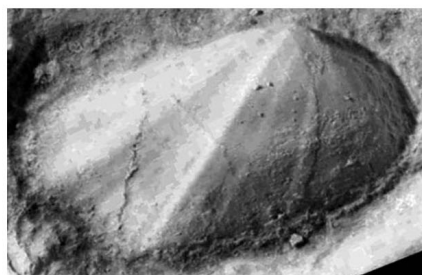
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L



M



N



O

Diagnosis. Ovate to subquadrate, posteriorly elongated shell; umbo placed in the anterior third of valve; anterior and posterior slopes well developed.

Etymology. From my grandson Juan Cruz.

Material. Holotype: internal mold of a left valve CEGH-UNC 20410, from the Floresta Formation, sierra de Mojotoro, Road 9, Km. 1651.5. **Paratypes:** left and right valves preserved as internal molds CEGH-UNC 20408, 20409, 20430, and 21901, from the Floresta Formation. Material with the suffix JUY-P 1-3 comes from the Caldera Formation. It is housed in the Museo de Geología, Mineralogía y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy. The museum label lists the horizon and locality as: sierra de Mojotoro, km 42, Road 9.

Description. Subquadrate, posteriorly elongate shells. Small -maximum length 20 mm, maximum height 10 mm-, orthogyrate beaks in anterior part of shell but not terminal; hinge line short; anterior margin broadly rounded; posterior margin acute; ventral margin gently rounded. Posterior slope limited by a slight, sometimes ill defined carina. Sculpture of very fine radial lines usually well preserved on the posterior slope, decreasing and gradually attenuating on the shell flank (Sánchez and Vaccari, 2003, p. 423).

Horizon and locality. Caldera Formation, Sierra de Mojotoro (Jujuy province), upper part of the early Tremadoc, *Kainella meridionalis* Zone, *Cordylodus angulatus* Zone; Floresta Formation, sierra de Mojotoro, lower part of the late Tremadoc, *P. deltifer* Zone (Sánchez and Vaccari, 2003).

Other occurrences. Cieneguillas Formation, lower Arenig, La Ciénaga (Sánchez, 2005).

Comments. Specimens assigned to *G. tenuicostata* Harrington by Sánchez (2005) coming from the La Ciénaga locality also lack a well defined carina, and are close to the material from the Floresta Formation. Therefore, they have been reassigned to the new species *Lossella juancruzi*.

Family UCUMARIIDAE Sánchez (in Sánchez and Vaccari, 2003)

Genus *Ucumaropsis* Sánchez, 2005

Type species. *Ucumaropsis lermaensis* Sánchez, 2005.

Ucumaropsis sp.
Figures 6.L, O

Material. Two articulated shells, preserved as composite molds CEGH-UNC 21902, 21903, and an internal mold of right valve CEGH-UNC 21901.

Horizon and locality. Santa Rosita Formation, upper Tremadoc, Village of Nazareno, Jujuy Province. Specimen CEGH-UNC 21901 comes from the base of the Rupasca Formation, lower late Tremadoc (*Bienvillia tetragonalis* Zone, *P. deltifer* Zone), Quebrada El Arenal, Jujuy Province (figure 1).

Description. Ovate shell; umbo not protruding, placed at midline of the valve; shell body slightly convex, without carina. Well developed posterior slope. Muscle scars not preserved. Ornament of very fine concentric and closely-packed radial costae covering the entire shell surface. Radial and concentric

Figure 6. A-C, *Goniophorina tenuicostata* Harrington, lower Tremadoc, Santa Rosita Formation, Iruya. **A**, left valve, reproduced from Harrington, 1938, pl. III, fig. 1, x 5 / *valva izquierda, reproducida de Harrington, 1938, pl. III, fig. 1, x 5*; **B**, right valve, ib., pl. III, fig. 4, x 1.8 / *valva derecha, ib., pl. III, fig. 4, x 1.8*; **C**, left valve, ib., pl. III, fig. 5, x 3.5 / *valva izquierda, ib., pl. III, fig. 5, x 3.5*; **D, E, *Goniophorina tenuicostata*** Harrington; **D**, composite mold of left valve, CEGH-UNC 7036, Acoite Formation, middle Arenig, Los Colorados, x 3.5 / *molde compuesto de valva izquierda, CEGH-UNC 7036, Formación Acoite, Arenigiano medio, Los Colorados, x 3.5*; **E**, composite mold of right valve, CEGH-UNC 15024, middle Arenig, Suri Formation, Cachiyuyo river (Famatina Basin), x 2.5 / *molde compuesto de valva derecha, CEGH-UNC 15024, Arenigiano medio, Formación Suri, río Cachiyuyo (cuenca de Famatina), x 2.5*; **F-I, *Lossella juancruzi*** gen. et sp. nov.; **F**, composite mold of right valve, JUY-P 3, lower Tremadoc, Caldera Formation, sierra de Mojotoro, Road 9, km. 42, x 2 / *molde compuesto de valva derecha, JUY-P 3, Tremadociano inferior, Formación Caldera, sierra de Mojotoro, Ruta 9, km. 42, x 2*; **G**, internal mold of left valve, holotype, CEGH-UNC 20410, upper Tremadoc, Floresta Formation, sierra de Mojotoro, Road 9, km 1651.5, x 3 / *molde interno de valva izquierda, holotipo, CEGH-UNC 20410, Tremadociano superior, Formación Floresta, sierra de Mojotoro, Ruta 9, km 1651.5, x 3*; **H**, internal mold of left valve, CEGH-UNC 20713, lower Arenig, Cieneguillas Formation, La Ciénaga, x 5 / *molde interno de valva izquierda, CEGH-UNC 20713, Arenigiano inferior, Formación Cieneguillas, La Ciénaga, x 5*; **I**, internal mold of right valve, CEGH-UNC 20711, x 2 / *molde interno de valva derecha, CEGH-UNC 20711, x 2*; **J, M, *Ucumaris conradoi*** Sánchez, upper Tremadoc, Floresta Formation, sierra de Mojotoro, Road 9, km 1651.5 / *Tremadociano inferior, Formación Floresta, sierra de Mojotoro, ruta 9, km 1651.5*; **J**, composite mold of left valve, holotype, CEGH-UNC 20250, x 8.5 / *molde compuesto de valva izquierda, holotipo, CEGH-UNC 20250, x 8.5*; **M**, detail of ornament, same specimen of figure J, x 17 / *detalle de la ornamentación del ejemplar de la figura J, x 17*; **K, *Ucumaropsis lermaensis*** Sánchez, composite mold of right valve, holotype, CEGH-UNC 20718, lower Arenig, San Bernardo Formation, cerro San Bernardo, x 3.5 / *molde compuesto de valva derecha, holotipo, CEGH-UNC 20718, Arenigiano inferior, Formación San Bernardo, cerro San Bernardo, x 3.5*; **L, O, *Ucumaropsis*** sp., upper Tremadoc, Santa Rosita Formation, Nazareno / *Tremadociano superior, Formación Santa Rosita, Nazareno*; **L**, right valve of articulated specimen preserved as composite mold, CEGH-UNC 21903, x 3 / *valva derecha de un ejemplar articulado preservado como molde compuesto, CEGH-UNC 21903, x 3*; **O**, detail of ornament, same specimen of figure L, x 17 / *detalle de la ornamentación del ejemplar de la figura L, x 17*; **N, *Lipanelia purmamarcensis*** Sánchez, upper Tremadoc, Upper Member of the Coquena Formation, quebrada Chalala, internal mold of right valve, CEGH-UNC 20686, x 3 / *Tremadociano superior, Miembro Superior de la Formación Coquena, quebrada Chalala, molde interno de valva derecha, CEGH-UNC 20686, x 3*. Figures reproduced by permissions of Museo de La Plata (figures A-C), Asociación Paleontológica Argentina (figures F, J), and The Paleontological Society (figures I, K, N) / *figuras reproducidas con autorización de: Museo de La Plata (figureas A-C), Asociación Paleontológica Argentina (figuras F, J), y The Paleontological Society (figuras I, K, N)*.

lines form a reticulate pattern with small pustules at the intersections (figure 6.O). Hinge area not known. **Discussion.** Development of pustules at intersections of radial and comarginal ornament is a diagnostic feature of ucumariids (Sánchez, in Sánchez and Vaccari, 2003). The pattern of radial ribs and pustules (a single order) is similar to that of the genus *Ucumaropsis* Sánchez. Although the material differs in some features from the type species such as the shell outline and the placement of the umbo, the small sample precludes the erection of a new taxon.

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