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Ucumariidae new family (Bivalvia, Anomalodesmata) and other bivalves from the Early Ordovician (Tremadocian) of northwestern Argentina

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Abstract. A new Tremadocian bivalve fauna is described from the Floresta Formation at Sierra de Mojotoro, Jujuy Province. The new genus *Ucumaris* is described and is the basis for a new family of Anomalodesmata, the Ucumariidae, extending the record of the anomalodesmatans back to the Tremadocian. *Intihuarella simplicidentata* nov. gen. et sp. included in a new family of Actinodontoida, the Intihuarellidae nov. and an undetermined Redoniidae?, are also described. Additionally, several specimens of *Goniophorina* (*Cosmogoniophorina*) cf. *tenuicostata* Harrington are described and illustrated. These taxa indicate a significant diversification of bivalves in Gondwanan shelves at the beginning of the early Ordovician.

Resumen. UCUMARIIDAE FAM. NOV. (BIVALVIA, ANOMALODESMATA) Y OTROS BIVALVOS DEL ORDOVÍCICO TEMPRANO (TREMADOCIANO) DEL NOROESTE DE ARGENTINA. Se describe una nueva fauna de moluscos bivalvos Tremadocianos proveniente de la Formación Floresta, Sierra de Mojotoro, Provincia de Jujuy. Se propone una nueva familia de Anomalodesmata, Ucumariidae nov., para incluir el nuevo taxón *Ucumaris conradoi* gen. et sp. nov., que extiende el registro de los anomalodesmata hasta el Tremadociano, y una nueva familia de Actinodontoida, Intihuarellidae nov., que incluye a *Intihuarella simplicidentata* gen. et sp. nov. Se reporta además un género indeterminado incluido con dudas en la Familia Redoniidae y la presencia de la especie *Goniophorina* (*Cosmogoniophorina*) cf. *tenuicostata* Harrington. Los nuevos taxones descritos confirman que los bivalvos experimentaron una rápida diversificación a comienzos del Ordovícico.

Key words. Tremadocian. Bivalves. Northwestern Argentina.

Palabras clave. Tremadociano. Bivalvos. Noroeste Argentino.

Introduction

Bivalves are virtually unknown from the interval spanning the Late Cambrian-earliest Tremadocian time. Currently, the oldest Argentinian bivalve faunas are those from the early Tremadocian rocks of northwestern Argentina. These bivalve faunas were described by Harrington (1938) in his paper on Ordovician Argentine faunas. There he reported *Palaeoneilo iruyensis* Harrington and *Goniophorina* (*Cosmogoniophorina*) *tenuicostata* Harrington, both from the *Kainella meridionalis* zone, which corresponds to the upper part of the lower Tremadocian (figure 2). Despite this time interval being critical to understanding the early diversification of bivalves, no further collections and descriptions have been made since Harrington's paper. The purpose of this report is to further describe bivalve faunas contained in the highly fossiliferous Tremadocian successions of Salta and Jujuy provinces of Argentina.

The material described here was obtained from the base of the Floresta Formation, a few meters above a sandstone bed bearing *Kainella meridionalis*, and consequently slightly younger than Harrington's specimens. The studied collection includes several specimens referred to the Ucumariidae, a new family of Anomalodesmata, constituting the first record of this subclass in beds of Tremadocian age. However, if the modiomorphids are included among the Anomalodesmata, as Fang and Morris (1997) and Waller (1990) suggested, the early Tremadocian species *Goniophorina (Cosmogoniophorina) tenuicostata* Harrington becomes the earliest record of the subclass. Additionally, the new actinodontoid family Intihuarellidae is erected to include the new genus *Intihuarella.* Associated forms include an undeterminated genus probably linked to the Family Redoniidae, and the modiomorphid *Goniophorina (Cosmogoniophorina)* cf. *tenuicostata* Harrington. Some poorly preserved specimens

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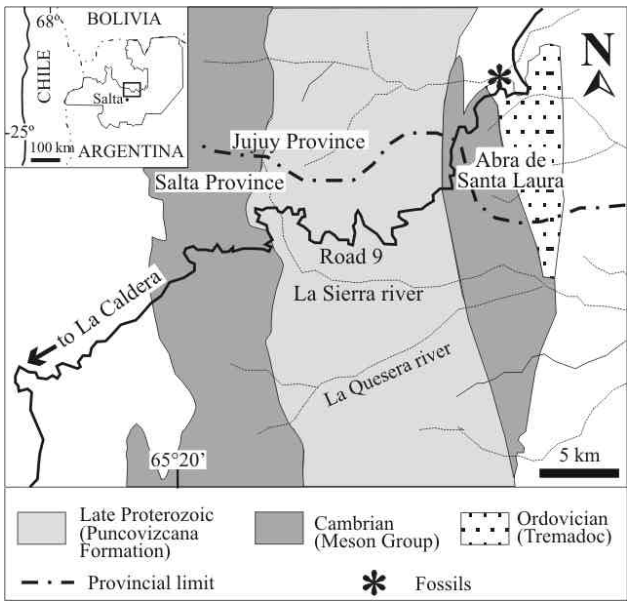

Figure 1. Location map. Based on Ferreira, 1997, cited in Moya, 1999. / *Mapa de ubicación. Basado en Ferreira, 1997, citado por Moya, 1999.*

representing probable additional new taxa were not included in the current study. The Floresta Formation fauna shows that bivalve diversity in the Tremadocian of the northwestern basin of Argentina is higher than has been previously recognized.

Geological setting

Fossiliferous strata are located in Jujuy Province, on the eastern flank of the Sierra de Mojotoro, which is part of the larger Cordillera Oriental (figure 1). In this region the early Ordovician succession (Santa Victoria Group, Turner, 1960) includes, from bottom to top, the La Pedrera, San José, Caldera, Floresta, and Aspero Formations (Moya, 1998). The bivalves described in this paper come from the lower part of the Floresta Formation exposed on the road-cut at km 1651.5 of Road 9 which runs between the cities of Salta and Jujuy. In the studied section the Floresta Formation is 82 m thick and consists mainly of light-green siltstones interbedded with some fine-grained sandstone beds. According to the regional geological map (Moya, 1998) and the evidence from sedimentary structures the exposed succession is overturned. The Floresta Formation overlies the amalgamated sandstone beds with *Kainella meridionalis* of the Caldera Formation, and its top is not exposed (figure 3).

Most of the bivalves described in this paper come from a 1 m thick interval of bioturbated siltstones. The thin interbedded fine-grained sandstones have yielded less well-preserved unidentifiable specimens (figure 3). A few meters above the level with bivalves there is a coquina bank containing well-preserved brachiopods (Benedetto and Carrasco, 2002).

Trilobites are very abundant in the interval containing the bivalves. They are represented by *Asaphelus catamarcensis* Kobayashi and *Bienvillia* sp. *A. catamarcensis* ranges from the *Neoparabolina frequens argentina* zone (late Cambrian-early Tremadocian) to the late Tremadocian (*Notopeltis orthometopa* and *Bienvillia tetragonalis-Conophrys minutula* zones, Harrington and Leanza, 1957). There is also a new species of *Parabolinella* Brogger which has been recorded in both the *Kainella meridionalis* and the *Bienvillia tetragonalis-Conophrys minutula* zones (figure 2). On the basis of the record of *K. meridionalis* in the underlying strata (see figure 3) as well as the fossiliferous content of the Floresta Formation at other localities (Moya *et al.*, 1994; Moya, 1998), the studied bivalve fauna can be referred to the *Bienvillia tetragonalis-Conophrys minutula* zone. The age of the trilobite zones is also supported by data from conodonts and graptolites (Aceñolaza and Albanesi, 1997; Albanesi and Moya, 2000; Albanesi *et al.*, 2001; Moya *et al.*, 1994; Ortega *et al.*, 1997; Tortello and Rao, 2000). According to this evidence the fossiliferous

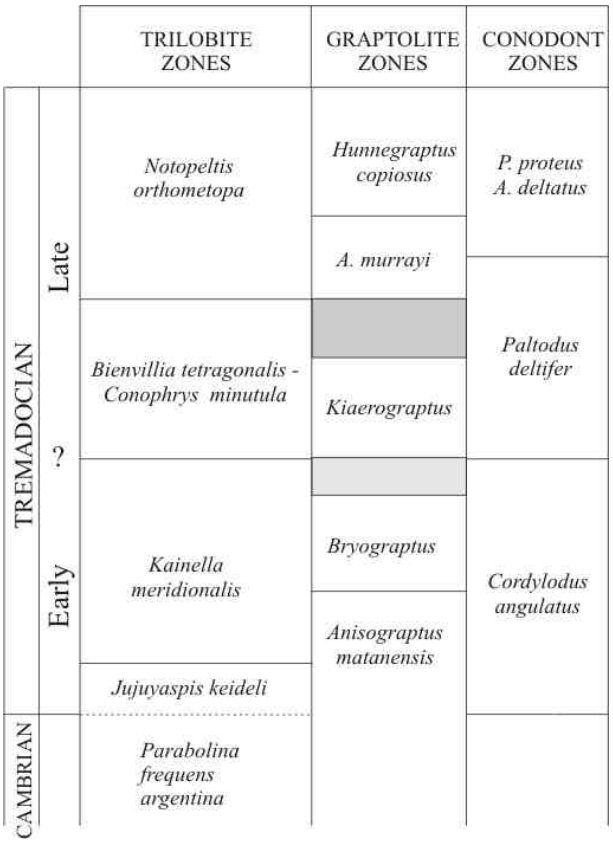

Figure 2. Correlation chart based on trilobites, graptolites, and conodonts. Data from Aceñolaza and Albanesi, 1997; Albanesi and Moya, 2000; Albanesi *et al.*, 2001; Harrington and Leanza, 1957; Moya *et al.*, 1994; Ortega *et al.*, 1997; Tortello and Rao, 2000. / *Cuadro de correlación basado en trilobites, graptolites y conodontos. Datos tomados de Aceñolaza and Albanesi, 1997; Albanesi and Moya, 2000; Albanesi* et al., *2001; Harrington and Leanza, 1957; Moya* et al., *1994; Ortega* et al., *1997; Tortello y Rao, 2000.*

strata could be referred to the lower part of the late Tremadocian (*P. deltifer* zone, figure 2).

Specimens of *Goniophorina* (*Cosmogoniophorina*) cf. *tenuicostata* Harrington included in this study belong to the R. Loss collection deposited in the Museo de Geología, Minería y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy. According to the label notation, they come from *K. meridionalis* horizon cropping out at the km 50 of Road 9, near La Caldera. Consequently, they are age-equivalent with the type specimens described by Harrington (1938) from Iruya.

Systematic paleontology (by Teresa M. Sánchez)

Material described in this paper is deposited in the paleontologic collection of the Cátedra de Paleontología (Escuela de Biología) and Estratigrafía y Geología Histórica, Universidad Nacional de Córdoba, Argentina, under the prefix CEGH-UNC. Some specimens belong to the collection of the Museo de Geología, Minería y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy, Argentina, prefix JUY-P.

Subclass HETEROCONCHIA Hertwig, 1895
Superorder PALAEOHETERODONTA Newell, 1965
Order ACTINODONTOIDA Douvillé, 1912
Superfamily CYCLOCONCHOIDEA Ulrich, 1884
Family REDONIIDAE ? Babin, 1966

Genus indeterminate
Figures 4.A, 6.I-O

Material. Seven specimens of left valves, and one right valve, all preserved as composite molds, CEGH-UNC 20551, and 20563 to 20569.

Horizon and locality. Floresta Formation, lower part of upper Tremadocian, *P. deltifer* zone. Sierra de Mojotoro, km 1651.5 of Road 9.

Description. Moderately inflated, ovate, small shells; prosogyrate umbo large and projecting, curved toward hinge line. Anterior adductor muscle scar well defined, more deeply impressed along posterior border, limited by a small myophoric buttress (figure 4.A); posterior adductor muscle scar rounded, only preserved in one specimen (CEGH-UNC 20551). Size of posterior adductor muscle scar nearly equal to that of anterior adductor scar. Two posterior pseudolateral teeth extending the length of dorsal margin of left valve; posterior dentition of right valve poorly preserved. Anterior and cardinal hinge features unknown. Shell ornamented with few irregular commarginal lines. Size of specimens ranges between 3 mm long and 2 mm high (smallest specimen), and 7 mm long and 4 mm high (largest specimen).

Discussion. Some features of the material, such as the posterior pseudolateral teeth and the recumbent umbo are diagnostic of the Family Redoniidae according to Babin (1966). However, the myophoric buttress limiting posteriorly the anterior adductor muscle is smaller and less marked than in typical redoniids. Additionally, there are no indications of structures in the anterior part of the hinge or the umbonal region. Although the specimens seem to be

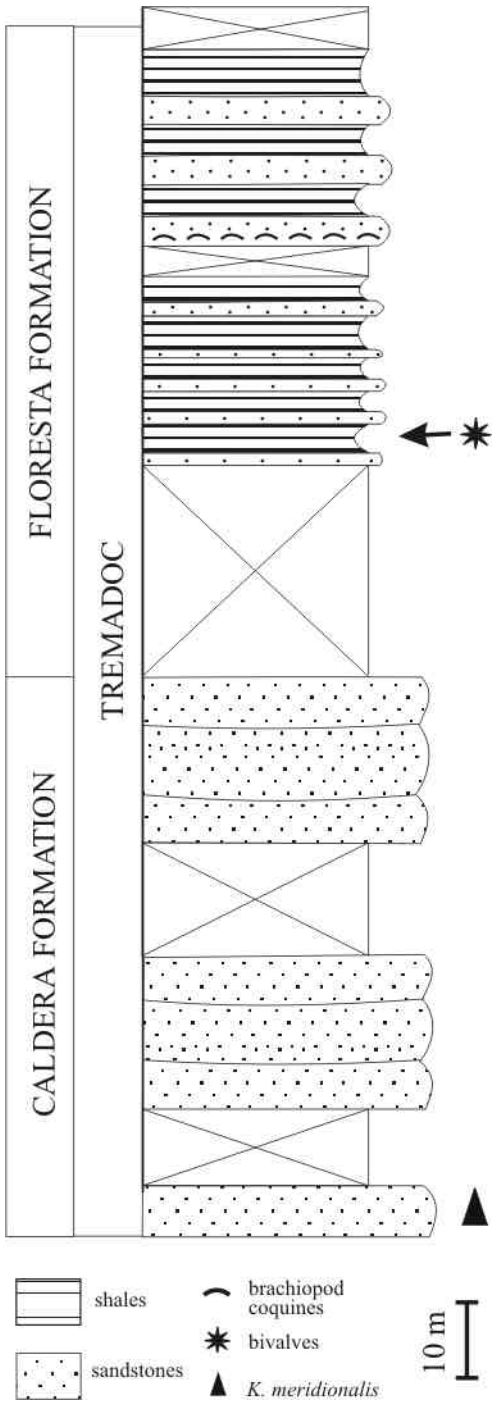

Figure 3. Stratigraphic location of fossiliferous level. Location of *K. meridionalis* zone follows chart of figure 2. / *Ubicación estratigráfica del nivel fosilífero. La ubicación de la zona de* K. meridionalis *está basada en el cuadro de la figura 2.*

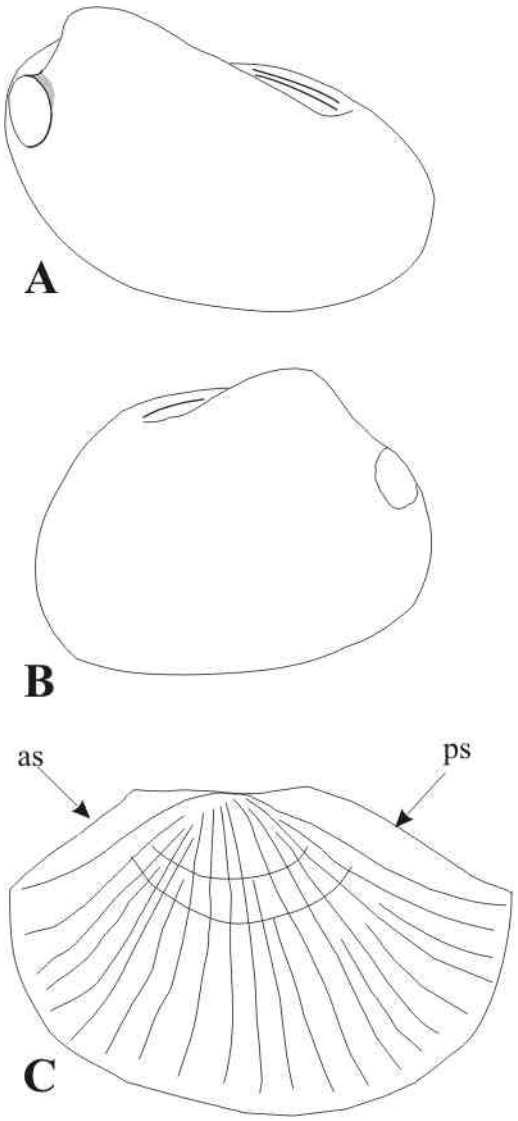

Figure 4. Schematic drawings of bivalves / *Figuras de los bivalvos*:: **A.** Redoniidae ? indet., **B.** ***Intihuarella simplicidentata*** gen. et sp. nov., **C.** ***Ucumaris conradoi*** gen. et sp. nov. (Not to scale). */ (No a escala).*

broadly similar to redoniids, these features make difficult to include them with certainty in this family. The relatively poor definition of some features, such as the myophoric buttress, could be related to their age.

Family INTIHUARELLIDAE new family

Type genus: *Intihuarella* gen. nov.

Diagnosis. Actinodontoida with a single pseudolateral posterior tooth which lacks denticles, slightly projected umbo, and anterior adductor muscle poorly impressed.

Remarks. The order Actinodontoida includes the families Cycloconchidae Ulrich and Redoniidae Babin (Carter *et al.*, 2000; Waller,1990). The two families differ on the basis of "numerous elongate teeth which lack denticles" in cycloconchids (Pojeta and Gilbert-Tomlinson, 1977, p. 29) and a reduced dentition in redoniids. Additionally, redoniids have a deep myophoric buttress supporting the anterior adductor muscle and a strongly curved umbo (Babin, 1966). In spite of the definition, some genera with reduced dentition have also been placed into the Cycloconchidae. These include *Fortowensia* Cope from the early Arenig of the Llangynog Inlier in Whales (Cope, 1996), and *Famatinadonta* Sánchez from the middle Arenig of the Sierra de Famatina (Sánchez, 2001). Both genera clearly differ from *Intihuarella* gen. nov. in the teeth pattern. *Fortowensia* has a single pseudocardinal tooth, and one anterior and one posterior pseudolateral teeth (Cope, 1996). *Famatinadonta* displays a single posterior pseudolateral and two strong pseudocardinal teeth (Sánchez, 2001). The new family is characterized by a simple dentition, with a single posterolateral tooth. In spite of the reduced dentition, which is close to that of redoniids, the absence of a myophoric buttress limiting the anterior adductor muscle and the slightly projected, not recumbent umbo, clearly separate Intihuarellidae fam. nov. from redoniids. The simple dentition of intihuarellids also differs from that of cycloconchids, and could be related to the primitive nature of the new family. It could imply that actinodontoids have originated from a *Intihuarella*-like type ancestor possessing a simple dental pattern. The early Arenig *Fortowensia* could represent a more advanced type, with well defined anterior and posterior lateral teeth.

Genus ***Intihuarella*** gen. nov.

Type species. *Intihuarella simplicidentata* sp. nov.

Derivation of name. From the quechua inti huara, that means dawn. Refers to the fact that this is one of the oldest records of the superfamily.

Diagnosis. Forms with a very reduced dentition limited to a single pseudolateral posterior tooth which lacks denticles, and slightly impressed adductor muscle scars.

Intihuarella simplicidentata sp. nov.
Figures 4.B, 5, 6.A-H

Holotype. An internal mold of right valve (CEGH-UNC 20411: figure 6.D).

Paratypes. Nineteen specimens preserved as composite molds and internal molds, CEGH-UNC 20412 to 20428, 20552, 20553, and 20255b.

Horizon and locality. Floresta Formation, lower part of upper Tremadocian, *P. deltifer* zone. Sierra de Mojotoro, km 1651.5 of Road 9.

Derivation of name. Refers to the simple dental pattern.

Diagnosis: As for the genus.

Description. Small shells (7.3 mm long, 5 mm high maximum size) with prosogyrate, slightly prominent umbos placed in the anterior third of shell (figure 4. B). Outline shell variable with size (table 1) from subrounded to subovate. Usually the smallest shells (juvenile individuals?) are rounded, slightly elongated, and the greatest shells, except the specimen CEGH-UNC 20421, are subovate (figure 5). Anterior, posterior, and ventral borders forming an ample curve; dorsal border slightly curved. Shell anisomyarian; anterior adductor muscle scar elliptic, posterior one slightly greater, subovate, usually ill defined. Pallial sinus not preserved. A very fine sulcus parallel to and above the posterior tooth is preserved in some specimens (e.g. CEGH-UNC 20552, figure 6.A). Posterior hinge of right valve with a single, non-denticulate tooth running along the complete dorsal margin. Left valve with the correspondent socket. Anterior and subumbonal parts of hinge edentulous. Shell ornamented with commarginal, fine growth lines and irregular, stronger ornament collinear with growth increments.

Remarks. The very fine sulcus above the posterior tooth in some specimens (CEGH-UNC 20552) can be interpreted as a ligamental sulcus of an opisthodetic ligament. The posterior tooth of *Intihuarella simplicidentata* sp. nov. resembles the posterior tooth of the tironuculid *Natasia boliviensis* (Babin and Branisa), especially the subspecies *N. boliviensis fragilis* Sánchez, recorded in the Acoite Formation (early Arenig, Cordillera Oriental; Sánchez, 1997a). But *Intihuarella* gen. nov. clearly differs from *N. boliviensis* in lacking changes in the dental pattern with growth.

Although there is not a close correspondence between the values of the relationship H / L (table 1) the general tendency shows a change of the shell outline with growth (figure 5). The smallest shells tend to be rounded whereas the greater become subovate.

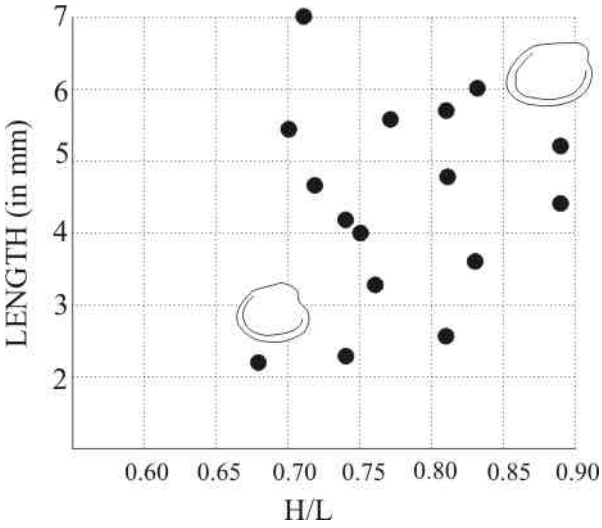

Figure 5. *Intihuarella simplicidentata* gen. et sp. nov. Relationship between size (L) and shell outline (H / L). H, height; L, length. / Intihuarella simplicidentata *gen. et sp. nov. Relación entre el tamaño (L) y el contorno de la valva (H/L). H, altura; L, longitud.*

Subclass ANOMALODESMATA Dall, 1889
Order PHOLADOMYOIDA Newell, 1965
Family UCUMARIIDAE nov.

Type genus. *Ucumaris* gen. nov.

Diagnosis. Equivalve bivalves with predominant radial ornamentation; shell surface ornamented with small pustules originated at the intersection of radial costae with fine commarginal lines. Shell with posterior slope. Radial and commarginal ornamentation covering all the shell surface except on the posterior slope. Shell without anterior or posterior gapes.

Remarks. According to Cox (1969) origination of pustules and tubercles is a consequence of the intersection of concentric threads and radial costae. The studied specimens show well developed pustules resulting from the intersection of the radial ornamentation and concentric lines. Due to the radial costae and the commarginal lines being developed over the entire shell, the shell surface is completely ornamented by radial arrays of pustules. This pustulate sculpture is similar to that of Anomalodesmata (see by example Newell, 1969; Runnegar, 1974) and consequently the new family has been included in this subclass. Although the radial ornamentation is a typical feature of the Family Pholadomyidae, the material of the new family does not show gapes nor nymph. Fang and Morris (1997, p. 55) stated that "a ligament nymph seems to be a primitive character of the Anomalodesmata". The absence of this structure in the studied material could be interpreted as evidence that nymphs developed later and allows for the placement of these specimens in a different group at the familial level.

The genera *Cuneamya* Hall and Whitfield and *Rhytimya* Ulrich have been viewed as early anomalodesmatans by Pojeta (1971) and Runnegar (1974), and placed in the Family Grammysiidae Miller (Pojeta, 1978). *Rhytimya* shows conspicuous radiating rows of tubercles (see Pojeta, 1978, pl. 15, 1), one of the features allowing Pojeta to place it into the anomalodesmatans. Cope (1996) describes *Arenigomya carinata* Cope from the early Arenig of Llangynog Inlier (South Wales) and places the genus *Arenigomya* into the Family Grammysiidae Miller. *Arenigomya* displays a granulose texture, with concentric and radial ornament, and a strong subumbonal carina (Cope, 1996). However, the Grammysiidae are characterized by a smooth surface or concentric ornamentation, the radial ornament being subordinate (Newell and La Rocque, 1969). It seems likely that *Arenigomya* Cope and *Ucumari*s gen. nov. are closely related genera which share a conspicuous radial sculpture and a granulose texture covering the entire body shell. On

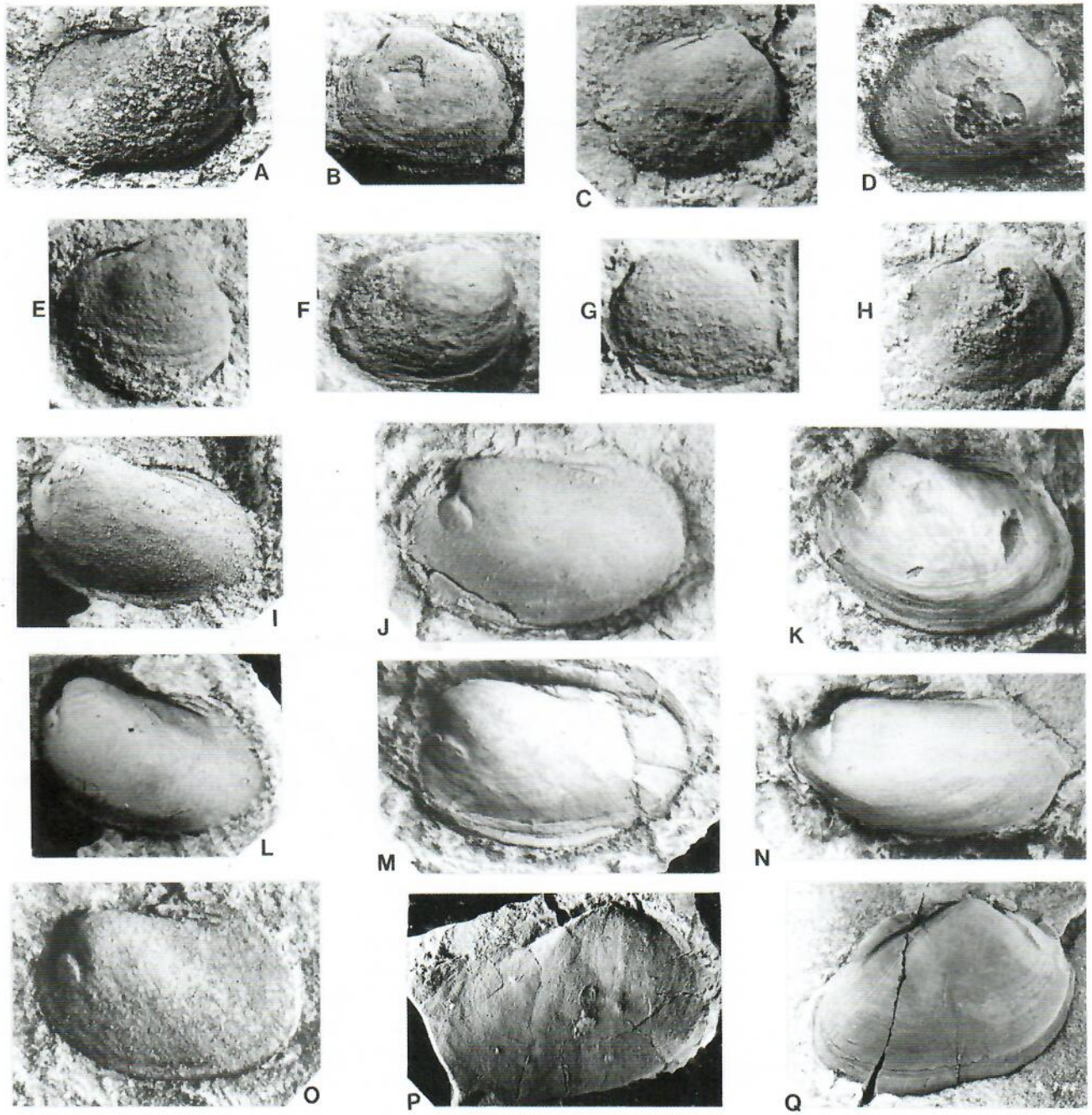

Figure 6. A-H, ***Intiluarella simplicidentata*** gen. et sp. nov. **A,** internal mold of right valve / *molde interno de valva derecha*, CEGH-UNC 20552 (x 6.5); **B,** composite mold of left valve / *molde compuesto de valva izquierda*, CEGH-UNC 20427 (x 7); **C,** internal mold of right valve /*molde interno de valva derecha*, CEGH-UNC 20414 (x 12); **D,** internal mold of right valve / *molde interno de valva derecha*, CEGH-UNC 20411, holotype (x 6.5); **E,** composite mold of right valve / *molde compuesto de valva derecha*, CEGH-UNC 20425 (x 8); **F,** internal mold of right valve / *molde interno de valva derecha*, CEGH-UNC 20428 (x 5); **G,** internal mold of left valve / *molde interno de valva izquierda*, CEGH-UNC 20416 (x 16); **H,** internal mold of right valve / *molde interno de valva derecha*, CEGH-UNC 20417 (x 6.5). **I-O,** Redoniidae? gen. indet. **I,** internal mold of left valve / *molde interno de valva izquierda*, CEGH-UNC 20568 (x 8); **J,** internal mold of left valve / *molde interno de valva izquierda*, CEGH-UNC 20567 (x 4); **K,** composite mold of left valve / *molde compuesto de valva izquierda*, CEGH-UNC 20563 (x 7); **L,** internal mold of left valve / *molde interno de valva izquierda*, CEGH-UNC 20568 (x 7.5); **M,** internal mold of left valve / *molde interno de valva izquierda*, CEGH-UNC 20565 (x 6); **N,** internal mold of left valve / *molde interno de valva izquierda*, CEGH-UNC 20566 (x 7); **O,** internal mold of left valve / *molde interno de valva izquierda*, CEGH-UNC 20564 (x 13). **P, Q,** ***Goniophorina* (*Cosmogoniophorina*) cf. *tenuicostata*** Harrington. **P,** composite mold of right valve / *molde compuesto de valva derecha*, CEGH-UNC 20430 (x 2.5); **Q,** composite mold of right valve / *molde compuesto de valva derecha*, JUY-P 3 (x 2).

this basis, *Arenigomya* Cope could be included in the new Family Ucumariidae. The familial placement of other Ordovician radially ornamented genera, such as *Rhytimya*, should be revised.

The flattened posterodorsal slope of *Ucumaris* gen. nov. is similar to that of some modiomorphids like *Goniophorina*. The association in this primitive family of a pustulate surface, an anomalodesmatan

Table 1. Measurements of *Intihuarella simplicidentata* gen. et sp. nov. / *Medidas de* Intihuarella simplicidentata *gen. et sp. nov.*

Specimen (CEGH-UNC)	Length	Height	H/L
20240	2.2	1.5	0.68
20414	2.3	1.7	0.74
20422	2.6	2.1	0.81
20413	3.3	2.5	0.76
20418	3.6	3.0	0.83
20416	4.0	3.0	0.75
20427	4.2	3.1	0.74
20417	4.4	3.9	0.89
20423	4.7	3.4	0.72
20411 (Holotype)	4.8	3.9	0.81
20426	5.2	4.6	0.88
20552	5.4	3.8	0.70
20419	5.6	4.3	0.77
20428	5.7	4.6	0.81
20415	6.0	5.0	0.83
20421	7.0	5.0	0.71

feature, and a posterodorsal slope, a *Goniophorina* type modiomorphid feature, is consistent with the relationship between modiomorphids and anomalodesmatan proposed by Fang and Morris (1997) and Waller (1990).

Genus ***Ucumaris*** gen. nov.

Type species. *Ucumaris conradoi* sp. nov.

Derivation of the name. From the quechua language ucumar that means body, the material part of living animals. It refers to the shell bodies.

Diagnosis: Ovate shell with regularly spaced costae separated by interspaces about 0.5 mm wide. Radial costae intersected by very fine, closely spaced commarginal lines. Radial costae increase by both bifurcation and intercalation. Secondary costae usually smaller than primary costae. Intersection of both primary and secondary radial costae with concentric ornament produces two order of pustules -great and small- over all the shell surface. Posterior slope conspicuous.

Discussion. *Ucumaris* gen. nov. differs from *Arenigomya* Cope by having two orders of costae (older and younger), by the absence of the strong subumbonal carina, and by its ovate shell outline, which is trapezoidal in *Arenigomya*. Both genera have a posterior slope but in *Arenigomya* it develops behind the subumbonal carina whereas in *Ucumaris* the slope is unbounded because of the absence of carina. Additionally, *Arenigomya* possesses a subumbonal articulation device which could be regarded as a chondrophore (Cope, 1996), though it is difficult to confirm this feature in the material of the new genus. However, giving the position of the articulation device (Cope, 1996) and taking into account the preservation of the specimens studied, such a structure in *Ucumaris* can not be completely rejected.

Finally, it is important to note that *Ucumaris* gen. nov., like the pholadomyoids (according to Fang and Morris, 1997) was a free burrowing (see Remarks in the next section).

Ucumaris conradoi sp. nov.
Figures 4.C, 7.A-J

Diagnosis. As for the genus.

Derivation of name. From my grandson Conrado.

Holotype. A composite mold of a left valve (CEGH-UNC 20250: figure 7.C).

Paratypes. Several isolated right and left valves, and a bivalved specimen, all preserved as composite molds, CEGH-UNC 20251 to 20254, 20255a, 20401 to 20407, 20429, and 20554 to 20562.

Horizon and locality. Floresta Formation, lower part of upper Tremadocian, *P. deltifer* zone. Sierra de Mojotoro, km 1651.5 of Road 9.

Description. Ovate, posteroventrally elongated shell; subdued umbo located in the anterior third of valves. Shells moderately inflated with maximum width at the mid length of the shell, beneath the umbo. Anterior and posterior margins rounded; posterior margin slightly higher than the anterior one. Ventral margin rounded. Hinge line short, about one half of the shell length. A flattened posterior slope extends from the beak along the posterior margin (figure 4. C). Posterior slope defined by the absence of surface ornamentation. Shell ornamented with regularly spaced radial costae intersected by very fine comarginal lines, generating a fine reticulate pattern. Increase in the number of costae is mostly by intercalation (figure 7.A, B, D) and occasionally some radial costae bifurcate (figure 7.G). Both types are irregular, and in portions of shell surface lack secondary costae. Secondary costae originating by bifurcation usually are thinner than the primary costa they originate from. Intercalated secondary costae begin small but can attain the size of the primary costae. Then, two order of costae could be recognized: first order -primary costae-, and second order (secondary costae). Primary costae are well marked and regularly spaced, about 4 per mm at the ventral margin, and are separated by flattened interspaces. Secondary costae are irregularly disposed into the interspaces, and attaining variable size, usually thinner than primary costae. Intersection of radial and concentric ornament produces small pustules which give a granulose texture on the shell surface. Depending on the size (age) of the costae intersected by the concentric lines, different sizes (small and coarse) of pustules can be recognized. Since no internal molds are preserved, both the muscular pattern and the pallial line

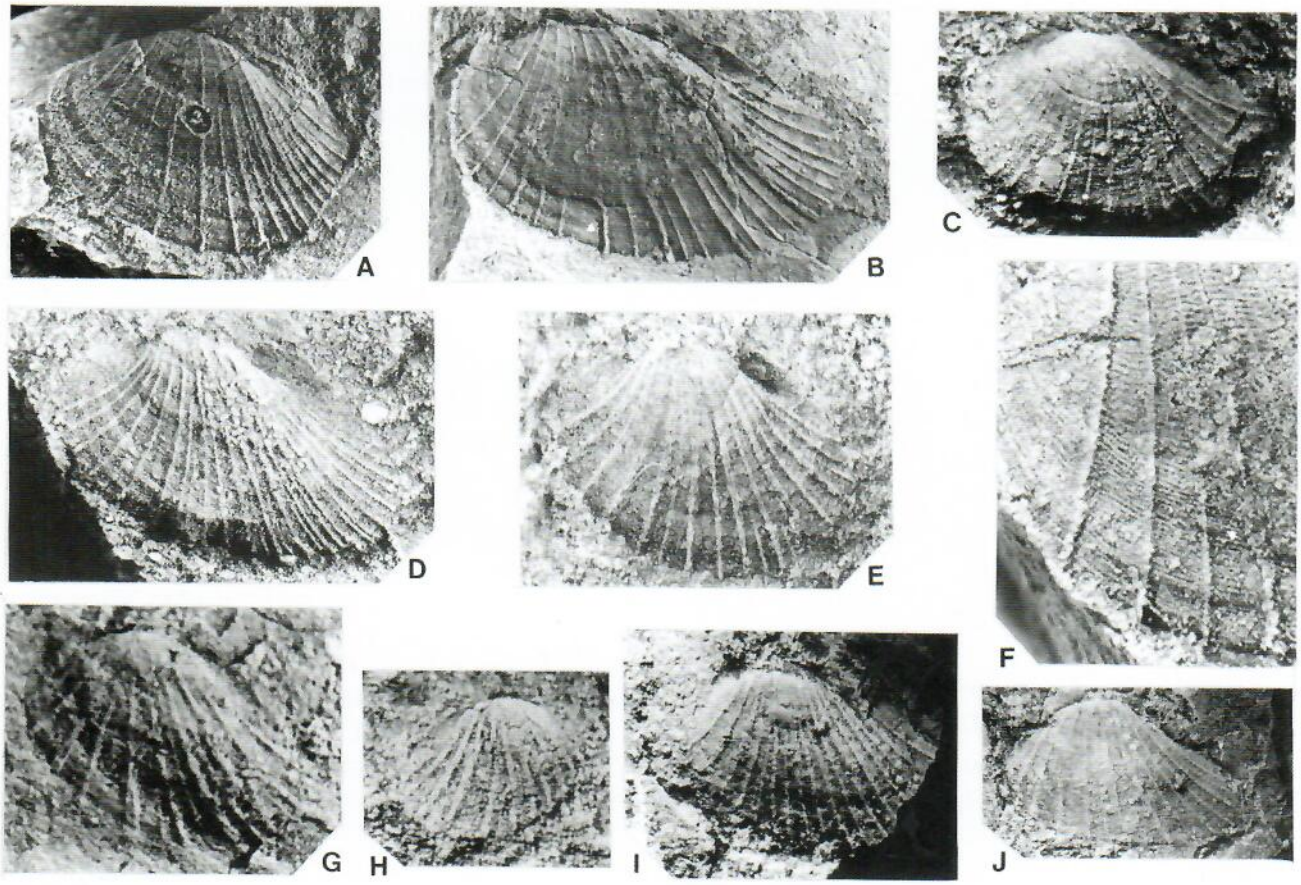

Figure 7. A-J, ***Ucumaris conradoi*** gen. et sp. nov. **A,** left valve, note intercalated costae / *valva izquierda mostrando las costillas intercaladas*, CEGH-UNC 20557 (x 5); **B,** left valve / *valva izquierda*, CEGH-UNC 20554 (x 4); **C,** left valve, holotype / *valva izquierda, holotipo*, CEGH-UNC 20250 (x 8); **D,** left valve / *valva izquierda*, CEGH-UNC 20558 (x 6); **E,** left valve / *valva izquierda*, CEGH-UNC 20559 (x 7); **F,** detail of ornamentation, same specimen as figure B (x 10) / *detalle de la ornamentación, ejemplar de la figura B*; **G,** left valve, note bifurcate costae / *valva izquierda mostrando las costillas bifurcadas*, CEGH-UNC 20402 (x 10); **H,** right valve / *valva derecha*, CEGH-UNC 20254 (x 7,5); **I,** left valve / *valva izquierda*, CEGH-UNC 20555a (x5); **J,** left valve / *valva izquierda*, CEGH-UNC 20404 (x 4). All specimens preserved as internal molds / *Todos los ejemplares están preservados como moldes internos.*

remain unknown. The specimens are edentulous. Size of specimens ranges between 3mm long and 2 mm high (smallest specimen), and 13 mm long and 8 mm high (greatest specimen). The holotype is 5 mm long and 3.8 mm high.

Remarks. Following Stanley (1970), the absence of a byssal sinus and the maximum shell width placed at mid-way of the body shell indicate that *Ucumaris conradoi* sp. nov. was a free burrower. The moderate inflation, elongated outline, and small shell size of the new species suggest that it was probably a rapid, shallow burrower.

Order MODIOMORPHOIDA Newell, 1969
Superfamily MODIOMORPHOIDEA Miller, 1877
Family MODIOMORPHIDAE Miller, 1877

Genus ***Goniophorina*** Isberg, 1934

Subgenus ***Goniophorina*** (***Cosmogoniophorina***) Isberg, 1934

Type species. *Cosmogoniophorina carinata* Isberg, 1934.

Goniophorina (***Cosmogoniophorina***) cf. ***tenuicostata*** Harrington, 1938
Figures 6.P, Q

Remarks. Placement of Modiomorphida into Anomalodesmata follows Fang and Morris (1997). Cladistic analysis from Carter *et al.* (2000) also supports this arrangement.

Material. Seven specimens of left and right valves preserved as internal molds. CEGH-UNC 20408 to 20410, and 20430, and JUY-P 1, 2, and 3.

Horizon and locality. Floresta Formation, lower part of upper Tremadocian, *P. deltifer* zone. Sierra de Mojotoro, km 1651.5 of Road 9 (U.N.C. collection), and Floresta Formation, *Kainella meridionalis* zone (= *C. angulatus* zone), Sierra de Mojotoro, km. 42, Road 9 (U.N.J. collection).

Occurrence. Tremadocian: The original report is from the *Kainella meridionalis* zone, Arroyo Colorado, Iruya (Harrington, 1938). Additional collections come from 9 Road, km 50 (U.N.J.), and Floresta Formation, *P. deltifer* zone, Sierra de Mojotoro (this paper). Middle

Arenig: Acoite Formation, Los Colorados, and Suri Formation, Sierra de Famatina (Sánchez, 1997b).

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.

Discussion. The *Goniophorina* specimens described herein show certain degree of similarity to Harrington's species *G.* (*G.*) *tenuicostata* but they differ in their less defined carina. Variations in *G.* (*G.*) *tenuicostata* are common and have been noted previously in populations from the middle Arenig Acoite and Suri Formations (Sánchez, 1997). However, the studied material is not abundant enough to evaluate to what extent such variations in the carina expression are due to intrapoblational variations or represent a different species.

Discussion

During the Tremadocian several bivalve clades developed (Babin and Hamman, 2001; Babin, 1995): babinkids (*Babinka*, Babin 1982), modiomorphids (*Cosmogoniophorina*, Harrington, 1938), colpomyids (*Colpantyx* and *Xestoconcha*, Pojeta and Gilbert-Tomlinson, 1977), and cyrtodontids (*Cyrtodontula* and *Pharcidoconcha*, Pojeta and Gilbert-Tomlinson, 1977). Tremadocian protobranchs include *Deceptrix* ?, Pojeta and Gilbert-Tomlinson, 1977, and the doubtful *Palaeoneilo* and *Ctenodonta*, Harrington, 1938 (their taxonomic status need to be revised). Paleontological evidence from the Floresta Formation adds two actinodontids (Intihuarellidae fam. nov. and an undeterminated genus possibly related to the Redoniidae) and a new anomalodesmatan clade (Ucumariidae fam. nov.) to the Tremadocian bivalve record.

Therefore, the available record confirms that the bivalve radiation began early in the Ordovician, or, more probably, in the upper Cambrian, and that in the Tremadocian most of the bivalve clades had already been differentiated. The lack of records from the late Cambrian and earliest Tremadocian (e.g. below the *Kainella meridionalis* zone in the northwestern basin) beds, however, precludes further delineation of the phylogenetic connection between the Argentine Tremadocian genera and the known Cambrian genera. On the other hand, the appearance of these new clades in the Tremadocian high-latitude, clastic successions of northwestern Argentina supports the suggestion by Babin (1993) that the early radiation of bivalves occurred in Gondwanan marine shelves.

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