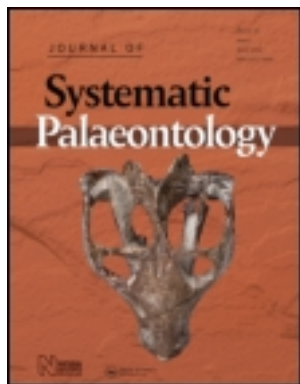


This article was downloaded by: [Juan Benedetto]

On: 01 August 2012, At: 09:58

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Systematic Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tjsp20>

Gatosella, a new basal plectambonitoid brachiopod with undercut cardinal process from Middle Ordovician limestones of the Precordillera terrane, Argentina

Juan L. Benedetto ^a

^a Centro de Investigaciones en Ciencias de la Tierra, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Córdoba, Av. Velez Sarsfield 299, X5000JJC, Argentina

Version of record first published: 01 Aug 2012

To cite this article: Juan L. Benedetto (2012): Gatosella, a new basal plectambonitoid brachiopod with undercut cardinal process from Middle Ordovician limestones of the Precordillera terrane, Argentina, *Journal of Systematic Palaeontology*, 10:3, 435-443

To link to this article: <http://dx.doi.org/10.1080/14772019.2011.590536>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

***Gatosella*, a new basal plectambonitoid brachiopod with undercut cardinal process from Middle Ordovician limestones of the Precordillera terrane, Argentina**

Juan L. Benedetto*

Centro de Investigaciones en Ciencias de la Tierra, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Córdoba, Av. Velez Sarsfield 299, X5000JJC, Argentina

(Received 23 March 2010; accepted 11 January 2011; printed 6 August 2012)

The plectambonitoid brachiopod *Gatosella muricata* gen. et sp. nov. is described from the uppermost nodular limestones of the San Juan Formation. The well-constrained early Darriwilian age of these beds leaves *Gatosella* as one of the oldest known plectambonitoideans possessing an undercut cardinal process. A phylogenetic analysis of representative genera bearing this character reveals that the new Precordilleran genus is a basal member of the subfamily Aegiromeninae (as presently defined). Parsimony analysis supports the existence of three subclades which may be considered as having familial rank in the Linnaean classification: Aegiromenidae, Hesperomenidae and Sowerbyellidae, and also indicates that the xenambonitins are more closely related to the sowerbyellids than to any other group.

Keywords: Brachiopoda; Plectambonitoidea; Ordovician; Precordillera; Argentina

Introduction

Taxonomic diversity of the rhynchonelliformean brachiopods increased dramatically during the Ordovician radiation. The main groups that radiated in the Lower Ordovician (Tremadocian–Floian) were the impunctate orthides, the syntrophidine pentamerides and the billingsellides, all of which have representatives in the Late Cambrian. The oldest reported member of the order Strophomenida is the plectambonitoid (?) *Akelina*, from the upper Tremadocian of Russia (Altai Mountains). The superfamily Plectambonitoidea, however, did not diversify significantly until the Dapingian–Darriwilian when more than 30 genera evolved on the carbonate and mixed carbonate-clastic platforms around the world (China, Baltica, Laurentia, Australia, Siberia, Precordillera terrane), reaching a maximum of 43 genera during the late Sandbian (approximately the mid Caradoc of British regional units). By the Sandbian–Katian, the plectambonitoids had spread across the temperate to high latitudes originating the well-known west Gondwanan *Aegiromena* Fauna (Havlíček 1986 and references therein). The Strophomenoidea, the other superfamily within the Strophomenida, also radiate during the second half of the Ordovician, reaching their first diversity peak by the late Katian (Harper *et al.* 2004) and becoming dominant during Silurian and Devonian. The plectambonitoids also survived the end-Ordovician biotic crisis but their diversity dropped

significantly at the end of the Ordovician, in particular the leptellinids (Candela 2010). Most of the Silurian survivors possess undercut cardinal process, becoming extinct before the Late Devonian faunal turnover.

Cocks & Rong (1989) considered the ‘undercut’ and ‘non undercut’ condition of the cardinal process as a key feature for familial grouping of plectambonitoidean brachiopods, later adopted in the revised *Treatise* (Cocks & Rong 2000). The families Xenambonitidae, Hesperomenidae and Sowerbyellidae have in common an undercut cardinal process in which the central part is not ankylosed anteriorly to the valve floor but supported laterally by variably developed socket plates, forming an arched, inverted V-shaped structure which may differ to some degree according to the genera. Its acquisition has been considered as the apomorphy that distinguishes the unnamed clade encompassing the above-mentioned three families (Cocks & Rong 1989, Fig. 5). According to this interpretation, this clade derives from an unidentified basal group of plectambonitoids having simple or trifid, not undercut cardinal process. The taxonomic significance of the undercut cardinal process has been questioned by Potter (1991) on the basis of its variable expression in the genus *Bimuria* Ulrich & Cooper, in which it ranges from simple not undercut to undercut, and also by Egerquist (1999) in her revision of the genus *Ujukella* Andreev. However, with rare exceptions, the undercut cardinal process is known to be a persistent character of this group of families, perhaps

*Email: jbenedetto@efn.uncor.edu

more diagnostic than other features commonly used to distinguish families and subfamilies within the plectambonitoids, such as lateral septa, bema, dorsal platform or ventral subperipheral rim, which may be plesiomorphic or have unclear polarity in a phylogenetic analysis.

One of the earliest published representatives of this clade is *Ujukella fastigata* Egerquist, from the upper Volkhov Stage of the East Baltic region (Russia). These levels belong to the *Baltoniodus norlandicus* Biozone, which indicates approximately the base of the Darriwilian Series. Although this species possesses an undercut cardinal process, its taxonomic placement is matter of debate. Cocks & Rong (2000) considered *Ujukella* Andreev as a junior synonym of *Calyptolepta* Neuman, 1976, and removed it from the sowebyelids, where it had been placed by Andreev (1993) because of its 'trifid' undercut cardinal process, to the grorudids. New well-preserved material from Baltoscandia described by Egerquist (1999) demonstrates that *Ujukella fastigata* has a simple, undercut cardinal process, and in a cladistic analysis it appears closely related to *Anechophragma* Neuman (type species *A. rarum* Neuman) from volcanogenic beds of mid Darriwilian (*D. artus* zone) age in Newfoundland. Egerquist (1999) referred both genera to the family Leptestiidae, whose diagnosis was modified to include genera that have a simple, undercut cardinal process (the 'transverse-ridge' type of Potter (1991)). Another early representative of the 'undercut cardinal process-bearing group' is *Aegiromena corolla* Havlíček & Branisa, 1980, from the 'Llanvirnian' sandstones of Bolivia. The precise age of these beds remains unknown but their association with a species of *Tissintia* is suggestive of a younger age, possibly late Darriwilian or Sandbian. The earliest Aegiromeninae so far reported is *Chonetoidea* from the mid Darriwilian (*Undulograptus intersitus* Zone, Dw2 'stage slice' of Bergström *et al.*, 2008) of South China (Zhan *et al.* 2008). This brachiopod, however, has apparently not yet been described and illustrated.

The purpose of this paper is to describe the new genus *Gatosella* as one of the earliest known occurrences not only of the subfamily Aegiromeninae (elevated to family rank here) but also of the clade encompassing the plectambonitoids bearing undercut cardinal process. The taxonomic placement of the new Precordilleran genus is analysed in a phylogenetic context.

Stratigraphy and age

The Precordillera (or Cuyania) is a low-latitude, Laurentian-derived terrane that accreted to the proto-Andean margin of Gondwana by the Late Ordovician (Benedetto 1993, 2004; Benedetto *et al.* 2009; Astini *et al.* 1995). Throughout the Cambrian and the first half of the Ordovician this microplate was the site of widespread carbonate sedimentation. Depositional

environments evolved from tidal flats, shoals, shallow subtidal and restricted subtidal settings during the Cambrian–early Tremadocian to open shelf settings in the late Tremadocian–Darriwilian (Cañas 1999). The open shelf carbonate succession, referred to as the San Juan Formation, consists of *c.* 350 m of burrowed skeletal wackestones and packstones (Fig. 1). The succession culminates with a 25–30 m thick package of nodular limestones – mainly grey mudstones – bearing a rich benthic fauna that includes brachiopods, trilobites, sponges, bryozoans, gastropods and crinoids (Benedetto 2003; Sánchez *et al.* 2003). The brachiopod association has been referred to the *Ahtiella argentina* Zone, the uppermost of the six biozones recognized through the San Juan Formation (Benedetto 2007; Sorrentino *et al.* 2009). These beds are particularly well exposed along the western slope of Cerro Viejo, about 20 km NE of Jáchal City, where the San Juan Formation forms a westward-dipping homoclinal sequence (Fig. 2). The plectambonitoid specimens described here were collected on the left side of the Los Gatos Creek (Quebrada Los Gatos) and in the Honda Creek, 2.5–3.1 m below contact with the overlying Los Azules Formation.

The age of the uppermost nodular limestones of the San Juan Formation is well constrained by conodonts belonging to the *Paroistodus horridus* Subzone of the *Lenodus variabilis* Zone (Ottone *et al.* 1999; Albanesi & Ortega 2002), of early Darriwilian age (Fig. 1). The immediately overlying black shales (lower member of the Los Azules Formation) have yielded a graptolite assemblage referred to as the *Undulograptus dentatus* Biozone, whereas the topmost beds of the San Juan Formation contain *Undulograptus austrodentatus* (Mitchell *et al.* 1998; Brussa *et al.* 2003; Ortega & Rickards 2003), the marker of the base of the Darriwilian Stage, corresponding to the Dw1 'substage' of Bergström *et al.* (2008).

Phylogenetic relationships of *Gatosella*

The origin of plectambonitoideans remains unresolved. Members of this superfamily have a fibrous shell structure (Williams 1970), whilst the Strophomenoidea have a laminar shell structure. Pseudopunctae are present in both groups. The cladistic analysis carried out by Williams *et al.* (2000) indicates that the superfamilies are related, having a common ancestor among the billingselloids. On the basis of shell structure and cardinal process morphology, Dewing (2004) postulated that Plectambonitoidea are more closely related to Clitambonitoidea than previously thought. A similar interpretation was anticipated by Cocks & Brunton (1996). Clitambonitoids also possess fibrous shells, and some genera display pseudopunctae (Wright & Rubel 1996). According to the phylogenetic scenario of Dewing (2004, Fig. 3). Strophomenoidea arose from a Cambrian laminar-shelled billingselloid, whilst the common ancestor

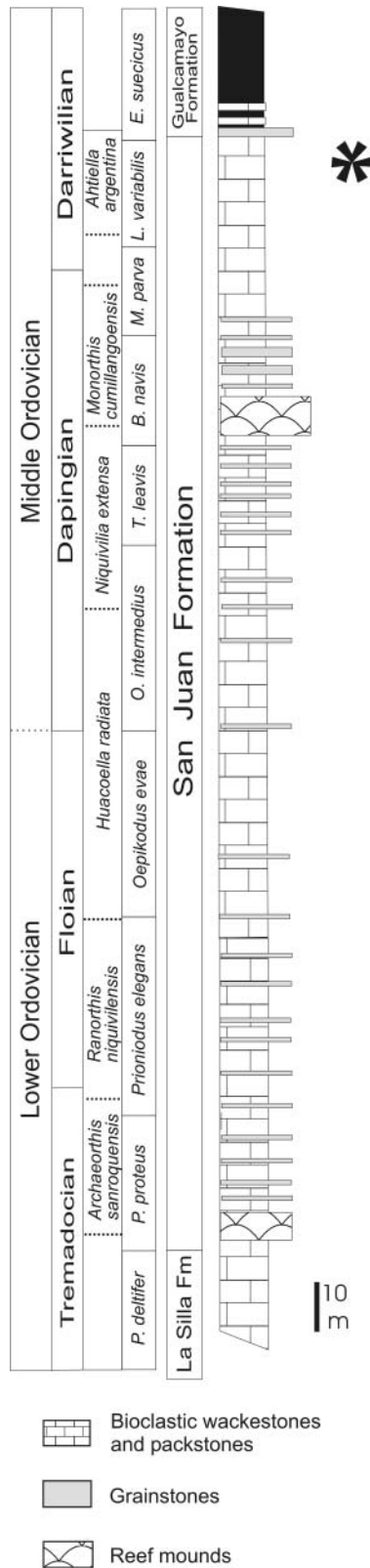


Figure 1. Stratigraphic column of the San Juan Formation showing distribution of lithofacies, conodont and brachiopod biozones, and levels yielding *Gatosella muricata* gen. et sp. nov. (asterisk). Modified from Carrera (2007) and Benedetto *et al.* (2008).

of the fibrous-shelled Plectambonitoidea and Clitambonitoidea remains unknown. The possibility that orthides – which share with the plectambonitoideans a fibrous secondary shell layer – are basal to the plectambonitoid clade needs to be explored.

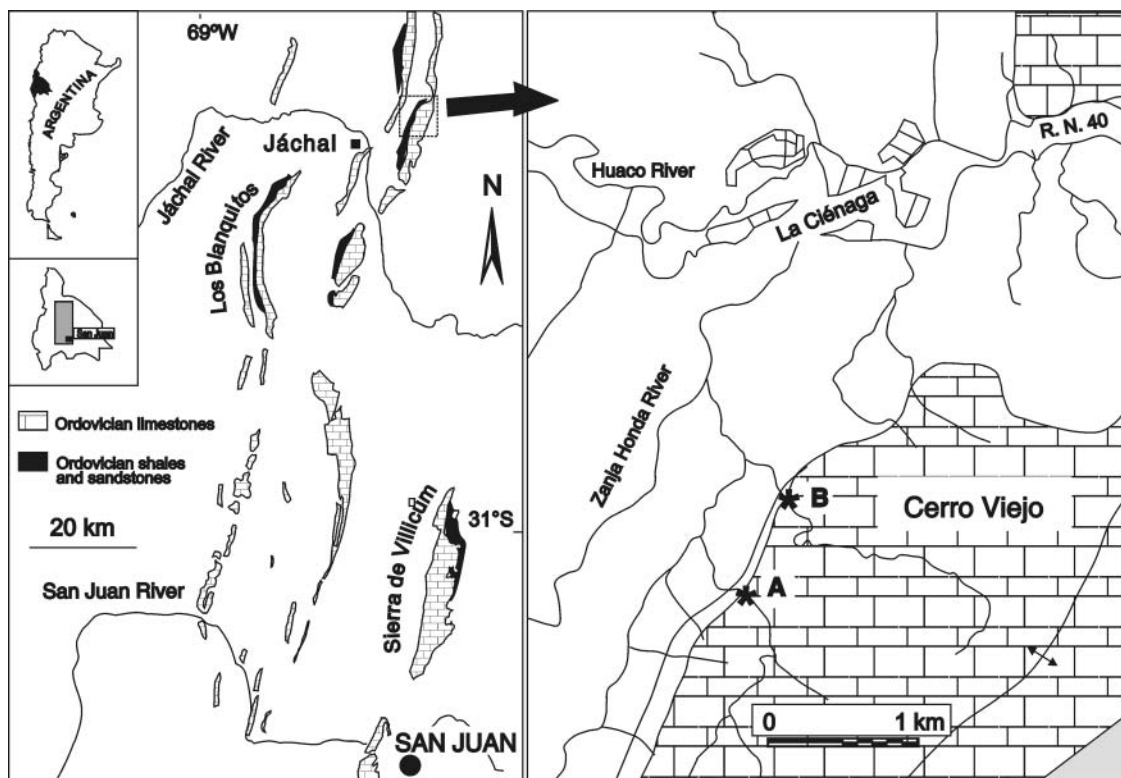
In this paper, cladistic analysis of plectambonitoids having undercut cardinal process was performed using TNT (Tree Analysis Using New Technology) version 1.0 (Goloboff *et al.* 2003). The 14-character matrix was analysed for 22 taxa (Table 1), and *Taffia* Butts, 1926, a basal taxon lacking the majority of apomorphies present in the group analysed here (including the undercut cardinal process), was chosen as outgroup for rooting the phylogenetic tree. A heuristic search of the data matrix in which all characters were unordered and equally weighted produced 11 minimal length trees, 33 steps long (Fig. 3). Phylogenetic relationships expressed in the 80% majority rule consensus tree are shown in Fig. 4; this tree is redrawn in Fig. 5 but with branch length calibrated to the age of the FADs (First Appearance Datum) of each taxon.

Although the cladogram of Fig. 3 supports a tripartite classification of the plectambonitoids bearing undercut cardinal process, arrangement of families and subfamilies is slightly different from that proposed by Cocks & Rong (1989, 2000). Perhaps the main difference is that the aegiromenins form a separate clade in which two subclades can be recognized. *Gatosella* appears as the basal member of the lineage that includes *Multiridgia* and *Jonesea*. The synapomorphy defining this lineage is the possession of a weak dorsal platform delineated by papillae and/or septules. The whole clade is stratigraphically parsimonious requiring a relatively long ghost lineage only for the Silurian genus *Mezounia*, which is placed at the base of the (*Chonetoidea* + *Aegiria* + *Aegiromena*) lineage (Fig. 5). This favours the classification of aegiromenins as a separate clade with family rank (family Aegiromenidae). The synapomorphy that defines node 1 is the presence of papillae and/or septules on the internal surface of both valves. In the 80% majority rule consensus tree (Fig. 4) part of this clade collapses and is replaced by a polytomy, indicating that considerable ambiguity exists over the relationships of the aegiromenid ingroup clade.

The remaining plectambonitoids considered in the parsimony analysis form two subclades. One of the subclades includes the genera currently referred to Hesperomenidae, with *Anoptambonites*, *Hesperomena* and *Rongambonites* as the more derived members. Monophyly of this subclade is supported by the synapomorphies (node 2) of having a well-developed, strong dorsal platform, and a high, bladeli-like dorsal septum. This node is preserved in the 80% majority rule consensus tree but partially collapses in the strict consensus tree. The third subclade is formed by members of the subfamily Xenambonitinae and the family Sowerbyellidae. Topology of this clade does not change significantly in the 80% majority rule consensus tree and constitutes

Table 1. Character state matrix used in TNT parsimony analysis of characters listed in the Appendix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Taffia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Xenambonites</i>	0	0	1	1	0	1	1	2	0	0	1	0	0	0
<i>Aegiromena</i>	0	0	0	2	02	02	013	3	0	0	1	0	0	1
<i>Chonetoidea</i>	0	0	1	1	2	0	0	2	0	0	1	0	0	1
<i>Mezounia</i>	0	1	0	1	0	0	2	0	0	0	1	0	0	1
<i>Aegiria</i>	0	0	1	2	0	0	01	2	0	3	1	0	0	1
<i>Multiridgia</i>	0	1	1	1	0	0	0	0	0	3	1	0	0	1
<i>Jonesea</i>	0	1	1	1	0	0	03	1	0	3	1	0	0	2
<i>Hesperomena</i>	0	0	0	1	0	0	0	1	0	2	1	1	0	0
<i>Anoptambonites</i>	0	0	0	1	0	0	0	1	0	2	1	1	0	0
<i>Kassinella</i>	0	1	1	2	0	0	0	1	0	2	1	0	0	0
<i>Sowerbyella</i>	0	0	0	1	2	0	02	0	1	0	1	0	0	0
<i>Anisopleurella</i>	0	1	0	1	2	0	2	0	1	0	1	0	0	0
<i>Eochonetes</i>	0	0	0	2	2	0	2	0	1	0	1	0	1	01
<i>Plectodonta</i>	0	0	0	1	2	0	03	0	1	0	1	0	1	12
<i>Metambonites</i>	1	0	1	1	2	0	1	2	0	0	1	1	2	0
<i>Aulie</i>	0	0	0	0	0	0	0	1	0	2	1	0	0	0
<i>Eoplectodonta</i>	0	02	0	2	2	0	2	0	1	0	1	0	1	0
<i>Synambonites</i>	1	0	0	1	0	1	1	0	0	0	1	1	0	0
<i>Gatosella</i>	0	1	1	1	0	2	0	2	0	3	1	0	0	1
<i>Chaganella</i>	1	0	0	1	0	0	0	1	0	2	1	0	0	0
<i>Rongambonites</i>	0	1	0	1	0	0	0	1	0	1	1	1	0	0

**Figure 2.** Index map of central San Juan Province showing Ordovician outcrops and location of the Cerro Viejo area (left). Collection sites are indicated by asterisks. A, Quebrada Los Gatos; B, Quebrada Honda.

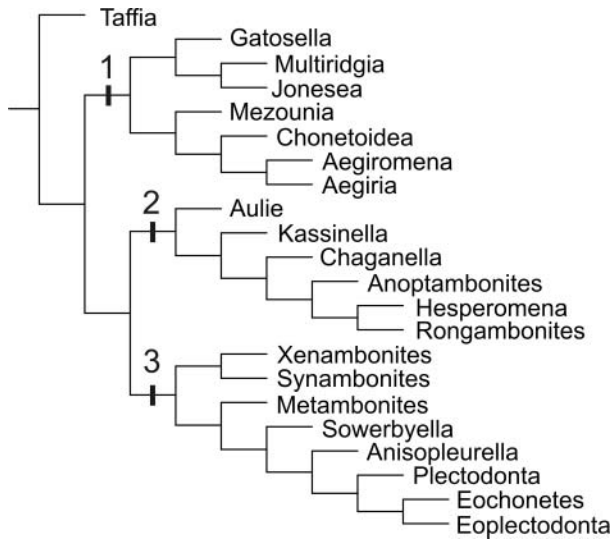


Figure 3. One of the 10 more parsimonious cladograms with a tree length of 11 steps, showing the nodes (1, 2, 3) discussed in the text.

the less ambiguous part of the cladogram (Fig. 4). The synapomorphy that characterizes this clade (node 3) is the possession of a well-defined, elevated bema. As the cladograms show, xenambonitins are more closely related to sowerbyellids than to any other group. *Xenambonites* and *Synambonites* appear as a basal subclade of the clade defined by having a ventral platform. The more derived members of this subclade are *Eochonetes*, *Eoplectodonta* and *Plectodonta*, which share a denticulate hinge. The FADs of these genera (Late Ordovician to Devonian) agree well with their placement in the phylogenetic tree.

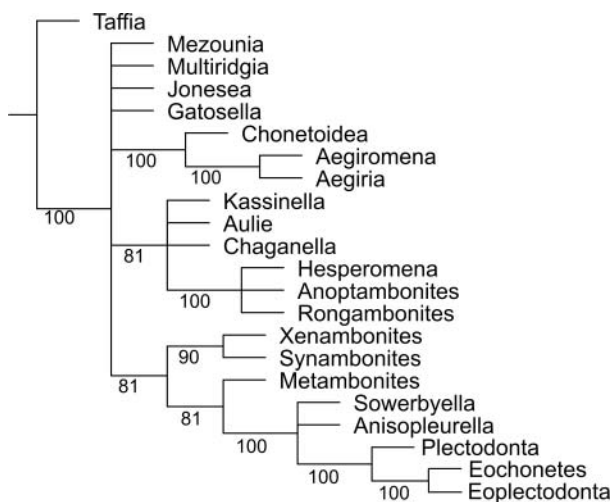


Figure 4. 80% majority rule consensus tree. Numbers on the branches indicate majority rule support for node. Note that phylogenetic relationships of *Gatosella* within the aegiromenid subclade are ambiguous.

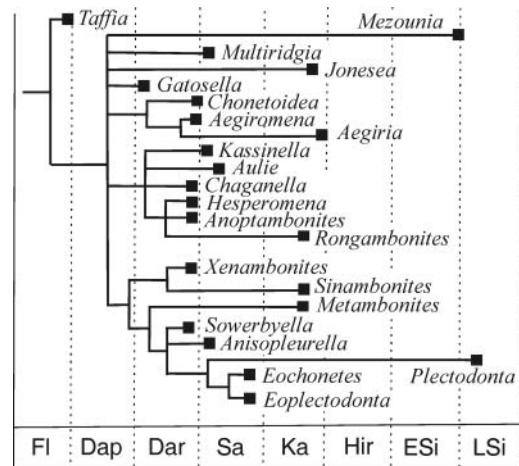


Figure 5. 80% majority rule consensus tree calibrated to chronostratigraphic scale. Black rectangles indicate the first appearance datum of each taxon. Fl, Floian; Dap, Dapingian; Dar, Darriwilian; Sa, Sandbian; Ka, Katian; Hir, Hirnantian; ESi, Early Silurian; LSi, Late Silurian.

The relationships inferred from cladistic analysis support a classification of the plectambonitoideans bearing undercut cardinal process into three families. This arrangement differs from the current Treatise classification as follows: (1) the subfamily Aegiromeninae should be elevated to the family rank (family Aegiromenidae); and (2) the xenambonitins do not appear closely related to the aegiromenids and should be included within the family Sowerbyellidae. The family Hesperomenidae, on the other hand, appears as a distinct, well-supported clade, as was recognized by Cocks & Rong (1989, 2000).

Systematic palaeontology

The material figured and cited in this paper is housed in the palaeontological collection of the Centro de Investigaciones Paleobiológicas (CIPAL), Córdoba University (CEGH-UNC collection numbers).

Order **Strophomenida** Öpik 1934
 Superfamily **Plectambonitoidea** Jones 1928
 Family **Aegiromenidae** Havlíček 1961
 (ex Aegiromeninae Havlíček 1961, p. 450)
 Genus ***Gatosella*** gen. nov.

Type species. *Gatosella muricata* sp. nov.

Derivation of name. After Quebrada Los Gatos, the type area.

Diagnosis. Shell small, gently concavo-convex. Ornament unequally parvicostellate. Dental plates vestigial. Ventral muscle field small, bilobed. Well-developed ventral

platform near the valve mid length formed by a series of elongate papillae and tubercles. Cardinal process undercut connecting with socket ridges laterally to form an inverted V-shaped structure. No bema. Incipient dorsal platform confined to the medial part of the valve delineated by short septules and isolated tubercles arranged radially flanking the anterior end of a stout median septum.

Occurrence. Uppermost San Juan Formation, lower Darriwilian.

Remarks. The new genus *Gatosella* is assigned to the family Aegiromenidae based on the absence of lateral septa and bema combined with a rudimentary dorsal platform delineated by elongate papillae. According to the diagnosis of Cocks & Rong (1989), aeginomenins differ from the xenambonitins in the lack of a platform. One of the most distinctive features of *Gatosella* is the rudimentary platform confined to the median part of the valve. It differs from the 'true' dorsal platform of hesperomenids and other plectambonitoids in that it is delineated by a few elongate papillae adjacent to the median ridge. In the aegiromenins the presence of rounded or gout-shaped papillae and/or elongate papillae or septules surrounding the ventral and dorsal muscle fields is very common (Havlíček 1991). In most of the genera they are arranged chaotically (*Jonesea*, *Chonetoidea*, *Nabiaioia*) or more or less radially (*Aegiromena*). In some species of *Aegiria* (e.g. *A. norvegica* Öpik) a low platform is suggested by a row of radial papillae. Among described aegiromenins, *Gatosella* is closest to *Multiridgia* Zeng 1987, from the Miaopo Formation of early Sandbian age (Zhan & Jin 2007). Externally, the Chinese genus (type species *M. elegans* Zeng) resembles *Gatosella* in its small shell and its unequally parvicostellate ornament. The latter, however, has a more transverse shell and a more convex ventral valve. Internally, *Multiridgia* bears an arcuate row of septules in both valves, though their shape, arrangement and location differ from those of *Gatosella*. In the new Precordilleran genus the ventral platform is much larger and formed by longer and more elevated septules reaching the mid length of the valve, whilst in *Multiridgia* it is low and confined to the posterior quarter of the valve. Moreover, in *Gatosella* the ventral muscle field is clearly defined in all growth stages whilst in *Multiridgia* it is smooth or weakly impressed. The dorsal interior in both genera is also clearly different. The new genus has a more prominent and longer median septum and the papillae are confined to both sides of its anterior termination, delineating an incomplete gently raised platform. This kind of incipient dorsal platform is infrequent in the plectambonitoideans; in *Aegiromena corolla* Havlíček & Branisa the median septum is accompanied laterally by septules beyond the bema. In *Aegiromena aquila* (Barrande) there is a row of coarse papillae radially arranged simulating a platform; however, they are not confined to the sides of the dorsal

septum but are more or less uniformly dispersed, forming a diffuse arch outside to the bema. In *Aegiromena glacialis* Benedetto, especially in juvenile shells, the median septum is flanked by 2–6 radial short septules and/or papillae that evolved to a moderately elevated large bema in mature specimens. There is no certainty that the incipient 'platform' of *Gatosella* represents an ancestral stage (ontogenetic or phylogenetic) in the development of a bema or is a 'true' platform in the sense of Cocks & Rong (1989). However, on the basis of its location close to the margin (at about 75% of shell length) this structure can be better interpreted as a platform.

Also distinctive for *Gatosella* is the relatively prominent ventral platform. Among plectambonitoids lacking undercut cardinal process *Calypsolepta* displays a somewhat similar ventral platform, but it differs in being more continuous (elongate papillae are only evident in some specimens of *C. rarum* (Neuman 1976)) and is bisected by a variably developed median septum that is absent in *Gatosella*. Of the plectambonitoids that have an undercut cardinal process, *Synambonites* Zhan & Rong and *Xenambonites* Cooper possess a high, continuous rim running close to the valve margin. In contrast, in the new Argentinian genus there is a true 'ventral platform' formed by a series of radially arranged septules, which clearly differs from the 'subperipheral rim' of other plectambonitoideans. The ventral platform of *Gatosella* is reminiscent of that of some species of *Aegiromena*, such as *A. descendens* Havlíček from the Bohdalec Shale of the Czech Republic (Katian) in which radial rows of septules and elongate papillae are present on the areas surrounding the anterior ends of muscle scars but are lacking in the central part of the valve (Havlíček 1967, pl. 4, Figs. 7–9).

Gatosella muricata sp. nov.
(Fig. 6A–Q)

Diagnosis. As for the genus by monotypy.

Derivation of name. Latin, *muricatus*, with spines.

Material. Holotype: CEGH-UNC 22044 (ventral internal mould, Fig. 6K–L); paratypes: CEGH-UNC 22040–22053 (seven external moulds, four internal moulds of ventral valves and one internal mould of dorsal valve).

Occurrence. Western slope of Cerro Viejo, uppermost San Juan Formation, 2.5–3.1 m below contact with the Los Azules Formation.

Description. Shell small, up to 5 mm wide, semielliptical in outline, with average length:width ratio of 0.64, gently concavo-convex; maximum width at the hinge line; cardinal extremities acute to nearly rectangular. Ventral valve moderately convex, with planar apsacline interarea

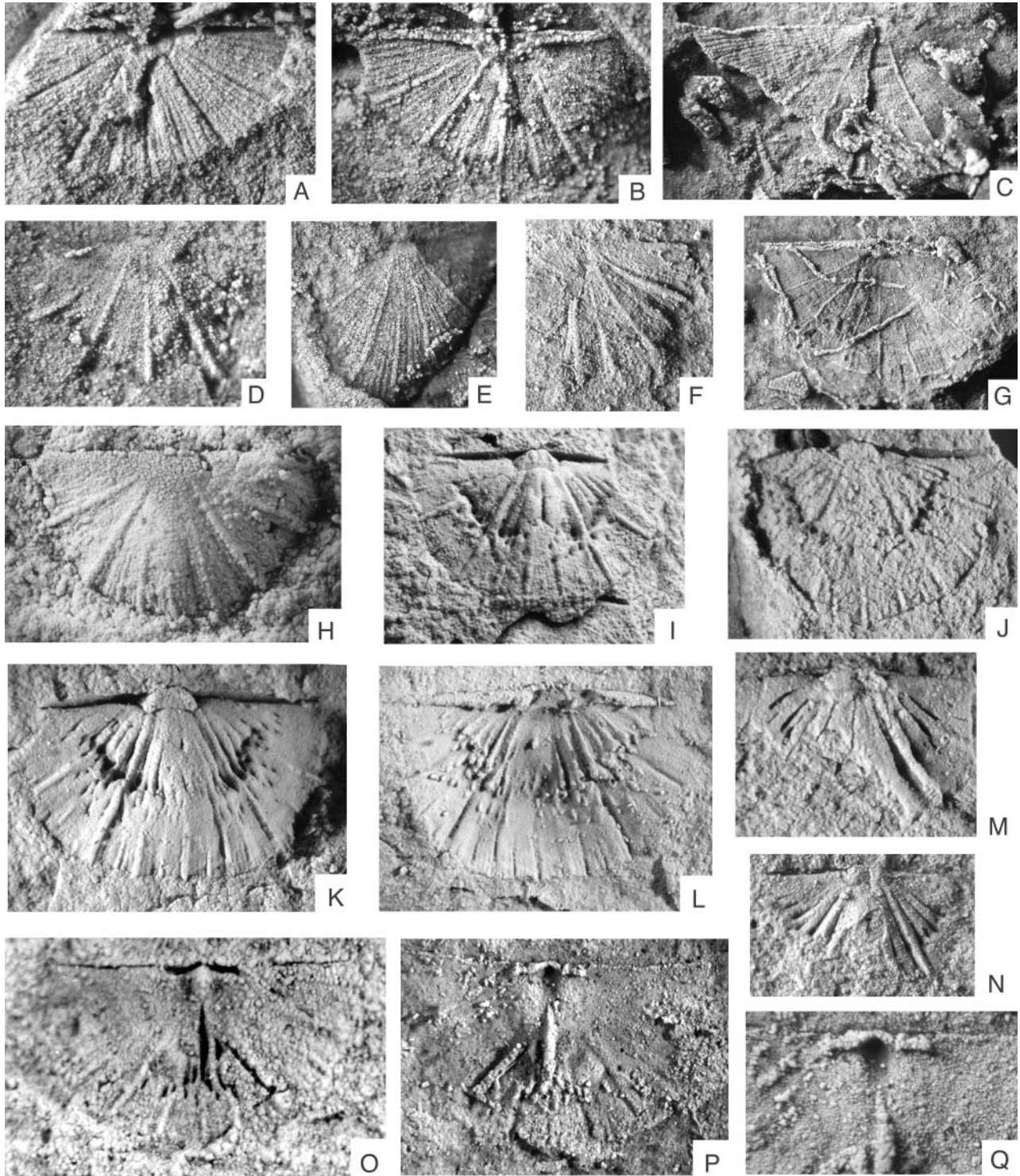


Figure 6. *Gatosella muricata* gen. et sp. nov. **A, B**, Dorsal valve external mould (CEGH-UNC 22040) and latex cast ($\times 12$); **C**, dorsal valve exterior, latex cast, CEGH-UNC 22041 ($\times 10$); **D**, dorsal valve exterior, latex cast, CEGH-UNC 22045 ($\times 12$); **E**, ventral valve exterior, latex cast, CEGH-UNC 22051 ($\times 8$); **F**, dorsal valve exterior, latex cast, CEGH-UNC 22047 ($\times 15$); **G**, dorsal valve exterior, latex cast, CEGH-UNC 22046 ($\times 10$); **H**, ventral valve exterior, latex cast, CEGH-UNC 22052 ($\times 13$); **I**, ventral valve internal mould CEGH-UNC 22053 ($\times 12$); **J**, ventral valve internal mould CEGH-UNC 22050 ($\times 12$); **K, L**, ventral valve internal mould, holotype CEGH-UNC 22044 and latex cast ($\times 14$); **M**, incomplete internal mould, juvenile ventral valve CEGH-UNC 22049 ($\times 22$); **N**, incomplete internal mould of ventral valve CEGH-UNC 22048 ($\times 12$); **O, P, Q**, dorsal valve internal mould CEGH-UNC 22043, latex cast ($\times 15$), and detail of cardinalia ($\times 30$).

and small convex pseudodeltidium. Dorsal valve gently concave, almost flat with hypercline dorsal interarea. Radial ornament unequally parvicostellate with 5–7 primary accentuated ribs originating at or near the umbo and one generation of less prominent ribs originating approximately at valve mid length; 4–6 fine, closely spaced parvicostellae between accentuated ribs along the anterior margin.

Ventral interior with robust teeth supported by very short dental plates, only present in adult specimens. Bilobed ventral muscle field well impressed, small, 50–60% as long as wide and extended forward approximately for 10% of the valve length; central adductor field wider than the more excavated, subtriangular diductor scars. Ventral platform ('visceral platform') extending to about the mid length of the valve, formed by a series of radially arranged elongate papillae and septules; isolated papillae irregularly disposed beyond the platform. A series of rounded radial grooves reflects the exterior accentuated ribs.

Dorsal interior with slender, undercut cardinal process, connecting laterally with thick widely divergent socket ridges to form an inverted V-shaped structure, with bounding minute slit-like dental sockets at their distal ends. Median septum prominent, originating anterior of alveolus, extending for two-thirds of valve length. A few short septules and isolated tubercles arranged radially on both sides of the median septum delineating an incipient, gently elevated platform confined to the medial part of the valve; septules disappear laterally, the valve floor becoming nearly smooth with only sparse small tubercles. Pallial markings not impressed.

Acknowledgements

I am grateful to D.A.T. Harper and Y. Candela for helpful reviews of the manuscript. Fieldwork was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (grant PIP-CONICET 00861), and Agencia Nacional de Promoción Científica y Técnica (grant FONCYT-PICT 16-21857).

References

- Albanesi, G. L. & Ortega, G.** 2002. Advances on conodont-graptolite biostratigraphy of the Ordovician System of Argentina. Pp. 143–166 in F. G. Aceñolaza (ed.) *Aspects of the Ordovician System in Argentina*. Serie Correlación Geológica 16, INSUGEO, Tucumán.
- Andreev, D. A.** 1993. New Ordovician Plectambonitaceans (Brachiopoda) from Tuva and the Leningrad region. *Palaeontological Journal*, **27**, 65–72.
- Astini, R. A., Benedetto, J. L. & Vaccari, N. E.** 1995. The Early Palaeozoic evolution of the Argentine Precordillera as a rifted, drifted and collided terrane: a geodynamic model. *Geological Society of America Bulletin*, **107**, 253–273.
- Benedetto, J. L.** 1993. La hipótesis de la aloctonía de la Precordillera Argentina: un test estratigráfico y biogeográfico. *Actas 12° Congreso Geológico Argentino*, **3**, 375–384.
- Benedetto, J. L.** (ed) 2003. *Ordovician Fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba, 560 pp.
- Benedetto, J. L.** 2004. The allochthony of the Precordillera ten years later (1993–2003): A new paleobiogeographic test of the microcontinental model. *Gondwana Research*, **7**, 1027–1039.
- Benedetto, J. L.** 2007. Brachiopod succession in the Lower-Middle Ordovician carbonate platform of the Precordillera terrane, western Argentina: an example of interplay between environmental, biogeographic and evolutionary processes. *Acta Palaeontologica Sinica*, **46**(Suppl.), 28–36.
- Benedetto, J. L., Sorrentino, L., Cech, N. & Sánchez, T. M.** 2008. Functional morphology of the Ordovician plectambonitoid brachiopod *Inversella* (*Reinversella*) *arancibiai* Herrera & Benedetto from the San Juan Formation, Argentine Precordillera. *Alcheringa: An Australasian Journal of Palaeontology*, **32**, 53–63.
- Benedetto, J. L., Vaccari, N. E., Waisfeld, B. G., Sánchez, T. M. & Foglia, R. D.** 2009. Cambrian and Ordovician paleobiogeography of Andean margin of Gondwana and accreted terranes. Pp. 199–230 in M. G. Bassett (ed.) *Early Palaeozoic Peri-Gondwanan Terranes. New Insights from Tectonics and Biogeography*. The Geological Society of London, Special Publications, **325**.
- Bergström, S. M., Chen, X., Gutierrez Marco, J. C. & Dronov, A.** 2008. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia*, **42**, 97–107.
- Brussa, E. D., Toro, B. A. & Benedetto, J. L.** 2003. Biostratigraphy. Pp. 75–90 in J. L. Benedetto (ed.) *Ordovician Fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba.
- Butts, C.** 1926. The Paleozoic rocks. Pp. 41–230 in G. I. Adams, C. Butts, L. W. Stephenson & C. W. Cooke (eds) *Geology of Alabama*. Alabama Geological Survey Special Report 14, Alabama.
- Candela, Y.** 2010. Phylogenetic relationships of leptellinid brachiopods. *Alcheringa: An Australasian Journal of Palaeontology*, **34**, 493–514.
- Cañas, F. L.** 1999. Facies sequences of Late Cambrian to Early Ordovician carbonates of the Argentine Precordillera: A physical stratigraphic comparison with Laurentian platforms. Pp. 43–62 in J. D. Keppie & V. A. Ramos (eds) *Laurentia-Gondwana connections before Pangea*. Geological Society of America, Special Paper 336, Boulder.
- Carrera, M. G.** 2007. Sponges as sea-level markers: an example from the Ordovician limestones of the Argentine Precordillera. *Acta Palaeontologica Sinica*, **46**(Suppl.), 71–76.
- Cocks, L. R. M. & Brunton, C. H. C.** 1996. The classification of the order Strophomenida. Pp. 47–51 in P. Copper & Jisuo Jin (eds) *Brachiopods*. A.A. Balkema, Rotterdam/Brookfield.
- Cocks, L. R. M. & Rong, J.** 1989. Classification and review of the brachiopod superfamily Plectambonitacea. *Bulletin of the British Museum (Natural History), Geology Series*, **45**, 77–163.
- Cocks, L. R. M. & Rong, J.** 2000. Strophomenida. Pp. 216–349 in R. L. Kaesler (ed.) *Treatise on Invertebrate Paleontology, part H, Brachiopoda (revised), vol. 2*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence.
- Dewing, K.** 2004. Shell structure and its bearing on the phylogeny of Late Ordovician-Early Silurian strophomenoid brachiopods from Anticosti Island, Québec. *Journal of Paleontology*, **78**, 275–286.

- Egerquist, E.** 1999. Revision of the plectambonitoid brachiopod *Ujukella* Andreev and related genera. *GFF*, **121**, 325–332.
- Goloboff, P., Farris, J. & Nixon, K.** 2003. T.N.T.: Tree Analysis Using New Technology. [Program and documentation available from the authors and at www.zmuc.dk/public/phylogeny].
- Harper, D. A. T., Cocks, L. R. M., Popov, L. E., Sheehan, P. M., Bassett, M. G., Copper, P., Holmer, L. E., Jin, J. & Rong, J.** 2004. Brachiopods. Pp. 157–178 in B. D. Webby, F. Paris, M. L. Droser & I. G. Percival (eds) *The Great Ordovician Biodiversification Event*. Columbia University Press, New York.
- Havlíček, V.** 1961. Plectambonitacea Im böhmischen Paläozoikum (Brachiopoda). *Vestník Ústředního ústavu Geologického*, **36**, 447–451.
- Havlíček, V.** 1967. Brachiopoda of the Suborder Strophomenina in Czechoslovakia. *Rozpravy Ústředního ústavu Geologického*, **33**, 1–235.
- Havlíček, V.** 1986. Climatic changes and development of benthic communities through the Mediterranean Ordovician. *Sborník geologických Ved, Geologie*, **44**, 79–116.
- Havlíček, V.** 1991. Genus concept in the Aegiromeninae and Leptellinae (Plectambonitacea, Brachiopoda). *Vestník Ústředního ústavu Geologického*, **66**, 151–162.
- Havlíček, V. & Branisa, L.** 1980. Ordovician brachiopods of Bolivia. *Rozpravy Československé Akademie Ved*, **90**, 1–53.
- Jones, O. T.** 1928. *Plectambonites* and some allied genera. *Memoirs of the Geological Survey of Great Britain, Palaeontology*, **1**, 367–527.
- Mitchell, C. E., Brussa, E. D., Toro, B. A. & Astini, R. A.** 1998. Late Ordovician graptolites from the Empozada Formation, Argentine Precordillera, an outer shelf, cool water, peri-Gondwanan assemblage? Pp. 224–226 in J. C. Gutierrez-Marco & I. Rábano (eds) *Proceedings of the 6th International Graptolite Conference & Field Meeting*. Temas Geológico-Mineros, **23**.
- Neuman, R. B.** 1976. Early Ordovician (late Arenig) brachiopods from Virgin Arm, New World Island, Newfoundland. *Geological Survey of Canada Bulletin*, **261**, 11–61.
- Öpik, A. A.** 1934. Über Klitambonitoid. *Acta et Commentationes Universitatis Tartuensis, Series A*, **36**, 1–239.
- Ortega, G. & Rickards, B.** 2003. A Darriwilian (Middle Ordovician) graptolite fauna of the lower member of the Los Azules Formation, Cerro Viejo, San Juan Precordillera. *Proceedings of the 7th International Graptolite Conference*. Serie Correlación Geológica, **18**, 87–92.
- Ottone, E. G., Albanesi, G. L., Ortega, G. & Holfeltz, G. D.** 1999. Palynomorphs, conodonts and associated graptolites from the Ordovician Los Azules Formation, Central Precordillera, Argentina. *Micropaleontology*, **45**, 225–250.
- Potter, A. W.** 1991. Discussion of the systematic placement of the Ordovician brachiopod genera *Cooperea* and *Craspedelia* by Cocks and Rong (1989). *Journal of Paleontology*, **65**, 742–755.
- Sánchez, T. M., Waisfeld, B. G., Carrera, M. G., Cech, N. & Sterren, A. F.** 2003. Paleoecology and biotic events. Pp. 111–142 in J. L. Benedetto (ed) *Ordovician Fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba.
- Sorrentino, L., Benedetto, J. L. & Carrera, M. G.** 2009. Diversidad taxonómica y distribución de morfotipos de braquiópodos en la Zona de *Ahtiella argentina* (Ordovícico Medio), Formación San Juan, Precordillera Argentina. *Ameghiniana*, **46**, 241–253.
- Williams, A.** 1970. Origin of laminar-shelled articulate brachiopods. *Lethaia*, **3**, 329–342.
- Williams, A., Carlson, S. J. & Brunton, C. H. C.** 2000. Brachiopod classification. Pp. 1–27 in R. L. Kaesler (ed.) *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised), Vol. 2*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence.
- Wright, A. D. & Rubel, M.** 1996. A review of the morphological features affecting the classification of clitambonitid brachiopods. *Palaeontology*, **39**, 53–76.
- Zeng, Q.** 1987. Brachiopoda. Pp. 489–555 in X. Wang, S. Ni, Q. Zeng, G. Xu, T. Zhou, Z. Li, L. Xiang & C. Lai (eds) *Biostratigraphy of the Yangtze Gorge Area, II. Early Palaeozoic Era*. Geological Publishing House, Beijing (in Chinese), 614 pp.
- Zhan, R. & Jin, J.** 2007. Ordovician–Early Silurian (Llandovery) stratigraphy and palaeontology of the upper Yangtze Platform, South China. *Post-Conference Field Excursion for the 10th International Symposium on the Ordovician System and the 3rd International Symposium on the Silurian System*. Science Press, Beijing, 169 pp.
- Zhan, R., Jin, J., Rong, J., Chen, P. & Yu, G.** 2008. Strophomenide brachiopods from the Changwu Formation (Late Katian, Late Ordovician) of Chun'an, western Zhejiang, South East China. *Palaeontology*, **51**, 737–766.

Appendix: List of coded characters and character states used in cladistic analysis

1. Shell profile: 0 concavo-convex; 1 biconvex
2. Ornament: subequally parvicostellate: 0; unequally parvicostellate 1; multicostellate 2
3. Dental plates: present 0; vestigial or absent 1
4. Ventral muscle field: subtriangular 0; small, bilobed 1; large, bilobed 2
5. Ventral median septum (or miophragm): absent 0; high, long: 1; short, confined posteriorly 2
6. Ventral platform: absent 0; high, continuous rim 1; delineated by papillae or tubercles 2
7. Bema: weak or absent 0; elevated, undercut 1; large, bilobed 2; defined by septules 3
8. Dorsal septum: absent 0; high, blade-like 1; short, confined to bema 2
9. Side septa: absent 0; present 1
10. Dorsal platform: absent 0; gently developed 1; strong, high 2; delineated by papillae 3
11. Cardinal process: not undercut 0; undercut 1
12. Cardinal process morphology: simple 0; strong, enlarged 1; small lobes differentiated 2
13. Denticles on hinge: absent 0; present 1
14. Internal surface: smooth 0; small tubercles 1; coarse papillae 2