Presence of punctae in the 'plectorthoidean' brachiopod *Famatinorthis turneri* (Middle Ordovician) from western Argentina: implications for early diversification of punctate orthides

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LETHAIA

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Famatinorthis Levy & Nullo is a distinctive orthide brachiopod of Dapingian age from the volcaniclastic rocks of the Famatina Range of western Argentina. Although it was originally classified among the plectorthoideans, a new collection from the La Escondida Formation has yielded exceptionally well-preserved moulds of *Famatinorthis turneri* in which silicified infillings of punctae are clearly visible, leading to the reassignment of the genus to the dalmanellidines. In this paper, phylogenetic analyses are used to determine the evolutionary relationships of *Famatinorthis*, the Tremadocian linoporellid *Lipanorthis*, and other Ordovician Gondwanan genera. The placement of Plectorthoidea in the same major clade as linoporellids, and the separation of Dalmanellidina as an independent clade are the most important features of all shortest trees, supporting the idea that linoporellids may have originated from a plectorthoid ancestor. Cladistic analysis reveals that *Lipanorthis* lies close to the ancestry of the linoporellid lineage, and *Famatinorthis* clusters within the more derived taxa of the clade with which it shares a large septalium. It seems that the presence of endopunctae in the orthides does not necessarily indicate close phylogenetic relationships as it could have occurred at different times in different clades. If the homoplasic nature of endopunctae in the order Orthida is supported by further morphologic and phylogenetic studies, the fundamental division of orthides in non-punctate (Orthidina) and punctate (Dalmanellidina) may need revision. □ *Brachiopods, Ordovician, Gondwana, Famatina, phylogeny, punctate orthides.*

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Famatinorthis Levy & Nullo 1973 is one of the most abundant and distinctive brachiopods of the Middle Ordovician volcanoclastic rocks of the Famatina Range, western Argentina. Its overall morphological features (see below) led to the genus being referred to the superfamily Plectorthoidea (Levy & Nullo 1973; Benedetto 1994, 2002). However, a new collection from the La Escondida Formation (Astini & Dávila 2002) yielded several ventral and dorsal internal moulds of *Famatinorthis turneri* Levy & Nullo on which silicified infillings of punctae are clearly visible. Punctae have also been observed in a series of partially silicified internal moulds of this species from the Molles Formation. Because of their very small diameter, preservation of these microscopic shell perforations seems to be relatively rare in the earliest punctate orthides. Preservation of punctae on internal moulds results from a combination of taphonomic factors, mainly the nature of the sediment (e.g. abundance of clay), and chemical environment (adequate supply of silica during early diagenesis), which may explain the apparent absence of punctae in large collections of *F. turneri* from other localities and horizons of the Famatina Range (Benedetto 2003b). Similarly, the punctate nature of the shell substance of *Lipanorthis* Benedetto (late Tremadocian of NW Argentina) was not originally discerned in neither the type species *L. andinus* Benedetto or in *L. santalaurae* Benedetto (in Benedetto & Carrasco 2002). The subsequent discovery of well-preserved radially-arranged punctae on internal moulds of *L. santalaurae* from the Saladillo Formation prompted Harper *et al.* (2004) to remove *Lipanorthis* from the plectorthoideans and transfer the genus to the dalmenellidines, leaving *Lipanorthis* as the oldest member of the suborder.

Lipanorthis and *Famatinorthis* are two recently documented examples that suggest, given an adequate preservational history, that punctae can be preserved in genera previously assigned to the Plectorthoidea. Since many plectorthids and giraldiellids are

morphologically close to the earliest forms of enteletoids (linoporellids), their assignment to either the suborders Orthidina or Dalmanellidina depends largely on the evidence of punctae. This raises the question as to whether the presence of punctae itself is really crucial for the major separation of the order Orthida into non-punctate and punctate forms. In other words, does the presence of punctae in the orthides necessarily indicate close phylogenetic relationships, or they could have originated independently in different clades?

The aim of the present paper is to document the presence of punctae in *F. turneri*, and to analyse the phylogenetic relationships of *Famatinorthis* and *Lipanorthis* to other Ordovician enteletoids, dalmanelloids and plectorthoids in order to provide insight on the origin of punctate orthides.

All the specimens of *Famatinorthis turneri* illustrated in this study (Fig. 3) are reposited in the palaeontological collections of CICTERRA (Centro de Investigaciones en Ciencias de la Tierra) under the prefix CEGH-UNC.

Geological setting and age

The material described here was sampled from the La Escondida Formation exposed in the central Famatina Range (Sierra de Famatina), about 15 km west of the town Angulos (Fig. 1). A detailed description of the lower Palaeozoic geology of the area was given by Astini & Dávila (2002) and Astini (2003). The Ordovician volcano-sedimentary rocks form a continuous, 2500 m-thick succession divided into the Famatina Group and the Cerro Morado Group (Fig. 2). The overall succession of the Famatina Group, which includes the Suri and Molles formations, shows a clear shallowing upward trend from dysaerobic graptolitic black mudstones to inner-platform richly fossiliferous siltstones and cross-bedded sandstones. The amount of volcanogenic rocks, including several ignimbrite units and volcanic breccias, increases towards the top of the group (mainly in the Molles Formation) recording the progradation of a slope-apron within active volcanic settings (Astini & Benedetto 1996; Mángano & Buatois 1996, 1997; Astini 1999). The volcanic succession continues into the overlying Cerro Morado Group, which starts with the El Portillo Formation, ac. 580 m thick unit formed by acidic volcanics and lava flows (rhyolites, rhyodacites) interbedded with ignimbrites and welded tuffs (Astini & Dávila 2002). The succession culminates with the La Escondida Formation, which consists of ignimbrites and laminated tuffs with fragmented lapilli formed by subaerial explosive volcanism. These volcaniclastic rocks are
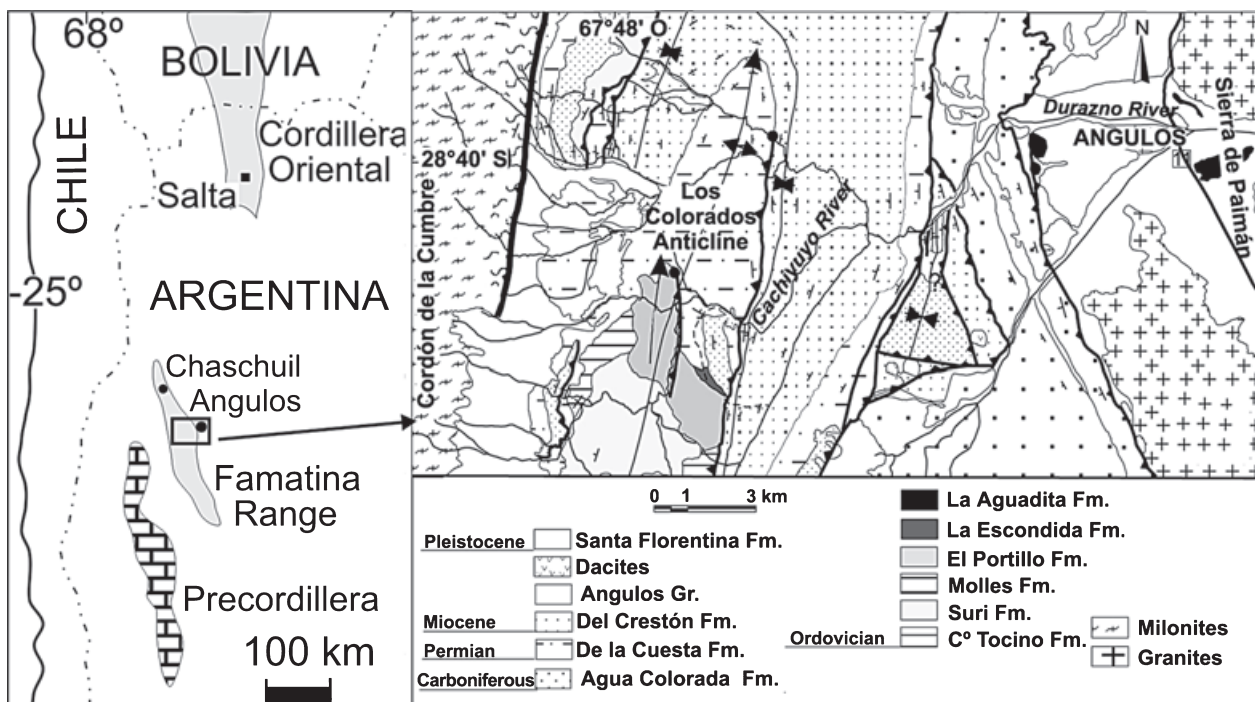

Fig. 1. Location of the Famatina Range and geological map of the studied area showing the collection site (asterisk) (modified from Astini 2003).
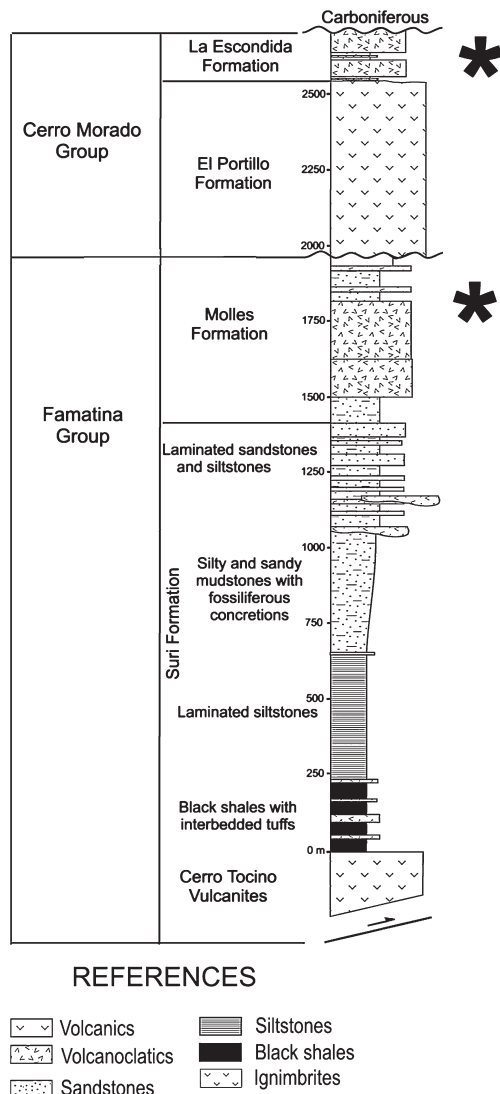
Fig. 2. Generalized stratigraphic column of the Famatina and Cerro Morado groups and levels bearing *Famatinorthis turneri* indicated by an asterisk (from Astini 2003).

interbedded with a rhythmic interval of marine shallow-water siltstones and fine-grained amalgamated sandstones with hummocky cross stratification. Shells beds are frequent at their bases, and oscillatory ripples may occur on their tops. Some sandstone beds are rich in trace fossils belonging to the *Cruziana* ichnofacies. The recurrent regressive-transgressive cycles within both the Famatina and the Cerro Morado groups have been interpreted as a result of active doming volcanism and cooling contraction, a distinctive feature of most volcanic-arc settings (Astini 1999, 2003).

The fossiliferous levels providing the specimens studied here are restricted to the middle part of the La Escondida Formation, within the interval of bioturbated green siltstones and fine-grained sandstones

mentioned above (Fig. 2). This c. 10 m thick transgressive interval rests sharply on a package of silicified pyroclastic rocks. Fossils occur mostly at the base of sandstone beds and form densely packed monotypical concentrations dominated by disarticulated shells of *Famatinorthis turneri*, with a similar proportion of ventral and dorsal valves. Most valves are randomly oriented, but in some beds display nested and stacked orientations perpendicular or oblique with respect to the bedding plane. According to Kidwell *et al.* (1986) and Kidwell (1991), these shell beds can be classified as sedimentological concentrations. Both taphonomic and sedimentological evidence indicates that they originated under sustained storm-generated oscillatory currents in a nearshore setting. Fossils are embedded in a muddy matrix which includes small fragments of brachiopod shells and dispersed small quartz grains. The largest shells are filled with a silicified matrix, the silicification probably due to the replacement of the original calcitic cement by silica during early diagenesis. As a result, internal structures of brachiopods, including punctae, are exceptionally preserved.

The age of the Famatinian volcaniclastic succession is well constrained on palaeontological (see compilation by Benedetto 2003a) and isotopic data. Conodonts recovered from shell beds bearing abundant specimens of *Famatinorthis turneri* in the Chaschuil region, north of the Famatina Range, were referred by Albanesi & Vaccari (1994) to the *Baltoniodus navis* Biozone of Dapingian age. The overlying rhyolite (Las Planchadas Formation) yielded a mean U-Pb SHRIMP dating of 468.3 ± 3.4 Ma (Baldo *et al.* 2003), an age close to the Dapingian/Darriwilian boundary (468.1 Ma according to Ogg 2004) or early Darriwilian in the graptolite calibrated timescale of Sadler *et al.* (2009). Conodonts from beds containing abundant specimens of *F. turneri* sampled from the lower part of the Molles Formation in the central Famatina Range correlate with the Dapingian *Paroistodus originalis* Biozone (Lehnert *et al.* 1997). Carbonate-rich, brachiopod-bearing coquinites from the base of the same formation at its type section of Molles River yielded a conodont association referable to the upper part of the *Oepikodus evae* Zone of Floian age (Albanesi & Astini 2000). Outside Famatina, a form comparable to *F. turneri* has been recorded in the volcaniclastic Shin Brook Formation of northeastern Maine, of Arenigian (~Dapingian) age (Neuman 1997). Thus, on the basis of the known record of *F. turneri*, the fossiliferous interval of the La Escondida Formation is tentatively dated as late Dapingian to early Darriwilian, but this age should be further corroborated by additional evidence.

Remarks on the morphology of *Famatinorthis turneri*

The monotypic genus *Famatinorthis* was erected by Levy & Nullo (1973) to include a large plectorthoid brachiopod from the Molles Formation considered morphologically close to *Mimella*. In fact, a series of shells from the same stratigraphic levels yielding *Famatinorthis turneri* were initially referred to *Mimella nova* Levy & Nullo 1973 on the basis of possessing a deeply impressed ventral muscle field (Levy & Nullo 1973). Morphology of *F. turneri* was re-assessed by Benedetto (1994) on the basis of material from the volcano-sedimentary rocks exposed along the Chaschuil River, in the northermost reaches of the Famatina Range, leading to emend the diagnosis of *Famatinorthis* and to regard *Mimella nova* as a junior synonym of *F. turneri*. New specimens of *F. turneri* collected from the Molles Formation at its type section of Molles River and at Quebrada La Leña revealed the presence of aditicules (Benedetto 2003b). It is significant that punctae were not detected in neither the Chaschuil or in the Molles River specimens.

Famatinorthis is characterized by its relatively large (25–35 mm wide) dorsibiconvex, gently uniplicate shell, multicostellate ornament, and well-developed aditicules (as defined by Jin *et al.* 2007; Jin 2012) arranged along the rib crests forming roughly concentric rows along the growth lamellae (Fig. 3K). The ventral muscle field is large (35–45% of valve length), pear-shaped, deeply impressed, delimited by lateral bounding ridges continuous posteriorly with dental plates that converge anteriorly forming a rounded anterior margin that becomes distinctly raised above the valve floor in adult and gerontic individuals (Fig. 3A, B). The ventral mantle canal system is saccate, with *vascula media* subparallel to each other or weakly divergent, originating from the anterior ends of diductor tracks, then diverging anterolaterally becoming broadly arcuate; the *vascula genitalia* are large bearing numerous radial, elongated ridges. The dorsal interior is characterized by a large concave septalium supported anteriorly by a median septum that anteriorly extends one-third to one-half of the valve length (Fig. 3G, I). The cardinal process is a long blade-like ridge always occupying the full length of septalium. The brachiophores are blunt, strongly diverging from each other; the sockets are deep, open laterally, bounded posteriorly by a strong rounded ridge and supported anterolaterally by well-developed fulcral plates. The dorsal muscle field is large, averaging one-half the length of shell, quadripartite, subrectangular in outline; the posterior pair of adductor muscle scars is deeply impressed and slightly larger than the anterior pair, and their posterior margin is digitate (Fig. 3J); the anterior pair is separated from the posterior pair by a broad transverse ridge. The dorsal mantle canal system, faintly impressed, seems to be of lemniscate type.

Infillings of punctae are preserved on the internal moulds obtained by etching original shells using 10% hydrochloric acid and can be seen under a stereomicroscope and in the photographs when the mould surface is coated with sublimated magnesium. Although punctae are present on the entire shell, they are better preserved on the posterolateral areas of both valves and, to a lesser degree, within the delthyrial chamber (Fig. 3B, C). In these regions punctae are randomly distributed and closely spaced, with a density of approximately 50 per mm^2. Individual punctae are straight, intersecting the inner shell layer at right angles (Fig. 3D, E), ranging in diameter from 40 to 50 μm. Outside the apical regions, punctae are arranged in a series of radial rows approximately 5–6 per millimetre (Fig. F, H).

Lipanorthis, the plectorthoidean cardinalia, and characters for phylogenetic analysis

Lipanorthis is an ubiquitous genus in the upper Tremadocian-Floian beds of northwestern Argentina. It is represented by several species, however only three species have been formally described: *L. andinus* Benedetto (Coquena Formation), *L. santalaurae* Benedetto (Floresta and Saladillo formations, Benedetto & Carrasco 2002; Harper *et al.* 2004), and *L. lipanensis* (Benedetto 1998). The latter, from the Acoite Formation, was originally attributed with interrogation to *Salopia* by Benedetto (1998) and reassigned to *Lipanorthis* by Harper *et al.* (2004), other species, not yet described, have been found by the author in the Azul Pampa and the San Bernardo formations and are awaiting documentation. The oldest member of the genus is *L. santalaurae*, recorded around the boundary of the *Cordylodus angulatus* and *Paltodus deltifer* conodont Biozones (upper Tr2 and Tr3), whilst the youngest is *L. lipanensis* of Floian age (*Didymograptellus bifidus* Biozone; Toro 1997). A detailed description of all *Lipanorthis* species is outside the scope of this work. Here, we discuss some features of *Lipanorthis* that are relevant for phylogenetic analysis, in particular the morphology of cardinalia. In the original diagnosis, *Lipanorthis* was described as having '…concave brachiophore bases converging onto low median ridge, bounding anteriorly bilobed notothyrial
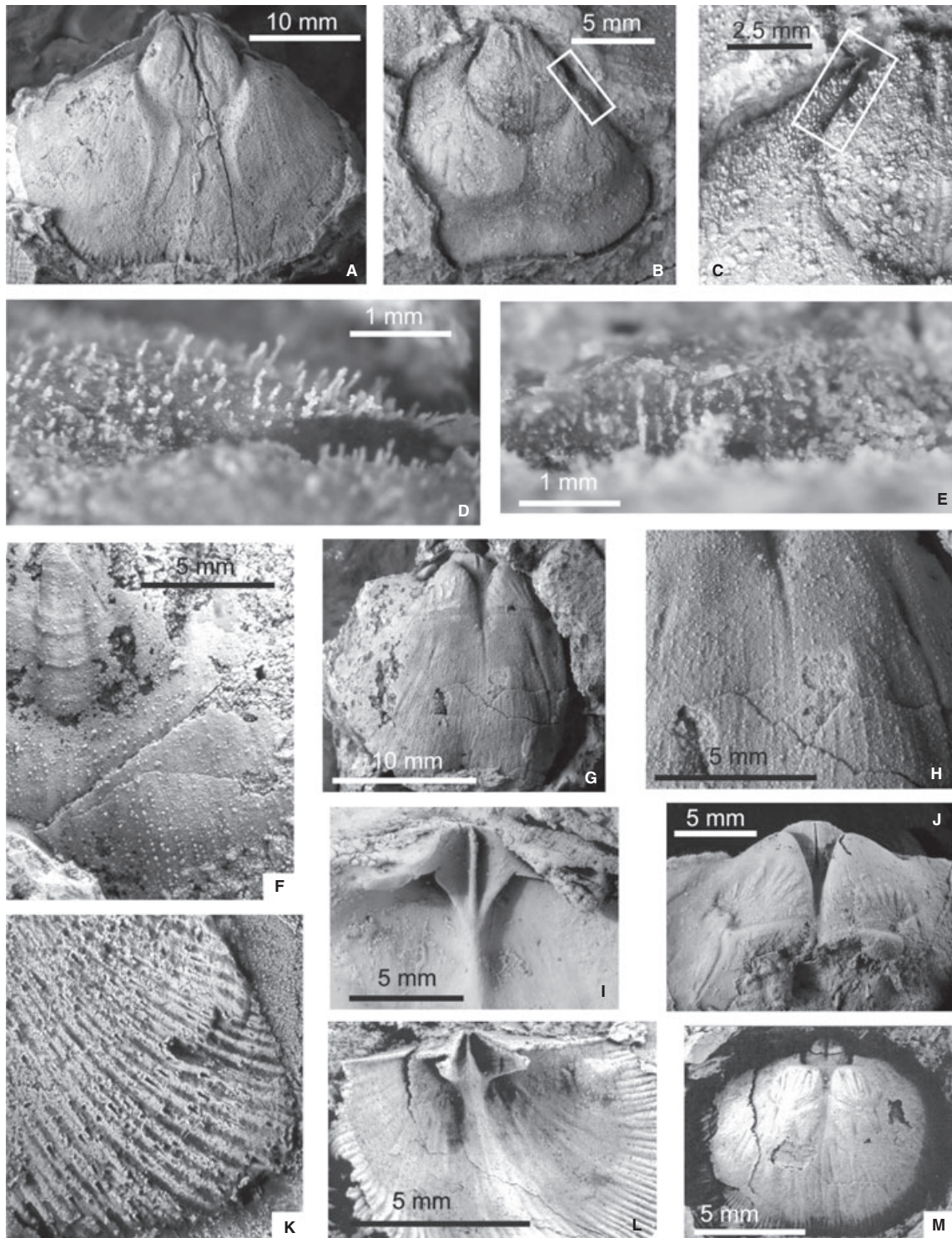
Fig. 3. (A–K) *Famatinorthis turneri* Levy & Nullo 1973; from the La Escondida Formation (A–H, K) and from the Molles Formation (I, J). A, internal mould of ventral valve, CEGH-UNC 25310. B, internal mould of ventral valve, CEGH-UNC 25312. C, detail of the same specimen as B showing punctae in delthyrial and posterolateral chambers. D, oblique view of infillings of puntae within the area delimited by a rectangle in C. E, cross section of carbonate shell remains showing subvertical equally spaced punctae, the same specimen as B (enlarged area delimited by a rectangle). F, incomplete ventral internal mould showing punctae arranged in radial rows, CEGH-UNC 25326. G, dorsal internal mould, CEGH-UNC 25315. H, detail showing punctae arranged in well defined rows, the same specimen as G. I, latex cast of cardinalia, CEGH-UNC 19823. J, internal mould of cardinalia showing digitate posterior adductor scars, CEGH-UNC 19820. K, latex cast of dorsal exterior showing aditicules, CEGH-UNC 19826. L-M *Lipanorthis santalaurae* Benedetto, Upper Tremadocian, Saladillo Formation. L, oblique view of latex cast of dorsal valve, CORD-PZ 30434-1 (from Harper *et al.* 2004). M, internal mould of dorsal valve, CORD-PZ 30434-1 (from Harper *et al.* 2004).

chamber' (Benedetto *in* Benedetto & Carrasco 2002, p. 656). The term 'notothyrial chamber' was preferred instead of 'septalium' because a V-shaped troughlike structure was not recognized in the available material. In the revised diagnosis by Harper *et al.* (2004, p. 276) *Lipanorthis* was described as having 'high brachiophore bases convergent onto the sides of median ridge, together forming short septalium with U-shaped profile' (illustrated here in Fig. 3L, M).

A true septalium, as defined by Williams & Brunton (1977) and Zuykov & Harper (2007) is absent in most plectorthoideans in which, instead, there is a concave, narrow notothyrial platform bounded laterally by convergent brachiophore bases, and anteriorly by variably developed ridges arising from the anterior ends of brachiophore bases (e.g. *Comatopoma*, *Gelidorthis*, *Geraldibella*, *Tazzarinia*, *Desmorthis*). In his diagnosis of the superfamily Plectorthacea, Havlíček (1977, p. 75) used the term 'notothyrial chamber' for this configuration. It differs from the septalium in that the brachiophopre bases are not fused medially. A further complication is that a sessile septalium may change gradually into a notothyrial chamber along a phyletic lineage (e.g. the *Protorthisina-Kvania-Nanorthis* lineage), or even through ontogeny, as observed in *Lesserorthis* (Benedetto 2007). In *Lipanorthis*, depending on the species, both a notothyrial chamber or a sessile septalium can be present. Thus, in order to elaborate the matrix for cladistic analysis, the following character states of brachiophore bases have been differentiated: (1) subperpendicular to valve floor bounding laterally the notothyrial platform; (2) converging to delimit a notothyrial chamber; (3) fused medially forming a small to medium-sized sessile septalium; and (4) fused medially forming a large, posteriorly sessile septalium (see Table 1).

Among brachiopods, the choice of those characters appropriate for cladistic analysis is particularly difficult, because many morphologies are subject to recurrent homoplasy, resulting in a questionable phylogenetic significance (Williams *et al.* 1996; Williams & Harper 2000). Good examples of highly homoplasic features are shell convexity and ornament, length and inclination of interareas, development of dorsal and ventral median ridges and size of muscle fields. Mantle canal systems also show a high degree of homoplasy because their basic patterns (e.g. saccate, pinnate, lemniscate) are recurrent in different groups of taxa, even at ordinal or supraordinal levels. These characters mentioned above, however, are useful for generic differentiation and have been widely used to diagnose families and subfamilies. The characters considered here as more phylogenetically informative (Table 1) refer to the shell structure (punctae, aditicules) and morphology of cardinalium (cardinal process, fulcral

Table 1. List of coded characters and character states.

1. Shell structure. 0: impunctate; 1: punctuate
2. Aditicules. 0: absent; 1: present
3. Shell convexity. 0: subequally biconvex; 1: dorsibiconvex; 2: ventribiconvex; 3: planoconvex; 4: convexoplane or convexoconcave
4. Ventral interarea. 0: low; 1: high apsacline; 2: high cataclite
5. Ornament. 0: costate; 1: coarsely costellate; 2: multicostellate; 3: parvicostellate; 4: fascicostellate
6. Rib curvature. 0: not incurved posteriorly; 1: incurved posteriorly to intersect hinge
7. Cardinal process. 0: absent; 1: short, simple; 2: long, thin ridge; 3: with shaft and enlarged non-lobate myophore; 4: myophore bi or trilobate
8. Brachiophore plates. 0: short, subperpendicular to valve floor; 1: converging to valve floor forming a notothyrial chamber; 2: forming a small septalium confined to the apical region; 3: forming a sessile medium-sized septalium; 4: forming a large septalium supported anteriorly by a septum
9. Fulcral plates. 0: absent; 1: present
10. Ventral muscle field. 0: short, subtriangular or suboval; 1: large, flabellate; 2: large suboval or subtriangular, deeply impressed and/or raised anteriorly; 4: on a pseudospondylium
11. Dorsal muscle field. 0: indistinct; 1: short, quadripartite; 3: large, posterior scars digitate
12. Dorsal median septum. 0: absent; 1: short ridge; 2: long and robust
13. Notothyrial platform. 0: low or rudimentary; 1: high, raised on valve floor; 2: notothyrial chamber/septalium
14. Brachiophores. 0: bladelike or rodlike, ventrally directed; 1: strongly divergent, subparallel to hinge line
15. Dental plates: 0: short, recessive; 1: long and subparallel or converging anteriorly; 2: absent
16. Pedicle callist. 0: absent; 1: present

plates, brachiophopre plates, notothyrial platform, septalium). The features lying in the ventral valve, such as dental plates, pedicle callist, and morphology of muscle field were also considered, but they are probably less significant phylogenetically because also show a high degree of homoplasy.

Cladistic analysis and results

The fundamental subdivision of the order Orthida into two suborders (Orthidina and Dalmanellidina) based on the non-punctate or punctate condition of the shell has been widely accepted for more than a half century (Moore 1952). This grouping is founded on the assumption that punctae constitute an evolutionary novelty (apomorphy) that appeared at one time in the early history of rhynchonelliformean brachiopods (Williams & Harper 2000). If correct (there is no conclusive evidence against this), punctate orthides are a monophyletic clade. The origin of punctate orthides is not yet resolved, current evidence suggest that non-punctate and punctate orthides may have shared a common ancestor in the mid Cambrian, prior to the brachiopod diversification in the Ordovician (Harper 2000).

Discovery of punctae in the late Tremadocian genus *Lipanorthis* Benedetto of northwestern Argentina (Harper *et al.* 2004) considerably extended the range of the whole suborder Dalmanellidina into older strata. This genus was reinterpreted as a linoporellid (Harper *et al.* 2004), a family that reached a diversification peak in the Late Ordovician (Sandbian-Katian). The linoporellid clade is characterized by a suite of derived characters, in particular their brachiophore plates that converge onto the median ridge to form a septalium. Other features of linoporellids, such as the proportionally high ventral interarea, variably developed aditicules and long, generally ridge-like cardinal process, may appear recurrently in other enteletoid families. Although the development of a septalium is unusual among dalmanellidines, it constitutes a diagnostic feature of many plectorthoideans (e.g. euorthisinids, finkelburgiids, phragmorthids, platystrophids). The presence of a small but well defined septalium in the Late Cambrian euorthisinid *Protorthisina* Benedetto, the earliest known rhynchonelliform from the Central Andean basin of northwestern Argentina and Bolivia, strongly suggests that this feature is an ancestral condition in the plectorthoidean clade (Benedetto 2007). A preliminary phylogenetic analysis of some upper Cambrian-Tremadocian plectorthoids from NW Argentina supports the hypothesis that *Protorthisina* gave rise to not only the lower Tremadocian-Floian *Kvania-Nanorthis* lineage but also a group of taxa characterized by the retention of a variably developed septalium (Benedetto 2007). They include the euorthisinids (*Protorthisina*, *Euorthisina*, *Notorthisina*), the enigmatic late Tremadocian *Lesserorthis* Benedetto (in which a V-shaped septalium is replaced by a delthyrial chamber configuration through ontogeny), and some related Gondwanan plectorthoids (e.g. *Irhirea* Havlíček) (Benedetto 2007).

In this paper the phylogenetic relationships among plectorthoids and punctate orthides are evaluated by using cladistic analysis. Perhaps the main difference relative to the phylogenetic approach carried out in the revised *Treatise* by Williams & Harper (2000, figs 521, 522) is that non-punctate and punctate orthides are analysed using a single node as the outgroup for rooting phylogenetic trees: the 'generalized' orthoid *Archaeorthis* or, alternatively, the basal plectorthoid *Protorthisina*. Thus, the presence of punctae is not assumed *a priori* as a criterion for separating the orthides into two main clades. The aim of this analysis is not to examine in detail the ingroup relationships of the linoporellids, which requires consideration of a set of morphological characters, but to reassess the phylogenetic position of the earliest known dalmanellidine *Lipanorthis*, and especially of *Famatinorthis*, which is placed here among the punctate orthides. The analysis

incorporates 37 genera including one orthoid, 13 plectorthoids, 14 dalmanelloids and 9 enteletoids (mainly linoporellids). Ordovician taxa from the Central Andean basin, North Africa and European peri-Gondwanan terranes were especially considered in our analysis on the assumption that the cold to temperate peri-Gondwanan shelves were the site of an important regional radiation event during the early Palaeozoic (Benedetto & Sánchez 2003). Selected taxa from Laurentia, Baltica, and other palaeocontinents were also included in the analysis. Morphological data used in the cladistic analysis were collected from different bibliographic sources, in particular Cooper (1956), Harper (2000), Harper *et al.* (2004), Havlíček (1971, 1977), and Benedetto (1994, 2002).

Cladistic analysis was performed using TNT (Tree Analysis Using New Technology) program version 1.0 (Goloboff *et al.* 2003) selecting the heuristic search option with multiple random addition sequences and the tree bisection reconnection branch-swapping algorithm (TBR), holding 10 trees in each addition sequence. A total of 16 binary and multistate characters (see Table 1) was analysed for the 37 taxa. The characters were treated as unordered and unweighted.

Phylogenetic analysis using *Archaeorthis* as outgroup resulted in 20 equally most parsimonious cladograms of 82 steps long with a CI (consistency index) of 0.317 and a RI (retention index) of 0.741. The strict consensus tree is shown in Fig. 4. The placement of plectorthoideans in the same major clade as linoporellids (Fig. 4, node 3), and the separation of dalmanellidines as an independent clade (Fig. 4, node 1) are the most important features of all shortest trees. The clade defined by node 3 is characterized by brachiophore bases converging to form a notothyrial chamber or a septalium and presence of fulcral plates. The euorthisinids *Protorthisina*, *Notorthisina* and *Euorthisina*, and the nanorthid *Kvania* are sister taxa that occupy the most basal position in the plectorthoid clade, which is consistent with their Cambrian-Lower Ordovician stratigraphical record. The euorthisinid? *Lesserorthis* appears as a basal form of the more derived members of the clade (giraldiellids and plectorthids), defined by the presence of a notothyrial chamber (Fig. 4, node 7). The other subclade includes all known linoporellids (plus *Irhirea*), with the plectorthoid *Scaphorthis* as ancestral form. The apomorphy that defines this clade (Fig. 4, node 4) is the presence of a medium to large septalium. The linoporellid clade is defined by the following apomorphic states (Fig. 4, node 5): simple cardinal process, presence of a well-developed septalium, and punctate shell substance. The Tremadocian *Lipanorthis* is invariably closely allied to *Salopia*, and both are sister taxa of the rest of linoporellids occupying the most basal position within the subclade.
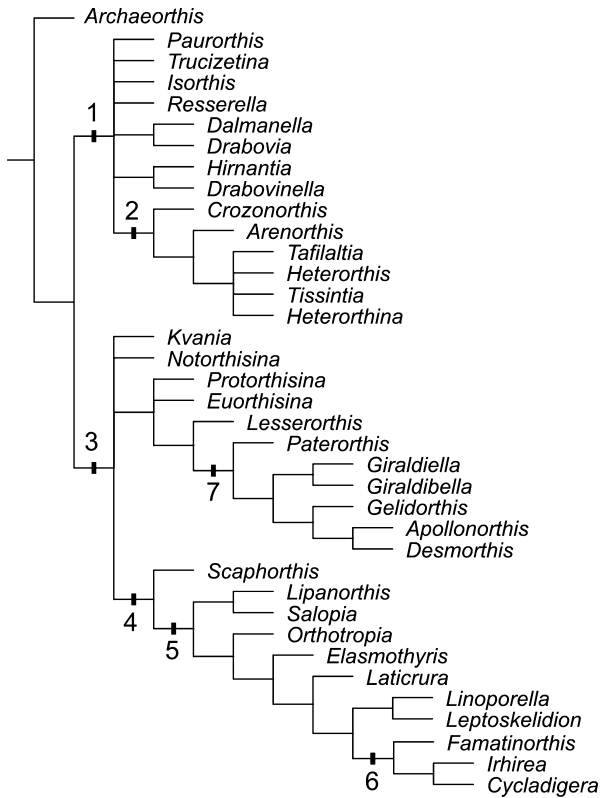
Fig. 4. Strict consensus of 20 trees using *Archaeorthis* as outgroup. Numbers below the branches indicate the nodes mentioned in the text.

significant that the enteletoids (e.g. *Hirnantia*, *Drabovinella*) tend to cluster among the dalmanelloids rather than with the linoporellids, which are currently classified among the Enteletoidea.

Cladistic analysis of the same dataset used above but selecting the late Cambrian euorthisinid *Protorthisina* as outgroup found 10 minimal length trees of 84 steps, with a CI of 0.302 and a RI of 0.732. The tree topology does not differ substantially from the cladogram constructed with *Archaeorthis* as outgroup. In the strict consensus tree (Fig. 5) dalmanellidines also form a single monophyletic clade with *Archaeorthis* occupying the most basal position of the clade. This clade is characterized by puntate shell substance, absence of septalium, and a cardinal process with expanded bi or trilobate myophore (Fig. 5, node 1).

The Tremadocian genera *Kvania* and *Notorthisina* are a paraphyletic grade at the base of both linoporellid and 'dalmanellidine' clades. The overall topology of the linoporellid clade is the same as using *Archaeorthis* as outgroup. Perhaps the main difference when comparing the two cladograms is that *Euorthisina* and *Lesserorthis* are closest to the outgroup in concordance with their early stratigraphic first appearance (Lower Ordovician). In both genera the small septalium is

Famatinorthis, in spite of its antiquity, falls within the more derived members of the clade to which shares a large, anteriorly supported septalium and a long simple cardinal process (Fig. 4, node 6). It is significant that the Moroccan plectorthoid *Irhirea*, in which punctae have not been detected, also clusters among the linoporellids to which shares a similar combination of morphological features. The Lower Devonian *Cicladygera*, from the Prague basin, appears closely allied to both *Irhirea* and *Famatinorthis*. However, as stated above, a more detailed morphological analysis based on a larger number of characters is needed in order to accurately resolve the ingroup relationships within the linoporellid clade.

The 'dalmanellidine' clade (Fig. 4, node 1) is characterized by punctate shells, brachiophore bases subperpendicular to valve floor bounding laterally the notothyrial platform, and well-developed cardinal process with lobate myophore. Dalmanellidine ingroup relationships are poorly resolved with the character set used in our analysis, but the genera referred to the family Heterorthidae appear as a homogeneous group of derived forms typified by a large ventral muscle field and costellae incurved towards the posterior margin (Fig. 4, node 2). It is
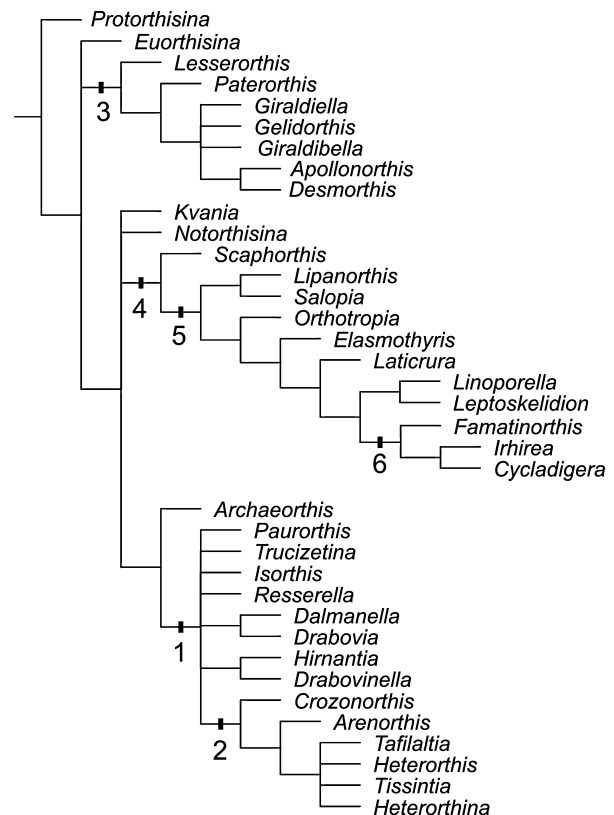

Fig. 5. Strict consensus of 10 trees using *Protorthisina* as outgroup. Numbers below the branches indicate the nodes mentioned in the text.

considered as a retained primitive feature since it occurs in the late Cambrian *Protorthisina*. In the 'plectorthoid' clade the septalium is lost and it is replaced by a typical notothyrial chamber and the cardinal process is simple (Fig. 5, node 3). As in the tree generated using *Archaeorthis* as outgroup, *Scaphorthis* appears as a basal form of the linoporellid clade. It shares with the linoporellids a simple cardinal process and a well-defined septalium, but lacks punctae (node 4). The apomorphies defining the other nodes depicted in the Fig. 5 have been enumerated in the cladogram of Fig. 4.

From the results of the parsimony analyses the following observations and inferences can be drawn:

1. The strict consensus topology supporting the linoporellids as a separate and distinctive clade was produced using both *Archaeorthis* and *Protorthisina* as outgroups;
2. Dalmanellidines are a monophyletic clade only if linoporellids are excluded from the suborder;
3. Plectorthoideans are placed in the same major clade as linoporellids using *Archaeorthis* as outgroup, or constitute a sister group to the linoporellids + dalmanellidines when trees are rooted with *Protorthisina* as outgroup;
4. Although a punctate shell is a distinctive character of the morphologically diverse dalmanellidine clade, cladograms suggest that this feature may have developed independently in the linoporellids. Consequently, the presence of endopunctae in the orthides does not necessarily indicate close phylogenetic relationships as it could have arisen at different times in different clades. As suggested by Havlíček (1977, p. 110–111), paurorthids may have evolved from a ranorthid-like impunctate ancestor (a 'pre-dalmanellid' form). On the other hand, linoporellids may have been derived from a basal plectorthoid like *Kvania* or *Notorthisina* (see emended diagnosis of the latter by Villas *et al.* 2009). The marked morphological differences between the Early Ordovician *Paurorthis*, one of the earliest dalmanelloids, and the almost coeval basal linoporellid *Lipanorthis* gives support to an early separation of the two lineages. If correct, differences in the punctae of both groups should exist and be evident by further detailed examination of their shell structure;
5. *Lipanorthis* lies close to the ancestry of the linoporellid lineage, and *Famatinorthis* clusters within the more derived Late Ordovician taxa characterized by a large, anteriorly unsupported septalium; and
6. Delineating a new suprafamilial grouping of taxa from the phylogenetic trees generated in this study seems to be inappropriate at this time. However, if

the homoplasic nature of endopunctae in the order Orthida is supported by further morphologic and phylogenetic studies, then the fundamental division of non-punctate (Orthidina) and punctate (Dalmanellidina) orthid brachiopods may need revision.

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