Early Silurian (Rhuddanian) brachiopods from the Argentine Precordillera and their biogeographic affinities



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Abstract. A brachiopod fauna dominated by *Hindella crassa* (J. de C. Sowerby), and also including an indeterminate pseudolinguloid, *Leangella* (*Leangella*) *america* sp. nov., *Eoplectodonta* (*Eoplectodonta*) *duplicata* (J. de C. Sowerby), *Fardenia* sp., *Glyptorthis vidari* (Baarli)., *Dolerorthis plicata* (J. de C. Sowerby), an indeterminate giraldiellid, *Dalmanella* sp., and *Stegerhynchus pusillum* (J. de C. Sowerby), is described from the La Chilca Formation exposed at Mogotes Azules, San Juan Province, Argentina. The age of the fauna is Early Silurian (Llandovery: Rhuddanian) and it is compared with other Rhuddanian brachiopod faunas both from Gondwana and elsewhere. The brachiopod faunas of Gondwana, despite their relatively low diversity, had much in common with those from Laurentia and Avalonia-Baltica, and heralded the cosmopolitanism that prevailed for all of the first half of the Silurian.

Resumen. BRAQIÓPODOS DEL SILÚRICO TEMPRANO (RHUDANIANO) DE LA PRECORDILLERA ARGENTINA Y SUS AFINIDADES BIOGEOGRÁFICAS. Se describe una fauna de braquiópodos proveniente de los niveles basales de la Formación La Chilca expuesta en Mogotes Azules, Precordillera Argentina. La misma está integrada por pseudolinguloideos indeterminados, *Leangella (Leangella) america* sp. nov., *Eoplectodonta (Eoplectodonta) duplicata* (J. de C. Sowerby), *Fardenia* sp., *Glyptorthis vidari* (Baarli), *Dolerorthis plicata* (J. de C. Sowerby), un giraldiéllido indeterminado, *Dalmanella* sp. *Stegerhynchus pusillum* (J. de C. Sowerby). La edad de la fauna es Silúrico Temprano (Llandoveriano, Rhuddaniano). Se compara esta asociación con otras faunas coetáneas de Gondwana y otras regiones. Las faunas de braquiópodos rhuddanianos de Gondwana, a pesar de su diversidad relativamente baja, tienen mucho en común con las de Laurentia y Avalonia-Baltica, confirmando el cosmopolitismo que prevaleció en la primera mitad del Silúrico.

Key words. Silurian. Rhuddanian. Brachiopods. Precordillera. Argentina. Gondwana.

Palabras clave. Silúrico. Rhuddaniano. Braquiópodos. Precordillera. Argentina. Gondwana.

Introduction

The Precordillera was originally an exotic terrane accreted to the South American margin of Gondwana in the early Palaeozoic. The thick Cambrian and Ordovician shallow-water carbonate succession indicates low latitude provenance, and its benthic faunas indicate a Laurentian derivation (Benedetto, 1993, 1998; Benedetto *et al.*, 1999; Astini *et al.*, 1995; Ramos *et al.*, 1996). The striking similitude between the Cambrian-Lower Ordovician faunas from the Argentine Precordillera and Laurentia would be very difficult to explain in the Finney (2007) reconstruction, in which the Precordillera is

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depicted as a para-autochthonous, eastern Gondwana-derived terrane. The precise timing of docking is still a matter of debate, but the overall evidence, including block faulting, cessation of carbonate deposition, basin rearrangement, coarse clastic influx, and K-bentonite layers, suggests a Mid-Ordovician age for the collision (Thomas and Astini, 2003; Benedetto, 2004). Fossils reveal increasing exchange between Precordillera and Gondwana from the Darriwillian onwards and especially during the Sandbian-Katian. The association of a Kosov-type Hirnantia Fauna with glacigenic diamictites indicate that the Precordillera was at high latitudes during Late Ordovician (Astini, 1999) and that it had previously accreted to Gondwana. However, the endemic highlatitude Gondwanan Siluro-Devonian Malvinokaffric faunas did not become widespread in the Precordillera basin until the Wenlock, when the typical Afro-South American assemblages (Clarkeia Fauna) evolved (Benedetto et al., 1992; Benedetto and Sánchez, 1996).

The purpose of this paper is to describe a new AMGHB2-0002-7014/09\$00.00+.50

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Figure 1. Simplified geological map of the San José de Jáchal area showing location of the stratigraphic sections mentioned in the text. The site yielding the brachiopods described herein in marked with an asterisk. References: **1**, Cambrian to Mid Ordovician limestones; **2**, Ordovician deep-water turbidites and olistsotromes; **3**, Mid Ordovician outer-ramp marls and black sales; **4**, La Chilca Formation (Lower Silurian); **5**, Los Espejos Formation (Wenlock-Pridoli); **6**, Devonian; **7**, Carboniferous-Permian; **8**, Triassic; **9**, Cenozoic. / mapa geológico simplificado de la región de San José de Jáchal mostrando la ubicación de las secciones estratigráficas mencionadas en el texto. El asterisco marca el sitio de donde provienen los braquiópodos descritos en este trabajo. Referencias: **1**, Calizas cambro-ordovícicas; **2**, Turbiditas y olistostromas ordovícicos; **3**, Margas y lutitas negras de plataforma externa (Ordovícico Medio); **4**, La Chilca Formation (Silúrico Inferior); **5**, Formación Los Espejos (Wenlockiano-Pridoliano); **6**, Devónico; **7**, Carbonífero-Pérmico; **8**, Triásico; **9**, Cenozoico.

brachiopod assemblage from near the base of lower Llandovery (Rhuddanian) La Chilca Formation, collected from below the two faunas from the same formation previously monographed by Benedetto (1995). These La Chilca faunas are of special interest because earliest Silurian megafossils are relatively rare in western Gondwana and, therefore, help to bridge the age gap between the *Hirnantia* Fauna and the typical Afro-South American assemblages of Wenlock to Pridoli age (Benedetto, 1986; Benedetto *et al.*, 1992). The fauna also sheds further light on the subsequent recovery of brachiopod faunas in the high-latitude cold-water shelves of Gondwana after the end-Ordovician extinction and also on the Early Silurian palaeobiogeography of western Gondwana.



Figure 2. Correlation between the Mogotes Azules, Cerro La Chilca/Cumillango and Cerro del Fuerte columns showing stratigraphic occurrence of Hirnantian/Llandovery brachiopod and graptolite assemblages. Asterisk marks the levels from which brachiopods described herein come from./ *Correlación entre las secciones estratigráficas de Mogotes Azules, Cerro La Chilca/Cumillango y Cerro del Fuerte mostrando la ubicación de las asociaciones de braquiópodos y graptolitos. El asterisco señala los niveles de donde proceden los braquiópodos descriptos en este trabajo.*

Stratigraphy and age of the fauna

On the basis of stratigraphic data, Thomas et al. (2002) (see previous references therein) inferred that a significant post-collision extension occurred in the Precordillera basin in response to the accretion of the Precordillera terrane. As a result, the uppermost Ordovician and Silurian succession overlies unconformably units of different ages, including the Floian-Darriwilian San Juan Limestone and Sandbian-Katian clastic units (black shales, marls and coarse breccias). The base of the Hirnantian-Silurian succession is formed by glacigenic deposits capped by Hirnantia-bearing shallow marine siltstones and sandstones. The two lithologies have been termed the Don Braulio Formation, but that unit is preserved only in a few places, where it infills a glacial palaeotopography. In contrast, the overlying La Chilca and Los Espejos formations -which constitute the Tucunuco Group -are widespread in the eastern and central Precordillera. The group, up to 700 m thick, has been interpreted as deposited in a strongly subsiding foreland basin developed after the collision of the Precordillera (Cuyania) terrane (Astini *et al.*, 1995).

The La Chilca Formation has its type locality at Cerro La Chilca, San Juan province (figura 1), where it is 135 m thick and overlies paraconformably the Hirnantian Don Braulio Formation (Astini and Benedetto, 1992). In the Mogotes Azules section, from which the fossils described here were collected, it overlies unconformably Upper Ordovician hemipelagic marls and black shales referred to Las Aguaditas Formation (figura 2). The La Chilca Formation thins to about 35 m in the Talacasto area, approximately 50 km southward Cerro La Chilca (figura 1). Despite the thickness variation, the lithology of the La Chilca Formation is fairly uniform. It begins with a thin chert conglomerate or a few beds of ferruginous sandstones and fine-grained sandstones. The material described here is from green siltstones immediately above the chert conglomerate. It

includes many broken shells and the specimens are largely disarticulated, indicating substantial postmortem transport from their original life position. In most of the sections, the La Chilca Formation continues with a succession of greyish-green bioturbated siltstones bearing graptolite remains, and grades to dark-grey laminated mudstones. The middle part of the unit consists of bioturbated siltstones interbedded with fine-grained, 7-10 cm thick sandstone beds with planar to low-angle lamination. The sandstone beds are rich in Chondrites and locally display Skolithos burrows on the top. This facies is gradationally overlain by quartz sandstone beds which thicken upward and become amalgamated. Hummocky cross-stratification and lenticular coquinas are fairly common, and there is an overall gradual shallowingupwards (Astini and Piovano, 1992). The sharp base and the muddy sediment in the lower third of the formation may indicate deposition during the transgression immediately after the end-Ordovician glaciation. The succession grades from a mud-dominated platform to chiefly sandy, storm-dominated shoreface deposits reflecting a general progradation of the shoreline. The succeeding outer-platform laminated green shales of the Wenlock Los Espejos Formation mark a new widespread transgressive pulse recorded not only in the Precordillera but also in the Central Andean basin of NW Argentina and Bolivia (Sánchez et al., 1991; Benedetto and Suárez Soruco, 1998).

Fossils recovered from the La Chilca Formation demonstrate that its base is possibly diachronous, reflecting the emergence of the Tambolar Arch to the south of the basin, which is also responsible for thickness variations. This structure has been interpreted as a peripheral bulge which was uplifted during the final stages of collision (Astini *et al.*, 1995).

In the Talacasto area the lowermost 0.60 m of the La Chilca Formation vielded a graptolite assemblage dominated by Persculptograptus persculptus (Salter) followed by species suggesting the Parakidograptus acuminatus Zone (from 0.6 m to 1.6 m), so that the Ordovician-Silurian boundary lies between those two zones (Cuerda et al., 1988). From the same section and approximately 20 m above the base, Albanesi et al. (2006) reported Monograptus cf. priodon (Bronn) and Pristiograptus aff. nudus (Lapworth) indicating a Telychian age. To the east of the basin, in the Cerro del Fuerte area (figures 1 and 2), a monotonous deep-water mudstone succession over 100 m thick underlies the La Chilca Formation. This unnamed unit is partially equivalent to the upper transgressive mudstone member of the Don Braulio Formation and the lower fine-grained member of the La Chilca Formation. According to Benedetto (2004), it may record deposition within a narrow, strongly subsid-

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ing remnant basin located in between the Precordillera terrane and Gondwana. Fossil content includes the graptolite P. persculptus and a low-diversity brachiopod fauna of Anisopleurella cf. gracilis (Jones), and Reuschella sp. (Benedetto, 1987). Rickards et al. (1996) concluded that graptolites from the basal fine-grained sandstones of the La Chilca Formation exposed there represent an interval from the Atavograptus atavus and Demirastrites triangulatus zones (Rhuddanian-lower Aeronian). The overlying 30 m of bioclastic sandstones have vielded conodonts of the Distomodus kentuckyensis Zone, of mid Rhuddanian-lower Aeronian age (Lehnert et al., 1999), and a moderately diverse brachiopod assemblage - named here the "Heterorthella precordillerana Assemblage" - including Dalmanella aff. testudinaria (Dalman), Heterorthella precordillerana Benedetto, Leptaena? sp., Eostropheodonta [Aphanomena] cf. mullochiensis (Reed), and Anabaia? sp. (Benedetto, 1995). A similar assemblage occurs in the type section at Cerro La Chilca (40-50 m above the base) and also in the Cerro Cumillango section. A quite different brachiopod fauna - named here the "Cordatomyonia umangoensis Assemblage"- occurs in the upper third of the La Chilca Formation at Cerro Agua de Felipe and consists of Dedzetina? sp. nov., Cordatomyonia umangoensis Benedetto, Homoeospira carinata Benedetto, H. antiqua Benedetto, Rafinesquina reliqua Benedetto, Eostrophedonta [Aphanomena] chilcaensis Benedetto, Anabaia? sp. and Rostricellula sp. In the Mogotes Azules section a comparable assemblage occurs 64 m above the base. An essentially similar fauna has been recorded from the upper part of the La Chilca Formation at its type section (due to structural complications these beds were erroneously assigned by the first author to the middle part of the unit; Benedetto, 1995).

The brachiopods described here are certainly Rhuddanian: there are no Hindella crassa dominated assemblages known from anywhere in rocks older? than Rhuddanian. The age within the Rhuddanian is less well constrained; whether it is early or late Rhuddanian is uncertain; but, nevertheless, by comparison with other Early Silurian faunas from around the world, and because the La Chilca fauna contains several well-known species, it is more likely to be mid to late Rhuddanian. Biostratigraphic correlation among selected sections of the La Chilca Formation (Fig. 2) aid to constrain the age of the H. crassa assemblage within the Rhuddanian. As stated above, the transgressive deposits immediately overlying the basal chert conglomerate have been dated as late Hirnantian to early Rhuddanian. The succeeding deep-water poorly-oxygenated deposits that characterize the lower third of the La Chilca Formation throughout the Precordillera basin are not older than mid-Rhuddanian (vesciculosus Zone) but no younger than early Aeronian (*triangulatus* Zone). Evidence from the Don Braulio Formation shows that the black shales immediately above the last appearance of *P. persculptus* and the last representatives of the *Hirnantia* Fauna are of early Rhuddanian age (*acuminatus* Zone), and data from the La Chilca section also indicate that the transgression started by the late Hirnantian-early Rhuddanian. According to these data, the *Hindella crassa* beds at Mogotes Azules section are of early (or just possibly mid) Rhuddanian age.

The fauna and its significance

The brachiopods we identified consist of an indeterminate pseudolinguloid, Leangella (Leangella) america sp. nov., Eoplectodonta (Eoplectodonta) duplicata (J. de C. Sowerby), Fardenia sp., Glyptorthis vidari (Baarli)., Dolerorthis plicata (J. de C. Sowerby), an indeterminate giraldiellid, Dalmanella sp., Stegerhynchus pusillum (J. de C. Sowerby) and Hindella crassa (J. de C. Sowerby). The fauna is dominated by H. crassa which comprises 35 % of individuals in the assemblage. E. (E.) duplicata (21 %), L. (L.) america sp. nov. (14 %) and D. plicata (13 %) constitute a significant part of the association, whereas Dalmanella sp., S. pusillum and Glyptorthis vidari occur sporadically and do not exceed 6 %. Fardenia sp. and the indeterminate giraldiellid are represented only by a single specimens. Shell fragments of linguliformean brachiopods are relatively common and are dispersed through the rock.

Apart from the two faunas described in the La Chilca Formation by Benedetto (1995), Rhuddanian faunas have been described from only a few other South American localities. The nearest comparableage fauna is that from near the Chilean border in the Salta Province of Argentina. There the Salar de Rincón Formation yielded the brachiopods identified by Isaacson et al. (1976) as Mendacella sp., dalmanellid indet., Fardenia filistriata Boucot and Johnson, stropheodontid indet., and Hindella [Cryptothyrella] cf. crassa (J. de C. Sowerby) as well as the gastropod Plectonotus sp., un-named trilobites and tentaculitids, and poorly-preserved graptolites which were identified as "of the Monograptus nudus group". However, M. nudus itself is confined to the crispus and turriculatus Biozones (upper Aeronian and lower Telychian), but nevertheless Cocks and Rong (in press) reassessed the age of the fauna as Rhuddanian. Additional sampling from the stratotype of the Salar del Rincón Formation led Benedetto and Sánchez (1990) to identify (as well as Fardenia and Hindella aff. crassa) Dalmanella sp., Aphanomena? sp., and Heterorthella

sp., the latter being relatively close to *H. africana* (Cocks and Brunton) from the South African Hirnantian Cedarberg Formation. The bivalve *Modiomorpha* sp. nov. is relatively common. Cryptospores and acritarchs recovered from the shell-beds indicate a latest Ordovician (Hirnantian) to early Llandovery age (Rubinstein and Vaccari, 2004). Although the Salar del Rincón brachiopod assemblage is closely similar to that of the La Chilca Formation, and in particular contains abundant Hindella, it is not identical.

Lower Silurian brachiopods have also been reported from the Ayala and Vargas Peña Formations of Paraguay, but the precise age of these units is still matter of discussion (Harrington, 1950; Wolfart, 1961; Gonçalvez de Melo and Boucot, 1990; Boucot et al., 1991; Benedetto, 2002; Uriz et al., 2006). Recently one of us (J.L.B) reviewed a brachiopod collection from the Ayala Sandstone collected by J. C. Galeano Inchausti (which remains unpublished) and the following taxa are preliminarily recognized: "Heterorthella" sp. nov. (this material was referred to Heterorthella freitana Clarke by Boucot et al., 1991, but it is in need of revision), Eocoelia paraguayensis (Harrington, 1950), Ancillotoechia sp., Eostropheodonta conradi (Harrington, 1950), and Hindella sp. The morphology of the species Eocoelia paraguayensis suggests an Aeronian to early Telychian age (Benedetto, 2002), but the presence of a species of Hindella comparable to H. crassa suggests a Rhuddanian age for the Paraguayan assemblage. Associated chitinozoans described by Grahn et al. (2000) and Grahn and Gutiérrez (2001) indicate that the lower part of the overlying Vargas Peña Shale may extend into the Rhuddanian. The graptolite Stimulograptus sedgwicki and other forms suggestive of a late Aeronian age were recovered recently from the uppermost 2 m of the Vargas Peña Formation (Uriz et al., 2006).

Farther to the north, Rhuddanian brachiopods occur in the Mérida Andes of Venezuela, from which Boucot *et al.* (1972) described a lower "*Meifodia* Fauna" with *Hesperorthis*? sp., *Dolerorthis* sp., *Skenidioides* sp., "*Resserella*" sp., *Leptaena* sp., *Eoplectodonta*? sp., *Meifodia* subundata prima and *Hindella* [*Cryptothyrella*]? sp., and an upper "*Eostropheodonta* Fauna" with "*Resserella*" sp., *Mendacella* cf. *uberis* (Billings), *Leptaena* cf. *valentia* Cocks, *Fardenia filistriata* Boucot and Johnson, *Eostropheodonta* cf. *mullochensis* (Reed), *Eoplectodonta* sp., "*Ancillotoechia*" sp., *Eospirigerina gaspeensis* (Cooper) and *Hindella* [*Cryptothyrella*] crassa (J. de C. Sowerby). Cocks and Rong (in press) assessed the lower fauna as certainly Rhuddanian and the upper one as either Rhuddanian or early Aeronian.

Thus, by the Rhuddanian, the brachiopod faunas of Gondwana, despite their relatively low diversity, had much in common with those from Laurentia and Avalonia-Baltica, and heralded the cosmopolitanism that prevailed for all of the first half of the Silurian except at the highest palaeolatitudes.

Systematic palaeontology

The collection, including the figured specimens, is held at the Centro de Investigaciones Paleobiológicas (CIPAL), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba (CEGH-UNC). The authors of the family and higher taxa names below are omitted from our reference list, but may be found in the recent Treatise (Kaesler 2000-2006).

> Superfamily LINGULOIDEA Menke, 1828 Family PSEUDOLINGULIDAE Holmer, 1991 Pseudolinguloid indet.

Discussion. Within the fauna there are several phosphatic fragments which are undoubtedly linguloids. The commonest linguloid in the Early Silurian is Pseudolingula, and the La Chilca fragments are very similar to Pseudolingula from the Silurian of Britain (Cocks and Popov, in press), but the Argentinian valves are not complete enough for firm generic identification.

Superfamily PLECTAMBONITOIDEA Jones, 1928 Family LEPTESTIIDAE Öpik, 1933

Genus Leangella Öpik, 1933

Type species. Plectambonites scissa (Davidson, 1871) var. triangularis Holtedahl, 1916.

Leangella (Leangella) america sp. nov. Figures. 3.1 - 3.12

Holotype. An internal mould of dorsal valve, CEGH-UNC 23489.

Paratypes. Two external moulds and seven internal moulds of ventral valves; three internal moulds of dorsal valves, CEGH-UNC 23449c, 23458d, 23459c, 23467, 23469, 23474b-c, 23476b, 23487b, 23488, 23489.

Etymology. After the American continent.

Type locality and type stratum. Base of the La Chilca Formation, Mogotes Azules, San Juan province.

Diagnosis. Like L. scissa apart from the evenly-rounded semicircular platform rim.

Description. Shell small, semielliptical, up to 11.5 mm wide, strongly concavoconvex, on average 65 % as long as wide. Cardinal extremities acute. Ventral valve strongly convex in lateral profile, with maximum thickness slightly posterior to mid-length. Ventral interarea plane, apsacline. Delthyrium partially filled by apical thickening. Dorsal valve moderately and evenly concave, with narrow, hypercline interarea. Radial ornament unequally parvicostellate with 7-9 accentuated fine ribs originated at the umbo. Parvicostellae not preserved.

Ventral interior with small, subtriangular, widely divergent teeth supported by thin dental plates prolonged anteriorly by ridges which bound laterally the muscle field. Highly raised, bilobed ventral muscle field about 50 % as long as wide, with strongly impressed diductor scars. Adductor scars indistinguishable. A low ventral platform usually present. Mantle canals with narrow vascula media subparallel or gently diverging anteriorly.

Dorsal interior with trilobate cardinal process and widely divergent socket ridges nearly parallel to hinge; dental sockets transversely elongated. Bema prominent, bilobed, strongly raised and free anteriorly, 50% as long as wide, extending anteriorly about 40-60% of valve length. Bema surface with fine radial ridges, more prominent near its margins. Platform evenly-rounded, semicircular, running subparallel close to the valve margin.

Discussion. The genus *Leangella* is of global distribution in rocks from Late Ordovician to Ludlow age

Figure 3. 1-12, números seguidos por comas en todos los casos Leangella (Leangella) america sp. nov. 1, Exterior of ventral valve/ exterior de valva ventral / CEGH-UNC 232474c, X5; 2, 3, Internal mould of ventral valve and latex replica / molde interno de valva ventral y réplica de látex / CEGH-UNC 232449c, X3.5; 4, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23467, X6; 5, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23487b, X7; 6, Interior of ventral valve / interior de valva ventral / CEGH-UNC 23474b, X7; 7, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23469, X5; 8, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23459c, X5; 9, 10, Internal mould of dorsal valve and latex replica/ molde interno de valva dorsal y réplica de látex / CEGH-UNC 23488, X8; 11, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23489, X7; 12, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23487a, X7. 13-24, Eoplectodonta duplicate (J. de C. Sowerby, 1839). 13, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23479c, X3; 14, Ventral valve exterior / exterior de valva ventral / CEGH-UNC 23471c, X3; 15, Dorsal valve exterior / exterior de valva dorsal / CEGH-UNC 23463b, X3; 16, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23457, X3. 17, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23481b, X3; 18, Ventral valve exterior / exterior de valva ventral / CEGH-UNC 23484b, X3; 19, Dorsal valve interior, latex replica / interior de valva dorsal, réplica de látex / CEGH-UNC 23459d, X3; 20, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23476a, X3; 21, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23490, X3; 22-23, Internal mould of dorsal valve and latex replica / molde interno de valva dorsal y réplica de látex / CEGH-UNC 23476b, X4; 25. Fardenia sp. Dorsal valve interior / interior de valva dorsal / CEGH-UNC 23468a, X2.5.



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and is common in deposits originally ranging from mid-shelf to deeper. The type species Leangella (Leangella) scissa (Davidson, 1871) occurs throughout the Rhuddanian and into the early Aeronian, and is the only species of the genus so far described from rocks of Rhuddanian age anywhere: it includes the subspecies L. scissa triangularis (Holtedahl) from the Oslo area, Norway, which was revised by Baarli (1995). The Argentinian form is close to the typical L. (L). scissa scissa from Wales, as revised and extensively illustrated by Cocks (1970), apart from the more evenly-rounded platform rim of L. america in contrast to the platform rim of L. scissa, which is even curved laterally but has a spatulate extension towards the anterior, as has the late Katian L. sholeshookensis (Jones, 1928) from Pembrokeshire, Wales. In addition, the new species is smaller than L. scissa, although not nearly so small as the earlier (late Katian) Leangella (L.) longae, which is abundant in the Boda Limestone Formation of Sweden (Cocks, 2005). Other late Katian and Hirnantian species are L. cylindrica (Reed) and L. discuneata Lamont, both revised by Harper (1989) from the late Katian (Pusgillian and Cautleyan) of Girvan, Scotland, and L. septata (Cooper, 1930) from the late Katian of Percé, Canada. L. discuneata and L. septata both have a variably developed median septum in the ventral valve, unlike L. america. The interiors of L. cylindrica are poorly known, but the species is larger, more convex and relatively wider than L. america. The Precordilleran species L. (L.) mutabilis Herrera and Benedetto (in Benedetto et al., 1992), from the lower part of the overlying Los Espejos Formation, of Wenlock age, differs from L. (L.) america in having a less convex ventral valve, a much more prominent radial ornamentation? which is also visible on internal moulds, and the presence, in adult individuals, of a double dorsal platform. The bema outline in the two species is relatively similar.

Family SOWERBYLLIDAE Öpik, 1930

Genus Eoplectodonta Kozlowski, 1929

Type species. Sowerbyella precursor Jones, 1928.

Eoplectodonta duplicata (J. de C. Sowerby, 1839) Figures 3.13 - 3.24

Material. External moulds of three ventral valves and two dorsal valves; internal moulds of five ventral valves and three dorsal valves, CEGH-UNC 23449b, 23457, 23459d, 23463b, 23471b-c, 23476a-b-c, 23479c, 23481b, 23484b, 23490.

Discussion. This species, which is the type species of *Eoplectodonta*, was also revised and extensively re-illustrated by Cocks (1970). The genus ranges from the Sandbian to the Ludlow, and the species throughout the Rhuddanian and into the early Aeronian. Its geographical range is extensive but it most commonly occurs in Avalonia-Baltica (which became united in the earliest Rhuddanian) and also Laurentia and Siberia.

Superfamily CHILIDIOPSOIDEA Boucot, 1959

Genus Fardenia Lamont, 1935

Type species. Fardenia scotica Lamont, 1935.

Fardenia sp. Figure 3.25

Material. A single interior of dorsal valve and an incomplete exterior of ventral valve, CEGH-UNC 23468a-b.

Discussion. The genus ranges from the Sandbian to the middle Llandovery (Aeronian), and is distinguished from the closely-related Coolinia in lacking an entire chilidium posterior to the cardinal process.

Figure 4. 1-10, Glyptorthis vidari (Baarli, 1995). 1. Dorsal valve exterior, latex replica / exterior de valva dorsal, réplica de látex / CEGH-UNC 23478a, X2.5; 2, Ventral valve exterior, látex replica / exterior de valva ventral, réplica de látex / CEGH-UNC 23483a, X2.5; 3, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23461c, X2; 4, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23453, X2.5; 5, 6, Internal mould of dorsal valve and exterior (latex replica) of the same specimen/ molde interno de valva dorsal y exterior (réplica de látex) del mismo espécimen / CEGH-UNC 23485 / 23486, X4.5; 7, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23481a, X2; 8, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23486b, X2.5. 9, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23461c, X3; 10, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23475b, X3.5. 11-26. Dolerorthis plicata (J. de C. Sowerby, 1839). 11, Ventral valve exterior, latex replica / exterior de valva ventral, réplica de látex / CEGH-UNC 23448, X3.5; 12, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23473, X3; 13, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 25452, X2; 14, 15, Internal mould of ventral valve and látex replica/ molde interno de valva ventral y réplica de látex / CEGH-UNC 23470, X2; 16, Internal mould of juvenile ventral valve / molde interno de valva ventral juvenil / CEGH-UNC 23492, X3.5; 17, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23458c, X2.5; 18, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23484a, X2; 19, External mould of dorsal valve / molde externo de valva dorsal / CEGH-UNC 23458b, X1.5; 20, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23461a, X2; 21, 22., Dorsal exterior (latex replica) and internal mould / exterior de valva dorsal (réplica de látex) y molde interno / CEGH-UNC 23450a-b, X2; 23, 24, Internal mould of dorsal valve and latex replica / molde interno de valva dorsal y réplica de látex / CEGH-UNC 232455a, X2.5; 25, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23491, X2; 26, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23462, X2. 27-26, Giraldiellidae gen. et sp. indet. Latex replica and internal mould of dorsal valve / réplica de látex y molde interno de valva dorsal / CEGH-UNC 23472, X3.



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Fortunately the only complete specimen is a dorsal valve, which makes the generic identification secure, but is not sufficient to identify a species.

Superfamily ORTHOIDEA Woodward, 1852 Family GLYPTORHIDAE Schuchert and Cooper, 1931

Genus Glyptorthis Foerste, 1914

Type species. Orthis insculpta Hall, 1847.

Glyptorthis vidari (Baarli, 1995) Figures 4.1 - 4.10

Material. One external mould and three internal moulds of ventral valves; two external moulds and four internal moulds of dorsal valves, CEGH-UNC 23453, 23461c, 23475b, 23478a, 23481, 23483a, 23485, 23486a, 23486b.

Discussion. This is the same species as the *Eridorthis* sp. of Temple (1987) from the Rhuddanian of Wales, which Baarli (1995) also recognised and named as Eridorthis vidari from the Rhuddanian Solvik Formation of the Oslo region, Norway. Glyptorthis is very similar to Eridorthis apart from the dorsal median sulcus in the former being replaced by a fold in the latter genus (Williams and Harper in Kaesler, 2000), but those features are only obvious in adult shells and the juveniles of the two genera are essentially identical. It cannot be ignored that a dorsal fold developed independently by heterochrony in some Glyptorthis lineages (cf. Bassett, 1972, p. 30) and this sole feature does not seem significant for generic separation. In any case, the single partially complete adult dorsal valve available in the sample (Fig. 2.1) shows a shallow persistent sulcus, also visible on internal moulds, so that our material is better referred to the genus Glyptorthis. The Precordilleran specimens differ from the topotype material of Eridorthis vidari figured by Baarli (1995) in their less clearly-developed dorsal myophragm, which in the type vidari almost becomes a median septum anteriorly in a few specimens, but we consider that this is well

within the limits of specific variability. *G. speciosa* Reed, from the upper Katian (Rawtheyan) of Scotland (Harper, 1984), differs in having a low ventral fold and a thicker cardinal process. Of the almost twenty species described by Cooper (1956) from the Middle Ordovician of North America, the La Chilca sample differs mainly in its incipient low, ridge-like cardinal process in both juvenile and adult individuals.

Family HESPERORTHIDAE Schuchert and Cooper, 1931

Genus Dolerorthis Schuchert and Cooper, 1931

Type species. Orthis interplicata Schuchert and Cooper, 1931,

Dolerorthis plicata (J. de C. Sowerby, 1839) Figures. 4.11 - 4.26

Material. Three external moulds and seven internal moulds of ventral valves; two external moulds and three internal moulds of dorsal valves, CEGH-UNC 23448, 23450a-b, 23452, 23455a, 23458b-c23461a, 23462, 23470, 23473, 23483b, 23484a, 23491, 23492.

Discussion. There are few named species of Rhuddanian age of this long-lived genus, which ranges from the Early Ordovician (Floian) to the Early Devonian (Emsian). However, both *D. plicata* (including its synonyms paucicostata, radians and sowerbyiana) and *D. gwalia* (Bancroft) have their type localities in the Rhuddanian of the type Llandovery area, Wales, and were revised by Temple (1987) and Cocks (in press). *D. plicata* has coarser ribbing than *D. gwalia* and is the same as the La Chilca material. The species is widespread, occurring in Baltica (Baarli, 1995) and Laurentia (Cocks, in press), as well as in the type area of Avalonia.

Superfamily PLECTORTHOIDEA Schuchert in Schuchert and LeVene, 1929 Family GIRALDIELLIDAE Williams and Harper, 2000

Figure 5. 1-12, *Dalmanella* sp. 1. Dorsal valve exterior, latex replica / exterior de valva dorsal, réplica de látex / CEGH-UNC 23459f, X3; 2, 3, Latex replica of exterior and internal mould of ventral valve / réplica de látex y molde interno de valva ventral / CEGH-UNC 23449c/23447b; 4, Exterior of juvenile dorsal valve / exterior de valva dorsal juvenil / CEGH-UNC 23480, X7; 5, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 25459e, X4; 6, 7, Internal mould of juvenile dorsal valve and latex replica / molde interno de valva dorsal juvenil y réplica de látex / CEGH-UNC 23465a, X4; 8, Interior of juvenile dorsal valve / interior de valva dorsal juvenil / CEGH-UNC 23465b, X3.5; 9, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23475a, X3. 10, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23475b, X3. 12, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 2347b, X3. 12, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 2347b, X3.5; 13, Exterior (latex replica) of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23475b, X3.5; 14, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23451, X2.5; 14, Internal mould of ventral valve / molde interno de valva dorsal / CEGH-UNC 23454, X2.5; 14, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23454, X2.5; 14, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23474a, X2.5; 18, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23474a, X2.5; 18, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23474a, X2.5; 18, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23453, X2.5; 16, Internal mould of ventral valve / molde interno de valva dorsal / CEGH-UNC 23454a, X2.5; 18, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23454a, X2.5; 19, Internal mould of dorsal valve / mold





23466, X3.5. **22**, **23**, Latex replica of exterior and internal mould of ventral valve / réplica de látex del exterior y molde interno de valva ventral del mismo individuo / CEGH-UNC 23449a/23447a, X3; **24**, Internal mould of ventral valve / molde interno de valva ventral / CEGH-UNC 23471a, X3; **25**, Internal mould of dorsal valve / molde interno de valva dorsal / CEGH-UNC 23474d, X3.5.

Gen. et sp. indet. Figures 4.27 - 4.28

Material. A single internal mould of dorsal valve CEGH-UNC 23472.

Discussion. The only material known is the internal mould of a dorsal valve which shows the characteristic subparallel dental plates of the family. Its generic attribution is uncertain but it may well be Giraldiella itself, which occurs in rocks of comparable age in many places, including the type Llandovery area of Wales.

Superfamily DALMANELLOIDEA Schuchert, 1913 Family DALMANELLIDAE Schuchert, 1913

Genus Dalmanella Hall and Clarke, 1892

Type species. Orthis testudinaria Dalman, 1828,

Dalmanella sp. Figures 5.1 - 5.12

Material. One external mould and two internal moulds of ventral valves; two external moulds and six internal moulds of dorsal valves, CEGH-UNC 23447b, 23449c, 23459 e-f, 23465a, 23465b, 23468c, 23475a, 23478b, 23479a-b, 23480.

Discussion. This is a rather variable species in the size and shape of the cardinal process and thickening of the brachiophore bases. Morphological changes are specially evident between smaller and the larger individuals (cf. Fig. 5.5 with 5.11). Morphological variability has been well documented in D. testudinaria (Williams and Wright, 1963; Cocks, 1982; Rong and Li, 1999). In general, the Mogotes Azules sample is close to D. aff. testudinaria (Dalman), which comes from the stratigraphically higher H. precordillerana assemblage in the same formation (Benedetto, 1995). Perhaps the main difference is the larger dorsal muscle field in the latter. In addition, both brachiophores and their supporting plates are more slender in our material. Specimens of D. testudinaria from the underlying Hirnantian Don Braulio Formation (Benedetto, 1986) differs from the Mogotes Azules specimens in having coarser ornament, more convex dorsal valve, larger dorsal muscle field, and more robust brachiophores. In addition, in our material the cardinal process does not seem to be bilobed posteriorly. However, in view of the morphological variations and the relative scarcity of material this taxon is left in open nomenclature.

Superfamily RHYNCHOTREMATOIDEA Schuchert, 1913 Family RHYNCHOTREMATOIDAE Schuchert, 1913

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Genus Stegerhynchus Foerste, 1909

Type species. *Rhynchonella* (*Stegerhynchus*) whitii-praecursor Foerste, 1909.

Stegerhynchus pusillum (J. de C. Sowerby, 1839) Figures 5.19- 5.25

Material. Two external moulds and four internal moulds of ventral valves; one external mould and two internal moulds of dorsal valves, CEGH-23447a, 23449a, 23453b, 23460, 23464, 23466, 23471a, 23472b, 23474d.

Discussion. The two genera Rhynchotrema and Stegerhynchus are very closely related, and the only substantial difference between the two is the presence of fila on the valve exterior of the latter and its absence on the former, and fila are seen on the Argentine material. Only two species of Stegerhynchus have been formally described from rocks of Rhuddanian age: S. pusillum (J. de C. Sowerby) from the Goleugoed Formation (upper Rhuddanian) in the Llandovery type area in Wales, and S. praecursor Foerste from the Rhuddanian of Tennessee, U.S.A. The latter species was revised by Jin (1989) who also identified it from the Rhuddanian of Anticosti Island, Canada, and Jin established that S. praecursor has only two ribs on the fold and sulcus. In contrast S. pusil*lum* has three or four ribs in the fold and sulcus, and these are also present in both the Welsh and Argentinian specimens. S. pusillum was revised, and its lectotype reillustrated, by Temple (1987).

Superfamily MERISTELLOIDEA Waagen, 1883 Family MERISTELLIDAE Waagen, 1883

Genus Hindella Davidson, 1882

Type species. Athyris umbonata Billings, 1862.

Hindella crassa (J. de C. Sowerby, 1839) Figures 5.13 - 5.18

Material. Two external moulds and three internal moulds of ventral valves; three internal moulds of dorsal valves, CEGH-23451, 23458a, 23459b, 23461b, 23463a, 23474a, 23491, 23492.

Discussion. Temple (1987) revised this species in detail and refigured the lectotype, which is from the late Rhuddanian Goleugoed Formation in the type Llandovery area of Wales. The species, often termed Cryptothyrella crassa, occurs abundantly at many localities around the globe in both the Hirnantian and the Rhuddanian, and often dominates its assemblage, but it is very rare in the early Aeronian and was extinct before the late Aeronian. The La Chilca Formation material is typical of the species in all aspects.

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