



HIGH-LATITUDE HIRNANTIAN (LATEST ORDOVICIAN) BRACHIOPODS FROM THE EUSEBIO AYALA FORMATION OF PARAGUAY, PARANÁ BASIN

by JUAN L. BENEDETTO^{1*}, KAREN HALPERN¹ and JULIO C. GALEANO INCHAUSTI²

¹Centro de Investigaciones en Ciencias de la Tierra, CICTERRA-CONICET, Universidad Nacional de Córdoba, Vélez Sarsfield 299, X5000JJC Córdoba, Argentina; e-mails: jbeneditto@efn.uncor.edu, karenhalpern@gmail.com

²Ministerio de Obras Públicas y Comunicaciones de Paraguay, Oliva y Alberdi, 1221 Asunción, Paraguay; e-mail: galeanojc@hotmail.com

*Corresponding author

Typescript received 15 August 2011; accepted in revised form 5 January 2012

Abstract: Examination of newly collected brachiopods from the Eusebio Ayala Formation of Paraguay reveals the occurrence of *Arenorthis paranaensis* sp. nov., *Plectothyrella? itacurubensis* sp. nov., *Hindella* sp. and *Eostropheodonta conradii* (Harrington). Associated graptolites of the *N. persculptus* Zone indicate that the age of the fossiliferous beds is Hirnantian. The overall generic composition of the fauna is similar to that of the atypical *Hirnantia* Fauna of the Bani Province. The record in Paraguay of *Arenorthis*, hitherto only known from North Africa, together with species of *Plectothyrella?* and

Eostropheodonta different from those recorded in the Kosovo Province, emphasizing the affinities between the Paraguayan fauna and the low-diversity African assemblages. Stratigraphic and faunal evidence indicates that biogeographical links between South America and Africa already existed by the end of the Ordovician when most of the intra-cratonic basins of Gondwana were flooded during the postglacial sea level rise.

Key words: brachiopods, Hirnantian, Paraguay, Paraná basin, palaeobiogeography.

THE Itacuribí Group of Paraguay is a lower Palaeozoic clastic succession deposited on the western margin of the vast Paraná basin, which extends through southern Brazil, Paraguay, Uruguay, and northern Argentina (Milani *et al.* 2007). Since the first mention of fossils in these rocks by Beder and Windhausen (1918), numerous taxa have been published, including brachiopods (Harrington 1950; Wolfart 1961; Gonçalves de Melo and Boucot 1990; Boucot *et al.* 1991; Benedetto 2002), trilobites (Baldis and Hansen 1980; Tortello *et al.* 2008), bivalves, gastropods, hyolithids (Harrington 1950; Wolfart 1961), tentaculitids (Godoy Ciguel 1988), conularids (Babcock *et al.* 1990), graptolites (Turner 1959; Harrington 1972; Uriz *et al.* 2008; Alfaro *et al.* 2010), organic-walled microfossils (Wood and Miller 1991; Gray *et al.* 1992; Grahn *et al.* 2000) and ichnofossils (Godoy Ciguel *et al.* 1987; Galeano Inchausti and Poiré 1999). The Itacuribí Group comprises, in ascending order, the Eusebio Ayala, Vargas Peña and Cariy formations (Harrington 1972). The Early Silurian age of the whole Itacuribí Group was based largely on the monograptid graptolites and palynomorph assemblages from the Vargas Peña

Formation. However, the recent discovery of a graptolite association including *Normalograptus persculptus* in the Eusebio Ayala Formation indicates that, at least in part, this unit is Hirnantian in age (Alfaro *et al.* 2010, 2012; Cingolani *et al.* 2011).

Most of the fossils mentioned in the literature come from the Vargas Peña and Cariy formations. The reddish micaceous sandstone of the underlying Eusebio Ayala Formation has yielded a few brachiopods that had previously been assigned to *Clarkeia antisimensis* (d'Orbigny, 1847) and *Heterorthella freitana* (Clarke, 1899) by Boucot *et al.* (1991). This study revises previous taxonomic identifications of the Eusebio Ayala Formation brachiopods on the basis of new extensive collections from the richly fossiliferous shell beds exposed in the clay quarries located northeast of the town of Itauguá (Fig. 1) and to report the occurrence of the genera *Hindella*, *Arenorthis* and *Plectothyrella?*, not previously recorded from this unit. We also discuss the biogeographic implications of the occurrence in the Paraná basin of a low-diversity Hirnantian brachiopod assemblage dominated by *Arenorthis*, hitherto known only from North Africa.

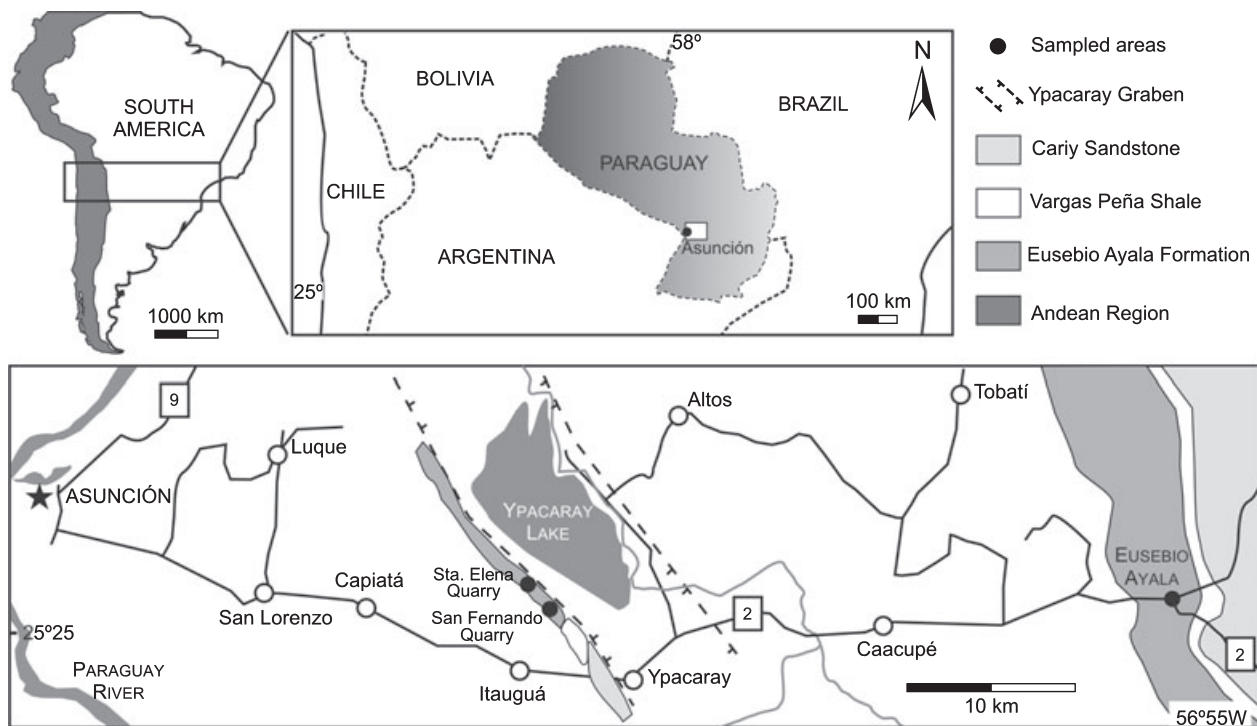


FIG. 1. Map showing the studied area and location of the Eusebio Ayala Formation exposures. Fossils come from the Santa Elena and San Fernando quarries and other small outcrops north-eastern Itaguá.

GEOLOGICAL SETTING AND AGE OF THE FAUNA

Lower Palaeozoic rocks are exposed discontinuously along the western border of the Ypacarai graben (Degraff *et al.* 1981), about 35 km east of the city of Asunción, in a series of isolated clay quarries, and around the town of Eusebio Ayala, the type locality of the eponymous formation. The material is from the San Fernando and the Santa Elena quarries, both located a few kilometres north-west of the town of Itaguá (Fig. 1). Harrington (1972) named these rocks the Itacurubí Group and subdivided it into the Eusebio Ayala, Vargas Peña and Cariy formations. The Itacurubí Group overlies conformably the nonfossiliferous Caacupé Group, of inferred Ordovician age, which consists of conglomerates and massive to cross-stratified yellowish feldspathic sandstones, probably estuarine or fluviodeltaic in origin (Fig. 2). The base of the Itacurubí Group marks the onset of a transgressive episode. The Eusebio Ayala Formation, *c.* 200 m thick, consists of reddish micaceous sandstone grading upward to fine-grained fossiliferous sandstone and siltstone. Rippled surfaces are common on the top of sandstone beds, which often display internally wavy and lenticular lamination. Vertical burrows referred to *Skolithos* by Godoy Ciguel *et al.* (1987) are very abundant suggesting lower

intertidal-shallow subtidal depositional settings. The shell beds yielding the brachiopods described in this study are confined to the upper part of the Eusebio Ayala Formation where they are interbedded with iron-rich levels (Fig. 2). The overall upward-fining trend of the Eusebio Ayala and Vargas Peña formations records the transition from shorface to platform deposits, the pale-grey fossiliferous claystones of the Vargas Peña Formation representing the maximum flooding. The overlying sparsely fossiliferous massive to cross-bedded quartz and feldspathic sandstone of the Cariy Formation denotes a shoreline progradation culminating the Itacurubí Group succession.

The Silurian age of the Itacurubí Group was first established by Harrington (1950, p. 23) on the basis of the identification by O. M. B. Bulman (later published by Turner 1959) of the graptolites *Climacograptus innotatus braziliensis* Ruedemann and *Diplograptus modestus* Lapworth in the Vargas Peña Formation, leading to postulate an early Llandovery (Rhuddanian) age. However, the re-study of graptolites from the Vargas Peña Quarry, the type locality, established the *D. convolutus* and *S. sedgwickii* Biozones of late Aeronian age (Rickards *in* Cocks 1972; see also Gonçalves de Melo and Boucot 1990). The graptolite fauna from the uppermost beds of the Vargas Peña Formation described by Uriz *et al.* (2008) also supports a late Aeronian-early Telychian age (*S. sedgwickii* –

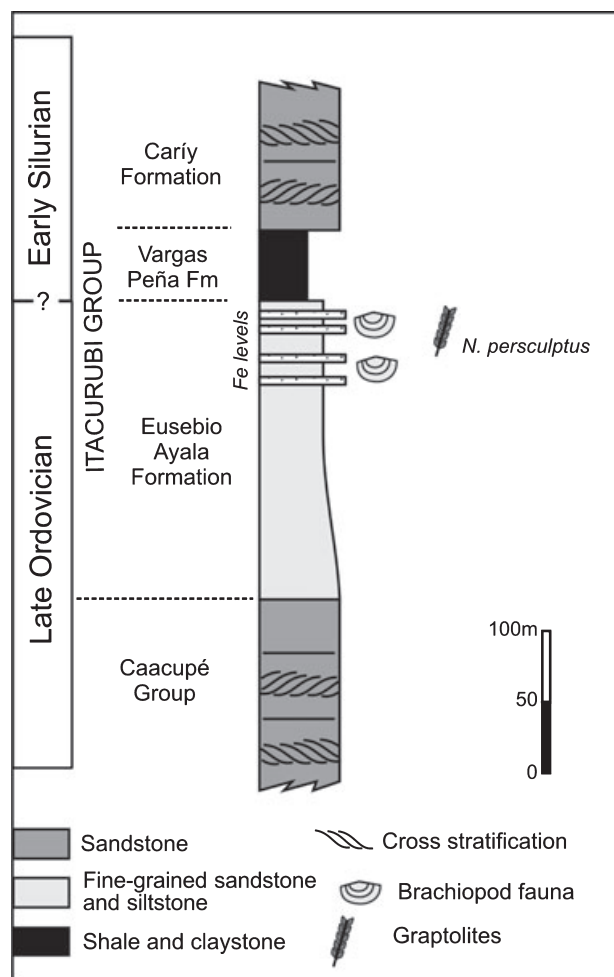


FIG. 2. Composite columnar section of the Itacurubi Group showing fossiliferous levels (modified after Cingolani *et al.* 2011).

S. turriculatus Biozones), which is compatible with the record of climacograptids of the *innotatus* group in beds as young as early Telychian in North Africa and Spain (Jaegger *in* Gray *et al.* 1992). The palynomorph assemblages recovered from the Vargas Peña Formation indicate a late Aeronian to mid-Telychian age (Gray *et al.* 1992), though Grahn *et al.* (2000) and Grahn and Gutiérrez (2001), on the basis of chitinozoans, placed tentatively the lower part of the Vargas Peña Formation into the Rhuddanian. Graptolites recovered from the lower part of the Vargas Peña Formation (under study by N. J. Uriz) also suggest a Rhuddanian age (Tortello *et al.* 2008, p. 396).

The age of the underlying Eusebio Ayala Formation was assumed as probably close to that of the Vargas Peña Formation on the basis of the presence of *Eocoelia paraguayensis* (Harrington, 1950) in both formations. New sampling from the Itacurubi Group, however, indicates that *E. paraguayensis* is absent in the Eusebio Ayala For-

mation, and that this species is confined to the Vargas Peña Formation (Benedetto 2002). Further evidence for the Silurian age of the Eusebio Ayala Formation is the occurrence of *Heterorthella freitana* (Clarke, 1899) and *Clarkeia antisiensis* (d'Orbigny, 1847) (Boucot *et al.* 1991). However, these species are reassigned here to *Arenorthis paranaensis* sp. nov. and *Plectothyrella? itacurubiensis* sp. nov., respectively, both taxa pointing to a Late Ordovician, rather than a Silurian, age. The discovery of *Normalograptus persculptus*, *N. medius* and *N. normalis* in the upper third of the Eusebio Ayala Formation indicates for the first time that the age of the lower part of the Itacurubi Group extends back into the Hirnantian (Alfaro *et al.* 2010, 2012; Cingolani *et al.* 2011). It is worth noting that though glacial sediments are not exposed in the studied area, a c. 50-m-thick succession of tillites underlying sandstones and shales bearing Late Ordovician to Early Silurian palynomorphs has been reported from drill cores (Figueredo 1995). Although the precise stratigraphic position of these glacial deposits remains unknown, they are probably older than the Eusebio Ayala Formation, based on their absence in the exposed stratigraphic sections of the Itacurubi Group.

The low-diversity brachiopod assemblage described here, although not fully diagnostic because three of four taxa are new species, is undoubtedly Hirnantian. *Hindella crassa* is not known from rocks younger than Rhuddanian, being a relatively common component of the *Hirnantia* fauna in many regions (Wales, Ireland, Norway, South China, Morocco, Quebec) (Rong and Harper 1988; Rong *et al.* 2002, and references therein). In southern South America, *Hindella crassa* occurs in the lowermost part of the La Chilca Formation of the Argentine Precordillera, dated as mid-late Rhuddanian by mean of associated brachiopods (Benedetto and Cocks 2009). *H. crassa* is also very abundant in beds of Hirnantian–earliest Silurian age (Salar del Rincón Formation) of the Puna region of north-western Argentina (Isaacson *et al.* 1976; Benedetto and Sánchez 1990; Rubinstein and Vaccari 2004), and in the probably coeval Quebrada Ancha Formation of northern Chile (Niemeyer *et al.* 2010). *Eostropheodonta* is another long-ranging cosmopolitan genus recorded from the Sandbian to the Wenlock, but most of its species are confined to the Hirnantian–Rhuddanian interval (Rong and Cocks 1994; Cocks and Rong 2000). Of them, *E. hirnantensis* (M'Coy, 1851) is a common component of the typical *Hirnantia* fauna, excepting in the African Hirnantian assemblages in which *Eostropheodonta* is represented by different species.

Of particular biostratigraphic interest is the genus *Arenorthis*, which has hitherto been reported only from beds of Hirnantian age. In North Africa (Morocco, Libya), it is commonly associated with *Plectothyrella* in the latest Ordovician Deuxième Bani Formation (Havlíček

1971; Mergl 1983). Therefore, we assume that the age of the upper part of the Eusebio Ayala is Hirnantian, a conclusion supported both by the graptolites of the *persculptus* Zone recovered from the same beds bearing the shelly fauna described here. Where within the Eusebio Ayala Formation the Ordovician/Silurian boundary should be drawn is uncertain, and the possibility that members of the described assemblage occur within Rhuddanian strata cannot be completely discarded. This issue could be resolved with a detailed sampling of graptolites and brachiopods from the uppermost part of the Eusebio Ayala Formation at different stratigraphic sections.

PALAEOBIOGEOGRAPHIC IMPLICATIONS

Since the publication of the classical study by Rong and Harper (1988) on the biogeographical distribution of the *Hirnantia* Fauna, numerous reports have been published worldwide (Owen *et al.* 1991; Rong and Li 1999; Rong *et al.* 2002; Sutcliffe *et al.* 2001, among others). Despite the nearly cosmopolitan distribution of the *Hirnantia* Fauna, two distinct biogeographical units have been recognized: the Kosov and Bani Provinces (Rong and Harper 1988). The Kosov Province developed at intermediate latitudes (approximately between 20° and 45° S), in well-oxygenated waters and a variety of substrate types ranging into the shallow subtidal zone. It has also been recorded in graptolite-bearing dark grey mudstones deposited in deeper waters, as in the Yangtze platform of south China (Rong *et al.* 2002). The Bani Province inhabited high-latitude sandy substrates marginal to the Gondwanan ice sheet. Its brachiopod assemblages are less diverse than the typical (Kosov) *Hirnantia* associations, and some of the key taxa (i.e. *Eostropheodonta*, *Plectothyrella*) are represented by different species. By the latest Ordovician, a different, high-diversity suite of brachiopods, named the Edgewood Province, developed in shallow warm waters with little or no siliciclastic input on the peri-Equatorial carbonate platforms of Laurentia, Kolyma and the Oslo region of Baltica (Owen *et al.* 1991). According to Delabroye and Vecoli (2010), the cause of the biogeographic segregation of brachiopods, graptolites and chitinozoans into low/mid-latitude and high-latitude faunal assemblages was the sea level drop during the end-Ordovician glaciation. However, as discussed below, the strong climatic gradient was probably the primary cause of provincialism during the Hirnantian.

Although *Hirnantia* itself has not been recorded in the Eusebio Ayala Formation, the overall generic composition of the fauna (presence of *Hindella*, *Eostropheodonta*, *Ar-enorthis* and *Plectothyrella*?) allows us to consider this brachiopod assemblage as representative of the *Hirnantia*

Fauna. The first three above-mentioned genera are key constituents of the majority of *Hirnantia* associations. *Ar-enorthis* is consistently associated with *H. sagittifera* in the Moroccan Anti-Atlas (Havlíček 1971, 1990; Mergl 1983; Destombes *et al.* 1985; Sutcliffe *et al.* 2001; Villas *et al.* 2006), and it is, together with *Destombesium*, one of the most distinctive brachiopods of the Bani Province. Its association with species of *Plectothyrella*? and *Eostropheodonta* different from those recorded in the Kosov Province (*P. crassicosis* and *E. hirnantensis*, respectively) strengthens the affinities between the Hirnantian faunas of Paraguay and North Africa.

The only *Hirnantia* Fauna hitherto recorded in South America comes from the Don Braulio Formation of the Argentine Precordillera (Benedetto 1986, 1990; Sánchez *et al.* 1991; Astini and Benedetto 1992). The fauna occurs in transgressive shallow subtidal fine-grained sandstones and siltstones that conformably overlie glacial deposits (Peralta and Carter 1990; Astini 1999). The uppermost dark grey mudstone yielding the *Hirnantia* Fauna contains numerous specimens of *N. persculptus* (Brussa *et al.* 2003). Towards the top of the Don Braulio Formation, there are some haematitic fine-grained sandstone beds of Rhuddanian age (Pothe de Baldis 1997). Overall, the brachiopod assemblage is dominated by *Hirnantia sagittifera*, *Dalmanella testudinaria*, *Paromalomena polonica*, *Eostropheodonta hirnantensis* and *Plectothyrella crassicosis chauveli*. Less common components are *Leptaena trifidum*, *Cliftonia oxoplecioides* and *Drabovia undulata*. Most of these taxa are conspicuous components of the Kosov-type assemblages, and the sole presence of a relatively thick-ribbed form of *Plectothyrella* does not justify to include the Precordillera in the Bani Province (Villas *et al.* 1999; Sutcliffe *et al.* 2001). A different low-diversity brachiopod assemblage of Hirnantian?–Lower Llandovery age has been recovered in the Puna region of NW Argentina (Salar del Rincón Formation). It consists of *Dalmanella* sp., *Eostropheodonta* sp., *Fardenia* sp., *Hindella crassa* and a species of *Heterorthella* close to *H. africana* (Cocks and Brunton) in Cocks *et al.*, 1970 (Isaacson *et al.* 1976; Benedetto and Sánchez 1990). The *Hindella*-dominated assemblage of northern Chile has been considered Lower Silurian but, as the authors stated, the few associated brachiopods are not useful for precise age determination (Niemeyer *et al.* 2010).

Here, we review the distribution of 42 taxa from 27 selected localities, which following Rong and Li (1999) were grouped in nine regions: Baltica, Avalonia, Central Europe, South China, Tibet, Sibumasu, North Africa, Eastern Canada and Argentina (Precordillera). A presence/absence matrix was built up considering all data available in the literature, including the Eusebio Ayala fauna of Paraguay described in this paper. Data were analysed using hierarchical clustering method with the

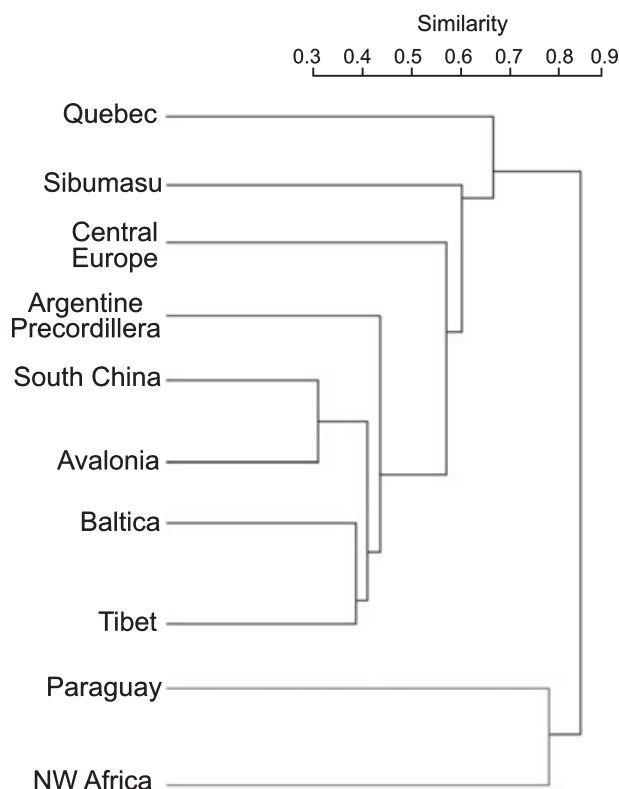


FIG. 3. Cluster analysis (using the Jaccard similarity index) of a selection of localities bearing *Hirnantia* faunas. Note the link between the Paraguay brachiopod fauna and the North African localities bearing Bani Province assemblages.

Jaccard coefficient as a similarity distance measure. The resulting dendrogram (Fig. 3) shows two main clusters. Within the first cluster, the regions classically ascribed to the Kosov Province display different degree of affinity reflecting local changes of faunal composition. The second cluster includes the low-diversity assemblages of North Africa (Morocco, Algeria and W Libya) and the Paraguay fauna. The South African assemblage from the Disa Member of the Cedarberg Formation (Cocks and Fortey 1986) was not included in the data matrix because only two brachiopod taxa (*Plectothyrella haughtoni* Cocks and Brunton, in Cocks *et al.*, 1970) and *Eostropheodonta decumbata* Cocks and Brunton (in Cocks *et al.*, 1970) are firmly established, the generic status of *Marklandella africana* Cocks and Brunton (in Cocks *et al.*, 1970) being in need of revision (it has been referred to *Heterorthella* by Harper *et al.* (1969) but subsequently ascribed to *Arenorthis* by Havlíček (1977)). Nevertheless, the South African fauna is by far closer to the Paraguayan-NW African assemblages than to any other Hirnantian fauna. It can also be compared to the Hirnantian?–Rhuddanian fauna of the Puna region of NW Argentina.

The presence of a Bani-type fauna in South America may result from a similar palaeolatitudinal position and

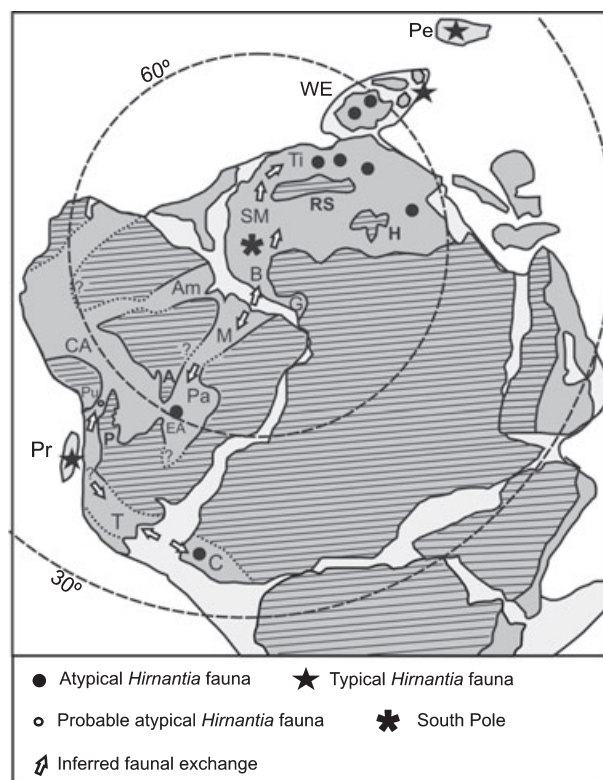


FIG. 4. Palaeogeographic map of the latest Ordovician (Hirnantian), showing epicontinental seas (gray), emerged areas (horizontal lines), and probable faunal connections between African and South American basins (arrows) (data from Benedetto *et al.* 1992; Cocks and Torsvik 2006; Villas *et al.* 1999; Fatka and Mergl 2009). A, Asunción Arch; Am, Amazonas basin; B, Bové basin; EA, Paraguay fauna (Eusebio Ayala Formation); C, Cape basin; CA, Central Andean basin; G, Ghana basin; H, Hoggar shield; M, Maranhao basin; P, Puna basin; Pa, Paraná basin; Pe, Perunica; Pr, Precordillera basin; RS, Reguibat shield; SM, Senegal-Mauritania basins (includes the Hodh basin); T, Tandil basin; Ti, Tindouf basin; WE, West European platform (includes Iberia, Armorica, Montagne Noire, Sardinia, and Carnic Alps).

a correspondence between the facies in which benthic faunas developed (Fig. 4). Overall, the decreasing diversity values towards the areas surrounding the Gondwana polar ice sheet agrees with the latitudinal diversity gradient hypothesis (*sensu* Jablonski *et al.* 2006). The latitudinal diversity gradient in the marine fossil record, and in particular in brachiopods, has persisted through most of the Phanerozoic (Powell 2009, and references therein). Besides, this pattern has been linked to periods of intense global climatic differentiation, such as the end-Ordovician cooling event. For instance, the low-diversity *Hirnantia* fauna from the Criadero Quartzite of Spain (Villas *et al.* 1999) is latitudinally intermediate between the high-diversity Kovov assem-

blages of Perunica (c. 40° S) and the much less diverse North African assemblages (more than 60° S). Also, the moderately low-diverse fauna from the Argentine Precordillera (c. 50° S) seems to be intermediate between the more temperate Kosov faunas and the Eusebio Ayala fauna, whose estimated palaeolatitude by plotting Paraguay on the Hirnantian maps (i.e. Cocks and Torsvik 2006) is c. 60° S, which is consistent with the impoverishment of the Kosov Province faunas caused by latitudinal gradient in species diversity (cf. Rong and Harper 1988).

The presence of a Bani-type brachiopod assemblage in Paraguay raises the issue of its connections with the African basins. Westward (present coordinates) dispersal to North Africa via the Central Andean basin of NW Argentina and Bolivia – to which the easternmost part of the Paraná Basin was connected by a narrow passage to the south of the Asunción Arch (Fig. 4) – is difficult to demonstrate because there are no reports of *Hirnantia* faunas from this basin, with the exception of the above-mentioned Puna assemblage of Hirnantian?–Lower Silurian age. On the other hand, faunal dispersal from the Paraná basin to North Africa via the Precordillera basin is highly improbable because the two basins were separated by a large upland area (the Pampean Arch). Moreover, the Precordillera basin was inhabited, as stated above, by a much more diverse and compositionally different *Hirnantia* Fauna.

A more reliable dispersal pattern is through an epicontinental seaway connecting directly the Paraná basin with the Ghana basins of West Africa through the Maranhao (Parnaíba) intra-cratonic basin of Brazil (Fig. 4). This hypothesis is supported by the similarity of the Upper Ordovician–Silurian successions of West Africa and Brazil. In the eastern and northern margins of the Paraná basin, the Iapó and Río Ivaí glaciogenic diamictites are overlain by sandstones and black shales (Vila María Formation) bearing palynomorphs of Llandovery age (Gray *et al.* 1985). In the Maranhao basin, the succession initiates with diamictites and cross-bedded sandstones (Ipu Formation) interpreted by Caputo and Crowell (1985) and Grahn and Caputo (1992) as having glacial origin, followed by Lower Silurian dark grey bioturbated mudstones (Tiangua Formation). The Ghana basins (Accra, and Takoradi-Elmina basins), exposed discontinuously along the Atlantic coast of West Africa, have been considered as remnants of the Maranhao basin preserved on the African plate as result of the opening of the South Atlantic Ocean (Villeneuve 2005). The Upper Ordovician–Llandovery stratigraphic succession in the Takoradi-Elmina basin consists of glacial deposits and marine shales (Ajua Formation). Towards the north, the Bové basin developed at the northern margin of the Ivory Coast shield, in Guinea, Guinea

Bisseau and Senegal. There, the upper part of the Pita Group includes Upper Ordovician glaciogenic conglomeratic claystones. The overlying Telimelé Group consists of graptolitic black shales of early Llandovery age (Villeneuve and Da Rocha Araujo 1984) followed by sandstones bearing a typical Afro-South American brachiopod assemblage (Racheboeuf and Villeneuve 1992). This is particularly significant as denotes that by the mid-Silurian, there was an active faunal exchange between the South American and West African basins (Benedetto and Sánchez 1996), suggesting that the Hirnantian biotas may have followed the same dispersal route. The Hodh basin of Mauritania (Underwood *et al.* 1998) could have been an intermediate step in the faunal exchange with the large Tindouf basin of Northwest Africa, which contains the classical localities of the Bani Province. It seems likely that such trans-Brazilian/West African epicontinental seaway was first established at the end of the Ordovician when the postglacial high stand produced, for the first time in the Phanerozoic, an extensive marine flooding of the intracratonic basins. Palynological evidence from South America also supports a second deglaciation event during the Lower Silurian (Aeronian–Telychian), which probably correlates with deposition of the offshore clays of the Vargas Peña Formation (Díaz-Martínez and Grahn 2007).

The link between South Africa and southern South America is more obvious because it is widely accepted that the Cape fold belt and the Ventana-Tandilia belts of eastern Argentina were in continuity before the opening of the South Atlantic Ocean. In both regions, passive-margin, shallow-marine lower Palaeozoic deposits (Cambrian?–Ordovician) are recorded. The recent detrital zircon age of the Sierra del Volcán diamictite exposed in the Tandilia belt of eastern Argentina setting a lower age limit for sedimentation in the Ordovician (instead of Neoproterozoic) supports its correlation with the Hirnantian Pakhuis Formation of South Africa (Zimmermann and Spalletti 2009; Van Staden *et al.* 2010). This age evidence is consistent with the trace fossils from the inner-shelf quartzites of the Balcarce Formation enclosing the glacial unit (Poiré *et al.* 2003), which can be correlated with the Peninsula and Cedarberg formations of the Table Mountain Group of South Africa. It should be noted, in addition, that both the Balcarce and the Peninsula formations contain not only a comparable suite of trace fossils but also share a similar palaeocurrent pattern towards the South (Poiré *et al.* 2003; Shone and Booth 2005). On this basis, a fluid marine connection between the South Africa and eastern Argentina during the Late Ordovician can be inferred. More difficult is to demonstrate a connection between the Tandilia and the Paraná basins because most of the Rio de La Plata Craton is covered unconformably by

glacigenic Upper Carboniferous–Permian sedimentary rocks. However, in one locality of north-eastern Argentina (Las Breñas borehole), a thick Cambro–Ordovician succession has been detected underlying iron-rich beds of Silurian age (Rapela *et al.* 2007). It is uncertain as to whether these sediments represent a relict of a formerly continuous marine sedimentary cover eroded during the late Palaeozoic glaciation or were deposited in an isolate, fault-bounded basin connected to the north-west with the Central Andean basin but not with the Balcarce basin.

SYSTEMATIC PALAEOONTOLOGY

(by J. L. Benedetto)

Remarks. All specimens are housed in the Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Córdoba (acronym CEGH-UNC). The systematic classification follows that of the Treatise on Invertebrate Paleontology, part H (revised) (Cocks and Rong 2000; Harper 2000; Alvarez and Rong 2002; Savage 2002).

Class RHYNCHONELLATA Williams *et al.*, 1996

Order ORTHIDA Schuchert and Cooper, 1932

Suborder DALMANELLIDINA Moore, 1952

Superfamily DALMANELLOIDEA Schuchert, 1913

Family HETERORTHIDAE Schuchert and Cooper, 1931

Genus ARENORTHIS Havlíček, 1970

Type species. By original designation, *Arenorthis arenaria* Havlíček, 1970, from the Deuxième Bani Formation (Upper Ordovician, Hirnantian) at Foum Hamia, Anti-Atlas Mountains, Morocco.

Arenorthis paranaensis sp. nov.

Figure 5C–W

1991 *Heterorthella freitana* (Clarke, 1899) in Boucot *et al.*, p. 513, figs 4–7.

Derivation of name. After the Paraná basin.

Holotype. An internal mould of dorsal valve (CEGH-UNC 24447a; Fig. 5U–W); from upper third of the Eusebio Ayala Formation (Hirnantian), San Fernando Quarry, Paraguay.

Paratypes. Five external moulds and four internal moulds of ventral valve, five external moulds and six internal moulds of dorsal valve CEGH-UNC 24432, 24444–24446, 24447b, 24447c,

24454–24460, 24493, 24496, from the San Fernando and Santa Elena quarries.

Diagnosis. Gently ventribiconvex, subcircular shells with fascicostellate ornament of 5–6 costae per 5 mm at anterior margin. Ventral muscle field large, suboval, extending for about 42 per cent valve length. Cardinal process expanded into a prominent, often trilobate myophore occupying the whole notothyrial platform. Thick brachiophores supported by proportionally short bases converging medially towards floor of valve.

Description. Shells up to 22 mm wide, most specimens ranging in width from 14 to 16 mm, gently ventribiconvex, nearly circular to transversely elliptical in outline. Ventral valve almost 85 per cent as long as wide and 20–25 per cent as deep as long and dorsal valve 90–95 per cent as long as wide. Anterior commissure weakly sulcate. Cardinal extremities rounded, maximum width near the mid-length. Hinge line about two-thirds as wide as maximum shell width. Ventral valve evenly and moderately convex, with maximum height about one-third length. Ventral interarea aplanate with open subtriangular delthyrium. Dorsal valve nearly flat in younger individuals, gently convex (6–8 per cent as deep as long) in medium to large specimens, with shallow sulcus originating at umbo. Dorsal interarea planar, anacline. Radial ornament fascicostellate with subangular costellae numbering 5–6 per 5 mm counted along the anterior margin of mature specimens. Posterior costellae incurved posterolaterally intersecting hinge line. A few accentuated growth lines (2–5) irregularly distributed.

Ventral interior with stout teeth supported by short dental plates continuous with low, curved ridges diverging anteriorly at 80–90 degrees. Muscle field large, suboval, extending in average for about 42 per cent valve length. Diductor scars large, flabellate, with scalloped margins; adductor scars narrowly subrectangular, generally not discernible. Pedicle callist low, forming a short platform.

Dorsal interior with cardinal process differentiated into a thick, rounded ridge-like shaft that often extends beyond the brachiophores bases, and a prominent myophore occupying the whole notothyrial platform. Myophore ovoid, its posterior face swollen often cleft by two weak fissures into three lobes. Long slender brachiophores projecting anterodorsally, supported by thick short bases converging medially towards floor of valve. Notothyrial platform slightly elevated, continuous anteriorly with variably developed, generally broad, rounded median ridge extended to about mid-valve length. Dental sockets suboval in outline excavated on valve floor. Muscle field large, 42–55 per cent as long as valve length, quadripartite, with the anterior pair subcircular considerably larger than the subtriangular posterior pair; anterior and posterior adductor scars separated by weak transverse ridges.

Remarks. The genus *Arenorthis* was erected by Havlíček in 1970 to include a distinctive heterorthid from the Hirnantian Deuxième Bani (Second Bani) Formation of Morocco characterized by a ventribiconvex shell and a

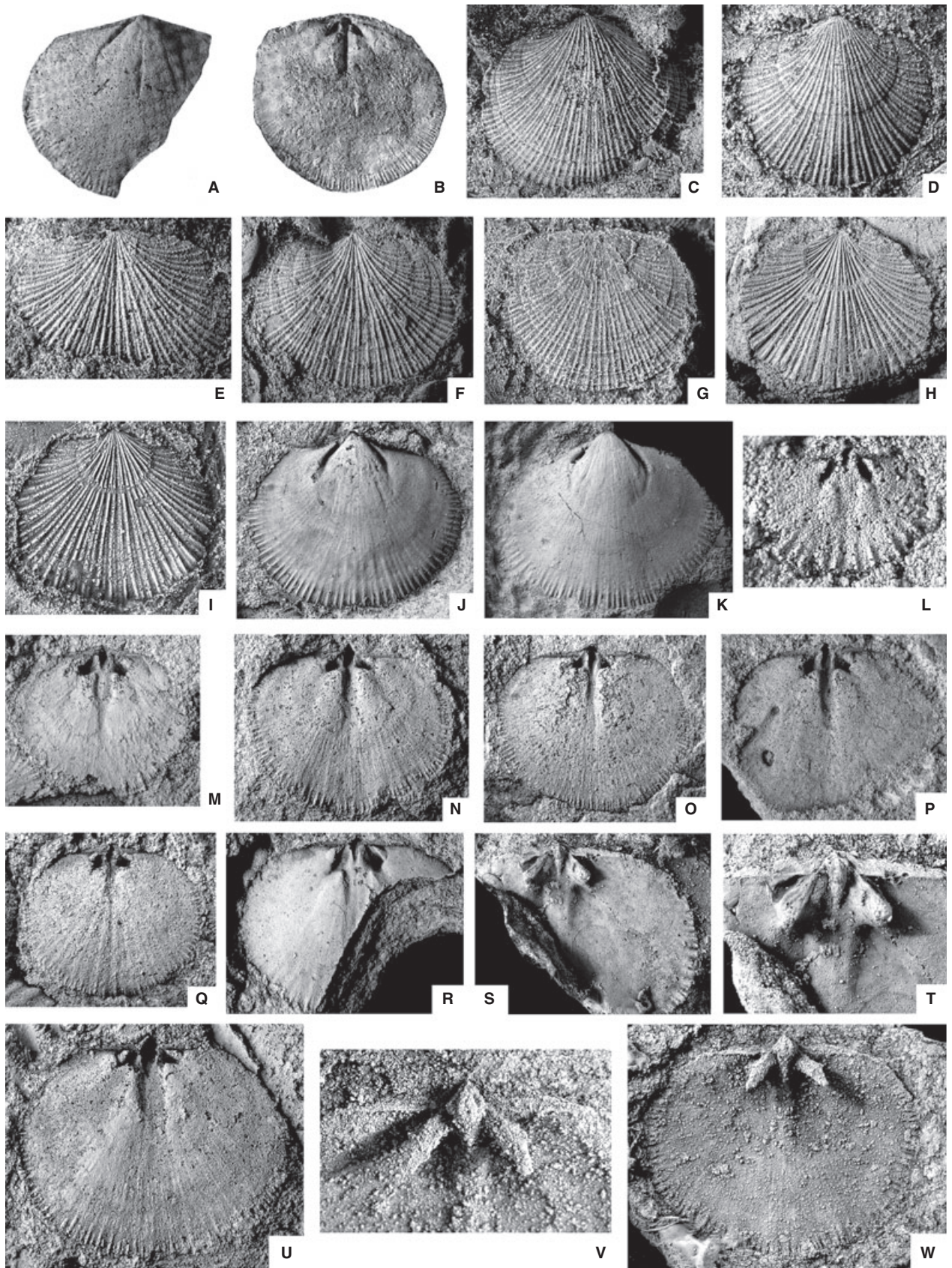
cardinal process bearing a bilobate or trilobate myophore. The type species is *Arenorthis arenaria* Havlíček, from the Fom Hamia locality, near Zagora, in the Anti-Atlas mountains. The only other species belonging to this genus is *Arenorthis circula* (Mergl 1983), which occurs a few metres below the levels bearing *A. arenaria*. This material was referred originally to the new genus *Fehamya* by Mergl (1983), but subsequently, it was regarded as a junior synonym of *Arenorthis* by Havlíček (1990) arguing that differences in the ventral muscle field and cardinal process do not justify the recognition of a separate genus. *Marklandella africana* Cocks and Bruton (*in* Cocks *et al.* 1970), from the Hirnantian Cedarberg Formation of South Africa (Cocks and Fortey 1986), was reassigned to the genus *Heterorthella* by Cocks (1972) but later *africana* was listed by Havlíček (1977) as a species of *Arenorthis*, not giving reasons for such an assignment. It is uncertain whether the South African species belongs to *Arenorthis*. The apparently simple cardinal process and the long, curved brachio-phore bases are more suggestive of *Heterorthella*, as Cocks (1972, p. 624) stated. It should be noted that basal forms of *Heterorthella*, such as *Heterorthella* sp., from the Salar del Rincón Formation of the Puna region (NW Argentina), of Hirnantian-early Llandovery age (Benedetto and Sánchez 1990), and *Heterorthella precordillerana* Benedetto, 1991, from the La Chilca Formation (Rhuddanian) of the Argentine Precordillera (Benedetto 1995) are morphologically close to, and slightly younger than, *Arenorthis*, suggesting that the latter is a potential ancestor of *Heterorthella*, a possibility that should be tested by a cladistic analysis. Outside Morocco, the genus *Arenorthis* was reported by Levy and Nullo (1974) from the Hirnantian of the Argentine Precordillera. However, from the description and illustrations provided by Levy and Nullo (1974, pl. 2, figs 11–13), we find no reasons for assigning these specimens to the heterorthids. The general form and shape of valves, the style of ornament, as well as the muscle fields and cardinalia morphology (e.g. presence of fulcral plates), are nearly identical to those of *Dalmanella testudinaria*, a very common species present in the same localities and

horizons yielding *A. cuyana*, and leave no doubt that this form is conspecific with *D. testudinaria*.

The material that served to erect the new species *Arenorthis paranaensis* was identified by Boucot *et al.* (1991) as *Heterorthella freitana* (Clarke, 1899). Harper *et al.* (1969) differentiated the genus *Heterorthella* (type species *H. maehli* Harper, Boucot and Walmsley, from the Wenlock of Nova Scotia, Canada) mainly on the basis of its planoconvex shell, its very long erect brachio-phore bases bounding posterolaterally the muscle field, and its high, simple, bladelike cardinal process. All these features are shared by other well-established species of the genus such as *H. freitana* (Clarke, 1899) (Llandovery of Amazonas basin, Brazil), *H. zaplensis* Benedetto, 1991 (Silurian of Sierra de Zapla, Argentina) and *H. tondonensis* Racheboeuf and Villeneuve, 1992 (Ludlow of Guinea, West Africa). The Paraguayan specimens have a gently convex dorsal valve (only the smallest valves are nearly planar), and their cardinalia are characterized by a bulbous trilobed myophore and relatively short brachio-phore supporting plates converging onto the notothyrial platform. These features, together with the large flabellate ventral muscle field, are all distinctive of the genus *Arenorthis*, to which we refer herein the Eusebio Ayala material.

The new species *Arenorthis paraguayensis* differs from the type species *A. arenaria* Havlíček in having somewhat coarser radial ornament (*A. arenaria* possesses 8–11 costellae per 5 mm). In addition, radial ornament in the Moroccan species is always strongly marked on the entire internal surface of both valves, and consequently muscle fields are poorly defined or even indistinguishable. The type species can also be distinguished from *A. paraguayensis* in its stronger bounding ridges originating at the end of brachio-phore bases. *A. paraguayensis* closely resembles *Arenorthis circula* (Mergl, 1983) (illustrated for comparison in Fig. 5A, B) in the general shape of the shell, ornament and arrangement of muscle scars, but differs in the absence of septum bisecting the ventral muscle field, in having weaker and shorter dorsal muscle bounding ridges, and a slightly wider dorsal median ridge. In addition, the myophore in *A. parana-*

FIG. 5. A, B, *Arenorthis circula* (Mergl, 1983), Fom El Fehamya, Morocco. A, VH 4015c dorsal valve internal mould; $\times 1$. B, VH 4015d, ventral valve internal mould; $\times 1.5$. C–W, *Arenorthis paranaensis* sp. nov. C, CEGH-UNC 24447b, ventral valve exterior, latex cast; $\times 2$. D, CEGH-UNC 24444, ventral valve exterior, latex cast; $\times 2$. E, CEGH-UNC 24456b, dorsal valve exterior, latex cast; $\times 2$. F, CEGH-UNC 24455b, dorsal valve exterior, latex cast; $\times 2$. G, CEGH-UNC 24458c, dorsal valve exterior, latex cast; $\times 2$. H, I, CEGH-UNC 24454, dorsal valve external mould and latex cast; $\times 2$. J, CEGH-UNC 24456a, ventral valve internal mould; $\times 2$. K, CEGH-UNC 24457, ventral valve internal mould; $\times 2.5$. L, CEGH-UNC 24445b, dorsal valve internal mould, juvenile specimen; M, CEGH-UNC 24447c, dorsal valve internal mould, juvenile specimen; $\times 3$. N, CEGH-UNC 24432, dorsal valve internal mould; $\times 2.5$. O, CEGH-UNC 24456, dorsal valve internal mould; $\times 2$. P, CEGH-UNC 24446, dorsal valve internal mould; $\times 2$. Q, CEGH-UNC 24458, dorsal valve internal mould; $\times 2.5$. R–T, CEGH-UNC 24445a, dorsal valve internal mould (R), latex cast (S), $\times 2.5$, and detail of cardinalia (T), $\times 6$. U–W, CEGH-UNC 24447a, holotype, dorsal valve internal mould (U), $\times 2.5$, detail of cardinalia (V), $\times 6$, and latex cast (W), $\times 2.5$.



ensis is trilobed, as in *A. arenaria*, whilst it is bilobed in *A. circula*.

Order RHYNCHONELLIDA Kuhn, 1949

Superfamily RHYNCHOTREMATOIDEA Schuchert, 1913

Family TRIGONIRHYNCHIIDAE Schmidt, 1965

Subfamily PLECTOTHYRELLINAE Bergström, 1968

Genus PLECTOTHYRELLA Temple, 1965

Type species. *Atrypa? crassicosis* Dalman, 1928, pp. 131–132, from the upper part of the *Dalmanitina* Beds (Hirnantian), Sweden.

Plectothyrella? itacurubiensis sp. nov.

Figure 6A–S

1991 *Clarkeia antisiensis* (d'Orbigny, 1847); Boucot *et al.*, p. 513, figs 1–3.

Derivation of name. After the Itacurubí locality.

Holotype. An internal mould of dorsal valve CEGH-UNC 24464b (Fig. 6O, P) from the upper third of the Eusebio Ayala Formation (Hirnantian), San Fernando Quarry, Paraguay.

Paratypes. CEGH-UNC 24462–24463, 24465–24475 from the San Fernando and Santa Elena quarries.

Diagnosis. A species of *Plectothyrella?* having two simple, rounded costae on the fold, one (rarely two) simple costa in the sulcus, and 5–7 rounded costae on each flank.

Description. Shell medium-sized (largest specimen 16 mm wide), nearly equibiconvex, averaging ($n = 12$) 92 per cent as long as wide and 58 per cent as deep as long. Shell outline longitudinally elliptical to subpentagonal. Hinge line slightly curved, about to one-half shell width. Maximum shell width at mid-length or two-thirds length. Anterior commissure uniplicate to weakly sulcinate. Ventral umbo low with small, slightly incur-

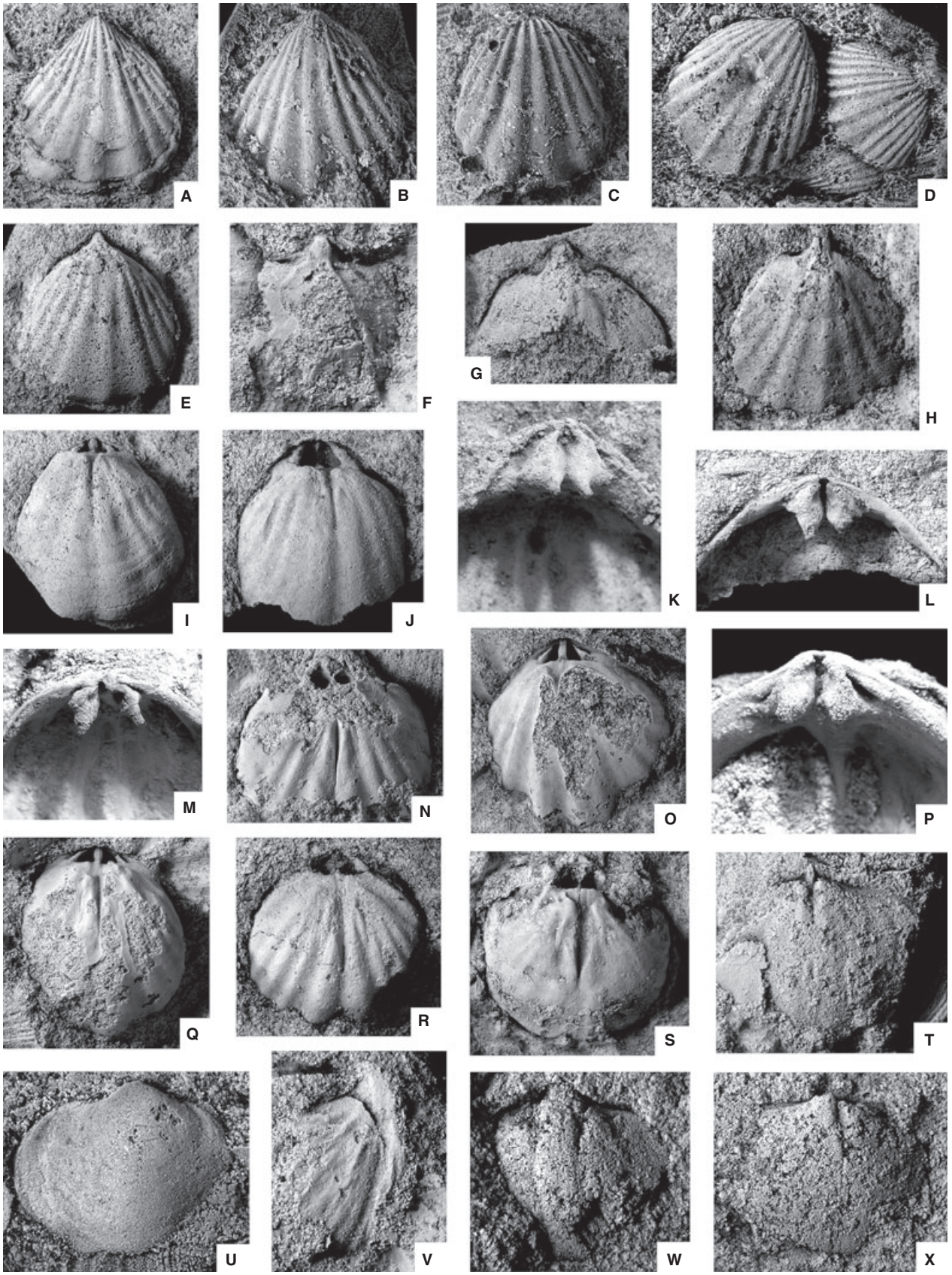
ved beak. Delthyrium open. Ventral sulcus broad, shallow, widening to about one-third shell width at anterior margin, bearing a simple, rounded median costa, though in large specimens a second narrow rib may be present. Brachial umbo inconspicuous. Notothyrium open, small, subcircular. Moderately high dorsal fold developed on anterior half of valve, of similar width as the sulcus, bearing two costae always larger than lateral ones. Each shell flank with 5–7 rounded simple costae. Fine growth lines and irregularly spaced growth lamellae usually present, more conspicuous at anterior margin.

Teeth moderately strong, transversely oval, partially supported by posterior shell wall; dental plates short, blade like in smaller specimens becoming nearly completely obliterated by callus deposits infilling apical cavities in medium-sized and large specimens. Pedicle chamber mostly undifferentiated in younger specimens, large, more profoundly excavated in largest specimens, in which valve floor deflects dorsally to form a moderately elevated, subtriangular 'ventral platform' (in the sense of Temple, 1965, p. 413) bearing a faintly impressed muscle field.

Hinge plates disjunct, massive, slightly divergent from each other; crural bases attached to inner surface of hinge plates, in some specimens preserved the proximal part of rodlike, gently curved radulifer crura extending ventro-anteriorly. Cardinal process absent. Dental sockets deep, slitlike, open distally, bounded posteriorly by strong, elongate outer socket ridges. Median septum variably developed, generally high and narrow, merged to the posterior wall of notothyrial chamber, tapering anteriorly, attaining about one-half, exceptionally two-thirds, shell length. Dorsal muscle field elongate, deeply impressed only in adult or gerontic specimens, with posterior adductor scars linear slightly divergent forwards, and anterior adductor scars narrow, pear-shaped, almost subparallel to each other.

Remarks. The genus *Plectothyrella* was erected by Temple (1965) to include strongly ribbed shells classified with interrogation as meristellids but subsequently reassigned to the rhyntonellids by Bergström (1968). According to his emended diagnosis, *Plectothyrella* includes biconvex, uniplicate, coarsely costate shells with strong dental plates hidden by secondary deposits, massive hinge plates and lacking cardinal process. The Eusebio Ayala rhyntonelloids were referred to *Clarkeia antisiensis* by

FIG. 6. A–S, *Plectothyrella? itacurubiensis* sp. nov. A, CEGH-UNC 24468a, dorsal valve exterior, latex cast; $\times 1.75$. B, CEGH-UNC 24468, ventral valve exterior, latex cast; $\times 2$. C, CEGH-UNC 24434, dorsal valve exterior, latex cast; $\times 2$. D, CEGH-UNC 24458, ventral (left) and dorsal (right) valve exteriors, latex cast; $\times 2$. E, CEGH-UNC 24467a, ventral valve internal mould; $\times 2$. F, CEGH-UNC 24463, ventral valve internal mould; $\times 3$. G, CEGH-UNC 24455c, incomplete ventral valve internal mould; $\times 2.5$. H, CEGH-UNC 24459a, ventral valve internal mould; $\times 2$. I, CEGH-UNC 24473, dorsal valve internal mould; $\times 3$. J, K, CEGH-UNC 24475, dorsal valve internal mould, $\times 3$, and detail of cardinalia, latex cast, $\times 6$. L, CEGH-UNC 24464c, dorsal valve latex cast, $\times 4.5$. M, Q, CEGH-UNC 24464a, detail of cardinalium (M), $\times 4$, and internal mould (Q), $\times 2$. N, CEGH-UNC 24466, dorsal valve, internal mould; $\times 2.5$. O, P, CEGH-UNC 24464b, holotype, internal mould of dorsal valve ($\times 2.5$), and detail of cardinalium, latex cast ($\times 4$). R, CEGH-UNC 24465a, dorsal valve internal mould; $\times 2.5$. S, CEGH-UNC 24462, dorsal valve internal mould; $\times 2$. T–X, *Hindella* cf. *H. crassa* (J. DE C. Sowerby, 1839). T, CEGH-UNC 24454b, dorsal valve internal mould; $\times 2.5$. U, CEGH-UNC 24450, dorsal valve exterior, latex cast; $\times 1.5$. V, CEGH-UNC 24454a, ventral valve internal mould; $\times 2.5$. W, CEGH-UNC 24460, ventral valve internal mould; $\times 3$. X, CEGH-UNC 24454c, dorsal valve internal mould; $\times 3.5$.



Boucot *et al.* (1991), but a careful observation of numerous well-preserved internal moulds from this formation reveals that there is no trace of cardinal process, which in *Clarkeia* constitutes a prominent, often bifid or trifid structure. Cocks (1972, p. 828) noted that the South African species *Plectothyrella haughtoni* Cocks and Brunton (*in* Cocks *et al.* 1970) is closely related to the South American *Clarkeia antisiensis* than to any other genus, and that both forms are probably related phylogenetically. New evidence from both internal and external features of the Eusebio Ayala material adds support to the probable origin of *Clarkeia* from *Plectothyrella? itacurubiensis* through the gradual development of a cardinal process and a series of less crucial morphological changes affecting muscle fields and ornament (Benedetto, *in progress*).

The commonest and more widespread species of the genus is *P. crassicostis* (= *P. platystrophoides* Temple 1965), whose type material is from the upper part of the *Dalmanitina* Beds of Sweden, but also has been reported from Poland, England, Canada (Quebec), Norway, Ireland, Czech Republic, South China and Argentina. In all of these localities, this species is associated with typical elements of the *Hirnantia* fauna. The new species *P.? itacurubiensis* can be easily distinguished from the type species because its fold is marked by two strong, rounded simple costae, and the sulcus bears a single costa: in *P. crassicostis* usually, there is three ribs in the sulcus (in populations of the Bohemian Kosov Formation, there is up to 7), four on the fold, and up to 14 on each flank. Moreover, in *P. crassicostis*, the ventral muscle field is deeply impressed posteriorly, its anterior part lying on a strongly raised ventral platform, which in the Paraguayan species is less prominent. *P. libyca* Havlíček and Massa, from Hirnantian beds of western Libya (Havlíček and Massa 1973) and Morocco (Havlíček 1990), recall *P.? itacurubiensis* in its coarser, generally nonbranched ribs numbering 4–7 on flanks (five in the Moroccan population), but differs in having 2–4 ribs in the sinus, and in some specimens, the two costae on the fold tend to bifurcate on its anterior half. Internally, *P. libyca* can be distinguished by its deeply excavated ventral muscle field in which adductor and diductor scars are clearly discernible. The cardinalia of both species are very similar, especially in the adult or gerontic specimens, in which hinge plates are cylindrical in cross section, becoming fused medially by progressive obliteration of the medial groove. The Moroccan species *P. chauveli* Havlíček (1971) differs from *P. libyca* in having finer radial ornament (up to eight costae on each flank and 5–7 in the sulcus). It should be noted that *chauveli* has been considered as a subspecies of *P. crassicostis* (Villas *et al.* 1999) because of the fact that rib thickness in the *Plectothyrella* specimens from the Criadero Quartzite of Spain is intermediate between *crass-*

icostis and *chauveli*. *P.? itacurubiensis* can be easily distinguished from *P. chauveli* by its less numerous costae and massive crural bases. However, the specimens from the Melez Chograne Formation of Lybia, referred to *P. crassicostis chauveli* by Sutcliffe *et al.* (2001, fig. 4), display a coarser ornament like that of *P. libyca*. Internally, the two North African species are quite similar, the differences noted by Havlíček and Massa (1973) in the muscle fields may be attributable to preservation. From the evidence available at present, it is uncertain whether the North African material belongs to a single highly variable species (different from *P. crassicostis*) or involves different taxa. The South African species *P. haughtoni* Cocks and Brunton (*in* Cocks *et al.* 1970), from the Hirnantian Cerdarberg Formation, is very similar to *P.? itacurubiensis* internally but clearly differs in having a much finer ribbing (up to 30 costae counted near the anterior margin). The Mauritanian rhynchonellid *Aratanea monodi* Schmidt, 1967, of Late Ordovician – Early Silurian age, was considered by Bergström (1968) as closely related to *Plectothyrella*, and Havlíček and Massa (1973) conclude that both genera are virtually identical and therefore are synonymous (see also Havlíček 1990). *P. monodi* (Schmidt, 1967) differs from other African species in its weaker ornament, slender crural bases and less impressed muscle fields, and from the Paraguayan species in its finer ribbing.

On balance, the ribbing style of the new Paraguayan material differs from other *Plectothyrella* species having costae that tend to be rounded instead of subangular, although abrasion could account for such a difference. In addition, the costae on the fold are simple while in *Plectothyrella* they bifurcate at valve midlength, and in the sulcus there are commonly 2–4 costae arising by intercalation. As a result, the total number of ribs in other species of *Plectothyrella* is generally greater than in the Paraguayan specimens, although *Plectothyrella* from the Bani Province are characterized by fewer costae. Considering such differences in the rib pattern, along with the more elongate shell, and the crura projected anteroventrally instead of dorsoventrally, the generic attribution of the Paraguayan species must be regarded as provisional.

Order ATHYRIDIDA Boucot, Johnson and Staton, 1964

Superfamily MERISTELLOIDEA Waagen, 1883

Family MERISTELLIDAE Waagen, 1883

Genus HINDELLA Davidson, 1882

Type species. By original designation *Athyris umbonata* Billings, 1862, p.144, from the Ellis Bay Formation, Anticosti Island, Canada (Late Katian).

Hindella cf. *H. crassa* (J. de C. Sowerby, 1839)

Figure 6T–X

Material. One external mould of dorsal valve, two internal moulds of dorsal valve, two internal moulds of ventral valve, CEGH-UNC 24454, 24458, 24460, 24461, 24464c. Upper part of the Eusebio Ayala Formation, San Fernando Quarry.

Description. Subequally biconvex, transversely oval shells, up to 25 mm wide. Faint dorsal fold developed anteriorly. Maximum width at about mid-length of valve. Exterior smooth. Growth lines poorly defined. Ventral interior with long, subparallel, proximally thickened dental plates converging slightly to valve floor. Pedicle chamber short, moderately deep, delimited in front by the posterior end of a deeply impressed muscle field, which expands narrowly forwards. Valve floor of umbonal cavities bears a series of ridges and grooves forming a roughly radial pattern. Dorsal interior with disjunct hinge plates separated by a narrow V-shaped cleft; short crural plates converging towards the median septum forming a septalium. Median septum prominent, extending over 30 per cent valve length. Dental sockets long, deep, excavated beneath distal ends of hinge plates. Dorsal muscle field faintly impressed, narrow, represented by subcircular posterior adductor scars and elongate anterior adductor scars.

Remarks. This species is infrequent in the Eusebio Ayala Formation sample. Fortunately, the Paraguayan specimens include a few exteriors and internal moulds of both valves showing most diagnostic features of the species. For generic attribution, we follow here the conclusion of Rong (1979) that *Cryptothyrella* Cooper, 1942, is a junior synonym of *Hindella* Davidson, 1882. The considerable morphologic variation within topotype material of *Hindella crassa* from Great Britain (Temple 1987) and other Hirnantian and Rhuddanian localities, together with the scarcity of available material from Paraguay, prevent a conclusive assignment to this species.

Class STROPHOMENATA Williams et al., 1996

Order STROPHOMENIDA Öpik, 1934

Superfamily STROPHOMENOIDEA King, 1846

Family LEPTOSTROPHIIDAE Caster, 1939

Genus EOSTROPHEODONTA Bancroft, 1949

Type species. *Orthis hirnantensis* M'Coy, 1851, from Hirnant Beds (Upper Ordovician, Hirnantian), near Bala, North Wales.

Eostropheodonta conradii (Harrington, 1950)

Figure 7

1950 *Australostrophia conradii* Harrington, p. 58, pl. 2, figs 1–5.

non 1961 *Australostrophia conradii* Harrington; Wolfart, p. 62, pl. 2, figs 2–7.

1978 *Aphanomena conradii* (Harrington, 1950); Harper and Boucot, p. 67.

Material. Three external moulds and six internal moulds of ventral valve, and one internal mould of dorsal valve, CEGH-UNC 24435–24441, 24459–24460, from the upper third of the Eusebio Ayala Formation, San Fernando Quarry.

Description. Outline transversely semi elliptical, with greatest width at hinge line, up to 24 mm wide and 20 mm long. Shell profile concave-convex. Gently convex ventral valve with maximum height at about one-quarter valve length. Ventral umbo inconspicuous. Ventral interarea apsacline, planar, low, transversely striated, with delthyrium covered apically by a convex deltidium. Dorsal interarea smaller and anacline. Hinge line lacking denticles. Unequally parvicostellate ornament of fine primary costellae numbering 5 per 5 mm at valve margin in between which are 2–3 parvicostellae. Ventral interior with stout rounded teeth diverging at about 120 degrees, supported by strong, proportionally long dental plates extending anteriorly at right angle. Ventral muscle field large, subtriangular, faintly impressed, bounded posterolaterally by anterior prolongation of dental plates. Cardinal process lobes discrete, directed ventrally, elongate, extending slightly beyond the anterior ends of socket ridges, diverging at about 40 degrees. Dorsal median ridge originating anterior to the cardinal process lobes, initially broad and undifferentiated, narrowing anteriorly. Socket ridges nearly straight, much slender than cardinal process lobes, diverging at about 90 degrees. Dorsal muscle field not impressed.

Remarks. Harper and Boucot (1978), in their revision of the Stropheodontacea, considered *Eostropheodonta* Havlíček (type species *E. hirnantensis* (M'Coy, 1851)) and *Aphanomena* Bergström (type species *A. schmalensei* Bergström, 1968) as separate genera included in separate families (Eostropheodontidae and Leptostrophiidae, respectively), and reassigned *Australostrophia conradii* Harrington, 1950 to the genus *Aphanomena*. According to these authors, the key character for differentiating the two genera is the external ornamentation, fasciculate in *Eostropheodonta* and parvicostellate in *Aphanomena*. Here, we follow Rong and Cocks (1994) in considering *Aphanomena* as a subjective junior synonym of *Eostropheodonta*, based on the fact that ornamentation of *E. hirnantensis* has proved to be highly variable (multicostellate, parvicostellate and fascicostellate) even in specimens of the same population, and internally the cardinalia, articulation and muscle fields are very similar. Following this generic concept, *Eostropheodonta* includes more than 20 species ranging in age from the late Sandbian (if *Hibernodonta* Harper is included in the synonymy) to the early Wenlock, with most species confined to the Hirnantian–Rhuddanian time interval (Rong and Cocks 1994; Cocks and Rong 2000).

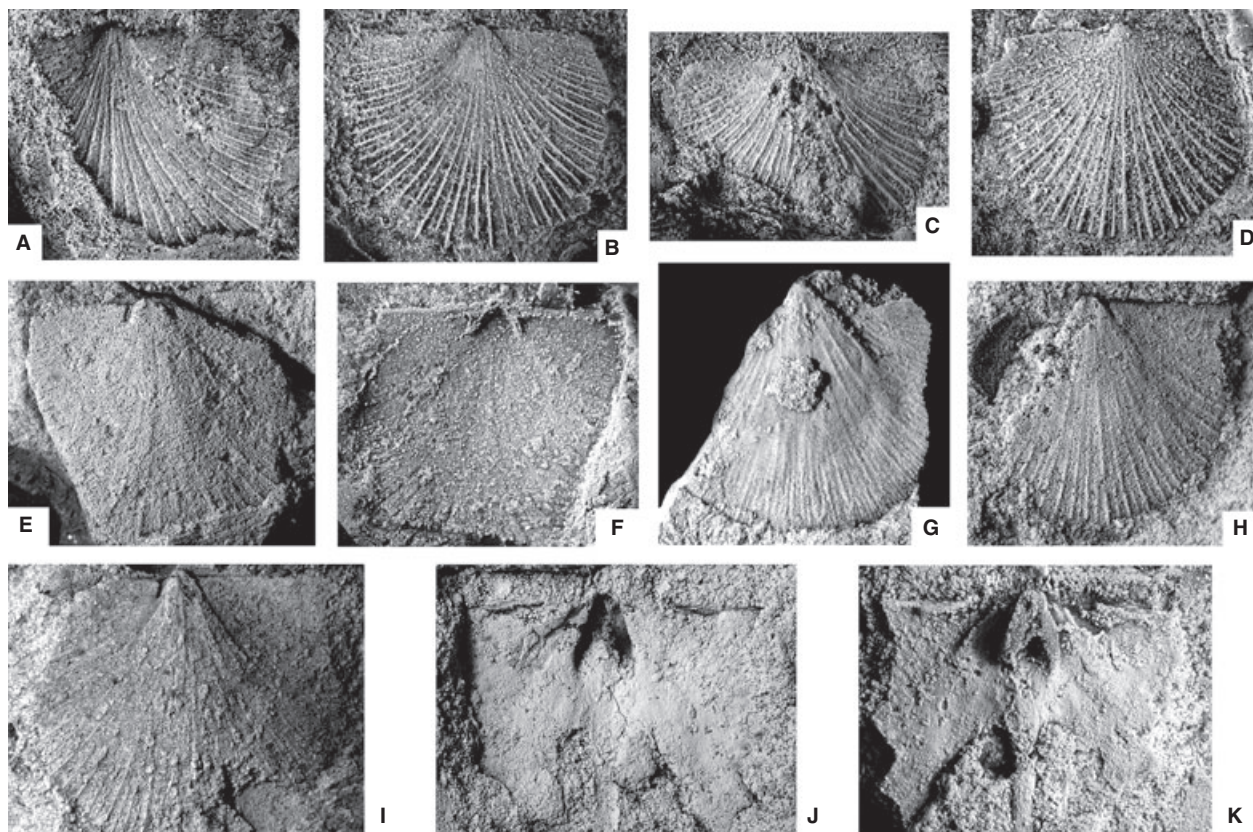


FIG. 7. *Eostropheodonta conradii* (Harrington, 1950). A, CEGH-UNC 24441, ventral valve exterior, latex cast; $\times 2$. B, CEGH-UNC 24439, ventral valve exterior, latex cast; $\times 2$. C, CEGH-UNC 24438, ventral valve exterior, latex cast; $\times 2$. D, CEGH-UNC 24440, ventral valve exterior, latex cast; $\times 2$. E–F, CEGH-UNC 24436, ventral valve internal mould and latex cast; $\times 2$. G, CEGH-UNC 24435, ventral valve internal mould; $\times 2$. H, CEGH-UNC 24437, ventral valve internal mould; $\times 3$. I, CEGH-UNC 24460b, ventral valve internal mould; $\times 1.5$. J–K, CEGH-UNC 24459, dorsal valve internal mould and latex cast; $\times 2.5$.

The Paraguayan species differs externally from *E. hirnantis* in its unequally parvicostellate ornament, which in the type species is rather variable, ranging from equally parvicostellate to fascicostellate with wavering costellae. Moreover, cardinal angles in the type species tend to be mucronate. Internally, *E. conradii* differs in having more prominent and elongate cardinal process lobes, and less diverging socket ridges. In addition, endopuctae in *E. conradii* are faintly marked or absent on internal moulds of both valves. *E. schmalensei* Bergström, from the Hirnantian of Sweden (Bergström 1968), differs from *E. conradii* in its larger size, subequally parvicostellate and considerably finer (3–4 costellae per mm) ornament, shorter and more divergent dental plates, and not discernible ventral muscle field. The cardinalia of *E. schmalensei* closely resemble those of *E. hirnantis*, then differences from the Paraguayan species are the same as noted above for the type species. *E. parvicostellata* Rong, 1984, from the Kuanyinchiao Bed (Hirnantian) of southwest China (Rong 1984) is distinguished from *E. conradii* by its much finer and almost equally parvicostellate ornament. In both

species, divergence of cardinal process lobes and socket ridges are quite similar, though in the Chinese species, the latter are slightly longer and robust than in *E. conradii*. The Moroccan species *E. tafilaltensis* Havlíček and *E. jebiletensis* Havlíček were erected on material lacking well-preserved dorsal interiors (Havlíček 1971) and are in need of revision. *E. tafilaltensis*, from the Upper Ordovician of Morocco, differs from *E. conradii* in having finer and subequally parvicostellate ornament and more divergent ventral muscle bounding ridges and socket ridges. *E. jebiletensis*, from the Hirnantian of central Anti-Atlas (see also Mergl 1983 for specimens referred to *E. cf. jebiletensis*), is very similar to *E. tafilaltensis* and probably both forms are conspecific. In ornament and internal features, the Paraguayan species resembles the material referred by Benedetto (1995) to *E. cf. mullochensis* (Reed), from the lower Llandovery La Chilca Formation of the Argentine Precordillera. The Argentine species can be differentiated in being smaller and more transverse in outline, in its higher notothyrial platform and its somewhat longer socket ridges. The species *E. chilcaensis*, from

slightly younger beds of the La Chilca Formation, clearly differs from *E. conradii* in its more uniform ornament and in the subequal size of cardinal process lobes and socket ridges. The material from the nearly coeval El Horno Formation of Venezuela (Boucot *et al.* 1972) described as *E. cf. mullochensis* closely compares with *E. conradii* in ornament pattern and ventral valve internal features, but differs in having slender cardinal process lobes and much longer socket ridges.

Wolfart (1961) referred to *E. conradii* some fairly well-preserved exteriors and interiors of a mucronate strophomenid from the uppermost part of the Itacurubi Group (Cariy Formation) of Paraguay. From the Wolfart's illustrations (pl. 2, figs 2–7), it is doubtful whether this form is related to the species described by Harrington. The material described by Wolfart has a finer ornament and uniform costellae, the shell is mucronate, the hinge line seems to be partially denticulate, the cardinal process lobes are prolonged anteriorly by a strong median ridge, and the dorsal muscle field is bounded laterally by strong ridges.

Acknowledgements. This work was supported by grants to J. L. B. from the Argentine Council of Research (CONICET, PIP 5599). We would like to thank M. Alfaro (Museo de La Plata) for providing some brachiopod specimens and stratigraphic data for this study, and to D. Balseiro (CICTERRA) for his help in the multivariate analysis. We are greatly indebted to Robin Cocks, Jisuo Jin, and David Harper for valuable comments on the manuscript, which substantially improved this work.

Editor. Fernando Alvarez

REFERENCES

- ALFARO, M. B., URIZ, N. J., CINGOLANI, C. A., BIDONE, A. R. and GALEANO INCHAUSTI, J. C. 2010. Hallazgo de la Biozona de *Persculptograptus persculptus* en la Formación Eusebio Ayala (Ordovícico Superior?–Llandovery), Paraguay oriental. *Actas Décimo Congreso Argentino de Paleontología y Bioestratigrafía y Séptimo Congreso Latinoamericano de Paleontología*, p. 41.
- — — TORTELLO, M. F., BIDONE, A. R. and GALEANO INCHAUSTI, J. C. 2012. Graptolites and trilobites from the Eusebio Ayala Formation (Hirnantian?–early Llandovery), Paraná Basin, eastern Paraguay. *Geological Journal*, doi:10.1002/gj.2448.
- ALVAREZ, F. and RONG, J. Y. 2002. Order Athyridida. 1475–1583. In KAESLER, R. L. (ed). *Treatise on invertebrate paleontology. Part H, Brachiopoda 4 (revised)*. Geological Society of America, Boulder, Colorado and University of Kansas Press, Lawrence, Kansas, 767 pp.
- ASTINI, R. A. 1999. The Late Ordovician glaciation in the Proto-Andean margin of Gondwana revisited: geodynamic implications. In KRAFT, P. and FATKA, O. (eds). *Quo vadis Ordovician? Acta Universitatis Carolinae, Geologica*, **43**, 171–174.
- and BENEDETTO, J. L. 1992. El Ashgilliano tardío (Hirnantiano) del Cerro La Chilca, Precordillera de San Juan. *Ameghiniana*, **29**, 249–264.
- BABCOCK, L. E., GRAY, J., BOUCOT, A. J., HIMES, G. T. and SIEGELE, P. K. 1990. First Silurian conularids from Paraguay. *Journal of Paleontology*, **64**, 897–902.
- BALDIS, B. A. and HANSEN, H. 1980. Trilobites dalmaníticos de Paraguay Oriental. *Actas Segundo Congreso Argentino de Paleontología y Bioestratigrafía y Primer Congreso Latinoamericano de Paleontología*, **1**, 49–67.
- BANCROFT, B. B. 1949. Welsh Valentian brachiopods and the *Strophomena antiquata* group of fossils brachiopods. 2–16. In LAMONT, A. (ed.). Privately printed, Mexnorough, 16 pp.
- BEDER, R. and WINDHAUSEN, A. 1918. Sobre la presencia del Devónico en la parte media de la República del Paraguay. *Boletín de la Academia Nacional de Ciencias de Córdoba*, **33**, 255–262.
- BENEDETTO, J. L. 1986. The first typical *Hirnantia* Fauna from South America (San Juan Province, Argentine Precordillera). 439–477. In RACHEBOEUF, P. R. and EMIG, D. (eds). *Les Brachiopodes fossiles et actuels*. Biostratigraphie du Paléozoïque, **4**, 500 pp.
- 1990. Los géneros *Cliftonia* y *Paromalomena* (Brachiopoda) en el Ashgilliano tardío de la Sierra de Villicum, Precordillera de San Juan. *Ameghiniana*, **27**, 151–159.
- 1991. Braquiópodos silúricos de la Formación Lipeón, flanco occidental de la Sierra de Zapla, Provincia de Jujuy, Argentina. *Ameghiniana*, **28**, 111–125.
- 1995. Braquiópodos del Silúrico temprano Malvinocáfrico (Formación La Chilca), Precordillera Argentina. *Geobios*, **28**, 425–457.
- 2002. The rhynchonellid brachiopod *Eocoelia* in the Llandovery of Paraguay, Paraná basin. *Ameghiniana*, **39**, 307–312.
- and COCKS, L. R. M. 2009. Early Silurian (Rhuddanian) brachiopods from the Argentine Precordillera and their biogeographic affinities. *Ameghiniana*, **46**, 241–253.
- and SÁNCHEZ, T. M. 1990. Fauna y edad del estratotipo de la Formación Salar del Rincón (Eopaleozoico, Puna Argentina). *Ameghiniana*, **27**, 317–326.
- — 1996. The 'Afro-South American Realm' and Silurian 'Clarkeia Fauna'. 29–33. In COPPER, P. and JISUO, J. I. N. (eds). *Brachiopods*. A. A. Balkema, Rotterdam, 373 pp.
- — and BRUSSA, E. D. 1992. Las cuencas Silúricas de América Latina. 119–148. In GUTIÉRREZ-MARCO, J. C., SAAVEDRA, J. and RÁBANO, I. (eds). *Paleozoico Inferior de Ibero-América*. Universidad de Extremadura, Cáceres, 630 pp.
- BERGSTRÖM, J. 1968. Upper Ordovician brachiopods from Västergötland, Sweden. *Geologica et Palaeontologica*, **2**, 1–35.
- BILLINGS, E. 1862. New species of fossils from different parts of the Lower, Middle and Upper Silurian rocks of Canada. *Geological Survey of Canada, Palaeozoic fossils*, **1**, 96–168.
- BOUCOT, A. J., JOHNSON, J. G. and STATON, R. D. 1964. On some atrypoid, retzioid, and athyroid Brachiopoda. *Journal of Paleontology*, **38**, 805–822.

- and SHAGAM, R. 1972. Braquiópodos del Silúrico de los Andes Merideños de Venezuela. Memorias IV Congreso Geológico Venezolano, Tome 2. *Boletín de Geología, Ministerio de Minas e Hidrocarburos Publicación Especial*, 5, 585–727.
- GONÇALVES DE MELO, J. H., SANTOS NETO, E. V. and WOLFF, S. 1991. First *Clarkeia* and *Heterorthella* (Brachiopoda; Lower Silurian) occurrence from the Paraná Basin in eastern Paraguay. *Journal of Paleontology*, 65, 512–514.
- BRUSSA, E. D., TORO, B. A. and BENEDETTO, J. L. 2003. Biostratigraphy. 75–90. In BENEDETTO, J. L. (ed.). *Ordovician fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba, 560 pp.
- CAPUTO, M. V. and CROWELL, J. C. 1985. Migration of glacial centers across Gondwana during Paleozoic Era. *Geological Society of America Bulletin*, 96, 1020–1036.
- CASTER, K. E. 1939. A Devonian fauna from Colombia. *Bulletin of American Paleontology*, 24, 1–218.
- CINGOLANI, C. A., URIZ, N. J., ALFARO, M. B., TORTELLO, F., BIDONE, A. R. and GALEANO INCHAUSTI, J. C. 2011. The Hirnantian–early Llandovery transition sequence in the Paraná Basin, eastern Paraguay. 103–108. In GUTIÉRREZ-MARCO, J. C., RÁBANO, I. and GARCÍA-BELLIDO, D. (eds). *Ordovician of the World*. Cuadernos del Museo Geominero, 14, 679 pp.
- CLARKE, J. M. 1899. A fauna Siluriana superior do Rio Trombetas, Estado do Pará, Brazil. *Archivos Museo Nacional do Rio do Janeiro*, 10, 1–174.
- COCKS, L. R. M. 1972. The origin of Silurian *Clarkeia* shelly fauna of South America, and its extension to west Africa. *Palaentology*, 15, 623–630.
- and FORTEY, R. A. 1986. New evidence on the South African Lower Palaeozoic: age and fossils reviewed. *Geological Magazine*, 123, 437–444.
- and RONG, J. Y. 2000. Order Strophomenida. 216–349. In KAESLER, R. L. (ed.). *Treatise on invertebrate paleontology. Part H, Brachiopoda 2 (revised)*. Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas, 423 pp.
- and TORSVIK, T. H. 2006. European geography in a global context from the Vendian to the end of the Palaeozoic. In GEE, D. G. and STEPHENSON, R. A. (eds). *European Lithosphere Dynamics. Memoirs of the Geological Society, London*, 32, 83–95.
- BRUNTON, C. H. C., ROWELL, A. J. and RUST, J. C. 1970. The first Lower Palaeozoic fauna proved from South Africa. *Quarterly Journal of the Geological Society of London*, 125, 589–603.
- COOPER, G. A. 1942. New genera of North American brachiopods. *Journal of the Washington Academy of Science*, 32, 228–235.
- DALMAN, J. W. 1928. *Upställning och Beskrifning af de i Sverige funne Terebratuliter. Kongliga Svenska Vetenskapsakademiens Handlingar för 1827*, 85–155.
- DAVIDSON, T. 1882. A monograph of the British fossil Brachiopoda, Devonian and Silurian Supplements. *Palaeontographical Society, Monographs (London)*, 5, 1–134.
- DEGRAFF, J. M., FRANCO, F. and ORUÉ, D. 1981. Interpretación geofísica y geológica del valle de Ypacaraí (Paraguay) y su formación. *Revista de la Asociación Geológica Argentina*, 36, 240–256.
- DELABROYE, A. and VECOLI, M. 2010. The end-Ordovician glaciation and the Hirnantian Stage: a global review and questions about Late Ordovician event stratigraphy. *Earth-Science Reviews*, 98, 269–282.
- DESTOMBES, J., HOLLARD, H. and WILLEFERT, S. 1985. Lower Palaeozoic rocks of Morocco. In HOLLAND, C. H. (ed.). *Lower Palaeozoic of North-western and West Central Africa*, 91, 91–336.
- DÍAZ-MARTÍNEZ, E. and GRAHN, C. Y. 2007. Early Silurian glaciation along the western margin of Gondwana (Perú, Bolivia and northern Argentina). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 245, 62–81.
- FATKA, O. and MERGL, M. 2009. The ‘microcontinent’ Perunica: status and store 15 years after conception. 65–101. In BASSETT, M. G. (ed.). *Early Palaeozoic Peri-Gondwanan terranes: new insights from tectonics and biogeography*, Vol. 325. Geological Society, London, Special Publications, London, 287 pp.
- FIGUEREDO, L. 1995. Descripción geológica del pozo RD 116 Santa Elena-Paraguay. In GONZÁLEZ NÚÑEZ, M., LAHNER, L., CUBAS, N. and ADELAIDA, D. *Mapa Geológico de la República del Paraguay, Hoja Coronel Oviedo 5670 1:100.000*. Cooperación Técnica BGR-MOPC, Asunción, 30 pp.
- GALEANO INCHAUSTI, J. C. and POIRÉ, D. G. 1999. Trazas fósiles de la Formación Caríy (Silúrico), Itacurubí, Paraguay. *Actas Decimocuarto Congreso Geológico Argentino*, 1, 359–362.
- GODOY CIGUEL, J. H. 1988. *Tentaculites itacurubiensis* n. sp. dos depósitos regressivos do Paraguai Oriental, Siluriano Inferior da Bacia do Paraná. *Revista Brasileira de Geociencias*, 18, 88–92.
- RÖSLER, O. and CLÉRICE, A. M. 1987. *Skolithos verticalis* e *Skolithos ayalis* nov. sp. da Formação Eusebio Ayala (Grupo Itacurubí, borda Ocidental da Bacia do Paraná no Paraguai) e sua importância no ambiente deposicional. *Revista Brasileira de Geociencias*, 18, 253–269.
- GONÇALVES DE MELO, J. H. and BOUCOT, A. J. 1990. *Harringtonina* is *Anabaia* (Brachiopoda, Silurian, Malvinokaffric Realm). *Journal of Paleontology*, 64, 363–366.
- GRAHN, Y. and CAPUTO, M. V. 1992. Early Silurian glaciations in Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 99, 9–15.
- and GUTIERREZ, P. R. 2001. Silurian and Middle Devonian Chitinozoa from the Zapla and Santa Bárbara ranges, Tarija Basin, Northwestern Argentina. *Ameghiniana*, 38, 35–50.
- PEREYRA, F. and BERGAMASCHI, S. 2000. Silurian and Lower Devonian Chitinozoan biostratigraphy of the Paraná Basin in Brazil and Paraguay. *Palaentology*, 24, 147–176.
- GRAY, J., COLBATH, G. K., FARIA, A., BOUCOT, A. J. and ROHR, D. M. 1985. Silurian age fossils from the Paleozoic Paraná Basin, southern Brazil. *Geology*, 13, 521–525.

- BOUCOT, A. J., GRAHN, Y. and HIMES, G. 1992. A new record of early Silurian land plant spores from the Paraná Basin, Paraguay (Malvinokaffric Realm). *Geological Magazine*, **129**, 741–752.
- HARPER, C. W. and BOUCOT, A. J. 1978. The Stropheodontacea, part I: Leptostrophiidae, Eostropheodontidae and Strophonellidae. *Palaeontographica, Series A*, **161**, 55–118.
- — — and WALMSLEY, V. G. 1969. The rhipidomellid brachiopod subfamilies Heterorthinae and Platyorthinae (new). *Journal of Paleontology*, **43**, 74–92.
- HARPER, D. A. T. 2000. Suborder Dalmanellidina. 782–844. In KAESLER, R. L. (ed.). *Treatise on invertebrate paleontology, Part H, Brachiopoda. 3 (revised)*. Geological Society of America, Boulder, Colorado and University of Kansas Press, Lawrence, Kansas, 485 pp.
- HARRINGTON, H. J. 1950. Geología del Paraguay Oriental. *Facultad de Ciencias Exactas, Contribuciones Científicas, Sección E (Geología)*, **1**, 1–82.
- 1972. Silurian of Paraguay. 41–50. In BERRY, W. B. N. and BOUCOT, A. J. (eds). *Correlation of South American Silurian rocks*, Vol. 133. Geological Society of America Special Papers, Boulder, 59 pp.
- HAVLÍČEK, V. 1970. Heterorthidae (Brachiopoda) in the Mediterranean Province. *Sbornik Geologických Věd, Paleontologie*, **12**, 7–39.
- 1971. Brachiopodes de l'Ordovicien du Maroc. *Notes et Memoires du Service Géologique du Maroc*, **230**, 1–130.
- 1977. Brachiopods of the Order Orthida in Czechoslovakia. *Rozprawy Ustředního ústavu geologického*, **44**, 1–327.
- 1990. Mediterranean and Malvinokaffric Provinces: new data on the Upper Ordovician and Lower Silurian brachiopods. *Casopis pro Mineralogii a Geologii*, **35**, 1–14.
- and MASSA, D. 1973. Brachiopodes de l'Ordovicien Supérieur de Libye occidentale. Implications stratigraphiques régionales. *Geobios*, **6**, 267–290.
- ISAACSON, P. E., ANTELO, B. and BOUCOT, A. J. 1976. Implications of a Llandovery (Early Silurian) brachiopod fauna from Salta Province, Argentina. *Journal of Paleontology*, **50**, 1103–1112.
- JABLONSKI, D., ROY, K. and VALENTINE, J. W. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.
- KING, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Annals and Magazine of Natural History, Series 1*, **18**, 26–42, 83–94.
- KUHN, O. 1949. *Lehrbuch der Paläozoologie*. E. Schweizerbart, Stuttgart, 326 pp.
- LEVY, R. and NULLO, F. 1974. La fauna del Ordovícico (Ashgilliano) de Villicun, San Juan, Argentina (Brachiopoda). *Ameghiniana*, **9**, 173–200.
- M'COY, F. 1851. On some new Cambro-Silurian fossils. *Annals and Magazine of Natural History (Series 2)*, **8**, 387–409.
- MERGL, M. 1983. New brachiopods (Cambrian-Ordovician) from Algeria and Morocco (Mediterranean Province). *Casopis pro Mineralogii a Geologii*, **28**, 337–348.
- MILANI, E. J., GONÇALVES DE MELO, J. H., DE SOUZA, P., FERNÁNDEZ, L. A. and BARROS FRANÇA, A. 2007. Bacia do Paraná. *Boletim de Geociências Petrobras*, **15**, 265–287.
- MOORE, R. C. 1952. Brachiopods. 197–267. In MOORE, R. C., LALICKER, C. G. and FISHER, A. G. (eds). *Invertebrate fossils*. McGraw-Hill, New York, 766 pp.
- NIEMEYER, H., ALVAREZ, F., BOUCOT, A. J. and BRUNA, M. 2010. Brachiopods from Cordón de Lila, Lower Silurian (Llandovery) Quebrada Ancha Formation, Antofagasta region, Chile. 287–307. In ALVAREZ, F. and CURRY, G. (eds). Evolution and development of brachiopod shell, *Special Papers in Palaeontology*, **48**, 287–307.
- ÖPIK, A. A. 1934. Über Klitamboniten. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis), (Series A)*, **26**, 1–239.
- ORBIGNY, A. d'. 1847. Considérations zoologiques et géologiques sur les Brachiopodes ou Palliobranches. *Comptes Rendues Hebdomadaires des Séances de l'Academie des Sciences*, **25**, 193–195, 266–269.
- OWEN, A. W., HARPER, D. A. T. and RONG, J. Y. 1991. Hirnantian trilobites and brachiopods in space and time. 179–190. In BARNES, C. R. and WILLIAMS, S. H. (eds). *Ordovician Geology*, Vol. 90–9. Geological Survey of Canada, Ottawa, 335 pp.
- PERALTA, S. H. and CARTER, C. 1990. La glaciación Gondwánica del Ordovícico tardío: Evidencias en fangolitas guijarrosas de la Precordillera de San Juan, Argentina. *Actas 11º Congreso Geológico Argentino*, **2**, 181–185.
- POIRÉ, D. G., SPALLETI, L. A. and DEL VALLE, A. 2003. The Cambrian-Ordovician siliciclastic platform of the Balcarce Formation (Tandilla System, Argentina): facies, trace fossils, paleoenvironments, and sequence stratigraphy. *Geologica Acta*, **1**, 41–60.
- POTHE DE BALDIS, E. D. 1997. Acritarcas del Llandoveryano temprano-medio de la Formación Don Braulio, Precordillera Oriental, Provincia de San Juan, Argentina. *Revista Española de Micropaleontología*, **29**, 31–68.
- POWELL, M. G. 2009. The latitudinal diversity gradient of brachiopods over the past 530 million years. *Journal of Geology*, **117**, 585–594.
- RACHEBOEUF, P. R. and VILLENEUVE, M. 1992. Une faune Malvino-Cafre de brachiopodes Siluriens du Bassin Bové (Guinée, Ouest de l'Afrique). *Geologica et Palaeontologica*, **26**, 1–11.
- RAPELA, C. W., PANKHURST, R. J., CASQUET, C., FANNING, C. M., BALDO, E. G., GONZÁLEZ-CASADO, J. M., GALINDO, C. and DAHLQUIST, J. 2007. The Río de la Plata craton and the assembly of SW Gondwana. *Earth-Science Reviews*, **83**, 49–82.
- RONG, J. Y. 1979. The Hirnantia fauna of China with comments on the Ordovician-Silurian boundary. *Journal of Stratigraphy*, **3**, 1–29. [in Chinese].
- 1984. Brachiopods of latest Ordovician in the Yichang District, western Hubei, central China. 111–176. In ACADEMIA SINICA (ed.). *Stratigraphy and palaeontology of systemic boundaries in China, Ordovician-Silurian boundary*, Vol. 1. Nanjing Institute of Geology and Palaeontology, Nanjing, 516 pp.

- and COCKS, L. R. M. 1994. True *Strophomena* and a revision of the classification and evolution of strophomenoid and 'stropheodontoid' brachiopods. *Palaeontology*, **37**, 651–694.
- and HARPER, D. A. T. 1988. A global synthesis of the latest Ordovician Hirnantian brachiopod faunas. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **79**, 383–402.
- and LI, R. Y. 1999. A silicified *Hirnantia* fauna (latest Ordovician brachiopods) from Guizhou, southwest China. *Journal of Paleontology*, **73**, 831–849.
- CHEN, X. and HARPER, D. A. T. 2002. The latest Ordovician *Hirnantia* Fauna (Brachiopoda) in time and space. *Lethaia*, **35**, 231–249.
- RUBINSTEIN, C. V. and VACCARI, N. E. 2004. Cryptospore assemblages from the Ordovician/Silurian boundary in the Puna region, North-West Argentina. *Palaeontology*, **47**, 1037–1061.
- SÁNCHEZ, T. M., BENEDETTO, J. L. and BRUSSA, E. D. 1991. Late Ordovician stratigraphy, paleoecology, and sea level changes in the Argentine Precordillera. 245–258. In BARNES, C. R. and WILLIAMS, H. (eds). *Advances in Ordovician Geology*. Geological Survey of Canada, Ottawa, Paper **90–9**, 336 pp.
- SAVAGE, N. M. 2002. Superfamily Rhynchotrematoidea. 1041–1046. In KAESSLER, R. L. (ed.). *Treatise on invertebrate paleontology. Part H, Brachiopoda 4 (revised)*. Geological Society of America, Boulder, Colorado and University of Kansas Press, Lawrence, Kansas, 767 pp.
- SCHMIDT, H. 1967. *Aratanea monodi* n. gen., n. sp. (Brachiopoda; W-Sahara). *Senckenberg Lethaea*, **48**, 91–97.
- SCHUCHERT, C. 1913. Class Brachiopoda. 355–420. In VON ZITTEL, K. A. (ed.). *Text-book of Palaeontology*, Vol. 1, part 1 and 2. MacMillan & Co., London, 1056 pp.
- and COOPER, G. A. 1931. Synopsis of the brachiopod genera of the suborders Orthoidea and Pentameroidea, with notes on the Telotremata. *American Journal of Science*, **22**, 241–255.
- — 1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. *Memoirs of the Peabody Museum of Natural History*, **4**, 270 pp.
- SHONE, R. W. and BOOTH, P. W. K. 2005. The Cape Basin, South Africa: a review. *Journal of African Earth Sciences*, **43**, 196–210.
- SOWERBY, J. D. E. C. 1839. Shells. 579–712. In MURCHISON, R. I. *The Silurian system, part 2, organic remains*. Murray and Sons, London, 768 pp.
- SUTCLIFFE, O. E., HARPER, D. A. T., ABDALLAH, A. S., WHITTINGTON, R. J. and CRAIG, J. 2001. The development of an atypical *Hirnantia* brachiopod fauna and the onset of glaciations in the Late Ordovician of Gondwana. *Transactions of the Royal Society of Edinburgh, Earth and Environmental Sciences*, **92**, 1–14.
- TEMPLE, J. T. 1965. Upper Ordovician brachiopods from Poland and Britain. *Acta Palaeontologica Polonica*, **10**, 379–450.
- 1987. Early Llandovery brachiopods of Wales. *Monograph of the Palaeontological Society*, **139**, 137 pp.
- TORTELLO, M. F., CLARKSON, E. N. K., URIZ, N. J., ALFARO, M. B. and GALEANO INCHAUSTI, J. C. 2008. Trilobites from the Vargas Peña Formation (Llandovery) of Itauguá, eastern Paraguay. 395–401. In RÁBANO, I., GONZALO, R. and GARCÍA BELLIDO, D. (eds). *Advances in trilobite research*. Cuadernos del Museo Geominero, **9**, 448 pp.
- TURNER, J. C. M. 1959. Faunas graptolíticas de América del Sur. *Revista de la Asociación Geológica Argentina*, **14**, 1–180.
- UNDERWOOD, C. J., DEYNOUX, M. and GHIENNE, J.-F. 1998. High palaeolatitude (Hodh, Mauritania) recovery of graptolite faunas after the Hirnantian (end Ordovician) extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **142**, 91–105.
- URIZ, N. J., ALFARO, M. B. and GALEANO INCHAUSTI, J. C. 2008. Silurian (Llandovery) monograptids from the Vargas Peña Formation (Paraná Basin, Eastern Paraguay). *Geologica Acta*, **6**, 181–190.
- VAN STADEN, A., ZIMMERMANN, U., CHEMALE, F., GUTZMER, J. and GERMS, G. J. B. 2010. Correlation of Ordovician diamictites from Argentina and South Africa using detrital zircon dating. *Journal of the Geological Society, London*, **167**, 217–220.
- VILLAS, E., LORENZO, S. and GUTIÉRREZ-MARCO, J. C. 1999. First record of a *Hirnantia* Fauna from Spain, and its contribution to the Late Ordovician palaeogeography of Northern Gondwana. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **89**, 187–197.
- VIZCAÍNO, D., ÁLVARO, J. J., DESTOMBES, J. and VENNIN, E. 2006. Biostratigraphic control of the latest Ordovician glaciogenic unconformity in Alnif (Eastern Anti-Atlas, Morocco), based on brachiopods. *Geobios*, **39**, 727–737.
- VILLENEUVE, M. 2005. Paleozoic basins in West Africa and the Mauritanide thrust belt. *Journal of African Earth Sciences*, **43**, 166–195.
- and DA ROCHA ARAUJO, P. R. 1984. Lithostratigraphie du bassin Paléozoïque de Guinée (Afrique de l'Ouest). *Bulletin de la Société Géologique de France*, **7**, 1033–2039.
- WAAGEN, W. 1883. Salt Range fossils. Volume 1, part 4. Productus Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica (Series 13)*, **3–4**, 547–728.
- WILLIAMS, A., CARLSON, S. J., BRUNTON, C. H. C., HOLMER, L. E. and POPOV, L. E. 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London (Series B)*, **351**, 1171–1193.
- WOLFART, R. 1961. Stratigraphie und Fauna des alteren Paläozoikums (Silur, Devon) in Paraguay. *Geologische Jahrbuch*, **78**, 29–102.
- WOOD, G. D. and MILLER, M. A. 1991. Distinctive Silurian chitinozoans from the Itacurubi Group (Vargas Peña Shale), Chaco Basin, Paraguay. *Palynology*, **15**, 181–192.
- ZIMMERMANN, U. and SPALLETTI, L. A. 2009. Provenance of the Lower Paleozoic Balcarce Formation (Tandilia System, Buenos Aires Province, Argentina): implications for paleogeographic reconstructions. *Sedimentary Geology*, **219**, 7–23.