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Orthid brachiopods from the Middle Ordovician of the Central Iberian Zone, Spain

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The present study of a large collection of orthid brachiopods from Middle Ordovician (middle Darriwilian) strata of Spanish regions of the Central Iberian Zone of the Iberian Massif, as well as the type collection of Portuguese species from the same Zone, revealed the occurrence of five genera of the family Orthidae, two of them new, and to which most of the seven previously reported species of *Orthis* from the same areas can be assigned. Besides the two new genera and species *Almadenorthis auriculata* Reyes-Abril and Villas gen. et sp. nov., and *Gutiorthis incurvata* Reyes-Abril and Villas gen. et sp. nov., three further new species are erected: *Paralenorthis estenaensis* Reyes-Abril and Villas sp. nov., *Paralenorthis lolae* Reyes-Abril and Villas sp. nov., and *Sivorthis calatravaensis* Reyes-Abril and Villas sp. nov. *Paralenorthis alata* and *Orthambonites* sp. are also identified in the same beds. *Orthis noctilio* is ascribed to the genus *Sivorthis,* and the species *Orthis lusitanica* and *Orthis miniensis* are restricted to only their type specimens. *Orthis duriensis* is poorly described and illustrated, its type material missing, and actually it may belong to *Sivorthis noctilio*. These brachiopod taxa invaded the cold waters of the Afro-South European Gondwanan margin from lower latitudes, coincident with the mid Darriwilian transgression, as they belonged to a family that diversified in temperate and tropical seas during the early Mid Ordovician.

Key words: Brachiopoda, palaeobiogeography, Ordovician, Darriwilian, Mediterranean, Gondwana.

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Introduction

Ordovician brachiopods have been known from the Iberian Massif since the works of Sharpe (1849; in Ribeiro et al. 1853) and Verneuil and Barrande (1855). These authors provided the earliest records and descriptions of several species of the genera *Orthis*, *Porambonites*, and *Leptaena*, occurring in various localities across the Portuguese and Spanish regions of the Central Iberian Zone (Fig. 1). Among the representatives of *Orthis* from Middle Ordovician strata, these pioneering works established six new Iberian species (*O. noctilio*, *O. miniensis*, *O. duriensis*, *O. lusitanica*, *O. ribeiroi*, and *O. bussacensis*; Sharpe 1849; Sharpe in Ribeiro et al. 1853). Verneuil and Barrande (1855) recognised one British (*O. vespertilio* Sowerby in Murchison, 1839) and one Baltic form (*O. calligramma* Dalman, 1828), later transferred respectively to *Harknessella* (Reed, 1917) and *Orthambonites* (Rubel, 1961). In the following 150 years, there have been only four taxonomic reviews of these species: Born (1918: *O. ribeiroi*, *O. calligramma*, *O. calligramma alata*); Mitchell (1974: *Cacemia ribeiroi*); Thadeu (1956: *O.* cf. *calligramma*, *Harknessella* cf. *vespertilio*, *Harknesella*? cf. *noctilio*); and Mélou (1976: *Cacemia ribeiroi*). Nevertheless, a few studies of other Middle Ordovician brachiopod faunas from Ibero-Armorica (Drot in Chauvel et al. 1969; Mélou 1973, 1975, 1976; Mitchell 1974; Havlíček in Arbin et al. 1978; Villas 1985) have been undertaken. Several brachiopod biozones based on the vertical distribution of some of the first-mentioned species were defined within the Middle Ordovician shales of Iberia, such as the *O. ribeiroi* and *O. noctilio* biozones of Delgado (1897, 1908) and the *O. ribeiroi* and *O. calligramma* biozones of Born (1918). All of these were redefined by Gutiérrez-Marco et al. (1984, 2002), assigning the "*O.*" *noctilio* Biozone to lower Oretanian strata, *Cacemia ribeiroi* Biozone to upper Oretanian strata, plus some other brachiopod biozones spanning the lower and upper Dobrotivian (chronostratigraphy according to the regional Mediterranean scheme; see Gutiérrez-Marco et al. 2002 and discussion below).

In the present work we analyse the Middle Ordovician representatives of the family Orthidae in the southern part of the Central Iberian Zone, which was largely ignored since the 19th century. It adds unexpected new data on the Ordovician

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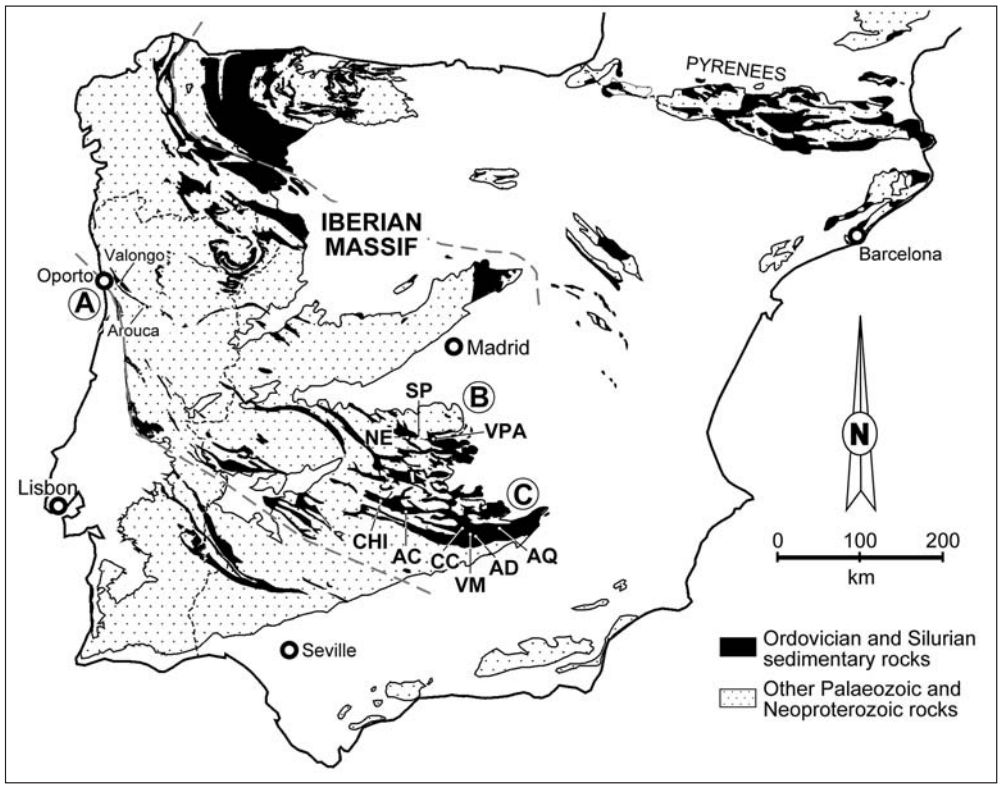

Fig. 1. Map of the main Ordovician–Silurian outcrops of Iberian Massif, with locations of the studied fossiliferous localities, including the Portuguese localities of Valongo and Arouca. Abbreviations: AC, Almodóvar del Campo; AD, Almuradiel; AQ, Aldeaquemada; CC, Calzada de Calatrava; CHI, Chillón; NE, Navas de Estena; SP, San Pablo de Los Montes; VM, Viso del Marqués; VPA, Ventas con Peña Aguilera. A, B, C are the representative areas of lithostratigraphic sections detailed in Fig. 2.

brachiopod biodiversity and palaeobiogeography of SW Europe, in part predicted by Reyes-Abril et al. (2006, 2008).

Institutional abbreviations.—MGM, Museo Geominero of Madrid, Spain (numbers MGM-5940-O to MGM-6328-O). NHM, Natural History Museum of London, UK (numbers NHM 82896 and NHM 82897, NHM 82902, NHM 82904, NHM 82907 and NHM 82908).

Other abbreviations.—m, mean; n, number; v, variance.

Geographical and geological setting

The studied material comprises several thousands of brachiopod specimens from tens of localities on the southern part of the Central Iberian Zone of the Iberian Massif. This large collection incorporates the original material of Gutiérrez-Marco et al. (1984), herein complemented by new sampling in some of the localities selected for this study.

The examined sections are located towards the middle part of the Ordovician succession overlying the ubiquitous Armorican Quartzite (Lower Ordovician, essentially Floian in age). The Middle Ordovician rocks are composed predominantly of dark shales and siltstones with more or less important sandstone intercalations, known as the "*Tristani* Beds" or "*Neseuretus* Shales and Sandstones" (Hammann et al. 1982; Gutiérrez-Marco et al. 2002), which ends in an upper succession (Sandbian to Hirnantian) of alternating shale, siltstone, and sandstone beds capped by limestone and glaciomarine diamictite beds. The studied brachiopods are from beds of mid Darriwilian age, in three partially correlative formations: the Navas de Estena, Río and Valongo formations (Fig. 2) cropping out in the core of the Los Yébenes, Navas de Estena and Almadén-Puertollano synclines, as well as in the eastern Sierra Morena and the Portuguese Valongo-Arouca areas (Fig. 1). The faunas are always preserved as internal and external moulds in shales and siliceous nodules (rarely as haematite casts). They are associated with a rich benthic fauna of trilobites, molluscs, echinoderms, ostracods, and other brachiopods (cremnorthids, linoporellids, strophomenids, and linguliforms,), as well as graptolites of the *Didymograptus artus* Biozone. The common record from these beds of several forms broadly known as "orthids of coarse ribs" (Tamain 1971), including *Orthis noctilio*, places all the studied localities within the "*Orthis*" *noctilio* Biozone of Gutiérrez-Marco et al. (1984, 2002). This implies a placement within the lower Oretanian Stage of the Mediterranean scheme, also equivalent to the basal Llanvirn (lower Abereiddian) of the revised British regional scale and to the middle Darriwilian in terms of the global Ordovician chrono-

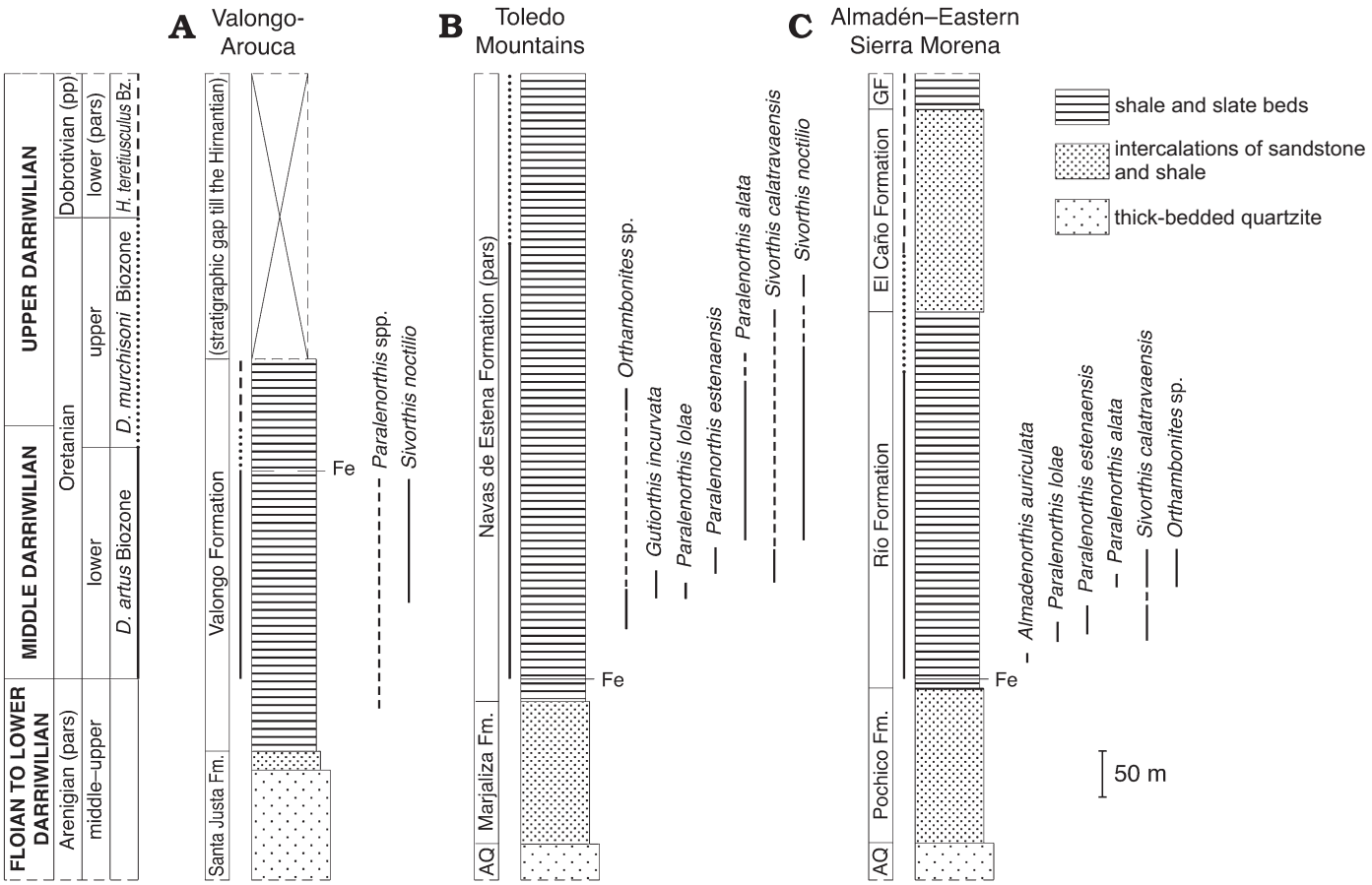

Fig. 2. Generalised stratigraphical columns of the Middle Ordovician rocks in the southern Central Iberian Zone, representatives of the three main areas (**A**–**C**) represented on Fig. 1, to show the vertical distribution of the studied brachiopod taxa. The left-hand column indicates the equivalence between the global chronostratigraphy and the north-Gondwanan regional scheme. Abbreviations: AQ, Armorican Quartzite; GF, Guindo Formation; Fe, thin oolithic ironstone bed. Note that the stratigraphic range of the graptolite biozones are directly annotated on the left side of each column.

stratigraphy (see Gutiérrez-Marco et al. 2002 and Bergström et al. 2009).

The orthid brachiopods from the Los Yébenes and Navas de Estena synclines occur in the lower half of the Navas de Estena Formation in the Acebrón stream section, 10 km south of Ventas con Pena Aguilera, Toledo Province (locality VPA in Fig. 1: lat 39°31’12’’N, long 4°11’33’’W; Greenwich Meridian); El Riscal, 3.7 km south of San Pablo de los Montes, Toledo Province (locality SP-II in Fig. 1: lat 39°30’33’’N, long 4°20’44’’W); and the Cuesta de Valderuelo section, 5.6 km southeast of Navas de Estena, Ciudad Real Province (locality NE in Fig. 1, from NE-I-base-, lat 39°27’32’’N, long 4°28’30’’W; to NE-IV-top-, lat 39°27’35’’N, long 4°28’25’’ W). The material from the Almadén-Puertollano syncline is from two selected exposures of the Río Formation placed 8.7 km north of Chillón, Ciudad Real Province (locality CHI in Fig. 1: lat 38°52’28’’N, long 4°53’46’’W) and 27 km west of Almodóvar del Campo, Ciudad Real province (locality AC in Fig. 1: lat 38°44’02’’N, long 4°29’34’’W).

Additional occurrences of orthid brachiopods from the lower half of the Río Formation were recorded across a large area of eastern Sierra Morena, from which five localities were selected: the first two lie 11 km southeast of Calzada de Calatrava, Ciudad Real Province (localities CC in Fig. 1: CC-III lat 38°36’52’’N, long 3°44’0’’W; and CC-IIIA lat 38°36’20’’N, long 3o44’25’’W, respectively); 2 km south of Viso del Marqués, Ciudad Real Province (locality VM in Fig. 1: lat 38°30’22’’N, long 3°35’05’’W); 3.3 km south of Almuradiel, Ciudad Real Province (locality AD in Fig. 1: lat 38°29’06’’N, long 3°30’15’’W); and 8.25 km northeast of Aldeaquemada, Jaén Province (locality AQ in Fig. 1: lat 38°28’06’’N, long 3°18’25’’W).

Finally, for comparative purposes, we have also examined orthid brachiopods from the Valongo area in the Oporto district, north Portugal, including the type specimens of the taxa defined by Sharpe (1849), which are presently stored in the Natural History Museum, London. Additional finds of the same orthids, whose original locality was only imprecisely located near San Pedro da Cova, were listed by Delgado (1892, 1908) and recovered by us from two localities within exposures of the Valongo Formation lying in the southern flank of the Valongo Anticline. The first situated at northeast of San Pedro da Cova and about 2 km south of Valongo (Fig. 1: lat 41°10’45’’N, long 8°30’09’’W). A second locality lies in the old Canelas quarry north of Arouca, Aveiro district (Fig. 1: lat 40°57’55’’N, long 8°13’08’’W),

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from where orthid brachiopods were illustrated by Thadeu (1956) and Sá and Gutiérrez-Marco (2006).

Apart from Spain and Portugal, some of the orthid brachiopods described in the middle Darriwilian beds of the Central Iberian Zone have been reported also from coeval beds in the French Armorican Massif (*O. noctilio*, *O. miniensis*, *O. duriensis*, and *O. lusitanica*: Tromelin and Lebesconte 1876, Pillet et al. 1990) and from Upper Ordovician strata in Sardinia, Italy (*O. noctilio* and *O. miniensis*: Meneghini 1857 and Vinassa de Regny 1927; *Harknessella noctilio*: Leone 1998). The latter identifications are only tentative and most probably (according to the illustrations) belong to different brachiopod taxa. However, the old collections from the former Sion-les-Mines locality, as well as recent collections from the Trélazé et Les Fresnaies localities south of Rennes (France), all housed in the museums of Nantes and Angers, probably represent the dispersal of some of the Iberian species to Armorica during the lower Oretanian. For example, *Sivorthis noctilio* was recovered by us from a new locality 700 m north of the "Laillé high", 3 km east from Guichen (Ille-et-Vilaine) and also south of the city of Rennes.

Systematic palaeontology

(by Jaime Reyes-Abril and Enrique Villas)

Order Orthida Schuchert and Cooper, 1932

Suborden Orthidina Schuchert and Cooper, 1932

Superfamily Orthoidea Woodward, 1852

Family Orthidae Woodward, 1852

Genus *Almadenorthis* Reyes-Abril and Villas nov.

Type species: *Almadenorthis auriculata* Reyes-Abril and Villas gen. et sp. nov.; lower Oretanian, Darriwilian, Middle Ordovician; central Spain.

Etymology: After the Almadén region, in central Spain, with important Palaeozoic fossiliferous localities where the first Spanish Ordovician orthids were discovered in the 19th Century.

Diagnosis.—Orthid with planoconvex, slightly sulcate to rectimarginate shell, with alate cardinal extremities, filate, capillate and coarsely ramicostellate ornament, short ventral interarea and divergent ventral vascula media.

Discussion.—These orthid shells do not fit within any of the defined genera in the family and merit formal taxonomic recognition. Within the family Orthidae, the most typical lateral profile is variably biconvex, planoconvex shells being only known in *Orthis* Dalman, 1828. Nevertheless, the planoconvex Iberian shells can be clearly discriminated, in having a costellate ornament, which is usually costate in *Orthis* itself. The alate cardinal extremities of the new genus are unusual within the family, in which obtuse extremities are common, although it is a feature known also from *Suriorthis* Benedetto, 2003a and some species of *Paralenorthis* Havlíček and Branisa, 1980 or *Sivorthis* Jaanusson and Bassett, 1993 (see below). From *Suriorthis* and *Paralenorthis*, the new genus can be distinguished readily in having a planoconvex profile, while it is dorsibiconvex and ventribiconvex respectively in the other two genera. With *Sivorthis* the new genus has in common a costellate ornament plus an alate outline of some of its species, nevertheless its short interarea and divergent ventral vascula media are clearly different from the typically long interarea and parallel vascula media of *Sivorthis*.

Stratigraphic and geographic range.—The genus is known only from its type locality and type horizon.

Almadenorthis auriculata Reyes-Abril and Villas sp. nov.

Fig. 3.

Etymology: For its auriculate cardinal extremities.

Type material: Holotype: MGM-5940-O, internal and external moulds of ventral valve. Paratypes: three internal moulds of ventral valves, one internal and external mould of ventral valve, and two internal and external moulds of dorsal valves, with numbers: MGM-5941-O to MGM-5945-O, from the lower horizons of the Río Shales.

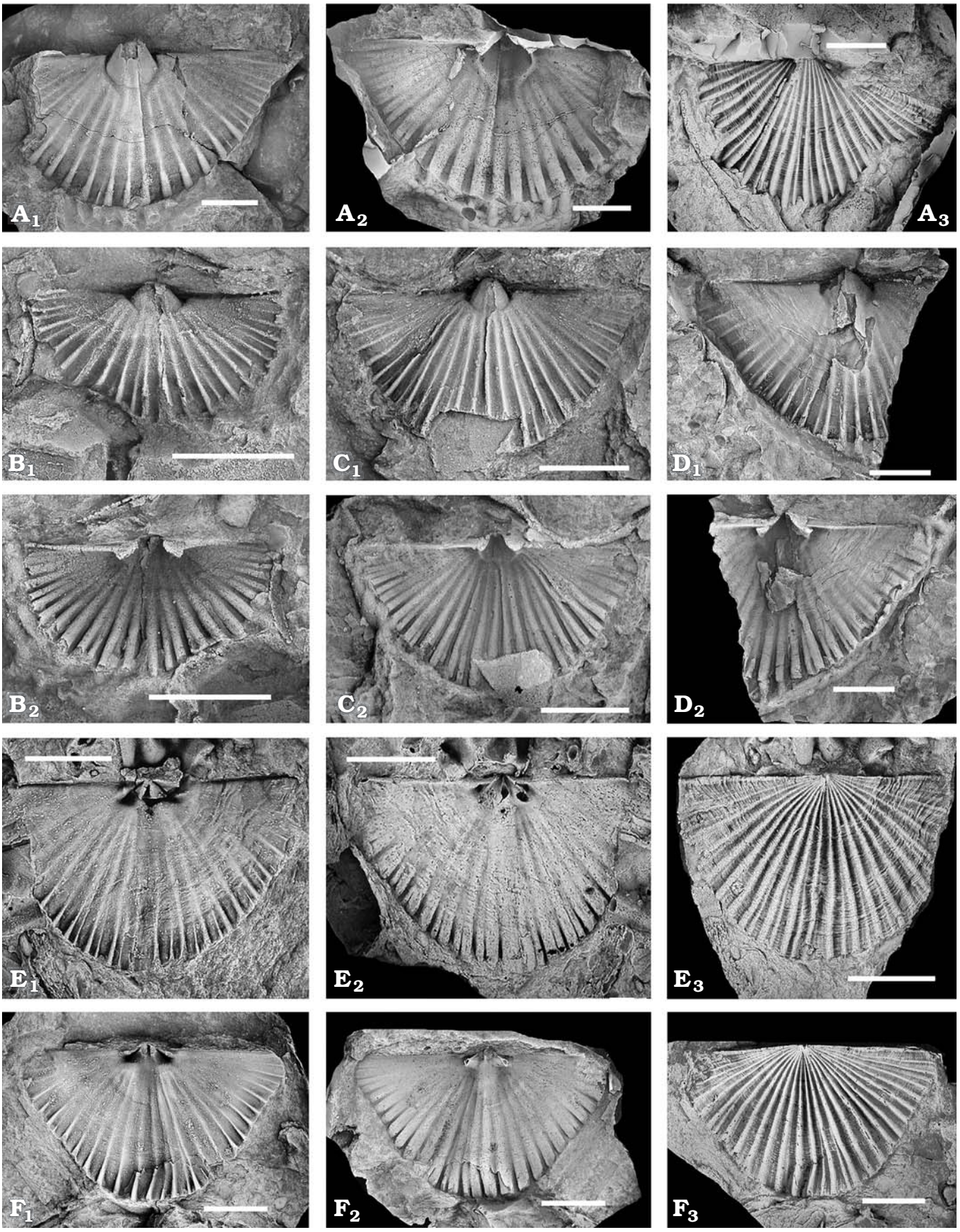
Type locality: AC-I, 5800 m SE of Fontanosas, but within the municipality of Almodóvar del Campo, Ciudad Real Province, Spain. UTM coordinates: lat 38°44'02''N, long 4°29'34''W.

Type horizon: Lower part of the Río Formation, *Didymograptus artus* Biozone, lower Oretanian, middle Darriwilian Stage of the Middle Ordovician Series.

Diagnosis.—Shell planoconvex, with transversally elongate semioval and auriculate outline, acute ears in young stages to rounded ears in adult stages; 51–71% as long as wide, with 60% the commonest value. Capillate, filate and coarsely ramicostellate ornament, with 26 to 33 ribs in adults; less than 60% of costae branching. Shell extremely thin, with all radial and concentric ornament strongly impressed on valve interiors.

Description.—Shell planoconvex, up to 15 mm long, very thin, transversely semioval in outline, with variably alate cardinal extremities, from acute ears in young forms to rounded ears in adults (see Fig. 3F_3), 51–58% as long as wide and slightly sulcate to rectimarginate anterior commissure. Ventral valve convex, with low fold, subplanar postero-lateral areas and maximum depth medially, 17–20% as deep as long; ventral interarea apsacline, short, planar to slightly curved, 3–5% as long as valve, with wide and open delthyrium. Dorsal valve planar, with shallow sulcus, progressively widening anteriorly; dorsal interarea anacline, planar, 2% as long

Fig. 3. Orthid brachiopod *Almadenorthis auriculata* Reyes-Abril and Villas gen. et sp. nov. **A**. Holotype, MGM-5940-O, internal mould (A_1), latex cast of interior (A_2) and latex cast of exterior (A_3) of ventral valve. **B**. MGM-5943-O, internal mould (B_1) and latex cast of interior (B_2) of ventral valve. **C**. MGM-5941-O, internal mould (C_1) and latex cast of interior (C_2) of ventral valve. **D**. MGM-5942-O, internal mould (D_1) and latex cast of interior (D_2) of ventral valve. **E**. MGM-5945-O, internal mould (E_1), latex cast of interior (E_2) and latex cast of exterior (E_3) of dorsal valve. **F**. MGM-5944-O, internal mould (F_1), latex cast of interior (F_2) and latex cast of exterior (F_3) of dorsal valve. Scale bars 5 mm. →



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as valve (measured on one valve), with open notothyrium. Radial ornament coarsely costellate, with ribs branching irregularly; less than 30% of costae branching in young stages, but up to 60% in adults; ribs narrow and high, subrounded in section, numbering 26 to 33 in shell margin, and 7–9 per 5 mm at 5 mm anteromedially from umbo; strongly capillate and filate, with 9–11 fila per mm.

Deltidiodont teeth, with crural fossettes, supported by very short dental plates, divergent toward valve floor; muscle field subtriangular, short, with rounded anterior margin, 22–29% as long as valve, 17–22% as wide as valve, diductor scars nearly as long as subtriangular adductor scar, not enclosing them anteriorly. Two narrow vascula media arise from anterior end of diductors and immediately diverge anteriorly, fading before mid length of valve.

Notothyrial platform short, posteriorly sloping and extending anteriorly as wide median ridge; cardinal process blade-like, high, thickening in adult stages; brachiophores rod-like, welded to nothothyrial platform; dental sockets excavated on valve floor; muscle field poorly impressed.

Shell with even finest radial and concentric ornamentation strongly impressed on interior of both valves (see Fig. $3D_1$, E_1). Crenulations (rib reflections) deeply impressed on inner surface of valve margin, narrower than reflactions of interspaces, which lack median sulci typical of many orthid species.

Stratigraphic and geographic range.—Known only from its type locality, AC-I, west of Almodóvar del Campo (Ciudad Real), in the lower horizons of the Río Formation.

Genus *Gutiorthis* Reyes-Abril and Villas nov.

Type species: *Gutiorthis incurvata* Reyes-Abril and Villas gen. et sp. nov.; lower Oretanian, middle Darriwilian, Middle Ordovician; central Spain.

Etymology: Named after our co-author Juan Carlos Gutiérrez-Marco, who made a great part of the brachiopod collection, and for his stratigraphical and palaeontological studies on the Spanish Ordovician.

Diagnosis.—Orthids with ventribiconvex shell of suboval outline and obtuse cardinal angles in adults; ornamentation costate, capillate and filate. Ventral valve with subtriangular muscle field and saccate mantle canal system; vascula media parallel and adjacent to anterior third of valve. Dorsal valve with high and strong notothyrial platform, thin rod-like divergent brachiophores, quadripartite muscle field and saccate mantle canal system. In both valves, posterior vascula terminalia markedly incurved posterolaterally, oblique to ribbing direction and intersecting posterior valve margin.

Discussion.—Externally and internally these large shells are very characteristic of the Orthidae, sharing with *Orthambonites* Pander, 1830 many of its diagnostic features. For example, the studied shells are very similar externally to *Orthambonites fundata* Rubel, 1961 among other species in the genus. Nevertheless, the attitude of its posterior vascula terminalia, oblique to the ribbing and intersecting the posterior valve margin, is a very peculiar feature within the orthids and is treated as a diagnostic feature of the new genus. Such a disposition of the vascula terminalia is known only within the family in *Sinorthis typica* Wang, 1955, as in its Chinese specimens (Zhan et al. 2006: pl. 3: 2) and in those from the Montage Noire, SE France (Mélou in Babin et al. 1982: pl. 3: 10–12). In any case, the taxonomic importance of this peculiar mantle canal system has not been evaluated up to now for the genus *Sinorthis* Wang, 1955, which displays clear differences from the Iberian shells; among them, the ramicostellate ribbing and the divergent ventral vascula media, different detail of costate ribbing, and proximally parallel ventral vascula media in the new genus. The posterodorsally incurved vascula terminalia is a feature well known in some dalmanellidine orthides with markedly circular outlines, such as the Heterorthidae or the Drabovidae. Nevertheless it is very rare within the orthidine orthides. Curiously, such an incurved vascula terminalia is also known in *Tarfaya* Havlíček, 1971, a genus assigned questionably to the family Heterorthidae (see Williams and Harper 2000; Villas and Herrera 2004; Benedetto 2007), but initially included among the Productorthidae (Havlíček 1971). Popov et al. (2009) have erected a new family Tarfayidae within the superfamily Orthoidea, including *Tarfaya* and *Xinanorthis* Xu et al., 1974, characterised, among other features, by the posterolateral regions of dorsal valve with vascula terminalia along the hinge line.

Stratigraphic and geographic range.—The genus is known only from its type locality and type horizon.

Gutiorthis incurvata Reyes-Abril and Villas sp. nov.

Fig. 4.

Etymology: For its posteriorly incurved vascula cardinalia and dentalia.

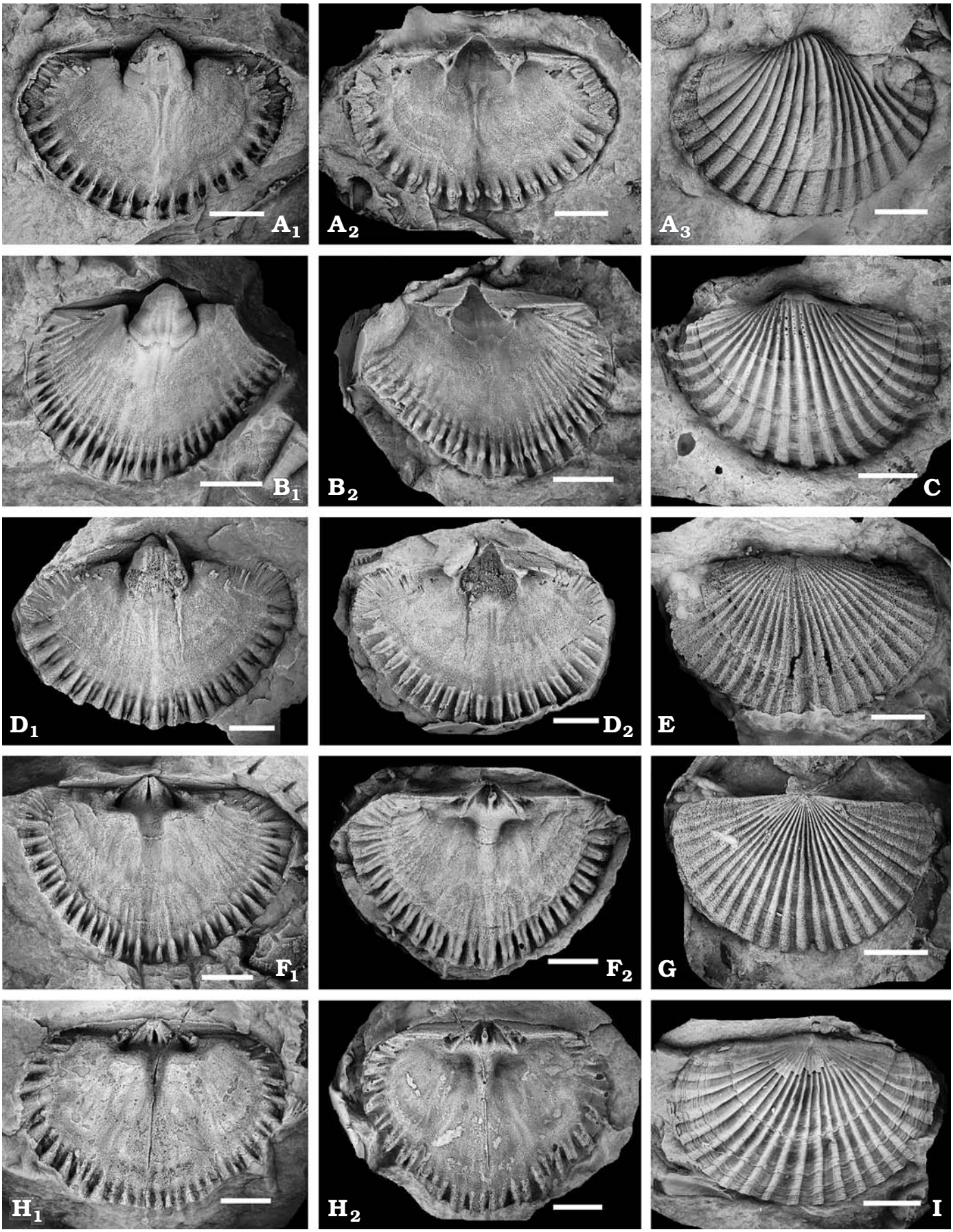
Type material: Holotype: MGM-5968-O, internal mould of ventral valve. Paratypes: twelve internal moulds and four external moulds of ventral valves, twelve external moulds and sixteen internal moulds of dorsal valves, and internal and external moulds of five ventral valves and three dorsal valves, with numbers: MGM-5946-O to MGM-5998-O.

Type locality: NE-IIA, 5600 m SE of Navas de Estena, Ciudad Real Province, Spain. UTM coordinates: lat 39°27'32''N, long 4°28'31''W.

Type horizon: About 110 metres above the base of the Navas de Estena Formation, *Didymograptus artus* Biozone, lower Oretanian, middle Darriwilian Stage of the Middle Ordovician Series.

Diagnosis.—*Gutiorthis* with rectangular to slightly acute cardinal angles at young stages, changing to obtuse with age; costate ribbing with high ribs of rounded cross section, nar-

Fig. 4. Orthid brachiopod *Gutiorthis incurvata* Reyes-Abril and Villas gen. et sp. nov. **A**. Holotype, MGM-5968-O, internal mould (A_1), latex cast of interior (A_2) and latex cast of exterior (A_3) of ventral valve. **B**. MGM-5946-O, internal mould (B_1) and latex cast of interior (B_2) of ventral valve. **C**. MGM-5948-O, latex cast of exterior of ventral valve. **D**. MGM-5950-O, internal mould (D_1) and latex cast of interior (D_2) of ventral valve. **E**. MGM-5996-O, latex cast of exterior of dorsal valve. **F**. MGM-5989-O, internal mould (F_1) and latex cast of interior (F_2) of dorsal valve. **G**. MGM-5995-O, latex cast of exterior of dorsal valve. **H**. MGM-5984-O, internal mould (H_1) and latex cast of interior (H_2) of dorsal valve. **I**. MGM-5973-O, latex cast of exterior of dorsal valve. Scale bars 5 mm. →



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rower than interspaces, numbering 17–22 at valve margin, including occasionally up to two costellae. Dorsal valve with high notothyrial platform; cardinal process flanked by two slender notothyrial ridges in adults.

Description.—Shell ventribiconvex, up to 26 mm long, with semicircular outline in young stages to suboval in adults. Maximum width along hinge line in young stages and along mid valve or posterior third of valve in adults; cardinal angles rectangular to slightly acute in young stages changing to obtuse in adults; 55–90% as long as wide, but part of that wide range due to deformation; hinge line 68–100% as wide as maximum valve width. Ventral valve strongly convex, weakly carinate, maximum depth at middle part of valve, 20–48% as deep as long (mean [m] = 34%, variance [v] = 1%, number [n] = 14); ventral interarea apsacline, slightly curved, 6–11% as long as valve (m = 8%, v = 0.2%, n = 11), with wide and open delthyrium. Dorsal valve weakly convex, 55–88% as long as wide (m = 69%, v = 1%, n = 29), slightly sulcate with up to 2 costae on sulcus; dorsal interarea planar, anacline, shorter than ventral interarea, with open notothyrium. Ornamentation costate, with high ribs of rounded section, narrower than intercostal spaces, numbering 17–22 at valve margin, 20 being the commonest number, including occasionally up to 2 costellae; with 6 ribs per 5 mm counted 5 mm anteromedially from umbo, about 3 capillae per 0.1 mm, well marked on ribs, and 4 fila per 0.1 mm well marked on intercostal spaces, as well as up to 4 conspicuous growth lines in largest valves.

Ventral interior with crural fosettes on massive, triangular teeth, supported by short dental plates, continuous anteriorly with short and incurved muscle bounding ridges; muscle field subtriangular, 24–43% as long as valve (m = 32%, v = 0.2%, n = 19), 21–35% as wide as valve (m = 25%, v = 0.1%, n = 24), with adductor scars 11–16% as wide as muscle field (m = 14%, v = 1%, n = 4), slightly shorter than diductor scars and not enclosed anteriorly; mantle canal system saccate, with vascula media parallel and adjacent, diverging at the anterior third of valve, and posterior distal branches incurving posterolaterally to intersect posterior valve margin, and oblique to ribbing.

Dorsal interior with high, prominent notothyrial platform in adult stages, continuous anteriorly with strong median ridge, reaching mid length of valve; cardinal process blade-like, high and thin, strengthened with age and flanked by slender notothyrial ridges; brachiophores rod-like, diverging at about 90°, thickening and welding to notothyrial platform with age; dental sockets excavated on secondary shell deposits; muscle field quadripartite, 38–57% as long as valve (m = 47%, v = 0.3%, n = 9), 23–34% as wide as valve (m = 31%, v = 1%, n = 15), with larger anterior pair than posterior pair, separated by curved, transverse ridges, diverging anteriorly; mantle canal system with vascula media strongly impressed, diverging from anterior adductor scars, and distal posterior branches incurving posterolaterally.

Shell with internal margins of both valves crenulated, with deep grooves, corresponding to crest of ribs, and wide eminences with shallow sulci on intercostal spaces.

Discussion.—These shells display external features similar to those illustrated in the drawings of *Orthis lusitanica* Sharpe, 1849, from the lower Oretanian of Valongo (Portugal). However, a precise comparison with this species is not possible since its internal features were not described; moreover, the two external moulds on which the brief description of *O. lusitanica* is based, could not be found in Sharpe's (1849) collection housed at NHM (Sarah Long, personal communication 2007). However, from a formal point of view, *O. lusitanica* is a valid taxon, since it was published including a description and figures. Nevertheless, since it is based on an incomplete sample, not allowing with certainty assignment of new specimens to the species, or allowing a precise generic attribution, it is proposed to restrict the species to the lectotype. For this purpose the lectotype is chosen herein as the external mould of a ventral valve, identified by Sharpe (1849: pl. 6: 5a) as a dorsal valve, where the costate ornamentation, pointed out by the author, can be observed. Regarding the second specimen assigned to *O. lusitanica* by Sharpe (1849: pl. 6: 5b), a dorsal valve, it is similar externally to those of *Gutiorthis incurvata* Reyes-Abril and Villas gen. et sp. nov. or even to *Paralenorthis estenaensis* Reyes-Abril and Villas sp. nov., although a precise comparison with them is again not possible, for the reasons stated above.

Stratigraphic and geographic range.—This species is known from both flanks of the Navas de Estena syncline (localities SP-II, south of San Pablo de los Montes, Toledo Province, and NE-IIA, southeast of Navas de Estena, Ciudad Real Province), in the lower part of the Navas de Estena Formation.

Genus *Orthambonites* Pander, 1830

Type species: *Orthis calligramma* Dalman, 1828 (see Jaanusson and Bassett 1993); Kundan regional stage, Middle Ordovician; Sweden.

Orthambonites sp.

Fig. 5.

Material.—Five internal moulds and one external mould of ventral valves, and nine internal moulds and four external moulds of dorsal valves, with numbers MGM-5999-O to MGM-6017-O.

Description.—Shell large, up to 26 mm wide and 19 mm long, slightly ventribiconvex, subrectangular in outline, maximum width along hinge line or close to it, depending on growth stage, cardinal angles acute in young stages and slightly obtuse in adults, 79–83% as long as wide, and with slightly sulcate anterior commissure. Ventral valve slightly convex, with weak median fold and almost flat posterolateral areas; ventral interarea apsacline, slightly curved and relatively short, 6–10% as long as valve, with open delthyrium. Dorsal valve slightly convex to subplanar, with shallow median sulcus, 70–89% as long as wide (m = 76%, v = 0.1%, n = 13); dorsal interarea anacline, flat and short, 4–9% as long as valve, with open notothyrium. Radial ornamentation costate with high ribs of rounded section, numbering 24–28 at dorsal valve margin, and 7–10 per 5 mm counted 5 mm anterolaterally from umbo; fila and capillae well marked on ribs and intercos-

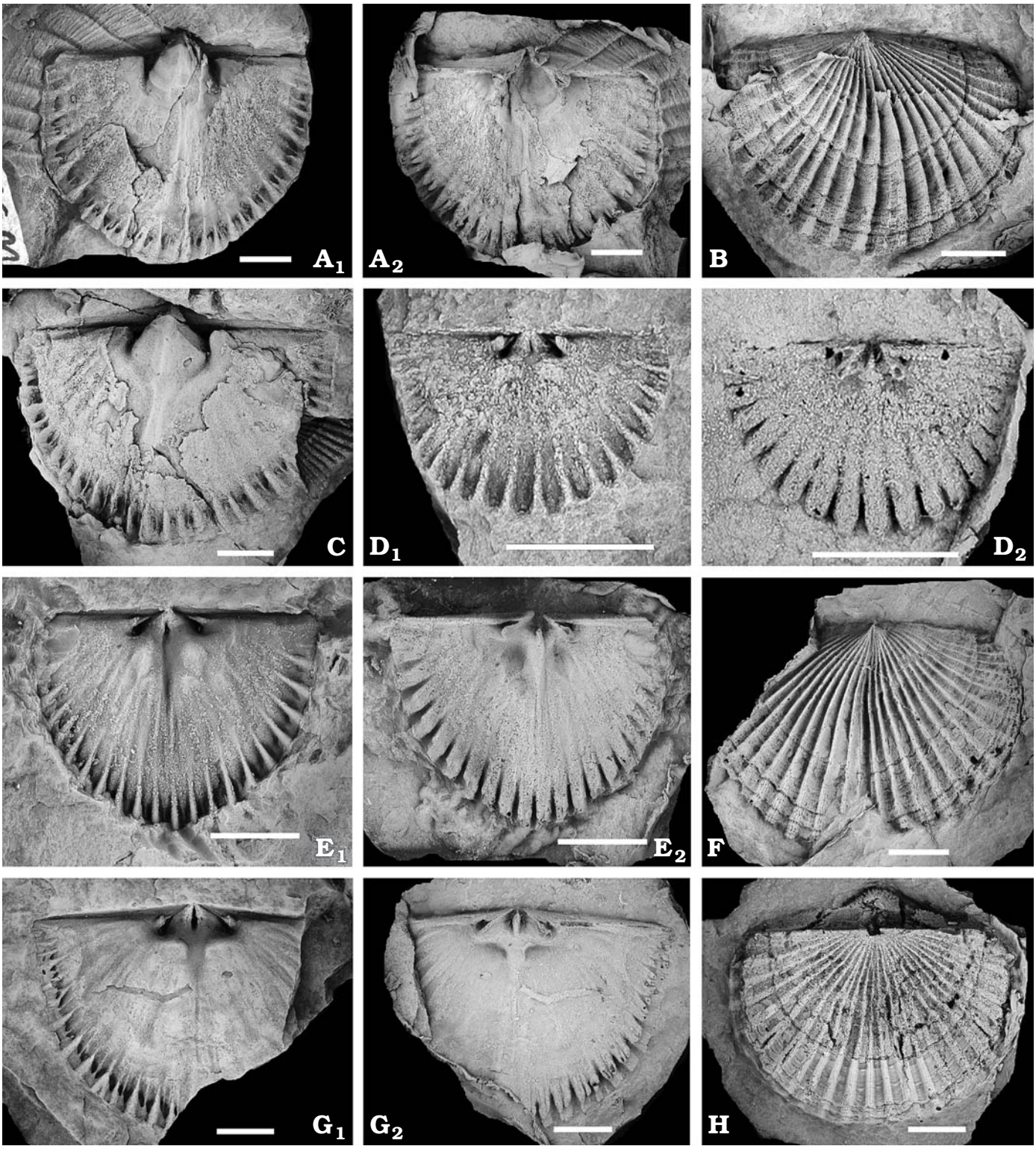

Fig. 5. Orthid brachiopod *Orthambonites* sp. **A**. MGM-5999-O, internal mould (A_1) and latex cast of interior (A_2) of ventral valve. **B**. MGM-6008-O, latex cast of exterior of dorsal valve. **C**. MGM-6002-O, internal mould of ventral valve. **D**. MGM-6006-O, internal mould (D_1) and latex cast of interior (D_2) of dorsal valve. **E**. MGM-6012-O, internal mould (E_1) and latex cast of interior (E_2) of dorsal valve. **F**. MGM-6013-O, latex cast of exterior of dorsal valve. **G**. MGM-6011-O, internal mould (G_1) and latex cast of interior (G_2) of dorsal valve. **H**. MGM-6007-O, latex cast of exterior of dorsal valve. Scale bars 5 mm.

tal spaces, with 4 capillae per 1 mm, 6 fila per 1 mm, as well as up to 3 strong growth lines.

Ventral interior with triangular teeth and large crural fossettes, short dental plates diverging onto valve floor, mus-

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cle field of subrhomboidal outline, 32–43% as long as valve, 21–36% as wide as valve, with adductor scar 3–5% as wide as muscle field; mantle canal system saccate, with parallel and adjacent vascula media until anterior third of valve, diverging close to anterior margin.

Dorsal valve with high ridge-like cardinal process, high notothyrial platform, continuous with wide median ridge that extends anteriorly 16–25% of valve length; brachiophores rod-like, strongly divergent, welded to notothyrial platform; dental sockets excavated on secondary shell deposits; muscle field quadripartite, 40–47% as long as valve, 26–33% as wide as valve, with posterior adductor scars of petaloid outline, twice as long as anterior scars, separated by curved transverse ridges, diverging anteriorly.

Ribbing strongly impressed on internal margins of both valves, with wide intercostal spaces divided shallow sulci.

Discussion.—In its profile, outline, ornamentation and arrangement of ventral vascula media, these orthid shells can be ascribed to *Orthambonites* Pander, 1830. They are close to *Orthambonites majusculus* Rubel, 1961 in the similar number of costae and in the subrectangular outline, although that species is more strongly convex. It is also close to *Orthambonites*? *novitas* Öpik, 1939 in the number of ribs, although that species displays some of them as being usually branched. However, the small Iberian sample, in which no specimen preserves both internal and external features, does not allow a specific identification.

Stratigraphic and geographic range.—This species is known from the localities SP-II (San Pablo de los Montes), NE-II (Navas de Estena) and VPA (Ventas con Peña Aguilera), in the lower part of the Navas de Estena Formation, and from CHI-I (Chillón), VM-I (Viso del Marqués) and CC-III-IIIA (Calzada de Calatrava), in the lower part of the Río Formation.

Genus *Paralenorthis* Havlíček and Branisa, 1980

Type species: *Paralenorthis immitatrix* Havlíček and Branisa, 1980; Floian Stage, Lower Ordovician; San Lucas, Bolivia.

Paralenorthis alata (J. de C. Sowerby in Murchison, 1839)

Fig. 6.

1839 *Spirifer alatus* sp. nov.; J. de C. Sowerby in Murchison 1839: 49, pl. 22: 7.
1849 *Orthis alata* (J. de C. Sowerby); Salter in Murchison 1849: 55, pl. 5: 3.
1869 *Orthis carausii* Davidson; Davidson 1869: 229, pl. 33: 1–7.
1869 *Orthis alata* (J. de C. Sowerby); Davidson 1869: 232, pl. 33: 17–21.
1912 *Orthis carausii* Davidson; Matley 1912: 78.
1918 *Orthis calligramma* var. *alata* Sow.; Born 1918: 336, pl. 24: 2a, b.
1969 *Lenorthis alata* (J. de C. Sowerby); Bates 1969: 10, pl. 2: 14; pl. 3: 1–7; pl. 4: 1–10; pl. 5: 1–6.
1993 *Paralenorthis alata* (J. de C. Sowerby); Jaanusson and Bassett 1993: 34.

Material.—Eleven internal moulds and eight external moulds of ventral valves, six external moulds and five internal moulds of dorsal valves, besides internal and external moulds of two ventral valves and four dorsal valves, with numbers MGM-6018-O to MGM-6055-O.

Emended diagnosis.—*Paralenorthis* with mucronate outline, acute cardinal angles, allometric growth, lowest values of length relative to width corresponding to largest valves, and sulcate anterior commissure; dorsal interarea steeply anacline to catacline; ornamentation costate with up to 38 ribs, of which some subcentral ribs have slightly delayed origin; ventral muscle field of subrhomboidal outline.

Description.—Shell ventribiconvex, up to 19 mm long, of mucronate outline, maximum width along hinge-line, acute cardinal angles, 47–69% as long as wide, corresponding lowest values to largest valves, and sulcate anterior commissure. Ventral valve convex, with variably developed median fold, subplanar postero-lateral areas, 24–38% as deep as long; ventral interarea apsacline to orthocline, curved, 6–11% as long as valve, with wide and open delthyrium. Dorsal valve slightly convex, with weak median sulcus, widening and deepening anteriorly, 50–73% as long as wide; dorsal interarea steeply anacline to catacline, 6–9% as long as valve, with open notothyrium. Radial ornamentation costate with 29–38 ribs, of which only 4 to 6 posterolateral ribs arise beyond umbo, and run subparallel to hinge line, besides 2 to 5 subcentral ribs with delayed origin along first 7 mm of growth; low ribs of subtriangular section in young stages, becoming more rounded in latest stages, numbering 4–7 per 5 mm counted 5 mm anteromedially from umbo, with intercostal spaces of similar width than ribs; fila and capillae poorly preserved (see Fig. 6F_2, F_3); up to 3 strong growth lines in largest shells.

Ventral interior with pedicle callist, triangular teeth and crural fossettes; short dental plates diverging onto valve floor and continuous with anteriorly converging muscle bounding ridges; bilobed muscle field, of subrhomboidal outline, 28–45% as long as valve, 19–26% as wide as valve, with longer and wider diductor scars than triangular adductor scar, not enclosing it anteriorly; adductor scar 8–17% as wide as muscle field; divergent vascula media (see Fig. 6D), arising from anterior end of diductor scars and not observable beyond mid length of valve.

Dorsal valve with high notothyrial platform, sloping posteriorly and continuous anteriorly with strong median ridge, widening forward and fading by mid length of valve; ridge-like, high and narrow cardinal process; rod-like brachiophores, welded to notothyrial platform; dental sockets excavated on secondary shell deposits; quadripartite muscle field, 34–56% as long as valve, 17–32% as wide as valve, with quadrangular adductor scars separated by transverse ridges.

Shell with radial ornamentation variably impressed on valve interiors, with grooves corresponding to crest of ribs as wide as intercostal impressions, divided by weak sulci at marginal areas.

Discussion.—*Spirifer alatus* J. de C. Sowerby in Murchison, 1839 was thoroughly re-described based on material from

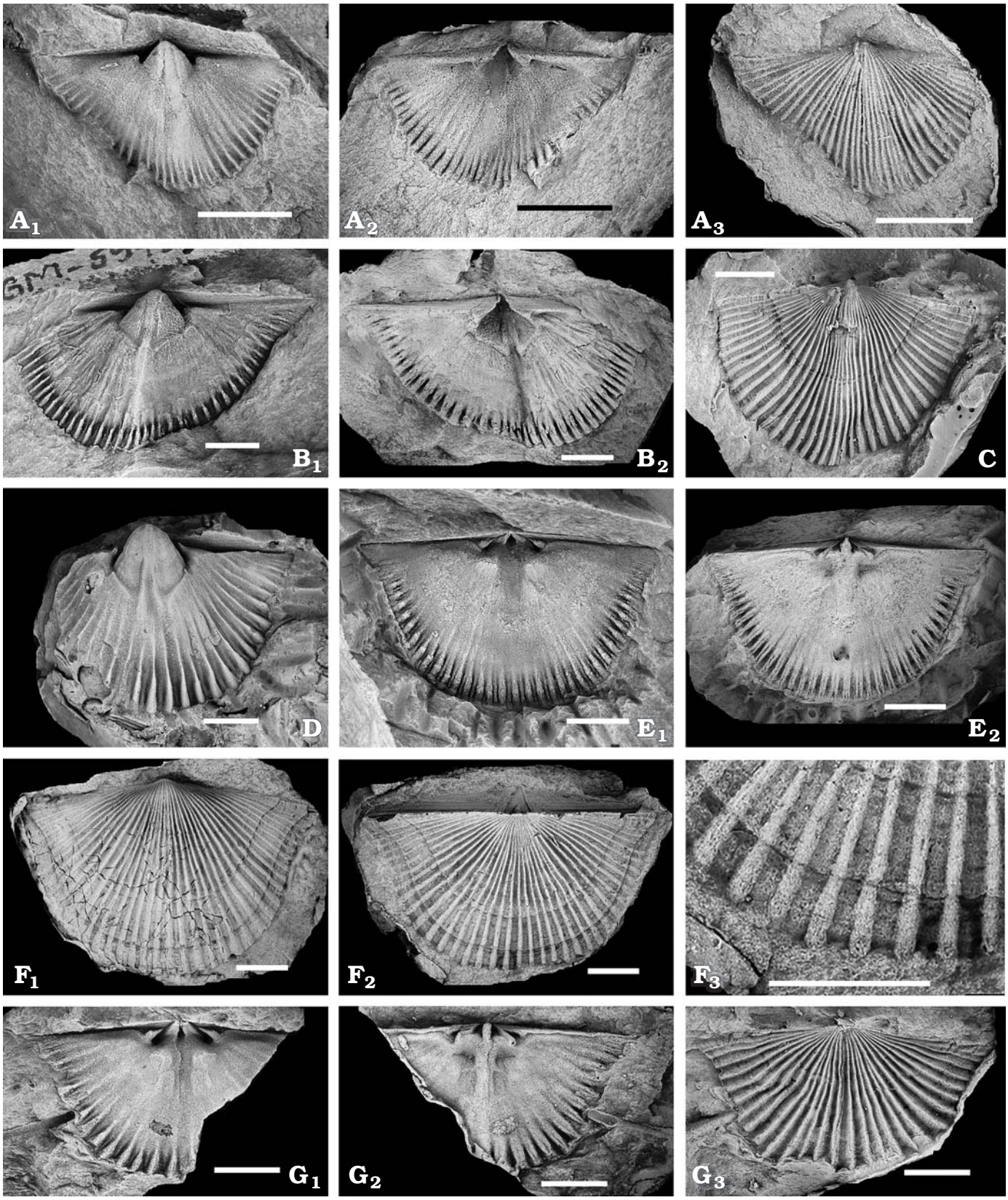

Fig. 6. Orthid brachiopod *Paralenorthis alata* (J. de C. Sowerby in Murchison, 1839). **A**. MGM-6021-O internal mould (A_1), latex cast of interior (A_2) and latex cast of exterior (A_3) of ventral valve. **B**. MGM-6030-O, internal mould (B_1) and latex cast of interior (B_2) of ventral valve. **C**. MGM-6038-O, latex cast of exterior of ventral valve. **D**. MGM-6037-O, internal mould of ventral valve. **E**. MGM-6048-O internal mould (E_1) and latex cast of interior (E_2) of dorsal valve. **F**. MGM-6027-O, latex cast of ventral exterior (F_1), latex cast of dorsal exterior (F_2), and detail of the latter (F_3) of a shell with conjoined valves. **G**. MGM-6042-O, internal mould (G_1), latex cast of interior (G_2) and latex cast of exterior (G_3) of dorsal valve. Scale bars 5 mm.

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South Wales, and assigned to *Lenorthis* Andreeva (in Nikiforova and Andreeva, 1961) by Bates (1969). Jaanusson and Bassett (1993), after the rejection of *Lenorthis* by Havlíček and Branisa (1980), re-ascribed the species to *Paralenorthis*, erected by these authors to replace *Lenorthis*. The strongly mucronate outline of the Iberian *Paralenorthis*, besides its allometric growth, with progressively higher values of valve length relative to width, and a very high number of ribs, with up to 38 ribs in adult shells, indicate clear assignment to *P. alata*. The main difference of the Iberian sample from the Welsh collection is in its lower variability of rib number, with 29 to 38 ribs on adults, versus 18–36 ribs on the Welsh shells. This difference could be due to the inclusion in the collections studied by Bates (1969) of some specimens of *Paralenorthis proava* (Salter, 1866), a species co-occurring at the same localities as *P. alata*, but with a much lower number of ribs: 16 to 20 (Bates 1968). The fine preservation of the Iberian sample allows the proposal of a more precise, diagnosis for *P. alata*, extracting its more clearly differentiating features from the lengthy diagnosis of Bates (1969).

Stratigraphic and geographic range.—Moridunian (Lower Arenig) beds of South-west Wales (Carmarthen, Pembrokeshire and Ramsey Island; see Bates 1969). Blue Schists of Carmarthen Mountains; Yellow Quartzites of North-East Tremanhire; Ogof Hên Formation of Ogof Hên Bahia and Ramsey Island. All from the Lower Arenig (Floian Stage, uppermost Lower Ordovician Series) of Wales (Bates 1969).

Lower half of the Navas de Estena Formation in the localities VPA (Ventas con Peña Aguilera, Toledo Province), NE-IV (Navas de Estena, Ciudad Real Province), and lower part of the Río Formation in the locality CHI-I 10E (north of Chillón, Ciudad Real Province). All lower Oretanian (middle Darriwilian Stage, Middle Ordovician Series).

Paralenorthis estenaensis Reyes-Abril and Villas sp. nov.

Fig. 7.

Etymology: After the type locality at Navas de Estena, Toledo Province.

Type material: Holotype: MGM-6068-O, internal mould of ventral valve. Paratypes: eighteen internal moulds and twelve external moulds of ventral valves, fourteen external moulds and twelve internal moulds of dorsal valves, and internal and external moulds of two ventral valves and three dorsal valves, with numbers: MGM-6056-O to MGM-6116-O.

Type locality: NE-IIIA, 5600 m SE of Navas de Estena, Province, Spain. UTM coordinates: lat 39°27'33''N, long 4°28'31''W.

Type horizon: About 130 metres above the base of the Navas de Estena Formation, *Didymograptus artus* Biozone, lower Oretanian, middle Darriwilian Stage of the Middle Ordovician Series.

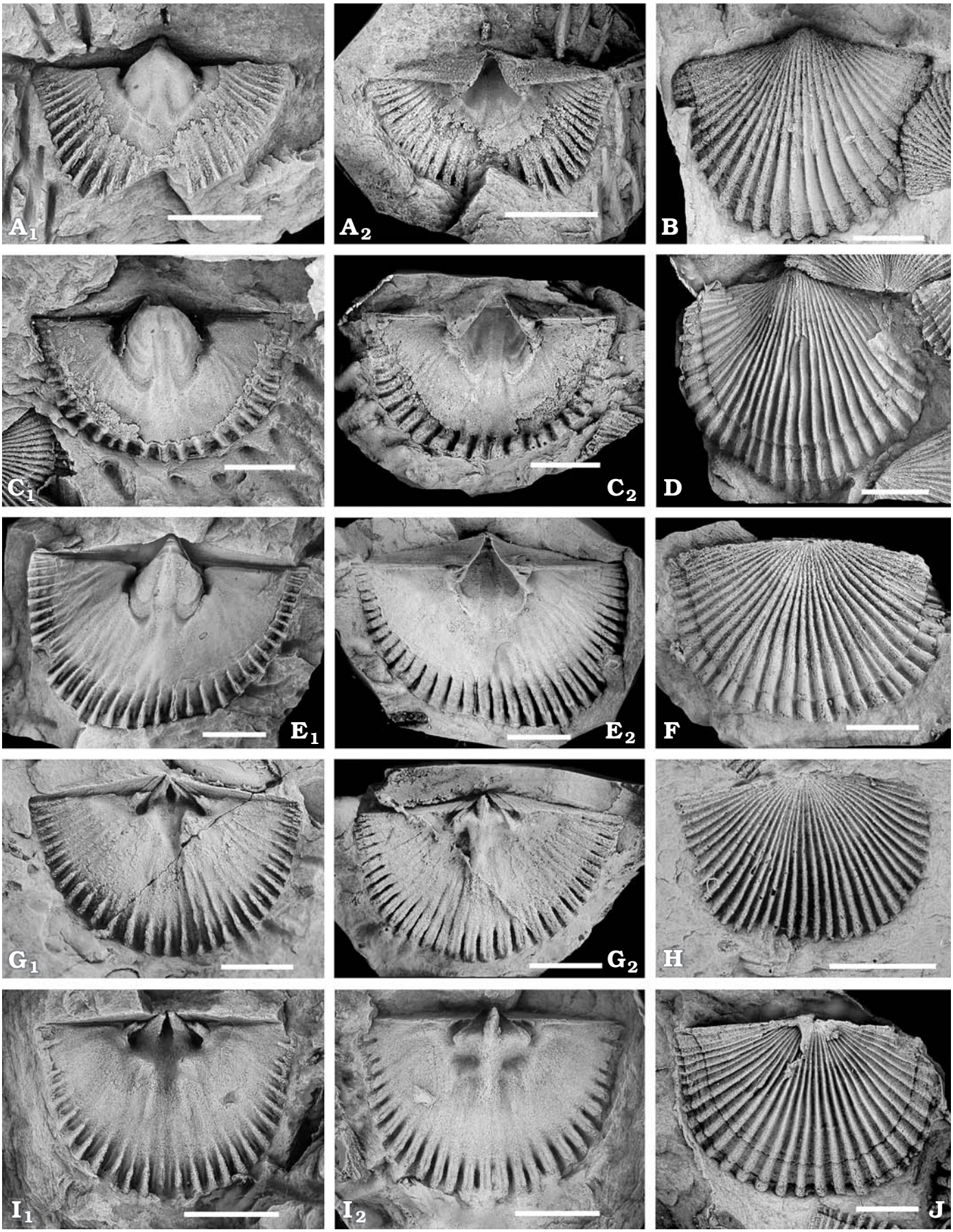
Diagnosis.—*Paralenorthis* species of subquadrangular outline, with acute cardinal angles in young stages, changing to rectangular to slightly obtuse in adult stages; ventral valve strongly convex, radial ornamentation costate with high ribs, numbering 26–38; bilobed ventral muscle field, deeply impressed, extending forward 28–44% of valve length; strong notothyrial platform with thick, ridge-like cardinal process, flanked by slender notothyrial ridges.

Description.—Shell ventribiconvex, up to 19.5 mm long, of subquadrangular outline, with maximum width at hinge line, acute cardinal angles in young stages and rectangular to slightly obtuse in adults, 63–84% as long as wide (m =75%, v = 0.5%, n = 43), with rectimarginate anterior commissure. Ventral valve strongly convex, 14–45% as deep as long (m = 24%, v = 1%, n = 27), with maximum depth at mid length of valve; ventral interarea apsacline, flat to slightly curve, 7–19% as long as valve (m = 12%, v = 0.1%, n = 25), with wide and open delthyrium. Dorsal valve slightly convex, 61–87% as long as wide (m = 71%, v = 0.5%, n = 43), with shallow median sulcus progressively widening forward; dorsal interarea flat, steeply anacline to catacline, 5–10% as long as valve, with open notothyrium, flanked by radial striae in adult shells. Radial ornamentation costate, with few postero-lateral ribs that run subparallel to hinge line, arising beyond umbo; ribs high, subtriangular in section, becoming rounded in latest growth stages, of similar width to intercostal spaces, numbering 26–38 at valve margin, with 29 the commonest number, and 4–6 per 5 mm counted 5 mm anteromedially from umbo; 10–12 capillae per mm, 5 fila per mm and up to 2 strong growth lines in largest shells.

Ventral interior with triangular teeth and strong crural fossettes; dental plates short, divergent onto valve floor, continuous with muscle bounding ridges, curved inwardly to bound diductor scars; muscle field large, bilobed and scalloped, with diductor scars longer and wider than adductor scar, not enclosing it anteriorly, 28–44% as long as valve (m = 35%, v = 0.5%, n = 28), 24–40% as wide as valve (m = 32%, v = 0.2%, n = 22), with highest values in adult stages; adductor scars progressively widening forward, 9–30% as wide as muscle field (m = 16%, v = 0.3%, n = 22); divergent vascula media, arising from anterior end of diductor scars and not observable beyond mid length of valve.

Notothyrial platform high, sloping posteriorly and continuous anteriorly with strong median ridge, lowering and occasionally narrowing forward; cardinal process blade-like and robust, flanked by slender notothyrial ridges in adult stages; brachiophores rod-like, divergent, welded to notothyrial platform; dental sockets excavated in secondary shell deposits, bisected posteriorly by short ridges; quadripartite muscle field, with anterior adductor scars lobate (see Fig. 7I$_1$) and longer

Fig. 7. Orthid brachiopod *Paralenorthis estenaensis* Reyes-Abril and Villas sp. nov. **A**. MGM-6068-O, internal mould (A_1) and latex cast of interior (A_2) of ventral valve. **B**. MGM-6077-O, latex cast of exterior of ventral valve. **C**. Holotype, MGM-6074-O, internal mould (C_1) and latex cast of interior (C_2) of ventral valve. **D**. MGM-6058-O, latex cast of exterior of ventral valve. **E**. MGM-6070-O, internal mould (E_1) and latex cast of interior (E_2) of ventral valve. **F**. MGM-6114-O, latex cast of exterior of dorsal valve. **G**. MGM-6097-O, internal mould (G_1) and latex cast of interior (G_2) of dorsal valve. **H**. MGM-6091-O, latex cast of exterior of dorsal valve. **I**. MGM-6098-O, internal mould (I_1) and latex cast of interior (I_2) of dorsal valve. **J**. MGM-6104-O, latex cast of exterior of dorsal valve. Scale bars 5 mm. →



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that posterior adductor scars, separated by straight ridges, diverging anteriorly, 22–61% as long as valve (m = 49%, v = 2%, n = 19) and 18–42% as wide as valve (m = 33%, v = 0.4%, n = 23).

Shell with internal margins of both valves crenulated, with deep and narrow grooves corresponding to crest of ribs, and wide eminences with shallow sulci on intercostal spaces.

Discussion.—The costate, capillate and filate ornaments, in addition to the ventribiconvex profile and the divergent ventral vascula media, indicate an affinity to *Paralenorthis* Havlíček and Branisa, 1981. The new species differs from other congeneric species in its subquadrangular outline, with changing cardinal angles, acute in young stages to rectangular in adults, the ponderous ventral muscle field and high and strong cardinal process, and more numerous ribs.

The studied shells display similar external features to *Orthis miniensis* Sharpe, 1849 (Middle Ordovician of Valongo, Portugal), which is based on two single external moulds. Its precise location within the Valongo Formation is not known and it has not been revised since its erection. Consequently, despite the fact that their ribs and intercostal spaces have a similar width to the Spanish sample, and their rib number ranges partly overlap, 20–30 in *Orthis miniensis* and 26–38 in the Spanish shells, it is not possible to make a precise comparison between the two. Actually, it is not even possible to make a generic assignment of this Portuguese species because a lack of internal features. In consequence, it is proposed herein to restrict the use of the name *O. miniensis* to the two specimens illustrated by Sharpe (1849: pl. 6: 3a, b), and stored at NHM with registration numbers NHM 82896 and NHM 82897. Additional Portuguese specimens of "*Orthis*" *miniensis* have been recently illustrated (fragments of valves) from the base of the Brejo Fundeiro Formation (Cacemes Group) of Bussaco (Romano et al. 1986) and from the middle part of the Moncorvo Formation of Trás-os-Montes (Rebelo and Romano 1986). Sá (2005) described as *Paralenorthis*? *miniensis* (Sharpe, 1849) the abundant material from 6 different fossil localities in the Moncorvo Formation, some of which could belong to *P. estenaensis*. The older records of *O. miniensis* from the Armorican Massif are based on incomplete descriptions (Tromelin and Lebesconte 1876) or illustrations (Péneau 1950), impossible to currently place within Sharpe's species because of the inconsistencies in its original description.

The rib number of this new *Paralenorthis*, up to 38 in adult shells, is much higher than in most of its co-generic species characterised by high rib numbers, like the type species, *Paralenorthis immitatrix* Havlíček and Branisa, 1980, with up to 28 ribs in the Peruvian specimens (Gutiérrez-Marco and Villas 2007). Nevertheless it is extraordinarily similar in rib number to *P. alata*, with 29–38 ribs, occurring in the higher horizons of the same Navas de Estena Formation; in any case, the mucronate outline of *P. alata* in all growth stages allows an easy distinction from the new species, with obtuse cardinal angles and subquadrangular outline in adult stages. In young stages, with acute cardinal angles and small ears, the new species is similar to *Paralenorthis subalata* (Ulrich and Cooper, 1938), but the rib number of this species, up to 29, is never so high as in *Paralenorthis estenaensis* Reyes-Abril and Villas sp. nov.

Stratigraphic and geographic range.—Known from both flanks of the Navas de Estena syncline (localities SP-II, south of San Pablo de los Montes, Toledo Province, and NE-III and IIIA, southeast of Navas de Estena, Ciudad Real Province), in the lower part of the Navas de Estena Formation. Also the species was recognised from the locality AD-I, (south of Almuradiel, Ciudad Real Province) in eastern Sierra Morena, from the lower part of the Río Formation.

Paralenorthis lolae Reyes-Abril and Villas sp. nov.

Fig. 8.

Etymology: Species dedicated to Dolores González-Mosquera, *Lola*, great defender of the palaeontological heritage of Navas de Estena and the nearby Cabañeros National Park.

Type material: Holotype: MGM-6121-O, internal mould of ventral valve. Paratypes: five internal moulds and twelve external moulds of ventral valves, nine external moulds and twelve internal moulds of dorsal valves, and internal and external moulds of three ventral valves and eleven dorsal valves, with numbers: MGM-6117-O to MGM-6169-O.

Type locality: SP-II, 5000 m SW of San Pablo de los Montes, Toledo Province, Spain. UTM coordinates: lat 39°30'33''N, long 4°20'44''W.

Type horizon: 110 metres above the base of the Navas de Estena Formation, *Didymograptus artus* Biozone, lower Oretanian, middle Darriwilian Stage of the Middle Ordovician Series.

Diagnosis.—Semicircular shells of *Paralenorthis* with rectangular to slightly acute cardinal angles, weakly carinate ventral valve and sulcate dorsal valve, short interareas and costate ornamentation, capillate and filate, with 18–26 ribs; subtriangular ventral muscle field, 23–36% as long as valve; thin and short blade-like cardinal process and wide median ridge reaching mid valve length.

Description.—Shell planoconvex to ventribiconvex, up to 17 mm long with semicircular outline, maximum width at hinge line, rectangular to slightly acute cardinal angles, 60–82% as long as wide and slightly sulcate anterior commissure. Ventral valve convex, slightly carinate, 15–38% as deep as long; ventral interarea short, 3–8% as long as valve, apsacline and curved, with open delthyrium. Dorsal valve plane to weakly convex, 52–73% as long as wide, weakly sulcate, with no more than 2 costae on sulcus; dorsal interarea anacline, plane, shorter than ventral interarea, with open notothyrium. Radial ornamentation costate, filate and capillate, with only a few postero-lateral ribs subparallel to hinge line, arising beyond umbo and thickened median costa, observed on ventral valve MGM-6242-O (Fig. 8D); ribs high with rounded crests, numbering 18 to 26 at valve margin, with commonest number 20, and 4–6 costae per 5 mm at 5 mm anteromedially from umbo.

Ventral interior with triangular, blunt teeth and well developed crural fossettes, dental plates short, divergent onto valve floor and continuous anteriorly with low muscle bounding ridges; subtriangular muscle field, with adductor track about the same width and length as diductor scars, not enclosed ante-

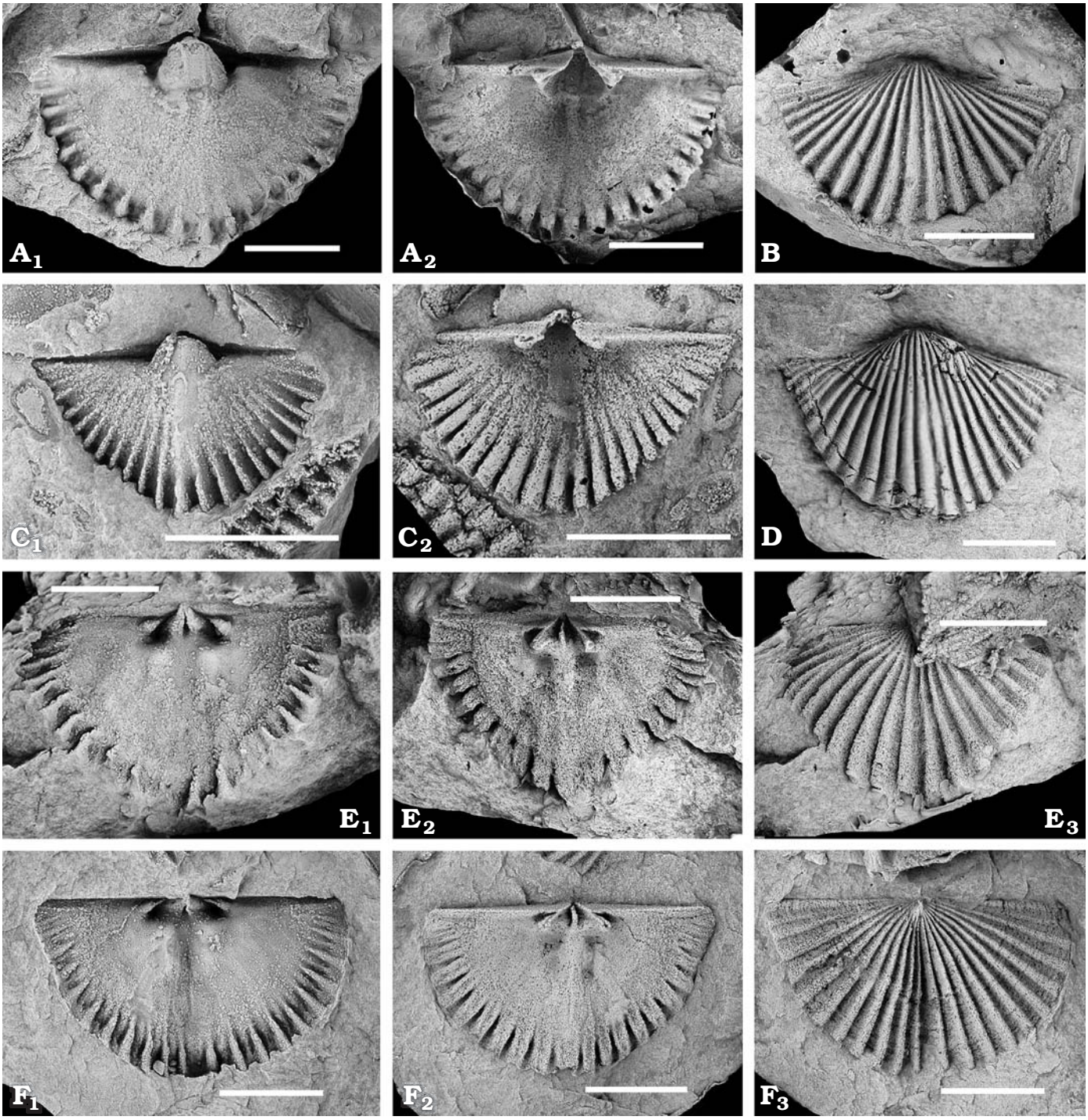

Fig. 8. Orthid brachiopod *Paralenorthis lolae* Reyes-Abril and Villas sp. nov. **A**. Holotype, MGM-6121-O, internal mould (A_1) and latex cast of interior (A_2) of ventral valve. **B**. MGM-6133-O, latex cast of exterior of ventral valve. **C**. MGM-6129-O, internal mould (C_1) and latex cast of interior (C_2) of ventral valve. **D**. MGM-6135-O, latex cast of exterior of ventral valve. **E**. MGM-6143-O, internal mould (E_1) latex cast of interior (E_2) and latex cast of exterior (E_3) of dorsal valve. **F**. MGM-6158-O, internal mould (F_1), latex cast of interior (F_2) and latex cast of exterior (F_3) of dorsal valve. Scale bars 5 mm.

riorly, 23–36% as long as valve (m = 29%, v = 0.1%, n =9), 18–26% as wide as valve (m = 22%, v = 0.1%, n = 9). Divergent vascula media, poorly impressed and strongly incurved postero-laterally by mid valve length.

Dorsal interior with short notothyrial platform, posteriorly sloping and continuous anteriorly with high and variably wide median ridge, reaching mid valve length and greatly enlarged in adult stages; cardinal process blade-like, short and thin; brachiophores rod-like, strongly divergent, welded to notothyrial platform; dental sockets excavated on secondary shell deposits; muscle field quadripartite, well impressed only in adult stages, with subequal adductor scars.

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Radial ornamentation strongly impressed on interior of young shell; internal margins of adult valves crenulated with deep and narrow grooves that correspond to crest of ribs, and wide eminences with shallow sulci on intercostal spaces.

Discussion.—These shells are externally very close to those of several *Paralenorthis* species with reduced rib numbers, as the Baltoscandian *Paralenorthis orbicularis* (Pander, 1830), the British *Paralenorthis proava* (Salter, 1866), the Chinese *Paralenorthis serica* (Martelli, 1901), the North American *Paralenorthis buttsi* (Schuchert and Cooper, 1932), *Paralenorthis parvicrassicostata* (Cooper, 1956) and *Paralenorthis robusta* (Neuman, 1964), the Argentine *Paralenorthis vulgaris* Herrera and Benedetto, 1989 and *Paralenorthis altiplanica* Benedetto, 1998, and the Peruvian *Paralenorthis carlottoi* Villas in Gutiérrez-Marco and Villas, 2007, but display a combination of features distinctive enough within *Paralenorthis* to propose the erection of a new species. Of the species above, it can be distinguished from *P. orbicularis* by its non mucronate outline and from *P. proava* by its weakly sulcate dorsal valve, with no more than two median costae on the sulcus, while there are four ribs in *P. proava*. It differs from *P. serica* in its longer ventral muscle field and longer nothotyrial platform (see Xu and Liu 1984: pl. 2: 15, 16, 19–29). The new species differs from *P. buttsi* in the form of their brachiophore bases, strongly convergent towards the bottom of the notothyrial cavity in the latter; from *P. parvicrassicostata* by the non capillate external surface of this species (see Williams 1974). Its semicircular, transversely elongated outline, allows easy distinction from *P. robusta,* of rounded outline. It can be distinguished from *P. vulgaris* by its transversely elongated outline and shorter ventral interarea, and from *P. altiplanica* by its much broader notothyrial platform and longer dorsal median ridge. Finally, it differs from *P. carlottoi* by its transversely elongated outline, with shells never more than 80% as long as wide, while *P. carlottoi* can be up to 98% as long as wide, as well as by its shorter ventral interarea that is no more than 8% as long as the valve, while those values range in *P. carlottoi* between 10% and 15%.

The lack of auriculation in the new species allows a ready distinction from the British *P. alata*, the Argentine *P. riojana* (Levy and Nullo, 1973) and *P. suriensis* Benedetto, 2003a, as well as the North American *P. marshalli* (Wilson, 1926), *P.*? *minuscula* (Phleger, 1933) and *P.*? *angulata* (Cooper, 1956). The new species can be also distinguished from *P. estenaensis* Reyes-Abril and Villas sp. nov. by its lower rib number, non-varying outline with growth and shorter ventral muscle field.

Stratigraphic and geographic range.—Known from the Navas de Estena syncline (localities NE-II and NE-IIA), in the lower horizons of the Navas de Estena Shales, and from eastern Sierra Morena (localities CC-IIIA, Calzada de Calatrava; VM-I, Viso del Marqués, Ciudad Real Province) and AQ-II, Aldeaquemada, Jaén Province), in the lower part of the Río Formation.

Genus *Sivorthis* Jaanusson and Bassett, 1993

Type species: *Sivorthis filistera* Jaanusson and Bassett, 1993; lower Dalby Limestone, upper Darriwilian, Middle Ordovician; Öland, Sweden.

Sivorthis calatravaensis Reyes-Abril and Villas sp. nov.

Figs. 9, 10A–D.

Etymology: After the Campo de Calatrava region (Ciudad Real), with important Ordovician fossiliferous localities.

Type material: Holotype: MGM-6199-O, internal and external moulds of ventral valve. Paratypes: twenty one internal moulds and fifteen external moulds of ventral valves, eighteen external moulds and thirteen internal moulds of dorsal valves, and internal and external moulds of four ventral valves and two dorsal valves, with numbers: MGM-6170-O to MGM-6247-O.

Type locality: NE-IIIA, 5600 m SE of Navas de Estena, Ciudad Real Province, Spain. UTM coordinates: lat 39°27’33’’N, long 4°28’31’’W.

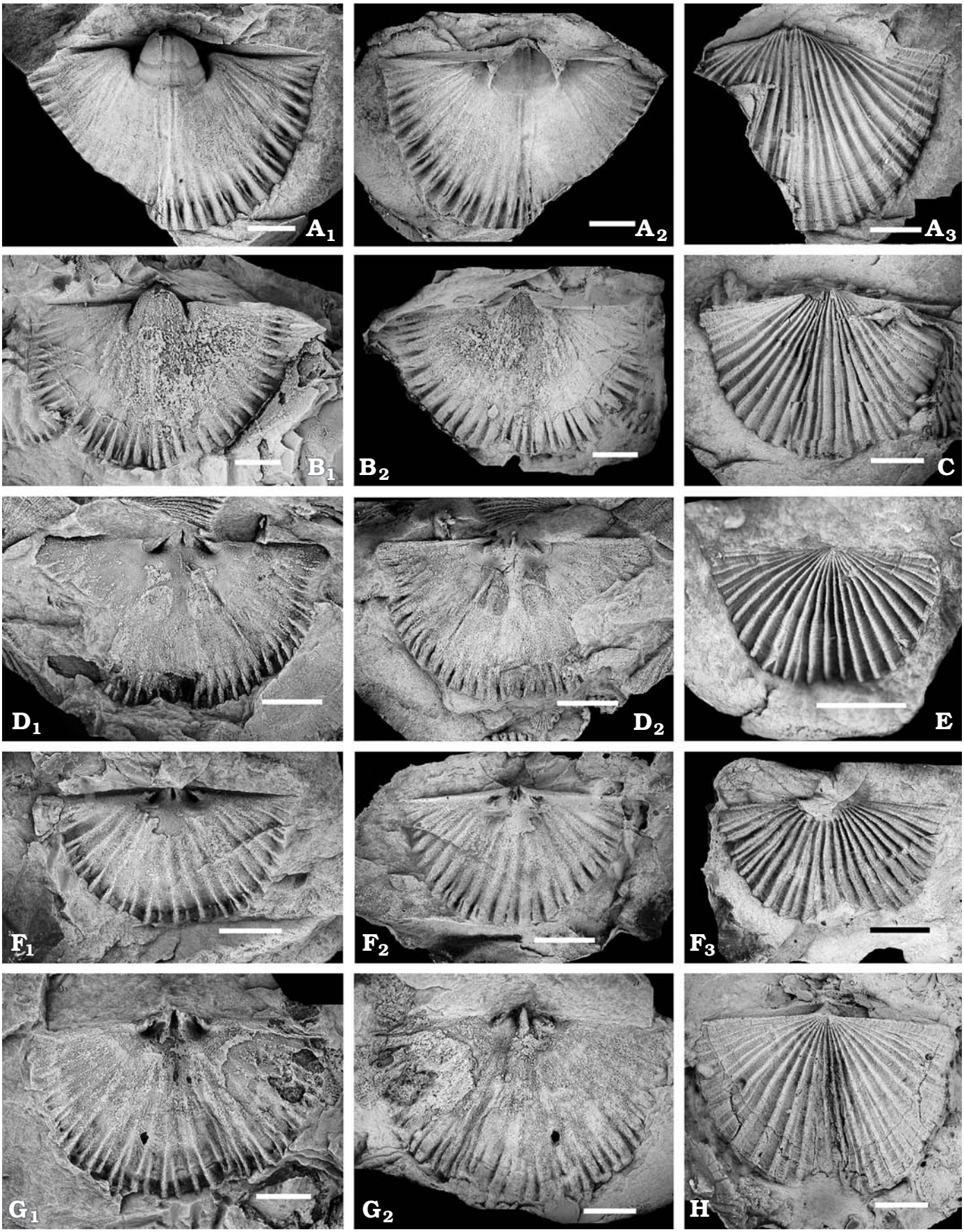
Type horizon: 130 metres above the base of the Navas de Estena Formation, *Didymograptus artus* Biozone, lower Oretanian, middle Darriwilian Stage of the Middle Ordovician Series.

Diagnosis.—*Sivorthis* species of variably auriculate outline, acute cardinal angles, 60–85% as long as wide and sulcate anterior commissure; radial ornamentation irregularly costellate, with 15–25% of costae ramified and 23–36 ribs in valve margin, capillate and filate; subtriangular ventral muscle field, 20–40% as long as valve; quadripartite dorsal muscle field, with anterior pair larger than posterior, and median ridge widest at its anterior end by mid valve length.

Description.—Shell ventribiconvex, up to 25 mm long, of variably auriculate outline, maximum width along hinge line, acute cardinal angles, 60–85% as long as wide (m = 72%, v = 1%, n = 36) and weakly sulcate anterior commissure, more accentuated in deformed valves. Ventral valve convex, with weak median fold and subplanar posterolateral areas, 20–46% as deep as long (m = 30, v = 1%, n = 13); ventral interarea planar to slightly curved, apsacline, 5–11% as long as valve (m = 7%, v = 0. 04%, n =13), with wide open delthyrium. Dorsal valve slightly convex, with shallow and wide median sulcus; dorsal interarea shorter than ventral interarea, with open notothyrium. Radial ornamentation irregularly costellate, with 15% of costae ramified by 10 mm growth stage and 25% ramified in largest valves; high ribs with rounded crests, numbering 23–36 at valve margins and 6–9 per 5 mm at 5 mm anteromedially from umbo; capillate and filate.

Ventral interior with pedicle callist weakly developed,

Fig. 9. Orthid brachiopod *Sivorthis calatravaensis* Reyes-Abril and Villas sp. nov. **A**. Holotype, MGM-6199-O, internal mould (A_1), latex cast of interior (A_2) and latex cast of exterior (A_3) of ventral valve. **B**. MGM-6203-O, internal mould (B_1) and latex of the interior (B_2) of ventral valve. **C**. MGM-6211-O, latex cast of exterior of ventral valve. **D**. MGM-6242-O, internal mould (D_1) and latex cast of interior (D_2) of dorsal valve. **E**. MGM-6219-O, latex cast of exterior of ventral valve. **F**. MGM-6239-O, internal mould (F_1), latex cast of interior (F_2) and latex cast of exterior (F_3) of dorsal valve. **G**. MGM-6241-O, (NEII), internal mould (G_1) and latex cast of interior (G_2) of dorsal valve. **H**. MGM-6247-O, latex cast of exterior of dorsal valve. Scale bars 5 mm. →



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triangular teeth and crural fossettes; dental plates short and perpendicular to valve floor, diverging anteriorly and continuous with muscle bounding ridges; subtriangular muscle field with anterior margin slightly rounded, 20–40% as long as valve (m = 29%, v = 0.2%, n = 24), 16–55% as wide as valve (m = 24%, v = 0.1%, n = 24), with adductor track halved by weak median ridge, 10–22% as wide as muscle field (m = 17%, v = 0.001%, n = 6), diductor scars about as long as adductor scars, not enclosing them anteriorly; ventral vascula media parallel and adjacent, arising from adductor track and diverging at anterior third of valve.

Notothyrial platform short and high, excavated anteriorly by posterior adductor scars and continuous with median ridge, widening forward and reaching about mid length of valve in adult stages (see Fig. $9D_1$, D_2); cardinal process ridge-like, narrow and short; brachiophores rod-like, short, welded to notothyrial platform; dental sockets broad, excavated on secondary shell deposits; muscle field quadripartite, 34–63% as long as valve (m = 48%, v = 0.5%, n = 15), 16–35% as wide as valve (m= 26%, v = 0.2%, n = 20), with anterior adductor scars at least double in width and length than posterior adductor scars, separated by curved ridges that diverge anteriorly.

Radial ornamentation impressed on interior of both valves, with internal margins crenulated with deep and narrow grooves, corresponding to crest of ribs, and wide eminences with shallow sulci on intercostal spaces.

Discussion.—The weakly sulcate anterior commissure, costellate ornamentation and parallel and adjacent ventral vascula media of these orthids are amongst the most distinctive diagnostic features of *Sivorthis*. But these specimens can be discriminated from all the known species of this genus by their auriculate outline, thus a new species is proposed.

The irregularly costellate ornamentation of the new species, with 23–36 ribs, most closely resembles that of *Sivorthis tenuicostata* (Cooper, 1956), with 30–40 ribs, and *Sivorthis friendsvillensis* (Cooper, 1956), with 32–36 ribs; they can be distinguished by the acute cardinal angles of the new species, the obtuse cardinal angles of *S. tenuicostata* and the rectangular to obtuse cardinal angles of *S. friendsvillensis*. The new species has more numerous ribs than in *Sivorthis ardmillanensis* (Reed, 1917), which has notably coarser ribs. Its auriculate outline distinguishes it from *Sivorthis eucharis* (Schuchert and Cooper, 1938) that has a rounded outline and obtuse cardinal angles. The relatively coarse costellation of the new species is very different from the finely costellate type species, *Sivorthis filistera* Jaanusson and Bassett, 1993, with 40–46 ribs. Its ribbing and weakly sulcate anterior commissure allows simple distinction from *Sivorthis noctilio* (Sharpe, 1849), with 36–52 observed ribs and strongly sulcate shell, occurring in the overlying horizons and described below.

Stratigraphic and geographic range.—Known from the Navas de Estena syncline (locality NE-IIIA), in the lower horizons of the Navas de Estena Formation, and from eastern Sierra Morena (localities CC-IIIA, Calzada de Calatrava; VM-I, Viso del Marqués, Ciudad Real Province; and AQ-II, Aldeaquemada, Jaén Province), in the lower part of the Río Formation.

Sivorthis noctilio (Sharpe, 1849)

Figs. 10E–I, 11.

1849 *Orthis noctilio* sp. nov.; Sharpe 1849: 151, pl. 6: 2a–2c.
1955 *Orthis vespertilio* Sow.; Ramírez y Ramírez 1955: 421, 422, pl. 71: B.
1956 *Orthis* (*Harknessella*?) cf. *noctilio* Sharpe; Thadeu 1956: 22, pl. 9: 1.
1984 *Monorthis noctilio* (Sharpe); Gutiérrez-Marco et al. 1984: 315, 316.
1994 "*Orthis*" *noctilio* Sharpe; Mayoral et al. 1994: pl. 1: 1–6.

Lectotype: Internal and external moulds of a dorsal valve, figured by Sharpe (1849: pl. 6: 2a, b) and stored at NHM with registration numbers NHM 82902 and NHM 82904.

Type locality: The lectotype was reported by Sharpe (1849) to have been "found in slate near Valongo" (north, south, or west of that city according with those stated in the original paper). The more accessible outcrop exposed today near Valongo is found about 2 km southeast of the city, along the road to San Pedro da Cova in the western flank of the Valongo anticline, where *S. noctilio* has been determined in one of the studied localities (grid reference lat 41°10'45''N, long 8°30'09''W).

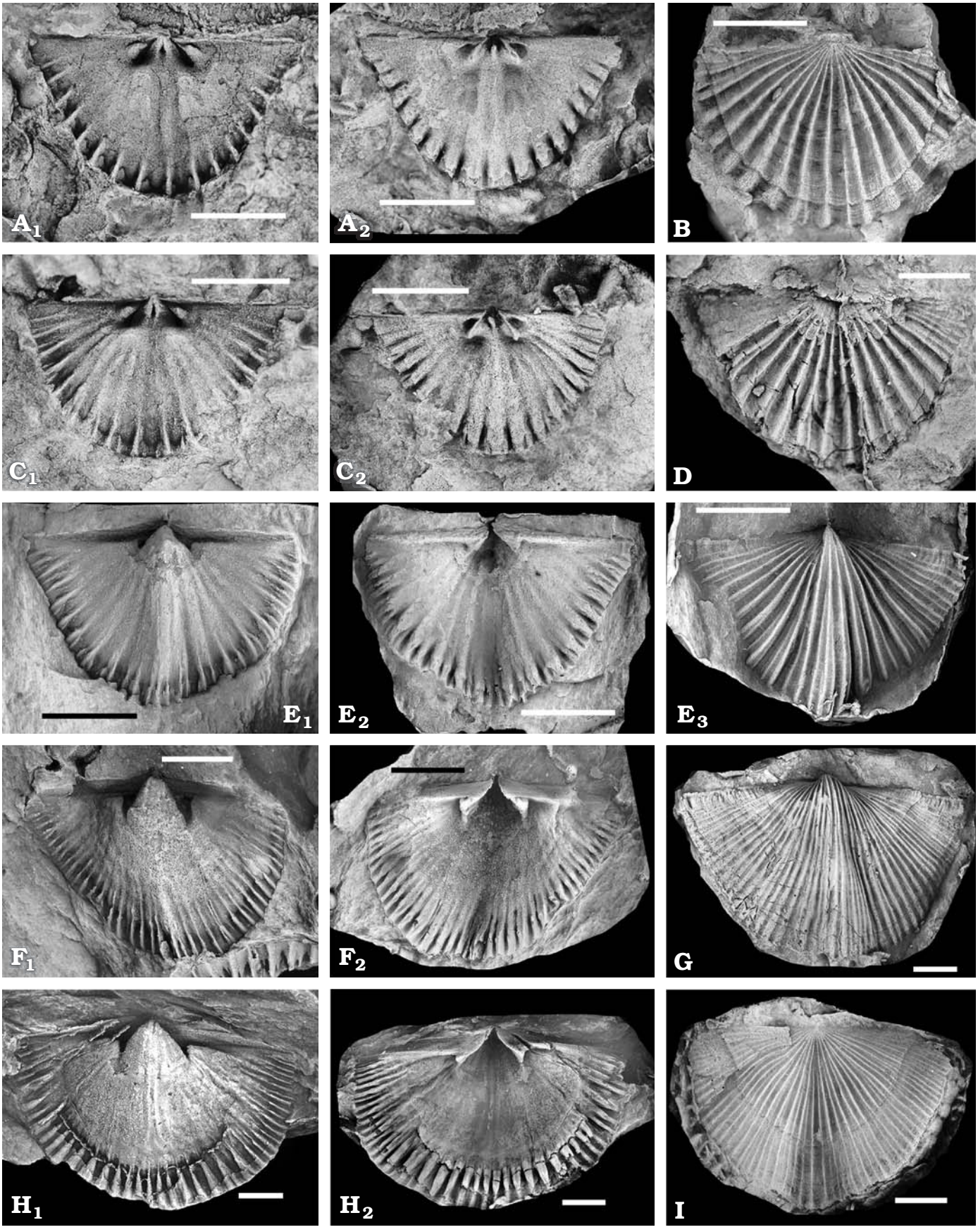
Type horizon: Lower part of the Valongo Formation, lower Oretanian, middle Darriwilian Stage of the Middle Ordovician Series.

Material.—Twenty nine internal moulds and twenty three external moulds of ventral valves, nine internal moulds and thirteen external moulds of dorsal valves, internal and external moulds of two ventral valve and three dorsal valves, and two shells with conjoined valves, with numbers: MGM-6248-O to MGM-6328-O.

Emended diagnosis.—*Sivorthis* with mucronate outline in young stages and semicircular outline in adults, cardinal angles acute to rectangular and strongly sulcate anterior commissure; radial ornamentation ramicostellate, with up to three generations of costellae in adult shells, and 36 to 52 ribs at valve margin.

Description.—Shell ventribiconvex, up to 28 mm long and 52 mm wide, of mucronate outline in young stages changing to semicircular in adults, maximum width along hinge line, cardinal angles acute to rectangular, rarely slightly obtuse in very large shells, 51–84% as long as wide (69% in lectotype), with highest values in largest shells; anterior commissure

Fig. 10. **A**–**D**. Orthid brachiopod *Sivorthis calatravaensis* Reyes-Abril and Villas sp. nov. **A**. MGM-6213-O, internal mould (A_1) and latex cast of interior (A_2) of dorsal valve. **B**. MGM-6236-O, latex cast of exterior of dorsal valve. **C**. MGM-6228-O, internal mould (C_1) and latex cast of interior (C_2) of dorsal valve. **D**. MGM-6226-O, latex cast of exterior of dorsal valve. **E**–**I**. *Sivorthis noctilio* (Sharpe, 1849). **E**. MGM-6269-O, internal mould (E_1) latex cast of interior (E_2) and latex cast of exterior (E_3) of dorsal valve. **F**. MGM-6266-O, internal mould (F_1) and latex cast of interior (F_2) dorsal valve. **G**. MGM-6303-O, latex cast of exterior of ventral valve. **H**. MGM-6285-O, internal mould (H_1) and latex cast of interior (H_2) of ventral valve. **I**. MGM-6322-O, latex cast of exterior of ventral valve. Scale bars 5 mm. →



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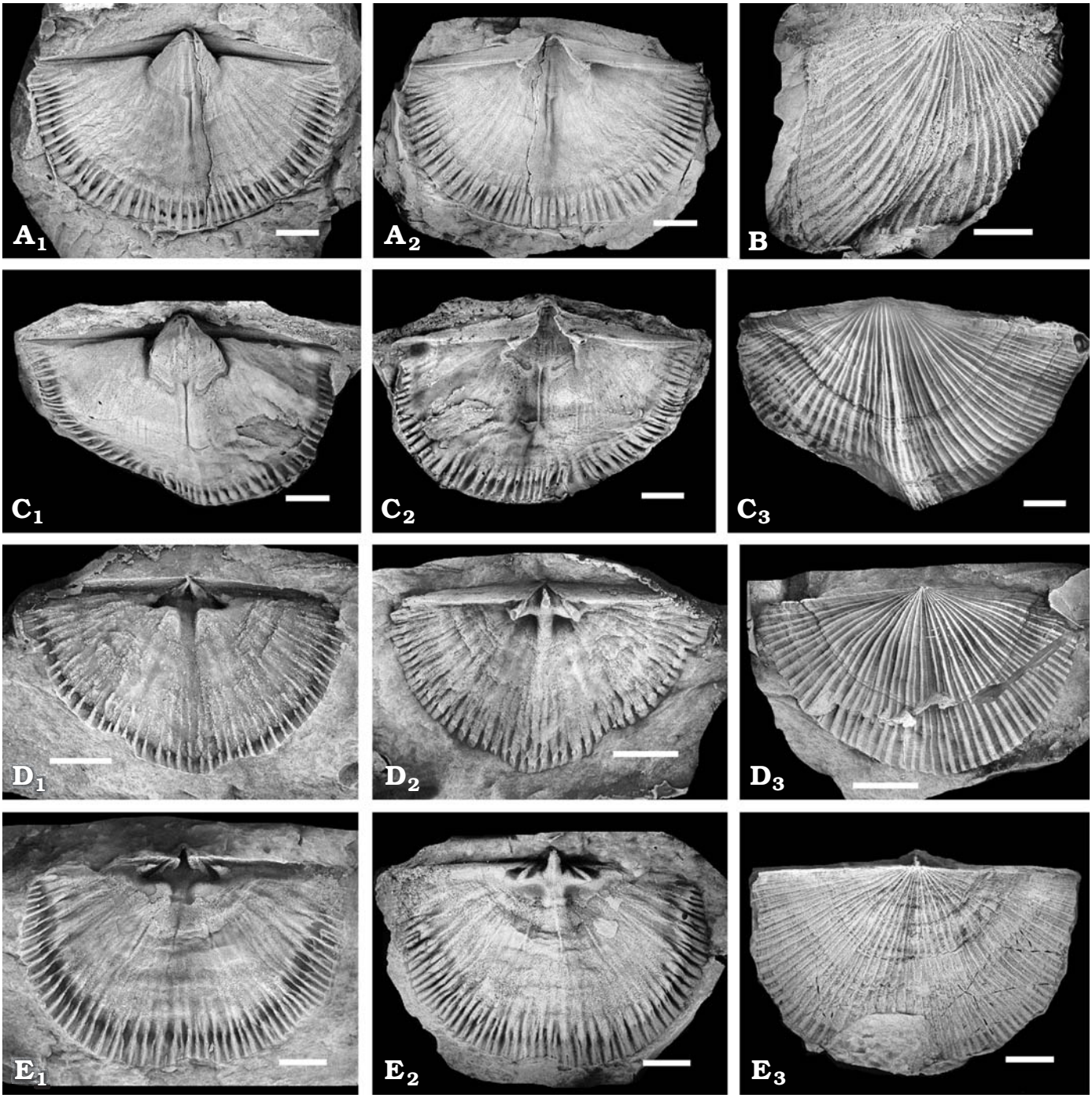

Fig. 11. Orthid brachiopod *Sivorthis noctilio* (Sharpe, 1849). **A**. MGM-6249-O, internal mould (A_1) and latex cast of interior (A_2) of ventral valve. **B**. Lectotype, NHM 82904, latex cast of exterior of dorsal valve. **C**. MGM-6273-O, internal mould (C_1), latex cast of interior (C_2) and latex cast of exterior (C_3) of ventral valve. **D**. MGM-6317-O, internal mould (D_1), latex cast of interior (D_2) and latex cast of exterior (D_3) of dorsal valve. **E**. MGM-6304-O, internal mould (E_1), latex cast of interior (E_2) and latex cast of exterior (E_3) of dorsal valve. Scale bars 5 mm.

strongly sulcate, more accentuated with deformation. Ventral valve convex, with strong median fold and subplanar posterolateral areas, 11–39% as deep as long (29% in lectotype), with highest values in deformed shells; ventral interarea planar to slightly curved, apsacline, 5–11% as long as valve, with wide and open delthyrium. Dorsal valve weakly convex with accentuated median sulcus, occupied by 4 to 6 ribs; dorsal interarea plane, anacline, 5–8% as long as valve, with radial striae parallel to open notothyrium. Radial ornament ramicostellate with high and narrow ribs on rounded crests, numbering 36–52 in adult valve margins and 3–8 per 5 mm at 5 mm anteromedially from umbo; up to three generations of costellae in adult shells, 25–30 fila per mm and 2–3 strong growth striae in adult shells.

Ventral interior with triangular teeth and crural fossettes; dental plates short, continuous with slender muscle bounding ridges and well developed pedicle callist; muscle field subcordate, 24–43% as long as valve (m =34%, v = 0.2%, n = 21), 18–32% as wide as valve (m = 24%, v = 0.2%, n = 20), with diductor scars longer than adductor scars, separated by slender median ridge, partially enclosing them anteriorly, and adductor track 9–16% as wide as muscle field. Ventral mantle canal system saccate, with parallel and adjacent vascula media, arising from adductor track and diverging at anterior third of valve.

Dorsal valve with short notothyrial platform, posteriorly sloping and continuous with wide, short median ridge; cardinal process ridge-like, thick and high, flanked by two notothyrial ridges; brachiophores rod-like, welded to notothyrial platform, and narrow dental sockets excavated on secondary shell deposits; muscle field with poorly impressed adductor scars, 18–30% as wide as valve.

Shell with radial ornamentation well impressed on interiors of both valves, often obscuring muscle fields; internal margins crenulated with deep and narrow grooves, corresponding to crest of ribs, and wide eminences with shallow sulci on intercostal spaces, not reaching valve margin.

Discussion.—*Orthis noctilio* Sharpe, 1849 was described originally from the Darriwilian horizons within the Valongo Formation, close to Valongo (Portugal). The description was based on the internal and external moulds of a dorsal valve and the internal mould of a ventral valve (Sharpe 1849: pl. 6: 2a–2c) and although referred to in several stratigraphic papers (e.g., Delgado 1908; Gutiérrez-Marco et al. 1984; Sá 2005), there has not been a taxonomic update until this study. In spite of the scarcity of the type material and the brief original description of *O. noctilio*, its features are distinctive enough to assign it with certainty the above described taxon. The study of the large Spanish sample and the revision of the Portuguese type material, stored at NHM have allowed an emended diagnosis and the proposal of a generic assignment for the species. The dorsal valve figured by Sharpe (1849: pl. 6: 2a, b) has been selected as the lectotype of the species. Another of the species defined by Sharpe (1849) from the Middle Ordovician of Valongo, *Orthis duriensis*, is similar externally to *O. noctilio*, and could be conspecific. Nevertheless, its revision has not been possible, since the dorsal valve illustrated by Sharpe (1849: pl. 6: 4a, b), could not be found among the other Valongo types, stored at NHM (Sarah Long, personal communication 2007).

The radial ornamentation of *O. noctilio*, finely costellate and filate, with one or two generations of costellae close to the umbo, besides its ventral vascula media, parallel and adjacent until the anterior third of the valve, allows assignment to *Sivorthis*. Within the genus, it can be discriminated from the other known species by its strongly sulcate anterior commissure and its high rib number. Most *Sivorthis* species are coarsely costellate, and even *S. filistera* Jaanusson and Bassett, 1993, with the finest ribs, numbering 40–46 at the valve margin, has a lower rib number than *Sivorthis noctilio*, with counts up to 52. Another clearly distinguishing feature from congeneric species is the outline, with obtuse cardinal angles for most shells, while they are acute to mucronate in *S. noctilio*.

Stratigraphic and geographic range.—Known from Valongo and Arouca localities, northern Portugal, in the middle part of the Valongo Formation (Sharpe 1849); from the locality VPA (Ventas con Peña Aguilera, Toledo Province, central Spain), in the lower part of the Navas de Estena Formation; and from Sion-les-Mines and "Laillé high" east from Guichen (south of Rennes, Armorican Massif, western France), in the lower part of the Traveusot Formation; all of them of early Oretanian age. All of these localities are of early Oretanian (mid Darriwilian) age.

Palaeobiogeographical remarks

The family Orthidae is mostly restricted to the Ordovician, with only a few genera surviving through the Silurian to the earliest Devonian (Williams and Harper 2000). By its first appearance datum, latest Early Ordovician (Floian or mid Arenig), the family was already diverse and dispersed throughout Gondwana and the neighbouring mid latitude continents of Baltica and South China: *Celsiorthis* Paterson and Brock, 2003 from the palaeoequatorial Australian margin of Gondwana; *Leoniorthis* Egerquist, 2003 from Baltica; *Paralenorthis* Havlíček and Branisa,1980 from the temperate proto-Avalonia (Bates 1968) and pre-Andean margins of Gondwana (Havlíček and Branisa 1980; Benedetto 2003b; Gutiérrez-Marco and Villas 2007), as well as from South China (Zhan and Jin 2005); and *Suriorthis* Benedetto, 2003a also from the pre-Andean margin of Gondwana. The family spread during the early Middle Ordovician (early Dapingian) to other tropical palaeocontinents, including Laurentia (Jaanusson and Bassett 1993) and Kazakhstan (Nikitina et al. 2006). By the same time it was consolidated on Baltica and Avalonia (Jaanusson and Bassett 1993). The only known Lower Ordovician (Floian) occurrence of the family at high latitudes is from the siltstone beds of the Montagne Noire (France), where Mélou (in Babin et al. 1982) recognised *Sinorthis typica* Wang, 1955 and described one species of *Sinorthis* Wang, 1955 and two species of *Orthambonites*, subsequently assigned by Jaanusson and Bassett (1993) to *Paralenorthis* and to an undetermined orthid genus. This incursion of the family within the Mediterranean region, or Afro-South European margin of Gondwana, is exceptional, since at that time the region was mostly occupied by inshore clastic deposits of the Armorican Quartzite facies, dominated by giant infaunal linguliform brachiopods. It was not until the mid Darriwilian transgression (early Oretanian/approx. early Abereiddian) when orthids became common in the Mediterranean region, as the Central Iberian collections studied herein demonstrate. Little can be said about their possible dispersion into other Mediterranean regions, since the

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early Oretanian is either rarely present or poorly fossiliferous. Nevertheless, our recovery of the Iberian species *Sivorthis noctilio* from a locality in the southern Armorican Massif, makes it possible that the highly diversified orthid fauna recorded from the middle Darriwilian of central Iberia is more widespread, reaching all the Ibero-Armorican Domain. Outside Ibero-Armorica virtually nothing is known about them, excepting some sporadic occurrences from Morocco (Havlíček 1971).

The two new orthid genera, *Almadenorthis* and *Gutiorthis*, are unknown outside the Mediterranean region, and are considered as adaptations to cold water within a family typically of temperate and tropical environments. The ancestor of the genus *Sivorthis* was apparently among these genera from warmer waters, but its first known species, mid Darriwilian in age, were adapted both to cold water, as in the Iberian *S. calatravaensis* and *S. noctilio*, and to warm waters as in Laurentian *Sivorthis eucharis* (Ulrich and Cooper, 1938) and *Sivorthis occidentalis* (Cooper, 1956). The genus disappeared from the Mediterranean area after the early Oretanian, but migrated into Baltica and Avalonia, persisting on this microcontinent and on Laurentia until the early Late Ordovician. The other two recorded genera, *Orthambonites* and *Paralenorthis*, belong to a group of pandemic orthids, dispersed through temperate and tropical continents during the Arenig (end of the Early Ordovician—beginning of the Mid Ordovician). They also migrated into the Mediterranean region, coinciding with the mid Darriwilian Oretanian transgression. Of all those genera migrating in and out of the North African margin of Gondwana, only one retained its specific identity through migration—*Paralenorthis alata*, originating in proto-Avalonia by the Floian (Bates 1969). It is unknown there after that age, but persisted on the South European margin of Gondwana until the mid Darriwilian, when Avalonia had already been detached from the continent. The extreme endemicity at the species level in Mediterranean orthids must be related to the high latitude of the region, with no other known equivalent during the Early Ordovician.

The orthids were the most common among the rhynchonelliformean brachiopods that invaded the siliciclastic North African Gondwana platforms during the mid Darriwilian transgression. Besides them, ranorthids, linoporellids, rafinesquinids and the earliest known draboviids and cremnorthids sporadically occur (Reyes-Abril et al. 2007). Nevertheless, the orthid incursion into the cold waters was very brief, and these immigrant taxa were all extinct by the late Oretanian (approximately late Abereiddian). In this sense, after the early Oretanian, the only relict "orthids of coarse ribs" known from the SW European-North African Gondwana platforms were those of an unassigned form widely distributed by the upper Oretanian on the northernmost part of the Central-Iberian Zone (Ollo de Sapo Domain: figured as "Orthacea indet." by Gutiérrez-Marco et al. 1999), as well as *Shoshonorthis tifletensis* (Havlíček, 1971) and "*Orthambonites*" *fraternus* Havlíček, 1971, from the upper Oretanian to the lower Dobrotivian (middle–upper Darriwilian) of Morocco, although their generic attribution requires further investigation (Jaanusson and Bassett 1993). *Schalidomorthis stubbefieldi* Bassett, 1981 has also been described from enigmatic olistoliths, of probable Ibero-Armorican origin and late Darriwilian age, within a Carboniferous olistostrome, overprinted by Variscan deformation on the Lizard terrane of southernmost Great Britain (Bassett 1981). By the late Katian, when the warming of the Mediterranean region allowed a generalised invasion of tropical and temperate faunas (Villas et al. 2002), the orthids were in marked decline and they never occupied the region again.

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