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Middle Ordovician strophomenoid brachiopods from the high latitude Gondwanan shelves (Central Spain) and their travel route

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KEY WORDS - Toledo Mountains, Darriwilian, brachiopods, taxonomy, Mediterranean Province, palaeobiogeography.

ABSTRACT - Two strophomenoid brachiopods from the Middle Ordovician of the Toledo Mountains, Central Spain, representing the first arrival of the group to the high latitude Gondwanan shelves are described. They are the new genus and species Oretanomena meloui*, from the Navas de Estena Shales and Río Shales, Oretanian (mid Darriwilian) in age, and* Dactylogonia asturica*, from the Guindo Shales, Dobrotivian (late Darriwilian) in age.* Oretanomena *is a primitive strophomenid of concavo-convex, dorsally geniculate profile, very close to the Iranian* Semnanostrophia*. They both settled during mid Darriwilian times on the high latitude Gondwanan shelves, much probably originating from South China ancestors after a migration along the western Gondwanan coast.* Dactylogonia asturica *settled on the Iberian platform slightly later, during the late Darriwilian, as the result of the dispersion of its genus from Laurentia, crossing the Iapetus Ocean up to Avalonia, and then also the Rheic Ocean, up to the Mediterranean margin of Gondwana.* Dactylogonia *is added to other rare rhynchonelliform brachiopods that succeeded in crossing the Rheic Ocean, during a time of strong faunal isolation of the high latitude margin of Gondwana.*

RIASSUNTO - [Brachiopodi strophomenidi nell'Ordoviciano Medio delle piattaforme gondwaniane di alte latitudini (Spagna Centrale) e loro rotte di dispersione] - *Vengono descritti due brachiopodi strophomenidi nell'Ordoviciano Medio dei Monti di Toledo (Spagna Centrale) che documentano il primo arrivo del gruppo nelle piattaforme di alte latitudini del Gondwana. Si tratta del nuovo genere e nuova specie* Oretanomena meloui*, dai Navas de Estena Shales e Río Shales, di età Oretanian (Darriwilian medio), e* Dactylogonia asturica*, dai Guindo Shales, di età Dobrotivian (tardo Darriwilian).* Oretanomena *è un primitivo Strophomeninae che mostra una morfologia concavo-convesso, genicolata dorsalmente, molto simile a quella del genere iraniano* Semnanostrophia*. La morfologia più comune della conchiglia degli Strophomeninae è resupinata con soli pochi generi convesso-piani, dorsi-biconvessi o concavo-convessi, quali* Oretanomena*. Il possesso di cardinalia di Tipo A ne permette l'inserimento entro gli Strophomeninae.* Oretanomena *è presente in una associazione a brachiopodi di substrati fangosi scuri, dominata da specie endemiche ed occasionalmente anche da generi endemici della famiglia Orthidae.* Dactylogonia asturica *documenta nella regione l'altra sottofamiglia Furcitellinae degli Strophomenidae. Il taxon, inizialmente descritto da rocce vulcanoclastiche della Zona Cantabrica (estremo nord della Spagna), viene ora segnalato in un singolo affioramento in una unità scistosa della Zona Centro-Iberica meridionale. Entrambi i taxa si stabilirono durante la metà del Darriwilian nelle piattaforme di alte latitudini del Gondwana, molto probabilmente a partire da forme più antiche della Cina meridionale dopo una migrazione lungo la costa occidentale del Gondwana.* Dactylogonia asturica *si stabilì successivamente nella Piattaforma Iberica, nel tardo Darriwilian, come risultato della dispersione del genere dal Laurentia, attraverso prima l'Oceano Giapeto fino ad Avalonia, e poi l'Oceano Reico, fino al margine mediterraneo del Gondwana.* Dactylogonia *si aggiunge ad altri rari brachiopodi rynchonelliformi che riuscirono ad attraversare l'Oceano Reico, durante un periodo di forte isolamento faunistico del margine di alte latitudini del Gondwana. Sebbene la presenza di questi strophomenidi sia molto rara nell'Ordoviciano Medio dell'Europa sud-occidentale, alcune segnalazioni in numerosi articoli di fine XIX e inizio XX secolo suggeriscono che la distribuzione geografica di alcuni di essi potrebbe estendersi anche alla parte portoghese della Zona Centro-Iberica.*

INTRODUCTION

Brachiopods of the order Strophomenida did not become relatively frequent at the North African-Mediterranean Gondwanan shelves until the Kralodvorian (late Katian), coinciding with the warming Boda event and the spreading of carbonate sedimentation on the region. During the Early and Middle Ordovician the dominant rhynchonelliformean brachiopods in the area were orthides, very often of endemic families, as Drabovidae, Euorthisinidae and Heterorthidae. They thrived on siliciclastic platforms at high latitudes, making up brachiopod communities of low diversity. The first conspicuous taxon in the region is the plectambonitoid *Aegiromena mariana* Drot (in Chauvel et al., 1969), abundant in the Dobrotivian (upper Darriwillian) of Iberia, Armorica and occasionally North Africa, where it frequently crowds many bedding planes. Besides this species, within an association where orthides are more diverse, *Dactylogonia asturica* (Villas in Villas et al., 1989) can occasionally be found, representing the other superfamily of the order, the Strophomenoidea. *D. asturica* was first described from volcaniclastic rocks of the Cantabrian Zone in northernmost Spain (locality CV in Fig. 1a), but it has been recently reported from dispersed outcrops of shaly units in Central Spain (Reyes-Abril et al., 2011). In lower horizons of Central Spain, Oretanian (middle Darriwilian) in age, a new strophomenoid genus and species assigned to the subfamily Strophomeninae occurs, within a brachiopod association that thrived on dark muddy substrates. This association is dominated by endemic species and occasionally also endemic genera of the family Orthidae. Both species represent the first arrival of brachiopods of the superfamily Strophomenoidea to the high latitude Gondwanan shelves. The earliest strophomenoid settled there during the first stages of the

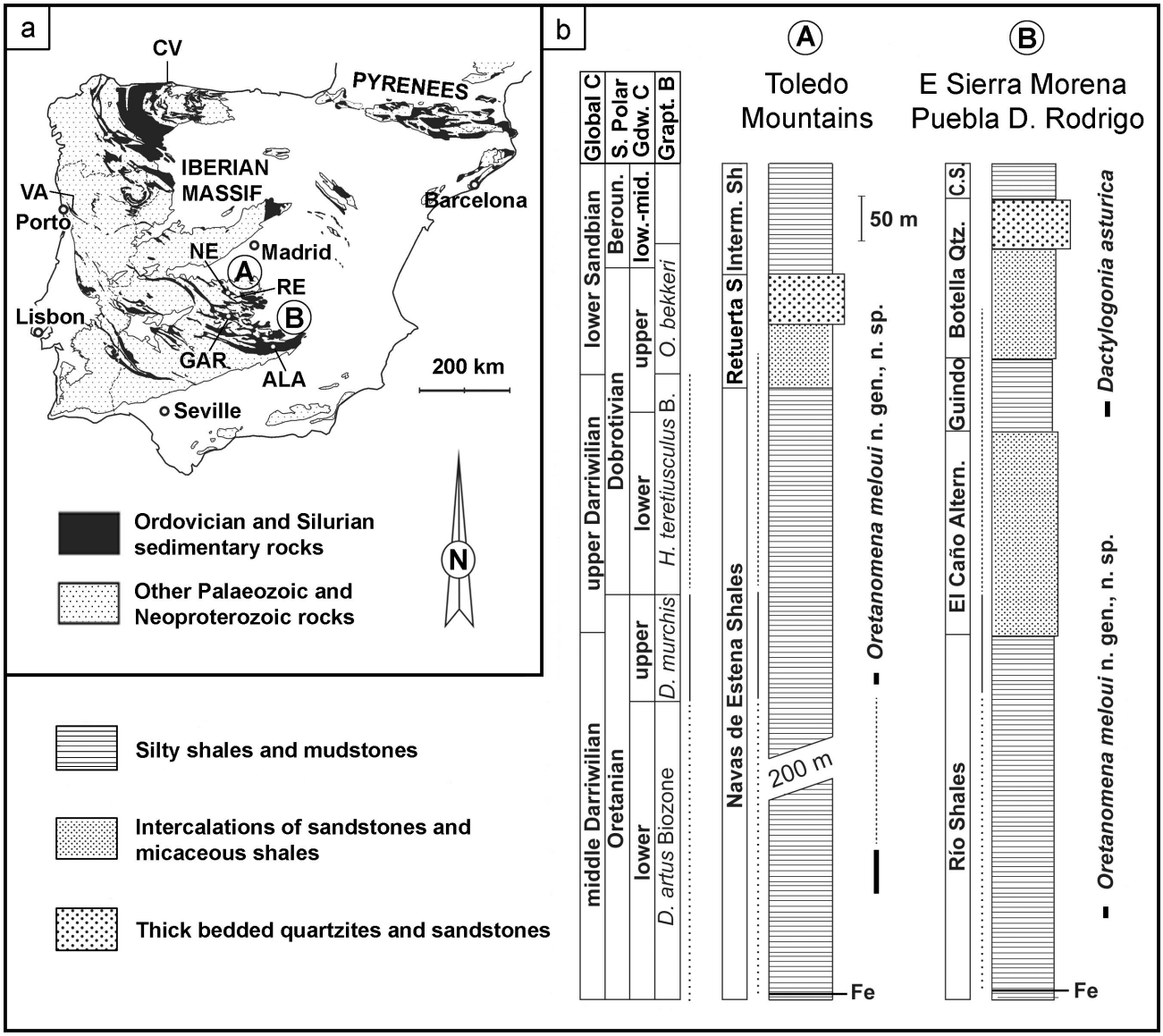


Fig. 1 - Location sketch-map and stratigraphical placement of the studied brachiopods. a) Map of the main Ordovician-Silurian outcrops of the Iberian Massif, with reference to the palaeontological localities mentioned in the text. Abbreviations: ALA, Alameda; CV, Cabo Vidrias; GAR, Puebla de Don Rodrigo; NE, Navas de Estena; RE, Retuerta del Bullaque; VA, Valongo Area (Portugal). 1 and 2 (encircled) are the representative areas of the lithostratigraphic units detailed to the right. b) Stratigraphical columns of the main Middle Ordovician formations in the southeastern Central-Iberian Zone (see map). The left-hand columns indicate the approximate equivalence between the global chronostratigraphy (Global C.), the South Polar Gondwanan regional scheme (S. Polar Gdw. C) and some graptolite biozones (Grapt. B). Other abbreviations: Altern., Alternations; B, Biozone; Beroun., Berounian; C.S., Cantera Shales; D., *Didymograptus* (and *D. murchisoni*); Fe, thin oolitic ironstone bed; Guindo, Guindo Shales; H, *Hustedograptus*; Interm. Sh, Intermediate Shales; O, *Oepikograptus*; Qtz, Quartzite; S, Sandstone. Note that the stratigraphical range of the graptolite biozones are directly annotated on the left side of each column.

mid Darriwilian transgression that drowned the platforms dominated since Floian times by the inshore clastic deposits of the Armorican Quartzite facies. Its arrival onto the Mediterranean margin of Gondwana coincided with the beginning of a major diversification of the superfamily Strophomenoidea in South China, at a time when it is poorly known from other palaeocontinents (Zhan et al., 2013). Simultaneously, *Dactylogonia* dispersed throughout the equatorial Laurentia, with at least five known species from the U.S.A. and Canada (Cooper, 1956; Ross, 1970).

After the preliminary analysis presented by Villas et al. (2014), in this paper we are describing those rare strophomenoids from the Oretanian and Dobrotivian of Central Iberia and analysing the path they could have followed to arrive into the high latitude Mediterranean margin of Gondwana during the late Mid Ordovician.

GEOGRAPHICAL AND GEOLOGICAL SETTING

Middle Ordovician brachiopods of the order Strophomenida (other than the plectambonitoid genus *Aegiromena*) are rare fossils in southwestern Europe. This is why the studied material only consists of fifty-four brachiopod specimens from five localities on the southern

part of the Central-Iberian Zone of the Iberian Massif. This strongly contrasts with the large collection of thousands of orthids and *Aegiromena* specimens from hundreds of localities in the same area, initiated by Gutiérrez-Marco et al. (1984), continued with the palaeontological works in more than 20 sheets of the Geological Map of Spain to 1:50,000 scale, and finally studied by Reyes-Abril (2009) and Reyes-Abril et al. (2010, 2011, 2013). The present work is a continuation of the former studies.

The examined localities are from beds of mid and late Darriwilian age placed respectively in two partially correlated formations: the Navas de Estena Shales and the Río Shales, cropping out in the core of the Navas de Estena and Puebla de Don Rodrigo synclines, and the Guindo Shales of eastern Sierra Morena (Fig. 1). The studied brachiopods are preserved as internal and external moulds in massive dark mudstones, and are always associated with a rich benthic fauna of trilobites, molluscs, echinoderms, ostracods, other brachiopods and rare graptolites. The endemic character of most of these benthic assemblages favoured its relative dating and correlation following the South Polar regional chronostratigraphic scheme (Gutiérrez-Marco et al., 2015, 2017; with previous references and suggested equivalences with the global scale).

The studied strophomenoid brachiopods from the Navas de Estena syncline occur in the lower half of the Navas de Estena Formation from two different sections. The first and westernmost is the Cuesta de Valderuelo section, 5.6 km southeast of Navas de Estena, province of Ciudad Real (locality NE-III, NE in Fig. 1a: 39º27´28.3″N, 4º28´34.6″W). The second locality is the south-eastern Raña section, 2-3.6 km southeast of Retuerta del Bullaque, province of Ciudad Real (loc. RE in Fig. 1a: horizons RE-II = loc. 3 in Montero, 1989, fig. 3: 39º26´11.6″N, 4º23´27.2″W; and RE-V = loc. 9 in Montero, 1989, fig. 3: 39º26´37″N, 4º23´57″W). Material from the Puebla de Don Rodrigo syncline is from an exposure in the lower part of the Río Formation situated in the Celadilla gorge (= garganta), 7 km southeast of Puebla de Don Rodrigo, province of Ciudad Real (loc. GAR in Fig. 1a: 39º2´30″N, 4º33´43″W). Fossiliferous localities NE-III, RE-II and GAR are placed in the middle Darriwilian (Dw2) *Didymograptus artus* graptolite Biozone (Bergström et al., 2009) and belong to the *Orthambonites-Sivorthis noctilio* brachiopod Biozone of Reyes-Abril et al. (2011), correlated with the lower Oretanian of the regional scale. Locality RE-V is placed on slightly higher beds, within the *D. murchisoni* Biozone of graptolites and the *Cacemia ribeiroi* Biozone of brachiopods, still in the Dw2 but already in the upper Oretanian (Fig. 1b).

The studied brachiopods from eastern Sierra Morena occur in the lower half of the Guindo Formation from a single section placed in the left bank of the Guadalén river, 2.2 km northeast of the La Alameda country house, and 13.8 km east of Aldeaquemada, province of Jaen (Andalusia, locality ALA-II: 38º25´46.3″N, 3º12´57.7″W; = loc. ALA in Fig. 1a). The fossiliferous assemblage includes some other brachiopods and trilobites indicative of the *Heterorthina kerfornei-Aegiromena mariana* Biozone and the *Morgatia hupei* sub-Biozone (top of the *Placoparia tournemini* Biozone). This trilobite sub-Biozone lies in a narrow interval of the upper lower Dobrotivian, being tentatively correlated with the "middle" upper Darriwilian (Dw3) of the global scale.

The record of rare strophomenids in some of the lower Oretanian localities here studied was first anticipated by Gutiérrez-Marco et al. (1984) and Montero (1989), who referred them to the genus *Macrocoelia* Cooper, 1956, but without any descriptions or figures. *Macrocoelia* is now considered as a junior synonym of the rafinesquinid genus *Colaptomena* Cooper, 1956, with a compressed plano- to concavoconvex profile (Cocks & Rong, 2000), similar to that of the shells studied herein, but lacking their dorsal geniculation. With reference to the Ibero-Armorican area, the only other place where strophomenids of similar age have been mentioned is the Valongo area in the Oporto district, North Portugal (loc. VA in Fig. 1a). Delgado (1892, 1908) reported from there several species of "*Strophomena*" from the so-called "*Didymograptus*" and "*Uralichas ribeiroi*" shales, now referred to the lower half of the Valongo Formation. This correlates well with beds in similar position occurring in the Navas de Estena Formation, which also bear the same fossil assemblages, including rather endemic orthid brachiopods (Reyes-Abril et al., 2010). Among the "*Strophomena*" species listed tentatively by Delgado (1892, 1908) we found, however, one Upper Ordovician form ("*S.* cf. *spiriferoides* McCoy, 1851" - now *Bicuspina*) and two Lower Devonian species ("*S. concomitans* Barrande, 1879" - now *Dalejodiscus*, and "*S.* cf. *phillipsi* Barrande, 1848" - now *Bojodouvillina*). As all of them are associated to typical Middle Ordovician trilobites, molluscs, echinoderms, brachiopods and other invertebrates, obviously the former identifications are wrong, but at the same time they are indicative that the geographical distribution of some of the present described taxa may range in the future into the Portuguese part of the Central-Iberian Zone. This could be solved with new field research in the relatively unexplored lower half of the Valongo Formation or, alternatively, after a future restudy of the original collections of J.F. Nery Delgado, which is stored in the National Laboratory of Energy and Geology (LNEG), Portugal.

SYSTEMATIC PALAEONTOLOGY

Repository - All the specimens are deposited in the Museo Geominero, Madrid, Spain (MGM-6447-O to MGM-6482-O, and MGM-7031-O to MGM-7039-O).

Order Strophomenida Öpik, 1934
Superfamily Strophomenoidea King, 1846
Family Strophomenidae King, 1846
Subfamily Strophomeninae King, 1846

Genus *Oretanomena* n. gen.
Type species *Oretanomena meloui* n. gen., n. sp., lower Oretanian (basal middle Darriwilian, Middle Ordovician), Toledo Mountains (Central Spain)

Derivation of name - Referred to the Cordillera Oretana, to which the Toledo Mountains and the Puebla de Don Rodrigo region belong, and from where the new genus is being described.

Diagnosis - Shell slightly concavoconvex, with both valves dorsally geniculate, unequally parvicostellate ornamentation, ventral muscle field flabellate, open anteriorly, socket ridges with gently to strongly postero-laterally curved anterior ends.

Remarks - This new genus can be ascribed to the family Strophomenidae King, 1846 as it possesses a cardinalia of Type A (see Rong & Cocks' [1994] classification), with a well-developed notothyrial platform and a postero-ventrally projected, bilobed cardinal process, as well as for the strong socket ridges, curved postero-laterally at their anterior ends. According to Cocks & Rong's (2000) subfamily diagnosis, the absence of muscle bounding ridges in the dorsal valve and the very weak side septa allow rejecting their inclusion in the subfamily Furcitellinae Williams, 1965 and locating them within the subfamily Strophomeninae King, 1846.

The most frequent shell profile within the Strophomeninae is resupinate, but several of its genera are convexoplanar or dorsibiconvex. Only two genera have been included within the subfamily with a concavoconvex profile, similar to that of the Iberian shells: *Drummuckina* Bancroft, 1949 from the Upper Ordovician of Girvan (Scotland) and *Ochyromena* Zhan, Jin, Rong & Liang, 2013 from the lower Middle Ordovician of South China. The Iberian Strophomeninae can be distinguished from these two taxa on the basis of a dorsally geniculate profile, as well as a parvicostellate ornamentation that is multicostellate in *Drummuckina*. According to Zhan et al. (2013) the Iranian genus *Semnanostrophia*, assigned originally to the family Glyptomenidae by Ghobadi Pour et al. (2011), must be also included within the strophomenines on account of its cardinalia of type A (Rong & Cocks, 1994). Although *Semnanostrophia* is very close to the Iberian strophomenine, with a planoconvex profile, as well as a parvicostellate ornamentation, it can be distinguished from the new genus based on non-geniculate shells and for its divergent socket ridges, not curved, as in the Iberian genus.

Oretanomena meloui n. sp.
(Figs 2a-g and 3a-e)

1984 *Macrocoelia* n. sp. 1 & n. sp. 2 Prieto - Gutiérrez-Marco, Rábano, Prieto & Martín, Tab. 1, p. 302.
1989 *Macrocoelia* sp. - Montero, p. 406, Tab. 1.
2011 *Dactylogonia* sp. nov. Reyes-Abril, Gutiérrez-Marco & Villas, Fig. 1.

Derivation of name - In honour of Michel Mélou, for his work on the Ordovician brachiopods of the Mediterranean region.

Diagnosis - As for the genus.

Type specimens - Holotype: internal mould of a dorsal valve (MGM-6480-O); paratypes: seventeen internal moulds and three external moulds of ventral valves, seven internal moulds and three external moulds of dorsal valves, as well as internal and external moulds of two ventral valves and three dorsal valves (MGM-6448-O, MGM-6455-O to MGM-6470-O, MGM-6472-O, MGM-6474-O, MGM-6478-O, MGM-6481-O, MGM-6482-O, and MGM-7031-O to MGM-7039-O).

Type horizon - Navas de Estena Shales (130 m above its base). *Didymograptus artus* graptolite Biozone, lower Oretanian, middle Darriwilian (Dw2, Middle Ordovician).

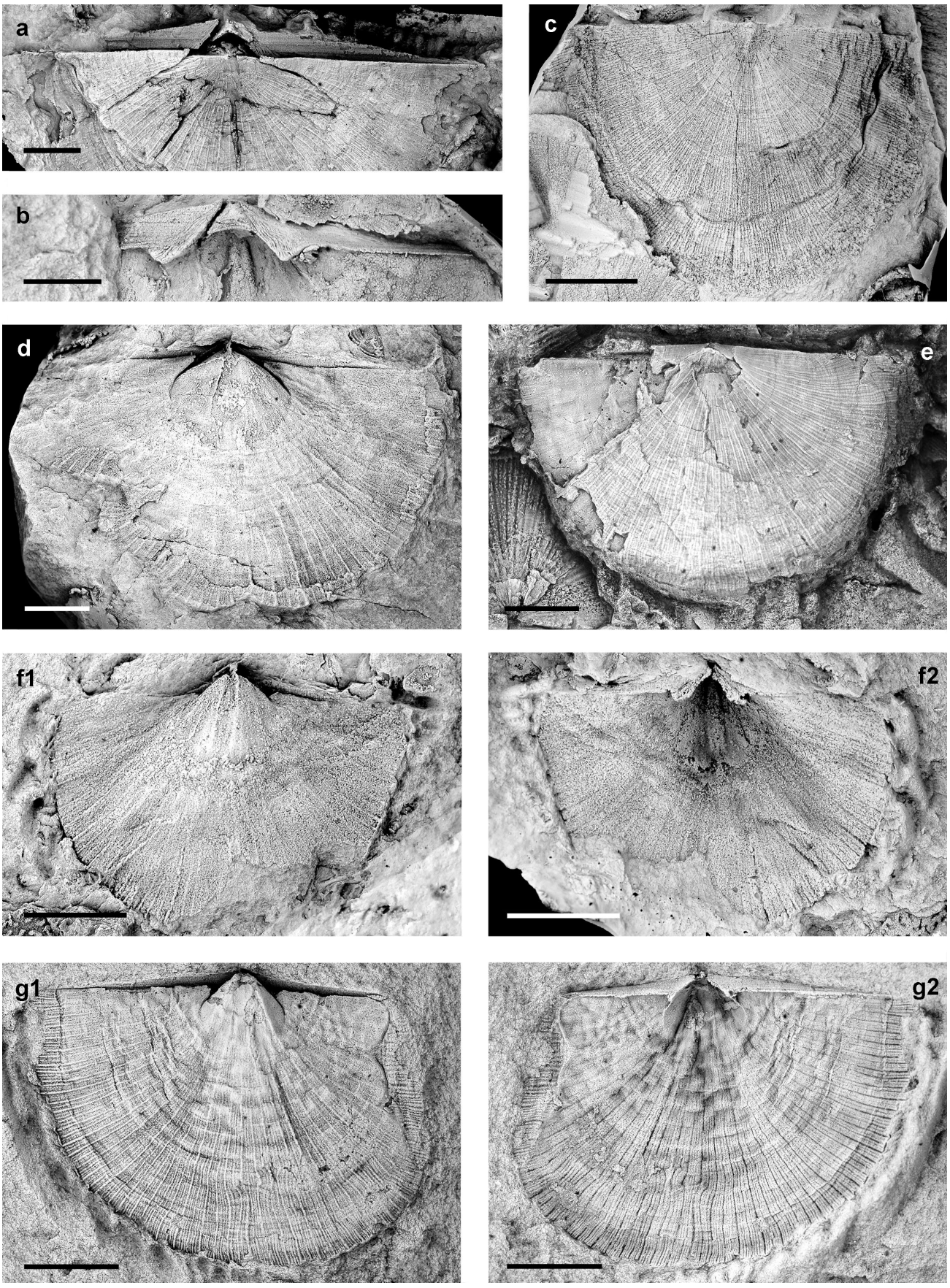
Type locality - NE-III: 5.6 km southeast of Navas de Estena, province of Ciudad Real, Spain (39º27′28.3″N, 4º28′34.6″W).

Description - Shell concavoconvex, up to 28 mm long, semicircular in outline, maximum width at hinge line, right to slightly acute cardinal angles, 58-85% as long as wide (mean [m] = 0.70; variance [v] = 0.01; number [n] = 20) and rectimarginate anterior commissure. Ventral valve slightly to moderately convex, 7-18% as deep as long (m = 0.11; v = 0.0008; n = 11), occasionally with dorsal geniculation at about 15 mm from posterior end, disc forming an angle of about 90º with trail; ventral interarea apsacline, short, 7% as long as valve (n = 4), with wide delthyrium and apically perforated pseudodeltidium, up to half as long as interarea. Dorsal valve slightly concave, with deep median sulcus developed in anterior half of largest valves, dorsally geniculate at about 18-20 mm from posterior end, 56-84% as long as wide (m = 0.67; v = 0.005; n = 14); dorsal interarea anacline, very short, 3% as long as valve (n = 3), notothyrium with apical chilidium reaching hinge line laterally. Radial ornament unequally parvicostellate and filate, of narrow ribs with rounded crests, numbering 30-36 ribs per 5 mm at 5 mm anteromedially from umbo, three-seven ribs per sector, and about ten filae per mm. Occasional growth lines usually related to mantle damage.

Ventral interior with small triangular teeth with irregularly crenulated dorsal face, supported by short dental plates, slightly divergent anteriorly and towards valve floor, and continuing anteriorly as short, curved muscle bounding ridges. Muscle field flabelliform, with suboval outline, poorly impressed anterior margin, 28-48% as long as valve (m = 0.39; v = 0.003; n = 17), with adductor scars as a narrow band, 19-32% as wide as muscle field (m = 0.28; v = 0.001; n = 17).

Dorsal interior with wide and low notothyrial platform, continuing anteriorly as a relatively wide median ridge, bifurcated anteriorly. Cardinal process lobes as high blades

Fig. 2 - *Oretanomena meloui* n. gen., n. sp. a) Paratype, latex cast of exterior of shell with conjoined valves, detail of posterior part in dorsal view (MGM-6448-O), locality GAR. b) Paratype, latex cast of ventral valve, detail of interarea (MGM-6461-O), locality NE-III. c) Paratype, latex cast of dorsal valve exterior (MGM-7033-1-O), locality NE-III. d) Paratype, internal mould of ventral valve (MGM-6464-O), locality RE-II. e) Paratype, ventral valve exterior (MGM-6469-O), locality RE-V. f) Paratype, internal mould (f1) and latex cast of interior (f2) of ventral valve (MGM-6459-O), locality NE-III. g) Paratype, internal mould (g1) and latex cast of interior (g2) of ventral valve (MGM-6458-O), locality NE-III. Scale bars correspond to 5 mm.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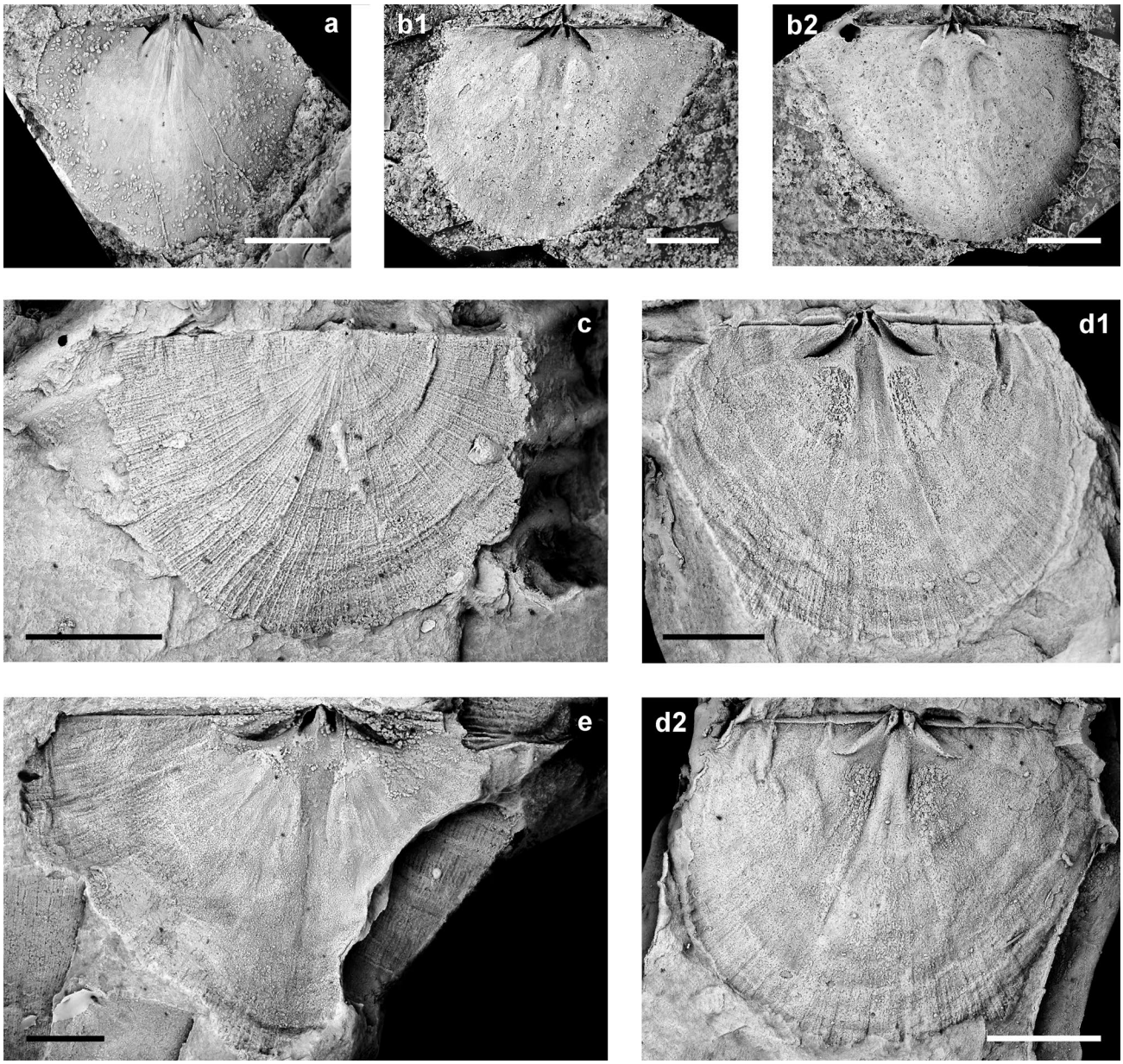

Fig. 3 - *Oretanomena meloui* n. gen., n. sp. a) Paratype, internal mould of ventral valve (MGM-6455-O), locality GAR. b) Paratype, internal mould (b1) and latex cast of interior (b2) of dorsal valve (MGM-6470-O), locality GAR. c) Latex cast of dorsal exterior (MGM-7039-O), locality NE-III. d) Holotype, internal mould (d1) and latex cast of interior (d2) of dorsal valve (MGM-6480-O), locality NE-III. e) Paratype, internal mould of dorsal valve (MGM-7031-O), locality NE-III. Scale bars correspond to 5 mm.

diverging anteriorly, discontinuous with socket ridges, and expanded postero-ventrally, with myophores developed posteriorly to hinge line. Socket ridges long, diverging anteriorly and with gently to strongly postero-laterally curved anterior ends in largest valves. Dorsal muscle field well impressed posteriorly only, with slender and straight transmuscle ridges, extending anteriorly for up to 35% of valve length. Side septa very slightly developed exclusively in largest valves.

Remarks - The main part of the collection is from the lower half of the Navas de Estena Shales, with an early Oretanian (Dw2) age, but one ventral valve exterior (MGM-6469-O) has been collected from the middle half of the same unit, with a late Oretanian (Dw2-3) age. There are no differences in the shape or ornamentation of this valve with the other ventral exteriors of the studied collection, but since neither shell interiors nor dorsal valves are known from the middle half of the Navas de Estena Shales, the range extension of the new species up to these upper Oretanian beds cannot yet be fully confirmed.

Occurrence - Localities NE-III, RE-II, RE-V, Navas de Estena Shales; GAR, Río Shales: Oretanian (middle Darriwilian), southern Central-Iberian Zone, Spain.

Subfamily Furcitellinae Williams, 1965

Genus *Dactylogonia* Ulrich & Cooper, 1942

Type species *Dactylogonia geniculata* Ulrich & Cooper, 1942, Middle Ordovician, Porterfield (Tennessee, U.S.A.)

Dactylogonia asturica (Villas in Villas et al., 1989)
(Fig. 4a-d)

1989 *Hesperinia asturica* Villas n. sp. - Villas, Gisbert & Montesinos, p. 561-564, Pl. 5, figs 6-13; Pl. 6, figs 1-12.
2011 *Dactylogonia asturica* (Villas, 1989) - Reyes-Abril, Gutiérrez-Marco & Villas, Fig. 1, Pl. 1, fig. B.

Material - Internal and external moulds of four ventral valves and five dorsal valves (MGM-6447-1-O, MGM-6447-2-O, MGM-6449-O to MGM-6454-2-O, and MGM-6473-O).

Description - Shell concavoconvex, up to 28 mm wide, dorsally geniculate, with semicircular outline, maximum width on hinge line, right or slightly acute cardinal angles, 79-94% as long as wide, and rectimarginate anterior commissure. Ventral valve homogeneously convex with high apsacline interarea and apical, perforated pseudodeltidium. Dorsal valve concave, dorsally geniculate at about 15 mm growth stage, with obtuse angle between disc and trail; anacline dorsal interarea, shorter than ventral, with small chilidium supported by slender mesocardinal ridge. Radial ornamentation multicostellate, with very thin ribs of rounded crest, numbering 22 to 26 in 5 mm, 5 mm anteromedially from umbo, intercostal spaces the same size as ribs, and variable number of growth lines coinciding with mantle damage.

Ventral valve interior with small cardinal teeth triangular in section, very short dental plates, flat and divergent anteriorly and towards valve floor, continuous anteriorly with low muscle bounding ridges. Ventral muscle field suboval, open anteriorly, 31-35% as long as valve length, 24-28% as wide as valve width, with diductor scars flanked posterolaterally by adjustors scars and divided in two lobes by radial ridges, longer and wider than adductor scars, not enclosing them anteriorly. Subperipheral rim low, more prominent on posterolateral sides.

Dorsal valve interior with long and high notothyrial platform, continuous anteriorly with robust median ridge extending anteriorly up to one third of valve length, with bifurcating anterior end unconnected to slender central median ridge; socket ridges strong and straight, diverging anteriorly, bounding large, triangular dental sockets, occasionally bounded externally by curved ridges in one of the two dental sockets; cardinal process lobes as thick and high, subparallel plates, with crenulated myophores posterior to hinge line, postero-ventrally facing; dorsal muscle field deeply impressed, with short transmuscle ridges and long sinuous side septa, about the same length as central median ridge; strong subperipheral rim separating disc from trail. Radial ornamentation well impressed on ventral interiors but only slightly on dorsal interiors, with exception of their valve margins. Mantle peripheral canals clearly impressed close to dorsal subperipheral rim.

Remarks - These shells coincide in their main features with *Hesperinia asturica* Villas (in Villas et al., 1989), known from the lower Dobrotivian (upper Darriwilian) of Asturias, north of Spain (Truyols et al., 1996; Gutiérrez-Marco et al., 1999), including profile, outline, ornamentation and dorsal and ventral interiors. Only the geniculation of ventral valves described in the largest valves of the Asturian collection, has not been identified in the shells studied herein. Villas (in Villas et al., 1989) assigned the species to *Hesperinia* Cooper, 1956 commenting also its great affinities with *Dactylogonia* Ulrich & Cooper, 1942, both genera having been included within the family Oepikinidae by Pope (1976), who considered that they could be synonymous. After Cocks & Rong's (2000) revision of the strophomenoids both genera were included in different families, *Dactylogonia* in the Strophomenidae King, 1846, and *Hesperinia* in the Glyptomenidae Williams, 1965, although the latter with uncertainty because of its poorly known cardinal process. Rong et al. (1999) contributed to a better knowledge of the genus and its type species, *Hesperinia kirki* Cooper, 1956 from the early Darriwilian of Nevada (U.S.A.), and included it within the Strophomenidae on account of its cardinalia of Type A (Rong & Cocks, 1994). According to Rong et al. (1999) both genera can be discriminated, since *Dactylogonia* has dorsal geniculation, much stronger transmuscle ridges, side septa, and median ridge, which are different from those of *Hesperinia*. Following these authors and the differential features between *Dactylogonia* and *Hesperinia* that they remarked, the Asturian species, now also identified from the Middle Ordovician of Central Spain, seems to be better allocated within *Dactylogonia*.

Dactylogonia is mainly known from Darriwillian to Katian beds in North America, Scotland and Northern Ireland, with more than 20 named species (see Cooper, 1956 and Cocks, 2008), most of them of parvicostellate ornamentation and thus easy to discriminate from the multicostellate *Dactylogonia asturica*. One of those parvicostellate species is the Bohemian *Dactylogonia blyskavensis* Havlíček, 1967, of early Berounian (Sandbian) age, the only other known species from the former high latitude Gondwanan areas. Havlíček (1976) erected a new genus, *Blyskavomena*, with *D. blyskavensis* as its type and only species, a posteriori regarded by Cocks & Rong (2000) a junior synonym of *Dactylogonia.*

The rare multicostellate species of the genus can also be readily differentiated from the Iberian species considering different features, as the much better developed ventral muscle bounding ridges of *Dactylogonia homostriata* (Butts, 1942) or the coarser ribbing of *Dactylogonia subaequicostellata* Cooper, 1956.

Occurrence - The Castro Formation, upper lower Dobrotivian (uppermost Darriwilian), Cantabrian Zone, Spain. Guindo Shales, upper lower Dobrotivian (uppermost Darriwilian), southern Central-Iberian Zone, Spain.

PALAEOBIOGEOGRAPHICAL REMARKS

It is not until the first stages of the mid Darriwilian transgression (early Oretanian/approx. early Abereiddian) that rhynchonelliform brachiopods became common on the high latitude Gondwanan shelves, covered until then by inshore clastic deposits of the Armorican Quartzite facies.

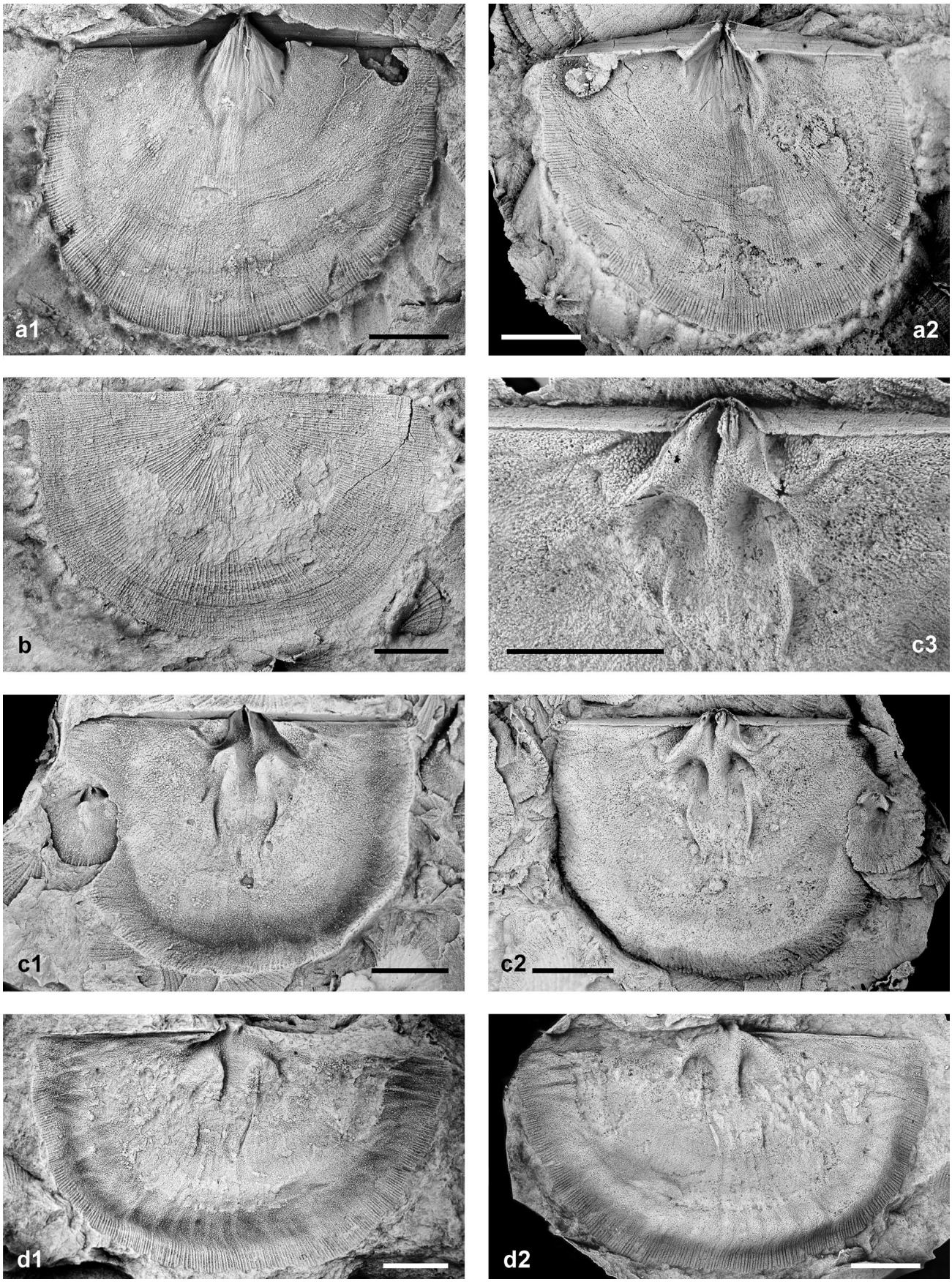

Fig. 4 - *Dactylogonia asturica* (Villas in Villas et al., 1989), all from locality ALAM-II. a) Internal mould (a1) and latex cast (a2) of ventral valve (MGM-6447-1a-O). b) Latex cast of dorsal valve exterior (MGM-6452-2-O). c) Internal mould (c1), latex cast of interior (c2), and detail of cardinalia in postero-ventral view (c3) of dorsal valve (MGM-6453-2-O). d) Internal mould (d1) and latex cast (d2) of interior of dorsal valve (MGM-6447-2a-O). Scale bars correspond to 5 mm.

Those first stages are well recorded in Central Spain, with low diversity brachiopod associations thriving on the dark muddy substrates resulting from the Darriwilian transgression. The associations are dominated by endemic species and occasionally also endemic genera of the family Orthidae (Reyes-Abril et al., 2010), with secondary occurrences of endemic drabovids, cremnorthids and strophomenids (Reyes-Abril et al., 2011). This is characteristic of the High latitude brachiopod province of Harper et al. (2013), well isolated from their Celtic, Baltic and Low latitude provinces. The isolation from these provinces would be a consequence of the clockwise gyre of the Rheic convergence, postulated by Pohl et al. (2015) between 40º S and 80º S. It is in this context that a member of the superfamily Strophomenoidea first arrives to the Mediterranean margin of Gondwana, coinciding with the beginning of a major diversification of the superfamily in South China (Zhan et al., 2013). It is the new genus *Oretanomena*, whose closest taxon is the Iranian genus *Semnanostrophia* Ghobadi Pour, Popov & Kebria-ee (in Ghobadi Pour et al., 2011). Both genera settled during mid Darriwilian times on the high latitudes Gondwanan shelves, much probably originating from South China ancestors after a migration along the western Gondwanan coast (Zhan et al., 2013).

The path followed by *Dactylogonia* to reach Iberia during the late Darriwilian must have been different than that of the older *Oretanomena* along the western Gondwana coast. The genus was well represented in the equatorial Laurentia, where it possibly originated, with at least five known species from mid and late Darriwilian of the U.S.A. and Canada (Cooper, 1956; Ross, 1970) and one unnamed species from Scotland (Williams, 1962). In spite of the almost endemic relationships of *Dactylogonia* with Laurentia, where it persisted until the Late Ordovician (Cooper, 1956; Williams, 1962), the genus demonstrated punctually its ability for dispersion. By the late Darriwilian *Dactylogonia* had crossed the Iapetus Ocean and arrived to Avalonia, with two unnamed species from Wales (MacGregor, 1961; Bates, 1968). It had also arrived to equatorial Gondwana following the equatorial west-ward current, with one known species from Tasmania (Laurie, 1991). Also by the late Darriwilian *Dactylogonia* crossed the Rheic Ocean and arrived to the high latitude Mediterranean margin of Gondwana, where it is represented by the Iberian *Dactylogonia asturica*, described above. The occurrence of a rhynchonelliform brachiopod genus at both sides of the Rheic Ocean is not frequent at all during the late Darriwilian, the Ordovician time of maximum isolation of the Mediterranean margin of Gondwana. The nearly 3000 km distance from north to south of the Rheic Ocean by the Darriwilian (Harper et al., 2013: fig. 11.6) would have prevented the exchange of most brachiopod species, with less dispersal potential. Nevertheless, a few eurythermal brachiopods could make the cross over from the Celtic province to the High-latitude province, probably by means of island hopping, as already hypothesised for the Sandbian by Villas et al. (2015). Besides *Dactylogonia*, at least three other genera are known to have come across the sea: *Mcewanella*, *Heterorthina* and *Tissintia*. They are well known from Iberia during the Middle Ordovician (Villas et al., 1989; Truyols et al., 1996; Reyes-Abril et al., 2011 and references therein), and have also been described from Avalonia (Williams, 1949; MacGregor, 1961; Bassett, 1981).

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