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Author: Colmenar, Jorge

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Ordovician rafinesquinine brachiopods from peri-Gondwana

JORGE COLMENAR

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The study of the strophomenide brachiopods of the subfamily Rafinesquininae present in the main Upper Ordovician sections, representing the Mediterranean margin of Gondwana, has revealed an increase in diversity of the group at the region during that time. The studied collections are from the Moroccan Anti-Atlas, the Iberian and the Armorican massifs, the Iberian Chains, Pyrenees, Montagne Noire, Sardinia, and Bohemia. Two genera of the subfamily Rafinesquininae have been recorded. Of them, the cosmopolitan *Rafinesquina* is the only one previously reported from the region and *Kjaerina* is found for the first time outside Avalonia, Baltica, and Laurentia. Additionally, two new subgenera have been described, *Kjaerina* (*Villasina*) and *Rafinesquina* (*Mesogeina*). Furthermore, the new species *Rafinesquina* (*Mesogeina*) *gabianensis, Rafinesquina* (*Mesogeina*) *loredensis*, *Kjaerina* (*Kjaerina*) *gondwanensis*, *Kjaerina* (*Villasina*) *pedronaensis*, *Kjaerina* (*Villasina*) *pyrenaica*, and *Kjaerina* (*Villasina*) *meloui* have been described. In addition, other species of these genera previously known from isolated localities in the region, such as *Rafinesquina pseudoloricata*, *Rafinesquina pomoides*, and *Hedstroemina almadenensis* are revised and their geographic range expanded. The adaptive radiation experienced by the rafinesquinines at the Mediterranean region during middle to late Katian, was probably related to changes in the regime of sedimentation and water temperature caused by the global warming Boda event.

Key words: Strophomenoidea, palaeobiogeography, adaptive radiation, Ordovician, Katian, Boda event, Gondwana, Mediterranean region.

Jorge Colmenar [colmenar@unizar.es], Área de Paleontología, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Pedro Cerbuna 12, E-50009, Zaragoza, Spain.

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Introduction

The Rafinesquininae Schuchert, 1893 is currently considered a subfamily within the Rafinesquinidae, including genera with shells lacking dorsal geniculation and often lacking rugae, except posterolaterally in gerontic specimens (Cocks and Rong 2000). According to the most recent data, the subfamily Rafinesquininae includes 14 genera ranging from Darriwilian to Ludlow and is spread worldwide (Cocks and Rong 2000). This subfamily shares some features with the closely related subfamily Leptaeninae Hall and Clarke, 1894, from which it differs, according to Cocks and Rong (2000), in not having either dorsal geniculation or concentric rugae over the whole shell. *Kjerulfina* Bancroft, 1929, in spite of its rugae over the whole disc, has been traditionally included within the Rafinesquininae (Cocks and Rong 2000) instead of within the Leptaeninae, denoting a certain difficulty to separate both subfamilies.

After their origin in North China during the early Middle Ordovician (Zhan et al. 2013), the rafinesquinine brachiopods experienced a great diversification and expanded their distribution all over the world. They spread during the late Middle Ordovician and early Late Ordovician to Baltica, Avalonia, and Laurentia palaeocontinents, to the Chu-Ili terrane (Kazakhstan), to the South American and Australian margins of Gondwana and also to the Mediterranean margin of Gondwana (Bohemia, Iberia, Anti-Atlas). The rafinesquinines colonized diverse marine environments, occupying typically middle shelf settings and becoming even dominant in some of them.

Prior to the Katian, the most common taxa in the cold-water siliciclastic shelves of the Mediterranean margin of Gondwana were heterorthids and draboviids (Villas et al. 2006). As a consequence of the middle to late Katian global warming Boda event (Fortey and Cocks 2005), optimal conditions for carbonate sedimentation at mid to high latitudes developed in the region, as an increasing of water temperature and a sea level rising, among others. Taking advantage of this event, temperate-water organisms previously

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unknown or rare in the region, colonized these platforms displacing the Mediterranean endemic taxa (Colmenar et al. 2013). Furthermore, from this moment on, rafinesquinines became more numerous and diverse in the area, accompanying by other strophomenoids such as *Longvillia* and other Dalmanellidine and Orthidine genera typically represented in Baltica and Avalonia (e.g., *Nicolella*, *Dolerorthis*, and *Eoporambonites*). The faunal signature of these low latitude immigrants suggests a Baltic-Avalonian influence.

According to the data published so far, the rafinesquinines seemed poorly represented in the Mediterranean region. There are only a few works describing or citing rafinesquinines in the region. The first one was carried out by Havlíček (1951), who assigned to *Rafinesquina* three species from the Ordovician of Bohemia, *Strophomena pseudoloricata* (Barrande, 1848), *Strophomena oculata* (Barrande, 1879), and *Strophomena vinicensis* (Barrande, 1879). Havlíček (1971) also described a new species of *Rafinesquina* (*R. pomoides*) from the Upper Ordovican rocks of Morocco, from where he also cited the occurrence of the Bohemian species *R. pseudoloricata.* The latest rafinesquinine species erected in the region was *Hedstroemina almadenensis* by Villas (1995) from Central Iberia. *Hedstroemina* has also been referred from other Ordovician localities of the studied region but mostly as indeterminate species (Villas 1985; Young 1985; Mélou 1990; Colmenar et al. 2013). They all represent a very small part of the brachiopod associations in which they are included but give clues on a bigger diversification of the subfamily in this region than hitherto expected.

The aim of this study is to analyze the diversification of Rafinesquininae at the Mediterranean margin of Gondwana during the Late Ordovician, mostly coinciding with the mid-late Katian global warming Boda event.

Institutional abbreviations.—DPZ, Museo Paleontológico of the Universidad de Zaragoza, Spain; IGM, Instituto Geológico e Mineiro, Lisboa, Portugal; LPB, Laboratoire de Paléontologie de Brest, France; MNHN.F.A, Muséum National d'Histoire Naturelle, Paris, France; MPZ, Museo Paleontológico of the Universidad de Zaragoza, Zaragoza, Spain; VOMN, field collection number Muséum National d'Histoire Naturelle, Paris, France.

Other abbreviations.— $\bar{x}$, mean; n, number of specimens; σ_n, variance.

Geographical and geological setting

For this work material from the main Ordovician outcrops from North Africa (Anti-Atlas) and Southern, Western, and Central Europe (the Armorican Massif, the Iberian Massif, the Montagne Noire, the Iberian Chains, the Pyrenees, the Carnic Alps, Sardinia, and the Bohemian Massif) have been studied. Most of them are relicts of the Variscan mountain chain.

The sampled formations range from the upper Sandbian to the upper Katian. The upper Sandbian–middle Katian units are predominantly siliciclastic. The most significant are the Louredo Formation at the Portuguese Central Iberian Zone, with alternating mudstone and sandstone beds (Young 1988); the "Bancos Mixtos" at the Spanish Central Iberian Zone, consisting in alternating shale, sandstone, and quartzite beds (Gutiérrez-Marco and Rábano 1987); the Fombuena Formation at the Iberian Chains with bryozoan marl, shale and sandstone (Villas 1983); the Cavá Formation at the Spanish Pyrenees, consisting in greywacke, siltstone, and quartzite (Hartevelt 1970); the Portixeddu Formation at Sardinia with predominantly siltstone, sandstone, and shale (Leone et al. 1991), the Glauzy Formation at the Montagne Noire composed of quartzitic sandstone (Colmenar et al. 2013); and the Lower Ktaoua and Upper Tiouririne formations from the Moroccan Anti-Atlas, both with alternating shale and sandstone beds (Destombes et al. 1985).

On the other hand, the upper Katian units are predominantly calcareous facies. The most representative are the Cystoid Limestone in the Iberian Chains, consisting of calcareous siltstone, marly limestone, and massive limestone (Villas 1983), the Gabian Formation at the Montagne Noire, with alternating marlstone and bioclastic limestone beds (Colmenar et al. 2013); and the Portilla de Luna Limestones at the Cantabrian Zone, consisting of limestone with marly intercalations (Gutiérrez-Marco et al. 1996).

Two other formations with different lithologies, also late Katian in age, crop out at the Portuguese Central Iberian Zone: the Porto de Santa Anna Formation, composed by volcaniclastic tuffs interbedded with silicified limestone (Young 1988); and at the Armorican Massif, the Rosan Formation, with alternating tuffs, dolerite sills, hyaloclastites, schists, and carbonates (Mélou 1990), both formations with abundant brachiopod content.

The logs of the most representative Upper Ordovician Mediterranean formations with the vertical distribution of the rafinesquinin taxa studied is summarized in Fig. 1. The detailed geographical and stratigraphical data of the sampled localities are provided in the Supplementary Online Material (SOM available at http://app.pan.pl/SOM/app61-Colmenar_SOM.pdf).

Systematic palaeontology

The use of open nomenclature follows recommendations by Bengtson (1988), and the synonymy lists follow recommendations by Matthews (1973).

Phylum Brachiopoda Duméril, 1806

Order Strophomenida Öpik, 1934

Superfamily Strophomenoidea King, 1846

Family Rafinesquinidae Schuchert, 1893

Subfamily Rafinesquininae Schuchert, 1893

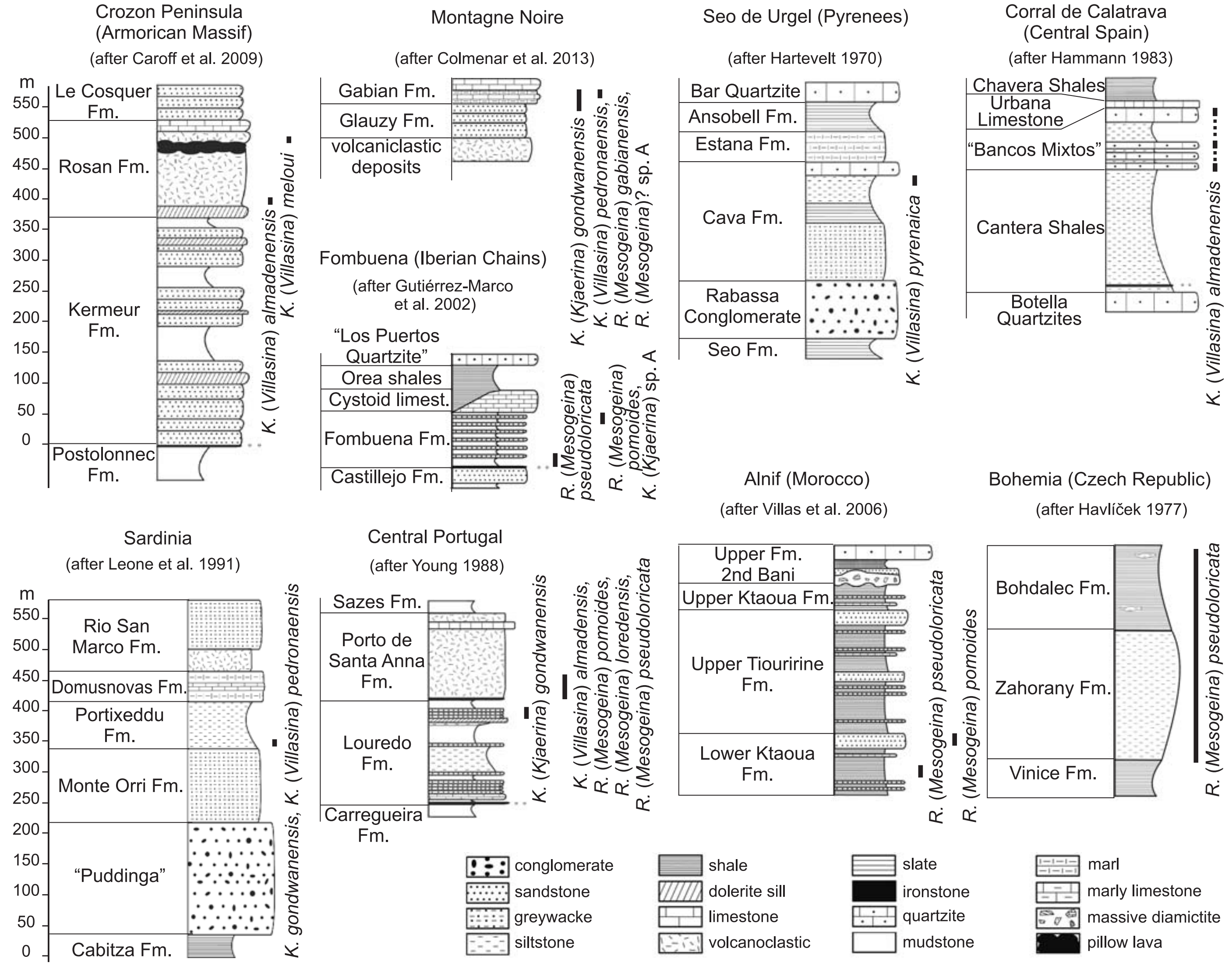


Fig. 1. Schematic stratigraphical columns and distributions of the taxa of subfamily Rafinesquininae in the most relevant SW Europe sections. Chronostratigraphical data of each section can be found in the referred papers.

Genus *Kjaerina* Bancroft, 1929

Subgenus *Kjaerina* (*Kjaerina*) Bancroft, 1929

Type species: *Kjaerina typa* Bancroft, 1929; Cheney Longville Formation, Cheneyan (lower Katian), Cheney Longville, Shropshire (UK).

Species included: *Kjaerina typa typa* Bancroft, 1929, Cheney Longville Formation, Cheneyan Stage (lower Katian), Shropshire (UK); *Kjaerina typa geniculata* Bancroft, 1929, Cheney Longville Formation, Cheneyan Stage (lower Katian), Shropshire (UK); *Strophomena bipartita* Salter in Murchison, 1854, Alternata Limestone and Cheney Longville formations, Cheneyan Stage (lower Katian), Shropshire (UK); *Leptaena complanata* Sowerby, 1839, Aurelucian Stage (lower Sandbian), Shropshire (UK); *Kjaerina jonesi* Bancroft, 1929, Horderley Sandstone Formation, Burrellian Stage (upper Sandbian), Shropshire (UK); *Kjaerina hedstroemi* Bancroft, 1929, Horderley Sandstone Formation, Burrellian Stage (upper Sandbian), Shropshire (UK); *Rafinesquina poljensis* Alichova, 1951, Hirmuse Formation, Oandu Stage (lower Katian), East Baltic and NW Russia; *Kjaerina hartae* Jin, Caldwell, and Norford, 1995, Red River Formation, Maysvillian Stage (lower Katian), southern Manitoba (Canada); *Kjaerina* (*Kjaerina*) *gondwanensis* sp. nov. Portixeddu Formation, lower middle Katian, Sardinia (Italy).

Emended diagnosis.—Rafinesquinine with abrupt dorsally directed geniculation (if present). Radial ornament parvicostellate. Concentric ornament consisting of irregular rugae sometimes covering the entire disc, sometimes restricted posterolaterally or even absent. Prominent median rib in the ventral valve often present. Dental plates always present, usually straight but may be gently curved and extending anteriorly into muscle-bounding ridges. Cardinal process bifid with plate-like lobes during all ontogeny. Socket ridges of variable strength bounding triangular dental sockets. Notothyrial platform anchor-shaped, continuous anteriorly with median ridge. Mesocardinal ridge sometimes present.

Remarks.—Since Bancroft (1929) erected *Kjaerina* and *Hedstroemina* for a group of very close species of Rafinesquininae with dorsally geniculate shells, their taxonomic validity have been questioned. Salmon (1942) considered both genera synonyms of *Rafinesquina* Hall and Clarke, 1892, considering as specific characters the differences in the amount of curvature in the dorsal valve and in the presence of a conspicuous median rib on the ventral valve of *Kjaerina*. Spjeldnaes (1957) considered them as two different subgenera within *Rafinesquina* differing in the divergence of the muscle bounding ridges and in their valve convexity. Similarly, Williams (1963) and Muir-Wood and Williams (1965) considered *Kjaerina* and *Hedstroemina* as two independent subgenera within *Kjaerina*.

Hurst (1979) observed enough differences between these two taxa to consider them as independent genera. The latter author considered that *Hedstroemina* has a less strongly developed median rib, more expressed rugae, more convex and more strongly dorsally geniculate ventral valves, wider and more impressed ventral musculature, more heavily calcified bilobed cardinal process, and thinner socket ridges than *Kjaerina*.

In spite of that, after the main revisions of the family since Hurst's (1979) work, *Kjaerina* and *Hedstroemina* have been considered as independent genera (Harper in Owen and Harper 1982; Cocks and Rong 2000; Cocks 2010), only one species remains today within *Hedstroemina* in addition to *H. fragilis*, its type species: *Oepikina*? *inaequiclina* Alichova, 1951 (Cocks and Rong 2000). *Hedstroemina almadenensis* Villas, 1995 was ascribed to the same genus but it is transferred to *Kjaerina* (*Villasina*) subgen. nov. herein.

Several Late Ordovician rafinesquinines share common features of *Kjaerina* and *Hedstroemina*, it is necessary therefore to discuss their taxonomic status, to more detail herein.

Analysis of the morphologic variability of the new species *K.* (*Kjaerina*) *gondwanensis* described (see below) allows to rule out as genus diagnostic two of the previously mentioned features: the median rib, frequent in some species of *Kjaerina,* and the rugation, considered more typical of *Hedstroemina*. The development of median rib is highly variable within the studied population of *K.* (*Kjaerina*) *gondwanensis*, displaying a continuous series of forms among the specimens with a prominent median rib (Fig. 2C, G, I) and specimens with the rib poorly developed (Fig. 2D, E, H). Similar pattern is present in the degree of rugation in *K.* (*Kjaerina*) *gondwanensis*; there is a continuity from specimens of without rugae (Fig. 2B, F), with rugae restricted posterolaterally (Fig. 2A, C–E, G, I) and rugae covering most of the shell surface (Fig. 2H). The variability of the rugation as an intraspecific feature was also stated for *Kjaerina* by Cocks (2010).

The strength of the geniculation also seems to be a variable intraspecific feature. For example, the type species of *Kjaerina* displays both geniculate (*K. typa geniculata*) and non-geniculate (*K. typa typa*) morphotypes. However, the geniculation in *Kjaerina* seems to be more abrupt than those displayed by *Hedstroemina* valves that appear to be more evenly convex (Cocks 2010).

With respect to the divergence of the dental plates, they are supposed to be narrowly divergent in *Kjaerina*, whereas they would be narrowly to widely divergent in *Hedstroemina*. Comparing the divergence angle of the dental plates in all the species of both genera (Table 1), it can be observed that the range of this feature in *Hedstroemina fragilis* is so large that it includes most of the means and ranges of this parameter in most of the species of *Kjaerina*. Thus, this character should not be used to differentiate between the discussed genera.

Table 1. Dental plates divergence in the *Kjaerina* species.

Species	Dental plates divergence angle range (mean)	Difference within ranges in each species	Reference
Hedstroemina fragilis	61–125° (96°)	64°	JC data
K. typa typa	42–89° (63°)	47°	Cocks 2010
K. typa geniculata	54–79° (63°)	25°	Cocks 2010
K. bipartita	69–98° (81°)	29°	Cocks 2010
K. complanata	89–102° (96°)	13°	Cocks 2010
K. jonesi	75–95° (86°)	20°	Cocks 2010
K. hedstroemi	41–90° (58°)	49°	Cocks 2010
K. poljensis	87°	–	JC data
K. gondwanensis sp. nov.	79–114° (90°)	35°	JC data

Ventral muscle field impression is a character too much variable among species and depends in many cases on the preservation of specimens.

The remaining diagnostic feature, i.e., strength of socket ridges has been observed in all the *Kjaerina* and *Hedstroemina* species. Typically, the socket ridges are thinner in most of *Kjaerina* species but specimens of *K. bipartita* display a similar expression of this character to the one observed in *H. fragilis*.

Finally, the supposedly more heavily calcified cardinal process lobes and thinner socket ridges of *Hedstroemina* need some comment. After revision of the topotypes of both genera housed in the Natural History Museum in London, UK, it turns out that the cardinal process lobes and the socket ridges are strongly variable features within the species of *Kjaerina*, including species with similar development to the one present in some of *Hedstroemina*. Moreover, the cardinal process lobes thicken in most brachiopod species during ontogeny, and its degree of calcification can not be used to distinguish between closely related genera.

In summary, due to the intraspecific variability in the majority of diagnostic characters of *Kjaerina* and *Hedstroemina*, without clear morphological boundaries between particular species, it does not seem to be justified to keep them in separate genera. Nevertheless, considering that there is a certain difference in the development of geniculation of their type species, it is proposed to maintain them as subgenera within *Kjaerina*, according to the criteria followed by Williams (1963) and Muir-Wood and Williams (1965). *Kjaerina* stands as the senior name for the genus, since *Hedstroemina* (= *Rakverina* Rõõmusoks, 1993 = *Virunites* Rõõmusoks, 2004) was introduced in the same paper 13 pages after *Kjaerina* (Bancroft 1929).

Kjaerina (*Kjaerina*) *gondwanensis* sp. nov.

Figs. 2, 3.

1985 *Hedstroemina* sp. A; Young 1985: 342, pl. 32: 1–13.
2013 *Hedstroemina* sp.; Colmenar et al. 2013: 159, fig. 4A–I.

Etymology: After the Gondwana supercontinent, where Mediterranean shelves were inhabited by this species.

Type material: Holotype: MPZ 2015/1335, external mould of ventral valve (Fig. $2A_1$). Paratypes: MPZ 2015/1336–1345, VOMN 2200, MNHN.F.A46450–46456.

Type locality: "Sa Siliqua", locality (Gon 1, see Hammann and Leone 1997: text-fig. 8 for exact location), Gonnessa, province of Carbonia-Iglesias, Sardinia, Italy.

Type horizon: Grey siltstone of the lower part of Portixeddu Formation, upper Berounian (lower–middle Katian, Ka1–2 stage slices).

Material.—Internal and external moulds of 39 ventral valves and 10 dorsal valves; MPZ 2015/1471–1500 from Gon1 locality, lower–middle Katian (Ka1–2).

Diagnosis.—Species of *Kjaerina* (*Kjaerina*) with variable outline during ontogeny from alate to semicircular; longitudinal profile concavoconvex. Radial ornament unequally parvicostellate with 5–8 ribs per 2 mm at 10 mm from umbo, often with prominent median rib; variable development of rugae, normally restricted to posterolateral extremities. Ventral muscle field triangular faintly impressed and without muscle bounding ridges.

Description.—Shells of medium to large size (largest specimen 31 mm wide), lateral profile concavoconvex; changing from weakly alate to semicircular in outline through ontogeny; maximum valve width at hinge line in most specimens, and more rarely slightly anteriorly to hinge line; slightly acute to rectangular cardinal angles and rectimarginate anterior commissure. Ventral valve ranging 62–130% as long as wide ($\bar{x} = 83\%$; $n = 31$; $\sigma_n = 0.16$) and 5–20% as deep as long ($\bar{x} = 10\%$; $n = 23$; $\sigma_n = 0.04$); in young specimens wider than long and vice versa in adult ones; moderately convex umbonal region and subplanar anteriorly, only one specimen with incipient dorsally directed geniculation at 17 mm long growth stage (Fig. 2E). Ventral interarea planar, apsacline, 6–13% as long as valve length, delthyrium with apical pseudodeltidium. Dorsal valve about 91% as long as wide and 9% as deep as long; with flat to slightly concave lateral profile. Dorsal interarea planar, anacline, about 2% as long as valve length; notothyrium covered by a medially grooved chilidium.

Radial ornament unequally parvicostellate with 5–8 ribs per 2 mm at 10 mm anteromedially from umbo, with up to 4–5 costellae intercalated between two costae; all of them with rounded crests; with prominent median costa in a few ventral valves. Concentric ornamentation of fila and variably developed discontinuous rugae, on posterolateral sides of valves, running oblique to hinge line; only a single specimen (Fig. 2H) with continuous rugae covering the entire valve.

Ventral interior with divergent, thin, blade-like dental plates extending forward approximately 10% of valve length and average dental plates divergence angle of 90° (range 79–114°; $n = 18$); muscle field triangular, very poorly impressed and without muscle bounding ridges.

Dorsal interior with strong and divergent socket ridges bounding triangular and elongated dental sockets; bifid cardinal process with elongated or plate-like and weakly anteriorly divergent lobes on low notothyrial platform, continuous with broad median ridge (Fig. 3A); between the cardinal process lobes a mesocardinal ridge (see Pope 1976) supporting the chilidium is present in some specimens (Fig. 3E); dorsal muscle field weakly elongated, about 90% as long as wide ($n = 1$). Shell structure finely pseudo-punctate.

Remarks.—The study of abundant and well-preserved material from Sardinia, together with material from the Glauzy Formation (Montagne Noire, France) allows now the formal description of a new species of *Kjaerina* (*Kjaerina*). Some specimens from the upper part of the Louredo Formation at Penha García Syncline (Portugal) figured by Young (1985: pl. 32: 1–13) as *Hedstroemina* sp. A, which show the same features as the studied shells, have also been included within the new species.

The presence of only one specimen with an incipient geniculation at 17 mm long growth stage (Fig. 2E) and having other much larger and without geniculation (Fig. 2B), suggests that it is an exceptional feature for the species. In some aspects *Kjaerina* (*Kjaerina*) *gondwanensis* sp. nov. resembles several species of the subgenus. The accentuated central costella, for instance, is a common feature in all species of *K.* (*Kjaerina*) except for *K.* (*Kjaerina*) *complanata* and *K.* (*Kjaerina*) *hartae.* The mucronate cardinal extremities and the posterolateral rugae are characters shared only with *K.* (*Kjaerina*) *typa typa* and *K.* (*Kjaerina*) *typa geniculata.* Nevertheless the dental plates not extending forward as muscle bounding ridges allow discriminating the studied material from these two species. *K.* (*Kjaerina*) *gondwanensis* differs from *K.* (*Kjaerina*) *hedstroemi* in lesser extension of the dental plates, in its shell outline, and presence of rugae. The new species also differs from *K.* (*Kjaerina*) *complanata* and *K.* (*Kjaerina*) *jonesi* in its shell outline and the absence of rugae. Finally *K.* (*Kjaerina*) *gondwanensis* differs from *K.* (*Kjaerina*) *bipartita* in the absence of muscle bounding ridges and possessing mucronate cardinal extremities and rugae.

Stratigraphic and geographic range.—In addition to the type locality, *K.* (*Kjaerina*) *gondwanensis* also occurs in the upper part of the Glauzy Formation (Ka1–2) and in the Gabian Formation (Ka2–4), Montagne Noire (France), as well as in the upper part of the Louredo Formation (Sa2–Ka1), Penha García Syncline (Portugal). Upper Sandbian–Katian.

Kjaerina (*Kjaerina*) sp. A

Fig. 4.

1985 *Hedstroemina* sp. 1; Villas 1985: 110, pl. 29: 4, 7; pl. 30: 1, 4, 6.
1985 *Hedstroemina*? sp. 2; Villas 1985: 111, pl. 30: 2, 3, 5, 7, 8.

Material.—Internal and external moulds of five ventral valves and one dorsal valve. MPZ 2015/1346, 1347, DPZ 368, 369, 372. Most of the specimens deformed by flattening. Lowermost Cystoid Limestone Formation at Alpartir 1 and Luesma 1 (see Villas 1985: figs. 2, 3 for exact location), Iberian Chains, Spain; upper Katian (Ka3–4 stage slices).

Description.—Shells of large size (largest specimen 46 mm wide), concavoconvex, semicircular in outline, or weakly alate in some specimens; maximum valve width normally at hinge line; slightly acute to rectangular cardinal angles. Ventral valve about 85% as long as wide; lateral profile with moderately convex disc and dorsally directed geniculation. Ventral interarea planar, apsacline, 10% as long as valve length. Dorsal valve with flat to concave disc; dorsal interarea anacline. Chilidium unknown.

Radial ornament parvicostellate with 8 ribs per 2 mm at 10 mm anteromedially from umbo, all of them with rounded crests; between two costae there are up to 6 costellae; prominent median costa present. Concentric ornamentation of irregular rugae covering the entire disc.

Ventral interior with strong, straight, short, blade-like dental plates; muscle field very well impressed, flabelliform, about 125% as long as wide and completely surrounded laterally by anteriorly convergent muscle bounding ridges. Diductor scars enclosing anteriorly lanceolate adductor scars.

Dorsal interior with thin, divergent socket ridges bounding triangular dental sockets; bifid cardinal process with anteriorly divergent, plate-like lobes. Strongly reduced anchor-shaped notothyrial platform continuous anteriorly with a short and narrow median ridge. Pseudopunctae thick, present in both valves coinciding with intercostal spaces and more developed posterolaterally to muscle scars.

Remarks.—All the external and internal characters of the studied specimens, the parvicostellate ornament with the prominent median costae, the rugae development, the ventral muscle field and the cardinalia, fit within *Kjaerina* (*Kjaerina*), according to the emended diagnosis above. The dorsally directed geniculation clearly excludes this species from *K.* (*Kjaerina*) *gondwanensis*, the only other known *Kjaerina* species from the Mediterranean margin of Gondwana. Another character that allows to demarcate this material from all the other known *K.* (*Kjaerina*) species are the parallel-sided or even convergent anteriorly muscle bounding ridges. Most likely it is a new species but it is left in open nomenclature here because of the scarcity of material and its poor preservation (most of the specimens are deformed by flattening) until more and better-preserved material is found.

Subgenus *Kjaerina* (*Villasina*) nov.

Etymology: Subgenus dedicated to Enrique Villas for his contributions in the study of the Late Ordovician brachiopods.

Type species: *Kjaerina* (*Villasina*) *pedronaensis* sp. nov.; middle to upper part of the Portixeddu Formation, Katian, Sardinia.

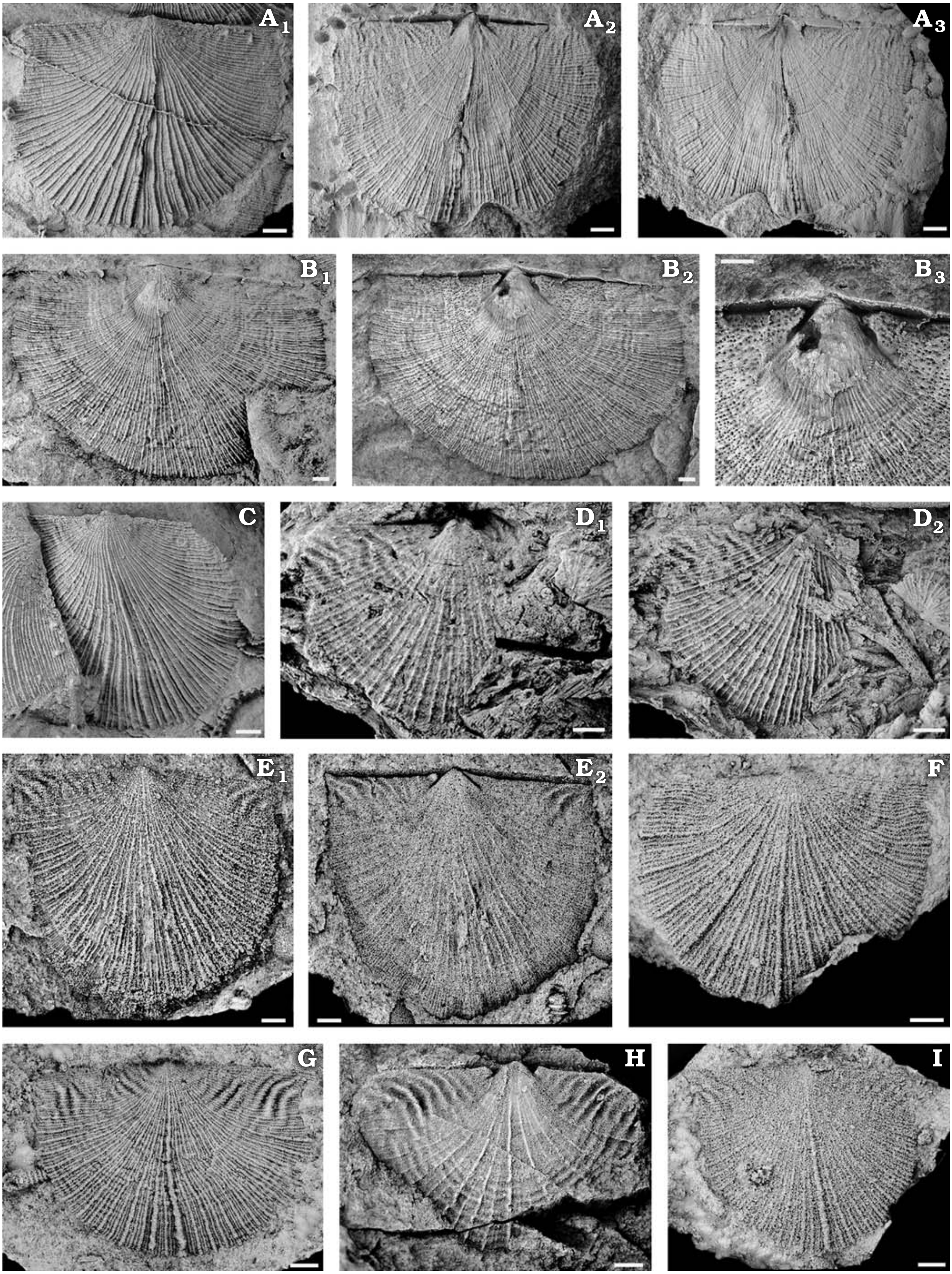
Species included: *Hedstroemina almadenensis* Villas, 1995, uppermost "Bancos Mixtos", middle Katian (Ka2 stage slice), Spanish Central Iberian Zone; *Kjaerina* (*Villasina*) *meloui* sp. nov., Tufs et Calcaires of the Rosan Formation, upper Katian (Ka3–4), Armorican Massif; *Kjaerina* (*Villasina*) *pyrenaica* sp. nov., Cavá Formation, lower–middle Katian (Ka1–2), Spanish Pyrenees.

Diagnosis.—Species of *Kjaerina* with longitudinal profile always geniculate dorsally. Radial ornament multicostellate. Concentric ornament consisting of more or less regular rugae normally covering the entire disc. Diductor scars not enclosing anteriorly adductor scars. Cardinal process lobes become extremely engrossed in some species during adult and gerontic stages.

Remarks.—Ornamentation is a character normally used to differentiate species. Nevertheless, sometimes it is also used as a key character at higher taxonomic levels. It is the case of the rugation used to distinguish between the subfamilies Rafinesquininae and Leptaeninae (Cocks and Rong 2000). Rong and Cocks (1994) in their revision of the strophomenoids, only conditionally accepted variations in the ornament as a valid character for generic and subgeneric differentiation. This is a logical criterion applied usually in all brachiopod groups, although occasionally in many brachiopod stocks and families, genera that differ exclusively in their ornamentation can be found (Cooper 1969). The ornamentation within the subfamily Rafinesquininae seems to be a good diagnostic character to demarcate genera because it allows to identify groups of species having a common ancestor.

Most of the genera in Rafinesquininae are unequally parvicostellate. Only *Megamyonia* Wang, 1949 from the Katian of North America, *Testaprica* Percival, 2009 from the Katian of central New South Wales, Australia, and *Shuangheella* Zhan and Jin, 2005 from the lower to middle Dapingian of China, are different in this respect and display multicostellate shells. Villas (1995), in erecting *Hedstroemina almadenensis* from the Upper Ordovician of central Spain considered its multicostellate ornamentation as a specific character, separating it from the parvicostellate type species *H. fragilis*. However, after a study of larger sample of rafinesquinins from several Upper Ordovician Mediterranean localities, it becomes evident that there was a radiation in the family during that time, spreading throughout the Mediterranean margin of Gondwana a close-knit group of multicostellate species, where *H. almadenensis* belongs to. This almost simultaneous occurrence of closely related and sharing an unusual ornamentation species in a previously almost uninhabited by this family region points to a common origin that merits taxonomic recognition. Nevertheless, considering the current reluctance to give generic significance to differences in the strophomenoid ornamentation (Rong and Cocks 1994), the Mediterranean spe-

Fig. 2. Ventral valves of rafinesquinine brachiopod *Kjaerina* (*Kjaerina*) *gondwanensis* sp. nov.; lower–middle Katian (Ka1–2), Upper Ordovician; Portixeddu Formation at Gonnesa, Sardinia, Italy (A–C); Gabian Formation at Tranchée Noire (D) and Glauzy Formation at Grand Glauzy hill (E–I), Montagne Noire, France. **A**. MPZ 2015/1335, holotype, latex cast of exterior (A_1), internal mould (A_2), and interior (A_3). **B**. MPZ 2015/1336, paratype, latex cast of ventral exterior (B_1), internal mould (B_2), and detail of the ventral muscle scar (B_3), showing the posterolateral pseudopunctae arrangement of a large specimen. **C**. MPZ 2015/1337, paratype, latex cast of ventral exterior. **D**. MPZ 2015/1338, internal mould (D_1) and latex cast of ventral exterior (D_2). **E**. MNHN.F.A46450, latex cast of ventral exterior (E_1) and internal mould (E_2), showing incipient geniculation. **F**. MNHN.F.A46454, paratype, latex cast of ventral exterior. **G**. MNHN.F.A46451, paratype, latex cast of ventral exterior. **H**. MNHN.F.A46452, paratype, internal mould showing rugation all over the ventral valve. **I**. MNHN.F.A46455, paratype, latex cast of ventral exterior showing a well developed median rib. Scale bars 2 mm. →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cies described below, close to *H. almadenensis*, are proposed to be grouped within a new subgenus *Kjaerina* (*Villasina*).

The concentric ornament of the studied material, consisting of irregular rugae sometimes covering the entire disc, sometimes restricted posterolaterally, as well as the bifid triangular cardinal process lobes, the straight socket ridges welded to the anchor-shaped notothyrial platform, continuous anteriorly with a median ridge, warrants its inclusion within the subfamily Rafinesquininae. Furthermore, the absence of a peripheral ridge and of socket ridges inwardly curved to bound the dorsal muscle scars, demarcates the studied material from the subfamily Leptaeninae, in spite of its well developed dorsally directed geniculation.

The material under discussion is very similar in many aspects to *Kjaerina* (*Kjaerina*) and *Kjaerina* (*Hedstroemina*), e.g., in displaying similar variable rugation as well as occasional dorsally directed geniculation. Nevertheless, its multicostellate ornamentation (Fig. 9D) allows a ready differentiation from these unequally parvicostellate subgenera.

The new subgenus also strongly recalls *Kjerulfina* Bancroft, 1929, but its shell is geniculate in dorsal direction, instead of the ventrally directed geniculation in *Kjerulfina*.

Kjaerina (*Villasina*) differs from *Megamyonia*, one of the other three multicostellate rafinesquinines, in its geniculate profile, in not having ventral transmuscle septa and in having much better developed socket ridges. It differs from *Testaprica*, also multicostellate, by its concavo-convex profile whereas the latter genus is convexo-concave to convexo-planar, or even resupinate (Percival 2009). Finally *K.* (*Villasina*) differs from *Shuangheella* in having a concavo-convex profile with very convex ventral valves, whereas *Shuangheella* is plano-convex with a very gently convex ventral valve. In addition, *K.* (*Villasina*) differs from *Shuangheella* in having a dorsal median ridge, absent in the latter, and in having straight socket ridges instead of the curved posterolaterally socket ridges of *Shuangeella*. The curved posterolaterally socket ridges is a feature typical of the family *Strophomenidae*, thus *Shuangheella* fits better within that family than in the subfamily Rafinesquininae.

Kjaerina (*Villasina*) *almadenensis* (Villas, 1995)

Figs. 5, 6.

1908 *Strophomena rhomboidalis* Wilkens; Delgado 1908: 31, 60.

1908 *Strophomena deltoidea* Conrad; Delgado 1908: 60.

1985 *Hedstroemina mundae* (Sharpe, 1853); Young 1985: pl. 34: 10 (non figs. 1–9, see remarks to *Rafinesquina* [*Mesogeina*] *pseudoloricata* below).

1985 *Hedstroemina* sp. B; Young 1985: 348, pl. 35: 1–14.

1995 *Hedstroemina almadenensis* sp. nov.; Villas 1995: 81, pl. 13: 8–13.

Holotype: MPZ 11570, internal and external moulds of dorsal valve, re-illustrated here in Fig. 2A.

Type locality: Al-1 locality, Almaden, Central Iberian Zone.

Type horizon: Calcareous sandstones of the uppermost "Bancos Mixtos".

Material.—Internal and external moulds of 30 ventral valves and 18 dorsal valves from the Spanish and Portuguese Central Iberian Zone and the Armorican Massif (France), uppermost upper Berounian (probably Ka2 stage slice, Katian).

Emended diagnosis.—Species of *Kjaerina* (*Villasina*) with ventral valve disc moderately convex; trail inclined with respect to disc 110–120°. Dorsal valve disc concave; trail inclined with respect to disc about 120°. Radial ornament with 6–8 ribs per 2 mm at 10 mm anteromedially from umbo; prominent median riboccasionally present; regular and continuous development of rugae. Ventral muscle field well impressed, flabellate. Cardinal process lobes, triangular in young specimens and extremely engrossed in adult and gerontic ones; myophores with concave and striated posteroventral surface; notothyrial platform strong; median ridge wide and high; broad transmuscle septa longer than median ridge.

Description.—Shell of medium size for the genus (largest specimen 36 mm wide), strongly concavoconvex, both valves geniculate dorsally, alate to semicircular in outline; maximum valve width at hinge line in young specimens and slightly anteriorly in adult ones; slightly acute cardinal angles in young stages and rectangular to obtuse cardinal angles in adult stages; rectimarginate anterior commissure. Ventral valve ranging 71–87% as long as wide ($\overline{x}$ = 79%; n = 5); lateral profile strongly geniculate dorsally, at approximately 20 mm long growth stage, with convex disc and trail of variable length inclined with respect to disc 110–120°; ventral interarea long, flat, apsacline with apical pseudodeltidium. Dorsal valve about 80% as long as wide; lateral profile strongly geniculate dorsally with moderately concave disc, trail of variable length inclined with respect to disc about 120°; dorsal interarea long, flat, anacline, notothyrium filled completely by cardinal process; medially grooved convex chilidium as long as dorsal interarea length, covering up to 50% of cardinal process lobes.

Radial ornament multicostellate with 6–8 ribs per 2 mm at 10 mm anteromedially from umbo; weakly prominent median costa not always present. Concentric ornamentation of fila, irregular but relatively continuous rugae with

Fig. 3. Dorsal valves of rafinesquinine brachiopod *Kjaerina* (*Kjaerina*) *gondwanensis* sp. nov.; lower–middle Katian (Ka1-2), Upper Ordovician; Portixeddu Formation at Gonnesa, Sardinia, Italy (A–E); Glauzy Formation at Grand Glauzy hill, Montagne Noire, France (F–J). **A**. MPZ 2015/1339, paratype, latex cast of dorsal interior (A_1) and detail of cardinalia of an incomplete specimen in anteroblique (A_2), posteroblique (A_3), and lateroblique (A_4) views. **B**. MPZ 2015/1340, paratype, latex cast of interior (B_1) and internal mould (B_2). **C**. MPZ 2015/1341, paratype, latex cast of dorsal exterior of an incomplete specimen. **D**. MPZ 2015/1342, paratype, latex cast of interior (D_1) and detail of cardinalia in anteroblique (D_2) and upper (D_3) views, showing the posteroventrally engrossed cardinal process lobes of a dorsal valve. **E**. MPZ 2015/1343, paratype, latex cast of interior (E_1) and detail of cardinalia (E_2), showing the mesocardinal ridge supporting the chilidium. **F**–**H**. Paratypes, latex casts of dorsal interior of an incomplete specimens. **F**. MNHN.F.A46456. **G**. MPZ 2015/1344. **H**. MNHN.F.A46453. **I**. MPZ 2015/1345, paratype, latex cast of dorsal exterior of an incomplete specimen. **J**. VOMN-2200, paratype, latex cast of dorsal exterior of a complete specimen. Scale bars 2 mm.

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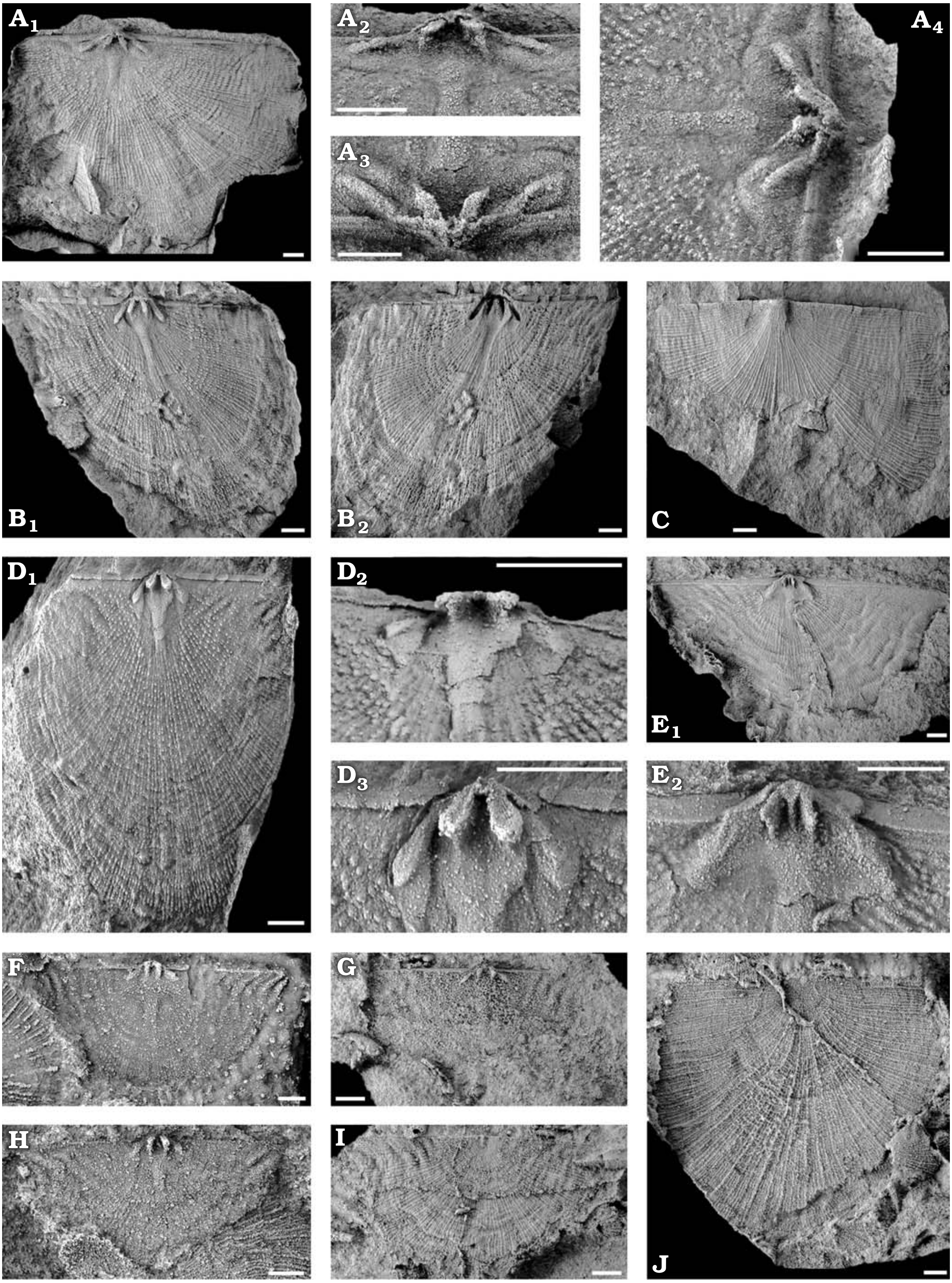
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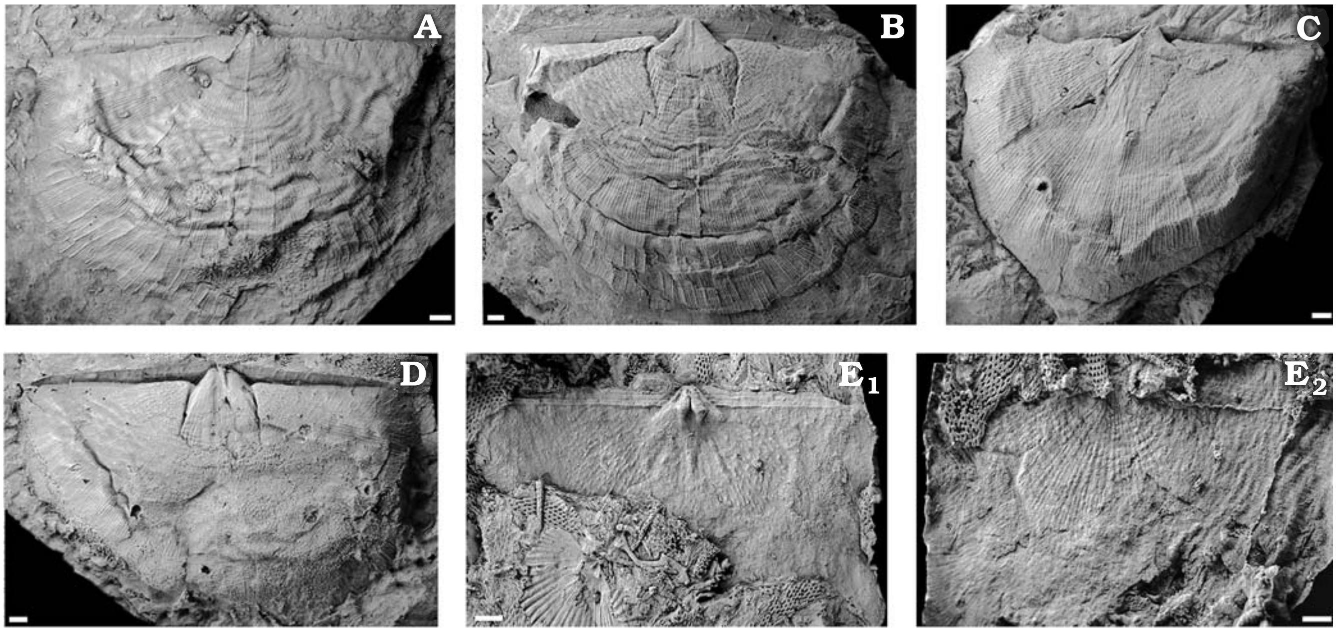

Fig. 4. Valves of rafinesquinine brachiopod *Kjaerina* (*Kjaerina*) sp. A.; upper Katian (Ka3–4), Upper Ordovician; Fombuena Formation at Alpartir (A, B, D) and Luesma (C, E), Iberian Chains, Spain. **A**. MPZ 2015/1346, latex cast of exterior of a complete and flattened ventral valve, showing the cardinal process lobes of the dorsal valve protruding in the vicinity of the hinge line. **B**. DPZ 368, internal mould of ventral valve. **C**. MPZ 2015/1347, internal mould of ventral valve, showing the convergent anteriorly muscle bounding ridges. **D**. DPZ 369, internal mould of ventral valve. **E**. DPZ 372, latex cast of interior (E_1) and exterior (E_2) of an incomplete dorsal valve. Scale bars 2 mm.

wave length of about 1 mm, which on posterolateral sides of valves run oblique to hinge line.

Ventral interior with short, thin, blade-like dental plates extending forward approximately 8% of valve length and average dental plates divergence angle of 107° (range 99–116°; n = 4), continuous anteriorly with less divergent muscle bounding ridges only developed in largest specimens; muscle field flabellate ranging 23–38% as long as valve length, approximately as long as wide and traversed by fine radial ridges; adductor scars ranging 25–30% as wide as muscle field maximum width; well developed myophragm located posteriorly to adductor scars.

Dorsal interior with strongly thickened cardinal process lobes in adult stages and myophores with concave and striated posteroventral surface; socket ridges ankylosed to posterolateral edges of strong anchor-shaped notothyrial platform continuous anteriorly with wide, high median ridge, bisecting deeply impressed adductor scars, traversed by broad transmuscle septa longer than median ridge. Both valves with coarse pseudopunctae, regularly arranged anteromedially coinciding with intercostal spaces and irregularly disposed posterolaterally.

Remarks.—This species was originally assigned to *Hedstroemina* by Villas (1995), who remarked its multicostellate radial ornament contrasting with the unequally parvicostellate *H. fragilis* (= *K.* [*H.*] *fragilis*). He considered the ornamentation as a specific character. Nevertheless, as discussed under the remarks of *K.* (*Villasina*) above, this character is considered herein as key subgeneric feature, and *H. almandenensis* is included within *K.* (*Villasina*). It is the species with the thickest cardinal process lobes within the subgenus. Also it has the most regular and continuous pattern of rugation, so its discrimination from the new species, introduced below, is very clear. Young (1985) assigned several valves from the Porto de Santa Anna Formation (Portuguese Central Iberian Zone) to an indeterminate species of *Hedstroemina*. Villas (1995), in his description of *H. almadenensis* from the uppermost "Bancos Mixtos" of the Spanish Central Iberian Zone, did not compare it with the material from Portugal. Now, after having studied both collections, I consider that the material from the Porto de Santa Anna Formation and the Spanish material belong to the same stock. In the same way, I include within this species material from the lower and middle part of the Rosan Formation of the Armorican Massif, due to the similarities in shell outline, ornamentation and ventral muscle field (Fig. 5H, K).

Fig. 5. Ventral valves of rafinesquinine brachiopod *Kjaerina* (*Villasina*) *almadenensis* (Villas, 1995); middle Katian (Ka2), Upper Ordovician; "Bancos Mixtos" Formation at Almadén (**A–D**), Spanish Central Iberian Zone, Spain; Porto de Santa Anna Formation at Louredo; Portuguese Central Iberian Zone, Portugal (E–G, I, J); lower part of Rosan Formation at Pointe de l'Aber, Armorican Massif, France (H, K). **A**. MPZ-11573, paratype, internal mould (A_1) and latex cast of exterior (A_2). **B**. MPZ 2015/1348, topotype, internal mould of a small valve showing the well developed median rib. **C**. MPZ-11574, paratype, ventral internal mould (C_1) and latex cast of interior (C_2), showing detail of dental plates. **D**. MPZ 2015/1349, topotype, latex cast of exterior of a small valve. **E**. IGM-3009A, latex cast of exterior. **F**. IGM-3006, internal mould of a small valve. **G**. IGM-3011, internal mould. **H**. MPZ 2015/1351, ventral internal mould (H_1) and latex cast of ventral exterior (H_2). **I**. IGM-3009B, latex cast of exterior. **J**. IGM-3005, ventral internal mould (J_1) and latex cast of ventral interior (J_2), showing detail of dental plates. **K**. MPZ 2015/1352, latex cast of exterior (K_1) and internal mould (K_2) of a small valve. Scale bars 2 mm.

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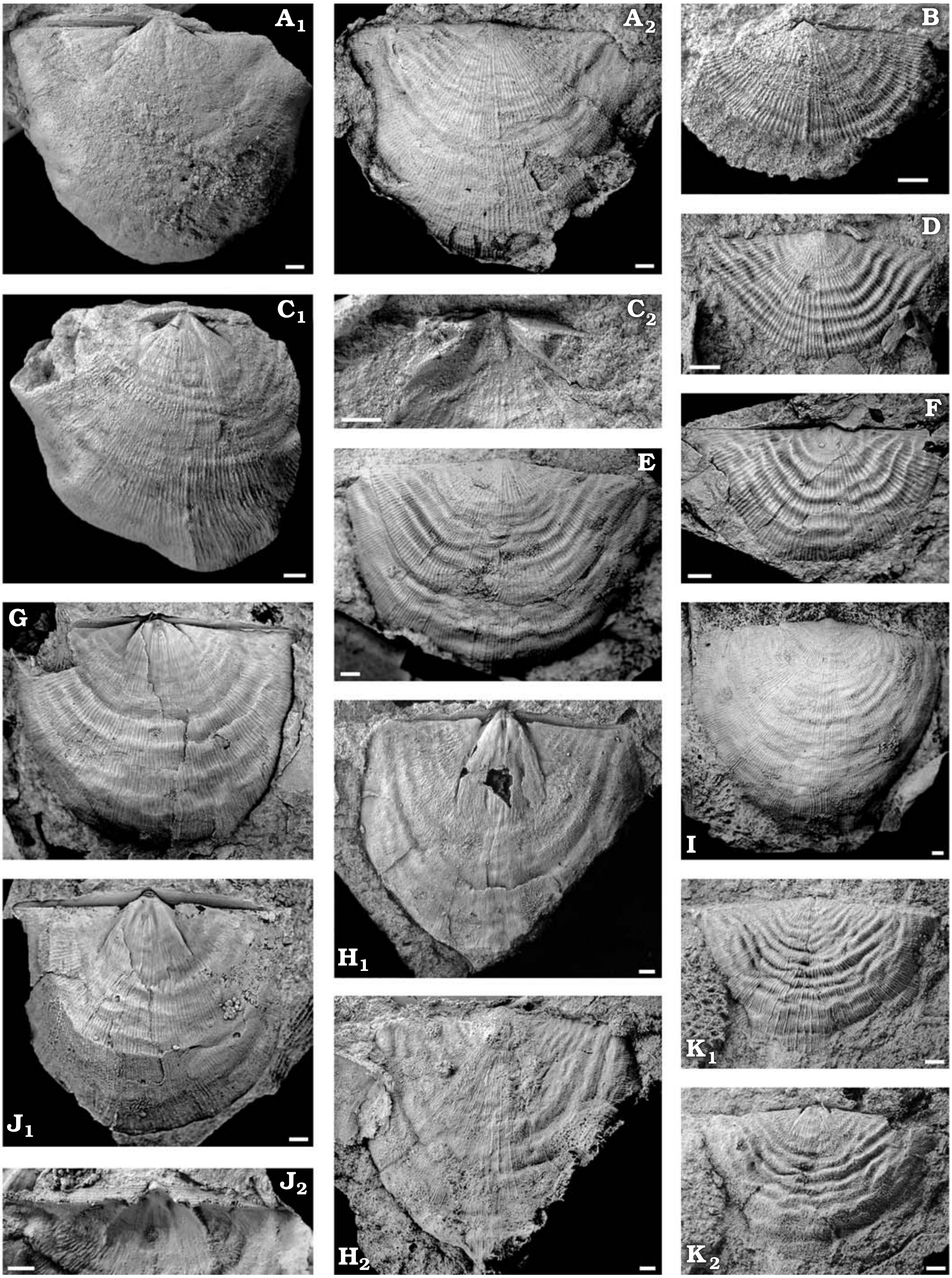
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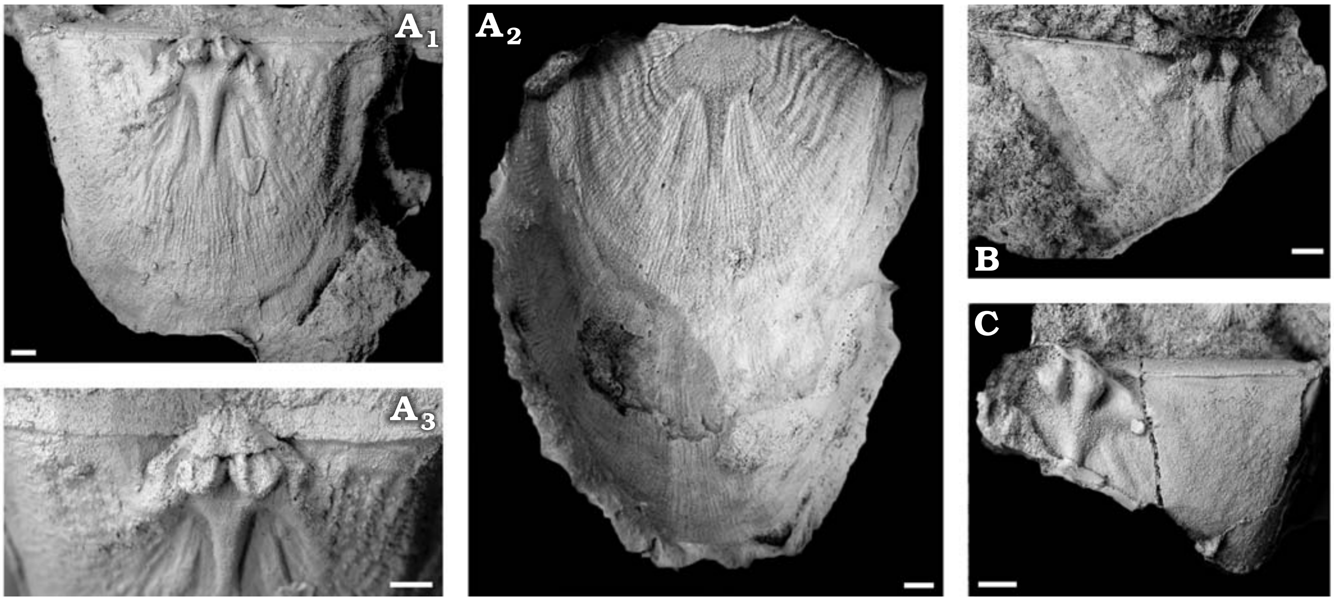

Fig. 6. Dorsal valves of rafinesquinine brachiopod *Kjaerina* (*Villasina*) *almadenensis* (Villas, 1995); middle Katian (Ka2), Upper Ordovician; "Bancos Mixtos" Formation at Almadén, Spanish Central Iberian Zone, Spain. **A**. MPZ 11570, holotype, latex cast of dorsal interior (A$_1$), posteroblique view (A$_2$), showing details of cardinalia, dorsal exterior (A$_3$) of a gerontic complete specimen. **B**. MPZ 11571, paratype, latex cast of dorsal interior of an incomplete specimen. **C**. MPZ 2015/1350, topotype, latex cast of dorsal interior of an incomplete specimen. Scale bars 2 mm.

Stratigraphic and geographic range.—Spanish Central Iberian Zone (Spain): Uppermost "Bancos Mixtos" at Fh 1 (Jabalón river section), Al-1 (Almadén), and Co-I (Corral de Calatrava) Hammann's (1976) localities, middle Katian (Ka2 stage slice); Portuguese Central Iberian Zone (Portugal): Porto de Santa Anna Formation at Louredo locality, middle Katian (Ka2 stage slice); Armorican Massif (France): lower part of Rosan Formation at Pointe de l'Aber locality, Katian.

Kjaerina (*Villasina*) *meloui* sp. nov.

Fig. 7.

1975 *Rafinesquina* sp.; Mélou and Plusquellec 1975: 15.
1985 *Hedstroemina* sp. C; Young 1985: 350, pl. 36: 1–10.
1990 *Hedstroemina* cf. *fragilis* Bancroft, 1929; Mélou 1990: 554, text-fig. 7, pl. 9: 1–8.

Etymology: Species dedicated to Michel Mélou for his contributions in the study of the Ordovician brachiopods.

Type material: Holotype: MPZ 2015/1353, internal mould of dorsal valve (Fig. 7A). Paratypes: LPB 17191–17195, MPZ 2015/1354.

Type locality: Lime kiln quarry, île de Rosan, Crozon (Finistère, France).

Type horizon: Stratigraphic layer 16 of the Tufs et Calcaires de Rosan Formation, upper Katian (Ka3–4 stage slices).

Material.—Internal and external moulds of two ventral valves and 13 dorsal valves; MPZ 2015/1501–1508 from the type locality and horizon.

Diagnosis.—*Kjaerina* (*Villasina*) species with ventral valve disc slightly convex. Dorsal valve disc flat to concave. Radial ornament with 9–12 ribs per 2 mm at 10 mm anteromedially from umbo; prominent median rib absent; irregular rugae development. Cardinal process stout; myophores with striated posteroventral surface; mesocardinal ridge always present; notothyrial platform strongly reduced; median ridge long and narrow; transmuscle septa narrow, longer than median ridge; dorsal median breviseptum, narrow, often present.

Description.—Shells of large size (largest specimen 50 mm wide), concavoconvex, with dorsally directed geniculation, semicircular in outline, maximum valve width at hinge line in young specimens and slightly anteriorly in older ones; acute cardinal angles in early growth stages, rectangular to slightly obtuse in adult stages. Ventral valve 80% as long as wide; lateral profile geniculate dorsally, at approximately 25 mm long growth stage, with slightly convex disc and with variable trail length; ventral interarea planar, apsacline, 8% as long as valve length; delthyrium open. Dorsal valve lateral profile geniculate dorsally with flat to concave disc and with variable trail length; dorsal interarea planar, anacline, 6% as long as valve length; notothyrium filled completely by cardinal process; medially grooved convex chilidium, as long as dorsal interarea length, covering up to 50% of cardinal process lobes.

Radial ornament multicostellate with 9–12 ribs per 2 mm at 10 mm anteromedially from umbo and without prominent median rib, all of them with rounded crests, small

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Fig. 7. Rafinesquinine brachiopod *Kjaerina* (*Villasina*) *meloui* sp. nov.; upper Katian (Ka3–4), Upper Ordovician; upper part of Rosan Formation, Armorican Massif, France. **A**. MPZ 2015/1353, holotype, latex cast of dorsal interior in upper view (A$_1$), lateroblique view of a dorsal valve (A$_2$), details of cardinalia in anteroblique (A$_3$), and posteroblique (A$_4$) views, dorsal exterior (A$_5$). **B**. LPB-17192, paratype, latex cast of dorsal interior in upper view (B$_1$), details of cardinalia in anteroblique (B$_2$) and posteroblique (B$_3$) views of dorsal valve. **C–E**. Paratypes, details of cardinalia of a dorsal valves. **C**. LPB-17194. **D**. MPZ 2015/1354. **E**. LPB-17195. **F**. LPB-17193, paratype, latex cast of exterior of a dorsal valve. **G**. LPB-17191, paratype, internal mould (G$_1$) and latex cast of interior (G$_2$) of a ventral valve. Scale bars 2 mm.

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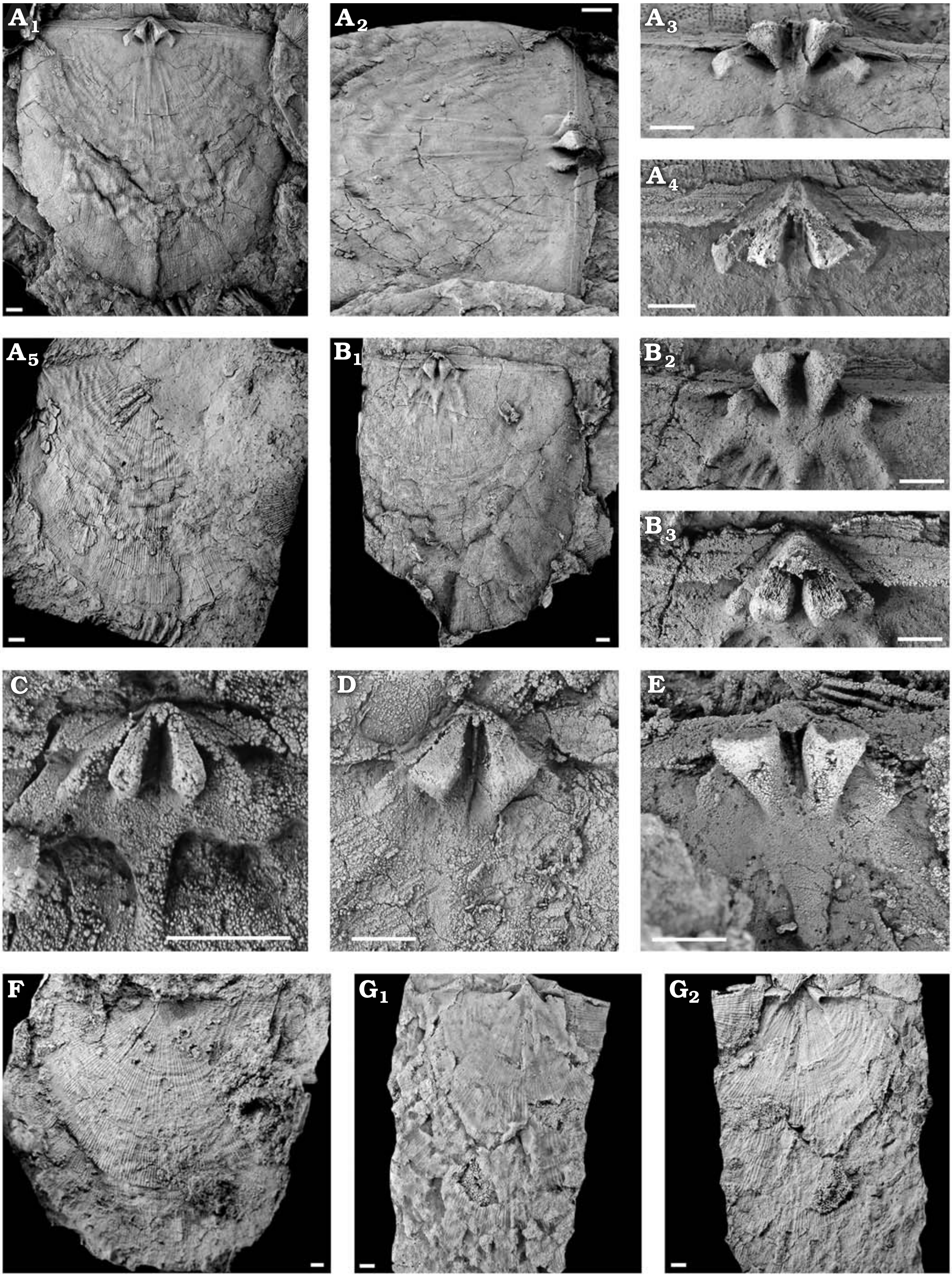
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intercostal spaces; concentric ornament of fila and irregular impersistent rugae well developed in the posterolateral sides of the disc and with wave length of about 1 mm.

Ventral interior with divergent, thin, blade-like dental plates extending forward approximately 7% of valve length and average dental plates divergence angle of 80°, continuous anteriorly with curved inwardly muscle bounding ridges; ventral muscle field triangular to flabellate, with divergent diductor scars not enclosing anteriorly narrow adductor scars; myophragm present posteriorly to adductor scars.

Dorsal interior with tabular, thin and divergent socket ridges bounding triangular dental sockets; bifid cardinal process with plate-like and weakly divergent lobes on a reduced notothyrial platform that continues anteriorly with long, narrow median ridge; porteroventral surface of myophores striated longitudinally; in adult specimens lobes become ponderous; between lobes, mesocardinal ridge supporting chilidium always present. Dorsal muscle field weakly elongated, crossed by long transverse transmuscle septa; thin dorsal median breviseptum often present anteriorly to median ridge. Both valves with very fine pseudopunctae, regularly arranged all over the shell, coinciding with intercostal spaces.

Remarks.—This species resembles in many characters *K.* (*Hedstroemina*) *fragilis* (Bancroft, 1929) as Mélou (1990) noted when referred provisionally the Armorican specimens to this species, but the multicostellate ornament of these shells allows a ready discrimination from the parvicostellate British species, as well as its inclusion in the new subgenus *Kjaerina* (*Villasina*). The high ribs density with 9–12 ribs per 2 mm at 10 mm anteromedially from umbo, *K.* (*Villasina*) *almadenensis* has 6–8 at the same growth stage, their weaker rugae development, the thin and long median ridge and the dorsal median breviseptum, are significant enough differences to erect a new species.

Stratigraphic and geographic range.—Type locality and horizon only.

Kjaerina (*Villasina*) *pedronaensis* sp. nov.

Figs. 8, 9.

1927 *Strophomena rhomboidalis* Wilk.; Vinassa de Regny 1927: 479, pl. 3: 40.
1948 *Leptaena rhomboidalis*; Dreyfuss 1948: 39, pl. 7: 11.
1981 *Leptaena* sp. A; Havlíček 1981: 26, pl. 6: 16.

Etymology: After the name of its type locality, the Punta Pedrona hill.

Type material: Holotype: MPZ 2015/1363, internal mould of dorsal valve (Fig. 9A). Paratypes: MPZ 2015/1355–1362, MPZ 2015/1364–1371.

Type locality: Punta Pedrona hill (Hammann and Leone 1997: see text-fig. 5 for exact location: Por 7), NE of Portixeddu, Province of Medio Campidano, Sardinia, Italy.

Type horizon: Greenish and grey silt and fine sandstone in tempestitic layers of the middle to upper part of the Portixeddu Formation, Katian.

Material.—Internal and external moulds of eight ventral valves and 16 dorsal valves from Sardinia (Italy) and Montagne Noire (France); MPZ 2015/1509–1515 from Punta Pedrona, Gonnesa, VCR-14 (Sardinia) and Tranchée Noire (Montagne Noire) localities, Katian.

Diagnosis.—*Kjaerina* (*Villasina*) species with ventral valve disc slightly convex. Dorsal disc flat to concave; both, ventral valve and dorsal valve trails, inclined with respect to disc about 90°. Radial ornament with 7–8 ribs per 2 mm at 10 mm anteromedially from umbo; prominent median rib present; strong and irregular rugae covering the entire disc, better developed posterolaterally. Ventral muscle field elongate, flabelliform, very well impressed in adults; muscle bounding ridges curved inwardly. Cardinal process with concave myophores, engrossed posteroventrally during adult and gerontic stages; notothyrial platform strongly reduced.

Description.—Shell of medium size for the genus (largest specimen 37 mm wide), concavoconvex, semicircular in outline, or weakly alate in some specimens; maximum valve width at hinge line; slightly acute to rectangular cardinal angles. Ventral valve ranging 59–86% as long as wide ($\bar{x}$ = 71%; n = 4; σ_n = 0.10); lateral profile geniculate dorsally, with moderately convex disc, forming an angle about 90° with variably developed trail; ventral interarea planar, apsacline, delthyrium with apical pseudodeltidium. Dorsal valve with lateral profile geniculate dorsally, with flat to very slightly concave disc forming angle of about 90° with trail; dorsal interarea anacline; notothyrium filled completely by cardinal process; medially grooved convex chilidium covering the notothyrium completely.

Radial ornament multicostellate with 7–8 ribs per 2 mm at 10 mm anteromedially from umbo, all of them with rounded crests; prominent median costa often present. Concentric ornamentation of fila and strong irregular rugae, covering the entire disc but better developed on posterolateral sides of valves where they run oblique to hinge line.

Ventral interior with straight, short, blade-like dental plates extending forward 7–10% of valve length and with average dental plates divergence angle of 96° (range 75–114°; n = 6); muscle field very well impressed in adults, elongate, flabelliform ranging 8–50% as long as valve length, 10–37% as wide as maximum valve width and completely surrounded laterally by inwardly curved muscle bounding ridges.

Dorsal interior with strong socket ridges with divergence angle of about 75°, bounding triangular dental sockets. Cardinal process bifid with triangular lobes, posteroventrally directed, discrete during young stages, become engrossed posteroventrally and even reaching out to touch each other during adult and gerontic stages; mesocardinal ridge sometimes present between lobes (Fig. 9A$_3$). Strongly reduced anchor-shaped notothyrial platform, continuous anteriorly with median ridge dividing the poor-impressed dorsal muscle field. Both valves with moderately coarse pseudopunctae, regularly arranged all over the shell, coinciding with intercostal spaces.

Remarks.—This new *Kjaerina* (*Villasina*) species resembles *K.* (*V.*) *almadenensis* in many aspects. These species share features such as the ornamentation and the concave myophores, but they clearly differ in the geniculation develop-

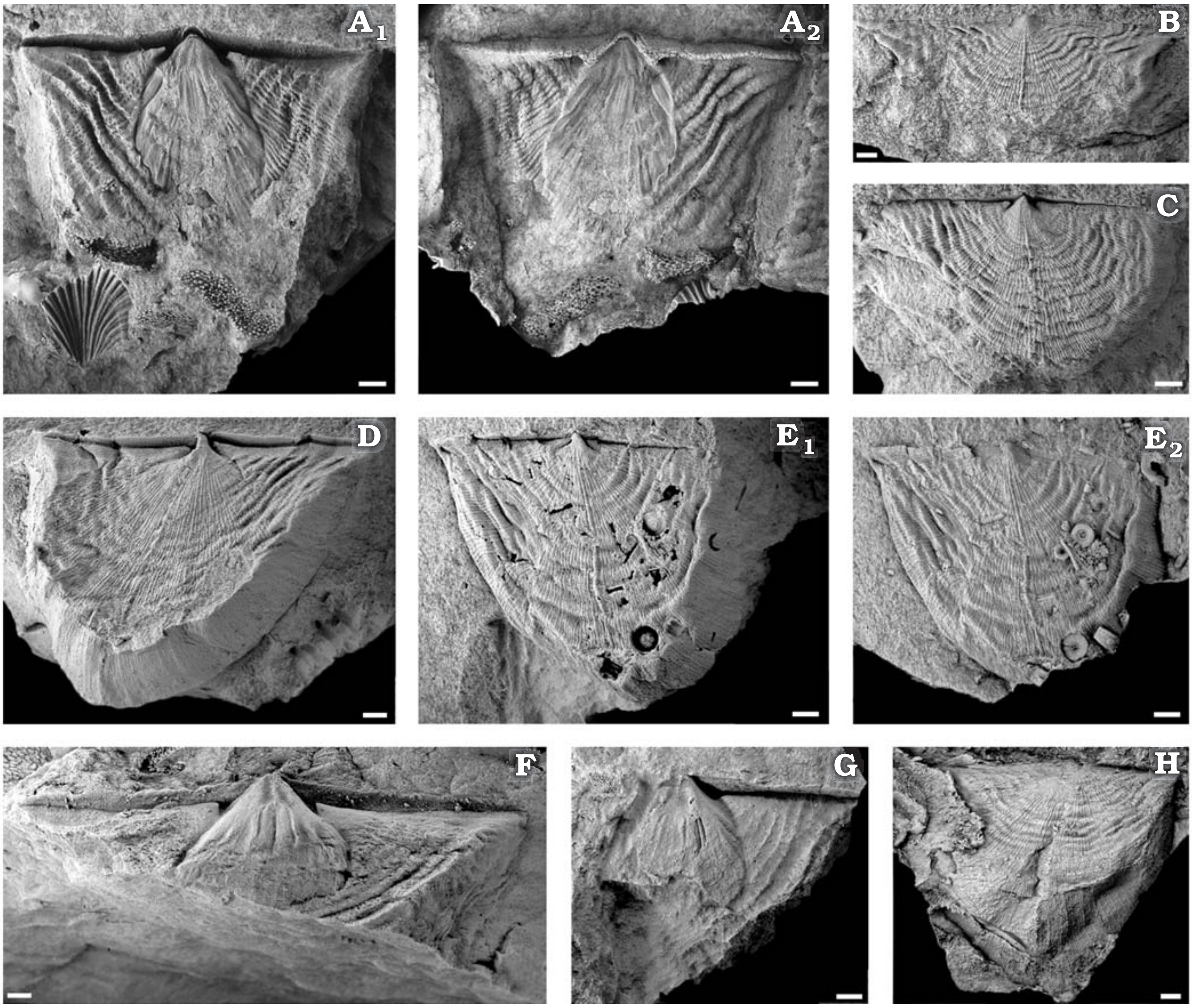


Fig. 8. Ventral valves of rafinesquinine brachiopod *Kjaerina* (*Villasina*) *pedronaensis* sp. nov.; Katian, Upper Ordovician; Portixeddu Formation at Punta Pedrona (A), Gonnesa (B–E), and VCR/14 (F), Sardinia, Italy; Gabian Formation at Tranchée Noire, Montagne Noire, France (G, H). **A**. MPZ 2015/1355, paratype, ventral internal mould (A_1) and latex cast of ventral interior (A_2) of an incomplete valve. **B**. MPZ 2015/1356, paratype, latex cast of ventral exterior. **C**. MPZ 2015/1357, paratype, internal mould. **D**. MPZ 2015/1358, paratype, internal mould. **E**. MPZ 2015/1359, ventral internal mould (E_1) and latex cast of ventral exterior (E_2). **F**. MPZ 2015/1360, internal mould of an incomplete valve. **G**. MPZ 2015/1361, internal mould of an incomplete valve. **H**. MPZ 2015/1362, latex cast of exterior. Scale bars 2 mm.

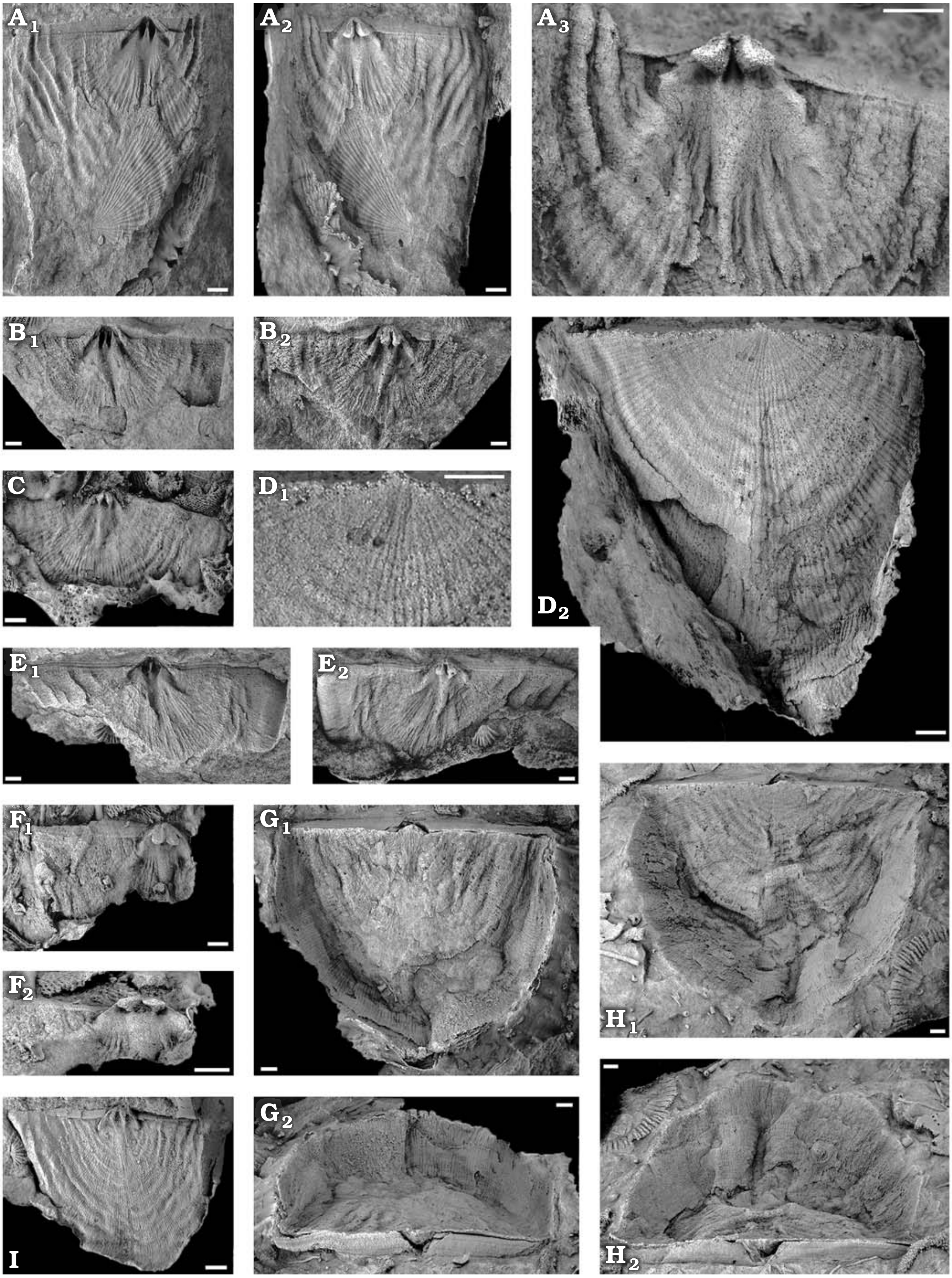
ment. The discs of both valves in *K.* (*V.*) *pedronaensis* are almost flat and make a sharp angle of about 90° with the trail whereas in *K.* (*V.*) *almadenensis* the inflexions between the convex discs and the trails are rounded. *Kjaerina* (*V.*) *pedronaensis* differs from *K.* (*V.*) *meloui* in having stronger rugae and geniculation, and lower ribs density. Vinassa de Regny (1927) assigned one valve from Portixeddu to *Strophomena rhomboidalis*. This shell shares all the characters with the new species described here, *K.* (*V.*) *pedronaensis*, so it is included herein in the synonymy of this species. Havlíček (1981: pl. 6: 16) figured a fragmented and poorly preserved ventral valve exterior as *Leptaena* sp. A. A larger sampling in the same levels of this formation has provided several specimens (Figs. 8G, 9C). This material has the same rib density, rugae development, ventral muscle field outline and cardinal process shape and thickening as those of type material of this new species, so I decided to include this material within *K.* (*V.*) *pedronaensis*.

Stratigraphic and geographic range.—In addition to the type locality *K.* (*V.*) *pedronaensis* occurs in the following localities: Sa Siliqua hill (locality Gon 1; Hammann and Leone 1997) and 900 m E-NE of Portixeddu (VCR/14 field number) both Portixeddu Formation, Katian, Sardinia (Italy); Tranche Noire, Gabian Formation, middle–upper Katian, Montagne Noire (France).

Kjaerina (*Villasina*) *pyrenaica* sp. nov.

Fig. 10A–H.

1970 *Rafinesquina* sp.; Hartevelt 1970: 174.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Etymology: After the Pyrenees Mountains.

Type material: Holotype: MPZ 2015/1372, internal mould of ventral valve (Fig. 10A). Paratypes: MPZ 11577–11580, 11582; MPZ 2015/1373–1375.

Type locality: Seo de Urgel, Spanish Pyrenees.

Type horizon: Thickly bedded sandstone of the Cavá Formation, lower –middle Katian (Ka1–2), Upper Ordovician.

Material.—Internal and external moulds of 11 ventral valves and eight dorsal valves; MPZ 2015/1516–1525 from the type locality and horizon.

Diagnosis.—Species of *Kjaerina* (*Villasina*) with ventral valve disc moderately convex. Dorsal valve disc flat to concave with shallow median sulcus; both, ventral and dorsal valve trails, inclined with respect to disc about 90°; chilidium unknown. Radial ornament with 4–5 ribs per 2 mm at 10 mm anteromedially from umbo; prominent median rib absent; strong and irregular rugae covering the entire disc, better developed posterolaterally. Muscle bounding ridges curved interiorly; ventral muscle field well impressed, elongate, flabelliform. Cardinal process lobes, plate-like in young specimens, engrossed postero ventrally in adult ones; notothyrial platform strong; broad median ridge.

Description.—Shell of medium to large size (largest specimen 30.8 mm wide), concavoconvex, both valves strongly geniculate dorsally; semicircular in outline, or weakly alate in some specimens; maximum valve width at hinge line; slightly acute to rectangular cardinal angles. Ventral valve ranging 71–102% as long as wide ($\bar{x}$ = 90%; n = 4; σ_n = 0.13) and 13–14% as deep as long ($\bar{x}$ = 14%; n = 4; σ_n = 0.003); longitudinal profile strongly geniculate dorsally with moderately convex disc forming an angle about 90° with trail ranging 45–65% as long as valve length. Ventral interarea planar, apsacline, 7% as long as valve length, delthyrium with apical pseudodeltidium. Dorsal valve with longitudinal profile strongly geniculate dorsally with flat to concave disc with shallow median sulcus, forming an angle about 90° with trail ranging 45–65% as long as valve length; dorsal interarea anacline; notothyrium filled completely by cardinal process. Chilidium unknown.

Radial ornament multicostellate with 4–5 ribs per 2 mm at 10 mm anteromedially from umbo, all of them with rounded crests; no prominent median costa. Concentric ornamentation of fila and strong irregular rugae, covering entire disc but better developed on posterolateral sides of valves where run oblique to hinge line.

Ventral interior with straight, short, blade-like dental plates extending forward approximately 10% of valve length and with average dental plates divergence angle of 95° (range 77–113°; n = 6); muscle field very well impressed, elongate, flabelliform ranging 55–61% as long as valve length, 25–51% as wide as maximum valve width and completely surrounded laterally by inwardly curved muscle bounding ridges.

Dorsal interior with strong socket ridges, diverging anteriorly about 85° and bounding triangular dental sockets; bifid cardinal process with elongate or plate-like lobes in young specimens (Fig. 10G), but engrossed in postero-ventral direction in gerontic specimens. The lobes are weakly divergent anteriorly and are situated on thick, anchor-shaped notothyrial platform, continuous anteriorly with broad median ridge halving dorsal muscle field. Shell structure unobservable due to grain size.

Remarks.—The ventral muscle field outline of this species resembles the one known from the species of *Kiaeromena*, but the multicostellate radial ornament, the less coarse rugation, as well as all the main dorsal internal characters differentiate this leptaenine genus from *Kjaerina* (*Villasina*). Especially the cardinal process, the straight socket ridges, not curving inwardly to bound the dorsal muscle scars and the absence in the studied material of transmuscle ridges. This new species clearly differs from the other *Kjaerina* (*Villasina*) species in having a very low ribs density, 4–5 ribs per 2 mm counted at 10 mm anteromedially from umbo (*K.* [*Villasina*] *almadenensis* has 6–8 at the same growth stage, *K.* [*Villasina*] *meloui* has 9–12 and *K.* [*Villasina*] *pedronaensis* 7–8 ribs), and by having a shallow dorsal median sulcus, autapomorphy of this species. Hartevelt (1970) cited the presence of *Rafinesquina* sp. in the Cavá Formation, probably referring to shells included now within this new species.

Stratigraphic and geographic range.—Type locality only.

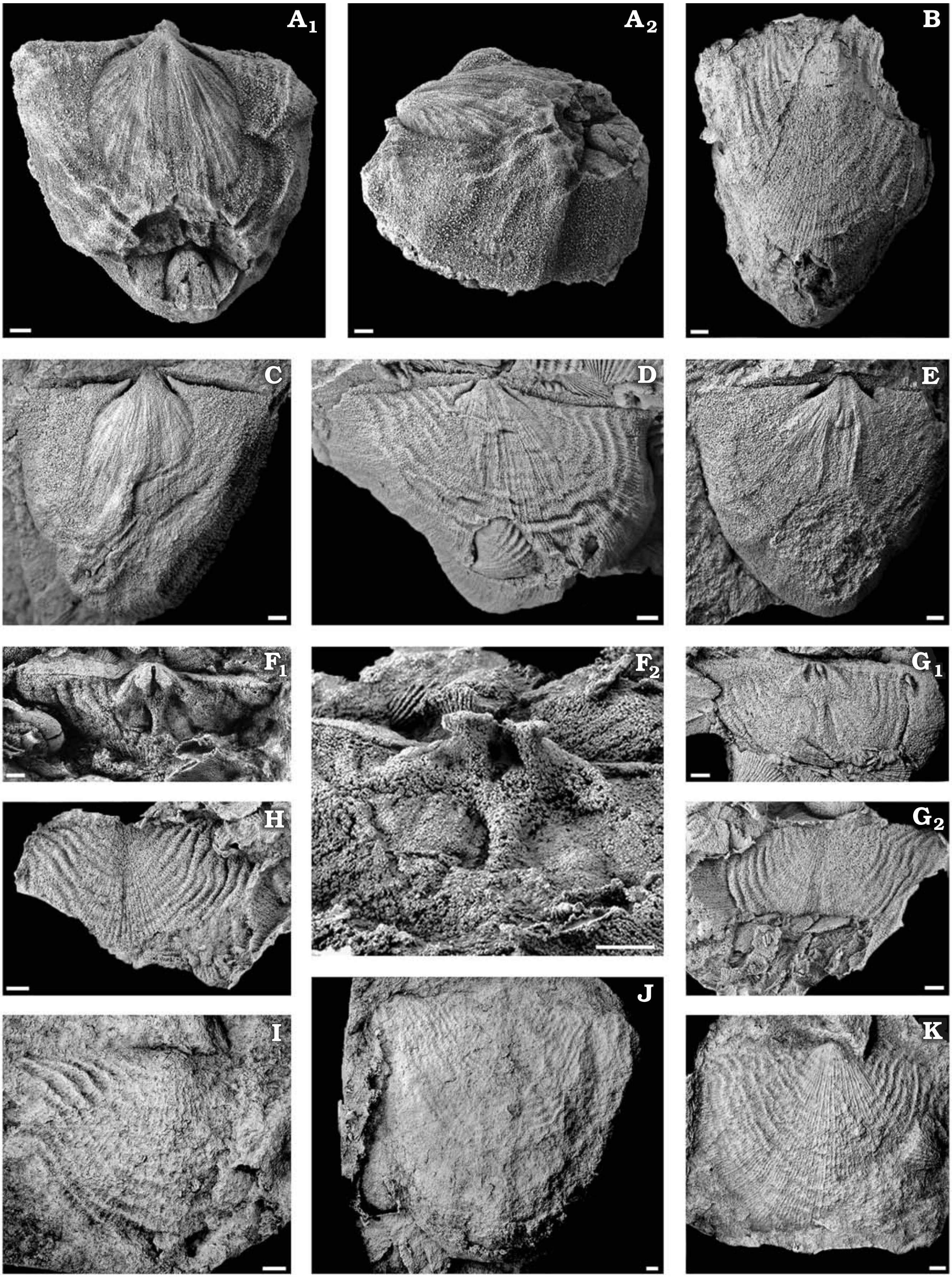
Kjaerina (*Villasina*) cf. *pyrenaica* sp. nov.

Fig. 10I–K.

Material.—Internal and external moulds of 3 poorly-preserved external and internal moulds of ventral valves (MPZ 2015/1379–1381) from microconglomeratic sandstone of the upper part of the Punta Serpeddi Formation, Katian, at Dolianova (Sardinia).

Remarks.—The multicostellate radial ornament with 4–5 ribs per 2 mm counted at 10 mm anteromedially from umbo and the rugation and shell outline resembles those of the spe-

← Fig. 9. Dorsal valves of rafinesquinine brachiopod *Kjaerina* (*Villasina*) *pedronaensis* sp. nov.; Katian, Upper Ordovician; Portixeddu Formation at Punta Pedrona (A, B, D–H) and Gonnesa (I), Sardinia, Italy; Gabian Formation, Montagne Noire, France (C). **A**. MPZ 2015/1363, holotype, internal mould (A$_1$), latex cast of dorsal interior (A$_2$), detail of cardinalia in anteroblique view (A$_3$). **B**. MPZ 2015/1364, paratype, internal mould (B$_1$) and latex cast of dorsal interior (B$_2$). **C**. MPZ 2015/1370, latex cast of interior of an incomplete valve. **D**. MPZ 2015/1365, paratype, detail of multicostellate radial ornament dorsal exterior (D$_1$) and latex cast of exterior (D$_2$) of a specimen with conjoined valves. **E**. MPZ 2015/1366, paratype, internal mould (E$_1$) and latex cast of dorsal interior (E$_2$). **F**. MPZ 2015/1367, paratype, latex cast of dorsal interior (F$_1$) and detail of cardinalia in anteroblique view (F$_2$), showing the posteroventrally engrossed cardinal process lobes of the specimen. **G**. MPZ 2015/1368, paratype, latex cast of exterior of a specimen with conjoined valves in dorsal (G$_1$) and posteroblique (G$_2$) views, showing the ventral interarea, chilidium, and hinge line. **H**. MPZ 2015/1369, paratype, latex cast of exterior of a specimen with conjoined valves in dorsal (H$_1$) and posteroblique (H$_2$) views, showing the ventral interarea, chilidium, and hinge line. **I**. MPZ 2015/1371, latex cast if interior. Scale bars 2 mm.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cies *Kjaerina* (*Villasina*) *pyrenaica,* but due to the absence of dorsal valves and the poor preservation of the available ventral interiors the species is left in open nomenclature.

Kjaerina (*Villasina*) sp. A

Fig. 11.

Material.—Internal and external moulds of one ventral valve and two dorsal valves (MPZ 2015/1379–1381) from Portilla de Luna Limestone, upper Katian (Ka3–4), at Portilla de Luna (northwestern Spain).

Description.—Shells of medium size (largest specimen 27 mm wide), concavoconvex, semicircular to longitudinally elongated semioval in outline, or weakly alate in some specimens; maximum valve width at hinge line; slightly acute to rectangular cardinal angles. Ventral valve with moderately convex disc and dorsally directed geniculation. Ventral interarea planar, apsacline, 10% as long as valve length, delthyrium partially covered by apical pseudodeltidium. Dorsal valve with flat to concave disc; dorsal interarea anacline. Chilidium moderately convex, as long as interarea and medially grooved.

Radial ornament multicostellate with 7 ribs per 2 mm at 10 mm anteromedially from umbo, all of them with rounded crests; very coarse but weakly marked discontinuous rugation present in both external and internal moulds, over the disc of specimen of Fig. 11A.

Ventral interior with straight, short, blade-like dental plates; muscle field very well impressed, elongate, flabelliform about 185% as long as wide and completely surrounded laterally by subparallel muscle bounding ridges.

Dorsal interior with divergent socket ridges bounding triangular dental sockets; bifid cardinal process with anteriorly divergent and posteroventrally directed triangular lobes. Strongly reduced notothyrial platform continuous anteriorly with broad median ridge. Shell structure pseudo-punctate.

Remarks.—The straight and thin socket ridges together with the triangular cardinal process lobes allow inclusion of this material to the subfamily Rafinesquininae. The multicostellate radial ornament, the valves with dorsally directed geniculation and the presence of rugation over the whole disc warrants the inclusion of this material to *Kjaerina* (*Villasina*). Due to the low number of available specimens and its degree of fragmentation the species is left in open nomenclature.

Genus *Rafinesquina* Hall and Clarke, 1892

Type species: *Leptaena alternata* Conrad, 1838; Hudson River Group, Caradoc, Cincinnati, Ohio (USA).

Subgenus *Mesogeina* nov.

Etymology: After *Mesogeios Thalassa*, ancient Greek name for the Mediterranean Sea.

Type species: *Leptaena pseudoloricata* Barrande, 1848; Zahorany and Bohdalec formations, upper middle Berounian–upper Berounian (lower–middle Katian, Ka1–2 stage slices), Upper Ordovician, Bohemia.

Species included: *Rafinesquina* (*Mesogeina*) *pomoides* Havlíček, 1971, Upper Tiouririne Formation, middle Katian (Ka2), Anti-Atlas (Morocco); *R.* (*Mesogeina*) *gabianensis* sp. nov., lower part of the Gabian Formation, middle–upper Katian (Ka2–4), Montagne Noire; *R.* (*Mesogeina*) *loredensis* sp. nov., lower part of Porto de Santa Anna Formation, middle Katian (Ka2), Portuguese Central Iberian Zone.

Diagnosis.—*Rafinesquina* with very well marked ventral muscle field, strong ventral muscle bounding ridges and subparallel and plate-like cardinal process lobes, engrossed posteroventrally only in adult specimens.

Remarks.—The species included below displays very similar features with *Rafinesquina* Hall and Clarke, 1892, especially in shell profile, outline and ornamentation. However, the internal features of these species are quite different to those of *Rafinesquina*, as the strong ventral muscle bounding ridges and the subparallel and the plate-like cardinal process lobes are not so thickened posteroventrally as it is typical of the *Rafinesquina* type species. These differences may warrant the erection of a new taxa. The morphological similarities of the species under discussion, as well as their differences to the rest of the species of *Rafinesquina*, besides their geographic restriction to the Mediterranean margin of Gondwana, points to a common ancestor with *Rafinesquina*. However, similarly to subgeneric divison of *Kjaerina*, the set of distinctive characters warrants erection of a new subgenus *Rafinesquina* (*Mesogeina*).

Rafinesquina (*Mesogeina*) *gabianensis* sp. nov.

Figs. 12, 13.

Etymology: After the Gabian Formation, from where the type material comes.

Type material: Holotype: MPZ 2015/1387, external and internal moulds of dorsal valve (Fig. 13A). Paratypes: MPZ 2015/1382–1386, MPZ 2015/1388, 1389.

Type locality: Tranchée Noire (Havlíček 1981), abandoned railway cutting close to the Gabian village, Montagne Noire (France).

Type horizon: Alternating marlstone and bioclastic limestone beds of the lower part of the Gabian Formation, middle–upper Katian (Ka2–4 stage slices), Upper Ordovician.

Material.—Internal and external moulds of 22 ventral valves and 15 dorsal valves; MPZ 2015/1526–1554 from the type locality and horizon.

← Fig. 10. Rafinesquinine brachiopod *Kjaerina* (*Villasina*) *pyrenaica* sp. nov. (**A**–**H**) from lower–middle Katian (Ka1–2), Upper Ordovician, Cavá Formation, Pyrenees, Spain and *Kjaerina* (*Villasina*) cf. *pyrenaica* (**I**–**K**) from Katian, Upper Ordovician, Bruncu de is Mallorus Member of the Punta Serpeddi Formation, Sardinia, Italy. **A**. MPZ 2015/1372, holotype, internal mould of ventral valve in upper (A_1) and lateroblique (A_2) views. **B**. MPZ 2015/1373, paratype, latex cast of exterior of a ventral valve. **C**. MPZ 11579, paratype, internal mould of ventral valve. **D**. MPZ 11580, paratype, internal mould of ventral valve. **E**. MPZ 11578, paratype, internal mould of ventral valve. **F**. MPZ 2015/1374, paratype, latex cast of dorsal valve (F_1) and anteroblique view of cardinalia (F_2). **H**. MPZ 11582, paratype, latex cast of exterior of an incomplete dorsal valve. **G**. MPZ 2015/1375, paratype, latex cast of interior (G_1) and exterior (G_2) of a dorsal valve. **I**. MPZ 2015/1376, latex cast of exterior of a ventral valve. **J**. MPZ 2015/1377, latex cast of exterior of a ventral valve. **K**. MPZ 2015/1378, latex cast of exterior of a ventral valve. Scale bars 2 mm.

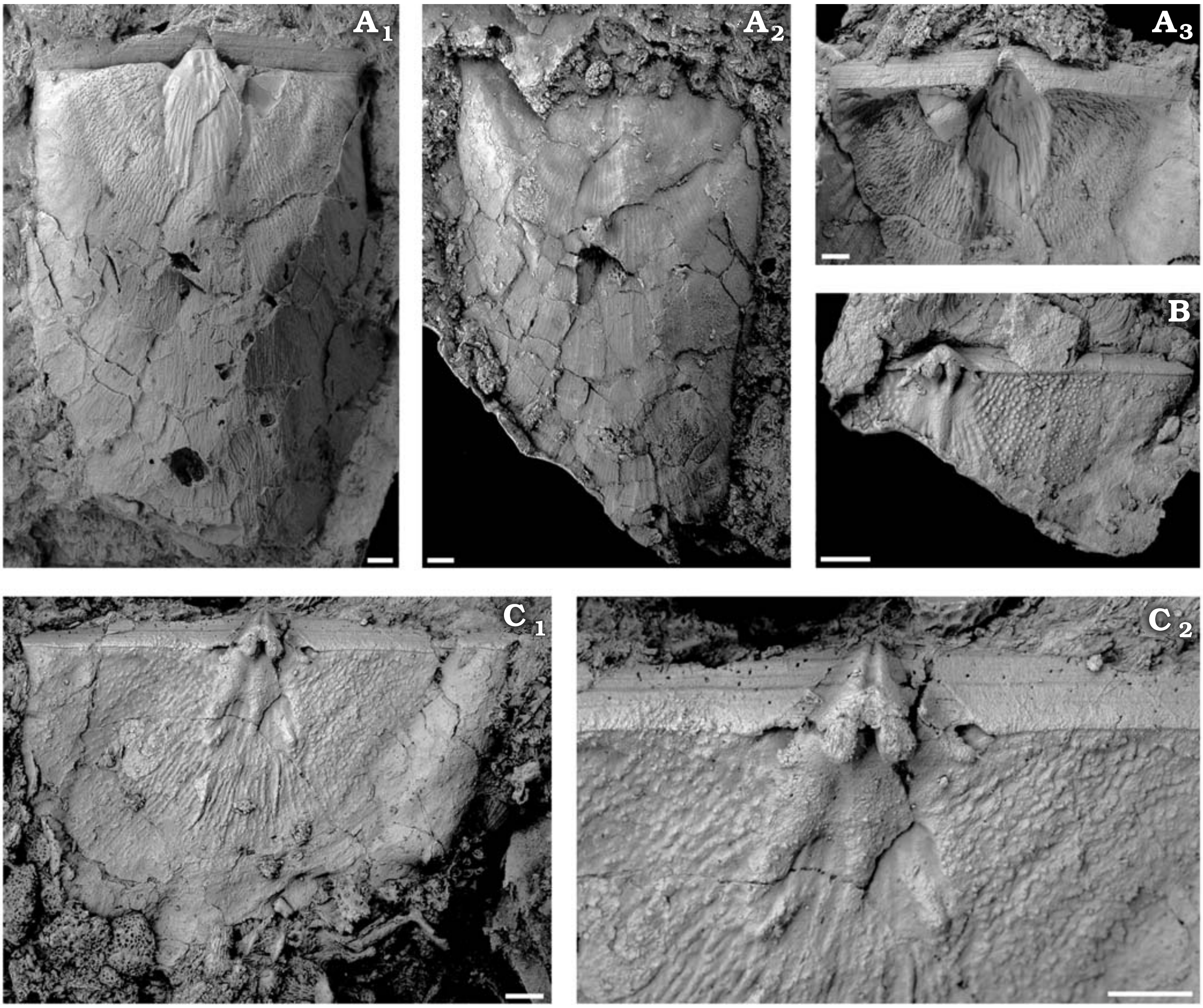

Fig. 11. Rafinesquinine brachiopod *Kjaerina* (*Villasina*) sp. A; upper Katian (Ka3–4), Upper Ordovician; the Portilla de Luna Limestone, Cantabrian Zone, Spain. **A**. MPZ 2015/1379, internal mould (A_1), latex cast of exterior (A_2) and interior (A_3) of a complete ventral valve. **B**. MPZ 2015/1380, latex cast of interior of an incomplete dorsal valve. **C**. MPZ 2015/1381, latex cast of interior of dorsal valve (C_1), detail of cardinalia (C_2). Scale bars 2 mm.

Diagnosis.—Species of *Rafinesquina* (*Mesogeina*) with shell slightly wider than long, often with weakly alate cardinal extremities. Ventral valves evenly convex, about 18% as deep as long and gently convex dorsal valves. Radial ornament with 4–6 ribs per 2 mm at 10 mm anteromedially from umbo, with up to three costellae between two costae; concentric ornament filate. Cardinal process lobes with concave and smooth myophores in adult specimens; notothyrial platform low, strongly reduced.

Description.—Shell of medium to large size (largest specimen 32.8 mm wide), concavoconvex, semicircular in outline; maximum valve width at hinge; slightly acute cardinal angles. Ventral valve evenly convex, 68–109% as long as wide ($\bar{x}$ = 89%; n = 8; σ_n = 0.15) and 15–22% as deep as long ($\bar{x}$ = 18%; n = 3; σ_n = 0.003). Ventral interarea planar, apsacline, very short, 3% as long as valve length, delthyrium with apical pseudodeltidium. Dorsal valve approximately 77% as long as wide ($\bar{x}$ = 14%; n = 4; σ_n = 0.003) and with gently concave lateral profile; dorsal interarea anacline, about 4% as long as valve length; chilidium not observed.

Radial ornament unequally parvicostellate, with commonly 6 ribs per 2 mm at 10 mm anteromedially from umbo but occasionally with only 4 or 5, all of them with rounded crests. Concentric ornamentation consisting of fine fila, with counts of 11 per mm, intersecting the radial ornament; some specimens show evidences of shell damage, reflected as discontinuities in the shell ornament (Fig. 12A, B, E).

Ventral interior with teeth triangular in section, dental plates short, straight, extending forward approximately 8% of valve length and with average dental plates divergence angle of 98° (range 75–109°; n = 10); muscle field poorly impressed anteriorly, subtriangular to flabelliform, approximately 35% as wide as maximum valve width and surrounded posterolaterally by very narrow and thin muscle bounding ridges.

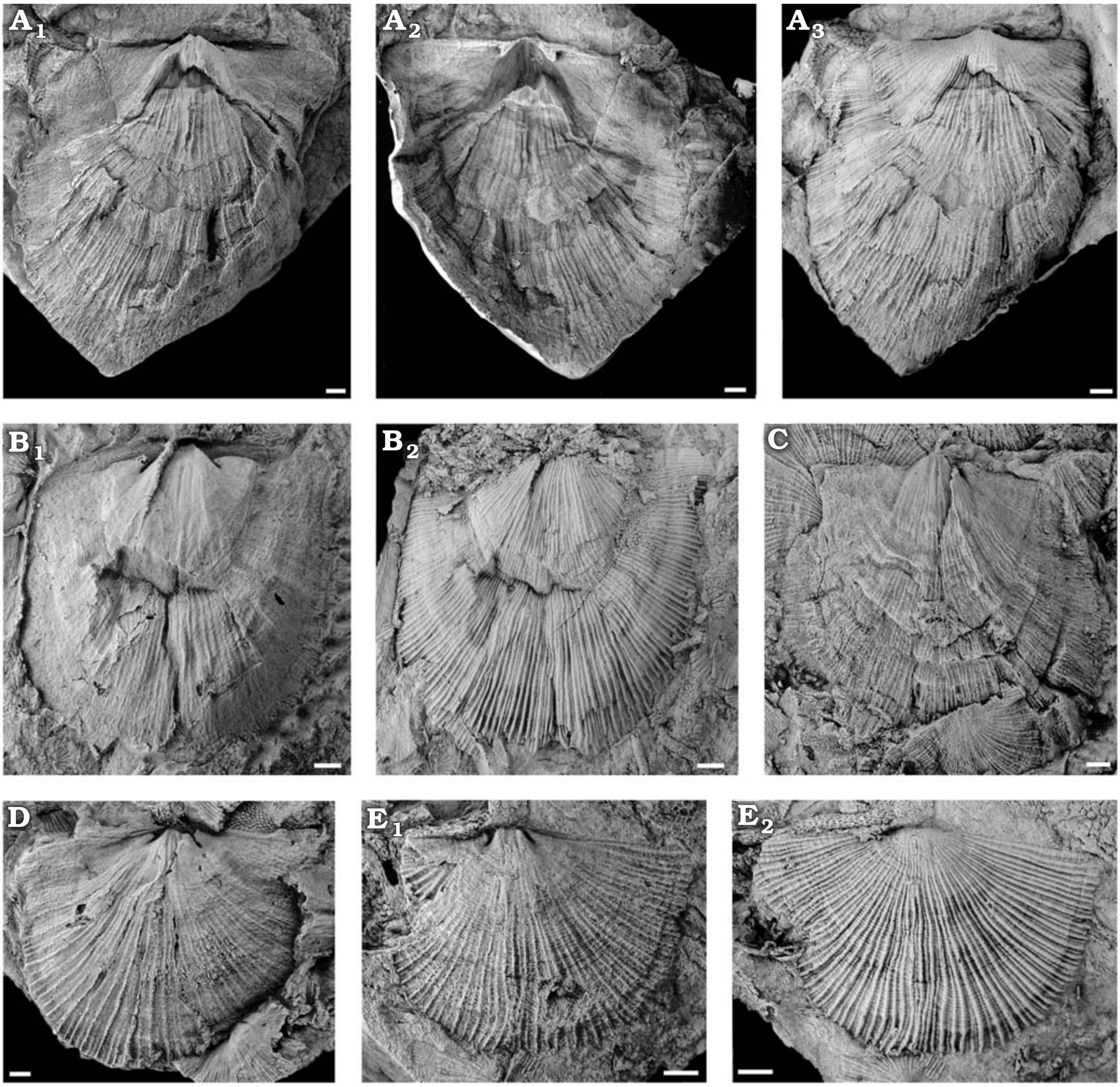

Fig. 12. Ventral valves of rafinesquinine brachiopod *Rafinesquina* (*Mesogeina*) *gabianensis* sp. nov.; middle–upper Katian (Ka2–4), Upper Ordovician; Gabian Formation, Montagne Noire, France. **A**. MPZ 2015/1382, paratype, internal mould (A_1) and latex cast of interior (A_2) and exterior (A_3). **B**. MPZ 2015/1383, paratype, internal mould (B_1) and latex cast of exterior (B_2) of a complete valve. **C**. MPZ 2015/1384, paratype, internal mould. **D**. MPZ 2015/1385, paratype, internal mould. **E**. MPZ 2015/1386, paratype, internal mould (E_1) and latex cast of exterior (E_2) of a small valve. Scale bars 2 mm.

Adductor scar lanceolate located between diductor scars and approximately 20% as wide as muscle scar maximum width.

Dorsal interior with thin and about 95° divergent socket ridges bounding posteriorly triangular dental sockets; bifid cardinal process, with ventrally divergent, elongate or plate-like lobes in young specimens (Fig. 13B), but triangular in outline and ponderous in adult specimens (Fig. 13A); the lobes are weakly divergent anteriorly and the myophores has a concave posteroventral surface; notothyrial platform, low, very reduced, continuous anteriorly with broad and low median ridge halving the poorly impressed dorsal muscle field. Pseudopunctae visible in both interiors, with radial regular arrangement over the entire shell excepting posterolaterally where exhibit a more irregular pattern. Ornamentation, both radial and concentric, impressed in interior of both valves.

Remarks.—Among all the species of this subgenus, the new species is most similar to *Rafinesquina* (*Mesogeina*) *pomoides* Havlíček, 1971 from the Upper Ordovician of Morocco and the Iberian Chains, in having a very convex ventral valve. As noted above, the new species has a very convex ventral valve about 14% as depth as long, but these values are lower than those of *R.* (*Mesogeina*) *pomoides*

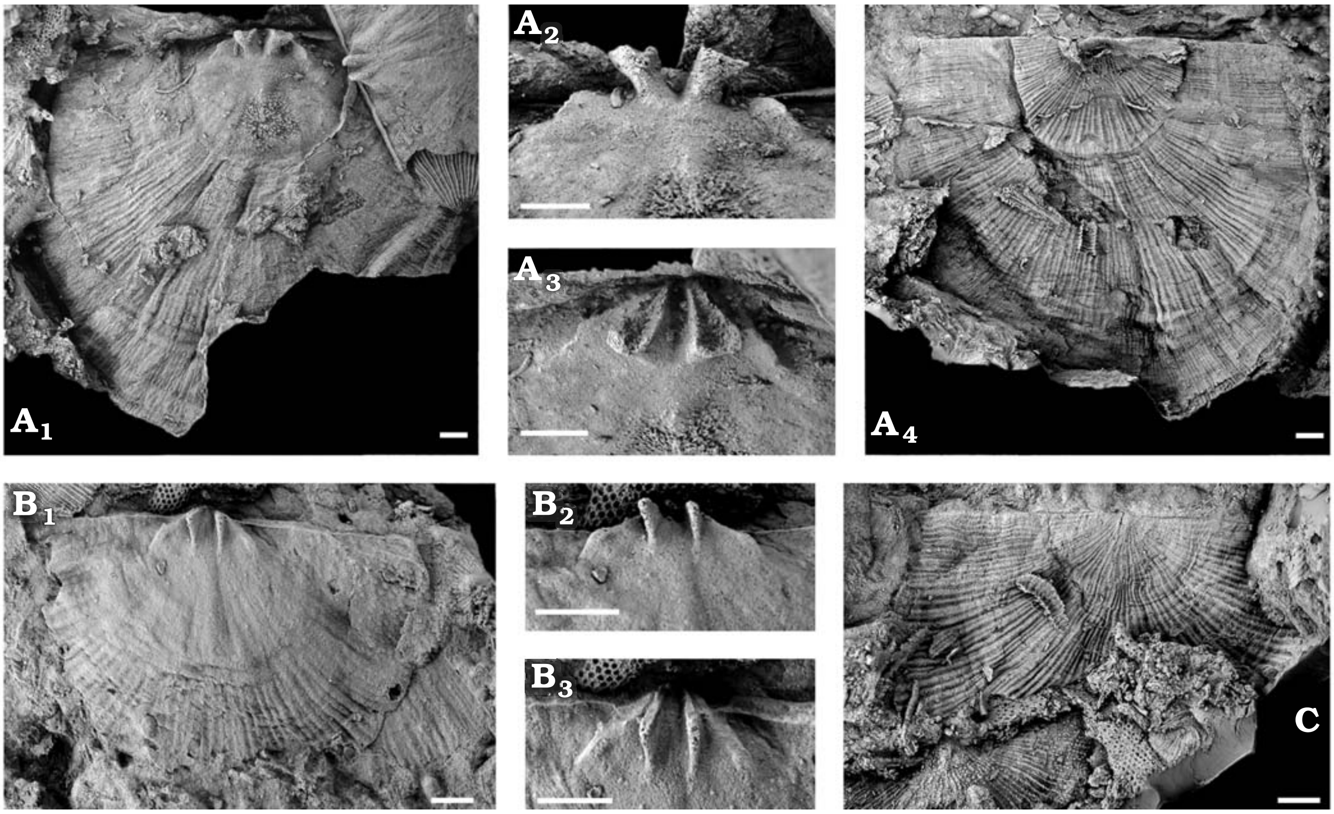

Fig. 13. Dorsal valves of rafinesquinine brachiopod *Rafinesquina* (*Mesogeina*) *gabianensis* sp. nov.; middle–upper Katian (Ka2–4), Upper Ordovician; Gabian Formation, Montagne Noire, France. **A**. MPZ 2015/1387, holotype, latex cast of interior (A_1), detail of cardinalia in anteroblique (A_2) and posteroblique (A_3) views, dorsal exterior (A_4). **B**. MPZ 2015/1388, paratype, latex cast of interior (B_1), detail of cardinalia in anteroblique (B_2) and posteroblique (B_3) views of a small specimen. **C**. VMN-1.22, paratype, latex cast of exterior. Scale bars 2 mm.

ventral valves, up to 27% as deep as long. Other characters that allow differentiating *R.* (*Mesogeina*) *gabianensis* from the Moroccan species are the absence of geniculation in *R.* (*Mesogeina*) *gabianensis* and the more alate cardinal extremities and the lower rib density of the new species, up to 6 ribs per 2 mm at 10 mm anteromedially from umbo in spite of 8–10 at the same growth stage of the Moroccan species. Finally the new species has concave myophores and a very small notothyrial platform whereas in *R.* (*Mesogeina*) *pomoides* the posteroventral surface of the myophores is flat and the notothyrial platform is much better developed.

Stratigraphic and geographic range.—Type locality and horizon only.

Rafinesquina (*Mesogeina*) *loredensis* sp. nov.

Fig. 14.

1985 *Hedstroemina mundae* (Sharpe, 1853); Young 1985: 345, pl. 34: 3, 8–9; non pl. 34: 1–2 (= *Orthis*? *mundae*), 4–7 (= *R.* [*Mesogeina*] *pseudoloricata*), 10 (*K.* [*Villasina*] *almadenensis*).

Etymology: After the name of the Loredo village.

Type material: Holotype: IGM-2919, internal mould of ventral valve (Fig. 14A). Paratypes: IGM-2923, 2925–2927.

Type locality: 250 m NE of the Louredo village, Aveiro district (Portugal).

Type horizon: Volcaniclastic rocks of the lower part of Porto de Santa Anna Formation, uppermost upper Berounian (probably middle Katian, Ka2 stage slice), Upper Ordovician at Louredo locality (Portuguese Central Iberian Zone).

Material.—Type material only.

Diagnosis.—Species of *Rafinesquina* (*Mesogeina*) with shell wider rather than long; ventral valves slightly convex, about 9% as deep as long and almost flat to slightly concave dorsal valves. Radial ornament with 6 ribs per 2 mm at 10 mm anteromedially from umbo, not clearly organized in sectors. Ribs subquadrate in section, twice as wide as the intercostal spaces. Ventral muscle field large, flabellate, poorly impressed anteriorly. Cardinal process lobes ponderous, with flat myophores; notothyrial platform low, very reduced.

Description.—Shell of large size (largest specimen 51.7 mm wide), lateral profile planoconvex to concavoconvex, semicircular in outline; maximum valve width at hinge line in young specimens and at mid valve length in adult ones; slightly acute cardinal angles in early growth stages and slightly obtuse in adult stages. Ventral valve 73–80% as long as wide ($\bar{x} = 76\%$; $n = 3$; $\sigma_n = 0.02$) and approximately 9% as deep as long, with slightly convex lateral profile. Ventral interarea planar, apsacline, 7% as long as valve length; delthyrium with apical pseudodeltidium. Dorsal valve almost flat to slightly concave, approximately 78% as long as wide; dorsal interarea anacline, 4% as long as valve length; notothyrium completely covered by a medially grooved, convex chilidium.

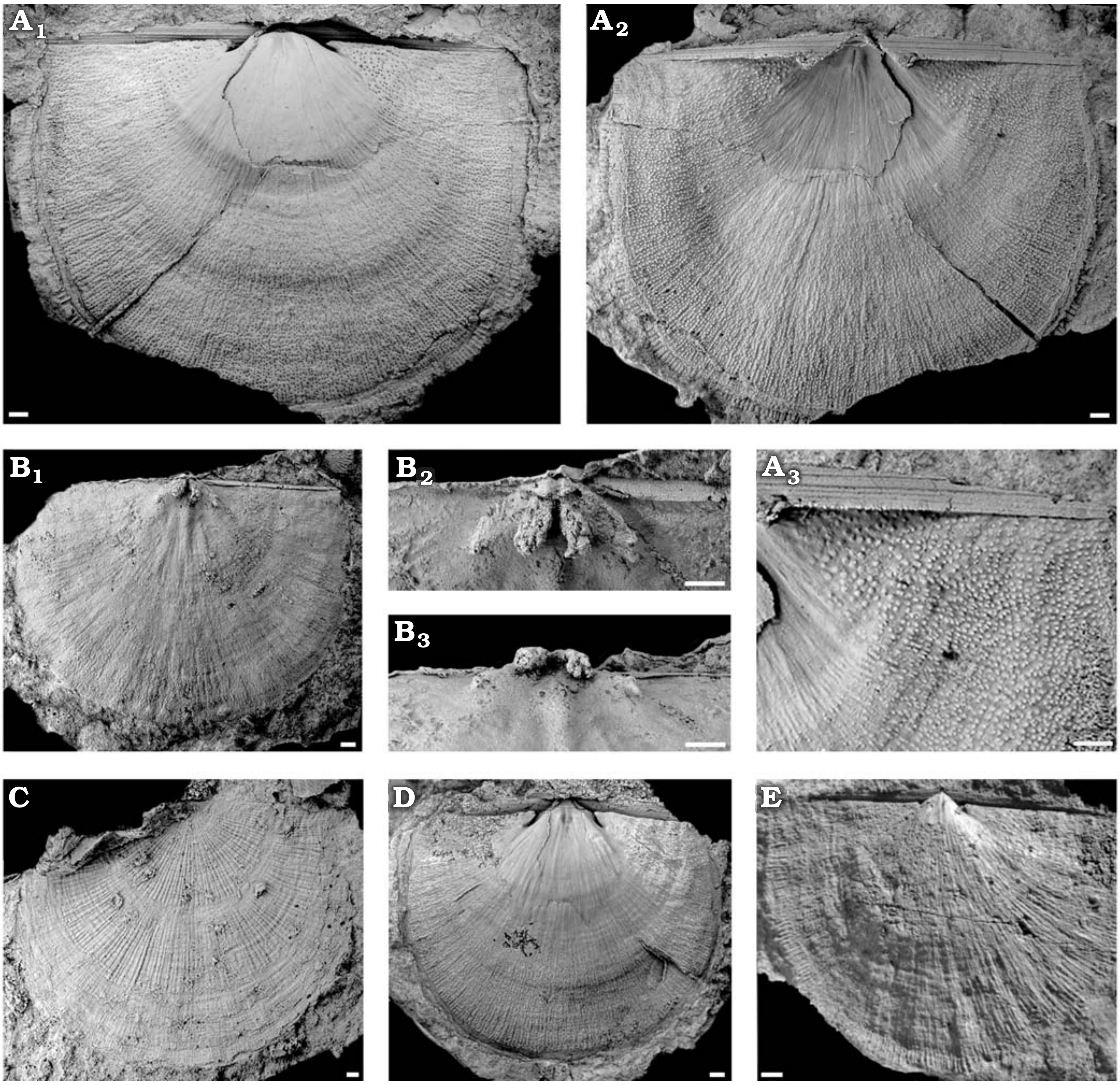

Fig. 14. Rafinesquinine brachiopod *Rafinesquina* (*Mesogeina*) *loredensis* sp. nov.; middle Katian (Ka2), Upper Ordovician; Porto de Santa Anna Formation, Portuguese Central Iberian Zone, Portugal. **A**. IGM-2919, holotype, internal mould (A_1), latex cast of interior (A_2), detail of pseudopunctae (A_3) of a ventral valve. **B**. IGM-2926, paratype, internal mould of dorsal valve (B_1), details of cardinalia in posteroventral (B_2) and anteroventral (B_3) views. **C**. IGM-2925, paratype, latex cast of exterior of dorsal valve. **D**. IGM-2927, paratype, internal mould of ventral valve. **E**. IGM-2923, paratype, internal mould of small ventral valve. Scale bars 2 mm.

Radial ornament parvicostellate, with 6 ribs per 2 mm at 10 mm anteromedially from umbo, all of them with subquadrate crests, not clearly organized in sectors; ribs twice as wide as intercostal spaces. Concentric ornamentation consisting of fine fila, with counts of 5 per mm, intersecting radial ornament; some specimens show evidences of shell damage, reflected as discontinuities in shell ornament varying the density of ribs per millimetre and even forming irregular lamellae close to the shell margins (Fig. 14C).

Ventral interior with strong teeth, short dental plates extending forward approximately 10% of valve length and with average dental plates divergence angle of 99° (range 93–103°; n = 3); muscle field large, poorly impressed anteriorly, flabelliform and surrounded posterolaterally by very narrow and thin muscle bounding ridges. Adductor scars lanceolate located between diductor scars and approximately 15% as wide as muscle scar maximum width; myophragm well developed posteriorly to adductor scars.

Dorsal interior with thin and about 85° divergent socket ridges, bounding anteriorly triangular dental sockets; bifid cardinal process with ponderous lobes, weakly divergent anteriorly, with flat myophores. They are located on very reduced, low notothyrial platform, continuous anteriorly with broad and low median ridge halving the poorly impressed dorsal muscle field. Pseudopunctae visible in both interiors, excepting on muscle scars, with radial regular arrangement over the entire shell except for posterolateral portion where it displays a more irregular pattern and coarseness.

Remarks.—Although the low number of available specimens is insufficient to study the intraspecific variability of this species of *Rafinesquina* (*Mesogeina*), the recorded material is appropriate to characterize its internal and external morphology and shows clear differences to the other *Rafinesquina* (*Mesogeina*) species described to date. *Rafinesquina* (*Mesogeina*) *loredensis* sp. nov. differs from the other Mediterranean species in having a more transversely elongate outline and ribs subquadrate in section, twice as wide as the intercostal spaces.

Young (1985) classified some rafinesquinid shells from Portugal as *Hedstroemina mundae* (Sharpe in Ribeiro et al., 1853). I propose to ascribe a part of that material to *Rafinesquina* (*Mesogeina*) *pseudoloricata* (Barrande, 1848) (see discussion under remarks of this species below). The rest of those Portuguese shells, with a clear transversally elongate outline (Young 1985: pl. 34: 3, 8, 9), are included herein in the new species *R*. (*Mesogeina*) *loredensis* (Fig. 14A, D, E). The Portuguese species *Orthis*? *mundae* Sharpe in Ribeiro et al., 1853 only known from a single ventral valve, is possibly also a rafinesquinine. However, its rounded outline and the remarkable inequality of its parvicostellate ornamentation discriminates the latter species from *R*. (*Mesogeina*) *loredensis* sp. nov., which possesses semicircular outline and parvicostellae only loosely arranged in sectors.

Stratigraphic and geographic range.—Type locality and horizon only.

Rafinesquina (*Mesogeina*) *pomoides* Havlíček, 1971

Figs. 15, 16.

1971 *Rafinesquina pomoides* sp. n.; Havlíček 1971: 71, pl. 22: 4–5; pl. 23: 2.

1979 *Strophonema* sp.; Hafenrichter 1979: pl. 9: 9.

1983 *Rafinesquina* aff. *pseudoloricata*; Villas 1983: pl. 3: 5–7.

1985 *Rafinesquina lignani* sp. nov.; Villas 1985: 105, text-figs. 11–13; pl. 24: 11–13; pl. 24: 1–6; pl. 25: 1–8; pl. 26: 1–6; pl. 27: 1–6.

1985 *Hedstroemina* sp. aff. *mundae* (Sharpe, 1853); Young 1985: 343, pl. 33: 6–12.

2006 *Rafinesquina*? *pomoides* Havlíček; Villas et al. 2006: figs. 4.5, 4.7, 4.8.

2007 *Rafinesquina pomoides* Havlíček, 1971; Álvaro et al. 2007: fig. 6C.

Holotype: Internal mould of ventral valve (Havlíček 1971: pl. 22: 4). [no specimen number in original publication] .

Type locality: Jbel Ahchahach, Anti Atlas, Morocco.

Type horizon: Upper Tiouririne Formation.

Material.—Internal and external moulds of 42 ventral valves and 11 dorsal valves: DPZ-318, 354b, 354b', 356 from the Iberian Chains and Spanish Central Iberian Zone; MPZ 2003/832, 833, 843 from the Anti Atlas, Morocco; MPZ 2015/1390 and IGM-2545A-B, 2945 from the Portuguese Central Iberian Zone; middle Katian (Ka2).

Emended diagnosis.—Species of *Rafinesquina* (*Mesogeina*) with shell approximately as wide as long. Ventral valve very convex with strong dorsal geniculation. Radial ornament with 8–10 ribs per 2 mm at 10 mm anteromedially from umbo. Ventral muscle field large, flabellate, poorly impressed anteriorly. Cardinal process lobes ponderous, triangular in outline, with flat and striated posteroventral surface; anchor-shaped notothyrial platform, high, well developed.

Description.—Shell of large size (largest specimen 38 mm wide), with strongly dorsal geniculation; semicircular in outline; maximum valve width at hinge line or slightly anterior to it; cardinal angles from acute to obtuse. Ventral valve ranging 82–123% as long as wide ($\bar{x}$ = 104%; n = 30; σ_n = 0.11); lateral profile geniculate dorsally, at approximately 25 mm long growth stage, with very convex disc and with variable trail length, ranging from 15% as deep as long in juvenile specimens and up to 40% as deep as long in adult ones ($\bar{x}$ = 27%; n = 28; σ_n = 0.06). Ventral interarea curved, apsacline, 8% as long as valve length; delthyrium open. Dorsal valve ranging 80–105% as long as wide ($\bar{x}$ = 96%; n = 7; σ_n = 0.09), gently concave; dorsal interarea anacline, 4% as long as valve length; notothyrium completely covered by a medially grooved, convex chilidium.

Radial ornament unequally parvicostellate with 8–10 ribs per 2 mm at 10 mm anteromedially from umbo, all of them with angular crests; ribs as wide as the intercostal spaces; between two costae there are up to 6 costellae. Concentric ornamentation consisting of fine fila disposed over the whole shell, as well as of more prominent growth lines occurring at different lengths from umbo but closer to each other, near shell margin; some specimens show evidences of shell damage, reflected as discontinuities in shell ornament (Figs. 15E, 16B).

Ventral interior with strong teeth well differentiated from hinge line, dental plates extending forward approximately 12% of valve length and with average dental plates divergence angle of 88° (range 80–94°; n = 6); muscle field poorly impressed anteriorly, flabelliform, ranging 24–55% as long as valve length, about 120% as long as wide and surrounded posterolaterally by narrow and thin muscle bounding ridges. Adductor scars lanceolate, about 15% as wide as muscle scars, completely surrounded by diductors.

Dorsal interior with strong and divergent socket ridges ($\bar{x}$ = 109°; n = 3) bounding triangular dental sockets; bifid cardinal process with elongate or plate-like lobes in young specimens, but triangular in outline and ponderous in adult specimens. Lobes weakly divergent anteriorly, with striated posteroventral surface of myophores. Situated on well developed, high, anchor-shaped notothyrial platform, continuous anteriorly with broad and well developed median ridge, halving subcircular dorsal muscle field; short transmuscle

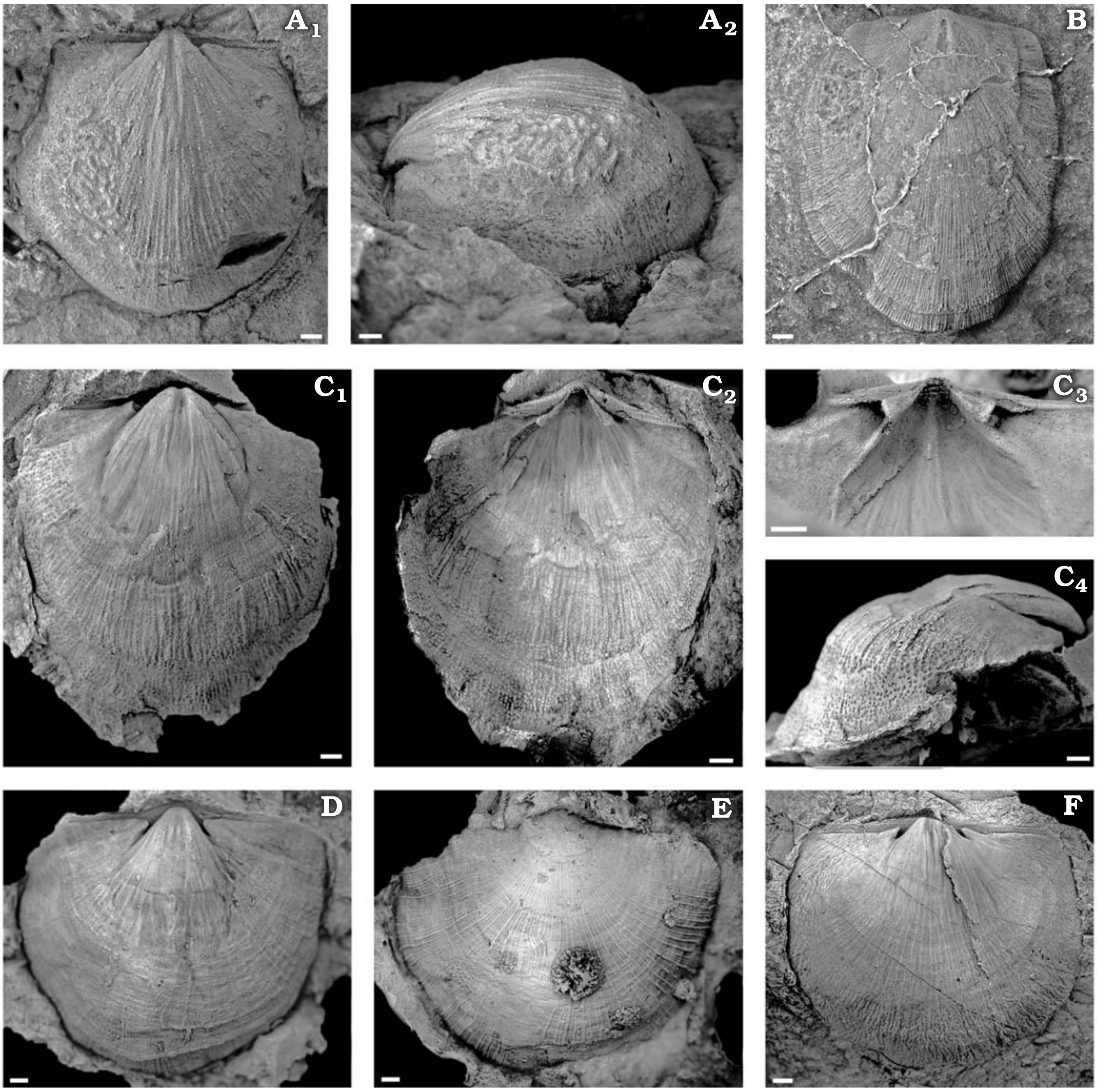

Fig. 15. Ventral valves of rafinesquinine brachiopod *Rafinesquina* (*Mesogeina*) *pomoides* Havlíček, 1971; middle Katian (Ka2), Upper Ordovician; Lower Ktaoua Formation (A) and Upper Tiouririne Formation (B), Morocco; Huerva Member of Fombuena Formation, Iberian Chains, Spain (C); Porto de Santa Anna Formation, Portuguese Central Iberian Zone, Portugal (D–F). **A**. MPZ_2003_832, ventral internal mould of a complete valve in upper (A_1) and lateroblique (A_2) views. **B**. MPZ 2015/1390, latex cast of ventral exterior of a ventral valve. **C**. DPZ-318 (ex-holotype of *Rafinesquina lignani* Villas, 1985), ventral internal mould (C_1), latex cast of ventral interior (C_2), detail of dental plates (C_3), and lateral view (C_4). **D**. IGM-2545A, ventral internal mould. **E**. IGM-2545B, latex cast of exterior. **F**. IGM-2945, internal mould. Scale bars 2 mm.

septa sometimes present in most posterior part of the muscle scars. Pseudopunctae with radial pattern visible in both interiors, but better marked in ventral ones.

Remarks.—This species was described by Havlíček (1971) based on a small collection from Morocco. Villas et al. (2006) and Álvaro et al. (2007), considered tentatively *Rafinesquina* (*Mesogeina*) *pomoides* as a senior synonym of the Spanish species *R.* (*Mesogeina*) *lignani* Villas, 1985. Following these authors and once confirmed the complete morphological similitude between both species, with the study of a new large collection from Mococco, I propose to synonymize them formally, being *R.* (*Mesogeina*) *pomoides* the senior synonym. Also some specimens classified by Young (1985: pl. 33: 6–12) as *Hedstroemina* sp. aff. *mundae* (Sharpe in Ribeiro et al., 1853), after examination of a large collection of these brachiopods from Portugal, belong to *R.*

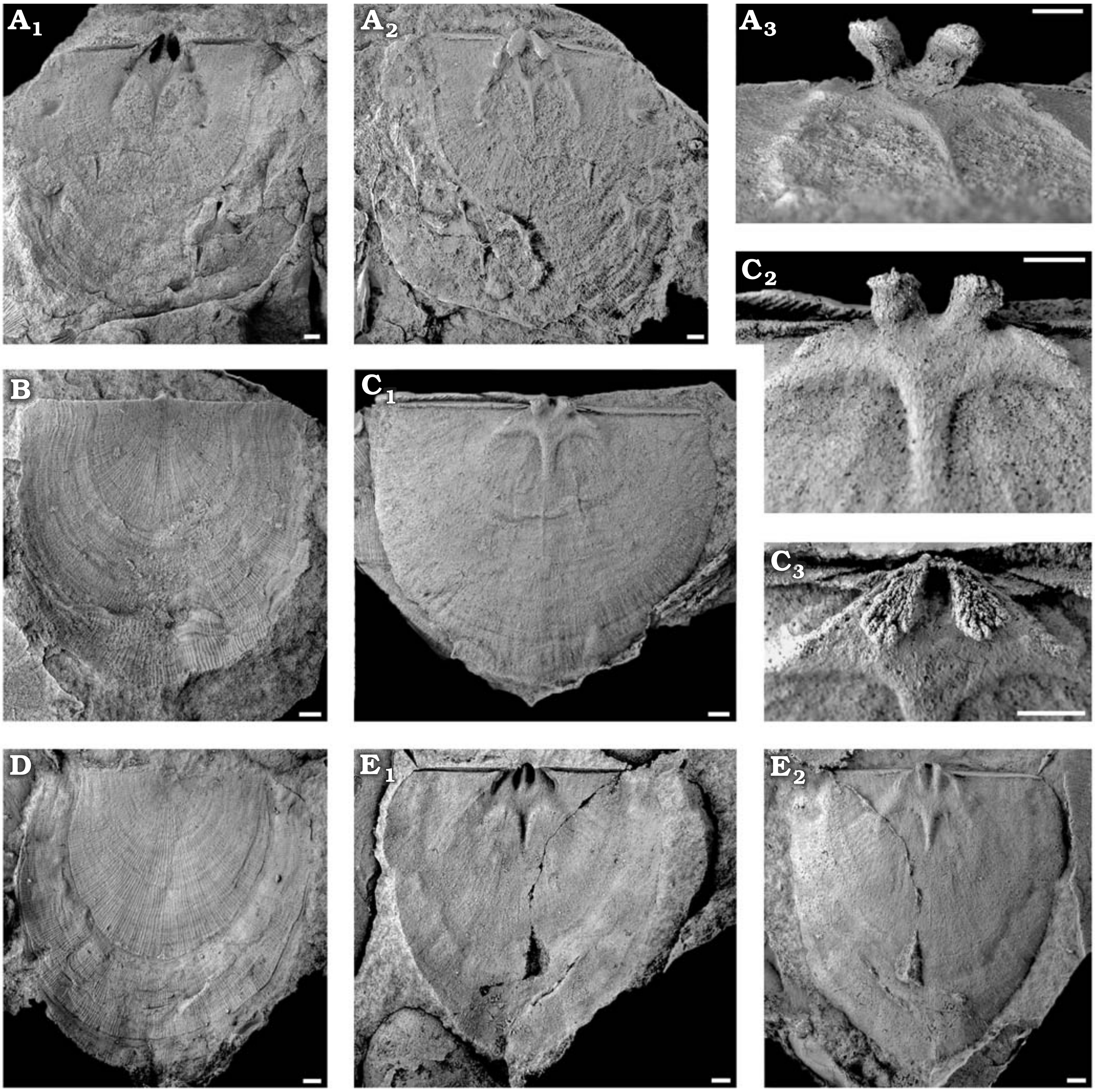

Fig. 16. Dorsal valves of rafinesquinine brachiopod *Rafinesquina* (*Mesogeina*) *pomoides* Havlíček, 1971; middle Katian (Ka2), Upper Ordovician; Lower Ktaoua Formation, Morocco (A, B); Huerva Member of Fombuena Formation, Iberian Chains, Spain (C–E). **A**. MPZ_2003_833, internal mould (A_1) and latex cast of interior (A_2), detail of cardinalia in anteroventral view (A_3). **B**. MPZ_2003_843, latex cast of exterior. **C**. DPZ-356, latex cast of interior of a dorsal valve (C_1), detail of cardinalia in anteroventral (C_2) and posteroventral (C_3) views. **D**. DPZ-354b, latex cast of exterior. **E**. DPZ-354b', internal mould (E_1) and latex cast of interior (E_2). Scale bars 2 mm.

(*Mesogeina*) *pomoides*, although the dorsal valves of the Portuguese shells remain unknown.

Stratigraphic and geographic range.—Katian of Morocco: middle part of Lower Ktaoua Formation at Jbel Ahchach (Havlíček, 1971); upper part of Lower Ktaoua Formation at Alnif (Villas et al. 2006; Alvaro et al. 2007) and Upper Tiouririne Formation at Jbel Adrar, Jbel Aroudane, and Jbel Tizi N'Rsoa; Portuguese Central Iberian Zone: Porto de Santa Anna Formation at Zuvinhal locality (Portugal); Spain: middle part of Huerva Member of the Fombuena Formation at Luesma 2, Fombuena 4, and Herrera 1 localities (see Villas 1985 for precise situation) from the Iberian Chains; "Bancos mixtos" at Corral de Calatrava (Hafenrichter 1979; Villas, 1995) from the Spanish Central Iberian Zone.

Rafinesquina (*Mesogeina*) *pseudoloricata* (Barrande, 1848)

Figs. 17, 18.

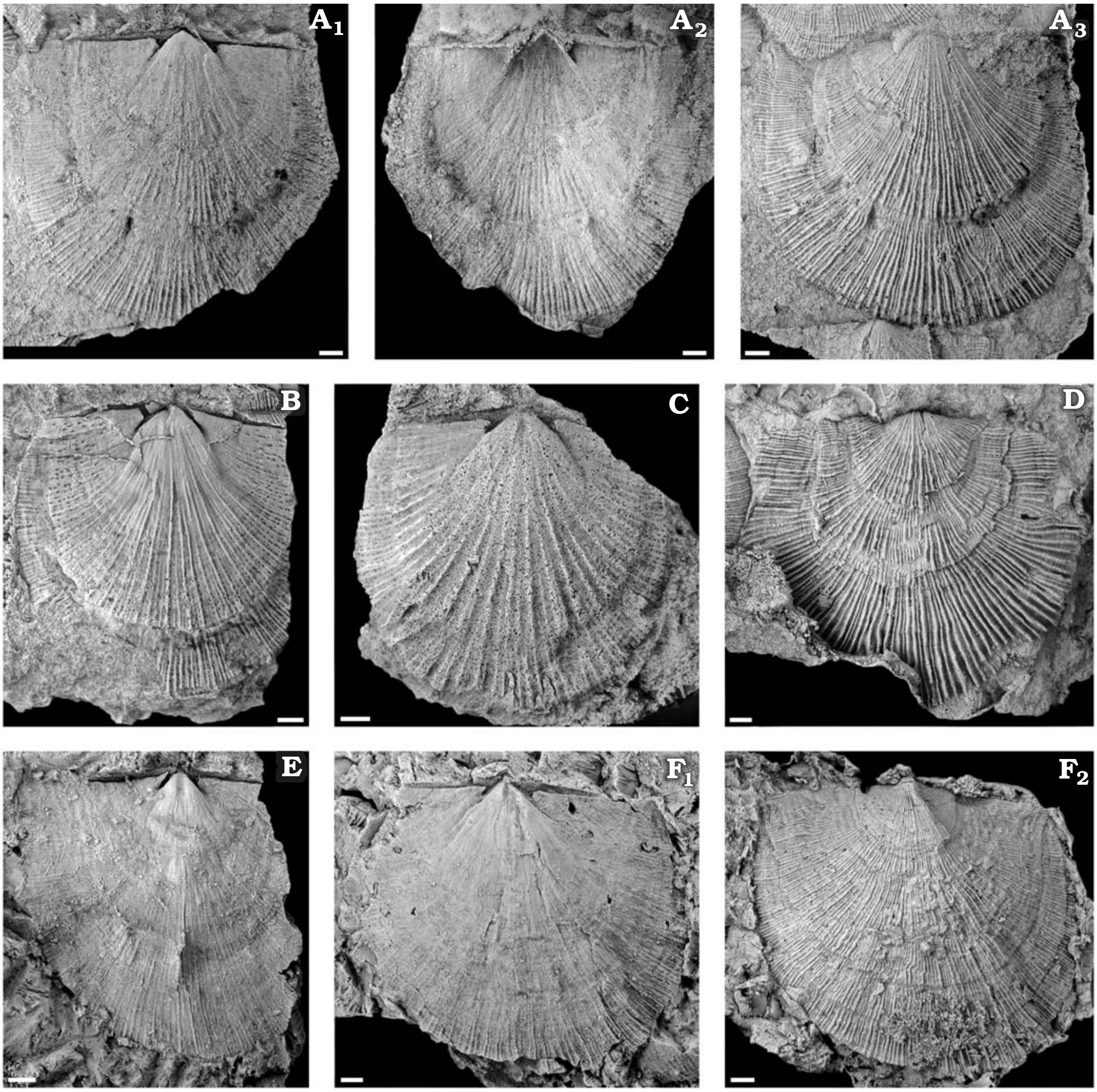

Fig. 17. Ventral valves of rafinesquinine brachiopod *Rafinesquina* (*Mesogeina*) *pseudoloricata* (Barrande, 1848); lower–middle Katian (Ka1–2), Upper Ordovician; Zahorany Formation, Bohemia, Czech Republic (A, B); Upper Tiouririne Formation, Morocco (C); Porto de Santa Anna Formation, Portuguese Central Iberian Zone, Portugal (D); Peña del Tormo Member of the Fombuena Formation, Iberian Chains, Spain (E, F). **A**. MPZ 2015/1391, internal mould (A_1), latex cast of interior (A_2) and exterior (A_3). **B**. MPZ 2015/1392, internal mould of an incomplete valve. **C**. MPZ 2015/1393, ventral internal mould. **D**. IGM-2952A, latex cast of ventral exterior. **E**. DPZ-359, internal mould of an incomplete valve. **F**. DPZ-362, internal mould (F_1) and latex cast of exterior (F_2). Scale bars 2 mm.

1848 *Leptaena pseudo-loricata*; Barrande 1848: 222, pl. 18: 9.
1853 *Leptaena beirensis*, n. s.; Sharpe in Ribeiro et al. 1853: 156, pl. 8: 8.
1853 *Leptaena ignava*, n. s.; Sharpe in Ribeiro et al. 1853: 157, pl. 8: 9.
1879 *Strophomena pseudo-loricata* Barr; Barrande 1879: pl. 54: 4.
1951 *Rafinesquina pseudoloricata* (Barr); Havlíček 1951: 23, pl. 3: 1, 6, 7.
1966 *Rafinesquina pseudoloricata* (Barr); Schulz and Jordan 1966: 703–705, figs. 1–3.
1967 *Rafinesquina pseudoloricata* (Barr); Havlíček 1967: 77, pl. 10: 7–14; pl. 11: 8.
1971 *Rafinesquina pseudoloricata* (Barr); Havlíček 1971: 70–71, pl. 21: 2–3.
1983 *Rafinesquina* sp. 1; Villas 1983: pl. 2: 2.
1985 *Rafinesquina pseudoloricata* Barrande, 1848; Villas 1985: 103–105, pl. 28: 1–8; pl. 29: 1–3, 5, 6, 8.
1985 *Hedstroemina mundae* (Sharpe, 1853); Young 1985: 345, pl. 34: 4–7; non figs. 1–2 (= *Orthis*? *mundae*), figs. 3, 8, 9 (= *Rafin-*

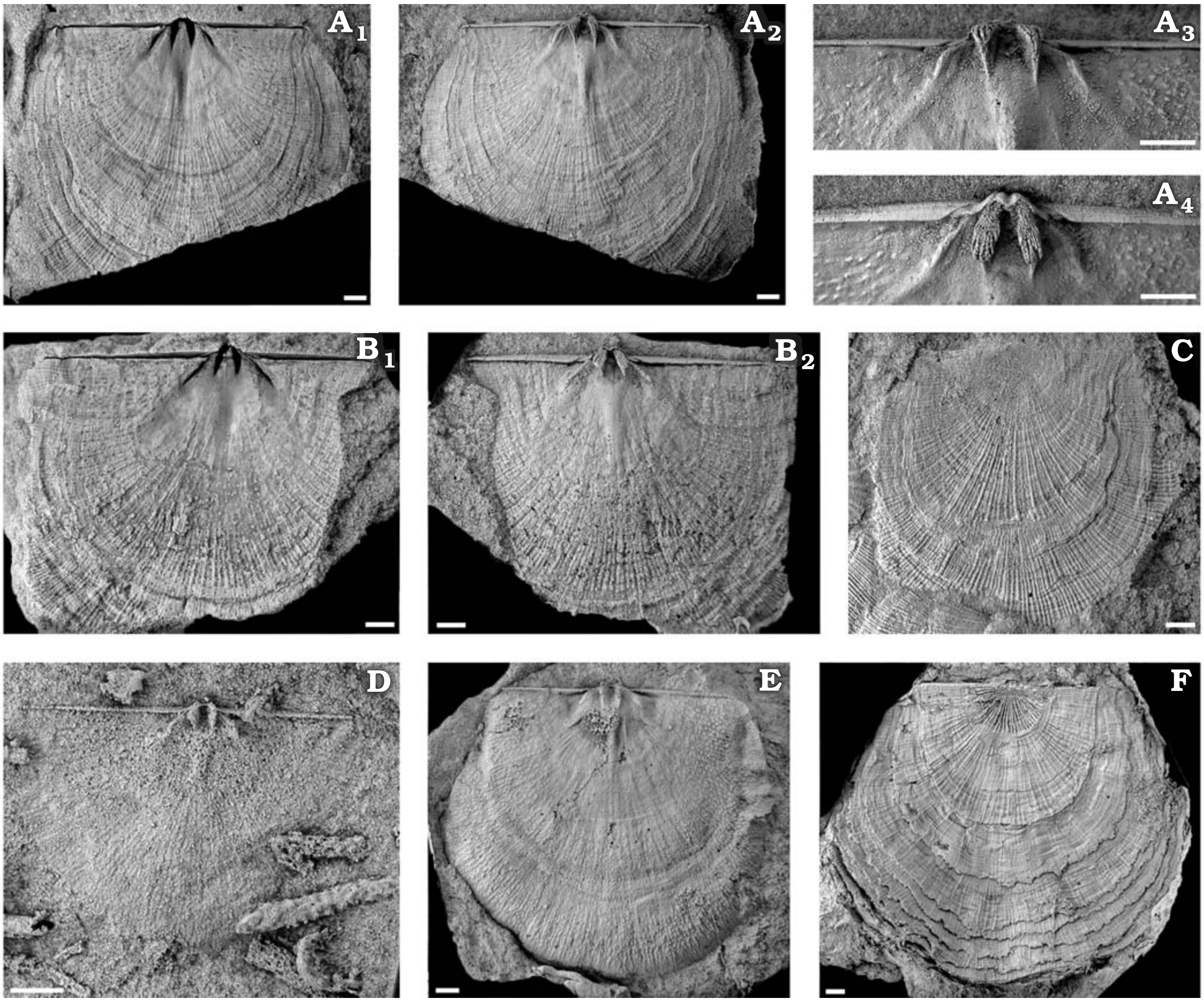

Fig. 18. Dorsal valves of rafinesquinine brachiopod *Rafinesquina* (*Mesogeina*) *pseudoloricata* (Barrande, 1848); lower–middle Katian (Ka1–2), Upper Ordovician; Zahorany Formation, Bohemia, Czech Republic (A–C); Peña del Tormo Member of the Fombuena Formation, Iberian Chains, Spain (D); Porto de Santa Anna Formation, Portuguese Central Iberian Zone, Portugal (E, F). **A**. MPZ 2015/1394, dorsal internal mould (A$_1$) and latex cast of dorsal interior (A$_2$), detail of cardinalia in anteroventral (A$_3$) and posteroventral (A$_4$) views. **B**. MPZ 2015/1395, internal mould (B$_1$) and latex cast of interior (B$_2$). **C**. MPZ 2015/1396, latex cast of dorsal exterior. **D**. MPZ 2015/1397, latex cast of interior of a small valve. **E**. IGM-2934, latex cast of interior. **F**. IGM-2936, latex cast of dorsal exterior. Scale bars 2 mm.

esquina [*Mesogeina*] *loredensis*, described above) and fig. 10 (= *Kjaerina* [*Villasina*] *almadenensis,* discussed above).

1995 *Rafinesquina* cf. *pseudoloricata* (Barrande, 1848); Villas 1995: 80, pl. 13: 2–7.

Material.—Internal and external moulds of 23 ventral valves and 10 dorsal valves: DPZ-359, 362 from the Iberian Chains, Spain; MPZ 2015/1391–1397 from Bohemia (Czech Republic); IGM-2934, 2936, 2952A from the Portuguese Central Iberian Zone; upper middle Berounian–upper Berounian (lower–middle Katian, Ka1–2 stage slices).

Description.—Shell of large size (largest specimen 37 mm wide), lateral profile concavoconvex, semicircular in outline; maximum valve width at hinge line in young specimens and at mid valve in adults; cardinal angles from acute to obtuse. Ventral valve gently convex, ranging 67–99% as long as wide ($\bar{x} = 87\%$; $n = 11$; $\sigma_n = 0.08$) and 6–12% as deep as long ($\bar{x} = 9\%$; $n = 5$; $\sigma_n = 0.04$); ventral interarea curved, apsacline, 6% as long as valve length; delthyrium open. Dorsal valve gently concave, approximately 87% as long as wide; dorsal interarea anacline, 1% as long as valve length; notothyrium completely covered by medially grooved, convex chilidium.

Radial ornament unequally parvicostellate, with 6–8 ribs per 2 mm at 10 mm anteromedially from umbo, normally displaying irregular layout from beak to shell margin and all of them with rounded crests; between two costae there are up to 5 costellae. Concentric ornamentation consisting of fila disposed over the whole shell but more abundant and closer among them near shell margin; some specimens showing evidences of shell damage reflected as discontinuities in shell ornament (Figs. 17A$_3$, D, 18C).

Ventral interior with strong teeth well differentiated from hinge line, dental plates extending forward approximately 12% of valve length and with average dental plates divergence angle of 99° (range 89–106°; n = 4); muscle field poorly impressed anteriorly, flabelliform, ranging 33–51% as long as valve length, approximately as long as wide and surrounded posterolaterally by narrow and thin muscle bounding ridges. Adductor scars lanceolate, faintly impressed located between diductors.

Dorsal interior with strong and divergent socket ridges ($\bar{x}$ = 96°; n = 4) bounding triangular and elongated dental sockets; bifid cardinal process with elongate or plate-like lobes in young specimens, but engrossed in adult specimens. Lobes weakly divergent anteriorly and myophores has striated posteroventral surface. Situated on low and delicate notothyrial platform, continuous anteriorly with broad and faintly impressed median ridge halving dorsal muscle field. Fine pseudopunctae with radial pattern visible in both interiors.

Remarks.—The unequally parvicostellate ornamentation, with 6–8 ribs per 2 mm at 10 mm anteromedially from umbo, the pseudopunctae development, the semicircular shell outline with the maximum valve width at hinge line in young specimens and at mid valve in adults and the cardinalia of the studied material from the Portuguese Central Iberian Zone and from the Spanish Iberian Chains and Spanish Central Iberian Zone, warrants their inclusion within the Bohemian species *Rafinesquina* (*Mesogeina*) *pseudoloricata* (Barrande, 1848). The Spanish collections had already been assigned to this species by Villas (1983, 1985, 1995), and are partly re-figured herein.

Two of the valves from Portugal, now revised, were used by Sharpe (in Ribeiro et al. 1853) to characterize two different species, *Leptaena beirensis* and *L. ignava*. The former based on one ventral valve and the latter on one dorsal valve. The same author (Sharpe in Ribeiro et al. 1853: 157) doubts about the validity of *L. ignava* in the remarks of both species arguing that "This shell (*L. beirensis*) closely resembles the next described, *L. ignava*, and perhaps they may prove the opposite valves of one species. (…) Only one valve of this shell (*L. ignava*) has been seen, and it may perhaps prove to be the ventral valve of the preceding species, *L. beirensis*, to which it is very nearly allied". Sharpe (in Ribeiro et al. 1853) did not compare his species with the Bohemian *R.* (*Mesogeina*) *pseudoloricata* described by Barrande (1848) little before. After the study of the type material of *L. beirensis* and *L. ignava*, as well as additional material from their type localities, I can confirm their synonymy, due to their identical radial and concentric ornamentation, pseudopunctae development, shell outline and cardinalia. In addition, the comparison of this material with topotypes of *R.* (*Mesogeina*) *pseudoloricata* from Bohemia, suggests inclusion of the Portuguese material to the Bohemian species and, therefore, *L. beirensis* and *L. ignava,* are junior synonyms of *R.* (*Mesogeina*) *pseudoloricata.*

Young (1985) also proposed to synonymize *L. beirensis* and *L. ignava* with the poorly known *Orthis mundae* Sharpe in Ribeiro et al. 1853, which he included to *Hedstroemina*. Young (1985) assigned to that reinterpreted species a wide range of rafinesquinines, which have been separated herein into three species of two different genera: *Kjaerina* (*Villasina*) *almadenensis*, *Rafinesquina* (*Mesogeina*) *loredensis*, and *R.* (*Mesogeina*) *pseudoloricata*. If the proposal by Young (1985) was right *O. mundae* would be a junior synonym of *R.* (*Mesogeina*) *pseudoloricata*. The only preserved valve or *O. mundae* displays some similarities in ornamentation to *R.* (*Mesogeina*) *pseudoloricata*, but clearly it is not sufficient to give a definite conclusion on its taxonomic status.

Stratigraphic and geographic range.—lower–middle Katian (Ka1–2), Upper Ordovician of Bohemia: Zahorany and Bohdalec formations (see Havlíček 1967); Germany: "Lederschiefer" pebbles from East Thuringia (see Schulz and Jordan 1966); Morocco: middle part of the Lower Ktaoua Formation (see Havlíček 1971); Portugal: Porto de Santa Anna Formation at Louredo locality; Spain: base of the Piedra del Tormo Member of the Fombuena Formation from the Iberian Chains.

Rafinesquina (*Mesogeina*)? sp. A

Fig. 19.

Material.—Internal and external moulds of 5 ventral valves and 4 dorsal valves (MPZ 2015/1398–1402) from alternating marlstone and bioclastic limestone beds of the lower part of the Gabian Formation, Montagne Noire (France), middle–upper Katian (Ka2–4), Ordovician.

Description.—Shells of large size (largest specimen 48 mm wide), lateral profile concavoconvex, semicircular in outline; maximum valve width at hinge line in early growth stages and at hinge line or near to it in adult stages; cardinal angles acute in early growth stages and right to obtuse in adult stages. Ventral valve approximately 92% as long as wide and approximately 7% as deep as long, lateral profile slightly convex. Ventral interarea planar, apsacline, 5% as long as valve length; delthyrium partially covered by apical pseudodeltidium. Dorsal valve with slightly concave lateral profile; notothyrium completely covered by medially grooved, convex chilidium.

Radial ornament unequally parvicostellate with 5–6 ribs per 2 mm at 10 mm anteromedially from umbo, all of them with angular crests; between two costae up to 6 costellae. Concentric ornamentation consisting of poorly marked, fine fila; well marked growth lines sometimes occur related to evidences of shell damage (Fig. 19A$_3$).

Ventral interior with strong teeth, dental plates extending forward approximately 12% of valve length and with average dental plates divergence angle of 85° (range 75–93°; n = 4); muscle field large, triangular, poorly impressed anteriorly, surrounded posterolaterally by outwardly curved muscle bounding ridges. Adductor scars lanceolate, about 20% as wide as muscle scars, located between diductor scars but not surrounded anteriorly.

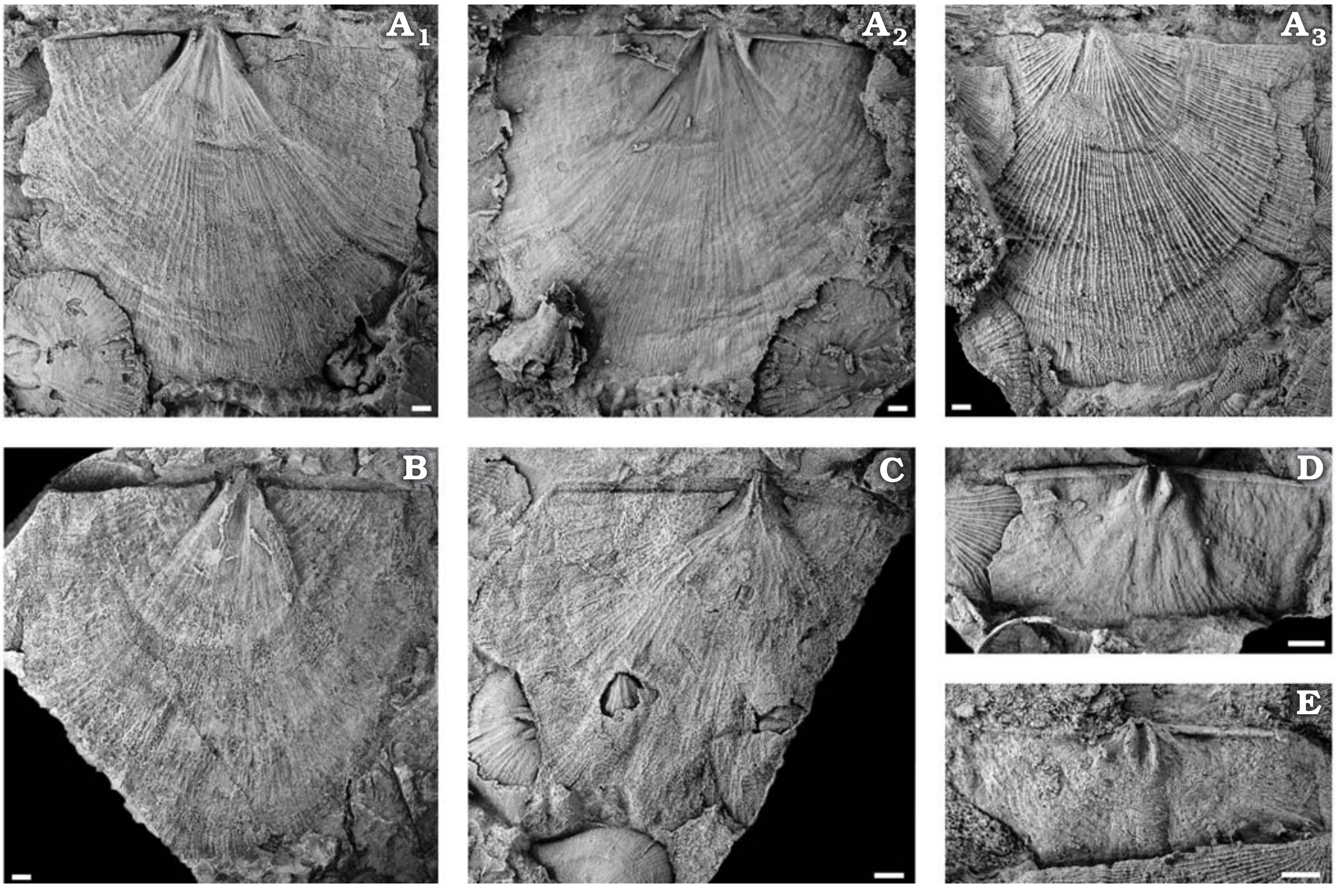

Fig. 19. Rafinesquinine brachiopod *Rafinesquina* (*Mesogeina*)? sp. A; middle–upper Katian (Ka2–4), Upper Ordovician; Gabian Formation, Montagne Noire, France. **A**. MPZ 2015/1398, internal mould (A_1) and latex cast of interior (A_2) and exterior (A_3) of an almost complete ventral valve. **B**. MPZ 2015/1399, internal mould of ventral valve. **C**. MPZ 2015/1400, internal mould of ventral valve. **D**. MPZ 2015/1401, latex cast of interior of an incomplete dorsal valve. **E**. MPZ 2015/1402, latex cast of interior of an incomplete dorsal valve. Scale bars 2 mm.

Dorsal interior with thin and divergent socket ridges (96°) bounding triangular dental sockets; bifid cardinal process with ridge-like, subparallel, medially convergent lobes. It is located on a very reduced or even absent notothyrial platform, continuous anteriorly with very thin and low median ridge halving poorly impressed dorsal muscle field. Pseudopunctae thin and poorly developed in both valve interiors.

Remarks.—All the external characters as well as dorsal internal characters suggest the inclusion of the studied material within *Rafinesquina* (*Mesogeina*), but the ventral internal features display some similarities with some leptostrophiids. It includes the triangular muscle field outline and the outwardly curved muscle bounding ridges, although the absence of denticles in the hinge line, a priori, discards the assignment of this material to the family Leptostrophiidae. As the studied material displays mixed features between the two families, it could belong to a new genus with an uncertain family position. On the other hand, the dorsal interior of the studied shells displays some features in common with *Rafinesquina* (*Mesogeina*), as the subparallel, plate like cardinal process lobes. To confirm the generic assignment and ascertain the family position of these shells, more material, especially adult dorsal valves, is needed.

Palaeobiogeographical remarks

The oldest known rafinesquinine is *Shuangheella* from the lower to middle Dapingian of South China (Zhan et al. 2013). During the late Darriwillian and the early Sandbian the group experienced a rapid westward dispersion from South China (Zhan et al. 2013) having colonized the main western palaeocontinents and terranes (see Fig. 20). By that time they are known from Baltica with *Kjerulfina* Bancroft, 1929 as the first rafinesquinine immigrant, from Avalonia with *Rafinesquina* Hall and Clarke, 1892 and *Kjaerina* Bancroft, 1929, from Laurentia with *Rhipidomena* Cooper, 1956, and from part of the Mediterranean margin of Gondwana (Perunica), with *Rafinesquina*. These genera proliferated in those regions during the late Sandbian–early Katian, while new genera as *Colaptomena* Cooper, 1956 and? *Hibernodonta* Harper and Mitchell in Harper et al. (1985) appear in Avalonia. Furthermore, *Rhipidomena* and *Testaprica* Percival, 2009, expanded their distribution during early Katian to middle Katian from Laurentia and Australia to the Chu-Ili and Chingiz terranes of Kazakhstan, respectively (Popov and Cocks 2006, 2014). Meanwhile, in the Mediterranean province the dominant

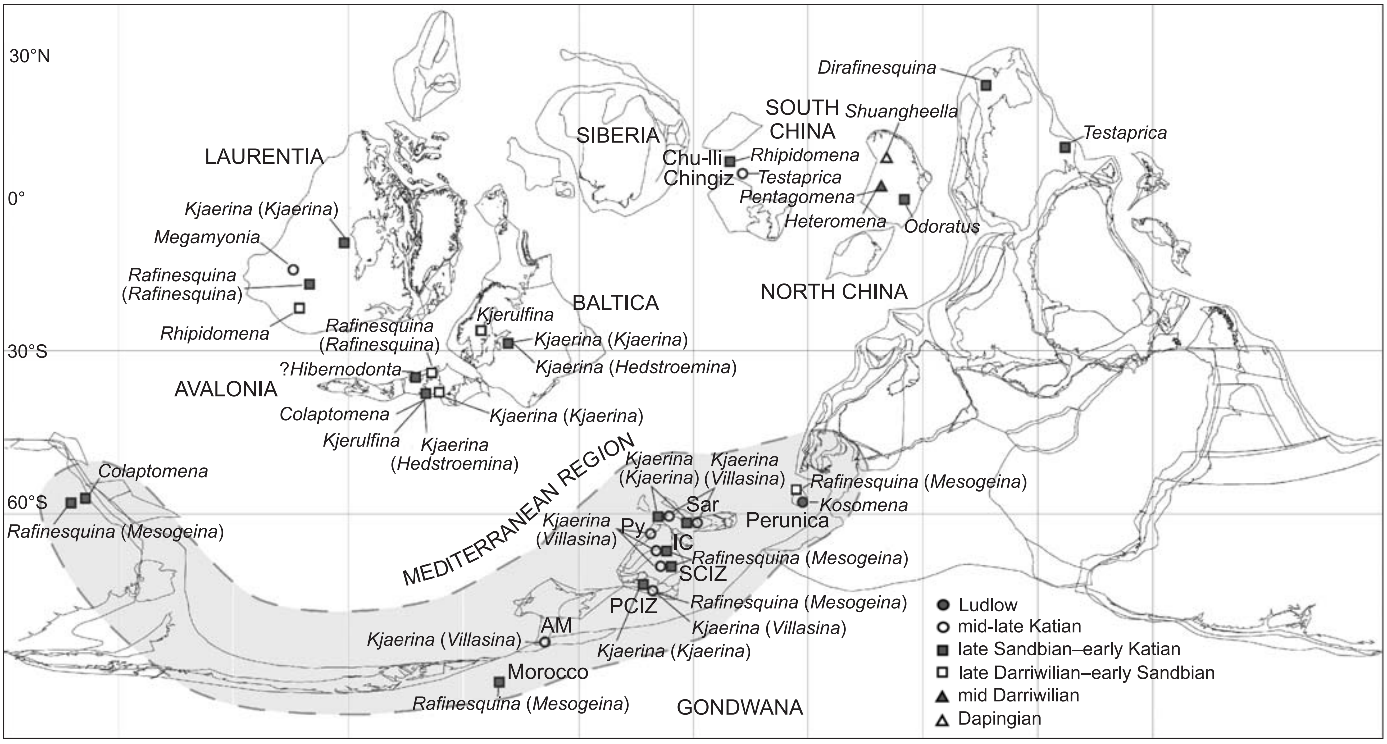

Fig. 20. First Appearance Datum (FAD) of all rafinesquinine genera in each palaeocontinent plotted over a palaeogeographical map for the late Katian time slice based on BugPlates and using a Mollweide projection. Present-day outlines of lands and seas are shown on each continent to aid recognition. AM, Armorican Massif; PCIZ, Portuguese Central Iberian Zone; SCIZ, Spanish Central Iberian Zone; IC, Iberian Chains; Py, Pyrenees; MN, Montagne Noire; Sar, Sardinia.

taxa were the heterorthids and draboviids while the strophomenoids were very rare.

The Mediterranean faunal province was first introduced by Spjeldnaes (1961) and subsequently refined by Havlíček (1976) to enclose a wide region on the high latitude northern Gondwana margin between present Arabia and northern South America. It was characterized during the Middle through the early Late Ordovician by low diversity brachiopod associations, dominated by endemic groups, mostly orthides (Heterorthidae and Drabovidae). The brachiopod diversity increased considerably during the rest of Late Ordovician, and the endemism in the associations diminished. The Mediterranean province is represented today mainly in the Central Andean Basin, the Anti-Atlas, the Armorican Massif, the Iberian Massif, the Montagne Noire, the Iberian Chains, the Pyrenees, the Carnic Alps, Sardinia and the Bohemian Massif. During the Upper Ordovician, it was located in mid-high latitudes, approximately 50–75° S (Harper et al. 2014).

Representatives of the superfamilies Plectambonitoidea (family Xenambonitidae) and Strophomenoidea (family Strophomenidae) were the first strophomenoids to appear in to the region (Middle Ordovician), but usually they occur in low proportions in the assemblages (Reyes-Abril et al. 2011). The rafinesquinines appeared in this region during the early Late Ordovician (early Sandbian), represented by a few species of *Rafinesquina* and restricted mainly to Perunica (Havlíček 1967). By the late Sandbian–middle Katian one of these species, *Rafinesquina* (*Mesogeina*) *pseudoloricata*, had expanded its distribution to the North African platforms and Iberia, surviving in the latter region until the late Katian.

Another genus that appears in the region during the early to middle Katian is *Kjaerina*. Its first record is from Avalonia (lower Sandbian), but in the interval of late Sandbian to early Katian it had already occurred in Baltica and Laurentia (Rõõmusoks 1993; Jin et al. 1995 respectively). The first known species of *Kjaerina* in the Mediterranean province is *K.* (*Kjaerina*) *gondwanensis,* which has been recorded in the lower to middle Katian of the Portuguese Central Iberian Zone, the Montagne Noire, and Sardinia. This species inhabited environments of thin-grained siliciclastic substrates within an upper offshore regime (lower Benthic Assemblage 3 [BA 3] of Boucot 1975). The arrival of *Kjaerina* to the high latitude margin of Gondwana coincides with the first pulse of the low latitude brachiopod invasion that became generalized during the late Katian (Fortey and Cocks 2005). From this moment on, something changed in the Mediterranean province, where the number of strophomenoide taxa increased exponentially. This circumstance was first noted by Havlíček (1967) in the Bohemian region but it is also clear in many other places of the province (Mélou 1990; Villas 1995). At this time, the regime of sedimentation change in the region from siliciclastic to carbonatic, even with development of reefs in Armorica and Central Spain (Boucot et al. 2003). Thanks to the appearance of new niches and simultaneously to the global warming of Boda event (Fortey and Cocks 2005), a diverse group of brachiopods, mainly belonging to the *Nicolella* fauna (Pickerill and Brenchley 1979; Havlíček 1981) coming from the temperate and tropical palaeocontinents (Avalonia, Baltica, Laurentia), invaded these carbonatic platforms and replaced in most part the high latitude endemic taxa (Colmenar et al. 2013).

Since this moment on, some genera previously rather marginal in the benthic assemblages in this region became more abundant. This is the case of the representatives of the subfamily Rafinesquininae, which proliferated in the new environments, such as several Mediterranean endemic species of *Rafinesquina* including *R.* (*Mesogeina*) *pomoides*, *R.* (*Mesogeina*) *gabianensis*, and *R.* (*Mesogeina*) *loredensis.* No other species of *Kjaerina* apart from *K.* (*Kjaerina*) *gondwanensis* is known to have thrived in this region after the starting of the Boda event (middle to late Katian), although diversified but well-knit group of multicostellate rafinesquinine species, probably descendant of *Kjaerina* itself, spreaded throughout majority of the Mediterranean margin of Gondwana during the middle to late Katian. They are *K.* (*Villasina*) *pedronaensis*, known from Sardinia and Montagne Noire, *K.* (*Villasina*) *almadenensis* from the Spanish and Portuguese Central Iberian Zone and from the Armorican Massif, as well as *K.* (*Villasina*) *meloui* exclusive to the Armorican Massif and *K.* (*Villasina*) *pyrenaica* from the Spanish Pyrenees.

There are some parts of the Mediterranean province, in which the rafinesquinines remained only a minor, poorly diversified component of brachiopod faunas. There are only two rafinesquinines known, *Rafinesquina* (*Mesogeina*) *pseudoloricata* and *R.* (*Mesogeina*) *pomoides*, from the middle–upper Katian of the southernmost Gondwanan platforms cropping out today in the Moroccan Anti-Atlas. This is interpreted to be related with the high latitudes of that region, close to the Antarctic Polar Circle (Harper et al. 2014), where the siliciclastic sedimentation continued to be dominant during the whole Late Ordovician. Another region where no rafinesquinine have been recorded in the upper Katian is Perunica—the most north-eastern part of the Mediterranean province. This could be related to the bathymetry in region because only the deeper facies are known from there (Havlíček 1982) where only small brachiopods of the *Foliomena* fauna (Havlíček and Mergl 1982) occur. This brachiopod association is characteristic of the BA 5–6 (Rong et al. 1999a), usually not inhabited by rafinesquinines, which are more frequent in shallower environments as those of the BA 3 (Percival 2009).

No rafinesquinine is known from the Hirnantian Stage, either from the cosmopolitan *Hirnantia* fauna or from coetaneous brachiopod associations from tropical latitudes (Rong and Harper 1988). It represents an abrupt disappearance of more than thirteen genera, known worldwide from the Upper Katian. This seems to include the subfamily Rafinesquininae within the list of losses related to the Hirnantian glaciation and the first of the big five mass extinctions. Nevertheless, there is a genus in the subfamily Rafinesquininae, *Kosomena* Havlíček, described from the Ludlow of Bohemia (Havlíček and Štorch 1990), which could be a Lazarus taxon. If the *Kosomena* ascription to the subfamily is correct, it must be assumed that some representative of the subfamily survived in unrecorded environments during the long period spanning the time interval between the early Hirnantian through the late Wenlock. No other rafinesquinine younger than *Kosomena* have been described so far.

Conclusions

The results reveal an increasing taxonomic diversity of subfamily Rafinesquininae in the Mediterranean region during middle to late Katian. Two genera of the subfamily Rafinesquininae have been recorded: *Rafinesquina*, the only one previously reported from the region and *Kjaerina*, cited for the first time outside Avalonia, Baltica, and Laurentia. Two new subgenera have been described, *Kjaerina* (*Villasina*) and *Rafinesquina* (*Mesogeina*), in which several species have been included. They are the new species *Rafinesquina* (*Mesogeina*) *gabianensis*, *R.* (*Mesogeina*) *loredensis*, *Kjaerina* (*Kjaerina*) *gondwanensis*, *K.* (*Villasina*) *pedronaensis*, *K.* (*Villasina*) *pyrenaica*, and *K.* (*Villasina*) *meloui*, and the previously known *Rafinesquina pseudoloricata*, *R. pomoides*, and *Hedstroemina almadenensis.* The great diversity of rafinesquinines found at the Mediterranean region, probably indicates an adaptive radiation of the group in response to changes in the regime of sedimentation and water temperature caused by the global warming Boda event.

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