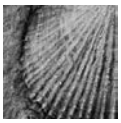
New and revised occurrences of rhynchonelliformean brachiopods from the middle Cambrian of the Iberian Chains, NE Spain

MICHAL MERGL & SAMUEL ZAMORA



New and revised occurrences of rhynchonelliformean brachiopods from the Languedocian (mid-late middle Cambrian) of the Iberian Chains are reported. The oldest assemblage corresponds to a level containing individuals of the new species *Brahimorthis alvaroi* and *Nisusia* sp. and is from the lower Languedocian Murero Formation. A younger assemblage is represented by *Chilidorthis tecta* from the Upper Languedocian Borobia and Torcas Formations. The geographic distribution and morphology of *Brahimorthis, Chilidorthis* and *Bohemiella* are reviewed and discussed. Moreover, evidence of the chilidium in *Bohemiella* and *Chilidorthis* and familial assignments of *Brahimorthis*, *Saesorthis, Chilidorthis* and *Bohemiella* are discussed. The new family Brahimorthidae fam. nov. is erected. • Key words: *Brahimorthis, Bohemiella, Nisusia,* Protorthida, Cambrian, Spain, Morocco, Czech Republic.

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Michal Mergl, Department of Biology, Faculty of Education, University of West Bohemia in Plzeň, Klatovská 51, 30619 Plzeň, Czech Republic; mmergl@kbi.zcu.cz • Samuel Zamora, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW75BD, UK; samuel@unizar.es

Apart from *Trematobolus* Matthew, 1893 and *Nisusia* Walcott, 1905, middle Cambrian rhynchonelliformean brachiopods are very rare in the Iberian Peninsula. They were first reported by de Verneuil & Barrande *in* Prado *et al*. (1860), who described *Orthisina* (= *Nisusia*) *vaticina* from the lower middle Cambrian of the Cantabrian Mountains (North Spain). This description has been subsequently cited and revised several times (Walcott 1912, Sampelayo 1935, Wotte & Mergl 2007). Havlíček & Josopait (1972) described two further species, *Chilidorthis tecta* Havlíček 1972 and *Brahimorthis* cf. *antiqua* Havlíček, 1971, both from the Languedocian (late middle Cambrian) of the Iberian Chains (NE Spain). Liñán & Mergl (2001) reported *Jamesella* sp. from the lower middle Cambrian of the Iberian Chains, and Gil Cid & Mélou (1986) described new species assigned to *Jamesella* Walcott, 1905 and *Yorkia* Walcott, 1897 from Sierra Morena (South Spain). Rhynchonelliformean brachiopods from the middle Cambrian of the Iberian Peninsula are, in most cases, a minor component of a generally diverse fauna that includes trilobites, echinoderms, lingulate brachiopods and several molluscan groups (Liñán & Gozalo 1986, Liñán & Mergl 2001, Clausen & Álvaro 2006, Wotte 2006, Zamora 2010). However, recent sampling in both classical and new localities from the Iberian Chains has provided new collections of rhynchonelliformeans. New specimens are compared with material from Morocco and Bohemia and the taxonomic positions of *Brahimorthis* and *Chilidorthis* are discussed.

Geological and stratigraphical sites

Within the Iberian Peninsula, the middle Cambrian (or Cambrian Series 3) is regionally subdivided into three stages named the Leonian, Caesaraugustan and Languedocian (Liñán *et al*. 1993, Álvaro & Vizcaïno 1998). Correlation of these west Mediterranean stages with global series proposed by the ISCS is not yet confidentially established because the lack of key trilobite taxa and is under discussion (Peng & Babcock 2011, Yuan *et al*. 2011). Base on chemostratigraphic data from Álvaro *et al*. (2008) the global Stage 5 probably corresponds with the Leonian, Caesaraugustan and part of the Languedocian stage while the two other Stages (Drumian and Guzhangian) probably fall within the Languedocian. For contrast other authors have been proposed the base of the Drumian within the Caesaraugustan stage base on poorly preserved trilobites which taxonomic assignment and utility in correlation are questionable (Gozalo *et al*.

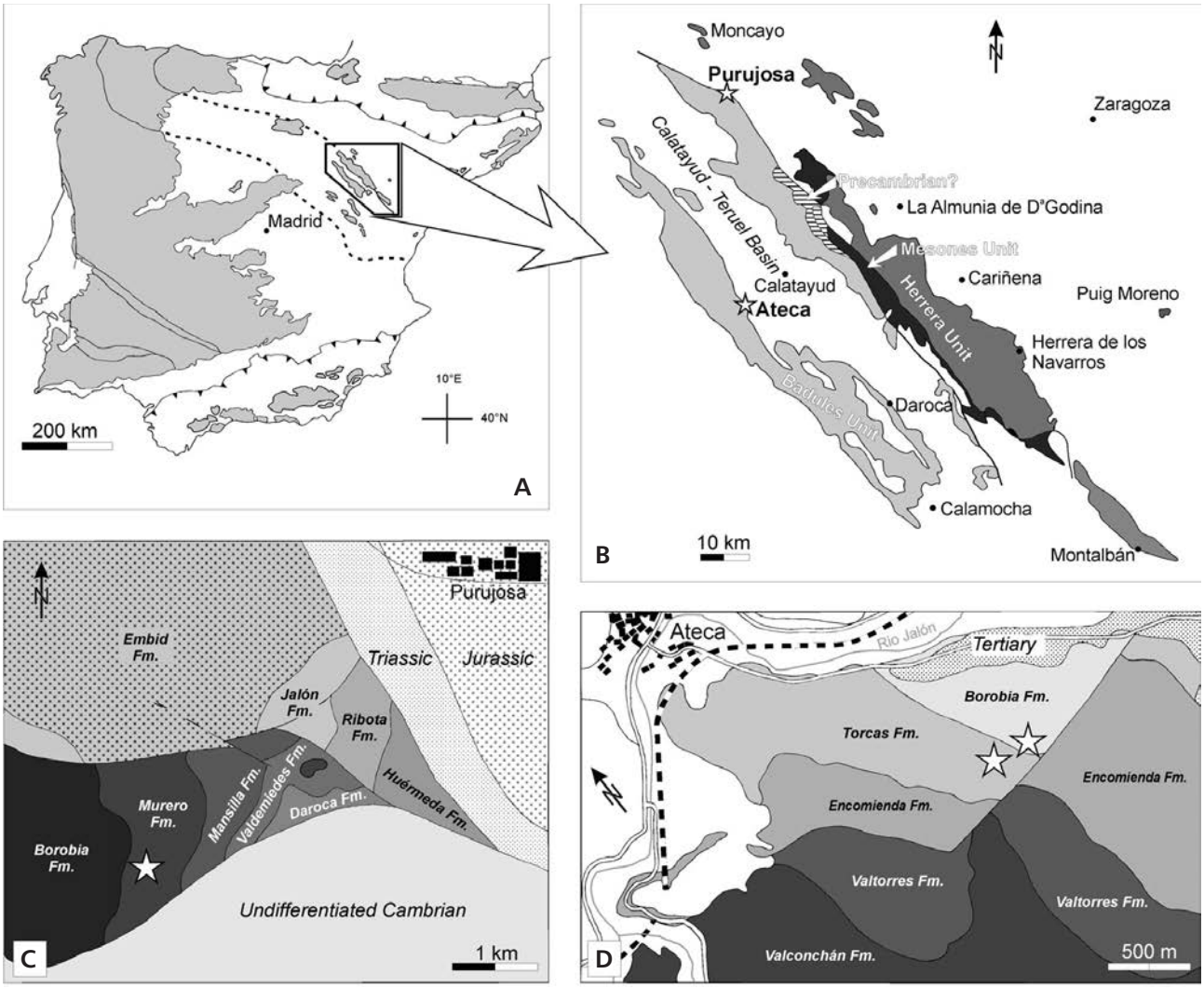


Figure 1. Geological settimg of sampled localities. • A – map of the Iberian Peninsula showing the position of the main pre-Hercynian outcrops. • B – detailed map of the Iberian Chains with the position of the studied localities. • C – geological map of Purujosa with the position of the Pur3 section (after Zamora 2009). • D – geological map of Ateca with the position of level AT22 (after Josopait 1972).

2011). Middle Cambrian rhynchonelliformean brachiopods from the Iberian Peninsula have been reported from two different basins: the northern Cantabro-Ebroan Basin (including the Cantabrian Zone and the Iberian Chains) and the southern Ossa-Morena Basin (Ossa Morena Zone) (Fig. 1).

The faunas from the Cantabrian Zone come from the Láncara Formation (Leonian-Caesaraugustan), and *Nisusia vaticina* is a common component that sometimes occurs in great numbers (Prado *et al*. 1860, Sampelayo 1935, Wotte & Mergl 2007). A few specimens of a new rhynchonelliformean taxon have been recovered from the lower Caesaraugustan Oville Formation in the Soto del Caso locality (Asturias), but this material awaits formal description. From the Iberian Chains, *Trematobolus* and *Jamesella* occur in the Bilbilian-Leonian Valdemiedes Formation, where the former genus is an important component of the assemblages sometimes forming shell coquine levels.

A younger occurrence of a rhynchonelliformean in the Murero Formation is reported for the first time in this paper. This assemblage is known solely from the Purujosa 3 section in the northern part of the Iberian Chains (NE, Spain), 2 kilometres south of Purujosa village (Fig. 1). Specimens come from the uppermost part of the Murero Formation and were collected from a thin layer (<1 m in thickness) of red lutites that is richly fossiliferous (Fig. 2). The associated fauna includes echinoderms – the edrioasteroid *Protorophus hispanicus* Zamora & Smith, 2010, the cinctan *Gyrocystis platessa* Jaekel, 1918, the stylophoran *Ceratocystis* sp., two different cothurnocystids and the blastozoans *Gogia gondi* Ubaghs, 1987, Lichenoididae indet. and *Dibrachicystis purujoensis* Zamora & Smith, 2012 (Zamora 2010; Zamora & Smith 2010, 2012), polymerid trilobites – *Eccaparadoxides pradoanus* Verneuil & Barrande (*in* Prado *et al*., 1960), *Conocoryphe heberti*

Munier-Chalmas & Bergeron *in* Bergeron, 1889, *Solenopleuropsis thorali* Sdzuy, 1958, *S. marginata* Sdzuy, 1958, *S. verdiagana* Sdzuy, 1958, agnostoids – *Condylopyge* sp., *Pseudoperonopsis sallesi* (Munier-Chalmas & Bergeron *in* Bergeron, 1889 and *Grandagnostus* sp. (Esteve *et al*. 2011, Zamora *et al*. 2011), lingulate brachiopods and the orthacean brachiopods described in this paper. Esteve *et al*. (2011) interpreted this level as consisting of multiple obrution events deposited in off shore shelf environments. The trilobite *Solenopleuropsis thorali* indicates a lowermost Languedocian age (*sensu* Álvaro & Vizcaïno 1998) for this level.

The Acon Group overlies the Murero Formation. This thick (more than 1000 m) siliciclastic series has been subdivided into several different formations (Álvaro 1995), which range from the basal lower Languedocian Borobia Formation to the Furongian Valtorres Formation (Fig. 2). All the middle Cambrian faunas reported in Havlíček & Josopait (1972) come from these levels. They described at least two middle Cambrian occurrences of rhynchonelliformeans. The lower level from the A1 unit (Borobia Formation *sensu* Álvaro 1995) provided individuals of *Chilidorthis tecta* Havlíček, 1971 associated with the trilobite *Bailiella* aff. *levyi* and is probably mid-late Languedocian in age. The second and younger assemblage comes from the A2 unit (Torcas Formation, *sensu* Álvaro 1995), and has provided, according to Havlíček & Josopait (1972), the species *Brahimorthis* cf. *antiqua* associated with trilobites (Shergold & Sdzuy 1991) that indicate an upper Languedocian age (*sensu* Álvaro & Vizcaïno 1998), as well as specimens of the cinctan echinoderm *Undatacinctus melendezi* (Schroeder 1973, Zamora & Álvaro 2010). Uncertainty concerning the morphology and taxonomic position of *Chilidorthis* was expressed by Williams & Harper (2000). This, combined with uncertainty about the occurrence of *Brahimorthis*, are the main reasons for resampling these levels.

Other rhyncholleniformean brachiopods from the Iberian Chains have been collected in the Borobia, Torcas and Valtorres formations (Fig. 1), but the material is too poorly documented and rare to be described in detail at present. Lastly, two species of rhyncholleniformean brachiopods, *Yorkia zafrensis* Gil Cid & Melou, 1986 and *Jamesella iberica* Gil Cid & Melou, 1986, were described from the Ossa Morena Zone in South Spain (Zafra, Province of Badajoz). They were sampled from the Playon Beds, and the associated trilobite fauna (Gozalo *et al*. 1994) indicates that they are uppermost Caesaraugustan–mid Languedocian in age.

Systematic palaeontology

All figured specimens are housed in the palaeontological collections of the Museum of Dr. B. Horák in Rokycany, Czech Republic (3RO), in the Department of Biology, University of West Bohemia in Plzeň (PCZCU) and in the Museo Paleontológico de la Universidad de Zaragoza, Spain (MPZ).

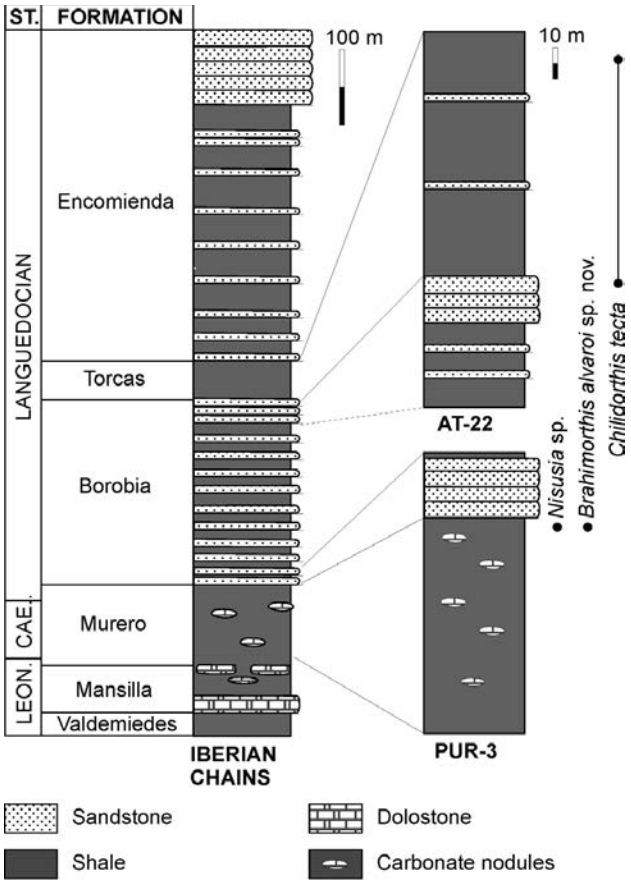


Figure 2. General stratigraphic section of Cambrian rocks in the Iberian Chains and detailed stratigraphy of Purujosa 3 and Ateca 22 sections showing the distribution of the studied rhynchonelliformean brachiopods.

Abbreviations. – W – width, L – length, n – number of specimens.

Order Kutorginida Kuhn, 1949
Superfamily Nisusoidea Walcott & Schuchert, 1908
Family Nisusidae Walcott & Schuchert, 1908

Genus *Nisusia* Walcott, 1908

Type species. – *Orthisina festinata* Billings, 1861; lower Cambrian; Vermont, USA.

***Nisusia* sp.**
Figure 3 A–E, I, L

Material. – Four ventral valves (MPZ2009/547, 549, 550a, 552); and one dorsal valve (MPZ2009/550b).

Description. – The shell is transversely subrectangular, with the L/W ratio ranging from 0.63 to 0.92 (n = 5); maximum width approximately midlength of the shell. The maximum width (14 mm) is estimated from the largest known specimen. The hinge line measures 85% of the maximum width. Cardinal extremities are obtuse to weakly alate (Fig. 3L).

Dorsal valve is gently convex, with a depressed median sector and prominent weakly curved apex. The maximum height is anterior to the apex. The dorsal pseudointerarea is steeply anacline. Dorsal interior is unknown.

Ventral valve is moderately convex in transverse profile and weakly convex along the shell axis. The apex is pointed, erect and pierced by a small foramen. A shallow sulcus is distinct from the midlength of the shell. The ventral interarea is high and apsacline, with a large and widely triangular delthyrium. Its sides subtend an angle of 90°. The pseudodeltidium is large and convex.

Ornamentation consists of numerous costellae originating from the apex. The size of costellae increases anteriorly. Primary costellae, numbering six to eight near the apex, are more prominent than intercalated ones. The largest preserved valve (Fig. 3L) has *ca* 70 costellae. Growth lines are distinct, wavy and irregularly spaced. The costellae on the ventral valve bear numerous low prostate spines; up to several in number on each primary costella, the spines are unknown on the dorsal valve. Preserved lengths of spines range from 1.2 to 1.5 mm. The diameter of the internal canal of the large spines is *ca* 200 μm.

The interior of ventral valve displays weak internal ribbing, with about 20 or more ribs in medium-sized shells. Teeth are large. Apical chamber is deep, anteriorly delimited by an indistinct triangular muscle field halved by a thin median ridge.

Remarks. – This is the first report of a nisusiid from the middle Cambrian of the Iberian Chains. The similar species *Nisusia vaticina* (Verneuil & Barrande *in* de Prado *et al*., 1860) was originally described from the Cantabrian Zone of northwest Spain, but its correct taxonomic position was not proposed before the revision of Walcott (1912). *Nisusia vaticina* is common in reddish limestone (Upper Member) of the early middle Cambrian Láncara Formation (Wotte & Mergl 2007). The shells described here are less transverse than those of *N. vaticina*, but there are only a few specimens to provide a detailed comparison with the Cantabrian species.

Occurrence. – Murero Formation, lower Languedocian; Purujosa, Iberian Chains, Spain.

Order Orthida Schuchert & Cooper, 1932
Suborder Orthidina Schuchert & Cooper, 1932
Superfamily Orthoidea Woodward, 1852

Brahimorthidae fam. nov.

Diagnosis. – Dorsibiconvex, strongly to weakly uniplicate, multicostellate and filose ornament, dental plates and spondylium absent; delthyrium and notothyrium open; ventral mantle canal system weakly impressed, with numerous radially disposed fine terminal canals along shell periphery; dorsal adductor field with four pairs of small radiating scars; notothyrium underlain by short transverse plate without distinct cardinal process; ventral muscle field of weakly defined small adductor scars anterior to the delthyrial chamber.

Remarks. – The new family is distinguished from the Protorthidae Schuchert & Cooper, 1931 by the absence of a distinct free spondylium, but there are other features which link the Brahimorthidae with the Protorthoidea Schuchert & Cooper, 1931. Adult shells of *Brahimorthis* lack an anterior extension of the transverse plate from the notothyrium and the cardinal process, which is characteristic of protorthids; however, juveniles of *Brahimorthis* (Fig. 4G) do show forward extensions of the free plate from the notothyrial chamber. The presence of this plate is assumed to be a plesiomorphic feature shared with the protorthids. Unlike other protorthoids that possess two pairs of scars, four pairs of scars are clearly impressed in the dorsal adductor field in *Saesorthis* (Geyer & Mergl 1997, fig. 5). In *Brahimorthis*, only two pairs are clearly defined; this is likely the result of fusion of attachment sites into one field, although asymmetrical shapes of imprints are reminiscent of an originally more complex arrangement (Fig. 4H).

The morphology of *Brahimorthis alvaroi* is less derived than that of *B. antiqua*. The former species retains a distinct transverse plate anterior to the notothyrium in the adult stage and has a shortly mucronate hinge line. The latter feature is common in most protorthoid genera (see review by Williams & Harper 2000) but may be seen also in some early orthoids. The Brahimorthidae is referred to Orthida due the lack of dental ridges uniting with free spondylium, but features mentioned above indicate some affinity to Protorthidae.

Genera assigned. – *Brahimorthis* Havlíček, 1971: middle Cambrian; Morocco, Spain, Bohemia, Czech Republic; *Saesorthis* Geyer & Mergl, 1997: middle Cambrian; Morocco; ?*Cymbricia* Roberts & Jell, 1990: middle Cambrian; Morocco.

Genus *Brahimorthis* Havlíček, 1971

Type species. – *Brahimorthis antiqua* Havlíček, 1971; middle Cambrian; Morocco.

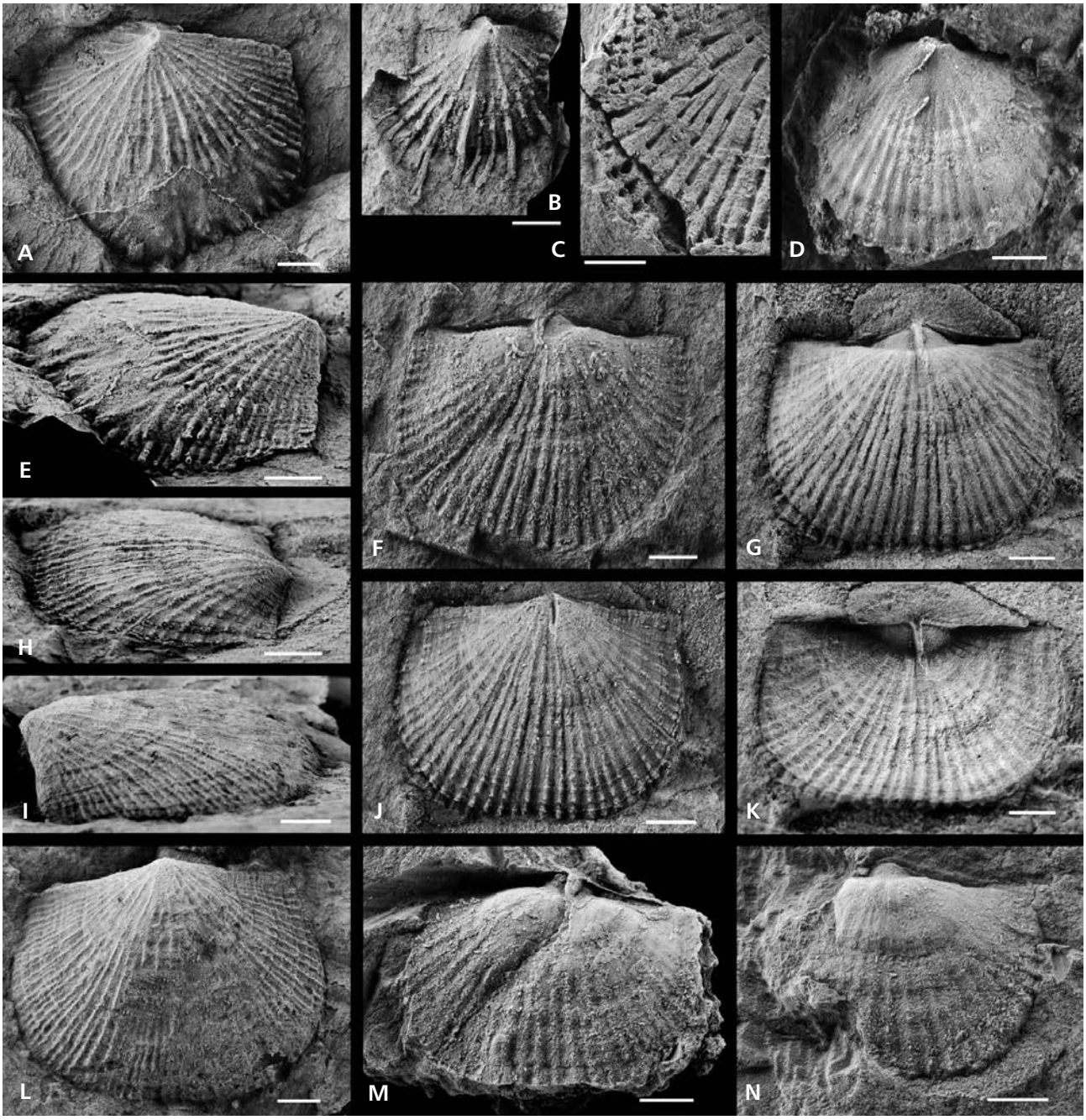


Figure 3. A–E, I, L – *Nisusia* sp. Age and locality: middle Cambrian, lower Languedocian, Murero Formation; Spain, Iberian Chains, Purujosa. Bar equals 2 mm. • A, C, E – ventral valve, latex cast of external mould (A, E) and fragment of shell (C), detail of spines on the external mould, and oblique lateral view, MPZ2009/550a, 547. • B – ventral valve, latex cast of external mould, MPZ2009/549. • D – internal mould of ventral valve, MPZ2009/552. • I, L – dorsal valve, latex cast of exterior in lateral and ventral views, MPZ2009/550b. • F–H, J, K, M, N – *Brahimorthis alvaroi* sp. nov. Age and locality: middle Cambrian, lower Languedocian, Murero Formation; Spain, Iberian Chains, Purujosa. Bar equals 2 mm. • F – ventral valve, internal mould, MPZ2009/551. • G, H, J, K – holotype, dorsal valve, internal mould, oblique lateral view to latex cast of exterior, latex cast of exterior, and internal mould in slightly posterior view, MPZ2009/554a, b. • M – ventral valve, internal mould, MPZ2009/556, N – dorsal valve, internal mould, MPZ2009/545.

Diagnosis. – See Havlíček (1971).

Remarks. – In his original description, Havlíček (1971) compared *Brahimorthis* to *Nisusia* Walcott, 1905, *Bohemiella* Schuchert & Cooper, 1931 and *Jamesella* Walcott, 1905. However, these genera have recently been assigned to different classes or orders. In 1977, Havlíček erected the new family Bohemiellidae. He included *Brahimorthis*,

Chilidorthis Havlíček, 1972, *Diraphora* Bell, 1941, *Oligomys* Schuchert & Cooper, 1931, *Pompeckium* Havlíček, 1970, *Wimanella* Walcott, 1908, *Shiragia* Kobayashi, 1935 and questionably, *Ocnerorthis* Bell, 1941 in this family. The systematic position of *Brahimorthis* and the concept of the Protorthacea were discussed by Geyer & Mergl (1997). They left *Brahimorthis* in the Bohemiellidae, although they expressed the opinion of a close evolutionary affinity of this genus with *Saesorthis* Geyer & Mergl, 1997, which they referred to the Protorthidae.

In the revised edition of *Treatise on Invertebrate Palaeontology*, Williams & Harper (2000) referred *Brahimorthis* to the Eoorthidae Walcott, 1908 within the Plectorthoidea. These authors also rejected the attribution of *Pompeckium* and *Ocnerorthis* to the Bohemiellidae. The rejection of *Brahimorthis* from the family Bohemiellidae seems reasonable. The bohemiellid genera have short brachiophores and simple and distinct cardinal process; both characters are absent in *Brahimorthis*. The absence of the dental plates is a common feature in many Cambrian families. Williams & Harper (2000) also noted the ramicostellate and filate ornament of *Brahimorthis* (Fig. 4E, F). Other eoorthid genera have a quite different ornament, varying from costellate to fascicostellate, and often having superimposed capillae. There are a few strange eoorthids known from the middle and late Cambrian (see Williams & Harper 2000) which placement within the eoorthids is questionable.

Brahimorthis shows a peculiar arrangement of the delthyrial chamber and ventral muscle field, which is different from *Bohemiella*. A triangular, transversely striated field is visible in the apical part of the delthyrial chamber (Fig. 4J, R). This small triangular field, originally interpreted by Havlíček (1971) as the ventral muscle field, is herein reinterpreted as an undivided scar of the diductor muscles. The axial deepening of this scar and anterior inflexion of growth striations are likely due the axially accommodated pedicle at the apical part of the delthyrial chamber. The bipartite callosity placed anterior to the delthyrial chamber (Fig. 4J, K, R; see also Geyer & Mergl 1997, figs 9-3, 9-8) probably borders two pairs of small adductor scars. The steep lateral sides of the delthyrial chamber display thin triangular impressions, which are about two times longer than the suggested diductor scar; these imprints are interpreted newly as the adjustor scars. The suggested placement of muscle imprints on the shell interior is shown in Fig. 5.

This interpretation of scars is based on the functional morphology of the muscle system. The dorsal valve floor has two distinct, posteriorly situated pairs of adductor scars. If the adductors were attached only in the apical part of the delthyrial chamber of the ventral valve (= striated area interpreted herein as the diductor scar), then their traction would have led to opening instead of closing of the shell. The attachment site of the adductors on the ventral valve should be somewhat anterior to the hinge line in order to facilitate rotation along the hinge and the closure of the shell. This could be achieved by an anteriorly extended transverse plate projecting from the delthyrial chamber (as in protorthids) or by the anterior shift of the adductor attachment sites on the valve floor (as in orthids). *Brahimorthis* does not show a proper transverse plate, as developed in protorthids. Small but deep scars of the adductor muscles are therefore placed just in front the delthyrial chamber, below the steep slope of the posterior valve floor.

A similarly unusual placement of the ventral adductor scars is known from the middle Cambrian genus *Cymbricia* Roberts & Jell, 1990. In this genus, the adductor scars are inserted in a heart-shaped pit located in anteriomedial position, and the diductor scars occupy the delthyrial chamber. The attachment site of the diductors in the dorsal valve of *Brahimorthis* is typically orthoid. The posterior part of the notothyrial chamber has a striated surface lacking any sign of the cardinal process. The transverse striation probably represents the wrinkled surface of the diductor site.

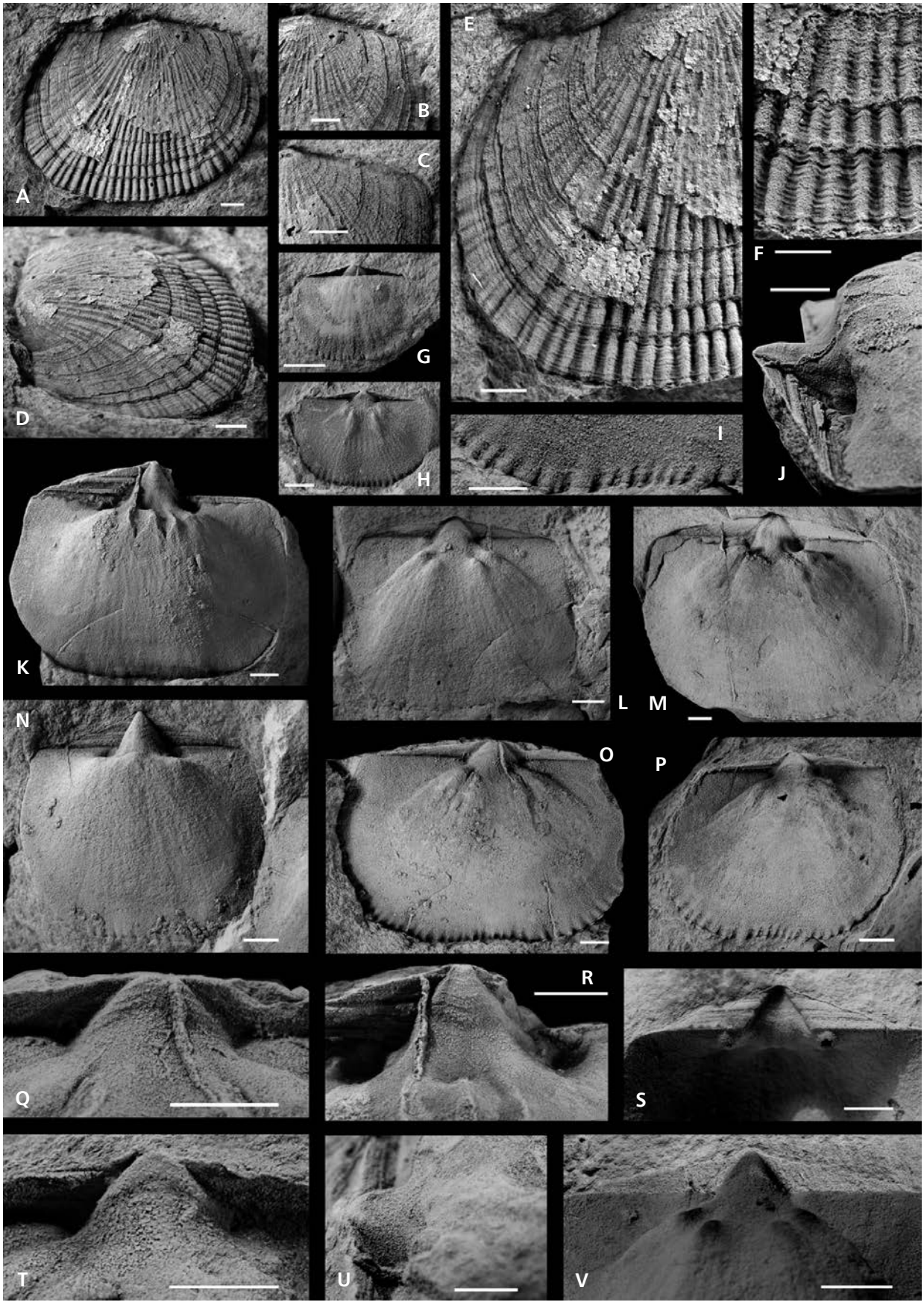
The disposition of the pallial markings in *Brahimorthis* is poorly known. One of the internal moulds of the topotypic specimens shows a weakly divergent proximal part of the ventral vascula media. The dorsal pallial markings are obscure.

Brahimorthis antiqua Havlíček, 1971

Figures 4A–V, 5

1971 *Brahimorthis antiqua* sp. n. Havlíček, p. 29, pl. 1, figs 1–10.

Figure 4. *Brahimorthis antiqua* Havlíček, 1971. Age and locality: middle Cambrian, Jbel Wawrmast Formation; Morocco, Hassi Brahim section, sampling horizon D 1887. Bar equals 2 mm. • A, B, D–F – dorsal valve, latex cast of exterior, slighly oblique view to cardinal extremity (B), oblique lateral view (D), detail of ornamentation (E), and detail of filose ornament (F), RO C805. C – dorsal valve, slighly oblique view to cardinal extremity, RO C802. • G – very small ventral valve, internal mould, RO C801. • H – small dorsal valve, internal mould, RO C806. • I, P, T – dorsal valve internal mould: detail of internal crenulation (I), internal moud (P), and detail of notothyrial chamber (T), RO C799. • J, K, R – ventral valve internal mould: detail of delthyrial chamber in oblique view (J), internal mould (K), and detail of delthyrial chamber (R), RO C810. • L, V – dorsal valve internal mould, and latex cast showing notothyrial chamber and adductor scars, RO C796b. • M – dorsal valve internal moud, RO C804. • N, S – ventral valve internal mould and its latex cast, RO C796a. • O, Q – dorsal valve internal mould and detail of notothyrial chamber, RO C812. • U – dorsal valve internal mould, detail of notothyrial chamber, RO C798.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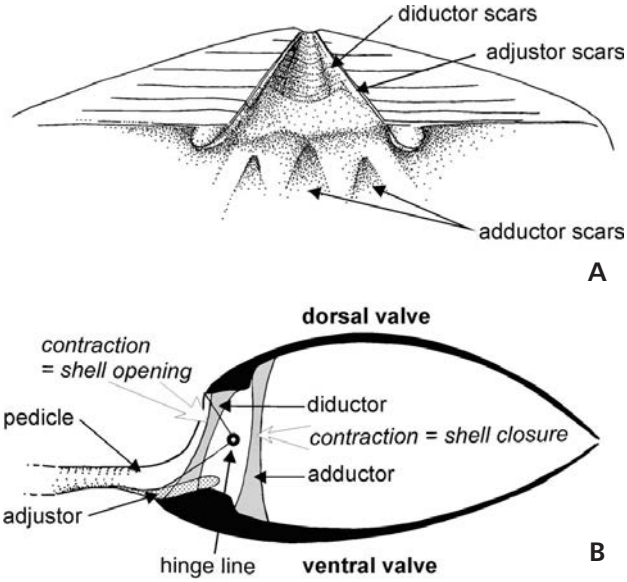


Figure 5. *Brahimorthis antiqua* Havlíček, 1971. Ventral valve interior with sites of muscle scars (A) and diagrammatical reconstruction of shell muscle system (B) along the shell axis; adductors are located anterior to the axis of rotation (= circle).

1983 *Brahimorthis antiqua* Havlíček, 1971. – Mergl, p. 340, pl. 1, figs 2, 3.

1997 *Brahimorthis antiqua* Havlíček, 1971. – Geyer & Mergl, p. 807, figs 8.16, 9.2–9.10, 9.12, 9.13.

Remarks. – This species were described by Havlíček (1971) and Geyer & Mergl (1997). Specimens of *Brahimorthis* n. sp. A are probably conspecific with *B. antiqua* because the differences noted by Geyer & Mergl (1997) fall within the range of variability now observed in *B. antiqua*.

Distribution. – Middle part of middle Cambrian, Jbel Wawrmast Formation, layers with *Badulesia tenera* (lower Caesaraugustan), Hassi Brahim section, Anti-Atlas, Morocco.

Brahimorthis pompeckiana Havlíček, 1977

Figure 6A–K

1977 *Brahimorthis pompeckiana* sp. n. Havlíček, p. 31, pl. 2, figs 15–19.

Material. – Two incomplete ventral valves (3RO 21307 = original number VH 1400a, 3 RO 21311 = VH 1400e), and three almost complete dorsal valves (3RO 21308 = VH 1400b, 3RO 21309 = VH 1400c, 3RO 21310 = VH 1400d).

Description. – See Havlíček (1977) for a complete description of this taxon.

Remarks. – Havlíček (1977) described and figured rare material of *Brahimorthis* from the Jince Formation (middle Cambrian) of Bohemia. Up to now, only three incomplete dorsal and two ventral valves have been collected. Havlíček noted that is rather difficult to compare *B. pompeckiana* with the type species due to the different modes of preservation. All known shells of *B. pompeckiana* were collected in coarse sandstones and many features are therefore poorly preserved. However, the general morphology of the shell is consistent with attribution to *Brahimorthis*. Havlíček (1977) used the ornamentation for discrimination of both species. Costellae in *B. pompeckiana* are subangular and separated by wider interspaces, while costellae of *B. antiqua* are wider and separated by narrow interspaces. In addition to this feature, the ventral interarea of *B. pompeckiana* is lower and less steep than that of *B. antiqua*. The dorsal valve of *B. pompeckiana* has a more convex axial profile with a less flattened anterior. This feature is not the result of differential preservation because all dorsal valves of *B. pompeckiana*, unlike valves of *B. antiqua*, lack this flattening. All shells have been collected from coarse sandstone and the associated fauna is rare and poorly represented by indeterminable fragments of large lingulate brachiopods.

Occurrence. – Middle part of middle Cambrian, Jince Formation, *Eccaparadoxides pusillus* Zone; Velcí, Příbram-Jince Basin, Czech Republic.

Brahimorthis alvaroi sp. nov.

Figures 3F–H, J, K, M, N

Holotype. – Dorsal valve figured on Fig. 3G, H, J, K (MPZ2009/545, 554, 556).

Paratype. – Ventral valve figured on Fig. 3F (MPZ2009/551).

Type horizon. – Pur3 section, level 10, top of the Murero Formation, lower Languedocian.

Type locality. – Purujosa, Iberian Chains, Spain.

Etymology. – In honour of Dr. Javier Álvaro for his contribution to the advancement of knowledge on the Languedocian Stage in the Mediterranean area and his help sampling in the studied areas.

Material. – Three dorsal and thee ventral valves MPZ2009/545, 551, 553, 554, 555, 556.

Diagnosis. – *Brahimorthis* with short alate cardinal extremities, distinct costellation on posterolateral flanks, and

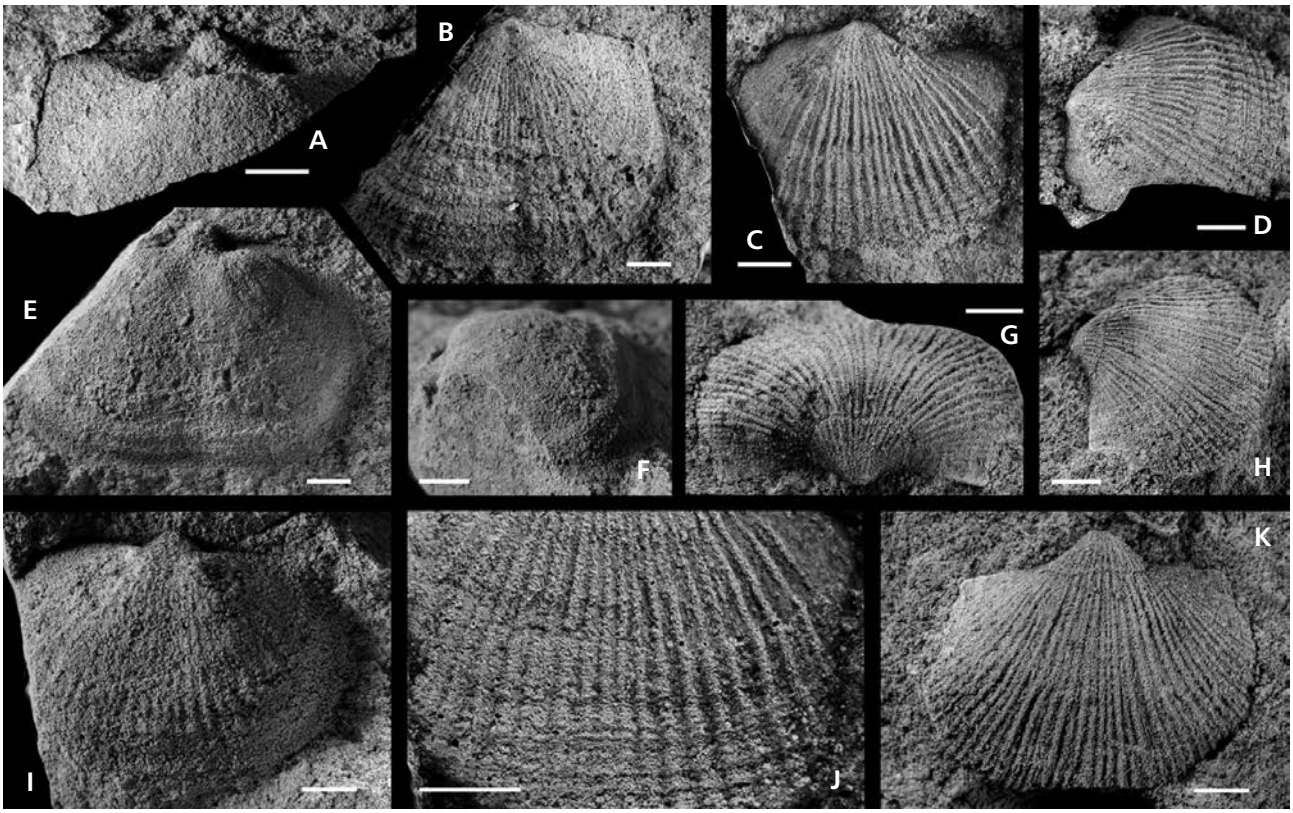


Figure 6. *Brahimorthis pompeckiana* Havlíček, 1977. Age and locality: middle Cambrian, Jince Formation, *Eccaparadoxides pusillus* Zone; Czech Republic, Příbram-Jince Basin, Velcí. Bar equals 2 mm. • A – internal mould of ventral valve, 3RO 21311. • B, E, F – dorsal valve, latex cast of exterior, internal mould, and oblique lateral view to internal mould, 3RO 21310. • C, D, I, J – dorsal valve, latex cast of exterior, the same on oblique lateral view, internal mould and detail of ornamentation, 3RO 21309. • G, H, K – ventral valve, latex cast of exterior in oblique posterior, oblique lateral, and ventral views, 3RO 21307.

broadly triangular notothyrial chamber; no median ridge in dorsal valve floor.

Description. – The shell is biconvex, subrectangular in outline and 15 mm wide in the largest known specimen. The maximum width is at the mid part of the valve.

The dorsal valve has acute cardinal extremities extended into short flattened alae. Flanks are evenly curved. The anterior margin is weakly curved. Transverse profile is gently convex. Axial profile is evenly convex, having the maximum height at the posterior one-third. A weakly defined sulcus is distinct from about the posterior third of the valve. The dorsal interarea is anacline, low and with a broadly triangular notothyrium. The sides of notothyrium subtend at an angle of 120°. The dorsal interior shows a broadly triangular notothyrial chamber. The cardinal process is absent, but the area of attachment of the diductors is marked by a fine arcuate striation. The dorsal adductor field consists of two pairs of small subcircular muscle scars placed anterior and anterolateral to the notothyrial chamber. In addition, there is a weakly impressed third pair of scars lateral to the notothyrial chamber. A fine and short median ridge is present.

The ventral valve is gently convex with a steeply apsacline interarea. The ventral muscle field is small and restricted to the delthyrial chamber and the surface of the short convex plate weakly raised above the valve floor.

The ornamentation is costellate consisting of subangular uniformly-sized costella. Primary costellae are distinct from the apex. Interspaces are wider than costellae. New costellae are rare, originating by implantation. There are some 40 costellae in the measured specimens (Fig. 3J). Growth lines are of uneven size, some approaching short growth lamellae.

Remarks. – The new species differs from *Brahimorthis antiqua* Havlíček, 1971 in the coarser costellation, the weaker shell convexity in the posterior third of shell, the lower ventral interarea, the absence of the dorsal median ridge and the wider notothyrial chamber. However, the main difference concerns the shell outline: the cardinal extremities of *B. antiqua* and *B. pompeckiana* are obtuse while in *B. alvaroi* are flattened and extended into short alae, which form an acute angle. This feature is clear in all specimens of *B. alvaroi* despite some shell compression in shale.

Occurrence. – Murero Formation, Languedocian; Purujosa, Iberian Chains, Spain.

Family Bohemiellidae Havlíček, 1977

Remarks. – When defining the Bohemiellidae, Havlíček (1977) discussed several unique features of the family. The absence of dental plates is one typical feature. Havlíček assigned nine genera to the family including *Chilidorthis* Havlíček & Josopait, 1972. Williams & Harper (2000) assigned seven genera to the Bohemiellidae and expressed some doubts (based on the poor state of preservation of the original material) about the familiar assignment of *Chilidorthis*. Bohemiellids are a group including (with the possible exception of *Murrinyinella* Kruse, 1990) planoconvex, subquadrate and costelate middle Cambrian orthoids. Presence of the chilidium or chilidial plates might be another significant feature of the family, but fine details of shell morphology are well known only in a few genera of Bohemiellidae.

Chilidorthis Havlíček & Josopait, 1972

Type species. – *Chilidorthis tecta* Havlíček & Josopait, 1972; middle Cambrian, Spain.

Remarks. – In the diagnosis of *Chilidorthis*, the presence of a large convex chilidium is the unique character that distinguishes this genus from other members of the Bohemiellidae. Based on this feature, Williams & Harper (2000) questioned the familiar assignment of this genus, but they also commented the poor state of preservation of *C. tecta*. *Chilidorthis* shows a large convex chilidium (Fig. 7G, H). Re-examination of *Bohemiella romingeri* Barrande, 1931 reveals the presence of a small, planar but distinct chilidium apically closing the notothyrium (Fig. 7U) and thin low chilidial plates extending from the chilidium and bordering the notothyrium.

Previously, Havlíček (1977) noted that the cardinal process of *Bohemiella* ranges from a thin setal plate to a broad ridge-like structure resting on a low notothyrial platform (Fig. 7S, T). The cardinal process has a distinct median separating ridge and lateral myophore ridges. There is no striated surface on the myophore in *Bohemiella*. Similarly broadly ridge-like cardinal process with a low median ridge and lateral myophore ridges are present in *Chilidorthis* (Fig. 7F, G). The notothyrial platform in *Bohemiella* and *Chilidorthis* extends forwards into a broad and low median ridge. The ventral muscle field of *Chilidorthis* is subtriangular, confined to a deep delthyrial chamber. It is clearly tripartite, with narrowly triangular diductor scars extending forwards from the delthyrial chamber and a narrower and shorter adductor track resting on an anteriorly elevated platform (Fig. 7M, Q). The shape of the ventral muscle field and the absence of dental plates also are other features shared with *Bohemiella*.

Due to their preservation in sandstones, the arrangement of the vascular system is not well known in *Chilidorthis*. It is of a saccate type in the ventral valve, and probably has a digitate or lemniscate condition in the dorsal valve. Weakly divergent *vascula media* divide at about the midlength of the ventral valve and continue by arcuate canals splitting into numerous *vascula terminalia* normal to valve margins (Fig. 7J, O–Q). The same saccate condition is known in the ventral valve of *Bohemiella* (see Havlíček 1977; pl. 2, figs 3, 4, 11). The vascular system in the dorsal valve of *Chilidorthis* is less known. There are undoubted arcuate *vascula media*, but imprints of *vascula myaria* are poorly preserved and *vascula genitalia* are not discernible (Fig. 7N, 8A). The same system is present in the dorsal valve of *Bohemiella*; re-examination shows finely preserved imprints of the *vascula media*, *vascula myaria* and *vascula genitalia* (Fig. 7S, 8B).

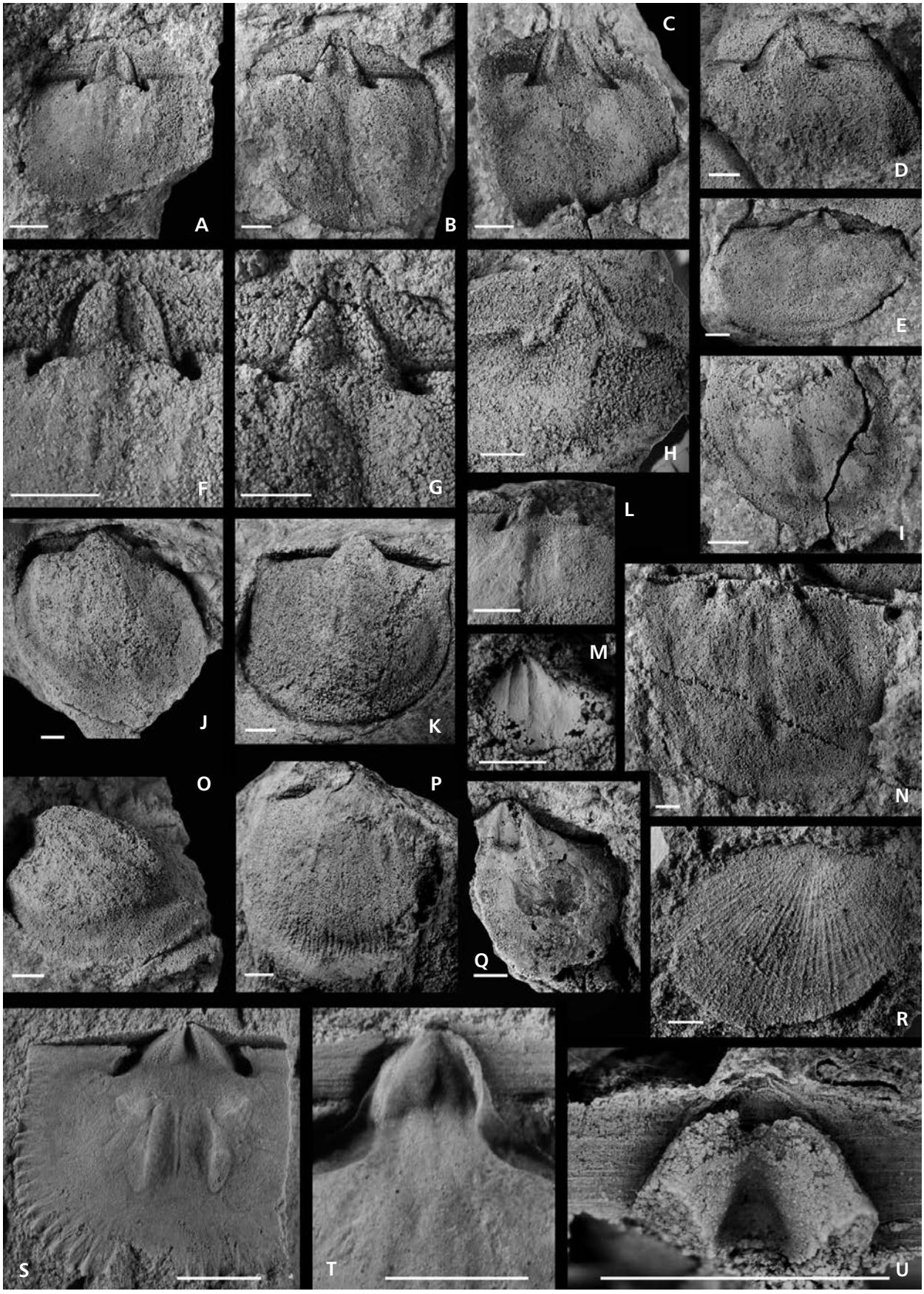
Chilidorthis tecta Havlíček & Josopait, 1972

Figures 7A–R, 8A

1972 *Chilidorthis tecta* Havlíček & Josopait, p. 343, figs 4:5, 5:1–8.

?1972 *Brahimorthis* cf. *antiqua* Havlíček, 1971, p. 346.

Figure 7. *Chilidorthis tecta* Havlíček & Josopait, 1972. Age and locality: middle Cambrian, Borobia Formation upper Languedocian; Spain, Iberian Chains, Valtorres, locality AT-22. Bar equals 2 mm. • A, F – medium-sized dorsal valve and detail of its cardinalia, internal mould, MPZ 2011/79. • B, G – dorsal valve, internal mould and latex cast its cardinalia, MPZ 2011/80. • C – dorsal valve, internal mould, MPZ 2011/81. • D, H – large dorsal valve and latex cast of cardinalia showing the chilidium, internal mould, MPZ 2011/82. • E – dorsal valve, deformed internal mould, MPZ 2011/83. • I – medium-sized dorsal valve, internal mould showing median ridge and subperipheral rim, MPZ 2011/84. • J, O – ventral valve, internal mould showing subperipheral rim, MPZ 2011/85. • K – ventral valve, internal mould, MPZ 2011/86. • L – medium-sized dorsal valve, internal mould showing well preserved brachiophore, MPZ 2011/87. • M – fragment of ventral valve, internal mould showing ventral muscle field, MPZ 2011/88. • N – large dorsal valve, internal mould, MPZ 2011/89. • P – ventral valve, internal mould showing pallial markings, MPZ 2011/90. • Q – ventral valve, internal mould showing ventral muscle field and proximal vascula media, MPZ 2011/91. • R – latex cast of dorsal valve exterior, MPZ 2011/92. *Bohemiella romingeri* (Barrande, 1848). Age and locality: middle Cambrian, Buchava Formation, Skryje Member, *Eccaparadoxides pusillus* Zone; Czech Republic, Skryje-Týřovice Basin, Biskoupky. Bar equals 2 mm. • S – medium-sized dorsal valve, internal mould showing adductor scars, PCZCU 1806. • T – dorsal valve, internal mould of cardinalia, PCZCU 1807. • U – dorsal valve, external mould showing the chilidium, PCZCU 1808.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Material. – Several dozen ventral and dorsal valves, mostly poorly preserved in coarse sandstone. Sixteen specimens figured (MPZ 2011/79–95) and about fifty more specimens.

Emended description. – The shell is planoconvex to weakly concavo-convex, 20 mm wide and thick-walled especially along the hinge line, which has a rectimarginate commissure.

The dorsal valve is planar, almost flat with a broadly subrectangular to transversely semielliptical outline. The maximum width is at hinge line. Cardinal extremities are rectangular to gently alate. A narrow, shallow sulcus may be developed in the posterior third of the valve, becoming obscure anteriorly. The dorsal interarea is low anacline, high, flat and covered by distinct growth striations of uniform size. The notothyrium is widely triangular, with the apical third closed by a gently convex chilidium, which continues by thin and low chilidial plates towards the hinge line.

The cardinal process is a large, broad, low ridge-like structure occupying the majority of the notothyrial chamber, halved by a low median separating ridge and bordered by low myophore ridges. The process extends from a low notothyrial platform, which extends anteriorly into a broad median ridge. The median ridge is high posteriorly, lower anteriorly and its anterior part is exaggerated by laterally adjacent proximal canals of *vascula media*. The anterior termination of the median ridge is fused with the low subperipheral rim. Brachiophores are short, ridge-like, widely divergent and with a short groove separating the brachiophore base from the inner socket ridge (Fig. 7L). Dorsal adductor scars are poorly impressed with a larger anterior pair placed in anteromedial position to a smaller posterior pair. The vascular system is poorly preserved, with subparallel proximal canals of *vascula media* divided into a very short inner branch and a long arcuate outer branch of *vascula media*. *Vascula myaria* are poorly impressed and extend between the inner and outer adductor scars.

The ventral valve outline changes from semicircular in early growth stages to subrectangular in adults, with rectangular to shortly alate cardinal extremities. The sides are evenly curved continuing into a less rounded anterior margin. The valve is from moderate to strongly convex both axially and transversally with somewhat depressed cardinal edges. The beak is short. The ventral interarea is steeply apsacline, high, gently concave, with transverse growth striation. The delthyrium is highly triangular, open and occupies some 25% of the hinge line.

Teeth are small and short, supported by a thick pad of the posterior shell wall. The dental plates are absent. The ventral muscle field is subtriangular, confined to the delthyrial chamber and occupies about 30% of the shell width and 25% of the shell length. Diductor scars are narrowly triangular, gently diverging and slightly flabellate along their anterior borders. The adductor scar is narrowly triangular, well-defined and slightly shorter than the diductor scars. The anterior part of the adductor track rests on a weakly elevated pad (Fig. 7Q). The ventral vascular system is saccate, with broad, laterally deep but axially shallow impressions of subparallel to weakly diverging proximal part *vascula media*. The main trunks of the *vasculum media* are divided into a short inner branch and a longer, arcuate and tapering outer branch of the *vascula arcuata* at around two-thirds of the shell length. Numerous thin radially arranged *vascula terminalia* extend from *vascula arcuata* along the majority of the shell periphery. The subperipheral rim is prominent and high in adult shells.

The ornamentation is multicostellate with uniformly sized radial costellae extending from the apex. Costellation is better developed in the dorsal valves (Fig. 7R) than the ventral valves, but this difference could be the result of surface abrasion of the ventral valve surface in all collected shells. New costellae mostly appear in front of growth lamellae. There are 2–3 costellae per 1 mm anteromedianly and 40–50 costellae in total on large shells. Interspaces are the same size as the costellae. Concentric ornament consists of a few weak growth lamellae, which are more crowded along the periphery of the large shells. Concentric filose ornament is very weak, being poorly preserved in all collected shells.

Remarks. – *Chilidorthis tecta* has been described from three localities (Havlíček & Josopait 1972) from the fossil horizon FH 1 near the road from Ateca to Valtorres in the Iberian Chains, Spain. From an overlying level in the same area, Havlíček & Josopait (1972) described two valves as *Brahimorthis*. Havlíček & Josopait (1972) noted that the dorsal valve interior of these shells show all the diagnostic features of *Brahimorthis*. These features, *e.g.* the high convexity of the dorsal valve, absence of the cardinal process and the raised notothyrial platform, are very characteristic of the genus. Unfortunately, we were not able to successfully review the original specimens collected by Josopait, which are currently stored in the Münster University palaeontological collections. However, sampling in the same level from which Josopait originally collected the material has provided a reasonable number of new specimens. Because of the lack of illustration in Havlíček & Josopait (1972), it is hard to judge whether there are two different brachiopod taxa or whether the attribution of two valves to *Brahimorthis* cf. *antiqua* by Havlíček & Josopait (1972) is due to the misidentification of *Chilidorthis tecta* because of poor preservation. Based on our observations we suggest that the second option is more plausible.

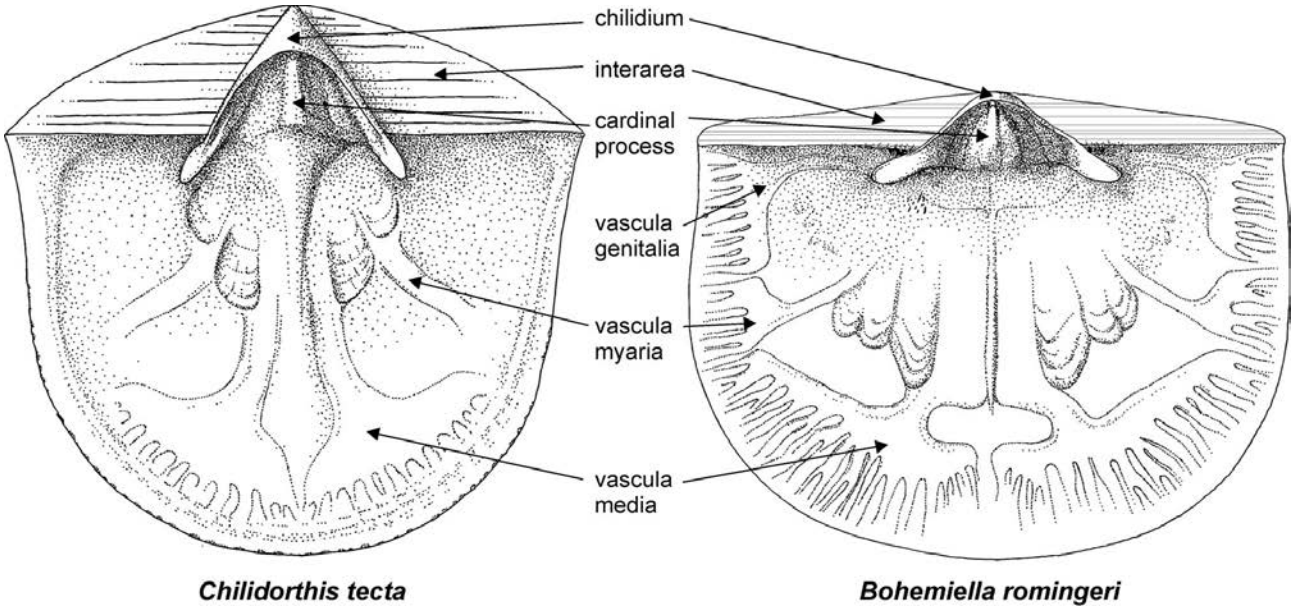

Figure 8. Dorsal valve interiors of *Chilidorthis tecta* Havlíček & Josopait, 1972 and *Bohemiella romingeri* (Barrande, 1848) with chilidia and reconstructed mantle canal systems.

Occurrence. – AT22 section, Valtorres Formation, Valtorres, Iberian Chains, Spain.

General discussion

Taxonomic relationships

The arrangement of the muscle imprints in *Brahimorthis* Havlíček, 1977 and *Saesorthis* Geyer & Mergl, 1997 represents a synapomorphy that justifies their separation into the new family within the superfamily Orthoidea Woodward, 1931. As pointed out by Geyer & Mergl (1997), *Brahimorthis* is best considered as the descendent of *Saesorthis.* The latter genus is known exclusively from Morocco and these authors broadly discussed its taxonomic position. Both genera share several common features: they lack dental plates and cardinal processes; have similar, highly raised delthyrial chambers which are not anteriorly extended into a distinct transverse plate; have weakly developed dental sockets and show parvicostellate ornamentation with prominent filose ornament; and have a weakly impressed vascular system. As stated by Geyer & Mergl (1997), *Brahimorthis* is more derived than *Saesorthis*. This hypothesis is also supported by the stratigraphic ranges of both genera. *Saesorthis* is restricted to the Jbel Wawrmast Formation, the *Hupolenus* Zone and the *Cephalopyge notabilis* Zone of the lower middle Cambrian of Morocco. *Brahimorthis* occurrences in North Africa, Spain and Bohemia are younger. *Brahimorthis antiqua* comes originally from Jbel Wawrmast Formation of the Hassi Brahim section. The sampling level (horizon D 1887: Havlíček 1971) is uncertain but appears to be from the middle part of the middle Cambrian, corresponding with *Badulesia tenera* layers (Geyer & Mergl 1997). Unnamed species of *Brahimorthis* (Geyer & Mergl 1997) from Jbel Wawrmast Formation of Morocco are also mid- middle Cambrian in age. *Brahimorthis* cf. *antiqua* has been reported from the Almunia layers (Torcas Fm. after this study) in the lower part of the Iberian Series of Spain (Havlíček & Josopait 1972) but this is most likely a misidentification. The new species of *Brahimorthis alvaroi* in Spain is of early middle Cambrian (lower Languedocian) age. *Brahimorthis pompeckiana* is known from four specimens (Havlíček 1977) which have been collected in a sandstone bank of uncertain age in the Jince area (Příbram-Jince Basin) of the Czech Republic. The now inaccessible locality has been referred to the *Eccaparadoxides pusillus* Zone of the Jince Formation (Fatka *et al.* 2004). The exact range of this zone is unknown, but likely represents the middle part of the middle Cambrian. In summary, all occurrences of *Brahimorthis* are thought to be from the lower to middle parts of the middle Cambrian. Only *Brahimorthis alvaroi* is associated with nisusiid brachiopods.

New morphological features observed in *Chilidorthis tecta*, especially the presence of the chilidium and observations of the chilidium of *Bohemiella* are in agreement with the original assigment of *Chilidorthis* in the Bohemiellidae by Havlíček (1977). *Bohemiellia* and *Chilidorthis* represent closely related orthids, both of which are Languedocian in age. *Bohemiella romingeri* is known only from the Buchava Formation, Skryje-Týřovice Basin in Central

Bohemia (Fatka e*t al.* 2011). Their shell morphology, distinguished by a planoconvex shell, shortly alate hinge line and fine ornament, is analogous to later Palaeozoic strophomenids. A similar mode of life and shell orientation (with the dorsal valve up) are suggested for *Bohemiella* and *Chilidorthis*.

Palaeobiogeographic implications

Current data on the morphology and distribution of rhynchonelliformean brachiopods of early to mid middle Cambrian age in Spain, Central Europe and NW Africa indicate closer phylogenetic relations between brachiopods from Bohemia (Czech Republic) and Morocco than to brachiopods from Spain: *Brahimorthis pompeckiana* is more closely related to *B. antiqua* than to *B. alvaroi. Bohemiella* was originally described from Bohemia and it is confidently known from Morocco (Geyer & Mergl 1997), but its presence in Spain is questionable. Obollelates and kutorginates are unknown in Bohemia and this is probably a true biological signal rather than a taphonomic and/or sampling bias. Obolellates and kutorginates are common in Spain (Gil Cid & Mélou 1986, Liñán & Mergl 2001, Wotte & Mergl 2007). Faunal similarities among early middle Cambrian obolellates, exemplified by the distribution of *Trematobolus*, exist between Spain, Morocco (Geyer & Mergl 1995), Jordan (Richter & Richter 1941) and Avalonian terranes (Walcott 1912, Rowell 1962). Kutorginates (*Yorkia, Nisusia*) are known from Spain and Avalonian terranes (Walcott 1912, Rowell 1962) but also from tropical East Gondwana (Brock 1998).

These differences are probably related to special ecological requirements of particular brachiopod groups, rather than the geographical distance of separation between Bohemia and Spain and the ability of larval migration.

Brahimorthis likely preferred the arenaceous sea floor. *Bohemiella* was common in finely arenaceous sea floor and had a restricted stratigraphical range. *Chilidorthis* likely preferred coarser arenaceous substrate and its known occurrence is also limited to a short stratigraphical interval. Obollelates and kutorginates were generally common in the lower Cambrian and extended up to the earliest middle Cambrian. Both groups preferred shallow carbonate shelves with deposition of calcarenites. In Bohemia, the shallow-water shelves with terrigenous depositions hosted mainly infaunal or epifaunal dwellers (lingulates, orthids and protorthids; Fatka *et al.* 2004, Mergl & Kordule 2008) and these shelves were not suitable for occupation by the latest obollelates and kutorginates. The few known occurrences of middle Cambrian brachiopods in western Gondwana argue that all these rhynchonelliformean brachiopod dominated faunas were intimately dependent on particular arenaceous environments.

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