

Late Viséan-Serpukhovian lasiodiscid foraminifers in Vegas de Sotres section (Cantabrian Mountains, NW Spain): potential biostratigraphic markers for the Viséan-Serpukhovian boundary

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Abstract

The Vegas de Sotres section (Cantabrian Mountains, Northern Spain) spans a continuous record of upper Viséan-Serpukhovian (Mississippian) marine carbonates. It contains distinctive bioclastic pale grey nodular and black limestones of the upper part of the Alba Formation, representative of more shallower-water facies than the classically described deeper-water red griotte limestones of the formation. Above the Alba Formation are dark grey laminated limestones typical facies of the Barcaliente Formation. The Alba Formation in Vegas de Sotres section is noteworthy for the common foraminifers. Systematic analysis of the lasiodiscid foraminifers allows the identification of diverse assemblages with twenty six species assigned to five genera. The dominant genus is *Howchinia*, in which 18 species have been identified. Six species were previously described in the literature, 5 species are identified in open nomenclature, and 7 new species are described (*H. acutiformis*, *H. cantabrica*, *H. enormis*, *H. hemisphaerica*, *H. plana*, *H. sotrensis* and *H. variabilis*). Also abundant are 5 species of the new genus *Hemidiscopsis*, formally described here for the first time. Another common genus is *Monotaxinoides* and more rarely, *Planohowchinia* and *Eolasiodiscus*. Owing to the abundance of taxa, including intermediate forms, phylogenetic relationships are recognized, with transitional forms occurring between distinct genera. Biostratigraphically, some species may help in the recognition of the Viséan/Serpukhovian boundary, as they are recorded close to the first occurrence of the conodont *Lochriea zieglerei*. *Howchinia hemisphaerica* nov. sp. first occurs in slightly older levels in the upper Viséan and *H. nov. sp. 4* in the same bed as *L. zieglerei*. Nine species of *Howchinia* first occur in slightly younger levels in the lower Serpukhovian and therefore also help potentially in the recognition of the base of the Serpukhovian.

Keywords:

Lasiodiscids

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Viséan

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1. Introduction

Representatives of the family Lasiodiscidae are some of the most useful biostratigraphic markers for different stages and substages of the Mississippian in the Western Palaeotethys. Thus, *Vissariotaxis* Mamet, 1970 is used for the recognition of the Cf6 zone (Asbian–Brigantian) in Western Europe (Conil et al., 1991) and Zone 15 in the Palaeotethys of Mamet and Skipp (1970). The genus *Howchinia* appears in the late Asbian (Vachard, 1977; Conil et al., 1980; Jones and Somerville, 1996). The genus *Monotaxinoides* was considered as representative of the uppermost late Brigantian (Conil et al., 1991), although it is difficult to know exactly what those authors potentially considered as *Monotaxinoides*, because the genus was not illustrated (nor were species listed), and the boundary between the continuum of *Howchinia* and *Monotaxinoides* can be readily disputed. Previously Laloux (1988) also considered the first occurrence of *Monotaxinoides* in the uppermost Viséan (upper Cf6δ zone) although he only illustrated "transition entre les genres *Howchinia* et *Montaxinoides*" from this period, which are juveniles (and of difficult identification) with a clear conical shape, and thus, considered here as *Howchinia*. *Eolasiodiscus donbassicus* is currently the basal zonal marker for the Serpukhovian in the Urals (Kulagina and Gibshman, 2002), although in Western Europe, as well as in other studies in Russia (Kulagina, 1988), it occurs together with *Turrispiroides*, and both are used as markers for the late Serpukhovian or Zone E2 in the Arnsbergian (Conil et al., 1991; Krainer and Vachard, 2002).

The Vegas de Sotres section contains rather diverse specimens of lasiodiscids as to be suitable for the characterization of the transition between the Viséan and Serpukhovian. In total, nearly 1400 thin-sections have been studied for the analysis of foraminifers. Stratigraphic sections in the southern Urals, mostly with slope to deep outer shelf limestone facies (Nikolaeva et al., 2009; Kulagina et al., 2009, 2011), also recorded lasiodiscid foraminifers. There, the basal biozone of the Serpukhovian is based on the first occurrence datum (FOD) of *Eolasiodiscus donbassicus* (Kulagina, 2001; Kulagina and Gibshman, 2002;), although it only occurs from the base of the Serpukhovian in shallow water facies (Kulagina et al., 2011).

Ar section in the southern Urals representative of deep-water facies, Verkhnyaya Kardailovka, is currently being investigated as a potential candidate for the GSSP for the Viséan–Serpukhovian boundary by Russian authors (Nikolaeva et al., 2009). The marker for the recognition of this boundary will be probably the conodont *Lochriea ziegleri* Nemyrovskaya, Perret and Meischner, 1994 (as it has been supported in the International Carboniferous Subcommission; Richards, 2005), which first occurs in an intermediate position within the traditional Venevian Russian Substage (Skompski et al., 1995; Gibshman et al., 2009). In the Verkhnyaya Kardailovka section, *Eolasiodiscus donbassicus* does not occur, although other lasiodiscids are recorded, in particular *Eolasiodiscus? muradymicus* (here considered as included in *Hemidiscopsis* nov. gen.), *Howchinia gibba* and *Monotaxinoides? sp.*, associated closely to the first occurrence of *L. ziegleri*, whereas *Howchinia bradyana*, *Monotaxinoides subplanus*, *M. convexus*, *M. gracilis* and *M. transitorius* occur higher up the section in the late Serpukhovian. Other sections in China, also investigated as potential candidates for the same GSSP, e.g. Nashui (deep-water facies) and Yashui (shallow-water facies) sections do not contain lasiodiscids (Hance et al., 2011; Groves et al., 2012).

The rich lasiodiscid assemblages of the Vegas de Sotres section may be considered as an excellent tool to understand the evolution of this family in the transition between the Viséan and the Serpukhovian, calibrated with the first occurrence of the conodont *Lochriea ziegleri*, as well as to clarify some taxonomic problems observed in the genera and species. Research on conodonts from the Vegas de Sotres section is still in progress, and additional sampling is currently under investigation. Lasiodiscid biostratigraphy will be discussed in relation to the first occurrence of *L. ziegleri*.

2. Stratigraphical setting

The Vegas de Sotres section is located three kilometres south of the small village of Sotres in the Picos de Europa Spanish National Park (Asturias; latitude 43° 12' 16" N and longitude 4° 45' 54" W; Fig. 1). It is on the western foothills of the Cueto de la Vezada peak at the east slope of the flat valley floor of the Duje River known as the Vegas del Toro (or Vegas de Sotres). The measured sections occur in Mississippian rocks located just above a Variscan thrust fault in the system of the Picos de Europa tectonic unit. The section passes through the upper part of the Alba Formation (Comte, 1959) and the lower part of the Barcaliente Formation (Wagner et al., 1971) (Fig. 2). The locality is unusual in the Cantabrian Mountains compared to most of the outcrops of the Alba Formation since upper Viséan to Serpukhovian foraminifers of the suborder Fusulinina are recognized together with some conodont species considered normally to dwell in shallow-water conditions (Martínez García et al.,

1984; Blanco-Ferrera et al., 2008, 2009). The succession is composite, comprising several short sections, because several late normal faults with metric-scale movement are significant for a thin succession. It has hampered the study and necessitated successive samplings led by biostratigraphic results (Figs. 2-3).

The lowest exposed beds of the Alba Formation in the Vegas de Sotres succession correspond to the Canalón Member of Wagner et al. (1971). This member consists of 11 m of red to pinkish-grey nodular mudstone in beds of decimetric thickness and with occasional centimetric marl layers (unit 1 of Blanco-Ferrera et al., 2008). Bioturbation, ferromanganese envelopes of intraclasts and skeletal debris, as well as hardground surfaces with ferromanganese oxides, are common. Within the fossils, pelmatozoan discrete sclerites, conodonts and agglutinated foraminifers often occur, whereas radiolarians, fragments of cephalopods and thin-shelled ostracods are present occasionally. Similar cephalopod condensed limestone facies is common in the Cantabrian Mountains and probably deposited reaching depths of some hundreds of metres (Wendt and Aigner, 1985).

Above the Canalón Member, 6.5 m of grey nodular limestones, sometimes, bioturbated include bioclastic limestone from centimetres to decimetres in thickness (unit 2 of Blanco-Ferrera et al., 2008). Bioclastic beds are commonly grain-classified and contain abundant pelmatozoan remains, together with foraminifers with different size and sorting (Fig. 3). Foraminifer abundance and diversity increases respect to the Canalón Member, and together with algaes and some conodont species suggest a continuous source from shallow water environments to the pelagic carbonate sedimentation of the nodular limestone.

The highest abundance in foraminifers is located in the succeeding 1.9 m of dark grey bioclastic limestones, locally rudstone, sometimes associated with fragments of brachiopods and corals (unit 3 of Blanco-Ferrera et al., 2008). Limestones contain silicified bioclasts and nodules, particularly upwards. This unit seems to have been deposited in the shallowest water setting in the studied section, and its age and stratigraphic position suggest its correlation with the San Adrián Member of the Alba Formation (Reuther, 1977). This member was located in the inner part of a carbonate ramp, which distal southwards part correspond to nodular limestones included in the Canalón Member (Sanz-López et al., 2004). The San Adrián Member consists of black, laminated lime mudstone, locally rudstone, where crinoids and rare corals can be occasionally observed in very scarce beds. Commonly, scarce fauna and high content of organic matter suggest poorly oxygenated sea-bottom conditions. The uppermost part of the Alba Formation is the Millaró Member (Sanz-López et al., 2004; Sanz-López and Blanco-Ferrera, 2012), here represented by about 2.7 m of chert-shale and limestone beds of a few centimetres in thickness (unit 4). It shows an irregular outcrop and is often poorly exposed (covered by Quaternary debris of limestone blocks of the Barcaliente Formation; Fig. 2). This member corresponds to a widespread drowning event on the Canalón/or San Adrián members in all the Cantabrian zone (Sanz-López et al., 2004, 2007).

The overlying Barcaliente Formation is typically formed by dark grey laminated limestones. The first beds include chert limestones with rare foraminifers. Late Serpukhovian conodonts are reported at 6 m above the base of the formation (Blanco-Ferrera et al., 2008; Sanz-López et al., 2013). The Barcaliente Formation corresponds to a carbonate ramp deposited in a restricted foreland basin. It was coeval with the deposition of siliciclastic turbidites in a foredeep, which located at the western and the southern border of the Cantabrian zone. Poorly oxygenated sea-bottom conditions (occasionally oxygenated) and subsidence increase respect to the Alba Formation. Stratified waters and marginal hypersaline conditions are suggested for the Cantabrian foreland basin close to the closure of the Rheic Ocean and the equatorial gateway (Sanz-López et al., 2013).

3. Systematic palaeontology (P. Cózar)

Family LASIODISCIDAE Reitlinger, 1956

Remarks: This family was considered as a superfamily by Vdovenko et al. (1993), and subdivided into three families, Vissariotaxidae Reitlinger in Vdovenko et al., 1993, Howchiniidae Martini and Zaninetti, 1988 emend. Rauser-Chernousova and Reitlinger in Vdovenko et al., 1993 and Lasiodiscidae Reitlinger, 1956.

The family Vissariotaxidae was not accepted by Mamet and Pinard (1990) and Pinard and Mamet (1998) because they transferred *Vissariotaxis* Mamet, 1970 into the family Pseudotaxidae Mamet, 1974. Those same authors created the family Turrspiroidae to include genera without a hyaline layer, comprising *Turrspiroides* Reitlinger in Voloshinova, Dain and Reitlinger, 1959, and *Hemidiscus* Schellwien, 1898. The second family, Howchiniidae, includes the genera with hyaline layers, such as *Monotaxinoides* Brazhnikova and Yartseva, 1956, *Eolasiiodiscus* Reitlinger, 1956, *Mesolasiiodiscus* Rauser-Chernousova and Chernmykh, 1990, and *Howchinia* Cushman, 1927. The latter genus was interpreted by Mamet and Pinard (1990) as a transitional genus

to the Tetrataxidae. The third and final family, Lasiodiscidae, would only include *Lasiodiscus* Reichel, 1946 and *Lasiotrochus* Reichel, 1946.

This family subdivision can be questioned, because transitional forms between *Vissariotaxis* and *Howchinia* can be suggested (primitive *Howchinia* auct.) and between *Vissariotaxis* and *Hemidiscopsis* [*H. declivis* (Ganelina, 1956) comb. nov.]. It is a rather controversial point that *Vissariotaxis* is not considered as a lasiodiscid, whereas *Howchinia* remains within the family. In addition, it is also possible to suggest some transitional forms between *Howchinia* and *Monotaxinoides* (*Howchinia enormis* nov. sp.), which do not support the published subdivision of the lasiodiscids.

A different classification scheme was proposed by Pille (2008), who emended the family Howchiniidae Martini and Zaninetti, 1988 by regrouping most of the primitive lasiodiscids, with or without a hyaline layer. She considered the hyaline layer only valid as for species identification, eventually as generic. Arguments for the regrouping of the genera with and without a hyaline layer was based on her observation of assemblages of *Howchinia* from the Montagne Noire, as well as those of *Hemidiscus* in the Carnic Alps reinterpreted by Vachard and Krainer (2001). In both cases, the hyaline layer was considered as a variable character. Pille (2008) considered the family Howchiniidae to be composed of *Howchinia*, *Vissariotaxis*, *Planohowchinia* Cózar and Mamet, 2001 and "*Monotaxinoides*" sensu Kulagina, 2001. On the other hand, Pille (2008) included the following planispiral genera in the family Lasiodiscidae: *Lasiodiscus*, *Mesolasiodiscus*, *Eolasiodiscus*, *Hemidiscus*, *Monotaxinoides* (part), "*Turrispiroides*" (auct.) and a new genus *Hemidiscopsis* (nomen nudum in Pille, 2008).

The latter subdivision can be also questioned, apart from the irrelevance of the hyaline layer for generic classification (generally considered as a valid character for most foraminifers), as some of the interpreted planispiral genera contain irregularities and they are not completely planispiral. Furthermore, the transitional forms listed above, do not support this family subdivision.

Thus, the validity of those families is not free of controversy due to the transitional forms between genera of both families (*Vissariotaxis* as ancestor of *Hemidiscopsis* and *Howchinia* as ancestor of *Monotaxinoides*), which would argue against the phylogenetic uniformity of each family. A more traditional (conservative) sense of the family Lasiodiscidae is retained herein, which include all of the following genera: *Eolasiodiscus*, *Hemidiscopsis*, *Hemidiscus*, *Howchinia*, *Lasiodiscus*, *Lasiotrochus*, *Mesolasiodiscus*, *Monotaxinoides*, *Planohowchinia*, *Turrispiroides*, and *Vissariotaxis*.

All the illustrated material is housed in the senior author's collection in the Department of Paleontology, Universidad Complutense de Madrid.

Genus *Eolasiodiscus* Reitlinger, 1956

Type species: *Eolasiodiscus donbassicus* Reitlinger, 1956.

Diagnosis: Discoidal test, with a tubular chamber more or less cylindrical with a discoidal coiling or slightly trochospiral. Bilayered wall with a poor development of the hyaline layer, which is developed in the umbilical area. Aperture simple at the end of the tubular chamber and small secondary apertures along the suture.

Eolasiodiscus donbassicus Reitlinger, 1956

Fig. 5 (24–27)

Description: Test of medium size for a high number of whorls (Table 1), discoidal or slightly concave. The tubular chamber with a planispiral coiling showing a slight but progressive deviation of the main coiling axis, and the proloculus is not observed. The lumen is wider than higher. Wall is bilayered, with a well-developed microgranular layer and a very thin to nearly absent hyaline layer in the whorls. Hyaline infilling poorly developed.

Remarks: This species was originally described from Bashkirian rocks, but later documented from the late Serpukhovian (e.g. Lipina and Reitlinger, 1971). More recently, the species has been used as marker for the early Serpukhovian (Kulagina, 2001; Kulagina and Gibshman, 2002), although it is only present at this level in some shallow-water sections of the southern Urals (Kulagina et al., 2011).

Genus *Hemidiscopsis* nov. gen.

Derivation of the name: Pille (2008, nomen nudum, unpublished Ph.D. Thesis) compared this genus with the genus *Hemidiscus* Schellwien, 1898.

Type species: *Monotaxinoides? caprariensis* Vachard, 1977, Les Mentaresses section, close to Vailhan, Brigantian (latest Viséan) in the Montagne Noire (France).

Composition: *Monotaxinoides? caprariensis* Vachard, 1977; *Monotaxinoides priscus* Brazhnikova and Yartseva, 1956; *Monotaxis declivis* Ganelina, 1956; *Eolasiotaxis muradymicus* Kulagina in Kulagina et al., 1992; *Hemidiscopsis? nov. sp. 1*; *Hemidiscopsis? nov. sp. 2*.

Diagnosis: Small nearly planispiral to planispiral test, with evolute whorls, proloculus generally large. Wall mostly microgranular, with thin to nearly absent hyaline layer in the spire and also very poorly developed to absent in one side of the test. Small protruding oblique spines in the suture between whorls. Simple terminal aperture.

Remarks: It differs from *Hemidiscus* in the small spines in the sutures (Fig. 5 (1-3, 5) and the presence of a rudimentary hyaline layer. It differs from *Monotaxinoides* and *Planohowchinia* by the presence of spines and a poorer development of the hyaline layer and umbilical infilling.

This genus was originally described Pille (2008) in her unpublished Ph.D. Thesis, although she considered the genus as exclusively composed of a microgranular wall. A very thin hyaline layer in the spire wall seems to be present in some of her specimens (Pille, 2008: pl. 45, figs. 19, 20, 24) as well as in one side of the test (pl. 45, figs. 4, 5, 6), a feature that is included in the diagnosis of the genus. In addition, secondary apertures along the sutures between whorls were also documented by Pille (2008: pl. 45, figs. 7-11) as characteristic for the genus, which is not observed in her illustrated specimens. Vachard (1977: p. 158) suggested previously the presence of those secondary apertures in the type species ["Il semble exister, du côté plan, des ouvertures secondaires suturales..."], although, this feature is not clearly observed in his equatorial specimens. In other species considered as included in this genus, the secondary apertures were not documented and apparently nor illustrated (Brazhnikova and Yartseva, 1956; Kulagina et al., 1992). Specimens attributed to those species in the Vegas de Sotres section, do not show clear secondary sutural apertures, although trace of small apertures are poorly preserved (Fig. 5 (17-18)). Owing to the ambiguous observation of this character, it is not included in the genus diagnosis.

Owing to the simple morphology of the tests only a few parameters seem to be representative for the species distinction: size of proloculus, relative width/height ratio of the test, shape of the lumen.

Hemidiscopsis caprariensis (Vachard, 1977) nov. comb.

Fig. 5 (10-18)

Description: Test of small size (Table 1), with similar growth in height and width of the lumen. Successive whorls are mostly planispirally coiled, but some whorls are displaced laterally from the main plane of coiling axis. In some specimens, the final whorl is situated in a distinct plane to the axis and located on the flank of the test. Hyaline layer is generally poorly developed in the spire and it can be also present on the concave side of the test (Fig. 5 (15-16)).

Remarks: It differs from *H. priscus* by a smaller proloculus and a more proportional growth of the spire, with more rounded lumen. It differs from other species of the genus by smaller size for similar number of whorls.

The species was formally published in Vachard (1977), although the types were previously described as *Monotaxinoides subcarbonicus* (Dain) by Vachard (1974: pl. 27, figs. 6-8;) in his unpublished thesis.

Pille (2008) considered specimens assigned to *H. caprariensis* with the displacement of the axis only on one side of the test, and thus, with a conical shape, as rather common in the assemblage from the Montagne Noire. Most of the conical specimens were recorded (together with flattened specimens) in Les Pascales outcrop, whereas in Roque Redonde, only flattened or slightly conical specimens were illustrated (Pille, 2008: pl. 45, fig. 20). In addition, one of the specimens from Les Pascales shows an irregular conical shape (Pille, 2008: pl. 45, fig. 13). It is also noteworthy that the proloculus is not sectioned in any of the conical specimens. Revision of the material from the Montagne Noire (collections D. Vachard, Lille, and M. Aretz, Toulouse) does not show intermediate forms between the discoidal and conical specimens which justify to include this variation in a single species. The dimensions, number of whorls and other parameters of the conical specimens are similar to *Hemidiscopsis? declivis* (Ganelina, 1956) comb. nov., to which they are assigned herein. The latter is considered as the transitional species between the conical *Vissariotaxis* and the discoidal *Hemidiscopsis*. Its inclusion in any of the genera could be debated, but here, it is referred to the genus *Hemidiscopsis* with question mark.

Hemidiscopsis muradymicus (Kulagina in Kulagina et al., 1992) nov. comb.

Fig. 5 (3–8)

Description: Large flattened discoidal test, with a low number of evolute whorls (Table 1). Some whorls can be slightly displaced from the main coiling axis. The spire grows progressively, with similar growth in height and width of the lumen, or slightly higher than wider. A very thin and incipient hyaline layer is observed in between some whorls, whereas in the rest of the whorls and sides, it is absent.

Remarks: The species differs from *Hemidiscopsis?* nov. sp. 2 by a lower number of whorls for similar size (specimens of 6 whorls measure about 300 microns in the latter, and in *H. muradymicus*, specimens of 6 whorls measure about 500 microns), and a wider lumen in the final whorls, and better development of the hyaline layer.

Hemidiscopsis muradymicus was originally described from the latest Serpukhovian and early Bashkirian from the south Urals (Kulagina et al., 1992), although it has been recorded close to, but above, the first occurrence of *Lochriea zieglerei* in the Verkhnyaya Kardailovka section (Nikolaeva et al., 2009).

Hemidiscopsis priscus (Brazhnikova and Yartseva, 1956) nov. comb.

Fig. 5 (19–23)

Description: Small flattened discoidal test, composed of a low number of evolute whorls (Table 1). The final whorls slightly displaced in one direction from the coiling axis. Large proloculus. The width of the lumen grows more rapidly than the height. Hyaline layer nearly absent, only observed in between some of the whorls of the spire.

Hemidiscopsis? nov. sp. 1

Fig. 5.9

Description: Large flattened discoidal test, with a moderate number of evolute whorls. The lumen grows proportionally in height and width. A well-developed hyaline layer is observed in between some whorls, and filling the umbilical area.

Remarks: The studied specimen contains similar parameters to *H. muradymicus*, however, this specimen shows a development of the hyaline infilling in the umbilical area, as well as clearly developed in between the whorls. The latter features are more typical in *Monotaxinoides*. However, the specimen occurs from the base of the section (Fig. 4), stratigraphically far below any representative of the latter genus, which suggests a closer relationship with the large *Hemidiscopsis* recorded in this lower part of the section. Alternatively, it could be an immature specimens of *Howchinia* nov. sp. 4, which is present at equivalent levels.

Hemidiscopsis? nov. sp. 2

Fig. 5 (1–2)

Description: Large flattened discoidal test, with a moderate number of evolute whorls. Some whorls can be slightly displaced from the main coiling axis. The lumen grows slightly more rapid in height than width in the inner whorls, and in contrast, wider than higher in the final whorls. A very thin and incipient hyaline layer is observed in between some whorls, whereas in the rest of the whorls and sides, it is absent.

Remarks: Specimens assigned to this species are poorly oriented sections, which do not allow a perfect observation of their morphology. Owing to their general size, parameters and numbers of whorls (Table 1), they are similar to *Eolasiotus donbassicus*, however, the shape of the lumen and irregularities in the coiling are closer to *Hemidiscopsis*.

Genus *Howchinia* Cushman, 1927

Type species: *Howchinia bradyana* (Howchin, 1888) emend. Davis, 1951

Diagnosis: Undivided second tubular chamber coiled in a medium to high conical spire. Umbilical area with hyaline infilling, in some cases with presence of pseudo-pillars. Bilayered wall of the tubular chamber, inner microgranular layer and outer hyaline layer.

Remarks: The presence of pseudo-pillars is a questionable feature in the literature, and for some authors, it is a valid taxonomic character, even assigning it to an advanced feature in the Serpukhovian (Lys, 1985), whereas for other authors, it is simply a diagenetic artifact and specimens with and without pseudo-pillars are illustrated together (Krainer and Vachard 2002). This structure was also recognized from uppermost Viséan (Brigantian) rocks (Cózar et al., 2005). Both facts suggest that the pseudo-pillars may represent a stage of preservation of the

umbilical hyaline infilling, although, it is only observed in specimens from the late Brigantian and early Namurian.

The distinction between *Howchinia* and *Monotaxinoides* is difficult to determine, and it seems to be based only on the height of the conical spire. Many authors have considered that difference rather subjective, and the intermediate forms can be arbitrarily included in the former or latter genus (Armstrong and Mamet, 1977; Pinard and Mamet, 1998; Pille, 2008). In this study, also arbitrarily, the flattened to nearly flattened forms are included in *Monotaxinoides*, whereas the more conical forms are included within *Howchinia*. Low conical shapes are observed in nine of the species included herein in *Howchinia* (*H. acutiformis*, *H. cantabrica*, *H. convexa*, *H. enormis*, *H. hemisphaerica*, *H. plana*, *H. subconica*, *H. subplana*, *H. variabilis*), that could be also considered as *Monotaxinoides*. All those nine species occur close the Viséan/Serpukhovian boundary.

Primitive transitional forms to *Vissariotaxis* are rarely recorded in the Vegas de Sotres section, characterized by a poor development of the hyaline layer in the wall (e.g., Cózar, 2004: pl. 1, fig. 20). These forms are the so-called primitive *Howchinia* of Laloux (1988) and Conil et al. (1991), however, they were interpreted by Pille (2008) as *Vissariotaxis*.

Dimensions for the different species (Table 2), show an overlap in the measurements of some species, although this is not a main criteria in distinguishing species. The main criteria area: the shape of the apical area, flanks and development of the layers in the wall .

Despite the numerous thin-sections prepared for this study (more than 1400), the assemblages are not particularly abundant in each species (Fig. 4, Table 2), and in some cases, scarce material does not allow to propose formal descriptions of each new species. Synonymies of well-known species are documented in Appendix .

Howchinia bradyana (Howchin, 1888) emend. Davis, 1951

Fig. 6 (10–16)

Description: Large specimens with proportional width and height ratio, and medium-sized proloculus compared to the size of the test (Table 2). Small apical angle between the initial whorls and the proloculus, passing into nearly flat to slightly convex flanks forming a high conical spire. Some of the large specimens develop wider final whorls, and the sections of the specimens are more triangular (Fig. 6.12). Microgranular layer changes from uniformly thick in the inner whorls and becomes thicker in the final whorls. Hyaline layer well developed in the spire and umbilical area. In between the whorls, the hyaline layer is poorly developed in the initial whorls, whereas it is well developed in the final whorls, where it is of the same thickness or thicker than the microgranular layer. Pseudo-pillars are observed in half of the studied specimens (Fig. 6 (11-12); Table 2).

Remarks: Mature specimens with a more triangular section are also included within the species, because immature specimens with wider final whorls are observed (Fig. 6.16), as well as variation in the width of the whorls (Fig. 6.11).

The diagnosis for this species is not clear enough in the literature, and other species can be frequently found illustrated under this species name (Appendix). Owing to this profusion of diverse illustrated material, a more restrictive definition for the species is acknowledged in this study.

Howchinia acutiformis nov. sp.

Fig. 7 (4–8)

1979. *Monotaxinoides* cf. *subconica* (Brazhnikova and Yartseva) – Malakhova in Wagner et al., pl. 3, fig. 16.

pars. 1987. *Howchinia subconica* (Brazhnikova and Yartseva) – Luo, pl. 2, fig. 7 [only].

pars. 2001. *Howchinia subconica* Brazhnikova and Yartseva (sic) forma *minima* – Vdovenko, pl. 4, fig. 43 [non fig. 42 = ? *H. cantabrica*].

2010. *Monotaxinoides subconica* (Brazhnikova and Yartseva) – Stephenson et al., fig. 5b.

Derivation of the name: Due to its acute test.

Material: Holotype VS 0117 (Fig. 7.8), and 10 paratypes (Fig. 7 (4–7)) (Table 2).

Type locality and horizon: Vegas de Sotres section, sample (VSC-2A1b), early Serpukhovian.

Occurrence: Serpukhovian in the Vegas de Sotres section, late Brigantian to Pendleian in England, latest Viséan of Donets, early Serpukhovian in Moscow Basin, and Serpukhovian in China.

Diagnosis: Conical test with an acute angle and irregular flanks with deviation of the main coiling plane from the fourth whorls. Hyaline layer in the spire poorly developed.

Description: Medium-sized conical test ($W= 120-230 \mu\text{m}$, $H= 50-90 \mu\text{m}$), with a marked apical angle, the first four or five whorls are flat with a progressive uniform deviation from the coiling plane, and the final 1-2 whorls are arranged also at a small deviation with the previous whorls. Small proloculus, inner diameter $15-25 \mu\text{m}$. Moderate number of whorls, less than 6. Microgranular layer uniformly thin throughout the spire, separated by a thinner hyaline layer apparently absent in the inner whorls. The umbilical area is wide, with a hyaline infilling that usually does not reach up to the final whorl, only up to half of the height of the lumen in the final whorl. This filling is generally flat at the base, although slightly concave bases are also observed.

Remarks: This species is similar to *Howchinia subconica* (Brazhnikova and Yartseva, 1956) in the general morphology of the test, with some displacements of some final whorls, and thus, slightly irregular flanks. Owing to the smaller dimensions with a lower number of whorls, it could be misinterpreted as a juvenile of *H. subconica*. However, the hyaline and microgranular layers, as well as the hyaline infilling are more reduced in *H. acutiformis*, with very poor development of the hyaline layer in between the microgranular layer, which is directly in contact in the inner whorls. In addition, for similar size, *H. acutiformis* has more whorls.

It differs from *H. variabilis*, a species which also presents flanks with an deviation in between different whorls, because the general shape of the flanks in *H. acutiformis* is convex, whereas it is mostly flat to concave in *H. variabilis*. In addition, *H. variabilis* does not present a similar acute apical angle.

Howchinia beleutensis Vdovenko, 1962

Fig. 8 (16–20)

Description: Medium-sized test with medium proloculus, convex flanks and slightly convex apical zone. Uniform microgranular layer which increases slightly but progressively in its thickness from the initial whorls. Hyaline layer in between the whorls is more or less uniform and relatively thin, with lower or similar thickness than the microgranular layer. Hyaline infilling is well developed in the umbilical area, with common presence of pseudo-pillars. Usually, the final whorls modified significantly the conical shape and the penultimate whorl is wider than the final whorl.

Remarks: The recognition of this species in most studies was based on the presence of the pseudo-pillars (mostly as *Howchinia* sp. 2 cf. Lys, 1985; Appendix), and thus, different morphologies were erroneously grouped in the same taxon. Additionally, the presence of those pseudo-pillars was considered as biostratigraphically significant, and attributed traditionally to the Namurian (Lys, 1985; Sebban and Lys, 1989; Skompski et al., 1989; Mamet et al., 1994; Cózar, 2003). However, those structures occur from uppermost Viséan rocks (Cózar et al., 2005), and in a wide variety of morphologies, attributed in this study to *H. bradyana*, *H. gibba* and *H. convexa*, and thus, apparently, with no taxonomic relevance. In the literature, pseudo-pillars can be also observed in specimens of *H. subplana* (see synonym list in Appendix).

This species differs from *Howchinia gibba* by a slightly more flattened conical form, and poorer development of the hyaline layer in the wall. It differs from *H. convexa* by more convex apical area and generally, slightly higher W/H ratios for specimens of similar whorls . It differs from *H. acutiformis* by better development of the hyaline layers in the spire and in the umbilical area, which cover all the whorls completely, as well as lower W/H ratios and a poorer development of the microgranular layer .

Howchinia cantabrica nov. sp.

Fig. 7 (9–16)

pars. 1956. *Howchinia* – Reitlinger, pl. 1, fig. 3 [only].

1973. *Howchinia subplana* (Brazhnikova and Yartseva) – Ivanova, pl. 20, fig. 19.

1973. *Howchinia* aff. *subplana* (Brazhnikova and Yartseva) – Perret, pl. 1, fig. 24.

pars. 1974. *Howchinia declive plana* n. ssp. – Monostori, pl. 2, fig. 5 [only].

1987. *Howchinia subplana* (Brazhnikova and Yartseva) – Luo, pl. 2, figs. 9.

1988. *Monotaxinoides* sp. – Laloux, pl. 2, fig. 38.

pars. 1988. *Monotaxinoides subplanus* (Brazhnikova and Yartseva) – Kulagina, pl. 3, figs. 20-21 [non pl. 2, fig. 23 = *H. subplana*].

pars. 1991. *Monotaxinoides subplana* Brazhnikova and Yartseva (sic) – Marfenkova, pl. 8, fig. 17 [only].

pars. 1992. *Monotaxinoides convexus* Brazhnikova – Kulagina et al., pl. 8, fig. 22.

1993. *Howchinia subplana* (Brazhnikova and Yartseva) – Perret, pl. FV, figs. 6, 9.

? 2001. *Howchinia subconica* Brazhnikova and Yartseva (sic) forma *minima* – Vdovenko, pl. 4, fig. 42 [non fig. 43 = *H. acutiformis*].

pars. 2009. *Monotaxinoides transitorious* Brazhnikova and Yartseva – Nikolaeva et al., pl. 1, fig. 40 [only].

2009. *Monotaxinoides subplana* Brazhnikova and Yartseva (sic) – Nikolaeva et al., pl. 1, fig. 48.

2010. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Stephenson et al., fig. 5c.

2011. *Monotaxinoides* ex gr. *subplana* (Brazhnikova and Yartseva) – Cózar et al., figs. 10.19, 10.21.

2013. *Howchinia* sp. 2 sensu Lys (= ? *H. beleutensis*) – Somerville et al., fig. 4.8.

pars. 2014. *Monotaxinoides subplanus* (Brazhnikova and Yartseva) – Kulagina et al., fig. 7.30 [only].

Derivation of the name: From the Cantabrian Mountains.

Material: Holotype VS 0163 (Fig. 7.15), and 25 paratypes (Fig. 7 (9–14, 16)) of diverse orientation (Table 2).

Type locality and horizon: Vegas de Sotres section, sample (VSC-2A1e), early Serpukhovian.

Occurrence: This species is present throughout the Serpukhovian in the Cantabrian Mountains and Morocco, in the late Serpukhovian of the Russian Platform, Urals and China, Arnsbergian in France and Belgium, as well as an undifferentiated Namurian in Hungary. It is noteworthy for its occurrence in the late Brigantian (to Arnsbergian) in England and from Limestone B₄ in the Donets Basin (Ukraine) correlated with a intervening position within the Venevian Substage by Davydov et al. (2010).

Diagnosis: Flattened conical test with the inner whorls nearly flat to slightly convex in the apical area. Microgranular layer of uniform thickness and hyaline layer in the spire very poorly developed. Hyaline infilling in the umbilical area moderately developed and does not cover completely the umbilical area up to the final whorl.

Description: Medium-sized very low conical test with a width generally ranging from 140 to 190 µm (with minimum of 115 µm and maximum of 240 µm) and a height 40 to 70 µm (with a maximum of 100 µm). The proloculus is of medium size, 20 to 30 µm in inner diameter. Low to moderate number of whorls, 3 to 5.5. The inner whorls are disposed nearly flat in the apical area or in a slightly convex shape. The rest of the flanks area more clearly convex. The microgranular layer is nearly uniform in thickness from the inner to the outer whorls, where its thickness may reach 8 µm. The hyaline layer is poorly developed in the inner whorls, where the microgranular layer of the successive whorls is nearly in contact with each other. In the outer whorls, the hyaline layer is slightly better developed, and may reach similar thickness as the microgranular layer. The hyaline infilling of the umbilical area does not cover completely the final whorl, in some specimens only up to the penultimate whorl. The hyaline infilling is flat in shape or slightly concave in its base.

Remarks: It is closely related to *Howchinia subplana*, to which it is commonly attributed (see synonymy). However, *Howchinia cantabrica* contains a poorer development of the hyaline infilling in the umbilical area and in between the whorls of the spire, with the microgranular layer of the successive whorls being more densely packed.

It differs from *Howchinia beleutensis* by slightly higher W/H ratio, more flattened tests, and poorer development of the hyaline layers in the wall and umbilical area. It differs from *H. acutiformis* by more convex and regular flanks and better development of the hyaline layer in between the microgranular layer.

Howchinia convexa (Brazhnikova in Aizenverg et al., 1983)

Fig. 7 (1–3)

Description: Small conical test with open apical angle, and the flank widening progressively except for the final whorls, which can be slightly narrower than the previous ones. Small to medium proloculus. Microgranular layer is uniformly thick, separated by a thin hyaline layer, and a well-developed hyaline layer in the umbilical area, with slight convex form in the base of the test. The umbilical area is flat to convex at the base, and convex to the upper part. Pseudo-pillars are rarely present (Fig. 7.3).

Remarks: The morphology of the flanks and the conical form are the most distinctive feature of this species, which allow to distinguish it from *H. gibba* and *H. hemisphaerica*.

It differs from *Howchinia acutiformis* by more regular convex flanks, better development of the microgranular layer, notably thicker in the final whorls than in *H. acutiformis*, and a better hyaline cover of the umbilical area, reaching and covering the final whorl.

Howchinia enormis nov. sp.

Fig. 7 (23–26)

?pars. 1985. *Howchinia* n. sp. 2 – Lys, pl. 2, fig. 5 [non pl. 1, fig. 16 = *H. subplana*].

pars. 1992. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Kulagina et al., pl. 5, fig. 20 [non fig. 17 = *H. subplana*].

2009. *Monotaxinoides* cf. *subplanus* Brazhnikova and Yartseva (sic) – Nikolaeva et al., pl. 1, figs. 45-46.

pars. 2014. *Monotaxinoides subplanus* (Brazhnikova and Yartseva) – Kulagina et al., (?) fig. 6.24, fig. 7.32.

Derivation of the name: Due to its large size.

Material: Holotype VS 1218 (Fig. 7.26), and 12 paratypes (Fig. 7 (23–25, 27)) (Table 2).

Type locality and horizon: Vegas de Sotres section, sample (VSC-2A), early Serpukhovian.

Occurrence: Serpukhovian in the Vegas de Sotres section, late Serpukhovian in the Urals and Bashkirian in Béchar (Algeria).

Diagnosis: Low conical test, nearly planispiral with a progressive but slow deviation to one side forming a shallow and wide umbilicus. Microgranular wall well developed with basal thickenings in the final whorls.

Description: Large test (up to 460 µm width and 150 µm high) in a very low conical shape, nearly planispiral coiling, in which the whorls (up to 9) show a slight displacement to one side of the test. The inner whorls form a small angle with the proloculus, and the flanks are slightly convex. Only one specimen (Fig. 7.23) shows a deviation of the final whorl, giving a higher conical test. The microgranular layer is well developed, increasing its thickness in the successive whorls, commonly with thickenings. The hyaline layer is well developed in the spire from the inner whorls, approximately 1/3 of the thickness of the microgranular layer. Umbilical area very wide, completely filled by hyaline material, with a flat shape in the base of the umbilical area.

Remarks: This species is very close to the morphology in *Monotaxinoides*, however, due to the slightly convex flanks it has been considered as a *Howchinia*. This feature of the flanks is more convex in the larger specimen (Fig. 7.23), with overall morphologies close to large *H. subplana* or *H. subconica*.

It differs from *Howchinia subplana* by the absence of the initial flat whorls, and a better development of the hyaline layer, with the presence of thickenings. The largest specimens, differs from *H. subconica* by the regularity of the flanks, in which only the final whorl is displaced.

The specimen illustrated by Lys (1985: pl. 2, fig. 5) is questionably attributed to this species because of the relatively poor development of the microgranular layer, without thickenings, although other parameters are similar.

Howchinia gibba (Moeller, 1879)

Fig. 8 (11–15)

Description: Large specimens with medium proloculus. Convex apical area and flanks with a moderate number of whorls. Well-developed hyaline layer in the spire and umbilical area, with a progressively thicker microgranular layer, even showing thickenings in the final whorls. The thickness of the hyaline layer is approximately the same as in the microgranular layer or slightly thicker in the final whorls. Pseudo-pillars are observed in more than half of the studied assemblage (Fig. 4, Table 2).

Remarks: This species has been often synonymed with *H. bradyana* in previous studies, although in more recent literature, both species were considered as independent (Krainer and Vachard, 2002). Nevertheless, both species are commonly confused (Appendix). *Howchinia gibba* differs from *H. bradyana* by having a more rounded form for specimens of similar number of whorls (higher W/H ratio), more convex flanks and apices, with lower number of whorls for similar size. The development of the microgranular layer is commonly better developed in mature specimens of *H. gibba* than in *H. bradyana*. Populations of both species are generally well distinguished by the comparison of the width and height, although the juvenile forms can overlap their parameters (Table 2).

Brazhnikova and Yartseva (1956) and Kulagina (2001) interpreted that the older species is *H. gibba*, and that *H. bradyana* arose from the former. The presence of *H. bradyana* in the late Asbian is well known, however the presence of *H. gibba* for that period can be questioned. In Western Europe, true large *H. gibba* are known from the early Brigantian (Cózar and Somerville, 2004), and in the Cantabrian Mountains, it is interpreted as derived from *H. nov. sp. 3*, a primitive *Howchinia* with a similar shape to *H. gibba*, and present from Asbian times.

Howchinia hemisphaerica nov. sp.

Fig. 8 (5–10)

1987. *Howchinia declivis* (Ganelina) – Luo, pl. 2, figs. 3-4.

pars. 1993. *Howchinia* cf. *subconica* (Brazhnikova and Yartseva) – Perret, pl. FV, fig. 2 [only].

pars. 2001. *Howchinia* ex gr. *declivis* (Ganelina) – Vdovenko, pl. 4, fig. 34 [only].

2001. *Howchinia subplana* Brazhnikova and Yartseva (sic) forma *minima* – Vdovenko, pl. 4, figs. 44-46.

Derivation of the name: Due to its hemispherical inflated shape in axial section.

Material: Holotype VS 1287 (Fig. 8.10), and 9 paratypes (Fig. 8 (5–9)) (Table 2).

Type locality and horizon: Vegas de Sotres section, sample (VSF-14c), early Serpukhovian.

Occurrence: End of the late Viséan to Serpukhovian in Vegas de Sotres section, France, Algeria, Donets; Serpukhovian in China.

Diagnosis: Small medium to low conical test, with hemispherical axial section. Thin microgranular layer, uniform in thickness. Hyaline infilling in the umbilical area flat in mature specimens.

Description: Test of medium to small size ($W=125-170\ \mu\text{m}$, $H=50-100\ \mu\text{m}$), nearly hemispherical in axial section, convex flanks and apical area. Low to moderate number of whorls (3.5 to 6). Small proloculus, but proportionally larger compared to the size of the test. Uniform thin microgranular and hyaline layers in the spire; the latter is thinner than the microgranular layer. Well-developed hyaline infilling in the umbilical area, with flat base in mature specimens.

Remarks: Specimens attributed to this species can be found as *Monotaxinoides* or *Howchinia subconica* in unpublished studies, such as Vachard (1974: pl. 27, figs. 4-5), Sebbar (2000: pl. 13, figs. 11, 13), and Pille (2008: pl. 44, figs. 35-36).

Measurements of *Howchinia hemisphaerica* are rather similar to those in small specimens of *H. beleutensis*. Both species can be distinguished by the distinct development of the microgranular and hyaline layers in the spire, that are more uniform and thinner in *H. hemisphaerica*.

It differs from *Howchinia* nov. sp. 3 by a poorer development of the microgranular layer, better hyaline infilling in the umbilical area, a more convex apical area, and the hemispherical axial section.

It differs from other species with similar measurements, such as *Howchinia acutiformis* and *H. cantabrica* by more convex flanks, lower W/H ratios, poorer development of the microgranular layer and well-developed hyaline infilling in the umbilical area, flat to nearly flat shape covering the final whorl.

It differs from *Howchinia convexa* by a poorer development of the microgranular layer and more flattened tests.

Howchinia plana nov. sp.

Fig. 6 (24–29)

Derivation of the name: Due to its very low conical shape, nearly flat.

Material: Holotype VS 1242 (Fig. 6.27), and 12 paratypes (Figs. 6 (24–26, 28–29)) (Table 2).

Type locality and horizon: Vegas de Sotres section, sample (VSC-3), early Serpukhovian.

Occurrence: Same as the type locality.

Diagnosis: Low conical test, nearly discoidal. Flanks are flat with slight irregularities (concave and convex). Microgranular wall well developed and hyaline layer poorly developed.

Description: Small flattened conical test ranging from 135 to 240 μm in width, generally very low, 25 to 60 μm in height, although two large specimens reach 90 μm in height. Flat flanks, with slightly concave or convex form. The axial section is a low triangle. Low to moderate number of whorls (3-6). Proportionally, large proloculus, reaching up to 32 μm in inner diameter. The microgranular wall is thin, uniform, separated by a poorly developed hyaline layer, less than 1/3 to 1/4 of the thickness of the microgranular layer. In some of the inner whorls it is nearly absent. The hyaline infilling is also poorly developed in the umbilical area, with concave form at the base, covering irregularly only some of the initial whorls or in those specimens with a better development, it does not cover completely the final whorl.

Remarks: The larger specimens are those with less discoidal shape (Fig. 6 (28–29)). Those specimens also show a low triangular section. This species differs from *Howchinia variabilis* by the more regular flanks, and the progressive growth in height and width of the lumen.

Howchinia sotrensis nov. sp.

Fig. 6 (5–7)

pars. 1948. *Monotaxis gibba* Moeller (sic) – Vissarionova, 1948, pl. 8, fig. 9 [only].

1983. *Howchinia gibba minima* Vdovenko – Aizenverg et al., pl. 14, figs. 9, 12, 13.
pars. 1993. *Howchinia gibba* (Moeller) – Ueno and Nakazawa, fig. 3.25 [only].
1993. *Howchinia* sp. – Ueno and Nakazawa, fig. 3.20.
pars. 2001. *Howchinia* sp. – Vdovenko, pl. 4, fig. 28 [only].
pars. 2001. *Howchinia* ex gr. *declivia* (Ganelina) – Vdovenko, pl. 4, fig. 29, 36 [only].
2005. *Howchinia bradyana* (Howchin) emend. Davis – Cózar et al., fig. 8.11.
2013. *Howchinia* sp. B – Cózar and Somerville, fig. 6d.

Derivation of the name: From the Sotres village.

Material: Holotype VS 0473 (Fig. 6.7), and 8 paratypes (Fig. 6 (5–6)) of diverse orientation (Table 2).

Type locality and horizon: Vegas de Sotres section, sample (VSF-15), early Serpukhovian.

Occurrence: This species is known in the late Viséan in Russia, Japan, Ireland, England, Venevian-Serpukhovian in the Donets, and Brigantian in Algeria and Scotland. In Vegas de Sotres, it is only known in the Serpukhovian part of the section.

Diagnosis: Small high conical test with the early whorls rapidly arranged at nearly 90° from the proloculus, and the flanks become flat, slightly expanding to the final whorls. Umbilical area with flat sides, nearly parallel. Poor development of the hyaline layer in the wall in the internal whorls.

Description: Small conical test, width 120 to 180 µm, height 110-170 µm (W/H ratio = about 1) with medium inner diameter proloculus (28-32 µm), proportionally large for the size of the test. Number of whorls moderate to high, and up to 8 has been recorded. Apical zone flat, with the first two whorls, forming a deviation in relationship with the succeeding whorls. Flanks are flat, slightly widening to the final whorls. Microgranular layer well developed, and the hyaline layer in the spire may reach approximately the same thickness in the final whorls, but it is poorly developed in the internal whorls. Lumen grows slightly more in width than in height, thus, the lumen in the final whorls is wider than high. Umbilical zone is significantly deeper than wider. Internal flanks of the umbilical area are nearly flat and parallel, of an approximate width similar to the outer diameter of the proloculus.

Remarks: This species was commonly illustrated from England by Strank (1981: pl. 75, fig. 5, pl. 84, fig. 12, pl. 87, figs. 18, 23, pl. 88, fig. 13) as *Howchinia bradyana*, and from Algeria by Sebbar (2000: pl. 13, fig. 6) as *Howchinia* sp. It differs from *Howchinia bradyana* by a poorer development of the hyaline layer in the spire, a more acute apical angle, and smaller size for a similar number of whorls. It differs from *Howchinia* nov. sp. 5 by a wider apical angle, and the deep umbilical area with parallel internal flanks. It differs from *Howchinia* nov. sp. 3 by a narrower umbilical area, more acute apical angle and a smaller size for a similar number of whorls.

Howchinia subconica (Brazhnikova and Yartseva, 1956)

Fig. 7 (20–22)

Description: Test of large size, moderately high conical spire, medium-sized proloculus (only sectioned in one specimen; Table 2). The initial whorls form a slight apical angle with the proloculus, and the flanks are convex with strong deviations of some whorls in the mature specimens. Microgranular layer well developed, progressively but slowly thicker, and separated by a hyaline layer, well developed and thicker than the microgranular layer. Wide and deep umbilical area, with a similar truncated conical shape as the outer morphology of the test. Hyaline infilling covering completely the umbilical area.

Remarks: It differs from *Howchinia subplana* by the conspicuous apical angle and the irregularities in some whorls, with flanks that can show also some deviations between the whorls.

Howchinia subplana (Brazhnikova and Yartseva, 1956)

Fig. 7 (17–19)

Description: Low truncated conical test of medium size and proloculus (Table 2). The apical zone contains several whorls flat or slightly convex, and the flanks are convex. Microgranular layer is well developed from the inner whorls. Hyaline layer well developed in the spire, of the same thickness or even thicker than the microgranular layer. Hyaline material is well developed in the umbilical area, filling it completely.

Remarks: The wide flat apical area composed of several planispiral whorls allows to distinguish *Howchinia subplana* from most other species of *Howchinia*, except for *H. cantabrica* (see remarks on this species).

Howchinia variabilis nov. sp.

Fig. 6 (18–21, ?22–?23)

1991. *Monotaxinoides subplana* Brazhnikova and Yartseva (sic) – Marfenkova, pl. 8, fig. 18 [only].

1991. *Monotaxinoides subconica* Brazhnikova and Yartseva (sic) – Marfenkova, pl. 8, fig. 21.

Derivation of the name: Due to the variable arrangement of some whorls.

Material: Holotype VS 1348 (Fig. 6.21), and 7 paratypes (Fig. 6 (18–20)) and 2 specimens attributed to this species with question mark (Fig. 6 (22–23)) (Table 2).

Type locality and horizon: Vegas de Sotres section, sample (VSF-14h), early Serpukhovian.

Occurrence: This species is only known in the Serpukhovian part of the Vegas de Sotres section and Kazakhstan.

Diagnosis: Small flattened conical test, angular apical area, with irregular flanks due to the rapid growth of the lumen from the third or fourth whorl. Well developed microgranular layer, and poor development of the hyaline layer in the spire and umbilical area.

Description: Small flattened test in a low conical axial section. Medium proloculus, with a inner diameter 20-33 µm. Apical angle between the juvenile whorls and the proloculus. Flanks are irregular, concave or convex, exceptionally nearly flat (Fig. 6.20). This irregularity in the flanks is due to an increase in the width of the lumen observed from the third whorl. However, the height of the lumen does not grow proportionally to the width. Microgranular wall thin, more or less uniform in thickness and separated by a poorly developed hyaline layer. Umbilical area wide and not uniformly filled by hyaline material, in some cases with concave shape, and covering only a few whorls, and in most cases it reaches up to the final whorl, but it does not cover completely the umbilical area.

Remarks: Some specimens (Fig. 6 (22–23)) show a different shape of the test, much more hemispherical, and thus, its inclusion in this species can be also questioned. However, from the third whorl, irregular growths of the lumen in width are observed, used for the attribution of the specimens to this species. Another species with irregularities in the flanks is recorded, *Howchinia* nov. sp. 4 (Fig. 6.17), although it contains a larger proloculus, better development of the hyaline layer in the spire, and a larger size than *H. variabilis*.

Howchinia nov. sp. 1

Fig. 6 (3–4)

1988. *Howchinia* primitive – Laloux, pl. 1, fig. 3.

1993. *Vissariotaxis exilis compressa* (Brazhnikova) – Vdovenko in Makhlina et al., pl. 18, fig. 24.

2004. *Vissariotaxis* transitional to *Howchinia* – Cózar, pl. 1, fig. 20.

Description: Moderate conical test, flanks are slightly convex, widening progressively, and convex apical area. The number of whorls is low (3.5-5.5). Sutures between the whorls can be depressed. The microgranular layer is well developed from the first whorl, and its thickness increases progressively up to the final whorls. The hyaline layer is poorly developed although present, about 1/4 of the thickness of the microgranular layer. The umbilical area is wide, also with conical shape, and poorly covered by hyaline infilling, which does not extend to the final whorl.

Howchinia nov. sp. 2

Fig. 6 (1–2)

1999. *Howchinia longa* (Brazhnikova) – Cózar and Rodríguez, pl. 2, fig. 6.

Description: Small cylindrical test (Table 2), with the flanks flat and parallel; the first whorl is arranged at 90° in relationship with the giant proloculus, the second and subsequent whorls are disposed also at approximately 90° from the first whorl. The total number of whorls is low to moderate (5-6), with depressed sutures. The microgranular layer is well developed from the first whorl and its thickness increases progressively but slowly up to the final whorls. The hyaline layer in between the microgranular layer is poorly developed, although present. The umbilical area is narrow, even narrower in between the final whorls than close to the proloculus due to the lateral increase of the lumen in the final whorls. This umbilical area (only observed in two specimens) seems not to contain hyaline infilling, and the microgranular layer of the final whorls seems to be directly in contact, closing completely the umbilical zone.

Remarks: Despite the short synonymy, the species is relatively common in unpublished thesis works. It can be found in France by Vachard (1974: pl. 27, figs. 9-12, as *Monotaxinoides* cf. *subcarbonicus*), or Pille (2008: pl. 45, figs. 40-42, as *Howchinia*? sp.; and pl. 45, fig. 22 as *Hemidiscopsis caprariensis*), as well as in England by

Strank (1981: pl. 13, fig. 9, as *Vissariotaxis* transitional to *Howchinia*; pl. 60, fig. 5, as deformed *Howchinia* sp.), and White (1992: pl. 3.20, fig. G, as 'extended' *Howchinia*).

Specimens of the Montagne Noire can be compared with those from the Vegas de Sotres, because the size of the proloculus and poor development of the hyaline layer is characteristic in both cases. They were interpreted as immature *Howchinia* or *Vissariotaxis* by Pille (2008). However, there is no other species of those genera with such a large proloculus, although the inner diameter of the proloculus in the specimens from the Montagne Noire is slightly lower (33-40 μm) than in the Vegas de Sotres section (40-50 μm). In general, all the dimensions are slightly lower in the specimens from the Montagne Noire than in Vegas de Sotres, but they do not seem significant enough as to be considered as two independent species. Other specimens from England or Southwest Spain are of similar parameters as those from the Vegas de Sotres section.

Howchinia nov. sp. 3

Fig. 8 (1-4)

1956. *Monotaxis gibba* (Moeller) – Brazhnikova and Yartseva, fig. 1.2.

1964. *Howchinia gibba* (Moeller) – Conil and Lys, pl. 14, fig. 264.

?. 1967. *Howchinia gibba* (Moeller) – Brazhnikova et al., pl. 15, fig. 9.

2010. *Howchinia* sp. – Cózar et al., fig. 4e.

2013. *Howchinia cummingsi* Hallett – Cózar and Somerville, fig. 6g.

Description: Test of medium size (Table 2), with flat apical area composed of the first two or three whorls, and convex flanks. Proloculus is not observed in the recorded specimens. Low to moderate number of whorls (5-7). Lumen grows slowly in height from one whorl to another, and more rapidly in width, thus in the final whorls the lumen is wider than high. Microgranular layer grows markedly but progressively, being 4 or 5 times thicker in the final whorls than in the inner whorls. Hyaline layer in the spire thickens progressively, being of similar thickness as the microgranular layer in the final whorls. The umbilical area is wide, with well developed hyaline infilling, with concave shape at the base or that does not cover completely the umbilical area.

Remarks: It differs from *Howchinia* nov. sp. 1 by a larger size, better development of the microgranular and hyaline layers, wider umbilical area, and flat apical area. Owing to its general shape, the species is also close to *H. gibba*, from which it differs by smaller dimensions for similar number of whorls, more flattened apical area, and a less development of the hyaline layer in the spire and umbilical area.

In England, the species was illustrated as *Vissariotaxis* aff. *cummingsi* and *Howchinia bradyana* by Strank (1981: pl. 60, fig. 11, pl. 84, fig. 9, pl. 87, figs. 16, 19).

Howchinia nov. sp. 4

Fig. 6.17

Description: Irregular conical test, with 7 whorls in a low conical shape, with irregularities in the arrangement of the successive whorls, and the final whorl, entirely displaced, and situated in a side, in the umbilical area. Large size with a low apical angle between the proloculus and the tubular chamber. Flanks are concave in the inner whorls and convex in the final ones. Microgranular and hyaline layers in the spire are well developed, uniform, only slightly thicker in the final whorls, and approximately of similar thickness. Hyaline infilling does not cover completely the umbilical area. Lumen grows progressively in height, but more rapidly in width. Umbilical area is irregular due to the displaced position of the final whorl.

Remarks: Only one specimen has been recorded in this species, which might be attributed to pathology.

Owing to the irregularities in the arrangement of some whorls it could be related to *H. variabilis*, from which it differs by a larger size for equivalent number of whorls and a better development of the hyaline layer in the spire in between the microgranular layers.

The most similar species is *H. plana*, although it does not present an irregular coiling and the development of the hyaline layer in the spire is poorer.

Howchinia nov. sp. 5

Fig. 6 (8-9)

1967. *Howchinia* sp. – Brazhnikova et al., pl. 17, fig. 13.

1980. *Howchinia* sp. – Conil et al., pl. 14, fig. 19.

1989. *Howchinia* sp. A – Ueno, pl. 7, fig. 15.

2009. *Howchinia bradyana* (Howchin) – Nikolaeva et al., pl. 1, fig. 43.

2013. *Howchinia* sp. A – Cózar and Somerville, fig. 6b.

Description: High conical test, large size (Table 2), with a highly acute apical angle between the early whorls and the proloculus. Flanks are striking, widening progressively. Axial section is nearly triangular. The number of whorls is high, up to 11. Microgranular and hyaline layers in the spire are well developed, uniform, only slightly thicker in the final whorls, and approximately of similar thickness. Hyaline infilling is observed in the entire umbilical area, in two specimens with pseudo-pillars. Lumen grows progressively in height, but more rapidly in width, thus in the final whorls, it shows a nearly rectangular shape. Umbilical area is also triangular-shaped in axial section, although less marked than the external shape.

Remarks: This species share many parameters with *H. bradyana*, from which it can be distinguished by the more triangular shape of the test and umbilical area as well as the more subquadratic shape of the lumen, and smaller size for similar number of whorls.

Owing to its larger size and higher number of whorls than *Howchinia sotrensis*, it could be proposed that *H. nov. sp. 5* is the mature growth stage of the former species. However, the shape of the umbilical area and the development of the hyaline layer in the spire are distinct in both species.

Genus *Monotaxinoides* Brazhnikova and Yartseva, 1956

Type species: *Monotaxinoides transitorius* Brazhnikova and Yartseva, 1956

Diagnosis: Test planispiral or slightly conical. Wall bilayered, with an inner microgranular layer and an outer hyaline layer. Hyaline infilling in the umbilical area. Aperture simple, at the end of the tubular chamber.

Monotaxinoides gracilis (Dain in Reitlinger, 1956)

Fig. 9 (4–11)

Description: Small planispiral test, composed of a moderate number of whorls (up to 7) (Table 3). The tubular chamber grows symmetrically in relationship with the coiling axis, and the test is nearly biconcave on both sides. Displacements of the successive whorls are rare, although present in the final whorl of some specimens. Proloculus of medium size. Microgranular and hyaline layers well developed. The hyaline infilling also well developed in the umbilical area, which corresponds to the less concave side of the test.

Genus *Planohowchinia* Cózar and Mamet, 2001

Type species: *Planohowchinia espielensis* Cózar and Mamet, 2001

Diagnosis: The coiling is planispiral to slightly trochospiral, with irregularities in the coiling axis. The wall is two-layered, with an inner microgranular layer and an outer hyaline layer covering all whorls. This thin hyaline layer separates the successive whorls, and in the umbilical area it covers the side of the microgranular layer, not filling this area. Simple main aperture and secondary elongated apertures are present along the sutures between the whorls.

Remarks: It differs from *Eolasiodiscus* and *Monotaxinoides* by the absence of hyaline material filling the umbilical area, and in addition *Monotaxinoides* has no well-defined secondary apertures along the suture.

Planohowchinia nov. sp. 1

Fig. 9 (1–3)

Description: Small discoidal or very low conical test (Table 3), with planispiral coiling in all the inner whorls, and in the mature specimens, a deviation of the coiling axis in the final whorl, which in some specimens is disposed laterally. Diameters range from 130 up to 400 μm , height from 30 to 100 μm , although, owing to the deviation of the final whorls, total height may reach up to 150 μm . Number of whorls moderate (up to 6.5). The proloculus is not intersected in any specimen. The width of the tubular chamber is usually larger than its height. Wall is bilayered, where the microgranular layer of the wall is well developed, with thickenings at the base of the lumen, and it is covered by a uniform hyaline layer, poorly developed or it may reach similar thickness as the microgranular layer. Pits in the sutures are observed in oblique sectioned specimens.

Remarks: It differs from *Planohowchinia espielensis* by a smaller size for similar number of whorls, less pronounced thickenings of the microgranular layer, lumen wider than higher, more discoidal tests with absence or poorer development of the umbilici of the tests.

It differs from *Planohowchinia? rara* Pille, 2008 (nomen nudum) by the smaller size (nearly half) and the discoidal shape. This species was questionably attributed to the genus by Pille (2008) due to its conical shape. The features of the wall are similar to those in *Planohowchinia*, although her single specimen (thin-section DV314D, late Asbian, near Roquessels, D. Vachard's collection, Lille) does not allow the observation of the secondary apertures. Another specimen from the Montagne Noire was published by Mamet (1968) in outcrops close to Vailhan, and assigned to the Brigantian. The latter is also a conical specimen, in which, secondary apertures could not be observed.

4. Evolution of the Lasiodiscidae in the Vegas de Sotres section (P. Cózar)

The Vegas de Sotres section is an excellent time slice to study some of the ancestral genera and species of the family Lasiodiscidae. Unfortunately, the geological record in that section seems to be too young for the occurrence of *Vissariotaxis*, which is considered herein the ancestral stock of the family, as for most authors (e.g., Vachard and Beckary, 1991; Kulagina, 2001; Pille, 2008). In contrast, Loeblich and Tappan (1988) and Pinard and Mamet (1998) assigned the genus *Vissariotaxis* to the family Tetrataxidae. The genus has been documented in the Namurian (Loeblich and Tappan, 1988), but it is extremely rare or absent above the lower part of the early Brigantian.

Owing to the morphological similarity with the transitional forms to *Howchinia*, it is interpreted that *Howchinia* nov. sp. 1 was derived from *Vissariotaxis exilis* (Vissarionova, 1948) in the early Asbian (Fig. 10), when both species co-existed (Laloux, 1988). It could be questioned if *Howchinia* nov. sp. 2 is a true *Howchinia*, although due to the presence of the incipient hyaline layer, here, this character is considered as typical of *Howchinia*. *Howchinia* nov. sp. 2 is interpreted as being derived from *Howchinia* nov. sp. 1, also in the early Asbian.

From the late Asbian, *Howchinia* with a well-developed hyaline layer occurs. The most primitive species is considered to be *Howchinia sotrensis*, from which, *H. bradyana* rapidly evolved also in the upper part of the late Asbian (Jones and Somerville, 1996). In this lineage, there is no further evolution up to the late Brigantian, when some specimens of *Howchinia* nov. sp. 5 are recorded (Fig. 11). Those specimens with a triangular shape probably arose from the more triangular forms of *H. bradyana*.

In contrast to Kulagina (2001), *Howchinia gibba* is considered herein as an independent lineage from that in *H. bradyana*. According to the phylogenetic scheme (Fig. 11), it is possible that the most primitive forms could be assigned to *Howchinia* nov. sp. 3 (Brazhnikova and Yartseva, 1956: fig. 1), which is considered to be present from the early Asbian, and taking into consideration its morphological characters, it is similar to *H. gibba*, but with a more rudimentary development of the hyaline and microgranular layers. This evolutionary step for the development of large true *H. gibba* is well established for the base of the Brigantian in Britain and Ireland (Cózar and Somerville, 2004; Somerville and Cózar, 2005), although it could be inferred that this step was recorded in the uppermost late Asbian, where some specimens of *H. gibba* might be present. However, because of the complex synonymy of *H. gibba* and *H. bradyana* (Appendix), where a significant confusion exists between these two species, it is difficult to know the precise first occurrence of those species.

Howchinia hemisphaerica is interpreted as another direct descendant from *H. nov. sp. 3*, where the development of the microgranular and hyaline layers in the spire still show primitive characteristics. This evolution occurred in the late Brigantian, or currently Serpukhovian (Fig. 11), although due to the rarity of this species, it is not precise enough. In the Vegas de Sotres section, the first *H. hemisphaerica* is recorded 10 cm below the first occurrence of *Lochriea zieglerei* (Fig. 4). In slightly younger levels in the section is observed the highest diversification in the genus *Howchinia*, all above the occurrence of that index conodont marker, but very close to it. Up to five new species of *Howchinia* are recorded, which notably complicate the reconstruction of its phylogeny. Two distinct tendencies seem to exist; the first lineage characterized by the well-developed microgranular layer separated also by a well-developed hyaline layer in the spire, and the second lineage, characterized by a poorly-developed hyaline layer separating the microgranular layer in the spire. In the first lineage and owing to the first occurrences in the Vegas de Sotres section, *Howchinia beleutensis* arose from *Howchinia gibba* (Fig. 11). Direct descendants from *H. beleutensis* seem to be *H. convexa* and *H. subplana*. Only the latter seems to have descendants, with *H. subconica* and *H. enormis*, although the first occurrences of those species are nearly synchronous. On the other hand, *H. hemisphaerica* is considered the direct ancestor of a second lineage with a poor hyaline layer in the spire. Similar to the first lineage, the general tendency is to more

flattened tests, nearly discoidal, in which the most probable phylogeny is *H. hemisphaerica* → *H. acutiformis* → *H. cantabrica* → *H. variabilis* → *H. plana* (Fig. 11).

The former lineage is interpreted to be the most significant for this period, because one of those species (*Howchinia enormis*) is considered as the ancestor of *Monotaxinoides* (Fig. 10). Within the *Monotaxinoides*, the first well-known species is *Monotaxinoides gracilis*, as already proposed by Vachard and Beckary (1991). The most probable ancestor species is *Howchinia enormis*, although intermediate *Howchinia* exist between *H. subplana* and *M. gracilis* in the Vegas de Sotres section. Higher in the succession is recorded the first occurrence of *M. transitorius*, which seems to be derived from *M. gracilis*. Thus, for the Serpukhovian, the complete lineage seems to be *H. enormis* → *M. gracilis* → *M. transitorius* (Fig. 10).

The evolution of *Eolasiiodiscus* is not as clear as that for *Monotaxinoides*. Traditionally, the genus *Eolasiiodiscus* was supposed to be derived from *Monotaxinoides* (e.g., Reitlinger, 1956), although currently, this hypothesis is not supported. The main argument against this phylogeny is the first occurrence of *Eolasiiodiscus*, from the lower part of the early Serpukhovian in Russia (Kulagina, 2001; Kulagina and Gibshman, 2002; Kulagina et al., 2003, 2009, 2011). In contrast, the first *Monotaxinoides* occurs in slightly younger levels and *M. transitorius* from the late Serpukhovian (e.g., Kulagina et al., 2003). Kulagina (2001) proposed that *Eolasiiodiscus* arose directly from *Vissariotaxis*. Pille (2008) adopted this hypothesis but suggested that *Hemidiscopsis* might bridge between these two genera. The latter hypothesis is considered as more appropriate, in the lineage *Vissariotaxis* → *Hemidiscopsis* → *Eolasiiodiscus*. In particular, the species involved in that phylogeny could be *Vissariotaxis exilis* → *Hemidiscopsis? declivis* → *H. caprariensis* → *H.? nov. sp. 2* → *Eolasiiodiscus donbassicus* (Fig. 10). This lineage is characterized by a change from conical to discoidal tests and a decrease in the hyaline layer in the whorls and umbilicus. It is not clear which species could be the direct ancestors of *H. priscus*, but it could be suggested that the *H. priscus* arose also from *H. caprariensis*.

There is still a puzzling role of the genus *Planohowchinia* within these phylogenetic lines. As proposed by Cózar and Mamet (2001), it could be an endemic form to the western extreme of the Palaeotethys and with a parallel evolution from the main lineages (Fig. 10).

5. Biostratigraphic relationship of the Lasiiodiscidae with the Viséan/Serpukhovian boundary in the Vegas de Sotres section

It is necessary to highlight the relative deep-water facies studied in the Vegas de Sotres section, and up unit 3, shallow-water facies are not recorded. Assemblages are thus facies controlled, and a typical suite of shallow-water platform foraminifers are virtually not recorded, except for some individual beds in the uppermost part of the section. Some well-known foraminiferal markers for the Serpukhovian in other basins [e.g., *Paramillerella tortula* (Zeller, 1953), *Janischewskina delicata* Malakhova, 1956; *Neoarchaediscus postrugosus* (Reitlinger, 1949); *Pseudoendothyra globosa* Rozovskaya, 1963] are rare and randomly distributed through the section. Taking into consideration the facies control on the shallowest-water foraminifers, the conodonts are the main tool for the biostratigraphic calibration, although they are not free of facies control.

However, the use of conodonts may lead to confusion between the currently valid Viséan/Serpukhovian boundary, and the proposal in progress on the International Subcommission on Carboniferous Stratigraphy (Richards, 2005) for the establishment of the base of the Serpukhovian at the first occurrence of *Lochriea ziegleri*. This conodont first occurs in intermediate positions in the Venevian Substage (Alekseev in Skompski et al., 1995; Gibshman et al., 2009) or close to the base of the late Brigantian (e.g., Varker in Skompski et al., 1995), or even in the early Brigantian (Sevastopulo and Barham, 2014). The references to the Viséan/Serpukhovian boundary are here based on the first occurrence of *L. ziegleri* in the Vegas de Sotres section (Fig. 12), and consequently in the new proposed horizon for the worldwide correlation.

The first occurrence of *L. ziegleri* is situated in the conodont sample VSC-1B3 (= as foraminifer sample VSF/0 in Fig. 3), but specimens are very rare (1 specimen per five kilos of rock processed) in the early range recorded in the section, from approximately the base of the late Brigantian or the proposed early Serpukhovian. Close to this boundary bed, the occurrence of some species of *Howchinia* is noteworthy. In a sample 10 cm below that boundary can be highlighted the first occurrence of *Howchinia hemisphaerica* (Fig. 12). It is also noteworthy for the occurrence of *Howchinia nov. sp. 4*, although this occurrence cannot be properly validated because only a single specimen has been recorded of this species.

Approximately 1-2 metres above the first occurrence of *L. ziegleri*, occurs nine species of *Howchinia*, and they can be used potentially in recognizing the Viséan/Serpukhovian boundary elsewhere (Fig. 12). Particularly,

the sequence of first occurrences consists of *H. beleutensis* - *H. subplana* (about 1.33 m above the first occurrence of *L. ziegleri*), *H. acutiformis* (at 1.40 m), *H. subconica* (at 1.60 m), *H. enormis* (at 1.78 m), *H. variabilis* - *H. cantabrica* (at 1.82 m), *H. plana* (at 2.33 m), and *Howchinia* nov. sp. 5 (at 2.54 m).

Pseudo-pillars are observed in specimens of *Howchinia gibba*, *H. bradyana* and *H. beleutensis* and *H. convexa* but not in others in the Vegas de Sotres section (Figs. 4, 12, , Table 2). All those specimens are recorded in the Serpukhovian part of the section, which suggests that it might be a modification in Serpukhovian times, but affecting different species, and thus, it should be considered as an intra-specific variation. In the literature, pseudo-pillars are also observed in specimens of *H. subplana* and *H. enormis* (e.g. see Lys, 1985), all of them in Serpukhovian rocks in a traditional sense. The oldest records of pseudo-pillars seem to correspond to *Howchinia bradyana* in latest Brigantian rocks from Ireland (Cózar et al., 2005). Thus, taking into consideration the base of the Serpukhovian as the FOD of *L. ziegleri*, those rocks in Northern Ireland should be also considered as Serpukhovian, and correlated with the lower part of the Serpukhovian in Vegas de Sotres section.

The record of *Hemidiscopsis* is not abundant up to the middle part of the Vegas de Sotres section. *Hemidiscopsis?* nov. sp. 1, and *H. muradymicus* are first recorded below FOD of *L. ziegleri* together with *Lochriea nodosa* (Bischoff, 1957), whereas *H. caprariensis* is first recorded 1.68 m above the boundary. Taking into consideration the records of *H. caprariensis* in France during the early Brigantian, this species seems to occur also in older levels than the first occurrence of *L. ziegleri*. The evolution between these *Hemidiscopsis* species seems to occur before the FOD of *L. ziegleri*, although it cannot be confirmed owing to the rarity in foraminifers in this lower part of the Vegas de Sotres section, as well as its absence in the lower levels. However, biostratigraphy of the Montagne Noire in France are being currently revised, and most of the outcrops dated as early Brigantian could be reassigned to the late Brigantian. Specimens of *H. priscus* are recorded in higher levels of the section, from 2.7 m above the boundary, even common in level VSC-14f (5.2 m). The rare *Hemidiscopsis?* nov. sp. 2 first occurs at 2.08 m above FOD of *L. ziegleri*. In summary, the occurrences of different species of *Hemidiscopsis* are not closely related to the Viséan/Serpukhovian boundary as defined by the conodont index taxon.

The primitive *Monotaxinoides*, *M. gracilis*, is also recorded at 2.08 m above *L. ziegleri*, in younger beds than the significant species of *Howchinia*. In addition, *Eolasiodiscus donbassicus* occurs only from the upper part of the succession, far above the Viséan-Serpukhovian boundary in the Vegas de Sotres. The first occurrence of *E. donbassicus* is only used to recognize the Viséan/Serpukhovian boundary in the shallow-water facies of the Khudolaz and Bolshoi Kizil section in the South Urals (Kulagina et al., 2011), and thus, its use in other basins and other platform settings are difficult.

6. Conclusions

Systematic analysis of the lasiodiscid foraminifers in the Vegas de Sotres section allows to recognize diverse assemblages with twenty-six species assigned to five genera. The section spans an interval between the late Viséan and the late Serpukhovian. The most abundant genus is *Howchinia*, represented by 18 species, of which 6 species are known in the literature, 5 species are identified in open nomenclature, and 7 new species are described (*H. acutiformis*, *H. cantabrica*, *H. enormis*, *H. hemisphaerica*, *H. plana*, *H. sotrensis* and *H. variabilis*). Also abundant are the representatives of the new genus *Hemidiscopsis*, with up to 5 species. In addition are recorded abundant *Monotaxinoides*, but rarely, *Planohowchinia* and *Eolasiodiscus*.

A phylogenetic relationship between these genera is proposed, in most cases established due to the presence of intermediate taxa, but more rarely where their precise ancestors are questionable (Figs. 10-11). Thus, it is proposed (1) the primitive *Howchinia* auct., such as *Howchinia* nov. sp. 1 is an intermediate form between *Vissariotaxis* and *Howchinia*; (2) *Howchinia enormis* nov. sp. is a transitional form between *Howchinia* and *Monotaxinoides*; (3) *Hemidiscopsis? declivis* is transitional between *Vissariotaxis* and *Hemidiscopsis*; and (4) *Hemidiscopsis?* nov. sp. 2 is the transition between *Hemidiscopsis* and *Eolasiodiscus*. No transitional forms related to *Planohowchinia* are recognized, probably due to the rarity of the genus, and thus, it is assumed a direct evolution from *Howchinia* during the late Asbian, as proposed by Cózar and Mamet (2001). In addition, evolution between the different species of *Howchinia* and *Hemidiscopsis* are established on the basis of their stratigraphic records in the Vegas de Sotres section. Species of other genera (*Eolasiodiscus* and *Monotaxinoides*) are in agreement with similar phylogenesis proposed in the literature.

Biostratigraphically, some species of *Howchinia* can help potentially in recognizing the Viséan/Serpukhovian boundary, and are closely related to the first occurrence of the conodont *Lochriea ziegleri*

in the Vegas de Sotres section. Other traditional markers included in the genera *Monotaxinoides*, *Eolasiiodiscus*, and even species of the new genus *Hemidiscopsis* do not show such a close relationship with the first occurrence of *L. ziegleri*. *Howchinia hemisphaerica* first occurs in slightly older levels and *H. nov. sp. 4* at the same bed as that conodont. Nine species of *Howchinia* first occurs in slightly younger levels (*H. acutiformis*, *H. cantabrica*, *H. convexa*, *H. enormis*, *H. plana*, *H. subconica*, *H. subplana*, *H. variabilis* and *H. nov. sp. 5*).

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Appendix. Supplementary data

Supplementary information with a full list of synonymies of well-known species (Appendix) can be found in the online version at: <http://dx.doi.org/10.1016/j.geobios.2015.02>.

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Table 1. Measurements of the *Eolasiotus* and *Hemidiscopsis* specimens in the Vegas de Sotres section. Nw = number of whorls; iDp = internal diameter of proloculus.

Specimen	Sample	Number specimens	W/H ratio	Height (H) (microns)	Width (W) (microns)	Nw	iDp (microns)
<i>Eolasiotus donbassicus</i>							
VS 0553	VSF-19(1)	5	4-5.4	30-50	130-280	5-8	--
VS 0647	VSF-22(4)		5.25	40	210	8	--
VS 1548	VSF-24(8)		4.8	30	145	6	--
VS 1549	VSF-24(10)		4.6	50	230	8	--
VS 1585	VSF-24a(6-2)		4	40	160	5.5	--
VS 1609	VSC-11b(9)		--	--	280	6	--
			5.4	50	270	>6	--
<i>Hemidiscopsis caprariensis</i>							
VS 0021	VS-B-1(2)	59	2.5-7.2	22-60	110-270	3-6	20-32
VS 0173	VSC-2A1e(4)		7.2	22	160	4	28
VS 0201	VSF-2(3)		5	40	200	>4	--
VS 0484	VSF-16(2)		--	--	150	6	--
VS 0497	VSC-3A(1)		5.25	40	210	>3.5	--
VS 0540	VS-00(2)		4	30	120	4.5	--
VS 0628	VSF-21(4)		--	--	150	4.5	--
VS 0686	VSF-23(3)		2.5	50	125	4	20
VS 0829	VSC-11B(4)		5.6	30	170	4	--
VS 0975	VS-01(1)		4.8	50	240	>4	--
VS 1046	VSC-2A1a(9)		5.4	50	270	>5	--
VS 1047	VSC-2A1a(10)		4.6	30	140	3.5	>15
VS 1058	VSC-2A1d(6)		3.1	45	140	4	20
VS 1061	VSC-2A1d(10)		3.4	40	135	3	26
VS 1066	VSC-2A1e(9)		6.3	30	170	3.5	26
VS 1148	VSF-4e(5-1)		--	--	110	3.5	25
VS 1285	VSF-14e(5-1)		3.2	45	145	3.5	23
VS 1302	VSF-14R(1-1)		4	50	200	4	25
VS 1303	VSF-14R(1-1)		4	30	120	4	--
VS 1304	VSF-14R(1-1)		5	30	150	4	--
VS 1307	VSF-14R(2-1)		--	--	170	5	--
VS 1309	VSF-14R(3-1)		--	--	160	4.5	--
VS 1312	VSF-14R(4-2)		3.5	40	140	4	--
VS 1321	VSF-14g(1-1)		--	--	170	5	--
VS 1333	VSF-14b(1-1)		4.25	40	170	4	--
VS 1336	VSF-14b(2-1)		--	--	120	>3	--
VS 1338	VSF-14b(2-1)		4.4	35	155	>4.5	--
VS 1340	VSF-14b(3-1)		--	--	130	4	22
VS 1345	VSF-14b(6-1)		4.2	50	210	3.5	32
VS 1357	VSF-15(9)		5.25	40	210	3.5	>15
VS 1371	VSF-16(9)		5.3	30	160	5	--
VS 1375	VSC-3A(6)		5.5	40	220	>3.5	--
VS 1391	VSF-16a(2-1)		--	--	110	3	25
VS 1395	VSF-16a(3-1)		--	--	200	>4	--
VS 1396	VSF-16a(3-2)		--	--	180	5.5	--
VS 1419	VSF-16b(5-1)		--	--	170	>5	--
VS 1424	VSF-16c(1-1)		6	30	180	5?	--
VS 1437	VSF-16c(4-1)		4.3	35	150	>4	--
VS 1447	VSF-16c(5-1)		--	--	140	3.5	30
VS 1448	VSF-16c(5-2)		4	40	160	>4	--
VS 1464	VSF-16d(3-1)		3.4	50	170	>4	--
VS 1487	VSF-16e(6-1)		3.8	40	155	4.5	--
VS 1489	VSC-4(7)		5	40	200	5	--
VS 1497	VSF-17(10)		--	--	185	6	28
VS 1499	VSF-18(6)		4	40	160	4.5	20
VS 1518	VSF-20(8)		--	--	150	>4	--
VS 1527	VSC-6A(10)		--	--	140	6	--
VS 1537	VSC-6A(9)		--	--	150	5.5	--
VS 1607	VSC-11b(7)		3.75	40	150	>5	--
VS 1746	VSC-8top(8)		5.2	25	130	4	23
VS 1749	VSC-9(6)		--	--	130	4.5	24
VS 1750	VSC-9(8)		--	--	130	5	27
VS 2124	VSF-118		4	50	200	>5	--
VS 2141	VSF-119		3.17	60	190	>3.5	30
VS 2143	VSF-119		4	40	160	>4.5	--
VS 2145	VSF-119		--	--	150	3	--
VS 2151	VSF-119		4.8	30	145	5	24
VS 2154	VSF-120		--	--	150	4	20
VS 2160	VSF-120		--	--	160	>4.5	--
<i>Hemidiscopsis murdyimicus</i>							
VS 2025	VSF-102	7	2.4-6	50-100	120-540	2-6.5	35-40
VS 2038	VSF-104		5.25	80	420	5.5	35
VS 2054	VSF-107		2.4	50	120	2	35
VS 2059	VSF-109		4.75	70	330	4?	--
VS 2073	VSF-113		5.4	75	410	4?	--
VS 2113	VSF-117		5.4	100	540	6.5	40
VS 2148	VSF-119		6	60	360	6	--
			3.6	60	220	3	40
<i>Hemidiscopsis prisus</i>							
VS 0122	VSC-2A1b(4)	16	2.7-7	20-60	110-230	2.5-5	30-40
VS 0375	VSC-2A*(5)		2.9	55	160	3	30
VS 0693	VSF-24(1)		3.75	40	150	3	32
VS 0989	VS-01(1)		3.33	45	150	3	30
VS 1049	VSC-2A1b(10)		3.4	50	175	3.5	30
VS 1064	VSC-2A1e(8)		3.4	50	170	3.5	30
VS 1310	VSF-14R(3-2)		2.7	60	160	3.5	30
VS 1319	VSF-14R(6-1)		--	--	130	3.5	30
VS 1323	VSF-14g(1-2)		--	--	140	4	35
VS 1343	VSF-14b(5-1)		2.78	45	125	2.5	40
VS 1346	VSF-14b(6-1)		4.6	28	130	3	35
VS 1358	VSF-15(10)		2.73	55	150	3.5	30
VS 1383	VSF-16a(1-1)		3.78	45	170	2.5	40
VS 1390	VSF-16a(1-2)		--	--	110	2	--
VS 1496	VSF-17(8)		4.5	50	230	5	>25
VS 1587	VSC-6A*(6)		--	--	200	>4	--
			7	20	140	4	30
<i>Hemidiscopsis ? nov. sp. 1</i>							
VS 2075	VSF-114	1	5.5	90	470	5.5	40
<i>Hemidiscopsis ? nov. sp. 2</i>							
VS 0294	VSF-7(4)	2	5.3-5.6	60	320-340	6	--
VS 0777	VSC-6A*(1)		5.6	60	340	>6	--
			5.3	60	320	6	--

Table 3. Measurements of the *Monotaxinoides* and *Planohowchinia* specimens in the Vegas de Sotres section. Nw = number of whorls; iDp = internal diameter of proloculus.

Specimen	Sample	Number specimens	W/H ratio	Height (H)	Width (W)	Nw	iDp (microns)
				35-100 (microns)	150-390 (microns)		
<i>Monotaxinoides gracilis</i>							
VS 0174	VSC-2A1e(4)	31	3.6	55	200	4.5	--
VS 0175	VSC-2A1e(4)		3.2	60	190	4	--
VS 0295	VSF-7(5)		--	--	250	>4	--
VS 0298	VSF-7(5)		--	--	350	6	--
VS 0342	VSC-2A(4)		4	50	200	4	--
VS 0467	VSC-3(4)		4.4	70	310	6	--
VS 0492	VSC-3A(1)		4.2	35	150	4	23
VS 0664	VSC-6A(3)		3.7	70	260	>5	--
VS 0681	VSF-23(2)		--	--	270	>4	--
VS 0779	VSC-6A(4)		--	--	260	>3	--
VS 0781	VSC-6A(4)		4.2	50	210	5	--
VS 0976	VS-01(1)		3.4	70	240	5?	--
VS 1000	VS-01(3)		3.6	80	290	6	--
VS 1040	VSC-2A1a(7)		3.25	40	130	3	24
VS 1059	VSC-2A1d(6)		3.5	80	280	>4	--
VS 1311	VSF-14f(3-2)		3.6	40	145	5	25
VS 1313	VSF-14f(5-1)		5.2	70	370	7	--
VS 1324	VSF-14g(2-2)		5.2	50	260	>5	--
VS 1329	VSF-14g(3-2)		3.7	100	370	6.5	28
VS 1350	VSC-3(10)		--	--	390	>5	--
VS 1367	VSF-16(7)		4	70	280	>6	--
VS 1368	VSF-16(7)		--	--	530	>6	--
VS 1408	VSF-16b(1-1)		4.1	55	230	4.5	30
VS 1435	VSF-16c(3-1)		5	50	250	4.5	--
VS 1470	VSF-16d(6-1)		3.6	60	200	4	--
VS 1483	VSF-16e(4-2)		4.6	50	230	>4	--
VS 1515	VSC-5(9)		--	--	360	--	--
VS 1542	VSF-23(8)		3.5	55	190	5.5	>20
VS 1573	VSF-24a(5-1)		3.6	70	250	5.5	30
VS 1594	VSC-6A(10)		--	--	280	>5	--
VS 2094	VSF-116		4.7	80	380	6.5	--
<i>Planohowchinia</i> nov. sp. 1							
VS 1109	VSF-4a(4-2)	8	2.13-4.5	30-150	130-400	4-6.5	--
VS 1325	VSF-14g(2-2)		4.33	30	130	4	--
VS 1327	VSF-14g(3-1)		--	--	360	--	--
VS 2057	VSF-109		--	--	320	6	--
VS 2076	VSF-115		4.5	40	180	>4	--
VS 2077	VSF-115		2.13	150	320	>4	--
VS 2085	VSF-115		2.33	150	350	6.5	--
VS 2150	VSF-119		2.66	150	340	6	--
		3.63	110	400	>6	--	

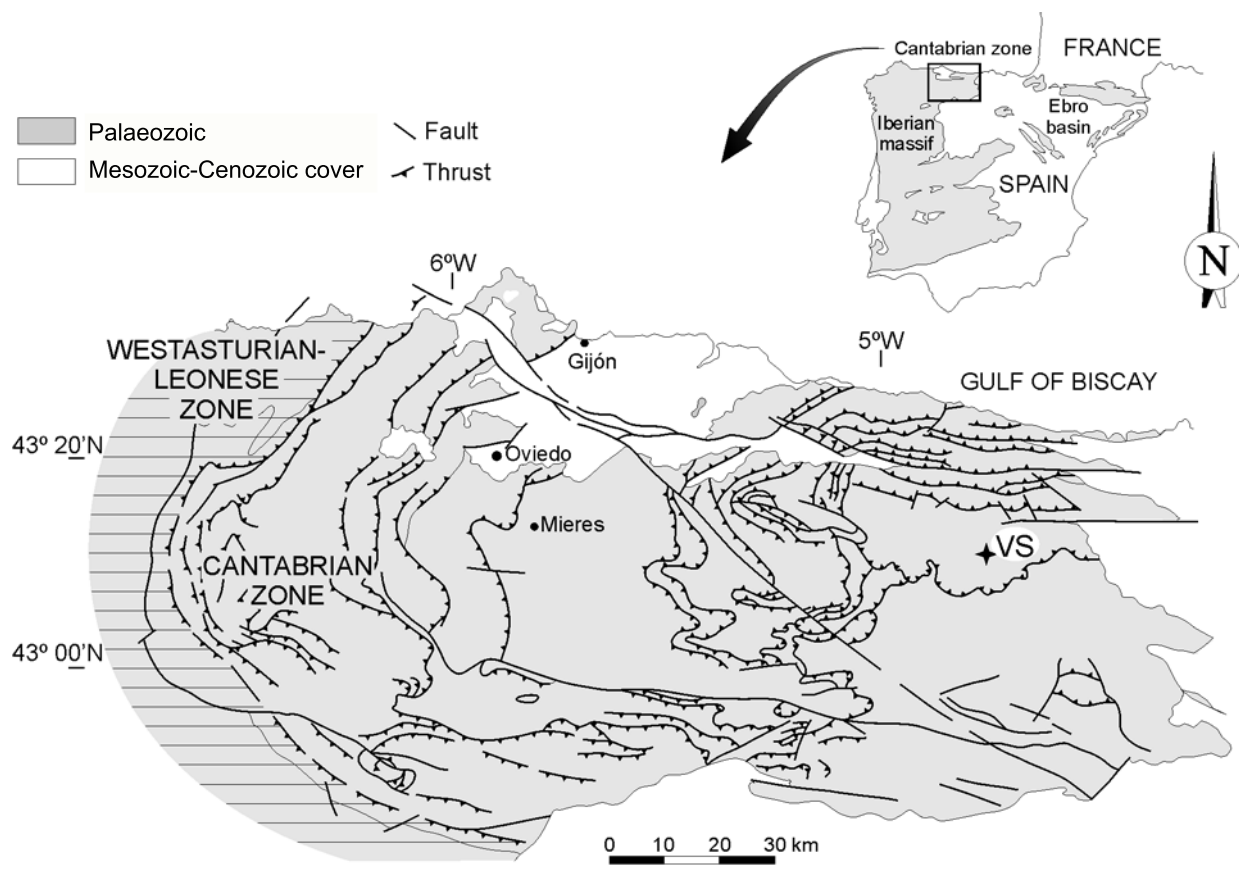


Figure 1. Geological sketch map of the Cantabrian Zone with the location of Vegas de Sotres section (VS).

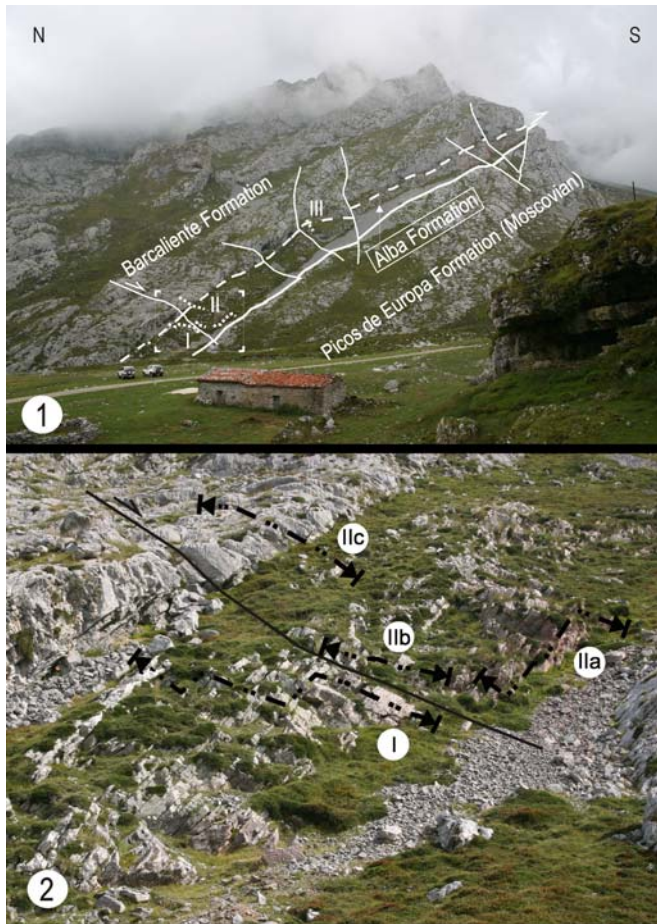


Figure 2. 1. Panoramic picture of the right slope of the Duje River valley with the location of the partial stratigraphic sections that form the Vegas de Sotres section. The Alba Formation rocks crops out between the Variscan thrust fault and the lower boundary of the Barcaliente Formation. 2. Detail of the location of the partial sections I, IIa, IIb and IIc.

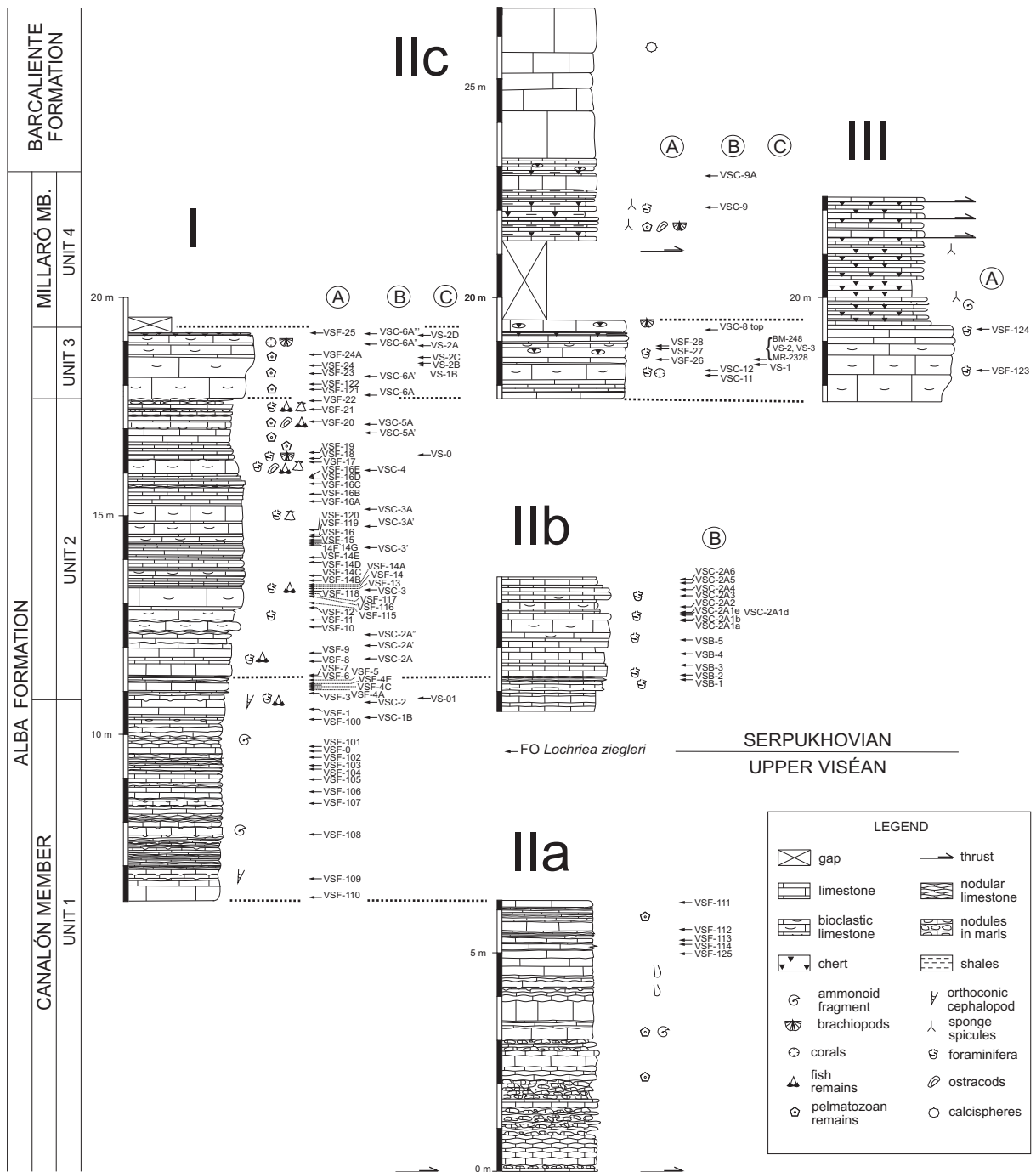


Figure 3. Composite stratigraphic Vegas de Sotres section with the location of the foraminifer samples. The short individual sections I to III, are located in Fig. 2. Dotted lines are the correlation levels between the individual sections established through conodont correlation. Periods of sampling is divided into (A) most recent and detailed sampling, (B) an older period of collection together with conodont sampling and (C) samples studied in Blanco-Ferrera et al. (2008).

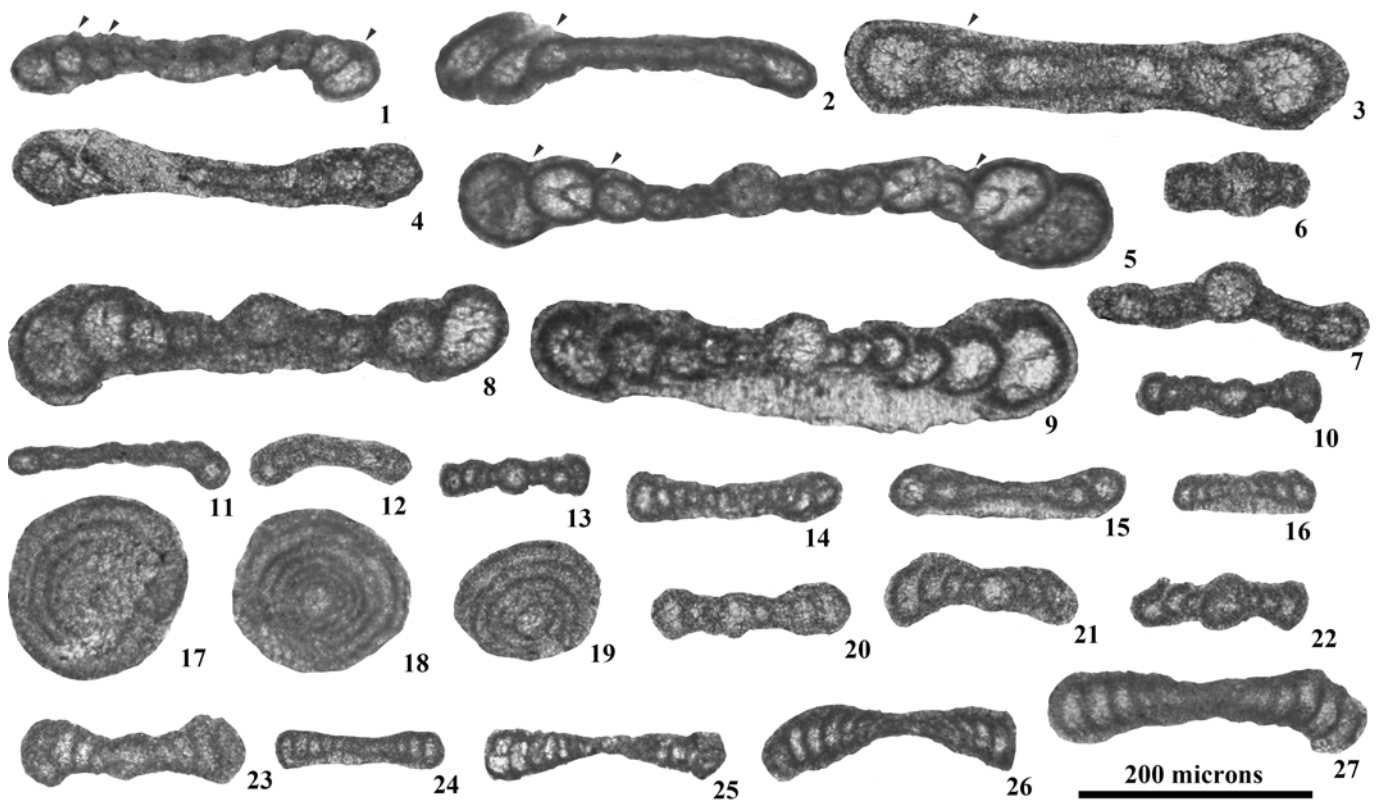


Figure 5. 1-2. *Hemidiscopsis?* nov. sp. 2, sutural spines highlighted with arrows, 1. specimen VS 0777, sample VSC-6A", 2. specimen VS 0294, sample VSF-7. 3-8. *Hemidiscopsis muradymicus* (Kulagina in Kulagina et al., 1992) nov. comb., sutural spines highlighted with arrows, 3. specimen VS 2059, sample VSF-109, 4. specimen VS 2113, sample VSF-117, 5. specimen VS 2073, sample VSF-113, 6. juvenile, specimen VS 2038, sample VSF-104 7. juvenile, specimen VS 2148, sample VSF-119, 8. specimen VS 2035, sample VSF-102. 9. *Hemidiscopsis?* nov. sp. 1, specimen VS 2075, sample VSF-114. 10-18. *Hemidiscopsis caprariensis* (Vachard, 1977) nov. comb., 10. specimen VS 1497, sample VSF-17, 11. specimen VS 1487, sample VSF-16e, 12. specimen VS 1046, sample VSC-2A1a, 13. specimen VS 1607, sample VSC-11b, 14. specimen VS 1419, sample VSF-16b, 15. specimen VS 0173, sample VSC-2A1e, 16. specimen VS 0628, sample VSF-21, 17. specimen VS 1307, sample VSF-14f, 18. specimen VS 1749, sample VSC-9. 19-23. *Hemidiscopsis priscus* (Braznikova and Yartseva, 1956) nov. comb., 19. specimen VS 1310, sample VSF-104. 20. specimen VS 1049, sample VSC-2A1b, 21. specimen VS 1064, sample VSC-2A1e, 22. specimen VS 0375, sample VSC-2A", 23. specimen VS 0989, sample VS-01. 24-27. *Eolasiiodiscus donbassicus* Reitlinger, 1956, 24. juvenile, specimen VS 0647, sample VSF-22, 25. specimen VS 0553, sample VSF-19, 26. specimen VS 1548, sample VSF-24, 27. specimen VS 1609, sample VSC-11b.

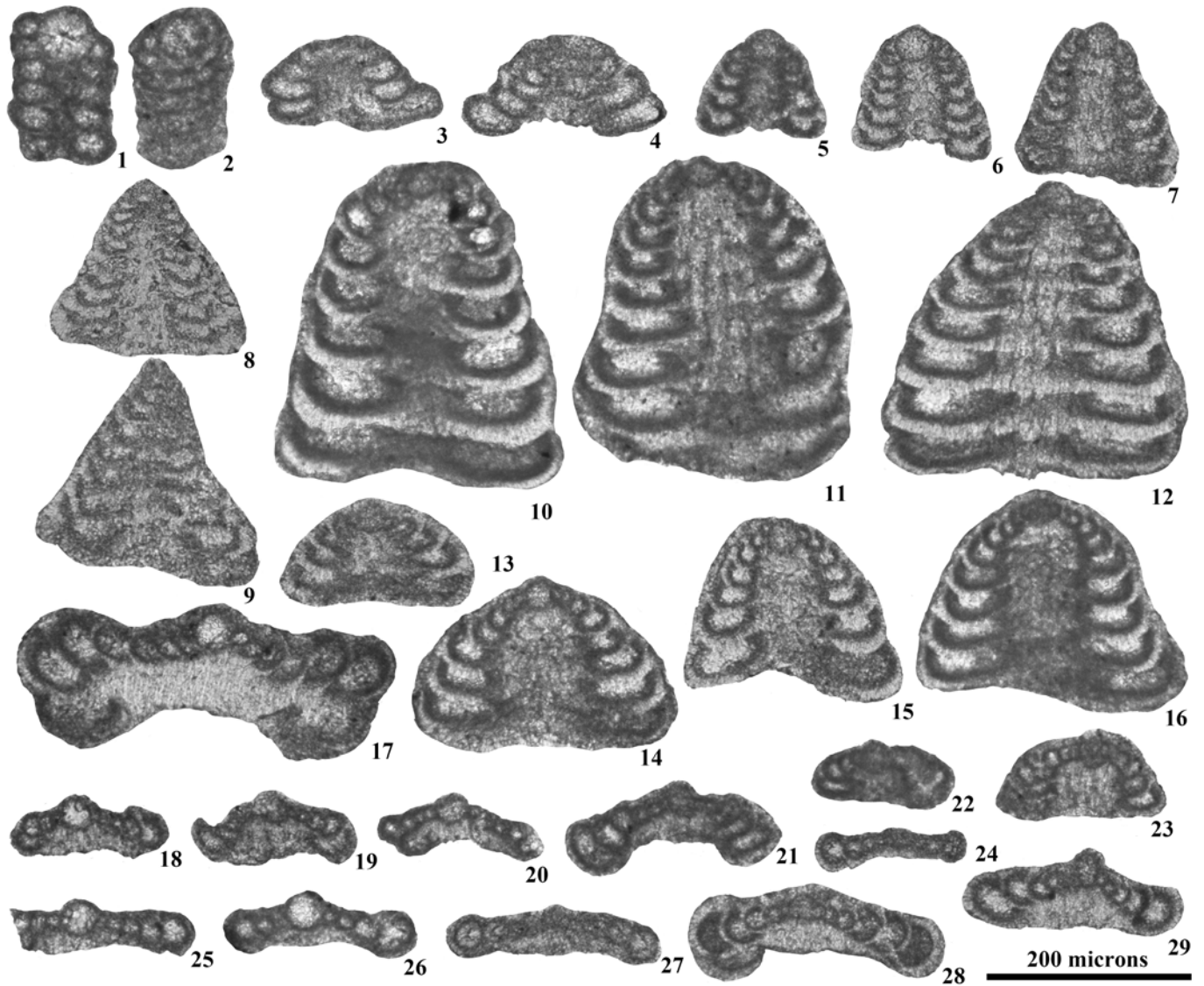


Figure 6. 1-2. *Howchinia* nov. sp. 2, 1. specimen VS 2047, sample VSF-106, 2. oblique section, specimen VS 2053, sample VSF-107. 3-4. *Howchinia* nov. sp. 1, 3. specimen VS 0626, sample VSF-21, 4. specimen VS 2014, sample VSF-103. 5-7. *Howchinia sotrensis* nov. sp., 5. paratype, specimen VS 0372, sample VSC-2A", 6. paratype, specimen VS 0302, sample VSF-8, 7. holotype, specimen VS 0473, sample VSF-15. 8-9. *Howchinia* nov. sp. 5, 8. specimen VS 1027, sample VSB-4, 9. specimen VS 0313, sample VSF-9. 10-16. *Howchinia bradyana* (Howchin, 1888) emend. Davis, 1951, 10. specimen VS 1153, sample VSF-4d, 11. pseudo-pillars well developed, specimen VS 0541, sample VS-00, 12. pseudo-pillars well developed, note the more triangular shape, specimen VS 1469, sample VSF-16d, 13. juvenile, specimen VS 0680, sample VSF-23, 14. juvenile specimens with development of pseudo-pillars, specimen VS 0262, sample VSF-5, 15. juvenile specimen, specimen VS 0240, sample VSF-3b, 16. juvenile specimen, specimen VS 1154, sample VSF-4d. 17. *Howchinia* nov. sp. 4, specimen VS 1069, sample, VSF-0. 18-21. *Howchinia variabilis* nov. sp., 18. juvenile, paratype, specimen VS 1286, sample VSF-14c, 19. paratype, specimen VS 1306, sample VSF-14f, 20. paratype, specimen VS 1431, sample VSF-16c, 21. holotype, specimen VS 1348, sample VSF-14h. 22-23. *Howchinia variabilis?* nov. sp., 22. specimen VS 1331, sample VSF-14g, 23. specimen VS 1344, sample VSF-14h. 24-29. *Howchinia plana* nov. sp., 24. paratype, juvenile, specimen VS 1231, sample VSC-2A", 25. paratype, specimen VS 1399, sample VSF-16a, 26. paratype, specimen VS 1291, sample VSF-14e, 27. holotype, specimen VS 1242, sample VSC-3, 28. paratype, specimen VS 0296, sample, VSF-7, 29. paratype, specimen VS 1044, sample VSC-2A1a.

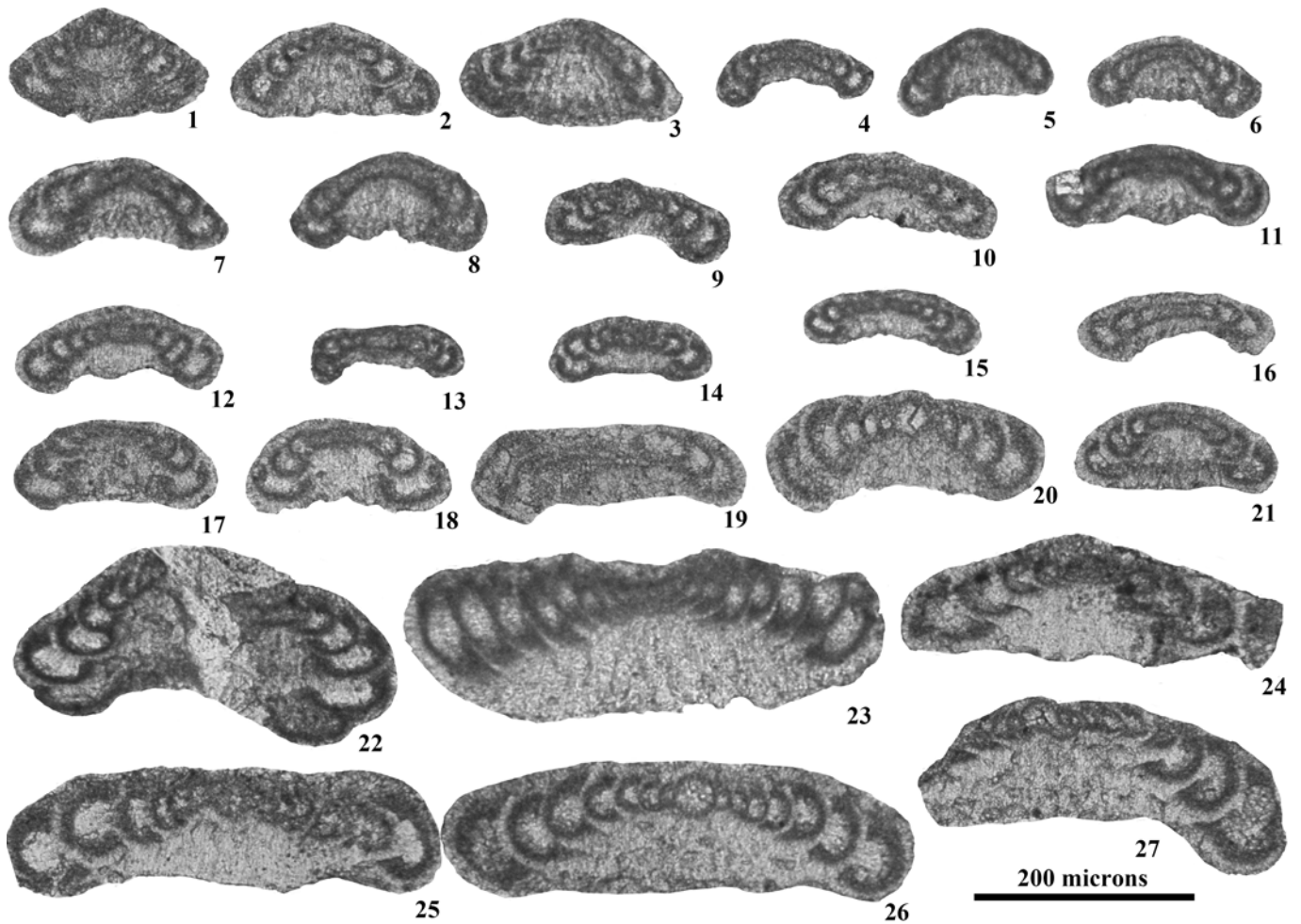


Figure 7. 1-3. *Howchinia convexa* (Brazhnikova in Aizenverg et al., 1983), 1. specimen VS 0079, sample VSB-4, 2. specimen VS 0166, sample VSC-2A1d, 3. pseudo-pillars well developed, specimen VS 1288, sample VSF-14d. 4-8. *Howchinia acutiformis* nov. sp., 4. paratype, specimen VS 0164, sample VSC-2A1d, 5. paratype, specimen VS 1342, sample VSF-14h, 6. paratype, specimen VS 1337, sample VSF-14h, 7. paratype, specimen VS 1097, sample VSF-4a, 8. holotype, specimen VS 0117, sample VSC-2A1b. 9-16. *Howchinia cantabrica* nov. sp., 9. paratype, juvenile, specimen VS 0076, sample VSB-4, 10. paratype, specimen VS 1510, sample VSF-19, 11. paratype, specimen VS 1267, sample VSF-14b, 12. paratype, specimen VS 1062, sample VSC-2A1e, 13. paratype, juvenile, specimen VS 0170, sample VSC-2A1e. 14. paratype, juvenile, specimen VS 0395, sample VSF-11, 15. holotype, specimen VS 0163, sample VSC-2A1d, 16. paratype, specimen VS 1224, sample VSC-2A". 17-19. *Howchinia subplana* (Brazhnikova and Yartseva, 1956), 17. specimen VS 0404, sample VSF-11, 18. specimen VS 1081, sample VSB-3, 19. specimen VS 0161, sample VSC-2A1d. 20-22. *Howchinia subconica* (Brazhnikova and Yartseva, 1956), 20. specimen VS 0591, sample VSC-5, 21. specimen VS 0167, sample VSC-2A1d, 22. specimen VS 1106, sample VSF-4a. 23-27. *Howchinia enormis* nov. sp., 23. paratype, specimen VS 0821, sample VSC-11B, 24. paratype, specimen VS 1207, sample VSF-8, 25. paratype, specimen VS 1201, sample VSF-8, 26. holotype, specimen VS 1218, sample VSC-2A', 27. paratype, specimen VS 1041, sample VSC-2A1a.

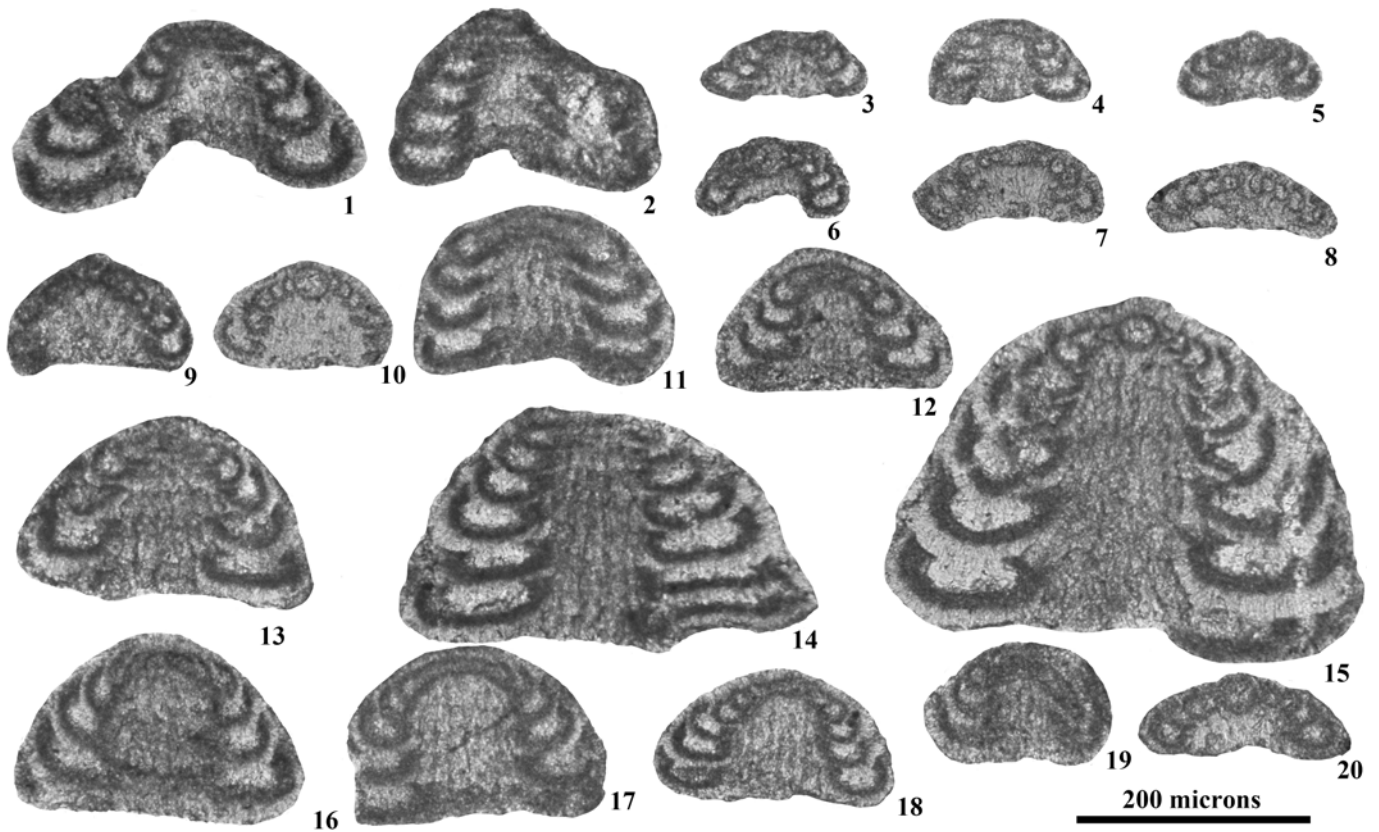


Figure 8. 1-4. *Howchinia* nov. sp. 3, 1. specimen VS 0617, sample VSF-20, 2. specimen VS 2068, sample VSF-110, 3. specimen VS 1458, sample VSF-16d, 4. specimen VS 0321, sample VSF-9, 5-10. *Howchinia hemisphaerica* nov. sp., 5. paratype, juvenile, specimen VS 0635, sample VSF-22, 6. paratype, juvenile, specimen VS 2007, sample VSF-102, 7. paratype, specimen VS 0578, sample VSF-19, 8. paratype, specimen VS 0462, sample VSF-3', 9. paratype, specimen VS 0365, sample VSC-2A", 10. holotype, specimen VS 1287, sample VSF-14c. 11-15. *Howchinia gibba* (Moeller, 1879), 11. juvenile with pseudo-pillars, specimen VS 0419, sample VSC-12, 12. juvenile, specimen VS 0356, sample VSC-2A", 13. juvenile specimen with development of pseudo-pillars, specimen VS 0366, sample VSC-2A", 14. pseudo-pillars well developed, specimen VS 1326, sample VSF-14g, 15. pseudo-pillars moderately developed, specimen VS 0119, sample VSC-2A1b. 16-20. *Howchinia beleutensis* Vdovenko, 1962, 16. pseudo-pillars well developed, specimen VS 1225, sample VSC-2A", 17. pseudo-pillars well developed, specimen VS 0475, sample VSF-15, 18. pseudo-pillars well developed, specimen VS 1260, sample VSF-14b, 19. juvenile, specimen VS 0110, sample VSC-2A1a, 20. oblique juvenile, specimen juvenile, specimen VS 0178, sample VSC-2A1c.

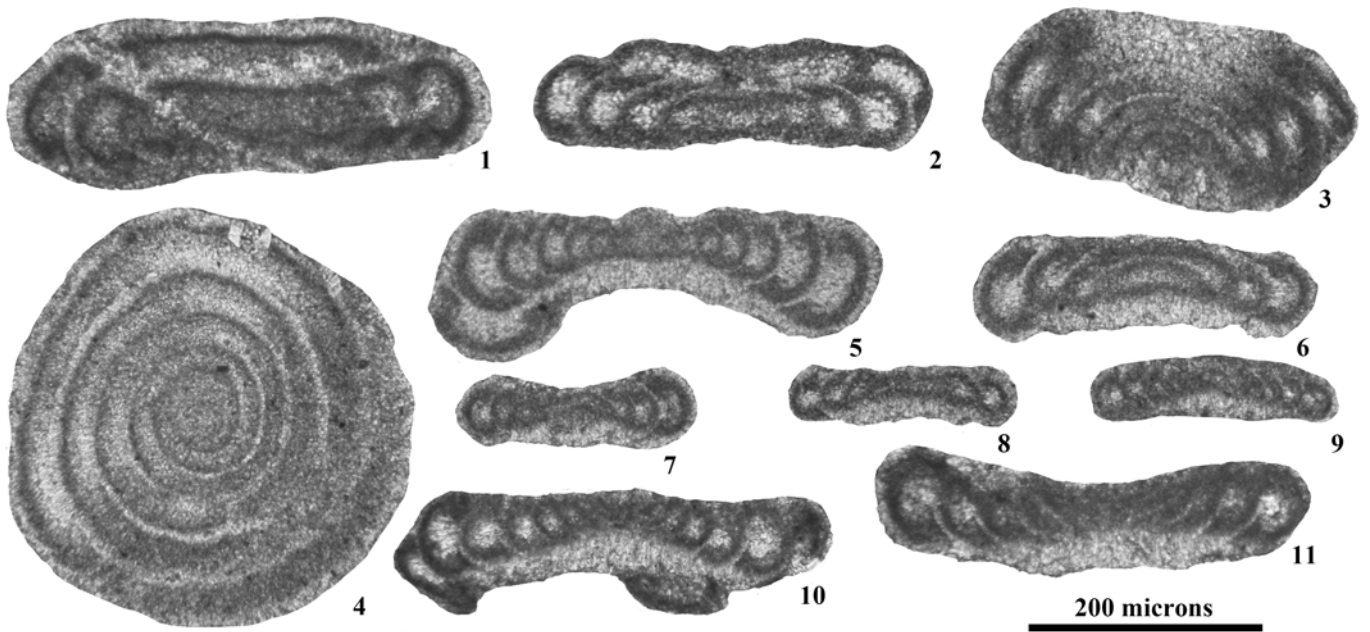


Figure 9. 1-3. *Planohowchinia* nov. sp. 1, 1. specimen VS 2150, sample VSF-119, 2. specimen VS 2085, sample VSF-115, 3. oblique section, specimen VS 1327, sample VSF-14g. 4-11. *Monotaxinoides gracilis* (Dain in Reitlinger, 1956), 4. specimen VS 1329, sample VSF-14g, 5. specimen VS 0298, sample VSF-7, 6. specimen VS 1059, sample VSC-2A1d, 7. specimen VS 0174, sample VSC-2A1e, 8. specimen VS 0342, sample VSC-2A', 9. VS 0781, sample VSC-6A", 10. specimen VS 1313, sample VSF-14f, 11. specimen VS 2094, sample VSF-116.

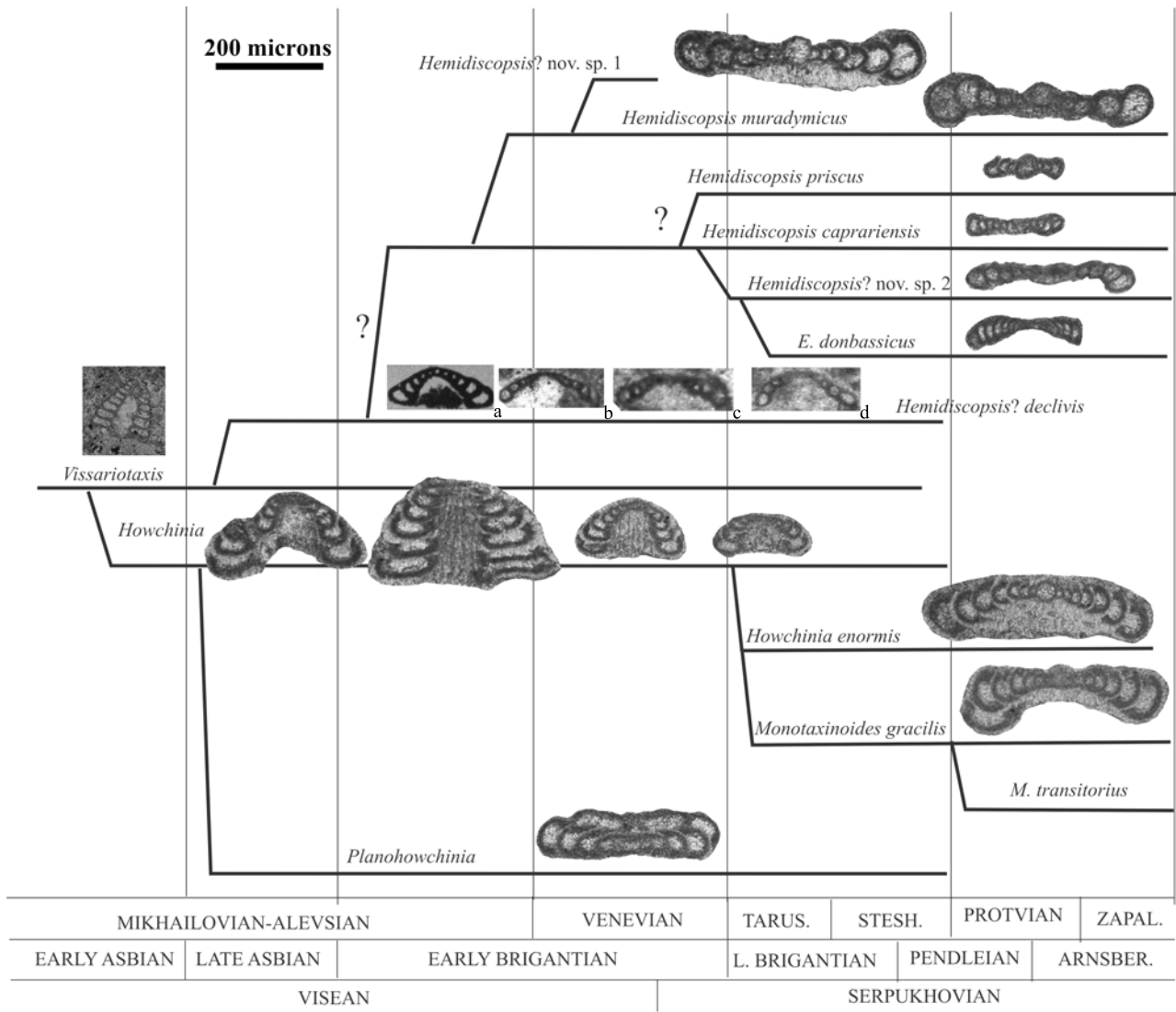


Figure 10. Proposed phylogeny for the primitive lasiodiscids. Illustrated species are those included in Figs. 5 to 9, except for *Vissariotaxis exilis* (unpublished specimen, Sierra del Castillo section, level PC-2164, late Asbian, see Cózar, 2004 for location of the stratigraphic level); *Hemidiscopsis? declivis*, a slightly modified from Ganelina, 1956, pl. 5, fig. 2; b-d modified from Pille, 2008 (from right to left, pl. 45, fig. 5, fig. 4 and fig. 13, as *Hemidiscopsis caprariensis*); note the irregular flanks in d, which is considered as a transitional feature to the planispiral *H. caprariensis*. Correlation of the western European and Russian substages are based on the biostratigraphy on shallow water facies from northern England in Cózar and Somerville (2014).

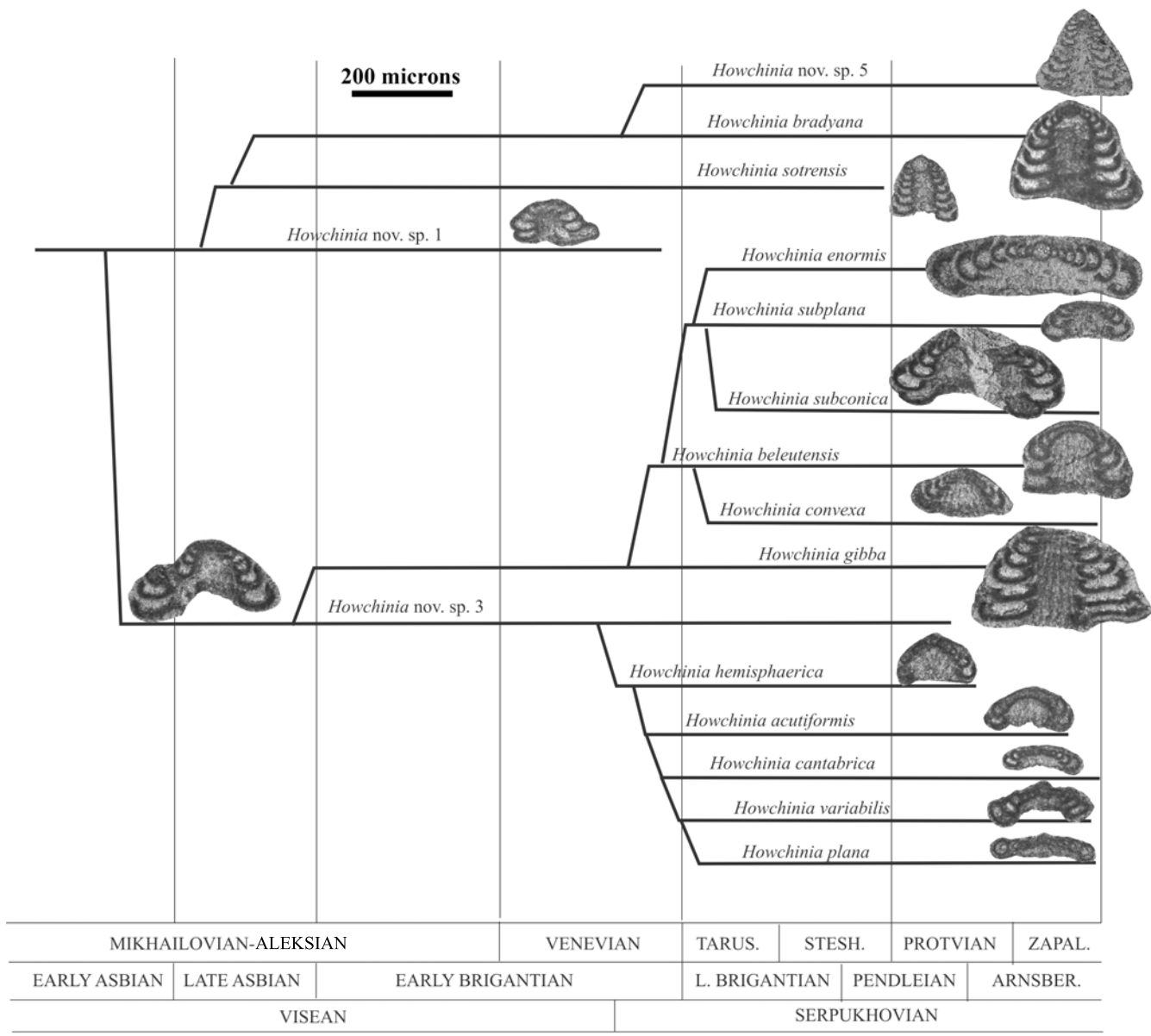


Figure 11. Proposed phylogeny in the *Howchinia* species. Illustrated species are those included in Figs. 6 to 8.

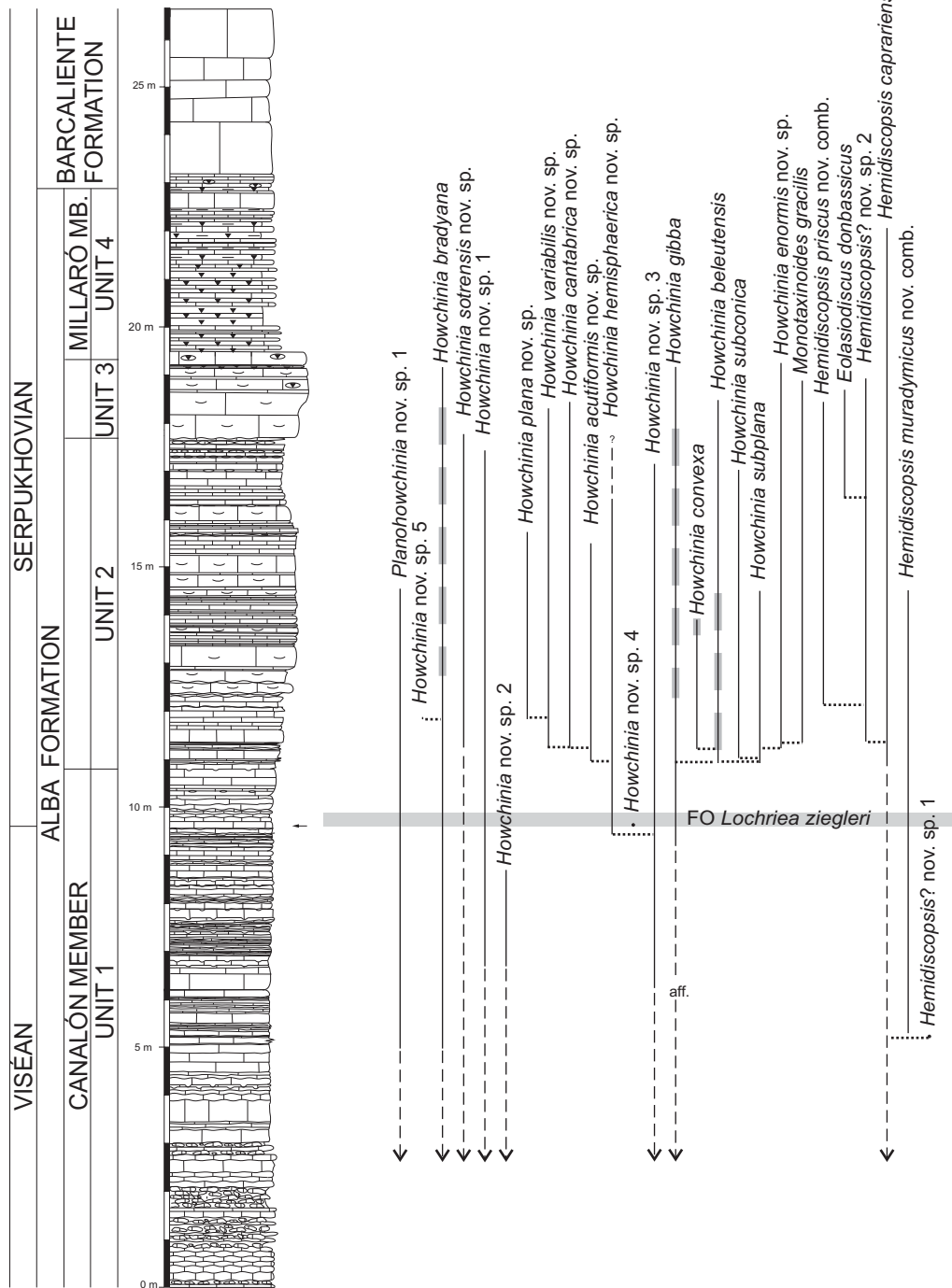


Figure 12. Summary of the stratigraphic ranges of the lasiodiscid species in the Vegas de Sotres section. Grey discontinuous thick bars correspond to the ranges of *Howchinia* specimens with pseudo-pillars.

Appendix 1

Species	Specimen	Sample	Number specimens	W/H ratio	Height (H) (microns)	Width (W) (microns)	Nw	iDp (microns)
<i>Eolasiodiscus donbassicus</i>			5	4–5.4	30–50	130–280	5–8	--
	VS 0553	VSF-19(1)		5.25	40	210	8	--
	VS 0647	VSF-22(4)		4.8	30	145	6	--
	VS 1548	VSF-24(8)		4.6	50	230	8	--
	VS 1549	VSF-24(10)		4	40	160	5.5	--
	VS 1585	VSF-24a(6-2)		--	--	280	6	--
	VS 1609	VSC-11b(9)		5.4	50	270	>6	--
<i>Hemidiscopsis caprariensis</i>			59	2.5–7.2	22–60	110–270	3–6	20–32
	VS 0021	VSB-1(2)		7.2	22	160	4	28
	VS 0173	VSC-2A1e(4)		5	40	200	>4	--
	VS 0201	VSF-2(3)		--	--	150	6	--
	VS 0484	VSF-16(2)		5.25	40	210	>3.5	--
	VS 0497	VSC-3A(1)		4	30	120	4.5	--
	VS 0540	VS-00(2)		--	--	150	4.5	--
	VS 0628	VSF-21(4)		2.5	50	125	4	20
	VS 0686	VSF-23(3)		5.6	30	170	4	--
	VS 0829	VSC-11B(4)		4.8	50	240	>4	--
	VS 0975	VS-01(1)		5.4	50	270	>5	--
	VS 1046	VSC-2A1a(9)		4.6	30	140	3.5	>15
	VS 1047	VSC-2A1a(10)		3.1	45	140	4	20
	VS 1058	VSC-2A1d(6)		3.4	40	135	3	26
	VS 1061	VSC-2A1d(10)		6.3	30	170	3.5	26
	VS 1066	VSC-2A1e(9)		--	--	110	3.5	25
	VS 1148	VSF-4c(5-1)		3.2	45	145	3.5	23
	VS 1285	VSF-14c(5-1)		4	50	200	4	25
	VS 1302	VSF-14f(1-1)		4	30	120	4	--
	VS 1303	VSF-14f(1-1)		5	30	150	4	--
	VS 1304	VSF-14f(1-1)		--	--	170	5	--
	VS 1307	VSF-14f(2-1)		--	--	160	4.5	--
	VS 1309	VSF-14f(3-1)		3.5	40	140	4	--
	VS 1312	VSF-14f(4-2)		--	--	170	5	--
	VS 1321	VSF-14g(1-1)		4.25	40	170	4	--
	VS 1333	VSF-14h(1-1)		--	--	120	>3	--
	VS 1336	VSF-14h(2-1)		4.4	35	155	>4.5	--
	VS 1338	VSF-14h(2-1)		--	--	130	4	22
	VS 1340	VSF-14h(3-1)		4.2	50	210	3.5	32
	VS 1345	VSF-14h(6-1)		5.25	40	210	3.5	>15
	VS 1357	VSF-15(9)		5.3	30	160	5	--
	VS 1371	VSF-16(9)		5.5	40	220	>3.5	--
	VS 1375	VSC-3A(6)		--	--	110	3	25
	VS 1391	VSF-16a(2-1)		--	--	200	>4	--
	VS 1395	VSF-16a(3-1)		--	--	180	5.5	--
	VS 1396	VSF-16a(3-2)		--	--	170	>5	--
VS 1419	VSF-16b(5-1)		6	30	180	5?	--	
VS 1424	VSF-16c(1-1)		4.3	35	150	>4	--	
VS 1437	VSF-16c(4-1)		--	--	140	3.5	30	
VS 1447	VSF-16c(5-1)		4	40	160	>4	--	
VS 1448	VSF-16c(5-2)		3.4	50	170	>4	--	
VS 1464	VSF-16d(3-1)		3.8	40	155	4.5	--	
VS 1487	VSF-16e(6-1)		5	40	200	5	--	

VS 1489	VSC-4(7)	--	--	185	6	28
VS 1497	VSF-17(10)	4	40	160	4.5	20
VS 1499	VSF-18(6)	--	--	150	>4	--
VS 1518	VSF-20(8)	--	--	140	6	--
VS 1527	VSC-6A(10)	--	--	150	5.5	--
VS 1537	VSC-6A'(9)	3.75	40	150	>5	--
VS 1607	VSC-11b(7)	5.2	25	130	4	23
VS 1746	VSC-8top(8)	--	--	130	4.5	24
VS 1749	VSC-9(6)	--	--	130	5	27
VS 1750	VSC-9(8)	--	--	130	3.5	30
VS 2124	VSF-118	4	50	200	>5	--
VS 2141	VSF-119	3.17	60	190	>3.5	30
VS 2143	VSF-119	4	40	160	>4.5	--
VS 2145	VSF-119	--	--	150	3	--
VS 2151	VSF-119	4.8	30	145	5	24
VS 2154	VSF-120	--	--	150	4	20
VS 2160	VSF-120	--	--	160	>4.5	--

Hemidiscopsis muradymicus

		7	2.4–6	50–100	120–540	2–6.5	35–40
VS 2035	VSF-102		5.25	80	420	5.5	35
VS 2038	VSF-104		2.4	50	120	2	35
VS 2054	VSF-107		4.75	70	330	4?	--
VS 2059	VSF-109		5.4	75	410	4?	--
VS 2073	VSF-113		5.4	100	540	6.5	40
VS 2113	VSF-117		6	60	360	6	--
VS 2148	VSF-119		3.6	60	220	3	40

Hemidiscopsis priscus

		16	2.7–7	20–60	110–230	2.5–5	30–40
VS 0122	VSC-2A1b(4)		2.9	55	160	3	30
VS 0375	VSC-2A"(5)		3.75	40	150	3	32
VS 0693	VSF-24(1)		3.33	45	150	3	30
VS 0989	VS-01(1)		3.4	50	175	3.5	30
VS 1049	VSC-2A1b(10)		3.4	50	170	3.5	30
VS 1064	VSC-2A1e(8)		2.7	60	160	3.5	30
VS 1310	VSF-14f(3-2)		--	--	130	3.5	30
VS 1319	VSF-14f(6-1)		--	--	140	4	35
VS 1323	VSF-14g(1-2)		2.78	45	125	2.5	40
VS 1343	VSF-14h(5-1)		4.6	28	130	3	35
VS 1346	VSF-14h(6-1)		2.73	55	150	3.5	30
VS 1358	VSF-15(10)		3.78	45	170	2.5	40
VS 1383	VSF-16a(1-1)		--	--	110	2	--
VS 1390	VSF-16a(1-2)		4.5	50	230	5	>25
VS 1496	VSF-17(8)		--	--	200	>4	--
VS 1587	VSC-6A"(6)		7	20	140	4	30

Hemidiscopsis ? nov. sp. 1

VS 2075	VSF-114	1	5.5	90	470	5.5	40
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Hemidiscopsis ? nov. sp. 2

		2	5.3–5.6	60	320–340	6	--
VS 0294	VSF-7(4)		5.6	60	340	>6	--
VS 0777	VSC-6A"(1)		5.3	60	320	6	--

Howchinia bradyana

		24	0.8–1.9	130–400	160–390	5–11	18–27
VS 0039	VSb-1(5)		1.4	130	190	5	--
VS 0240	VSF-3b(5)		1	210	210	7	25
VS 0328	VSF-9(4)		0.8	390	310	10	--
VS 0262	VSF-5(2)		1.6	160	260	7.5	23

	VS 0680	VSF-23(1)	1.9	110	210	5	27
	VS 0687	VSF-23(3)	0.94	>180	170	7	--
	VS 0689	VSF-23(4)	0.91	230	210	7?	--
	VS 0803	VSF-25(1)	0.95	240	220	6	--
	VS 1153	VSF-4d(1-1)	0.84	320	270	9	18
	VS 1154	VSF-4d(1-1)	1.3	200	260	8.5	21
	VS 1160	VSF-4d(3-1)	1.28	180	230	8	20
	VS 1219	VSC-2A'(6)	0.91	330	300	11	20
with pseudo-pillars	VS 0165	VSC-2A1d(3)	1.12	310	350	8?	--
with pseudo-pillars	VS 0531	VS-00(1)	0.97	400	390	9	--
with pseudo-pillars	VS 0541	VS-00(2)	0.81	320	260	10	18
with pseudo-pillars	VS 0605	VSC-5'(1)	0.8	250	200	8	--
with pseudo-pillars	VS 0842	VSC-12(4)	1.06	150	160	8	--
with pseudo-pillars	VS 1050	VSC-2A1b-c(9)	1	220	220	7	--
with pseudo-pillars	VS 1359	VSF-15(10)	1.25	320	400	11	--
with pseudo-pillars	VS 1398	VSF-16a(5-1)	1.1	320	360	9?	--
with pseudo-pillars	VS 1468	VSF-16d(4-2)	0.92	270	250	10	--
with pseudo-pillars	VS 1469	VSF-16d(6-1)	0.97	300	290	10	20
with pseudo-pillars	VS 1608	VSC-11b(9)	1.03	290	300	9	20
with pseudo-pillars	VS 2088	VSF-115	0.89	280	250	6	--

Howchinia acutiformis

		10	2–2.5	50–90	120–230	4–6	15–25
	VS 0117	VSC-2A1b(2)	2.25	80	180	6	20?
	VS 0147	VSC-2A1c(1)	2.13	80	170	4.5	--
	VS 0164	VSC-2A1d(3)	2.3	60	140	5.5	15
	VS 0238	VSF-3b(3)	2.4	50	120	4	--
	VS 0326	VSF-9(4)	2.15	70	150	4	25
	VS 1097	VSF-4a(1-2)	2.11	90	190	5	--
	VS 1337	VSF-14h(2-1)	2.3	65	150	5	--
	VS 1342	VSF-14h(4-2)	2	70	140	5	20
	VS 1416	VSF-16b(4-2)	3.3	65	220	5.5	--
	VS 2062	VSF-109	2.5	90	230	4	--

Howchinia beleutensis

		13	1.48–2.5	85–250	150–370	4–7	20–30
	VS 0118	VSC-2A1b(2)	2.5	90	230	4	25
	VS 0219	VSF-3a(3)	1.8	90	170	4	30
	VS 0509	VSC-3A'(4)	1.55	90	140	6	--
	VS 1055	VSC-2A1c(7)	2.3	85	200	5	--
	VS 1056	VSC-2A1c(9)	1.73	110	190	6	--
	VS 1406	VSF-16a(5-2)	2.08	120	250	6.5	20
with pseudo-pillars	VS 0064	VSB-3(1)	1.48	250	370	7?	--
with pseudo-pillars	VS 0110	VSC-2A1a(4)	1.66	90	150	5	--
with pseudo-pillars	VS 0475	VSF-15(1)	1.69	130	220	6	--
with pseudo-pillars	VS 1002	VSB-1(6)	1.94	170	330	6	--
with pseudo-pillars	VS 1225	VSC-2A"(8)	1.79	140	250	6	--
with pseudo-pillars	VS 1260	VSF-14b(1-2)	1.9	110	210	6	>15
with pseudo-pillars	VS 1315	VSF-14f(5-1)	2.08	130	270	6.5	--

Howchinia cantabrica

		26	2.4–4	40–100	115–240	3–5.5	20–30
	VS 0046	VSB-2(1)	2.8	50	140	3	23
	VS 0061	VSB-2(5)	2.4	50	120	3	20
	VS 0076	VSB-4(3)	2.6	60	160	4.5	25
	VS 0163	VSC-2A1d(3)	3.6	50	180	5.5	--
	VS 0170	VSC-2A1e(2)	3.1	45	140	4.5	--
	VS 0200	VSF-2(3)	2.8	40	115	4	25
	VS 0274	VSF-5(5)	3.2	45	145	3.5	25
	VS 0352	VSC-2A"(2)	3	50	145	4	22
	VS 0395	VSF-11(1)	3.5	40	140	4.5	--
	VS 0499	VSC-3A(1)	3.75	40	150	5.5	--
	VS 0697	VSF-24(2)	2.8	60	170	4	--
	VS 0995	VS-01(2)	2.7	70	190	4.5	30

VS 1034	VSB-5(8)	2.28	70	160	5	--	
VS 1062	VSC-2A1e(7)	2.91	100	240	5	27	
VS 1078	VSF-2(8)	3	50	150	4	--	
VS 1210	VSF-8(9)	3.25	40	130	4	22	
VS 1224	VSC-2A"(7)	4	40	160	4	--	
VS 1267	VSF-14b(4-1)	2.85	70	200	5.5	--	
VS 1334	VSF-14h(1-1)	3.25	40	130	3.5	--	
VS 1433	VSF-16c(2-2)	2.7	60	160	4	--	
VS 1441	VSF-16c(4-2)	2.4	70	150	4	25	
VS 1455	VSF-16d(1-2)	3.6	50	180	4	20	
VS 1510	VSF-19(10)	3.3	55	185	4.5	--	
VS 2131	VSF-118	3.9	50	195	4	23	
VS 2157	VSF-120	3.2	50	160	4.5	--	
VS 2158	VSF-120	3	50	150	4	--	
<i>Howchinia convexa</i>		5	1–2.4	80–160	140–180	4–5	22–25
VS 0079	VSB-4(4)	1	160	160	5	23	
VS 0148	VSC-2A1c(1)	--	--	140	4.5	25	
VS 0166	VSC-2A1d(4)	2.25	80	180	4	22	
VS 0265	VSF-5(3)	1.45	110	160	4	22	
with pseudo-pillars	VS 1288	VSF-14d(5-1)	2	90	180	5	25
<i>Howchinia enormis</i>		16	2.86–4.8	70–150	250–460	5–9	30
VS 0335	VSC-2A'(1)	2.86	150	430	8	--	
VS 0489	VSF-16(5)	4.8	70	340	>6	--	
VS 0684	VSF-23(2)	--	--	460	8	--	
VS 0821	VSC-11B(2)	3.3	130	430	9	--	
VS 0945	VSC-8top(4)	4.5	90	410	6?	--	
VS 1007	VSB-1(8)	>3.3	75	>250	5?	--	
VS 1041	VSC-2A1a(8)	>2.7	130	>350	7.5?	30	
VS 1065	VSC-2A1e(9)	--	--	450	7.5	30	
VS 1075	VSF-2(6)	5.6	80	450	7	--	
VS 1201	VSF-8(6)	<4	<100	400	7	30	
VS 1207	VSF-8(8)	>3.3	100	>330	>5	--	
VS 1216	VSF-9(8)	3.45	110	380	>5.5	--	
VS 1218	VSC-2A'(6)	3.8	110	420	7	30	
VS 1339	VSF-14h(3-1)	3.1	120	380	>5	--	
VS 1362	VSF-15(10)	3.4	100	340	7?	--	
VS 2179	VSF-122	2.9	100	290	4.5?	--	
<i>Howchinia gibba</i>		17	1–2.1	110–300	230–400	5–8	20–25
VS 0027	VSB-1(3)	2.1	120	260	6?	--	
VS 0272	VSF-5(4)	1.1	270	300	8	--	
VS 0356	VSC-2A"(3)	1.8	110	200	6?	--	
VS 0413	VSF-12(4)	1.36	220	300	6	--	
VS 1185	VSF-5(7)	1.6	180	290	7	--	
VS 2021	VSF-104	1.38	210	290	6	25	
with pseudo-pillars	VS 0119	VSC-2A1b(2)	1.4	280	400	8	23
with pseudo-pillars	VS 0141	VSC-2A1b-c(3)	1.1	300	330	7	--
with pseudo-pillars	VS 0155	VSC-2A1c(4)	1.07	260	280	7	--
with pseudo-pillars	VS 0366	VSC-2A"(4)	1.6	150	250	6	20
with pseudo-pillars	VS 0419	VSF-12(5)	1.46	150	220	5?	--
with pseudo-pillars	VS 0633	VSF-21(5)	1.50	153	230	7	--
with pseudo-pillars	VS 1326	VSF-14g(2-2)	1.71	210	360	7	--
with pseudo-pillars	VS 1422	VSF-16b(6-1)	1	230	230	6?	--
with pseudo-pillars	VS 1528	VSC-6A(10)	1.5	120	180	6	--
with pseudo-pillars	VS 2106	VSF-116	1.64	140	230	6	--
with pseudo-pillars	VS 2169	VSF-121	1.47	190	280	7	--
<i>Howchinia hemisphaerica</i>		10	1.6–2.9	50–100	125–170	3.5–6	18–28
VS 0178	VSF-0(1)	2.4	70	170	4	26	
VS 0365	VSC-2A"(4)	1.6	100	160	5	--	
VS 0408	VSF-12(1)	2.3	60	140	4	22	
VS 0446	VSC-3(5)	1.66	90	170	4	25	

	VS 0462	VSC-3'(3)	2.9	50	145	4	21	
	VS 0578	VSF-19(3)	2.46	65	160	6	18	
	VS 0635	VSF-22(2)	1.9	65	125	4	23	
	VS 1287	VSF-14c(6-1)	2.14	70	150	5	25	
	VS 1361	VSF-15(10)	1.8	100	180	5	--	
	VS 2007	VSF-102b	1.85	70	130	3.5	28	
<i>Howchinia planiformis</i>			12	2.3–5.4	25–90	135–240	3–6	22–32
	VS 0077	VSB-4(3)	3	50	150	4	27	
	VS 0987	VS-01(1)	3.5	40	140	3.5	22	
	VS 1076	VSF-2(6)	4.1	30	125	3	28	
	VS 1231	VSC-2A"(10)	4.14	35	145	>5	>20	
	VS 1242	VSC-3(9)	4.1	50	205	5?	>20	
	VS 1290	VSF-14c(2-1)	2.33	60	140	3.5	30	
	VS 1291	VSF-14c(2-1)	3.01	60	185	3.5	32	
	VS 1294	VSF-14c(2-2)	3.67	45	165	4	28	
	VS 1399	VSF-16a(5-1)	5	40	200	5	28	
	VS 1440	VSF-16c(4-1)	5.4	25	135	4	28	
	VS 0296	VSF-7(5) ?	2.6	90	240	6	22	
	VS 1044	VSC-2A1a(8) ?	2.61	80	210	5	30	
<i>Howchinia sotrensis</i>			9	0.92–1.09	110–170	120–180	5–8	28–32
	VS 0075	VSB-4(2)	1.07	140	150	6	--	
	VS 0302	VSF-8(1)	1	130	130	7.5	32	
	VS 0372	VSC-2A"(4)	1.09	110	120	5	30	
	VS 0473	VSF-15(1)	0.94	160	150	8	28	
	VS 1187	VSF-5(8)	1.09	110	120	6	30	
	VS 1200	VSF-8(6)	0.93	160	150	7.5	30	
	VS 1271	VSF-14c(1-1)	0.92	140	130	7	30	
	VS 1381	VSC-3A(9)	1.05	170	180	7	>20	
	VS 2147	VSF-119	1.08	120	130	6.5	30	
<i>Howchinia subconica</i>			5	2.4–2.84	65–150	185–470	5–7	27
	VS 0167	VSC-2A1d(4)	2.84	65	185	4.5	>15	
	VS 0310	VSF-8(5)	2.7	100	270	>5	--	
	VS 0591	VSC-5(1)	2.4	100	240	5	27	
	VS 1106	VSF-4a(4-2)	--	>150	>330	7	--	
	VS 1512	VSC-5(5)	--	--	>470	>6	--	
<i>Howchinia subplana</i>			6	2.4–3.5	70–100	190–230	4–6	22
	VS 0035	VSB-1(4)	2.7	70	190	4	--	
	VS 0161	VSC-2A1d(1)	3.5	60	240	5	--	
	VS 0404	VSF-11(5)	2.57	70	180	6	--	
	VS 0491	VSF-16(5)	2.3	100	230	6	22	
	VS 1018	VSB-3(5)	2.4	75	180	6	--	
	VS 1081	VSF-3a(7)	2.4	75	180	6	--	
<i>Howchinia variabilis</i>			10	2.1–3	50–90	150–240	3.5–6	20–33
	VS 0407	VSF-12(1)	2.1	70	150	3.5	33	
	VS 1182	VSF-5(7)	3	50	150	4	--	
	VS 1202	VSF-8(6)	2.5	60	150	5	25	
	VS 1286	VSF-14c(6-1)	2.7	55	150	4	21	
	VS 1306	VSF-14f(1-2)	2.7	60	160	5	28	
	VS 1348	VSF-14h(6-1)	2.5	80	200	5.5	20	
	VS 1431	VSF-16c(2-2)	3	50	150	5	27	
	VS 2144	VSF-119	2.8	60	170	4.5	25	
	VS 1331	VSF-14g(5-1) ?	2.3	60	140	4	24	
	VS 1344	VSF-14h(5-2) ?	2	80	160	5	20	
<i>Howchinia nov. sp. 1</i>			4	2–2.28	70–100	160–210	3.5–5.5	--
	VS 0299	VSF-8(1)	2	80	190	4	--	

VS 0626	VSF-21(1)	2	90	180	4.5	--	
VS 2014	VSF-103'	2.1	100	210	5.5	--	
VS 2055	VSF-109	2.28	70	160	3.5	--	
<i>Howchinia</i> nov. sp. 2		3	0.42–0.5	180–200	90–100	5–6	40–50
VS 2047	VSF-106	0.5	200	100	5	50	
VS 2053	VSF-107	0.42	210	90	6	40	
VS 2067	VSF-109	0.5	180	90	5	50	
<i>Howchinia</i> nov. sp. 3		5	1.8–2.8	60–140	130–240	5–7	--
VS 0321	VSF-9(2)	1.8	130	240	7	--	
VS 0617	VSF-20(2)	1.8	70	130	4.5	--	
VS 1458	VSF-16d(1-2)	2.3	60	140	4.5	--	
VS 2050	VSF-106	2.8	80	230	5	--	
VS 2068	VSF-110	1.64	140	203	5.5	--	
<i>Howchinia</i> nov. sp. 4		2	2.7–4.5	60–130	270–360	5–7	35
VS 1069	VSF-0(9)	2.7	130	360	7	35	
<i>Howchinia</i> nov. sp. 5		2	0.94–1.05	170–200	160–210	7–10	20
VS 0313	VSF-9(1)	1.05	200	210	7	--	
VS 1027	VSB-4(10)	0.94	170	160	10	20	
<i>Monotaxinoides gracilis</i>		31	2.9–5.2	35–100	150–390	4–7	23–30
VS 0174	VSC-2A1e(4)	3.6	55	200	4.5	--	
VS 0175	VSC-2A1e(4)	3.2	60	190	4	--	
VS 0295	VSF-7(5)	--	--	250	>4	--	
VS 0298	VSF-7(5)	--	--	350	6	--	
VS 0342	VSC-2A'(4)	4	50	200	4	--	
VS 0467	VSC-3'(4)	4.4	70	310	6	--	
VS 0492	VSC-3A(1)	4.2	35	150	4	23	
VS 0664	VSC-6A(3)	3.7	70	260	>5	--	
VS 0681	VSF-23(2)	--	--	270	>4	--	
VS 0779	VSC-6A"(4)	--	--	260	>3	--	
VS 0781	VSC-6A"(4)	4.2	50	210	5	--	
VS 0976	VS-01(1)	3.4	70	240	5?	--	
VS 1000	VS-01(3)	3.6	80	290	6	--	
VS 1040	VSC-2A1a(7)	3.25	40	130	3	24	
VS 1059	VSC-2A1d(6)	3.5	80	280	>4	--	
VS 1311	VSF-14f(3-2)	3.6	40	145	5	25	
VS 1313	VSF-14f(5-1)	5.2	70	370	7	--	
VS 1324	VSF-14g(2-2)	5.2	50	260	>5	--	
VS 1329	VSF-14g(3-2)	3.7	100	370	6.5	28	
VS 1350	VSC-3'(10)	--	--	390	>5	--	
VS 1367	VSF-16(7)	4	70	280	>6	--	
VS 1368	VSF-16(7)	--	--	530	>6	--	
VS 1408	VSF-16b(1-1)	4.1	55	230	4.5	30	
VS 1435	VSF-16c(3-1)	5	50	250	4.5	--	
VS 1470	VSF-16d(6-1)	3.6	60	200	4	--	
VS 1483	VSF-16e(4-2)	4.6	50	230	>4	--	
VS 1515	VSC-5(9)	--	--	360		--	
VS 1542	VSF-23(8)	3.5	55	190	5.5	>20	
VS 1573	VSF-24a(5-1)	3.6	70	250	5.5	30	
VS 1594	VSC-6A"(10)	--	--	280	>5	--	
VS 2094	VSF-116	4.7	80	380	6.5	--	

Planohowchinia nov. sp. 1

		8	2.13–4.5	30–150	130–400	4–6.5	--
VS 1109	VSF-4a(4-2)		4.33	30	130	4	--
VS 1325	VSF-14g(2-2)		--	--	360	--	--
VS 1327	VSF-14g(3-1)		--	--	320	6	--
VS 2057	VSF-109		4.5	40	180	>4	--
VS 2076	VSF-115		2.13	150	320	>4	--
VS 2077	VSF-115		2.33	150	350	6.5	--
VS 2085	VSF-115		2.66	150	340	6	--
VS 2150	VSF-119		3.63	110	400	>6	--

Appendix 2. Lists of synonymies

Eolasiodiscus donbassicus Reitlinger, 1956

1956. *Eolasiodiscus donbassicus* n. sp. – Reitlinger, p. 76, pl. 2, figs. 1, 3-4.
1962. *Monotaxinoides transitorius* Brazhnikova and Yartseva – Bogush and Juferev, pl. 9, fig. 25.
1967. *Eolasiodiscus donbassicus* Reitlinger – Brazhnikova et al., pl. 20, fig. 5, pl. 22, fig. 7(?), pl. 25, 6-7.
pars. 1969. *Amodiscus* cf. *curvus* Potievskaya – Manukalova-Grebenyuk et al., pl. 2, figs. 19, 20, 21.
1970. *Eolasiodiscus donbassicus* Reitlinger – Lys and Raoult, pl. 1, fig. 2.
1973. *Eolasiodiscus donbassicus* Reitlinger – Einor, pl. 9, figs. 22-24.
1973. *Eolasiodiscus?* sp. – Einor, pl. 9, figs. 25-27.
pars. 1973. *Monotaxinoides* – Browne and Pohl, pl. 26, figs. 4, 6 [only].
1976. *Eolasiodiscus donbassicus* Reitlinger – Lys, pl. 37, fig. 2.
1978. *Eolasiodiscus donbassicus* Reitlinger – Lys et al., pl. 3, fig. 7.
1979. *Eolasiodiscus* ex gr. *donbassicus* Reitlinger – Brazhnikova in Wagner et al., pl. 5, figs. 17-18.
1982. *Eolasiodiscus donbassicus* Reitlinger – Villa, pl. 2, fig. 9.
1983. *Eolasiodiscus* ex gr. *donbassicus* Reitlinger – Aizenverg et al., pl. 12, figs. 30-39.
1983. *Eolasiodiscus donbassicus* Reitlinger – Groves, pl. 6, figs. 3-4.
1985. *Eolasiodiscus donbassicus* Reitlinger – Adachi, pl. 21, figs. 16-19.
1985. *Eolasiodiscus* sp. B – Adachi, pl. 21, figs. 22-24.
pars. 1985. *Monotaxinoides transitorius* (Brazhnikova and Yarseva) (sic) – Lys, pl. 2, fig. 3 [only].
1985. *Eolasiodiscus donbassicus* Reitlinger – Lys, pl. 2, fig. 4.
non. 1987. *Eolasiodiscus donbassicus* Reitlinger – Delvolvé and Perret, pl. 2, figs. 8, 10.
1987. *Eolasiodiscus transitorius* (Brazhnikova and Yartseva) – Delvolvé and Perret, pl. 2, figs. 9,
11.
1987. *Eolasiodiscus* sp. ou *Monotaxinoides* sp. – Laloux, pl. 3, fig. 85.
1987. *Eolasiodiscus donbassicus* Reitlinger – Laloux, pl. 3, fig. 86.
pars. 1988. *Monotaxinoides* aff. *transitorius* Brazhnikova and Yartseva – Laloux, pl. 2, fig. 40
[only].
1988. *Eolasiodiscus donbassicus* Reitlinger – Kulagina, pl. 3, fig. 22-23.
1989. *Eolasiodiscus donbassicus* Reitlinger – Sebbar and Lys, pl. 2, fig. 8.
1989. *Eolasiodiscus donbassicus* Reitlinger – Vachard et al., pl. 5, figs. 5, 6, 8.
?. 1991. *Eolasiodiscus maximus* Potievskaya – Marfenkova, pl. 8, fig. 23.
pars. 1991. *Monotaxinoides transitorius* Brazhnikova and Yartseva – Vachard and Beckary, pl. 1,
fig. 1; pl. 4, figs. 8, 9, 10, 11, 14.
1992. *Eolasiodiscus donbassicus* Reitlinger – Kulagina et al., pl. 5, figs. 16, 18; pl. 9, fig. 25; pl. 10,
fig. 29; pl. 11, fig. 22.
1993. *Eolasiodiscus donbassicus* Reitlinger – Vdovenko et al., pl. 13, figs. 10-11.
1993. *Eolasiodiscus donbassicus* Reitlinger – Mamet et al., pl. 12, fig. 14.
1993. *Eolasiodiscus* sp. – Ueno and Sakagami, fig. 2.5.
?. 1994. *Eolasiodiscus donbassicus* Reitlinger – Ueno et al., fig. 7.13-7.20.
1996. *Eolasiodiscus donbassicus* Reitlinger – Mamet, pl. 1, fig. 27.
1997. *Eolasiodiscus* sp. A – Matsusue, pl. 1, figs. 17-18.
1997. *Eolasiodiscus* sp. B – Matsusue, pl. 2, figs. 1-2.
1998. *Hemidiscus?* sp. – Pinard and Mamet, pl. 25, fig. 5.
2002. *Eolasiodiscus donbassicus* Reitlinger – Kulagina and Gibshman, figs. 17-18.
2009. *Eolasiodiscus donbassicus* Reitlinger – Stepanova and Kucheva, figs. 6.28, 13.28, (?) 9.27.

Hemidiscopsis caprariensis (Vachard, 1977) nov. comb.

1977. *Monotaxinoides? caprariensis* n. sp. – Vachard, pl. 6, figs. 18-20.
pars. 1992. *Monotaxinoides priscus* Brazhnikova and Yartseva – Kulagina in Kulagina et al., pl. 5, fig. 8 [only].
non. 1997. *Howchinia* trans *Monotaxinoides* sp. – Gallagher and Somerville, fig. 9f. [= *H. declivis*]
non. 2005. cf. '*Monotaxinoides*' sp. – Somerville and Cózar, pl. 1, fig. 1 [= *H. declivis*].
2011. "*Turrispiroides*" sp. – Cózar et al., fig. 10.17 [only].

Hemidiscopsis priscus (Brazhnikova and Yartseva, 1956) nov. comb.

1956. *Monotaxinoides priscus* sp. nov. – Brazhnikova and Yartseva, p. 65, pl. 1, figs. 4, 6.
1969. *Ammodiscus diadema umbonata* Potievskaya – Manukalova-Grebenyuk et al., pl. 2, figs. 25-28.
non. 1976. *Eolasiiodiscus priscus* (Brazhnikova and Yartseva) – Crousilles et al., pl. 38, fig. 21 [= *Planohowchinia espielensis*].
1983. *Monotaxinoides priscus* Brazhnikova and Yartseva – Aizenverg et al., pl. 14, fig. 10.
1989. *Monotaxinoides priscus* Brazhnikova and Yartseva – Sebbar and Lys, pl. 2, fig. 6.
non. 1992. *Monotaxinoides priscus* Brazhnikova and Yartseva – Groves, pl. 3, figs. 34-40.
pars. 1992. *Monotaxinoides priscus* Brazhnikova and Yartseva – Kulagina in Kulagina et al., pl. 5, fig. 10 [only].
?. 2001. *Monotaxinoides priscus* Brazhnikova and Yartseva – Vdovenko, pl. 4, fig. 41.
2003. *Monotaxinoides priscus* Brazhnikova and Yartseva – Brenckle and Milkina, pl. 5, fig. 26.
2010. *Monotaxinoides priscus* Brazhnikova and Yartseva – Stephenson et al., fig. 5a.
2011. *Monotaxinoides priscus* Brazhnikova and Yartseva – Cózar et al., fig. 10.18.

Hemidiscopsis muradymicus (Kulagina in Kulagina et al., 1992) nov. comb.

?. 1976. *Eolasiiodiscus curvus* (Potievskaya) – Crousilles et al., pl. 38, fig. 22.
1992. *Eolasiiodiscus muradymicus* sp. nov. – Kulagina in Kulagina et al., p. 72, pl. 5, figs. 9, 11.
2009. *Eolasiiodiscus muradymicus* Kulagina – Nikolaeva et al., pl. 1, fig. 41.
2014. *Eolasiiodiscus muradymicus* Kulagina – Kulagina et al., fig. 7.29.

Howchinia bradyana (Howchin, 1888) emend. Davis, 1951

1888. *Patellina bradyana* n. sp. – Howchin, p. 544, pl. 9, figs. 22-25.
1951. *Howchinia bradyana* (Howchin) – Davis, p. 248-253, pl. 10-11.
1956. *Monotaxis gibba* (Moeller) – Brazhnikova, pl. 2, fig. 8, pl. 10, fig. 16-17, pl. 13, figs. 3, 5.
1956. *Monotaxis gibba* (Moller) *longa* – Brazhnikova and Yartseva, pl. 1, figs. 1, 7.
1956. *Monotaxis* aff. *gibba* (Moller) *longa* – Brazhnikova and Yartseva, pl. 1, fig. 12.
1956. *Monotaxis ex gr. gibba* (Moller) – Brazhnikova and Yartseva, pl. 1, fig. 15.
pars. 1956. *Howchinia* – Reitlinger, pl. 1, figs. 1, 4.
pars. 1956. *Howchinia bradyana* (Howchin) – Reitlinger, pl. 1, figs. 5-7.
pars. 1967. *Howchinia gibba* (Moeller) – Brazhnikova et al., pl. 17, figs. 9, 15 [non pl. 15, fig. 8, pl. 17, fig. 9 = *H. gibba*].
1968. *Howchinia bradyana* (Howchin) – Mamet, pl. 5, figs. 5-6.
1970. *Howchinia bradyana* (Howchin) Davis – Austin et al., pl. 2, fig. 5.
1971. *Howchinia bradyana* (Howchin) – Hallett, pl. 4, fig. 17.
1973. *Howchinia bradyana* (Howchin) – Perret, pl. 1, figs. 25-26.
pars. 1973. *Howchinia gibba* (Moeller) – Bozorgnia, pl. 29, figs. 5, 7 [non fig. 8 = *H. gibba*].
pars. 1973. *Howchinia gibba* (Moeller) – Ivanova, pl. 9, fig. 22, pl. 20, fig. 14, pl. 31, fig. 23 [non pl. 20, fig. 15 = *H. gibba*].
1973. *Howchinia gibba longa* (Brazhnikova) (sic) – Ivanova, pl. 20, fig. 16, pl. 34, fig. 1.
1977. *Howchinia bradyana bradyana* (Howchin) – Vachard, pl. 6, fig. 9.

1977. *Howchinia bradyana longa* (Brazhnikova) – Vachard, pl. 6, fig. 13.
 non. 1978. *Howchinia bradyana* (Howchin) – Lys et al., pl. 1, fig. 20 [= *H. gibba*].
 1979. *Howchinia gibba* (Moeller) – Malakhova in Wagner et al., pl. 3, fig. 15.
 1980. *Howchinia bradyana* (Howchin) – Conil et al., pl. 14, figs. 21-26, pl. 30, fig. 14.
 1980. *Howchinia longa* (Brazhnikova) – Conil et al., pl. 14, fig. 20.
 pars. 1981. *Howchinia bradyana* (Howchin) – Fewtrell et al., pl. 10, figs. 9-10. [non pl. 3.9, fig. 13. = *H. gibba*].
 1983. *Howchinia gibba longa* Brazhnikova – Aizenverg et al., pl. 14, fig. 8.
 1984. *Howchinia bradyana* (Howchin) – Herbig, pl. 7, figs. 12-15.
 1985. *Howchinia gibba longa* Brazhnikova – Lys, pl. 1, fig. 3.
 1987. *Howchinia bradyana* (Howchin) Davis – Luo, pl. 2, fig. 8.
 1988. *Howchinia bradyana* (Howchin) – Laloux, pl. 1, figs. 5-6.
 pars. 1988. *Howchinia gibba* (Moeller) – Kulagina, pl. 1, fig. 9 [non pl. 1, fig. 10, pl. 3, fig. 18 = *H. gibba*].
 1990. *Howchinia bradyana* (Howchin) – Strogon et al., fig. 11b.
 1991. *Howchinia gibba* (Moeller) – Marfenkova, pl. 8, figs. 14-15.
 1991. *Howchinia gibba longa* Brazhnikova – Marfenkova, pl. 8, figs. 16.
 non. 1991. *Howchinia bradyana* (Howchin) – Amler et al., pl. 1, fig. 15 [= *H. gibba*].
 1991. *Howchinia* cf. *longa* (Brazhnikova) – Amler et al., pl. 1, fig. 14.
 1991. *Howchinia bradyana* (Howchin) – Vachard and Fadli, pl. 1, figs. 3, 10.
 1992. *Howchinia gibba* (Moeller) – Kulagina et al., pl. 6, fig. 37.
 1992. *Howchinia gibba longa* Brazhnikova – Kulagina et al., pl. 5, fig. 19.
 1992. *Howchinia bradyana* (Howchin) – Vachard and Berkhli, pl. 1, fig. 14.
 1992. *Howchinia bradyana longa* Brazhnikova – Somerville et al., Fig. 6d.
 non. 1993. *Howchinia bradyana* (Howchin) – Perret, pl. FV, fig. 11 [= *H. gibba*].
 pars. 1993. *Howchinia gibba* (Moeller) – Ueno and Nakazawa, fig. 3. 26 [only].
 1997. *Howchinia bradyana* (Howchin) – Gallagher and Somerville, fig. 9i.
 1997. *Howchinia bradyana* (Howchin) – Gallagher, pl. 2, fig. 14.
 non. 1999. *Howchinia bradyana* (Howchin) emend. Davis – Cózar and Rodríguez, pl. 2, fig. 1 [= *H. gibba*].
 pars. 2000. *Howchinia bradyana* (Howchin) Davis – Cózar, pl. 2, fig. 15 [non fig. 11 = *H. gibba*].
 non. 2001. *Howchinia bradyana bradyana* (Howchin) – Vdovenko, pl. 4, figs. 24-25 [= *H. gibba*].
 2001. *Howchinia bradyana longa* (Brazhnikova and Yarseva) (sic) – Vdovenko, pl. 4, figs. 26, 31,
 32.
 pars. 2001. *Howchinia* sp. – Vdovenko, pl. 4, fig. 27 [only].
 pars. 2002. *Howchinia gibba* (Moeller) – Krainer and Vachard, pl. 4, fig. 7 [only].
 non. 2003. *Howchinia bradyana* (Howchin) Davis – Cózar, fig. 40 [= *H. gibba*].
 2003. *Howchinia* sp. – Brenckle and Milkina, pl. 5, figs. 29.
 2004. *Howchinia bradyana* (Howchin) Davis – Cózar and Somerville, figs. 10.3-10.5.
 2004. *Howchinia bradyana* (Howchin) Davis – Cózar, pl. 1, fig. 17.
 2005. *Howchinia bradyana* (Howchin) Davis – Cózar and Somerville, fig. 13.23.
 2005. *Howchinia bradyana* (Howchin) Davis – Somerville and Cózar, pl. 1, fig. 3.
 2005. *Howchinia bradyana* (Howchin) Davis – Cózar et al., fig. 8.11.
 2005. *Howchinia gibba* (Moeller) – Cózar et al., fig. 8.12.
 pars. 2005. *Howchinia* ex gr. *gibba* (*Howchinia* sp. 2 cf. Lys) – Cózar et al., fig. 8.13 [only].
 2006. *Howchinia bradyana* (Howchin) – Gallagher et al., fig. 14.14.
 non. 2009. *Howchinia bradyana* (Howchin) – Nikolaeva et al., pl. 1, figs. 43 [= *H. sp.* 4].
 non. 2009. *Howchinia bradyana* (Howchin) – Gibshman et al., pl. 6, fig. 4 [= *H. gibba*].
 2013. *Howchinia bradyana* (Howchin) Davis – Cózar and Somerville, fig. 6a.

Howchinia beleutensis Vdovenko, 1962

1962. *Howchinia beleutensis* n. sp. – Vdovenko, p. 44, pl. 4, figs. 7-8.

1973. *Howchinia* cf. *subconica* (Brazhnikova and Yartseva) – Ivanova, pl. 31, fig. 24.
 1973. *Howchinia* aff. *subconica* (Brazhnikova and Yartseva) – Perret, pl. 1, fig. 25.
 ?. 1978. *Howchinia* n. sp. (à pseudotubes) – Lys et al., pl. 2, fig. 8.
 non. 1985. *Howchinia* n. sp. 2 – Lys, pl. 1, fig. 16 [= *H. subplana*], pl. 2, fig. 5 [= ?*H. enormis*].
 pars. 1985. *Howchinia* sp. – Adachi, pl. 22, figs. 2-3 [only].
 non. 1989. *Howchinia* sp. 2 Lys – Sebbar and Lys, pl. 2, fig. 5 [= *H. bradyana*].
 non. 1989. *Howchinia* à tubulures ombilicales – Skompski et al., pl. 6, fig. 16 [= *H. gibba*].
 1991. *Monotaxinoides acuta* Manukalova – Marfenkova, pl. 8, figs. 19-20.
 non. 1993. *Howchinia* sp. 2 Lys – Perret, pl. FV, figs. 7, 8, 10. [= *H. subplana*].
 pars. 1993. *Howchinia* cf. *subconica* (Brazhnikova and Yartseva) – Perret, pl. FV, fig. 3 [only].
 pars. 1993. *Monotaxinoides?* *subconicus* (Brazhnikova and Yartseva) (transition between *Monotaxinoides* and *Howchinia*) – Mamet et al., pl. 12, fig. 16 [only].
 1996. *Monotaxinoides subconica* Brazhnikova and Yartseva (sic) – Marfenkova in Einor, pl. 41, fig. 26.
 2000. *Howchinia* sp. 2 – Cózar, pl. 2, fig. 16.
 2003. "*Howchinia*" sp. 2 – Cózar, fig. 5L.
 2004. *Howchinia gibba* (Moeller) – Cózar et al., fig. 3, 17.
 2005. *Monotaxinoides belutensis* (Vdovenko) (sic) – Brenckle, pl. 11, fig. 8.
 non. 2005. *Howchinia* ex gr. *gibba* (*Howchinia* sp. 2 cf. Lys) – Cózar et al., fig. 8.13-8.15 [13 = *H. bradyana*; 14, 15 = *H. gibba*].
 2011. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Cózar et al., fig. 10.16.
 ?. 2011. *Monotaxinoides* ex gr. *subplana* (Brazhnikova and Yartseva) – Cózar et al., fig. 10.19, 10.21.
 non. 2013. *Howchinia* sp. 2 sensu Lys (= ? *H. beleutensis*) – Somerville et al., fig. 4.8 [= *H. cantabrica*].

Howchinia convexa (Brazhnikova in Aizenverg et al., 1983)

1979. *Monotaxinoides* sp. 1 – Brazhnikova in Wagner et al., pl. 5, figs. 8-9.
 1983. *Monotaxinoides convexus* sp. nov. – Brazhnikova in Aizenverg et al., pl. 14, figs. 17-18.
 pars. 1985. *Howchinia* sp. – Adachi, pl. 22, fig. 4 [only].
 ?. 1987. *Howchinia gibba* (Moeller) – Luo, pl. 2, fig. 5.
 1989. *Monotaxinoides* sp. – Skompski et al., 1989, pl. 6, fig. 20.
 non. 1992. *Monotaxinoides convexus* Brazhnikova – Kulagina et al., pl. 8, fig. 22.
 1993. forme de passage *Howchinia subconica*-*Howchinia bradyana* – Perret, pl. FV, fig. 4.
 pars. 1993. *Howchinia* cf. *subconica* (Brazhnikova and Yartseva) – Perret, pl. FV, figs. 5 [only].
 pars. 1993. *Monotaxinoides?* *subconicus* (Brazhnikova and Yartseva) (transition between *Monotaxinoides* and *Howchinia*) – Mamet et al. pl. 12, fig. 16 [only].
 pars. 2005. *Monotaxinoides?* sp. – Cózar et al., fig. 8.17 [only].
 2010. *Howchinia* sp. – Cózar et al., fig. 4f.

Howchinia gibba (Moeller, 1879)

- pars. 1879. *Tetrataxis conica* var. *gibba* n. var. – Moeller, p. 173, pl. 7, fig. 3 [only].
 non. 1956. *Monotaxis gibba* (Moeller) – Brazhnikova, pl. 2, fig. 8, pl. 10, fig. 16-17, pl. 13, figs. 3, 5 [= *H. bradyana*].
 non. 1956. *Monotaxis gibba* (Moller) *longa* – Brazhnikova and Yartseva, fig. 1.3, pl. 1, figs. 1, 7 [= *H. bradyana*].
 non. 1956. *Monotaxis* ex gr. *gibba* (Moller) – Brazhnikova and Yartseva, pl. 1, fig. 15 [= *H. bradyana*].
 1956. *Howchinia* – Reitlinger, pl. 1, fig. 2 [only].
 1956. *Monotaxis* aff. *gibba* (Moller) *longa* – Brazhnikova and Yartseva, pl. 1, figs. 12 [= *H. bradyana*].

- ? 1963 *Howchinia gibba* (Moeller) – Conil, pl. 1, fig. 5.
 non. 1964. *Howchinia gibba* (Moeller) – Conil and Lys, pl. 14, fig. 264 [= *H. sp.* 3].
 pars. 1967. *Howchinia gibba* (Moeller) – Brazhnikova et al., pl. 15, fig. 8, pl. 17, fig. 9. [non pl. 17, figs. 9, 15 = *H. bradyana*].
 non. 1967. *Howchinia gibba* (Moeller) forma *minina* – Brazhnikova et al., pl. 15, fig. 5. [= ?*H. bradyana*].
 ? 1970. *Howchinia sp.* – Gorecka and Mamet, pl. 3, fig. 8
 pars. 1973. *Howchinia gibba* (Moeller) – Bozorgnia, pl. 29, fig. 8 [non figs. 5, 7 = *H. bradyana*].
 pars. 1973. *Howchinia gibba* (Moeller) – Ivanova, pl. 20, fig. 15 [non pl. 9, fig. 22, pl. 20, fig. 14, pl. 31, fig. 23 = *H. bradyana*]
 non. 1973. *Howchinia gibba longa* (Brazhnikova) (sic) – Ivanova, pl. 20, fig. 16, pl. 34, fig. 1 [= *H. bradyana*].
 1978. *Howchinia bradyana* (Howchin) – Lys et al., pl. 1, fig. 20.
 1979. *Howchinia gibba* (Moeller) – Brazhnikova in Wagner et al., pl. 2, fig. 5.
 pars. 1981. *Howchinia bradyana* (Howchin) – Fewtrell et al., pl. 3.9, fig. 13 [only].
 1980. *Howchinia gibba longa* (Brady) (sic) – Skompski and Sobon-Podgorska, pl. 4, figs. 1, 3.
 pars. 1985. *Howchinia sp.* – Adachi, pl. 22, figs. 1, 5 [only].
 non. 1985. *Howchinia gibba longa* Brazhnikova – Lys, pl. 1, fig. 3 [= *H. bradyana*].
 non. 1987. *Howchinia gibba* (Moeller) – Luo, pl. 2, fig. 5 [= ? *H. convexa*]
 pars. 1988. *Howchinia gibba* (Moeller) – Kulagina, pl. 1, fig. 10, pl. 3, fig. 18 [non pl. 1, fig. 9 = *H. bradyana*].
 1988. *Howchinia gibba* (Moeller) – Ivanova, pl. 2, fig. 23.
 1989. *Howchinia* à tubulures ombilicales – Skompski et al., pl. 6, fig. 16.
 1989. *Howchinia gibba* (Moeller) – Ueno, pl. 7, fig. 14.
 1991. *Howchinia bradyana* (Howchin) – Amler et al., pl. 1, fig. 15.
 non. 1991. *Howchinia gibba* (Moeller) – Marfenkova, pl. 8, figs. 14-15 [= *H. bradyana*].
 non. 1991. *Howchinia gibba longa* Brazhnikova – Marfenkova, pl. 8, figs. 16 [= *H. bradyana*].
 non. 1992. *Howchinia gibba longa* Brazhnikova – Kulagina et al., pl. 5, fig. 19 [= *H. bradyana*].
 non. 1992. *Howchinia gibba* (Moeller) – Kulagina et al., pl. 6, fig. 37 [= *H. bradyana*].
 1993. *Howchinia bradyana* (Howchin) – Perret, pl. FV, fig. 11.
 1993. *Howchinia bradyana* (Howchin) – Vdovenko in Makhlina et al., pl. 18, fig. 23.
 non. 1993. *Howchinia gibba* (Moeller) – Ueno and Nakazawa, fig. 3.25 [= *H. sp.* 5], fig. 3. 26 [= *H. bradyana*].
 1996. *Howchinia gibba* (Moeller) – Marfenkova in Einor, pl. 41, fig. 27.
 1999. *Howchinia bradyana* (Howchin) emend. Davis – Cózar and Rodríguez, pl. 2, fig. 1.
 pars. 2000. *Howchinia bradyana* (Howchin) emend. Davis – Cózar, pl. 2, fig. 11 [only].
 2001. *Howchinia bradyana bradyana* (Howchin) – Vdovenko, pl. 4, figs. 24-25.
 pars. 2002. *Howchinia gibba* (Moeller) – Krainer and Vachard, pl. 4, figs. 5, 6, 8 [non fig. 7 = *H. bradyana*].
 2003. *Howchinia bradyana* (Howchin) emend. Davis – Cózar, fig. 40.
 2004. *Howchinia gibba* (Moeller) – Cózar and Somerville, figs. 10.3-10.5.
 2005. *Howchinia gibba* (Moeller) – Cózar and Somerville, pl. 1, fig. 4.
 non. 2005. *Howchinia gibba* (Moeller) – Cózar et al., fig. 8.12 [= *H. bradyana*].
 pars. 2005. *Howchinia ex gr. gibba* (*Howchinia sp.* 2 cf. Lys) – Cózar et al., fig. 8.14-8.15 [only].
 2009. *Howchinia bradyana* (Howchin) – Gibshman et al., pl. 6, fig. 4.
 2010. *Howchinia gibba* (Moeller) – Cózar et al., figs. 4d, 4q.
 2013. *Howchinia gibba* (Moeller) – Cózar and Somerville, figs. 6c.

Howchinia subconica (Brazhnikova and Yartseva, 1956)

1956. *Montaxis subconica* n. sp. – Brazhnikova and Yartseva, pl. 1, figs. 13-14, 16.
 1973. *Howchinia subconica* (Brazhnikova and Yartseva) – Ivanova, pl. 20, fig. 17-18.

- non. 1973. *Howchinia* cf. *subconica* (Brazhnikova and Yartseva) – Ivanova, pl. 31, fig. 24 [= *H. beleutensis*].
- non. 1973. *Howchinia* aff. *subconica* (Brazhnikova and Yartseva) – Perret, pl. 1, fig. 25 [= *H. beleutensis*].
- non. 1979. *Montaxinoides* cf. *subconica* (Brazhnikova and Yartseva) – Brazhnikova in Wagner et al., pl. 3, fig. 16 [= *H. acutiformis*].
1979. *Montaxinoides subconica* (Brazhnikova and Yartseva) – Brazhnikova in Wagner et al., pl. 9, fig. 6.
1985. *Howchinia subconica* (Brazhnikova and Yartseva) – Adachi, pl. 21, fig. 32.
- pars. 1985. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Adachi, pl. 21, fig. 31 [only].
- pars. 1987. *Howchinia subconica* (Brazhnikova and Yartseva) – Luo, pl. 2, fig. 6 [non fig. 7 = *H. acutiformis*].
1988. *Howchinia subconica* (Brazhnikova and Yartseva) – Kulagina, pl. 3, fig. 19.
- non. 1991. *Monotaxinoides subconica* Brazhnikova and Yartseva (sic) – Marfenkova, pl. 8, fig. 21 [= *H. variabilis*].
- non. 1993. *Howchinia* cf. *subconica* (Brazhnikova and Yartseva) – Perret, pl. FV, figs. 2 [= *H. hemisphaerica*], 3 [= *H. beleutensis*], 5 [= *H. convexa*].
- pars. 1993. *Monotaxinoides? subconicus* (Brazhnikova and Yartseva) (transition between *Monotaxinoides* and *Howchinia*) – Mamet et al., pl. 12, fig. 17 [non fig. 16 = *H. beleutensis*].
- non. 1996. *Monotaxinoides subconica* Brazhnikova and Yartseva (sic) – Marfenkova in Einor, pl. 41, fig. 26 [= *H. beleutensis*].
- ?. 2001. *Howchinia subplana* Brazhnikova and Yartseva (sic) forma *minima* – Vdovenko, pl. 4, figs. 44-46.
- pars. 2001. *Howchinia subconica* Brazhnikova and Yartseva (sic) forma *minima* – Vdovenko, pl. 4, fig. 43 [non fig. 42 = *H. cantabrica*].
- non. 2010. *Monotaxinoides subconica* (Brazhnikova and Yartseva) – Stephenson et al., fig. 5b [*H. acutiformis*].

Howchinia subplana (Brazhnikova and Yartseva, 1956)

1956. *Monotaxis subplana* n. sp. – Brazhnikova and Yartseva, p. 64, pl. 1, figs. 9-11.
- pars. 1974. *Howchinia declive plana* n. ssp. – Monostori, pl. 2, fig. 4 [only].
1981. *Monotaxinoides* sp. B – Igo and Adachi, pl. 6, fig. 22.
1983. *Monotaxinoides subplanus* (Brazhnikova and Yartseva) – Aizenverg et al. 1983, pl. 14, figs. 4-5.
- pars. 1985. *Howchinia* n. sp. 2 – Lys, pl. 1, fig. 16 [non pl. 2, fig. 5 = ?*H. enormis*].
- pars. 1985. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Adachi, pl. 21, fig. 30 [non fig. 31 = *H. subconica*]
- non. 1987. *Howchinia subplana* (Brazhnikova and Yartseva) – Luo, pl. 2, fig. 9.
- pars. 1988. *Monotaxinoides subplanus* (Brazhnikova and Yartseva) – Kulagina, 1988, pl. 2, fig. 23 [non pl. 3, figs. 20-21 = *H. cantabrica*]
1990. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Vdovenko et al., pl. 1, fig. 30.
- non. 1991. *Monotaxinoides subplana* Brazhnikova and Yartseva (sic) – Marfenkova, pl. 8, figs. 17 [= *H. cantabrica*], 18 [= *H. variabilis*].
1991. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Gibshman and Akhmetshina, pl. 3, fig. 18.
1992. *Monotaxinoides* sp. – Kulagina et al., pl. 5, fig. 14.
- pars. 1992. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Kulagina et al., pl. 5, fig. 17, pl. 8, fig. 23 [non fig. 20 = *H. enormis*].
- non. 1993. *Howchinia subplana* (Brazhnikova and Yartseva) – Perret, pl. FV, figs. 6, 9.
1993. *Howchinia* sp. 2 Lys – Perret, pl. FV, figs. 7, 8, 10.
- pars. 1993. *Monotaxinoides? subconicus* (Brazhnikova and Yartseva) (transition between *Monotaxinoides* and *Howchinia*) – Mamet et al., pl. 12, fig. 17 [only].

- non. 2001. *Howchinia subplana* Brazhnikova and Yartseva (sic) forma *minima* – Vdovenko, pl. 4, figs. 44-46 [= *H. hemisphaerica*].
2002. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Kulagina and Gibshman, pl. 1, fig. 12.
- non. 2003. *Monotaxinoides cf. subplanus* (Brazhnikova and Yartseva) – Brenckle and Milkina, pl. 5, fig. 25 [= ? *M. gracilis*]
- non. 2010. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Stephenson et al., fig. 5c [= *H. cantabrica*].
2011. *Monotaxinoides subplana* (Brazhnikova and Yartseva) – Cózar et al., fig. 10.16.
- pars. 2014. *Monotaxinoides subplanus* (Brazhnikova and Yartseva) – Kulagina et al., figs. 6.24, 7.31 non figs. 7.30 [= *H. cantabrica*], 7.32 [*H. enormis*].
- non. 2014. *Monotaxinoides ex gr. subplanus* (Brazhnikova and Yartseva) – Kulagina et al., fig. 7.25 [= *M. gracilis*].

Monotaxinoides gracilis (Dain in Reitlinger, 1956)

1956. "*Ammodiscus*" *gracilis* n. sp. – Dain in Reitlinger, pl. 1, fig. 8.
1973. *Monotaxinoides gracilis* (Dain) – Ivanova, pl. 31, fig. 26.
1973. *Eolasiiodiscus* du type *Monotaxinoides gracilis* Dain? – Perret, pl. 1, fig. 23.
1979. *Monotaxinoides gracilis* (Dain) – Brazhnikova in Wagner et al., pl. 5, fig. 7.
1983. *Monotaxinoides gracilis* (Dain) – Aizenverg et al., pl. 14, fig. 6.
1985. *Eolasiiodiscus* sp. A – Adachi, pl. 21, figs. 20-21.
1991. *Eolasiiodiscus gracilis* (Dain) – Marfenkova, pl. 9, fig. 19.
- pars. 1991. *Monotaxinoides transitorius* Brazhnikova and Yartseva – Vachard and Beckary, pl. 4, fig. 12 [only].
1992. *Monotaxinoides gracilis* (Dain) – Kulagina et al., pl. 5, figs. 5, 7; pl. 15, fig. 24.
- pars. 1992. *Monotaxinoides transitorius* Brazhnikova and Yartseva – Kulagina et al., pl. 6, fig. 36.
1992. *Monotaxinoides* sp. – Kulagina et al., pl. 15, fig. 25.
1993. *Monotaxinoides? gracilis* Dain (sic) – Perret, pl. FV, fig. 1.
1997. *Monotaxinoides* sp. – Harris et al., Fig. 8.13.
2002. *Monotaxinoides gracilis* Dain (sic) – Kulagina and Gibshman, figs. 13-15.
2003. *Monotaxinoides cf. subplanus* (Brazhnikova and Yartseva) – Brenckle and Milkina, pl. 5, fig. 25.
2009. *Monotaxinoides gracilis* Dain – Nikolaeva et al., pl. 1, fig. 47.
- ? 2009. *Monotaxinoides* sp. – Nikolaeva et al., pl. 1, fig. 42.
2014. *Monotaxinoides gracilis* Dain – Kulagina et al., figs. 7.24, 7.26.
2014. *Monotaxinoides ex gr. subplanus* (Brazhnikova and Yartseva) – Kulagina et al., fig. 7.25.

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