Isostrophic molluscs (Tergomya and Gastropoda) from the Upper Ordovician of Norway

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Ten species of Upper Ordovician isostrophic Tergomya and Gastropoda (Mollusca) are described from the Oslo Region, Norway. *Sinuitina*, represented by *Sinuitina*? *planilata* sp. nov., is considered a cyrtonellid tergomyan, based on interpretation of the umbilico-lateral sinuses as inhalant emarginations, though it differs from the type species in possessing a selenizone. Three species of cap-shaped gastropods are referred to *Archinacella,* demonstrating a wide variation in shell morphology. Muscle scars in *Sinuites usitatus*? Isakar, 1991 resemble those found in comparable species in Bohemia. *Tropidodiscus laticonchus* sp. nov. and *T. maximus* sp. nov. differ markedly from the type species in their large size, wide umbilici and the high number of whorls, while *T.* sp. differs in having narrow (for the genus) umbilici. *Cymbularia pachygaster* (Koken *in* Koken & Perner 1925) and *C. bullatus* (Koken *in* Koken & Perner 1925) are synonymized, and it is shown that the umbilici of the species are not plugged but partially covered by infolding of the lateral lip.

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Introduction

In this paper we revise Norwegian Upper Ordovician isostrophic tergomyan and gastropod molluscs from the Oslo Region, Norway. Their distinctive shells, coiled in one plane normal to the axis of coiling and bilaterally symmetrical about the plane in which they coil, makes them conspicuous elements of Palaeozoic communities. In Baltoscandia they are diverse but usually represented by few specimens. This is the fourth paper revising such molluscs from the Ashgill of Norway (Yochelson 1977; Ebbestad 1999a, b). Yochelson (1977) described five genera with eight species of tergomyan monoplacophoran molluscs from the Oslo Region, therefore there is no need to re-illustrate or redescribe these here, but the distributions of these molluscs are included in Fig. 2.

The recently revised classification of monoplacophoran molluscs outlined by Peel (1991a) and partly by Wahlman (1992) is followed here. Peel (1991a) formalized the two classes Tergomya and Helcionelloida to replace the class Monoplacophora in terms of formal systematics. Material presented here of assumed untorted molluscs falls within the tergomyan Order Cyrtonellida (e.g. *Sinuitina*? *planilata* sp. nov.), while the remaining specimens are considered gastropods, i.e. molluscs that have undergone torsion in their early ontogeny. A total of 10 species from 12 localities in three districts of the Oslo Region (Fig. 1) are discussed in the light of the modern Ordovician stratigraphy of the Oslo Region (Owen et al. 1990; Heath & Owen 1991). Eight new taxa are recognized, though 6 out of the 10 species are represented by fewer than 3 specimens, mostly from old collections around the turn of the 19th century. Detailed information on stratigraphy is only known for a few specimens, and accordingly only a sketchy distribution can be constructed (Fig. 2). Nevertheless, several interesting morphological features are demonstrated or highlighted within this material, usually showing uncertainties in generic concepts rather than solving key questions on morphology or systematics (e.g. emarginations in *Sinuitina*? *planilata* sp. nov.; shell size, nature of the umbilici and number of whorls in *Tropidodiscus laticonchus* sp. nov., *T. maximus* sp. nov. and *T.* sp.;

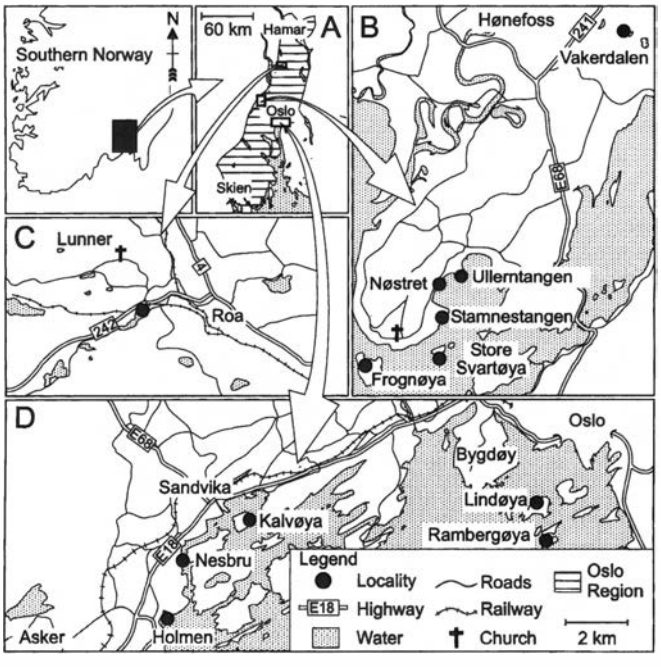


Fig. 1. Locality map showing the Oslo Region. A: Palaeozoic sedimentary and igneous rocks marked with crosses. B: Ringerike district. C: Hadeland district. D: Oslo–Asker district.

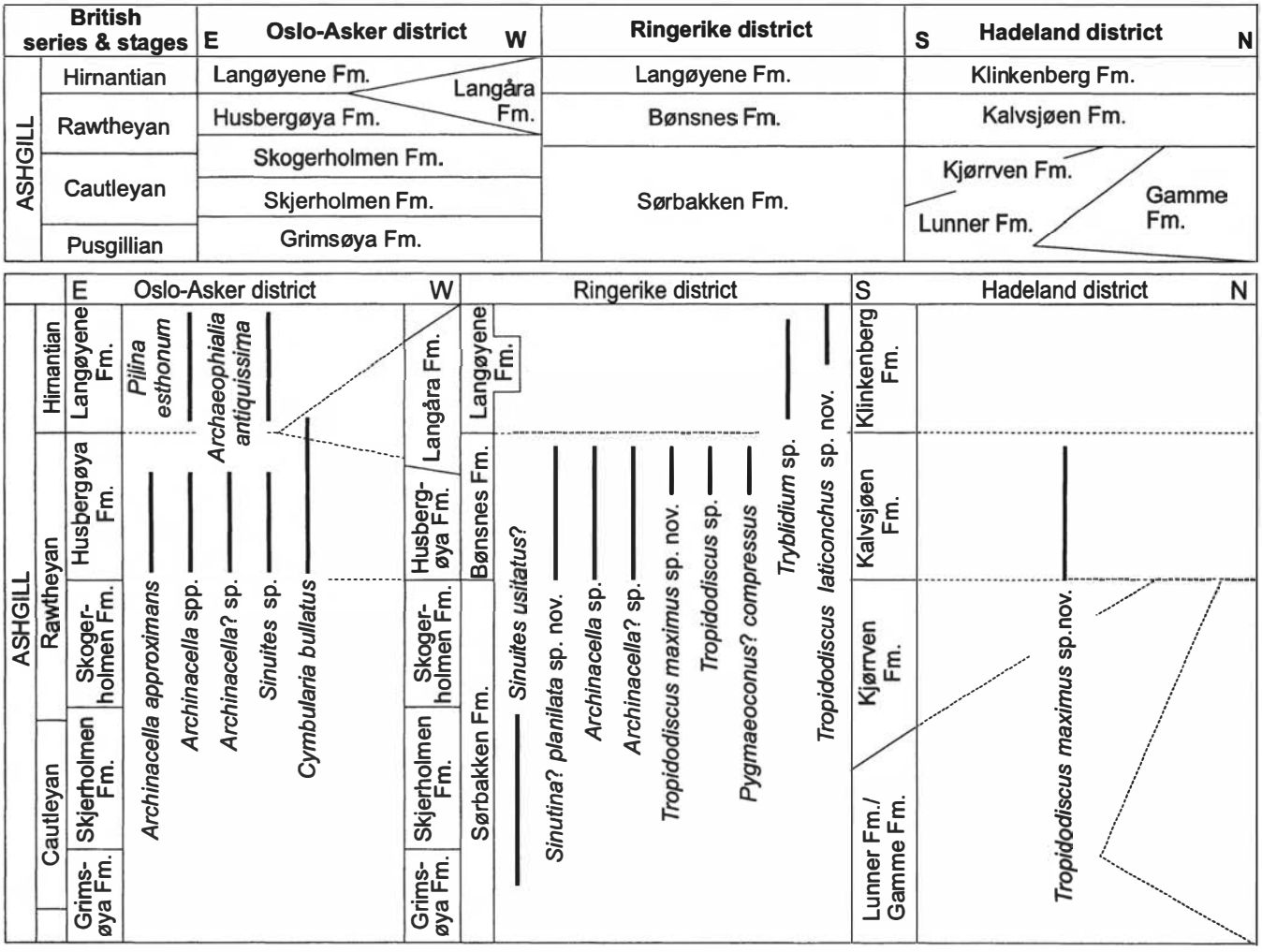


Fig. 2. Stratigraphical framework (upper half) and distribution of Upper Ordovician Tergomya and Gastropoda of the Oslo Region (lower half). Stratigraphical scheme based on Owen et al. (1990) and Heath & Owen (1991). Specimens described by Yochelson (1977) included.

ontogeny and infolding of lateral lips in *Cymbularia bullatus* (Koken *in* Koken & Perner 1925)).

The material discussed here is housed in the Palaeontological Museum, University of Oslo (PMO) and in the Swedish Museum of Natural History, Stockholm (RM). Where known, the localities are indicated with their UTM coordinates (Norwegian topographical maps, series M 711, scale = 1:50 000). Prior to photography, the specimens were painted with photographic opaque and whitened with ammonium chloride sublimate. All photographs were taken by J. O. R. Ebbestad.

Systematic palaeontology

Class Tergomya Horný, 1965

Order Cyrtonellida Horný, 1963

Genus *Sinuitina* Knight, 1945

Type species. – By original designation of Knight (1945, p. 333); *Tropidocyclus cordiformis* Newell, 1935, p. 349, pl. 36, fig. 1b–d, from the Missourian Lansing shales near Wann, Washington County, Oklahoma, USA.

Remarks. – The type species and at least 10 species represent this long-ranging genus in the Upper Ordovician to the Carboniferous of Laurentia, Baltica and Gondwana. Lower Palaeozoic species include *S.*? sp. *sensu* Yu (1975) from the Ordovician of China, *S.*? *planilata* sp. nov. from the Ashgill of Norway and *S. reyesi* Fischer, 1969 from the Wenlock? of Bolivia. The position of *Sinuitina* is not well understood and it has been interpreted both as an exogastric tergomyan (Starobogatov 1970; Runnegar & Jell 1976) and an endogastric gastropod (Knight 1945; Rollins et al. 1971; Knight et al. 1960; Wahlman 1992). Interpretation of possible muscle scars in the Devonian *S. spinari* Horný, 1963 from Bohemia is controversial and has not contributed towards resolving the taxonomic position of the genus (see Horný 1963b; Runnegar & Jell 1976; Berg-Madsen & Peel 1978).

Starobogatov (1970) interpreted *Sinuitopsis* as an untorted mollusc, based on a functional interpretation of the median anterior and two umbilico-lateral sinuses. He argued that the maximum oxygen supply to the gills (single

pair) and the most efficient discharge of water would be achieved with the median dorsal sinus acting as the exhalant opening and the lateral sinuses working as inhalant openings. Comparison was made with *Bucanella, Sinuitina* and *Trigyra* sharing a similar morphology. Along the same lines of argument, Berg-Madsen & Peel (1994) reconstructed *Telamocornu cambriense* from the Upper Cambrian of Wales as an exogastric tergomyan mollusc, also including *Sinuitella, Sinuitopsis* and *Pharetrolites* within this group. These functional considerations also allow an interpretation of *Sinuitina* as an untorted cyrtonellid tergomyan. Besides the distinct umbilico-lateral sinuses, all genera mentioned above share a typical broad, rapidly expanding shell with few whorls, an acute dorsum, slight embracing of earlier whorls and circumbilical angulations associated with the lateral sinuses.

Sinuitina? *planilata* sp. nov.

Fig. 3A–H

Derivation of name. – From Latin *Planus,* meaning level or flat, and *Latus,* meaning side, referring to the near vertical lateral surfaces in this species.

Diagnosis. – A species of *Sinuitina*? with a markedly changed whorl profile during ontogeny; from ovate in early whorls to development of peripheral angulations yielding near vertical upper whorl surfaces just above the periphery in last whorl.

Holotype. – PMO 17640, Fig. 3A–H, from the Bønsnes Formation, Stamnestangen, Ringerike (NM 681597). An internal mould with patchy shell preservation.

Paratype. – PMO 18125b. A fragmentary specimen from the same locality and formation as the holotype.

Description. – The shell is about 25 mm in length and 15 mm in width, with three rapidly expanding whorls. About half the height of a whorl is embraced by the succeeding whorl. Profile of upper surface acute above periphery, with an angle of about 35° to the plane of symmetry, and culminating in a distinctly raised median dorsal keel. Whorl profile rounded in early ontogeny, with circumbilical angulation developing in the penultimate whorl. The periphery of the last whorl is at median height of the whorl, with near vertical lateral surfaces above umbilical angulation. Umbilical surfaces are slightly concave in the last whorl, sloping towards shallow sutures. Umbilici narrow and deep. Circumbilical angulations end in a small but prominent sinus on each umbilico-lateral margin; a second angulation is formed at the peripheries during the last 1/3 of the whorl (adaperturally) with a weakly concave area between the two angulations. The median dorsal sinus is probably narrow and with a short notch-like slit, but is unknown in detail. A median dorsal keel is developed with an apparent median line and gently concave lateral transitions to lateral surfaces. Prosocyrt growth lines meet the selenizone at a high angle to form spiral bordering lirae; other ornamentation unknown. The lunulae are more strongly expressed than the growth lines, being distinctly V-shaped and raised medianly, creating a cord-like impression and the illusion of a raised median line in the selenizone.

Remarks. – The changed inclination of the umbilical and lateral surfaces during ontogeny is a distinctive feature of *S.*? *planilata,* though the lateral angulations of the periphery and transition to the umbilici do not develop until the final whorl. Given the large size of the specimen, it may be a feature related to maturity. Circumbilical angulations are seen to develop late in the ontogeny of the much smaller type species *S. cordiformis* (Newell 1935) as well, but this lacks the prominent peripheral angulation of *S.*? *planilata.* The distinct umbilico-lateral sinuses forming in the last whorl are typical of *Sinuitina*, which is also characterized by a rapidly expanding, broad shell with few whorls, acute dorsum, and a 'pseudoselenizone' (Knight 1945) formed by the V-shaped growth lines on the median dorsal area. In all but this respect, *S.*? *planilata* conforms well with the general morphology of the type species, but the median dorsal cord-like keel in the former species is distinctly delimited and is probably made by a small notch-like slit, creating a true selenizone. In so far as the distinction between a sinus and a short parallel-sided slit in this morphology need only be slight, assignment to *Sinuitina* is not ruled out. In proposing a tentative generic placement for *S.*? *planilata* account is taken of this difference and consideration is taken of the functional similarities. The stratigraphical distinction between *S.*? *planilata* and the type species would allow structural modifications of certain characters (e.g. median and lateral sinuses) without drastically changing their function, but may of course also allow time for convergence to take place.

The morphologically similar *S.*? *planilata* and *S. reyesi* Fischer, 1969 from the Lower Silurian of Bolivia may be compared in sharing a distinct concave lateral area between the periphery and umbilico-lateral angulation on the last whorl, and the cord-like median dorsal band, features not seen in other species of *Sinuitina.* However, the delimitation of the median area in *S. reyesi* seems to conform well with *Sinuitina* proper, and the reticulated ornamentation differs also from that of *S.*? *planilata.*

Yochelson (1963) redescribed two lower Llanvirn species, *Pharetrolites*? *elegans* (Koken *in* Koken & Perner 1925) and *P.*? *tumidus* (Koken *in* Koken & Perner 1925) from Norway, but stated that they could just as well be placed within *Sinuitina.* Their exact stratigraphical position is unknown. Morphologically, the two species are close and differ mostly from *S.*? *planilata* in having a more lenticular shell with a somewhat greater rate of whorl expansion, lacking umbilical angulation and not showing distinct umbilico-lateral sinuses. The median dorsal sinus is developed without a slit and selenizone, though a minor

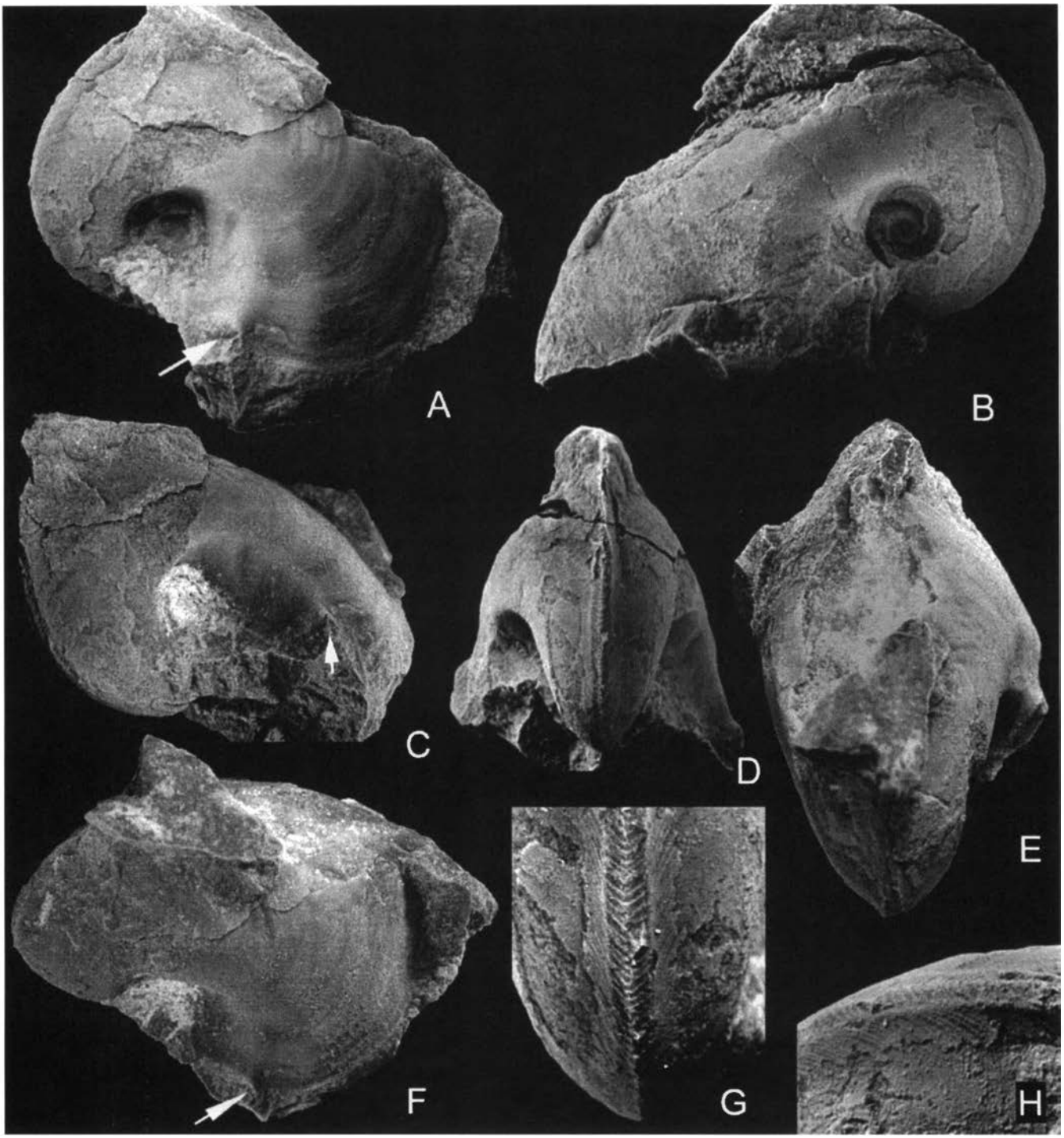


Fig. 3. A–H: *Sinuitina*? *planilata* sp. nov. from the Bønsnes Formation, Stamnestangen, Ringerike (NM 681597). Left, right, anterior oblique, anterior, dorsal, dorsal oblique, dorsal detail and oblique detail views of holotype PMO 17640. A–F ×3; G, H ×6. Coll.: J. Kiær 1914.

median dorsal elevation creates a cord-like line similar to that seen in *S.*? *planilata.*

Class Gastropoda Cuvier, 1797

Family Archinacellidae Knight, 1956
Genus *Archinacella* Ulrich & Scofield, 1897

Type species. – By original designation; *Archinacella powersi* Ulrich & Scofield, 1897, p. 829, pl. 61, figs. 3, 5, from the Blackriverian Platteville Limestone at Beloit, Wisconsin, USA.

Remarks. – More than 50 species, mostly of Ordovician age in Laurentia, Baltica and Gondwana, have been attributed to this genus (see Ulrich & Scofield 1897; Bassler 1915; Koken & Perner 1925; Horný 1963a, 1996b; Yochelson 1977; Wahlman 1992; Peel & Horný 1999).

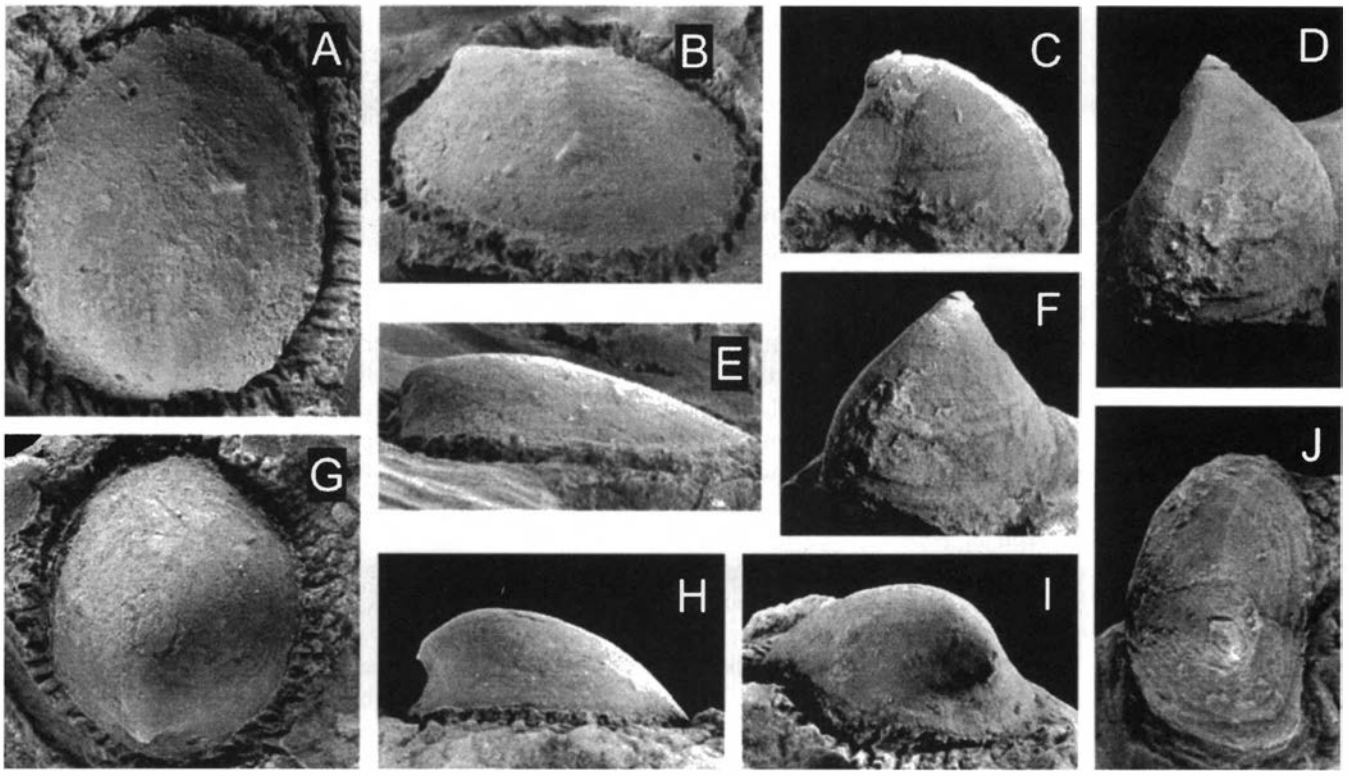


Fig. 4. A, B, E: *Archinacella* sp. 1 (PMO 55863) from the Bønsnes Formation, Nøstret in Sælabonn, Ringerike (NM 677607). Dorsal, lateral and anterior oblique views, ×2.25. Coll.: J. Kiær. C, D, F, J: *Archinacella* sp. 2 (PMO 165.666) from the Husbergøya Formation, Rambergøya, Oslofjord (NM 960395). Dorsal, right lateral, anterior and anterior oblique views, ×4.5. Coll.: M. Høyberget 1996. G–I. *Archinacella*? sp. (PMO 55867) from the Bønsnes Formation, Nøstret in Sælabonn, Ringerike (NM 677607). Dorsal, right lateral and posterior oblique views, ×2.5. Coll.: J. Kiær.

The genus is characterized by a patelliform shell, an entire muscle band around the periphery of the shell interior and tear-like attachment areas laterally to the apex (see Horný 1996b and references therein). Horný (1963a) distinguished *Archinacellina,* from the Ordovician of Bohemia, in which the muscle band leaves discontinuous scars around the periphery of the shell. A detailed summary of the history and views on the systematic position of *Archinacella* and related genera was given by Peel & Horný (1999), who concurred with the point of view that *Archinacella* and allied forms without multiple series of muscle scars should be regarded as gastropods (Starobogatov 1970; Harper & Rollins 1982; Yochelson 1988; Peel 1990; Horný 1996b; but see Wahlman 1992 for different views).

Yochelson (1977) described all the then known cap-shaped species of assumed untorted molluscs from the Ashgill of the Oslo Region. Only a few new patelliform shells, all tentatively referred to *Archinacella sensu lato,* have been collected from these strata. Apart from displaying morphological variation, they contribute little towards the taxonomy and detailed morphology of this group. However, for the sake of completeness they are presented here.

Archinacella sp. 1

Fig. 4A, B, E

Remarks. – This specimen (PMO 55863), from the Bønsnes Formation at Nøstret, Ringerike (NM 677607), is 20 mm long, 17 mm wide and 5 mm high, and resembles in its general morphology the type species of *Archinacella.* The most important differences are the lower profile and the relatively more elongated shell in the Norwegian species. Weak lateral lines on the right side of the shell may indicate muscle scars, but can equally well represent impressions of shell ornamentation or just be artefacts of preservation.

Archinacella sp. 2

Fig. 4C, D, F, J

1977 *Archinacella* sp.; Yochelson, p. 306, pl. 2I, J.

Remarks. – Yochelson (1977, p. 306) described a specimen (PMO 11847) from what is now the Husbergøya Formation on Lindøya in the Oslofjord (NM 960403), having a laterally compressed high-coned shell with the apex close to the margin. An additional specimen (PMO 165.666) from the same formation on Rambergøya in the Oslofjord (NM 960395) is here attributed to this species. Both are internal moulds, but the new specimen shows weak impressions of growth ornamentation. The fact that the shell on the right lateral side seems to have been pushed inwards, possibly during burial, affects the appearance of the shell and the position of the apex; otherwise it matches the morphology of the specimen described by Yochelson (1977). Measurements of specimen PMO 165.666: maxi-

mum length is 9 mm, width equals 55 mm and height is 7 mm.

Archinacella? sp.

Fig. 4G–I

Remarks. – PMO 55867 is an internal mould from the Bønsnes Formation at Nøstret, Ringerike (NM 677607). This species is distinguished by the almost circular aperture (length = 14 mm; width = 12 mm) and the distinct curvature of the apex area. Maximum height is 5 mm and is reached at 2/3 the length of the shell measured from the anterior margin. The convex lateral profile displays an increased curvature towards the apex, which is not overhanging the posterior margin; the sub-apical wall is strongly concave. A comparable species is *Archinacella approximans* Perner *in* Koken & Perner, 1925 from the same level in Norway, which is only known from a single, much smaller specimen. Other Baltoscandian species differ in the shape of the shell, but intergradation of morphologies may be an important factor among these cap-shaped shells (Yochelson 1977).

Family Sinuitidae Dall *in* Eastmann, 1913

Genus *Sinuites* Koken, 1896

Type species. – By subsequent designation of Bassler (1915, p. 1159); *Bellerophon bilobatus* Sowerby, 1839, p. 643, pl. 19, fig. 13, from the Caradoc at Horderley, Shropshire, England.

Remarks. – Much controversy surrounds this genus regarding the discussion on preserved muscle scars of torted versus untorted molluscs (see Wahlman 1992; Horný 1990, 1991, 1992, 1996a; Peel 1991a for references to the extensive literature). Horný (1990, 1992) found that *Sinuites* was a torted mollusc, i.e. a gastropod, partly based on extensive studies of morphology and muscle scars in the Czech Lower Ordovician species *Sinuites sowerbyi* Perner, 1903 and *S. reticulatus* Perner, 1903, a view that is also taken here (see also Peel 1991a, p. 28).

A large number of *Sinuites* species have been named, with widespread distribution in Laurentia, Baltica and Gondwana during the Ordovician. However, the broad concept of the genus is reflected in the number of sinuitid genera erected from species originally attributed to *Sinuites: Sinuitopsis* Perner, 1903, Middle Ordovician, Czech Republic; *Sinusinuites* Yu, 1961, Ordovician, China; *Strangulites* Horný, 1962, Upper Ordovician, the Czech Republic; *Sylvestrosphaera* Peel, 1980, Upper Silurian, Britain; *Hispanosinuites* Frýda & Gutierrez-Marco, 1996, Lower Ordovician, Spain; *Selesinuites* Horný, 1997, Middle Ordovician, Czech Republic; *Quasisinuites* Horný, 1997, Middle Ordovician, Morocco.

Wahlman (1992) did not acknowledge the generic status of *Strangulites* based on comparison with North American species of *Sinuites,* but Horný (1996a) anticipated that future studies related to the subinductural deposits would clarify its position. In his detailed study of this character, Horný (1996a) also addressed a number of the problems related to morphology, systematic delimitation and ecology of *Sinuites,* proposing a semi-infaunal, predatory lifestyle for this genus.

Sinuites usitatus? Isakar, 1991

Fig. 5A–I

Material. – Three internal moulds (9148, PMO 9149, PMO 11310) from the Sørbakken Formation on Frognøya (NM 653577), Ringerike district, and three internal moulds (PMO 55413a/1-3) from an unspecified locality in Ringerike. PMO 9148 preserves patches of shell, while specimens PMO 55413a/1 and PMO 55413a/2 preserve faint outlines of muscle scars (Figs. 5A, C, H, I; 6).

Remarks. – The Norwegian specimens compare well with the Estonian material of *Sinuites usitatus* Isakar, 1991, both in shell morphology and stratigraphical position. In Estonia, this species appears in the Kõrgessaare Formation of the Vormsi Stage (F_1b, equivalent of the lowermost Ashgill) within the upper part of the *Pleurograptus linearis* Graptolite Zone. Most of the Norwegian material is from the lower part of the Sørbakken Formation on Frognøya in Ringerike. Owen (1979) correlated the lower part of the unit with the Cautleyan beds in North England, which would approximately correspond to the *Dicellograptus complanatus* Graptolite Zone and thus a slightly higher stratigraphical position than that of the Estonian specimens.

The largest Norwegian specimen (PMO 55413a/1) has a maximum length and width of 22 mm and 17 mm, respectively, and shows a deep, relatively wide U-shaped median sinus and a long (adaperturally) lateral apertural lips. The shell is generally bulbous with a well-rounded dorsum, but the specimens PMO 55413a/1-3 have a somewhat steeper angle of the dorsal surface relative to the plane of symmetry, while PMO 11310 shows an intermediate curvature of the dorsal surface. Immediately behind the anterior margin of the latter specimen is a distinct trough-like constriction, which is absent in immature specimens. A similar constriction can be seen in the holotype in the Museum of Geology, University of Tartu, Estonia (TÜG 2/3) of *Sinuites usitatus* which is 22 mm and 20 mm in maximum preserved length and width respectively. Internal moulds of Estonian specimens suggest that narrow umbilici are present (Isakar 1991), but in both Estonian and Norwegian specimens the umbilici are plugged with shell material when the shell is preserved.

A characteristic feature of *S. usitatus* is the post-apertural constriction on the last whorl. Similar constrictions were described in *Strangulites* Horný, 1962, but are probably of no generic value (Horný 1963b, p. 75). Whorl constriction excepted, *S. usitatus* shows little similarity with species of *Strangulites* which Horný (1963b) found to have a general *Bellerophon*-like shell shape.

Prior to the description of *S. usitatus* by Isakar (1991),

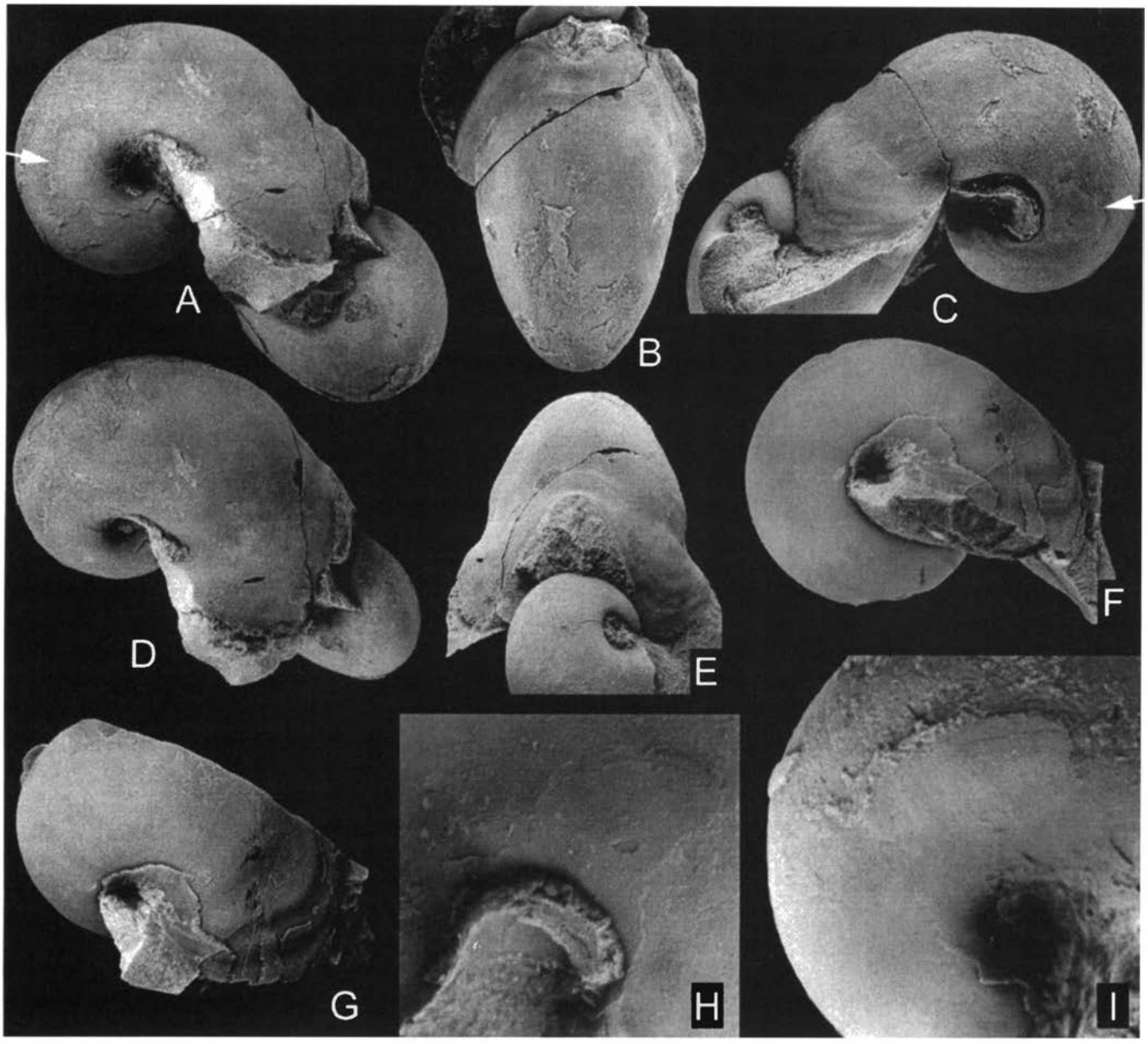


Fig. 5. A–I: *Sinuites usitatus*? *Isakar, 1991 from the Sørbakken Formation, Ringerike. A–E, H, I: Right lateral, dorsal oblique, detail of right umbilical wall, dorsal, anterior, detail of left umbilical wall and left lateral views of PMO 55413a/1, from unknown locality. The arrows in A and C indicate muscle scars (details in H, I). A–E ×2.25; H, I ×4.5. Coll.: Unknown. F, G. Right lateral and dorsal oblique views of PMO 9148 from Frognøya (NM 653577), ×2.25. Coll.: W. C. Brøgger.*

Sinuites bilobatus (*sensu lato*) was the only recognized species of this genus from the Ashgill of Norway, whereas several monotypic species are known from the Ashgill (Harjuan) of Estonia; *Sinuites angulatus* (d'Eichwald, 1840), *Sinuites navicula* (d'Eichwald, 1842), *Sinuites nitens* (d'Eichwald, 1860) and *Sinuites quadratus* Koken *in* Koken & Perner, 1925. The museum label of the specimens described here (PMO 9148-PMO 9149) identified the species as *S. corpulentus* Koken *in* Koken & Perner, 1925 from the Llanvirn Elnes Formation in the Oslo Region. This species has shorter lateral apertural lobes than *S. usitatus*? and seemingly also a more prominent spiral ornamentation. Kiær (1897) reported a specimen of *Bellerophon* sp. cf. *B. bilobatus* from the Bønsnes Formation at Stamnestangen, Ringerike, but the specimen has not been located in the collections at PMO.

Muscle scars

Two specimens (PMO 55413a/1, PMO 55413a/2) preserve faint outlines of muscle scars. The best-preserved scar appears as a continuous circumbilical muscle field visible on the right side of PMO 55413a/1 from the initial part of the last whorl, stretching almost half a whorl adaperturally (Figs. 5A, C; 6). The position, shape and extension of the muscle scar are almost identical to some described in *S. sowerbyi* Perner, 1903 by Horný (1992), though proportionally the attachment area is larger in *S. usitatus*? The

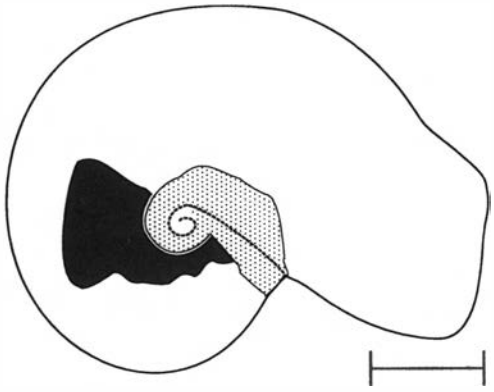


Fig. 6. Muscle scars (black) on the right circumbilical margin of specimen PMO 55413a/1. Dotted area indicates cover by matrix. Scale bar = 5 mm.

preservation of the Norwegian material is too poor to reveal further details of features, such as the continuous migration observed in similar types of scars (see Horný 1992, p. 98).

Sinuites sp.

Fig. 7A, B

Material. – Three internal moulds (PMO 11844, PMO 11846, PMO 11848) from Lindøya in the Oslofjord (NM 960403), and one internal mould (PMO 5519) from Nesbru in Asker (NM 840370), all from the Husbergøya Formation in the Oslo–Asker district.

Remarks. – This species is stratigraphically younger than *S. usitatus*? It is more laterally compressed and without the bulbous appearance, but this may be a preservational artefact. Otherwise, this material resembles *S. usitatus*? only in the expression of the aperture and the U-shaped sinus. Brenchley & Cocks (1982) interpreted the shale-dominated Husbergøya Formation as a deep shelf environment within their *Tretaspis/Tretaspis-Onniella* association. *Sinuites* has been reported elsewhere in various environments, from lagoonal through nearshore to outer shelf facies (see Horný 1996a for references).

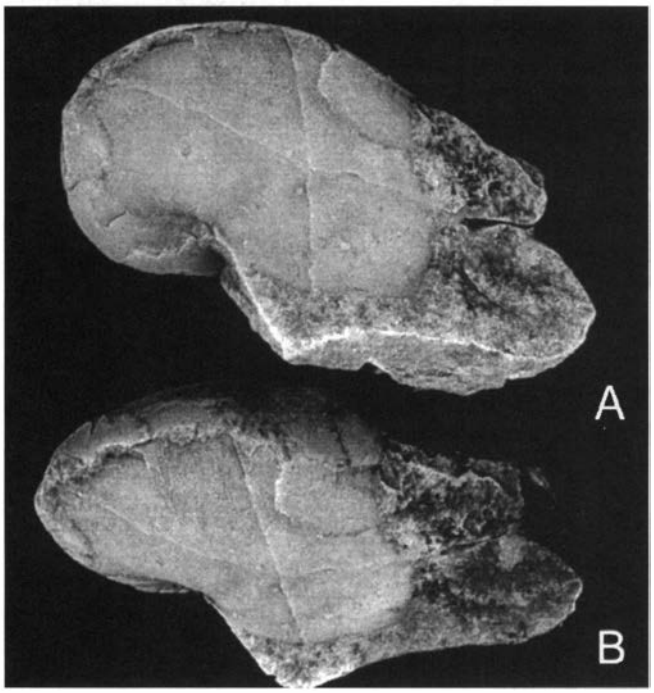


Fig. 7. A, B. *Sinuites* sp. (PMO 11844) from the Husbergøya Formation, Lindøya, Oslofjord. Right lateral and dorsal oblique views, ×3. Coll.: J. Kiær 1891.

Family Tropidodiscidae Knight, 1956

Genus *Tropidodiscus* Meek & Worthen, 1866

Type species. – By original designation of Meek & Worthen (1866, p. 160); *Bellerophon curvilineatus* Conrad, 1842, p. 269, pl. 16, fig. 7, from the Lower Devonian (Eifelian) Onondaga Limestone at Schoharie, New York, USA.

Remarks. – This long-ranging genus is found in Lower Ordovician to Devonian rocks of Laurentia, Baltica, Siberia, Kazakhstan and Gondwana, and includes more than 50 named species. Knight (1941) gave a detailed account of the complicated synonymy problems of *Tropidodiscus,* which were also summarized by Wahlman (1992). Horný (1962) erected the subgenus *Peruniscus,* but it has received little support (Horný 1997a, p. 233). The basic morphology is of a lenticular shell of several whorls, wide umbilici with deep sutures and strongly prosocyrt growth lines curving backwards medianly into a V-shaped sinus that leads into a deep narrow slit. The species ranges in size from a few millimetres across, e.g. *T. minimus* Gynda (1983) from the Middle Ordovician of Siberia, to more than 3 cm across, e.g. *T. giganteus* Twenhofel, 1928 from the Upper Ordovician of Anticosti Island, or *T. maximus* sp. nov., described here. The slender shell with the elongated aperture of *Tropidodiscus* has been interpreted as well suited for high mobility (Linsley 1978; Wahlman 1992), but minute members of the genus could also have been dwellers on algal foliage (Peel 1977, 1978; Horný 1997c).

Wahlman (1992) included in the Family Tropidiscidae such genera as *Temnodiscus* Koken, 1896 and *Phragmolites* Conrad, 1838. Peel (1991b) retained *Phragmolites* in the Bucaniinae despite the great similarity in shell shape with *Tropidodiscus,* and pointed out the different shapes of the median sinus in the two, a view supported by Ebbestad (1999a).

Tropidodiscus laticonchus sp. nov.

Fig. 8A–G

Derivation of name. – From Latin *Latus* meaning broad, and *Concha* meaning shell, which refers to the broad character of the shell in this species.

Diagnosis. – A large species of *Tropidodiscus* in which whorl height and width are equal; weak circumbilical

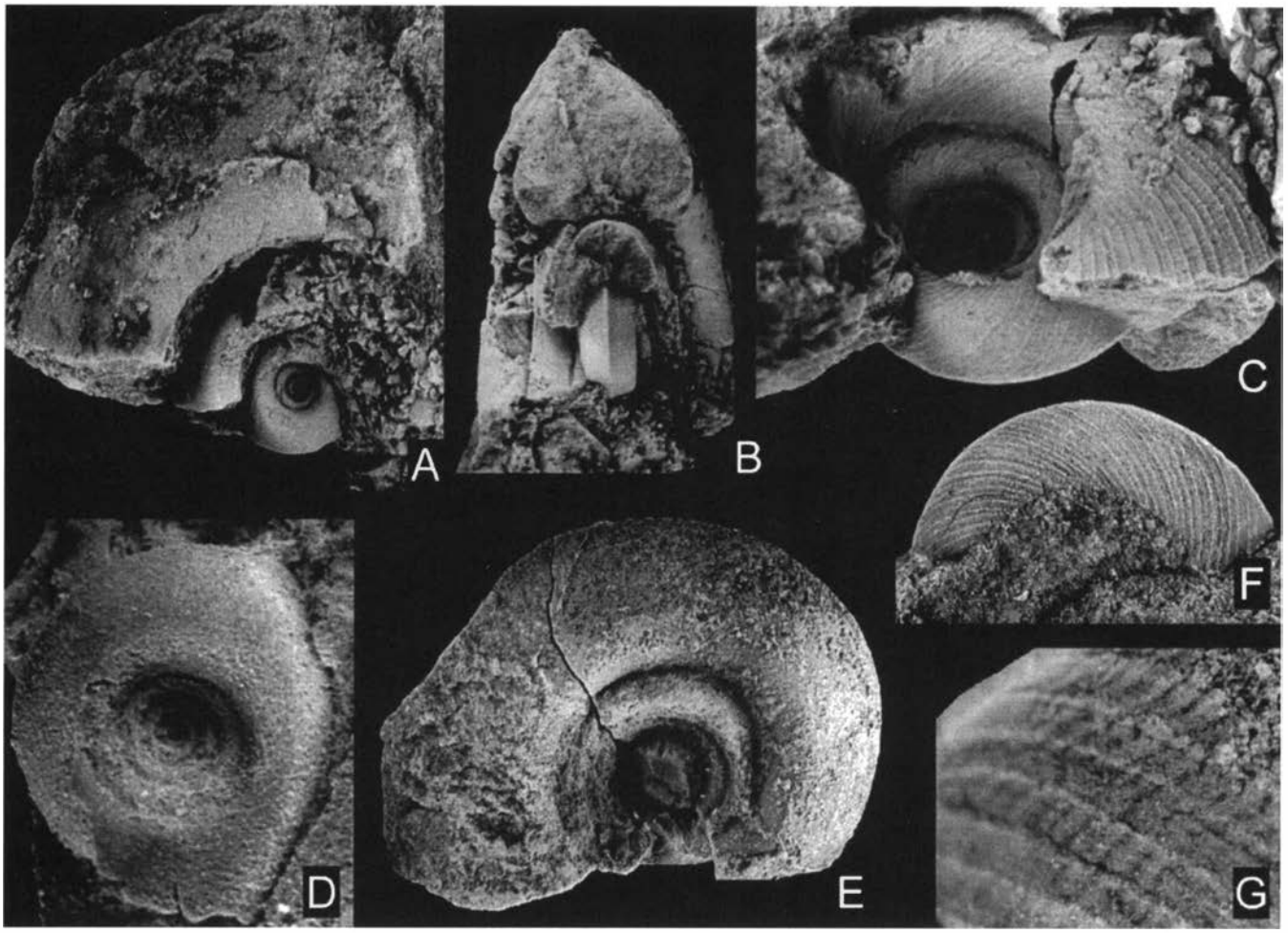


Fig. 8. A–G: *Tropidodiscus laticonchus* sp. nov. from the Langøyene Formation, Ringerike. A–C: Right lateral, posterior and ventral oblique views of the holotype (PMO165.667) from Grunntjern in Vakerdalen (NM 73869), A, B ×2.5; C ×5.5. Coll.: N.-M. Hanken 10/7-1997. D: Right lateral view of paratype specimen (PMO 16875) from Store Svartøya (NM 680584), ×6.5. Coll.: J. Kiær (31/8-1915). E–G: Left lateral view and details of inner whorl in paratype specimen (PMO165.668) from Ullerntangen (NM 685610), D ×2.5; E ×10; F ×40. Coll.: N.-M. Hanken 1972.

angulations are present, and the thick shell has both spiral and collabral ornamentation.

Holotype. – An incomplete specimen (PMO 165.667, Fig. 8A–C) from the uppermost part of the Langøyene Formation at Grunntjern in Vakerdalen, Ringerike (NM 738690).

Paratypes. – A partly preserved specimen (PMO 165.668, Fig. 8E–G) found at Ullerntangen (NM 685610), two external moulds (PMO 16875, Fig. 8D; PMO 16932) from Store Svartøya (NM 680584), a fragment (PMO 165.669) found at Grunntjern in Vakerdalen and an external mould from Store Svartøya. All specimens from Ringerike, and from the same formation as the holotype.

Description. – Shell large, maximum observed length more than 3.5 cm, and inflated lenticular with 5–5.5 whorls of uniform expansion rate. Periphery is at 1/3 of the whorl height and about half the height of a whorl is embraced by the succeeding whorl. Height and width of whorls about equal, giving the shell a broad appearance. Whorls have a typical heart-shaped transverse cross-sectional profile. The angle of the upper surface is about 45° to the plane of symmetry, with a slightly concave transition to a low and narrow, but distinctly raised median dorsal selenizone. Transition to umbilical surfaces evenly rounded and turning inwards at the deep sutures on the internal mould. The sutures appear moderately deep when the thick shell without parietal thickening is preserved. Umbilici wide, the umbilical angle being about 110°, and with all whorls visible. Anterior median sinus narrow and V-shaped, formed by the median apertural margin turning sharply abaperturally. Slit narrow, of unknown depth. Ornamentation consists of fine prosocyrt growth lines expressed as stronger lirae on regular intervals, crossed by a finer, subordinate pattern normal to the direction of the growth lines.

Remarks. – This species is unusual for the genus in having a large number of inflated lenticular whorls and deep but wide umbilici. It differs further in having less distinct

circumbilical angulations and narrow sutures when the shell is preserved. Expressed on internal moulds, these characters are similar to those seen in members centred around the type species of *Tropidodiscus,* but become obscured by the thick shell developed in this species. The ornamentation of the shell is, however, typical of *Tropidodiscus,* with prosocyrt growth lines creating the distinct deep V-shaped sinus followed by a narrow and deep slit. A large number of whorls may suggest affinity with *Megalomphala,* but the development of the sinus excludes all members of the Bucaniinae.

The only Baltoscandian species of *Tropidodiscus* having some resemblance to *T. laticonchus* is *T. lenticularis* (Koken, 1897), which has similar deep umbilici and an inflated lenticular shell. All other Baltoscandian species conform to the typical *Tropidodiscus* form of a narrow lenticular shell having shallow umbilici, although a species like *T. maximus* sp. nov. combines these characters with a large number of whorls.

Tropidodiscus maximus sp. nov.

Fig. 9A–H

Derivation of name. – From Latin *Maximus,* meaning greatest, referring to the magnificent appearance of this large species.

Diagnosis. – A large species of *Tropidodiscus* with wide umbilici, 5–6 whorls and a deep, relatively wide sinus.

Holotype. – PMO 14351 (Fig. 9A–D) from the upper part of the Bønsnes Formation on Store Svartøya, Ringerike (NM 680584). Preserved as an internal mould with some traces of shell.

Other material. – PMO 16459 (Fig. 9E–H) from the same locality and unit as the holotype is tentatively referred to the species. Preserved as an internal mould.

Description. – Shell large (maximum observed length = 3.8 cm) and lenticular with 5–6 whorls of uniform expansion rate. Periphery is at 1/3 of the whorl height on the internal mould, but placed slightly more adumbilically when the shell is preserved owing to parietal thickening. Slightly less than half the height of a whorl is embraced by the succeeding whorl. Whorl profile of internal moulds shows the typical heart-shape of the genus with the whorl height larger than the whorl width. The upper surface is at an angle of about 35° to the plane of symmetry, with a slightly concave transition to a weakly raised and narrow median dorsal selenizone. Umbilici shallow and wide, with all whorls visible. The anterior median sinus is wide and deep, V-shaped, and leading into a narrow and deep slit that reaches slightly more than 2/3 of a whorl back abaperturally. Ornamentation consists of only weak prosocyrt growth lines.

Remarks. – The holotype and the tentatively assigned specimen differ considerably in size, but the variations in morphology may be ontogenetic. However, the rate of whorl expansion, the proportional width of the umbilici, parietal thickening and direction of the growth lines in the smaller specimen matches generally well with the larger specimen, though a wider range of specimens is needed to enable assessment of the full morphological variation of this species.

Tropidodiscus maximus differs from the type species mainly in being larger, with a lower rate of whorl expansion, having wider umbilici, proportionally lower height of the whorls and less arched growth lines. In these characters it is more similar to *T. imitator* Koken, 1896 from the Devonian (Eifelian) of Germany, sometimes considered the type species of *Oxydiscus* Koken, 1896, an objective synonym of *Tropidodiscus* (see Knight 1941). Comparable Baltoscandian species in terms of whorl expansion rate and width of the umbilici are *T. planissimus* d'Eichwald, 1860 from the Llanvirn of Estonia and *T. orbiculus* (Lindström, 1884) from the Ludlow of Sweden. The latter is only known from a partial specimen measuring 13 mm in width, and is distinguished by a carina and coarse growth lines on regular intervals. *T. planissimus* is 15 mm wide with a very narrow and acute lenticular shell. All other described Norwegian species (Table 1) are smaller at mature size with coarser ornamentation, a higher rate of whorl expansion and narrower umbilici.

At least 17 species of *Tropidodiscus* have been named from the Ordovician and Silurian of Baltica (Table 1). Yochelson (1963) synonymized *T. imbricatus* Koken *in* Koken & Perner, 1925 with *T. sphenonotus* (Koken, 1897), from the Llanvirn of Norway. He also discussed the Arenig? *Cymbularia lenticularis* (Koken, 1897), from Swedish? drift material, as an atypical species of that genus, emphasizing the laterally compressed phaneromphalous shell. Koken & Perner (1925, p. 7) described the deep umbilici and a circumbilical angulation of the species, illustrating a distinct heart-shaped cross-section of the whorl, which suggest placement in *Tropidodiscus.* If compared with species of *Cymbularia,* the shell can be seen as laterally compressed, but with respect to *Tropidodiscus* the shell is actually inflated lenticular. Thus, it resembles *T. laticonchus* (see above), but is closer to species of *Tropidodiscus* with narrow umbilici.

Tropidodiscus sp.

Fig. 9I, J

Material. – A specimen (PMO 165.670, Fig. 9I, J) from the middle or upper part of the Kalvsjøen Formation, near Skøyen in Hadeland (NM 868852).

Remarks. – The incomplete specimen is slender with a great many whorls, steep dorsal surfaces, periphery relatively low on the whorl and moderately wide and deep umbilici. The umbilici are narrow for the genus, but their appearance is amplified by parietal thickening of the

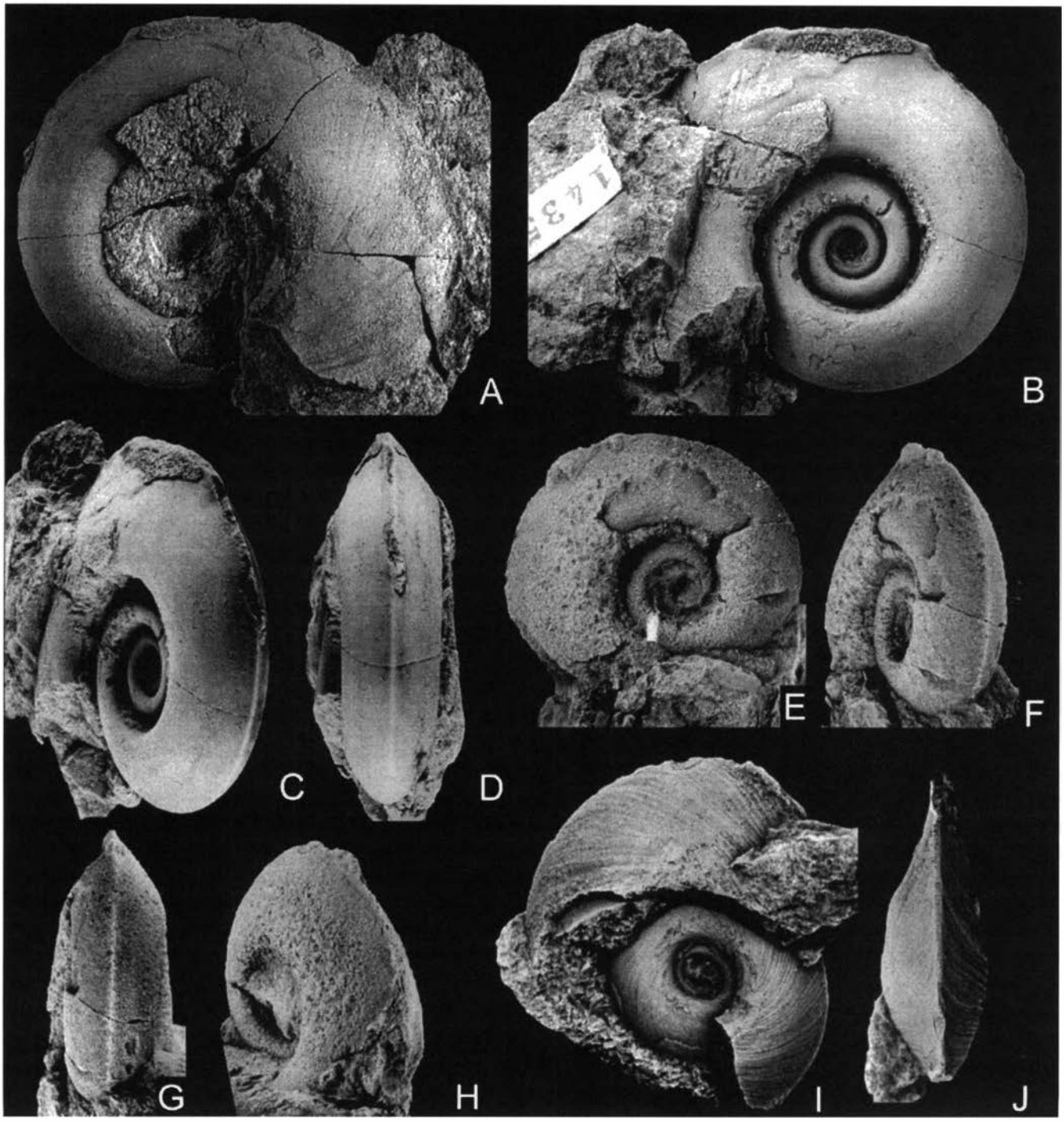


Fig. 9. A–H. *Tropidodiscus maximus* sp. nov. A–D: Right lateral, left lateral, posterior oblique, and posterior views of the holotype (PMO 14351) from the Bønsnes Formation, Svartøya, Ringerike (NM 680584), ×2. Coll.: T. Münster. E–H: Left lateral, posterior oblique, posterior and anterior oblique views of paratype (PMO 16459) from the Bønsnes Formation, Svartøya, Ringerike (NM 680584), ×4. Coll.: J. Kiær 26/8-1915. I, J. *Tropidodiscus* sp. Right lateral and dorsal views of PMO165.670 from the Kalvsjøen Formation, near Skøyen, Hadeland (NM 868852), ×4. Coll.: A. Marques Guedes 24/8-1997.

already robust outer shell. The growth lines are distinct and typical of the genus, while a high number of whorls and the nature of the umbilici are atypical. Similar developments of these features are found only in *T. laticonchus* (see above) and *T. lenticularis* (see above). While *T.* sp. is similar to the latter in the general shell morphology, it differs from *T. laticonchus* in most aspects of the shell characters.

Family Bellerophontidae McCoy, 1851

Subfamily Cymbulariinae Horný, 1963

Genus *Cymbularia* Koken, 1896

Type species. – By subsequent designation of Perner (1903, p. 148); *Cymbularia galeata* Koken, 1896, p. 393, from the Kukruse Stage (late Llanvirn-early Caradoc),

Table 1. Distribution of Lower Palaeozoic species of *Tropidodiscus* Meek & Worthen, 1896 in Baltoscandia. Species are listed according to their relative stratigraphical appearance. LO, MO and UO mean Lower, Middle and Upper Ordovician respectively, while LS and LU mean Lower and Upper Silurian respectively.

		NORWAY	SWEDEN	ESTONIA
LS:US	LUDLOW	*Tropidodiscus discus* (Lindström, 1884) *T. orbiculoides* (Lindström, 1884)		
UO	ASHGILL	*T. laticonchus* sp. nov; *T. maximus* sp. nov.; *T.* sp. *T. nautilinus* (Koken *in* Koken & Perner, 1925) *T. parvus* (Koken *in* Koken & Perner, 1925)		
	CARADOC			*T. viator* (Koken *in* Koken & Perner, 1925) *T. ingricus* (De Verneuil, 1845) *T. planissimus* (d'Eichwald, 1860) *T. karki* (Öpik, 1930)
MO	LLANVIRN	*T. sphenonotus* (Koken, 1897) *T.? ogygiae* (Koken *in* Koken & Perner 1925) *T.* sp. *sensu* Strand (1932)		*T. minutus* (Koken *in* Koken & Perner, 1925) *T.? ogygiae* (Koken *in* Koken & Perner, 1925)
LO	ARENIG		*T. lenticularis* (Koken, 1897) *T. suecicus* (Koken *in* Koken & Perner, 1925)	

Viivikonna Formation (formerly Brandschiefer, C_2), at Kuckers, Estonia.

Remarks. – The whereabouts of the holotype of *C. galeata* from Estonia was uncertain (Knight 1941; Horný & Vizcaïno 1995), but it is now known to be housed in the Koken and Perner collection at the Central Scientific-Research Geological Exploration Museum, St. Petersburg, Russia (sample CNIGRM 10903/256). Horný & Vizcaïno (1995) gave a detailed account of 20 species of *Cymbularia* and other taxa formerly attributed to this genus, and discussed the generic delimitation compared with their new genus *Thoralispira* from the Arenig of France. The total number of species named exceeds 30 and they have been described from the Tremadoc to the Ludlow of Laurentia, Baltica, Siberia and Peri-Gondwana (see Koken & Perner 1925; Peel 1977; Horný & Vizcaïno 1995).

Morphologically, *Cymbularia* is allied with the cyrtonellid tergomyan *Thoralispira,* but is distinguished by a less deep slit and a broad selenizone. Horný & Vizcaïno (1995) hesitated to draw a closer comparison, which would have lead to a relocation of the entire Cymbulariinae, and left *Thoralispira* under open nomenclature. Muscle scars are not found in the Norwegian material described here, which thus cannot help us to make a closer comparison between the two genera. The Norwegian material illustrates some of the uncertainty surrounding the nature of the umbilici in this genus; they are not completely plugged but rather shut or nearly so by thin extensions or infolding of the lateral lips (see below). Reed (1921) also recognized this feature in *C. galeata,* while several other species may have closed umbilici (Knight 1941; Yochelson 1963; Peel 1977). Yochelson (1963) assumed that the condition of the umbilici is of generic value and that species of *Cymbularia* described in Koken & Perner (1925) could thus be incorrectly assigned.

Cymbularia bullatus (Koken *in* Koken & Perner, 1925)

Figs. 10A–M, 11A, B

1925 *Bellerophon bullatus* sp. nov., Koken *in* Koken & Perner, p. 2, pl. 26, fig. 16.
1925 *Cyrtolites pachygaster* sp. nov., Koken *in* Koken & Perner, pp. 56–57, pl, 25, figs 32–34.

Holotype. – By monotypy. The original (PMO 40449, Fig. 10A–C) of Koken & Perner (1925, p. 2, pl. 26, fig. 16), from Husbergøya or Langåra formations, in Asker.

Material. – The holotype and 10 specimens are known from the central Oslo–Asker district: the specimen (PMO 11439) attributed to *Cyrtolites* by Koken & Perner (1925, pp. 56–57, pl. 25, figs. 32–34) from Asker; four specimens (PMO 97150–PMO 97153) from Rambergøya (NM 960395); three specimens (RM Mo87829–RM Mo87831) from Lindøya (NM 960403); a specimen (PMO 5518) from Holmenskjæret (NM 836362); one specimen (PMO 144.025) from Kalvøya (NM 863399). With the exception of the last of these specimens, they are all from the Husbergøya or the Langåra formations (eastern and western parts of the Oslofjord, respectively). The Kalvøya specimen comes from the Langøyene Formation.

Diagnosis. – A species of *Cymbularia* with shell of equal length and width, markedly changed width and depth of the sinus during ontogeny and covering of the umbilici by infolding of the lateral lips.

Description. – (Emended from Koken & Perner 1925). Shell narrowly phaneromphalous, of about equal length and width, bulbous with 5 involute, almost convolute whorls of almost uniform expansion rate. Whorl profile evenly rounded, with the height of a whorl being 1/3 its width on an internal mould. At maturity the dorsal surfaces show higher angles to the plane of symmetry. Periphery is at 1/3 of the whorl height, with rounded transition to near horizontal umbilical surfaces. The umbilici are narrow and the umbilical angle is 25°. The median anterior sinus is V-shaped, but becoming more widely V-shaped in later ontogeny. This leads into a narrow slit of unknown length

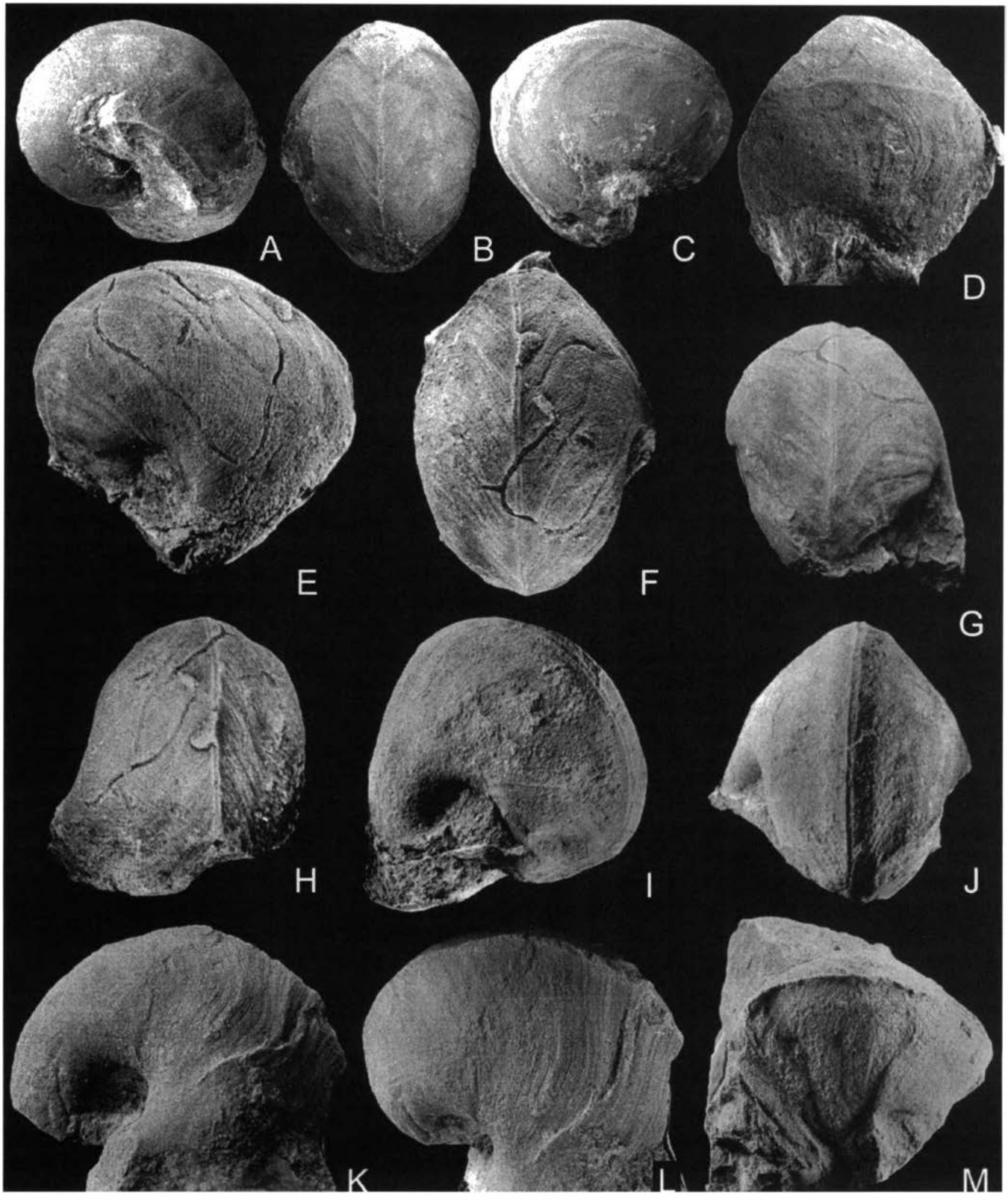


Fig. 10. A–M: *Cymbularia bullatus* (Koken *in* Koken & Perner, 1925) from the Husbergøya and Langåra formations, Oslo–Asker district. A–C: Right lateral, dorsal and dorsal oblique views of holotype (PMO 40449) from Asker. This is the original of Koken & Perner (1925, p. 2, pl. 26, fig. 16), ×3. Coll.: Unknown. D: Dorsal view of a fragment (PMO 5518) from Holmenskjæret, Asker, ×3. Coll.: J. F. Bockelie 7/3-1965. E–H: Right lateral, dorsal, posterior and anterior views of specimen RM Mo87829 from Lindøya, Oslofjord (NM 960403), ×3. Coll.: G. Holm 1879. I, J. Posterior oblique and posterior views of specimen PMO 97152 from Rambergøya, Oslofjord (NM 960395), ×3. Coll.: P. Brenchley. K, L: Right lateral and dorsal oblique views of specimen PMO 11439 from Asker. This is the original of Koken & Perner (1925, pp. 56–57, pl. 25, figs. 32–34), ×3. Coll.: Unknown. M. Dorsal oblique view of PMO 97150 from Rambergøya, Oslofjord (NM 960395), ×3. Coll.: P. Brenchley.

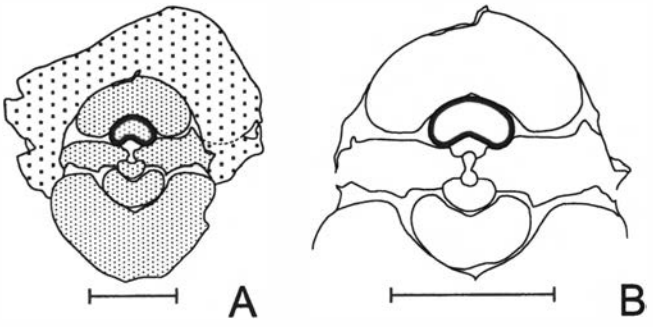


Fig. 11. A: Transverse cross-section of *Cymbularia bullatus* (Koken *in* Koken & Perner, 1925) (PMO 97151) from the Husbergøya Formation, Rambergøya, Oslofjord (NM 960395). Differential shading illustrates differential infilling of matrix. B: Detail of inner whorls, with location of same whorl in A and B marked with black outlines. Coll.: P. Brenchley. Scale bars = 5 mm.

with a slightly concave selenizone between spiral lirae. The shell is thin on the upper surface, but thicker on parietal walls and umbilical surfaces. On the penultimate and perhaps also the last whorl, thin vertical extensions of the thick parietal shell are developed that cover or nearly cover the umbilici. Ornamentation consists of prosocyrt growth lines with increased curvature (abaperturally) closer to the median dorsal area, changing from an angle of 45° to the selenizone in early ontogeny to about 65° in mature stages. The changed curvature is also reflected in the change of the V-shaped median sinus.

Remarks. – Originally both *Bellerophon bullatus* and *Cyrtolites pachygaster* Koken *in* Koken & Perner, 1925 were known from single specimens from the same stratigraphical level in the Oslo–Asker district. The large number of new samples of various sizes demonstrates clearly all intermediate morphologies from the initial rounded whorls to the acute profile in the last whorl and the changing nature of the sinus and growth lines. The two species are therefore synonymized, with the better-preserved *C. bullatus* being given priority. By the same characters, but also including the narrow umbilici and narrow selenizone, the species is placed with *Cymbularia,* though some authors (e.g. Yochelson 1963; Horný & Vizcaïno 1995) have questioned the concept of the genus with special reference to the Baltoscandian species.

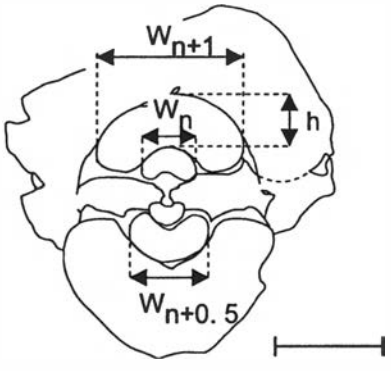
The cross-section of PMO 97151 (Fig. 11A, B) shows differential infilling of matrix, highlighting the phaneromphalous umbilici. The matrix of the inner whorls has a darker colour than that of the last whorl (indicated with different shading in Fig. 11A), which suggests that after the inner parts of the shell were filled with matrix (dark colour), the shell was redeposited and completely filled (lighter colour). Brenchley & Cocks (1982, p. 786) found that transportation of assemblages in the Ashgill succession in the central Oslo Region was limited, and though part of the shell of the specimen described here is missing in the last whorl, this is believed to be associated more with weathering and dissolution than abrasion by transport.

In size and shape *C. bullatus* can be compared to *C. cultrijugata* (Roemer, 1876) and *C. roemeri* Koken *in* Koken & Perner, 1925 from the Caradoc of Estonia. They both differ in having less-rounded whorls and collabral ornamentation. The British Ashgill *C. drummuckensis* Reed, 1921 is similar to *C. bullatus* in size, shape and ornamentation, but it has a narrower aperture relative to the length of the shell.

Ontogeny

The largest nearly complete specimen (PMO 11439) measures 2 cm in length, with a preserved apertural width of 1.8 cm, while the holotype measures 1.5 cm in length with a preserved apertural width of 1.4 cm. The lateral extensions and infolding of the apertural lip are distinct when the shell is preserved (Fig. 10I), and unless the cross-section is known (Fig. 11A, B) this would suggest plugged or anomphalous umbilici. Ontogenetic change is the key to explaining the condition of the umbilici, and the approach towards this follows that of Peel (1974), who described ontogenetic changes in *Plectonotus* from the Silurian Nova Scotia. A simple set of measurements was applied to the cross-section of *C. bullatus* on whorls 2–5 (Table 2). These are the width/height relationship (w/h) and the whorl expansion rates (W) measured at whorl intervals (w_n) and half whorl intervals $V = w_{n+1}/w_{n+0.5}$). These values indicate that, during ontogeny, *C. bullatus* shows a relative increase of the width to height (w/h) of the fourth whorl, coinciding with a general decrease in whorl expansion rate seen as a marked drop in the values of w_n and V of last

Table 2. Simple measurements on a transverse cross-section (PMO 97151) of *Cymbularia bullatus* (Koken *in* Koken & Perner, 1925) to show ontogenetic variation.



Whorl #	w/h	Whorl #	w_n	Whorl #	V
5	~2.60	5–4	2.27	5–4.5	1.57
4	2.60	4–3	2.63	4–3.5	1.87
3	2.30	3–2	2.75	3–2.5	1.80
2	2.25	2–1	–	2–1.5	–

Abbreviations: h = height of whorl measured along median plane, w = general width of a whorl, w_n and w_{n+1} express width of consecutive whorls while $w_{n+0.5}$ equals width a half whorl after W_n. The rate of whorl expansion is expressed as $W = w_{n+1}/w_n$ while the rate of whorl expansion at half whorls (V) is expressed as $V = w_{n+1}/w_{n+0.5}$ (modified from Peel 1974). Scale bar = 5 mm.

whorl and last half whorl. Thus, the almost involute character develops late in the ontogeny but after the covering of the umbilici (fourth whorl, Fig. 11A, B). The transformation of the last whorl increases the width of the sinus while at the same time making it shallower (abaperturally), and gives the acute profile of the upper surface, characteristic of the genus.

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