Bucaniidae (Gastropoda) from the Upper Ordovician of Norway

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Fourteen species of bellerophontoid gastropods of the Family Bucaniidae are described from the Upper Ordovician succession of the Oslo Region, Norway. *Bucania* sp. is compared with several species of *Bucania* that stand out morphologically by having a median dorsal carina, moderate to wide umbilici and an ornamentation consisting of crenulated growth lines. *Salpingostoma carnatum* sp. nov. from the Kalvsjøen Formation in Hadeland illustrates the problems of generic delimitation within the Bucaniidae by showing morphological characters similar to both *Bucania* and *Salpingostoma. Megalomphala crassiuscula* Koken, 1897 is figured for the first time, but the species may eventually prove to be conspecific with *M. contorta* (d'Eichwald, 1856). Based on new material, the poorly known species *Phragmolites pinguis* (Koken *in* Koken & Perner, 1925) is transferred to *Megalomphala.* Norwegian material of *Tetranota conspicua* (d'Eichwald, 1840) is conspecific with the Estonian form *sensu lato*, though the original Estonian concept of this conspicuous Baltic species needs to be revised.

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Introduction

Though conspicuous elements of the fossil fauna, gastropods of the Lower Palaeozoic successions in the Oslo Region are only known from a few works (see Yochelson 1963, p. 140; Peel & Yochelson 1976), most importantly through the monographic treatment of Baltic Ordovician gastropods by Koken & Perner (1925). Yochelson (1963) discussed the history behind this work and pointed out several problems and confusions with the taxonomic and stratigraphic handling of the taxa. Some of these problems will be addressed here with the revision and description of 14 species of bellerophontoid gastropods of the Family Bucaniidae, including four forms described earlier by d'Eichwald (1840) and/or Koken & Perner (1925). These taxa amount to only a few of the Ashgill bellerophontoid gastropods known in the Oslo Region, but species outside the Bucaniidae will be treated in a separate study.

Bellerophontiform shells are isostrophically coiled in one plane normal to the axis of coiling, and are bilaterally symmetrical about the plane in which they coil. Isostrophism is uncommon in the Gastropoda where the shell is usually helically coiled. Some gastropod limpets are isostrophic, but among fossil groups the most conspicuous isostrophically coiled shells belong to the Palaeozoic Bellerophontoidea. Members of the Bucaniidae are a coherent group of bellerophontiform gastropods ranging from the Early Ordovician to Devonian with affinities mainly to Laurentia and Baltica. Besides the nature of the coiling, they can be recognized by their numerous, slightly overlapping whorls, moderately narrow to wide umbilici, an apertural slit with a subsequent selenizone and ornamentation usually with both collabral and spiral components. Several schemes of classification have been developed for this group (Ulrich & Scofield 1897; Wenz 1938; Knight et al. 1960; Horný 1961; Peel 1991; Wahlman 1992). In this paper the scheme developed by Wahlman (1992) is followed, viewing the Bucaniidae as a separate family with two subfamilies; the Bucaniinae Ulrich & Scofield, 1897 with nine included genera (see Peel 1991; Wahlman 1992; Ebbestad 1999) and the Plectonotinae Boucot & Yochelson, 1966 containing three genera (see Wahlman 1992).

Peel (1972) transferred *Salpingostoma* Roemer, 1876 to the Bucaniinae, and later he (Peel 1991) demonstrated that the formation of a single exhalant opening in the last whorl (trema) was also developed in species of *Bucania* Hall, 1847 and *Megalomphala* Ulrich & Scofield, 1897. This feature was earlier considered diagnostic of *Salpingostoma* (see Koken & Perner 1925; Knight et al. 1960) but seems to be a function of maturing. Other morphological characters in *Salpingostoma* provide a generic separation, but also link it closer to other members of the Bucaniinae. The Subfamily Undulabucaninae established by Wahlman (1992) cannot be supported (see below; Ebbestad 1999).

The present revision is largely based on museum collections with some additional new sampling made for this study. Where known, the exact positions of localities are indicated with their UTM grid coordinates on Norwegian topographical maps, series M 711 (scale = 50,000). The Norwegian material presented here is housed in the Palaeontological Museum in Oslo (PMO) and is registered in the museum database. Additional material mentioned or discussed in the text is found in collections in the Swedish Museum of Natural History, Stockholm (RM), the Estonian Natural History Museum, Tallinn, Estonia (RLM), Museum of Geology, University of Tartu, Estonia (TUG), the Central Scientific-Research

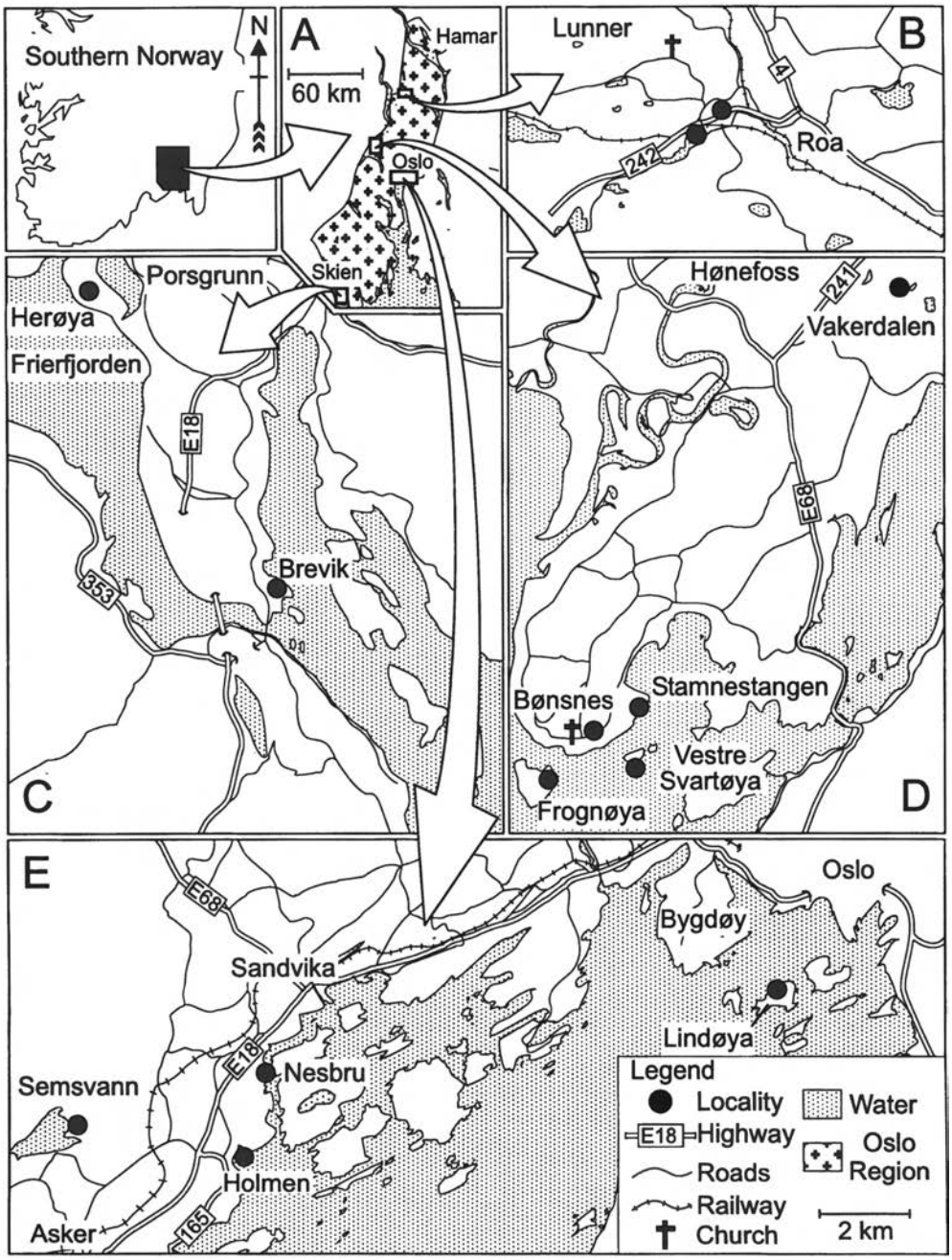

Fig. 1. Locality map showing the Oslo Region with Palaeozoic sedimentary and igneous rocks marked with cross hatches (A) and with indicated positions of parts of the Hadeland (B), Skien Langesund (C), Ringerike (D) and Oslo–Asker (E) districts, shown on the larger maps.

Geological Exploration Museum, St. Petersburg, Russia (CNIGRM) and the Department of Historical Geology, St. Petersburg University, Russia (PSM). Prior to photography, the specimens were painted with photographic opaque and whitened with ammonium chloride sublimate. All photographs were taken by the author.

Stratigraphy

Typically, most gastropod samples in museum collections from the Oslo Region lack precise information on stratigraphical level, which renders their vertical distribution somewhat uncertain. Their stratigraphical range, however, can be constrained somewhat since most samples originate from a few 'classical' localities (Fig. 1) in the Oslo Region (i.e. most localities around the Oslo fjord and Svartøya and Stamnestangen in Ringerike). Combined with the scarcity of specimens, this in turn limits information on the regional distribution of species across the Oslo Region. With one exception (*Kokenospira* sp. from the Grimsøya Formation, formerly the Tretaspis Limestone (4cβ)) all species described here come from the Late Ordovician, Ashgill (Rawtheyan to Hirnantian stages)

succession of the Oslo Region. The stratigraphy largely follows that of Owen et al. (1990), and includes the Herøya, Husbergøya, Langåra, Sørbakken, Bønsnes, Kalvsjøen, Klinkenberg and Langøyene formations (Fig. 2). These broadly correspond to the Gastropod Limestone (5a) and the Calcareous Sandstone (5b) levels of the older *etasje* system applied to the sedimentary rocks of the Oslo Region.

Systematic palaeontology
Family BUCANIIDAE Ulrich & Scofield, 1897
Subfamily BUCANIINAE Ulrich & Scofield, 1897

Genus *Bucania* Hall, 1847

Type species. – By subsequent designation of Waagen (1880, p. 130); *Bellerophon sulcatinus* Emmons, 1842, p. 312, fig. 4, from the Middle Ordovician (Chazyan Stage) Chazy Limestone at Chazy in New York State, USA.

Remarks. – Traditionally, the numerous species of *Bucania* have been divided into two informal groups, the *B. sulcatina* and *B. lindsleyi* groups, (Ulrich & Scofield 1897; Wahlman 1992). Transitional morphologies exist between the two, with the presumed primitive group of *B. sulcatina* having a thin shell, wide umbilici, broad whorls, relatively low expansion rate and a deep slit. Wahlman (1992) distinguished three North American species of *Bucania*, ranging from the Kirkefieldian to the Maysvillian stages, in a new genus *Undulabucania* characterized by a small shell having wide umbilici, a deep slit and a distinct ornamentation of closely spaced undulating collabral threads forming a net-like meshwork. He placed the genus in his new Subfamily Undulabucaninae, but the close relationship with *Bucania* suggests that it should be regarded a member of the Bucaniinae (see Ebbestad 1999; please note the misspelling of *Undulabucania* in that paper).

A number of species somewhat similar to *Undulabucania* mainly by the expression of the ornamentation can be recognized: *B. reticulata* (Koken *in* Koken & Perner 1925), middle Caradoc, Norway, here transferred from *Phragmolites*? as designated by Yochelson (1963); *B. gracillima* Koken, 1897, late Caradoc, Sweden; *B. oelandica* Koken, 1896, middle Caradoc, Sweden; *B.* sp., Ashgill, Norway, described herein; *B.* cf. *punctifrons* sensu Reed (1920), Ashgill, Scotland; *B. groenlandica* Peel, 1991, Llandovery, Greenland; *B. squamosa* (Lindström, 1884), Wenlock, Sweden. These species are of different sizes, but all have regularly coiled whorls with a slightly increased rate of expansion in the last whorl, a thin shell with pronounced periodically crenulated growth lines, moderately wide to narrow umbilici, a deep slit, a dorsal median carina and flaring of the aperture in mature specimens of some species (e.g. *B. squamosa*). With respect to the ornamentation, they compare closely with *Undulabucania*, with *U. punctifrons* (Emmons, 1842) showing an ornamentation very similar to that of, for instance, *B.* cf. *punctifrons*, *B. reticulata* and *B.* sp. They differ generally in the size, shell shape and development of the aperture and possession of a carina in the last three. Some of the *Bucania* species discussed above could be reassigned to *Undulabucania* on the basis of their comparable ornamentation. Given the few but important variations in characters and the tendency for the development of transitional morphologies within all groups of *Bucania* (see Wahlman 1992, p. 127) this approach would be premature. However, these species do stand out morphologically within *Bucania* and though they broadly resemble the *B. sulcatina* group, they differ markedly in their wavy ornamentation, the presence of a carina and the more slender and thinner shell. Only *B. oelandica* and possibly *B.* sp. have comparably broad and small-sized shells similar to those seen in the *B. lindsleyi* group. In *B. squamosa* there is parietal thickening combined with a flared, and explanate aperture with thickening in mature specimens, but Peel (1991) showed that this feature may be developed in a range of bucaniid species and is related to maturity and the mode of life. *B. squamosa* is also similar to *B. stephnae* from the Wenlock of Sweden prior to the flaring of the former, although the latter lacks the distinct ornamentation and is closer to the *B. lindsleyi* group in that respect. It is stressed that all groupings of *Bucania* remain informal, and serve no known phylogenetic base suitable for taxonomy.

Earlier assignment of *B. reticulata* and *B. gracillima* to *Phragmolites* Conrad, 1838, is not supported. The crenulated ornamentation in these species lacks the pronounced flaring seen in *Phragmolites* and the shells have relatively low whorl expansion, the whorl being broad and well rounded without an angulated transition to the umbilical surface; umbilici are moderately wide to wide.

Bucania sp.

Fig. 3

Only one partly preserved external mould is known (PMO 94373b), from the Husbergøya Formation at Semsvann in Asker (NM 802366). It is a small (1.25 cm in length), regularly coiled shell with its periphery at one-third of the whorl height. The transition from the lateral surface to the median wide umbilici is rounded. Ornamentation consists of lamellose growth lines that periodically develop crenulations (about 7 crenulations from periphery to dorsum). Each crenulated growth increment is set distinctly apart from adjacent ones, but forms a pronounced spiral pattern running normal to the growing edge. The median dorsum suggests development of a carina but it cannot be observed. The nature of the slit, early whorls, umbilici and apertural margin are unknown.

The species can be compared with *B. reticulata* from the upper Caradoc Furuberget Formation in the northern part of the Oslo Region, Norway, originally recognized as *Phragmolites* by Koken (1896) and Yochelson (1963).

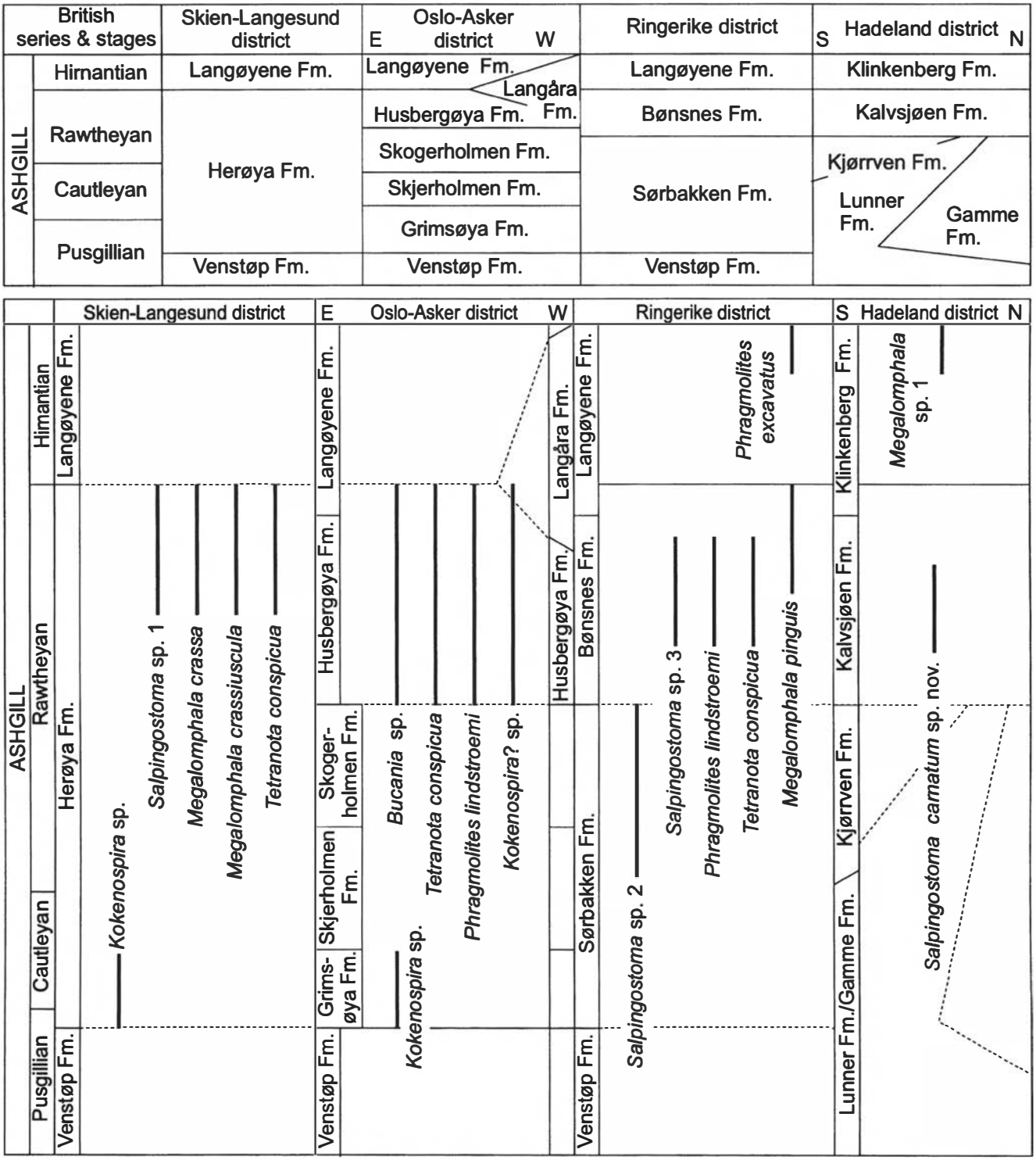

Fig. 2. Stratigraphical framework (upper half) and distribution of Upper Ordovician bucaniid gastropods of the Oslo Region (lower half). Stratigraphical scheme based on Owen et al. (1990) and Heath & Owen (1991).

This differs from *B.* sp. mainly by its more rounded whorl profile, wider umbilici and much denser crenulated ornamentation, with a higher number of smaller and fewer sinuous crenulations on each increment. The Swedish *B. oelandica*, known from one specimen in drift material of middle Caradoc age at Gräsgård on Öland, may provide a closer match. This species has a small shell (2 cm in length) with similar narrow umbilici and a rounded transition from the lateral to umbilical surfaces. It differs from *B.* sp. mainly in the ornamentation by having more widely spaced growth lines and a more prominent spiral component.

The shells of *B. reticulata*, *B. oelandica* and *B.* sp. are much smaller than the Swedish upper Caradoc *B.*

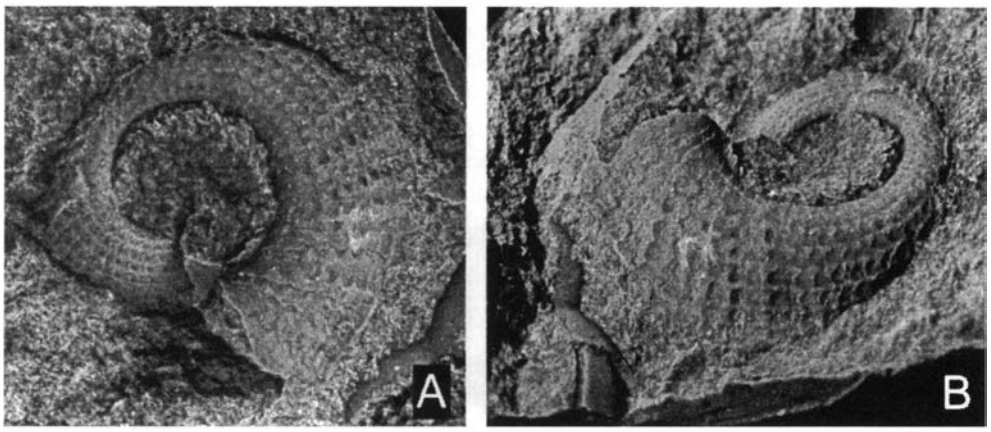

Fig. 3. A–B. *Bucania* sp. (PMO 94373b) from the Husbergøya Formation at Semsvann, Asker (NM 802366). Lateral and lateral oblique views of latex cast of external mould, ×4. Coll.: L. Koch 9/10-1966.

gracillima Koken, 1896, which may be the largest species of the genus (see Ebbestad 1998) but is otherwise comparable in the ornamentation and a median dorsal carina. While *B. oelandica* and *B.* sp. have narrow umbilici, those of *B. reticulata* are wide and similar to the larger *B. gracillima.* Swedish Silurian species differ from *B.* sp. in shell shape, but exhibit similar ornamentation. Both Norwegian species of *Bucania* may be compared closely with *B. groenlandica* from the Llandovery of Greenland while other Baltoscandian species from Estonia are more similar to the *B. sulcatina* (Caradoc species) or the *B. lindsleyi* groups (Ashgill species).

Genus *Phragmolites* Conrad, 1838

Type species. – By monotypy; *Phragmolites compressus* Conrad, 1838, p. 119, from the Middle Ordovician Black River Group (Turinian Stage) at Burgin, Mercer Co. in Kentucky, USA.

Remarks. – Morphological and taxonomic aspects of *Phragmolites* were discussed by Peel (1991), Wahlman (1992) and Ebbestad (1999). Peel (1991) included the genus in the Bucaniinae on the basis of growth lines that suggest a tangential aperture and a wide shallow sinus passing abruptly into a narrow slit. More than 20 species are recognized, mainly of Baltic and Laurentian affinities (Ebbestad 1999).

Two Norwegian species of *Phragmolites* are known; *P. lindstroemi* (Koken *in* Koken & Perner, 1925) and *P. excavatus* (Koken *in* Koken & Perner, 1925) from the uppermost Ashgill Bønsnes and Langøyene formations, respectively (Ebbestad 1999). The latter was found in the uppermost 1–1.5 m of the Langøyene Formation at Grunntjern in Vakerdalen (NM 738690), Ringerike (N. -M. Hanken pers. comm.). Both species are unusual for the genus in possessing a large number of whorls, a deep slit, unusually wide periodical flarings and strong linear ornamentation resembling that of *Offleya* Poulsen, 1974 from the Llandovery of Greenland.

One additional specimen (PMO 143.939) attributed to *P. lindstroemi* is illustrated here from the Husbergøya Formation at Holmenskjæret (NM 836362) in the Asker district (Fig. 4). It differs markedly from other known specimens by its large size (3.3 cm in length excluding carina), nearly twice the size of the previously largest specimen, making it the largest specimen of the species and genus. The shell is slender with deep sutures and a very high, pointed dorsal median carina. Ornamentation preserved on the umbilical surface shows regular growth lines crossed by fine spiral lines. The typical flarings of the species are only discernible as cross-sections in two places at the suture on the onset of the last whorl. They are not strongly developed and crenulation of the flared margins cannot be confirmed. Two distinct transverse lines on the internal mould (see Fig. 4A) may relate to periodical growth, but flared and crenulated growth lines cannot be associated on the preserved sutural shell. The early whorls are not preserved, preventing a closer comparison with the other specimens of *P. lindstroemi.* However, in the largest of these the periodical flaring evidently becomes progressively more widely spaced during ontogeny. If the trend were to continue in larger shells, even more widely spaced flarings as in the Asker specimen would be seen.

Following the International Code of Zoological Nomenclature, Article 32d, the species name *Phragmolites lindströmi* as named by Koken *in* Koken & Perner (1925) and subsequently *P. lindstromi* as used by Yochelson (1963) are mandatorily emended to *P. lindstroemi.*

Genus *Salpingostoma* Roemer, 1876

Type species. – By monotypy; *Bellerophon megalostoma* d'Eichwald, 1840, p. 111, from the lower Middle Ordovician Väo Formation (Lasnamägi Stage, C_Ib), on the island of Odinsholm, Estonia.

Remarks. – Some 37 species of this genus are named from the lower Arenig to Wenlock sediments (see Bassler 1915; Koken & Perner 1925; Peel 1991; Wahlman 1992). Peel (1991) redescribed the type species of *Salpingostoma* and

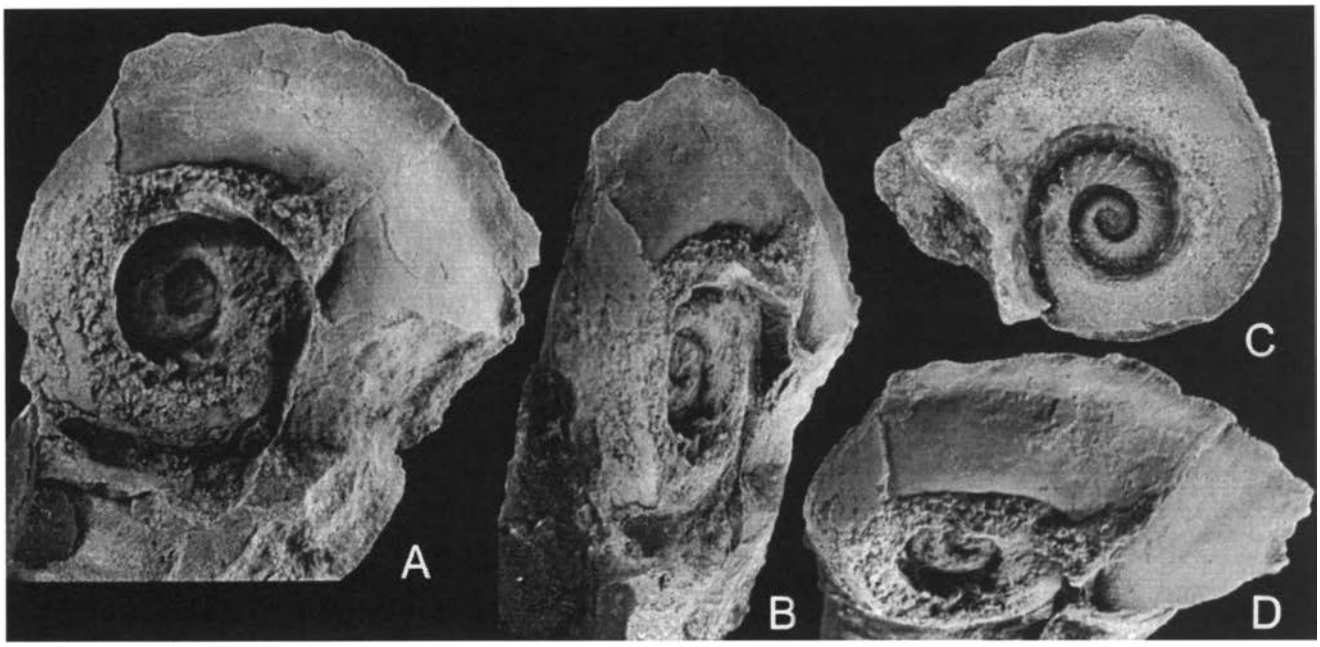

Fig. 4. A–D. *Phragmolites lindstroemi* (Koken *in* Koken & Perner, 1925). A-B, D. Large specimen (PMO 143.939) from the Husbergøya Formation at Holmenskjæret (NM 836362), Asker. Coll.: J. F. Bockelie 27/4-1965. Lateral, posterior oblique and dorsal oblique views of internal mould, ×1.8. C. Lateral view of the lectotype (PMO 20735) from the Bønsnes Formation, Ringerike, with partially preserved shell in the umbilicus, ×4. Figured by Koken & Perner (1925, pl. 27, fig. 3) and Ebbestad (1999, plate 1A).

suggested that 5 of the 14 Ordovician species described from Baltica by Koken & Perner (1925) may prove to be synonymous. Teichert's (1932) placement of the Estonian Ashgill *Bucania cornu* Koken, 1897 in *Salpingostoma* is not accepted, while the Tremadoc *B. macera* Koken, 1897 from Estonia is included in *Salpingostoma*. The Ordovician species *S. caudatus* Perner, 1903 and *S*? *plicosus* Perner, 1903 from Bohemia were referred to an unnamed genus and *Tremanotus* respectively by Horný (1963). *S*? *attava* Perner, 1903 was recognized as inorganic by Horný (1963, p. 143).

Horný (1962) made the Ashgill (Kralodvor local series) *S. grande* Perner, 1903 from Bohemia the type species of *Grandostoma*, which typically lacks a slit band. He (1963, p. 86) suggested that the British Ashgill species *S. asteroideum* Reed, 1921 and *S. etheridgei* Reed, 1921 were conspecific with *G. grande*, a relationship originally also commented on by Reed (1921). A topotype specimen of *S. asteroideum* was figured by Owen & Harper (1996). While a distinct slit band is described and clearly expressed in *S. asteroideum*, the description of the median band in *S. etheridgei* is more vague. It is stated to be very narrow and usually concealed by the carina (Reed 1921, p. 75). Based on the original descriptions and illustrations, *S. asteroideum* is therefore retained in *Salpingostoma* while *S. etheridgei* is tentatively referred to *Grandostoma*.

Traditionally the presence of an anteriorly closed slit, forming a trema, has been viewed as diagnostic for the genus *Salpingostoma*, but Peel (1991) also described this character in species of *Bucania* and *Megalomphala*. He explained the condition as a function of mature age and a deep slit, where a functional exhalant current is stationary and the slit need not be open all the way to the apertural margin (Peel 1991, p. 76). It was pointed out that the possession of a trema is still a useful taxonomic trait for *Salpingostoma* when viewed in combination with other features of shell morphology, but that some species currently assigned to the genus based on the trema alone may prove to belong in *Bucania*.

The specimens discussed below are assigned to *Salpingostoma* owing to a combination of characters including whorl profile, expression of the umbilici, the number of whorls and the tremate condition. As with other species of *Salpingostoma*, the broad whorls and low rate of whorl expansion leave the earlier whorls visible in the umbilici. In contrast comparable species of *Bucania*, like *B. stephnae*, have a more rapid whorl expansion and a more compact appearance with more overlap of the whorls. The aperture is too poorly preserved in most of the Norwegian species to allow an appreciation of its shape, but expansion or flaring appears to be present.

Salpingostoma carnatum sp. nov.

Fig. 5

Derivation of name. – From Latin *carnatus*, meaning fleshy or fat, referring to the large soft parts that must have been housed in the voluminous shell.

Holotype. – Here selected; a well-preserved specimen (PMO 164.008, Fig. 5A–F) from the middle part of the Kalvsjøen Formation near Kalvsjø, Hadeland (NM 868852). Other specimens unknown.

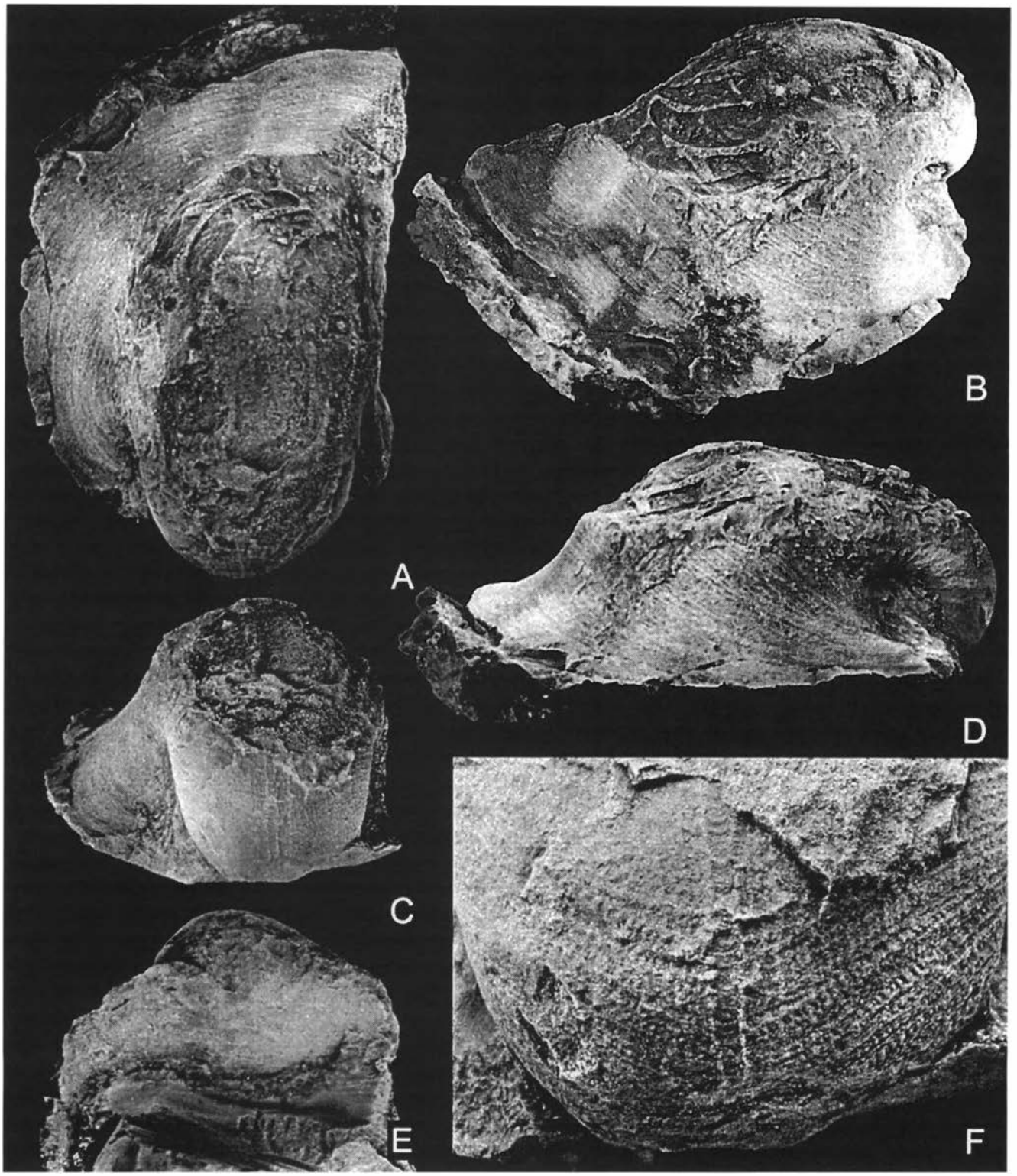

Fig. 5. A–F. *Salpingostoma carnatum* sp. nov. (PMO 164.008) collected from the Kalvsjøen Formation at the easternmost end of the road section on high way 242 near Skøyen, Hadeland (NM 869852). A–E. Dorsal, anterolateral, anterior oblique, posterior, lateral and apertural views, respectively, ×1.5. F. Detail of selenizone and ornamentation on last whorl, ×4.5. Coll.: J. O. R. Ebbestad 24/8-1997.

Diagnosis. – A species of *Salpingostoma* with a very broad shell in which the rapidly expanding last whorl produces a wide explanate aperture; an abrupt apertural flaring is lacking and no marginal brim or border is developed.

Description. – Shell large, about 6 cm in length, with broad whorls of unknown number that are well rounded at the dorsum. Transition to umbilical surfaces rounded with somewhat increased curvature. Umbilici appear to be

narrow and deep, with the last whorl largely concealing the early whorls. Median dorsal sinus wide, shallow and gently concave abaperturally, leading into a deep slit that reaches about two-thirds of a whorl back abaperturally. The slit is closed adaperturally for approximately one-quarter of its length to form a single dorsally placed trema. The selenizone is well defined, with conspicuous lunulae. The already broad last whorl expands gradually with steep and concave transitions into a broad but not abruptly flaring explanate apertural margin. The concave curvature increases slightly towards the apertural margins, but no brim or border zone is developed. Ornamentation consists of irregular prosocline growth lines crossed by thicker irregular spiral lines normal to the margin.

Remarks. – The specimen described is well preserved, though somewhat dorso-ventrally compressed and skewed lengthwise. Originally, the whorls must therefore have been less broad, more rounded and sitting in a more upright position relative to the aperture. This would increase the effect of a wide expansion of the last whorl with a steep transition to a correspondingly broad aperture.

Morphologically, *S. carnatum* is quite far removed from the type species, and in many respects similar to species of *Bucania*. The tightly coiled shell with narrow umbilici and compact appearance is similar to that of *B. stephnae* Peel, 1991 from the Wenlock of Sweden or *B. cornu* Koken, 1897 from the Ashgill of Estonia and the ornamentation resembles that of the *B. lindsleyi* (Safford, 1869), *B. rugatina* Ulrich *in* Ulrich & Scofield, 1897 or *B. cornu*. With about 50 species of *Bucania* and almost as many species of *Salpingostoma,* the morphological variation is large in both genera, and comparison can be made both ways. This only reflects the poor understanding of bucaniid phylogeny and the current lack of systematic delimitation of the genera, especially in view of the much wider distribution of a tremate condition in genera other than *Salpingostoma* as demonstrated by Peel (1991). In this respect *S. carnatum* has a more abaperturally located trema, than, for instance, the comparable *B. cornu*, but not as extreme as in *S. megalostoma*. Within the current classification a cautious approach is taken and the species is included in *Salpingostoma*.

Salpingostoma dilatatum (d'Eichwald, 1840) is the only other species described from the Baltoscandian Ashgill. It differs markedly from *S. carnatum* in being larger, having wider umbilici, a strongly elongated last whorl, a less steep transition to the well-defined anterior and lateral brim of expanded aperture and in having more strongly developed and wrinkled spiral ornamentation. Owing to the expanded last whorl, the closed anterior part of the slit is longer, with a smaller trema positioned almost posteriorly on the last whorl.

The shell of the Swedish early Arenig species *S. crispatum* Koken *in* Koken & Perner, 1925 approximates to that of *S. carnatum* in the steep transition to the apertural margins and the broad shell gradually expanding into a broad aperture. The two species differ mainly in the much broader and more expanded last whorl of the latter, but also in the more pronounced wavy ornamentation of *S. crispatum*. This contrasts with the more markedly expanding last whorl and abruptly flaring aperture of the type species, leaving the whorls raised upright above the explanate surface.

Salpingostoma sp. 1

Fig. 6A–C, 7

Material. – Two specimens; an internal mould (PMO 40451, Fig. 6A–C) labelled Brevig (NL 400464) in Skien and a poorly preserved sectioned internal mould (PMO 13103, Fig. 7) labelled Frierfjorden in Skien. The stratigraphical position is likely to be the upper part of the Herøya Formation, with reference to the distribution of fossils indicated by Kiær (1897).

Remarks. – The two specimens represent a species with at least four whorls, having a broad and rounded dorsal whorl profile and almost horizontal umbilical surfaces. The rate of whorl expansion is moderate in early whorls with marked increased anterior expansion of the last whorl giving very deep umbilici with an umbilical angle of about 80°. The aperture is tangential but poorly preserved. A tremate condition is indicated by a raised median ridge that extends slightly less than two-thirds of a whorl back abaperturally and is absent from the median anterior margin of the aperture.

This species is the only Norwegian form comparable to *S. carnatum*. It has a somewhat smaller, but equally compact shell with moderately wide umbilici. It differs by having a stronger posterior expansion of the last whorl, with less steep transition to the margin. Without a preserved shell or aperture, the true nature of these characters cannot be assessed more closely.

Salpingostoma sp. 2

Fig. 6D–F

Material. – One internal mould (PMO 10618) from the upper part of the Sørbakken Formation on the east side of Frognøya, Ringerike (NM 652575).

Remarks. – This is a slender form with a steeply curved dorsal whorl profile on the anterior part of the last whorl and gently rounded umbilical surfaces. A tremate condition is indicated by a pointed median crest that extends slightly less than two-thirds of a whorl back abaperturally but is absent from the median anterior margin of the aperture. A faint impression of spiral ornamentation is present on the side of the last whorl. The partial preservation indicates a bell-shaped aperture.

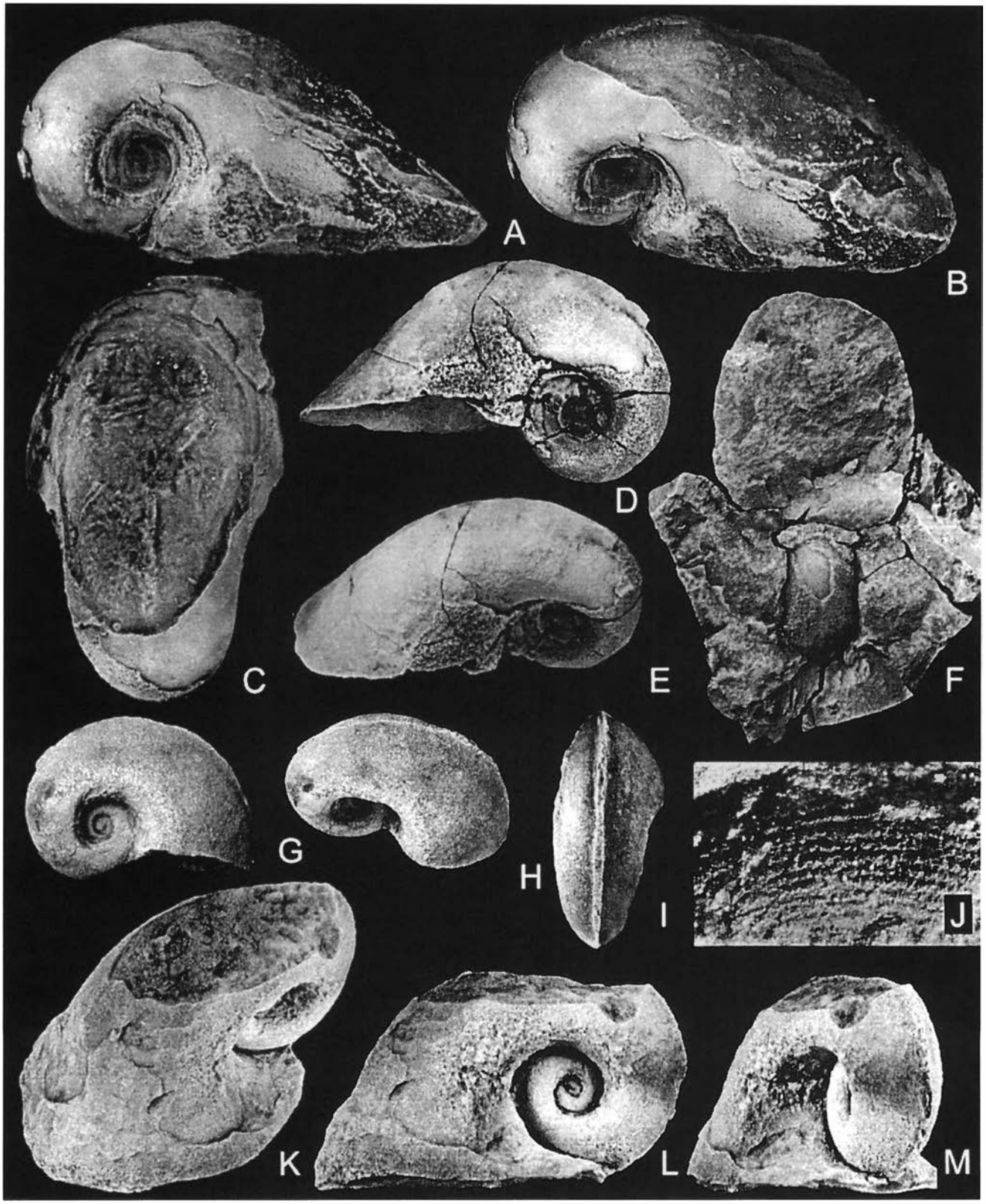

Fig. 6. A–C. *Salpingostoma* sp. 1 (PMO 40451) from the Herøya Formation at Brevig (NL 400464), Skien. Lateral, dorsal oblique and dorsal views, internal mould, ×1.5. Coll.: unknown. D–F. *Salpingostoma* sp. 2 (PMO 10618) from the Sørbakken Formation at Frognøya (NM 652575), Ringerike. Lateral, dorsal oblique and ventral views, internal mould, ×1.5. Coll.: J. Kiær 1915. G-M. *Salpingostoma* sp. 3. G–J. Lateral, dorsal oblique, dorsal and detailed views of a specimen (PMO 15898) from the Herøya Formation, Skien, internal mould, G-I ×1.5; J × 13. Coll.: J. Kiær 1915. K–M. Anterior oblique, lateral and posterior oblique views of a specimen (PMO 16611) from the Bønsnes Formation at southern Vestre Svartøya (NM 679582) respectively, Ringerike, internal mould, ×1.5. Coll.: J. Kiær 9/9-1915.

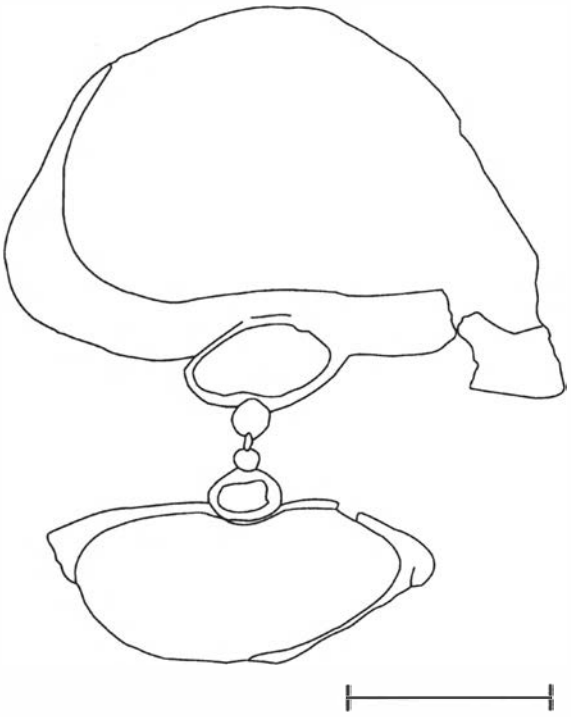

Fig. 7. Transverse cross-section of *Salpingostoma* sp. 1 (PMO 13103) from the upper part of the Herøya Formation at Frierfjorden in Skien. Coll.: unknown. Scale bar = 1 cm.

Salpingostoma sp. 3

Fig. 6G–M

Material. – Two internal moulds (PMO 15898; PMO 16611) from the upper part of the Bønsnes Formation at Stamnestangen (NM 680594) and southern Vestre Svartøya (NM 679582) respectively, in Ringerike.

Remarks. – This species differs markedly from *Salpingostoma* sp. 1 and *S.* sp. 2 in the sloping upper surface of the whorl and the stronger slope of the dorsal surface forming an acute angle to the dorsum, with a slightly raised selenizone band. The periphery is at one-third of the whorl height with gently sloping, almost horizontal umbilical surfaces. The overlap of the preceding whorls is slight and all whorls are visible in the umbilici. A small patch of the preserved shell in the right side umbilicus (shell viewed dorsally) and impressions on the right upper surface of the last-preserved whorl of PMO 15898 indicate dominantly spiral ornamentation (Fig. 6J).

Genus *Megalomphala* Ulrich & Scofield, 1897

Type species. – By original designation of Ulrich *in* Ulrich & Scofield (1897, p. 850); *Bellerophon contortus* d'Eichwald, 1856, p. 587, from drift material of the Middle Ordovician Kahula Formation (Keila Stage, D_{II}), at Pühalepa (Pyhalep) on the Island Hiiumaa (Dagö), Estonia.

Remarks. – The type species *Megalomphala contorta* (d'Eichwald, 1856) was redescribed in detail by Peel (1991). The Orthoceras limestone is given as the stratigraphical level of the type specimen, which Koken (1897, p. 123) claimed is from drift material of the Kegelschen Schicht (D_{II}). This corresponds to the Kahula Formation of the Keila Stage (D_{II}).

Species of *Megalomphala* are typified by a large number of slowly expanding whorls with impressed whorl profile and a deep, narrow slit, but the expression of these characters is variable in the about 15 species described (see Ebbestad 1999). Seven Baltoscandian species of *Megalomphala* are known in the literature, ranging from Tremadoc to Ashgill, but synonymies may exist. All taxa are morphologically very similar, with the exception of *M. pinguis* redescribed here and the Ashgill *M.? carinata* from Sweden (Ebbestad 1999). Minor variations in the position of the periphery, relative width of whorls and the shape of whorl profile serve as distinguishing characters.

Megalomphala crassa (Koken, 1896)

Fig. 8A–E, G–H

1896 *Bucania crassa* sp. nov., Koken, p. 391.
1897 *Bucania crassa* Koken; Koken, p. 123.
1925 *Megalomphala crassa* (Koken); Koken & Perner, p. 67, pl. 25, figs. 10, 14, 15.
1925 *Megalomphala crassiuscula* Koken; Koken & Perner, p. 68, *non* fig. 17A, pl. 25, figs. 20, 21.

Norwegian material. – Three specimens (PMO 40452, PMO 40453, RM Mo87611) from the upper part of the Herøya Formation in Skien. PMO 40452 is the original of Koken & Perner (1925, pl. 25, figs. 20, 21). The largest specimen (RM Mo87611) measures 2.6 cm in length and 1.4 cm in width.

Remarks. – Koken (1896, 1897) recorded *M. crassa* from the Kõrgessaare Formation of the Vormsi Stage (F_Ib) at Lyckholm and the Adila Formation of the Pirgu Stage (F_Ic) at Piirsalu (Piersal), Kirna and Hiiumaa (Dagö-Kertel) in Estonia. Potential lecto- and paralectotype specimens collected by Koken exist in the CNIGRM, RLM and TUG collections, while Norwegian material was only later assigned to the species (Koken & Perner 1925), leaving it outside the original type series.

Koken & Perner (1925) stated that *M. crassa* occurs in '*etasje* 5a' in Skien, Norway, and both Norwegian specimens of *M. crassa* in the PMO are identified on the original label in Koken's handwriting to this stratigraphical level and species. It is also clearly indicated that this is figured material, and one specimen (PMO 40452) can be matched with the figure of Koken & Perner (1925, pl. 25, figs. 20, 21, see Fig. 8A). However, the published text and plate caption for this illustration give *M. crassiuscula* as the name of this specimen; level or locality is not mentioned. In the CNIGRM collection in St. Petersburg, an Estonian

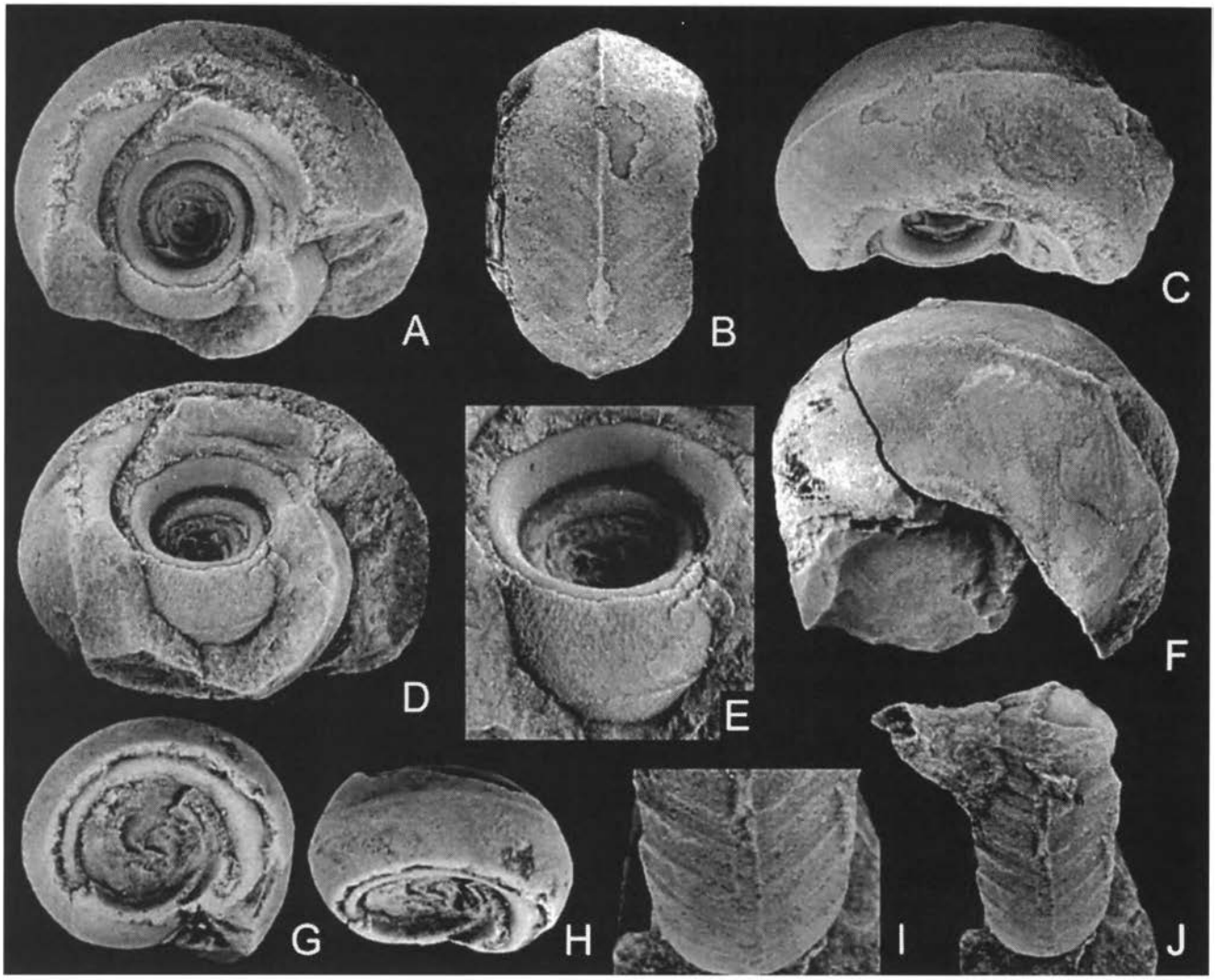

Fig. 8. A–E, G–H. *Megalomphala crassa* (Koken, 1896) from the upper part of the Bønsnes Formation in Skien. A–E. Lateral, dorsal, dorsal oblique, ventral oblique and detail of umbilicus respectively of the specimen (PMO 40452) figured by Koken & Perner (1925, pl. 25, figs. 20, 21), A–D × 3, E × 4.8. Coll.: unknown. G–H. Lateral and dorsal oblique views of small specimen (PMO 40453), ×3. Coll.: unknown. F. *Megalomphala crassiuscula* (Koken, 1897) (PMO 11013), from the Herøya Formation? at Langesund, Skien. ×3. Coll.: B. Esmark 1892. I–J. *Megalomphala* sp. 1 (PMO 164.009) found in the Klinkenberg Formation near Skøyen, Hadeland (NM 868852), I ×4.8, J ×3. Coll.: M. Høyberget 24/8-1997.

specimen (CNIGRM 10903/40) is wrongly identified as the figured specimen (Koken & Perner 1925, pl. 25, figs. 20–21). Only one Norwegian specimen (PMO 11013, Fig. 8F), supposedly from the Venstøp Formation in Langesund, is identified as *M. crassiuscula* in Koken's handwriting. This is probably the specimen referred to as such in Koken & Perner (1925, p. 68) under the description of this species. Therefore, since the only illustration in Koken & Perner (1925) supposedly of *M. crassiuscula* matches the *M. crassa* specimen, it seems that the figure caption and figure of *M. crassa* and *M. crassiuscula* have been mixed up on the published plate and that the latter species in fact has never been figured.

The Norwegian material of *M. crassa* has a more compact shell with height less than twice the width and better-expressed growth lines when compared with the Estonian samples; in other respects they compare well. *M. crassa* differs from the type species mainly in being much broader with a more flattened dorsum and stronger growth lines. An Estonian specimen (CNIGRM 10903/290) from Matthis (D_I), collected and identified as *M. crassiuscula* by Koken, appears very similar to *M. crassa* but has a more elevated, less flattened dorsum. A more rounded dorsum is seen in *M. cycloides* Koken, 1896, which is also a wider form. This in turn is in many respects similar to the type species *M. contorta.* All species mentioned above, with the exception of *M. crassa*, occur at approximately the same stratigraphical level, the Jõhvi Substage (D_I) and Keila Stage (D_{II}).

Megalomphala crassiuscula (Koken, 1897)

Fig. 8F

1897 *Bucania crassiuscula* sp. nov., Koken, p. 123.

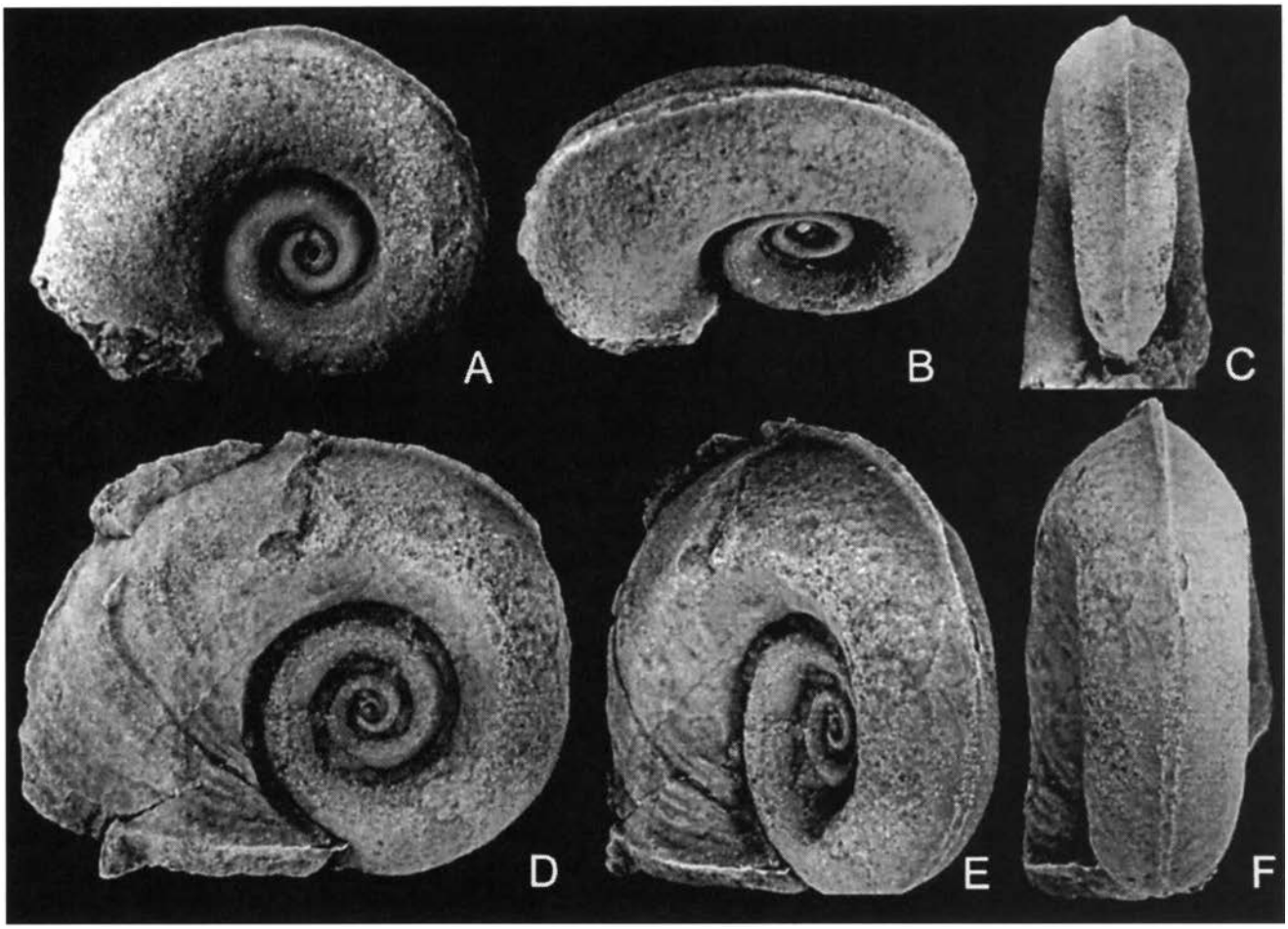

Fig. 9. Megalomphala pinguis (Koken *in* Koken & Perner, 1925) from the Bønsnes Formation in Ringerike. A–C. The holotype (PMO 20731) found at Bønsnes Church (NM 666588), internal mould. Figured by Koken & Perner (1925, pl. 27, figs. 16–18), ×1.8. Coll.: unknown. D–F. Left lateral, posterior oblique and posterior views of a large specimen (PMO 5523) from Stamnestangen (NM 680594), internal mould, ×2. Coll.: J.Kiær 1915.

1925 *Megalomphala crassiuscula* Koken; Koken & Perner, p. 68, fig. 17A, *non* pl. 25, figs. 20, 21.

Occurrence. – *M. crassiuscula* was reported from the Kahula Formation of the Jôhvi Substage (D_I) and Keila Stage (D_{II}) at Matthis and Paesküll, respectively (Koken 1897). It was later also recorded from the Venstøp Formation in Langesund, Norway, but this may be wrong (see below). It has also been found in drift material at Ellerbeck, Germany (Koken & Perner 1925).

Remarks. – The confusion concerning samples and illustrations related to *M. crassa* described above leaves this species unfigured until now. Two specimens (CNIGRM 10903/290, 291) in the type collection in St. Petersburg from Matthis (D_I), and a specimen from Paesküll in the Koken & Perner (1925) reference collection in Tallinn (RLM g8:70) are likely to be the specimens recorded by Koken (1897, p. 123). The affinity of the specimen (CNIGRM 10903/40 wrongly noted as *M. crassiuscula*, figured by Koken & Perner (1925, pl. 25, figs. 20, 21) is uncertain since the original label is missing. Material outside Estonia was recorded subsequently to the original description and is not part of the type series. Further systematic treatment of *M. crassiuscula* is postponed, pending investigation of possible synonymies with other Baltoscandian species of *Megalomphala.*

The Norwegian specimen (Fig. 8F, PMO 11013) is only partly preserved, but shows a rather inclined dorsum with a slightly concave transition to the angular periphery. This is one character used to distinguish the species from *M. crassa.* The original label indicates that the specimen comes from the Trinucleus Shale in Langesund, equivalent to the Venstøp Formation in the recent stratigraphy. Lithologically, the sample is not typical for this unit and it seems more likely that it originated from one or other of the bounding formations.

Megalomphala pinguis (Koken *in* Koken & Perner, 1925)

Figs. 9A–G; 10

1925 *Conradella pinguis* sp. nov., Koken *in* Koken & Perner, p. 70, pl. 27, figs. 16–18.
1963 *Phragmolites pinguis* (Koken): Yochelson, p. 164.

Fig. 10. Transverse cross-section of *Megalomphala pinguis* (PMO 15675) from the Bønsnes Formation at Stamnestangen, Ringerike (NM 680594). Coll.: J. Kiær 1915. Scale bar = 1 cm.

Holotype. – By monotypy; the specimen (PMO 20731) from the Bønsnes Formation at Bønsnes Church in Ringerike (NM 666588). Figured by Koken & Perner (1925, pl. 27, figs. 16–18).

Additional material. – Two large specimens (PMO 5523, PMO 15675) from the upper part of the Bønsnes Formation at Stamnestangen (NM 680594) in Ringerike.

Diagnosis. – A species of *Megalomphala* with a low carina on almost circular whorls. Minor impression of earlier whorls gives shallow sutures.

Description. – Shell with 5–6 uniformly expanding whorls, expansion rate = 3, and widely phaneromphalous with an umbilical angle of about 120°. Whorl profile semicircular and only with periphery moving to just below mid-height of whorl in the final coil giving a more inclined upper surface. Minor whorl impression produces shallow sutures. Aperture tangential without flaring, with a wide and shallow V-shaped sinus turning abruptly into a narrow slit of unknown length. Slit and selenizone on low carina revealing lunulae in the selenizone when broken. Shell without significant peripheral or parietal thickening and with ornamentation consisting of weakly prosocline growth lines with an angle of 60° to the median dorsal plane.

Discussion. – This species was placed in *Phragmolites* by Koken & Perner (1925) based on the supposed preserved ornamentation typical of that genus. This view was later advocated by Yochelson (1963, p. 164), but examination of the type specimen gives little reason to support this. It is preserved as an internal mould with partly coarsely recrystallized umbilici, which could give the impression of reticulate or wavy ornamentation. The typical wide umbilici and large number of rounded whorls suggest an affinity with *Megalomphala* and the species is here described as such.

Two additional specimens (PMO 5523, PMO 15675) from the same unit are tentatively attributed to this species. Both samples are much larger than the original, but compare closely in the uniform rate of whorl expansion, the whorl profile and the dorsal median carina. The poor preservation of the holotype precludes further comparison. Originally the only other comparable species in the unit in Ringerike was attributed to *Temnodiscus lindstroemi* by Koken & Perner (1925), who pointed out similarities with *M. pinguis.* Two specimens from the *T. lindstroemi* type series have been assigned to a new species, *M.? carinata* Ebbestad, 1999 based on comparison with material from the Ashgill Boda Limestone of Sweden. *M.? carinata* differs from *M. pinguis* in having a slender shell with a more strongly inclined upper surface, an angular dorsum with an elevated selenizone and wider umbilici.

Megalomphala pinguis can be compared with *M. marjorae* (Wenlock) and *M. gotlandica* (Ludlow) of Sweden and *M. dawesi* (Llandovery) from Greenland, all described by Peel (1991). A common trait is the wide umbilici and rounded whorls, compared with the deep umbilici and depressed, lenticular whorls seen in the type species. These features also apply to the Llandovery *M. septentrionale* (Poulsen, 1974) from Greenland, which has a more-rounded whorl profile similar to that of *M. pinguis* but with deeper sutures. A combination of shallow sutures and almost circular whorls with a low carina distinguish *M. pinguis* from other species of *Megalomphala.*

One specimen of *M. pinguis* (PMO 5523) occurs with *Catachisma pillula* (Koken *in* Koken & Perner, 1925), reported both from the Skien–Langesund and Ringerike districts, the Bønsnes and Herøya formations, respectively (Fig. 2).

Megalomphala sp. 1

Fig. 8I, J

Material. – A partly preserved specimen (PMO 164.009) from the Klinkenberg Formation near Skøyen in Hadeland (NM 868852). Possibly belonging to lithofacies 3 or 4 of Heath & Owen (1991).

Remarks. – The partly preserved specimen resembles *M. crassa* but differs in having stronger growth lines at regular intervals and in having a distinct, relatively broad selenizone with lunulae (Fig. 8I, J). The form is unlike

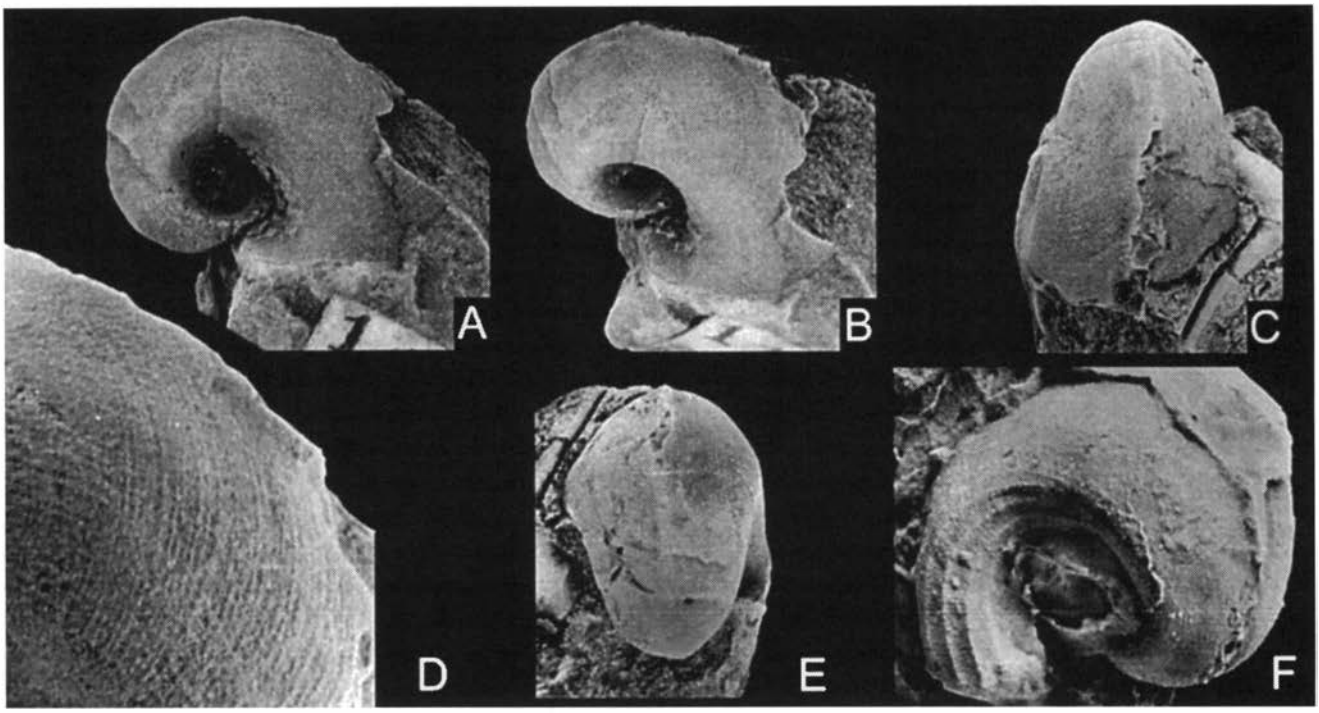

Fig. 11. A–E. *Kokenospira*? sp. Specimen PMO 11855 from the Langåra Formation on Lindøya, Oslo (NM 960403). Lateral, dorsal oblique, anterior, posterior views and detail of ornamentation, respectively, A–C, E ×3, D × 20. Coll.: unknown. F. *Kokenospira* sp. (PMO 11546/11556) from the Grimsøya Formation at Lindøya, Oslo (NM 960403). Posterior oblique view of latex cast, ×6. Coll.: W. C. Brøgger.

any of the Baltic species of this genus, but until additional material is found, its affinity remains unresolved.

Genus *Kokenospira* Bassler, 1915

Type species. – By original designation of Bassler (1915, p. 687); *Bucaniella esthona* Koken, 1889, p. 389, pl. 13, figs. 1, 1a, from Ordovician strata of Estonia, found as Pleistocene drift at Berlin, Germany.

Remarks. – Originally named *Kokenia* by Ulrich & Scofield (1897), an already occupied name that was subsequently changed to *Kokenospira* by Bassler (1916). The genus is characterized by a rounded shell with moderately wide umbilici, no flaring of the aperture, a short slit passing into a raised median selenizone and numerous revolving lines or ribs. Transverse growth lines may be prominent, but are always subordinate to the spiral ornamentation. About 20 species can be recognized from the Ordovician and Silurian of Laurentia and Baltica (see Koken & Perner 1925; Reed 1920; Ulrich & Scofield 1897; Wahlman 1992), though Wahlman (1992) stated that only two species of *Kokenospira* are known (*K. esthona* (Koken, 1889), Ordovician drift material, Germany; *K. costalis* (Ulrich & Scofield, 1897), Edenian, USA). Yochelson (1963) synonymized *K. glabrata* (Koken *in* Koken & Perner, 1925) with *K. insularis* (Koken *in* Koken & Perner, 1925). Yochelson (1963) found that the number of spiral lirae in *Kokenospira* varies during ontogeny and postulated that a revision of the described taxa may lead to new generic assignments. Wahlman (1992) pointed out the close relationship to *Tetranota*, placed in a different subfamily.

Kokenospira sp.

Fig. 11F

Material. – One external impression (PMO 11546/11556) from the Grimsøya Formation at Lindøya, Oslo (NM 960403) and two internal moulds (PMO 13155, PMO 13156) from the Herøya Formation in Skien.

Remarks. – The narrow umbilici, a raised median dorsal area and ornamentation of numerous spiral lines place these specimens with *Kokenospira*, but poor preservation permits no assignment to the species level. The typical ornamentation is impressed on a latex cast made from the external mould (PMO 11546/11556, Fig. 11F), showing numerous prominent spiral lines with prominent, but subordinate, growth lines normal to the spiral element. The other two specimens only show a similar shell shape, with narrow umbilici and a raised median area that tentatively places them in *Kokenospira*. The strong ornamentation is similar to that seen in the middle Caradoc *K. depressa* (Koken *in* Koken & Perner, 1925) from Estonia and the Ashgill *K. lingualis* var. *girvanensis* Reed, 1920 from Scotland.

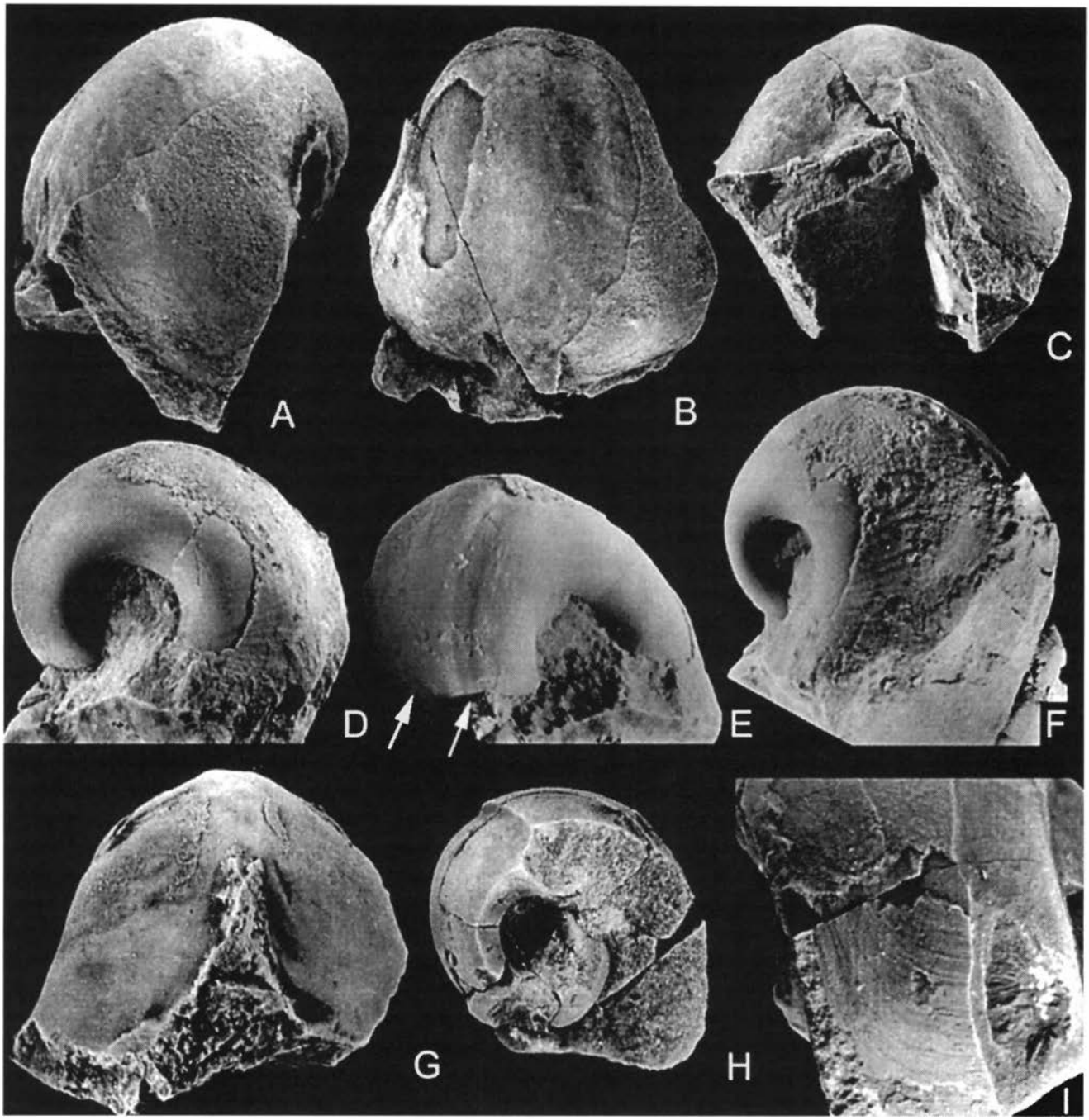

Fig. 12. A–I. *Tetranota conspicua* (d'Eichwald, 1840). A–F, H–I from the Bønsnes Formation at Stamnestangen, Ringerike (NM 680594); G from the Herøya Formation in Brevik, Skien. A–C. Specimen (PMO 13918) figured by Koken & Perner (1925, pl. 23, figs. 32–33). Anterior oblique, dorsal and anterior views, internal mould, ×2. Coll.: J. Kiær 1894. D–F. Specimen PMO 17788. Lateral, posterior oblique and anterior oblique views, with partially preserved shell. Arrows point to grooves possibly representing the position of the gills, ×3. Coll.: J. Kiær. G. Anterior view of a specimen (PMO 13114), internal mould, ×3. Coll.: unknown. H-I. Lateral view and detail of ornamentation of specimen (PMO 17641), H ×3, I ×4.5. Coll.: J. Kiær 1914.

Kokenospira? sp.

Fig. 11A–E

Material. – A specimen (PMO 11855) from the Langåra Formation on Lindøya, Oslo (NM 960403) with preserved impressions of ornamentation, and an internal mould (PMO 144.046) from the Husbergøya Formation at Nesbru, Oslo (NM 840370).

Description. – Shell having at least three rapidly expanding whorls with evenly rounded, gently convex dorsum. The periphery is at one-third of the whorl height, where lateral areas pass via a rounded angulation into narrow umbilici with gently convex almost horizontal umbilical surfaces. Shell ornamentation consisting of fine, densely spaced, gently prosocyrt growth lines forming an angle of 45° to the selenizone. They are crossed by equally fine and numerous spiral lines, which are more distinct on the early

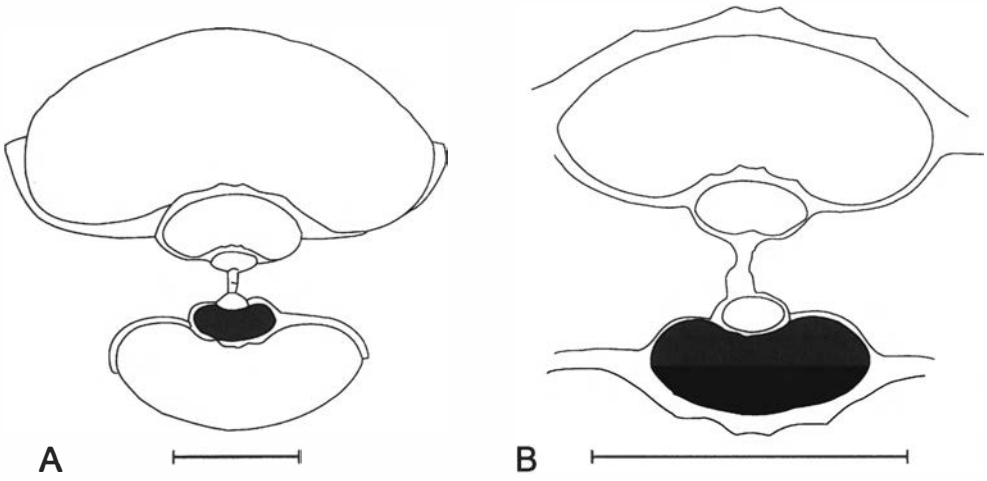

Fig. 13. A. Transverse cross-section of *Tetranota conspicua* (PMO 17644) from the Bønsnes Formation at Stamnestangen, Ringerike (NM 680594). B. Detail of inner whorls. Coll.: J. Kiær. Scale bars = 0.5 cm.

part of the body whorl. Aperture tangential, without flaring, and with a wide V-shaped sinus curving into slit of unknown length, followed by narrow, slightly raised selenizone. Lunulae not visible.

Discussion. – With the limited material at hand, the generic position of this species is uncertain. The raised selenizone is similar to typical *Kokenospira* species, but except at the initial part of the body whorl, the strong spiral lines are lacking. The change in the nature and expression of the spiral lines reflects the variability of this character within the genus as pointed out by Yochelson (1963).

The regional distribution of *Kokenospira*? sp. suggests that it lived in a shelf environment in the *Onniella* association of Brenchley & Cocks (1982).

Subfamily PLECTONOTINAE Boucot & Yochelson, 1966

Genus *Tetranota* Ulrich & Scofield, 1897

Type species. – By original designation of Ulrich & Scofield (1897, p. 849); *Bucania bidorsata* Hall, 1847, p. 186, from the upper Middle Ordovician (Mohawkian) Trenton Limestone in the Jefferson County, New York, USA.

Remarks. – Wahlman (1992) redescribed the type species *Tetranota bidorsata* (Hall, 1847), placing the genus in the Plectonotinae. At least 20 species can be attributed to this genus (see Reed 1920; Koken & Perner 1925; Teichert 1932; Wahlman 1992), distributed in Arenig to Ashgill strata of the Laurentian and Baltic palaeocontinents. *Tetranota* is usually distinguished by an involute shell with narrow to moderate umbilici, largely expanded aperture laterally, a broad and elevated selenizone bordered by two revolving threads and two or three pairs of dorsolateral revolving ridges (Wahlman 1992, p.144).

As pointed out by Peel (1974) a number of bellerophontoidean gastropods develop a trilobate dorsum, and this can be explained as an evolutionary response to increased respiratory efficiency of the mantle and separation of inhalant from exhalant currents. Both *Tetranota* and other genera placed in the Plectonotinae have a V-shaped sinus passing into a relatively short true slit that generates a selenizone. This may occupy only part of the median lobe as in species of *Plectonotus* or the entire width as in species of *Tritonophon*. In *Tetranota bidorsata* (Hall, 1847) from the Edenian of North America and *T. conspicua* (d'Eichwald, 1842) from the Ashgill of Baltoscandia, the median elevation and selenizone are developed much in the same way as in *Tritonophon*. However, most other species of *Tetranota* show modest elevation of the selenizone, which usually is distinctly delimited by revolving threads. *Tetranota* is stratigraphically older than *Tritonophon* and *Plectonotus* and Wahlman (1992) considered it to be ancestral to the later genera.

Wahlman (1992) placed the Subfamily Plectonotinae in the Family Bucaniidae based on the depressed whorls, a laterally flaring aperture, spiral ornamentation and open umbilici. He also pointed out the close affinity between *Kokenospira* and *Tetranota*, but besides lacking the numerous revolving lines, the latter tends to expand laterally and have a more pronounced elevation of the median dorsal area. Teichert (1932) found that some Baltic species of *Tetranota* have very narrow umbilici, and it was suggested that they perhaps represent a separate lineage. This character is also found in some North American species, such as the late Caradoc *T. obsoleta* Ulrich & Scofield, 1897 and even the type species *T. bidorsata* (Hall, 1847).

Tetranota conspicua (d'Eichwald, 1840)

Fig. 12A–I, 13

1840 *Bellerophon conspicuus* sp. nov., d'Eichwald, p. 112.
1856 *Bellerophon conspiquus* d'Eichwald: d'Eichwald, p. 587.

1858 *Bellerophon conspicuus* d'Eichwald; Schmidt, p. 207.
1859 *Bellerophon conspicuus* d'Eichwald; d'Eichwald, pl. 42, fig. 14.
1860 *Bellerophon conspicuus* d'Eichwald; d'Eichwald, p. 1078.
?1896 *Bucaniella conspicua* (d'Eichwald); Koken, p. 392.
?1897 *Bucaniella conspicua* (d'Eichwald); Koken, p. 126.
?1925 *Bucaniella conspicua* (d'Eichwald); Koken & Perner, pp. 19–20, pl. 23, figs. 1, 2, 24, 32, 33.
?1932 *Tetranota conspicua* (d'Eichwald); Teichert, p. 266.
?1963 *Tetranota conspicua* (d'Eichwald); Yochelson, p. 165.

Material. – About 20 specimens known. The specimen (PMO 13918) illustrated by Koken & Perner (1925, pl. 28, figs. 32, 33) is rephotographed. Additionally, three samples are figured (PMO 13114, PMO 17641, PMO 17788) and a transverse cross-section (PMO 17644) is shown.

Distribution. – This is a common species in the Kõrgessaare Formation ($F_{II}a$) in Estonia and is also recorded in drift material on Öland, Sweden, and Germany. In Norway several specimens were found in the Bønsnes Formation in the Ringerike district, the Langåra Formation in the Oslo–Asker district, and the upper part of the Herøya Formation in the Skien–Langesund district.

Remarks. – d'Eichwald (1840, p. 112) described this species from drift material at Odinsholm and later figured it (d'Eichwald 1859, pl. 42, fig. 14). In the collections at PSM in St. Petersburg a single specimen (PSM 1/2324) is attributed to *Tetranota conspicua*, but labelled as a replacement for the type specimen. The typical grey colour of the matrix on this specimen suggests material from the Keila Stage (D_{II}) in Estonia (M. Isakar, Tartu pers. comm.). Koken (1897, p. 126) and Koken & Perner (1925, p. 19) stated that d'Eichwald's (1859) drawing was not very exact, and though the figure of d'Eichwald (1859) is similar it is not a perfect match to the available specimen in PSM.

When comparing all specimens assigned to this species in the original collections in PSM and CNIGRM (both St. Petersburg), it seems that Koken (1897) and Koken & Perner (1925) established a concept of *Tetranota* different from that used by d'Eichwald (1840, 1859, 1860). Specimens assigned to *T. conspicua* by Koken & Perner (1925) refer to material with a bright-yellow fine micritic (aphanitic) matrix typical of the Vormsi Stage ($F_{II}a$) in Estonia. These are morphologically removed from the species presented by d'Eichwald (1840, 1859). Especially noticeable are the wide umbilici in d'Eichwald's (1859) species compared with the narrower umbilici in the species of Koken & Perner (1925). Later studies on *T. conspicua* tend to follow the concept established by the latter authors. This practice will also be followed here with respect to the Norwegian specimens, pending a closer study of the material of d'Eichwald (1840, 1859, 1860) and Koken & Perner (1925).

Most samples from Estonia are preserved as internal moulds that provide little information on the ornamentation. Size, shell morphology, including cross-sectional characters, and stratigraphical position of the Norwegian material otherwise correspond well with that of the Estonian species and they may be viewed as conspecific. A general description of the Norwegian material is given here.

The shell has four depressed whorls showing a uniform expansion rate in early ontogeny, with increased rate in the last whorl, thus narrowing the umbilical angle from 70° in early ontogeny to 45° at mature size. In cross-section, the whorls are lenticular, with a slightly more convex upper surface, and well-rounded periphery but without thickening of the shell. The height of the whorls is about one-third of the width. Preceding whorls are embraced to the periphery, giving shallow sutures. Trilobation is not pronounced, as there is a flat, relatively broad selenizone bordered laterally by concave trenches. Small patches of shell show an ornamentation of prosocline growth lines with somewhat stronger lines developed at regular increments. Spiral ornament is lacking. The broad last whorl widens anterolaterally, giving a wide V-shaped sinus with a weak convex (adaperturally) curve seemingly merging with a short slit followed by the selenizone. Lunulae are unknown.

The trilobation of the type species *T. bidorsata* is much more pronounced than in *T. conspicua*, with stronger lateral spiral lines near the selenizone and on the upper whorl surface. It also shows greater lateral and anterior expansion of the last whorl and has stronger growth lines. Other Baltic Ordovician and Silurian species attributed to *Tetranota* (see Teichert 1932) generally show minor elevation of the median dorsum, and in *T. rudicostata* (Koken *in* Koken & Perner, 1925) the lateral expansion of the last whorl is also small. Along with this species, *T. silurica* (Koken *in* Koken & Perner, 1925) and *T. undata* (Koken *in* Koken & Perner, 1925) have a higher convexity of the upper whorl surface, and the latter also has an acute periphery when compared with *T. conspicua.*

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