NAUTILOIDS WITH MULTIPLE PAIRED MUSCLE SCARS FROM LOWER–MIDDLE ORDOVICIAN OF BALTOSCANDIA

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Abstract: The number, outline and arrangement of muscle scars on the internal mould of the body chamber of five species of Early and Middle Ordovician nautiloids from Baltoscandia are described. The ellesmeroceratids *Oelandoceras haelluddenense* Foerste and *Pictetoceras oliviae* King have 9–10 pairs of muscle scars. The oncoceratid *Phtanoncoceras ellipticum* (Lossen), and *Botellusoceras torpense* gen. et sp. nov., order and family indeterminate, have eight and nine pairs of muscle scars, respectively. The tarphycerid *Estonioceras imperfectum* (Quenstedt) has four pairs of muscle scars.

Key words: cephalopods, muscle system, nautiloid phylogeny.

ALL shelled cephalopods must have had some way of anchoring their body to the shell wall. Recent *Nautilus* is attached by two strong, head-retractor muscles and two sheet-like tendons (aponeuroses). These muscles form two characteristic imprints on the inner surface and a continuous band around the posterior end of the shell of the body chamber (see e.g. Wells 1988; Mutvei *et al.* 1993; Isaji *et al.* 2002). Imprints of such muscles are preserved in numerous nautiloids (Dzik and Korn 1992). The shape and number of the complex of muscle scars differs strongly between taxa in both lower and higher taxonomic ranks. Accordingly, muscle scars bear at least some potential for information about the soft anatomy of extinct forms and can be used for systematic grouping of the taxa. This paper contributes new information on the value of muscle scar shape for understanding nautiloid relationships.

PREVIOUS STUDIES ON THE MUSCLE SCARS IN NAUTILOIDS

More than 100 years ago, muscle scars were described, mostly by German writers, in several Palaeozoic nautiloids from erratic boulders in Baltoscandia (for review, see Mutvei 1957). At that time, however, such scars were used neither in taxonomy nor for interpretation of soft anatomy. A detailed study of several Early Palaeozoic genera was published by Mutvei (1957) who discussed muscle scars with regard to the soft part anatomy of nautiloids.

Sweet (1959) described some additional attachment structures and discussed their taxonomic value. Mutvei (1964) provisionally distinguished three groups of fossil nautiloids on the basis of shell morphology combined with the number and position of muscle scars. He differentiated between Oncoceratomorphi, Nautilomorphi and Orthoceratomorphi. The Oncoceratomorphi were distinguished as comprising taxa currently referred to the orders Oncoceratida and Discocerida. They were characterized by 7–25 pairs of retractor muscle scars, the ventral pair being the largest. The Nautilomorphi comprise the recent *Nautilus* and the fossil orders Tarphyceratida, Barrandeoceratida and Nautilida. They have either a single lateral pair, a single ventral pair, or ventral and lateral pairs of muscle scars. The Orthoceratomorphi, as defined, comprise the fossil orders Orthoceratida and Ellesmereoceratida, and are characterized by a paired or a single dorsal muscle scar. Recently, Mutvei (2002*a*, *b*) classified Orthoceratomorphi as the order Orthoceratida Kuhn 1940 (*sensu* Mutvei) including Orthoceratida and Actinoceratida, which both possess dorsal muscle scars and an inner calcified-perforate layer of the connecting ring.

MATERIAL

Most of the material was collected by G. Holm in the late nineteenth and early twentieth centuries, and by one of

us (HM) from the Häludden outcrop on the north-east coast of the island of Öland, Sweden. The lower part of the Orthoceratite Limestone crops out on Öland along a cliff north of Byxelkrok. The outcrop extends from the lower Lanna Limestone, Volkovian Stage, up to the Holen Limestone Formation of the Kundan Stage and gives, therefore, a profile at the boundary interval of Arenig–Llanvirn. The cephalopods collected came mainly from the lower Holen Limestone Formation of Hunderumian Stage. The Holen Limestone Formation, which is only 7–10 m thick, consists of greyish, thinly bedded glauconitic or oolitic, sometimes strongly phosphatized limestones (see Jaanusson 1960; Jaanusson and Mutvei 1982). Numerous discontinuity surfaces occur in the highly condensed section. The abundant cephalopods are partly phosphatized, showing exceptionally good preservation of minute details of the shell.

A minor part of the material was collected by G. Holm from different outcrops of the Folkeslunda Limestone Formation, throughout Öland and during his visits to Estonia. The Folkeslunda Limestone Formation (Lasnamägian, Llanvirn) consists of greyish, thinly bedded glauconitic, oolitic, bioclastic limestones with several omission or hardground surfaces. These surfaces are often phosphatized or haematitic. The Folkeslunda Limestone in Öland is about 3 m thick and highly fossiliferous with a diverse cephalopod fauna; also common are hyolithids, gastropods and trilobites. The fauna is well preserved, and sometimes slightly phosphatized (see Jaanusson 1960; Jaanusson and Mutvei 1982).

Repository abbrevations. NRM, Naturhistoriska Riksmuseet Stockholm; SGU, Sveriges Geologiska Undersökning, Uppsala; MB, Museum für Naturkunde der Humboldt Universität zu Berlin.

TERMINOLOGY

In Recent *Nautilus* the retractor muscles, the longitudinal mantle muscles and the subepithelial muscles from the septal portion of the body all have their origin on an annular myoadhesive band of the mantle (Mutvei and Doguzhaeva 1997, text-fig. 10B). This band, termed by Owen (1832) the annulus, secretes a more or less pronounced elevation on the inner surface of the shell wall immediately anterior to the mural part of the last septum. This elevation was therefore termed the annular elevation (Mutvei 1957). As in *Nautilus* (Mutvei and Doguzhaeva 1997, text-fig. 9C, pl. 9, fig. 1, pl. 10) the anterior border of the annular elevation often forms a ridge that appears as a furrow on the internal mould of the living chamber. In fossil shells the position of the muscle scars is indicated by anteriorly extending lobes of this annular elevation or in places where its width increases. In certain cases the annular elevation is more pronounced on the muscle scars than elsewhere. Additionally, discrete circular to subquadrangular areas are developed posterior to the lobes.

SYSTEMATIC PALAEONTOLOGY

Order ELLESMEROCERIDA Flower, *in* Flower and Kummel 1950 emend. nov.

Diagnosis. Small cyrto-, ortho- and gomphoceracones, usually laterally compressed or rounded in cross-section, mostly with short chambers. Siphuncle marginal or submarginal, mostly ventral, comparatively wide, sometimes with diaphragms. Siphuncular segments concave with largest diameter at septal necks. Connecting ring of a thick spherulitic–prismatic outer layer. Multiple paired muscle scars located at base of living chamber.

Remarks. There is one main reason for emending of the Ellesmerocerida. This order was originally said to comprise all 'archaic' (Flower 1964) or 'ancient' (Furnish and Glenister 1964) nautiloids. This initial, intuitive definition was very broad, subjective, far from a natural grouping, and includes very different nautiloids that can easily be divided into some taxa of ordinal rank. Consequently, the original pool of Ellesmerocerida was restricted later by the outgrouping of the Plectronocerida (Chen and Teichert 1983), Protactinocerida (Chen *et al.* 1979) and Yanhericerida (Chen *et al.* 1979). Furthermore, Mutvei (2002*a*, *b*) showed that the Baltoceratidae belong to the Orthoceratida, as is evident from the typical structure of the connecting ring as well as the shape of the muscle impressions and general shell shape. Frey (1995, p. 27) pointed out that 'other distinctive groups within the Ellesmerocerida that may constitute separate order-rank taxa are … Protocyloceratidae, the strongly compressed Bassleroceratidae, and the Bathmoceratidae and Cyrtocerinidae'. Thus since 1950, when Flower erected the Ellesmerocerida, the order has become more and more eroded. The remaining taxa, which represent the families Ellesmeroceratidae and Cyclostomiceratidae, share a relatively large set of morphological characters, marginal–subcentral, concave siphuncle, endo- or exogastric shell, a connecting ring consisting of a relatively thick spherulitic–prismatic layer and common diaphragms in the siphuncle. The diagnosis above summarizes this remaining set of features.

In this paper only two genera of the Ellesmerocerida are dealt with: *Oelandoceras* and *Pictetoceras*. Both belong to the youngest representatives of the order, which comprises mainly Canadian forms.

Family CYCLOSTOMICERATIDAE Foerste, 1925

Genus PICTETOCERAS Foerste, 1926

Pictetoceras oliviae King, 1998
Text-figures 1B, 3D–H, 5B

*1998 *Pictetoceras oliviae* King, pp. 341–342, text-figs
3A–D, 4, 6A

Holotype. NRM Mo 158460a.

Type locality and horizon. Hälludden at Öland, Sweden; Grey Vaginatum Limestone, Lower Holen Limestone Formation (upper Arenig/Kunda).

Material. Twenty-six specimens in the repository of the NRM.

Diagnosis. Small, straight or slightly cyrtocone, slightly compressed, gomphoceroid shell. Smooth or weakly ornamented with growth lines. Sutures slightly undulatory with dorsal and ventral saddles. Siphuncle tubular, in contact with shell wall. Septal necks orthochoanitic. Thick spherulitic–prismatic layer of the connecting ring.

Description of muscle scars. The annular elevation with muscle scars is most completely preserved in the specimen NRM Mo-158460 (Text-fig. 3D–E). It forms a narrow band around the base of the body chamber. This band is only slightly broader on the ventral than on the dorsal side. Its posterior margin is marked by a thin, rather distinct ridge on the internal mould of the body chamber. This ridge runs more or less parallel to the last suture. It forms several, indistinct, adapically directed lobes. The anterior margin of the annular elevation is likewise distinct,

but without forming a ridge. Here the annular elevation forms indistinct, adorally directed lobes opposite the adapically directed lobes. The muscle scars are slightly oval with the largest diameter in a lateral direction. Most scars have a somewhat irregularly pitted, rough surface. The adjacent scars are mostly in contact with each other; only a few are separated by narrow interspaces. The position of each scar on the annular elevation is indicated by the adapical-adoral lobes. The scar occupies the entire distance between the anterior and posterior margins of the annular elevation. There are about 9–10 pairs of muscle scars situated around the entire body chamber. As in *Oelandoceras*, the most ventral muscle scars are larger than the remaining scars.

In specimen NRM Mo-160671 (Text-fig. 3F–H) the annular elevation forms a distinct groove on the mould of the body chamber. The muscle scars are well preserved on the ventral side of the body chamber but indistinct and worn off on the dorsal side. They show similar morphological features to the first specimen, and consist of about the same number.

Remarks. The following characters in this species show considerable intraspecific variation: the maximum dorsoventral diameter at the base of the body chamber in adult shells varies between 9 and 12 mm, and the cross-section of the shell is depressed to a varying degree.

According to King (1998) the connecting ring in this species consists of two structurally different layers. These two layers could not be distinguished by us in the type material. Instead there seem to have been slight differences in compaction of acicular crystallites in a single outer spherulitic–prismatic layer of the connecting ring. The effect of differences in compaction may well have been increased during diagenesis by recrystallization and
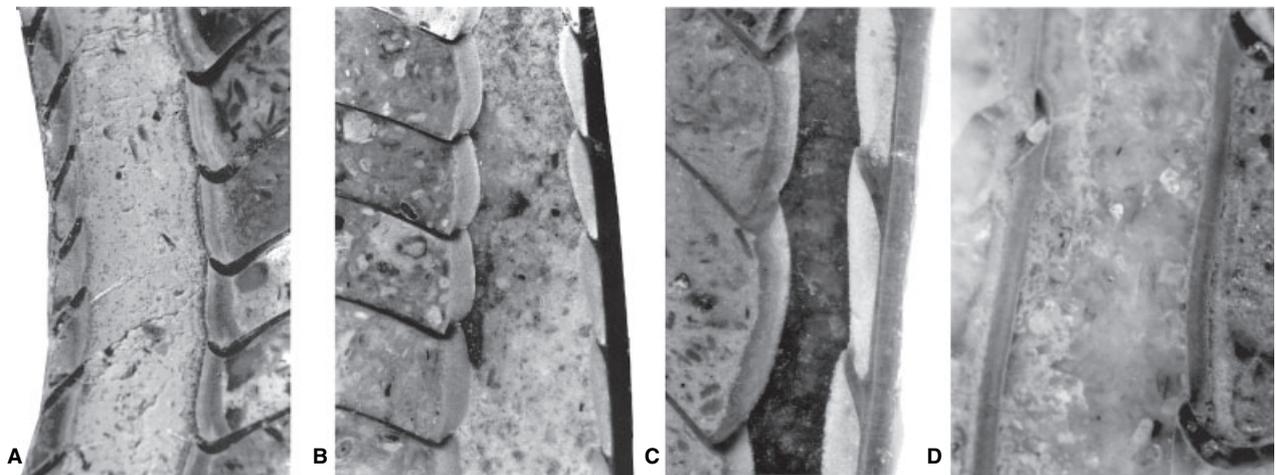
TEXT-FIG. 1. A, *Oelandoceras haelludenense* Foerste, 1932; NRM-Mo 160711, Öland; Holen Formation (late Arenig); polished section of the phragmocone; × 13. B, *Pictetoceras oliviae* King, 1998; NRM-Mo 160671, Hälludden, Öland; Holen Formation (late Arenig); polished section of the phragmocone; × 11. C, *Phtanoncoceras oelandense* Evans and King, 1990; NRM-Mo 1584153b, Hälludden, Öland; Holen Formation (late Arenig); polished section of the phragmocone; × 10. D, *Botellusoceras torpense* sp. nov.; NRM-Mo 160707, Torp, Öland; Folkeslunda Formation (Llanvirn); polished section of the phragmocone; × 10.

phosphatization (Text-fig. 1B). As in *Nautilus*, the connecting ring must have had a second, inner, layer composed of glycoprotein, but this layer is usually not preserved in fossil nautiloids (Mutvei 2002*b*).

Occurrence. The genus is reported from the uppermost Arenig and the Llanvirn of the Ordovician of Baltoscandia.

Family ELLESMEROCERATIDAE Kobayashi, 1934

Genus OELANDOCERAS Foerste, 1932

Oelandoceras haelluddenense Foerste, 1932
Text-figures 1A, 2A–C, 5A

*1932   *Oelandoceras haelluddenense* Foerste, p. 170, pl. 1, fig. 3A–B, text-fig. 6A–B.

1935   *Oelandoceras haelluddenense*; Biese, pp. 63–64, text-fig. 3.1.

1962   *Oelandoceras haelluddennse* [*sic*]; Balashov, pl. 5, fig. 11.

1964   *Oelandoceras haelluddenense*; Flower, p. 98, text-fig. 33.

1977   *Oelandoceras haelluddenense*; Aceñolaza, Durand and Taddei, p. 230.

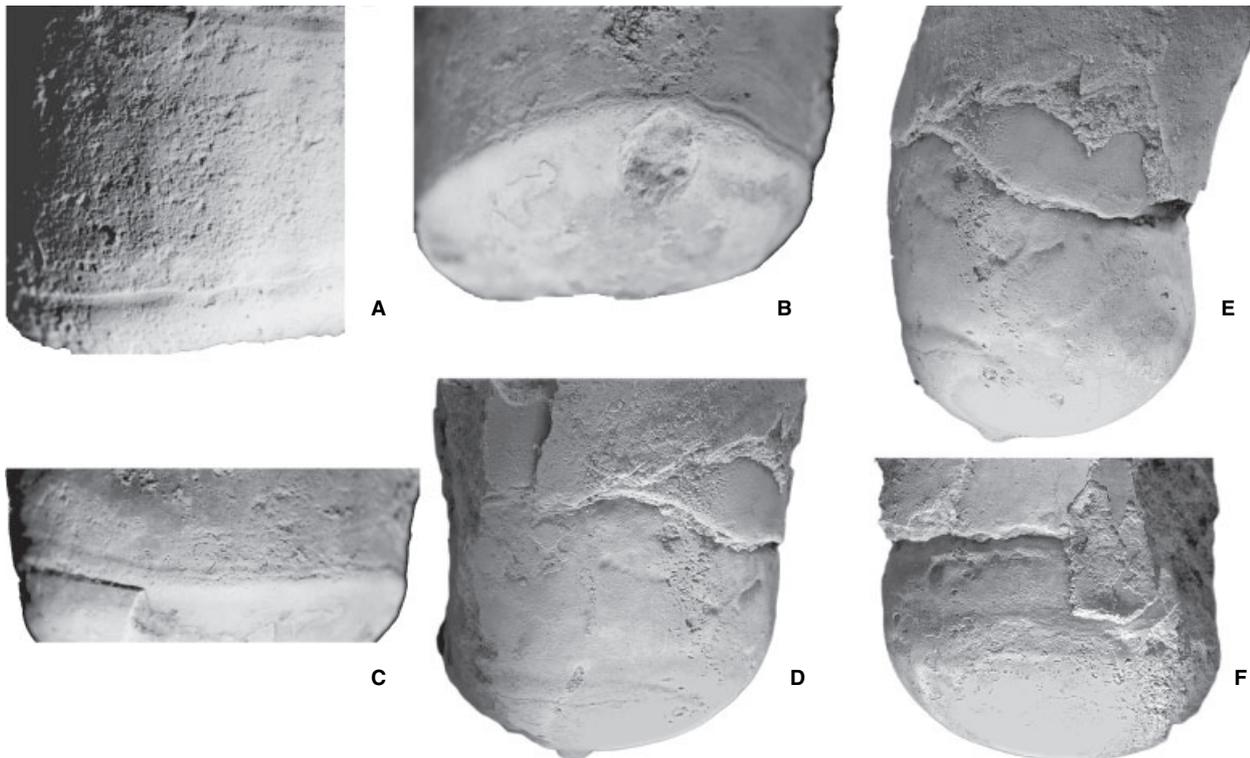1984   *Oelandoceras haelluddenense*; Dzik, p. 20, text-fig. 2.35.

Holotype. SGU type 06714 MO10.

Type locality and horizon. Hälludden at Öland, Sweden; Grey Vaginatum Limestone, Lower Holen Limestone Formation (upper Arenig/Kunda).

Material. Eight specimens in the repository of the NRM

Diagnosis. Small endogastric cyrtocones, slightly compressed in cross-section, surface smooth; sutures with faint lateral lobes, slightly inclined forwards to convex (dorsal) side of shell; siphuncle narrow, tubular, close to concave (ventral) side of shell; septal necks short, orthochoanitic; connecting ring of thick spherulitic–prismatic layer; multiple pairs of muscle scars around base of body chamber.

Description. External characters of the shell were described by Foerste (1932) but the structure of the siphuncle and the type of muscle scars have hitherto remained unknown.

TEXT-FIG. 2. A–C, *Oelandoceras haelludenense* Foerste, 1932. A, NRM-Mo 160699, Hälludden, Öland; Holen Formation (late Arenig); muscle scars at the base of the mould of the body chamber, dorso-lateral view; × 5. B–C, NRM-Mo 160684, Hälludden, Öland; Holen Formation (late Arenig); muscle scars at the base of the mould of the body chamber; B, ventral view; C, lateral view; × 5. D–F, *Estonioceras imperfectum* (Quenstedt, 1845); NRM-Mo 160762, Kandel, Estonia; Middle Ordovician; muscle scars at the base of the living chamber; D, ventral view; E, lateral view; F, dorsal view; × 1·5.

The siphuncle is situated close to the concave (ventral) side of the shell. It is tubular in shape and narrow, having a diameter of about one-tenth of the dorsoventral shell diameter. Septal necks are relatively short and orthochoanitic. The connecting rings are composed of a thick spherulitic–prismatic layer. The inner glycoprotein layer of the connecting ring is not preserved.

Description of muscle scars. The annular elevation in specimen NRM Mo.160684 is discernible only on ventral concave side and on the dorsal convex side where it forms indistinct, adorally directed lobes (Text-fig. 2B–C). As in *Pictetoceras oliviae*, the annular elevation seems to have a uniform width on the ventral and dorsal sides. The adoral lobes of the annular elevation mark the position of the muscle scars, which seem to have a morphology similar to those in *Pictetoceras*.

In the second specimen, NRM Mo. 160699, the body chamber is much smaller than in the first specimen (Text-fig. 2A). The annular elevation is narrow and shows five small, somewhat indistinct, muscle scars on the ventral and ventro-lateral sides of the body chamber. In both specimens the number of muscle scars agrees with that in *Pictetoceras*, being about 9–10 pairs.

Remarks. The genus *Oelandoceras* agrees with the members of the family Ellesmeroceratidae in its endogastric shell and siphuncular structure (Text-fig. 1A). The shape of the annular elevation and the arrangement of the muscles scars show a close similarity to those in *Pictetoceras oliviae*. The latter characters are still unknown in the rest of the ellesmerocerids.

Occurrence. The genus is reported from the uppermost Arenig and lower Llanvirn (Holen Limestone Formtion) of the Ordovician of Baltoscandia.

Order ONCOCERIDA Flower, *in* Flower and Kummel 1950
Family PHTANONCOCERATIDAE Evans and King, 1990

Genus PHTANONCOCERAS Evans and King, 1990

Phtanoncoceras ellipticum (Lossen, 1860)
Text-figures 1C, 3A–C, 5D

*1860   *Cyrtoceras ellipticum* Lossen, p. 27, pl. 1, fig. 3A–B.
1889   *Cyrtoceras ellipticum*; Rüdiger, p. 65.
1992   *Phtanoncoceras ellipticum*; Dzik and Kiselev, pp. 62–65, figs 1a–e, 3a–e.

Lectotype. MB C.873.

Type locality and horizon. Erratic boulder from the Folkeslunda Limestone, Zary (Lower Silesia), Poland.

Material. One specimen in the repository of the NRM, Mo 160695, from Lerkaka, Öland, Folkeslunda Limestone, coll. G. Holm 1882.

Diagnosis. Exogastric cyrtocones with slightly compressed shell. Conch section laterally compressed with broadly rounded venter and obtusely rounded dorsum. Living chamber long. Sutures with faint lateral lobes. Narrow, tubular siphuncle, orthochoanitic septal necks. Thin to moderately thick spherulitic prismatic layer of the connecting ring.

Description of muscle scars. The specimen NRM Mo-160695 (Text-fig. 3A–C) shows a well-preserved annular elevation with muscle scars. The adapical margin of the annular elevation follows a parallel course to the last suture. The adapertural margin forms a paired, broad, adorally directed lobe on the ventral side. Midventrally the two lobes are separated by an acute sinus. The width of the annular elevation at the ventral lobes is about 3 mm. On the ventro-lateral side of the body chamber there follow four acute, prominent lobes separated by rounded sinuses. The annular elevation is 3 mm wide at the lobes but only 2 mm wide between them. The lobes become somewhat narrower in the dorsal direction. In places the surface of the lobes shows longitudinal striae. On the dorso-lateral and dorsal sides the annular elevation forms three low, rounded lobes. The width of the annular elevation at the latter lobes is about 2 mm. The position of the muscle scars on the annular elevation is indicated by nine lobes on both sides of the body chamber. The most ventral pair of the scars is the largest, and the remaining eight pairs decrease somewhat in size in dorsally.

Remarks. As in the case of *Pictetoceras oliviae* (King 1998) the connecting ring of *Phtanoncoceras* was interpreted as double-layered by Evans and King (1990). In order to confirm this interpretation, we restudied the type of *Phtanococeras oelandense* Evans and King, 1990. Evans and King (1990, text-fig. 2) illustrated a diagrammatic cross-section of the apical part of the siphuncle of this specimen. Our current observations show, however, that the outer layer of the connecting ring is not double-layered. This subject is discussed further under *P. oliviae* ('Remarks' and Text-fig. 1B).

Occurrence. Llanvirn of Baltoscandia.

Order and family indeterminate

Genus BOTELLUSOCERAS gen. nov.

Derivation of name. Latin, *botellus*, small sausage.

Type species. *Botellusoceras torpense* sp. nov.

Diagnosis. Shell loosely coiled or cyrtoconic, moderately expanding, exogastric; body chamber contracted, gibbous adorally; cross-section of shell nearly circular; sutures transversal; siphuncle tubular, near venter but not marginal; septal necks orthochoanitic; connecting ring with a thin outer spherulitic–prismatic layer.

TEXT-FIG. 3. A–C, *Phtanoncoceras ellipticum* (Lossen, 1860); NRM-Mo 160695, LerkakA, Öland; Folkeslunda Formation (Llanvirn); muscle scars at the base of the mould of the body chamber; A, dorsal view; B, lateral view; C, ventral view; × 1·5. D–H, *Pictetoceras oliviae* King, 1998. D–E, NRM-Mo 158460; F–H, NRM-Mo 160671; Hälludden, Öland; Holen Formation (late Arenig); Folkeslunda Formation (Llanvirn); muscle scars at the base of the mould of the body chamber; D, ventral view; E, lateral view; × 2; F, lateral view; G, dorso-lateral view; × 4; H, dorsal view; × 20.

Remarks. At present it is impossible to classify the genus with certainty in either the Tarphycerida or the Oncocerida. The close relationship between the two orders has already been discussed by Flower (1964). The borderline between Tarphyceratida and Oncoceratida is very narrowly drawn within Lower–Middle Ordovician exogastric cephalopods.

The genus differs from the tarphycerid *Estoniceras* on account of its short, bent and gibbous body chamber, a larger apical angle and lack of a hyponomic sinus. It differs from the oncocerid *Piersaloceras* in its smaller apical angle, shell ornamentation and spacing of septa.

Occurrence. Folkeslunda Limestone Formation, Lasnamägian, upper Llanvirn of Öland and Dalarna, Sweden.

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Botellusoceras torpense sp. nov.
Text-figures 1D, 4A–D, 5C

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Derivation of name. From Torp, village on Öland, Sweden.

Holotype. NRM Mo 160707, coll. Holm 1909.

Type locality and horizon. Torp, Öland, Sweden; Folkeslunda Limestone Formation, Lasnamaegian, Llanvirn.

Material. Paratype Mo-14555, 8656, 160694 and three unnumbered specimens, in the repository of the NRM.

Diagnosis. As for genus.

Description. The shell is cyrtoconic, circular in cross-section; its maximum dorsoventral diameter is 22 mm. The shell surface is smooth with straight, slightly irregular and non-equidistant growth lines. Chamber length is 7 mm at a shell diameter of 19 mm. Sutures with faint lateral lobes. Concavity of septa is 8 mm at a shell diameter of 20 mm. Siphuncle is situated near the ventral side (5 mm from the ventral side at a shell diameter of 20 mm). It is tubular and its diameter is about one-tenth of the total shell diameter. Septal necks are short and orthochoanitic. Connecting ring consists of a moderately thick, outer spherulitic–prismatic layer (Text-fig. 1D). Living chamber long (about 40 mm). Adult living chamber is sausage-like and widens slightly at the aperture.

Description of muscle scars. In the specimen NRM Mo 160707 the annular elevation is *c.* 3 mm wide on the ventral side of the shell but its width decreases gradually towards the dorsal side where it is about 1 mm (Text-fig. 4A–D). Its posterior margin is distinct. It runs parallel to the last suture and forms indistinct, adapically directed lobes. The anterior margin is also distinct. In contrast to the posterior margin, it forms well-defined, rounded, adorally directed lobes on the opposite side of the adapical lobes. The muscle scars on the annular elevation are clearly discernible, oval depressions with the largest diameter laterally. Each scar occupies the distance between one adapical and adoral lobe. The

ventral scars are the largest. They are separated by a rather wide interspace midventrally. On the lateral and dorsal sides there are seven scars of similar appearance to the ventral scars but their size decreases successively dorsally. The latter scars are separated by narrow interspaces.

In specimen NRM Mo160694 the annular elevation is well preserved on the lateral and dorsal sides. It shows muscle scars that are identical to those in the former specimen.

Occurrence. Folkeslunda Limestone Formation, Lasnamägian, upper Llanvirn of Öland and Dalarna, Sweden.

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Order TARPHYCERIDA Flower, *in* Flower and
Kummel 1950

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Remarks. The muscle scars of species of this order have in the past been interpreted in different ways. Mutvei (1957) figured the muscle scars of *Estonioceras perforatum* (Schröder, 1891), *Estonioceras impressum* (Hyatt, 1894) and *Discoceras angulatum* (Saeman, 1854), which preserved two large ventral scars and several scar-like structures on the lateral parts of the annular elevation. Additionally he figured an *Estonioceras imperfectum* (Quenstedt 1845–49) and *Planctoceras falcatum* (v. Schlotheim 1820) with annular elevation but without discernible muscle scars. This material led him to conclude a simple pair of 'retractor muscles' had been present in the Tarphycerida. Sweet (1959) argued that both dorsal and ventral muscle attachment sites occur in tarphycerids. Such dorsal sites, however, are known in lituitids that belong to the orthocerids and not to the tarphycerids (Mutvei 2002*b*). Sweet's conclusion that the position of the muscle scars have a limited taxonomic significance is, therefore, invalid.

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Family ESTONICERATIDAE Hyatt, *in* Zittel 1900

Genus ESTONIOCERAS Noetling, 1883

Estonioceras imperfectum (Quenstedt, 1845)
Text-figures 2D–F, 5E

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1821   *Lituites imperfectus* Wahlenberg, p. 84.
1845   *Lituites imperfectus* Quenstedt, pl. 2, fig. 17.
1849   *Lituites imperfectus*; Quenstedt, p. 51, pl. 2, fig. 3a–b.
1953   *Estonioceras imperfectum*; Balashov, pp. 220–222, pl. 2, figs 1–3 (see for prior synonymy).
1959   *Estonioceras imperfectum*; Sweet, p. 299.
1964   *Estonioceras imperfectum*; Chang, pp. 132–133, 138, pl. 1, fig. 5.
1971   *Estonioceras imperfectum*; Neben and Krüger, pl. 18, fig. 4.

TEXT-FIG. 4. A–D. *Botellusoceras torpense* sp. nov.; NRM-Mo 160707, Torp, Öland; Folkeslunda Formation (Llanvirn); A, dorsal view; B, lateral view; C, ventral view; D, detail of ventral area of muscle scars; × 2.

Type locality and horizon. Orthoceratite Limestone, Middle Ordovician, Tallinn, Estonia.

Material. Two specimens in the repository of the NRM, Mo 160763, from Torp, Öland, Folkeslunda Limestone, coll. G. Holm 1882, Folkeslunda Limestone Formation, Lasnamaegian, Llanvirn; Mo 160761, 160762 (two fragments belonging to one specimen) from Kandel, Estonia, Middle Ordovician, coll. Holm 1883–84.

Diagnosis. Large *Estonioceras*, openly coiled, slowly expanding, whorls nearly touch each other, shell smooth with faint growth lines, growth lines with ventral suture. Conch section depressed with broad rounded
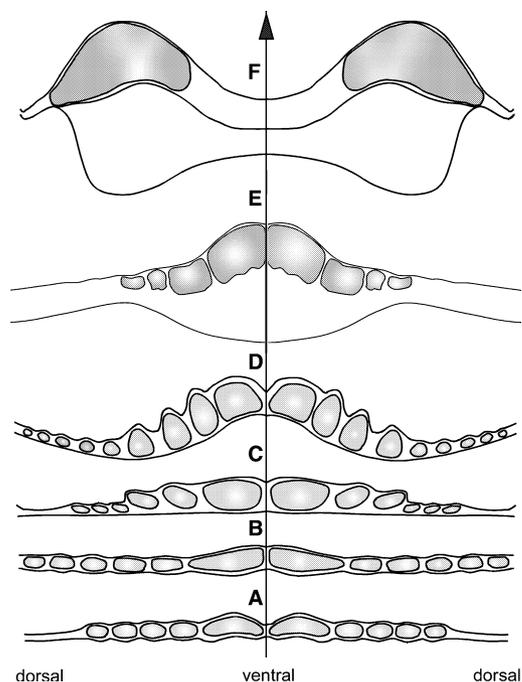
TEXT-FIG. 5. Idealized muscle scar shapes in some nautiloids; note that largest attachment areas of retractor muscles occur in the ventral part except in *Nautilus*. A, *Oelandoceras haelludenense* Foerste, 1932. B, *Pictetoceras oliviae* King, 1998. C, *Botellusoceras torpense* sp. nov. D, *Phtanoncoceras ellipticum* (Lossen, 1860). E, *Estonioceras imperfectum* (Quenstedt, 1845). F, *Nautilus pompilius* L.; after Mutvei and Doguzhaeva (1997); arrow in direction of growth.

venter and slightly concave dorsum, Living chamber long. Sutures with faint lateral lobes. Narrow, tubular siphuncle, subventral; orthochoanitic septal necks; thin to moderately thick spherulitic prismatic layer of the connecting ring.

Remarks. The external characters of the genus are well described by Balashov (1953). The connecting ring and septal neck system is described in detail by Mutvei (2002*b*) on *Estonioceras imperfectum* from Tallinn. A supplementary description is given below on well-preserved muscle scars in this species.

Description of muscle scars. The adult specimen, NRM Mo 160762 (Text-fig. 2D–F), shows the annular elevation with exceptionally well-preserved muscle scars. The entire shell diameter is about 80 mm and the dorso-ventral diameter at the base of the body chamber is 28 mm. The annular elevation appears as a rather deep depression on the internal mould of the body chamber. Its adapical margin is marked by a weak furrow that runs parallel to the last suture. Its adoral margin is marked by a distinct edge. The annular elevation forms a broad, rounded and high lobe on the ventral side, being 20 mm wide here. Midventrally the lobe shows a shallow, rounded sinus. On the lateral

and dorsal sides the annular elevation has a uniform width of 5 mm. Four pairs of muscle scars are distinctly visible as depressions on the annular elevation. The ventral pair is large and oval shaped with a longitudinal dimension of 8 mm and a transverse dimension of 10 mm. Midventrally these scars are in a broad contact with each other. The adapical portion of the scars has several shallow pits. On the ventro-lateral sides there are three, closely situated, somewhat quadrangular scars that decrease rapidly in size dorsally. Each of these scars has an irregularly pitted adapical portion. The rest of the annular elevation shows, on the dorso-lateral and dorsal sides, several small pits of irregular shape.

Occurrence. The genus is reported from the Llanvirn and Llandeilo of Baltoscandia and from China.

DISCUSSION

As pointed out (Boletzky 1987; Wells 1988), Recent decapod coleoids have two pairs of pedal retractor muscles, cephalic and hyponome retractors. Octopods have an additional, second pair of cephalic retractors. Recent *Nautilus* has two pairs of pedal retractors, seemingly homologous to those in the majority of coleoids, but the hyponome retractors are here much smaller in size and situated on the ventral surface of the powerful cephalic retractors (Wells 1988; Mutvei *et al.* 1993, fig. 8B). Early Palaeozoic cephalopods show even more pairs of muscles, four pairs of cephalic retractors in tarphycerids, about 9–10 pairs in ellesmerocerids and up to 25 pairs in oncocerids and discocerids (see Text-fig. 5 and e.g. Mutvei 1964; Mjagkova 1967; Zhuravleva 1972; Dzik 1984).

Two pairs of pedal retractors in *Nautilus* correspond to two pairs of nephridia, gills and atria. Several authors have considered the occurrence of two pairs of these organs as primitive features, indicating metamery (e.g. Naef 1926; Lemche and Wingstrand 1959; Wingstrand 1985), whereas others have considered these organs as secondarily duplicated (e.g. Morton and Yonge 1964). It was shown later by Wingstrand (1985) and Haszprunar and Schaefer (1996) that whereas serial repetition of organs is an autapomorphy of monoplacophorans, such serial repetition of organs also seems to be a primitive feature of the Mollusca in general (Haszprunar and Wanninger 2000). Furthermore, there is a tendency for reduction of serially repeated organs in the various molluscan subclades. This trend can now also be demonstrated for cephalopods (see Text-fig. 5).

Nevertheless, the functional reason for the complex muscle system in monoplacophorans as well as in early cephalopods remains enigmatic. Haszprunar and Wanninger (2000, p. 162) pointed out that 'it is very improbable

that a muscle can "survive" phylogenetically, if there is no functional need for it'. If the multiple pedal muscles in fossil nautiloids were inherited from primitive molluscs, such as monoplacophorans and polyplacophorans, they must have acquired rapidly a new, and still unknown function. On the other hand, it is possible that the multiple muscles in fossil nautiloids have arisen by a secondary subdivision of a few retained pedal muscles, as in various Recent gastropods, notably in patellogastropods (Wanninger *et al.* 1999).

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