Discosorids and Oncocerids (Cephalopoda) of the Middle Ordovician Kunda and Aseri Regional Stages of Baltoscandia and the early evolution of these groups

Original article

Céphalopodes discosoridés et oncocéridés des étages régionaux Kunda et Aseri de l’Ordovicien moyen de Baltoscandinavie et premiers stades évolutifs de ces groupes

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Abstract

Discosorid and oncocerid cephalopods of the Kunda and Aseri Regional Stage (Darriwilian, Middle Ordovician) from Öland Island, Sweden and North Estonia are described for the first time. We demonstrate that a high generic and specific diversity of Oncocerida was already established in the earliest Darriwilian. The new oncocerid species Neumatoceras borense nov. sp., N. breviborense nov. sp., Paramiamoceras breviventrum nov. sp., Richardsonoceras gastroscopium nov. sp., R. gerhardi nov. sp., R. goldmanni nov. sp., R. haelluddenense nov. sp., Richardsononoceroides kingi nov. sp., R. oelandense nov. sp., and R. rhytium nov. sp. are erected; Richardsonoceroides schiefferdeckeri (Dewitz) is revised. The new graciloceratid Kundoceras evansi nov. gen., nov. sp. is erected. A review of records of early oncocerids from China shows that Richardsonoceras Foerste is probably the most primitive oncocerid and supports the hypothesis that oncocerids evolved in the early Floian or latest Tremadocian from a Bassleroceras Ulrich and Foerste-like ancestor. The new discosorid genus Paldoceras nov. gen. and species Paldoceras paldiskense nov. sp. and P. neptunsakerense nov. sp. are erected. These discosorids record the morphological link between the late Darriwilian Ruedemannoceras Flower and the early Floian Apocrinoceras Teichert and Glenister, which is considered to be the earliest discosorid.

Résumé

Les céphalopodes discosorides et oncocérides des étages régionaux Kunda et Aseri (Darriwilien, Ordovicien Moyen) de l’île Öland, Suède et du Nord de l’Estonie sont décrits pour la première fois. Nous démontrons qu’une très forte diversité spécifique et générique des Oncocérides était déjà établie au début du Darriwilien. De nouvelles espèces d’oncocérides sont décrites : Neumatoceras borense nov. sp., N. breviborense nov. sp., Paramiamoceras breviventrum nov. sp., Richardsonoceras gastroscopium nov. sp., R. gerhardi nov. sp., R. goldmanni nov. sp., R. haelluddenense nov. sp., Richardsononoceroides kingi nov. sp., R. oelandense nov. sp., et R. rhytium nov. sp. L’espèce Richardsononoceroides schiefferdeckeri (Dewitz) est révisée. Un nouveau gracilocératide est décrit : Kundoceras evansi nov. gen., nov. sp. Une observation des enregistrements des oncocérides primitifs de Chine montre que Richardsonoceras Foerste est probablement le plus primitif des oncocérides et conforte l’hypothèse que les oncocérides ont évolué durant le Floien ancien ou le Trémadocien récent depuis un ancêtre ressemblant à Bassleroceras Ulrich et Foerste. Un
nouveau genre et deux nouvelles espèces de discosorides ont été créés : Paldoceras nov. gen., Paldoceras paldiskense nov. sp. et P. neptunsakerense nov. sp. Ces discosorides enregistrent le lien morphologique entre Ruedemannoceras Flower du Darriwilien récent et Apocrinoceras Teichert et Glenister du Floien ancien qui est considéré comme le discosoride le plus ancien.

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Mots clés : Darriwilien ; Oncocéridés ; Discosoridés ; Baltoscandinavie

1. Introduction

Oncocerids and discosorids are a highly diverse group of nautiloids that contributed significantly to the diversity of many Ordovician–Devonian shallow-water fossil cephalopod associations. The two groups comprise mainly stumpy (breviconic), curved conch forms with sometimes highly modified adult body chambers.

The systematic differentiation of the two orders is difficult. In both evolutionary lineages the siphuncle is considered to be tubular or expanded, the connecting ring is considered to be thick or thin, and characteristic actinosiphonate deposits occur. Although the position of the siphuncle in oncocerids is generally exogastric and in discosorids endogastric, in both groups taxa with a central siphuncle position occur. These difficulties are classically interpreted as a result of repeated homeomorphy and morphological conversion of two originally clearly separated higher taxa during their evolutionary history (Flower and Kummel, 1950; Flower and Teichert, 1957; Sweet, 1964; Teichert, 1964).

Because the systematics of several oncocerid and discosorid families was discussed very contrarily in the past (Dzik, 1984), depending of the interpretation of their phylogeny, the tracing of the early evolutionary history of these orders is crucial for the diagnostic differentiation of younger families. The discovery of early Floian oncocerids in South China in the early 1980s, published in Chinese language (Chen in Qi et al., 1983) failed to reach a broader readership. Awareness of this assemblage, combined with the discovery of a new exceptionally preserved, Darriwilian oncocerid–discosorid association from the north Estonian Darriwilian Aseri Regional Stage (discovered B.K. and M.I.) and with a comparison of these specimens with the partly undescribed collection of early Darriwilian oncocerids from the Island of Öland of Sweden housed in the Naturhistoriska Riksmuseet, have provided the motive opportunity to review the conflicting ideas of earlier authors and attempt to trace the early evolution of discosorids and oncocerids.

2. Material

The majority of the material reported here is from part of the collections of Gerhard and Olivia Holm at the Naturhistoriska Riksmuseet Stockholm, Sweden (RM, NRM-PZ Mo- numbers). Gerhard Holm was curator of the fossil collection of the Riksmuseet from 1901–1923 and during repeated visits in the 1890s and early 1900s to the Öland Island (Fig. 1) the two collected a great number of cephalopods, mainly from the Hälludden cliff at the very northeast of the island. Holm published only very little from this collection (e.g., Holm, 1897, 1900), but numerous notes, available at the Riksmuseet testify for plans to write a comprehensive work on the coiled nautiloids. Several specimens are named by him as nomina nuda. A significant number of tarphycerids of this collection still remains to be described in a future work.

The second part of the material comes from our own collections (B.K. and M.I.) in summer 2006. A single 4 m × 4 m large block at the cliff about 2 km northwest of Paldiski at the Pakri Peninsula, Estonia yielded about 50 specimens of small nautiloids on a bed surface ca. 0.02 m above the base of the Aseri Limestone, comprising small discosorids, oncocerids, tarphycerids and orthocerids. The material is in the Paleontological collection of the University of Tartu, Museum of Geology, Tartu, Estonia (TUG).

3. Geological and palaeoecological setting

3.1. Hälludden cliff section

The Hälludden is a cliff exposure at the very northeast of the Öland Island, Sweden, a few kilometres north of Byxelkrok (Fig. 1). At the Hälludden section a grey to yellow to green thin-bedded glauconitic wackestone of the Kundan Gillberga Formation and the lowermost part of the Formation C (Stouge, 2004), Darriwilian, Middle Ordovician crops out. These Formations comprise the Lanna and Holen Limestones sensu Jaanusson (1982) (compare Ebbestad and Högström, 2007).

Fig. 1. Regional overview on the early Palaeozoic of the Baltoscandian with the two main discosorid and oncocerid collection sites (stars) (map after Jaanusson, 1976).
The Hälludden section was intensively studied since more than a century. Jaanusson and Mutvei (1982) investigated the faunal composition of the section bed by bed using index horizons for the determination of the occurrences. The boundary between Formation C and the Gullhögen Formation is a prominent discontinuity surface (horizon D). The limestones below the horizon D contain commonly arenitic glauconite grains (Stouge, 2004) and correspond to the Hunderumian Asaphus (Asaphus) expansus Biozone and the basal Valastean Asaphus (Asaphus) raniceps Biozone (Jaanusson and Mutvei, 1982).

Stouge (2004, p. 104) listed conodonts indicative of the Baltionodus triangularis–Yangtzeplacognatus crassus conodont-zone for this section (Fig. 2).

Almost all cephalopods collected at Hälludden by O. and G. Holm are from the green thin bedded glauconitic limestones of the upper part of the Gillberga Formation. A few specimens of the Riksmuseet, collected by Mutvei, have detailed horizon information; all came from within the upper metre of the Gillberga Formation. Jaanusson and Mutvei (1982, Fig. 6) list common cephalopods in the half-metre below horizon D. Therefore it is concluded that the Hälludden cephalopods described herein are exclusively from the early Darriwilian, Timeslice 4a of Webby et al. (2004).

Earlier descriptions of cephalopods from this horizon comprise several ellesmerocerids (Holm, 1900; Evans and King, 1990; King, 1998, 1999; Kröger, 2006), endocerids (Holm, 1897; Mutvei, 1997), and orthocerids (Foerste, 1928; Kröger, 2004; Kröger and Mutvei, 2005). However, a number of cephalopods, especially taphycerids and actinocerids, from this section are still undescribed. The non-cephalopod macrofauna of this section comprises common trilobites, echinoderms, paragastropods, and other mollusks (Jaanusson and Mutvei, 1982). The fossils are slightly phosphatized with exceptionally preserved conch microstructures.

The depositional environment of the Hälludden Limestones has been equivocally debated (see in Stouge, 2004), but a deposition above storm wave-base is considered to be likely. The cephalopod conchs are often broken and the broken conchs are sometimes overgrown by bryozoans. Thus, transport and repeated reworking of the material appears to have taken place, and it is not clear whether the nautiloids were deposited and reworked at the location of their original habitat or had drifted in from elsewhere. However, given the small size of many of the conchs a parautochthon provenance can be assumed.

3.2. Pakri cliff section

The Pakri cliff section northwest of Paldiski, northern Estonia, spans a sedimentary succession from the Lower Cambrian to Uhakuan, Middle Ordovician. The collected cephalopods come from a single 4 m x 4 m large block of the cliff, ca. 2 km northwest of Paldiski at 59°21’694 N, 024°02’390 E, which had fallen from the cliff, exposing a weathered surface in the basal 0.02 m of the Ojaküla Member (Cephalopod Limestone), Kandle Formation of the Aseri Regional Stage. This limestone is slightly younger than the Gillberga Formation of Öland, representing roughly the Eoplacognathus suecicus conodont-zone, which corresponds to the late Darriwilian, timeslice 4c of Webby et al. (2004) (Fig. 2). At the Pakri Peninsula the Ojaküla Member of Kandle Formation (Aseri limestone) comprises a 0.15 m thick green-grey, quartz-arenitic packstone with dark phosphatic Fe-oxhydroxide (limonite) ooids. The limestone consists of two sedimentation intervals, which are divided by a prominent hardground. The lower part is marly; a deeper green colour than the upper part appears on the weathered surface. The lower boundary of the Aseri Stage (Limestone) is a nearly plane, strongly phosphatized dark hardground. In the lower levels of the upper part, fragments of large endocerids are very common. However, the discosorids and oncocerids described herein are exclusively from a layer ca. 0.02 m above the basal hardground of the Aseri Stage, where large endocerids are absent or very rare. Besides the discosorids and oncocerids described herein, small fragments of smooth orthocerids and taphycerids (e.g. Estonioceras Noetling, 1883) were relatively common at the block surface. The non-cephalopod macrofauna comprises echinoderm ossicles, trilobites, hyolithids, gastropods and paragastropods.

Similar to Hälludden, the cephalopod conchs are often broken and sparite-filled broken conchs were sometimes subsequently broken, as indicated by bryozoan overgrows, suggesting transport and repeated reworking of the material. However, given the small size of many of the conchs a parautochthonous provenance probably from slightly deeper waters is likely, similar to that represented by the Gillberga Formation at the Hälludden cliff, from the Livonian Tongue in the south. The strongly condensed section, the high content of sand and the reworking of shells suggest a relatively shallow depositional environment, clearly above storm wave-base close to the northern shoreline of the Baltic Basin (compare also paleogeographic reconstructions of Männil, 1966).

4. Evolutionary importance of the described associations

Since Flower and Kummel (1950) the classification of the Discosorida and Oncocerida is strongly connected with the phylogenetic concepts of the two groups. The Oncocerida were
4.1. Early evolution of the Discosorida

The evolutionary plasticity of post-Middle Ordovician Discosorida is reflected by the diagnoses in Sweet (1964: K283) and Teichert (1964: K324), respectively. The Oncocerida are characterized by an exogastric or endogastric conch curvature, tubular or “considerably inflated” siphuncular segments. The Oncocerida are described as brevicones which are “endogastric; rarely exogastric” and have expanded siphuncular segments and thick connecting rings. Therefore, the investigation of the early evolution of these groups is crucial in order to understand their later composition, their changes and interdependences.

4.1. Early evolution of the Discosorida

The Chazyan (late Darriwilian) Ruedemannoceras was classically considered to be the ancestral discosorid (Flower and Teichert, 1957). Flower (1976) mentioned Ruedemannoceras from the Whiterockian of Nevada, and Loganceras Foerste, 1933 from the Whiterockian (late Darriwilian) of Newfoundland as earliest records of the Discosorida. Flower (1979) described another Chazyan ruedemannoceratid from the Cape Webster Formation of north Greenland. These occurrences were long thought to be the oldest Discosorids, although a middle Darriwilian discosorid Sangzhioceras chinense Lai, 1982 had been recorded from the Shihtzupu Formation of Hunan, China, but was not recognized in the western literature. Ruedemannoceratids are only moderately curved, relatively slender brevicones with a widely expanded, eccentric siphuncle. In Ruedemannoceras, the early portions of the siphuncle are subcentral, suggesting a migration of the siphuncle from a dorsal position to a ventral position during early ontogeny (Flower and Teichert, 1957, p. 44). Although, Flower and Teichert (1957) never seriously discussed the possibility that the conch flipped its curvature during ontogeny in Ruedemannoceras, this scenario remained an alternative to the ideas of these authors until today.

Flower and Teichert (1957) favored a model that regards电子商务ers as more or less direct ancestors of discosoridians. The problem with this model is the large stratigraphic gap between the youngest electrornocrinid (late Cambrian) and the earliest discosorids. Earlier, Teichert and Glenister (1954) considered the early Floian nautiloid Apocrinoceras talboti Teichert and Glenister, 1954 as an ancestral discosorid. But, according to Flower and Teichert (1957, p. 44): “It became apparent that the resemblance between the siphuncles of Westonoceras and Apocrinoceras did not extent to Apocrinoceras and Ruedemannoceras. Yet all evidence indicates that Ruedemannoceras is primitive in relation to Westonoceras,” and thus Apocrinoceras was rejected as discosorid ancestor. The discosorid occurrences from the earliest and middle Darriwilian described herein as Paldoceras nov. gen. allows a new interpretation of Apocrinoceras. In fact, Apocrinoceras is very similar to Paldoceras; it has a simple, expanded marginal siphuncle, short cyrtoconoid septal necks and a slightly cyrtoconic shell form. The connecting ring and septal neck shape of the newly discovered specimens and that of Apocrinoceras are very similar. Ruedemannoceras differs from the former two in having a siphuncle that is clearly removed from the conch margin, thicker and with shallow bulletes. Paldoceras with its simple and relatively thin, but widely expanded connecting ring, is the morphologic and stratigraphic link between Apocrinoceras, and Ruedemannoceras. Beside Apocrinoceras only a few pre-Darriwilian brevicones with expanded siphuncles at the concave side of conch are known; all are questionable, because of the fragmentary and poor preservation. The enigmatic and poorly known brevicones Clelandoceras (?) rarum Flower, 1964 from Fort Cassin equivalent (early Floian) of the El Paso group and Muriceras (?) obscurum Flower, 1964 from the Stairsian equivalent “first pilocerid zone”, are potentially early discosorids. Both species have an expanded, marginal siphuncle at the concave side of the conch, but details of the connecting ring and septal necks are not known. Further finds may show if these cephalopods are related to Apocrinoceras and if the discosorids had already originated by the middle Tremadocian (Stairsian equivalent).

4.2. Early evolution of the Oncocerida

The Chazyan (late Darriwilian) Graciloceras was classically considered as the earliest oncicerid. Findings of graciloceratids in the Antelope Valley Limestone of Nevada (Flower, 1968) gave first evidence for a pre-Chazyan origin of the Oncocerida, but detailed stratigraphic comparisons were unavailable in the

Fig. 3. Schematic drawings of Early Ordovician oncocerids. 1. Valhalloceras floweri Evans and King, 1990, from the Olenidletta Member, Valhalla Formation (Billingen equivalent), Flowian. 2. Langyashanoceras circulare Chen in Qi et al., 1983. 3. Richardsonoceras langyashanense Chen in Qi et al., 1983. Both from the early Flowian of the Hunghuayuan Formation from Chuxian, Anhui, China. Not to scale.
late 1960s. Flower (1971) mentioned a slightly older *Gracioceras* from Lehman Limestone of Utah, USA, but again, a detailed stratigraphic comparison was not available at that time. Therefore, Flower (1971, 1976) considered that oncocerids and discosorids originated during the Whiterockian (Middle Ordovician).

An improved stratigraphy of the Antelope Valley Limestone revealed a late Dapingian–early Darriwilian age for the graciloceratids *Ikesoceras* Flower, 1968 and *Leonardoceras* Flower, 1968 (see Siewers, 1993). Evans and King (1990) presented records of unequivocal graciloceratids from the middle or late Floian of the Valhalla Formation of Spitzbergen (*Valhalloceras floweri* Evans and King, 1990), but note that the second species *Phtanococeras oelandi* Evans and King, 1990 described therein, is an ellesmerocerid with clearly concave, thick connecting ring segments, although it remained under the Oncocerida in Evans and King, 1990). However, already in the late 1970–1980s several pre-Chazyan occurrences of Oncocerida of the Far-East were reported from the latest Tremadocian to early Floian (*Langyashanoceras circulare* Chen in Qi et al., 1983; *Richardsonoceras langyashanense* Chen in Qi et al., 1983: Fig. 3(2, 3)), Dapingian (*Richardsonoceras yongshunense* Lai and Qi, 1977, *Richardsonoceras beianense* Ying, 1989) and early Darriwilian (*Oncoceras katoi* Kobayashi, 1928). But these records remained largely unnoticed by western workers. Interestingly, one of the earliest oncoceridan records *L. circulare* from the Hunhuayuan Formation of Anhui, China is a form with a flanged shell (Fig. 3(2)), similar to *Diastoloceras perplexum* Teichert and Glenister, 1954,

![Fig. 4. Darriwilian discosorids from Baltoscandia. 1–6. *Paldoceras paldiskense* nov. gen., nov. sp., from cliff northwest of Paldiski, Pakri Peninsula, north Estonia, Aseri Regional Stage. 1–3. TUG 1285-42: 1: lateral view; 2: view of convex antiprosphuncular side, note overgrown bryozoan above eroded conch with sparite filled chambers; 3: view of concave prosphuncular side. 4. TUG 1285-47, median section, note the short body chamber, same specimen as Fig. 5(3). 5. TUG 1285-35 with adult septal crowding and parts of body chamber. 6. TUG 1285-10, note marginal expanded siphuncle in earliest growth stages preserved, same specimen as Fig. 5(1). 7–8. *Paldoceras neptunsakerense* nov. gen., nov. sp., NRM-PZ Mo 161118, holotype, from Halludden cliff, Öland Island, Sweden, from Gillberga Formation, Kunda Regional Stage, same specimen as Fig. 5(2); 7, median section; 8, lateral view. Scale bar 10 mm.](image-url)
Fig. 5. Median sections of siphuncle and septal necks of Middle Ordovician Discosorida and Oncocerida from Baltoscandia (note: all figures orientated with apex up). 1. *Paldoceras paldiskense* nov. gen., nov. sp., 1285-10, from cliff northwest of Paldiski, Pakri Peninsula, north Estonia, from Aseri Regional Stage, apicalmost part of specimen, showing expanded siphuncular segments of marginal siphuncle, same specimen as Fig. 4(6), scale: 0.5 mm. 2. *Paldoceras neptunsakerense* nov. gen., nov. sp., NRM-PZ Mo 161118, holotype, from Hälludden cliff, Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage, note the short cyrtochoanitic...
known from the early Floian of the Emanuel Limestone of Western Australia. The latter was provisionally placed to the Protocycloceratidae by Teichert and Glenister (1954) but clearly represents an oncocerid with an only slightly curved shell and a marginal slightly expanded siphuncle. Another early oncocerid is “Bassleroceras” annulatum Teichert and Glenister, 1954 from the early Floian of the Emanuel Limestone in Western Australia, which is described as having a marginal siphuncle at the convex side of the conch that is “tubular in outline [...]” appears to consist of short orthochoanitic septal necks joined by thin connecting rings. The siphuncular segments expand slightly between successive foramina’.

All these early Oncocerida, known from the latest Tremadocian to early Floian, have marginal siphuncles with short septal necks similar to Richardsonoceras. Therefore, graciloceratids with eccentric siphuncles and orthochoanitic septal necks hardly represent the starting point of the oncocerid evolutionary lineage, as suggested earlier (e.g., Flower, 1976). Likewise, the middle Floian graciloceratid Valhalloceras floweri (Fig. 3(1)) represents not the ancestral oncocerid morphology. Instead it will be evident that a morphologically diverse oncocerid fauna goes back as early as in the Floian Stage. The Hälludden association impressively shows that gibbous forms (Neumatoceras Foerste, 1935) and slender curved forms (Richardsonoceras) existed in the earliest Darriwilian, as well as typical graciloceratids (Kundoceras nov. gen.). In contrast only Richardsonoceras and breviconic, nearly straight oncoceratids, but no graciloceratids are known from the early Floian.

The structure of the siphuncle and septal necks of Richardsonoceras is preserved in the Hälludden specimens, showing very short, recumbent septal necks and thin marginal, only very slightly expanded connecting rings. The conch morphology and the thin marginal siphuncle are suggestive of Bassleroceras Ulrich and Foerste, 1936, which is very common in the late Tremadocian to Floian in Laurentia. Richardsonoceras differs from Bassleroceras mainly in having a thinner connecting ring with slightly expanded or tubular segments and short, recurved septal necks. Therefore, the available data strongly suggest a descent of the oncocerids from longiconic ellesmerocerids such as Bassleroceras in the latest Tremadocian (Tulean equivalent).

5. Systematic palaeontology

Order DISCOSORIDA Flower in Flower and Kummel, 1950

Family APOCRINOCERATIDAE Flower and Teichert, 1957

Genus Paldoceras nov. gen.

Derivation of name: Referring to the type locality, Paldiski, the harbour in the south of the Pakri Peninsula, Estonia.

Type species: Paldoceras paldiskense nov. gen., nov. sp. from the Aseri Regional Stage, Darriwilian, of the Paldiski cliff at Pakri Peninsula, northwest of Paldiski, Estonia.


Diagnosis: Small, relatively slender cyrtocerids with elliptically compressed cross section. Conch only slightly curved and with nearly straight adult body chamber. Conch surface nearly smooth. Body chamber short and without apertural constriction and hypostomonic sinus. Siphuncle expanded, forming globular segments, but without conspicuous adnate area at adapical surface of septa. Connecting ring apparently thin and simple. Septal necks short, suborthochoanitic to cyrtoceroanitic. No endosiphuncular and cameral deposits known.

Other included species: P. neptunsakerense nov. gen., nov. sp.

Remarks: This genus differs from Apocrinoceras in having a nearly smooth conch and a more compressed cross section.

Paldoceras paldiskense nov. gen., nov. sp.

Figs. 4(1–6), 5(1, 3), 6(1) and 7

Derivation of name: Referring to the type locality.

Holotype: Specimen TUG 1285-18.

Type locality and horizon: Paldiski cliff at Pakri Peninsula, northwest of Paldiski, Estonia; Aseri Regional Stage, Darriwilian.

Material: Holotype and 10 specimens (TUG 1285-10, 14, 26, 32-36, 42, 47) from type locality, Aseri Regional Stage, and one specimen (TUG 1285-1) from Lasnamägi Regional Stage, Pliiku Ots, Väike Pakri Island, Estonia.

Occurrence: Aseri–Lasnamägi Regional Stage, Darriwilian; Pakri Peninsula and Väike Pakri Island, Estonia.

Diagnosis: Slender cyrtocerid conchs, with elliptically compressed cross section with width/height ratio: 0.85 and a medium angle of expansion of up to 20°. Conch surface smooth with faint directly transverse growth lines without hyponomic sinus. Conch in later growth stages shallowly undulated. Body chamber short. Eight chambers at distance similar to conch height. Sutures nearly transverse forming faint lateral lobe and
Fig. 6. Middle Ordovician Oncocerida and Discosorida from Baltoscandia. 1. *Paldoceras paldiskense* nov. gen., nov. sp., TUG 1285-18, holotype, from cliff northwest of Paldiski, Pakri Peninsula, north Estonia, Aseri Regional Stage, same specimen as Fig. 7, lateral view. 2–5. *Kundoceras evansi* nov. gen., nov. sp., from Hälludden cliff, Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage; 2–3: NRM-PZ Mo 161122, juvenile growth stages; 2: view of prosiphuncular, convex side of conch curvature, note the healed shell damage; 3: lateral view; 4: NRM-PZ Mo 158694, holotype, note the nearly tubular eccentric siphuncle, and the
shallow saddle at prosiphuncular side. Siphuncle marginal at concave side of conch curvature with broadly expanded segments and thin connecting ring with diameter 0.15 of conch height. Septal necks short and cyrtochoanitic.

**Description:** Holotype consists of fragment of complete apical part with length of 24 mm (Fig. 6(1,7)). Cross section elliptically compressed with adoral conch height 8 mm, width 6.8 mm (width/height ratio: 0.85). Conch surface smooth with directly transverse faint growth lines. Sutures with faint lateral lobe and shallow but distinctive saddle at prosiphuncular side. Eight chambers occur at distance similar to conch height. Apex conical, compressed. Siphuncle marginal at concave side of conch curvature, globular segments with 0.5 mm diameter at conch height 3.4 mm and septal distance 0.5 mm. Specimen TUG 1285-42 apical fragment with 32 mm length and in adoral parts slightly shallowly undulated shell (Fig. 4(1–3)). The angle of expansion varies between 9° in late growth stages and 20° in early growth stages (mean of early and late stages = 14°, n = 6). The conch width/height ratio varies between 0.75–0.89 (mean = 0.85, n = 6) with tendency toward more circular cross section in later growth stages.

Siphuncle marginal at concave side of conch curvature throughout entire length (Fig. 5(1, 3)). Septal necks short, suborthochoanitic to cyrtochoanitic. Connecting ring equally expanded, simple, slightly thicker than septa.

**Remarks:** This species differs from *P. neptunsakerense* in having a more strongly curved conch and a higher angle of expansion at comparative growth stages.

*Paldoceras neptunsakerense* nov. gen., nov. sp.  
**Figs. 4(7–8) and 5(2)**

**Derivation of name:** From Neptuns Åker, the old name of the Hälludden cliff, Öland Island.

**Holotype:** Specimen NRM-PZ Mo 161118.

**Type locality and horizon:** Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

**Material:** Holotype only.

**Occurrence:** Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

**Diagnosis:** Slender cyrtoconic conch, with elliptically compressed cross section and angle of expansion of 13°. Conch surface smooth with faint straight growth lines. Eight chambers at distance similar to conch height. Sutures nearly transverse. Siphuncle marginal at concave side of conch curvature with expanded segments and diameter 0.13 of conch height. Connecting ring thin and simple. Septal necks suborthochoanitic.

**Description:** Fragment of part of 20 mm long phragmococone with conch height 4.5 mm, increasing to 9 mm and maximum conch width ca. 8 mm. Conch surface smooth with faint straight growth lines. Without hyponomic sinus. Shell slightly undulated in adoral part. Eight chambers occur at distance similar to conch height. Sutures slightly oblique toward direction perpendicular to growth axis, sloping in adoral direction at prosiphuncular side, with faint lateral lobe forming distinctive shallow saddle at prosiphuncular side.

Siphuncle marginal at concave side of conch curvature with clearly expanded segments, diameter 0.8 mm at conch height 6.2 mm and septal distance 0.5 mm. Connecting ring simple, thin, equally expanded between two succeeding chambers (Fig. 5(2)), slightly thicker than septa.

**Remarks:** This species differs from *Paldoceras paldiskense* in having a less curved and more slender shell.

**Order ONCOCERIDA Flower in Flower and Kummel, 1950**

**Family GRACILOCERATIDAE Flower in Flower and Kummel, 1950**

**Genus Kundoceras** nov. gen.

**Derivation of name:** Referring to the type horizon.

**Included species:** *Kundoceras evansi* nov. gen., nov. sp.

**Type species:** *Kundoceras evansi* nov. gen., nov. sp. from the Gillberga Formation, Kunda Regional Stage, Darriwilian, of Hälludden cliff at Öland Island, Sweden.

long body chamber with thickened shell at peristome, same specimen as on Fig. 5(7); 5: NRM-PZ Mo 158458a, lateral view of adult body chamber. 6–8, 11. *Paramiamoceras breviventrum* nov. sp., from Hälludden cliff, Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage; 6–8: NRM-PZ Mo 161124, holotype; 6: apical view, note trapezoidal cross section and the marginal siphuncle; 7: view of antisiphuncular, concave side of conch curvature; 8: lateral view; 11: NRM-PZ Mo 1611123, lateral view, note the adult septal crowding at adoralmost chambers. 9–10. *Neumatoceras* sp. A from Hälludden cliff, Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage, 9, NRM-PZ Mo 161117, lateral view, specimen with part of adapical body chamber, 10, NRM-PZ Mo 161116, lateral view, same as on Fig. 5(4). 12. *Neumatoceras boreense* nov. sp, NRM-PZ Mo 161119, holotype, from Hälludden cliff, Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage, lateral view. 13. 15. *Neumatoceras parviborense* nov. sp, NRM-PZ Mo 161114, holotype, from Hälludden cliff, Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage, same specimen as Fig. 8(6); 13: lateral view; 15: cross section. 14, 16. *Neumatoceras* ? sp, B, NRM-PZ Mo 161121, from Hälludden cliff, Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage; 14: lateral view; 16: apical view, note ovate cross section and the marginal siphuncle at narrower side of cross section. Scale bar: 10 mm.
Occurrence: Kunda Regional Substage, Darriwilian; Öland Island, Sweden.

Diagnosis: Slender cyrtoconic conchs, with subcircular cross section and angle of expansion of 5–7°, with maximum conch height of 14 mm. Conch surface annulated with nearly straight transverse, slightly irregularly spaced acute ridges. Adult body chamber slightly contracted with thickened shell at adult aperture. Five–six chambers at distance similar to conch height. Sutures nearly transverse. Siphuncle between centre and convex side of conch curvature with tubular segments and thin connecting ring with diameter 0.07 of conch height. Septal necks orthochoanitic. No endosiphuncular and cameral deposits known.

Remarks: This genus resembles Piersaloceras Teichert, 1930 in having an elongated, curved conch with transverse ornamentation and a nearly tubular, eccentric siphuncle. However, Piersaloceras differs in having a conspicuous crenulated shell and a larger angle of expansion. The Black River genus Ehlersoceras Foerste, 1933 is similar in having a slender, only slightly transversely curved ornamented conch, but differs in having a slightly depressed cross section and a siphuncle that is only slightly removed from the shell margin on the convex side of conch curvature.

Kundoceras evansi nov. gen., nov. sp.
Figs. 5(7), 6(2–5) and 8(4)
1999. Piersaloceras sp. - King, p. 152, Fig. 8C.

Derivation of name: In honour of David H. Evans, Peterborough, UK, for his decades-long study of Paleozoic cephalopods.

Holotype: Specimen NRM-PZ Mo 158694.

Type locality and horizon: Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Material: Holotype and four specimens (Mo 158458a–c, 161122) from Hälludden, Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Occurrence: Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

Diagnosis: Same as for genus because of monotypy.

Description: Holotype fragment of 66 mm long part of phragmocone and 29 mm long adult body chamber (Fig. 6(4)). Maximum height of body chamber at adapical third 15.5 mm, adorally contracting toward 13 mm at peristome. Conch surface with slightly irregular annulations, showing acute nearly transverse ridges (Fig. 8(4)), 1 mm distant at base of body chamber. Ridges in adult growth stages more pronounced. Shell
of adult peristome thickened (Fig. 6(4)). Septal distance at 15 mm conch height 2 mm and siphuncle 2.5 mm from conch margin at convex side of conch curvature. Siphuncular diameter 1.1 mm with tubular segments and orthochoanitic septal necks of 0.3 mm length (Fig. 5(7)).

Juvenile fragment Mo 161122 (Fig. 6(2–3)) with length 33 mm, conch height 7–12 mm, conch width 6–12 mm with apical angle higher than in later growth stages. Specimen NRM–PZ Mo 158458a 46 mm long fragment of adult specimen with nearly identical adult size and conch shape similar to the holotype.

Specimen NRM–PZ Mo 158458c 24 mm long body chamber with 13 mm conch cross section diameter and 14 mm at base of body chamber, showing traces of thin annular band with multiple muscle attachment sites along circumference (Fig. 6(5)).

Remarks: The adult size of two of the described specimens is indicated by the apertural constriction and the strong thickening of the peristome at apertural diameter 13–14 mm. A very well preserved additional specimen (NRM–PZ Mo 158452) of this species from the Hälludden was figured by King (1999: Fig. 8c), but this specimen could not be located in the collection during the visits of B.K. at the RM. It shows the straight sutures and the conspicuously curved body chamber, contracted towards the aperture.

Family ONOCERATIDAE Hyatt, 1884
Genus Neumatoceras Forerste, 1935
Type species: Neumatoceras gibberosum Forerste, 1935 from the basal part of Bighorn formation, Richmondian Regional Stage, Late Ordovician of the Medicine Mountain, Big Horn County, Wyoming, USA; by original designation.

Occurrence: Mid to Late Ordovician; North America, Baltoscandia.

Diagnosis: Compressed strongly curved brevicones with maximum height behind base of body chamber. Conch margin at concave side of conch curvature nearly straight, concave or slightly convex. Conch margin at convex side of conch curvature geniculate on phragmocone. Siphuncle close to margin at convex side of conch curvature, segments almost cylindrical (compiled from Forerste, 1935, p. 31, and Sweet, 1964, p. K288).

Neumatoceras borense nov. sp.
Figs. 6(12) and 9(17)

Derivation of name: From Latin, boreas, north. The name was informally given to this species by Holm in the 1890s but never published.

Holotype: Specimen NRM–PZ Mo 161119.

Type locality and horizon: Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Material: Holotype and one additional specimen (Mo 161115) from Hälludden, Öland Island, and one specimen (Mo 14051) from Enerum, Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Occurrence: Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

Diagnosis: Strongly cyrtoconic gibbous brevicone, with compressed cross section with width/height ratio ca. 0.75 (Fig. 6(12)). Angle of expansion of apical conch portion = 22°. Maximum conch height 20 mm at position of last septum. Body chamber curved and with length of 23 mm. Conch surface ornamented with fine but distinctive irregular growth lines which form sharp lobes on convex side of curved conch (Fig. 9(17)). Growth lines more regularly spaced in early growth stages. Sutures form wide, shallow lateral lobes with saddles on convex and concave sides of shell. Thin marginal siphuncle on convex side of conch curvature.

Description: Cross section ovate in early growth stages with narrowly rounded side at convex side of conch curvature. At base of body chamber cross section slightly more broadly rounded on concave side of conch. Adult body chamber aperture ovate. Ratio conch width/height: 0.8 at conch height 8 mm, 0.75 at conch height 20 mm (maximum height, base of body chamber) and 0.72 at aperture. More compressed in adoral conch parts. Antisiphuncular conch margin concave throughout entire growth in longitudinal view, siphuncular side convex. More curved conch margin at antisiphuncular side in longitudinal view resulting in half-moon shaped outline of holotype in longitudinal view.

Second specimen with apical conch height of 4 mm, conch width 3.7 mm, larger height 7.3 mm and width 6.5 mm.

Remarks: N. borense is the largest of the two species known from the Hälludden. Both Hälludden species are unique within Neumatoceras in having a combination of a high angle of expansion and a very strong conch curvature. The conch margin at the convex side of conch curvature is concave throughout the entire length, but with a slightly lesser curvature at the part of latest phragmocone chambers and basal body chamber.

Neumatoceras parviborense nov. sp.
Figs. 6(13, 15) and 8(6)

Derivation of name: From Latin, parvus, small, referring to N. borense nov. sp., which is nearly similar in conch size but larger in general dimensions.

Holotype: Specimen NRM–PZ Mo 161114.

Type locality and horizon: Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Material: Holotype and one additional specimen (Mo 161115) from Hälludden, Öland Island, and one specimen (Mo 14051) from Enerum, Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Occurrence: Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

Diagnosis: Strongly cyrtoconic gibbous brevicone, with compressed cross section with width/height ratio of 0.8. Angle of expansion of apical conch portion = 18°. Maximum conch height 15 mm at base of body chamber. Body chamber curved. Conch surface ornamented with fine but distinctive irregularly spaced growth lines which form sharp lobe at convex side of curved conch. Growth lines more regularly spaced in early growth stages. Sutures form wide shallow lateral lobe, sinus at convex and concave side of shell.

Description: In holotype, ratio conch width/height is 0.94 at conch height of 8.5 mm, 0.8 at base of body chamber, and 0.72 at...
Fig. 9. Oncocerida from Hälludden cliff, Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage, Darriwilian. 1–4, Richardsonoceras gastroscopium nov. sp.; 1–2: NRM-PZ Mo 161084, juvenile specimen; 1: lateral view; 2: view of prosiphuncular, convex side of conch curvature, note shallow hyponomic sinus of ornamentation; 3: NRM-PZ Mo 161081, holotype, lateral view, note conch undulation in mature growth stages; 4: NRM-PZ Mo 161080, conch cross section.
aperture (Fig. 6(13)). At base of body chamber 14 mm high, 12 mm wide. More compressed in apertural conch parts. Second specimen consists of fragment of phragmocone with apical conch height of 6.9 mm, conch width of 6.3 mm, increasing respectively to height 12.5 mm and width 10 mm adorally.

Specimen NRM-PZ Mo 14051 represents portion of base of body chamber and adoral part of phragmocone with conch height of 12.5–13.5 mm, and conch width of 10–13 mm. Conch height at base of body chamber 15 mm, conch width 13 mm. Conch is smooth or with very fine growth lines (Fig. 8(6)). Marginal siphuncle with tubular segments with diameter of ca. 1 mm.

Remarks: Conch shape and ornamentation is similar in N. borense, but N. parviborense is somewhat less compressed, with lower angle of expansion and, more importantly, the adult is of a smaller size. The phragmocone of N. parviborense is more curved compared with that of N. borense.

Figs. 5(4) and 6(9–10)
1999. Neumatoceras sp. - King, p. 154, Fig. 8D.

Material: Two specimens (Mo 161116-17) from Hälludden cliff, Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darrwiilian.

Description: Specimen NRM-PZ Mo 161116 consists of 32 mm long portion of phragmocone and base of body chamber with angle of expansion of 9° (Fig. 6(10)). Apical conch height 8.7 mm, adorally with conch height: 13.9 mm and conch width: 12 mm (ratio of conch width/height: 0.86). Length of preserved part of body chamber = 8 mm. Concave side of conch curvature clearly less curved than convex side. Conch surface nearly smooth, but with fine symmetrical ribs, occurring at about five per millimetre, irregularly spaced. Chamber height: 1 mm. Siphuncle marginal in position with diameter of 0.9 mm at conch height of 13.2 mm. Siphuncular segments nearly tubular. Septal necks short, either cyrtochoanitic or suborthochoanitic (Fig. 5(4)).

Second specimen (Fig. 6(9)) slightly larger in its general dimensions but with similar angle of expansion and conch curvature.

Remarks: Both specimens have a relatively weakly coiled phragmocone combined with a nearly straight margin on the convex side of conch curvature, generating the maximum conch height at the base of the body chamber and when projected adorally results in a characteristic gibbous body chamber of Neumatoceras. However, the body chamber is not preserved in either specimen, making a specific determination impossible. Both fragments are unique in having a comparatively low angle of expansion combined with a weak curvature.

Neumatoceras? sp. B

Fig. 6(14, 16)

Material: Specimen NRM-PZ Mo 161121 from Hälludden cliff. Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darrwiilian.

Description: Specimen consists of strongly cyrtoconic portion of phragmocone and basal part of body chamber. Conch cross section ovate with more narrowly rounded side on convex side of conch curvature (Fig. 6(16)). Apical conch height: 18 mm and conch width: 15 mm respectively, with ratio conch width/height: 0.83. Dimensions at base of body chamber 25 mm height, 21 mm respectively. Septa narrowly spaced. Siphuncle marginally positioned on convex side of conch curvature with tubular or slightly expanded segments with diameter: 1.5 mm at apical end of fragment. Conch surface with weak narrowly spaced ribs or growth lines.

Remarks: The fragmentary character of this specimen does not allow any specific determination, but the large adult size is unique amongst the known species of oncocerids from the Middle Ordovician of Baltoscandia.

Genus Paramiamoceras

Chen, 1987

Type species: Paramiamoceras minutum Chen, 1987 from the Late Ordovician of Tibet, China; by original designation.

Occurrence: Mid to Late Ordovician; Tibet, Baltoscandia.

Diagnosis (from Chen, 1987, p. 186): Weakly compressed, weakly curved gradually enlarging shells with marginal siphuncle on convex side of conch curvature and nearly tubular segments, but slightly expanded at side directed toward conch margin. Septal necks orthochoanitic to suborthochoanitic.

Remarks: This genus is similar to Ehlersoceras Foerste, 1933 but differs in having a nearly smooth conch surface and an ovate to trapezoidal conch cross section. Miamoceras Flower, 1946 differs in having a clearly higher angle of expansion and subcardioid siphuncular segments.

Paramiamoceras breviventrum nov. sp.

Fig. 6(6–8, 11)

Derivation of name: From the Latin brev, broad, referring to the wide convex side of conch curvature.

Holotype: Specimen NRM-PZ Mo 161124.

Type locality and horizon: Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darrwiilian.
Material: Holotype and specimen NRM-PZ Mo 161123 from type locality and horizon.

Occurrence: Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

Diagnosis: Slightly cyrtoconic conchs, with compressed juvenile and nearly circular later growth stages, and angle of expansion of 13°. Adult conch height about 16 mm. Cross section is ovate with narrowly rounded keel on convex side of conch curvature to broadly rounded on opposite side, and with maximum width of conch in prosiphuncular half of conch cross section. Conch surface smooth, with fine growth lines. Eight chambers in distance similar to conch height. Sutures form wide shallow lateral lobes, with saddles at convex and concave sides of shell. Siphuncle marginal in position at convex side of conch curvature with diameter ca. 0.08 of conch height. Siphuncular segments slightly convex with thin connecting ring. Septal necks suborthochoanitic to achoanitic.

Description: Holotype consists of parts of phragmocone and nearly complete body chamber with total length of 36 mm (Fig. 6(7, 8)). Conch surface nearly smooth, with fine growth lines that form shallow lobe at convex side of conch curvature. Angle of expansion of phragmocone: 13° between conch heights of 11–15 mm and widths of 8.6–13.5 mm. Body chamber with length of 23 mm enlarges gradually from height of 15 mm at base to 16 mm at aperture. In second specimen, base of body chamber with conch height of 15 mm and width of 13.5 mm (Fig. 6(11)). Most adoral chambers of second specimen crowded. Cross section ovate with slightly flattened venter and dorsum with ratio conch width/height of 0.78 at apical end, 0.89 at base of body chamber and nearly circular at base of body chamber. Cross section at apical end ovate with greatest width at prosiphuncular half. Siphuncle marginal in position at convex side of conch curvature. Cross section at apical end of second specimen trapezoidally rounded with its greatest width within prosiphuncular half. Siphuncle marginal in position and on convex side of conch curvature. At conch height of 12 mm, siphuncle is 1 mm in diameter. Suture lines are nearly transverse or slope slightly adorally on prosiphuncular side of conch, with shallow lateral lobes. Approximately eight chambers in distance similar to conch height.

Remarks: This species differs from the Chinese species in having an ovate to trapezoidal conch cross section with slightly flattened venter.

Genus Richardsonoceras Foerste, 1933

Type species: Cyrtoceras simplex Billings, 1857 from the Leray beds, Ottawa formation, Black River Regional Stage, Middle Ordovician of Nepean township, Ottawa, Ontario, Canada; by original designation.

Occurrence: Darriwilian-Katian; Baltoscandia, North America, North China, Siberia.


Richardsonoceras gastroscopium nov. sp.

Figs. 5(5), 8(1) and 9(1–4)

Derivation of name: From gastroscope, an endoscope that is inserted through the mouth and used for examining the interior of the stomach, referring to the conch form of this species.

Holotype: Specimen NRM-PZ Mo 161081.

Type locality and horizon: Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Material: Holotype and 23 specimens from Hälludden (Mo 14085, 154573, 154575–76, 161073, 161075, 161079-80, 161082-84), near Torp (161074, 161078), Toknäs (Mo 161076-77), Enerum (Mo 15209), Nerika near Mossby (Mo 161069-70) and Byrum (Mo 161067, 161072), Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Occurrence: Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

Diagnosis: Strongly cyrtoconic conchs, with compressed cross section of width/height ratio of ca. 0.89 and angle of expansion of 8°. Cross section more broadly rounded at concave side of conch curvature and with narrowly rounded keel on convex side of conch curvature. Ornamented with distinctive, slightly irregularly, narrowly spaced ribs which are oblique, sloping in adapical direction toward convex side of conch curvature where they form shallow angular lobe. Conch is slightly undulated in late growth stages. Chamber height one-eighth of conch height. Sutures form wide lateral lobes, conspicuous saddles on convex side of shell and wide shallow saddle on concave side of shell. Almost ventrally positioned siphuncle with diameter of ca. 0.06 of conch height, slightly convex segments and short cyrtochoanitic septal necks. Connecting ring very thin.

Description: Strongly cyrtoconic, almost gyroconic shells, known to reach maximum diameter of at least ca. 23 mm (Mo 161069). Conch cross section compressed, ratio conch width/height of 0.85 at conch height of 17 mm in holotype (mean = 0.83, n = 13 measured specimens). Conch cross section tends to be more compressed in later growth stages (Fig. 10). Conch grows at an angle of expansion of 8° in holotype (mean = 7°, n = 13). Expansion rate decreases with conch height in all specimens (Fig. 11). Length of body chamber 21 mm where base of body chamber is 17 mm high (specimen NRM-PZ Mo 161084, Fig. 9(1)).

Ornament consists of conspicuous oblique growth lines, sloping in adapical direction towards convex side of conch curvature and forming narrow hyponomic sinus on convex side (Fig. 9(2)). Growth lines irregularly spaced, with more than five per mm in holotype. At conch height greater than 20 mm, surface of conch exhibits slightly irregular undulations, parallel to growth lines (Fig. 9(3), holotype).

Sutures slightly oblique, sloping adapically towards convex side of shell and forming a shallow lateral lobe and a conspicuous ventral saddle. Approximately eight chambers in distance equivalent to conch height. Septal necks very thin
compared with septa, relatively short and cyrtochoanitic on side of siphuncle closest to conch axis.

Remarks: This species is similar to *R. simplex* (Billings, 1857), but differs in possessing a more strongly curved conch. Specimens assigned to *R. simplex* (Billings, 1857) by Chen (1987: Pl. 5, Figs. 4, 6) from the Darriwilian of Tibet differ in having a lower angle of expansion.

*Richardsonoceras gerhardi* nov. sp.
Figs. 8(2, 7) and 9(6, 7)

**Derivation of name:** In honour of Gerhard Holm, Intendant of the Paleontological Collections of the Naturhistoriska Riksmuseet Stockholm and collector of the largest part of the Öland cephalopod collection of the NRM.

**Holotype:** Specimen NRM-PZ Mo 158419 and Mo 158411 (fragments of this specimen was given two numbers).

**Type locality and horizon:** From Hälludden cliff at Öland Island, Sweden, Gillberga Formation, Kunda Regional Stage, Darriwilian.

**Material:** Holotype and eight specimens (Mo 158420, 158408a–b, 161091-92, 161093-95) from Hälludden, one from Enerum (Mo 14069), Gillberga Formation, Kunda Regional Stage, and one specimen (Mo 14114) from Folkeslunda Limestone, Lasnamägi Regional Stage, Lerkaka; all from Öland Island, Sweden, Darriwilian.

**Occurrence:** Kunda Regional Stage, Darriwilian, of Öland Island, Sweden.

**Diagnosis:** Large cyrtoconic conchs, with compressed cross section and angle of expansion of 11°. Cross section more broadly rounded on concave side of conch curvature and more narrowly rounded on convex side of conch curvature. Ornamented with distinctive, narrowly spaced ridges, which are oblique, sloping adapically towards convex side of conch curvature where they form shallow angular lobes. Ridges are regularly spaced, where conch height less than ca. 25 mm, but irregularly spaced and conch slightly undulated in later growth stages. Chamber height one-ninth of conch height. Sutures form wide shallow lateral lobes, with shallow saddles at convex and concave sides of shell. Nearly ventrally positioned siphuncle with diameter ca. 0.06 of conch height. Siphuncular segments slightly convex at side directed toward conch margin, tubular or slightly concave in side directed toward conch centre. Septal necks suborthochoanitic. Connecting ring thin.

**Description:** Cyrtoconic shells, only slightly less curved in latest growth stages. Known maximum diameter ca. 27 mm (Mo 104069). Conch cross section compressed, more broadly rounded on concave side of conch curvature and narrower rounded on convex side, ratio conch width/height of 0.75–0.85 at holotype, more compressed in late growth stages (Fig. 10). Conch grows with angle of expansion of 11°. Adult body chamber of holotype 32 mm long, with 25 mm conch height at its base and with angle of expansion of 6° (Fig. 9(6, 7)).

Ornament consists of conspicuous, oblique, fine rounded ridges, sloping adapiacally towards convex side of conch curvature, forming narrow hyponomic sinus at convex side (Fig. 8(2, 7)). Ridges are regularly spaced, with two ridges per mm at conch height less 25 mm and irregularly spaced in later growth stages.

Suture lines nearly transverse with shallow lateral lobe. Approximately nine chambers in distance equivalent to conch height. Septal necks suborthochoanitic. At conch cross section diameter 20 mm siphuncle 1.2 mm in diameter, and septal distance 2.2 mm. Connecting ring thin, sometimes covered with calcareous layer within the cameral side of siphuncle that is thickest close to adoral septum of each segment.

Remarks: This species differs from *R. ellipticum* (Lossen, 1860) nov. comb., in having a stronger conch curvature and a...
larger angle of expansion. In contrast to \textit{R. ellipticum}, \textit{R. gerhardi} nov. sp. is ornamented with fine obliquely transverse ridges. Dzik and Kiselev (1995, p. 64) assigned \textit{R. ellipticum} to \textit{Phtanoncoceras} Evans and King, 1990, and stated that \textit{R. ellipticum} is "virtually indistinguishable" from \textit{Phtanoncoceras oelandense} Evans and King (1990), the type of this genus. This statement is wrong. \textit{P. oelandense} has an adult body chamber with convex conch margins in longitudinal perspective, a much smaller adult size, concave siphuncular body chamber with convex conch margins in longitudinal perspective. Siphuncle marginal on convex side of conch. Approximately eight chambers at length. Ornament consists of fine regularly spaced, rounded, shallow, rounded ridges, oriented obliquely transverse, sloping adapically towards, and forming shallow lobe at convex margin of conch (Fig. (8(3, 8))). Approximately five ridges occur per millimetre.

At conch cross section of 11 mm (NRM-PZ Mo 161096) marginal siphuncle with diameter of 0.8 mm (0.07 of conch cross section), and length of segments 2 mm. Connecting ring composed of two layers, inner layer thin, outer layer forms wedge, thickest at adoral part of segment (Fig. (5(8, 9)). Siphuncular segments slightly expanded. Septal necks very short, cythrochoanitic.

**Remarks:** The regularly transverse ornamentation of this species is characteristic also for \textit{Richardsonoceras priscum} (Eichwald, 1860) nov. comb. (note: Dzik and Kiselev, 1995 cited "Cyrtoceras priscum" Eichwald, 1861, p. 327, Pl. 1, Fig. 5" as first description, however there exists no "Eichwald, 1861" and their reference must correctly be \textit{C. priscum} Eichwald, 1860, p. 1285, Pl. XLVII, Fig. 10a–c). In contrast to the oblique ornamentation of \textit{R. goldmanni} the ornamentation of \textit{R. priscum} is straight and directly transverse. The latter differs also in having a lower expansion rate, a less curved conch and a nearly circular conch cross section.

\textit{Richardsonoceras goldmanni} nov. sp.

Figs. (5(8–9), 8(3, 8) and 9(5, 9, 15))

**Derivation of name:** In honour of the architecture theorist Nikolaus Goldmann (1611–1665), the inventor of the Volute, a form element for the construction of Ionic steles, that has some similarity with the species in consideration.

**Holotype:** Specimen NRM-PZ Mo 161098.

**Type locality and horizon:** Hälludden, Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Dariwilian, Middle Ordovician.

**Material:** Holotype and 16 specimens Mo 158397, 191096-97, 161099, 161100-04, 161106-12 from Hälludden cliff, and Enerum, Mo 14047–14048, 161105, Öland Island, all Gillberga Formation, Kunda Regional Stage. Two specimens (TUG 1285-31, 51) from Paldiski cliff, Pakri Peninsula, Aseri Regional Stage, Dariwilian.

**Occurrence:** Kunda Regional Stage, Dariwilian; Öland Island, Sweden, and Aseri Regional Stage, Dariwilian; Pakri Peninsula, Estonia.

**Diagnosis:** Slightly compressed cyrtocones with adult size of 12–14 mm. Late growth stages less curved than juvenile growth stages. Body chamber height approximately equals length. Ornament consists of fine regularly spaced, rounded, obliquely transverse ridges. Ridges form shallow sinus on convex side of conch. Approximately eight chambers at length similar to conch height. Sutures form shallow lateral lobe and conspicuous ventral sinus. Siphuncle marginal on convex side of conch with slightly expanded siphuncular segments. Siphuncular segments slightly convex with thin connecting ring. Septal necks very short cythrochoanitic.

**Description:** Curved conchs with maximum observed conch cross section height 14 mm (specimen NRM-PZ Mo 161112, Fig. 9(15)). Angle of expansion varies between 5° in adult body chamber of holotype and 7° in juvenile section of specimen NRM-PZ Mo 161105 (mean = 6°, \(n = 5\), Fig. 11). Conch cross section variable within observed specimens, with mean value of conch width/height ratio of 0.85 (\(n = 11\)) and with tendency of more compressed cross sections in larger specimens (Fig. 10). Cross section more widely rounded on concave side of conch and narrowly rounded on convex side of conch. Length of body chamber in specimen NRM-PZ Mo 161109 15 mm, in NRM-PZ Mo 161112 12 mm (maximum height: 14 mm), in Mo 161105 height and length = 12 mm. Ornament consists of shallow, rounded ridges, oriented obliquely transverse, sloping adapically towards, and forming shallow lobe at convex margin of conch (Fig. 8(3, 8)). Approximately five ridges occur per millimetre.

At conch cross section of 11 mm (NRM-PZ Mo 161096) marginal siphuncle with diameter of 0.8 mm (0.07 of conch cross section), and length of segments 2 mm. Connecting ring composed of two layers, inner layer thin, outer layer forms wedge, thickest at adoral part of segment (Fig. 5(8, 9)). Siphuncular segments slightly expanded. Septal necks very short, cythrochoanitic.

**Remarks:** The regularly transverse ornamentation of this species is characteristic also for \textit{Richardsonoceras priscum} (Eichwald, 1860) nov. comb. (note: Dzik and Kiselev, 1995 cited “Cyrtoceras priscum” Eichwald, 1861, p. 327, Pl. 1, Fig. 5” as first description, however there exists no “Eichwald, 1861” and their reference must correctly be \textit{C. priscum} Eichwald, 1860, p. 1285, Pl. XLVII, Fig. 10a–c). In contrast to the oblique ornamentation of \textit{R. goldmanni} the ornamentation of \textit{R. priscum} is straight and directly transverse. The latter differs also in having a lower expansion rate, a less curved conch and a nearly circular conch cross section.

\textit{Richardsonoceras haelluddenense} nov. sp.

Figs. 5(11), 8(9) and 9(13, 16)

**Derivation of name:** Referring to the Hälludden cliff at Öland Island, Sweden, the type locality.

**Holotype:** Specimen NRM-PZ Mo 161087.

**Type locality and horizon:** Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Dariwilian.

**Material:** Holotype and three specimens (NRM-PZ Mo 161088-90) from Hälludden, Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Dariwilian.

**Occurrence:** Kunda Regional Stage, Dariwilian; Öland Island, Sweden.

**Diagnosis:** Slender cyrtoconic conchs, with compressed cross section of conch width/height ratio ca. 0.80 and angle of expansion of 2°. Cross section more widely rounded on concave side of conch and narrowly rounded on convex side of conch. Ornamented with distinctive, slightly irregular, narrowly spaced ridges, which are oblique, sloping in adaxial direction toward convex side of conch, forming shallow angular lobes. Conch is very slightly undulated in late growth stages. Chamber height one-ninth of conch height. Sutures form wide lateral lobe, conspicuous saddle on convex side of conch and wide shallow saddle on concave side of conch. Siphuncle nearly ventrally positioned, with diameter ca. 0.07 of conch height, with very slightly convex segments and very short adnate cythrochoanitic or achoanitic septal necks. Connecting ring thin.

**Description:** Slender conch, nearly equally cythroconic throughout entire length, less curved in latest growth stages (Fig. 9(13, 16)). Known maximum diameter ca. 15 mm (NRM-PZ Mo 161088). Conch cross section compressed, with ratio conch width/height of 0.79 at conch height 13 mm in specimen NRM-PZ Mo 161089. Conch grows with angle of expansion of 2° in holotype. Mean angle of expansion of four measured specimens = 2°. Length of body chamber 19 mm and height of base of body chamber 13 mm in holotype.
Ornament consists of conspicuous oblique, fine rounded ridges, which slope in adapically towards convex side of conch, forming narrow hyponomic sinus on convex side. Ridges are irregularly spaced and sometimes strongly developed, sometimes very fine and shallow. More than seven ridges per millimetre at holotype. Conch is slightly irregularly undulated.

Suture lines slightly oblique, sloping in adapical direction toward convex side of shell forming shallow lateral lobe and conspicuous ventral saddle. Approximately nine chambers per distance equivalent to conch height. Septal necks are very short recumbent, touching adapical surface of septa in entire length, or achoanitic (Fig. 5(11)). Siphuncular segments slightly expanded, with diameter of 1 mm at conch cross section 15 mm and length of segments of 1.5 mm in holotype.

**Remarks:** This species is unique within *Richardsonoceroides* in its combination of very low angle of expansion and the finely ribbed ornamentation.

**Genus:** Richardsonoceroides Chen, 1987  
**Type species:** Richardsonoceroides typicum Chen, 1987 from the Darriwilian of Tibet, China; by original designation.

**Occurrence:** Darriwilian; North China, Baltoscandia.

**Diagnosis:** Slender, compressed cyrtocones with oval cross section. Angle of expansion larger in apical portions. Adoral portions of mature specimens nearly straight and with low angle of expansion. Chambers narrowly spaced. Body chamber not contracted. Thin siphuncle is marginal at convex side of curved conch. Siphuncle thin, marginal with slightly expanded segments which are higher than wide. Septal necks are very short, suborthochoanitic (from Chen, 1987, p. 185).

**Remarks:** This genus differs from the entirely cyrtoconic *Richardsonoceras* in having an almost straight or only slightly curved dorsal conch portion at maturity. The siphuncle is only one-twentieth of conch height and therefore clearly thinner than that of *Richardsonoceras*, which is larger than one-fifteenth of conch height. The septal necks of *Richardsonoceroides* are very short, nearly achoanitic, in contrast to septal necks in *Richardsonoceras*, which are clearly cyrtochoanitic. The genus was known formerly exclusively from China and Tibet.

*Richardsonoceroides kingi* nov. sp.  
**Fig.** 9(10)  
**Derivation of name:** In honour of Andrew H. King, for his unpublished Dissertation about the Middle Ordovician Baltoscandic cephalopods (King, 1990).

**Holotype:** Specimen NRM-PZ Mo 161065.

**Type locality and horizon:** Toknäs “Butan” cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

**Material:** Holotype and one additional specimen (NRM-PZ Mo 161066) from Halludden, Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

**Occurrence:** Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

**Diagnosis:** Cyrtococonic conchs, with compressed cross section, angle of expansion of 7°, and with maximum conch height of 14 mm. Cross section ovate with greatest width near midlength between venter and dorsum. Conch surface smooth with fine growth lines. Late growth stages of conch slightly undulated. Eight chambers at distance similar to conch height. Sutures form wide shallow lateral lobe, sinus on convex and concave side of shell. Siphuncle marginal on convex side of conch with diameter ca. 0.05 of conch height.

**Description:** Strongly cyrtococonic shell in juvenile growth stages, slightly curved in latest growth stages. Known maximum diameter ca. 14 mm (holotype, Fig. 9(10)). Conch cross section compressed, with ovate shape, more narrowly rounded on convex side of conch. Ratio conch width/height of 0.80–0.85 in holotype, more compressed in later growth stages. Conch grows with angle of expansion of 7.4° in holotype. Body chamber length: 14 mm in holotype with 12 mm conch height at base of body chamber.

Suture lines are nearly transverse with shallow lateral lobe. Approximately eight chamber occur in distance equivalent to conch height. Siphuncle marginal on convex side of conch with diameter 0.4 mm at conch cross section 8 mm.

**Remarks:** This species is strongly curved in juvenile conch portions and the straight conch portion is shorter than in *R. rythium*. *R. oelandense* has a similar conch shape but is generally smaller in conch dimensions.

*Richardsonoceroides oelandense* nov. sp.  
**Fig.** 9(11, 14)  
**Derivation of name:** Referring to the Öland Island, the type region of this species.

**Holotype:** Specimen NRM-PZ Mo 161071.

**Type locality and horizon:** Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

**Material:** Holotype only.

**Occurrence:** Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

**Diagnosis:** Small initially cyrtococonic conchs, adorally nearly straight conch, with ovate compressed cross section and angle of expansion of 11°, and with maximum conch height of 11 mm. Cross section ovate with rounded keel at convex side of conch curvature. Conch surface smooth, with fine growth lines. Late growth stages slightly undulated. Five chambers at distance similar to conch height. Sutures form wide shallow lateral lobes, and saddles on convex and concave sides of shell. Position of siphuncle marginal at convex side of conch. Siphuncular diameter ca. 0.05 of conch height. Siphuncular segments slightly convex with thin connecting ring. Septal necks suborthochoanitic to achoanitic.

**Description:** Conch moderately curved, but slightly curved in latest growth stages. Known maximum diameter less than 10 mm. Conch cross section compressed, with ovate shape, more narrow-rounded on convex side of conch. Ratio conch width/height of 0.85 (holotype). Conch of holotype grows with angle of expansion rate 11° in apical part. Suture lines nearly transverse with shallow lateral lobe. Approximately five chambers at distance equivalent to conch height. Siphuncular diameter 0.3 mm at conch cross section diameter 6 mm, and segments with length of 1 mm. Connecting ring thin.
Remarks: This species differs from R. kingi in having a smaller adult size and a more slender conch.

Richardsonoceroides rhytium nov. sp.

Figs. 5(10), 8(5) and 9(8)

Derivation of name: From Latin rhytium, drinking-horn, referring to the conch form.

Holotype: Specimen NRM-PZ Mo 161113.

Type locality and horizon: Hälludden cliff at Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Material: Holotype and eleven specimens (NRM-PZ Mo 161043-45, 161052-57, 16113) from Hälludden, Öland Island, Sweden; Gillberga Formation, Kunda Regional Stage, Darriwilian.

Occurrence: Kunda Regional Stage, Darriwilian; Öland Island, Sweden.

Diagnosis: Slender cyrtoconic conchs, with compressed cross section and angle of expansion of 5°, and with maximum conch height of 14 mm. Cross section ovate narrower at convex side of conch curvature. Conch surface smooth, with fine growth lines. Late growth stages with slightly undulated conch. Eight chambers at distance equivalent to conch height. Sutures form wide shallow lateral lobe and saddle on convex and concave side of shell. Siphuncle marginally positioned at convex side of conch with diameter ca. 0.05 of conch height. Siphuncular segments slightly convex with thin connecting ring. Septal necks suborthocoanitic to achoanitic.

Description: Cyrtoceras shells, less curved in latest growth stages. Known maximum diameter ca. 14 mm (holotype, Fig. 9(8)). Conch cross section compressed, with ovate shape, narrower rounded on convex side of conch. Ratio conch width/height of 0.81–0.92 in holotype, more compressed in later growth stages (mean = 0.82, n = 6; Fig. 10). Conch grows with angle of expansion of 4.6° in holotype. Body chamber length 19 mm in holotype with 13 mm conch height at body chamber base. Ornamented with irregularly spaced growth lines and with irregularly spaced undulations in later growth stages (Fig. 8(5)). Suture lines nearly transverse with shallow lateral lobe. Approximately eight chambers at distance equivalent to conch height. Septal necks very short or absent. Septum slightly thickened and slightly curved adapically on septal perforation (Fig. 5(10)). Siphuncular diameter 0.7 mm at conch cross section diameter 12.9 mm, and with length of segments of 1.8 mm. Connecting ring thin.

Remarks: This species is the largest Richardsonoceroides known from Baltoscandia. It intermediates between R. typicum and R. hubeiense Xu in Xu and Liu, 1977 with respect to adult conch height and angle of expansion. R. kingi nov. sp. and R. oelandense nov. sp. differ in having a higher conch curvature in juvenile portions.

Richardsonoceroides schiefferdeckeri (Dewitz, 1880)

Figs. 5(6) and 9(12)

1880. Cyrtoceras schiefferdeckeri nov. sp. - Dewitz, p. 179, Pl. 4, Fig. 7a-c.

Holotype: not stated. The Königsberg collection of H. Dewitz of which the Holotype was probably part of, has been lost during the World War II, and the type cannot be located. Therefore, the neotype NRM-PZ Mo 161086 is designated herein.


Material: Seven specimen (NRM-PZ Mo 161047-51, 161058, 161061) from Hälludden, Öland Island, Hunderumian and Valaste Substage, Gillberga Formation, Kunda Regional Stage. Eight specimens (TUG 1285-9, 15, 22, 25, 41, 45, NRM-PZ Mo 161059-60) from Paldiski cliff, Paldiski, Estonia, Aseri Regional Stage, all Darriwilian.

Occurrence: Kunda Regional Stage, Darriwilian of Öland Island, Sweden, in erratic boulders of Kaliningrad oblast, Russia, and Aseri Regional Stage, Darriwilian of Pakri Peninsula, Estonia.

Diagnosis: Small, slender cyrtoconic conchs, with compressed cross section, angle of expansion 7°, and with maximum conch height of 7 mm. Conch less curved in latest growth stages. Cross section ovate. Conch surface smooth with faint growth lines, forming ventral lobe on convex side of conch curvature. Five or six chamber at distance equivalent to conch height. Sutures form wide shallow lateral lobes, saddles at convex and concave side of shell. Siphuncle marginal on convex side of conch with diameter ca. 0.09 of conch height. Siphuncular segments slightly convex with thin connecting ring. Septal necks achoanitic.

Description: Known maximum diameter ca. 7 mm (NRM-PZ Mo 161048-50, 161061, TUG 15, 22). Conch cross section ovate compressed, more narrowly rounded on convex side of conch. Ratio conch width/height of 0.88 at NRM-PZ Mo 161050 and specimen TUG 1285-45. Conch grows with angle of expansion of 7.4° in complete holotype. Angle of expansion of body chamber = 4° in NRM-PZ Mo 191050 (Fig. 9(12)). In early growth stages apical angle larger, in late growth stages conch nearly tubular and only slightly curved. Body chamber length of 11.5 mm in holotype with 6.7 mm conch height at body chamber base. Body chamber length of 14 mm in specimen NRM-PZ Mo 161048 and of 13 mm in specimen NRM-PZ Mo 161049. Suture lines nearly transverse, with shallow lateral lobe. Approximately eight chambers at distance equal to conch height. Septal necks achoanitic (Fig. 5(6)). Marginal siphuncle with slightly expanded segments. Siphuncular diameter of 0.01 mm at conch cross section diameter of 2 mm, and with length of siphuncular segments of 1.5 mm. Connecting ring thin.

Remarks: The six largest of the known specimens from Paldiski and Öland show a maximum conch height of 7 mm or slightly more, the known body chamber length in these
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