

The oldest ascocerid cephalopod from the Silurian of Estonia and notes on the biogeography of the order Ascocerida (class Cephalopoda)

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Abstract. The early Palaeozoic order Ascocerida is a group of morphologically unique and rare cephalopods known from the Ordovician and Silurian rocks of Avalonia, Baltica, Laurentia and Perunica. The limited Estonian record of Silurian ascocerids is complemented with a specimen from the Pähkla locality (Island of Saaremaa; Paadla Regional Stage, Ludlow Series) representing the stratigraphically oldest known occurrence of ascocerids in the Silurian of Estonia. The strata that were formerly exposed in Pähkla are likely correlated to the Hemse Group of the Island of Gotland (Sweden) having a remarkable record of ascocerids. The appearance of Silurian ascocerids in Estonia is confined to a time interval when the group had the highest species diversity and the widest geographic dispersion, reaching also outside Baltica for the first time.

Key words: Estonia, Baltica, Pähkla, Silurian, Ascocerida, biogeography, stratigraphy.

INTRODUCTION

Representatives of the order Ascocerida are enigmatic, morphologically unique early Palaeozoic cephalopods characterized by periodical truncation of the cyrtoconic juvenile shell portion (Barrande 1855, 1877; Furnish & Glenister 1964). Phragmocone chambers in an inflated mature (ephebic) shell are separated by thin sigmoidal septa and located above the living chamber.

The ascocerids are rarely found in the Ordovician and Silurian strata of North America (Canada, USA) and Europe (Bohemia, Estonia, Norway, Poland, Sweden, United Kingdom) (for a summary see Miller 1932; Flower 1941; Sweet 1958; Kesling 1961; Furnish & Glenister 1964; Holland 1999). The largest collections of Silurian ascocerids consisting of 190 and 130 specimens were collected and described by Barrande (1865, 1877) from the Prague Basin and Lindström (1890) from the Island of Gotland. Outside Gotland, the Silurian record of ascocerids in Baltica is rather scarce, being limited to only two occurrences in Poland (Dzik 1984) and a few ones on the Island of Saaremaa, Estonia (Kaljo 1970; Klaamann 1970). The latter record is complemented herein with the description of a specimen from the Paadla Regional Stage (Ludlow Series) of Estonia. The specimen was identified in the palaeontological collections of the Natural History Museum of the University of Tartu. It comes from the Pähkla locality

(Saaremaa, Estonia) and represents the stratigraphically oldest ascocerid cephalopod in the Silurian of Estonia.

MORPHOLOGICAL CHARACTERISTICS OF ASCOCERID CEPHALOPODS

Two portions of the shell are recognized in ascocerids. They can be characterized as follows (modified after Furnish & Glenister 1964):

1. The juvenile portion, which is a cyrtoconic longicone with a low expansion rate, and a narrow, tubular, ventrally shifted siphuncle. The apex of the juvenile portion is known in only two specimens of the species *Parascoceras decipiens* and one specimen of *Parascoceras fistula* (see Lindström 1890); it is cup-shaped, without constriction, initially smooth on the surface, with the first segment of the siphuncle being inflated and in contact with the ventral shell wall (Furnish & Glenister 1964).
2. The mature (ascocerid) portion, which is inflated and breviconic. The phragmocone is situated above the living chamber, individual phragmocone chambers are separated by thin, sigmoidally curved septa that overlap each other adapically. The siphuncle is restricted to the ventral part of the ascocerid apex and is strongly modified (short siphuncular segments, extremely expanded, thin connecting rings and rather

short septal necks). The living chamber forms the so-called neck adorally.

Finds of both parts of the shell conjoined are, however, extremely rare and usually only the mature ascocerid shell portions are found. Up to now, only twenty specimens with a completely or partly preserved juvenile shell are known from Gotland (Lindström 1890, pl. 1, figs 3–6) and one specimen is known from Bohemia (Barrande 1877, pl. 491, figs 3–7). This is most likely due to periodical truncation of the juvenile part during ontogeny. Once the juvenile shell is truncated, it is very difficult to assign a specimen to *Ascocerida*.

Overall scarcity of fossil records of this cephalopod group likely represents a sampling artefact caused by the rarity and low preservation potential of their thin, fragile shells and also by the fact that ascocerids could easily be overlooked by the collectors and researchers owing to their peculiar morphology.

THE PÄHKLA LOCALITY

The old Pähkla Quarry is rarely mentioned in publications, although it has been known for a very long time. The first record of this locality can likely be traced back to the middle of the 19th century (*Pechel* in Schmidt 1858, pp. 173–174). The quarry has been listed among the ‘principal localities’ of the Paadla Regional Stage (Klaamann 1970, No. 51 in table 44). The total thickness of the exposed strata was 1.3 m in the middle of the 20th century (Klaamann 1970).

The only published log of the section (Kõrts 1991) is rather generic and documents 0.4 m of lagoonal argillaceous dolomites, overlain by 0.2 m of pelletal limestones and 0.4 m of open shelf nodular limestones.

The exposure was correlated to the middle part of the Himmiste Beds (Paadla Formation) in the Kipi borehole (Kõrts 1991, fig. 1).

The present-day situation in this locality is considerably different. In November 2015 only the argillaceous dolomites of the lower part of the former succession were exposed in a thickness of 0.12 m (Fig. 1). Few loose blocks in the northern part of the quarried area consist of up to 0.3 m thick nodular limestones. The quarry is extensively overgrown, the higher (northern) escarpment is partly covered with waste and the eastern margin is partly recultivated.

As the lagoonal dolomites are usually poor in fossils, it appears more likely that the cephalopod specimen came from the upper part of the section that is currently inaccessible in situ.

DESCRIPTION OF THE SPECIMEN FROM ESTONIA AND ARGUMENTS FOR ITS ASSIGNMENT TO THE ORDER ASCOCERIDA

Order ASCOCERIDA Kuhn, 1949
Family ASCOCERATIDAE Barrande, 1867
Genus *Ascoceras* Barrande in Hauer 1847

Type species. *Ascoceras bohemicum* Barrande, 1855; from locality Kozotz (Barrande 1855) = Hvižďalka Quarry (Kříž 1999), central Bohemia, Kopanina Formation, Přídolí Series, Silurian.

Diagnosis. Mature shell generally robust in proportions; smooth or sculptured only by straight and transverse striae; aperture simple, unmodified; four to five phragmocone chambers usually present.

A



B



Fig. 1. A view of the Pähkla Quarry (A) and the available outcrop section (B, a detail of the lower right corner of figure A).

Remarks. *Ascoceras* differs from *Aphragmites* in lacking the annulation on the surface. It differs from *Lindstroemoceras* in greater shell size and in lacking the annulation and the basal septum, and from *Glossoceras* in having a shorter and wider ascocerid shell with a lower number of phragmocone chambers and a simple, unmodified aperture. It is generally larger and more robust than *Parascoceras* and lacks the duplicature at the first ascocerid connecting ring present in the latter.

Ascoceras sp.

Locality and horizon. Pähkla Quarry, Island of Saaremaa, Estonia; Paadla Regional Stage, Ludlow Series, Silurian.

Description and remarks. The studied specimen (Fig. 2) is 42 mm long, the maximum dorsoventral diameter reaches 14 mm and its cross section is circular. Although the specimen is only a poorly preserved fragment, its typical shape and dimensions suggest that it represents the adapical half of an ascocerid living chamber. An imprint of one sigmoidal septum and a septal foramen of the septum of truncation are clearly visible. Conjoined sigmoidal septa are visible in the most adapical part of the convex side. These morphological features prove that the specimen can be confidently assigned to the order Ascocerida. The shape and dimensions of the fragment suggest assignment of this specimen to the genus *Ascoceras*. Species-specific characters are not preserved.

STRATIGRAPHIC DISTRIBUTION AND BIOGEOGRAPHY OF THE SILURIAN ASCOCERIDS

Ascocerids from Laurentia

Laurentian ascocerids of Ordovician age are well known (Billings 1857, 1865, 1866; Hyatt 1883; Foerste 1928, 1929, 1930; Foerste & Savage 1927; Miller 1932; Flower 1941, 1952, 1963; Kesling 1961; Frey 1985). The Silurian ascocerids from Laurentia are, however, insufficiently described and mostly unrevised since their original description (Foerste 1930; Miller 1932). The following four species assigned to *Ascoceras* by original descriptions are known from this palaeocontinent but the precise ages of specimens could not be specified, due to scarcity of primary stratigraphic information:

- *A. croneisi* Foerste, 1930 – from the locality Wauwatosa and the quarry at Milwaukee, Wisconsin, USA; Racine Dolomite, upper Niagaran Regional Series; corresponds to the lower Ludlow Series, Silurian (Watkins 2007);
- *A. indianense* Newell, 1888 – from the limestones at Delphi, Indiana; Niagaran Regional Series; corresponds to the upper Wenlock–lower Ludlow Series, Silurian (Ault & Carr 1978);
- *A. townsendii* Whiteaves, 1884 – from the locality Durham, Owen Sound, Ontario, Canada; Guelph, Niagaran Regional Series; corresponds to the upper Wenlock–lower Ludlow Series, Silurian (Percival & Wright 2005);

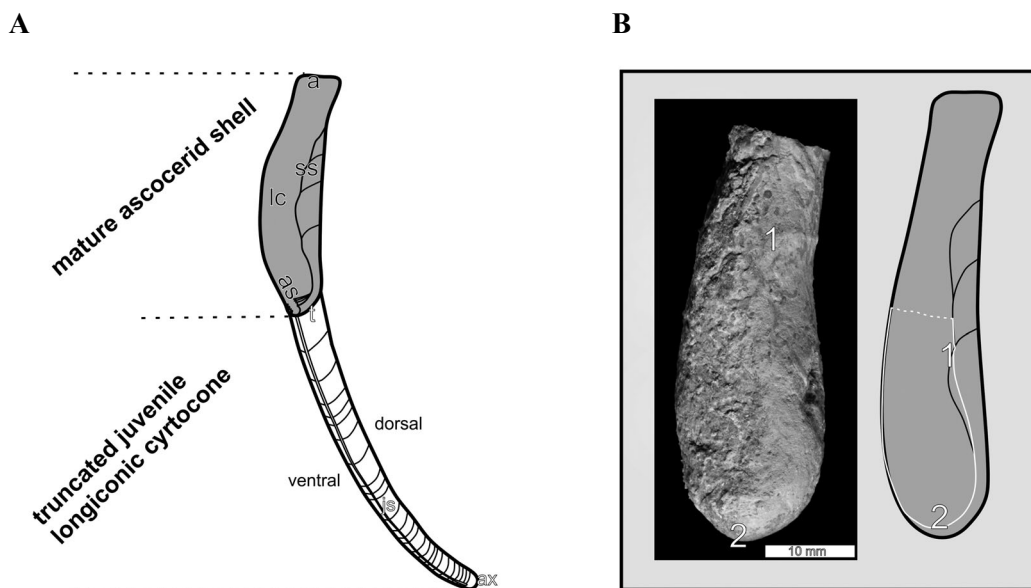


Fig. 2. General morphology of the ascocerids (A) and photograph and reconstruction of the studied specimen (B); a, aperture; as, ascocerid siphuncle; ax, apex; js, juvenile siphuncle; lc, living chamber; ss, sigmoidal septa. Adapted from Lindström (1890), terminology modified after Furnish & Glenister (1964).

- *A. southwelli* Worthen, 1890 – from Port Byron, Illinois, USA; Port Byron Dolomite, Niagaran Regional Series; corresponds to the upper Wenlock–lower Ludlow Series, Silurian (Foerste 1930).

Ascocerids from Baltica

The oldest ascocerids of the Baltoscandian region have been recorded (Fig. 3; Lindström 1890) in the Lower

Visby Formation (boundary interval of the Llandovery and Wenlock series) of Gotland, Sweden. Four ascocericid species have been identified in the upper Sheinwoodian Slite Group. No ascocerids are known from the Homeric Stage and the lowermost Gorstian Stage of Gotland. The peak of species diversity (seven ascocericid species) is confined to the upper Gorstian and lower Ludfordian. Ascocerids are not found in the *Neocucullograptus kozlowskii* Biozone but re-appear in the upper Ludfordian

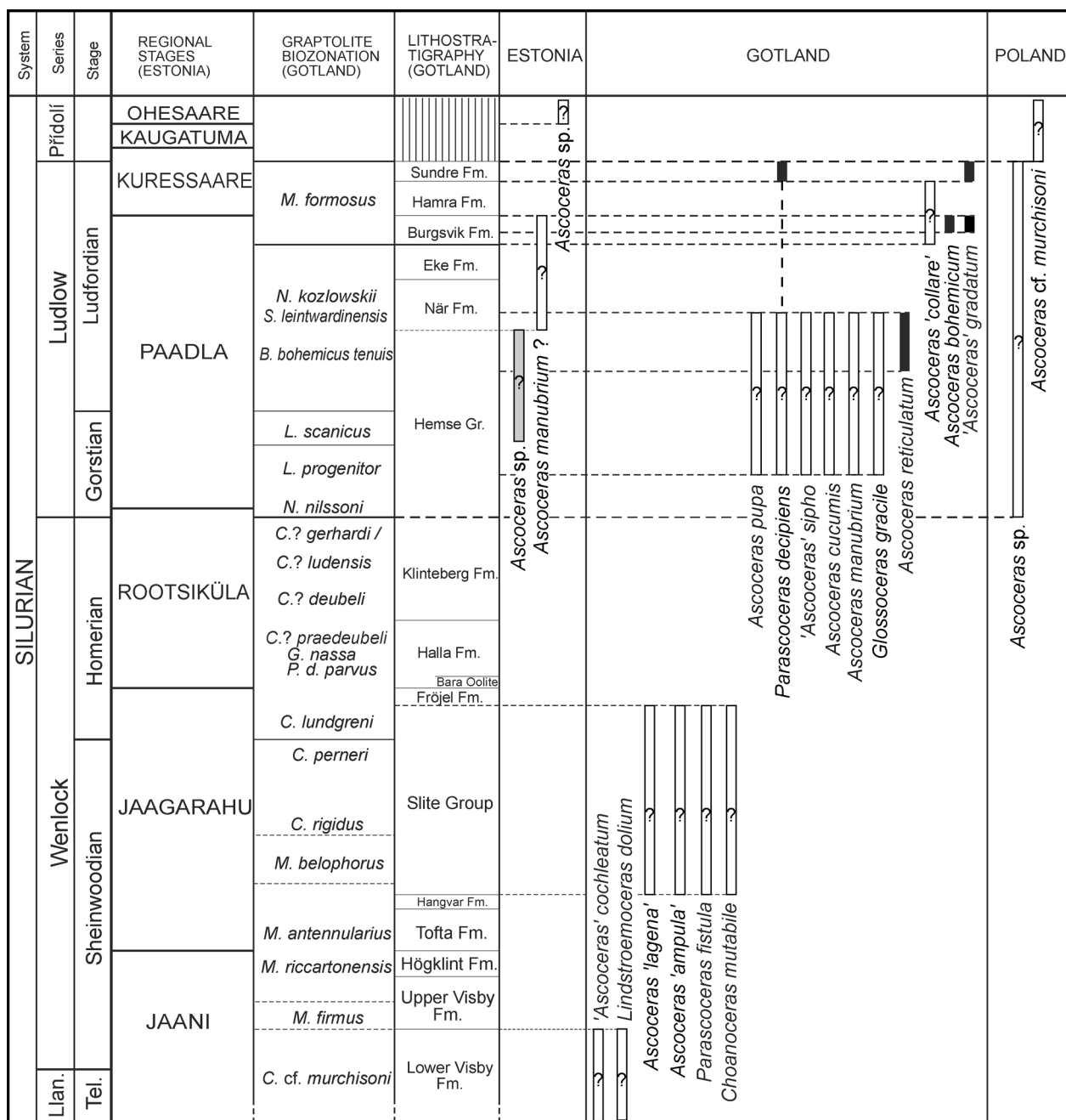


Fig. 3. Stratigraphic distribution of ascocerids on Baltica. The bars indicate possible lower and upper limits of the distribution of the documented specimens. Taxonomic revision of the group is currently being prepared for publication. For this reason the original and/or most recently valid taxonomic names for the genera and species were used for individual taxa.

Stage, with three species present. The latest occurrence of ascocerids in the Sundre Formation (uppermost Ludfordian Stage) of Gotland is represented by two species. This formation corresponds to the youngest Silurian strata on Gotland.

Dzik (1984) assigned two specimens found in the Silurian erratic boulders from the Pleistocene sediments in Poland to the order Ascocerida – *Ascoceras* sp. (Ludlow Series) and *Ascoceras* cf. *murchisoni* (Přídolí Series). The datings of boulders are based on conodont evidence (Dzik 1984, p. 9).

The specimen recently discovered in Estonia comes from the Paadla Regional Stage. The occurrence level is correlated to the Hemse Group on Gotland (Hints 2008). The Estonian record contains also *Ascoceras manubrium* Lindström (Kaljo 1970, table 16; Klamann 1970, table 46) that is tentatively (with a question mark) reported from the uppermost part of the Paadla Regional Stage (Uduvere Beds) and *Ascoceras* sp. from the Ohesaare Regional Stage (Kaljo 1970, table 16).

Ascocerids from Perunica

The only occurrence of Silurian ascocerids outside the Laurentia, Avalonia and Baltica palaeocontinents is known in Perunica (Prague Basin, Bohemia). There, the stratigraphic distribution of ascocerids is well documented in the context of modern stratigraphy of the Silurian strata of the Prague Basin; see Kříž et al. (1986, 1993), Kříž (1991, 1992), Štorch (1994, 1995a, 1995b), Manda & Kříž (2006), Manda et al. (2012), Frýda & Manda (2013), Slavík et al. (2013), Štorch et al. (2014) and also references therein.

The stratigraphically oldest, early Gorstian ascocerid species from Perunica was illustrated by Barrande (1877). The ascocerids are represented by only two species (*Ascoceras verneuilli* and *Glossoceras gracile*) in the late Gorstian and most of the Ludfordian stages. The group's acme on Perunica is reached in the Ludlow–Přídolí boundary interval, with eight ascocerid species (*Aphragmites buchi*, *Aphragmites deshayesi*, *Aphragmites goldfussi*, *Aphragmites keyserlingi*, *Ascoceras bohemicum*, *Ascoceras bronni*, *Ascoceras murchisoni* and *Parascoceras decipiens*) recorded. Two further ascocerid species in the upper Přídolí Series (*Parascoceras* nov. sp., *Ascoceras murchisoni*) comprise the youngest known occurrence of ascocerids in the Prague Basin.

Ascocerids from Avalonia

Two species of the genus *Ascoceras* are mentioned from England by Holland (1999). *Ascoceras barrandei* Salter,

1858 comes from Stansbatch in Herefordshire, Whitcliffe, and *A. vermiforme* Blake, 1882 from Ledbury in Herefordshire, Whitcliffe, both from the Whitcliffe Formation (Ludlow Series).

Notes on the biogeography of the Silurian ascocerids

The overall fossil record of ascocerid cephalopods is scarce but some aspects of biogeography could still be emphasized.

Ascocerids occur in sediments that accumulated in subtropical or tropical seas (see, for example, Manda & Kříž 2006). The group was exclusively restricted to Laurentia and Baltica from the Middle Ordovician up to the early Wenlock (Lindström 1890; Foerste 1928, 1929; Miller 1932; Sweet 1958; Kesling 1961; Flower 1963; Furnish & Glenister 1964; Frey 1985; Kröger 2007, 2013).

The appearance of the genus *Ascoceras* on Gotland is well documented by Lindström (1890). The North American record lacks the necessary detail but may slightly postdate the stratigraphically oldest occurrence of *Ascoceras* on Gotland (see the chapter 'Ascocerids from Laurentia' above). The oldest record of ascocerids from Estonia comes from the time interval where the group has its maximum species diversity and dispersion. This is contemporaneous with the appearance of ascocerids outside Baltica. The occurrence of the Ascocerida in Perunica was documented already by Barrande (1877). Considering the palaeobiogeography of ascocerids (confinement to low-latitude areas), this migration to Perunica may be related to the shift of the Perunica Microcontinent towards the palaeoequator during the Silurian (Kříž et al. 2003).

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Vanim askotseriid Eesti Silurist ja seltsi Ascocerida (klass Cephalopoda) biogeograafiast

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Varapaleosoiiline selts Ascocerida on erilise morfoloogiaga haruldaste peajalgsete rühm, mis oli levinud Avaloonia, Baltica, Laurentia ja Perunica paleokontinendil Ordoviitsiumi ning Siluri ajastul. Väheseid levikuandmeid Eesti Silurist võimaldab täiendada Pähkla läbilõikest (Saaremaa, Paadla lade, Ludlow) leitud eksemplar, mis on ühtlasi Eesti vanim selle seltsi esindaja leid. Pähkla läbilõikes kunagi paljandunud kihid on arvatavasti korreleeritavad märkimisväärsel hulgal askotseriidide kivistisi sisaldava Hemse kihtkonnaga Gotlandil. Askotseriidide ilmumine Eesti Siluris leidis aset geoloogilise aja momendil, mil selts oli suurima liigilise mitmekesisuse ja maksimaalse arealiga, mis esmakordselt ulatus ka väljapoole Baltica paleokontinenti.