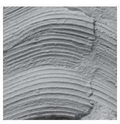
Lituitid cephalopods from the Middle Ordovician of Bohemia and their paleobiogeographic affinities

Martina Aubrechtová & Vojtěch Turek



Cephalopods of the order Lituitida Starobogatov, 1983 are a common component of low-latitude, warm-water fossil assemblages of the Middle and Upper Ordovician strata of Baltica and the Chinese paleocontinents (North and South China, Tarim, Tibet). The lituitids are also known from Laurentia, Siberia and mid-latitude Avalonia and Argentine Precordillera. By contrast, in the high-latitude regions of peri-Gondwana, the group is known only from a ?*Trilacinoceras* Sweet, 1958 from the late Darriwilian rocks of the Iberian peninsula and *Rhynchorthoceras* cf. *angelini* (Boll, 1857) from the upper part of the Klabava Formation (uppermost Dapingian Stage) of Bohemia. The single specimen of the latter species is the earliest known lituitid known from European and African peri-Gondwanan basins. The timing of its appearance coincides with a time interval of an increased faunal interchange between Perunica and Baltica during the late Dapingian time. Six specimens of two lituitids, *Lituites lituus* de Montfort, 1808 and *Trilacinoceras* cf. *discors* (Holm, 1891), are for the first time reported from the late Darriwilian Dobrotivá Formation. Finds of these lituitids are coeval with an occasional dispersion event of another typically low-latitude cephalopod group, the Tarphyceratida, to high latitudes. • Key words: Lituitida, Middle Ordovician, Prague Basin, Bohemia, Baltica, paleobiogeography, migration.

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The Ordovician strata of the Prague Basin (Figs 1, 2) contain a rich invertebrate fossil assemblage that has been studied intensively since the 40's of the 19th century. Besides studies on taxonomy, paleoecology and taphonomy (including exceptional preservation), numerous works have dealt with paleobiogeographic affinities of the fossil associations. Havlíček (1981, 1982, 1989) defined various brachiopod-based communities (= associations), each bound to a characteristic environment and/or time interval. The author concluded that in the Prague Basin, during the Ordovician, periods of faunal interchange and migration repeatedly changed with periods of a more pronounced faunal isolation associated with a high endemism. Havlíček *et al.* (1994) then used these differences in fossil assemblages to establish a separate microcontinent (microplate) Perunica involving a major part of the Bohemian Massif. Fatka & Mergl (2009) revised the original concept of Perunica, which they supported not only by paleontological but also paleomagnetic and sedimentological data. Havlíček *et al*. (1994) summarized brachiopod and trilobite taxa established in the Ordovician of Bohemia and discussed their changing paleobiogeographical relationships to the fossil assemblages known from European and African peri-Gondwana, Avalonia, Baltica, Laurentia or other regions. By contrast, according to Servais & Sintubin (2009) Perunica should be considered as a paleobiogeographical province only.

Paleobiogeographic affinities were studied also for other fossil groups, such as acritarchs (Servais & Fatka 1997, Vavrdová 1997), bivalves (Polechová 2013), bryozoans (Mergl 2004), chitinozoans (Paris & Mergl 1984), conodonts (Dzik 1983), gastropods (Frýda 1988) or ostracods (Lajblová & Kraft 2014). Generally, the benthic fauna shows a stronger affinity to other European and African peri-Gondwanan basins and/or Avalonia, while nektonic/planktonic groups contain more elements from distant regions of mainly Baltica but also Laurentia and South China (see Fatka & Mergl 2009 and references therein). Note, however, that, *e.g.* actritarchs, some bivalves, bryozoans and ostracods contradict this pattern (*e.g.* Polechová 2013).

Cephalopods may be helpful from the paleobiogeographic point of view, too, as shown by numerous paleobiogeographic studies from other parts of the world (*e.g.* Evans 2007, Kröger *et al.* 2007, Kröger & Lefebvre 2012, Evans *et al.* 2013, Kröger 2013a). In the Prague Basin, however, the group and its paleobiogeographic significance has not received a sufficient attention with the exception of only three more recent studies of Marek (1999), Manda (2008) and Aubrechtová (2015).

Earliest cephalopods in Bohemia are known from higher levels of the Klabava Formation (Dapingian Stage, Fig. 1; Kraft & Kraft 1994, Havlíček 1998, Marek 1999) and then occur throughout the rest of the overlying Ordovician strata. Most abundant and most diverse are straight shelled cephalopods with a relatively thin, tubular siphuncle assigned to orders Orthocerida and Pseudorthocerida (35 species; Marek 1999). Note that the unambiguous assignment of species to either of these two orders is mostly difficult and out of scope of this paper. Some orthocerid and pseudorthocerid taxa have, however, been briefly discussed, synonymised or re-assigned by, *e.g.* Dzik (1981), Kröger (2004, 2012), Kröger & Isakar (2006), Evans (2005), Evans *et al.* (2013) and Aubrechtová (2015). It is an interesting fact, that other cephalopod orders that are represented in the Ordovician of the Prague Basin, are restricted only to rather narrow intervals during the Darriwilian (Šárka and Dobrotivá formations) and upper Katian (Králův Dvůr Formation) stages (Fig. 1). In the Šárka Formation, three endocerid species and a cyrtocerinid *Bathmoceras complexum* (Barrande, 1868, see Mutvei 2015) are known. Rather common is also "*Orthoceras*" *bonum* Barrande, 1868, the assignment of which to the order Actinocerida (Marek 1999, Manda 2008, Evans *et al.* 2013) is, however, uncertain. In the strata of the Dobrotivá Formation, an undetermined endocerid (Turek & Aubrechtová unpublished data) and a tarphycerid *Trocholites fugax* Babin & Gutiérrez-Marco, 1992 (= ?*Lituites primulus* Barrande, 1865) have been found (Manda 2008). In the Králův Dvůr Formation, a single actinocerid and an endocerid have been identified (Turek & Aubrechtová, personal observation). Additionally, *Diestoceras primum* (Barrande, 1865) is so far the only representative of the Oncocerida in the Ordovician of the Prague Basin (*cf.* Strand 1934, Flower 1946, Marek 1999).

In this work, cephalopods of the order Lituitida Starobogatov, 1983 from the Prague Basin are for the first time investigated and interpreted. Generally, the lituitids can be distinguished from other cephalopod groups owing to their peculiar morphology. They have an initially coiled but then rapidly uncoiling shell, sinuous transverse

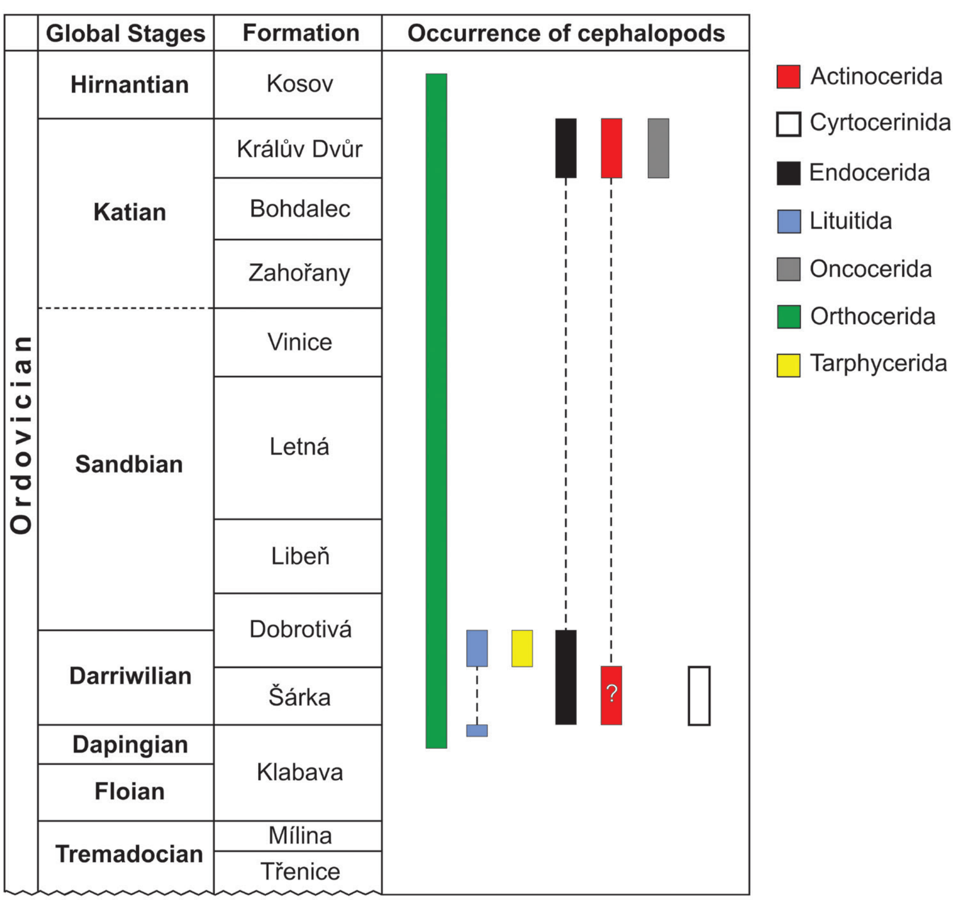

Figure 1. Stratigraphic occurrence of cephalopod orders in the Ordovician of the Prague Basin (generalized with the exception of the Lituitida). Modified after Marek (1999) and Lajblová & Kraft (2014).

ornamentation and a modified aperture (see Furnish & Glenister 1964). These cephalopods were among most common faunal elements during the Middle and Late Ordovician, especially on Baltica (*e.g.* Sweet 1958) and the Chinese paleocontinents (*e.g.* Lai 1986, Fang *et al.* 2017a), *i.e.* regions of a probably low-latitude position (Figs 3, 4). Nevertheless, occurrence data suggest a wider paleogeographic extent of the group (at least during the Middle Ordovician) – lituitids were reported from mid-latitude Argentine Precordillera (Kröger *et al.* 2007) and Avalonia (Evans 2005) and even as scarce elements from high-latitude European peri-Gondwana (Iberian Peninsula: Guttiérrez-Marco *et al.* 1984, Babin & Guttiérrez-Marco 1992, Sá & Guttiérrez-Marco 2009; and Perunica). From Perunica, the lituitids are known only from a single specimen assigned by Marek (1999) to *Rhynchorthoceras* cf. *angelini* (Boll, 1857) of the family Sinoceratidae (see Kröger *et al.* 2007). Here, we illustrate and describe this specimen for the first time. We also describe six newly identified lituitid fragments from the collections of the National Museum Prague. Five of the specimens are assigned to the genus *Lituites* Bertrand, 1763 and one to the genus *Trilacinoceras* Sweet, 1958.

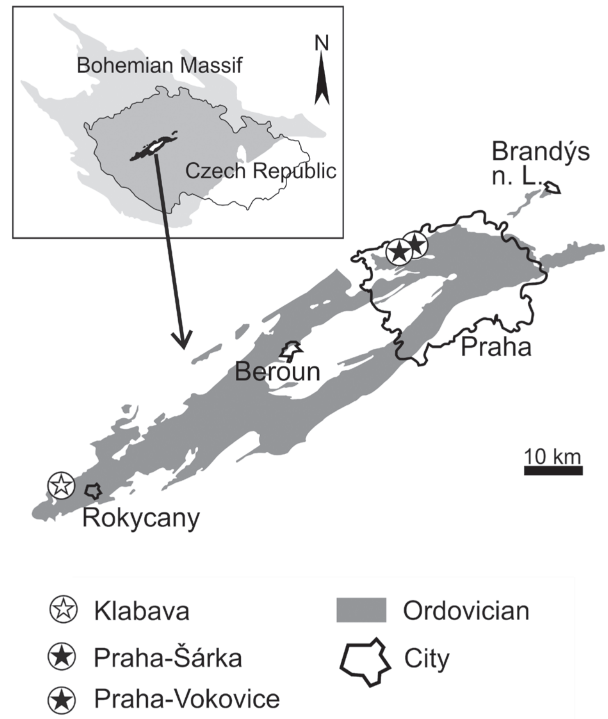

Figure 2. Position of the lituitid occurrences in the Prague Basin. Modified after Manda (2008).

Geological setting, material and methods

Main occurrences of the Ordovician rocks within the Bohemian Massif are restricted to the Teplá-Barrandian area, namely the Prague Basin (Fig. 2). The Basin is an infilling of a tectonically predisposed, narrow linear depression situated in central Bohemia, between cities Plzeň and Prague, and with its deepest part and maximum thickness along its central longitudinal axis (Havlíček 1981, 1982). The present-day denudation relict does not exceed 25 km in width but the sea extended far from the linear depression at least in some time-spans (Havlíček 1981).

The Prague Basin contains a continuous and uninterrupted succession of sedimentary and volcanic rocks ranging from Early Ordovician to Middle Devonian in age. The sedimentary complex of the Prague Basin rests with a marked angular unconformity either on the deformed late Proterozoic (Cadomian) or undeformed Cambrian basement (Havlíček 1998). The sedimentation in the Prague Basin took place under an extensional regime as the Prague Basin, along with other European and African peri-Gondwanan basins, drifted towards Baltica and Avalonia paleocontinents. The tectonic unrest led to extensive volcanic activity, segmentation of the Prague Basin and subsequent facial differentiation. The sedimentation ended with the Variscan orogeny that first manifested itself in the region during the Middle Devonian (Chlupáč 1998).

The Ordovician of the Prague Basin is represented by an unmetamorphosed, richly fossiliferous, continuous succession of various clastic sediments accompanied with volcanic rocks. The sedimentation began in the Tremadocian Stage (Třenice and Mílina formations), when the sea first invaded central Bohemia and probably created a very shallow, narrow sea bay. The central, rapidly subsiding depression was not yet developed (Havlíček 1998).

The overlying strata of the Klabava Formation (Floian to Dapingian stages, Lower to Middle Ordovician; Fig. 1) represent a time interval of initial deepening of the Prague Basin, sea-level rise and segmentation. The Formation was deposited under transgressive systems tract conditions (Havlíček 1998). It consists of an up to 300 m of shales associated with local developments of iron ores and rocks of volcanic origin (Kraft & Kraft 2003a). The most characteristic facies of the Klabava Formation are grey-green clayey shales deposited in the rapidly subsiding axial segment of the basin (Havlíček 1998). They may pass laterally into greenish greywackes and red shales. The deeper-water environments are also represented by dark grey graptolitic shales (Havlíček & Šnajdr 1957). Towards, and in proximity to the former shore, a series of shallow-water facies developed (Kukal 1959, 1963), including red greywackes and silty shales with frequent volcanic glass and locally underlain by basal conglomerates. Tuffs and tuffites represent another facies

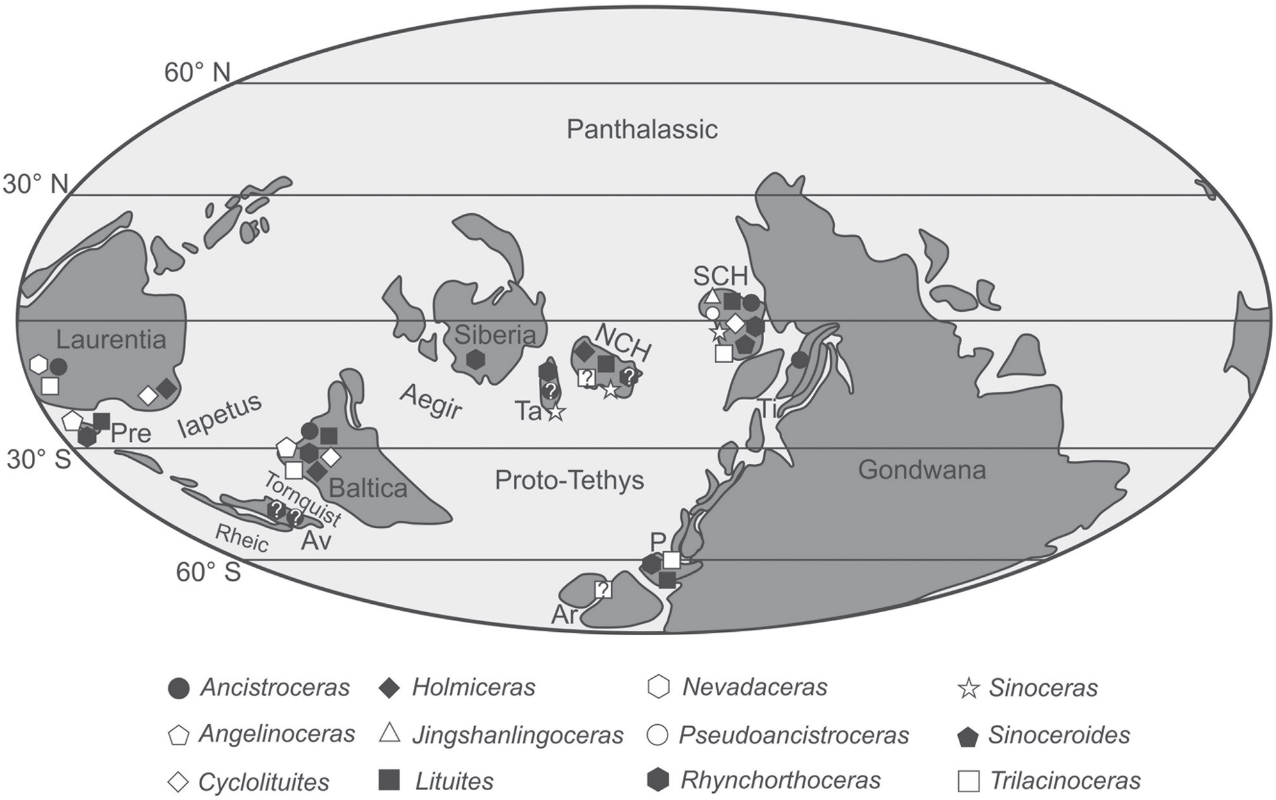

Figure 3. Paleogeographic distribution of the lituitid cephalopods during the Mid Ordovician. Adopted from Torsvik & Cocks (2017), lituitid occurrences after Sweet (1958), Flower (1975), Lai (1986), the Paleobiology Database (*fossilworks.org*), Kröger (2013a), Fang *et al.* (2017a, b) and references therein (*Tapinolituites* Gao, 1982 is not included due to lack of reliable stratigraphic data.). Abbreviations: Ar – Armorica; Av – Avalonia; NCH – North China; P – Perunica; SCH – South China; Pre – Argentine Precordillera; Ta – Tarim; Ti – Tibet.

developed close to the former shore, under an inter-tidal to shallow sub-tidal conditions. Basin-ward progression of shallow water facies coincides with the Walhall regression event (Havlíček & Šnajdr 1957, Mergl 1984, Havlíček *et al.* 1994, Havlíček 1998, Mergl & Vohradský 2000).

A single specimen of *Rhynchorthoceras* cf. *angelini* studied herein was collected by M. Mergl in an abandoned iron ore mine near Ejpovice (Fig. 2; Dzik 1983, Mergl & Vohradský 2000). It comes from tuffitic rocks, *c.* three meters below the base of the Šárka Formation, which corresponds to the *Azygograptus ellesi-Tetragraptus reclinatus abbreviatus* Zone (Kraft & Kraft 1994, Marek 1999) of the uppermost Dapingian Stage (Kraft & Kraft 2003b). The specimen is held at the collections of the Museum of Dr. Bohuslav Horák in Rokycany.

The Šárka Formation (lower–mid Darriwilian Stage, Middle Ordovician; Fig. 1) formed during the time of a further transgression, deepening and strong volcanic activity that resulted in a rapid change of facies (Havlíček 1998, Servais *et al.* 2008). The Formation is an up to 350 m thick succession that consists of clayey shales associated locally with iron ores and volcanitic rocks (Havlíček 1998, Servais *et al.* 2008). The clayey shales contain originally carbonatic, secondarily silicified (Kukal 1962) nodules with 3D preserved fossils including brachiopods, mollusks, arthropods, echinoderms and other fauna. Despite the rich cephalopod fossil assemblage known from the Šárka Formation (Barrande 1865–1870; Marek 1999), no lituitid has been recorded so far (Fig. 1).

The lithology of the Dobrotivá Formation (upper Darriwilian to lowermost Sandbian stages, Middle Ordovician Series; Fig. 1) is similar to the preceding Šárka Formation and no abrupt changes in the facial development can be recognized (Havlíček *et al.* 1994). The deepening of the Prague Basin progressed with black-shale sedimentation continuing. This deepening was accompanied by a rise of the marginal segments and subsequent accumulation of sandy deposits along both sides of the Basin (note that the sandstones are generally missing in its western part).

The best preserved fossil assemblage of the Dobrotivá Formation comes from carbonatic nodules that originate from shelly facies. From black shales, however, well-preserved fossils have also been locally gathered (Havlíček & Vaněk 1990). Body fossils are, by contrast, rare within the sandy deposits; the fossil assemblage

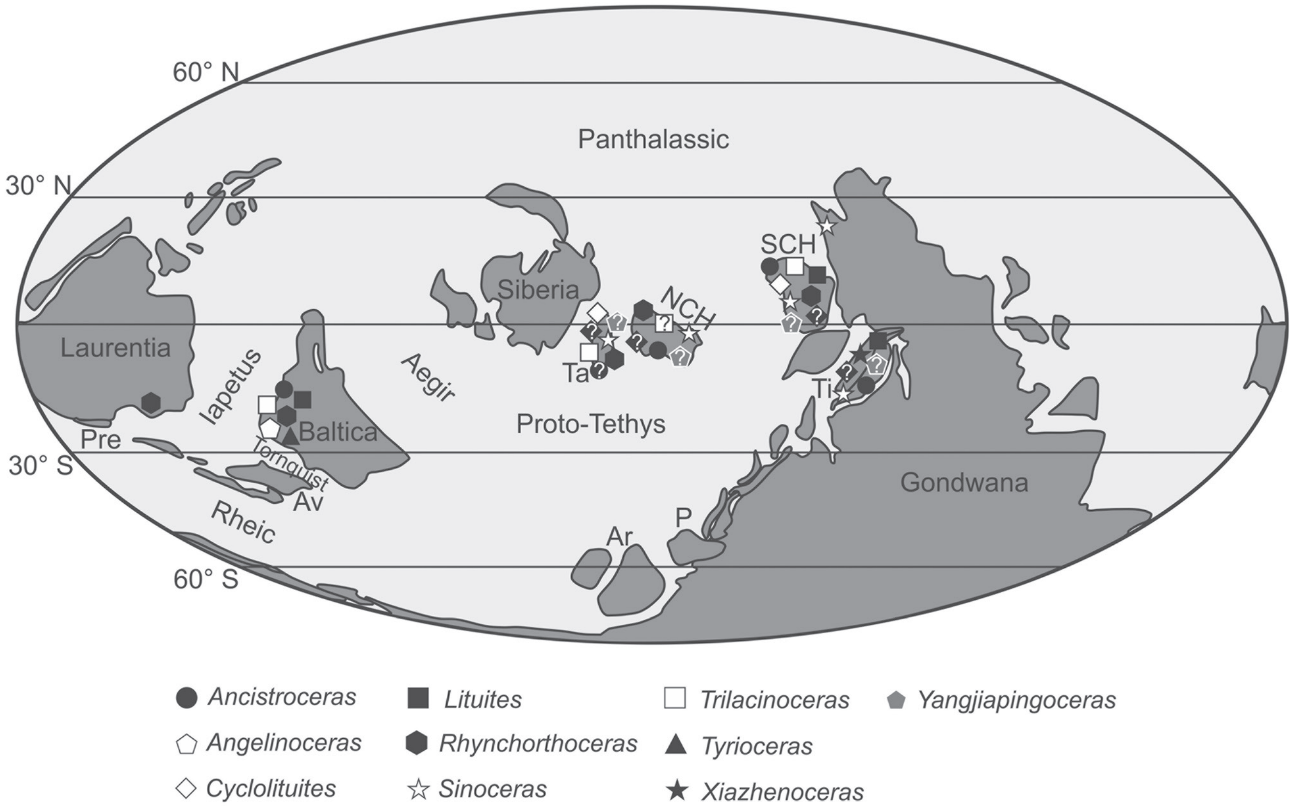

Figure 4. Paleobiogeographic distribution of the lituitid cephalopods during the Late Ordovician (sources and abbreviations as for Fig. 3).

mainly consists of ichnofossils (Havlíček 1998). Benthic and nectobethic assemblages of the Šárka and Dobrotivá formations are analogical in both formations around their boundary. By contrast, the pelagic elements are rather different (Havlíček 1998, Marek 1999, Manda 2008).

Specimens assigned to the lituitid genera *Lituites* and *Trilacinoceras* studied herein are preserved within nodules and come from two localities: Praha-Šárka (field near Villa Hamerník) and Praha-Vokovice (Fig. 2). Klouček (1916) clearly assigned the nodules from the former locality to the Dobrotivá Formation and also described their lithological characteristics. This is in agreement with information later provided by F. Hanuš on labels attached to specimens collected by him. František Hanuš strictly distinguished older fossil assemblages of the Šárka Formation from stratigraphically younger assemblages of the Dobrotivá Formation (Hanuš 1923). Additionally, the location of the site corresponds to the position of outcrops of the Dobrotivá Formation indicated in the detailed geological map of the area (Králík *et al.* 1983, 1984). Associated index trilobite *Placoparia zippei* (Boeck, 1828) preserved in a nodule with the specimen NM L 46559, lithology of nodules and other fossils known from the locality all support a stratigraphical origin of the above lituitid specimens from the lower part of the Dobrotivá Formation. This part of the Dobrotivá Formation probably corresponds to the regressive or post-regressive stagnant phase in the Prague Basin (for stratigraphical occurrence of *P. zippei* see Moravec 1990 and Havlíček & Vaněk 1996).

Nodules from localities collectively referred to as Praha-Vokovice contain both fossil assemblages of the Šárka Formation and the Dobrotivá Formation. The stratigraphic determination of the single lituitid specimen from this locality, NM L 46569, is indicated by collector C. Klouček on an attached label, as well as on the specimen. According to Klouček (1916, p. 39), his inscription "X" in black ink directly on nodules indicates the Dobrotivá Formation. The lithology of the nodule with the lituitid specimen also corresponds to that of the Formation.

It is noteworthy, that all of the above cephalopod fragments come from localities in the eastern part of the present day denudation relict of the Prague Basin (Praha-Šárka and Praha-Vokovice; Fig. 2), although collecting activity has been also intensive in the western part of the Basin. Four specimens are fragments of internal moulds of body chambers of subadult individuals, two specimens are counterparts of internal moulds. The material is only slightly diagenetically flattened or damaged. All six specimens studied herein are held in the collection of the National Museum, Prague.

Morphological terminology used in this study follows Furnish & Glenister (1964), Korn (2010; terminology concerning the coiled growth stages) and Kröger (2008; terminology concerning the type of ornamentation). In the course of a separate study on Baltic Middle Ordovician lituitids by one of the authors of the present paper (MA), comparison was also possible with the type and other illustrated specimens (Remelé 1880a, b, 1881a, b, 1882, 1890; Foerste 1930; Neben & Krüger 1971) collected from Pleistocene erratics of Baltic origin in northern Germany (Museum für Naturkunde in Berlin) and with lituitid cephalopods from the Middle Ordovician of Estonia (University in Tartu, Tallinn Technical University and the Estonian Museum of Natural History in Tallinn).

Systematic paleontology

Class Cephalopoda Cuvier, 1797
Order Lituitida Starobogatov, 1983
Family Lituitidae Phillips, 1848

Genus *Lituites* Bertrand, 1763

Type species. – *Lituites lituus* de Montfort, 1808, Middle Ordovician of Baltoscandia (type locality unknown), designated as the type species of *Lituites* by Sweet (1958).

Diagnosis. – "Gradually expanded annulate conchs with whorls of spiral portion in contact or loosely coiled but not impressed dorsally; body chamber may equal or exceed length of weakly sigmoid orthoconic phragmocone; fully mature aperture characterized by pair of pronounced ventrolateral lappets and similar but shorter dorsolateral lappets; dorsal sinus generally divided by low salient; siphuncle subdorsal (after Furnish & Glenister 1964, K366)."

Remarks. – *Lituites* differs from all other lituitid genera in the combination of a moderate angle of expansion (not exceeding 8° in adult individuals), pronounced annulation with multiple deep sinuses and saddles, compressed cross section in early growth stages that becomes less compressed to circular later during shell growth, subdorsal position of the siphuncle that becomes subcentral in ontogeny and development of the five-lappeted aperture with deep ventral sinus, two deep lateral (ocular) sinuses and two shallow dorso-lateral sinuses at maturity.

Occurrence. – Middle to lower Upper Ordovician (lower Sandbian Stage) of Baltoscandia and Pleistocene erratics of Baltoscandic origin of Germany, Poland and Russia; Middle Ordovician of North and South China; Upper Ordovician of South China and Tibet; Middle Ordovician (upper Darriwilian Stage) of Perunica (Bohemia) and Precordillera (Argentina).

***Lituites lituus* de Montfort, 1808**
Figures 5E–G, 6

1731 *Tubulos concameratos*. – Klein, pp. 6, 10, 25, pl. 5, fig. b.
1732 *Lituites*. – Breyn, p. 26, pl. 2.
1808 *Lituites lituus* sp. nov.; de Montfort, pp. 278–280, text-fig. on p. 278.
1808 *Hortolus convolvans*. – de Montfort, pp. 284, 285, text-fig. on p. 282.
1811 *Lituites*. Parkinson, p. 110, pl. 6., fig. 11, pl. 7, fig. 18.
1813 *Lituites lituus* Montfort. – Schlotheim, p. 34.
1813 *Lituites convolvens*. – Schlotheim, p. 35.
1820–1821 *Orthoceratites undulatus*. – Schlotheim, pp. 55, 58, pl. 9, fig. 1.
1821 *Lituites perfectus* sp. nov.; Wahlenberg, p. 83.
1837 *L. lituus*. – Bronn, pp. 102–104, pl. 1, figs 3a, 6.
1837 *Lituites lituus*. – Hisinger, p. 27, pl. 8, fig. 5a, b.
1846 *O. undulatus*. – Quenstedt, p. 44.
1846 *Lituites lituus* Montfort. – Quenstedt, p. 50.
1849 *Orthoceratites undulatus*. – Quenstedt, pl. 1, fig. 24a, b.
1849 *Lituites lituus* Montfort. – Quenstedt, pl. 1, fig. 25.
1852 *Lituites lituus*. – Quenstedt, p. 344, pl. 26, fig. 12.
1857 *Lituites perfectus* Wahlb. – Boll, p. 85, pl. 9, fig. 30.
1857 *Lituites sinuatus* sp. nov. var nov.; Boll, p. 85, 86, pl. 9, fig. 31a–c, e, f.
1860 *Lituites lituus*. – Lossen, pp. 15–19, pl. 1a–d.
1860 *Lituites perfectus* Wahlenberg 1821. – Lossen, pp. 19–21.
1876 *Lituites lituus*. – Römer, pl. 6, fig. 7.
1880 *Lituites lituus* Montfort. – Remelé, pp. 432–435.
1880 *Lituites perfectus* Wahlenberg. – Remelé, pl. 1, fig. 2a, b.
non 1880 *Lituites perfectus* Wahlenberg. – Remelé, pl. 1, fig. 3. (= *Trilacinoceras discors* Holm).
1880 *Lituites lituus* Montf. – Angelin & Lindström, pp. 8, 9, pl. 9, fig. 8.
? 1880 *Lituites anguinus* Angel. – Angelin & Lindström, pl. 11, fig. 9.
? 1880 *Lituites anguinus* Angel. – Angelin & Lindström, pl. 11, figs 12, 13.
1882 *Lituites lituus* Montf.. – Schöder, pp. 58, 59, pl. 2, fig. 3.
1882 *Lituites lituus* de Montfort. – Noetling, pp. 156–193, pl. 11, fig 1.
1884 *Lituites lituus* Montfort. – Noetling, p. 129.
1884 *Lituites perfectus* Wahlenberg. – Noetling, p. 129.
1885 *Lituites lituus* Montf. – Holm, pp. 17, 20, 24, 25, pl. 5, figs 2–4.
1889 *Lituites perfectus* Wahl. – Rüdiger, pp. 42, 43.
1890 *Lituites lituus* Mtf. – Steinmann & Döderlein, pp. 370, 371, text-fig. 429.

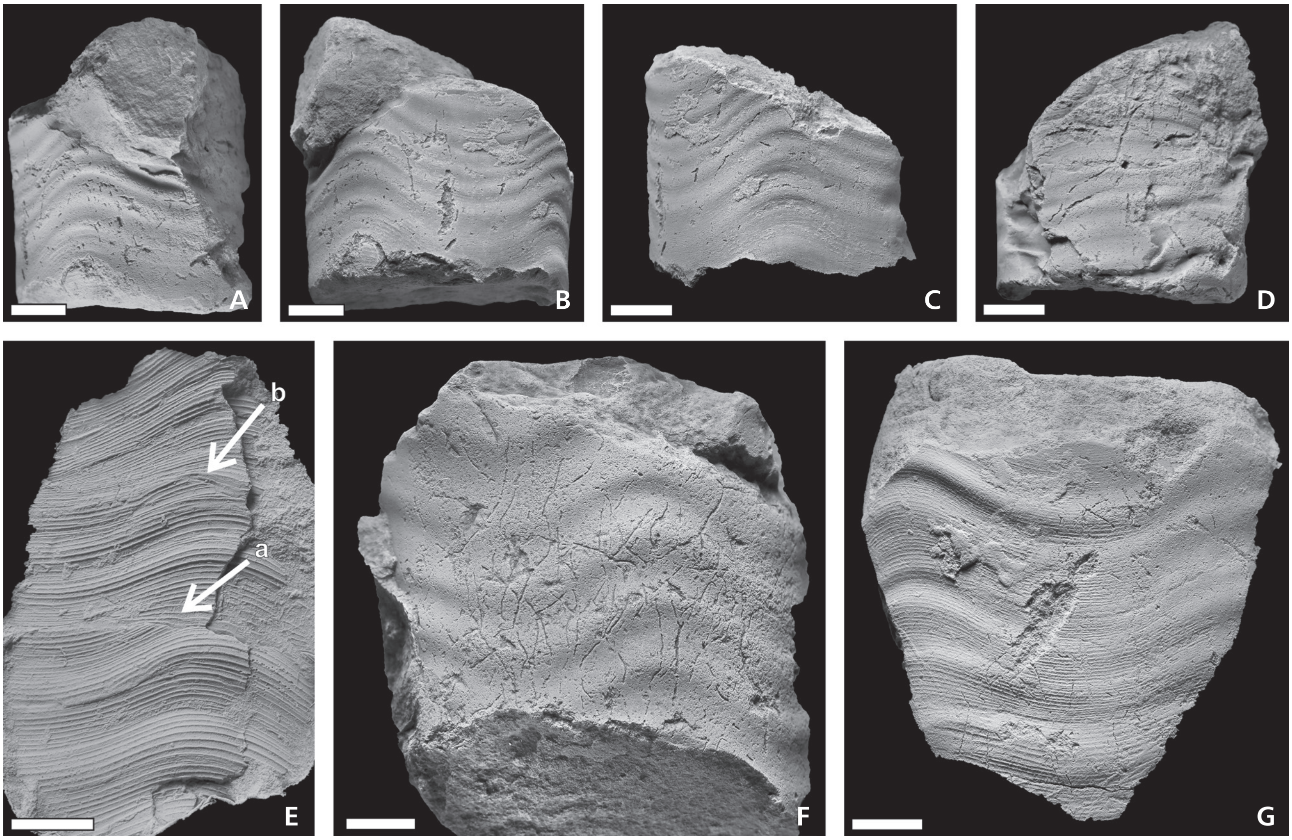

Figure 5. Lituitid cephalopods from the lower part of the Dobrotivá Formation (latest Darriwilian, Middle Ordovician) at Praha-Šárka (field near Villa Hamerník). • A–D – *Trilacinoceras* cf. *discors* (Holm, 1891); A – lateral view; B – ventral view; C – ventrolateral view; D – dorsal view; NM L 46557. • E–G – *Lituites lituus* de Montfort, 1808; E – lateral view, latex cast, NM L 46559, arrows point to a sublethal shell damage (a) and an anomalous growth of the shell (b); F – lateral view, NM L 46558, latex cast; G – lateral view, NM L 46564. All specimens oriented with apex down; coated in ammonium chloride. Scale bar 5 mm.

1890 *Lituites lituus* Montfort. – Remelé, pp. 7–12, pl. 1, fig. 1.
1890 *Lituites perfectus* (Wahlenb.) – Remelé, pl. 1, fig. 2a, b, pl. 6, fig. 3.
1890 *L. tenuicaulis* Remelé. – Remelé, pl. 3, fig. 2a, b.
1890 *Lituites perfectus*? (Wahlenb.). – Remelé, pl. 6, fig. 4.
1891 *Lituites lituus* de Montfort. – Holm, pp. 753–759, pl. 12, figs 1, 2.
1891 *L. perfectus* Wahlenb. – Holm, pp. 745–753, pl. 11, figs 1–5.
1897 *Lituites perfectus*. – Holm, pp. 469–474, pl. 9.
1926 *Lituites lituus* Montfort. – Patrunky, pp. 115, 118, 119.
1953 *Lituites perfectus* Wahlenberg. – Balashov, pp. 334, 335, pl. 14, fig. 4.
1958 *Lituites perfectus* Wahlenberg. – Sweet, pp. 144–147, pl. 14, figs 2, 3, ?pl. 16, figs 2, 4.
1958 *Lituites lituus* Montfort, 1808. – Sweet, pp. 141, 142–144, pl. 14, fig. 5, pl. 15, fig. 4.
1965 *Lituites lituus* de Montfort. – Müller, p. 129, text-fig. 175.
? 1971 *Lituites* sp. – Neben & Krüger, pl. 21, fig. 7.
? 1971 *Lituites* cf. *lituus*. – Neben & Krüger, pl. 21, fig. 1.
? 1971 *Lituites* sp. – Neben & Krüger, pl. 21, figs 3, 4, 6–8.
1984 *Lituites lituus*. – Dzik, p. 137, pl. 41, fig. 1.
1984 *Lituites perfectus* Wahlenberg. – Dzik, pp. 137–139, text-figs 53c, d, 55.14, pl. 41, figs 4, 5.
? 1984 *Lituites lituus*. Dzik, p. 137, pl. 41, figs 2, 3.

Material. – Five specimens, from localities Praha-Šárka (field near Villa Hamerník) (NM L 46558–46560, 46564) and Praha-Vokovice (NM L 46569), Prague Basin, central Bohemia; Dobrotivá Formation, upper Darriwilian Stage, Middle Ordovician.

Diagnosis. – Coiling typically tight, with whorls in contact or only slightly separated from each other, slightly impressed or not impressed. Coiled shell diameter between 20 and 30 mm. Whorls moderately compressed in cross-section (WWI of *c*. 0.8). Shell strongly curved upon uncoiling, the longitudinal axis of the cyrtoconic/orthoconic shell may reach or exceed the position of the central part of the coiled shell. The curved shell has an angle of expansion of *c*. 5–7° and is compressed in cross-section. Orthoconic growth stage has an angle of expansion of up to 6–8° and is nearly circular in cross-section. Sculpture consists of coarse and broad annulations up to 10 mm apart and fine (4–5/mm) to moderately coarse (up to 1/mm) lirae that follow the course of the annulation. Weak dorso-lateral sinuses develop on the sculpture later in growth. Adult diameter of the shell varies between 27 and 50 mm (compiled from Remelé 1880a, b, 1890; Noetling 1882 and Holm 1891).

Description. – Specimen NM L 46558 (Fig. 5F) is a moderately diagenetically compressed internal mould of a body chamber. The apertural margin is not preserved but the rather large diameter of the fragment indicates a near-adult growth stage of the individual. The total length of the fragment is 29 mm. The maximum dorsoventral diameter is 33 mm and maximum (reconstructed) lateral diameter is *c.* 34 mm; the original cross-section was circular or subcircular. The original shell wall is not preserved but the internal mould shows distinct, widely spaced annuli; adapically, three annuli correspond to 10 mm of shell length and their distance slightly increases adorally. The dorsal side of the shell is incompletely preserved but the annuli indicate a presence of a low and wide dorsal saddle. The annuli laterally and ventrally form broad and moderately deep lobes. The ventral lobe is only slightly deeper than the lateral lobe; this additionally supports the assumption of the near-adult growth stage of the individual.

Specimen NM L 46559 (Fig. 5E) is a counterpart of a shell fragment of a large individual, laterally secondarily broken, with an exceptionally well preserved sculpture. The total length of the fragment is 34 mm. The annuli are distinct and widely spaced. The distance between individual annuli clearly decreases adorally (3 annuli per 10 mm adapically *vs*. 6 annuli per 10 mm adorally), possibly indicating the proximity of the apertural margin. Distinct lirae run subparallel to the course of the annuli (2–3 lirae per 1 mm adapically *vs*. 4 lirae per 1 mm adorally). Healed damage of the shell wall is apparent in the adapical half of the specimen (a in Fig. 5E). Additionally, an area of anomalous shell growth in the adoral part of the fragment indicates local minor damage to the secretionary part of the mantle (b in Fig. 5E).

Specimen NM L 46564 (Fig. 5G) is a fragment of the adapertural part of the shell with a damaged apertural margin. Shell sculpture is well preserved. The total length of the shell fragment is 29 mm. The annuli are widely spaced; three annuli correspond to ten mm of shell length. The last annulus is more raised above the shell surface and may indicate the proximity of the aperture. Lirae run subparallel to the course of annuli (3–5 lirae per 1 mm).

Specimen L 46569 (Fig. 6A) is a counterpart of the adoral part of the shell. The total length of the fragment is 26 mm. Shell sculpture shows a broad and shallow lobe and a saddle. The annuli are distinct, widely spaced, two annuli correspond to ten mm of shell length. The annuli are regular in spacing. Distinct lirae run subparallel to the course of the annuli (3 lirae per 1 mm adorally).

Specimen NM L 46560 (Fig. 6B) is a diagenetically compressed fragment of an internal mould of a body chamber. One of the lateral sides of the shell is weathered away entirely. The shape and density of annuli indicates that the fragment probably represents an almost mature individual. The total length of the fragment is 18 mm, the maximum dorsoventral diameter is 29 mm. The lateral diameter cannot be measured but the original cross section was probably circular or subcircular. The transverse annuli are rather indistinct and densely spaced (7–8 per 10 mm ventro-laterally, 6 per 10 mm laterally and 12 per 10 mm of shell length dorsolaterally). Insertion of additional annuli occurs dorsolaterally. The annulli form a very low saddle dorsally, which passes into a shallow and wide lateral lobe. Ventrolateral saddle is narrow and ventral lobe is broad and distinct. The annuli are paralleled with lirae (4–5 per 1 mm), which are preserved dorsolaterally in the adoral part of the shell fragment.

Remarks. – The general dimensions of the fragments and the character of ornamentation (widely spaced annuli paralleled with coarse lirae that together form distinct sinuses and lobes) fully correspond to the specific diagnosis of *L. lituus*. However, the distinction between *L. lituus* de Montfort, 1808 and morphologically similar *L. perfectus* Wahlenberg, 1821 is barely possible in fragmentary material, especially when nothing of the coiled growth stage or the adult aperture is preserved (see, *e.g.* Noetling 1882 for discussion). However, recent observation (M. Aubrechtová) of coeval lituitids from Estonia indicates that *L. lituus* and *L. perfectus* are synonymous. Based on priority, the above described specimens are assigned to *L. lituus*.

Occurrence. – Middle Ordovician of Baltoscandia; Middle Ordovician (upper Darriwilian Stage) of Bohemia.

Genus *Trilacinoceras* Sweet, 1958

Type species. – *Lituites discors* Holm, 1891 (by original designation), from the Darriwilian (uppermost Red *Lituites* Limestone = *Platyurus* Limestone) age strata of Dalarna and the Island of Öland, Sweden.

Diagnosis. – Conch lituiticonic with two to three open or approximated (but not impressed), compressed, planispiral whorls adapically, and adorally an essentially straight, slightly compressed orthoceraconic segment, of which nearly half the length is body chamber. Conch expands rather gradually, hence appears to be essentially tubular adorally. Growth-lines and annulations prominent, forming conspicuously deep ventral sinus and five salients adapically, but only three salients (ventrolateral and dorsal) throughout most of uncoiled part. Peristome with incurving, tongue-shaped ventrolateral lappets, deep ventral sinus, and broad, low dorsal lappet. A secondary dorsolateral lappet pair may be formed in some species, but the development of these is not heralded in either the growth-lines or annulations at the extreme adoral end of the body chamber. Siphuncle dorsad of center throughout length of phragmocone (adapted after Sweet 1958).

Remarks. – Dzik (1984) regarded the genus *Trilacinoceras* Sweet, 1958 as a junior synonym to the genus *Lituites* Bertrand, 1763. *Trilacinoceras* and *Lituites* are closely related but according to Sweet (1958), they differ in overall shell proportions and complexity of aperture. *Trilacinoceras* is smaller in shell size and its aperture possesses three lappets, instead of five as in *Lituites* (see Sweet 1958 and Furnish & Glenister 1964, K367). We do not have at our disposal sufficient data to fully discuss or resolve this issue. However, the morphological differences as described by Sweet (1958) are in our opinion relevant and we thus regard *Trilacinoceras* and *Lituites* as separate genera.

Occurrence. – Middle Ordovician of Nevada; Middle to Upper Ordovician of Baltoscandia; Middle Ordovician of S. China and ?N. China; Upper Ordovician of S. China, Tarim and ?N. China; Middle Ordovician (upper Darriwilian Stage) of Bohemia and ?Iberian peninsula.

***Trilacinoceras* cf. *discors* (Holm, 1891)**
Figure 5A–D

Material. – Single specimen NM L 46557 from locality Praha-Šárka, field near Villa Hamerník, Prague Basin, central Bohemia; Dobrotivá Formation, upper Darriwilian Stage, Middle Ordovician.

Description. – Specimen NM L 46557 (Fig. 5A–D) is an internal mould of the adapertural part of the body chamber. The specimen is slightly secondarily compressed dorsoventrally. The dorsal side of the specimen is damaged (Fig. 5D). The total length of the fragment is 18 mm, maximum dorsoventral diameter is 21 mm and maximum lateral diameter is 23 mm. The reconstructed shell cross-section is circular. The shell ornamentation consists of undulated transverse annuli, seven of which correspond to ten mm of shell length. The annulation is more densely spaced adaperturally. The annulation forms a low saddle dorsally (Fig. 5D), a broad and shallow asymmetric lobe laterally (Fig. 5A) and a broad distinct lobe ventrally (Fig. 5B). Fine lirae run parallel to the annuli (4–5 per 1 mm). The course of ornamentation indicates that the specimen represents a subadult growth stage.

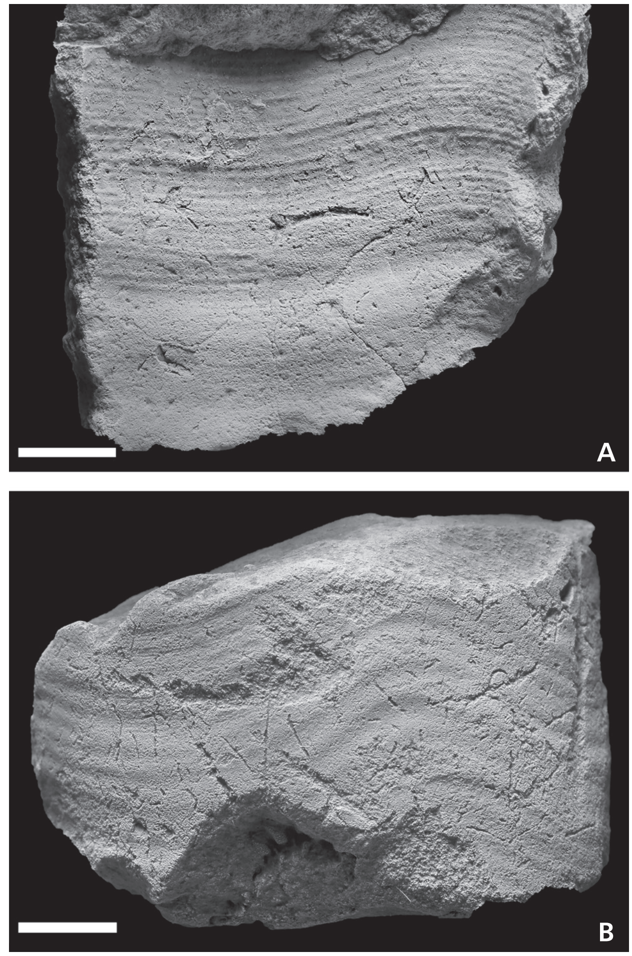

Figure 6. *Lituites lituus* de Montford, 1808 from the lower part of the Dobrotivá Formation (latest Darriwilian, Middle Ordovician) of the Prague Basin (Bohemia); A – lateral view, latex cast, NM L 46569; B – lateral view, NM L 46560. All specimens coated in ammonium chloride. Specimen NM L 46560 from Praha-Šárka (field near Villa Hamerník), specimen NM L 46569 from Praha-Vokovice. Both specimens oriented with apex down; coated in ammonium chloride. Scale bar 5 mm.

Remarks. – The straight shell of *Trilacinoceras discors* expands slowly (3–6°) and its maximum diameter upon maturity is about 23 mm. Maximum length of the whole individual is up to about 160 mm. The adult growth stage has a compressed cross-section. The fully developed aperture has only three lappets; two small and widely tongue-shaped and a wide and entire dorsal lappet, which in length does not exceed the ventro-lateral lappets. The lateral sinuses of aperture are very shallow and broad; the ventral sinus is short and wide. The surface is ornamented with annuli and lirae. The annuli are very fine adapically (less than 1 mm apart) and gradually become coarser with ontogeny (2.7 mm apart in adult stages). (For further description and discussion see Holm 1891 and Sweet 1958.)

The preserved part of the sub-adult individual from Bohemia corresponds to the diagnosis and published illustrations of *T. discors* (Sweet 1958). The specimen's ornamentation indicates, that the aperture was trilobate. However, the specimen studied is a rather short fragment with incomplete preservation of the aperture. For these reasons, we questionably assign the specimen to *T.* cf. *discors*.

Of the Baltic species of the genus, *T. norvegicum* Sweet, 1958, differs from *T. discors* in being markedly larger in general shell size (25 mm in maximum diameter in the latter *vs*. 44 mm in the former), in having a more compressed cross-section (0.88 in *T. norvegicum* vs. > 0.9 in *T. discors*) and in the possession of secondary dorso-lateral lappets at the aperture. *Lituites tornquisti* is similar in adult size and angle of expansion to *T. discors* but differs from it in having five lappets at the fully-grown aperture instead of three.

Family Sinoceratidae Shimizu & Obata, 1935

Genus *Rhynchorthoceras* Remelé, 1882

Type species. – *Lituites breynii* Boll, 1857, by original designation, from a Middle Ordovician *Orthoceras* Limestone collected in Pleistocene erratics, northern Germany.
Diagnosis. – "Lituitidans with orthoconic longicone conchs with slight curvature at apex. Siphuncle is tubular or slightly expanded within chambers, large (diameter one-sixth of conch diameter), subcentral and displaced toward convex side of shell. Septal necks are orthochoanitic, cameral deposits cover septal necks in some specimens. Cameral deposits with single vertical lamella on concave side of shell (after Kröger *et al.* 2007)."

Remarks. – Genus *Rhynchorthoceras* differs from all other lituitid genera in that its shell apex is not coiled but only curved and that its sculpture does not show prominent sinuses and lobes. The internal structures, however, fully correspond to those of all other lituitid genera. *Rhynchorthoceras* may be mistaken for *Ancistroceras* Boll, 1857 in specimens in which the apical portion is not preserved. For further discussion on the genus, see Kröger *et al.* (2007).

Occurrence. – Middle Ordovician of Baltoscandia; Middle Ordovician of Avalonia; Middle Ordovician of North China; Middle Ordovician (Dapingian Stage) of Argentine Precordillera and Perunica.

***Rhynchorthoceras* cf. *angelini* (Boll, 1857)**
Figure 7

Material. – Single specimen MBHR 66902 from locality Klabava, Prague Basin, central Bohemia; uppermost part of the Klabava Formation, uppermost Dapingian Stage, Middle Ordovician.

Description. – Specimen MBHR 66902 (Fig. 7) is a fragment of a phragmocone cut in a median plane, with remains of two septa and the outer shell. The total length of the fragment is 42 mm, adapical diameter is 23 mm and adoral diameter is 27 mm (angle of expansion is 9°). The shape of the cross section is circular. The shell is ornamented with straight, rather evenly spaced lirae (two per 1 mm adapically and three per 1 mm adorally). The lirae are slightly inclined adapically at the lateral side of the shell and indicate a very shallow and broad ventral lobe (hyponomic sinus). Traces of a septum and a suture of the preceding septum are preserved adorally (Fig. 7A, E). The preserved phragmocone chamber is 11.4 mm in length (corresponding diameter 29 mm; relative chamber height is 0.4). Septa were almost symmetric with straight, directly transverse sutures. Marked asymmetry of the adapical end of the phragmocone is due to a deep corrosion. The phragmocone is entirely filled with sparitic calcite, thus any internal structures, except fragments of the adoral septum (see above), are not preserved. However, sparitic calcite probably protruding from the phragmocone through the septal perforation of the adoralmost septum (Fig. 7E) suggests a subcentral, slightly ventrally shifted position of the siphuncle.

Remarks. – The internal structures of this specimen are entirely destroyed by recrystallization and it thus cannot be proven, whether the specimen possessed the type of siphuncle and cameral and endosiphuncular deposits typical for the lituitids. On the other hand, the sculpture, cross-section and angle of expansion correspond fully to those in the lituitids and in *Rhynchorthoceras*. The angle of expansion of 9° and the ornamentation of straight, obliquely oriented lirae, which do not form distinct lobes and saddles are within the range of variability of the species *R. angelini* (Boll, 1857). However, the poor and fragmentary preservation of the specimen from Bohemia does not allow its unequivocal assignment to that species.

Discussion

The stratigraphically earliest lituitids have been described from the Dapingian Stage strata of Sweden (Kröger 2013a), Laurentia (Flower 1975), the Argentine Precordillera (Kröger *et al.* 2007) and North China (Qi 1980). The group reached its peak diversity and abundance during the middle and upper Darriwilian Stage (see discussions in Kröger & Zhang 2009 and Kröger *et al.* 2009). The latest lituitids are reported from the Katian of Baltica (Strand 1934, Sweet 1958, Kröger 2013a, b) and China (South China, North China, Sibumasu, Tarim and Tibet; Lai 1981, 1986; Lai & Wang 1986; Kröger

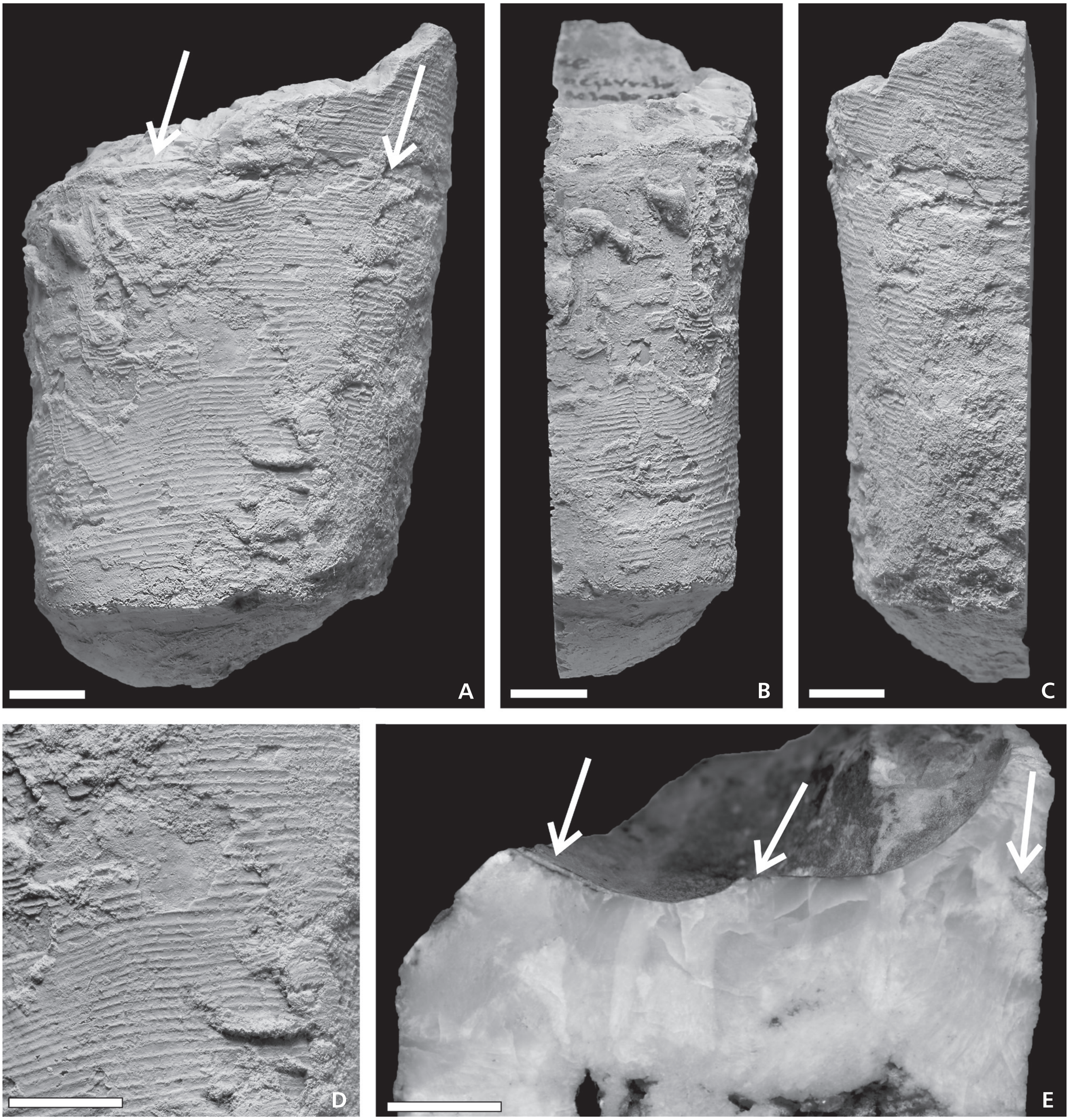

Figure 7. Lituitid cephalopod *Rhynchorthoceras* cf. *angelini* (Boll, 1857) from the upper part of the Klabava Formation (latest Dapingian, Middle Ordovician) of the Prague Basin (Bohemia); A–C – adapertural part of the phragmocone showing ornamentation of straight, nearly transverse lirae; A – lateral side, arrows indicate the suture (see in the text above); B – dorsal view; C – ventro-lateral view; D – detail of sculpture; E – median section, detail of adapertural part, arrows indicate remains of the most adoral septum, suture of the preceding septum and inferred position of the siphuncle (see in the text above). Specimen oriented with apex down; coated in ammonium chloride. Scale bar 5 mm.

2013a). An assignment of the peculiar Silurian genus *Sphooceras* Flower, 1962 and the early-mid Devonian lamellorthoceratid *Arthrophyllum* Beyrich, 1850 to the Lituitida (Dzik 1984, Kröger 2008) is not accepted here (see also Turek & Manda 2012).

The lituitids were relatively abundant especially in the low-latitude seas (Figs 3, 4) of Baltica (see Balashov 1953, Sweet 1958 and references therein) and China (North and South China, Tarim, Tibet; *e.g.* Lai 1986, 1989; Yun 1999, 2002, 2003; Xiao *et al.* 2006; Fang *et al.* 2017a). In these regions, the lituitids may even be used for biostratigraphic purposes (Evans *et al.* 2014). The group is known also from Laurentia (Flower 1975), Siberia (Kröger 2013), Avalonia (Evans 2005) and the Argentine Precordillera (Kröger *et al.* 2007). The paleogeographical position of the latter region during the Ordovician has been debated (see Keller *et al.* 1998, Keller 1999, Benedetto *et al.* 2009, Carrera *et al.* 2014) but mid-latitude position in the southern hemisphere is indicated, *e.g.* by the cephalopod fossil assemblages (Kröger *et al.* 2007).

The lituitids have previously been mentioned from high-latitudes only exceptionally (Figs 3, 4). Marek (1999) reported a single specimen of *Rhynchorthoceras* cf. *angelini* Boll, 1857 from the uppermost part of the Klabava Formation (uppermost Dapingian Stage, Fig. 1) of the Prague Basin. This is the stratigraphically earliest lituitid known to date from the high-latitude regions of European peri-Gondwana. Also, the species appeared in the Prague Basin during a period of an increased exchange of nektonic fauna between Baltica and Perunica (*e.g.* Dzik 1983, Manda 2008, Kröger 2013a, Aubrechtová 2015). Note, however, that the benthic fauna of that time is more similar to that of Avalonia and/or Armorica and Gondwana (see, *e.g.* Frýda 1988; Mergl 1991, 1992; Havlíček *et al.* 1994; Fatka & Mergl 2009).

From the upper Darriwilian Stage (Dobrotivian Regional Stage) of the Iberian Peninsula, Guttiérrez-Marco *et al.* (1984), Babin & Guttiérrez-Marco (1992) and Sá & Guttiérrez-Marco (2009) reported an occurrence of ?*Trilacinoceras* (Fig. 3). The two lituitids studied herein, *Lituites lituus* and *Trilacinoceras* cf. *discors* from the Dobrotivá Formation (upper Darriwilian Stage; Fig. 1) of the Prague Basin, are roughly coeval with the above occurrence from Iberia. Additionally, the three lituitid species occur in the high-latitudes of European peri-Gondwana approximately at the same time, when another typical low-latitude cephalopod *Trocholites* Conrad, 1838 (order Tarphycerida Flower, 1950) appears in the region, as well (Manda 2008). It is notable, that lituitids (and tarphycerids also) are absent in the Prague Basin in the preceding early–mid Darriwilian time interval (Šárka Formation), when the cephalopod fauna was comparatively richer and more diverse (Fig. 1) and contained several taxa of Baltic affinity (*Bathmoceras* Barrande, 1867, *Bactroceras* Holm, 1898, endocerids; see Manda 2008 and Aubrechtová 2015 for summary and references).

The occurrence of lituitids in high-latitudes supports previous presumptions of their high migratory potential in relation to the small size of the cup-shaped initial chamber (Kröger 2006, Fang *et al.* 2017b), which suggests a pelagic life-style of the larvae (*e.g.* Shimansky & Zhuravleva 1961, Mutvei 2002, Kröger & Zhang 2009, Kröger *et al.* 2009, Manda & Frýda 2010). Additionally, the mature lituitids are thought to have been slowly swimming, vertical migrants preferably inhibiting open water, pelagic environments (*e.g.* Mutvei 2002, Kröger & Zhang 2009, Kröger *et al.* 2009, Kröger 2013a).

Limited record on lituitids from high-latitudes (Figs 3, 4) shows that these cephalopods were relatively rare in European and African peri-Gondwanan basins. The marine environment conditions there were probably close to their ecological limits. It is hard to say, whether the lituitids formed stable populations there or represented stray immigrants. A relatively long period of their occurrence in peri-Gondwana may point to the former possibility. The Iberian and Perunican lituitids were members of nektonic marine faunas of Baltic affinity and their appearance coincides with a peak of lituitid and orthocerid diversity reported by Kröger *et al.* (2009). However, these faunal elements are currently unknown from other peri-Gondwanan basins.

Occurrence of *Rhynchorthoceras* in the Klabava Formation corresponds to a regressive time interval in the Prague Basin and is correlated with the Walhall regression event (Havlíček & Šnajdr 1957, Mergl 1984, Havlíček *et al.* 1994, Havlíček 1998, Mergl & Vohradský 2000). Likewise, the lower part of the Dobrotivá Formation originated during a regressive phase (Havlíček *et al.* 1994, Havlíček & Vaněk 1996, Fatka & Mergl 2009) and globally, it represents a time interval of a long-term sea level rise with pronounced short-term sea-level falls (Nielsen 2004, Haq & Schutter 2008).

Conclusions

Three lituitid species are described from the Middle Ordovician strata of the Prague Basin (central Bohemia). *Rhynchorthoceras* cf. *angelini* (family Sinoceratidae), previously reported from the uppermost part of the Klabava Formation (upper Dapingian Stage), is the earliest lituitid known from the high-latitude European and African peri-Gondwana. *Lituites lituus* and *Trilacinoceras* cf. *discors* (family Lituitidae) from the Dobrotivá Formation (uppermost Darriwilian Stage) are newly recorded. Cephalopod faunas of Dobrotivá Formation are much less abundant and less diverse than cephalopods from the underlying Šárka Formation (lower–upper Darriwilian Stage).

The lituitids of the Dobrotivá Formation are coeval with the first appearance of the tarphycerid *Trocholites* in high-latitudes. The lituitid occurrences in peri-Gondwana coincide with the peak of the global abundance and diversity of lituitids globally.

The lituitids described from the Prague Basin are conspecific with those known from Baltica. This supports the concept of faunal interchange between the two regions during the late Dapingian–Darriwilian time interval. This also justifies presumption of a high migratory potential of the lituitid early growth stages and tolerance of pelagic, deeper-water environments by adults. By contrast, the benthic assemblages studied by previous authors from the Prague Basin generally show a close similarity with those of Armorica, Avalonia and/or Gondwana.

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