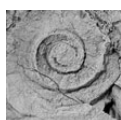


# *Trocholites* Conrad, 1838 (Nautiloidea, Tarphycerida) in the Middle Ordovician of the Prague Basin and its palaeobiogeographical significance

ŠTĚPÁN MANDA



Nautiloids of the order Tarphycerida are a characteristic component of warm-water Ordovician faunas of Baltica and Laurentia but are usually absent from the cooler high latitude marine environments. The presence of the tarphycerid *Trocholites*, reported from the Middle Ordovician, Dobrotivian (late Darriwilian) strata of the Iberian Chain and Armorican Massif (peri-Gondwanan Europe), provide an exception. *Lituities primulus* Barrande, 1865, represented by a single poorly-preserved individual was reported from coeval strata in the Prague Basin (Perunica) and doubtfully assigned to *Curtoceras* or *Trocholites*. New biostratigraphically well-constrained specimens of *Trocholites* described and discussed from the early Dobrotivian of the Prague Basin, are conspecific with *Trocholites fugax* previously described from the Iberian Chain and Armorican Massif. The contemporaneous presence of *Trocholites fugax* in Perunica and peri-Gondwanan terranes is additional evidence for faunal connections between these microcontinents during the Dobrotivian. By comparison with the preceding Llanvirnian (early Darriwilian) fauna, the low diversity Dobrotivian cephalopod fauna of the Prague Basin suggests an increasing faunal separation between Perunica and Baltica. The occurrence of *Trocholites* in early Dobrotivian strata of Perunica, the Iberian Chain and Armorican Massif reflects an unusual dispersion event of tarphycerids into lower latitude seas coinciding with a distinct climate perturbation during the Ordovician. • Key words: Middle Ordovician, Dobrotivian, Darriwilian, Cephalopoda, Tarphycerida, taxonomy, Prague Basin.

MANDA, Š. 2008. *Trocholites* Conrad, 1838 (Nautiloidea, Tarphycerida) in the Middle Ordovician of the Prague Basin and its palaeobiogeographical significance. *Bulletin of Geosciences* 83(3), 327–334 (4 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received August 11, 2008; accepted in revised form September 1, 2008, issued September 30, 2008.

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The Ordovician cephalopod fauna of the Prague Basin was described by J. Barrande in his classic “*Système silurien du Centre de la Bohême*” (1865–1877). Barrande erected 35 species of *Orthoceras* Bruguière, 1789, two species of *Bathmoceras* Barrande, 1867, three species of *Endoceras* Hall, 1847, and a single species each of *Tretoceras* Salter, 1858, *Bactrites* Sandberger, 1843, *Gomphoceras* Sowerby, 1839 (in Murchison 1939), and *Lituities* Bertrand, 1763. Despite continual and intensive research on the Ordovician strata of the Prague Basin since Barrande’s time, only a single new cephalopod species has been added (Marek 1999). This suggests that our knowledge of the Ordovician cephalopod fauna of the Prague Basin is relatively complete. Dzik (1981) synonymized *Tretoceras parvulum* Barrande, 1868 with *Bactroceras sandbergeri* (Barrande, 1868); see also Hewitt & Stait (1985) and Evans (2005). Marek (1999) suggested that *Bathmoceras complexum* (Barrande, 1856) is conspecific with *Bathmoceras praeposterum* Barrande, 1867. Many researches have provided information about the

stratigraphic ranges of Barrande’s species (for example Prantl 1952; Havlíček & Vaněk 1966; Mergl 1978; Kraft & Kraft 1990, 1993, 1994; Budil 1999), although the identity of certain taxa is in need of revision. The last short summary of cephalopod distribution in the Ordovician of the Prague Basin was published by Marek (1999).

As a rule, cephalopods are rather uncommon in the Ordovician of the Prague Basin. The fauna usually consists of one species or a few taxa of orthocone cephalopods belonging to the orders Orthocerida and Pseudorthocerida (and where unrevised, commonly referred to the genus *Orthoceras*). Ellesmerocerids are known from the Klabava Formation (Arenigian; Dapingian–earliest Darriwilian), the Šárka Formation (early Darriwilian; latest Arenigian–Llanvirnian) and the Králův Dvůr Formation (Kralodvorian; early Hirnantian). Endocerids and a single actinocerid are restricted to the Šárka Formation. A single oncocerid shell has been described from the Králův Dvůr Formation (see Marek 1999).

Tarphyceratids are known only from the Dobrotivá Formation (Dobrotivian, late Darriwilian). Barrande (1865) described a single poorly-preserved shell, assigning it to “*Lituites*” *primulus*. Klouček (1909), Vaněk (1999), and Marek (1999) all referred to the presence of “*Lituites*” *primulus* or *Curtoceras*, respectively, but without providing descriptions. This paper describes a suite of newly-collected specimens regarded as belonging to *Trocholites fugax* Babin & Gutiérrez-Marco, 1992. The occurrence of tarphycerids in the low diversity cephalopod fauna of the early Dobrotivian is of palaeobiogeographic significance because they are only known from Perunica and peri-Gondwanan Europe during Dobrotivian time (e.g., Babin *et al.* 1996, Bogolepova 1999).

The order Tarphycerida Flower, 1950 includes nautiloids with a bilaterally symmetrical, evolute or convolute shell and a relatively thick siphonal tube. Lithuitids originally grouped together with tarphyceratids (see Flower 1950, Furnish & Glenister 1964) in fact comprise an independent clade “*Lituitina*” Dzik, 1984 within the Orthoceratoidea Khun, 1940 (see Dzik 1981, 1984). In addition, some authors considered the order Barrandeocerida Flower, 1950 as a suborder within the Tarphycerida (see Turek 2008), but more data concerning early ontogeny and structure of the siphuncle are needed. Tarphyceratids appeared during the latest early Ordovician and their diversity rapidly reached its maximum just before the Middle Ordovician (Frey *et al.* 2004). During the Ordovician tarphycerids inhabited shallow and warm seas of carbonate platforms, e.g., Baltica, Laurentia, and Kazakhstania. The end-Ordovician extinction event reduced the diversity of the Tarphycerida, and the few surviving clades became extinct during the Silurian (for summary see Dzik 1984, Stridsberg & Turek 1997). The tightly-coiled nautiliconic shell of tarphyceratids suggests that they might have been active swimmers (see Westermann 1998).

## Cephalopod distribution in the Middle Ordovician of the Prague Basin

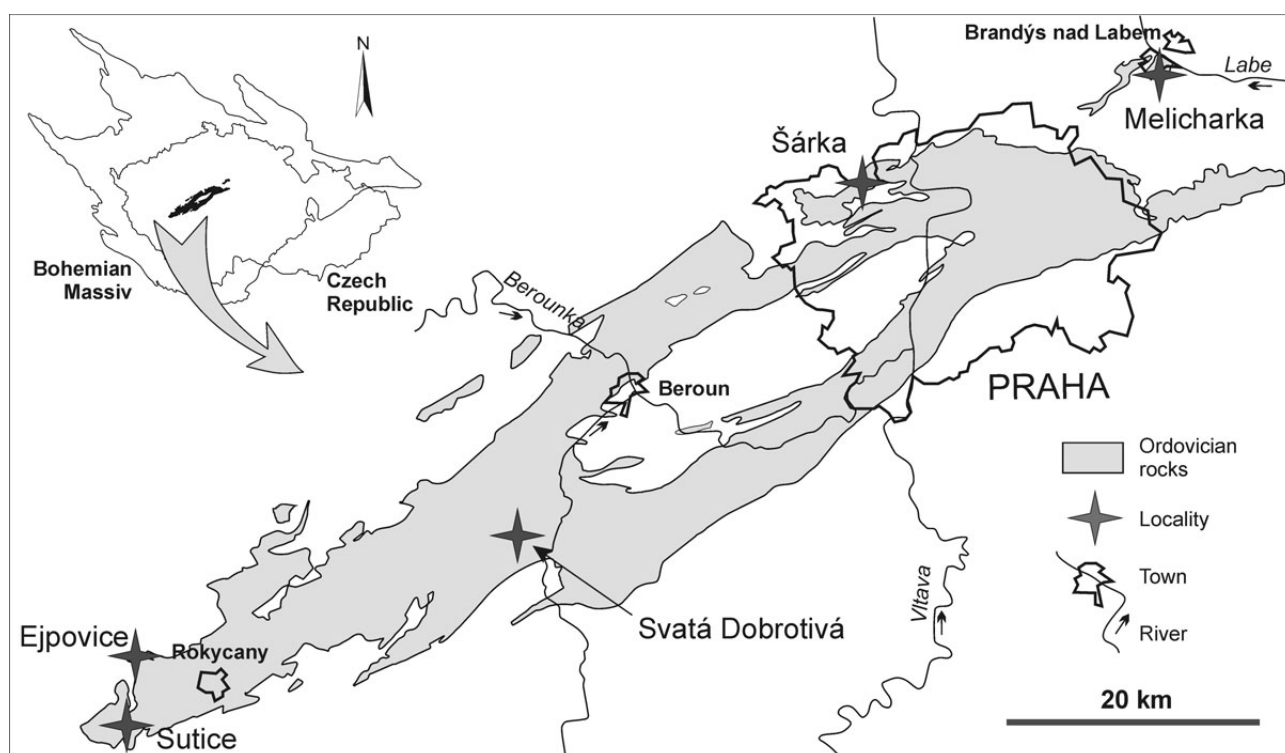
The Middle Ordovician sequence of the Prague Basin is divided into the Klabava, Šárka and Dobrotivá formations. In the classic concept (for summary see Havlíček 1998), the Klabava Formation corresponds with the Arenigian–earliest Llanvirnian, the Šárka Formation with the Llanvirnian and the Dobrotivá Formation with the Dobrotivian. The recent international division of the Middle Ordovician does not fit well with the British and Mediterranean stages and the correlation of Bohemian to international remains unclear. Following the concept of P. Kraft and O. Fatka and presented by various authors (see Kraft & Fatka 1999), the Middle Ordovician is here taken to have started within the Klabava Formation and ended close to the boundary between the Dobrotivá and Libeň formations.

## Klabava Formation: Arenigian-earliest Llanvirnian (Dapingian–earliest Darriwilian)

Cephalopods appear in the Prague Basin at the beginning of the Middle Ordovician in the upper part of the Klabava Formation, which consists mainly of yellow-grey and reddish shales. Two indeterminable species of orthocone cephalopods and the ellesmerocerid *Bathmoceras complexum* (Barrande, 1856) have been reported from the shales of the *Holograptus tardibrachiatus* Zone, Arenigian, Dapingian (Kraft & Kraft 1993, Marek 1999). The ellesmerocerid *Bactroceras* cf. *sandbergeri* (Barrande, 1867), and lituitid *Rhynchorthoceras* cf. *angelini* (Boll, 1857) occur rarely in the shales and tuffites of the succeeding *Azygograptus ellesi*–*Tetragraptus reclinatus abbreviatus* Zone (Kraft & Kraft 1994, Marek 1999). The appearance of ellesmerocerid and lituitid genera in the upper Klabava Formation is considered to be a reflection of the initiation of communication between Perunica and Baltica during the late Arenigian (Frýda 1988, Mergl 1991, Frýda & Rohr 1999). Dzik (1983) pointed out that the conodont fauna of the late Klabava Formation contains some Baltic taxa although diversity is low in comparison with Baltica probably due to cold water conditions (see also Zusková 1993). The same distribution pattern is exhibited amongst trilobite and gastropod faunas as well as cephalopod faunas.

## Šárka Formation: Llanvirnian (early Darriwilian)

The Šárka Formation (Llanvirnian; early Darriwilian) consists mainly of dark shales and contains the most diverse cephalopod fauna in the Ordovician of the Prague Basin. Cephalopods have been collected mainly from siliceous nodules in the Rokycany and Praha town areas. The most common material consists of orthoconic cephalopods belonging to the orders Orthocerida and Pseudorthocerida, which need to be revised. The ellesmerocerids *Bactroceras sandbergeri* (Barrande, 1867) (including *Tretoceras parvulum* Barrande, 1868, see Dzik 1984) and *Bathmoceras complexum* (Barrande, 1856) (including *Bathmoceras praeposterum* Barrande, 1867, see Marek 1999) are less common. Endocerids are represented by three rare species: *Vaginoceras novator* (Barrande, 1870), *Cameroceras peregrinum* (Barrande, 1870) and “*Endoceras*” *conquassatum* Barrande, 1870 (see Marek 1999). The single actinocerid species “*Orthoceras*” *bonum* is also rare (Marek 1999). The presence of ellesmerocerids, endocerids and actinocerids reflects a period of enhanced faunal exchange between Baltica and Perunica during the Llanvirnian (Marek 1999). The cephalopod fauna of the Šárka Formation exhibits the strongest affinity within the Ordovician sequence of the Prague Basin with Baltic cephalopod faunas (e.g., Holm 1899a, b; Balashov 1968). By contrast, the



**Figure 1.** Distribution of the Ordovician rocks in the Prague Basin, Czech Republic and the location of *Trocholites*-bearing localities.

benthic fauna that consists of trilobites and brachiopods shows only weak affinities with Baltic assemblages (Havlíček *et al.* 1994).

### Dobrotivá Formation: Dobrotivian (late Darriwilian)

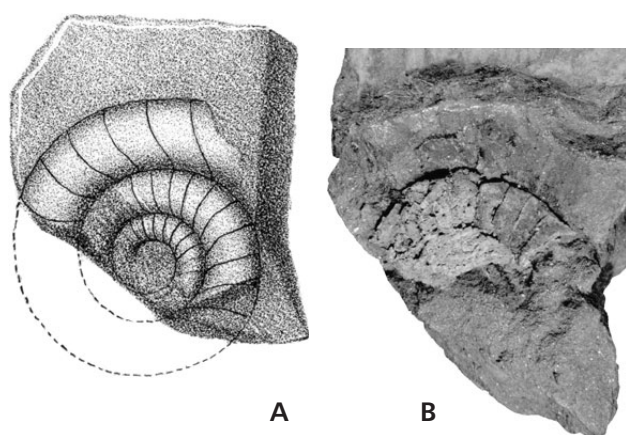
The Dobrotivá Formation is developed as black shales similar to those of the underlying Šárka Formation. The two formations differ in the nature of their faunal communities rather than facies. The cephalopod fauna of the Dobrotivá Formation is reduced in diversity by comparison with the Šárka Formation. The Baltic genera represented in the Šárka Formation are missing from the Dobrotivá Formation. Three rare species of longiconic orthocerids occur in siliceous nodules and more rarely in shale (Klouček 1909, Havlíček & Vaněk 1966). In addition, Barrande (1865) described a poorly-preserved portion of a coiled shell from the Svatá Dobrotivá (Sancta Benigna) locality as *Lituities primulus* Barrande, 1865 (see Fig. 2). Klouček (1909) also reported *Lituities primulus* from the Šárecké Valley at Praha and Vaněk (1999) listed “*Lituities*” *primulus* from siliceous nodules from the lower part of the Dobrotivá Formation at locality Melicharka in Brandýs nad Labem Town. An additional specimen was reported by Mergl (1996) from a shale of the *Hustedograptus teretiusculus* Zone at Ejpovice Village (Fig. 1).

### Palaeobiogeographical significance of *Trocholites*

Tarphycerid nautiloids originated in the late Early Ordovician and form a characteristic component of Middle to Upper Ordovician cephalopod faunas, inhabiting warm-water carbonate platforms (for summary see Furnish & Glenister 1964, Dzik 1984). Thus tarphycerids may be considered as an indicator of warm-water masses or might suggest connections with such water bodies. *Trocholites* Conrad, 1838 including 42 species is widely distributed in Middle and Upper Ordovician strata of Baltica, South and North China, Tibet, Laurentia, and Australia (for summary see Schröder 1891, Whiteaves 1904, Chen & Liu 1976, Dzik 1984, Stait *et al.* 1985, Babin & Gutiérrez-Marco 1992 and Guo 1998).

Havlíček *et al.* (1994, p. 37) emphasized the “absolute difference in benthic and necto-benthic association” between Baltica and Perunica during the Dobrotivian. According to Havlíček *et al.* (1994), Tornquist’s Ocean “functioned as an effective barrier” during Dobrotivian times. Kraft & Kraft (1990) and Fatka *et al.* (1998) described a single specimen of the Baltic graptolite *Gymnograptus linnarsoni* (Moberg, 1896) from the *Hustedograptus teretiusculus* Zone of the Prague Basin. The presence of *Trocholites* in the Prague Basin further suggests a degree of connection with Baltica during the *Hustedograptus teretiusculus* Zone. The presence of *Trocholites* in early Dobrotivian contrasts with the absence of any other





**Figure 2.** “*Lituites primulus*” Barrande, 1865; holotype by monotypy. Svatá Dobrotivá (Sancta Benigna) d1 locality. Most probably Middle Ordovician, lower Dobrotivian, Dobrotivá Formation. • A – reproduction of a specimen illustrated by Barrande (1865) on pl. 99 as fig. 12,  $\times 1.2$ . • B – the same specimen, lateral view,  $\times 1.2$ . National Museum, L 40460.

cephalopod genus shared with Baltica during this time as well as the absence of tarphycerids in the underlying Llanvirnian where five Baltic genera are present.

*Trocholites fugax* was described by Babin & Gutiérrez-Marco (1992) from the early Dobrotivian of Spain. Babin *et al.* (1996) described the same species from the Dobrotivian of the Armorican Massif. Thus the presence of *Trocholites fugax* in the Prague Basin, Iberian Chain and Armorican Massif are coeval, suggesting that faunal exchange took place between these areas during the early Dobrotivian, which is in agreement with the conclusions of Havlíček *et al.* (1994). More recently Ausich *et al.* (2002) described a Dobrotivian echinoderm fauna from the Iberian Chain and suggested that there was faunal isolation between peri-Gondwana and Perunica. In addition, Evans (2000) noted the presence of *Trocholites* even in the Middle Ordovician of Bolivia, Northwestern Gondwana, but this material has not yet been described nor figured.

## Conclusions

The appearance of the coiled tarphycerid *Trocholites fugax* in the early Dobrotivian of Perunica and peri-Gondwana seem to reflect an unusual dispersion event of tarphycerids to higher latitudes (Fig. 4). It suggests that isolation between Baltica and Perunica was not absolute, as was previously stated. Havlíček *et al.* (1994) explained the isolation between the Prague Basin and Baltica through enhanced surface currents of Tornquist’s Sea. However, there is no reason why such currents should have confined faunal exchange. Contrarily, faunal isolation would be more likely where surface current activity is low, leading to prolonged transport of invertebrate larvae and the higher pro-

bability of their mortality. With more occasional instability common in weak currents, this would cause mass mortality of the larvae. Babin & Gutiérrez-Marco (1992) proposed that the presence of *Trocholites* in Spain during the early Dobrotivian might be explained by a prolonged period of climatic disturbance in which storm systems that developed in temperate palaeolatitudes in the vicinity of Baltica, transferred bodies of water carrying planktic and nektonic animals southward onto peri-Gondwana.

The nektonic habit of *Trocholites* is clearly suggested by its small nautiloid shell (see Westerman 1998). In addition, the very small size of the embryonic shell of *Trocholites* might indicate the planktotrophy of the early post-hatching stage. Evans (2000) studied an Ordovician cephalopod fauna from Saudi Arabia that included warm-water elements, *i.e.* northern shelf of Gondwana, using the hypothesis of Babin & Gutiérrez-Marco (1992) to explain their presence there. The occurrence of *Trocholites fugax* in the Prague Basin also appears to support this hypothesis.

## Systematic palaeontology

Subclass Nautiloidea Agassiz, 1847

Order Tarphycerida Flower, 1950 (*in* Flower & Kummel 1950)

Family Trocholitidae Chapman, 1857

### Genus *Trocholites* Conrad, 1838

*Type species.* – *Trocholites ammonius* Conrad, 1838.

### *Trocholites fugax* Babin & Gutiérrez-Marco, 1992

Figure 3A–E

?1865 *Lituites primulus* Barr.; Barrande, pl. 99, fig. 12.

1992 *Trocholites fugax* n. sp.; Babin & Gutiérrez-Marco, pp. 530–534, figs 3a–h, 4a–f. See for further synonymy of Spanish material.

?1992 *Lituites primulus*. – Babin & Gutiérrez-Marco, p. 534.

1996 *Trocholites fugax*. – Babin *et al.*, p. 107, pl. 1, figs 1–3.

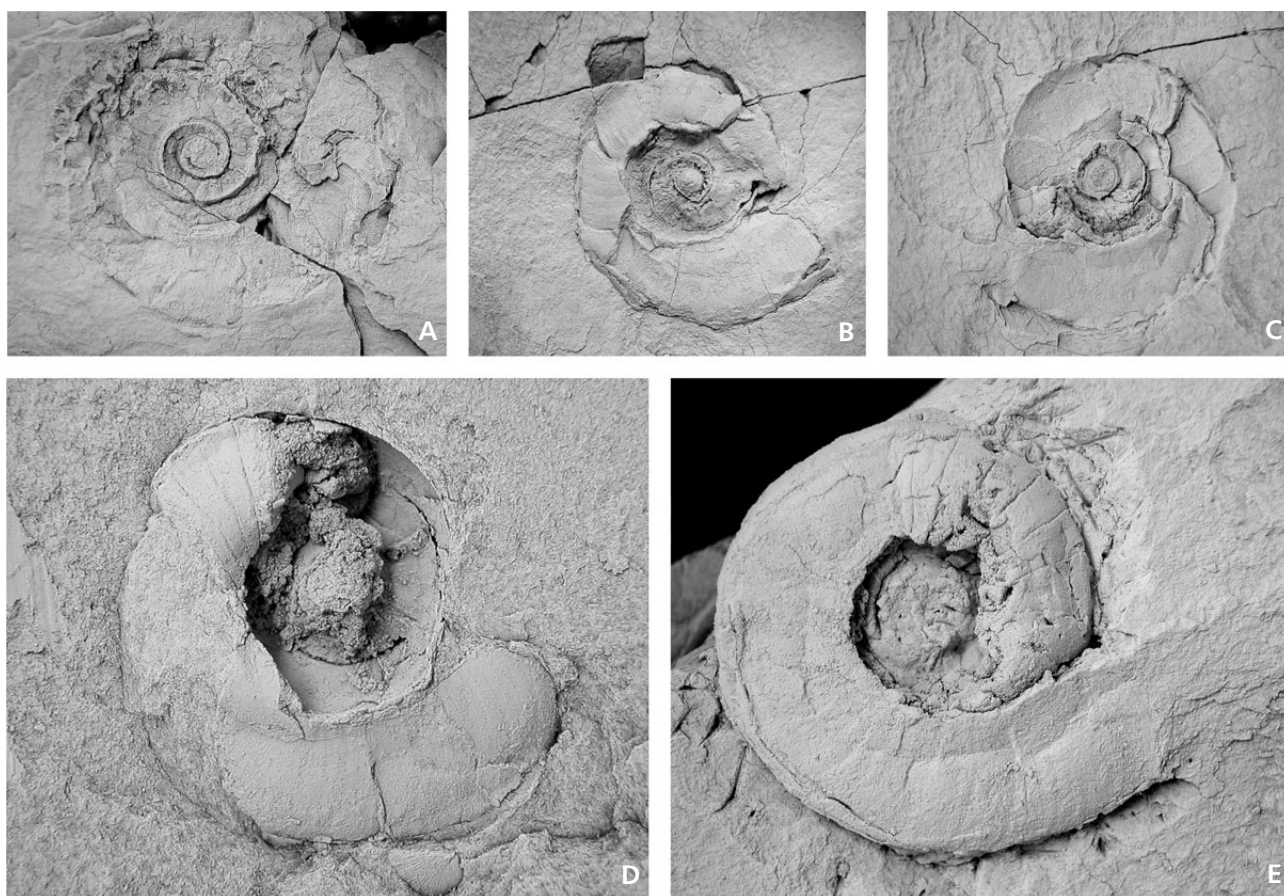
1996 “cyrtokonní nautiloid”. – Mergl, p. 32.

1999 “*Lituites*” *primulus* Barrande. – Vaněk, p. 8.

?1999 *Curtoceras primulus*. – Marek, pp. 415, 416.

*Holotype.* – Specimen No. NE VII 2639 (Museo GeoMinero, Madrid) designated by Babin & Gutiérrez-Marco (1992) and figured by them as fig. 3D. Middle Ordovician, early Dobrotivian. Navas de Estena, Massif Hesperian, Spain.

*Material.* – Seven more or less flattened shells preserved in shale: specimens No. 11484, 11518, 11521, 11560, 11664,



**Figure 3.** *Trocholites fugax* Babin & Gutiérrez-Marco, 1992. Prague Basin, Ordovician, Middle Ordovician, lower Dobrotivian. Dobrotivá Formation.  
 • A – Týmákov, Sutice 1, western slope, lateral view,  $\times 1.4$ , specimen No. 11675, collection of M. Mergl, Museum of Doctor Bohuslav Horák, Rokycany.  
 • B – Týmákov, Sutice 1, western slope, lateral view,  $\times 1.3$ , specimen No. 11518, collection of M. Mergl, Museum of Doctor Bohuslav Horák, Rokycany.  
 • C – Týmákov, Sutice 1, western slope, lateral view,  $\times 1.2$ , specimen No. 11484, collection of M. Mergl, Museum of Doctor Bohuslav Horák, Rokycany.  
 • D – Ejpovice, Ejpovice, northern slope of Čilina Hill, lateral view,  $\times 1.8$ , CGS MM 517a. • E – Týmákov, Sutice 1, western slope, lateral view,  $\times 2.3$ , specimen No. 11521, collection of M. Mergl, Museum of Doctor Bohuslav Horák, Rokycany. All specimens are coated with ammonium chloride.

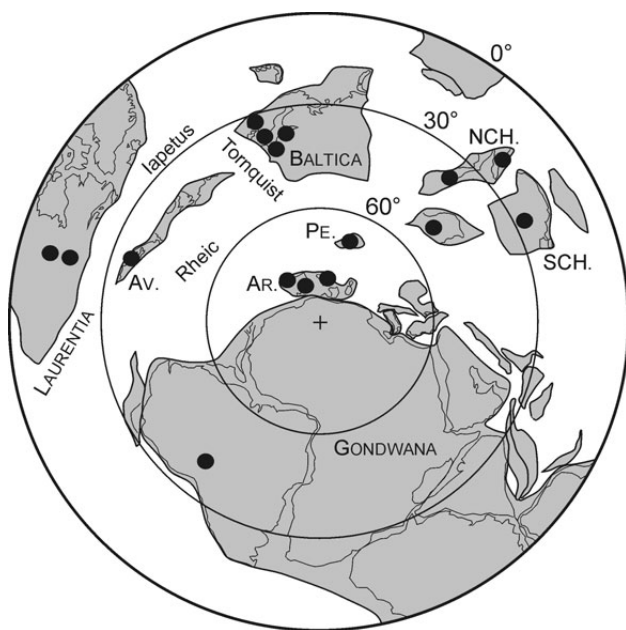
11675 are housed in the Museum of Doctor Bohuslav Horák in Town of Rokycan, West Bohemia; specimen MM 517a, b is deposited in the Czech Geological Survey, Praha, Collection of M. Mergl. Two additional unnumbered specimens are housed in the private collection of O. Karoušek.

**Description of the Bohemian material.** – Gradually expanding exogastric convolutedly coiled shells. Whorl cross section depressed and rounded across the venter and flanks. Siphuncle dorsal and submarginal, its diameter is about 0.5 mm where the lateral diameter of the shell is about 6 mm. Body chamber long, about two-thirds of a volution. Cameral depth is about  $1/3$ – $1/4$  of the dorsoventral diameter of the whorl. Sutures are poorly preserved, probably almost straight with weak dorsal lobe. First three whorls exhibit almost straight, densely-packed growth lines that later become irregular and more distant. Hyponomic sinus is shallow and broad. Approximately five whorls

are developed. Embryonic shell is not visible, but must be very small with a diameter less than 0.5 mm. Dimensions are giving in Table 1.

**Discussion.** – Barrande (1865, pl. 99 as fig. 12) first illustrated *Lituities primulus* as a new species (holotype by monotypy, see Fig. 2). This type specimen is a small part of a convolute phragmocone with three whorls preserved in a slightly flattened state in dark shale. As noted by Babin & Gutiérrez-Marco (1992), the preservation of the specimen figured by Barrande as *Lituities primulus* excludes a precise comparison with better-preserved specimens showing more diagnostic features. The mode of coiling and the depth of the camerae are similar to that of *Trocholites fugax*. The holotype of *Lituities primulus* came from the Svatá Dobrotivá – Sancta Benigna d1 locality, the exact site of which is unknown. However, the brachiopods and trilobites described by Barrande from this locality clearly suggest a Dobrotivian age, and the lithology of the matrix is similar





**Figure 4.** Distribution of *Trocholites* in the Middle Ordovician. Palaeogeographic reconstruction adopted from Cocks & Torsvik (2002). For data see Schröder (1891), Chen & Liu (1976), Dzik (1984), Babin & Gutiérrez-Marco (1992), Babin *et al.* (1996), and Frey (1995). Abbreviations: Ar. – Armorica, Av. – Avalonia, NCH. – North China, SCH. – South China, Pe. – Perunica.

**Table 1.** Dimensions of *Trocholites fugax*. Abbreviations: dv – diameter of shell (ventral), dd – diameter of shell (dorsal), wh – whorl height, uw – umbilical width (diameter of whorl), n – number of visible whorls. All measurements are in mm.

Specimen	dv	dd	wh	uw	n
MM 517	24	21	8	11.5	5
11484	30	25.5	10	12	5
11518	29	24	11	14	5
11521	27	21	8	10.5	4
11560	19	16	5	9	4
11664	13	12	4	8	4
11675	30.5	26.5	12	14	5

to that of the Dobrotivá Formation. This suggests that *Trocholites fugax* and *Lituities primulus* are coeval and probably conspecific, but the poor preservation of the holotype of the latter leaves some uncertainty as to this and therefore the type species is not proposed as a senior synonym of *Trocholites fugax*.

**Occurrence.** – Dobrotivian of Spain and the Armorican Massif, France (Babin & Gutiérrez-Marco 1992; Babin *et al.* 1996).

Prague Basin (Bohemia): Middle Ordovician, early Dobrotivian (early Llandeillan, late Darriwilian), *Hustedograptus teretiusculus* Zone. Lower Dobrotivá Formation.

1. Ejpvovice, northern slope of Čilina Hill, W of Rokycany Town, West Bohemia; black shale with brachiopods, conularids, graptolites, bivalves, hyolithids, orthocone cephalopods, trilobites, machaerids, ostracods and echinoderms (for detail of fossil contents see Mergl 1996); single specimen was collected by M. Mergl.

2. Tymákov, Sutice 1, western slope, West Bohemia, dark grey shale with numerous trilobites and brachiopods (see Mergl 1978); all available specimens were collected by M. Mergl.

3. Melicharka, field at Melicharka factory, Brandýs nad Labem, Central Bohemia; shale with small siliceous nodules rich in trilobites, brachiopods, graptolites, orthocone cephalopods, conularids, bivalves and echinoderms (for detailed descriptions see Vaněk 1999); two specimens of *Trocholites* are present in private collection of O. Karoušek from Brandýs nad Labem.

## Acknowledgments

Special thanks are given to Michal Mergl from the University of West Bohemia, Plzeň who kindly lend me specimens from his collection. Many thanks to David H. Evans (Natural England, Peterborough), Vojtěch Turek (National Museum, Prague) and Susan Turner (Queensland Museum, Brisbane) for the help with the critical reading of the manuscript and for language corrections. Vojtěch Turek also kindly gave access to Barrande's collection. This paper is contribution to the UNESCO-IUGS IGCP Project 503 "Ordovician Palaeogeography and Palaeoclimate". The work was supported by the project VaV DE08P04OMG002 (Czech Republic Ministry of Culture).

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