**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. *Lituites primulus* Barrande, 1865, represented by a single poorly-preserved individual was reported from coeval strata in the Prague Basin (Perunica) and doubtfully assigned to *Cartoceras 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 dispersal 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.


Štěpán Manda, Czech Geological Survey, Klárov 3, P.O.B. 85, 118 21 Praha 011, Czech Republic; manda@cgu.cz

The Ordovician cephalopod fauna of the Prague Basin was described by J. Barrande in his classic “Système silurien du Centre de la Bohème” (1865–1877). Barrande erected 35 species of Orthocerida Bruguëire, 1789, two species of Bathmoceras Barrande, 1867, three species of Endoceras Hall, 1847, and a single species each of Tretoceras Saller, 1858, Bactrites Sandberger, 1843, Gomphoceras Sowerby, 1839 (in Murchison 1839), and Lituites 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 (Dobrotovian, 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 tarphycerids (see Flower 1950, Furnish & Glenister 1964) in fact comprise the order Lithuitidae (see also Zusková 1993). The same distribution pattern is exhibited amongst trilobite and gastropod faunas as well as cephalopod faunas. The common material consists of orthoconic cephalopods being collected mainly from siliceous nodules in the Rokycany and Praha town areas. The most diverse cephalopod fauna in the Ordovician of the Prague Basin consists mainly of yellow-grey and redish 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, Dapinigan (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 elles–Tetragraptus reclinatus 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 Batica 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 Batica 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.

Klabava Formation: Arenigian-earliest Llanvirnian (Dapinigan–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 redish 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, Dapinigan (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 elles–Tetragraptus reclinatus 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 Batica 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 Batica 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 Pseudorthoerida, 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” conquisatum 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 Batica 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...
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 *Lituites primulus* Barrande, 1865 (see Fig. 2). Klouček (1909) also reported *Lituites primulus* from the Šárecké Valley at Praha and Vaněk (1999) listed “*Lituites* 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 linnarsonii* (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
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 reflects 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 probability 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 nautiliconic 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 ammoinius_ 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.
1996 _Trocholites fugax._ – Babin et al., p. 107, pl. 1, figs 1–3.

_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,
11675 are housed in the Museum of Doctor Bohuslav Horák in Town of Rokycany, 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 Lituites 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 Lituites 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 Lituites 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.
to that of the Dobrotivá Formation. This suggests that Trocholites fugax and Lituites 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.

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.

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Figure 4. Distribution of Trocholites in the Middle Ordovician. Palaeogeographic reconstruction adopted from Cocks & Torsvik (2002).


1. Ejpovice, northern slope of Čilina Hill, W of Rokycany Town, West Bohemia; black shale with brachiopods, conularids, graptolites, bivalves, hyoliths, 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.

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