

Two new orthothecids from the Cambrian of the Barrandian area (Hyolitha, Skryje-Týřovice Basin, Czech Republic)

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Two orthothecid hyoliths *Probactrotheca briketa* new genus and new species and *Circotheca smetanai* new species are described from the Middle Cambrian Buchava Formation of the Skryje-Týřovice Basin in the Czech Republic. The new forms are based on about twenty well-preserved external and internal moulds of opercula and conchs. The stratigraphic range and geographic distributions for both taxa are well known. • Key words: hyoliths, orthothecids, *Circotheca*, *Probactrotheca*, Cambrian Series 3, Skryje-Týřovice Basin, Teplá-Barrandian region, Czech Republic.

VALENT, M., FATKA, O., SZABAD, M., MICKA, V. & MAREK, L. 2012. Two new orthothecids from the Cambrian of the Barrandian area (Hyolitha, Skryje-Týřovice Basin, Czech Republic). *Bulletin of Geosciences* 87(2), 241–248 (5 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received August 31, 2011; accepted in revised form November 11, 2011; published online December 14, 2011; issued March 30, 2012.

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Cambrian sediments of the Teplá-Barrandian region contain a common and well diversified invertebrate fauna, including several types of tubular and conical fossils. Microscopic to submicroscopic nonbiomineralized tubes were described as *Rhabdotubus robustus* Maletz *et al.*, 2005. The rare occurrence of *Vermes* indet. and *Selkirkia* Walcott, 1911 was reported by Fatka *et al.* (2004, p. 379) and Mergl & Kordule (2008), respectively; Fatka *et al.* (in press) described two species of the genus *Sphenothallus* Hall, 1847.

Sixteen usually gregarious and locally very common hyolith species have been collected from different stratigraphical levels of the Jince Formation in the Příbram-Jince Basin (Fatka *et al.* 2004; Valent 2004, 2006; Valent *et al.* 2009) and the Skryje Member of the Buchava Formation in the Skryje-Týřovice Basin (Marek 1983a, Fatka 1990, Valent 2006, Valent *et al.* 2011a, b).

The first Cambrian hyolithids from the Teplá-Barrandian region were established by Barrande (1867) and Novák (1891). New taxa, as well as revisions of selected earlier forms, were published in a series of short papers by Marek (1972, 1975, 1980, 1981) and Valent *et al.* (2009, 2011a, b). Recently, Martí Mus & Bergström (2005) revised the morphology of the genus *Maxilites* Marek, 1972. All so far described taxa are classified within the Order

Hyolithida Sysoev, 1957. However, knowledge concerning forms of the Order Orthothecida Marek, 1966 is much more restricted, being briefly mentioned in three papers only: Marek (1975) cited the presence of an orthothecid in the Skryje-Týřovice Basin; Marek (1976, fig. 5B) published a reconstruction of an undescribed species of *Circotheca*, this species is described herein as *Circotheca smetanai* sp. nov.; Fatka *et al.* (2004) reported the stratigraphic distribution of *Orthotheca* sp. and *O.* sp. B within the Jince Formation of the Příbram-Jince Basin. Valent *et al.* (in press) formally described five new species known already to Marek as the orthothecids *Gracilitheca mirabilis* Valent *et al.*, *G. triangularis* Valent *et al.*, *Gracilitheca* sp., *Nephrotheca betula* Valent *et al.* and *Nephrotheca* sp.

This contribution describes two additional forms of orthothecids based on material from several classical localities in the Skryje Member of the Buchava Formation in the Skryje-Týřovice Basin. Both new taxa, together with eight other hyolith species, were previously distinguished, but invalidly described, by Marek (1983a) in an unpublished report prepared for the Academy of Science of the Czech Republic. In his manuscript, Marek described both taxa in detail but he did not unambiguously designate or illustrate any type specimens and left no photographs. This paper is dedicated to the fond memory of Dr. Ladislav Marek.

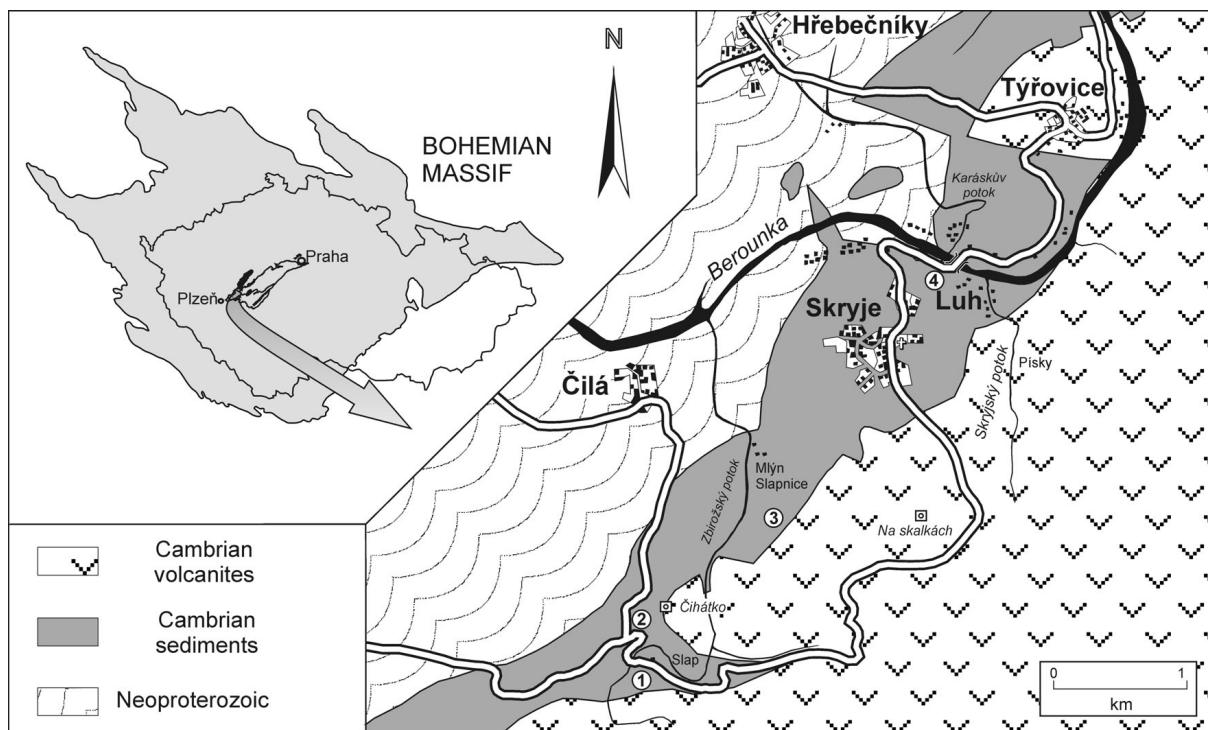


Figure 1. Simplified sketch map showing the location of fossil sites in the Middle Cambrian Buchava Formation within the Skryje-Týřovice Basin, Central Bohemia. (Geology modified from Mašek *et al.* 1997.) 1 – Buchava locality, 2 – rocks near Zbíroh stream opposite the Buchava quarry, 3 – Dlouhá hora Hill and 4 – Skryje-Luh locality (southern slope above the Skryje stream).

Systematic palaeontology

Class Hyolitha Marek, 1963
Order Orthothecida Marek, 1966
Family Circothecidae Missarzhevskij, 1969

Genus *Circotheca* Sysoev, 1958 emend. Berg-Madsen & Malinky, 1999

Type species. – *Hyolithus (Orthotheca) stylus* Holm, 1893;
Cambrian Series 3, Sweden, *Paradoxides forchhammeri* Regional Stage, *Solenopleura brachymetopa* and *Lejopyge laevigata* zones.

Discussion. – Berg-Madsen & Malinky (1999, pp. 873 to 875) selected a lectotype for the type species and figured the internal and external surfaces of both opercula and conchs; they also provided a new description of the type species, including detailed information on its stratigraphic range. Using the internal morphology of the operculum as the most important diagnostic feature, the concept of *Circotheca* was restricted by Berg-Madsen & Malinky (1999). On account of the presence of bent growth lines, corroborating the non planar aperture, they did not accept the emendation proposed by Missarzhevskiy (1969).

Occurrence. – Middle Cambrian to Ordovician. Specimens assigned to this genus are reported from Baltica (Sweden), Laurentia (U.S.A., Mexico), Siberia, and different European and Asian peri-Gondwanan regions (Bohemia, France, England, India and China), respectively.

Species. – At least 38 species have been included in this genus (see Berg-Madsen & Malinky 1999), but the true number of species recognized in the literature is impossible to enumerate.

Circotheca smetanai sp. nov.

Figures 2A–D, G, K, 3

- 1975 *Circothecid.* – Marek, p. 66.
- 1976 *Circotheca* sp. nov. – Marek, fig. 5B.
- 1983a *Circotheca smetanai* sp. n. – Marek, pp. 10–12 (MS).

Holotype. – Outer surface of operculum; L40465 (Fig. 2C, D), Buchava locality. Deposited in the collection of the National Museum, Prague, Czech Republic.

Paratypes. – Inner surface of operculum; L40469 (Fig. 2A), Biskoupky locality. External mould of conch; L40467 (Fig. 2K), Buchava locality. All specimens are deposited in

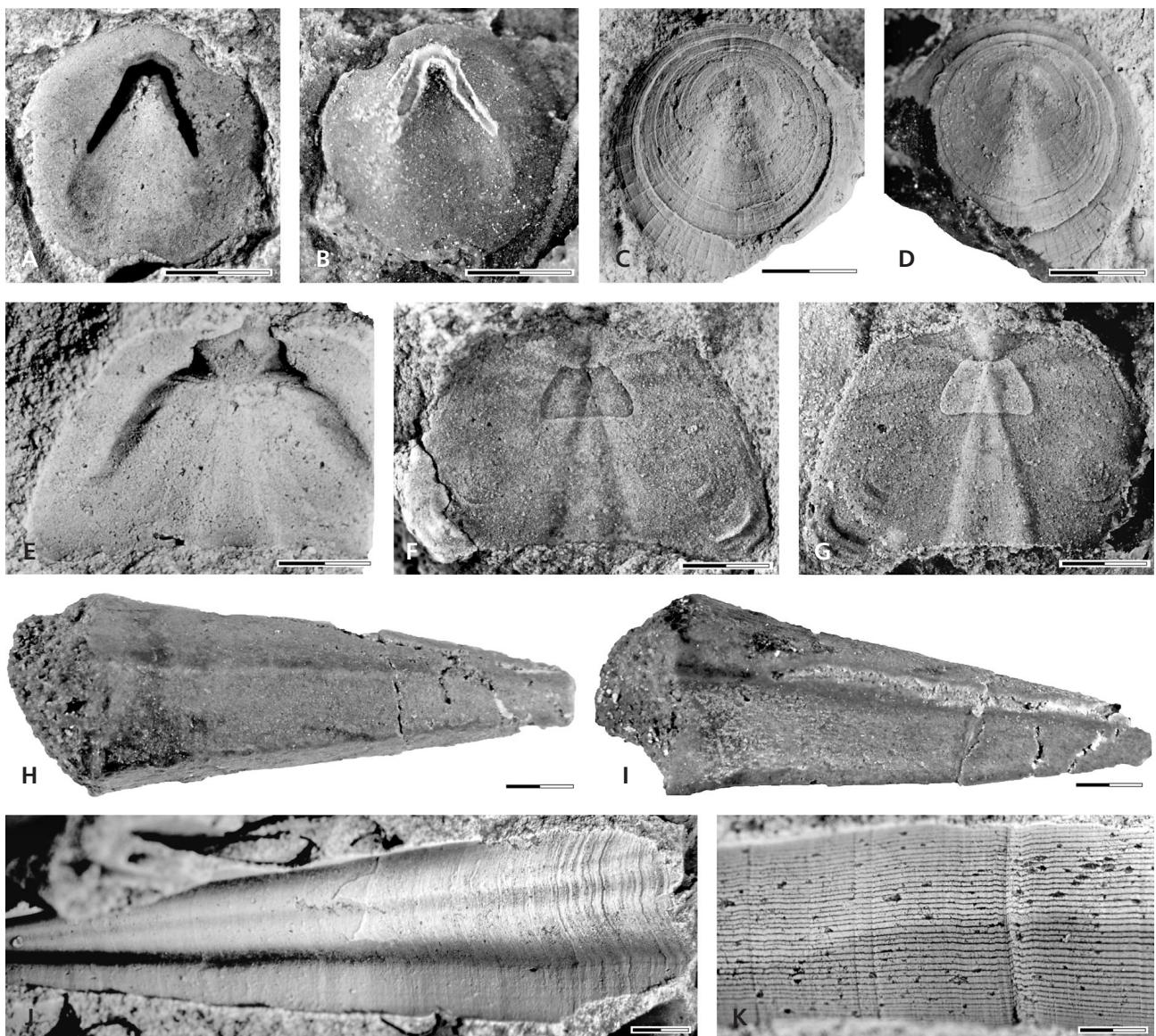


Figure 2. *Circotheca smetanai* sp. nov. (A–D, K) and *Probactrotheca briketa* gen. et sp. nov. (E–K); Middle Cambrian, Buchava Formation, Skryje Member, *Paradoxides (Eccaparadoxides) pusillus* Zone. Scale bar = 1 mm. All specimens are deposited at the Palaeontological Department of the National Museum, Prague. *Circotheca smetanai* sp. nov. • A – inner surface of operculum, Biskoupy locality. L40469 (paratype). • B – inner surface of operculum. Latex cast of L40469 (paratype). • C – outer surface of operculum, Buchava locality. L40465 (holotype). • D – outer surface of operculum. Latex cast of L40465 (holotype). • K – external mould of conch, Buchava locality. L40467 (paratype). *Probactrotheca briketa* gen. et sp. nov. • E – inner surface of operculum, Biskoupy locality. L40472 (paratype). • F – outer surface of operculum, Buchava locality. L40473 (holotype). • G – outer surface of operculum. Latex cast of L40473 (holotype). • H – dorsal view of isolated conch, Biskoupy locality. L40470 (paratype). • I – ventro-lateral view of isolated conch, Biskoupy locality. L40470 (paratype). • J – dorsal outer surface of conch, Biskoupy locality. L40572 (paratype).

the collection of the National Museum, Prague, Czech Republic.

Type horizon and locality. – Cambrian Series 3, Buchava Formation, Skryje Member, *Paradoxides (Eccaparadoxides) pusillus* Biozone; Skryje-Plazy locality, Skryje-Týřovice Basin, Teplá-Barrandian region, Czech Republic.

Derivation of name. – After Vojtěch Smetana, for his contribution to the understanding of the Bohemian Cambrian.

Material. – Twelve conchs and six opercula.

Diagnosis. – *Circotheca* with sub-circular operculum, summit of operculum displaced slightly dorsally. External surface of operculum with well developed concentric

irregularly disposed growth-lines. Outer surface of conch bears very narrow, corrugate ribs which are T-shaped in cross-section.

Description. – Narrow orthocone conch (Fig. 3C) of sub-circular cross-section; slightly dorso-laterally curved (V+, D–). The angle of divergence reaches about 8 degrees. The aperture is slightly bowed from the dorsal to the ventral margin. A distinct wall surrounding the aperture is developed on internal moulds, representing a sudden tapering of the wall. Muscle scars were not ascertained. The preservation state of the internal moulds excludes any detection of apical septa.

The sculpture of the conch surface consists of very narrow and corrugating ribs (Fig. 2K). The distal ends of ribs form a T-like shape in the cross-section.

The operculum is sub-circular in outline, slightly concave in cross-section (Fig. 2A–D). The apex of the operculum situated excentrically, being slightly displaced dorsally. A narrow, flat and poorly developed depression runs ventrally from the opercular summit (Fig. 2D). The external surface sculpture consists of infrequent, irregularly disposed but clearly visible concentric growth-lines (Fig. 2C, D); regularly spaced radial ribs are well developed.

The internal surface of the operculum bears a pair of large bilobate cardinal processes (Fig. 2A, B). The prominent lobes are broadly rounded frontally and laterally; distal parts are postero-laterally elongated. The cardinal processes attain two thirds of the opercular length; their bases diverge at the angle of about 80 degrees.

Dimensions. – The maximum length of the conch reaches at least 40 mm; width of the aperture ranges around 5 mm.

Discussion. – *Circotheca smetanai* sp. nov. is the third species of the genus *Circotheca* in which both the conch as well as the operculum are known [the others are *C. stylata* (Holm, 1893), Cambrian of Sweden and *C. caperai* Marek, 1983b, Ordovician of Morocco]. A restudy of Holm's (1893) material showed that the original specimen is preserved in limestone and the surface sculpture of the conch is eroded; only a small part of the conch shows bases of the wavy warped longitudinal ribs (see Berg-Madsen & Malinky 1999, pp. 874, 875, text-fig. 9). Only the bases of the cardinal processes, diverging at the angle of about 60 degrees, are developed on the inner surface of the operculum which Holm (1893) assigned to this species. However, the angle of divergence is markedly smaller than in *C. smetanai*.

Circotheca caperai Marek, 1983b ("Arenigian" of Montagne Noire, France) differs from the mentioned species with regard to the shorter bases of cardinal processes and in the sharply undulating longitudinal ribs developed on the outer surface of conch.

Occurrence. – *Circotheca smetanai* sp. nov. is quite a rare species in the Skryje Member (Buchava Formation) of the Skryje-Týřovice Basin. The species is known from the Bis-koupk locality, Buchava locality, rocks near Zbíroh stream opposite the Buchava quarry, Dlouhá hora and Skryje-Luh localities (southern slope above the Skryje stream) (Figs 1, 5).

Remarks on stratigraphy. – The presence of *C. smetanai* has been established in the lower third of the Buchava Formation, near the base of the *Paradoxides (Eccaparadoxides) pusillus* Biozone (Fig. 5), in levels which are correlated with the upper Leonian regional Stage (Álvaro *et al.* 2004, fig. 5). The Leonian Stage corresponds to the *Paradoxides oelandicus* regional Stage of Baltica (Geyer & Shergold 2000, table 1). Until now, the oldest species of *Circotheca*, *C. stylata*, has been described from the *Solenopleura brachymetopa* trilobite zone of south Sweden (Berg Madsen and Malinky 1999, pp. 844, 874, 875; Malinky 2009, p. 589). Specimens described and figured recently by Peel (2010) and Peel & Ineson (2011) from the early Cambrian Sirius Passet Lagerstätte of Greenland show surface sculpture of conch and circular operculum and could belong to *Circotheca*.

C. smetanai thus represents the oldest described occurrence of the genus *Circotheca*.

Family uncertain

Genus *Probactrotheca* gen. nov.

Type species. – *Probactrotheca briketa* sp. nov.; Cambrian Series 3, Buchava Formation, Skryje Member, Skryje-Týřovice Basin, Teplá-Barrandian region, Czech Republic.

Diagnosis. – Medium sized orthocone conch with a small angle of divergence, and trapezoid cross-section. Ventral side concave; dorsal side divided longitudinally into three parts: the middle part with slightly raised rounded keel on the mould and with slightly vaulted lateral shoulders. The boundaries between these three parts are rounded, as is the junction with the ventral side. The ventral apertural margin is straight; the dorsal margin is slightly arched adapically cut out. The sculpture of the conch consists of fine growth-lines.

The flat operculum is sub-trapezoid in outline. Its inner side bears narrow broadly diverging cardinal processes with subparallel edges. The lower walls are distinct. Plicae are well developed on the outer side; the slightly convex triangulum is distinct. The sculpture of the operculum consists of fine distinct growth-lines.

Discussion. – *Probactrotheca* gen. nov. is reminiscent of the genera *Bactrotheca* Novák, 1891, *Quadrotheca* Sysoev,

1958, *Trapezotheca* Sysoev, 1958 and *Holmitheca* Sysoev, 1968.

In *Trapezotheca*, based on the Lower Ordovician type species *Hyolithus (Orthotheca) aemulus* Holm, 1893, the ventral side is much less concave and the conch sculpture consists of longitudinal elements. The Lower Cambrian genus *Holmitheca* (type species *Holmitheca obvia* Sysoev, 1968) shows well rounded edges of the conch especially those, which separate middle part of the dorsal side from the lateral sides. Opercula of *Trapezotheca* and *Holmitheca* are unknown. The similar genus *Quadrotheca* Sysoev, 1958 emended Malinky, 2002 [type species: *Hyolithes (Orthotheca) quadrangularis* Holm, 1893], the only genus of the Family Quadrothecidae Malinky, 2002, differs in possessing a flat dorsum and venter. The genus *Bactrotheca* Novák, 1891 (type species *Hyolithes teres* Barrande, 1867) shows a flat venter without a broad shallow furrow and flat dorsum.

All orthothecids with a “quadrate” cross-section were traditionally classified within the family Orthothecidae Sysoev, 1958. Malinky (1987) provided the following emended diagnosis of this family: “Orthothecids with inflated, angular dorsum and slightly inflated venter, forming a subtriangular transverse outline; ornament on exterior of shell may be longitudinal, transverse, or combination of both. Unlike Fisher (1962), Malinky (1987, p. 947) proposed to exclude from this family seven genera including *Bactrotheca* and *Quadrotheca*. Consequently, Malinky (2002, p. 541) established a new family, Quadrothecidae, with only one genus *Quadrotheca*. In their most recent paper Malinky *et al.* (2009) refrained from classifying *Bactrotheca* within any family. Malinky (2009) changed the concept of the family Orthothecidae and included its type genus *Orthotheca* Novák, 1886 and six other genera. This most recent concept excludes the genera *Bactrotheca* and *Quadrotheca* from this family. In conclusion, the new genus *Probactrotheca* does not fall within any recognised family as they are presently diagnosed.

Species. – Monotypic genus with species *Probactrotheca briketa* sp. nov.

Occurrence. – Middle Cambrian, Skryje-Týřovice Basin, Bohemia.

***Probactrotheca briketa* sp. nov.**

Figure 2E–J, 4

1983a *Probactrotheca briketa* sp. n. – Marek, pp. 15–17 (MS).

Holotype. – L40473 (Fig. 2F, G). Outer surface of opercu-

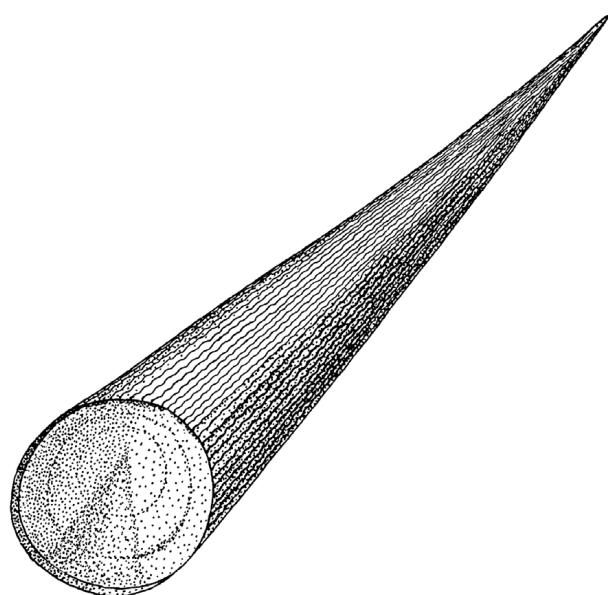


Figure 3. *Circotheca smetanai* sp. nov., reconstruction of conch with attached operculum. (Modified from Marek 1976.)

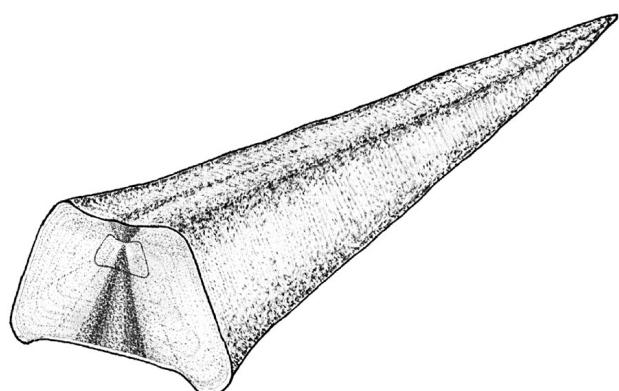


Figure 4. *Probactrotheca briketa* sp. nov., reconstruction of conch with attached operculum.

lum deposited in the collection of the National Museum, Prague, Czech Republic. Buchava locality.

Paratypes. – Inner surface of operculum; L40472 (Fig. 2E). Internal mould of the conch; L40470 (Fig. 2H, I). External mould of conch; L40572 (Fig. 2J). All specimens come from the Biskoupy locality and are deposited in the collection of the National Museum, Prague, Czech Republic.

Type horizon and locality. – Cambrian Series 3, Buchava Formation, Skryje Member, *Paradoxides (Eccaparadoxides) pusillus* Biozone; Biskoupy locality, Skryje-Týřovice Basin, Teplá-Barrandian region, Czech Republic.

Material. – In addition to the holotype and paratypes, two other incomplete moulds and five external conch imprints.

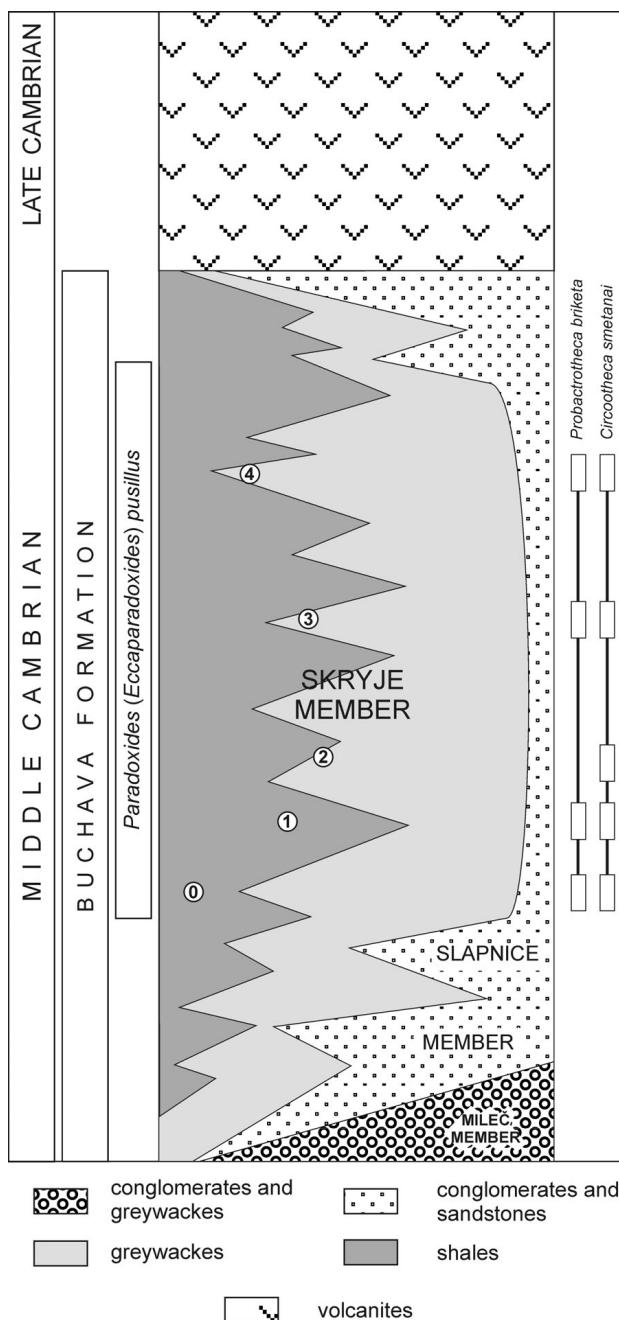


Figure 5. Stratigraphic distribution of *Circotheeca smetanai* sp. nov. and *Probactrotheca briketa* gen. et sp. nov. within the Buchava Formation of the Skryje-Týřovice Basin (biostratigraphy after Fata et al. 2011). 0 – Biskoupy locality; 1 – Buchava locality; 2 – rocks near Zbiroh stream opposite the Buchava quarry; 3 – Dlouhá hora Hill and 4 – Skryje-Luh locality (southern slope above the Skryje stream).

Diagnosis. – The same as for the genus.

Description. – Orthocone conch, subtrapezoidal in cross-section. The angle of divergence ranges from 10 to 12 degrees, w/h index = 1.55. The ventral side is strongly concave; the concavity is about one seventh of the height of

the conch. On the dorsal surface of the conch, the slightly arched dorsal flat part carries an indistinct, broadly rounded medial keel and the almost flat lateral sides can be recognised (Fig. 4). The keel is more distinct on internal moulds. Strongly rounded edges separate the lateral sides from the ventral as well as the dorsal surfaces of the conch. The aperture is perpendicular to the conch axis. The ventral apertural margin is excavated slightly backward. Muscle scars were not found. The apical part is not preserved in any of the conchs, hence it is not known if apical septa were developed.

In the best preserved specimens, indistinct, very fine growth-lines are developed on the outer surface of the conch (Fig. 2J).

The flat operculum is sub-trapezoidal in outline (Fig. 2E–G), its ventral margin slightly arched. The cardinal processes are narrow (exsag.), broadly diverging and virtually of the same width. Their proximal ends are strongly internally curved to the inner surface of the operculum and merge with its surface. The distal ends of the cardinal processes are free. Narrow, distinct but low walls extend from about half of the length (tr.) of the cardinal processes in a shallow arch towards the anterior lateral opercular margins (Fig. 2E). Plicae are distinct and separated by a shallow furrow; their outer margins reach an angle of about 55 degrees. A small and slightly vaulted triangular area lies between the summit and the dorsal opercular margin. A thin conical projection with a diameter of 0.3 mm is developed in the centre of the opercular summit and is interpreted as a proto-operculum. This clearly visible shield, which rises above the remainder of the operculum, represents an early ontogenetic stage. A distinctly separated, centrally located sub-trapezoidal shield representing the earliest ontogenetic stages rises above the rest of operculum. The shield differs in shape from the adult specimen's opercula in its straight anterior margin and in sharper corners.

The outer surface of operculum is covered by fine growth-lines (Fig. 2F, G).

Dimensions. – The conch of the adult specimen was at least 30 mm long.

Discussion. – *Probactrotheca briketa* sp. nov. differs from all other orthothecids of similar cross-section in the distinct ridges separating the different parts of the conch. The most similar species is the Lower Ordovician (Dapitanian) *Quadrotheca quadrangularis* (Holm, 1893) from Sweden but the sculpture in this species consists of longitudinal riblets.

Occurrence. – *Probactrotheca briketa* sp. nov. is known only from the Skryje Member (Buchava Formation) of the Skryje-Týřovice Basin at the Biskoupy, Buchava, Dlouhá Hora Hill, and Skryje-Luh localities (Figs 1, 5).

Stratigraphy and palaeoecology

Both new species have been recognized in different stratigraphical levels at several localities of the Skryje Member, Buchava Formation, within the *Paradoxides (Eccaparadoxides) pusillus* Biozone (Fig. 5).

Dzik (1978) and Nützel *et al.* (2006) documented the large size of early ontogenetic shells (= protoconchs) in several groups of early molluscs, including specimens of the Ordovician orthothecid *Bactrotheca* Novák, 1891. This morphological feature has been suggested as a decisive argument for the presence of lecithotrophic (= nonfeeding) larvae in molluscs and hyoliths (Nützel *et al.* 2006). Unfortunately, protoconchs are broken off in all accessible specimens of both *Circotheca smetanai* and *Probactrotheca briketa*. According to the interpretation of hyolithids by Marek & Yochelson (1976) and Marek *et al.* (1997), adult specimens of *P. briketa* and *C. smetanai* were suspension feeders living most probably on and/or partly embedded in muddy substrates in relatively shallow water settings.

Acknowledgements

The authors are indebted to Pavel Štys (Charles University in Prague) for consultation on nomenclatorial rules. This study was supported by MSM 0021620855, the Czech Science Foundation through the Project No. 205/09/1521 (Feeding strategies in Cambrian to Middle Ordovician of the Barrandian Region) and by project of Ministry of Culture CR No. DE06P04OMG009. This contribution benefited from the constructive suggestions made by John S. Peel (Uppsala University, Uppsala, Sweden) and Jan Bergström (Swedish Museum of Natural History, Stockholm, Sweden).

References

- ÁLVARO, J.J., VIZCAÍNO, D., KORDULE, V., FATKA, O. & PILLOLA, G.L. 2004. Some solenopleurine trilobites from the Langue docian (Late Mid Cambrian) of Western Europe. *Geobios* 37, 135–147. DOI 10.10116/j.geobios.2003.03.009
- BARRANDE, J. 1867. *Système Silurien du centre de la Bohême*. Vol. 3. 179 pp. Prague & Paris.
- BERG-MADSEN, V. & MALINKY, J.M. 1999. A revision of Holm's Mid and Late Cambrian hyoliths of Sweden. *Palaeontology* 42(5), 841–885. DOI 10.1111/1475-4983.00099
- DZIK, J. 1978. Larval development of hyolithids. *Lethaia* 11, 293–299. DOI 10.1111/j.1502-3931.1978.tb01884.x
- FATKA, O. 1990. Das Kambrium von Skryje und Týřovice, 12–17. In WEIDERT, K.H. (ed.) *Klassische Fundstellen der Paläontologie, Band 2*. Goldschneck, Korb.
- FATKA, O., KORDULE, V. & SZABAD, M. 2004. Stratigraphical distribution of Cambrian fossils in the Příbram-Jince Basin (Barrandian area, Czech Republic). *Senckenbergiana lethaea* 84(1/2), 369–384. DOI 10.1007/BF03043477
- FATKA, O., KRAFT, P. & SZABAD, M. in press. A first report of *Sphenothallus* Hall, 1847 in Cambrian of Europe. *Comptes Rendus Palevol* 11.
- FATKA, O., MICKA, V., SZABAD, M., VOKÁČ, V. & VOREL, T. 2011. Nomenclature of Cambrian lithostratigraphy of the Skryje-Týřovice Basin. *Bulletin of Geosciences* 86(4), 841–858. DOI 10.3140/bull.geosci.1284
- FISHER, D.W. 1962. Small conoidal shells of uncertain affinities, 98–143. In MOORE, R.C. (ed.) *Treatise on invertebrate paleontology, part W*. University of Kansas Press & Geological Society of America.
- GEYER, G. & SHERGOLD, J.H. 2000. The quest for internationally recognized divisions of Cambrian time. *Episodes* 23, 188–195.
- HALL, J. 1847. *Paleontology of New York. Volume I. Containing descriptions of the organic remains of the Lower Division of the New York system (equivalent to the Lower Silurian rocks of Europe)*. 338 pp. C. Van Benthuysen, Albany.
- HOLM, G. 1893. Sveriges Kambrisk-Silurska Hyolithidae och Conularidae. *Sveriges Geologiska Undersökning, Afhandlingar och uppsatser, Ser. C* 112, 1–172.
- MALETZ, J., STEINER, M. & FATKA, O. 2005. ‘Middle’ Cambrian pterobranchs and the Question: What is a graptolite. *Lethaia* 38(1), 73–85. DOI 10.1080/00241160510013204
- MALINKY, J.M. 1987. Taxonomic revision of lower and middle Paleozoic Orthothecida (Hyolitha) from North America and China. *Journal of Paleontology* 61(5), 942–959.
- MALINKY, J.M. 2002. A revision of Early to Mid Ordovician hyoliths from Sweden. *Palaeontology* 45(3), 511–555. DOI 10.1111/1475-4983.00248
- MALINKY, J.M. 2009. First occurrence of *Orthotheca* Novák, 1891 (Hyolitha, Early Devonian) in North America. *Journal of Paleontology* 83(4), 588–596. DOI 10.1666/08-164R.1
- MALINKY, J.M., ERIKSSON, M.E. & AHLBERG, P. 2009. ‘Mediterranean Province’ hyoliths from the middle Cambrian and Upper Ordovician of Sweden. *GFF* 131(4), 281–291. DOI 10.1080/11035890903458693
- MAREK, L. 1963. New knowledge on the morphology of Hyolithes. *Sborník geologických věd, Paleontologie* 1, 53–73.
- MAREK, L. 1966. New hyolithid genera from the Ordovician of Bohemia. *Časopis Národního muzea, Oddíl přírodovědný* 135(2), 89–92.
- MAREK, L. 1972. Middle Cambrian hyolithes *Maxilites* gen. nov. [Maxilites gen. nov. ze středního kambria (Hyolitha)]. *Časopis Národního muzea, Oddíl přírodovědný* 141(1–2), 69–72.
- MAREK, L. 1975. Objev nové hyolithové fauny ve skryjsko-týřovickém kambriu (The discovery of a new hyolithid fauna in the Skryje-Týřovice Cambrian). *Bohemia centralis* 4, 64–71.
- MAREK, L. 1976. The distribution of the Mediterranean Ordovician Hyolitha, 491–499. In BASSETT, M.G. (ed.) *The Ordovician System: Proceedings of a Palaeontological Association Symposium*. University of Wales Press and National Museum of Wales, Cardiff.
- MAREK, L. 1980. *Slapylites* gen. nov. z českého středního kambria Hyolitha. *Časopis Národního muzea, Oddíl přírodovědný* 149(3), 156–160.
- MAREK, L. 1981. Middle Cambrian Hyolithid family *Parentilitidae* fam. nov. (*Parentilitidae* fam. nov., nová čeleď hyolithů

- ze středního kambria). *Časopis Národního muzea, Oddíl přírodovědný* 150(3), 163–168.
- MAREK, L. 1983a. *Hyolithi českého středního kambria (Hyoliths of the Bohemian Middle Cambrian)*. Unpublished manuscript, Ústav geologie a geotechniky Československé akademie věd, Prague.
- MAREK, L. 1983b. The hyoliths in the Arenigian of Montagne Noire. *Mémoire de la Société d'Etudes Scientifiques de l'Aude*, 57–62.
- MAREK, L., PARSLEY, R.L. & GALLE, A. 1997. Functional morphology of hyoliths based on flume studies. *Věstník Českého geologického ústavu* 72(4), 277–283.
- MAREK, L. & YOCHELSON, E.L. 1976. Aspect of the biology of Hyolitha Mollusca. *Lethaia* 9, 65–82.
DOI 10.1111/j.1502-3931.1976.tb00952.x
- MARTÍ MUS, M. & BERGSTRÖM, J. 2005. The morphology of hyolithids and its functional implications. *Palaeontology* 48(6), 1139–1167. DOI 10.1111/j.1475-4983.2005.00511.x
- MAŠEK, J., STRAKA, J., HRAZDÍRA, P., PÁLENSKÝ, P., ŠTĚPÁNEK, P. & HÚLA, P. 1997. *Geological and nature conservation map. Protected landscape area and biosphere reserve Křivoklátsko*. Czech Geological Survey, Prague.
- MERGL, M. & KORDULE, V. 2008. New Middle Cambrian lingulate brachiopods from the Skryje-Týřovice area (Central Bohemia, Czech Republic). *Bulletin of Geosciences* 83(1), 11–22. DOI 10.3140/bull.geosci.2008.01.011
- MISSARZHEVSKIY, V.V. 1969. Descriptions of hyolithids, gastropods, hyolitelmintins, camenids and forms of an obscure systematic position, 105–175. In ROZANOV, A.Y., MISSARZHEVSKIY, V.V., VOLKOVA, L.G., KRYLOV, I.N., KELLER, B.M., KOROLYUK, I.K., LENDZION, K., MIKHNYAK, R., PYKHOVA, N.G. & SIDOROV, A.A. *Tommotsky jarus i problema niznej graničny Kembrija. Trudy Ordena Trudvogo krasnogo znameni Geologicheskogo instituta* 206.
- NOVÁK, O. 1886. Zur Kenntnis der Fauna der Etage F-Fl in der paläozoischen Schichtengruppe Böhmens. *Aus den Sitzungsberichten der königlichen Böhmens Gesellschaft der Wissenschaften*, 1–27.
- NOVÁK, O. 1891. Revision der paläozoischen Hyolithiden Böhmens. *Abhandlungen Böhmischen Gesellschaft Wissenschaften* 7(4), 1–48.
- NÜTZEL, A., LEHNERT, O. & FRÝDA, J. 2006. Origin of planktontrophy – evidence from early molluscs. *Evolution & Development* 8(4), 325–330.
DOI 10.1111/j.1525-142X.2006.00105.x
- PEEL, J.S. 2010. Articulated hyoliths and other fossils from the Sirius Passet Lagerstätte (early Cambrian) of North Greenland. *Bulletin of Geosciences* 85(3), 385–394.
DOI 10.3140/bull.geosci.1207
- PEEL, J.S. & INESON, J.R. 2011. The extent of the Sirius Passet Lagerstätte (early Cambrian) of North Greenland. *Bulletin of Geosciences* 86(3), 535–543.
DOI 10.3140/bull.geosci.1269
- SYSOEV, A.V. 1957. K morfologii, sistematicheskemu položeniu i sistematike chiolotov (To the morphology, systematic position and systematics of hyoliths). *Doklady Akademii nauk SSSR* 116(2), 304–307.
- SYSOEV, A.V. 1958. The superorder Hyolithoidea, 184–190. In ORLOV, Y.A., LUPPOV, N.P. & DRUSHITS, V.V. (eds) *Principles of Palaeontology. Mollusca, Cephalopoda* 6. 359 pp. Gosgeotekhizdat, Moscow.
- SYSOEV, A.V. 1968. *Stratigrafija i khiloty drevnejshikh sloev nizhnego kembrija Sibirskoj platformy [Stratigraphy and hyoliths of the oldest Lower Cambrian beds of the Siberian Platform]*. Akademiya Nauk SSSR. 67 pp. Yakutskiy filial Sibirskego otdeleniya Instituta Geologii, Yakutsk. [in Russian]
- VALENT, M. 2004. *Hyolithi středního kambria skryjsko-týřovické oblasti (Middle Cambrian hyoliths of the Skryje-Týřovice area)*. 88 pp. Mgr. dissertation, MS Charles University, Prague. [in Czech]
- VALENT, M. 2006. Stratigraphic distribution of the class Hyolitha (Mollusca) in the Barrandian area (Czech Republic). *Acta Universitatis Carolinae, Geologica* 47(1–4), 183–188.
- VALENT, M., FATKA, O. & MAREK, L. in press. *Gracilitheca* and *Nephrotheca* in Cambrian of the Barrandian area (Hyolitha, Orthothecida, Czech Republic). *Alcheringa*.
- VALENT, M., FATKA, O., MICKA, V. & SZABAD, M. 2009. *Jincelites vogeli* gen. et sp. nov. (Hyolitha) from the Cambrian of Czech Republic (Příbram-Jince Basin, Teplá-Barrandian region). *Bulletin of Geosciences* 84(1), 179–184.
DOI 10.3140/bull.geosci.1084
- VALENT, M., FATKA, O., SZABAD, M., MICKA, V. & MAREK, L. 2011a. *Skryjelites auritus* gen. et sp. nov. and *Quasimolites quasimodo* gen. et sp. nov. – two new hyolithids (?Mollusca) from the Middle Cambrian of Czech Republic. *Zootaxa*.
- VALENT, M., FATKA, O., SZABAD, M. & VOKÁČ, V. 2011b. Carinolithidae fam. nov., *Carinolithes bohemicus* sp. nov. and *Slehoferites slehoferi* gen. et sp. nov. – new hyolithid taxa from the Bohemian Middle Cambrian (Skryje-Týřovice Basin, Czech Republic). *Palaeobiodiversity and Palaeoenvironments* 91(2), 101–109.
DOI 10.1007/s12549-011-0049-1
- WALCOTT, C.D. 1911. Cambrian geology and paleontology II, no. 5 – Middle Cambrian annelids. *Smithsonian Miscellaneous Collections* 57(5), 109–144.