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SCHIZOCRANIA (BRACHIOPODA, DISCINOIDEA): TAXONOMY, OCCURRENCE, ECOLOGY AND HISTORY OF THE EARLIEST EPIZOAN LINGULATE BRACHIOPOD

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Abstract: The lingulate brachiopod *Schizocrania* (Trematidae, Discinoidea) is reviewed. *Ptychopeltis* is definitively synonymized with *Schizocrania*, because new data indicate that convexity of the shell, profile of the anterior margin commissure, density of the dorsal valve costellation, ornamentation of the ventral valve and shape of the pedicle notch are worthless for separation of these genera. Four Ordovician species of *Schizocrania* are reported from the Barrandian area: *S. multistriata* (Darriwilian), *S. hornyi* (Sandbian), *S. incola* (Sandbian) and the new species *S. equestra* sp. nov. (Katian). Occurrence of *Schizocrania striata* is confirmed for the first time around the S/D boundary in the Barrandian area. *Schizocrania* has a wide geographic range with mid-Ordovician to early Devonian occurrences in Laurentia, Avalonia, West Gondwana and the Silurian occurrence in Baltica. *Schizocrania* was the earliest lingulate brachiopod adhering to floating objects in an open sea (both living cephalopods and their empty drifting shells), but it was highly opportunistic, and used any vacant hard surface on the sea floor (conulariids, strophomenid brachiopods, trilobites) as a suitable substrate for settlement of the larva. Decline of the genus coincided with disappearance of planktic graptolites, and might have been caused by competition of rapidly evolving planktic dacryoconarids, increased predation pressure, and rebuilding of the trophic structure in the early Devonian seas.

Key words: Discinoidea, Trematidae, *Schizocrania*, Ordovician, Devonian, ecology, plankton, Barrandian

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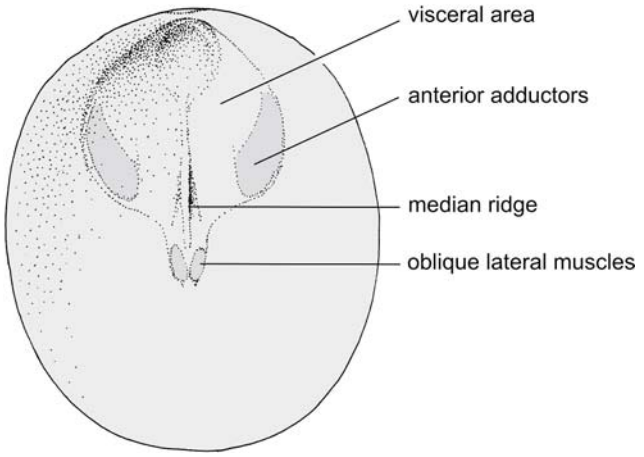
Introduction

The brachiopod genera *Drabodiscina* Havlíček, 1972, *Orbiculothyris* Wolfart, 1968, *Ptychopeltis* Perner, 1903, *Schizocrania* Hall et Whitfield, 1875, *Trematis* Sharpe, 1848, and *Tethyrete* Havlíček, 1994 form a morphologically distinctive discinoidean group, with known range from the Darriwilian (Havlíček 1972, Williams 1974, Sutton et al. 2000, Mergl 2002) to the Lower Devonian (Hall and Clarke 1892). Geographic distributions of particular genera range from almost cosmopolitan in *Schizocrania* and *Trematis* to very restricted in *Drabodiscina*, *Orbiculothyris* and *Tethyrete*. Differences between these genera are matters for discussion (Havlíček 1972, Havlíček and Vaněk 1996). Holmer and Popov (2000) synonymized *Ptychopeltis* and *Orbiculothyris* with *Schizocrania*, although Havlíček and Vaněk (1996) argued that the relationship of *Ptychopeltis* and *Schizocrania* needed further investigation. Recent discoveries in both genera indicates that mineralization of the posterior closure of the pedicle notch, its outline and other features are not as straightforward for distinction of particular genera as suggested by Havlíček (1994).

The mode of life of trematid brachiopods has also been contentious (Havlíček 1972, Lockley and Antia 1980, Harland and Pickerill 1987), although new observations (Gabbott 1999, Basset et al. 2009) have brought unequivocal evidence for their fixosessile and pseudoplanktic habitat. Here we review available data about relationships, geographic and stratigraphic distributions, and mode of life of species referred to *Ptychopeltis* and/or *Schizocrania*.

In the Czech Republic, several successive species of *Schizocrania* are moderately common in the Middle and Upper Ordovician of the Burundian area (Prague Basin). The earliest species were found in the Šárka Formation (Darriwilian) (Mergl 2002), with successive occurrences from the Dobrotivá Formation (Darriwilian), Libeň Formation (early Sandbian) and Letná Formation (mid-Sandbian) (Havlíček 1972, Mergl 2002). New specimens of *Schizocrania* are recorded here from the Bohdalec Formation (Katian). The genus has been assumed absent in the Silurian and Lower Devonian of Bohemia (Mergl 2001), although it occurs in the Silurian or Lower Devonian of Gotland (Mergl 2010), Ukraine (Kozlowski 1929), France (Bassett 1986),



Text-fig. 1. *Schizocrania incola* (Perner, 1903). Drawings of visceral area and muscle scars.

Great Britain (Davidson 1848, Lockley and Antia 1980, Mergl 2006) and eastern USA and Canada (Hall 1847, Hall and Whitfield 1875, Barrett 1878, Hall and Clarke 1892). Two specimens of *Schizocrania* have been found among brachiopods in the collection of Vladimír Havlíček currently stored in the the Museum of West Bohemia (Museum of Dr. B. Horák at Rokycany). Because it is the first report of this genus from near of the S/D boundary in Central Europe, it is briefly reported.

Material

The material studied is housed in the palaeontological collections of the National Museum Prague (NM), in the palaeontological collections of the Museum of Dr. B. Horák, Rokycany, the Czech Republic (3RO), and in the palaeontological collections of the University of West Bohemia at Plzeň (PCZCU). Locality names are according to Mergl (2002).

Abbreviations

VvW – ventral valve width, VvL – ventral valve length.

Systematic part

Order Lingulida Waagen, 1885
Superfamily Discinoidea Gray, 1840
Family Trematidae Schuchert, 1893

Genus *Schizocrania* Hall et Whitfield, 1875

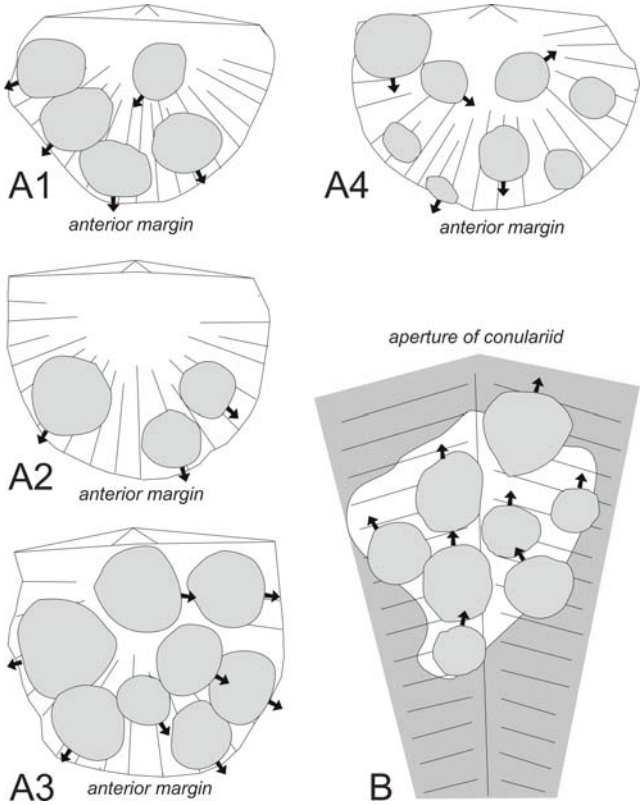
Type species. ?*Orbicula filosa* Hall, 1847; Trenton Group, Ordovician; New York State, USA.

Remarks. In his emended diagnosis of *Ptychopeltis* Perner, 1903, and comment to this genus, Havlíček (1972) noted that there are two main differences between *Ptychopeltis* and *Schizocrania* Hall et Whitfield, 1875: the very high dorsal valve and the narrow, parallel-sided pedicle notch of the former genus. Later, Havlíček and Vaněk (1996) stated that distinction between these genera needs further investigation.

The parallel-sided pedicle notch of *Ptychopeltis* is distinctly seen in newly sampled specimens of *S. multistriata* (Reed, 1905) (Pl. 1, Figs 11, 14) from the Barrandian area. Unfortunately, the outline of the pedicle notch is unknown in the majority of species formerly referred to *Ptychopeltis* and *Schizocrania*, from Bohemia and elsewhere. Only a few illustrated specimens (Hall and Clarke 1892, Havlíček 1972, Lockley and Williams 1981, Bassett 1986, Sutton et al. 2000, Mergl 2006, 2010) indicate that the pedicle notch shape may vary from parallel-sided (*S. multistriata*), moderately triangular (*S. striata* (J. de C. Sowerby, 1839), *S. verneuilii* (Davidson, 1848), *Schizocrania* sp. A sensu Basset (1986)) to very broad (*S. filosa*, *S. striata*). The shape of the pedicle notch can vary between individuals referred to the same species (Sutton et al. 2000), and its outline can be changed by post-mortem process. Dorsally flexed margins of the pedicle notch in living specimens are easily broken off and compressed (Mergl 2006) in deformed specimens. Thus, the broadly triangular pedicle notch can be an artifact of flexible compression. The broadly wide outline of the notch of *S. filosa* figured by Hall and Clarke (1892) could have been exaggerated by preservation, because shells of *S. filosa* are generally collapsed and flattened. An undeformed ventral valve of *S. multistriata* in a nodule retains the original parallel-sided outline (Havlíček 1972, Mergl 2002).

High convexity of the dorsal valve is the second difference noted by Havlíček (1972), and is prominent in numerous specimens currently referred to *Schizocrania* (= *Ptychopeltis incola*, *P. hornyi*) in Sandbian sandstone (Libeň and Letná formations) in the Barrandian area. The convexity of specimens preserved in shale varies widely, from low to highly conical. Lockley and Antia (1980: text-fig. 2A), Bassett (1986: pl. 8, fig. 15), Mergl (2006) figured originally strongly convex dorsal valves of *Schizocrania*, but the dorsal valves of *S. verneulii* (Mergl 2006, 2010) are only gently arched. The shell convexity and nature of anterior commissure were influenced by the substrate and its relief, by mode of preservation, and by sediment compaction; they therefore have weak taxonomic value.

The observed absence of radial costellae on the ventral valve in some early species of *Schizocrania* clade is seemingly stable, and significantly different from the later Silurian and Devonian species. The latter regularly bear radial costellae on the ventral valve exterior (Mergl 2006, 2010). The Ordovician species of *Schizocrania* are much complicated. Some species are erected only on the dorsal valves (Reed 1917, Havlíček 1972, Harper 1984), and the ventral valve ornamentation is unknown. The figured ventral valves of *Schizocrania multistriata* Reed, 1905 from the Middle Ordovician of Wales (Lockley and Williams 1981) and the Darriwilian of Bohemia (Havlíček 1972, Mergl 2002) lack radial costellation, but other specimens referred to the same species (Sutton et al. 2000: pl. 14, fig. 4) show distinct radial costellation. The type species *Schizocrania filosa* is illustrated (Hall and Clarke 1892) without radial costellation of the ventral valve, and the newly well-illustrated specimens referred to *S. filosa* (http://drydredgers.org/brachschizo.htm, accessed 20 November 2016) show only concentric ornamentation. In summary, because there is no distinct feature that might be useful for discrimination of *Ptychopeltis* from *Schizocrania*, the former is designated here as a junior synonym of *Schizocrania*.



Text-fig. 2. (A) Orientation of *Schizocrania filosa* (Hall, 1847) on articulated shells of benthic brachiopod *Rafinesquina* sp. (A1–A3 – on dorsal valve of articulated shells, A4 – on ventral valve of articulated shell; forward growth direction is unclear in three specimens) from Upper Ordovician, Corryville Formation, Lawrenceburg, Indiana (after www.drydredgers.org/scizo.htm). (B) Orientation of *Schizocrania multistriata* (Reed, 1905) shells on outer face of conulariid *Metaconularia imperialis* test (Dobrotivá Formation, Kařízek mine, Barrandian area; after Havlíček and Vaněk 1996); preserved conulariid shell in white, suggested outline of incomplete conulariid test in grey. Arrows indicate direction of forward growth of *Schizocrania* specimens.

The genus *Orbiculothyris* Wolfart, 1968 was synonymized with *Schizocrania* by Holmer and Popov (2000), but that needs further confirmation. A distinct feature is the posteriorly closed pedicle opening of *Orbiculothyris*, unknown in any species of *Schizocrania*, which indicates relationship to other trematids and supports the validity of *Orbiculothyris*.

Some occurrences of *Schizocrania* are poorly known, and relationship of the described shells need revision (Barrett 1878, Douglas 1933, Newell and Tafur 1944, Hede 1951). Among the problematic species, Hurst (1979) described and illustrated *Schizocrania hewardi* from the Upper Ordovician, Onny Shale Formation (Early Katian; Streffordian) of Shropshire, England (Cocks 2008). Due to its unusual ornamentation with subdued capillate ornamentation, absence of distinct larval shell, very small size (only 1.2 mm shell length), and highly convex dorsal valve at this growth size, we consider that figured specimens is not a trematid brachiopod. The figured specimens of Hurst (1979: figs 78–83) might be an ostracod or a primitive mollusc.

Species previously referred to genus:

Schizocrania asteroidea Reed, 1917; Upper Ordovician, Katian (Rawtheyan); Girvan, Scotland.

Schizocrania filosa (Hall, 1847); Upper Ordovician; NE of USA and Canada.

Schizocrania helderbergia Hall et Clarke, 1892; Lower Devonian, Lower Helderberg Group; NE of USA.

Schizocrania hewardi Hurst, 1979; Upper Ordovician, Katian; Shropshire, England (likely it is not a brachiopod).

Schizocrania multistriata (Reed, 1905); Middle Ordovician, Darriwilian; Pembrokeshire, Wales; Barrandian area, Bohemia.

Schizocrania schucherti Hall et Clarke, 1892; Upper Ordovician, Hudson River Group; USA (likely junior synonym of *S. striata*).

Schizocrania striata (J. de C. Sowerby, 1839); Silurian to Early Devonian, Ludlow to Lochkovian; Shropshire, England; Barrandian area, Bohemia; Gotland, Sweden; Podolia, Ukraine.

Schizocrania superincreta Barrett, 1878; Lower Devonian, Oriskany Sandstone; USA.

Schizocrania? *turnbulli* (Reed, 1905); Upper Ordovician, Katian; Pembrokeshire, Wales.

Schizocrania verneuilii (Davidson, 1848); Silurian, Wenlock; Herefordshire, England.

Schizocrania sp.; Middle Ordovician, Darriwilian; Carmarthenshire, Wales (Lockley and Antia 1980); Upper Ordovician; Quebec, Canada (Harland and Pickerill 1987); Silurian to Lower Devonian, Pridoli to Lochkovian; North France (Bassett 1986).

Schizocrania hornyi (Havlíček, 1972)

Pl. 1, Figs 16–24, Pl. 2, Figs 1–8

1972 *Ptychopeltis hornyi* sp. n.; Havlíček, p. 232, pl. 1, figs 3–6.

D e s c r i p t i o n . Havlíček (1972).

R e m a r k s . The distinguishing feature of this species is coarse costellation (Havlíček 1972) of high rounded costellae, with narrower interspaces rarely supplemented by a secondary intercalated costellae. Preservation is exclusively in quartzitic sandstone, which preserves the original convexity, but fine ornamentation details are absent. Almost all preserved specimens have rectimarginal anterior commissure, apart from the single specimen figured by Havlíček (1972: pl. 1, fig. 3). *S. hornyi* apparently preferred conulariid hosts or large orthocone cephalopods.

O c c u r r e n c e . Libeň Formation, Řevnice Quartzite (lower Sandbian) (localities: Cekov (small hill south of the village), Čilina hill near Rokycany (abandoned quarry at Plzeňská Čilina, north slope of Čilina hill, summit platform of the hill), Kařezská hora hill near Kařízek, Stradiště hill near Starý Plzenec, Tymákov (NW slope Sutice hill)). Letná Formation, lower part (mid-Sandbian) (localities: Děd hill at Beroun, Starý Plzenec (Černá stráň, valley of Úslava river NW from the town), Trubín).

Schizocrania incola (Perner, 1903)

Pl. 3, Figs 1–16, Text-fig. 1

1903 *Ptychopeltis incola* Barr.; Perner, p. 42, text-figs 15, 16, pl. 43, figs 8–15.
1963 *Ptychopeltis incola* Perner; Horný, p. 63, pl. 15, figs 1–7, pl. 16, figs 1–8.
1972 *Ptychopeltis incola* Perner; Havlíček, p. 232, text-fig. 1, pl. 2, figs 2, 3.

Description. Perner (1903), Horný (1963).

Remarks. The main differences of *Schizocrania incola* (Perner, 1903) from the ancestral *S. hornyi* (Havlíček, 1972) are the high convexity of the dorsal valve, highly arcuate anterior commissure, and finer (capillate instead of costellate) ornamentation in the dorsal valve. The last difference is the most significant. The number of costellae near the anterior margin ranges between 2–4 costellae per 1 mm in the largest preserved dorsal valves *S. multistriata* (Reed, 1905) and *S. hornyi*, but there is at least 7–8 costellae in *S. incola* (Pl. 3, Figs 9, 11, 12–14). This difference is even more striking because the number of costellae per 1 mm in all species of *Schizocrania* decreases with the shell size, and the measured valves of *S. incola* are larger than the largest available valves of *S. multistriata* and *S. hornyi*. *Schizocrania incola* is also prominent in high convexity of the dorsal valve. One of the type specimens of *S. incola* (NM-L 5404) shows a distinct impression of a large visceral area, with clearly defined anterior projection (Text-fig. 1, Pl. 3, Fig. 16).

Occurrence. Letná Formation, upper part (mid- to late Sandbian) (localities: Trubská gorge, Zahořany).

Schizocrania multistriata (Reed, 1905)

Pl. 1, Figs 1–15

1905 *Trematis multistriata*, sp. nov.; Reed, p. 446, pl. 23, figs 1, 1a.
1972 *Ptychopeltis* sp. n.; Havlíček, p. 233, pl. 2, figs 4, 5.
1974 *Schizocrania salopiensis* sp. nov.; Williams, p. 44, pl. 6, figs 22–26.
1978 *Trematis multistriata* Reed; Cocks, p. 25.
1978 *Schizocrania salopiensis* Williams; Cocks, p. 26.
1979 *Schizocrania salopiensis* Williams; Hurst, p. 229, figs 72–77.
1981 *Schizocrania* cf. *salopiensis* Williams; Lockley and Willliams, p. 24, figs 60–65.
1981 *Schizocrania multistriata* (Reed); Lockley and Willliams, p. 24, figs 66.
1996 *Ptychopeltis salopiensis* (Williams); Havlíček and Vaněk, p. 234, pl. 1, figs 1, 2, pl. 2, fig. 1.
2000 *Schizocrania multistriata* (Reed); Sutton et al., p. 83, pl. 13, figs 11–13, pl. 14, figs 1–7.
2008 *Schizocrania multistriata* (Reed); Cocks, p. 22.

Description of Bohemian material. Havlíček and Vaněk (1996) and Mergl (2002).

Remarks. Newly sampled ventral valves and re-examination of specimens from the Dobrotivá Formation prove that the ventral valve of the specimens from the Barrandian area lacks the radial costellation, and the pedicle notch is parallel-sided and gently tapering posteriorly. Although this differentiates the Bohemian specimens from the British ones (Sutton et al. 2000: pl. 14, fig. 4), we prefer to maintain the name *S. multistriata* (Reed, 1905) for the Barrandian specimens. Similarly to the British specimens (Sutton et al. 2000: 84), the variation of density of costellae is remarkably high in the Barrandian specimens (Pl. 1, Figs 5, 6). New costellae originate exclusively by intercalation (Pl. 1, Fig. 4). Unlike the stratigraphically younger species, the costellae of *S. multistriata* from the Barrandian area are wider than the interspaces, and the interspaces have concave profiles (Pl. 1, Fig. 4). The type specimens of *S. multistriata* came from the Darriwilian of Pembrokeshire in Wales (uppermost Llandeilian or lowermost Aurelucian: Cocks (2008)) and that is of comparable age to the Bohemian specimens.

Occurrence. In the Barrandian area, the species is very rare in the Šárka Formation (lower Darriwilian) (locality: Osek (field)), and moderately common in the Dobrotivá Formation (upper Darriwilian) (localities: Ejpovice (highway cut, quarry, temporary excavations in industrial park), Kařízek (Veronika mine), Malé Přílepy (field), Osek (highway cut), Praha – Liboc (temporary excavations), Praha – Motol (railway cutting), Praha – Vokovice (field), Sedlec (Sutice, well excavations in village), Starý Plzenec (Černá stráň)). In England and Wales, the species occurs sporadically (about 50 shells are known, mostly in argillaceous rocks) from the latest Fennian (Arenig) to lowermost Caradoc (= latest Dapingian? to early Sandbian) (Sutton et al. 2000).

Schizocrania striata (J. de C. Sowerby, 1839)

Pl. 3, Figs 17–22

1839 *Orbicula striata*; J. de C. Sowerby in Murchison, p. 610, pl. 5, fig. 12.
1854 *Orbicula striata*, Sow.; Murchison, pl. 20, fig. 3.
1859 *D.* (*Orbicula*) *striata*, Sow.; Murchison, pl. 20, fig. 3.
1866 *Discina striata* Sow. (sp.); Davidson, p. 67, pl. 6, figs 1–4.
1867 *D. striata*, Sow. [*Orbicula*, Sil. Syst.]; Murchison, pl. 20, fig. 3.
1872 *D. striata*, Sow. [*Orbicula*, Sil. Syst.]; Murchison, pl. 20, fig. 3.
1902 *Orbicula striata* J. de C. Sowerby; Blake, p. 6.
1963 *Schizocrania striata* (J. de C. Sowerby); Holland et al., p. 154.
1978 *Schizocrania striata* (J. de C. Sowerby); Cocks, p. 26.
1980 *Schizocrania striata* (Sowerby); Lockley and Antia, text-figs 2A–C.
2006 *Schizocrania striata* (J. de C. Sowerby); Mergl, p. 217, fig. 3A–I.
2008 *Schizocrania striata* (J. de C. Sowerby); Cocks, p. 22.
2010 *Schizocrania striata* (J. de C. Sowerby); Mergl, p. 368, fig. 3J–L.

Material. One dorsal valve (3RO 85502, original label VH 12788), and one ventral valve (3RO 72443, original label VH 13755).

Description. Shell thin-walled, considering its size, 20 mm wide, circular. Dorsal valve moderate and evenly convex in transverse and axial profiles, without any sign of fold or sulcus, and without flattening in posterolateral part. Lateral and anterior margins evenly curved. Dorsal apex low, placed near posterior margin, but poorly preserved due to compression and moderate breakage of valve.

The ventral valve is flat, circular, with dorsally inflexed surface adjacent to the pedicle notch. Posterior margin extends backwards slightly, breaking the otherwise regularly rounded outlines of the lateral and anterior margins. The apex is flat, situated at one-fourth of VvL. The posterior margin has developed deep V-shaped emargination of the pedicle notch, occupying 20 % of VvL and 12 % of VvW. Details of the pedicle notch are unknown. Interior of the ventral valve bears fine and short (10% of VvL), median ridge extending below the apex.

The ornamentation of the dorsal valve consists of fine elevated radial costellae regularly spaced over the entire surface. Density of costellae depends on their distance from the apex. There are 7 costellae per 1 mm at 5 mm distance from the apex. New costellae are intercalated on the flat floor of the interspaces, where the interspaces are approximately 150 μm wide. Intercalated new costellae appear anteriorly to prominent concentric growth bands, and rapidly attain the same size as the primary costellae. Concentric ornamentation consists of low ridges distinct on the floors of the interspaces. The intersections of radial costellae with low concentric fila form fine but distinct reticulate ornamentation.

The ventral valve exterior bears prominent, thin, high, radially arranged costellae of uniform shape and size. The first costellae emerges from the apex, and with the newly formed costellae, evenly cover the entire surface of the valve. Costellae are also evenly spaced in the posterolateral sectors of the valve. They are absent only on inflexed shell surface close to the pedicle notch. New costellae originate by implantation at flat interspaces when adjacent bordering costellae are 0.8 mm apart. There are 9 costellae per 5 mm near the anterior margin of the 20 mm long valve. Costellae gently project outside the shell margin. It is likely that originally there was a non-mineralized organic sheet between their tips. Interspaces have a flat floor. The concentric ornamentation is distinct on the floor of interspaces, consisting of low broad bands separated by weak furrows. There are some 13–15 growth lines at 10 mm distance from the apex. Concentric bands become narrower with shell growth. Drape-like structures extending and vanishing backwards are distinct along sides of the interspaces. The structure indicates a tension and folding of the first-formed organic sheet of the shell near tough and already mineralized costellae.

Remarks. The two available shells are referred to *Schizocrania striata* (J. de C. Sowerby, 1839), because there is no distinct difference between them and specimens from Shropshire, England. *Schizocrania verneuilii* (Davidson, 1848) has the radial costellation absent in the posterolateral sectors of the valve (Mergl 2006: fig. 34O, P).

Occurrence. In the Barrandian area, the species is very rare in the top of the Požáry Formation (Pridoli) (locality: Klonk stratotype (bed No. 7)) and the Kotýs Limestone, Lochkov Formation (Lochkovian) (locality: Svatý Jan pod Skalou (Solway's quarries)). The species is present in the Gorstian and Ludfordian (Upper Ludlow Beds) of Shropshire, England (Lockley and Antia 1980, Mergl 2006), and in the Homerian to Ludfordian of Gotland (Mergl 2010).

Schizocrania equestra sp. nov.

Pl. 2, Figs 9–19

Holotype. Dorsal valve figured on Pl. 2, Fig. 11 (PCZCU 2085).

Etymology. Latin *equestra* means rider.

Type horizon and locality. Katian, Bohdalec Formation; Praha – Michle, temporary excavations at Chodovská Street (in year 1985).

Material. Four valves attached to incomplete compressed orthocone cephalopod shell and 25 dorsal valves of variable size in black shale.

Diagnosis. Moderately convex *Schizocrania* with circular outline, low dorsal apex and costellate ornamentation of low rounded costellae as wide as shallow interspaces; 3–4 costellae per 1 mm anteromedianly in large specimens; new costellae rare, intercalated, concentric fila absent.

Description. The shell is almost circular in adults, plano-convex, 17 wide in the largest known specimen. The ventral valve is unknown. The dorsal valve has evenly rounded margins, and moderate convex transverse and lateral profiles. The apex is located near the posterior margin, separated from it by a short band of thickened shell. The visceral area is poorly defined. Ornamentation consists of regular costellae, originating at the dorsal apex. Costellae are straight in midsector, but gently curved in posterolateral parts of the valve. Costellae are always arranged perpendicularly to shell margin and are rounded, gently increasing in size anteriorly, and separated by shallow interspaces of the same size. New costellae originate exclusively by intercalation. Concentric fila are absent, and only weak broad concentric bands (Pl. 2, Fig. 14) indicate irregularity of shell growth.

Remarks. The new species is distinct in its fairly coarse and regular costellate ornamentation, with about half the number of costellae as on comparably sized shells of *S. incola* (Perner, 1903). *Schizocrania hornyi* (Havlíček, 1972) has a similar density of costellation, but its costellae are coarser, separated by narrower interspaces and the dorsal apex protrudes more posteriorly. Specimens referred to *Schizocrania multistriata* (Reed, 1905) from the Barrandian area differs from the new species by the less rounded posterior margin of the dorsal valve, and generally finer costellation.

Occurrence. Type locality only.

Functional morphology and ecology of *Schizocrania*

A distinctly smaller diameter of the ventral valve compared to the dorsal valve in particular individuals is a unique feature of *Schizocrania*. This peculiarity was noted by Hall and Clarke (1892) in *S. filosa*, and the same differences are seen in *S. verneuilii* and *S. striata* (Mergl 2006). The ventral valve ornamentation never copies the structures (ribbing, spinosity) of the substrate or the ornamentation of the dorsal valve. The concentric and radial ornamentation of the ventral valve of *Schizocrania* is always distinct, though its irregularity may be seen in some specimens (Pl. 1, Fig. 12). That observation led Hall and Clarke (1892) to the conclusion that the ventral valve was firmly attached at some distance above the host surface by a sufficiently large and stout pedicle. Only the periphery of the convex dorsal valve was in narrow contact with the surface of the host shell, although profile and outline of the dorsal valve might more or less follow the relief of the host shell. That explains the common variation in the dorsal valve shape (Pl. 1, Fig. 21), and in the curvature of the anterior commissure (Pl. 2, Fig. 10, Pl. 3, Fig. 10) of *Schizocrania* shells, and also means that differences in the commissure profile are taxonomically worthless.

The deep insertion of the ventral valve inside the highly convex dorsal valve of *Schizocrania* implies that the gap opened between the dorsal valve and host surface was very narrow when feeding. The elevation of the dorsal valve was provided by backward contraction of anterior body wall. This hydraulic opening mechanism pushed away the dorsal valve from the ventral valve and the host substrate by rotation along a narrow swollen band bordering the posterior margin of the dorsal valve. This made possible the gentle elevation of the dorsal valve periphery, which facilitated inflow and outflow of water inside the shell. This thickening is apparent in the very low posterior slope and moderate impression of the apical chamber into the posterior shell wall (Pl. 3, Figs 7, 8), ands distinguishes *Schizocrania* from its homeomorph *Orbiculoidea* (s.s.) (Mergl 2006). In *Orbiculoidea*, a similarly conical dorsal valve has a much more centrally situated apex, and its posterior slope is higher and weakly thickened.

For more than forty years there have been speculations about the benthic or pseudoplanktic mode of life of *Schizocrania* (Hall and Clarke 1892, Holland 1971, Havlíček 1972). A fine review and some conclusive data about the habitat of this genus were presented by Lockley and Antia (1980) and Harland and Pickerill (1987). The pseudoplanktic mode of life of the discinoid brachiopods on cephalopod shells was extensively discussed by Gabbott (1999) and Bassett et al. (1999). The data about the occurrence of *Schizocrania* in the Barrandian area, and new evidence of a benthic mode of life of conulariids (Van Iten et al. 2013) have brought some new insights into the autecology and unique features of *Schizocrania*.

All the available data indicate that *Schizocrania* specimens were (always?) attached by a stout pedicle to any hard substrate, and thus neither living individuals nor particular species were host specific. *Schizocrania* has been found on the surface of benthic corals (Mergl 2006), trilobites (Key et al. 2010), on strophomenid brachiopod shells (Hall and Clarke 1892, Cooper 1956, Rowell 1965), on the outer surface of a conulariid test (Harland and Pickerill 1987, Havlíček and Vaněk 1996, Mergl 2002) and on cephalopod shells (Havlíček 1972, Lockley and Antia 1980, Mergl 2010). Lockley and Antia (1980) observed shells of *Schizocrania* inside the abandoned body chamber of broken and probably drifted cephalopod shells. Other data (Hall and Clarke 1892, Douglas 1933, Newell and Tafur 1944, Hede 1951, Cisne 1973, Sempere 1991) and relevant data from the Barrandian area (Havlíček and Vaněk 1996) indicate that isolated *Schizocrania* shells are generally preserved in deep water deposits with a depleted benthic fauna. Cephalopod shells and graptolites are often associated with specimens of *Schizocrania* (Sempere 1991). Cisne (1973) and Lockley and Antia (1980) noted that isolated dorsal valves are common, but ventral valves are rare. Ventral valves have been observed more often inside dorsal valves in bivalved specimens attached to the host shell (Hall and Clarke 1892, Mergl 2002).

The profile of the anterior commissure indicates that many, but not all species of *Schizocrania* adhered to cylindrical objects. *Schizocrania* shells adhered to cylindrical objects are known from the Barrandian area (Havlíček 1972), Anglo-Welsh Basin (Lockley and Antia 1980), and Gotland (Mergl 2010). Low (Pl. 2, Fig. 10) to high (Pl. 3, Fig. 10) convexity of the anterior commissure of the dorsal valve indicates that the host surfaces were on cylindrical objects of variable diameter. Highly convex and narrow dorsal valves probably represent individuals attached to a highly convex substrate, doubtless small cephalopod shells, or their apical part. Preferred orientation of attached shells of *Schizocrania* has not been proved unequivocally, but there are a few samples to indicate that. However, in the group of four specimens attached to the outer surface of the body chamber of an orthocone host, two specimens were adhered on opposite outer sides of the cephalopod shell (Pl. 2, Fig. 19). The third observed specimen is near the cephalopod shell aperture. The fourth specimen is poorly preserved, with unclear orientation. Three shells are aligned with the cephalopod shell and have apices towards the cephalopod aperture. Obviously, this shell orientation of *Schizocrania* was hydrodynamically convenient, and supports suggestions about the life colonization on an actively swimming cephalopod (cf. Gabbott 1999). In the case of necroplanktic drift, the shells of *Schizocrania* would likely have occupied also the internal surface of the cephalopod shell. Rock surrounding four specimens yielded other broken shells of orthocone nautiloids and numerous isolated (> 20 specimens) dorsal valves of *Schizocrania*. These shells unequivocally represent shells attached to the outer surface of a living cephalopod, or drifted cephalopod shell, as indicated by their weakly to moderate arched ("uniplicate") anterior commissure. No specimen has a concave ("unisulcate") anterior margin, which would have indicated attachment to the internal surface of the empty cephalopod shell. Loose dorsal valves probably represent specimens that dropped out of the cephalopod shell shortly before burial by sediment. We speculate that rapid deep submergence of cephalopod shells

brought the *Schizocrania* specimens into deeper hypoxic waters. Their death led to the separation of the dorsal valves from the ventral valves, and explains the often-reported preponderance of dorsal valves relative to ventral valves in fossil records (Cisne 1973, Williams 1974, Sutton et al. 2000). The ventral valves of *Schizocrania* remained attached to the cephalopod shells by the pedicle, which was more resistant to decay than the soft parts of the brachiopod body inside the shell, especially the musculature that holds the dorsal valve to the ventral valve. However, some shells of *Schizocrania* have been observed in an adhered situation on the internal surface of body chamber (Lockley and Antia 1980: text-fig. 2A). This indicates settlement on empty cephalopod shells, and a necroplanktic drift of the shell. Interpretations about taphonomy of attached discinoid brachiopods to cephalopod shells have been published by Gabbott (1999).

An absence of specimens having convex lateral margins indicates that settlement of larva was controlled by the hydrodynamic property of the host substrate. The larvae which attempted to adhere anticoincidently with elongation of the cephalopod shells were generally unsuccessful, or became detached before reaching any great size.

Numerous individuals of *Schizocrania filosa* and some specimens of *S. verneuilii* (Mergl 2010) and *S. striata* (Pl. 3, Fig. 19) have been observed on benthic hosts. Hall and Clarke (1892) noted a preferential settlement onto *Rafinesquina* shells. The same habit of *Schizocrania* has been stated by Cooper (1956), and figured by Rowell (1965). There are few published data about this phenomenon, but some unpublished data indicate that the specimens of *Schizocrania* attached to *Rafinesquina* shells show a preferential orientation on the host shells (Text-fig. 2a). Their anterior margins are consistently oriented with the periphery of particular *Rafinesquina* shells.

Preferred orientation might be envisaged on conulariid shell, but the results are ambiguous (Harland and Pickerill 1980). However, the group of six specimens attached to a large but incomplete *Metaconularia imperialis* from the Veronika mine (Darriwilian, Dobrotivá Formation) (Havlíček and Vaněk 1996) shows distinct preferred orientation (Text-fig. 2B). Havlíček (1972) suggested that conulariids were planktic animals, and that *Schizocrania* drifted together with the conulariids. However, conulariids were probably benthic invertebrates (Van Iten et al. 2015). The *Schizocrania* exploited the hard surface of the conulariids because a conulariid test was a moderate elevated hard substrate, suitable for settlement of larva on otherwise unsuitable soft bottom. The conulariid *Metaconularia imperialis* was a large (> than 25 cm high) benthic animal, with its aperture facing up, toward open water. In that case, the preferred position of *Schizocrania* was with the apex directed down toward the sea floor, and the anterior margin facing open water. This is consistent with position of *Schizocrania* individuals on the benthic strophomenid *Rafinesquina*, if it is assumed that an active feeding current of *Rafinequina* was directed towards the centre of its anterior commissure. The opportunistic strategy of *Schizocrania* is evident from its use of other hard substrates: large reclining brachiopod shells (Hall and Clarke 1892), coral skeletons (Mergl 2006) or exposed glabella surface of trilobites (Key et al. 2010).

An encrusting trepostome bryozoan colony has been found on the small shell of *Schizocrania hornyi* from the Řevnice Quartzites (Pl. 1, Figs 16, 17). This indicates that the *Schizocrania* shells might have been suitable hosts for other sclerobionts. The bryozoan colony is preserved only on the counterpart, but its lower face nicely preserves the radial ornamentation of the brachiopod. The zoarium entirely covers the exterior of the dorsal valve, and its growth over the periphery of the host shell likely killed the brachiopod in the juvenile growth stage.

Conclusions

In summary, *Schizocrania* larvae did not search for a special host. The primary restrictions for their settlement and subsequent growth were an environment wholly marine, shallow but calmer rather than rough water, and a sufficiently oxygenated and nutrient-rich environment. *Schizocrania* used any accessible vacant hard surface on the sea floor as well as any available substrate in open shallow sea. The live swimming cephalopods and drifting empty cephalopod shells represented suitable but rare nektic or planktic (necroplanktic) substrates in the Ordovician and Silurian open seas. A similar habitat strategy was evidenced by the related and similarly shaped discinoidean genera *Trematis* and *Kosoidea* (Gabbott 1999, Basset et al. 2009), known from the Soom Shale (Upper Ordovician) of South Africa. The morphology of *Schizocrania*, *Trematis* and *Kosoidea* shells indicate adjustment to this drifting mode of life. The shell was firmly attached by a large pedicle. The edges of the dorsal valve of *Schizocrania* were wedged into the host's surface, whereas the ventral valve held the whole individual firmly on the host shell. It is worthwhile to point out that a similar life strategy is applied by recent cap-like gastropods (e.g. *Acmaea*, *Crepidula*, *Patella* and many unrelated others) on hard surfaces in rough waters.

The shell of *Schizocrania* was thin and light, but strengthened by fine costellation. The costae indicate a richly setigerous periphery of *Schizocrania* (Lockley and Antia 1980). The evenly convex dorsal valve was hydrodynamically suitable for weak but multidirectional currents around the drifting substrate or on benthic reclining strophomenid brachiopods, where weak tidal water movement might be expected.

Occurrence of *Schizocrania* in the Lower Devonian (Oriskany Sandstone and Helderberg Group; Hall and Clarke (1892)) indicates that the genus was able to survive the Hirnantian glaciation, the Silurian climatic changes, and the Silurian/Devonian boundary. The cause of the decline of *Schizocrania* is not obvious, but coincides with the decline of graptolites in the early Devonian. The competition of rapidly evolving dacryoconarid tentaculites among marine plankton might the main cause of the disappearance of this trematid genus from this particular open sea habitat. Data about cephalopod encrusters were extensively reviewed by Radwanski (2011), and indicate that cephalopod shells were not used as the host for large organophosphatic brachiopods from the Middle Devonian. Other sclerobionts (crinoids, cornulites, bryozoans, edrioasteroids, microconchids, "worm tubes") occupied shells of dead cephalopods from the late

Ordovician (Radwanski 2011). In the Mesozoic, additional groups of invertebrates, such as barnacles, oysters and other bivalves (Taylor 1990) also attached to similar substrates.

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Explanations to the plates

PLATE 1

Schizocrania multistriata (Reed, 1905)

1. Dorsal valve in nodule, PCZCU 626, Darriwilian, Šárka Formation, Osek (field).
2. Dorsal valve in nodule, PCZCU 627, Darriwilian, Šárka Formation, Osek (field).
3., 4. Dorsal valve in nodule, and detail of ornamentation with partly preserved shell substance, PCZCU 2094, Darriwilian, Šárka Formation, Osek (field).
5. Small dorsal valve in shale, PCZCU 2095, Darriwilian, Dobrotivá Formation, upper part, Ejpovice (temporary excavation).
6. Dorsal valve with preserved convexity in shale, PCZCU 624+, Darriwilian, Dobrotivá Formation, lower part, Sedlec (excavation of well).
7. Dorsal valve with muscle scars and trace of median ridge in shale, PCZCU 625, Darriwilian, Dobrotivá Formation, lower part, Sedlec (excavation of well).
8. Dorsal valve in nodule, 3RO 23094 (original label VH 1370), Darriwilian, Dobrotivá Formation, Praha – Vokovice.
9., 10. Compressed dorsal valve with preserved muscle scars, and counterpart with fragment of ventral valve, PCZCU 628, Darriwilian, Dobrotivá Formation, lower part, Sedlec (excavation of well).
11. Small ventral valve in shale, PCZCU 2096, Darriwilian, Dobrotivá Formation, lower part, Ejpovice (open cast mine).
12., 15. Ventral valve in nodule in ventral and oblique views, 3RO 23094 (original label VH 1370), Darriwilian, Dobrotivá Formation, Praha – Vokovice.
13., 14. Ventral valve in shale in oblique and ventral views, PCZCU 2097, Darriwilian, Dobrotivá Formation, lower part, Ejpovice (open cast mine).

Schizocrania hornyi (Havlíček, 1972)

16., 17. Small dorsal valve in sandstone, with limonitised shell, with encrusting bryozoan on shell (distinct in counterpart) in side and dorsal views, PCZCU 2098, Sandbian, Libeň Formation, Řevnice Quartzite, Čilina Hill (N slope) near Rokycany.
18., 23. Holotype, medium sized dorsal valve (internal mould in sandstone) in oblique and dorsal views, 3RO 50889 (original label VH 1472a), Sandbian, Libeň Formation, Řevnice Quartzite, Čilina Hill near Rokycany; figured by Havlíček (1972) on pl. 1, fig. 6.
19., 24. Large dorsal valve, internal mould in sandstone, detail of ornamentation and dorsal view, PCZCU 2080, Sandbian, Libeň Formation, Řevnice Quartzite, Čilina Hill (summit platform).
20., 21. Dorsal valve, internal mould in sandstone, posterior and dorsal views, PCZCU 2099; Sandbian, Libeň Formation, Řevnice Quartzite, Čilina Hill (N slope).
22. Medium-sized dorsal valve, internal mould in sandstone, 3RO 50896 (original label VH 1479), Sandbian, Libeň Formation, Řevnice Quartzite, Kařezská hora.

Scale bars 3 mm (1–3, 5–24) and 1 mm (4).

PLATE 2

Schizocrania hornyi (Havlíček, 1972)

1., 5., 6. Small dorsal valve, internal mould in sandstone in dorsal (1), posterolateral (5), and anterolateral (6) views, PCZCU 2081, Sandbian, Letná Formation (lower part), Starý Plzenec.
2. Dorsal valve, internal mould in sandstone, PCZCU 2082, Sandbian, Letná Formation (lower part), Starý Plzenec.
3. Dorsal valve, internal mould in sandstone, 3RO 51697 (original label VH 1476), Sandbian, Letná Formation, Trubín.
4., 7. Dorsal valve, internal mould in sandstone in dorsal (4) and lateral (7) views, 3RO 51696 (original label VH 1475), Sandbian, Děd (Drabov) (old collections)
8. Dorsal valve, compressed internal mould in sandstone PCZCU 2083, Sandbian, Letná Formation (lower part), Starý Plzenec.

Schizocrania equestra sp. nov., all specimens (9–19) are from late Sandbian, Bohdalec Formation, Praha – Michle (temporary excavations in Chodovská street)

9., 10. Small undeformed dorsal valve in phosphate nodule, PCZCU 2084.
11. Holotype, compressed dorsal valve in shale, PCZCU 2085.
12. Compressed small dorsal valve in shale, PCZCU 2086.
13. Compressed dorsal valve in shale, PCZCU 2087.
14. Compressed large dorsal valve in shale, PCZCU 2088.
15. Compressed large dorsal valve in shale, PCZCU 2089.
16. Compressed large dorsal valve in shale, PCZCU 2090.
17. Elongate dorsal valve in shale, PCZCU 2091.
18. Compressed large dorsal valve in shale, detail of ornamentation, PCZCU 2092.
19. Compressed orthocone cephalopod with four attached shells (two at top right, two below), PCZCU 2093.

Scale bars 3 mm (1–19).

PLATE 3

Schizocrania incola (Perner, 1903)

1., 2., 11., 13. Dorsal valve in carbonate nodule, dorsal (1) and anterodorsal (2) views, detail of ornamentation (11) and details of costellation (13), 3RO 51700 (original label VH 998), Sandbian, Letná Formation (upper part), Zahořany.

3. Dorsal valve in sandstone, 3RO 51701 (original label VH 1477), Sandbian, Letná Formation (upper part), Trubská gorge.

4., 6., 9., 12., 15. Paralectotype, dorsal valve, internal mould in sandstone in dorsal (4), posterolateral (6) and anterior (15) views, and detail of ornamentation in left (9) and right (12) anterolateral margins, NM-L 5406, Sandbian, Letná Formation, probably upper part, Trubská; figured by Perner (1903) on pl. 43, fig. 10.

5., 8. Paralectotype, dorsal valve, internal mould in sandstone in dorsal (5) and anterior (8) views, NM-L 5405, Sandbian, Letná Formation, probably upper part, Trubská; figured by Perner (1903) on pl. 43, fig. 9.

7., 10., 16. Lectotype, dorsal valve, internal mould in sandstone showing visceral platform (16) in lateral (7), dorsal (16) and anterior (10) views, NM-L 5404, Sandbian, Letná Formation, probably upper part, Trubská; figured by Perner (1903) on pl. 43, figs 11, 12.

14. Paralectotype, dorsal valve, internal mould in sandstone, detail of ornamentation in right posterolateral margin, NM-L 5407, Sandbian, Letná Formation, probably upper part, Trubská; figured by Perner (1903) on pl. 43, figs 14, 15.

Schizocrania striata (J. de C. Sowerby, 1839)

17., 18., 20., 21. Ventral valve in limestone (17) and counterpart (20), detail of apex (18) and detail of ornamentation at anterior margin (21), 3RO 72443 (original label VH 13755), Přídolí, Požáry Formation, upper part, Suchomasty, Klonk, bed No. 7.

19., 22. Shell in limestone attached to strophomenid shell, with fragment of ventral valve preserved inside dorsal valve (19), and detail of ornamentation (22), 3RO 85502 (original label VH 12788), Lochkovian, Lochkov Formation, Kotýs Limestone, Svatý Jan pod Skalou, Solway's quarries.

Scale bars 3 mm (1–8, 10, 15–21), and 1 mm (9, 11–14, 22).

PLATE 1

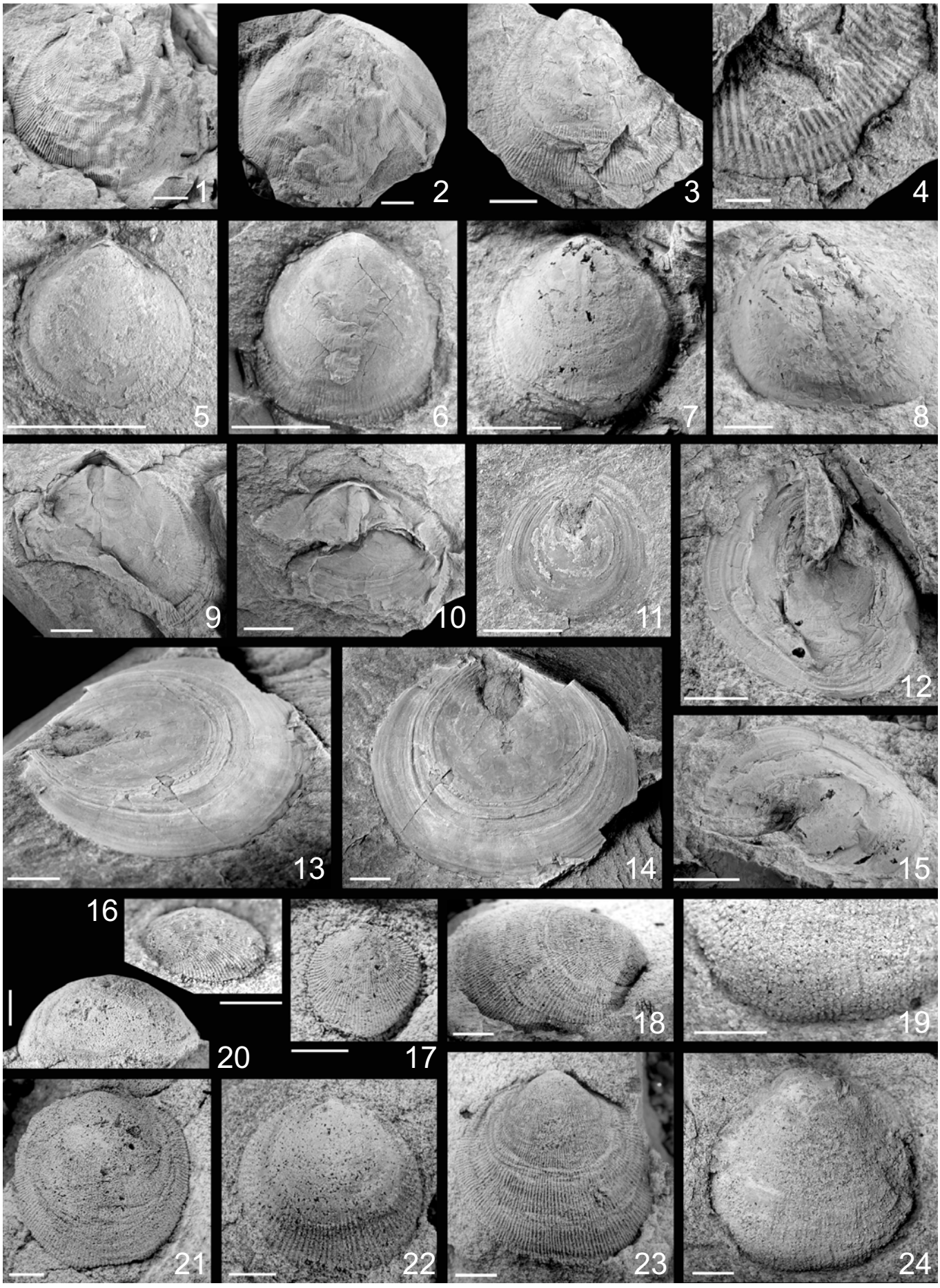

PLATE 2

PLATE 3