Ptychopariid trilobites in the Middle Cambrian of Central Bohemia (taxonomy, biostratigraphy, synecology)

Vratislav Kordule



A revision of ptychopariid trilobites from the Middle Cambrian of central Bohemia is presented. With a few exceptions, they were previously referred only to *Ptychoparia striata*. Three genera are recently distinguished: *Ptychoparia* Hawle & Corda, 1847, *Ptychoparioides* Růžička, 1940, and *Mikaparia* gen. nov. Seven species are described: three are revised, four are new, and two is left in open nomenclature; their stratigraphical ranges and significance are discussed. A new stratigraphical subdivision of the Middle Cambrian of the Skryje-Týřovice area is suggested, including three assemblage zones and three barren zones. Four substrate and bathymetrically controlled trilobite associations are recognized in the Skryje-Týřovice area. • Key words: Bohemia, Middle Cambrian, trilobites, new taxa, biostratigraphy.

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Vratislav Kordule, Dlouhá 104, 261 01 Příbram III, Czech Republic; Vkordule@seznam.cz

Representatives of the genera *Ptychoparia* Hawle & Corda 1847, *Ptychoparioides* Růžička, 1940, and *Mikaparia* gen. nov. are significant components of the trilobite fauna of the Middle Cambrian marine deposits in the Jince and Skryje-Týřovice areas. Specimens referred to these taxa were already described in part by Emmrich (1839), but a modern revision has appeared necessary since the paper of Šnajdr (1958). It is apparent that some formerly described ptychopariid species constitute so-called "cumulative" taxa.

Several authors have studied this trilobite group on material from Central Bohemia. The earliest detailed study by Barrande (1852) was followed by the contributions of Pompeckj (1896), Jaekel (1901), Růžička (1940, 1944), Richter (1940), and Šnajdr (1958, 1982). Růžička (1940) described several new genera and species from the basal Mileč Sandstone from the Na Kamenných hůrkách locality near Týřovice in the Skryje-Týřovice area. However, the majority of these species has been based on tectonically deformed specimens. Richter (1940) and Šnajdr (1958) critically evaluated this article. Both authors referred all of Růžicka's species to the genus *Ptychoparia* and to the species Ptychoparia striata (Emmrich, 1839). A new study of the original and new material confirmed the validity of some taxa described by Růžička (1940, 1944), primarily of the genus Ptychoparioides Růžička, 1940. Vokáč (1997) also studied ptychopariids, but there are some uncertainties in his systematic. Although the present author was unable to study the materials in Vokáč's private collection, the specimens described and figured by Vokáč (1997) can be identified, and their taxonomic position is revised.

Following the previous stratigraphical models (their summary is given in Havlíček 1998 and Fatka *et al.* 2004, Fatka 2006), Fatka & Kordule (1992), and Kordule (1996), presented a detail biostratigraphical scheme for the Middle Cambrian of the Jince area, based on distribution of index trilobites. A similarly detailed stratigraphy of the Middle Cambrian in the Skryje-Týřovice is missing. Stratigraphical schemes of the Middle Cambrian of the Skryje-Týřovice have been presented by Kettner (1923), and refined by Šnajdr (1958) and Havlíček (1971, 1998), but all are too general. The taxonomical revision of ptychopariid species with a compilation of their distributive data allows some corrections and additions to actual stratigraphic subdivision of the Middle Cambrian in the Skryje-Týřovice area; some ptychopariids are the valuable index species.

Material and methods

The specimens of studied collections are preserved in a variety of rock types, from coarse-grained quarzitic sandstone, greywacke, de-calcified siltstone, mudstone to carbonatic nodules. Some specimens from fine-grained sediments show minute details (tubercles, genal caeca) that are absent in those coming from coarse-grained rocks. Most of the specimens are slightly tectonically distorted; therefore the biometrical data are employed with a caution.

Locality names are consistent with names used by Šnajdr (1958; pp. 25–29) and Fatka & Kordule (1992). All figured specimens are covered by ammonium chloride if not otherwise stated.

Abbreviation of the collections: NM – Palaeontological collections of the National Museum, Prague; ČGÚ MŠ – Palaeontological collection of M. Šnajdr stored in the Czech Geological Survey, Prague; ČGÚ VK – Author's collection stored in the Czech Geological Survey, Prague; ČGÚ XB – Palaeontological collection of the Czech Geological Survey, Prague.

Systematic part

Superfamily Ptychopariacea Matthew, 1887 Family Ptychopariidae Matthew, 1887 Subfamily Ptychopariinae Matthew, 1887

Genus Ptychoparia Hawle & Corda, 1847

Type species. – Conocephalus striatus Emmrich, 1839; Middle Cambrian, Bohemia, Czech Republic.

Emended diagnosis (Snajdr 1958). – Glabella tapering forward, with weakly rounded anterior; four pairs of glabellar furrows; cephalic border prominent, rather long (sag.); anterior border furrow deep; genal spine prominent, short, rapidly tapering, extending backward toward the third segment; genal caeca prominent on external surface of preglabellar field, preocular field of fixigenae and librigenal field of librigenae; pygidium with 5 to 6 axial rings and terminal piece; pleural lobes with distinct pleural and interpleural furrows; exoskeleton surface with finely tuberculate sculpture.

Discussion. – E. & R. Richter (1941, p. 53) selected *Pty-choparia sternbergiana* Boeck, 1827 as the type species. However, this species is considered to be a *nomen dubium* (see Šnajdr 1986, p. 21). Neither the subsequent descriptions of the cranidium and the pygidium given by Šnajdr (1958), nor his generic diagnosis of *Ptychoparia* are correct because of a mismatch of the features of more than one species. The revised taxonomy therefore requires an emended diagnosis for the genus *Ptychoparia*.

The most valuable morphological features of the dorsal exoskeleton of *Ptychoparia* and allied genera that are used for their classification are:

1. the length of cranidium (sag.) relative to the length (sag.) of the anterior border (LCr/LAB index);

2. the morphology of the genal caeca and the sculpture of the cephalon;

3. the morphology of the pleural lobes on the pygidium;

4. the number of pygidial axial rings.

Based on these features, three morphological groups that likely represent particular evolutionary lineages have been distinguished. The first lineage (*Ptychoparia* Group) comprises several species of *Ptychoparia*, some of which are rare and insufficiently known. The second lineage (*Mikaparia* Group) comprises two species. The third lineage (*Ptychoparioides* Group) comprises three species, although Šnajdr (1958) synonymised *Ptychoparioides* Růžička, 1940 with *Ptychoparia* and all species of *Ptychoparoides* considered invalid. Members of all three lineages have been observed in a substantial part of the Middle Cambrian succession in central Bohemia, and are present both in the Jince and Skryje-Týřovice areas.

By comparing the original and the new specimens it has been observed that the diagnoses of the genus *Ptychoparia* given by Barrande (1852) and Šnajdr (1958) involved lumping particular species of the *Ptychoparia* and *Mikaparia* lineages. Their diagnoses therefore do not reflect the actual morphology of *Ptychoparia*. Some specimens used in their diagnoses are now grouped into the new genus *Mikaparia* sp. nov. In addition, new specimens that are comparable with those studied by Růžička (1940) indicate the validity of *Agraulopsis resseri*, the species referred by Šnajdr (1958) to *P. striata*; the revision of this species is out of scope of the present paper.

Species included. – Ptychoparia striata (Emmrich, 1839); Middle Cambrian, Bohemia, Czech Republic. Ptychoparia dubinka sp. nov.; Middle Cambrian, Bohemia, Czech Republic. Ptychoparia cf. striata (Emmrich, 1839); Middle Cambrian, Bohemia, Czech Republic. Ptychoparia? sp. A.; Middle Cambrian, Bohemia, Czech Republic.

Ptychoparia striata (Emmrich, 1839)

Figures 1A–M, 2J, K

- 1825 Trilobites Sulzeri var. γ. Sternberg, pl. 2, fig. 1 A.
- 1839 Conocephalus striatus Emmrich; Emmrich, p. 43.
- 1847 Ptychoparia striata nob. Hawle & Corda, p. 25, pl. 2, fig. 11.
- 1852 Conocephalites striatus Emmrich. Barrande (partim), pl. 14, fig. 3, non figs 1, 2, 4–7.
- 1896 ?Solenopleura spec. Pompeckj, pl. 15, fig. 21.
- 1906 Ptychoparia striata Emmrich. Lorenz, p. 58.
- 1940 Ptychoparia lobifera Růžička; Růžička, p. 4, pl. 1, figs 10–12.
- 1940 *Ptychoparia gracilis* Růžička; Růžička, p. 4, pl. 1, figs 13–15.
- 1940 ?*Lobocephalus cylindricus* Růžička; Růžička, p. 9, pl. 1, fig. 22.

- 1940 *Ptychoparioides nobilis* Růžička; Růžička (partim), p. 5, pl. 2, fig. 5.
- 1952 Ptychoparia striata (Emmrich). Prantl, fig. on p. 261.
- 1953 Ptychoparia striata (Emmrich, 1839). Přibyl, p. 62.
- 1953 Ptychoparia gracilis Růžička. Přibyl, p. 62.
- 1958 Ptychoparia striata (Emmrich, 1839). Šnajdr (partim), p. 185, pl. 38, figs 16, 19, non figs 18, 20; pl. 39, figs 4, 6–7, non figs 1–3, 5; pl. 40, fig. 1, non figs 2, 4, 6–7.
- 1959 Ptychoparoides Růžička. Moore (partim), p. 232, fig. 170-8b (non 170-8a).
- 1970 *Ptychoparia striata* (Emmrich, 1839). Horný & Bastl (partim), pp. 25, 147, 193, 301; non pl. 4, fig. 1 (= *Mikaparia milena* gen. et sp. nov.).
- 1983 *Ptychoparia striata* (Emmrich, 1939). Šnajdr, p. 196, pl. 3, fig. 2 (= invalid holotype selection by Šnajdr).
- 1989 Ptychoparia striata (Emmrich, 1939). Pek & Vaněk, p. 28.
- 1989 Ptychoparia lobifera Růžička, 1940. Pek & Vaněk, p. 43 (= noted as ?Ptychoparia mutica by Pek & Vaněk).
- 1989 Ptychoparia striata. Prokop, fig. on pl. 5, fig. 2.
- 1993 Ptychoparia striata (Emmrich). Levi-Setti, p. 179, pl. 103.
- 1997 Ptychoparia striata (Emmrich, 1839). Vokáč, pl. 1, figs 7–9.
- 2001 *Ptychoparia striata* (Emmrich, 1839). Vaněk & Valíček, p. 6.

Neotype. – Designated and figured by Šnajdr (1958, pl. 38, fig. 19), the complete specimen (catalogue numbers: old number ČC 330, No. 536; new number L 15177a) selected from the specimens of Barrande's collection stored in the National Museum, Prague, figured herein in Fig. 1B. It comes from material with the same catalogue number for several specimens. This specimen was never figured by Barrande. This explains that later references quoting this specimen as being figured by Barrande (1852, pl. 29, fig. 39) are incorrect, and refer to another specimen with the same catalogue number (ČC 330, No. 536).

The original specimens of Emmrich's collection have been lost. The selection of the holotype by Šnajdr (1983) is invalid because there is no evidence that this specimen comes from Emmrich's original collection. This specimen coming from Hawle's collection (Hawle & Corda 1847, pl. 2, fig. 11; refigured by Šnajdr, 1983, pl. 3, fig. 2), is almost complete though damaged, and is preserved as the internal mould in shale with the original label attached. This specimen is actually housed in the palaeontological collection of the National Museum, Prague, catalogue number NM L 17634.

Type horizon and locality. – Jince Formation, probably Paradoxides gracilis Zone; Czech Republic, Jince, slope called Vinice or Vystrkov Hill (determination based on lithology and mode of preservation).

Material. – Several tens of complete specimens and other parts of exoskeletons, mainly from the *Paradoxides gracilis* Zone.

Diagnosis. – Ptychoparia with S1, S2 very conspicuous, S3 distinct, S4 poorly marked, S1 unforked; paradoublure line poorly defined; pygidium with five rings and axial piece; pleural fields with four distinct ribs and a weakly defined fifth rib; genal caeca prominent on librigenae and frontal parts of fixigenae.

Emended description: Some new data is added to the descriptions of former authors (Šnajdr 1958). Anterior border is high, robust, highly convex, with maximum length at sagittal axis, tapering abaxially. Average LCr/LAB index is 5 (range 4.5-7 based on tectonic deformation). Genal spines are of moderate length. The exoskeleton is densely penetrated by fine punctae, including the lateral borders of the hypostome, the frontal part of rostrum and the cephalic doublure. Genal caeca prominent on librigenae and frontal parts of fixigenae. Caeca consist of radial canals essentially normal to lateral and anterior margins of the cephalon. The anastomosing canals are located more anterolaterally. The caecal morphology is clearly impressed on internal surface but only partly distinct on the outer surface of the cephalon. The fine tubercles cover bottom of interspaces between the caecal canals. The pygidial axis bears five distinct axial rings and the terminal piece. Pleural fields with four distinct ribs, fifth rib developed as weak elevation near the terminal axial piece. Pleural and interpleural furrows clearly differentiated.

The common length of a complete exoskeleton is 50 mm, rarely attaining nearly 70 mm.

Remarks. – The most accurate description of this species was presented Šnajdr (1958, pp. 185–190). However, this author used several different taxa in his general description, which must therefore be revised. The cephalon figured by Šnajdr (1958, p. 187, pl. 40) and referred to *Ptychoparia striata* (Emmrich) belongs to *Mikaparia milena* sp. nov. This cephalon has LCr/LAB of about 10 (anterior border is sagittally very short). Also the specimen figured by Barrande (1852) and refigured Moore *et al.* (1959, fig. 170:6 on p. O232) as *P. striata* is actually *M. milena*. The pygidium figured by Šnajdr (1958, Fig. 41) bears six axial rings and a terminal piece, and shows a distinct differentiation of the pleural and interpleural furrows; it actually belongs to *Ptychoparia dubinka* sp. nov.

Remains of soft and weakly sclerotised parts have been observed in several new specimens. Similar structures were made known by Jaekel (1901) from the closely related species *P. dubinka* sp. nov. However, Šnajdr (1958) expressed doubt about the origin of these impressions. Description of these soft and weakly sklerotised parts will be published elsewhere.

The earliest occurrence of *P. striata* is known from the basal sandstone of the Mileč Formation in the Skryje-Týřovice area. The species *Ptychoparia lobifera* and *P. gracilis*, both described as new taxa by Růžička (1940) from the Mileč Formation, were synonymized with *P. striata* by Šnajdr (1958). Newly discovered pygidia with five axial rings and the terminal piece support this opinion. The early specimens of *P. striata* from the Skryje-Týřovice area support the assumption that the species appeared in the Jince area slightly later, as the earliest and rare remains of the species are known from the *Acadolenus snajdri* Subzone. The species reached its maximum abundance in the *Paradoxides gracilis* Zone. All known complete exoskeletons of the species come from this zone.

Barrande (1852) presented the first description of *P. striata*. He described in detail the morphology of exoskeletons and evaluated the opinions of former authors. Pompeckj (1896) and Růžička (1940) included all now distinguished species of this genus in *P. striata*. In addition, Šnajdr (1958) used specimens from various stratigraphic levels of the Skryje-Týřovice and Jince areas in his redescription. However, the specimens referred by him to *P. striata* are now considered as particular species of three separate genera. Contrary to the synonymy list published by Šnajdr (1958), the following taxa are considered to be valid: *Conocoryphe mutica* Hawle & Corda, 1847, *Solenopleura torifrons* Pompeckj, 1896, and *Agraulopsis resseri* Růžička, 1940.

Several complete specimens figured by Barrande (1852) and Šnajdr (1958) from the *Paradoxides gracilis* Zone do not belong to the *Ptychoparia* Group. They are referred here to *Mikaparia milena* gen. and sp. nov. Both Richter (1940) and Šnajdr (1958) referred *Agraulopsis resseri* Růžička, 1940 to *P. striata*, as they believed that the original material represented extremely deformed individuals. Vokáč (1997) expressed some doubts about the type specimen selection of Šnajdr (1983).

This author preferred the type specimen of *Ptychoparia striata* that Šnajdr (1958) selected from the Barrande's collection. Because all original specimens of Emmrich's

(1839) collection have been misplaced among other specimens or were lost, it is wholly impossible to identify the original type specimen. In his description of P. striata, Barrande (1852) used the specimens from two genera, namely from the species Ptychoparia striata (Emmrich) and Mikaparia milena gen. et sp. nov. In addition, the neotype selected by Snajdr (1958, pl. 38, fig. 19) had never been figured earlier, despite the mistaken claims of other authors (Vokáč 1997, Vaněk &Valíček 2001) that it had been figured by Barrande (1852). This specimen has the same catalogue number as several unfigured specimens from Barrande's collection. Such ambiguity probably led Šnajdr (1983) to select the new type specimen (holotype by monotypy) from the Hawle's collection, because this specimen is the earliest collected, described, figured, and hitherto preserved specimen of P. striata. It is probable that this specimen originates from the same locality as Emmrich's specimen. It is noteworthy to add that the neotype by Snajdr (1958) and the more recently chosen holotype (Šnajdr 1983) belong to the same species. Moreover, Šnajdr's (1983) selection is consistent with the original description of Emmrich (1839), as well as the later description by Barrande (1852). The subsequent selection of the supposed holotype by Šnajdr (1983) is invalid.

Occurrence. – Skryje-Týřovice area: basal conglomerates and sandstones of the Mileč Formation; localities Malá Pleš near Kouřimecká hájovna, Na Kamenných hůrkách near Týřovice, Mileč Hill, and Slapnický mlýn. Jince Formation, Týřovice Greywackes, localities Hlohovice, and Čilá (new locality "U tří chat").

Jince area: Jince Formation; in all localities from the *Acadolenus snajdri* Subzone to *Paradoxides gracilis* Zone.

Ptychoparia dubinka sp. nov. Figures 2A–I, 3A–F

- 1896 Ptychoparia striata Emmr. sp. Pompeckj, pp. 541, 542, pl. 17, figs 6–8.
- 1901 *Ptychoparia striata* Emm. sp. Jaekel, pp. 133, 136–138, pls 4–6.
- 1941 Ptychoparia striata (Emmrich). Prantl, p. 118.

Figure 1. *Ptychoparia striata* (Emmrich, 1839). Jince Formation, probably *Paradoxides gracilis* Zone (A, B), *Paradoxides gracilis* Zone (C, D, F, G, M), Interval zone between *Eccaparadoxides pusillus* Zone and *Paradoxides gracilis* Zone (E), Mileč Formation (H–J). Localities: Jince, exact locality unknown (A, B), Jince, Vystrkov Hill (C, E, G), Jince, slope called Vinice (D, F, M), Skryje, Slapnický mlýn (K, L), Malá Pleš Hill near Kouřimecká myslivna (H–J). • A – complete small specimen, internal mould, NM L 17634, × 1.6 (designated as holotype by Šnajdr 1983). • B – complete specimen, internal mould, NM L 15177a, × 1.2 chosen by Šnajdr (1958) as neotype. • C – cephalon with part of thorax, internal mould, ČGÚ VK 215, × 1.4. • D – hypostom, internal mould, ČGÚ VK 216, × 3.1. • E – pygidium, internal mould, ČGÚ VK 217, × 2.5. • F – incomplete specimen with hypostome *in situ*, internal mould, ČGÚ VK 218, × 1.9. • G – laterodorsal view of cephalon with free cheek, internal mould, ČGÚ VK 215, × 1.7. • H – free cheek, internal mould, ČGÚ VK 219, × 2.8. • I – incomplete cranidium, internal mould, ČGÚ VK 220, × 3.0. • J – incomplete specimen showing sediment infilling of a gut, internal mould, NM L 6104, × 1.7.



- 1958 Ptychoparia striata (Emmrich, 1839). Šnajdr (partim), pp. 185, 189, text-fig. 41, pl. 39, fig. 3.
- 1997 *Ptychoparia tenuis* Pompeckj. Vokáč, p. 16 (partim), pl. 1, figs 2–4, non fig. 5 (=*Mikaparia mutica*).
- 1999 *Ptychoparia dubinka* sp. n. Kordule, p. 18 (*nomen nudum*).

Holotype. – Pygidium preserved as internal mould in siltstone, figured in Fig. 2E, housed in the collections of the Czech Geological Survey, Prague (ČGÚ VK 225).

Derivation of name. - After Dubinky Hill near Skryje.

Type horizon and locality. – Jince Formation, Skryje Shale, lower part of *Eccaparadoxides pusillus* Zone; Czech Republic, Skryje, hillside of Dubinky Hill in Zbiroh Creek valley (2.5 km SW of Skryje).

Material. – Several hundred complete specimens from a sandstone intercalation at the Pod trním locality near Týřovice, and several tens of cranidia, pygidia, librigenae, hypostomes from other localities in Skryje-Týřovice area.

Diagnosis. – Ptychoparia with S1, S2, S3 and S4 deeply incised and clearly defined; adaxial portion of S1 forked; anterior border prominent, with average LCr/LAB cca 6.0; genal caeca with anastomosing canals very prominent in external surface of the cephalon; paradoublural furrow distinctly separated from border furrow; distal ends of pleurae extended into short spines in all segments; pygidial axis with six axial rings and terminal piece; pygidial pleural fields with five pairs of ribs and rudimentary sixth rib; exoskeleton generally larger than in *P. striata*.

Description. - Dorsal exoskeleton heteropygous, elongately oval in outline, generally 70 mm in length, but might reach 100 mm as maximum. Cephalon broadly semicircular, less convex adaxial than abaxial periphery. Genal angle with prominent, although rapidly tapering genal spines that extend backward to approximately fifth thoracic segment. Glabella trapezoidal, tapering forward, weakly rounded anteriorly, defined by deep and wide axial and preglabellar furrows. Glabella bears four pairs of glabellar furrows. S1 longest, oblique, strongly curved backward, forked adaxially, with weaker and shallower anterior branch. S2, S3 are shorter and shallower; S2 curved backward, S3 almost normal to sagittal axis; S4 very short, transverse, weekly impressed anterior to ocular ridge. Occipital ring highly vaulted with small median node. Occipital furrow deeper abaxially, with shallow axial portion arched forward. Preglabelar field long, moderately vaulted. Anterior border strongly convex, long, with LCr/LAB cca 6.0, rapidly tapering abaxially. Anterior border furrow deep and wide (sag.), paradoublure furrow well defined in front of preglabellar furrow and adjacent part of fixigenae. Fixigena as wide (tr.) as glabella, gently convex (exsag.). Palpebral lobe of moderate size, feebly convex, situated opposite to S1, weakly raised above surface of fixigena. Ocular ridge prominent, inclined backward, slightly curved, uniting palpebral lobe with axial furrow slightly behind to S4. Librigena subtriangular in general outline, gently vaulted (exsag.), with evenly wide (tr.) border and narrow and shallow border furrow. Facial sutures differentiated; α - β convex adaxially, β - γ convergent, and ϵ - ω divergent to the genal angle. Preocular area of fixigena and librigena as well as preglabellar area covered by distinct, anastomosing ridges of genal caeca in chevron-like arrangement. Postocular fixigena with similar but much finer and less regular ridges.

Hypostome with prominent anterior lobe, distinct and much shorter posterior lobe separated by distinct middle furrow. Borders highly raised laterally and posteriorly. Anterior margin almost flat and weakly differentiated from anterior lobe. Dorsal surface of exoskeleton densely covered by fine hollow tubercles.

Long thorax of fourteen segments gently tapering backward. Axis strongly vaulted (tr.), almost evenly broad (tr.) along whole length, well defined by deep axial furrows. Pleurae fulcrate, with horizontal proximal and steeply sloping distal parts. Pleural furrow broad, concave (exsag.) tapering and deepening toward pleural tip. Anterior pleural band narrower than posterior band, which is gently expanding abaxially. Pleural extremities shortly pointed, gradually extending in posterior segments, with long, almost backward-directed spines.

Pygidium semicircular, gently vaulted. Pygidial axis long, highly convex, with six rings and terminal subtriangular piece. Lateral lobes with five distinct ribs on each pleural field and weakly defined sixth rib. Ribs separated by deep pleural furrows distinct toward very narrow (exsag.) and steeply sloping border. Interpleural furrows shallower than pleural furrows, but well defined and distinct all the way to the border. The pygidial doublure is narrow, gently extending anterolaterally.

External surface of exoskeleton densely covered by minute uniformly sized tubercles.

Remarks. – Vokáč (1997) suggested that *Ptychoparia striata tenuis* Pompeckj, 1896 is a valid taxon. However, the type specimen belongs to *Mikaparia mutica* (Hawle & Corda, 1847) and remains a subjective synonym. This corrected attribution is based on LCr/LAB, which is cca 9.5. As evident from his synonymy list and illustrations, Vokáč (1997) confused two different species: *Ptychoparia dubinka* sp. nov. and *Mikaparia mutica* (Hawle & Corda, 1847). In addition, Vokáč (1997) referred *Ptychoparia mutica* to the genus *Conocoryphe*, although shapes of the pygidia of *Mikaparia* and *Conocoryphe* are quite different.



Figure 2. *Ptychoparia dubinka* sp. nov. Jince Formation, Skryje Shale, lower part of *Eccaparadoxides pusillus* Zone. Localities: Skryje, Dubinky Hill (A, B, D–I), Týřovice, Studená hora Hill (C). • A – incomplete cranidium, internal mould, ČGÚ VK 222, × 1.8. • B – incomplete cranidium with left free cheek, internal mould, ČGÚ VK 223, × 1.5. • C – hypostome, internal mould, ČGÚ VK 224, × 4.3. • D – hypostome, internal mould, ČGÚ VK 223, × 1.5. • C – hypostome, internal mould, ČGÚ VK 224, × 4.3. • D – hypostome, internal mould, ČGÚ VK 227, × 4.2. • E – holotype, pygidium, internal mould, ČGÚ VK 225, × 2.2. • F – librigena, internal mould, ČGÚ VK 226, × 2.0. • G – pygidium, internal mould, ČGÚ VK 229, × 1.8. • I – detail of microornament in fixigena, ČGÚ VK 230, × 6.5. • *Ptychoparia striata* (Emmrich, 1839). Mileč Formation, Mileč Sandstone (J, K). Locality: Malá Pleš near Kouřimecká myslivna (J, K). • J – pygidium, internal mould, ČGÚ VK 232, × 3.5. • *Ptychoparia sp. Jince* Formation, *Eccaparadoxides pusillus* Zone, *Acadolenus snajdri* subzone. Locality: Jince, temporary excavation = locality No. 2 of Fatka & Kordule (1992). • L – incomplete cranidium, internal mould, ČGÚ VK 233, × 2.5.

Ptychoparia dubinka sp. nov. is probably a descendant of *Ptychoparia striata* from the basal conglomerates and sandstones of the Mileč Formation. A comparison with the specimens of *P. striata* from the Mileč Formation is difficult because of their rarity and poor preservation. New material allows confident differentiation of the species based on the higher number of axial rings in the pygidial axis of *P. dubinka*. Even complete specimens of *P. dubinka* have formerly been confused with *P. striata*, probably due to less favourable preservation in the sandstone at the Pod trním locality. The majority of well preserved specimens of *P. dubinka* have been found at Dubinky Hill (Kordule 1999).

The exoskeleton of *P. dubinka* is generally larger than that of *P. striata*. Jaekel (1901) figured the complete specimen of *P. dubinka* from the sandstone intercalation from the Pod trním locality near Týřovice. In this specimen, poorly preserved paired structures below the first to sixth axial rings of the axis are visible. He suggested that these structures are the remains of appendages of the ventral exoskeleton (coxa and endopodite). Šnajdr (1958, p. 190) did not support this opinion. However, new finds by the present author indicate that the original opinion of Jaekel (1901) was correct.

Occurrence. – Skryje-Týřovice area: Jince Formation, lower and middle part of the Skryje Shale and their stratigraphical equivalents (intercalation of the Týřovice Conglomerate in NE part of the area); localities Studená hora Hill near Týřovice, SE slope of Mileč Hill, Pod trním, slope Dlouhá hora, Dubinky Hill, Podmokelský mlýn, Lípa Hill, Mlečice, and Biskoupky.

Ptychoparia cf. *striata* (Emmrich, 1839) Figure 6N

Material. - One slightly deformed cranidium.

Description. – The specimen is similar to *Ptychoparia striata*, but differs in shortly conical glabella with preserved S1, S2 and S3, by poorly defined genal caeca, and external surface of cephalon covered by coarser tubercles than in *P. striata*. LCr/LAB 6.4. Other parts of the exoskeleton are unknown.

Remarks. - The specimen undoubtedly belongs to Ptycho-

paria, but differs from *P. striata* by its coarser ornament with larger tubercles. The number of glabellar furrows is unclear because S4 is not distinct; its absence may be a result of incomplete preservation.

Occurrence. – Jince area; Jince Formation, lower parts of the *Eccaparadoxides pusillus* Zone; Vystrkov, small hill N of the road from Jince to Velcí.

Ptychoparia? sp. A Figure 6M

Material. – Single cranidium preserved as internal mould in fine-grained brown-purple sandstone.

Description. – The cranidium is 16 mm long and 24 mm wide, slightly deformed. It differs from *Ptychoparia striata* (Emmrich) by wide (tr.) and convex cephalic border of unusual length (sag.). LCr/LAB about 6. Cephalic border separated from the glabella by a narrow and deep border furrow. Glabella slightly elevated above surface of fixigenae, of bluntly conical outline and with inconspicuous S1 to S4. Preglaberal field bears narrow and weakly defined transverse ridge, which joins the fixigenae. Fixigenae vaulted with ocular ridges, anterodorsally extended and connected with palpebral lobes of moderate size. Other parts of dorsal exoskeleton are unknown.

Remarks. – The preservation obscures the presence of S4 and the convexity of preglaberal field. Despite the described differences, the possibility that the cranidium is an unusually deformed cephalon of *P. striata* cannot be entirely excluded.

Occurrence. – Jince area; Jince Formation, lower part of the *Eccaparadoxides pusillus* Zone (*Acadolenus snajdri* Subzone); locality Rejkovice – Ve žlutých.

Mikaparia gen. nov.

Type species. – Mikaparia milena gen. et sp. nov.; Middle Cambrian, Czech Republic.

Derivation of name. – After the nickname for the female name Milena.

Figure 3. *Ptychoparia dubinka* sp. nov. Jince Formation, Skryje Shale, lower part of *Eccaparadoxides pusillus* Zone (A–F). Localities: Skryje, Dubinky Hill (A–C, E, F), Skryje, Pod trním (D). • A – incomplete specimen, internal mould, ČGÚ VK 234, \times 1.4. • B – cranidium, internal mould, ČGÚ VK 235, \times 1.7. • C – cranidium, latex cast of external mould, ČGÚ VK 236, \times 2.0. • D – complete specimen, internal mould uncoated with ammonium chloride, showing spinose pleurae, ČGÚ XB 46a, \times 1.6. • E – incomplete cranidium, latex cast of external mould, ČGÚ VK 237, \times 2.4. • F – cranidium, internal mould, ČGÚ VK 238, \times 1.6.

Vratislav Kordule • Ptychopariid trilobites in the Middle Cambrian of Bohemia



Diagnosis. – Glabella tapering forward, with weakly rounded anterior; four pairs of glabellar furrows; cephalic border short (sag.); anterior border furrow deep; genal spine conspicuous, long, weakly tapering; genal caeca weakly defined on external surface of preglabelar field, preocular field of fixigenae and librigenal field of librigenae; pygidium with six to eight rings and terminal piece, pleural field with distinct pleural furrows; interpleural furrows obscure or weakly defined; surface of cephalon with minute tubercles.

Discussion. – Mikaparia is closely related to *Ptychoparia*, but differs by its less prominent and shorter (sag.) cephalic border. Unlike *Ptychoparia*, the genal caeca of *Mikaparia* is less prominent on the external surface of the cranidium, and the courses of the canals are often overprinted by dominant minute tubercles. Genal spine of *Mikaparia* is long, almost straight and only gently tapering backward; the spine of *Ptychoparia* is shorter, curved and rapidly tapering. Ribs in pygidial pleural field are fused in *Mikaparia*, with only pleural furrows present. Unlike *Ptychoparia*, interpleural furrows are generally absent in *Mikaparia*. Pygidium of *Ptychoparia* is shorter, more transverse, with 5–6 rings on a gently tapering axis in contrast to the longer and narrower (tr.) axis of *Mikaparia*.

The new genus is present both in the Jince and Skryje-Týřovice areas, but particular species are restricted to distinct stratigraphical levels. Mikaparia mutica is restricted to the upper half of the Eccaparadoxides pusillus Zone in the Skryje-Týřovice area. Mikaparia milena sp. nov. is very rare in the lower two-thirds of the Jince Formation in the Jince area, but becomes abundant in the Paradoxides gracilis Zone. In 30 metre-thick succession of this zone, the species M. milena sp. nov. is slightly more frequent than Ptychoparia striata (Emmrich). It is noteworthy that this is also evident from the disproportion of the illustrations by Barrande (1852, pls 14, 29), and new collecting has supported this disparity. It is difficult to undertand why almost all ptychopariid trilobites have been incorporated under the name Ptychoparia striata. This confusion is probably historically based. Because P. striata was one of the earliest described trilobites in Bohemia, it has since been considered as the perfectly known, unproblematic taxon, and its splitting into several particular species has been difficult to accept.

Species included. – Mikaparia mutica (Hawle & Corda, 1847); Middle Cambrian, Bohemia, Czech Republic. *Mi-kaparia milena* sp. nov.; Middle Cambrian, Bohemia, Czech Republic.

Mikaparia milena sp. nov. Figure 4A–H

- 1852 Conocephalites striatus Emmrich. Barrande (partim), pl. 14, figs 1, 6, pl. 29, fig. 39.
- 1944 Ptychoparia striata (Emmrich). Růžička, p. 6, text-fig. 4 (refigured by Šnajdr, 1958, pl. 39, fig. 2).
- 1955 Ptychoparia striata Emmrich. Hupé, p. 129, fig. III/1.
- 1958 Ptychoparia striata (Emmrich, 1839). Šnajdr (partim), p. 185, text-fig. 40, pl. 38, figs 17, 18, pl. 39, figs 1, 2, pl. 40, figs 3, 5.
- 1959 Ptychoparia striata (Emmrich). Moore, p. O233, fig. 170:6.
- 1970 *Ptychoparia striata* (Emmrich, 1839). Horný & Bastl (partim), pl. 4, fig. 1, Catalogue pp. 301, 302.
- 1989 Ptychoparia striata. Prokop, fig. on p. 155.
- 1990 *Ptychoparia striata* (Emmrich, 1839). Šnajdr, p. 94, fig. on p. 95.
- 1992 Ptychoparia sp. nov. Fatka & Kordule, pl. 2, fig. 7.
- 1993 Ptychoparia striata (Emmrich). Chlupáč, p. 156, pl. 1, fig. 11.
- 1996 Ptychoparia sp. nov. Kordule, pl. 2, fig. 6.
- 2002 ?*Ptychoparioides* sp. Valíček & Szabad, p. 80, pl. 1, fig. 5.

Holotype. – Complete, slightly deformed specimen preserved as internal mould in silt shale, figured in Fig. 4H, housed in the palaeontological collections of the Czech Geological Survey, Prague (ČGÚ VK 243).

Derivation of name. - After a woman named Milena.

Type horizon and locality. – Jince Formation, middle part of the *Eccaparadoxides pusillus* Zone; Czech Republic, Rejkovice near Jince (locality No. 14 *in* Fatka & Kordule 1992).

Material. - Several tens of complete specimens and nume-

Figure 4. *Mikaparia milena* sp. nov. Jince Formation, *Acadolenus snajdri* Subzone (G), middle part of *Eccaparadoxides pusillus* Zone (H), Interval Zone between *Eccaparodoxides pusillus* Zone and *Paradoxides graci*lis Zone (B), *Paradoxides graci*lis Zone (A, C–F). Localities: Jince, probably slope called Vinice Hill (A, D, F), Jince, Vystrkov Hill (B), Felbabka (C, E), Rejkovice, Ve žlutých (G) = locality No. 11 of Fatka & Kordule (1992) (H). • A – complete specimen, internal mould, specimen figured by Barrande (1852) on pl. 29, fig. 39, NM L 15178 (IT 537, ČC 327), × 1.3. • B – cephalon, internal mould, ČGÚ VK 239, × 3.2. • C – cephalon with part of thorax, internal mould, ČGÚ VK 240, × 1.5. • D – complete specimen, internal mould, NM L 15176a, × 1.2. • E – pygidium with posterior part of thorax showing terminal parts of pleurae, internal mould, ČGÚ VK 241, × 1.5. • F – pygidium, internal mould, specimen figured by Barrande (1852) on pl. 14, fig. 6, NM L 12665 originally figured with 7 rings, but actually only with 6 rings and terminal piece, × 2.1. • G – pygidium, internal mould, ČGÚ VK 242, × 2.3. • H – holotype, complete specimen, internal mould, ČGÚ VK 243, × 1.5.

Vratislav Kordule • Ptychopariid trilobites in the Middle Cambrian of Bohemia



rous isolated parts of the exoskeletons mainly from the *Pa-radoxides gracilis* Zone.

Diagnosis. – Mikaparia with subtrapezoidal, forward tapering and anteriorly rounded glabella; S1 long, strongly curved backward, S2, and S3 shorter and shallower, S3 almost normal to sagittal axis; S4 weekly impressed; anterior border conspicuous, short (sag.), gently convex; average LCr/LAB cca 10.0; pygidial axis with six rings and subtriangular terminal piece; five ribs on pleural field.

Description. - Dorsal exoskeleton heteropygous, elongated oval in outline, generally 60 mm in length, exceptionally nearly 90 mm long. Cephalon semicircular with long genal spines that extend backward to fifth thoracic segment. Glabella subtrapezoidal, tapering forward, rounded anteriorly, defined by deep and wide axial and preglabellar furrows. Glabella bears four pairs of glabellar furrows, S1 longest, oblique, strongly curved backward; S2, S3 are shorter and shallower; S3 runs almost normal to sagittal axis; S4 weekly impressed. Occipital ring highly vaulted with small median node. Occipital furrow deep abaxially, with shallow axial portion curved forward. Preglabelar field vaulted, low. Anterior border strongly convex, short, with LCr/LAB near 10.0. Anterior border furrow deep and wide (sag.). Paradoublure furrow is not present. Fixigena as wide (tr.) as glabella, gently convex (exsag.). Palpebral lobe of moderate size, opposite to L2 and L3, slightly raised above surface of fixigena. Ocular ridge prominent, slightly inclined backward, uniting palpebral lobe with axial furrow opposite to S4. Librigena subtriangular in general outline, gently vaulted (exsag.), with evenly wide (tr.) border and narrow and shallow border furrow. Facial sutures differentiated; α - β convex adaxially, β - γ convergent, and ε - ω divergent to the genal angle. The rostral plate is transversally elongated, convex in ventral view. Hypostome with robust median body anterolaterally extended into short rounded extensions. Preocular area of fixigena and librigena, and the preglabellar area, covered by weakly defined genal caeca composed of radially arranged anastomosing fine ridges.

Long thorax of fourteen segments gently tapering backward. Axis strongly vaulted (tr.), almost evenly broad (tr.) along whole length, well defined by deep axial furrows. Pleurae fulcrate, with horizontal proximal and steeply sloping distal parts. Pleural furrow broad, concave (exsag.) tapering and deepening toward pleural tip. Anterior pleural band narrower than posterior band, which gently expands abaxially. Pleural extremities shortly pointed.

Pygidium subpentagonal. Pygidial axis convex, with six rings and terminal subtriangular piece. Lateral lobes with five ribs on each pleural field. Ribs separated by deep pleural furrows distinct toward narrow (exsag.) border. The first and second ribs bear shallow interpleural furrow, but repining ribs are without furrows. The pygidial doublure is narrow, gently extending anterolaterally.

External surface of exoskeleton densely covered by minute, uniformly sized tubercles.

Remarks. – Valíček & Szabad (2002, pl. 1, fig. 5) figured a cranidium from the basal beds of the Jince Formation. These authors referred this specimen to *Ptychoparioides* sp., but it probably belongs to *Mikaparia milena* sp. nov. However, the specimen is kept in a private collection that was not available to the present author.

The earliest occurrence of the new species is in the middle of the *Eccaparadoxides pusillus* Zone of the lower Jince Formation. The specimens are rare there and in the following sequence cca 230 m thick of siltstone and mudstone. The species becomes abundant in the *Paradoxides gracilis* Zone, in association with *Ptychoparia striata*. This explains why all specimens as yet figured come from this upper level (Barrande 1852, Šnajdr 1958).

Mikaparia milena sp. nov. is probably an ancestor of *Mikaparia mutica* (Hawle & Corda, 1847), which is known from the Skryje-Týřovice area. The latter has seven to eight rings on the pygidial axis and terminal piece. Barrande (1852, pl. 14, fig. 6) figured a pygidium that belongs to *M. milena* from the Jince area. This specimen has seven rings on its pygidial axis, but this feature is the combination of a damaged axis and schematic drawing. A similar situation concerns another pygidium (Barrande 1852; pl. 29, fig. 39). All studied specimens have only six rings and a terminal piece.

Occurrence. – Jince area, Jince Formation, in all trilobitebearing localities from the *Acadolenus snajdri* Subzone (rare) to *Paradoxides gracilis* Zone (frequent).

Mikaparia mutica (Hawle & Corda, 1847)

Figures 5, 6, 7

- 1847 *Conocoryphe mutica* Hawle & Corda, 1847; pp. 24, 167.
- 1852 Conocephalites striatus Emmrich. Barrande (partim), pl. 14, fig. 7.
- 1896 Ptychoparia striata tenuis Pompeckj. Pompeckj, p. 542, pl. 17, fig. 9.
- 1958 Conocoryphe Hawle & Corda, 1847. Šnajdr (partim), p. 156.
- 1958 *Ptychoparia striata* (Emmrich, 1839). Šnajdr (partim), p. 185, pl. 39, fig. 5, pl. 40, figs 2, 4, 6, 17.
- 1970 Ptychoparia striata (Emmrich, 1839). Horný & Bastl (partim), p. 301.
- 1982 *Conocoryphe mutica* Hawle & Corda. Šnajdr, p. 67, pl. 3, fig. 4.



Figure 5. *Mikaparia mutica* (Hawle & Corda, 1847). Jince Formation, Skryje Shale, middle and upper part of *Eccaparadoxides pusillus* Zone. Localities: Skryje, Buchava (B, C, F), Skryje, slope Dlouhá hora (A, G), Dubinky Hill (H), Týřovice, Pod hruškou (D), Skryje, Plazy (E). • A – cranidium, latex cast of external mould, ČGÚ VK 248, × 2.8. • B – librigena, internal mould, ČGÚ VK 249, × 1.4. • C – pygidium, internal mould, ČGÚ VK 250, × 2.8. • D – pygidium, internal mould, NM L 17851, × 1.7, figured as lectotype by Šnajdr (1982) on pl. 3, fig. 4. • E – pygidium, of small specimen, internal mould, ČGÚ VK 251, × 6.5. • F – pygidium, internal mould, ČGÚ VK 252, × 2.3. • G – pygidium, internal mould, ČGÚ VK 253, × 1.7. • H – pygidium, latex cast of external mould showing spinose ornament, ČGÚ VK 247, × 2.4.

- 1983 mutica, Conocoryphe Hawle & Corda. Šnajdr, p. 174 [as Ptychoparia mutica (H. & C. 1847)].
- 1989 Ptychoparia mutica (Hawle & Corda). Pek & Vaněk, pp. 28, 51 (for striata tenuis, Ptychoparia Pompeckj, 1895).
- 1997 *Ptychoparia tenuis* Pompeckj, 1895. Vokáč, p. 16, pl. 1, fig. 5.
- 2001 Ptychoparia tenuis Pompeckj, 1895. Vaněk & Valíček, p. 6.

Lectotype. – (SD Šnajdr 1958, p. 185). Deformed pygidium preserved as internal mould in siltstone, from the Hawle collection, with original label attached, figured here in Fig. 5D), housed in the palaeontological collection of the National Museum, Prague (L 17851).

Type horizon and locality. – Jince Formation, upper part of the *Eccaparadoxides pusillus* Zone; Czech Republic, Tý-řovice, Pod hruškou locality.

Material. – Two damaged complete specimens, about twenty cranidia, twenty pygidia.

Diagnosis. – Mikaparia with subtrapezoidal, forward tapering and anteriorly rounded glabella; S1 long, strongly curved backward, S2 and S3 shorter and shallower, S3 almost normal to sagittal axis; S4 weekly impressed; anterior border narrow (sag.), gently convex; average LCr/LAB cca 9.0; pygidial axis with seven to eight rings and subtriangular terminal piece; six ribs on pleural field; interpleural furrows absent; genal caeca obscure on external surface of cephalon.



Figure 6. *Mikaparia mutica* (Hawle & Corda, 1847). Jince Formation, Skryje Shale, middle part of *Eccaparadoxides pusillus* Zone. Locality: Skryje, Buchava. • A – incomplete cranidium, internal mould, ČGÚ VK 244, × 1.5. • B – cranidium, internal mould, ČGÚ VK 245, × 1.8.

Remarks. – The exoskeleton is generally similar to that of *M. milena* sp. nov. Major differences are as follows: (1) LCr/LAB about 9, depending on tectonic deformation and the age of specimen, range between 8 and 10; (2) internal surface of the cephalic shield has the same radial canals of genal caeca and very small tubercles, but the external surface of cephalon shows only tubercles; (3) pygidial axis of seven rings and terminal piece, occasionally with eight rings and terminal piece; (4) deep pleural furrows define six ribs in the pleural field of the pygidium. Interpleural furrows are absent (rarely their traces may be seen only on first three ribs, but this may be due to deformation).

It has been suggested that the name *Conocoryphe mutica* (Hawle & Corda, 1847) is invalid (Barrande 1852, Šnajdr 1958). It seems likely that the main reason for this lies in the incorporation of Hawle's specimens into Barrande's collections, in which the type specimen of *Conocoryphe mutica* was not stored separately. Revising Barrande's collection, Šnajdr (1982, pl. 3, fig. 4) found and figured one of the original syntypes of Hawle & Corda (1847). This specimen (an internal mould of a pygidium) is labeled in original ink, and was selected by Šnajdr (1958) as the lectotype of *Conocoryphe mutica* Hawle & Corda, 1847, but the same author synonymised *C. mutica* with *Ptychoparia striata*.

The common length of holaspid specimens is 60 to 70 mm, but some specimens seem to have reached 100 mm as might be inferred from exoskeletal fragments. Pygidia of M. mutica generally have seven axial rings and a terminal piece. However, the large pygidia rarely show eight axial rings and the terminal piece. This variation in the number of axial rings is unknown in any other ptychopariid taxon. This might be explained by phenotypic variability, because it seems unlikely that these pygidia belong to another ptychopariid species. Šnajdr (1982) noted that the lectotype (pygidium) of *P. mutica* bears weakly preserved interpleural furrows, but that the pygidial shield is deformed along the sagittal axis. Weak furrows reminiscent of interpleural furrows in several available pygidia are likely to have originated by compression along the sagittal axis.

The lower half of the sequence referred to the *Eccaparadoxides pusillus* Zone in the Skryje-Týřovice area yielded only *Ptychoparia dubinka* sp. nov. In the higher part of the zone, *P. dubinka* is gradually substituted by *Mikaparia mutica* (Hawle & Corda, 1847). Within approximate beginning of the upper third of the *Eccaparadoxides pusillus* Zone, there is an overlap of the older faunal assemblage characterised by *P. dubinka*, *Ptychoparioides henkli* sp. nov., and *Germaropyge germari* with a younger assemblage. A sequence about ten metres thick, known from all accessible sites with this stratigraphical interval in the Skryje-Týřovice area, yielded both *P. dubinka* and *M. mutica*.

Mikaparia mutica is an important index species of the youngest faunal assemblage in the Skryje-Týřovice area, associated with *Sao hirsuta*, *Eccaparadoxides rohanovicus*, *Solenopleurina tyrovicensis*, *Agraulos ceticephalus*, *Jincella prantli*, *Peronopsis umbonata*, *Condylopyge rex*, *Diplorrhina cuneifera* and other agnostids.

Occurrence. – Skryje-Týřovice area: Jince Formation, upper part of the Skryje Shale; localities Studená hora Hill near Týřovice, Pod hruškou near Týřovice, Luh and Plazy near Skryje, slope Dlouhá hora, Dubinky Hill, and Buchava.

Genus Ptychoparioides Růžička, 1940

- 1940 Ptychopairoides Růžička; Růžička, p. 5.
- 1953 Ptychoparioides Růžička, 1939. Přibyl, p. 63.
- 1958 Ptychoparioides Růžička. Šnajdr, pp. 184, 186, 190.
- 1959 Ptychoparoides Růžička. Moore (partim), p. O233,
 - pl. 170/8a, non 8b (= *Ptychoparia striata*).

- 1989 Ptychoparioides Růžička 1940. Pek & Vaněk, p. 57 (by the authors considered as Ptychoparia mutica Hawle & Corda, 1847).
- 2001 Ptychoparioides Růžička, 1940. Vaněk & Valíček, p. 7.

Type species. – Solenopleura torifrons Pompeckj, 1896; Middle Cambrian, Czech Republic.

Remarks. – According to chapter 70.3 of the Zoological Code (fourth edition), the type species of the genus *Ptychoparioides* Růžička, 1940 is defined as *Solenopleura torifrons* Pompeckj, 1896. The selection of *Ptychoparioides nobilis* Růžička, 1940 as the type species is invalid because it is based on an incorrectly identified specimen, which actually belongs to *Solenopleura torifrons* Pompeckj, 1896. In addition, the type specimen selected by Růžička (1940) did not originate from the original collection of Pompeckj (1896).

Emended diagnosis (Růžička 1940). – Glabella highly convex, bluntly conical, anteriorly rounded, extending nearly toward border furrow; axial furrows deep; occipital ring vaulted, with small median node; S1, S2 and S3 shallow; preglabellar field flat; anterior border short (sag.), high, convex, separated from glabella by deeply concave border furrow; ocular ridges prominent; palpebral lobes small; genal caeca obscure; genal spine short; thorax of 14 segments; pygidium transverse, with axis with three to five rings and large terminal piece; pleural furrows present, interpleural furrows absent; surface of exoskeleton finely tuberculate.

Discussion. – Ptychoparioides differs from Ptychoparia and Mikaparia by having a conical instead of a trapezoidal or subtrapezoidal glabella. The preglabellar field of Ptychoparioides is low and depressed, and the anterior border is shorter (sag.) and raised and shelf-like, unlike the convex and broad preglabellar field of Ptychoparia. Librigena of Ptychoparioides extend into short spines not extending beyond the second segmnet of the thorax. Pygidium of Ptychopariodes is shorter, less arched and more transverse than in Ptychoparia and Mikaparia, with weakly defined pleural and interpleural furrows. It is worth noting that the general morphology of Ptychopariodes is similar to that of Conocoryphe, but there are striking differences in the facial suture courses between these genera. The genal caeca of Ptychoparioides is obscure compared to Ptychoparia.

The diagnosis of the genus given by Růžička (1940) is inaccurate because it is based on poorly preserved specimens from sandstone. The genus was therefore considered invalid by Richter (1940) and Šnajdr (1958). It was synonymised with *Ptychoparia* Hawle & Corda, 1847 and its type species put into synonymy with *Ptychoparia striata*



Figure 7. *Mikaparia mutica* (Hawle & Corda, 1847). Jince Formation, Skryje Shale, upper part of *Eccaparadoxides pusillus* Zone. Locality: Skryje, slope Dlouhá hora (A), Dubinky Hill (B). • A – librigena, latex cast of external mould, ČGÚ VK 246, \times 2.0. • B – librigena showing long spine, latex cast of external mould, ČGÚ VK 247, \times 1.6.

(Emmrich, 1839). However, the well preserved specimens from fine-grained sediments of the Skryje-Týřovice and Jince areas (Kordule 1996) indicate the validity of the genus and allow further refinement of the generic diagnosis.

Ptychoparioides torifrons (Pompeckj, 1896) Figure 8A–G

- 1896 Solenopleura torifrons Pompeckj; Pompeckj, p. 546, pl. 15, fig. 22.
- 1907 Solenopleura torifrons Pompeckj. Kafka & Perner, fig. 243/7.
- 1940 *Ptychoparioides nobilis* Růžička; Růžička, p. 5, pl. 2, figs 1–4, pl. 3, figs 4, 5.

- 1940 Ptychoparioides torifrons Růžička; Růžička, p. 6, pl. 2, figs 6–9, pl. 3, figs 6–8.
- 1944 Ptychoparioides nobilis Růžička; Růžička, p. 5, text-fig. 5.
- 1953 Ptychoparioides nobilis Růžička. Přibyl, p. 63.
- 1955 Ptychoparoides nobilis Růžička. Hupé, p. 129, fig. 11/4.
- 1958 Ptychoparia striata (Emmrich, 1839). Šnajdr,
 p. 184 (partim), pp. 186, 190, pl. 38, fig. 20.
- 1959 Ptychoparoides nobilis. Moore, p. O233, fig. 170:8a, non 8b (= Ptychoparia striata).
- 1970 Ptychoparioides nobilis Růžička, 1940. Horný & Bastl, p. 217, as Ptychoparia striata.
- 1989 nobilis, Ptychoparioides. Pek & Vaněk, p. 45, as Ptychoparia mutica.
- 2001 Ptychoparioides torifrons Růžička, 1940. Valíček, p. 7.

Lectotype. – Cranidium preserved as internal mould in sandstone, figured by Pompeckj (1896, pl. 15, fig. 22a), housed in the Geologische Bundesanstalt, Wien, Austria, coll. No. 1896/04/0047. The original selection of Růžička (1940) is invalid because the lectotype was not selected from the type specimens of Pompeckj (1896).

Type horizon and locality. – Middle Cambrian, Mileč Formation, upper part of the formation; Czech Republic, Týřovice, Na Kamenných hůrkách locality.

Material. – Eight cranidia and five pygidia.

Diagnosis. – Ptychoparioides with highly convex, anteriorly subtruncate glabella; S1 and S2 are shallow, inclined backward, S3 and S4 are short, shallow, transverse; preglabelar field flat; cephalic border conspicuously convex anteriorly; anterior border short, evenly broad (sag.), convex; separated from preglabelar field by broadly concave border furrow; ocular ridges strongly inclined backward; pygidium transverse, with axis cca 25% of pygidial width; five axial rings and terminal piece; two flat, weakly defined ribs on pleural lobes.

Remarks. – Fine details of the morphology such as genal caeca and tubercles are not preserved by the coarse sandstone of the original locality. New data about the morphology of the pygidia are based on new material from Malá Pleš Hill near Týřovice. Růžička (1940) distinguished two species, *Ptychoparioides nobilis* Růžička, 1940 and *P. torifrons* (Pompeckj, 1896). Revision of the specimens figured by Růžička (1940) and newly collected specimens indicate that both species are variably deformed specimens of the same species. This opinion is supported also by the drawings of Růžička (1940, pl. 3, figs 4–8), which, apart the deformation, do not show any other differences. The name *P. nobilis* is considered a subjective synonym of *P. torifrons*.

Occurrence. – Skryje-Týřovice area: basal conglomerates and sandstones of the Mileč Formation; localities Malá Pleš near Kouřimecká hájovna, Na Kamenných hůrkách near Týřovice, Mileč Hill, Slapnický mlýn. Jince Formation, Týřovice Greywackes, lower part; locality Hlohovice.

Ptychoparioides henkli sp. nov. Figure 9A–J

- 1997 Ptychoparioides cf. torifrons (Pompeckj, 1895). Vokáč, p. 17, pl. 1, fig. 6.
- 1999 Ptychoparioides henkli sp. nov. Kordule, p. 18 (nomen nudum).

Holotype. – Complete, slightly damaged specimen, preserved as internal mould in shale, figured in Fig. 9E. Housed in the collection of the Czech Geological Survey, Prague (ČGÚ VK 265).

Derivation of name. – After Luboš Henkl, a private fossil collector.

Type horizon and locality: Jince Formation, lower part of the *Eccaparadoxides pusillus* Zone; Czech Republic, Skryje, Dlouhá hora locality.

Figure 8. *Ptychoparioides torifrons* (Pompeckj, 1896). Mileč Formation, Mileš Sandstone (A–G). Localities: Týřovice, Na Kamenných hůrkách (A–C), Skryje, Slapnický mlýn (D, E), Malá Pleš near Kouřimecká myslivna (F, G). • A – cranidium, internal mould, NM L 28206, × 2.0. • B – cranidium, internal mould, NM L 28200, × 2.0. • C – cranidium, internal mould, NM L 19652, × 2.3. • D, E – cranidium, internal mould and its oblique view, ČGÚ MŠ 9770, × 3.9. • F – pygidium, internal mould, ČGÚ VK 254, × 3.2. • G – pygidium, internal mould, ČGÚ VK 255, × 3.8. • *Ptychoparioides chlupaci* sp. nov. Jince Formation, *Acadolenus snajdri* Subzone (H, P), *Litavkaspis rejkovicensis* Subzone (I–K). Localities: Rejkovice, Ve žlutých (H, P) = locality No. 11 of Fatka & Kordule (1992); Rejkovice, Potůček (I–K). • H – cranidium, internal mould, ČGÚ VK 256, × 3.5. • I – cranidium, external mould showing spinose surface, ČGÚ VK 257, × 4.0. • J – cranidium, internal mould, ČGÚ VK 257, × 2.1. • K – holotype, damaged complete specimen, internal mould, ČGÚ VK 258, × 2.7. • O – cranidium, internal mould, ČGÚ VK 263, × 2.4. • *Mikaparia mutica* (Hawle & Corda, 1847). Jince Formation, Skryje Shale (L, M). Locality: Skryje, slope Dlouhá hora. • L – nearly undeformed cranidium preserved in siltstone with longer preglaberal field, internal mould, ČGÚ VK 260, × 1.2. • M – cranidium, internal mould, ČGÚ VK 261, × 4.5. • *Ptychoparia cf. striata* (Emmrich, 1839). Jince Formation, lower part of *Eccaparadoxides pusillus* Zone. Locality: Velcí. • N – cranidium, internal mould, ČGÚ VK 262, × 2.5. • ?*Ptychoparia* sp. A. Jince Formation, *Acadolenus snajdri* Subzone. Locality: Rejkovice, Ve žlutých = locality No. 11 of Fatka & Kordule (1992). • P – cephalon with part of thorax, internal mould, ČGÚ VK 259, × 1.8.



Material. – Five complete specimens, several cranidia and pygidia.

Diagnosis. – Ptychoparioides with highly convex, forward rapidly tapering glabella, which is distinctly higher than fixigenae; S1 and S2 are moderately deep and inclined backward, S3 and S4 are short, shallow, transverse; preglabelar field flat, very short; anterior border short, evenly broad (sag.), weakly convex, with edge directed anterodorsally, separated from preglabelar field by broadly concave border furrow; ocular ridges conspicuous, almost straight, strongly inclined backward towards small palpebral lobes; pygidium transverse, with axis 30–35% of pygidial width; five axial rings and terminal piece; two distinct and third weakly defined pleural furrows in lateral pygidial lobe; interpleural furrow weakly defined between the first and second pleura; third and fourth ribs poorly defined.

Differential description. – The species resembles *Ptychoparioides torifrons* but differs by the following features: (1) lower cephalic border less convex anteriorly and dorsally; (2) pygidium broadly rounded posteriorly, with distinctly vaulted pygidial axis having five rings and the terminal piece; (3) lateral lobes with four weakly marked ribs; three anterior pairs with distinct pleural and interpleural furrows, furrow in the fourth pair obscure.

Remarks. – This rare species is known only from the Skryje-Týřovice area. It is a probable descendent of *P. to-rifrons* (Pompeckj, 1896), which stratigraphically preceded it. *Ptychoparioides henkli* sp. nov. is similar to *P. chlupaci* sp. nov. but differs from the latter in having deeper S1–S4, less vaulted fixigenae, and a glabella highly raised above the fixigenae. The pygidium of *P. henkli* is larger and longer (sag.), with five rings in the axis. The length of adult specimens is larger than *P. chlupaci*.

General shape, outline of the glabella and especially the shape of the pygidium of *P. henkli* are very similar to *Conocoryphe*, particularly to *Conocoryphe sulzeri cirina* Šnajdr, 1982.

Ptychoparioides henkli, Ptychoparia dubinka and *Germaropyge germari* are the index taxa of the association of the lower and middle part of the *Eccarapadoxides pusillus* Zone in the Skryje-Týřovice area.

Occurrence. - Skryje-Týřovice area: Jince Formation,

Skryje Shale; localities slope Dlouhá hora, Dubinky Hill, Podmokelský mlýn, and Mlečice.

Ptychoparioides chlupaci sp. nov. Figure 8H–K

1996 Ptychoparioides sp. nov.; Kordule, pl. 2, fig. 4.

Holotype. – Almost complete, slightly damaged specimen, preserved as internal mould in sandstone, figured in Fig. 8. K. Housed in the collection of the Czech Geological Survey, Prague (ČGÚ VK 258) (from Knížek coll.).

Derivation of name. – In honour of the late Professor Ivo Chlupáč (1931–2002), a famous Czech palaeontologist.

Type horizon and locality. – Jince Formation, *Eccaparadoxides pusillus* Zone, *Litavkaspis rejkovicensis* Subzone; Czech Republic, Rejkovice, Potůček locality.

Material. – The holotype, a cephalon with four attached thoracic segments and four cranidia.

Diagnosis. – Ptychoparioides with slightly convex glabella, weakly tapering forward as high as fixigena, with evenly rounded anterior lobe; S1 and S2 are shallow, inclined backward, S3 and S4 are short, shallow, transverse; preglabelar field flat, very short; anterior border short, evenly broad (sag.), weakly convex anteriorly and dorsally, with edge directed dorsally, separated from preglabelar field by broadly concave border furrow; ocular ridges conspicuous, weakly curved and inclined backward towards small palpebral lobes; pygidial width; three axial rings and terminal piece; two distinct and third weakly defined pleural furrows in lateral pygidial lobe; interpleural furrow weakly defined between the first and second pleura; third and fourth ribs poorly defined.

Differential description. – The species resembles *Ptychoparioides torifrons*, but differs by the following features: (1) cephalic border less vaulted anteriorly and dorsally; (2) fixigenae more convex, raised to almost the same level as the glabella; glabella is slightly convex; (3) librigenae extended into very short spines; (4) external surface of cepha-

Figure 9. *Ptychoparioides henkli* sp. nov. Jince Formation, Skryje Shales, lower part of *Eccaparadoxides pusillus* Zone (A–J). Localities: Skryje, Buchava (A), Skryje, slope Dlouhá hora (C–E), Skryje, locality Jahn (B, F–J). • A – cranidium, internal mould, ČGÚ VK 264, × 2.2. • B – cranidium, internal mould, ČGÚ VK 266, × 2.5. • C, D – cephalon with thorax, internal mould and its oblique view; note hypostome *in situ*, ČGÚ P 2713, × 1.8. • E – holotype, complete specimen, internal mould with hypostome *in situ*, ČGÚ VK 265, × 1.3. • F – pygidium, internal mould, ČGÚ VK 268, × 2.0. • H – pygidium of small specimen, internal mould, ČGÚ VK 269, × 5.5. • I – pygidium, internal mould, ČGÚ VK 270, × 4.6. • J – pygidium, latex cast of external mould showing fine granulation, ČGÚ VK 267, × 2.3.



lon densely covered by very fine spines; (5) pleurae with deep pleural furrow, the terminal points of pleurae rounded; (6) Pygidium short (sag.), extended laterally; the axis has three rings and a terminal piece.

Remarks. – The new species resembles *Ptychoparioides torifrons* (Pompeckj, 1896), but differs by its less vaulted cephalic border and conspicuously convex fixigenae. A very short and transverse pygidium distinguishes *P. chlupaci* from *P. torifrons* and *P. henkli* sp. nov. Less convex and less tapering glabella with shallow glabellar furrows distinguish *P. chlupaci* from *P. henkli*. Some morphological features, such as the librigenal spines and the thorax, are unknown in *P. torifrons* and cannot be used in the discrimination of other species.

The first report of *Ptychoparioides* in the Jince area was published by Kordule (1996). *Ptychoparioides chlupaci* sp. nov. could be a descendent of *P. torifrons* from the Skryje-Týřovice based on some common morphological features, for example short transverse pygidium with narrow (tr.) axis.

Occurrence. – Jince area; Jince Formation, lower and middle parts of the *Eccaparadoxides pusillus* Zone, (*Litavkaspis rejkovicensis* and *Acadolenus snajdri* Subzones); localities Potůček and Ve žlutých near Rejkovice.

Synecology of the ptychopariid trilobites in the Skryje-Týřovice area

In the Skryje-Týřovice area, the ptychopariid trilobites occur in various lithofacies that likely reflect diverse palaeobathymetric conditions. The diverse palaeobathymetry of recent fossil-bearing sites in the Skryje-Týřovice area was already suggested by Havlíček (1971) and Kukal (1971). In the Jince area, the ptychopariids occur in a lithofacially less varied succession with a presumably less steep sea-floor gradient. However, in contrary to taxonomic studies, little attention has been given to taphonomy and palaeoecology of the fossils assemblages in both areas. There are reports on brachiopods (Mergl & Šlehoferová 1989), miomerid trilobites (Kordule 1996), generalised models (Fatka 1998, 2000) and trophic models or analysis of some special groups (Lefebvre & Fatka 2003, Fatka 2005).

The important topic is to determine how indigenous are the fossil assemblages. The model presented here is based on lithological, palaeoecological and taphonomical criteria compiled from numerous sites in the Skryje-Týřovice area. In is worth to note, that part of the fossils collected in the area in last two centuries derived from heterofacial intercalations with drifted and probably mixed or sorted bioclasts. Some heterofacial fossil intercalations have lithology of distal storm-generated beds with size-sorted lithoclasts and bioclast, or show signs of rapid deposition and burial of dead animals (e.g., Pod trním locality). In almost all such sites the ptychopariids are present and are often a significant component of fossil assemblages. Four depth-related, level-bottom benthic associations could be recognized here.

The ptychopariid-mollusc association is characterised by species that lived in deeper littoral to shallow sublitoral. Among the trilobites, the dominance of ptychopariids and ellipsocephalids is characteristic. Helcionellid molluscs are fairly common, but the most numerous benthic animals in this low-diversity were fixo-sessile orthid (*Pompeckium*) and protorthid (*Jamesella*) brachiopods. *Ptychoparia striata*, *Ptychoparioides torifrons*, *Perneraspis conifrons*, *Germaropyge* cf. *germari*, and the brachiopod *Pompeckium kuthani*, are the characteristic fossils of the stratigraphically oldest known assemblage of the Skryje-Týřovice area. Most of the taxa are unknown in younger sedimentary succession in the area. Na Kamenných hůrkách and Hlohovice localities are the typical sites with the association.

The ptychoparid-ellipsocephalid association includes species of shallow inner sublittoral zone. The ptychoparids and ellipsocephalids are dominant. These groups are associated with other trilobites, mainly *Lobocephalina*, *Skreiaspis*, *Conocoryphe, Ctenocephalus* and *Acadoparadoxides*, and locally with the orthid brachiopod *Bohemiella*.

This association possesses the highest taxonomic diversity and is the most spatially and stratigraphically widespread association in the Skryje-Týřovice area. *Ptychoparia dubinka, Mikaparia mutica*, together with *Germaropyge germari, Eccaparadoxides pusillus* and *Ptychoparioides henkli* belong to the index species of the lower and middle part of the *Eccaparadoxides pusillus* Zone in the Skryje-Týřovice area. The Dubinky Hill locality is the typical site with the association.

The paradoxid-solenopleurid association includes species living in a moderately deep sublittoral zone. Some eurytopic species penetrate shoreward into the ptychopariid-ellipsocephalid association, and in rare cases, some elements spread more basinward into the agnostidparadoxid association. The paradoxid-solenopleurid association includes some paradoxid taxa (*Hydrocephalus carens, Luhops exspectans, Eccaparadoxides pusillus, E. rohanovicus*), a ptychopariid *Mikaparia mutica*, a conocoryphid (*Bailiella granulata*), solenopleurids and other trilobites (*Solenopleurina tyrovicensis, Sao hirsuta, Agraulos ceticephalus*), and rarely some, depth-related miomerid trilobites (*Phalagnostus, Peronopsis, Condylopyge*). Luh and Plazy localities are the typical sites of the association.

The agnostid-paradoxid association includes species occupying outer sublittoral zone. Agnostoid trilobites are dominant. Whether associated polymerid trilobites (*Ag*-



Figure 10. Diagrammatic section showing the bathymetric range of the benthic associations in the Skryje-Týřovice area and their genera.

raulos ceticephalus, Sao hirsuta, Solenopleurina tyrovicensis and an uncommon *Hydrocephalus carens*) are autochthonous has not been definitely solved. The Pod hruškou locality and upper part of the Luh locality area represent the typical sites for this association.

Spatial distributions of trilobites and lithofacies development imply that ptychopariid (*s.s.*) mostly preferred very shallow-water to shallow sublittoral environment with firm sand and silt on sea floor. This is evident from early occurrences of *Ptychoparia striata* and *Ptychoparioides torifrons* in the Mileč Formation. The species *Ptychoparia* sp. A is similarly known only from siltstones of the Jince area.

The assumption of a shallow sublittoral habitat of ptychopariids is supported by the abundant occurrence of Ptychoparia dubinka associated with Germaropyge germari in heterofacial sandstone lens at the Pod trním locality near Týřovice. Extensive intercalation of sand with abundant complete trilobite specimens (Ptychoparia, Germa*ropyge*) inside mudstone succession can be explained by a slumping of unconsolidated sand from shoals into slightly deeper environment. Apparent rapid killing of the trilobite individuals happened by their deep burial in unconsolidated sand and, possibly, by dysaeroby of surrounding deeper environment. The instant burial of the trilobites in sand is indicated by completeness of exoskeletons with hypostoma in place, enrollment of the specimens, and traces of unsclerotised parts. Other ptychopariid taxa (Mikaparia) probably preferred a slightly deeper and calm environment in shallow sublittoral zone.

Occurrence of ptychopariids in the Skryje-Týřovice and Jince areas

Pre-Ordovician erosion and the incomplete stratigraphy of the Middle Cambrian marine successions in central Bohemia makes any assumption about faunal interchange with other regions highly speculative. Havlíček (1971) originally suggested that marine transgression came to the Skryje-Týřovice area from the Jince area. Subsequently, the same author (Havlíček 1980, 1992, 1998) suggested faunal immigration from Bavaria (Frankenwald), following the path of the suggested Middle Cambrian seaway over the Skryje-Týřovice area to the Jince area.

Representatives of *Ptychoparia* and *Ptychoparioides* are present as separate taxa in the Skryje-Týřovice area in the very beginning of the marine transgression. *Mikaparia* appeared slightly later.

There is diachroneity of the earliest occurrences of *Ptychoparia* and *Mikaparia* in the Skryje-Týřovice and Jince areas. In the Jince area the FAD of *Mikaparia milena* is in the lower part of the *Eccaparadoxides pusillus* Zone, and the species continues, without any distinct morphological change, into the *Paradoxides gracilis* Zone (Fig. 12). Its is probable, that the morphologically similar species *Mikaparia mutica*, restricted to the Skryje-Týřovice area, is derived from the stratigraphically earliest population of *M. milena*, because *Mikaparia* is unknown in the lower part of the *Eccaparadoxids pusillus* Zone in Skryje-Týřovice area, In the same manner as *M. milena* in the Jince area,

Trilobite species	Pt-M Ass.	Pt-E Ass.	Pa-S Ass.	A-Pa Ass.
Agraulopsis resseri				
Perneraspis conifrons				
Ptychoparia striata				
Ptychoparioides torifrons				
Lobocephalina emmrichi				
Germaropyge germari				
Ellipsocephalus cf. hoffi				
Ptychoparia dubinka				
Mikaparia mutica				
Ptychoparioides henkli				
Ctenocephalus coronatus				
Skreiaspis spinosa				
Acadoparadoxides cf. sirokyi				
Plutonides kozaki				
Eccaparadoxides pusillus				
Eccaparad. rohanovicus				
Luhops expectans				
Hydrocephalus carens				
Conocoryphidae (s.s.)				
Bailiella granulata				
Solenopleura sp.				
Jincella prantli				
Peronopsis sp.				
Phalagnostus nudus				
Solenopleurina tyrovicensis				
Sao hirsuta				
Agraulos ceticephalus				
Condylopyge rex				
Diplorrhina cuneifera				
Phalacroma bibullatum	common			
Pleuroctenium granulatum		aro		
Peronopsis umbonata	ia	aic		
Skryjagnostus pompeckji	· v	ery rare		

Figure 11. Distribution of trilobites in the benthic associations of the Skryje-Týřovice area. Pt-M Ass. – ptychopariid-mollusc association, Pt-E Ass. – ptychopariid-ellipsocephalid association, Pa-S Ass. – paradoxid-solenopleurid association, A-Pa Ass. – agnostid-paradoxid association.

also *Mikaparia mutica* pass over the upper limit of the *Eccaparadoxides pusillus* Zone in the Skryje-Týřovice area.

Ptychoparia striata is the characteristic ptychopariid of the *Eccaparadoxides pusillus* to *Paradoxides gracilis* zones in the Jince area (Fig. 12). Outside the Jince area, it is known in the Mileč Formation and in the lowest succession of the Jince Formation of the Skryje-Týřovice area (Týřovice Conglomerate and Greywackes below the *Eccaparadoxides pusillus* Zone) (Figs 12, 13). Higher in the succession in the Skryje-Týřovice area, *P. striata* is substituted by the closely related *P. dubinka*, which disappears in the upper part of the *Eccaparadoxides pusillus* Zone (Figs 12, 13). Unlike *P. striata*, the species *P. dubinka* is unknown in the Jince area.

Additional differences between the Skryje-Týřovice and Jince areas include the particular species of *Ptychopa*-

rioides (P. torifrons, P. henkli in the Skryje-Týřovice area and *P. chlupaci* in the Jince area) present in successions of approximately same age (lower part of the *Eccaparadoxides pusillus* Zone or older zones.

Despite general similarity of the benthic marine biota of the Jince and Skryje-Týřovice areas, there are striking taxonomic differences in their ptychopariid trilobite associations. This difference, together with occurrence of particular taxa restricted to one of the two areas (e.g., in brachiopods), indicates remarkably independent evolution of marine communities in both the areas, despite their geographical proximity at the present time. This is consistent with existence of a palaeogeographic barrier that restricted interchange of marine biota.

Stratigraphy – a review

Although the total thickness of the Cambrian sediments in the Skryje-Týřovice area attains some 200 m (Havlíček 1998), a finer biostratigraphical subdivision of these beds has not been undertaken. This is due in part to the deformation and erosion of the Middle Cambrian sediments towards the SW, and the scantiness of exposures of the Mileč and Jince formations, especially at their boundary interval. Another difficulty is the accurate correlation of particular localities because of uneven lithofacies development and presence of various faunal assemblages.

A review of the different approaches taken in studying the stratigraphy of the Skryje-Týřovice area since 1884 was given by Šnajdr (1958, pp. 19–21). The most valuable information were presented in articles of Jahn (1896) and Kettner (1923). There are a few additional stratigraphical reports on the area. Jarka (1940) published a list of species from various stratigraphical levels of the Skryje Shale at the slope Dlouhá hora near Skryje. This author attempted to correlate the ranges of these taxa with those from the Jince area. He did not subdivide the Skryje Shale, but reported restriction of *Sao hirsuta* and *Solenopleura tyrovicensis* to the upper part of the succession. Přibyl & Jarka (1946, p. 289) applied data from Jarka (1940), with a brief note that the beds with *Sao hirsuta* constitute a biostratigraphical horizon.

Prantl (1947) took notice of a horizon with Sao hirsuta, Pleuroctenium granulatum and Solenopleura tyrovicensis in the upper part of the Skryje Shale without any detailed definitions. He suggested that this horizon is overlain by horizon with Ceratocystis perneri and Lobocephalina emmrichi. However, these species have a longer stratigraphical span and are present below the Sao hirsuta horizon.

Šnajdr (1958) incorporated all fossiliferous levels into the *Eccaparadoxides pusillus* Zone due the presence of paradoxid trilobites in the basal sandstones of the Mileč Fm. Lithofacies Skryje-Týřovice area Fm. Jince area Zones Ellipsocephalus hoffi Rejkocephalus Lingulella zone Paradoxides gracilis TRZ HIATUS Eccaparadoxides pusillus Paradoxides gracilis ikaparia milena ^Dtychoparia striat Onymagnostus hybridus - TRZ Jince Formation Ptychoparioides chlupaci Skryje Shale vchoparioides henkli Jince Formation Ptvchoparia dubinka Eccaparadoxides pusillus Mikaparia milena taxon-range zone Týřovice Conglomerate Ptvchoparioides and Greywacke rons milena ^otychoparia M.Fm. ţ Ornamentaspis Mileč striata 5 Conocoryphe horizon Conglomerate N.

Vratislav Kordule • Ptychopariid trilobites in the Middle Cambrian of Bohemia

Figure 12. Ranges of particular ptychopariid trilobites in the Skryje-Týřovice area and Jince area. Stratigraphy modified after Kordule (1996) and Fatka *et al.* (2004). Abbreviations: TRZ – taxon-range zone, M.Fm. – Mileč Formation.

Formation. However, among the paradoxid remains in the Mileč Formation, the presence of Eccaparadoxides has not been proved yet; the fragments of skeletons belong to another genus, probably Hydrocephalus. Havlíček (1971) presented a different approach; this author defined two brachiopod zones in the Skryje-Týřovice area. The older is characterised by *Pompeckium kuthani* and the younger by Bohemiella romingeri. The latter species is restricted to the Skryje Shale facies only. The range of the older zone includes the Mileč Conglomerate and Sandstone and the lower part of the Týřovice Greywacke (Havlíček 1971). The Týřovice Greywacke extends into the upper half of the Jince Formation, and thus overlaps the upper part of the Eccaparadoxides pusillus Zone of the clayey lithofacies. In Havlíček's original concept (1971), the Mileč Sandstone and Conglomerate is only a local stratigraphical unit, absent in other parts of the basin. Based on his opinion, the younger Týřovice Greywacke and Skryje Shale should directly cover the Proterozoic bedrocks at some sites, especially in the NE part of the basin (Havlíček 1971, p. 41, fig. 4). However, this concept contradicts with finds of fossiliferous conglomerate and sandstone that has been made by M. Szabad and the present author at Malá Pleš in 1996, in the NE extremity of the preserved Cambrian sediments of the Skryje-Týřovice area. The Czech Stratigraphic Subcommission incorporated the Mileč Conglomerates and Sandstones into the Mileč Formation (Havlíček *in* Klomínský 1994).

The Eccaparadoxides pusillus Range Zone in the Skryje-Týřovice area was subsequently defined with a new Acadoparadoxides cf. sirokyi Subzone. The index species of the youngest preserved beds of the Eccaparadoxides pusillus Range Zone in the Skryje-Týřovice area were listed by Kordule (1999). This fauna includes Mikaparia mutica, Sao hirsuta, Plutonides kozaki, Agraulos ceticephalus and some agnostids (e.g., Condylopyge rex, Diplorrhina cuneifera, Peronopsis umbonata).

Kettner (1923, pp. 17–24) named specific lithological units of the Middle Cambrian in the Skryje-Týřovice area that had been distinguished by Jahn (1896) and Kettner &

Kodym (1919). Kettner (1923) separated the "Orthis Sandstone" ("orthisové pískovce" in Czech) from the Mileč Sandstone and Conglomerate, and united the former with the Týřovice Conglomerate in a new unit called the Týřovice Conglomerate and Sandstone. He suggested that the fauna of the Mileč Sandstone from the Na Kamenných hůrkách and Mileč Hill localities is older than fauna of the "Orthis Sandstone" from the Luh, Slapnický mlýn, and Lohovice localities. Růžička (1940, p. 11) revised the trilobite fauna from the basal sandstone of the Mileč Sandstone, and observed that it is undistinguishable from that of the "Orthis Sandstone" in Skryje and Lohovice. He suggested the same faunal age for both units. New observations by the present author in Hlohovice and outcrops in the Zbiroh Creek valley support the opinion of Růžička (1940). For instance, the trilobite Perneraspis conifrons, which was hitherto known from the Mileč Conglomerate and Sandstone, has now been found in the Týřovice Conglomerate and Greywacke at Hlohovice and the new locality U tří chat near Čilá. This species might be useful as an index species for the Perneraspis conifrons Range Zone, but the definition of such a zone is premature at present.

New proposal of biostratigraphic zonation in the Skryje-Týřovice area

Summarizing the available data (including new investigations of time and space distributions of ptychoparid trilobites), the new proposal of biostratigraphical zonation based on assemblage zones and barren intervals is suggested for the Mileč and Jince formations (in ascending order; Fig. 11):

- a) Barren interval in the lower part of the Mileč Formation (oldest Cambrian sediment in the area);
- b) *Ptychoparia striata* Assemblage Zone containing the index species *Ptychoparia striata*, *Perneraspis conifrons*, *Ptychoparioides torifrons*.
- c) Barren interval in the lower part of the Jince Formation, from the top of the preceding zone to the lower boundary of the *Acadoparadoxides* cf. *sirokyi* Abundance Zone.
- d) Acadoparadoxides cf. sirokyi Abundance Zone.
- e) *Ptychoparia dubinka* Assemblage Zone, containing the index species *Ptychoparia dubinka*, *Germaropyge germari*, *Ptychoparioides henkli*, and *Eccaparadoxides pusillus*.
- f) Mikaparia mutica Assemblage Zone, containing the index species Mikaparia mutica, Sao hirsuta, Agraulos ceticephalus, Jincella prantli, Diplorrhina cuneifera, Condylopyge rex, Peronopsis umbonata, and Phalagnostus nudus.
- g) Barren interval in the uppermost part of the Jince Formation.

Ptychoparia striata Assemblage Zone

The *Ptychoparia striata* Assemblage Zone is known in the Mileč Formation, but it extends to lower part of the Týřovice Conglomerate and Greywacke. The Týřovice Conglomerate and Greywacke have been referred to the Jince Formation (Havlíček 1971, Havlíček *in* Klomínský 1994) and are mainly present in the lower part the formation. Total estimated thickness of the zone is 8 to 20 m.

Acadoparodoxides cf. sirokyi Abundance Zone

The index species *Eccaparadoxides pusillus* is rare in the lowest beds referred to the *Eccaparadoxides pusillus* Taxon Range Zone. This led Kordule (1999) to definition of this interval as the *Acadoparadoxides* cf. *sirokyi* Taxon Range Zone. The zone includes about 10 m thick interval exposed on the slope of Dubinky Hill, which is the type-locality of the zone. Apart from the index species, *Ellipsocephalus* cf. *hoffi* is rarely present. At this site, the highest part of the zone yielded one cranidium of *Eccaparadoxides pusillus*.

A more diversified assemblage is known at a locality near the Hlaváč's village near the Podmokelský mlýn locality (Kordule 1999). Associated with Acadoparadoxides cf. sirokyi, the trilobites Ptychoparia dubinka, Lobocephalina emmrichi, Ptychoparioides henkli, Ellipsocephalus cf. hoffi, Peronopsis sp. and an orthid Bohemiella romingeri were collected there. However, the index species Eccaparadoxides pusillus is absent. This difference may be explained by the heterochrony of the lower boundary of the Acadoparadoxides cf. sirokyi and the Eccaparadoxides pusillus zones. It appears likely that Acadoparadoxides cf. sirokyi should be found even in older beds than is currently known; therefore, the succession with Acadoparadoxides cf. sirokyi is renamed to the Acadoparadoxides cf. sirokyi Abundance Zone. Total estimated thickness is about 10 m.

Ptychoparia dubinka Assemblage Zone

The beds overlying the Acadoparadoxides cf. sirokyi Abundance Zone are rich in fossils, and the succession is defined as the Ptychoparia dubinka Assemblage Zone. This zone is defined by the presence of Ptychoparia dubinka, Germaropyge germari, Ptychoparioides henkli, and Eccaparadoxides pusillus. The zone contains a more diversified association, with Ptychoparia dubinka, Lobocephalina emmrichi, Conocoryphe sulzeri atlanta, Ellipsocephalus cf. hoffi, Skreiaspis spinosa, Eccaparadoxides pusillus, and an orthid Bohemiella romingeri. The trilobites Germaropyge germari, Hydrocephalus carens,

Vratislav Kordule • Ptychopariid trilobites in the Middle Cambrian of Bohemia



Figure 13. Correlation of the biostratigraphy of the Middle Cambrian in the Skryje-Týřovice area after Šnajdr (1958), Havlíček (1971), corrected ranges of taxon-range and abundance zones, newly defined assemblage zones, and ranges of the index species. Abbreviations: M.Fm. – Mileč Formation.

Ctenocephalus coronatus, and Peronopsis cf. integer are less common. The rare trilobites are Ptychoparioides henkli, Luhops expectans, Parabailiella granulata, and Peronopsis umbonata (Jarka's collection, exact level unknown). Hyolithids are generally less common. Lichenoides, Stromatocystites, Ceratocystis, and Etoctenocystis represent echinoderms. The typical occurrence of the Ptychoparia dubinka Assemblage Zone is in the middle part of the slope of Dlouhá hora and Dubinky Hill near Skryje (Kordule 1999). Other known occurrences of this zone are situated at the NE slope of Karáskova rokle (Pod trním locality), in the NW slope of the Buchava locality, at Čihátko Hill, and Biskoupky. Total estimated thickness of the zone is 60 m.

Mikaparia mutica Assemblage Zone

The *Ptychoparia dubinka* Assemblage Zone is substituted by the *Mikaparia mutica* Assemblage Zone approximately in the middle part of the Skryje Shale. The base of the *Mikaparia mutica* Assemblage Zone is defined by the last occurrence of the species *Ptychoparia dubinka*. The co-occurrence of *P. dubinka* and *M. mutica* is known from the approximately 8 m thick succession at the top of the *Ptychoparia dubinka* Assemblage Zone. The *Mikaparia mutica* Assemblage Zone occupies a nearly 60 m thick succession, and is characterized by a rich association of polymerid and miomerid trilobites. This zone is also characterised by occurrence of Sao hirsuta, Agraulos ceticephalus, Jincella prantli, Diplorrhina cuneifera, Condylopyge rex, Peronopsis umbonata, and Phalagnostus nudus. Trilobites Solenopleura tyrovicensis, Conocoryphe sulzeri cirina, Conocoryphe sulzeri atlanta, and Bailiella granulata are less common. The paradoxid Hydrocephalus carens is very frequent, while Eccaparadoxides pusillus is restricted to the lower two-thirds of the zone. Less frequent are Eccaparadoxides rohanovicus, Jincella prantli, Skreiaspis spinosa, Ellipsocephalus aff. hoffi, and Ctenocephalus coronatus. Species Plutonides kozaki, Luhops expectans, Germaropyge germari, and Solenopleura sp. nov. are rare.

The suggested deepest part of the basin near Týřovice and Skryje (Kukal 1971) yielded common agnostoids. Some of them are important for local biostratigraphical subdivision as well as for extrabasinal correlations. In this, probably the deepest part of the basin, their abundant occurrence indicates the base of the *Mikaparia mutica* Assemblage Zone, while in sites only some 2 km toward the SW, the base is defined by the index species *Mikaparia mutica*. The miomerid trilobites are represented by *Diplorrhina cuneifera*, *Phalagnostus nudus*, *Condylopyge rex*, *Phalacroma bibullatum*, *Skryjagnostus pompeckji*, *Peronopsis umbonata*, *Pleuroctenium granulatum*, and *Peronopsis* cf. *integra*. Echinoderms are represented by the abundant *Trochocystis bohemica*, while *Trochocystoides parvus*, *Etoctenocystis* cf. *bohemica*, *Luhocrinus monicae*, and *Ceratocystis perneri* are rare. Brachiopods are represented by small and generally rare species of *Lingulella* and *Luhotreta*, and also by the orthid *Bohemiella romingeri* in more shoreward sites of the basin. Hyoliths are represented by several species. Helcionellids are rare, and *Volborthella* has been found.

The range of the *Mikaparia mutica* Assemblage Zone continues above the upper limit of the *Eccaparadoxides pusillus* Range Zone. Stratigraphical ranges of particular species of the *Mikaparia mutica* Assemblage Zone are different. *Mikaparia mutica, Jincella prantli*, and *Ctenocephalus coronatus* are known from the entire range of the zone (about 60 m in thickness). The ranges of other species are more restricted. *Sao hirsuta* is known from an approximately 40 m thick succession in the middle of the zone. *Agraulos ceticephalus* occurs only in the middle part of the zone, in cca 10 m thick succession. In addition, a poorly outcropping Skryje Shale and strong tectonic deformation locally obscure their actual ranges.

The *Mikaparia mutica* Assemblage Zone is the best-known zone of the Cambrian sequence in the Skryje-Týřovice area. The type area with passage of the *Ptychoparia dubinka* Assemblage Zone to the *Mikaparia mutica* Assemblage Zone is on the wooded slope close to Podmokelský mlýn. The adjacent lowest succession of *Mikaparia mutica* Assemblage Zone is in adjacent Buchava Quarry.

Numerous historical collecting sites lie within this zone. The zone is known at more localities: Studená hora Hill, a gorge near Týřovice, Lůmek near Týřovice, Pod hruškou locality, an opening of Karáskova rokle, Luh, Plazy, Skryje village, upper outcrops at slope of Dlouhá hora and Dubinky Hill. Approximate total thickness of the zone is 70 m.

Barren intervals

Some parts of the Middle Cambrian succession in the Skryje-Týřovice area did not yield any fossils; these sucessions are defined as barren intervals. Kordule (1996) suggested that the succession in the upper part of the Týřovice Conglomerate and Greywacke and the lower part of the Skryje Shale (about 40 m) are unfossiliferous, but new data indicate that the Barren Interval (Kordule 1996) has thickness of 20–30 m. This barren interval is developed as alternation of thin layers of greywackes (Týřovice Conglomerate and Greywacke) and mudstones (Skryje Shale).

Conclusions

Numerous localities in the Skryje-Týřovice area and their fauna have been studied since the mid-nineteen century

(Jahn 1896; Kettner 1923; Jarka 1940; Růžička 1940; Prantl 1941, 1947; Přibyl & Jarka 1946; Chlupáč *et al.* 1998; Vokáč 1997 *etc.*). However, many localities in the same area were overlooked. The Dubinky Hill locality should be noted as an example (Kordule 1999). It had never been studied before, although its significance for stratigraphy and the taxonomy of ptychopariids is outstanding. These exposures on the steep slope of the Zbirožský Creek valley constitute the most complete sequence of the Skryje Shale, with basinward, deepening trends in the succession. A weak tilting and faulting, good outcropping, and rich fossil content are other advantages of this sequence, so that this section currently represents one of the most significant sections of the Jince Formation in the Skryje-Týřovice area.

New data about spatial and stratigraphical distribution of ptychopariid trilobites allow to propose a bathymetrical model for the benthic, trilobite-dominated associations in the Skryje-Týřovice area. A new proposal of biostratigraphical subdivisions of the Mileč and Jince formations is presented with three new assemblage zones: Ptychoparia striata Assemblage Zone, Ptychoparia dubinka Assemblage Zone, and Mikaparia mutica Assemblage Zone. Stratigraphical ranges of index taxa are plotted (Fig. 13). There are striking differences in the taxonomic composition of ptychopariids, other trilobites, as well as the invertebrates (see review of Havlíček 1998, Fatka et al. 2004) in fossils assemblages between the Jince and Skryje-Týřovice areas, and also in the stratigraphical ranges of particular ptychoparioid species. This difference indicates palaeogeographic separation of both areas in the Middle Cambrian.

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