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TREMADOCIAN TRILOBITES OF THE PRAGUE BASIN, CZECH REPUBLIC

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Abstract: A revision of the trilobites of the Třenice and Mílina Formations (Upper Tremadocian) confirms the presence of 29 species. *Celdometopus* gen. n. is established, and six new species, *Agerina clymene, Hemibarrandia klouceki, Holoubkocheilus asopus, Parabathycheilus krafti, Platypeltoides perseis*, and *Pricyclopyge oceanitis* are described. All formerly described species of the genera *Geragnostus, Ottenbyaspis, Hemibarrandia, Holoubkovia, Anacheirurus, Parapilekia, Parabathycheilus, Holoubkocheilus, Proteuloma, Harpides, Holubaspis, Dikelokephalina, Ceratopyge, Niobina, Apatokephalus, Celdometopus*, and *Eulomina,* are re-described or further commented on. Old and new data about their morphology, distribution, and affinity are summarized. The fauna contains numerous cosmopolitan taxa, but most of the species show Gondwanan affinity, especially among calymenaceans and by the presence of an early cyclopygid. Compared with other regions, the total absence of olenid trilobites is characteristic. A high taxonomic diversity with dominant cheirurids and illaenids makes this one of the richest late Tremadocian trilobite faunas ever described.

■ Trilobita, taxonomy, Tremadocian, Ordovician, Barrandian area, Prague Basin, Bohemia, Czech Republic.

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Introduction

The first report of the Tremadocian trilobites from the Barrandian area was written by Celda Klouček in the year 1914. However, a unique specimen of *Harpiges grimmi* BARRANDE, 1872 had been known since the mid nineteenth century. The Bohemian Tremadocian trilobites have been described by many authors (Růžička 1926, 1931, Klouček 1931, Vaněk 1965, Pek 1977, Mergl 1984a, 1994), but some species were established on poorly preserved or too few specimens. They have not been properly studied, and are sometimes described as being insufficiently known by other authors (Moore 1959, Peng 1990, Fortey and Owens 1991, Ebbestad 1999).

Most of the newly studied material was collected during the past twenty years at the classical and new localities. Earlier authors (Klouček 1917, 1925, 1926a, Koliha 1937, Růžička 1926, 1931) noted the remarkably high diversity of the trilobite fauna in the known localities. The main purpose of the present research is to utilize small fragments and morphologically less attractive exoskeletal parts (librigenae, doublures, smooth fragments, and thoracic segments). In this way, the author attempt to reveal the morphology of hitherto unknown but taxonomically significant exoskeletal parts. The results enable a better reconstruction of the species. Furthermore, the new evaluation of the remarkably rich Tremadocian trilobite of the Prague Basin fauna might bring some new views to the evolutionary history of benthic faunas in the southwest periphery of Gondwana in the early Ordovician.

Historical overview

Harpides grimmi BARRANDE, 1872 is the earliest known trilobite of Tremadocian age in the present stratigraphical framework. The horizon and locality at which a unique and nearly complete specimen of this species was found is not precisely known. The specimen, sometimes called the rarest trilobite of Bohemia (Prantl 1945), was found in the iron ores at Holoubkov iron works in or around 1840, and its exact locality has remained unknown since the first report. The suggestions of locating the site near Dobřív (Krejčí 1877) or Mirošov (Purkyně 1914, Prantl 1945) are probably incorrect. Uncertainty about the locality led to speculations that the species is of younger Arenig age (Barrande 1872).

In August 1914, Professor Celda Klouček found the remains of trilobites in the reddish chert cobblestones of a road near Hořovice. After a short search he found the original trilobite-bearing bed at a local quarry at the Olešná village near Komárov in the SW part of the Prague Basin. This bed is situated in the upper part of the Mílina Formation, and its lithology and petrography have been described in detail by Kettner (1916). Until Klouček's find, the fauna of the reddish cherts was considered to be very poor, consisting only of linguliform brachiopods, sponges, and an orthid *Jivinella incola*. In 1917, Klouček listed eleven trilobite species, with only approximate generic attributions. Modified versions of this list of trilobite taxa were repeatedly published in the following years (Koliha 1924, 1937, Klouček 1926a). In 1920, Klouček found a similar trilobite fauna in the Úvaly east of Prague. From this region he reported fifteen trilobite species (Klouček 1922), among which occurred *Harpides* cf. *rugosus*. In 1924, a private collector named Vojtěch Kraft, together with Klouček, discovered a diverse but very fragmental trilobite fauna in the dumps of the abandoned "V Ouzkém" iron ore mine near Holoubkov. Klouček (1925) suggested the same age of the trilobite fauna, but the haematite in which these fossils occur has recently been referred to the subjacent Třenice

Formation. Klouček (1925) listed thirteen trilobite species from the Mílina Formation. However, only one species was diagrammatically figured by the author (Klouček 1926b), and another trilobite fragment from Holoubkov was figured without any formal description (Klouček 1931). According their manuscripts and short notes, Klouček and Jan Koliha intended to publish a trilobite monograph based on their own findings from the years 1914 to 1931 (Klouček and Koliha 1927, Klouček 1931). However, the preparation of this work was halted by Klouček's death in 1935.

In the meantime, a private collector named R. Růžička (1926) had published a study of trilobites collected at the "V Ouzkém" locality near Holoubkov. He reported 21 species. Eight of them he described as new, but his determination and illustrations were of poor quality. This paper was immediately criticised by Klouček and Koliha (1927), and was followed by a short reply from Růžička (1928). Five years later, Růžička (1931) published another short paper describing additional finds from the "V Ouzkém" locality with the formal description of one new species. Two more short papers by Růžička (1935, 1941) dealt with the trilobites from the Olešná locality of the overlying Mílina Formation.

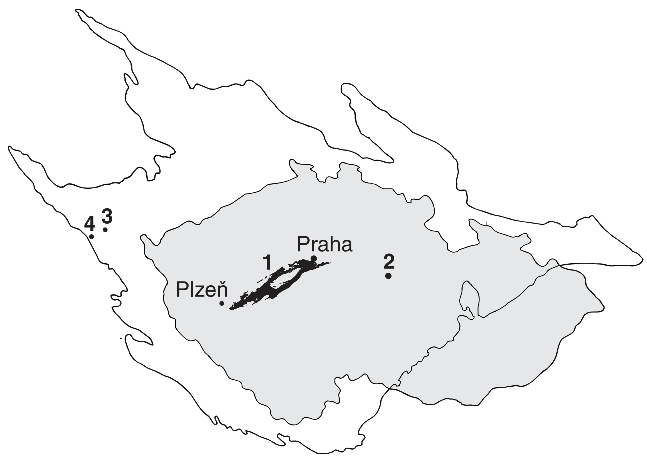
After the Second World War, the investigation of the Tremadocian trilobite fauna produced only short reports based on old material collected between the wars. The systematics, nomenclature, and morphology of selected taxa were reviewed by several authors (Prantl and Přibyl 1947, 1949a, Přibyl 1950, 1953, Vaněk 1959). Kalat (1949) briefly reported the discovery of a new trilobite locality in Úvaly east of Prague. In the mid-1960s, Vaněk published a short paper and a larger trilobite monograph of the Tremadocian trilobites of Central Bohemia (Vaněk 1964, 1965). This monograph is the first complete review of the trilobites of the Třenice and Mílina Formations. Subsequently, Havlíček and Vaněk (1966) reviewed the results. Vaněk (1965) reported 23 trilobite species, mostly based on the material collected by the previous authors and collectors. However, the validity of Vaněk's taxonomic determination has to be considered as somewhat questionable. For example, some of his locality data is erroneous, and the trilobites are not well illustrated. Some drawings were adopted from the papers of Růžička (1926, 1931), and the new photos illustrated only a few specimens. Therefore his results must be taken with some reserve.

In a review of the agnostid trilobites from the Barrandian, Pek (1977) re-described two species from the Mílina Formation, adopting Vaněk's (1965) determination. A monograph on the fauna of the Mílina Formation, based mostly on newly gathered material collected from 1977 to 1980, has been published by Mergl (1984a). The new material derived from the Olešná locality and from a new trilobite-bearing locality near the small village of Kvaň, near Zaječov. The author described sixteen species of trilobites, leaving open taxonomic positions for only three of them. Ten years later, the same author (Mergl 1994) revised the trilobites of the Třenice Formation. This revision is based exclusively on the material collected by Klouček, Kraft, and Růžička, because, with rare exceptions, no trilobites had been found in the known localities since the 1930s. The find of the trilobite *Bavarilla* cf. *hofensis* at Popovice near Brandýs, east of Prague, was briefly commented on by Vaněk (1999), but this specimen was not accessible to the present author.

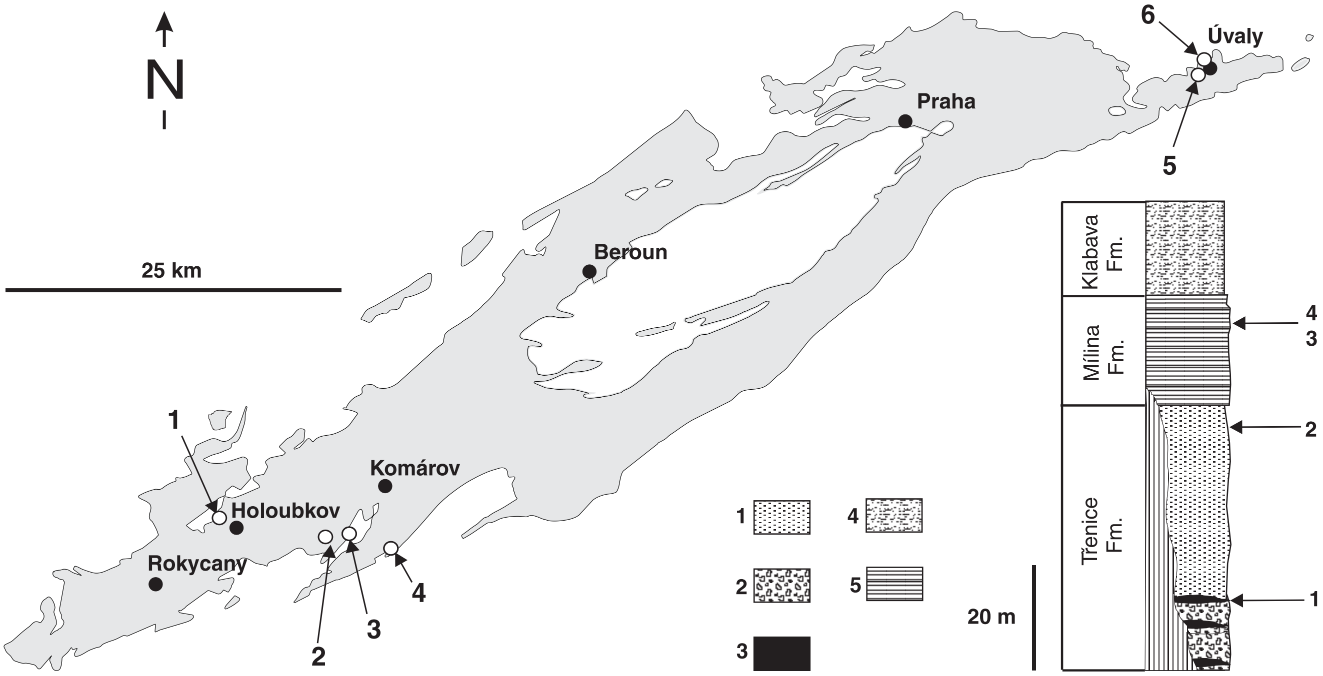
Geological setting

The early Ordovician sedimentation in the Prague Basin started by the deposition of coarse grained siliciclastics in a narrow, tectonically based trench extending from Rokycany in the SW to the Úvaly in the NE (Text-figs. 1, 2). The transgression of the basal Třenice Formation overlies an uneven surface formed by Precambrian or Cambrian rock. The Třenice Formation is comprised of coarse- to medium-grained sandstones (lithic greywackes and arkoses) and, at its base, by petromictic conglomerates of a local provenience. Eroded Upper Cambrian volcanics surrounding the basin were the main source of rhyolite and andesite clasts in the sandstones. Local haematite impregnations in conglomerates and sandstones are common. On the contrary, thin lenticular haematitic beds, often quartzitic and associated with stromatolitic structures, are very local. The thickness of the Třenice Formation ranges from 0 to 30 m, and rarely up to 70 m (Havlíček 1998).

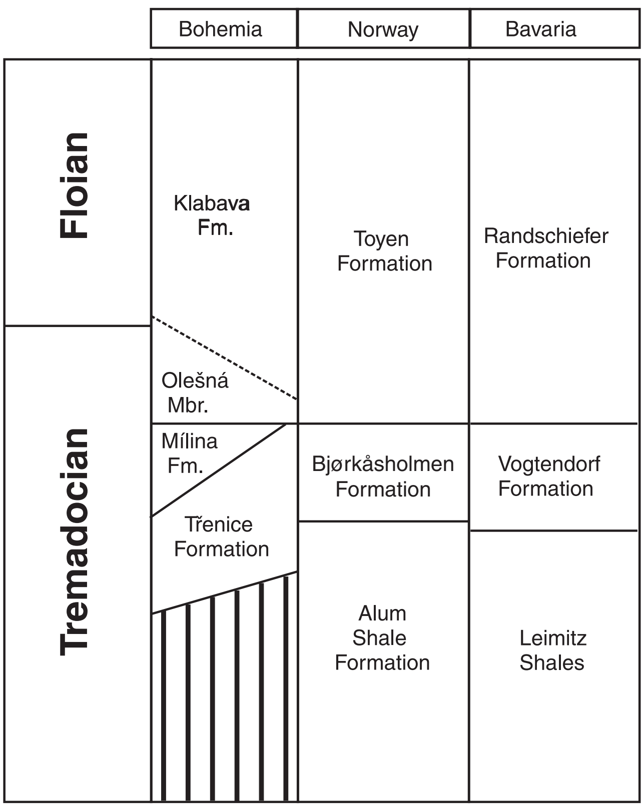
The overlying Mílina Formation has comparatively smaller extent, and has been considered to be of a regressive character by many authors (Kettner 1921, Bouček 1947, Havlíček and Šnajdr 1956). However, the Mílina Formation in the Komárov area rests on Upper Cambrian volcanics, thus having rather a transgressive than regressive character. For the formation pink, red-brown, and grey chert beds intercalated with fine red-brown greywackes and thin interbeds of silty shales are typical. The facies development of the Mílina Formation in the Úvaly area is characteristic by fine-grained sandstones and quartzitic shales. The thickness of the formation ranges from 0 to 30 m (Havlíček 1998).



Text-fig. 1. The Bohemian Massif with the Ordovician of the Barrandian area (1) and the trilobite-bearing localities in Železné hory area in East Bohemia (2), Hof (Leimitz Shales) (3) and Vogtendorf (Vogtendorf Formation) (4) in Bavaria.



Text-fig. 2. The Ordovician of the Prague Basin (A) with trilobite-bearing localities (1 – Holoubkov, 2 – Cheznovice, 3 – Olešná, 4 – Kvaň, 5 – Úvaly, Škvorec enclosure, 6 – Úvaly, Vinice) and general lithostratigraphy of the Tremadocian of the Prague Basin (1 – greywacke, 2 – conglomerate, 3 – haematite, 4 – siltstone, 5 – chert).



Text-fig. 3. Correlation of the Tremadocian to Floian successions discussed in this study.

The Třenice Formation has been correlated with the lower Tremadocian, and the Mílina Formation with the upper Tremadocian (Havlíček 1998). This arbitrary subdivision does not seem valid, as it is based on a tentative and perhaps incorrect correlation with the Bavarian sequence (Vaněk 1964, Havlíček and Vaněk 1966). The entire sequence is more probably of upper Tremadocian age because of the composition of fossil associations. It began with rapid transgression immediately followed by a short regressive event, which is probably coeval with the *Ceratopyge* regressive event (Erdtmann 1995, Erdtmann and Paalis 1995). The next transgression began in the earliest Arenig (approximately Hunneberg Stage) and brought a different fauna into the basin.

Localities

The trilobites considered here are known from both the Třenice and Mílina formations, but only at eight localities. Their presence and mode of preservation were strongly affected by taphonomic processes (Mergl 1997). Their remains are therefore present only in thin layers associated with other abundant benthic fauna.

Holoubkov ("V Ouzkém")

The locality "V Ouzkém" or "Ouzký" is situated 1000 m NW from the centre of the Holoubkov village. It is an iron-ore mine that was opened in 1794 and abandoned in the second half of the 19th century (Lipold 1863).

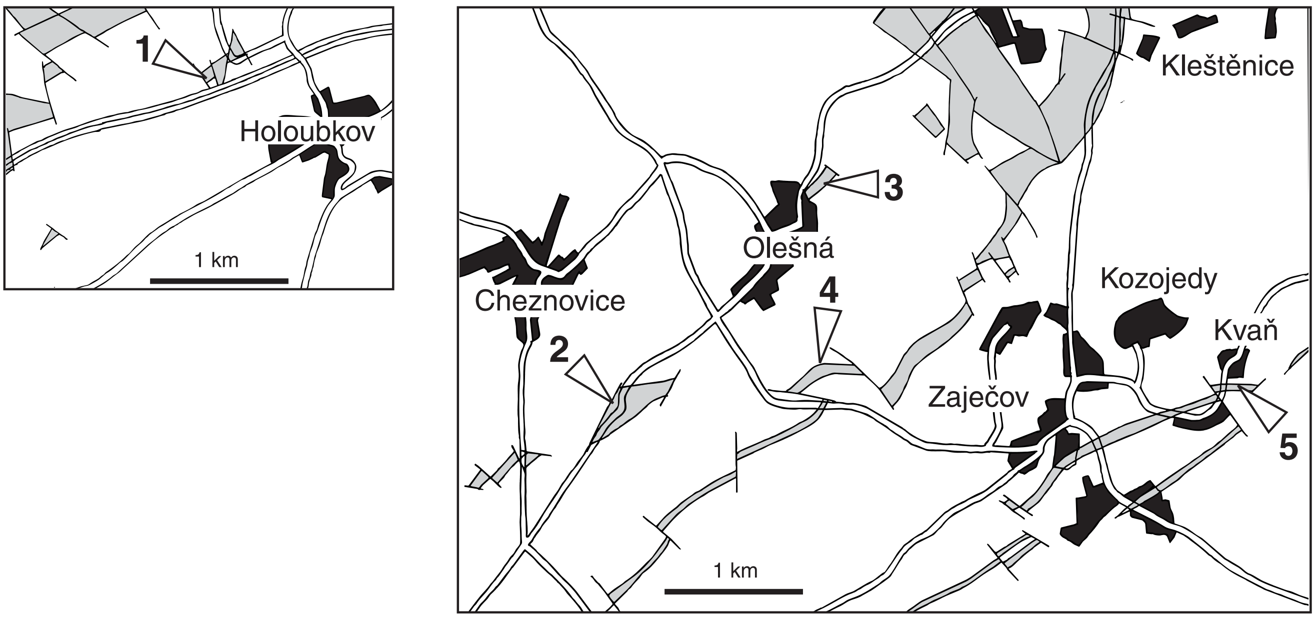
The orthid brachiopods and cystoids from this locality, called "Auskyer Zeche," were described by Barrande (1879, 1887). The trilobites were discovered by Klouček during the summer of 1924 (Klouček 1924). According to Klouček (Klouček 1924, 1925), there is a trilobite-bearing succession less than 20 cm thick or (?) even several associated beds of a compact quartzose haematite. The composition of the associated fossils indicates that they came from a laminated, quartzitic haematite body, the so called "Stahlertz" (Lipold 1863). The lamellae are probably of biogenic origin, and were recently compared with stromatolites (Lehnert et al. 2003). The fauna of trilobite and associated cystoids and brachiopods is remarkably rich. Indirect evidence about the stratigraphic situation at this locality indicates that it begins with beds of petromictic conglomerate that are several metres thick, with up to 50 cm sized boulders, followed by or intercalated with conglomerates of sorted gravel, the clasts of which are only a few mm in size. The boulders are encrusted by a problematicum *Marcusodictyon* (Mergl 1984b), thus indicating a shallow, littoral, high-energy environment. Massive haematites ("dichten Rotheisenstein" of Lipold 1863) occur above or intercalated with the conglomerates. These beds yield a rich fauna of rhynchonelliform brachiopods and cystoids dominated by *Echinosphaerites* and *Glyptosphaerites*, but without any trilobite remains. The fossils described by Barrande (1879, 1887) originate from these beds. The overlying laminated haematite beds yield different brachiopod and trilobite fauna, predominated by small organophosphatic brachiopods, and different rhynchonelliform brachiopods and cystoids. This fauna was found and collected by Klouček (1924, 1925). Red-brown siltstones and shales with an abundant admixture of coarse sand grains form the top of the succession. The siltstones contain a different fauna of small organophosphatic brachiopods, conodonts, and reworked small, bulbous stromatolites. These siltstones belong to the lowermost part of the Klabava Formation.

Although age estimations of the iron ores range from early Tremadocian (Třenice Formation) to the lowermost Arenigian (Klabava Formation), the distinct faunas in the lower and middle parts of the succession are referred to the Třenice Formation (Havlíček 1977).

Cheznovice ("Žlebec")

The locality "Žlebec" or "Ve Žlebci" locality is situated cca 1100 m SE from the Cheznovice village near Mýto (Figs 1, 4), and concerns two small quarries near the road from Strašice to Olešná. The fauna in the larger quarry S of the road was known to Koliha (1924). The coarse greywackes in this quarry are referred to the Třenice Formation due to the presence of the large lingulid brachiopod *Hyperobolus feistmanteli* (BARRANDE, 1879). The second smaller old quarry lies N of the road, in NW margin of an abandoned mining area with small shallow pits and dumps. The edge of the small quarry adjacent to the mining field yields loose rocks with trilobites and associated fauna. These yellow-green, distinctly laminated medium- to coarse-grained, platy greywackes are characterised by haematite impregnations. The greywackes with trilobites are of finer grain size, being composed almost exclusively of small, rounded, flattened, and parallel-bedded clasts of weathered Upper Cambrian volcanics.

The trilobite fauna is rare and poorly preserved, and is associated with orthid and lingulate brachiopods. The thickness of the bed, or perhaps several beds, is at least 10 cm. Subjacent greywackes that are coarser and less distinctly bedded outcrop few metres south of the collecting site. These subjacent greywackes only yield large lingulid



Text-fig. 4. Outcropping Tremadocian rocks in the Holoubkov area (A) and the Komárov area (B) with discussed trilobite-bearing localities (1 – Holoubkov, 2 – Cheznovice, 3 – Olešná, 4 – Mílina, 5 – Kvaň).

brachiopods (Mergl 2002), and might correlate with the greywackes at the larger quarry.

A stratigraphical succession can be inferred from the loose rocks and adjacent outcrops. It is evident that a succession of coarse, thick-bedded greywackes is 10–20 metres or even more thick. This is overlain by fine-grained, well-sorted greywackes, locally impregnated with haematite. A rich fauna of trilobites and brachiopods appear at this level. This layer lies below a local conglomerate intercalation, which is followed by cherts of the Mílina Formation. Indeed, the trilobite-bearing bed forms the top of the Třenice Formation immediately below the base of the Mílina Formation (Fig. 5). This locality was unknown to former authors, and new fossils were collected here from 1992 to 2005.

Olešná (quarry)

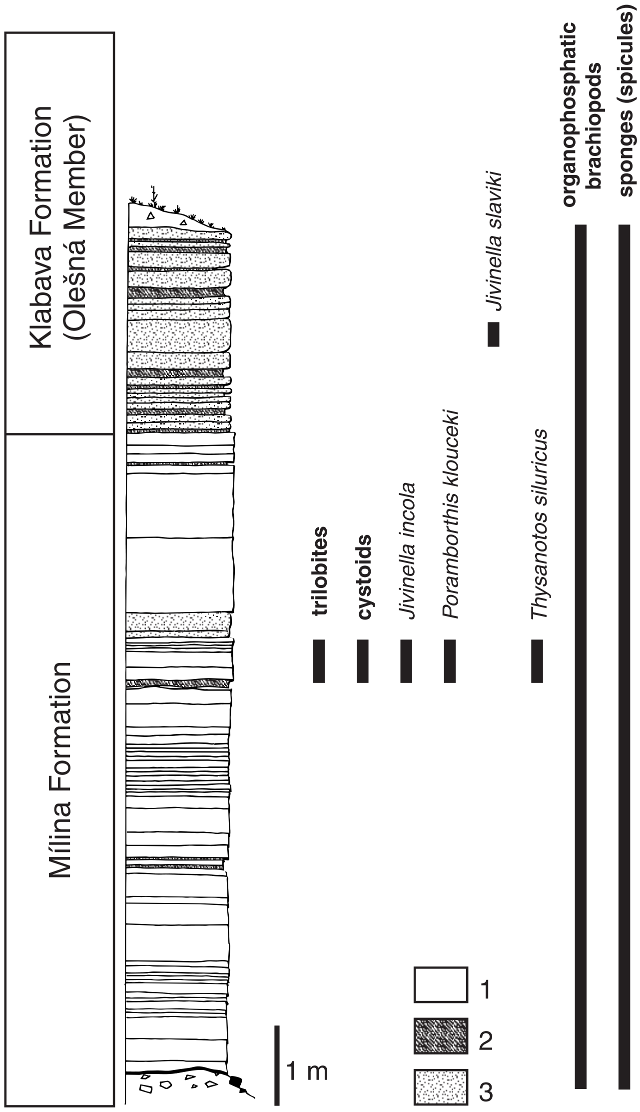
The Olešná locality is the earliest known trilobite-bearing locality in the Mílina Formation. It is situated near the NE margin of Olešná village, south of the road from Olešná to Komárov, 650 m NNE from the road crossing in Olešná. The small wooded hill was originally cut by two quarries. The east quarry, the original trilobite-bearing locality of Klouček and Růžička, is now totally destroyed and all new material was gathered from the second west quarry.

The trilobite-bearing succession is formed by several beds of grey, pink, or pale red cherts, which have an almost uniform lithology along the entire length of the trench. The subjacent chert beds yielded only spicules of siliceous sponges and shells of lingulate brachiopods. The thin basal chert layer that contains trilobites is lenticular, less than 5 cm thick, and lies within thin greywacke layers. Overlying chert beds are 2–18 cm thick, platy to massive, and affected by tectonic cracks. The fossil preservation in this section is strongly affected by the limonitization and weathering, with some parts being soft and lacking any well-preserved fossils. The most well preserved material, including minute trilobite fragments, have been collected in a 3 cm thick bed in the upper third of trilobite-bearing sequence. The quality of the preservation in this part is better in slightly weathered and leached cherts. Therefore, the old material (Klouček's and Růžička's collections) from the east quarry is of better quality than most of the newly collected specimens coming from fresh rock. Lateral lithological changes also affect the quality of fossil preservation. The taxonomic composition within the trilobite-bearing sequence slightly vary. The lower and middle beds are characterized by the prevalence of larger species (*Holubaspis, Hemibarrandia, Parapilekia*), while the upper thin beds are characterised by smaller taxa (*Celdometopus, Apatokephalus, Anacheirurus, Geragnostus*). This might reflects a gradual change of taxonomic composition of the living assemblage, an environmental change, or merely altered hydrodynamic conditions with different sorting processes.

The trilobite-bearing layers are succeeded by a fine-grained, red-brown greywacke (22 cm), followed by thick beds of grey cherts (170 cm), and several red chert beds (40 cm). The disappearance of cherts is a significant lithological boundary. The following succession of fine-grained, red-brown greywackes, siltstones, and silty shales belongs to the base of the Olešná Member of the Klabava Formation. This succession, including its distribution the fossils, has been described by Mergl (1986). The lithology and fossil content in the quarry is typical of the upper Mílina Formation and the lower Olešná Beds in the area. The sequence can be precisely correlated with other sections in the Komárov area.

Kvaň (field)

The Kvaň trilobite-bearing locality has been discovered in 1977. It is situated near the S margin of the village of Kvaň, 1200 m NNE from the school building in Zaječov. The small SW-NE ridge with a ploughed field yields loose rocks from the entire succession of the Mílina Formation and the lowermost part of overlying Olešná Member of the



Text-fig. 5. Stratigraphical column of the upper Mílina Formation and the lower Klabava Formation (Olešná Member) in Olešná with marked trilobite-bearing level (1 – chert, 2 – siltstone, 3 – greywacke).

Klabava Formation. An attempt to uncover the succession by digging a small trench was unsuccessful, but the distribution of loose rock enables an approximate reconstruction of the succession. Above the Upper Cambrian volcanics are several metres of conglomerate, followed by a succession of fine red cherts (some 10 m) that abound with spicules and lingulate microbrachiopods. The overlying trilobite-bearing bed should be only 0.3 to 0.4 m thick (estimated maximum is 0.6 m), with one 0.15 to 0.20 m thick bed which is more resistant; the other beds are only a few cm thick. The lateral changes of the beds are significant. The most well preserved fossils came from a thin, pink to pale grey bed with abundant small accumulations of finely fragmented trilobites and brachiopods, among which trilobites the *Agerina*, *Apatokephalus*, *Holubaspis*, and agnostids are dominant. The fossil association in the trilobite-bearing cherts is dominated by the orthid *Jivinella incola* and the lingulate brachiopods *Orbithele* and *Leptembolon*. However, trilobite remains are less common than at the Olešná locality.

Mílina (quarry)

The old quarries in low Mílina hill, 1200 m SSE from the crossing in the Olešná village, is the type locality of the Mílina Formation. The lithology and thickness of the Mílina Formation and the lower Olešná Beds of the Klabava Formation is nearly the same as in the quarries at Olešná (Kettner 1916, Mergl 1986). The Mílina equivalent of the trilobite-bearing layers in Olešná is the 70 cm thick succession of two dark red-brown chert beds. Klouček (1917) noted findings of trilobite fragments, but recent searches for trilobite remains have not been successful, although the commonly associated species *Jivinella incola* a *Poramborthis klouceki* were found. The preservation of orthids is poor and indicates a taphonomic loss of less resistant calcareous remains. Vaněk (1965) noted numerous trilobite taxa from this locality, but this assertion does not seem reliable.

Úvaly

Four trilobite-bearing of the Mílina Formation are known in the Úvaly area east of Prague. They were described by Kalat (1949). The original localities of Klouček (1920, 1922) are situated near the western periphery of Úvaly, near the Prague – Úvaly road. An old dump some 50 m south of the road on east margin of the Škvorec enclosure is the first locality noted by Klouček (1920, 1922). The second locality is on the opposite side of the road in the pit of an abandoned iron ore mine. This open pit structure was accessible to Kalat and Marek after the Second World War. The third locality is the most eastward of the row of pits between the Úvaly and Škvorec enclosures (Kalat 1949). The collecting of fossils at all three sites is currently not possible. The new locality, unknown to Klouček and Koliha, was observed by Kalat (1949). At the steep slope "Na Vinici" above Výmola creek, N of Úvaly, Kalat (1949) described a succession of cherts, greywackes, and pink quartzitic shales. These shales yielded rich and abundant, but very fragmental and tectonically deformed trilobite fauna associated with the orthids *Jivinella incola* and *Poramborthis klouceki*. Unlike the Komárov area, the trilobite fauna here is dominated by *Proteuloma kettneri*, *Ceratopyge mareki, Platypeltoides perseis*, and *Geragnostus peki*, while *Holubaspis*, *Parapilekia*, *Hemibarrandia*, and other genera are less common. The fossils at all localities in the Úvaly area are strongly deformed and preserved as moulds with a fine mineral cover, but they are less fragmental than in the Komárov area. Stratigraphic data concerning the trilobite-bearing beds are poor (Klouček 1920, 1922). According to the section published by Kalat (1949), the trilobite-bearing layers are succeeded by pale-grey to red cherts with sponge spicules and lingulid brachiopods, followed by red-violet shales and greywackes, probably an equivalent to the Olešná Member of the Klabava Formation. The succession is similar to that in the Komárov area, but tectonic deformation obscures the lithological data.

Preservation

The preservation of fossils significantly differs at the localities considered here. High fragmentation and early-diagenetic deformation, with few exceptions, make quantitative and biometrical data less reliable, and therefore rarely reported.

The preservation of fossils in the haematitic iron ores of the Třenice Formation ranges from well-preserved external and internal moulds to poor specimens covered by a glossy haematitic cover. The original calcareous substance was replaced by crystalline quartz and covered by a thin haematite film. Some specimens show fine details in the dorsal and inner surfaces, and have preserved the original thickness and some structures (e.g. pores) of the exoskeleton. The remains are highly fragmental, often broken into small pieces (e.g. thoracic segments are often broken into several parts). Some more massive parts have worn edges indicating abrasion. Complete specimens are so far unknown, but one thorax with an entire cephalon (*Ottenbyaspis*), and one cranidium (*Holubaspis*) with attached librigena, have been found. These finds indicate the rapid burial of unsorted material.

The trilobites in coarse platy greywackes of the Třenice Formation are poorly preserved. Only the more resistant parts, mostly librigenae, are preserved by a thin haematitic film on bedding planes. The original convexity of the librigenae is not preserved, and large sand grains are impressed through the walls. Associated, poorly preserved shells of orthid brachiopods indicate the significant deformation of thick-walled bioclasts, probably due to dissolution of the calcareous material.

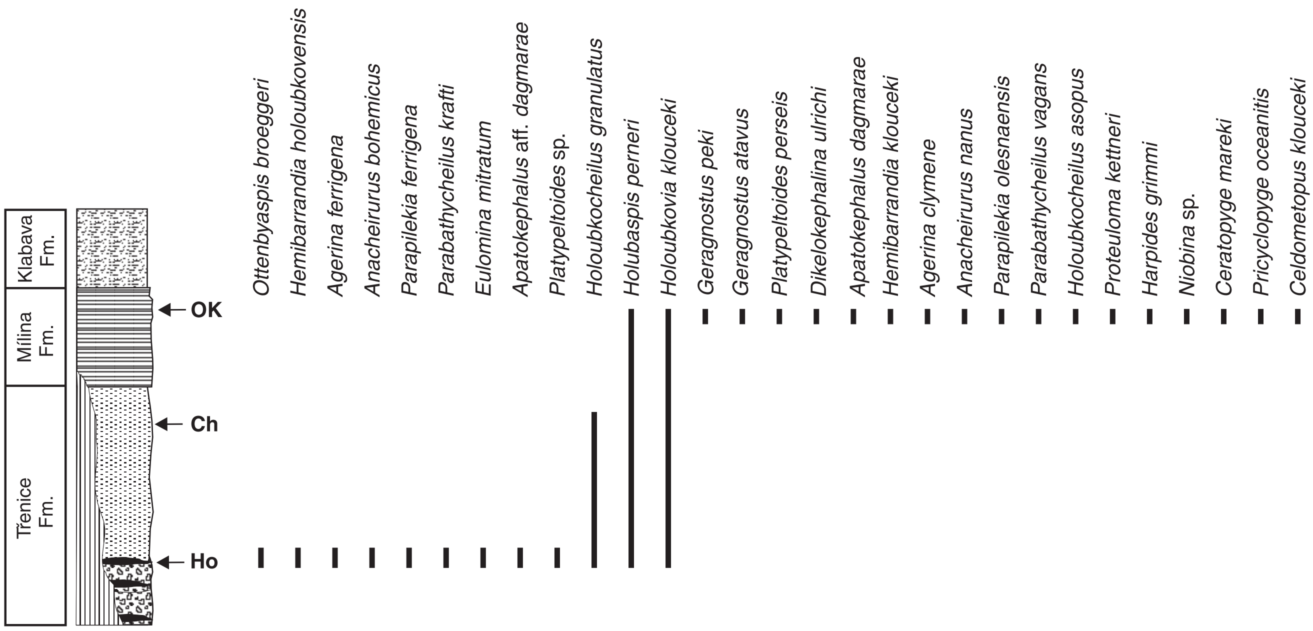
The fossils in the red-brown to pale grey cherts of the Mílina Formation are preserved as internal and external moulds, with the original calcitic material replaced by a yellow limonitic material, or by empty spaces covered by a secondary film or infillings of crystalline quartz. The quality of the preservation ranges from undistorted, three-dimensional specimens to flattened and ghostly imprints. Entire pygidia or cranidia are rare, and the finds of several jointed segments with pygidium or cephalon attached are also uncommon. Librigenae are almost always removed. Although the exoskeletons are highly fragmental, none of the remains are abraded or worn. The fossils underwent some distortion shortly after burial, as evinced by compression and fractures in all directions. The fracturing by sediment compaction affected almost all larger larger parts of exoskeletons with convex parts collapsed. That this deformation occurred immediately after deposition but probably before a lithification is evindenced by the limited displacement of the fragments. The accumulations of fragments on the bedding planes resulted from the washing and winnowing of the fractured specimens from an unconsolidated sediment. A pattern of taphonomic loss of some skeletal material is apparent. The less resistant calcareous material sometimes disappeared, and selective dissolution left only phosphatic fossils. This loss was perhaps controlled by the amount of calcareous, mostly calcitic material in the sediment (Mergl 1997).

The fossils from the pale yellow and pink quartzitic shales of the Mílina Formation in the Úvaly area are generally more complete than those from the cherts. Exoskeletal parts (e.g. pygidia and cranidia) are commonly complete, and a few almost entire specimens have been found. Fossils are preserved as internal and external moulds, strongly distorted and considerably flattened. The main distortion is tectonic. The folds often exaggerate original structures (e.g. the weakly expressed axial rings of the pygidium). Fragments of the exoskeletons are usually clustered on the bedding planes. Some individuals show fracturing with or without the weak displacement of fragments. Although the fossils have undergone considerable distortion, some more complete exoskeletal parts have provided valuable information about the morphology of the particular species. However, these fossils have no importance for biometry, because the tectonic distortion considerably altered the original proportions of the exoskeletal parts.

Biostratigraphy and associated fauna

The stratigraphically earliest trilobite fauna from this area occurs at the Holoubkov locality. The trilobites are known from a surprisingly rich and oft-mentioned fossil assemblage (Havlíček and Vaněk 1966, Havlíček 1982a, 1982b, 1989, 1992, 1998, Chlupáč and Kukal 1988). Trilobites are associated with rhynchonelliform, lingulate, and craniate brachiopods, a hyperstrophic gastropod, sponges, and cystoids (Růžička 1927, Havlíček 1949, 1977, 1980, 1982a, Prokop 1964, Mergl 1981, 2002, Mergl and Prokop 2006). This locality is significant for the presence of the problematic encrusting *Marcusodictyon* (Mergl 1984b). New evidence indicates that there are at least three stratigraphically different faunas at this site. The oldest consists only of the problematic encrusting *Marcusodictyon*. A younger assemblage is dominated by large to small rhynchonellaceans (*Poramborthis grimmi* and *P. anomala, Protambonites, Eoorthis, Robertorthis, Apheoorthina*), rare lingulate brachiopods, and cystoids *Echinosphaerites* and *Glyptosphaerites*. Trilobites and gastropods are still unknown. The youngest horizon is characterized by smaller rhynchonellaceans (*Poramborthis, Jivinella, Apheoorthina, Kvania*), diversified small sized lingulate brachiopods, craniates, the hyperstrophic gastropod *Mimospira*, the cystoids *Palaeosphaeronites* and *Pyrocystites* (?), and the first trilobites. An equivalent of the second assemblage was reported from the Jivina quarries near Komárov (Klouček 1915, Havlíček 1977), and trilobite-bearing beds from the Cheznovice locality are an equivalent of the trilobite-bearing third assemblage.

The trilobite-bearing beds of the overlying Mílina Formation are characterized by the presence of *Jivinella incola*, smaller *Poramborhis klouceki* and *Kvania kvanica,* a less



Text-fig. 6. Stratigraphical column of the Třenice and Mílina Formations in the southwestern part of the Prague Basin and distribution of trilobites. Localities: Ch – Cheznovice, Ho – Holoubkov, OK – Olešná and Kváň.

diverse but abundant fauna of the lingulate and craniate brachiopods, the gastropod *Mimospira*, and the cystoids *Macrocystella*, *Paleosphaeronites*, *Echinosphaerites* and *Pyrocystites* (?). This level is distinct in the Komárov area 3.5 to 4.0 m below the top of the formation, and approximately 10 m above the trilobite-bearing beds of the Třenice Formation. The occurrence of a rich fauna is only local, probably due taphonomic or diagenetic loss at the other localities. The data from the Úvaly area are less complete. The trilobites are associated with *Jivinella incola* and *Poramborthis klouceki*. This indicates that the beds bearing trilobites might correlate with those containing *Jivinella incola* and the trilobites in the Komárov area.

The overlying Olešná Member of the Klabava Formation begins with a red greywacke with a poor fauna of lingulate brachiopods and sponges associated with *Jivinella slaviki* (0.7 to 1.5 m above the boundary). This species has also been found 4 m above the boundary in a very rich but slightly different fauna of lingulate brachiopods (Mergl 1986, 2002).

The absence of organic-walled microfossils (chitinozoans, hystrichosphaerids), a lack of graptolids, and insufficient knowledge of the associated but yet unstudied conodonts prevent the direct correlation of the sequence with the standard conodont and graptolite zonations.

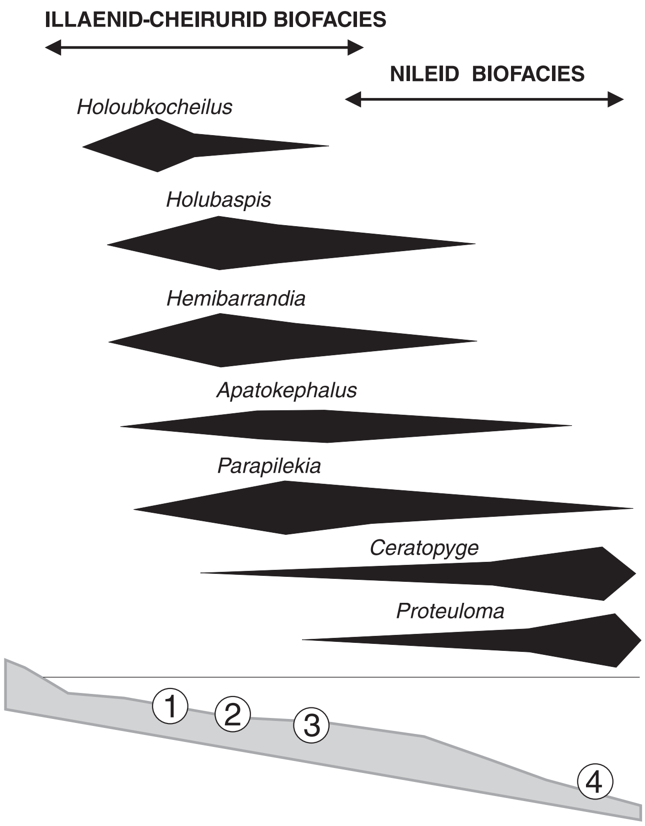
Palaeoenvironment

The lithology, taphonomy, and taxonomic composition of the fossil assemblages are consistent with a shallow littoral, wholly marine environment. The lithology of the trilobite-bearing beds in the Třenice Formation indicates a shallow, high-energy environment, and proximity to an ancient shore (Havlíček and Šnajdr 1956, Kukal 1963) in both the Holoubkov and Cheznovice localities. Tightly packed and sometimes nested convex shell accumulations and fragmentation indicate deposition on a shallow sea floor with oscillatory (wave) currents at a maximum depth of several tens of metres. The small shell fragments are sometimes preserved in small traps between the stromatolitic mounds, indicating the transport of bioclasts over a floor. However, a chaotic accumulation of fragmented fossils in the trilobite-bearing beds originated very probably by the rapid deposition of unsorted bioclasts and scattered small pebbles in a ferruginous matrix (probably sideritic clay). The presence of echinoderms indicates an entirely marine environment.

The environment during deposition of the trilobite-bearing beds of the Mílina Formation was similar, though less of the coarse siliciclastic material was deposited from the nearby land. The extensive growth of siliceous sponges probably formed local "sponge gardens". In these "gardens" flourished organophosphatic lingulate microbrachiopods and spinose and pedunculate rhynchonelliform brachiopods, possibly resting on the sponges. Unconsolidated sediment was often rewashed, leaving sorted bioclastic material (tiny spicules and biogenic detritus to coarse bioclasts of cm size, e.g. whole shells) on bedding planes or forming small lenticular accumulations. The colour banding of the cherts is similar to hummock or flaser cross bedding, but diagenetic silicification obscures the textures. A maximum depth of several tens of metres has been suggested, though a depth of even just a few metres is not entirely excluded. The presence of well developed eyes in almost all trilobites of both formations, including the illaenimorphs *Hemibarrandia*, *Ottenbyaspis*, and *Platypeltoides*, and the absence of atheloptic trilobites, also indicate a habitat within the photic zone. Somewhat less consistent is the rare presence of *Pricyclopyge*, which is thought to represent mesopelagic genus (Fortey and Owens 1997).

Biofacies

Trilobite biofacies patterns in onshore-offshore transects have been recognized by Fortey (1975a, 1975b) in the Lower Ordovician of Spitzbergen; similar trilobite based biofacies have since been recognized in the Ordovician, Silurian, and Devonian (for example Fortey and Owens 1978, 1987, Cocks and Fortey 1988, Chlupáč 1983, 1987). In the Lower Ordovician, Fortey (1975b) described a basinward succession of illaenid-cheirurid, nileid, and olenid biofacies. In the same relation to the shore, the equatorial carbonate mounds or algal buildups were replaced by near-shore siliciclastic facies in higher palaeolatitudes. Despite a lithological difference, most of the Bohemian Tremadocian trilobite assemblages might be well compared with the illaenid-cheirurid biofacies of the lower palaeolatitudes.



Text-fig. 7. Reconstruction of depth-related distribution of index trilobite genera in the Mílina Formation. Number indicate approximate depth-related position of trilobite-bearing localities (1 – Holoubkov, 2 – Kvaň, 3 – Olešná, 4 – Úvaly).

The trilobite assemblage from the south-western part of the Prague Basin is dominated by the cheirurids *Parapilekia* and *Anacheirurus*, illaenimorph genera *Hemibarrandia* and *Ottenbyaspis*, an eurekiid (?) *Holubaspis*, and the early calymenaceans *Holoubkocheilus* and *Parabathycheilus.* The proetid-like *Eulomina* is also present. The trilobite association of the Třenice Formation is consistent with the illaenid-cheirurid biofacies.

The composition of the trilobite association of the Mílina Formation is generally similar. The illaenid-cheirurid biofacies continues, with the dominance of the genera *Parapilekia*, *Hemibarrandia* and *Holubaspis*. However, some new taxa appear while the proportions of others become less significant, indicating more an open and deeper (? or shaded in sponge "gardens") environment. A remopleuriid *Apatokephalus*, associated with *Celdometopus*, *Ceratopyge*, *Pricyclopyge, Platypeltoides, Harpides*, and *Dikelokephalina*, together with agnostids, appear more commonly in the SW part of the basin. The east part of the basin, in the Úvaly area, shows a higher degree of similarity to the nileid biofacies. The cheirurids, illaenimorphs and *Holubaspis* are less common or rare, and the trilobite assemblage is dominated by *Proteuloma*, *Ceratopyge, Platypeltoides*, and agnostids. However, many taxa characteristic of the nileid biofacies are absent in the Barrandian. With the exception of *Platypeltoides* and the very rare *Niobina*, the asaphids, shumardiids and nileids are unknown. The deeper biofacies, often associated with olenid trilobites, are unknown in the Prague Basin. This might be explained by a shallower environment and absence of oxygen deficient sea floor in the basin. The absence of the olenid biofacies is consistent with a shallow epicontinental character for the sedimentary basin in the area between Rokycany and Prague, gradually deepening toward the northeast. The dark shale intercalations with a graptolite fauna are known from the most eastward outcrop of the Tremadocian succession in the Prague Basin (the "Na Chrástnici" quarry near Břežany; Koliha 1926). The intercalation yielded *Rhabdinopora flabelliforme intermedium* and *Callograptus kodymi* (Prantl and Přibyl 1949b, Kraft 1975). However, no trilobites are associated with this remarkable graptolite fauna.

Affinity and correlation of the fauna

There is quite a general consensus about the Ordovician position of most of the terranes that constitute Europe (Scotese and McKerrow 1991, Cocks and Fortey 1988, 1998). The Bohemian area, referred to by some authors as the Perunica terrain (Havlíček et al. 1994), was situated in the south-western periphery of West Gondwana with other marginal terranes (Fortey and Cocks 2003, Cocks and Torsvik 2005). The European Tremadocian successions of the Welsh Basin (Avalonia), Spain and southern France (Armorica), and Bavaria (Perunica) are sufficiently known for comparative purposes. The data from northern Africa are more scattered (Legrand 1973, 1985). Brachiopod and trilobite data concerning these terrains have been summarized several times (Cocks and Fortey 1988, 1990, Havlíček 1989, Havlíček et al. 1994, Cocks and Torsvik 2002, Fortey and Cocks 2003).

The open shelf olenid biofacies extended onto some European shelves from the late Cambrian to its next expansion in the early Tremadocian (Clarkson and Taylor 1995). The olenid genera *Bienvillia, Hypermecaspis, Peltocare, Parabolinella, Saltaspis,* and *Tropidopyge* are known from Scandinavia (Henningsmoen 1957, 1959, Tjernvik 1956, Nikolaisen and Henningsmoen 1985, Ebbestad 1999), while *Angelina, Beltella*, *Bienvillia, Leptoplastides, Peltocare*, and *Parabolinella* are significant olenid genera in Great Britain (Whittington et al. 1983, Fortey and Owens 1989, 1991, 1992). The olenid genera *Parabolinella* and *Triarthrus* are also present in Bavaria (Sdzuy 1955), and olenids are reported also from the Iberian Chains of Spain (Josopait 1972). This is consistent with the deeper, outer-shelf marginal position of olenid biofacies in Baltica (Norway and southern Sweden), the continental margins of Avalonia (South Wales) and Perunica (Bavaria), and the deeper sites of Armorica (Iberian Chain). The olenid biofacies is similar to those in the external sides of East Gondwana. Tremadocian successions in Argentina, Bolivia, and Mexico contain similar, very rich fauna including *Angelina, Bienvillia*, *Hypermecaspis, Leptoplastides, Jujuaspis, Parabolina, Parabolinella, Peltocare,* and *Triarthrus* (Harrington and Leanza 1957, Robison and Pantoja-Alor 1968, Přibyl and Vaněk 1980, Waisfeld and Vaccari 2003). This indicates (Fortey and Cocks 2003) that these biofacies are almost independent of biogeography and palaeolatitude. Nevertheless, the olenid biofacies is absent in the Prague Basin. Even the deepest sites east of Prague (Úvaly area), with more common *Ceratopyge* and *Proteuloma*, lacks any olenid species. This indicates rather equivalent of the nileid biofacies. The basin in the Lower Ordovician was never deep enough to enable the immigration of the open-shelf elements, which also explains the absence of the brachiopod *Broeggeria* association, which is common elsewhere with the olenids.

Numerous cosmopolitan genera are significant in the composition of the Tremadocian trilobite fauna of the Prague Basin, e.g. *Apatokephalus, Agerina, Ceratopyge, Geragnostus, Dikelokephalina, Harpides, Parapilekia, Platypeltoides*, and *Proteuloma*. Their presence indicates rather weak influence of climate on their spread. The trilobite genera listed above expanded along the margins of Gondwana and adjacent terrains, with the evolution of local endemic species from pandemic ancestors. Other genera are much more restricted. Illaenimorph *Ottenbyaspis* and *Hemibarrandia* have their analogies in Baltica (*Panderia, Ottenbyaspis*), Kazakh, and neighbouring terranes (*Parakoldinia* and its relatives). These illaenimorphs as a whole indicate a shallower environment and are therefore rare in the deeper nileid biofacies of the Scandinavian Lower Ordovician. *Parapilekia* and other cheirurids (*Pliomeroides, Anacheirurus*) are rare in the Tremadocian of Baltica, and in the other southwest Gondwana occurrences (Barrande 1868, Szduy 1955, Fortey and Owens 1991, Sdzuy et al. 2001). Unlike other areas in western and south-western Europe, the cheirurids represented by *Parapilekia* and *Anacheirurus* belong to the predominant elements in the Prague Basin. That they are associated with the endemic calymenaceans

Parabathycheilus and *Holoubkocheilus*. *Parabathycheilus* is known from Armorica and marginal Perunica (Bavaria), but calymenaceans are absent in a deeper sites of Avalonia. Calymenacenas are rare outside southwest Gondwana, being represented by the generally rare and depth-related *Pharostomina* in other more marginal sites (Mexico, Argentina, Bolivia, and Hunan). *Holubaspis* is predominant and highly endemic, and is undoubtedly a shallow-water genus restricted to Perunica only (Sdzuy et al. 2001). Its origin and affinity are uncertain, but it shares many common features with a late Cambrian but somewhat problematic eurekiid genus *Arcadiaspis* of Laurentia. A cyclopygid *Pricyclopyge* in the Mílina Formation may indicate a deeper environment, as indicated by its common presence in the axial and deeper eastern part of the basin.

In summary, Lower Ordovician trilobite fauna of the Prague Basin is similar to the cheirurid-illaenid biofacies common in shallow-water environment in a low palaeolatitude during the Tremadocian time because of the predominance of cheirurid and illaenimorphs. Apart from the cosmopolitan taxa common in other continents and mostly associated rather with a nileid biofacies, the Prague Basin became an important area for some endemic calymenaceans (*Holoubkocheilus, Parabathycheilus*) and taxa of unclear systematic position (*Holubaspis, Holoubkovia, Eulomina*). Its similarity with the late Tremadocian fauna of Scandinavia (Mergl 1984a, Havlíček et al 1994) actually reflects similar depth-related nileid biofacies with cosmopolitan genera.

Affinity to other Bohemian faunas

Trilobite faunas of the Třenice and the Mílina formations are closely related. It is not surprising that the first authors who dealt with this fauna (Klouček 1925, 1926a, Koliha 1937) suggested the same stratigraphic age for all known occurrences. However, there are phylogenetically related couplets of the same genera. The species *Hemibarrandia holoubkovensis* precedes *H. klouceki, Anacheirurus bohemicus* precedes *A. nanus*, *Parapilekia ferrigena* precedes *P. olesnaensis*, *Parabathycheilus krafti* precedes *P. vagans*, *Holoubkocheilus granulatus* precedes *H. asopus*, and *Agerina ferrigena* precedes *A. clymene*. Some rare trilobites from the Třenice Formation show close relations to the species of the Mílina Formation, and thus are tentatively referred to the same species (*Apatokephalus dagmarae*, *Platypeltoides perseis*, *Dikelokephalina ulrichi*, and *Holoubkovia klouceki*). *Holubaspis perneri* is only species present in both formations with certainty. Finally, there are taxa that are present in only one of the formations. *Eulomina mitratum* and the illaenimorph *Ottenbyaspis broeggeri* are moderately common but confined to the Třenice Formation. On the contrary, the Mílina Formation bears many unknown in the Třenice Formation. These are represent by new immigrants into the basin; *Harpides grimmi*, *Celdometopus klouceki, Proteuloma kettneri, Pricyclopyge oceanitis, Ceratopyge mareki*, and the agnostids *Geragnostus atavus* and *G. peki* are the characteristic representatives. Unlike the Třenice Formation, the fauna of the Mílina Formation has more cosmopolitan taxa typical for of the late Tremadocian.

The trilobite fauna of the Třenice and Mílina formations has no obvious descendants in the younger Ordovician units in the basin and almost entirely disappeared before the Arenigian. The trilobites of the Klabava Formation are known from several stratigraphic levels (Holub 1911, Mergl 1991), but the fauna is wholly different except for the cosmopolitan agnostid *Geragnostus* and mesopelagic cyclopygid *Pricyclopyge*. The deepening of the basin brought a new depth-related fauna including asaphids, some atheloptic trilobites, and abundant meso- to bathypelagic cyclopygids. The illaenid-cheirurid biofacies with pliomerids, cheirurids, illaenids, isocolids, and possibly a descendant of *Holubaspis*, only continued along the shoals of submarine volcanic elevations (Mergl 1991) in the Komárov area.

Repository of studied material

All of the materials studied and illustrated in the present contribution are housed in the following institutions:
1) Czech Geological Survey, Prague: The collection of J. Vaněk (prefix JV), the collection of the author (prefix MM), and the small collection of V. Havlíček (prefix VH), from the Olešná, Kvaň, and Úvaly localities.
2) National Museum, Prague: The large collections of C. Klouček and R. Růžička from the Olešná, Holoubkov, and Úvaly localities, and the small collections of N. Kalat and F. Hörbinger from the Úvaly area (prefix L NM).
3) Museum of Dr. B. Horák, Rokycany: The small collection of V. Kraft from the Holoubkov locality (prefix MR).
4) University of West Bohemia, Praha: The collection of the author (prefix PCZCU) from the Olešná and Kvaň localities.

Abbreviations

Lc – length of cranidium, Lp – length of pygidium, Wc – width of cranidium, Wp – width of pygidium.

Acknowledgment

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Systematic part

Class **Trilobita** WALCH, 1771
Order **Agnostida** SALTER, 1864
Family **Metagnostidae** JAEKEL, 1909
Subfamily **Metagnostinae** JAEKEL, 1909

Genus ***Geragnostus*** HOWELL, 1935

Type species: *Agnostus sidenbladhi* LINNARSSON, 1869; Upper Tremadocian, Ceratopyge Limestone; Sweden.

Geragnostus peki (MERGL, 1984)

Text-fig. 8A-O

1922 *Agnostus* cf. *bavaricus* BARR.; Klouček, p. 1.
1926a *Agnostus* sp.; Klouček, p. 192.
1926a *Agnostus* cf. *bavaricus* BARR.; Klouček, p. 192.
1937 *Agnostus* sp.; Koliha, p. 486.
1937 *Agnostus* cf. *bavaricus* BARR.; Koliha, p. 486.
1964 *Geragnostus bavaricus* (BARRANDE, 1868); Vaněk, p. 107.
1965 *Geragnostus bavaricus* (BARRANDE, 1868); Vaněk, p. 265, pl. 22, figs 1, 2.
1965 *Leiagnostus franconicus* SDZUY, 1955; Vaněk, p. 266, pl. 22, figs 3, 4.
1977 *Leiagnostus franconicus* SDZUY, 1955; Pek, p. 21, pl. 4, figs 1, 2.
1977 *Geragnostus bavaricus* (BARRANDE, 1868); Pek, p. 9, pl. 1, figs 1–5, text-fig. 3.
1984a *Neptunagnostella peki* sp. n.; Mergl, p. 18, pl. 2, figs 5, 6, text-fig. 1.
2001 *Geragnostus peki* (MERGL, 1984); Vaněk and Valíček, p. 45.

Holotype: Pygidium figured by Mergl (1984a) on pl. 2, fig. 6, re-figured here in text-fig. 8K, O, deposited in the collections of the Czech Geological Survey, Prague (MM 100).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Zaječov (part Kvaň), small hill SW of the village.

Material: Fifteen cephala, 11 pygidia, and one thoracic segment.

Diagnosis: *Geragnostus* with strongly convex shields; cephalon with relatively short and narrow glabella, weak transverse furrow and small posterolateral spines; pygidium with weak axial furrows, long and wide axis, M3 wider (tr.) than M2; M2 with minute median node slightly anterior to its posterior end; pygidial border narrow with minute posterolateral spines.

Emended description: Cephalon highly convex, subcircular, widest at posterior margin, with slightly depressed preglabellar field. Glabella moderately convex, tapering gently forward, cca 60 % as long as cephalon. Anterior lobe shorter and less convex than the much more prominent, subcircular, highly and evenly convex posterior lobe, which is slightly extended toward posterior margin. Transglabellar furrow weakly impressed. Axial node small, at anterior portion of posterior lobe.

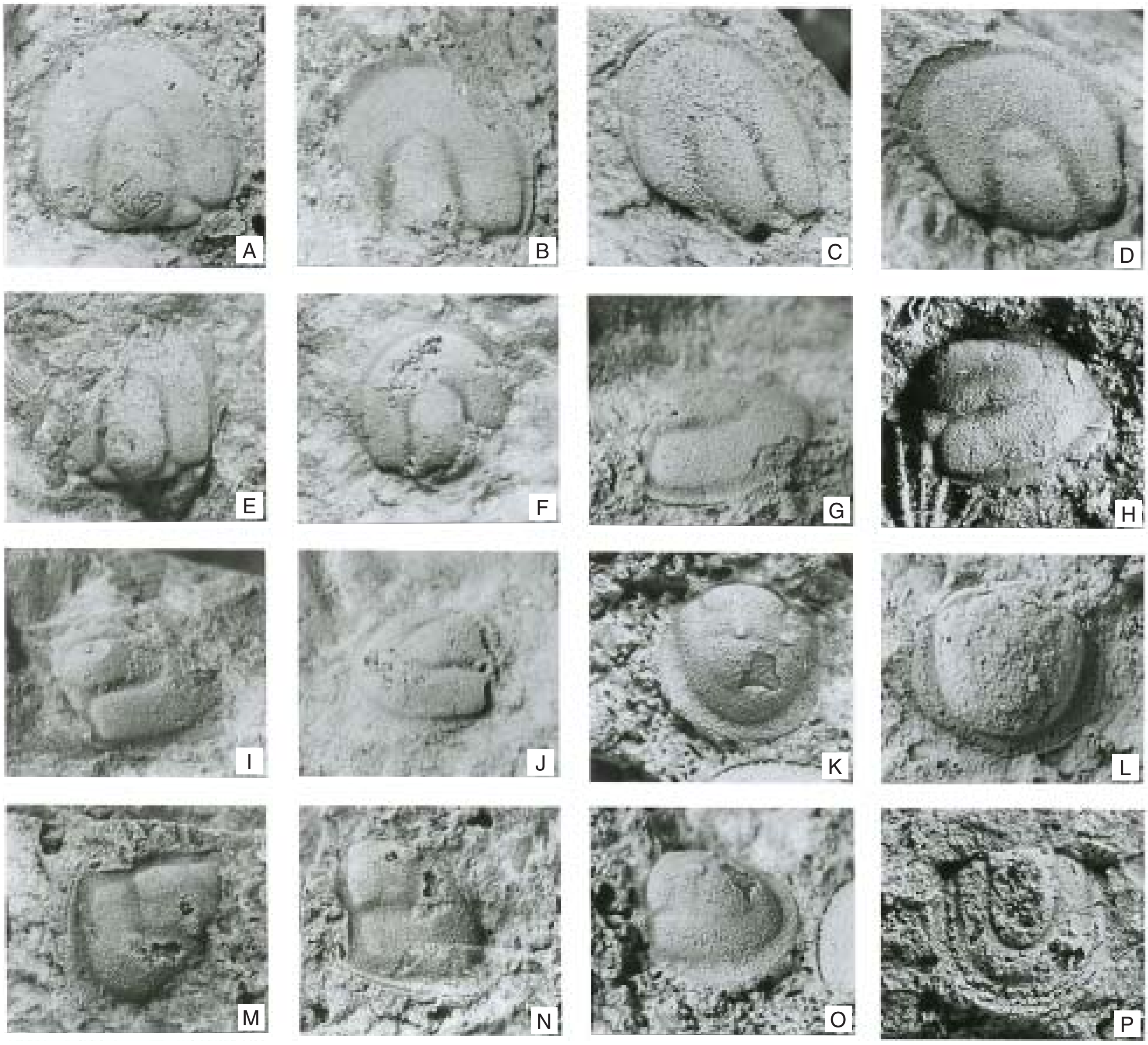
Axial furrows deep and broad. Basal lobe subtriangular, much shorter than its width (sag. and tr.), and connected medially, with rounded abaxial margin, and separated from genae and glabella by deep and well impressed furrows. Genae smooth, steeply downsloping. Anterior border is broad, and tapers posteriorly. Border furrow is broad, tapering and deeply incised posteriorly. Genal angles with small, short posterolateral spines are directed posterodorsally.

The thorax is poorly known. The only fragment of the first thoracic segment shows short, gently convex median lobe, laterally with adjacent highly raised lateral lobe. Pleural furrow and band are not clearly developed.

Pygidium highly convex, subcircular in outline, subequal in length and width, with maximum width at about anterior one-third. Axis tapers backward, some 65 % as long as pygidial length, gently convex, with low relief. Axial furrows weak, converging near M1, subparallel near M2, and converging and curved around M3. M1 subrectangular, longer than M2. Median ridge low and broad anteriorly and continues to a prominent axial node at posterior of M2. Pleural fields strongly downsloping, gently convex, each narrower (tr.) than the axis. Anterior margin deeply concave in dorsal view, with forward extended shoulder with acute tip. Articulating furrow deep, short. Border gently convex with border furrow distinct anteriorly, becoming obscure posteriorly. Posteriolateral border spines very small and short.

Remarks: Among the various early Ordovician metagnostids, *Geragnostus wimani* TJERNVIK, 1956 (see Ahlberg 1992) strongly resembles *G. peki* (MERGL, 1984). This species from the Latorp Limestone (*Megistaspis planilimbata* Zone, Hunneberg Stage) of Scandinavia has a similar backward tapering pygidial axis with low relief, anteriorly tapering glabella with a weak transverse furrow, and very small posterolateral border spines. Unlike *G. peki*, the frontal lobe of the median ridge on pygidial axis is very prominent, and the preglabellar part of the cephalon is shorter (sag.). Two species of *Geragnostus* from the Ceratopyge Limestone of Västergötland and Öland (Ahlberg 1989, 1992), and the Bjørkåsholmen Limestone (Ebbestad 1999), are less similar to *G. peki*. The type species *G. sidenbladhi* (LINNARSSON, 1869) has less convex shields, narrower (tr.) pygidial axis with deeper axial furrows and larger M3, stronger posterolateral border spines, narrower (tr.) genal field on cephalon, and more clearly incised furrows and lobes on the glabella. *Geragnostus crassus* TJERNVIK, 1956 differs from *G. peki* by having a distinct transglabellar furrow, a longer glabella, larger posterolateral border spines, and a wider (tr.) M3 on the uniformly wide pygidial axis.

The Tremadocian metagnostids from the Montagne Noire, France (Howell 1935) are poorly preserved and illustrated, making a comparison with *G. peki* impossible. The presence of three agnostid species in the Tremadocian of the Barrandian was noted by Klouček (1922) from the Úvaly area. He referred one to *Agnostus bavaricus* BAR-



Text-fig. 8. ***Geragnostus peki*** **(MERGL, 1984)**
A, H – cephalon, internal mould and latex cast in oblique view, PCZCU 1600, ×12, ×14; B, G – cephalon, internal mould and its oblique view, PCZCU 1601, ×12; C – cephalon, deformed internal mould, NM L 38472 ×12; D – cephalon, deformed internal mould, NM L 38473, ×12; E, I – cephalon, internal mould and its oblique view, PCZCU 1602, both ×12; F, J – incomplete cephalon, internal mould and its oblique view, PCZCU 1603, both ×12; K, O – holotype, pygidium, internal mould and its oblique view, MM 100, both ×12; L – pygidium, latex cast of exterior, PCZCU 1604, ×14; M, N – incomplete pygidium, internal mould and its oblique view, PCZCU 1605, ×12; Mílina Formation, Kvaň (A, B, E–K, M–O), Úvaly, Vinice (C, D) and Olešná (L).
Geragnostus atavus **MERGL, 1984. P – holotype, internal mould, MM 101, ×12; Mílina Formation, Olešná.**

RANDE, 1868, leaving two others unassigned. The first illustrations of the Tremadocian agnostids were given in Vaněk (1965), followed by Pek (1977). All of the specimens illustrated by those authors are poorly preserved and tectonically deformed. The nearly effaced pygidia were referred (Vaněk 1965, Pek 1977) to *Leiagnostus franconicus* SDZUY, 1955, while the cephala with distinct and (because of tectonic deformation) exaggerated axial furrows were attributed to *Geragnostus bavaricus*. New material from the Úvaly area indicates the occurrence of only one species that is morphologically identical with the specimens from the Komárov area.

Occurrence: Mílina Formation; Olešná (rare), Kvaň (abundant), Úvaly-Vinice (abundant).

Geragnostus atavus MERGL, 1984
Text-fig. 8P

1965 *Geragnostus bavaricus* (BARRANDE, 1868); Vaněk, p. 265, pl. 22, figs 1, 2.
1984a *Geragnostus atavus* sp. n.; Mergl, p. 19, pl. 2, fig. 7, text-fig. 2.
2001 *Geragnostus atavus* MERGL, 1984; Vaněk and Valíček, p. 44.

Holotype: Pygidium figured by Mergl (1984a) on pl. 2, fig. 7, re-figured here in text-fig. 8P, deposited in the collections of the Czech Geological Survey, Prague (MM 101).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Material: Three pygidia.

Diagnosis: *Geragnostus* with subquadrate pygidium of low convexity having deep parallel axial furrows; pygidial border narrow with prominent posterolateral spines.

Description: See Mergl (1984a).

Remarks: Knowledge of this species is still poor. The less convex pygidium, deeply incised axial furrows, and distinct posterolateral border spines indicate that it is a different species from the much more common *G. peki* (MERGL, 1984). This species is known only from the Olešná locality, and new, better preserved specimens must be obtained to compare and evaluate this species with other metagnostids.

Occurrence: Mílina Formation; Olešná (very rare).

Order **Corynexochida** KOBAYASHI, 1935
Suborder **Scutelluina** HAWLE et CORDA, 1847
Superfamily **Illaenoidea** HAWLE et CORDA, 1847
Family **Illaenidae** HAWLE et CORDA, 1847
Subfamily **Panderinae** BRUTON, 1968

Genus *Ottenbyaspis* BRUTON, 1968

Type species: *Illaenus oriens* MOBERG et SEGERBERG, 1906; Upper Tremadocian, Bjørkåsholmen Formation; Öland, Sweden.

Ottenbyaspis broeggeri (RŮŽIČKA, 1926)
Text-figs 9, 10

1925 *Symphysurus* sp. I; Klouček, p. 1.
1926 *Symphysurus Bröggeri* n. sp.; Růžička, p. 10, pl. 2, figs 10–12.
1926 *Symphysurus Bröggeri* n. sp.; Růžička, p. 18, pl. 3, fig. 10.
1926b *Symphysurus bohemicus* KLOU. n. sp.; Klouček, fig. on p. 54.
1926a *Symphysurus bohemicus* KLOU.; Klouček, p. 192.
1927 *Symphysurus Bröggeri* n. sp.; Klouček and Koliha, p. 3.
1928 *Symphysurus Bröggeri* n. sp.; Růžička, p. 53.
1931 *Symphysurus Bröggeri* RŮŽ.; Růžička, p. 391, pl. 1, fig. 7.
1949a *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Prantl and Přibyl, p. 11.
1970 *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Horný and Bastl, p. 85.
1994 *Ottenbyaspis* (?) *broeggeri* (RŮŽIČKA, 1926); Mergl, p. 18, pl. 5, figs 1–6.
2001 *Ottenbyaspis* (?) *broeggeri* (RŮŽIČKA, 1926); Vaněk and Valíček, p. 33.

Lectotype: Pygidium, internal mould, figured by Růžička (1926) on pl. 2, fig. 11, re-figured here in text-fig. 9A–C, E, F, H, deposited in the collection of the National Museum, Prague (NM L 18905).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the adandoned "V Ouzkém" iron ore mine.

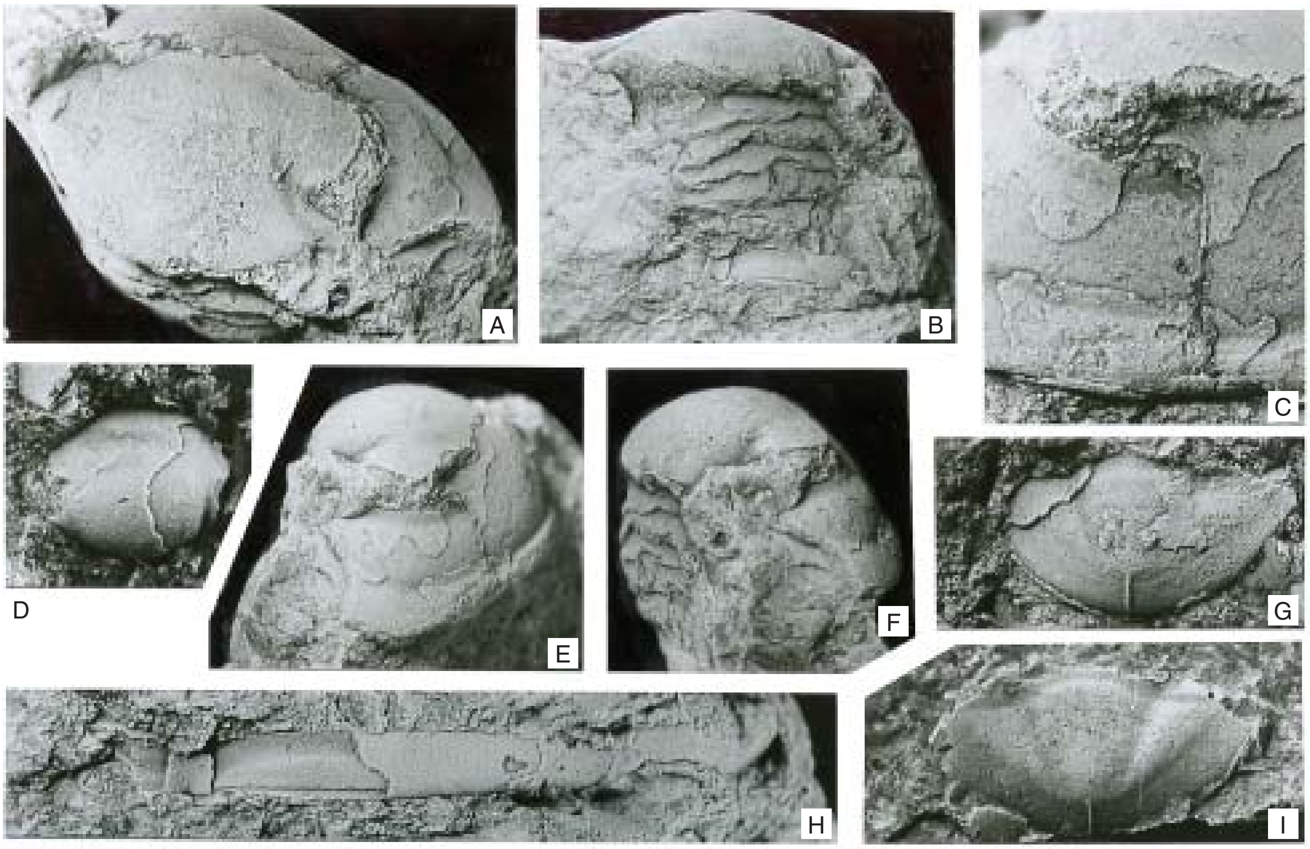
Material: One cephalon with incomplete thorax, 3 fragments of cephalon, and 6 pygidia.

Description: Mergl (1994).

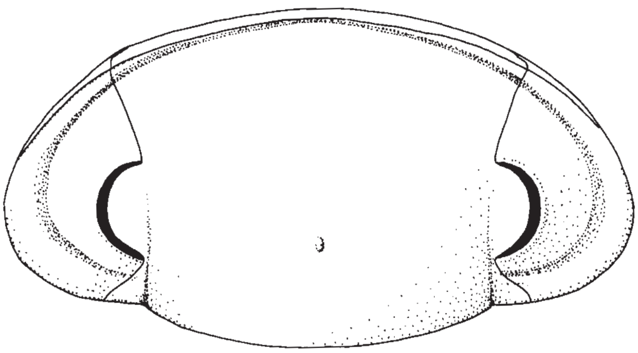
Remarks: *Ottenbyaspis broeggeri* (RŮŽIČKA, 1926) was originally referred to *Symphysurus* GOLDFUSS, 1843 by Růžička (1926, 1931). However, the original generic assignment has been corrected by Mergl (1994), who compared the species with both *Ottenbyaspis* BRUTON, 1968 and *Parakoldinia* ROZOVA, 1984. The latter genus is broadly distributed throughout the late Cambrian to early Tremadocian (Rozova 1984, Shergold and Sdzuy 1984) in Asia. Stratigraphically successive European species were referred to *Ottenbyaspis* by Bruton (1968). Although the attribution of *Ottebyaspis* to the subfamily Panderiinae BRUTON, 1968 is not unambiguous, the opinion of Lane and Thomas (1983) is followed here. Neither the Scandinavian nor the Bohemian species show the course of the ventral sutures, which are important for classification.

Outside Bohemia, three species of *Ottenbyaspis* occur in the Upper Tremadocian of Sweden and Norway (Tjernvik 1956, Bruton 1968, Ebbestad 1999), and in the lower Arenigian of Bornholm, Denmark (Poulsen 1965, Nielsen 1995). The cranidium of *Ottenbyaspis oriens* (MOBERG et SEGERBERG, 1906) from the Bjørkåsholmen Formation (Upper Tremadocian) is wider (tr.) between the anterior branches of the facial sutures, and this species has a less distinct anterior border than the cranidium of *O. broeggeri*. The anterior part of the cranidium of the early Arenigian (*Megistaspis planilimbata* Zone, Hunneberg Stage) species *O. perseverans* (TJERNVIK, 1956) is wider (tr.) than that of *O. broeggeri*, but a raised anterior border is about the same length (sag.) as in the Bohemian species. Unlike *O. oriens*, the weakly divergent anterior branch of the facial sutures is common in *O. broeggeri* and *O. perseverans*. Both Swedish species differ by lack of the postaxial ridge in the pygidium. The rare species *Ottenbyaspis* sp. from the late Arenigian (*Megistaspis polyphemus* Zone, Komstad Limestone, Volkhov Stage) (Nielsen 1995) has an anteriorly wider (tr.) cranidium, smaller palpebral lobes, and deeper axial furrows; its pygidium is unknown.

Ottenbyaspis broeggeri is somewhat similar to young specimens of *Hemibarrandia holoubkovensis*. The main difference is the postaxial ridge on the inner surface of the pygidium. The cephalon of *O. broeggeri* differs by a smaller palpebral lobe on a very narrow (tr.) palpebral part of fixigena. The axial furrows are longer in *H. holoubkovensis* and run almost parallel, while in *O. broeggeri* they are anteriorly divergent. This is distinct even in a small specimen (Text-fig. 9D), which is very similar to the *Panderia* figured by Bruton (1968). On the posterior part of the glabella, small-sized specimens of *H. holoubkovensis* have three to four



Text-fig. 9. ***Ottenbyaspis broeggeri*** **(RŮŽIČKA, 1926).**
A–C, E, F, H – specimen with incomplete thorax, cranidium with librigena, thorax, detail of anterior rim and facial suture, anterolateral and lateral views to the specimen, and detail of segments showing doublure, NM L18905, ×6, ×4, ×10, ×4, ×4, ×7; D – cranidium of small specimen, NM L 18931b, ×12; G – pygidium, internal mould, NM L 30834a, ×5.5; I – pygidium, internal mould, NM L 18921, ×5.5; Třenice Formation, Holoubkov.



Text-fig. 10. ***Ottenbyaspis broeggeri*** **(RŮŽIČKA, 1926). Reconstruction of the cephalon. Approximately ×6.**

arched terrace ridges, with steep slopes facing backward, and the surface of the glabella and genae are covered by fine pits. In *O. broeggeri* these posterior terrace ridges are absent and the glabella lacks distinct pitting. A small axial node is present on the external surface of the exoskeleton in some fragments referred to *Ottenbyaspis broeegeri.* This posterior part of the glabella was figured by Růžička (1926: pl. 2, fig. 12) and has a distinct axial node. Segments of *Ottenbyaspis* have a very broad (tr.), gently convex axis, and much shorter, considerably fulcrate pleural parts. The doublure of the pleurae show very fine terrace lines. The pleural furrow is weakly defined.

O. broeggeri was described by Růžička (1926) as a different species than *S. bohemicus* KLOUČEK. The latter name denominates the drawing of a nileid by Klouček (1926a), but there is no associated formal description of *S. bohemicus*, and this name should be considered as a *nomen nudum*. Klouček and Koliha (1927) suggested the identity of both species, but Růžička (1931) argued for their independence. It is noteworthy that Klouček's drawing (Klouček 1926) and statements by Klouček and Koliha (1927: p. 3) imply that in the reconstruction of *S. bohemica*, the pygidium of *O. broeggeri* was by Klouček erroneously referred to as a somewhat idealised cephalon of *Hemibarrandia*. Prantl and Přibyl (1949a) deduced that *S. broeggeri* and *S. bohemicus* are synonymous with *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926). In attempting to support such a statement, they incorrectly presumed the course of the anterior branch of the facial sutures in Klouček's (1926b) original reconstruction of *S. bohemicus*, and did not mention any other evidence. Summarizing all of the data, *S. bohemicus* is considered as an invalid, and *H. holoubkovensis* and *O. broeggeri* are independent valid species restricted to the Třenice Formation.

Occurrence: Třenice Formation, locality Holoubkov (rare).

Genus ***Hemibarrandia*** PRANTL et PŘIBYL, 1949

Type species: *Nileus holoubkovensis* RŮŽIČKA, 1926; Upper Tremadocian, Třenice Formation; Barrandian, Bohemia.

Species assigned:
Hemibarrandia holoubkovensis (RŮŽIČKA, 1926); Tremadocian, Bohemia.
Hemibarrandia cf. *holoubkovensis* (RŮŽIČKA, 1926); Tremadocian, Bavaria.
Hemibarrandia klouceki sp. n.; Tremadocian, Bohemia.
Hemibarrandia triangula SDZUY, 1955; Tremadocian, Bavaria.
Hemibarrandia sp.; Tremadocian, Bavaria.

Remarks: The systematic position of *Hemibarrandia* PRANTL et PŘIBYL, 1946 has been discussed by numerous authors (Růžička 1926, Prantl and Přibyl 1949a, Sdzuy 1955, Vaněk 1965, Courtessole and Pillet 1975, Mergl 1984a, 1994). The genus was taken as an unusual taxon of the family Nileidae ANGELIN, 1854. Courtessole and Pillet (1975) established the new subfamily Hemibarrandinae COURTESSOLE et PILLET, 1975, but their drawing of the cephalon of *Hemibarrandia* is over-generalized. Fortey and Chatterton (1988) expressed doubts about the assignment of *Hemibarrandia* to the family Nileidae and the validity of the subfamily Hemibarrandinae. Despite the remarkably large size of *Hemibarrandia*, its general morphology is similar to that of the subfamily Panderiinae BRUTON, 1968. The main differences concern the small size of *Panderia* BRUTON, 1968. A panderinid *Ottenbyaspis* BRUTON, 1968 is also of small size. The late Cambrian genera *Koldinia* WALCOTT et RESSER, 1924 and *Parakoldinia* ROZOVA, 1960 are similar to the panderines. The effaced, strongly convex (sag.) cranidia with striated anterior margin or rim, narrow (tr.) fixigenae, distinct palpebral lobes, and nearly effaced pygidia of these genera indicate that *Hemibarrandia* might be the late survivor of these Upper Cambrian genera. The morphology of *Hemibarrandia* closely resembles the genus *Ottenbyaspis* BRUTON, 1968. The latter has a similarly transverse cephalon, an effaced glabella, weak and short axial furrows, a raised marginal rim, and a weak, posterior median glabellar tubercle. However, *Hemibarrandia* differs by having a much larger size and a more divergent anterior branch of the facial suture. A distinct border furrow on librigena is a common feature of *Hemibarrandia*, *Ottenbyaspis*, and *Panderia*. Some features apparently indicate a relationship to illaenids (e.g. pitted surface), but the details of the preglabellar ventral structures are unknown in *Hemibarrandia*. A highly extended adaxial librigenal doublure, with an oblique, anteriorly rapidly diverging rostral suture, indicates that the rostral plate probably does exist, being short (sag.), broadly triangular, and apparently of the same form as in the illaenids and the early panderines.

The genus is present in the Upper Tremadocian of Bohemia (Růžička 1926, Mergl 1984a, 1994), the Lower and Upper Tremadocian of Bavaria (Sdzuy 1955, Hammann and Sdzuy in Sdzuy et al. 2001), and possibly also occurs in the Lower Tremadocian of the Montagne Noire, France (Sdzuy 1958).

Hemibarrandia holoubkovensis (RŮŽIČKA, 1926)

Text-fig. 11

1925 *Symphysurus* sp. II; Klouček, p. 1.
1926 *Nileus Holoubkovensis* n. sp.; Růžička, p. 8, pl. 2, figs 5–8.
1926a *Symphysurus* (*Hemibarrandia*) sp.; Klouček, p. 193.
1931 *Nileus Holoubkovensis* RUŽ.; Růžička, p. 391, pl. 1, fig. 8.
1937 *Nileus holoubkovensis* RUŽ.; Koliha, p. 485.
1949a *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Prantl and Přibyl, p. 11, pl. 2, fig. 3.
1951 *Pseudonileus holoubkovensis* (RŮŽIČKA, 1926); Kobayashi, p. 41.
1953 *Hemibarrandia holoubkovensis* (RŮŽIČKA); Přibyl, p. 44.
1964 *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Vaněk, p. 108.
1965 *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Vaněk, p. 273, pl. 26, figs 47–49.
1970 *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Horný and Bastl, p. 168, pl. 5, fig. 10.
1975 ? *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Courtessole and Pillet, p. 260, fig. 2q.
1994 *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Mergl, p. 20, pl. 6, figs 1–7, pl. 7, figs 1–4, 6, text-fig. 2.
2001 *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Vaněk and Valíček, p. 35.

Lectotype: Selected by Prantl and Přibyl (1949a), pygidium figured by Růžička (1926) on pl. 2, fig. 8, re-figured here in text-fig. 11E, deposited in the collection of the National Museum, Prague (NM L 18903).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the abandoned “V Ouzkém” iron ore mine.

Material: About 40 fragments of cephalons, 5 librigena, and 8 pygidia.

Diagnosis: *Hemibarrandia* with shorter (sag.) pygidium (Lp/Wp = 0.52), with distinct axis; anterior arch of the pygidium occupying less than 50 % of width; surface of exoskeleton, apart of articulating surfaces, almost completely covered by circular pits of 0.2 mm size.

Description: Mergl (1994).

Remarks: Several species of *Hemibarrandia* have been reported from Europe. Sdzuy (1955) described the species *H. triangula* SDZUY, 1995 from the Leimitz Shales (Lower Tremadocian) of Bavaria (*Macrocystella* ? *bavarica* Zone). The Bavarian species is known from a single specimen that differs from *H. holoubkovensis* by having longer axial furrows on the cranidium and a rounded triangular outline of the pygidium.

Occurrence: Třenice Formation, locality Holoubkov (abundant).

Hemibarrandia klouceki sp. n.

Text-figs 12, 13

1917 *Barrandia-Symphysurus* ? n. sp.; Klouček, p. 7.
1922 *Symphysurus* sp.; Klouček, p. 1.
1926a *Symphysurus* (*Hemibarrandia*) sp.; Klouček, p. 193.
1937 *Symphysurus bohemicus* KLOU.; Koliha, p. 486.
1964 *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Vaněk, p. 108.
1965 *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Vaněk, p. 273, pl. 26, figs 47–49.
1984a *Hemibarrandia holoubkovensis* (RŮŽIČKA, 1926); Mergl, p. 25, pl. 7, figs 1–4.

Holotype: Pygidium figured here in text-fig. 12M, deposited in the palaeontological collection of the Czech Geological Survey, Prague (VH 5025).

Paratype: Almost complete cranidium figured here in text-fig. 12A, F deposited in the palaeontological collection of the University of West Bohemia at Plzeň (PCZCU 1647).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Name: After Professor Celda Klouček, a famous collector of fossils from the Bohemian Tremadoc.

Material: One complete cranidium, 4 larger fragments of cranidium, 10 librigena, one thorax with pygidium, 10 pygidia and numerous fragments of various parts of exoskeleton.

Diagnosis: *Hemibarrandia* with longer (sag.) pygidium (Lp/Wp = 0.55–0.62) having poorly defined axis; anterior arch of the pygidium occupying about 50 % of width; surface of exoskeleton, apart of articulating surfaces, almost completely covered by circular pits of 0.2 mm size.

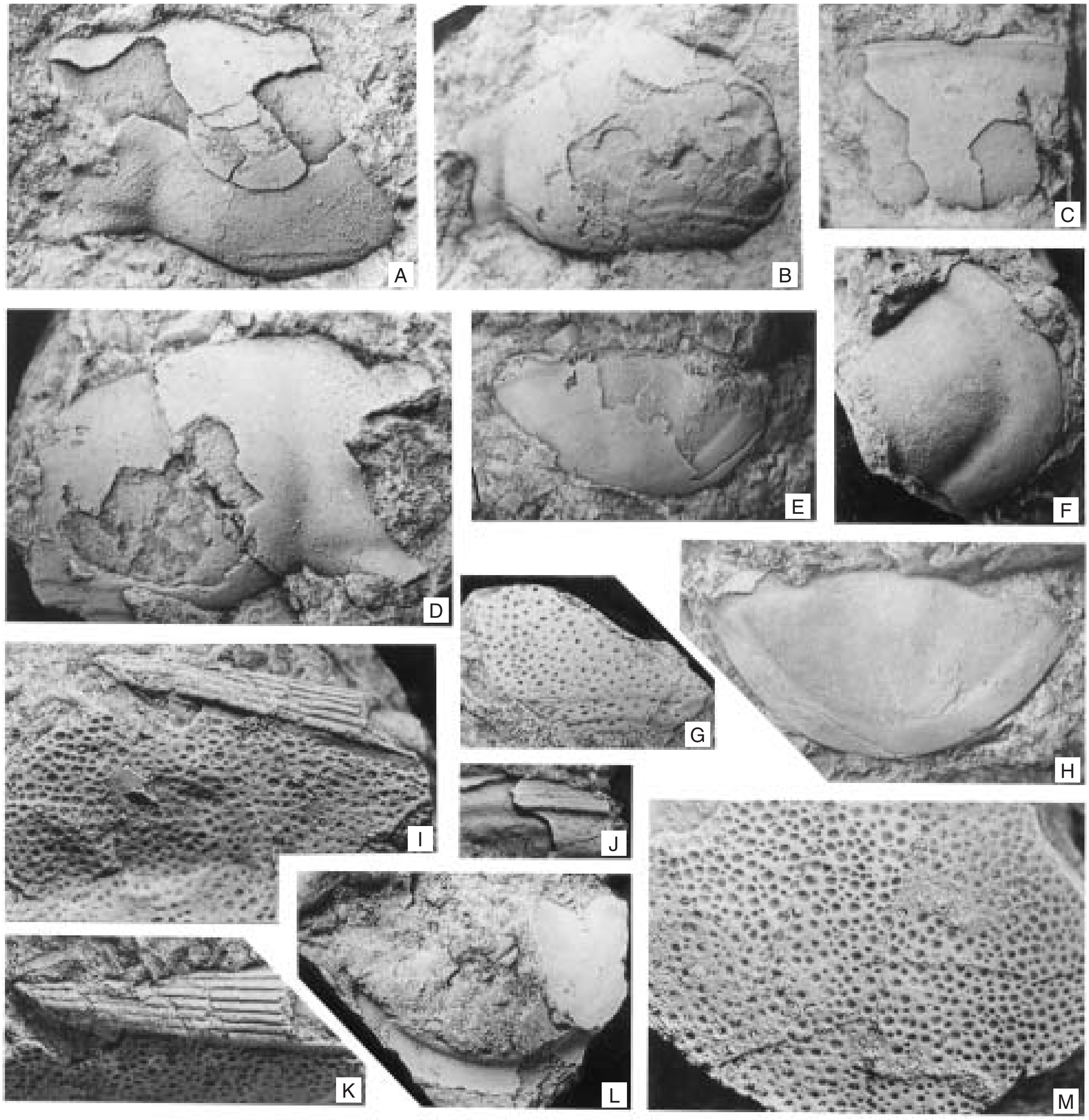
Description: Entire exoskeleton may reach 120–150 mm, large pygidia are 60 or even more mm wide. Cephalon transversely broadly oval, gently convex in transverse profile, with sloping librigenae and gently dorsally arched frontal margin. Glabella ill-defined, effaced, delimited posteriorly by broad (tr.) and short (sag.) axial furrows. Axial furrows disappear at anterior one-forth of length. Glabella continues forward to less convex field toward border furrow. No trace of occipital groove or ring. Posterior margin of glabella gently convex backward. Glabella gently convex (tr.), in side view with conspicuously curved posterior portion becoming less convex forward. Anterior border short, high, conspicuously convex, separated from weakly convex preglabellar and glabellar region by narrow distinct border furrow. This is deepest and narrowest (sag.) near sagittal axis, becoming shallower and wider abaxially. Anterior face of the border with raised marginal rim bearing transverse terrace ridges parallel to edges of cephalon. These ridges continue onto anterolateral parts of fixigena but rapidly disappear laterally. Fixigena conspicuously narrow (tr.), with large horizontal palpebral lobe bearing weak and broad palpebral groove. Anterior branch of facial suture widely diverging anteriorly, broadly S-shaped. Posterior branch of facial suture almost straight, much shorter than anterior branch, and inclined cca 45° toward posterior margin. Posterior part of fixigena very small. Posterior border furrow weak, widening abaxially. Posterior border weakly convex (exs.). Librigena broadly (tr.) crescentic, with rounded genal angle. Lateral border broad, weakly convex (tr.), librigenal part of the posterior border tapering adaxially. Lateral border with raised, narrow marginal rim extending toward the genal angle. Genal field gently convex (exs. and tr.). Eye socle low, smooth, indicating low, long (sag.), crescentic eyes with subvertical visual surface.

Doublure slightly narrower than lateral border (exs. and tr.), with weakly convex ventral surface. Doublure is extended far forward by narrower, conspicuously convex anterior (sag.) part. Adaxial points of doublure cut obliquely, which may indicate presence of transverse, short (sag.) rostral plate. Surface of doublure with coarse terrace ridges parallel with lateral margin. The widest lateral part of doublure with cca 8 to 10 terrace ridges. External surface of cephalon covered by small uniform circular pits of 0.2–0.3 mm diameter. The glabellar surface near the posterior margin probably smooth. Hypostome unknown.

Thorax of eigth segments. Thorax slightly tapering backward, with axial region about two-times wider (tr.) than pleural regions. Axis gently convex, externally defined by weak axial furrows. Pleural region consists of horizontal inner portion and gently sloping and slightly backward curving outer portion of nearly same width (sag.). Pleural furrows become indistinct adaxially, but they are distinct on ventral surface of outer portion of pleurae. Anterior pleural band higher and abaxially curved backward, posterior pleural band weak. Articulating facet broadly triangular, facing anterolaterally. Ventral surface of axial ring with fine acute ridge along its posterior margin. The axial ring thickened forward, being very thin near posterior edge of segment. Dorsal surface of segment is covered by shallow circular pits except for a smooth band bordering the anterior edge of pleura.

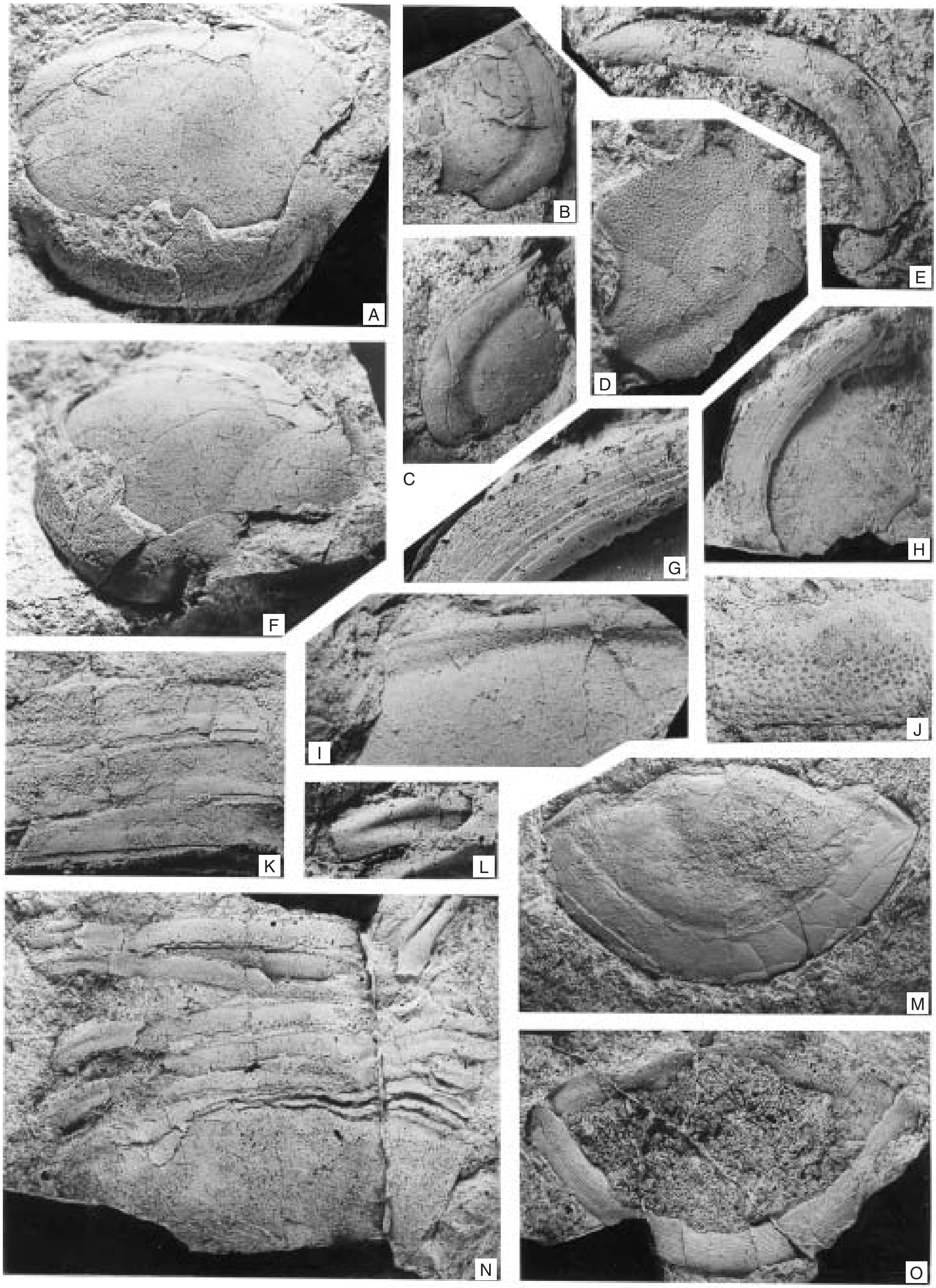
Pygidium transversely oval, with evenly curved posterior and lateral margins. Anterior margin weakly arched at the axis, and slightly curved backward in pleural regions. Pygidium gently convex, nearly effaced, with Lp/Wp 0.52–0.66,. Axis with rounded tip, weakly defined by curved, converging axial furrows, at anterior margin about 50 % as wide as the pygidium. Axial furrows are more perceptible on ventral surface, externally the axis is marked by weak convexity of surface. Pleural region weakly defined. Border furrow weak, narrow, limiting evenly broad (sag.) and weakly convex border. Anterior pygidial pleural furrow weakly inclined backward, separated from the anterior margin by conspicuous articulating facet and high transverse anterior pleural band. Doublure narrow (sag.), about 20 % of pygidial length, with convex ventral surface, almost evenly wide along entire length apart from the slightly tapering and dorsally bent lateral extremities. Surface of the doublure covered by coarse, regularly spaced, rarely branching terrace ridges, 8 to 15 in number, with steeper slopes facing posteriorly.

Remarks: The new species is very similar to *H. holoubkovensis* (RŮŽIČKA, 1926), and has been confused



Text-fig. 11. ***Hemibarrandia holoubkovensis*** **(RŮŽIČKA, 1926).**
A – incomplete cranidium of small specimen, NM L 18901, ×6; B – incomplete cranidium of medium-sized specimen, NM L 30825, ×2.2; C – anterior part of cranidium showing marginal rim, JV 2656, ×5; D – incomplete cranidium of small specimen, NM L 18902, ×6; E – lectotype, pygidium, NM L 18903, ×2.2; F – left librigena, internal mould, NM L 30824, ×6; G – posterior part of glabella showing terrace ridges and pitted sculpture, NM L 38509, ×4; H – pygidium, internal mould, NM L 18922, ×2.2; I, K – anterior margin of glabella showing pitted sculpture and ridges on anterior rim, and anterior view to rim, NM L 38508, both ×5.5; J – anterior margin of glabella preserved as internal mould (left) and exterior (right), NM L 38510, ×6; L – pygidium, internal mould showing doublure, NM L 38511, ×2.5; M – sculpture on anterior part of glabella, NM L 38512, ×5.5; Třenice Formation, Holoubkov.

with this species by previous authors (Vaněk 1965, Mergl 1984a). However, there are sufficient features to differentiate the new species on the material from the Mílina Formation. *H. klouceki* differs by less transverse outline of the pygidium, with wider (tr.) axis and narrower pleural region. Pygidial length/width ratio is about 0.55–0.62 in *H. klouceki* compared with cca 0.50 in *H. holoubkovensis*. The new species is probably larger, with a cephalon width of nearly 70 mm.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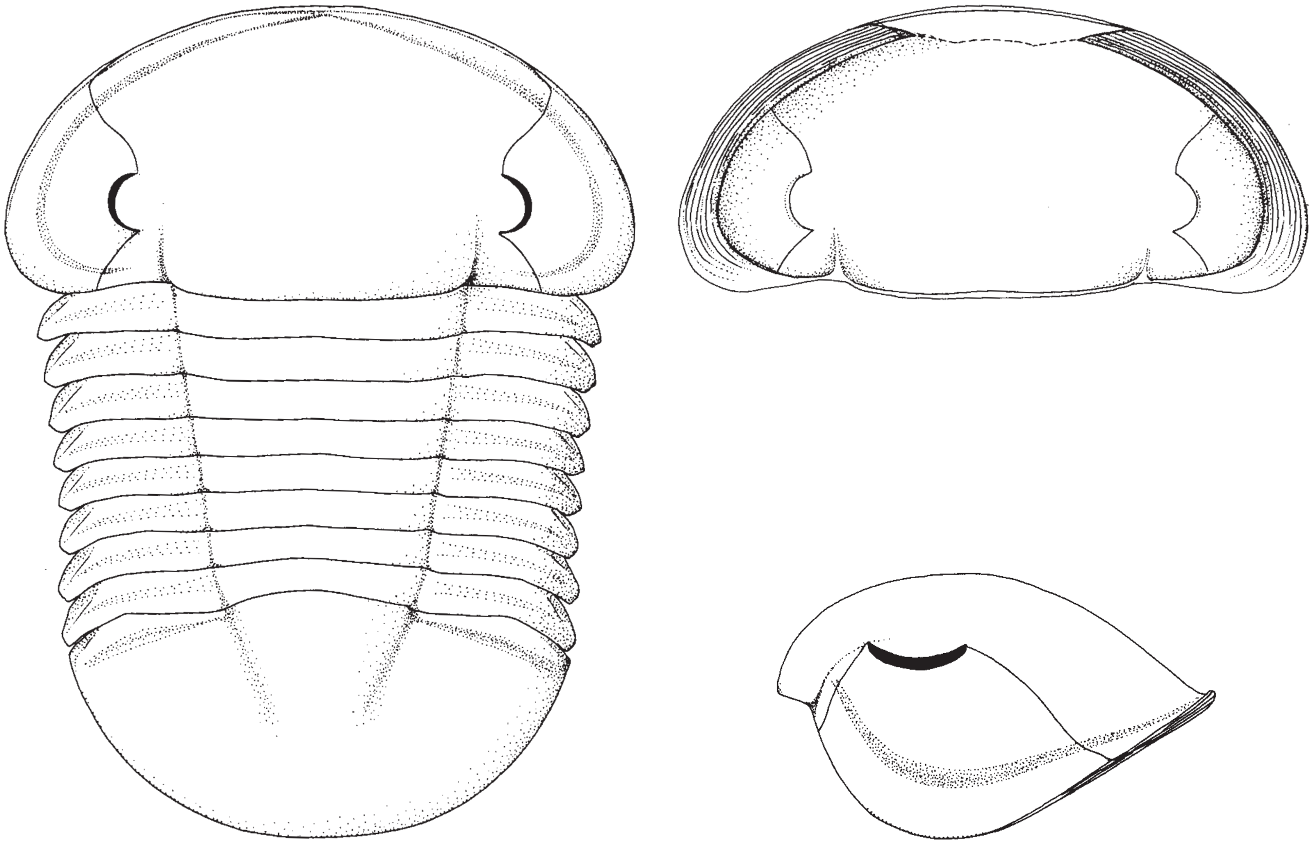


Text-fig. 13. *Hemibarrandia klouceki* sp. n. Reconstruction of the exoskeleton, ventral side of the cephalon and lateral view to the cephalon. Approximately ×1.5.

Hemibarrandia is known also from Bavaria; Sdzuy (1955) described *H. triangula* SDZUY, 1955 from the Leimitz Shales (Lower Tremadocian), while two imperfectly known species are reported from the Vogtendorft Formation (Upper Tremadocian). Hammann and Sdzuy (in Sdzuy et al. 2001) extensively discussed the affinity of all Bavarian species to *H. holoubkovensis*. The new species differs from *H. triangula* by having a more divergent anterior branch of the facial suture, a more rounded outline of the pygidium, and a convex and poorly defined pygidial border, which is concave in *H. triangula*. *Hemibarrandia* sp. from the Vogtendorf Formation has a conspicuously broad pygidial axis and a narrow pleural region. The specimen of *Hemibarrandia* cf. *holoubkovensis* from the same formation is so poorly preserved that a satisfactory comparison with the Bohemian species is impossible.

The species *H. triangula,* the only complete specimen referred to the genus, shows eight thoracic segments (Sdzuy 1955). An incomplete specimen of *H. klouceki* has eight segments (Mergl 1984a; pl. 7, fig. 1). Another incomplete specimen *H.* sp. from Bavaria has seven segments (Hammann and Sdzuy in Sdzuy et al. 2001). The cluster of segments with an associated incomplete pygidium from Klouček's original collection (NM L 38614) consists of eight partly incomplete segments of uniform size and a small piece of a smooth exoskeletal part, probably the posterior margin of the cranidium. The entire cluster of parts might belong to the same specimen, but the possibility of two individuals

◀ **Text-fig. 12. *Hemibarrandia klouceki* sp. n.**
A, F – almost complete cranidium and oblique view showing its convexity, internal mould, PCZCU 1647, both ×1.7; B – right librigena, internal mould, NM L 38515a, ×1.5; C – left librigena, internal mould, NM L 38515b, ×1.5; D – right librigena, latex cast of exterior, NM L 38517, ×2.5; E – doublure of librigena in ventral view, internal mould, NM L 38516, ×3; G, H – right librigena, detail of doublure with terrace lines and latex cast of ventral surface, MM 128, ×3.5, ×1.8; I – anterior part of cranidium showing marginal rim, PCZCU 1649, ×2.5; J – sculpture of axis on thoracic segment, latex cast, PCZCU 1648, ×5; K, L, N incomplete pygidium with thorax, detail of internal mould of axis showing doublure, and internal mould of pleura, VH 5023, ×3, ×3, ×1.7; M – holotype, pygidium, internal mould, VH 5025, ×1.7; O – pygidium showing doublure, latex cast, NM L 38518, ×1.7; Mílina Formation, Olešná (A–I, K–O), Kvaň (J).

having become mixed cannot be excluded. Despite this uncertainty, the reconstruction of *H. klouceki* (Text-fig. 13) exhibits eight segments. This number of segments indicates the affinity of *Hemibarrandia* to panderines that have eight segments (Brunton 1968). Segments of *Hemibarrandia* lack any articulating furrow or its equivalent in the thoracic axial rings. The axial rings are conspicuously thickened in the anterior portion, with a narrow acute transverse ridge along the posterior margin of the ventral side of the axial ring. This fine ridge is an anteriorly thickened edge of a narrow (sag.) doublure. The articulating surface of each axial ring is evident from a smooth anterior band occupying about one-third of the segment length (sag.), while the posterior two-third bears a pitted ornament. The absence of the articulating furrow is considered as diagnostic for nileids and illaenids (Whittington 2000). The possible presence of eight thoracic segments, the distinct marginal rim, and the pitted surface of the exoskeleton favour the attribution of *Hemibarrandia* to panderines and not to nileids (Whittington 1965). The oldest known illaenids, the panderines, are from the late Tremadocian of Scandinavia (Bruton 1968) and North China (Zhou and Fortey 1986). *Hemibarrandia* pre-dates these panderines, being known from the Lower Tremadocian (Sdzuy 1955), and extending to the Upper Tremadocian (Mergl 1984a, 1994, Hammann and Sdzuy in Sdzuy et al. 2001). It is noteworthy, that some Lower Ordovician illaenids from the Table Head Formation of Newfoundland (Whittington 1965) are remarkably similar to *Hemibarrandia*. The species *Illaenus marginalis* RAYMOND, 1925 and *I. alveolatus* RAYMOND, 1925 have remarkably similar transverse outlines of cephala. Although both lack border furrows on the librigenae that is characteristic of *Hemibarrandia*, the latter species has a shallow posterior border furrow. Otherwise, they have similar morphologies with transverse, highly convex, effaced cephalons having a distinct anterior rim, large palpebral lobes, and a nearly effaced pygidium.

In the first published list of the trilobite fauna from the Mílina Formation, *H. klouceki* was named *Barrandia-Symphysurus*? n. sp. by Klouček (1917), but in a subsequent paper the same author (Klouček 1926a) listed this species under name *Symphysurus* (*Hemibarrandia*). This later name was also used on the original labels attached to Klouček's *H. klouceki* specimens stored in the National Museum in Prague. In the subsequent faunal lists (Koliha 1937) this species is confused with *Symphysurus bohemicus* KLOUČEK (nomen nudum), although Klouček and Koliha (1927) stated that *S. bohemicus* is identical with *S. Bröggeri* n. sp. (= *Ottenbyaspis broeggeri* RŮŽIČKA, 1926).

Occurrence: Mílina Formation; Olešná (abundant), Kvaň (rare), Úvaly, Vinice (rare).

Suborder **Leiostegiina** BRADLEY, 1925
Superfamily **Leiostegiodea** BRADLEY, 1925
Family **Leiostegiidae** BRADLEY, 1925

Genus ***Agerina*** TJERNVIK, 1956

Type species: *Agerina erratica* TJERNVIK, 1956; Arenigian, Planilimbata Limestone; Sweden.

Agerina ferrigena (RŮŽIČKA, 1926)
Text-fig. 14A–E

1931 *Niobe ferrigena* n. sp.; Růžička, p. 7, pl. 3, figs 6a–b.
1931 *Holometopus Grönwalli* n. sp.; Růžička, p. 392, pl. 1, figs 14, 15 (not pl. 1, fig. 12).
1931 *Niobe ferrigena* RŮŽIČKA; Růžička, p. 289.
1965 *Holometopus Grönwalli* RŮŽIČKA; Vaněk, p. 289.
1965 *Diceratopyge* ? sp.; Vaněk, pl. 26, fig. 57, 58.
1970 ? *Diceratopyge* ? *ferrigena* (RŮŽIČKA 1931); Horný and Bastl, p. 151.
1994 *Proteuloma* cf. *kettneri* (RŮŽIČKA, 1941); Mergl, p. 17, pl. 3, fig. 7.

Holotype: Incomplete cranidium figured here in text-fig. 14B, D, deposited in the palaeontological collection of the National Museum, Prague (NM L 18911).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the abandoned "V Ouzkém" iron ore mine.

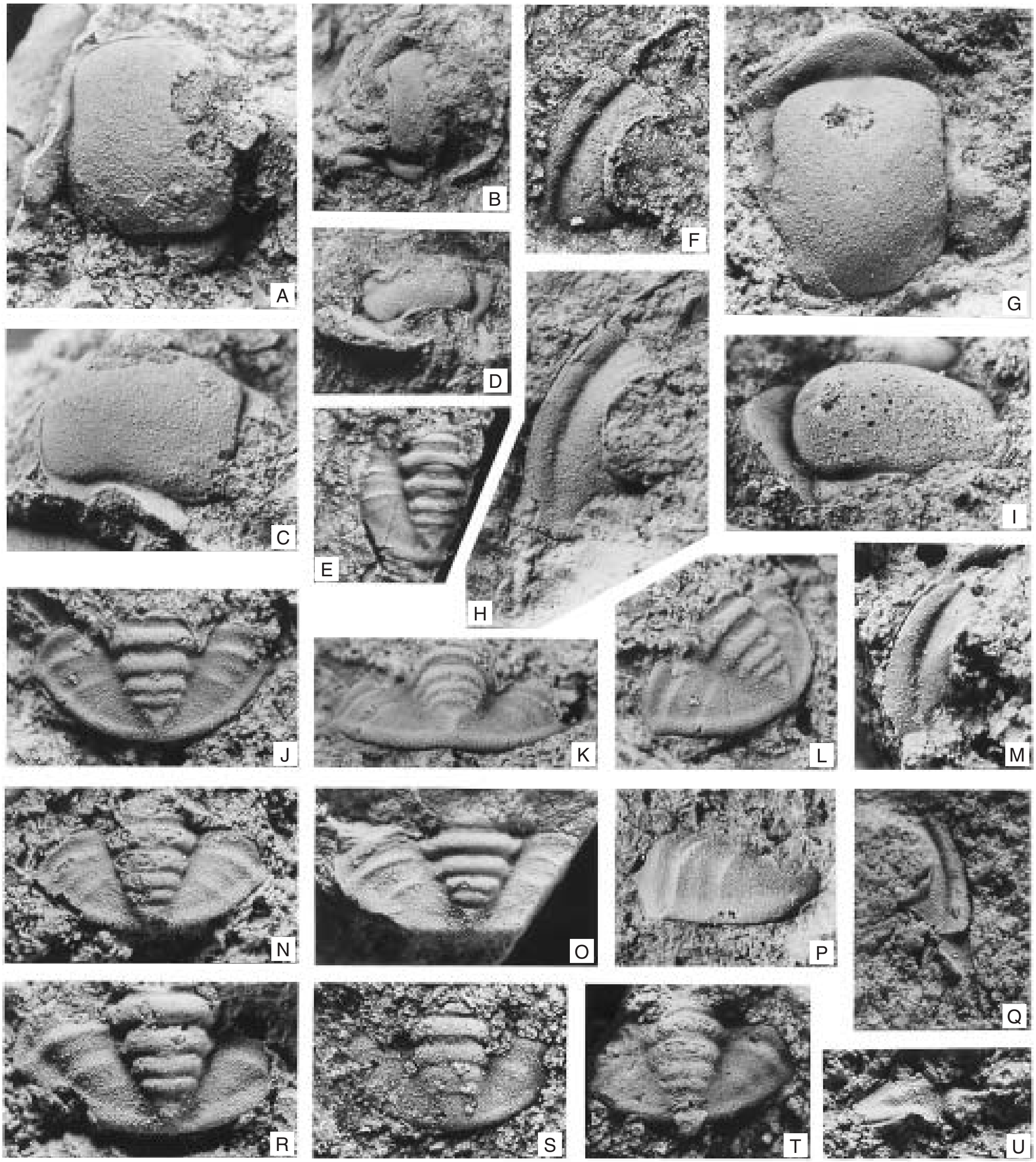
Material: Two cranidia and one pygidium.

Diagnosis: *Agerina* with gently arched (sag. and tr.) narrowly trapezoidal glabella without glabellar furrows; preglabellar field long (sag.), shortly triangular in outline, evenly rounded anteriorly with fine raised peripheral ridges; anterior branch of facial suture weakly diverging; palpebral lobes large, broadly reniform; pygidial axis with four rings and small triangular terminal piece.

Description: Růžička (1926, 1931) and Mergl (1994).

Remarks: The species *Agerina ferrigena* (RŮŽIČKA, 1926) is similar to *A. praematura* TJERNVIK, 1956. The lateral profile of the cranidium, the preglabellar field with fine raised ridges, and the weak axial depression in frontal glabellar lobe are the same in both species. The Bohemian species differs by having a shorter and backward widening glabella, a gently widening (sag.) preglabellar field, and shallower axial and preglabellar furrows.

The species *Niobe ferrigena* RŮŽIČKA, 1926 has been referred by Vaněk (1965) to the genus *Diceratopyge* TROEDSSON, 1937. However, the holotype can be reliably referred to *Agerina* TJERNVIK, 1956. This is evident especially from the effaced, posteriorly gently widening and highly convex glabella, an axially forward extended preglabellar field, and a short (exs.) posterior fixigena with shallow border furrow. Vaněk (1965) also referred the pygidium of *A. ferrigena* to *Diceratopyge* ? sp. Růžička (1931) attributed this pygidium to the newly established *Holometopus Grönwalli* RŮŽIČKA, 1931. However, this species is based on a very small, poorly preserved, smooth cranidium that cannot be referred to *Agerina* due the oc-



Text-fig. 14. ***Agerina ferrigena*** **(RŮŽIČKA, 1926).**
A, C – glabella with part of fixigena, NM L 38489, both ×10; B, D – lectotype, small incomplete cranidium, NM L 18911, both ×12; E – pygidium, NM L 18932, ×7; Třenice Formation, Holoubkov.
Agerina clymene **sp. n.**
F, H – right librigena, latex cast and internal mould, PCZCU 1560, ×10, ×10; G, I – incomplete cranidium, internal mould and latex cast in oblique view, PCZCU 1561 ×10, ×10; J–L, S – holotype, pygidium, internal mould in posterior and oblique views, and latex cast of exterior, PCZCU 1562, all ×10; M – incomplete left librigena, internal mould, PCZCU 1563, ×10; N, T – pygidium, internal mould and latex cast of exterior, PCZCU 1565, both ×10; O – pygidium, internal mould, PCZCU 1566, ×10; P – incomplete pygidium in oblique view, internal mould showing short pleural spine, PCZCU 1567, ×10; Q – right librigena, internal mould, PCZCU 1564, ×10; R – pygidium, internal mould, PCZCU 1568, ×10; U – incomplete segment, internal mould, PCZCU 1570, ×10. Mílina Formation, Kvaň.

cipital node and undivided broad fixigena. This specimen is probably a meraspid stage of an unclear taxonomic position. Finally, the pygidium of *A. ferrigena* has been referred to *Proteuloma kettneri* (RŮŽIČKA, 1931) by Mergl (1994), following the earlier misidentifications. However, the rarity of well preserved material does not permit a more detailed comparison with other *Agerina* species.

Occurrence: Třenice Formation, Holoubkov (very rare).

Agerina clymene sp. n.

Text-figs 14F–U, 15

1965 *Proteuloma geinitzi* (BARRANDE, 1868); Vaněk, p. 266, pl. 22, figs 5–9.

1984a *Proteuloma kettneri* (RŮŽIČKA, 1941); Mergl, p. 38, pl. 5, figs 8–12.

Holotype: Pygidium figured in text-fig. 14J–L, deposited in the palaeontological collection of the University of West Bohemia at Plzeň (PCZCU 1562).

Paratypes: Incomplete cranidium figured in text--fig.14G, I (PCZCU 1561), and librigena figured in text-fig. 14F, H (PCZCU 1560), both deposited in the palaeontological collections of the University of West Bohemia at Plzeň.

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Zaječov (part Kvaň), small hill SW of the village.

Name: Latin, *Clymené*, from Greek mythology, a daughther of Ókeanos and Téthys.

Material: Three small nearly complete cranidia, 10 incomplete cranidia, 28 librigenae, and 34 pygidia.

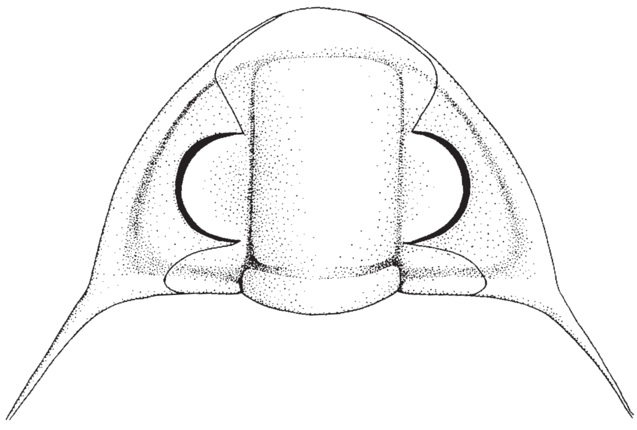
Diagnosis: *Agerina* with strongly arched (sag. and tr.) rectangular glabella without glabellar furrows; preglabellar field long (sag.), shortly triangular, evenly rounded, without fine elevated ridges; anterior branch of facial suture weakly diverging; palpebral lobes large, broadly reniform; librigenal spines long, thin, directed ventrolaterally; pygidial axis with four rings and small triangular terminal piece; vestigial marginal spine on the first pygidial pleura.

Description: Small species with maximum width of cranidium (estimated) about 10 mm and total length of exoskeleton some 12–15 mm. Glabella rectangular, about 1.5 times longer than its width, effaced, strongly convex (sag. and tr.), marked by deep and narrow axial furrows. Occipital furrow transverse, evenly deep. Occipital ring short (sag.), evenly wide (sag.). Preglaberal field flat, slightly extended anteriorly, forming rounded angle of the anterior margin. Anterior part of fixigena very narrow (tr.) with anterior branch of facial suture weakly diverging anteriorly. Palpebral lobes large, broadly reniform in outline, gently depressed near axial furrows, much higher than posterior fixigena, indicating large semicircular eyes with steep visual surface. Posterior fixigena short (tr.), flat, with broad and shallow border furrow which rapidly disappears abaxially. Posterior branch of facial suture transverse, abaxially turning rapidly posteriorly, and turning adaxially near the very posterior margin. Therefore, lateral tips of fixigena are nearly rounded. Librigena triangular, with weakly convex genal field steeply sloping toward border furrow. Genal angle extended into long and narrow lateroventrally directed cylindrical genal spine. Narrow and deep border furrow distinct anteriorly, shallowing toward genal angle. Border evenly wide (tr.), flat, with acute edge. Narrow, evenly wide (tr.) doublure convex, ventrally covered with weak parallel terrace ridges. Doublure extends adaxially almost toward sagittal line.

Number of segments unknown. One incomplete segment has very short pleura with posterolaterally inclined and flattened distal extremity, which is mostly occupied by large articulating facet. Anterior pleural band triangular and flattened, posterior pleural band very short (exs. and tr.), forming high edge at the posterior margin of pleura. Pleural furrow inclined at about 45° angle to sagittal axis.

Pygidium short (sag.), with Lp/Wp = 0.40–0.50, of broadly semielliptical outline. Axis prominent, strongly convex (tr.), slightly tapering backwards and highly raised above pleural fields. It occupies about 30–40 % of the pygidium width at the anterior margin. There is prominent articulating half-ring, four highly convex rings and small, flattened triangular terminal piece, which touches the posterior border. Ring furrows are narrow (sag.) and deep. Axial furrows are distinct and narrow (tr.). Pleural fields gently convex, with two pleurae and weak pleural furrows. Distinct narrow rib between the first and second pair of pleurae present. Anterior pleura extends into vestigial pleural spine on lateral margin. Border furrow broad and shallow. Border narrow, slightly convex, with rounded edge, smooth. Doublure short (sag.), convex ventrally. Articulating facets large, facing anterolaterally. Posterior arch small and low.

Remarks: An extensive discussion about the genus *Agerina* TJERNVIK, 1956 has been given by Hammann and Sdzuy (in Sdzuy et al. 2001). Some species formerly referred to *Agerina* were transferred to *Hexianella* ZHANG, 1983 by Adrain and Fortey (1997), but the latter genus, according to Hammann and Sdzuy (in Sdzuy et al. 2001), is a junior subjective synonym of *Brackebuschia* HARRINGTON et LEANZA, 1957. Hammann and Sdzuy (in Sdzuy et al. 2001) described *Agerina alkleini* HAMMANN et SDZUY, 2001 from the Vogtendorf Formation (Upper Tremad-



Text-fig. 15. *Agerina clymene* sp. n. Reconstruction of the cephalon. Approximately ×10.

ocian) of Bavaria, Germany. Their material includes several complete cranidia and one poorly preserved pygidium. The cranidium is very similar to *A. clymene*, but the new species has a longer and more rounded preglabellar field bordered by less divergent anterior branches of the facial sutures, wider (tr.) palpebral lobes, narrower (tr.) librigena, and a less posteriorly inclined genal spine. Based on these characteristics, the species *A. clymene* is more similar to the Scandinavian species *A. praematura* than to *A. alkleini*. However, the glabella of the new species and of *A. alkleini* is effaced and differs from that of the typical specimen of *Agerina praematura* TJERNVIK, 1956 from the Bjørkåsholmen Formation (Upper Tremadocian) of Västergötland, Sweden. However, Ebbestad (1999) noted that glabellar furrows are barely visible in the Norwegian material of *A. praematura*. The librigena of *A. praematura* is not illustrated, and the length of the genal spine is unknown, making these features useless for a comparison. Only one pygidium of A. *alkleinii* is known, and it is very poorly preserved. The pygidium of Scandinavian *A. erratica* (early Arenig, *Planilimbata* Limestone) has the axis about as wide as the pleural field, and the posterior border bears irregular terrace ridges; the posterior margin of the pygidium is slightly pointed behind the axis. The axis of *A. praematura* is narrower (tr.) and its terrace ridges are less distinct while in *A. clymene* it is narrower (tr.) than in *A. erratica*, and the border is longer (sag.) and flattened in comparison with those of *A. praematura* and *A. erratica*. The pygidial axis of *A. clymene* has a distinct triangular terminal piece. This piece is absent in the Scandinavian species, but it is clearly developed in the pygidium of *Brackebuschia acheila* HARRINGTON et LEANZA, 1957 from the Lower Tremadocian of Argentina. In addition, the pygidial axis of *B. acheila* is similarly narrow (tr.) as in *A. clymene*, but the former has four pairs of faint glabellar furrows; these are absent on the effaced glabella of *A. clymene*. Based on the available data, *A. clymene* is similar to the Bavarian species *A. alkleini* by having an effaced glabella, though the morphology of its pygidium is closer to *Brackebuschia*. *A. clymene* with a less advanced pygidium is probably directly derived from the Lower Tremadocian *Brackebuschia*, and it is less related to the Scandinavian species of *Agerina*; the affinity of *A. alkleini* to the genus *Brackebuschia* must be evaluated based on new pygidia material. The species *Hoekaspis*? *quadrata* DEAN, 1966 from the Landeyran Formation (Arenig) of the Montagne Noire (Dean 1966), France, probably belongs to *Agerina* or to another closely related leiostegiid genus. The French species differs from *A. clymene* by having a shorter preglabellar field with distinctly raised border, and fewer transverse palpebral lobes; the pygidium of the French species is unknown.

Previous authors (Vaněk 1965, Mergl 1984a) have misidentified the pygidium of *A. clymene* with *Proteuloma kettneri* (RŮŽIČKA, 1941). Almost all specimens of *A. clymene* derive from a single bed of the Mílina Formation in the Kvaň locality. A thin chert layer, less than 5 cm thick, frequently contains thin laminae with fragments of trilobites. Fragments are usually smaller than 2–5 mm. Among these fragments, complete pygidia and crushed librigenae of *A. clymene* are remarkably dominant (40 % of all trilobite remains). The other common trilobites in these laminae are *Apatokephalus dagmarae* MERGL, 1984 and agnostids. Other polymerid trilobites are significantly rarer. Because the species *Proteuloma kettneri* RŮŽIČKA, 1931 is unknown from this bed, it is fairly certain that this pygidium does not belong to *P. kettneri*, as suggested by previous authors (Vaněk 1965, Mergl 1984a). In contrast to the Kvaň locality, the species *A. clymene* is very rare in the Olešná locality.

Occurrence: Třenice Formation, Holoubkov (very rare). Mílina Formation; Olešná (very rare), Kvaň (abundant); Úvaly,Vinice (abundant).

Order **Lichida** MOORE, 1959
Superfamily **Lichoidea** HAWLE et CORDA, 1847
Family **Lichidae** HAWLE et CORDA, 1847
? Subfamily **Trochurinae** PHLEGER, 1936

Genus ***Holoubkovia*** PŘIBYL et VANĚK, 1969

Type species: *Lichas klouceki* RŮŽIČKA, 1926; Upper Tremadocian, Třenice Formation; Barrandian, Bohemia.

Holoubkovia klouceki (RŮŽIČKA, 1926)

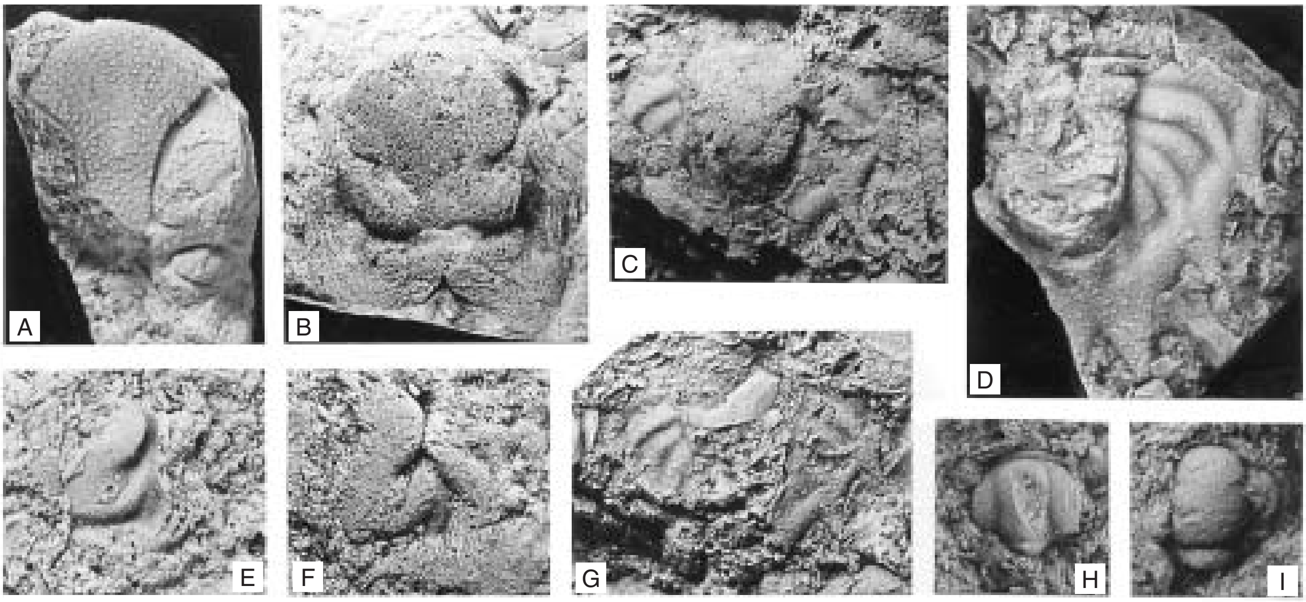
Text-fig. 16

1925 *Lichas* sp.; Klouček, p. 1.
1926a *Lichas* sp.; Klouček, p. 193.
1926 *Lichas Kloučeki* n. sp.; Růžička, p. 16, pl. 3, fig. 3.
1926 *Lichas* sp.; Růžička, p. 17, pl. 3, fig. 4.
1926 *Lichas* sp.; Růžička, p. 17, pl. 3, fig. 5.
1931 *Lichas Kloučeki* n. sp.; Růžička, p. 393, pl. 1, fig. 10.
1959 *Platylichas kloučeki* (RŮŽIČKA, 1926); Vaněk, p. 115, pl. 1, fig. 3.
1964 *Platylichas kloučeki* (RŮŽIČKA, 1926); Vaněk, p. 108.
1965 *Platylichas kloučeki* (RŮŽIČKA, 1926); Vaněk, p. 288, pl. 25, fig. 40, pl. 26, fig. 56.
1969 *Holoubkovia klouceki* (RŮŽIČKA, 1926); Přibyl and Vaněk, p. 373, pl. 2, fig. 10.
1970 *Platylichas klouceki* (RŮŽIČKA, 1926); Horný and Bastl, p. 183.
1988 *Metopolichas klouceki* (RŮŽIČKA, 1926); Thomas and Holloway, p. 214, pl. 11, figs 236, 239, 240.
1994 *Holoubkovia klouceki* (RŮŽIČKA, 1926); Mergl, p. 23, pl. 8, figs 10, 11.
1994 *Apatokephalus* (?) sp.; Mergl, p. 23, pl. 1, fig. 10.
2001 *Metopolichas* (?) *klouceki* (RŮŽIČKA, 1926); Vaněk and Valíček, p. 34.

Lectotype: Selected by Vaněk (1959), incomplete pygidium figured by Růžička (1926) on pl. 3, fig. 3, re-figured here in text-fig. 16D, deposited in the collection of the National Museum, Prague (NM L 11437).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the abandoned “V Ouzkém” iron ore mine.

Material: In addition to the holotype, 2 pygidia, one incomplete glabella, and 4 hypostomes.



Text-fig. 16. *Holoubkovia klouceki* (RŮŽIČKA, 1926).
A – incomplete glabella, NM L 18909, ×7; B – hypostome, latex cast of exterior, PCZCU 1645, ×7; C, G – pygidium, latex cast of exterior and internal mould, NM L 38513, both ×7; D – lectotype, incomplete pygidium, NM L 11437, ×7; E, F – incomplete hypostome, internal mould and latex cast of exterior, PCZCU 1646, both ×7; Třenice Formation, Holoubkov (A, C, D, G). Mílina Formation, Kvaň (B, E, F).
H – gen. et sp. indet. A, small cranidium, a specimen referred by Růžička (1931) to *Holometopus Grönwalli* n. sp., NM L 18931a, ×12; Třenice Formation, Holoubkov.
I– gen. et sp. indet. B, small cranidium, NM L 18927, ×12; Třenice Formation, Holoubkov.

Diagnosis: *Holoubkovia* with short posterior median termination in pygidium and deep emargination between short and convex posterior pleural spines; hypostome broad, with high, tuberculate middle body, coarse raised ridges on lateral border and deep notch at posterior border; sculpture of unevenly sized, and large tubercles.

Emended description: Length of the entire exoskeleton between 20–30 mm. Cranidium incompletely known. Median lobe semicircular, rather short (sag.), strongly expanded anteriorly, narrowest at about one-third of cephalic length opposite to postero-mesian corners of bullar lobes. Frontal part of median lobe considerably curved downwards. Bullar lobes gently convex, obliquely ovoid. Adaxial parts of basal lateral lobes are short (sag.), weakly arched (tr.); their abaxial part unknown. Occipital lobes are large, transverse, acute adaxially, gently arched (tr. and sag.). S2 run oblique but at mid-length rapidly turn backward, weakly converging adaxially. Distal parts of S2 curved abaxially and probably not joined with S1. Ornament of evenly scattered small tubercles of uniform size covering dorsal surface of lobes; ventral surface of glabellar furrows smooth.

Hypostome subpentagonal, with deep subangular notch in posterior margin. Maximum width between shoulders in posterior one-third. Middle body subpentagonal, gently convex (tr.), posterior border furrow shallow. Anterior lobe evenly arched, broadly pear-shaped, with very steep sides. Posterior lobe short, with high prominent anterolateral projections forming conspicuously high lobes. Maculae not observed. Anterior border rounded, extended into short, laterodorsally directed anterior wings. Lateral border evenly wide (tr.), continuous into flattened, long, rather acute posterior border spines with rounded points. Ventral surface of anterior lobe finely pitted. Proximal parts of anterior wings and lateral borders in front of posterior spines with faint terrace lines running almost parallel to hypostomal margins. Length of the largest observed hypostome is 8 mm.

Pygidium subtriangular, with prominent axis occupying one-third (tr.) of the width. Axis 60–70% as long as pygidium, gently tapering posteriorly, abruptly sloping at the posterior end. Axis strongly convex (tr.), bordered by narrow and deep axial furrows, with three rings and the terminal piece defined by distinct ring furrows at least near sides of the axis. A weakly defined triangular, weakly convex (tr.) postaxial ridge extends to posterior margin. Pleural fields with two distinct pairs and third less distinct pair of pleurae, which extend into short, acute, backward directed pleural spines. Dorsal surface of spines gently convex. Pleural furrows transverse in adaxial parts, rapidly curved backward in distal parts. Interpleural furrows distinct. Anterior and posterior pleural bands slightly convex. Weakly convex border well defined by narrow border furrow, which is distinct across anterior pleural bands but missing at posterior pleural bands.

Remarks: The validity of the genus *Holoubkovia* PŘIBYL and VANĚK, 1969 has been questioned by Thomas and Holloway (1988), who suggested the possible synonymy of this genus with *Metopolichas* GÜRICH, 1901.

This interpretation was adopted by Pollitt et al. (2005). However, this suggestion was not supported by Sdzuy and Hammann (in Sdzuy et al. 2001) and Whittington (2002), all of whom preferred to retain *Holoubkovia* as a separate genus. The development of the pygidial posterior border in *Holoubkovia* is unusual in Lichidae HAWLE et CORDA, 1847, and is unknown in lichakephalids (Pollitt et al. 2005). The pygidial posterior border and short axis is similar to the genera of the subfamily Trochurinae PHLEGER 1939.

Apart of *H. klouceki*, a pygidium tentatively referred to the genus has been described by Sdzuy and Hammann (in Sdzuy et al. 2001) from the Vogtendorf Formation (Upper Tremadocian) of Bavaria. A single specimen of *Holoubkovia* ? sp. found in Bavaria is poorly preserved, but of a comparable size with *H. klouceki*. The figured pygidium (Sdzuy and Hammann in Sdzuy et al. 2001: pl. 7, figs 10a, b) seems to have a more backward extended posterior median termination than that of *H. klouceki*. A broad, high, and bluntly ending axis followed by a postaxial triangular ridge, and the narrow pygidial doublure of *H. klouceki* are similar to trochurinids (which appeared in the Llanvirn; Pollitt et al. 2005), but also to some Ordovician species of Dicranopeltini PHLEGER, 1936, e.g. *Dicranopeltis polytoma* (ANGELIN, 1854) from the Cystoid Limestone (Ashgill) of Spain (Hammann 1992). This similarity is supported by the development of a short median lobe of the glabella, and by the coarsely tuberculate surface of the exoskeleton. Because Thomas and Holloway (1988) and Pollitt et al. (2005) did not accept the validity of this genus, and many features of the genus are unknown, the phylogenetic position of *Holoubkovia* remains unclear.

All three pygidia, one cranidium, and two hypostomes from the Třenice Formation were derived from small, less than 15–20 mm long individuals, as might be assumed from the sizes of known specimens. This may indicate that small size is a characteristic feature of the species. Two lichid hypostomes have been found among the newly collected trilobite specimens from the Mílina Formation. The smaller one is identical in size and outline to the hypostome of *H. klouceki* illustrated by Růžička (1926). The second hypostome is much larger, with a length of (sag.) almost 8 mm, and having the same morphology. Indeed, the inferred length of the entire exoskeleton of *H. klouceki* can reach 50–60 mm, as the lichid hypostomes are relatively large (Whittington 2002). However, it is not excluded that the hypostomes from the Mílina Formation might belong to another related but larger species.

In a redescription of *L. klouceki*, Vaněk (1959) pointed out that the cranidium and hypostome figured by Růžička (1926) were not available for him to study, and he described only the pygidium. The same author (Vaněk 1965) also stated that the species is known from one external mould of a pygidium also from the Olešná locality in the Mílina Formation. However, this specimen has not been identified amongst the material stored in the National Museum, Prague. A poorly preserved counterpart of a lichid hypostome has been misidentified by Mergl (1994: pl. 1, fig. 10) as a cranidium of *Apatokephalus dagmarae* MERGL, 1984. Klouček (1917, 1926a) noted fragments of cephala, a pygidium, and a hypostome of *Lichas* sp. in cherts of the Mílina Formation in the Olešná locality. Klouček probably misidentified *Lichas* sp. with fragments of conspicuously convex tuberculate cranidia of a calymenid *Parabathycheilus vagans* MERGL, 1984. This misidentification implies from the attached labels in Klouček's collection stored in the National Museum, Prague.

Occurrence: Třenice Formation, Holoubkov (very rare). Mílina Formation; Kvaň (very rare).

Order **Phacopida** SALTER, 1864
Suborder **Cheirurina** HARRINGTON et LEANZA, 1957
Family **Pilekiidae** SDZUY, 1955
Subfamily **Pilekiinae** SDZUY, 1955

Genus ***Anacheirurus*** REED, 1896

Type species: *Cheirurus* (*Eccoptochile*) *frederici* SALTER, 1864; Upper Tremadocian, Tremadocian Slates; Wales.

Anacheirurus bohemicus (RŮŽIČKA, 1926)

Text-fig. 18G

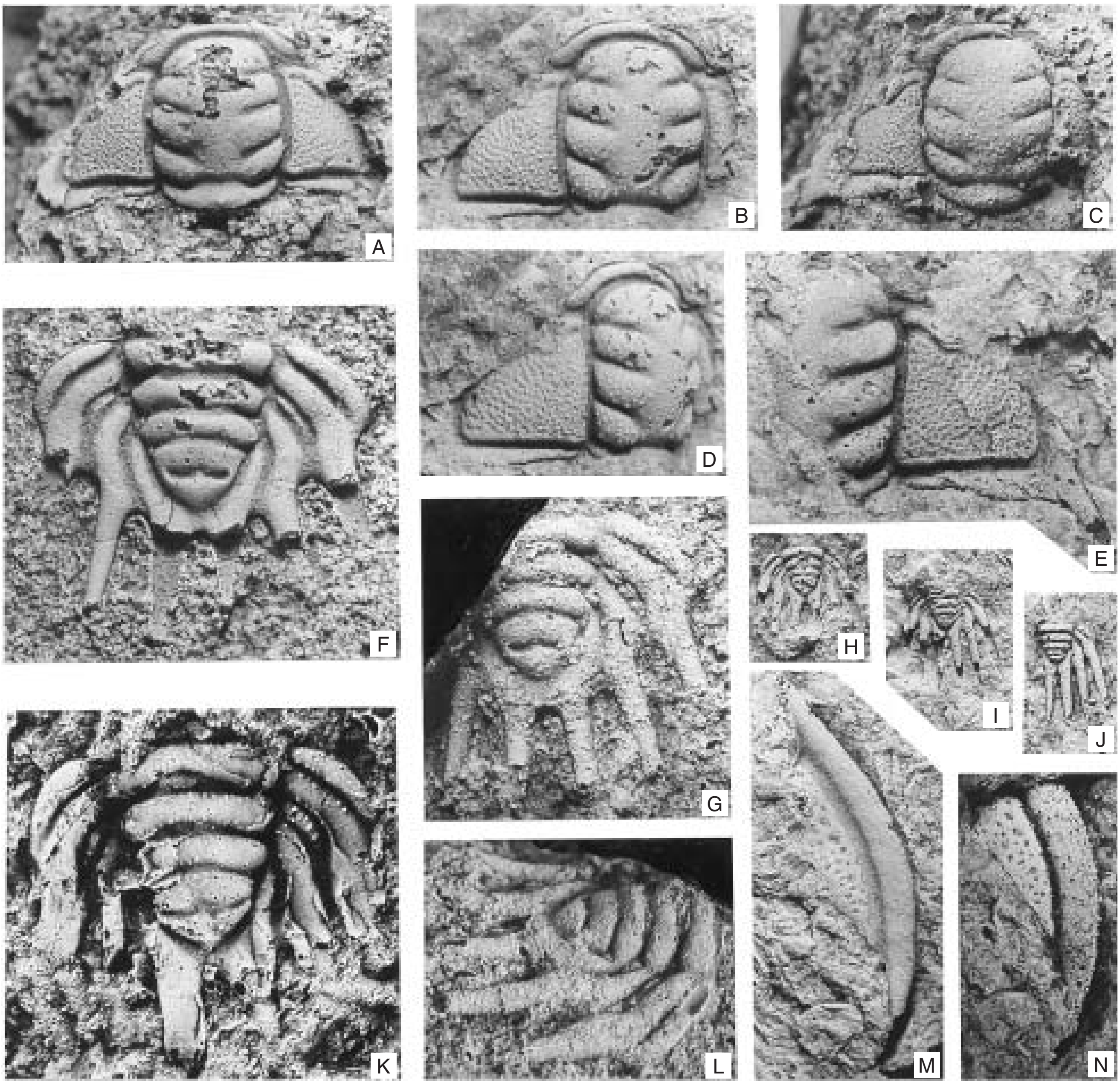
1926 *Cyrtometopus bohemicus* n. sp.; Růžička, p. 14, pl. 3, fig. 2, (not pl. 3, fig. 1).
1947 *Parapilekia bohemica* (RŮŽ.); Prantl and Přibyl, p. 24.
1964 *Pilekia bohemica* (RŮŽIČKA, 1926); Vaněk, p. 108.
1965 *Pilekia bohemica* (RŮŽIČKA, 1926); Vaněk, p. 279, pl. 26, fig. 53, (not pl. 26, figs 51, 52).
1970 *Pilekia bohemica* (RŮŽIČKA, 1926); Horný and Bastl, p. 79.
1985 *Parapilekia bohemica* (RŮŽIČKA, 1926); Přibyl et al., p. 119.
1995 *Anacheirurus bohemicus* (RŮŽIČKA, 1926); Mergl, p. 11, pl. 1, fig. 8.
2001 *Anacheirurus bohemicus* (RŮŽIČKA, 1926); Vaněk and Valíček, p. 19.

Lectotype: Selected by Vaněk (1965), the incomplete pygidium figured by Růžička (1926) on pl. 3, fig. 2, re-figured here in text-fig. 18G, deposited in the collection of the National Museum, Prague (NM L 18908).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the adandoned "V Ouzkém" iron ore mine.

Material: Only the lectotype.

Remarks: The pygidium is very similar to that of the species *A. nanus* (MERGL, 1984) from the Mílina Formation (Mergl 1984a), and it is not excluded that the name *A. nanus* is a subjective synonym of *A. bohemica*. However, the rarity of *A. bohemica* does not permit a detailed comparison. The pygidium of *A. plutonis* BULMAN et RUSHTON, 1973 described from a borehole from central England differs from *A. bohemicus* in having short radiating spines. The type species *A. frederici* (SALTER, 1864) from the Shineton Shales (Upper Tremadocian) is similar to the Bohemian species by having spines that are strongly direc-



Text-fig. 17. *Anacheirurus nanus* (MERGL, 1994).
A, C – holotype, cranidium, internal mould and latex cast of exterior, MM 110, both ×8; B, D – cranidium, internal mould and its oblique view, MM 107, both ×8; E – incomplete cranidium showing genal spine, MM 109, ×8; F, G, L – pygidium, internal mould, latex cast of exterior and its oblique view, MM 112, ×8; H – minute pygidium, internal mould, PCZCU 1650, ×8; I, J – minute pygidium, internal mould and latex cast, PCZCU 1651, ×8; K – pygidium, latex cast of exterior showing spinose sculpture, NM L 38519, ×8; M, N – librigena, internal mould and latex cast of exterior, PCZCU 1562, both ×5.2; Mílina Formation, Olešná.

ted backwards. The British species is strongly deformed, and illustrations of it do not allow a comparison with either of the Bohemian species.

The species was established by RŮŽIČKA (1926) as *Cyrtometopus bohemicus* n. sp. on the basis of cranidial and pygidial fragments, but without selection of the holotype. VANĚK (1965) selected as the lectotype of *Pilekia bohemica* the pygidium figured by RŮŽIČKA (1926) on pl. 3, fig. 2, but this pygidium does not belong to *Pilekia* BARTON, 1915 but to *Anacheirurus* REED, 1896. The different generic attribution is based on the presence of only three pairs of spines on the pygidium, while *Pilekia* has four pairs (Whittard 1967, Bulman and Rushton 1973, Peng 1990). Fragments of cranidia figured by Růžička (1926) belong to *Parapilekia ferrigena* MERGL, 1994.

O c c u r r e n c e : Třenice Formation, Holoubkov (very rare).

Anacheirurus nanus (MERGL, 1984)
Text-fig. 17

1917 *Amphion* sp. n. ?; Klouček, p. 7.
?1922 *Amphion* sp. n.; Klouček, p. 1.
1926a *Amphion* sp.; Klouček, p. 193.
1984a *Parapilekia nana* sp. n.; Mergl, p. 23, pl. 5, figs 1–6, text-fig. 4.
1985 *Parapilekia nana* MERGL, 1984; Přibyl and al., p. 120.
2001 *Anacheirurus nanus* (RŮŽIČKA, 1926); Vaněk and Valíček, p. 19.

Holotype: Cranidium figured by Mergl (1984a) on pl. 5, fig. 4, re-figured here in text-fig. 17A, C, deposited in the palaeontological collections of the Czech Geological Survey, Prague (MM 110).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Material: Twenty cranidia, 3 librigenae, and 18 pygidia.

Diagnosis: *Anacheirurus* with oval (sag.) glabella, with short distinct S4, small occipital node; pygidium with four axial rings and imperfectly separated broadly triangular terminal piece; three long, strongly inclined backward, subparallel, long, tubular spines; exoskeletal surface finely spinose; glabella conspicuously spinose; anterior and lateral borders with numerous fine spines on frontal edges and larger and more scattered spines on dorsal surface; fixigenae with fine pits; pygidium with rows of fine spines along margins of pleural bands and axial rings.

Description: See Mergl (1984a). The length of entire individual, estimated after largest fragemnts, may reach 30–40 mm. New material indicates that posterior branch of facial suture is curved backwards more strongly than suggested by original reconstruction (Mergl 1984a). Pleural spines of the pygidium are longer, cylindrical, and more backward-directed than suggested in the original description. Very small, probably early holaspid (or late meraspid?) specimens have conspicuously long pleural spines. The pygidia, being 2–3 mm long, all have three pairs of pleural spines of nearly the same length.

Remarks: Both Mergl (1984a) and Přibyl et al. (1985) erroneously referred the species to *Parapilekia* KOBAYASHI, 1934, until Peng (1990) attributed it to *Anacheirurus* REED, 1896. Apart from two British species, Bulman and Rushton (1973) referred *Anacheirurus* to the species *Parapilekia sougyi* DESTOMBES, 1969 from the Arenigian of Mauritania (Destombes et al. 1969) and *P. atecae* HAMMANN, 1971 from the early Tremadocian of North Spain (Hammann 1974). The North African species is remarkable by having only three glabellar furrows disconnected with axial furrows. Unlike *A. nanus,* the glabella of *P. sougyi* is shorter (sag.), with its anterior border less curved. The pygidium of the African species is unknown. It is unlikely that the Mauritanian species belongs to *Anacheirurus*. The cranidium outline of the Spanish species *P. atecae* is similar to that of *A. nanus*, but the former differs by having longer (tr.) eye ridges and a less forward extended anterior border. However, the pygidium of *P. atecae* is unknown, and its generic position remains unclear, although Hammann (1971) noted its possible affinity to *Anacheirurus*. The conspicuously spinose surface of the exoskeleton, and especially on the surface of the glabella, distinguishes *A. nanus* from other species referred to the genus. The mere presence of a branched S3 (respectively fused S3 and S4) is not acceptable as a diagnostic feature for *Anacheirurus*; Whittard (1967) stated the presence of an unbranched S3 in the redescription of the type species *A. frederici* SALTER, 1864 from the highest Tremadocian Slates of North Wales. The number of axial rings on the pygidium of the type species is unclear. Based on the data of Whittington et al. (1984), *A. frederici* is roughly comparable in age with *A. nanus.* The pilekiids *P. discreta* (BARRANDE, 1868) and *P. anxia* SDZUY, 1955 from the Leimitz Shales (Lower Tremadocian) of Bavaria have distinctly branched S3 similar to *Anacheirurus*, but the associated pygidia have four pleural spines are diagnostic of *Parapilekia* KOBAYASHI, 1934.

Among the specimens of Klouček's collection stored in the National Museum in Prague, one pygidium has been found with a label *Amphion* sp. n. It therefore seems reasonable to suggest that *Amphion* n. sp. listed by Klouček (1917, 1926a) is identical with *A. nanus*.

The species *A. nanus* is rare in the lower and middle part of the trilobite-bearing red chert beds at the Olešná locality, but becomes fairly abundant higher in the succession, associated mainly with *Celdometopus klouceki* (VANĚK, 1965) and *Harpides grimmi* BARRANDE, 1872.

Occurrence: Mílina Formation; Olešná (moderately abundant), Kvaň (very rare), Úvaly, Vinice (very rare).

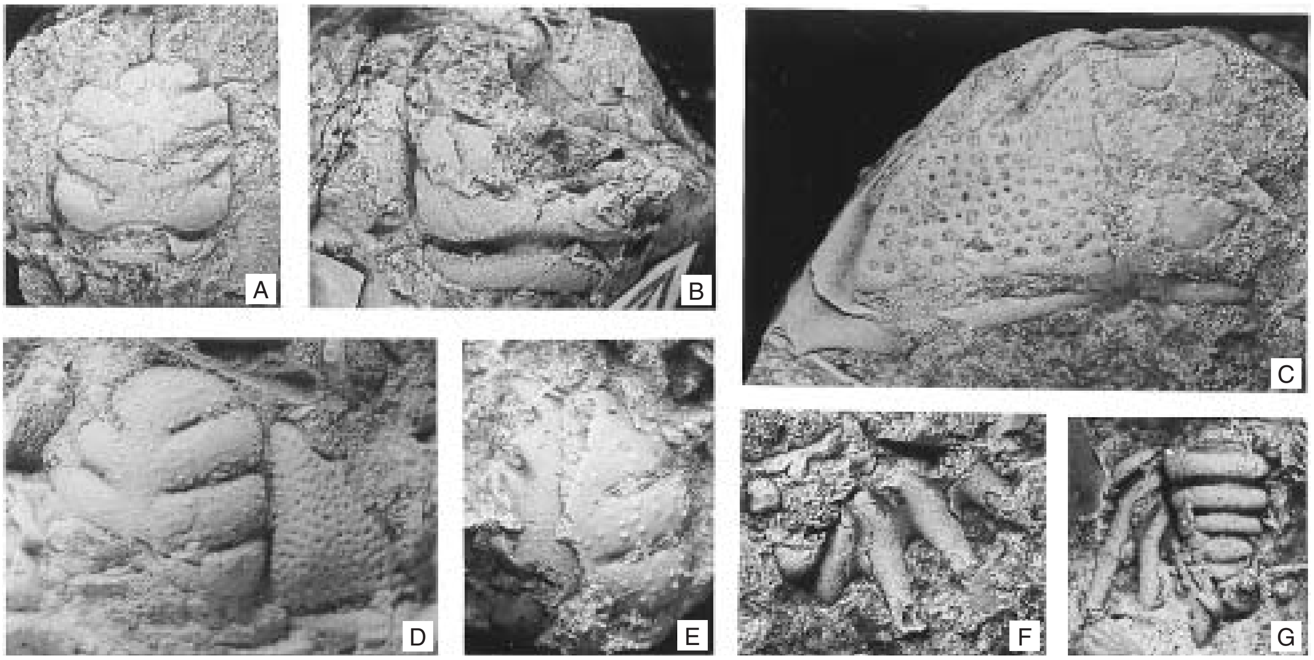
Genus *Parapilekia* KOBAYASHI, 1934

Type species: *Calymene ? speciosa* DALMAN, 1827; Upper Tremadocian, Ceratopyge Limestone; Öland, Sweden.

Remarks: The genera of the family Pilekiidae SDZUY, 1955 have been discussed by Přibyl et al. (1985). Species belonging to the genus *Parapilekia* KOBAYASHI, 1934 were listed by Fortey (1980), followed by Peng (1990) and Ebbestad (1999). The first modern revision of the type species was presented by Ebbestad (1999). However, knowledge about the hypostomal morphology and the details of pleural fields of *P. speciosa* remains poor. Ebbestad (1999) noted that the anterior pleural band is extended laterally into a pleural spine. However, in the species *P. olesnaensis* (RŮŽIČKA, 1935) and *P. latilus* (LIU, 1977), the anterior pleural bands are cut abaxially by a transverse pleural furrow, and the pleural spine extends from the posterior pleural band. This difference is probably a misinterpretation of the pleural morphology based on a unique, a poorly preserved, but almost entire specimen of *P. speciosa* from Norway (Ebbestad 1999; figs 79A, 79B and 80).

Parapilekia ferrigena MERGL, 1994
Text-fig. 18A–F

1926 *Cyrtometopus bohemicus* n. sp.; Růžička, p. 14, pl. 3, fig. 1, (not pl. 3, fig. 2).
1926 *Pliomera* sp.; Růžička, p. 15, pl. 1, figs 9, 10.
1925 *Cheirurus* sp.; Klouček, p. 1.



Text-fig. 18. *Parapilekia ferrigena* MERGL, 1994.
A – glabella, internal mould, NM L 18923, ×3; B – incomplete glabella, NM L 18891, ×3; C – lectotype, incomplete cranidium, NM L 18907, ×3; D – incomplete cranidium, NM L 30828, ×6; E – incomplete glabella showing tuberculate sculpture, NM L 18892, ×3; F – incomplete pygidium, NM L 18924, ×2.7. Třenice Formation, Holoubkov.
***Anacheirurus bohemicus* (RŮŽIČKA, 1926).**
G – lectotype, incomplete pygidium, NM L 18908, ×8. Třenice Formation, Holoubkov.

1926a *Cheirurus* sp. I; Klouček, p. 193.
1931 *Pliomera* sp.; Růžička, p. 392, pl. 1, fig. 9.
1931 *Cheirurus* sp.; Růžička, p. 392, pl. 1, fig. 11.
1947 *Parapilekia bohemica* (Růž.); Prantl and Přibyl, p. 24.
1964 *Pilekia bohemica* (RŮŽIČKA, 1926); Vaněk, p. 108.
1965 *Pilekia bohemica* (RŮŽIČKA, 1926); Vaněk, p. 279, pl. 26, figs 51, 52 (not pl. 26, fig. 53).
1970 *Pilekia bohemica* (RŮŽIČKA, 1926); Horný and Bastl, p. 79.
1994 *Parapilekia ferrigena* sp. n.; Mergl, p. 10, pl. 1, figs 1–7, 9.
2001 *Parapilekia ferrigena* MERGL, 1994; Vaněk and Valíček, p. 20.

Holotype: Incomplete cranidium, figured by Růžička (1926) on pl. 3, fig. 1, re-figured here in text-fig. 18C, deposited in the collection of the National Museum, Prague (NM L 18907).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the abandoned "V Ouzkém" iron ore mine.

Additional material: Six incomplete cranidia, two fragments of glabella, 14 fragments of fixed cheeks, one free cheek, one incomplete pygidium, and one minute fragment of pygidium.

Diagnosis: *Parapilekia* with somewhat oval glabella, wholly covered by scattered tubercles; S3 undivided; genae laterally extended, lacking distinct inflexion of posterior margin near genal angle; long fixigenal spine; pygidial axis rapidly tapering; four pairs of pygidial pleural spines radially arranged; pleurae with prominent lateral flange projections.

Description: Estimated length of entire specimens is 100–120 mm. No data concerning thorax morphology is noted in the original description (Mergl 1994). Segments are nearly the same as those in *P. olesnaensis*. In adaxial part of the pleura is a distinct flange with prominent projection at its anterolateral corner.

Remarks: The material of *P. ferrigena* MERGL, 1994 is scarce and very fragmentary. Some features of the exoskeleton are still unknown, especially the details of thorax and the length of pygidial spines, both of which are of taxonomical significance. *Parapilekia ferrigena* is distinguished from the closely related, stratigraphically subsequent species *P. olesnaensis* (RŮŽIČKA, 1935) from the Mílina Formation (Růžička 1935, Mergl 1984a) and also from the type species *P. speciosa* (DALMAN, 1827) from the Bjørkåsholmen Formation (Upper Tremadocian) of Scandinavia (Ebbestad 1999) by its absence of a distinct inflexion of the posterior margin near the genal angle and by tubercles covering the entire surface of the glabella. The genal angle is perhaps less acute in *P. olesnaensis*, but this difference is somewhat less distinct due to the deformation and fragmentation of the genae of *P. ferrigena*. The large, distinct articulating projection of the flange on the sides of the pleurae in *P. ferrigena* seems to be smaller in *P. olesnaensis*. The genal spine in *P. speciosa* is more laterally directed; it extends from a somewhat rounded genal angle instead of the acute genal angle terminated by a posterolaterally directed spine in *P. ferrigena*. The pygidial axis of *P. speciosa* is less tapering and has a wider (tr.) axial piece than in *P. ferrigena*. A comparison with other species of the genus is given by Mergl (1994).

Occurrence: Třenice Formation; Holoubkov (rather abundant).

Parapilekia olesnaensis (RŮŽIČKA, 1935)

Text-figs 19, 20

1917 *Cheirurus* sp. I; Klouček, p. 6.
?1917 *Cheirurus* sp. II; Klouček, p. 6.
1922 *Cheirurus* sp.; Klouček, p. 1.
1926a *Cheirurus* sp. I; Klouček, p. 193.
?1926a *Cheirurus* sp. II; Klouček, p. 193.
1935 *Cyrtometopus olešnaensis* n. sp.; Růžička, p. 1, pl. 1, figs 1–3.
1937 *Cyrtometopus olešnaensis* RUŽ.; Koliha, p. 486.
?1937 *Cyrtometopus* sp.; Koliha, p. 486.
?1937 *Cyrtometopus* cf. *discretus* BARR.; Koliha, p. 486.
1947 *Parapilekia olešnaensis* (RŮŽIČKA); Prantl and Přibyl, p. 2, pl. 6, figs 6, 7.
1965 *Pilekia olešnaensis* (RŮŽIČKA, 1935); Vaněk, p. 108.
1965 *Pilekia olesnaensis* (RŮŽIČKA 1935); Vaněk, p. 281, pl. 24, figs 27–29; pl. 25, fig. 32.
1966 *Pilekia olešnaensis* (RŮŽ.); Havlíček and Vaněk, pl. 3, figs 6, 7.
1970 *Pilekia olesnaensis* (RŮŽIČKA 1935); Horný and Bastl, p. 223.
1984a *Parapilekia olesnaensis* (RŮŽIČKA, 1935); Mergl, p. 21, pl. 6, figs 1–8, text-fig. 3.
1985 *Parapilekia olesnaensis* (RŮŽIČKA, 1935); Přibyl et al., p. 119.
2001 *Parapilekia olesnaensis* (RŮŽIČKA, 1935); Vaněk and Valíček, p. 20.

Lectotype: Selected by Vaněk (1965), incomplete cranidium, figured by Růžička (1935) on pl. 1, fig. 1, deposited in the collection of the National Museum, Prague (NM L 18934).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Material: Forty cranidia, ten hypostoma, four librigenae, five incomplete thoraxes, twenty pygidia and numerous small fragments of various parts of exoskeleton in various quality of preservation.

Diagnosis: *Parapilekia* with oval glabella, small spine in librigena, and distinct inflexion near genal angle; pygidial axis rapidly tapering, with small externally imperfectly separated terminal piece; long, slender, cylindrical pleural spines in posterior thoracic segments bent dorsally; pygidial pleural spines radially and regularly arranged, with tips bent dorsally; rows of small tubercles on sides of L1, L2, and L3 but absent in axial part of glabella.

Emended description: Although a description of this species was given by Růžička (1935), and was followed by Mergl (1984a), this emended description is based on new material.

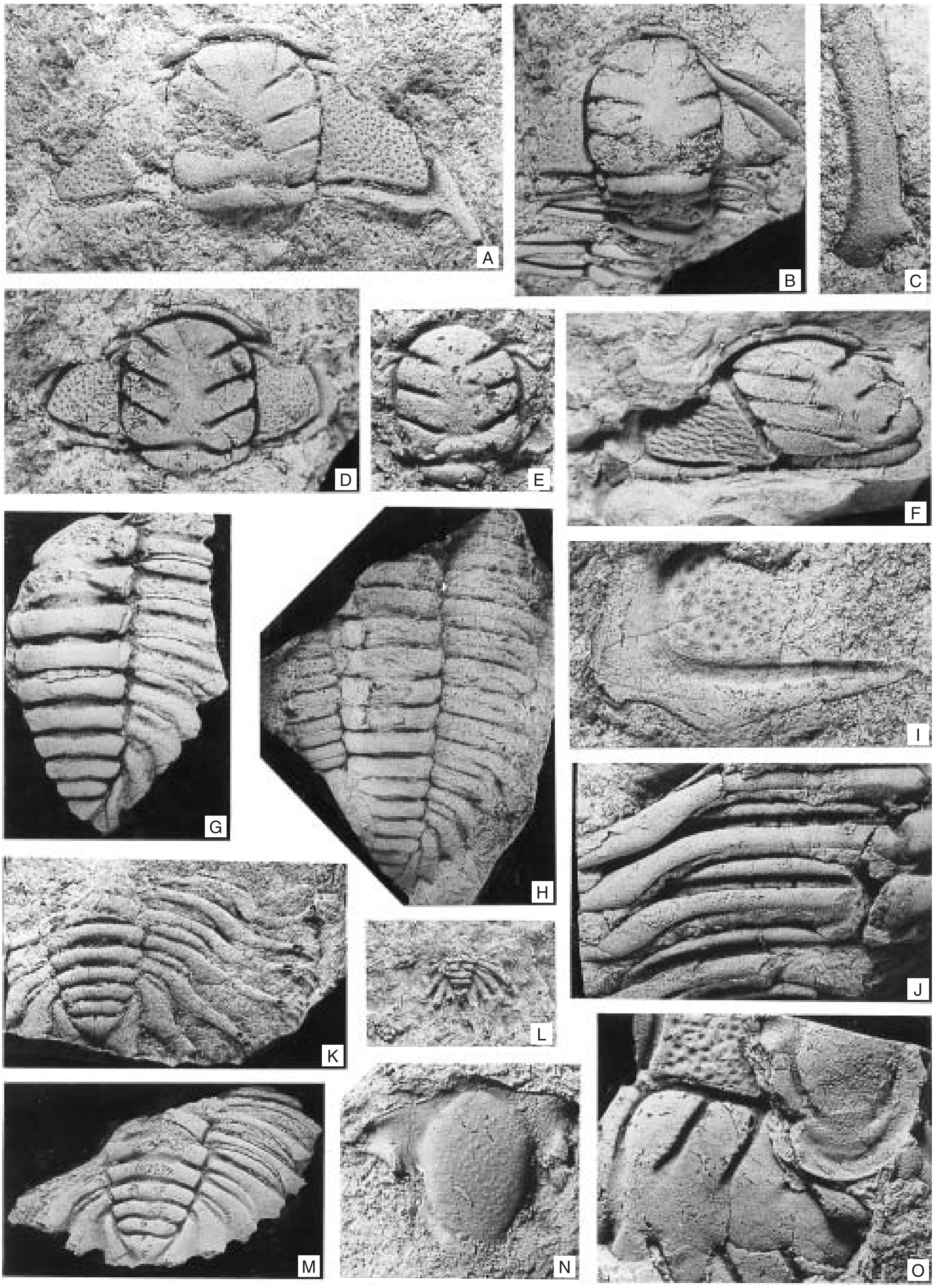
Exoskeleton thick-walled, with remarkable morphological differences in inner and dorsal surfaces, especially concerning the strength of dorsal furrows and the sculpture. The entire length of large individuals may attain 130–150 mm.

Cephalon semielliptical, moderately convex (tr.), with Lc/Wc = 0.50. Glabella subquadrate, anteriorly rounded, gently tapering anteriorly, moderately convex, with a maximum width at L1. S1, S2, and S3 narrow, deep, directed obliquely backwards, extending about one-third across the glabella. Glabellar furrows rapidly shallowing adaxially. Axial furrows are narrow and conspicuously deep. Preglabellar furrow narrow, deep, anteriorly arched. Occipital ring convex, widest at axis, length (sag.) about half of L1 (exs.). Occipital furrow deep abaxially, curved forward in shallower axial part. Anterior border gently convex, evenly wide, forming evenly convex, weakly dorsally arched anterior margin. Anterior border furrow forming a deep, narrow, and forward arched groove. Frontal lobe moderately convex, anteriorly evenly rounded. Fixigenae slightly narrower (tr.) than glabella, triangular in outline, moderately convex, gently downsloping abaxially. Surface of fixigena covered by small shallow subcircular pits in large holaspid specimens. Posterior border highly convex and narrow adaxially, lowering and rapidly widening abaxially. Genal angle extending into slightly flattened, inward curved oblique genal spine. Posterior margin near the genal spine is conspicuously bent forward, forming large gently flattened articulating boss at about two-thirds of fixigena (abax.). Posterior border furrow is deep adaxially, shallower and broader towards lateral border furrow. Palpebral lobe fused with short, high, curved to weakly S-shaped eye ridges, separated by a deep palpebral furrow from postocular area of fixigena. Anterior branch of facial suture short, running forwards and slightly inwards from anterior end of palpebral lobe. Posterior branch of facial suture long, running slightly backward to cut lateral margin at about mid-length of the cephalon.

Librigena small, with narrowly triangular genal field. Field covered by several shallow small circular pits of the same size as on fixigenae. Lateral border narrow, slightly flattened abaxially. Lateral border furrow deeper anteriorly, shallower abaxially. Small short librigenal spine extends posterolaterally from the lateral margin of librigenae, opposite to S1. Doublure of librigenae weakly convex ventrally, almost evenly wide (tr.) but weakly tapering anteriorly. Rostral plate unknown. Doublure of fixigenae is a small, narrowly subtriangular area below genal angle and genal spine, continuing adaxially into a tapering strip below articulating boss of posterior border.

Surface of glabella and librigenae covered by fine, densely spaced, spinose tubercles. Coarser tubercles surround lateral glabellar lobes L1, L2, and L3, but they are never present in centres of lobes or on central area. There are about eight coarse tubercles in each row on L1 and L2.

Hypostome large, broadly oval, equal in length and width, with highly arched large anterior lobe of middle body separated by shallow middle furrow from much shorter (sag.) posterior lobe. Maculae small, weakly convex. Anterior margin anteriorly gently arched, passing laterally to dorsally inclined, triangular and flattened anterior wings. Lateral notches deep. Shoulders high, long, subparallel to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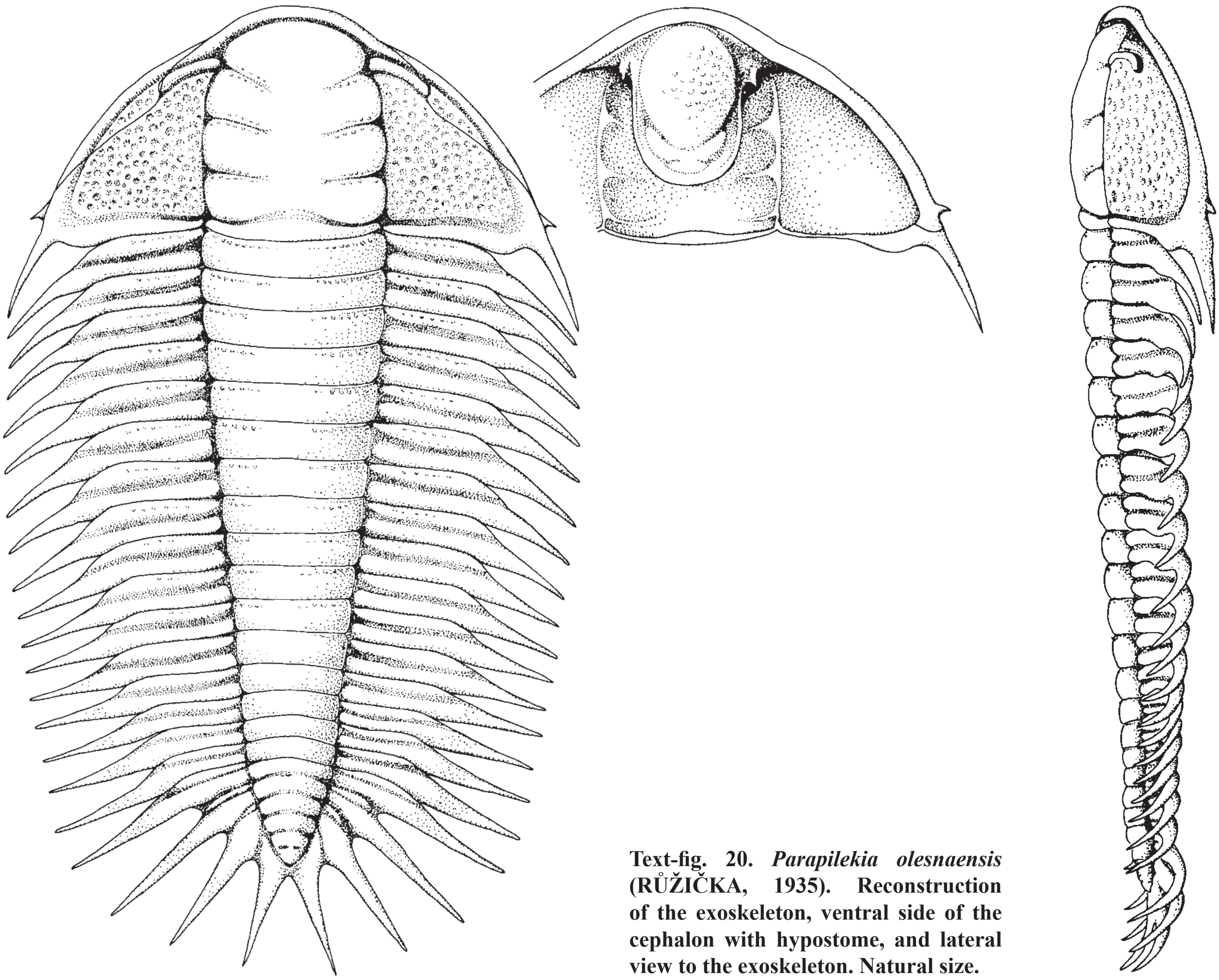


Text-fig. 20. ***Parapilekia olesnaensis*** **(RŮŽIČKA, 1935). Reconstruction of the exoskeleton, ventral side of the cephalon with hypostome, and lateral view to the exoskeleton. Natural size.**

each another, posteriorly lowering, and continuing into evenly curved posterior border. Border furrow shallow and wide. Posterior portion of middle body covered by large, low circular pustulae.

Thorax consisting of probably 14 segments; 13 distinct segments are present in most complete specimens with attached small piece of (?) fourteenth segment. Axis evenly tapering, pleural region widening backwards, slightly fulcrate, posteriorly with decreasing portion of subhorizontal pleural bands compared with fulcrate parts and pleural spines on each segment. The flat pleural band almost as wide (tr.) as the axis (tr.) in anterior segments, but only 60–70% as wide in posterior segments. Axial rings moderately convex, weakly longer (sag.) abaxially, in axial part extended into broad and deep articulating furrow. Articulating half-ring is short (sag.) and broad (tr.), arched anteriorly and highly convex dorsally. Overlap (sag.) of axial rings is 20–30% in an unrolled specimen. Pleural field flattened, with outer portion of pleurae extended into long, evenly tapering and backward inclined tubular spines. Spines slightly bent ventrally in anterior part of the thorax. In posterior half of the thorax and especially in the last three segments, the pleurae

◀ **Text-fig. 19.** ***Parapilekia olesnaensis*** **(RŮŽIČKA, 1935).**
A – cranidium, latex cast of exterior, PCZCU 1653, ×2.5; B – cranidium with librigena, internal mould, PCZCU 1654, ×2.5; C – ventral side of librigena showing small librigenal spine, internal mould, PCZCU 1655, ×2.5; D – cranidium, internal mould, PCZCU 1656, ×2.5; E – small cranidium, internal mould, PCZCU 1657, ×7; F – cranidium, internal mould tectonically deformed, NM L 38618, ×2.5; G, H – incomplete thorax with part of pygidium, internal mould and latex cast of exterior, NM L 38619, ×2.5, ×2; I – incomplete fixigena, internal mould, PCZCU 1658, ×2.5; J – pleural negion showing extended posterior pleural bands, internal mould, NM L 38521, ×3.5; K, M – pygidium, latex cast of exterior and internal mould, NM L 38520, both ×1.6; L – minute pygidium, latex cast of exterior, PCZCU 1659, ×7; N – incomplete hypostome, internal mould, PCZCU 1660, ×4; O – hypostome and associated cranidium showing relative size of both, internal mould, PCZCU 1661, ×3.5.
Mílina Formation, Olešná (A–E, G–O), and Úvaly (Vinice) (F).

extended into long cylindrical spines that have proximal parts slightly curved ventrally but distal ends are reversely bent and pointing laterodorsally (Text-figs 19K, 20). Pleural furrows are deep, almost transverse grooves from axial furrows to inclined outer portion of pleura. Anterior pleural band highly convex, tapering abaxially, terminated by small anterolateral projection of flange. This projection is more conspicuous in posterior than in anterior segments. Posterior pleural band high, wide near the axial furrow, tapering abaxially but abruptly extended into prominent, tumid, and slightly depressed articulating boss at about mid-width (tr.) of pleural region. External surface of segments covered by fine tubercles. A row of prominent elongate large tubercles in chevron-like arrangement runs along the anterior margin of each axial ring. Doublure of thorax is restricted to ventral face of spines and short (tr.) adjacent part of pleural bands. Ventral surface of doublure is finely spinose.

Pygidium large, with high, rapidly tapering axis bordered by deep axial furrow. Anterior margin slightly arched anteriorly. Articulation half-ring is prominent, with deep smooth articulating furrow. Axial rings tapering (tr.) and shorter (sag.) posteriorly, separated by deep, shorter (sag.) ring furrows. There are five axial rings and the axial piece. The last ring furrow is imperfect, being disconnected from axial furrow. Axial piece widely triangular, extending nearly to posterior margin. Pleural fields slightly narrower (tr.) than the axis, with four distinct pleurae, extended into radially arranged pleural spines. Interpleural furrows are deep grooves, oblique and slightly curved in the first and second pleura, but almost in axial direction between third and fourth pleurae. Pleural furrows deep in the first and second pleurae, weak in the third pleura, and absent in the fourth pleura. Anterior pleural bands are smaller and less robust that posterior pleural bands, which extend into long, narrowly conical spines. Proximal parts of spines are slightly turned ventrally, but the thinner distal parts of spines bend laterodorsally. Doublure restricted to narrow band below the pleural region and short postaxial part. Doublure surface is ventrally convex, densely covered by very fine spines.

Ontogeny: Only early holaspid specimens are known, with a cranidium length of only 3 mm. The smallest pygidium is 2 mm long (sag.), including the spines (exs.). Even the smallest specimens have three lateral glabellar furrows, six axial rings in the pygidium, and four pairs of pleural spines, with proportional lengths of spines and an axis similar to large specimens.

Remarks: The type species *Parapilekia speciosa* (DALMAN, 1827), which is a rare trilobite in the Bjørkåsholmen Limestone (Upper Tremadocian) of Scandinavia, is closely related to *Parapilekia olesnaensis* (RŮŽIČKA, 1935). In addition to differences already noted by Mergl (1984a) and Ebbestad (1999), it is worth adding that the spines on the pygidium of *P. olesnaensis* are longer and ventrally curved, and the thorax tapers more rapidly posteriorly than the thorax of *P. speciosa*. Small tubercles covering the surface of the glabella in *P. speciosa* are restricted to transverse bands bordering the glabellar furrows in *P. olesnaensis*. A small prolibrigenal spine at the lateral border of the librigenae is the unique feature of *P. olesnaensis*, unknown in other species of the genus; only *P*. sp. reported by Fortey and Owens (1991) has a similar but profixigenal spine.

Differences between *P. olesnaensis* and the Bavarian species *P. anxia* (SDZUY, 1955) and *P. discreta* (BARRANDE, 1868) have already been commented on by Mergl (1984a). Newly described P. *vogtendorfensis* HAMMANN et SDZUY, 2001 differs from *P. olesnaensis* by having unevenly radiating spines (Hamman and Sdzuy, in Sdzuy et al. 2001). The cranidium described by Hammann and Sdzuy (in Sdzuy et al. 2001) as Pilekiidae ? gen. et sp. indet. differs from *P. olesnaensis* by having a much more anterior S3 and by a forward widening glabella. *Parapilekia latilus* (LIU, 1977) from the Panjiazui Formation (Lower Tremadocian) of Hunan, South China (Peng 1990) differs by having a distinct S4, longer (sag.) and narrower (tr.) glabella, and by distinctly larger fixigenae. Pilekiids from the Tremadocian of Tasmania and Victoria, Australia, described by Jell (1985) and Jell and Stait (1985) are imperfectly known. One way in which they differ is by the lack of a distinct inflexion near the genal angles (Jell 1985: pl. 32, fig. 5). However, the cranidium of a pilekiid figured by Jell (1985: pl. 12, fig. 1) is almost identical to this of *P. olesnaensis*. The only distinct difference is a well-developed last ring furrow on the pygidial axis.

Klouček (1922, 1926a) distinguished several cheirurid trilobites in the Mílina Formation, but did not illustrate any species; he referred three species to genera *Amphion* and *Cheirurus*. The specimen he listed as *Amphion* n. sp. belongs to *Anacheirurus nanus* (MERGL, 1984), as noted above. However, it is unknown why Klouček differentiated the other two cheirurids in his fossil lists (Klouček 1917, 1926a). The specimen listed as *Cheirurus* sp. I is probably identical with *P. olesnaensis*, because Klouček's (1917) paper implies that this species is abundant. This is consistent with the frequency of *P. olesnaensis* in the Olešná locality. The second specimen, *Cheirurus* sp. II, is represented only by a pygidium (Klouček 1917). It is likely that Klouček was influenced by published data about the composition of the *Ceratopyge* fauna (Moberg and Segerberg 1906). He was anxious to differentiate more cheirurid taxa in a suggested "*Euloma-Niobe*" fauna of the Mílina Formation to support relationships between the Scandinavian and Bohemian faunas.

The formal description of the species was made by Růžička (1935). He figured two medium-sized cranidia (about 20–25 mm wide) and one incomplete pygidium, but also stated that the species could be fairly larger, with cranidium widths of nearly 60 mm. Newly collected fragments indicate even larger sizes, with cephalic widths of nearly 80 mm. The length of the complete exoskeleton can thus reach 130–150 mm. The species is the commonest and most well known large trilobite in the Mílina Formation, with several finds of more complete parts of the exoskeleton.

Occurrence: Kvaň (abundant), Úvaly, Vinice (abundant).

Suborder **Calymenina** SWINNERTON, 1915
Superfamily **Calymenoidea** BURMEISTER, 1843
Family **Bathycheilidae** PŘIBYL, 1953
Subfamily **Bathycheilinae** PŘIBYL, 1953

Genus ***Parabathycheilus*** MERGL, 1984

Type species: *Parabathycheilus vagans* MERGL, 1984; Upper Tremadocian, Mílina Formation; Barrandian, Bohemia.

Remarks: The genus *Parabathycheilus* MERGL, 1984 has been defined based on material from the Upper Tremadocian of Bohemia (Mergl 1984a, 1994). Rabano (1990) questioned the validity of the genus, but Hammann and Sdzuy (in Sdzuy et al. 2001) subsequently supported its validity and presented a short new diagnosis of the genus. In addition to the characters noted by Hammann and Sdzuy (in Sdzuy et al. 2001), the lack of spines on the edge of the librigenal border should be considered a characteristic feature of the genus. Outside of Bohemia, the genus is represented by *P. gallicus* (DEAN, 1965) in the Lower Arenig of the Montagne Noire, and by an unnamed species *Bathycheilus* ? n. sp. in the Santed Formation (Upper Tremadocian) of the Iberian Chains, Spain (Hammann 1983). The poorly known *Parabathycheilus* sp. has also been reported from the Vogtendorf Formation (Upper Tremadocian) of Bavaria (Sdzuy et al. 2001). *Prionocheilus* sp. from the early Arenig of Mauritania (Destombes et al. 1969) might belong to *Parabathycheilus*. This poorly known species has a librigena without spines, short and high eyes, and a small tuberculate pygidium. Chen and Zhou (2002) compared *Bathycheilus sinensis* CHEN et ZHOU, 2002 from the Lower Llanvirnian of China with *P. gallicus*. The differences stated by these authors are consistent with the generic characters of *Parabathycheilus*. Although having a shorter pygidium with less rings and pleurae than it is in the type species *B. complexus* (BARRANDE, 1872), thus being similar to *Parabathycheilus*, the Chinese species is more probably *Bathycheilus*. Indeed, *Parabathycheilus* is restricted to the late Tremadocian and the early Arenigian in the European part of the Gondwana periphery.

The early pharostomatinid *Prionocheilus languedocensis* (COURTESSOLE et PILLET, 1975) from the Tremadocian and the Lower Arenig of the Montagne Noire, France has a very similar pygidium and a narrowly parabolic outline of the glabella with three glabellar furrows (Henry and Vizcaïno 1996). It differs from *Parabathycheilus* by the absence of the border and preglabellar field, and by having preserved interpleural furrows on the pygidium.

Parabathycheilus vagans MERGL, 1984
Text-fig. 21A–R

?1917 *Lichas* sp.; Klouček, p. 7.
1964 *Pharostomina ferentaria* SDZUY, 1955; Vaněk, p. 108.
1965 *Pharostomina ferentaria* SDZUY 1955; Vaněk, p. 283, pl. 25, figs 33–35.
1966 *Pharostomina ferentaria* SDZUY; Havlíček and Vaněk, pl. 3, fig. 4.
1984a *Parabathycheilus vagans* sp. n.; Mergl, p. 32, pl. 2, figs 8–12, text-fig. 7.
2001 *Bathycheilus vagans* (MERGL, 1984); Vaněk and Valíček, p. 15.

Holotype: Cranidium figured by Mergl (1984a) on pl. 2, fig. 2, re-figured here in text-fig 21L, M, deposited in the palaeontological collections of the Czech Geological Survey, Prague (MM 102).

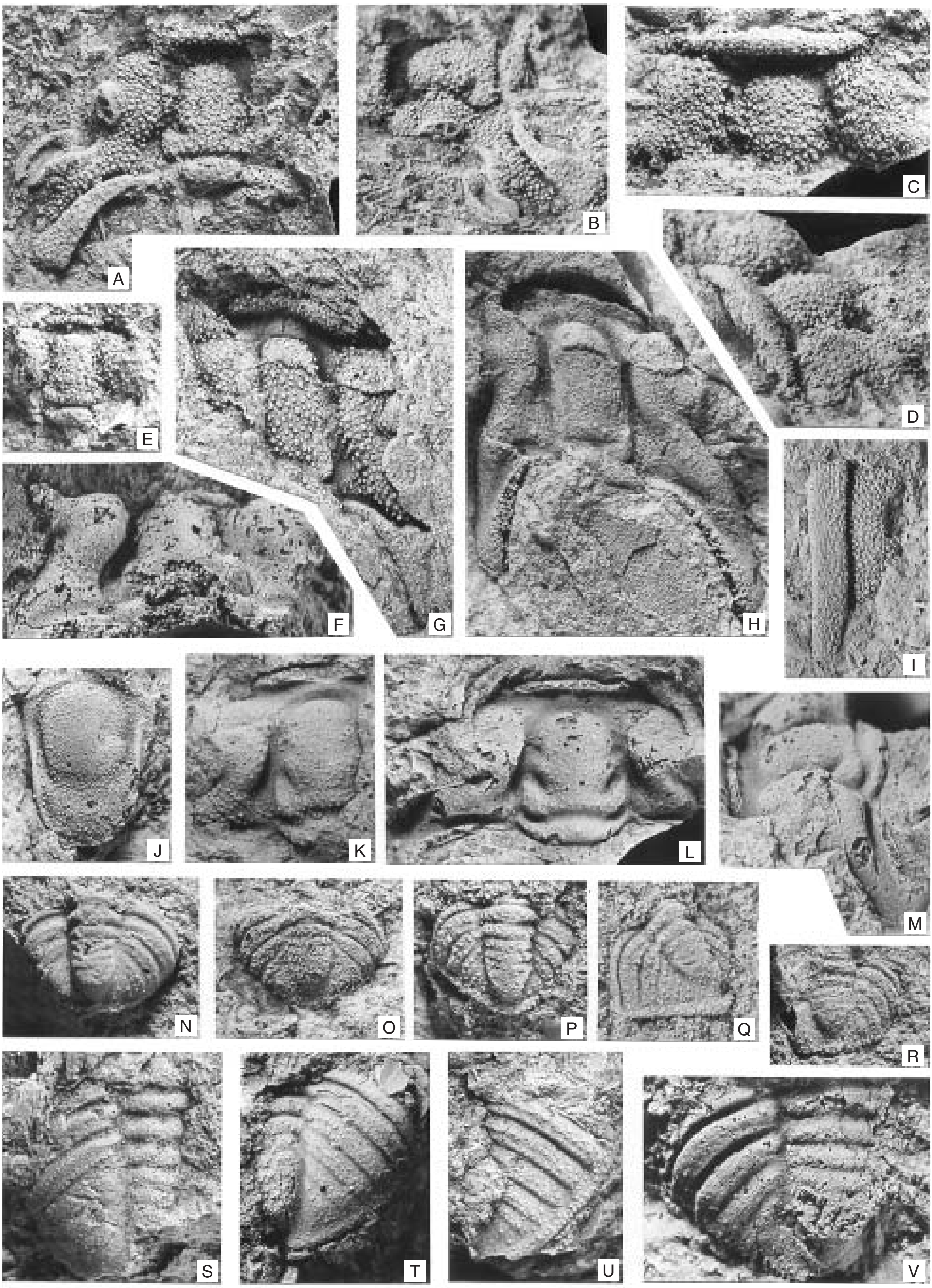
Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Material: Twenty cranidia (mostly incomplete), 6 librigenae, and 12 pygidia.

Diagnosis: *Parabathycheilus* of small size, with weakly tapering pygidial axis having five rings and conspicuous terminal piece; pleural field with four pleural furrows; pygidial border short (sag.), distinctly convex; cephalon densely covered by somewhat tubular, highly conical coarse tubercles.

Emended description: Species of small size, width exceeding 15 mm; suggested length of entire specimen 20 to 25 mm. There is strong difference between dorsal and inner exoskeletal surfaces; the latter is smooth in large individuals.

Cephalon semicircular, wider (tr.) than long (sag.), with conspicuous relief. Glabella elongate parabolic, widest posteriorly, highly convex (sag. and tr.) with evenly arched frontal lobe bordered by evenly curved preglabellar furrow. Three pairs of glabellar furrows distinct; S1 very deep, strongly inclined backward; S2 short, deep near axial furrows, rapidly shallowing, situated at mid-length of glabella; S3 very short, distinct near axial furrows. L1 large, triangular, L2 and L3 weakly defined. Sides of glabella steeply downsloping, central area subhorizontal (sag.). Occipital ring short (sag.), with lateral occipital lobes curved slightly forwards. Occipital furrow deep abaxially, shallow and longer (sag.) axially. Preglabellar field short (sag.), flat, fused with distinct border furrow. Anterior border short (sag.), transverse, very high, with convex dorsal surface (sag.), weakly arched in frontal view. Axial furrows deep. Fixigenae strongly convex, narrow in anterior and palpebral areas, extended laterally in posterior area. Anterior and palpebral areas considerably convex, with surface nearly vertical opposite to L2 and L3. Posterior area less convex, tapering backward and abaxially. Paraglabellar fields weakly defined, narrow (tr.), marked by nearly smooth surface. Palpebral lobes conspicuously extended dorsally, with adaxially steeply downsloping surface, forming almost stalk-like character of eyes. Eye ridges imperceptible. Posterior border furrow deep, broad (exs.), rapidly curved, and shallowing backward. Posterior border high and narrow adaxially, rapidly curved backward, becoming broader and flattened in abaxial portion, facing laterodorsally. Librigena triangular, with low and wide border separated from gently convex genal field by narrow and smooth subangular border furrow. Eye socle high, short (exs.), slightly curved, indicating short (exs.) but high eyes. Posterior doublure short, smooth. Surface of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glabella, borders and genal fields densely covered by prominent, narrowly conical, somewhat tubular tubercles. Tubercles of variable size, but generally considerably large in relation to size of the specimen. Scattered smaller tubercles intercalated between the larger ones. All tubercles show infilling of axial canal. Bottoms of axial and border furrows, eye socle, and preglabellar field smooth. This smooth surfaces flanked by bands of smaller tubercles; these smaller tubercles also cover surface of palpebral lobes. Inner surface of the cranidium almost smooth, without any traces of tubercles. Small fossulae present anterolateral to frontal lobe. Hypostome and thorax unknown, but unassigned hypostome figured on pl. #, fig. might belong to this species.

Pygidium short, broadly subtriangular, with slightly curved posterior margin. Axis about the same width (tr.) as associated pleural region, and about 80% as long as pygidium. Axis strongly convex (tr.), defined by weakly converging, deep axial furrows. Four to five rings, gradually narrowing (sag.) and triangular, large and highly raised terminal piece distinct externally. Ring furrows are narrow (sag.), distinct anteriorly, but ill defined posteriorly; they are much prominent on the inner surface. Articulating half ring prominent, smooth. Pleural regions subhorizontal adaxially, steeply sloping laterally towards weak and narrow border furrow. Four pleural furrows distinct, the third and fourth pairs short and inclined more backward. Interpleural furrows ill-defined between the first and second pleura, others pairs of interpleural furrows missing. Articulating facets small. Posterior border short, evenly broad, (sag.), convex, forming narrow strip-like doublure. Surface of the pygidium covered by irregularly spaced small tubercles, some forming short rows between pleurae.

Remarks: This species has been compared with *P. gallicus* (DEAN, 1965) by Mergl (1984a). A rare, poorly preserved specimen referred to *Bathycheilus* ? sp. n. by Hammann (1983) from the Upper Tremadocian of Spain is probably conspecific with *P. vagans* or with another closely related species. The morphology of the pygidium is the same and the finer ornament of the Spanish specimens is probably the result of a different mode of preservation in the shale. The pygidium and cephalon referred to *Prionocheilus* cf. *languedocensis* (COURTESSOLE et PILLET, 1975) from the Santed Formation of Spain (Hammann 1983: pl. 2, figs 18–20) probably belong to the same species; this has already been recognized by Hammann and Sdzuy (in Sdzuy et al. 2001).

The poor remains of *P. vagans* available to Vaněk (1964, 1965) were misinterpreted as the Bavarian species *Pharostomina ferentaria* SDZUY, 1955, but substantial differences in the morphology of the cephalon were described by Mergl (1984a). A coarsely tuberculate or spinose surface of small fragments led Klouček (1926a) to identify these remains as a lichid, as is evident from labels attached to some specimens stored in the National Museum, Prague.

Occurrence: Mílina Formation; Olešná (abundant), Kvaň (rare), Úvaly, Vinice (rare), Úvaly, test pit (rare).

Parabathycheilus krafti sp. n.

Text-fig. 21S–U

1926 *Asaphid* (*Megalaspis* ?); Růžička, p. 8, pl. 3, figs 8, 9.
1926 *Niobe* sp.; Růžička, p. 8, pl. 3, fig. 7.
1965 Trilobitarum inc. fam. et gen. I; Vaněk, pl. 26, figs 62, 63.
1970 *Holubaspis perneri* (RŮŽIČKA, 1926); Horný and Bastl, p. 199.
1994 *Parabathycheilus* sp.; Mergl, p. 12, pl. 2, fig. 3, pl. 7, fig. 5, pl. 8, figs 1–3.
2001 *Bathycheilus* sp.; Vaněk and Valíček, p. 15.

Holotype: Pygidium figured by Mergl (1994) on pl. 8, fig. 2, re-figured here in text-fig. 21T, deposited in the collection of the National Museum, Prague (NM L 30823).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the abandoned "V Ouzkém" iron ore mine.

Name: After the late private collector Vojtěch Kraft, who collected fossils in the type locality.

Material: Ten incomplete pygidia.

Diagnosis: *Parabathycheilus* of large size, with long, narrower and distinctly tapering pygidial axis having seven rings and small terminal piece; pleural field with five pleural furrows; on internal surface distinct six pairs of pleural furrows; pygidial border narrow, weakly convex.

Description: Pygidium moderately sized (6 mm long or even larger size), broadly triangular in outline, with semi-elliptical posterior margin. Axis bordered by deep axial furrows, gently tapering posteriorly, straight (sag.),

◄ **Text-fig. 21. *Parabathycheilus vagans* MERGL 1984.**
A, B – cranidium, latex cast of exterior and its oblique view, PCZCU 1616, both ×8; C, D – incomplete cranidium, latex cast of exterior and its oblique view showing high anterior border, PCZCU 1617, both ×8; E – small cranidium, latex cast of exterior, PCZCU 1618, ×8; F – cranidium, internal mould, posterior view showing high palpebral lobe, PCZCU 1619, ×6; G, H – incomplete cranidium tectonically deformed, latex cast of exterior and internal mould, NM L 38615, both ×8; I – incomplete librigena, latex cast of exterior, PCZCU 1620, ×8; J – hypostome, internal mould, PCZCU 1621, ×8; K – incomplete cranidium, internal mould, PCZCU 1622, ×8; L, M – holotype, cranidium, internal mould and its oblique view, MM 102, both ×5.5; N – pygidium, internal mould, PCZCU 1623, ×8; O – pygidium, latex cast of exterior, PCZCU 1624, ×8; P, Q – pygidium latex cast of exterior, NM L 38490, ×8; R – incomplete pygidium, internal mould, PCZCU 1625, ×8; V – large pygidium, internal mould, PCZCU 1626, ×8; Mílina Formation, Olešná (A–F, I–M, O–Q), Kvaň (N, R) and Úvaly, Vinice (G, H).
***Parabathycheilus krafti* sp. n.**
S – incomplete pygidium, internal mould, NM L 18914, ×5.5; T – holotype, incomplete pygidium, internal mould, NM L 30823, ×5.5; U – incomplete pygidium, internal mould, NM L 18913, ×5.5; Třenice Formation, Holoubkov.

moderately convex (tr.), with large articulating half ring, six well defined rings and small terminal piece. Ring furrows distinct. Pleural field narrowly triangular, moderately convex. Five pairs of pleurae with obscure borders except for the first and second interpleural furrows. Five deeply incised, narrow and oblique pleural furrows are distinct toward border furrow on dorsal surface. Sixth pair of pleural furrow distinct on inner surface of the pygidial shield. Border narrow, slightly depressed, convex dorsally. Border furrow narrow and weak. Surface of the pygidium covered by fine tubercles of uneven size, often arranged in short rows tracing interpleural furrows. Doublure semi-tubular, short (sag.), and smooth.

Remarks: This new species differs from *Parabathycheilus vagans* MERGL, 1984 from the Mílina Formation by having a larger size, a narrower (tr.) pygidial axis, more rings and pleural furrows on the pygidium, and a less conspicuous pygidial border. The pygidium of the new species differs from *P. gallicus* (DEAN, 1965) from the early Arenig of the Montagne Noire, France (Dean 1965; Courtessole et al. 1983) by having a narrower (tr.) pygidial axis and a more rounded posterior margin of the pygidium.

Parabathycheilus krafti sp. n. was referred by Růžička (1926) to an unnamed asaphid, although he was aware that finely tuberculate sculpture is unusual in this trilobite group. In the species list compiled by Klouček (1926a), only the species *Megalaspis* sp. might be correlated with the new species. Koliha (1937) merely adopted the determination of Růžička (1926). Vaněk (1965) incorrectly referred the pygidium to *Holubaspis perneri* (RŮŽIČKA, 1926); its shape probably led Vaněk (1965) to assign *H. perneri* to the hystricurids.

Occurrence: Třenice Formation, Holoubkov (rare).

Subfamily **Pharostomatinae** HUPÉ, 1953

Genus ***Holoubkocheilus*** MERGL, 1994

Type species: *Euloma granulatum* RŮŽIČKA, 1926; Upper Tremadocian, Třenice Formation; Barrandian, Bohemia.

Remarks: When first established (Mergl 1994), *Holoubkocheilus* was referred to Pharostomatinae HUPÉ, 1953. *Holoubkocheilus* has a cephalon with a broadly parabolic glabella and only two pairs of glabellar furrows, similar to the species *Pharostomina opiki* SDZUY, 1955, the type species of *Pharostomina* SDZUY, 1955. Unlike the latter genus, *Holoubkocheilus* has a distinct preglabellar field and terrace ridges on the librigenae, which are absent in *P. oepiki* (Sdzuy 1955; pl. 2, fig. 99). Additionally, the pygidia of both genera are quite similar, with only three axial rings, two pleural furrows, and weak interpleural furrows on the pygidium. Unlike *P. oepiki*, the species *P. ferentaria* SDZUY, 1955 has three pairs of glabellar furrows, while the pygidial axis has four to five rings and at least four distinct pleural furrows on the pleural fields. There is no doubt that *P. ferentaria* belongs to another genus. The species *P. trapezoidalis* (HARRINGTON et LEANZA, 1957) and *P. mexicana* ROBISON et PANTOJA-ALOR, 1968 are very similar to *P. ferentaria*. In view of the pygidial morphology, *P. ferentaria* is the nearest to the genus *Prionocheilus* ROUAULT, 1847, or may represent a new genus, as suggested by Henry and Vizcaïno (1996). The stratigraphically earliest known pharostomatine, the species *Prionocheilus languedocensis* (COURTESSOLE et PILLET, 1975) from the latest Tremadocian and Lower Arenig of the Montagne Noire, France, has three glabellar furrows (Henry and Vizcaïno 1996), and its pygidial morphology is generally consistent with that of *P. ferentaria*. The paraglabellar fields that are well developed in *Pharostomina* and characteristic for other bathycheilids are weakly defined but present in *Holoubkocheilus*.

By contrast, the genus *Holoubkocheilus* has an unusual pygidial morphology for pharostomatines. The pygidia of both known species of *Holoubkocheilus* are transverse with a short and broad axis, having only three rings and a rounded terminal piece. A transverse intra-annular furrow on the second ring (Text-fig. 22K), dividing it into a shorter (sag.) praeannulus and a longer postannulus, is an unusual characteristic in the calymenids. The pleural fields are rather small, having prominent pleural furrows, short and weak interpleural furrows and shallow and broad border furrow. The border bears fairly coarse terrace ridges on the dorsal surface, while the same ridges are present on the narrow doublure. A row of small spines along the edge of the librigena, a typical character of pharostomatines, is absent in *Holoubkocheilus*.

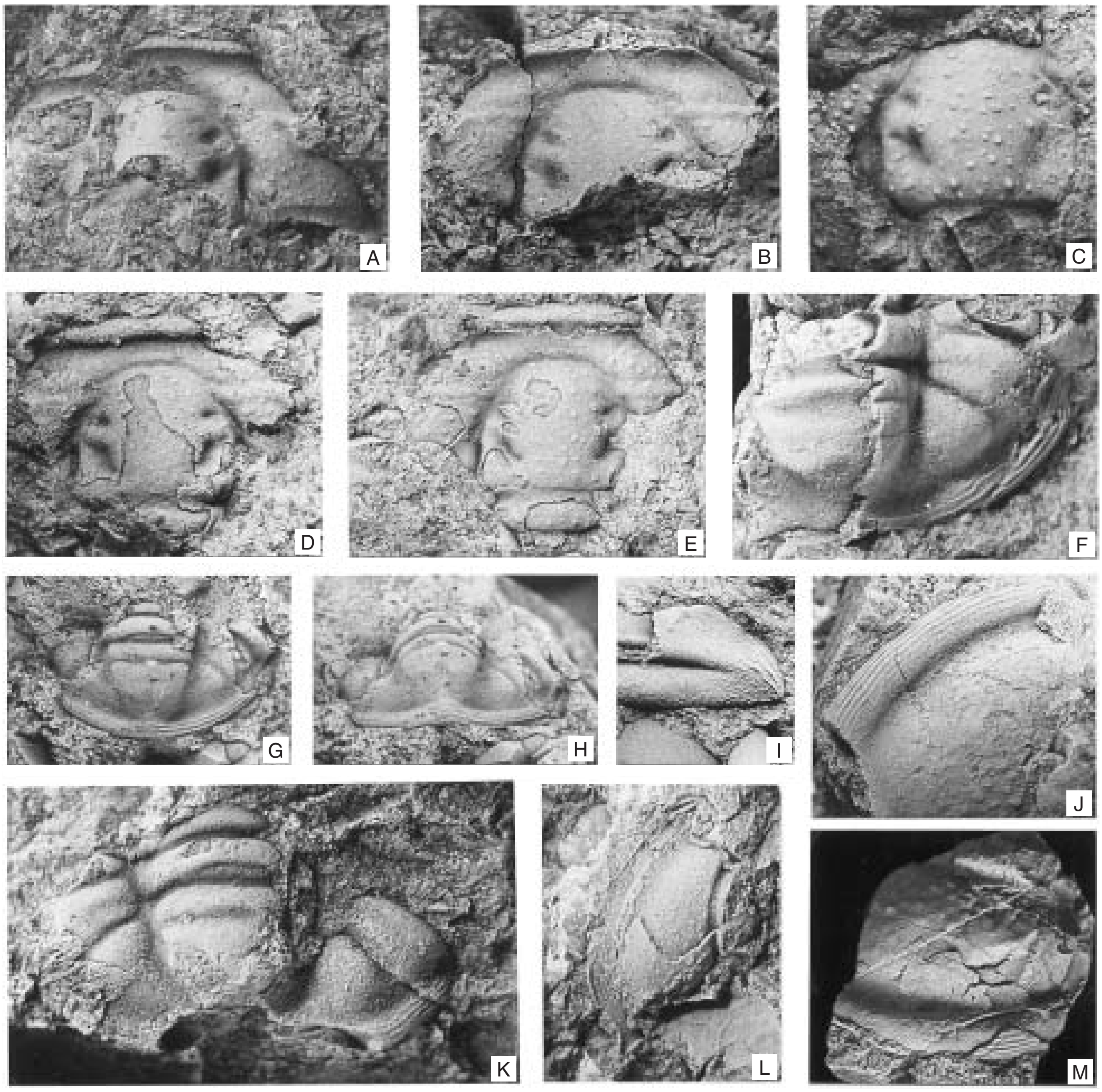
Mergl (1994) referred *Holoubkocheilus* to Pharostomatinae, but the genus might be rejected from calymenids. Its short, transverse pygidium with a few pleurae and rings, a cranidium with glabellar furrows disconnected with the axial furrows, a long genal spine, tubular borders on the cephalon, large eyes, and a pygidial border covered by prominent parallel terrace ridges are remarkably similar to some early Ordovician hystricurids (Jell and Stait 1985, Jell 1985, Dean 1989). Terrace ridges are essentially unknown in calymenids (Campbell 1967), while glabellar furrows disconnected to axial furrows, are present in some hystricurid genera. Because of the lack of knowledge about early calymenid evolution, *Holoubkocheilus* and *Pharostomina* are left in Bathycheilidae. They represent primitive calymenaceans that might be separated into a new subfamily.

The pygidium of *Holoubkocheilus* shows some resemblance to *Bavarilla* (BARRANDE 1863), but the cranidium of *Bavarilla* is quite different, with an anteriorly more expanded preglabellar field, and a long (sag.) and low anterior border with three well developed pairs of glabellar furrows and a finer ornament similar to homalonotids (Sdzuy 1955, 1957).

Holoubkocheilus granulatus (RŮŽIČKA, 1926)

Text-fig. 22

1926 *Euloma granulatum* n. sp.; Růžička, p. 3, pl. 1, figs 1–3.
1927 *Euloma granulatum* n. sp.; Klouček and Koliha, p. 3.
1928 *Euloma granulatum* n. sp.; Růžička, p. 52.
1931 *Euloma granulatum* RŮŽ.; Růžička, p. 387, pl. 1, figs 1–4.



Text-fig. 22. ***Holoubkocheilus granulatus*** **(RŮŽIČKA, 1926).**
A – incomplete cranidium, JV 2659, ×4.5; B – incomplete cranidium, NM L 18918, ×4.5; C – incomplete cranidium showing coarse tuberculate sculpture, NM L 30821, ×8; D – incomplete cranidium, NM L 30822, ×4.5; E – incomplete cranidium, NM L 18884, ×4.5; F – incomplete pygidium, partly preserved as internal mould, showing terrace ridges, NM L 18920, ×4.5; G, H – lectotype, pygidium and its posterior view, NM L 18885, both ×6; I – part of pleura, NM L 38481, ×6; J – incomplete librigena with terrace ridges on border, NM L 38482, ×4.5; K – large pygidium, NM L 18919, ×4.5; L – librigena, internal mould, NM L 30834b, ×5.5; M – librigena in low-angle light showing ridges on border and tuberculate surface of genal field, NM L 38484, ×4.5; Třenice Formation, Holoubkov.

1953 *Euloma granulatum* RŮŽIČKA; Přibyl, p. 42.
1965 *Eulomina granulatum* (RŮŽIČKA, 1926); Vaněk, p. 108.
1965 *Eulomina granulata* (RŮŽIČKA, 1926); Vaněk, p. 286, pl. 25, figs 38, 39.
1970 *Eulomina granulata* (RŮŽIČKA, 1926); Horný and Bastl, p. 148.
1994 *Holoubkocheilus granulatus* (RŮŽIČKA, 1926); Mergl, p. 14, pl. 2, figs 1–9, pl. 3, figs 1–6.
2001 *Holoubkocheilus granulatus* (RŮŽIČKA, 1926); Vaněk and Valíček, p. 16.

Lectotype: Selected by Vaněk (1965), pygidium figured by Růžička (1926) on pl. 1, fig. 3, re-figured here in text-fig. 22G, H, deposited in the collection of the National Museum, Prague (NM L 18885).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the abandoned "V Ouzkém" iron ore mine.

Material: Fourteen incomplete cranidia, 7 librigenae, and 18 pygidia and one fragment of pleura.

Diagnosis: *Holoubkocheilus* with broadly parabolic glabella having two deep glabellar furrows disconnected from axial furrows; S1 deepest adaxially, inclined backward, S2 shorter, less inclined backwards; preglabellar field long (sag.); distinct transverse eye ridges; anterior border transverse, only weakly arched forward; lateral border tubular, with conspicuous, parallel terrace ridges; ornament of sparsely and fairly coarse tubercles on glabella and genal fields; pygidium with weak posterior arch; tubular posterior border on pygidium and distinct praeannulus and postannulus on the second ring of pygidial axis.

Description: Cephalon broadly semi-elliptical. Glabella broadly parabolic, with evenly curved preglabellar furrow and deep axial furrows. Glabella gently (sag.) and moderately (tr.) convex, equally long as wide. Occipital ring long (sag.), lacking axial node. Occipital furrow broad (sag.), deeper abaxially, weakly curved forward. S1 deep, inclined backward in cca 45° to the sagittal axis, deepest at mid-length, shallowing abaxially, disconnected with axial furrows. Posterior glabellar lobe triangular, highly arched. S2 shorter and shallower than S1, slightly inclined backward, disconnected to axial furrows. Preglabellar field long (sag.), nearly flat, passing forward into deep anterior border furrow. Anterior border conspicuous, highly convex, rounded in profile, almost transverse, widest near sagittal axis. Fixigenae about 50% as wide (exs.) as the glabella in palpebral area, with elevated large palpebral lobe. Preocular field tapering forward, gently convex (sag. and tr.). Postocular field gently convex, lowering abaxially, as wide as glabella (tr.), with prominent posterior border and abaxially widening and shallowing posterior border furrow. Eye ridges transverse, distinct both internally and externally, evenly wide, extending anterior to S2. Librigena triangular, with deep border furrow in anterior part, becoming shallower and broader posterolaterally. Lateral border tubular, highly and evenly convex, evenly wide along whole length, covered by parallel terrace ridges, numbering 7–9 in large librigena. Genal field strongly convex, widening backward, slightly flattened near genal angle. Eye socle almost vertical, high, and bordered by deep evenly curved concave eye socle furrow. Visual surface is not preserved, but eyes have elongate reniform (exs.) outline. Genal angle extended into long, backward directed and almost flat genal spine. Surface of glabella and genal fields covered by prominent coarse tubercles, often of uneven size. Bottoms and adjacent slopes of axial furrows, glabellar furrows, and border furrows are smooth.

Thorax poorly known. The pleurae have deep, fairly narrow, slightly backward inclined pleural furrow extending to long lateral end of pleura. Anterior and posterior bands evenly long (exs.). Outer portion of pleura slightly flattened, with short and flat pleural spine with a few fine terrace ridges.

Pygidium transverse, with evenly curved posterior margin and transverse anterior margin. Axis is wide, occupying about 40% of pygidial width, strongly and evenly convex (tr.), moderately tapering posteriorly, extending nearby the posterior border. Articulating ring conspicuously long (sag.). Three rings and large terminal piece distinct, separated by conspicuous ring furrows, the last of which is much weaker than the anterior two. The second ring divided into shorter (sag.) praeannulus and a longer postannulus. Axial furrows deep, wide (tr.), with smooth bottom. Facets small. Pleural field with narrow, subhorizontal adaxial portion and marginal portions rapidly sloping down toward the border. Two pairs of pleural furrows rapidly curved backward and extending toward border furrow. One pair of short interpleural furrow transverse, weakly defined adaxially. Border furrow broad and shallow. Lateral and posterior borders short (sag.), tubular, distinctly convex, evenly wide, covered by fine terrace ridges parallel to posterior margin. Doublure short (sag.), flat, covered by fine terrace ridges. Short (tr.) posterior arch distinct behind the axis. Surface of the pygidium has fine tubercles.

Remarks: This species was described by Růžička (1926, 1931). Although this author referred the species to *Euloma* ANGELIN, 1854, he stated that its morphology is not entirely consistent with *Euloma*, and it represents an unusual group of eulomids. This generic attribution was criticised by Klouček and Koliha (1927). Vaněk (1965) referred this species to *Eulomina* RŮŽIČKA, 1931, but this genus differs by having a finely pitted cephalon surface, prominent anterior border, and broadly trapezoidal glabella with very weak glabellar furrows. The pygidium referred to *Eulomina* by Vaněk (1965) belongs to *Holubaspis* PŘIBYL, 1950, as pointed out Mergl (1984a, 1994).

Occurrence: Třenice Formation, Holoubkov (abundant), Cheznovice (abundant).

Holoubkocheilus asopus sp. n.

Text-fig. 23

1941 *Euloma kettneri* n. sp.; Růžička p. 22, fig. 3 (partim).
1984a *Eulomina* sp.; Mergl, p. 34, pl. 34, fig. 14.
2001 *Eulomina* sp.; Vaněk and Valíček, p. 16.

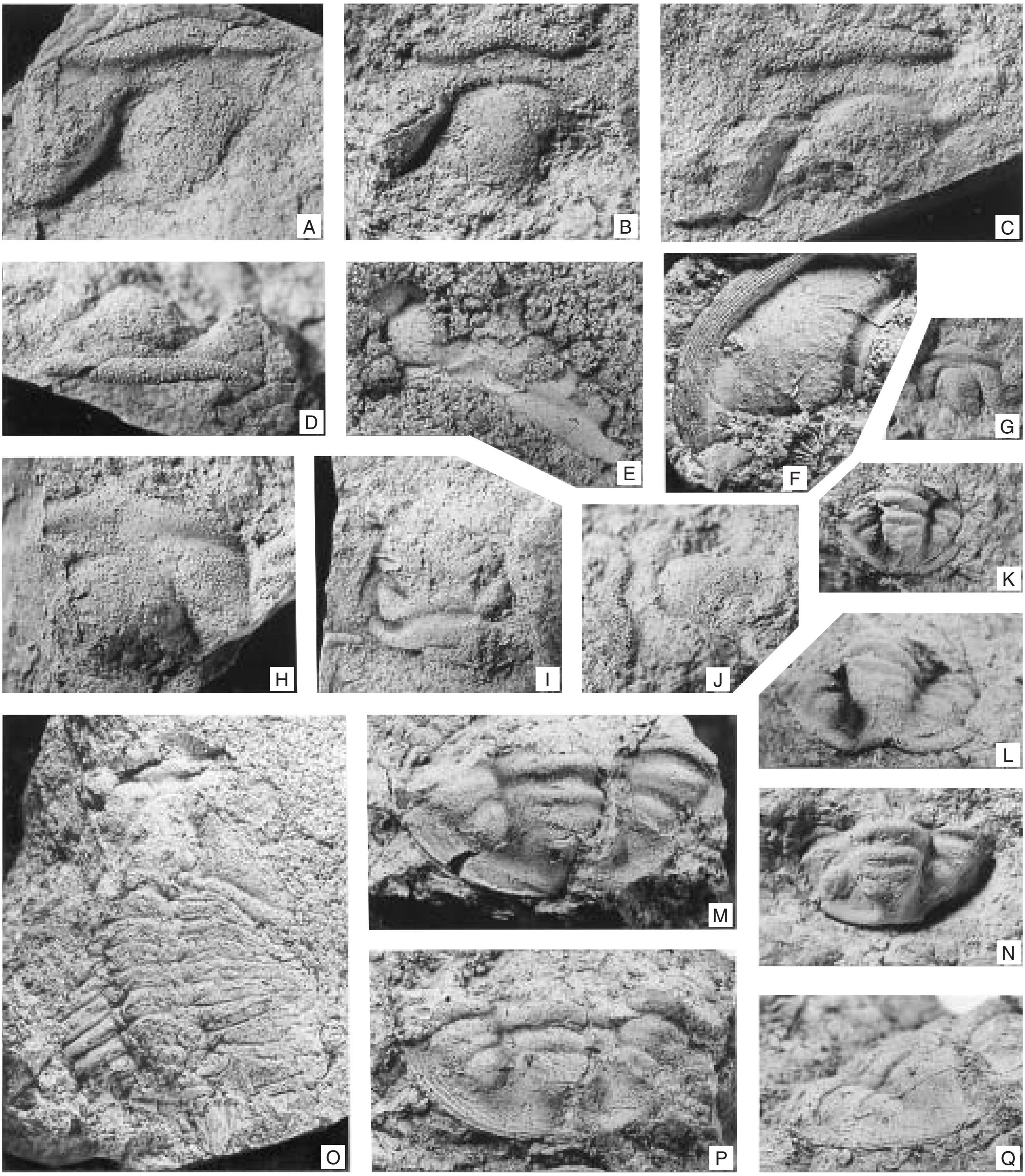
Holotype: Incomplete cranidium figured here in text-fig. 23C deposited in the palaeontological collection of the University of West Bohemia at Plzeň (PCZCU 1629).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Name: Latin, *Ásópos*, from Greek mythology, the son of Ókeanos and Téthys.

Material: Eight cranidia, 1 librigena, 6 pygidia and incomplete poorly preserved cranidium with thorax.

Diagnosis: *Holoubkocheilus* with angular front margin of anterior border; broadly parabolic glabella; eye ridges obscure; paraglabellar fields distinct.



Text-fig. 23. ***Holoubkocheilus asopus*** **sp. n.**
A, D – incomplete cranidium, internal mould, and its anterior profile, PCZCU 1627, both ×3.5; B, J – incomplete cranidium, internal mould, and its oblique view, PCZCU 1628, both ×3.5; C – holotype, incomplete cranidium, internal mould, PCZCU 1629, ×3.5; E – posterior fixigena, latex cast of exterior, NM L 38485, ×3.5; F – librigena, latex cast of exterior, NM L 38486, ×4; G – small cranidium, internal mould, PCZCU 1630, ×3.5; H – incomplete cranidium, internal mould, PCZCU 1631, ×3.5; I – incomplete glabella, latex cast of exterior, PCZCU 1632, ×3.5; K, L – pygidium, internal mould and its posterior view, NM L 38487, ×3.5, ×6; M, P, Q – pygidium, internal mould, latex cast of exterior and its oblique view, PCZCU 1633, all ×6; N – pygidium, internal mould, PCZCU 1634, ×3.5; O – cranidium with incomplete thorax, NM L 38488, ×2.2; Mílina Formation, Olešná (A–L, O) and Kvaň (M, N, P, Q).

D e s c r i p t i o n : Cranidium with broadly parabolic glabella, cca 85–90% as long as its width, gently convex, with steeper frontal lobe (sag.) and moderately convex in transverse profile. S1 deep, inclined backward, expanding into shallow depression in adaxial ends. S2 much shorter and shallower, slightly inclined backward, S3 absent. Occipital furrow deep, and forward inclined abaxially, shallow and transverse medially. Occipital ring broad, without occipital node. Axial furrows deep, preglabellar furrow separated from gently curved and deep border furrow by short, weakly convex (sag.) preglabelar field. Anterior border prominent, highly convex, angular and expanding forward into short angular projection. Paraglabelar field small and distinct. Fixigenae narrow near palpebral lobes, expanding anteriorly, by highly convex lobe extending toward preglabelar field. Anterior branch of facial suture gently diverging forward. Postocular fixigenae highly convex, lowering and tapering backward and abaxially. Posterior border furrow deep, transverse near axial furrow; abaxial portion of fixigenae broad (exs.), with subrectangular margin. Cranidium covered by coarse tubercles that are unevenly and sparsely scattered over the surface.

Thorax poorly known, almost parallel sided, with gently arched axis and broad pleural bands. Pleurae slightly sloping adaxially, extended into flattened, laterally directed, short spines.

Pygidium transverse, with evenly curved posterior margin and transverse anterior margin. Axis rather wide, occupying about 40% of width of the pygidium, strongly and evenly convex (tr.), moderate tapering posteriorly, extending almost toward the posterior border. Articulating ring large. Three rings and the terminal piece distinct, separated by backward less distinct ring furrows. Axial furrows deep, with smooth bottom. Pleural field with narrow subhorizontal adaxial portion and rapidly downsloping marginal portions. Two pairs of pleural furrows, rapidly curved backward and extending to border furrow. The first pair of interpleural furrows shallow and short. Border short, convex, evenly wide, covered by fine terrace ridges parallel to margin. The ridges absent on anterior band of the first pleura. Doublure short (sag.), flat, bearing similar terrace ridges. Small posterior arch distinct behind the axis. Surface of the pygidium with fine tubercles.

R e m a r k s : The species is imperfectly preserved, and due to its rarity the librigenae and some parts of cranidium are unknown. It differs from *H. granulatus* (RŮŽIČKA, 1926) by having an angular, forward extended anterior border and obscure eye ridges, while in *H. granulatus* the anterior border is transverse, and eye ridges are distinct and transverse. The pygidial characters of both species are nearly the same. The only difference is that the first axial ring is divided by a transverse furrow into a praeannulus and postannulus in *H. granulatus*; in the new species this ring is probably undivided, but its poor state of preservation makes this difference less certain.

The species was known to Klouček, who referred a small fragment of the cephalic posterior border to *Euloma*. His hand-written label correlates with the name *Euloma* sp. à la V Ouzkém in his fossil list (Klouček 1931). The pygidium of *H. asopus* was confused with *Proteuloma kettneri* in the original description of the latter species by Růžička (1941); this discrepancy was corrected by Mergl (1984a).

O c c u r r e n c e : Mílina Formation; Olešná (very rare), Kvaň (rare).

Order **Ptychopariida** SWINNERTON, 1915
Suborder **Ptychopariina** RICHTER, 1933
Superfamily **Ptychopariodea** MATTHEW, 1887
Family **Eulomidae** KOBAYASHI, 1955

Genus ***Proteuloma*** SDZUY, 1958

T y p e s p e c i e s : *Conocephalites geinitzi* BARRANDE, 1868; Lower Tremadocian, Leimitz Shales; Bavaria, Germany.

Proteuloma kettneri (RŮŽIČKA,1941)

Text-fig. 24

?1917 *Euloma* sp.; Klouček, p. 6.
1922 *Euloma* sp.; Klouček, p. 1.
1924 *Euloma* sp.; Koliha, p. 36.
1926a *Euloma* sp. I.; Klouček, p. 192.
1931 *Euloma* cf. *ornatum*; Klouček, p. 363.
1937 *Euloma* cf. *geinitzi*; Koliha, p. 480.
1937 *Euloma* cf. *ornatum*; Koliha, p. 486.
1941 *Euloma Kettneri* n. sp.; Růžička, p. 22, figs 1, 2, (not fig. 3).
1965 *Proteuloma geinitzi* (BARRANDE, 1868); Vaněk, p. 107.
1966 *Proteuloma geinitzi* (BARR.); Havlíček and Vaněk, pl. 3, fig. 5.
1965 *Proteuloma geinitzi* (BARRANDE, 1868); Vaněk, p. 266, pl. 22, figs 5–9.
1970 *Proteuloma geinitzi* (BARRANDE, 1868); Horný and Bastl, p. 182.
1984a *Proteuloma kettneri* (RŮŽIČKA, 1941); Mergl, p. 38, pl. 5, figs 8–12.
2001 *Proteuloma kettneri* (RŮŽIČKA, 1941); Vaněk and Valíček, p. 30.

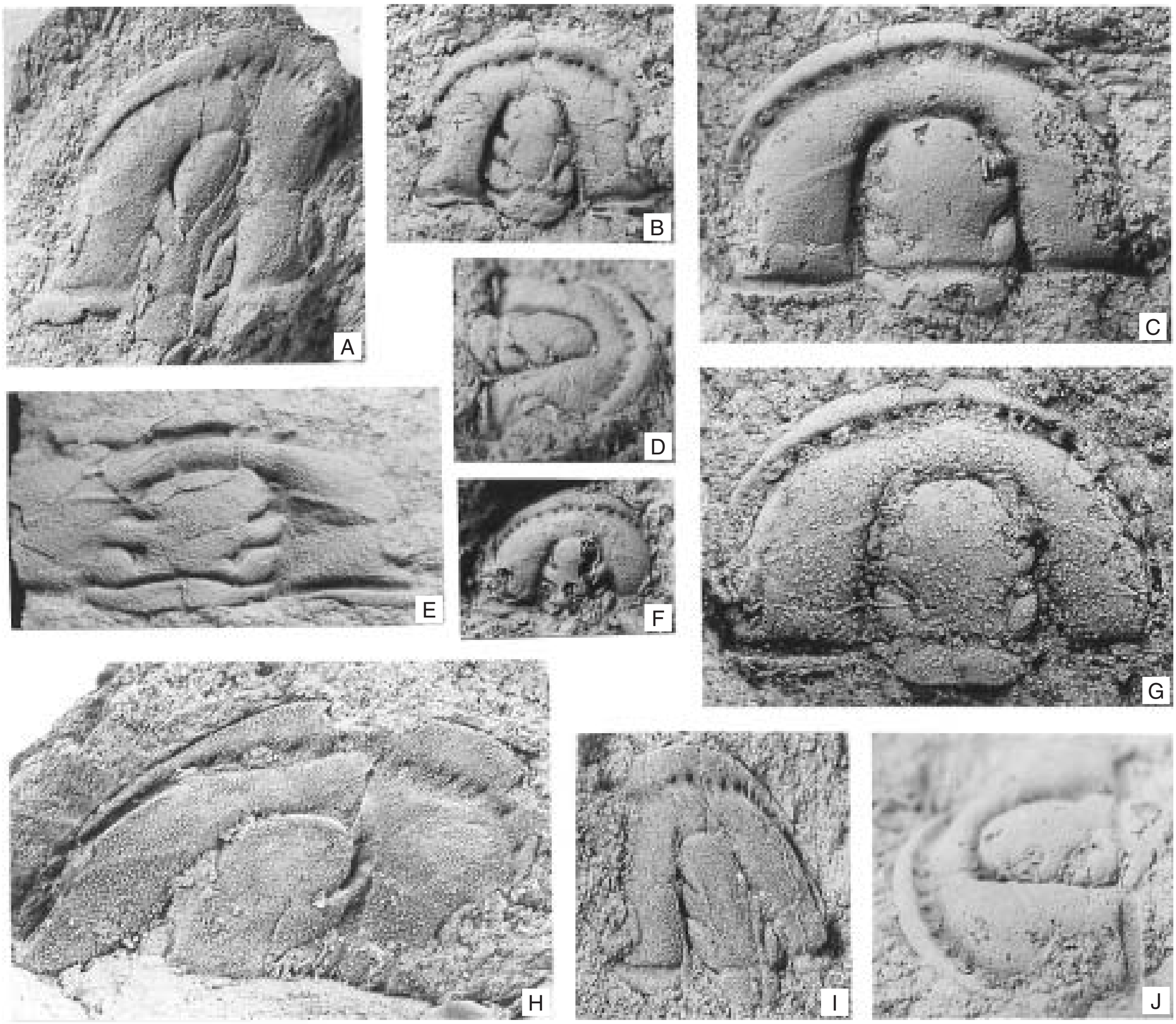
L e c t o t y p e : Selected by Mergl (1984a), the cranidium figured by Růžička (1941) as text-figs 1 and 2, re-figured here in text-fig. 24B, D, deposited in the collection of the National Museum, Prague (NM L 18975).

T y p e h o r i z o n a n d l o c a l i t y : Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

M a t e r i a l : Ten cranidia in chert, and 20 mostly strongly deformed cranidia in shale.

D i a g n o s i s : *Proteuloma* with small palpebral lobes behind mid-length of the cranidium; wide, weakly plicate preglabellar field; evenly curved anterior and lateral borders and small librigena; S1 and S2 deep, S1 long, adaxially considerably curved backward; eye ridges weak, inclined 60% toward sagittal axis; border furrow with cca 20 circular pits; surface with fine spinose sculpture.

E m e n d e d d e s c r i p t i o n : Small species, with maximum length of 20–25 mm. Cephalon semicircular, conspicuously convex (sag. and tr.), 60% as long as its width in the largest known non-deformed specimen, 13.3 mm wide



Text-fig. 24. ***Proteuloma kettneri*** **(RŮŽIČKA, 1941).**
A – tectonically deformed cranidium, latex cast of exterior, NM L 38474, ×5; B, D – lectotype, cranidium, internal mould and its oblique view, NM L 18975, both ×5; C, G, J – cranidium, internal mould, latex cast of exterior and its oblique view, PCZCU 1642, all ×5; E – tectonically deformed cranidium, internal mould, NM L 38475, ×6; F – small cranidium, internal mould, PCZCU 1641, ×5; H – tectonically deformed cranidium, latex cast of exterior showing finely spinose sculpture, NM L 38476, ×6; I – tectonically deformed cranidium, latex cast of exterior, NM L 38477, ×5; Mílina Formation, Olešná (B–D, F, G, J), Úvaly (Škvorec enclosure) (A, H, I), and Úvaly (Vinice) (E).

cranidium. Glabella broadly parabolic, 85 % as long as its width, considerably convex (tr.), widest (tr.) at occipital furrow, defined by narrow and deep axial furrows. Preglabellar furrow deep, evenly rounded. Occipital ring short (sag.) with distinct occipital node, separated by deep occipital furrow. S1 long, deep, adaxially turns backward almost to occipital furrow. S2 shorter, conspicuously inclined backwards. S3 absent. L1 largest of the glabellar lobes, the one-third long (exs.) and one-fourth wide (tr.) as glabella. Frontal lobe transversally oval. Preglabellar field long and gently convex (sag.). Fixigenae conspicuously vaulted (exs. and tr.), widest at posterior margin. Posterior border highly convex, short (sag.), gently widening abaxially, defined by deep transverse border furrow. Palpebral lobe small, opposite to S1, reniform, defined by distinct palpebral furrow. Eye ridges ill-defined on dorsal surface, but distinct on inner surface, narrow, nearly straight with adaxial part bent forward, at about 60° to sagittal axis. Anterior branch of facial suture gently diverging forward, posterior branch shorter, runs towards genal angle at about 45°. Anterior and lateral margins evenly curved. Anterior border short (sag.), 10 % of glabellar length, highly and evenly arched, slightly tapering abaxially to narrower lateral border. Anterior and lateral border furrows deep, concave, with a row of uniform circular pits. There are about 18 to 20 pits in a row in large individuals. Posterior glabellar doublure rather long (sag.), almost equal to length of occipital ring and posterior border (sag. and exs.). Surface of the cranidium densely covered by fine spines of uniform size. Librigena, hypostome and thorax unknown.

Pygidium small, transverse, with short axis equal to about 60 % of pygidial length. Axis conspicuously convex (tr.) and raised above pleural regions. Two (?) axial rings are distinct on available but deformed material. Axial furrow weakly converging backward. Tip of axis regularly rounded and raised above posterior area. Pleural field almost horizontal, with weakly defined pleural furrows. Lateral and posterior borders very narrow (sag. and tr.), convex. Doublure very narrow (sag.).

R e m a r k s : The species *P. kettneri* (RŮŽIČKA, 1940) is similar to *P. geinitzi* (BARRANDE, 1868) from the Leimitz Shales (Lower Tremadocian) of Bavaria, Germany. The Bavarian species differs by having larger and more forward-situated palpebral lobes and a less curved anterior margin of the cranidium (Sdzuy 1955, 1958). The same differences are distinct in specimens from Turkey, referred to *P.* cf. *geinitzi* by Shergold and Sdzuy (1984). The Turkish *P.* cf. *geinitzi* from the Seidişehir Formation (Early Tremadocian) has larger and more anterior palpebral lobes, and a less curved anterior border than *P. kettneri*. Several species referred to *Proteuloma* from the early Ordovician of Kazakhstan (*P. limitaris* APPOLONOV et TSCHUGAEVA, 1983, *P. acutiscula* APPOLONOV et TSCHUGAEVA, 1983, *P. rectangulata* APPOLONOV et TSCHUGAEVA, 1983) have less curved anterior borders, larger palpebral lobes, and narrower (tr.) preocular fixigenae. The species *P. monile* (SALTER, 1873) from the Shineton Shales of England and the Lower Tremadocian rocks of South Wales (Lake 1940, Owens et al. 1982) differs by having larger palpebral lobes and eye ridges that are less inclined backward, and correspondingly larger postocular fixigenae. In addition, the cranidium of *E. monile* is more rectangular, with a less convex anterior margin. Owens et al. (1982) stated that the degree of backward obliquity of eye ridges must be treated with caution. However, in *P. kettneri*, the backward inclined eye ridges and small palpebral lobes are remarkably stable characters, distinct both in rare material from the Komárov area south-western part of the Prague Basin, and in deformed but numerous specimens from the Úvaly area east of Prague. Hammann and Sdzuy (in Sdzuy et al. 2001) reported and figured the species *Euloma ornatum* ANGELIN, 1854 from the Vogtendorf Formation (Upper Tremadocian) of Bavaria. These specimens, although associated with similar trilobite taxa, clearly differ from *P. kettneri* by having larger and more anterior palpebral lobes, narrower (tr.) fixigenae, and a subangular anterior border.

The pygidia that Vaněk (1965: pl. 22, fig. 9) and Mergl (1984a: pl. 5, fig. 9; 1994: pl. 3, fig. 7) referred to *P. kettneri* actually belong *Agerina clymene* sp. n.

The first report of *Euloma* ANGELIN, 1854 in the Mílina Formation was given by Klouček (1922). The species *E.* cf. *ornatum* or *E.* cf. *geinitzi* were listed by Koliha (1937). These references surely concern the species *P. kettneri*. However, Klouček (1931) also noted *Euloma* sp. à la Ouzký from the Mílina Formation. This author, as evident from hand-written labels in Klouček's collection in the National Museum in Prague, gave this name to a small fragment (external mould of a fixigena) of *Holoubkocheilus asopus* sp. n. This species is very similar to *H. granulatus* (RŮŽIČKA, 1926), and was originally referred to *Euloma* (Růžička 1926, 1931). In addition, Klouček (1917) also used the name *Euloma* ? on the labels attached to the spinose glabellae of a calymenid *Parabathycheilus vagans* MERGL, 1984.

O c c u r r e n c e : Mílina Formation; Olešná (rare), Úvaly, Vinice (abundant), Úvaly, test-pit (abundant).

Order **Asaphida** SALTER, 1864
Superfamily **Asaphoidea** BURMEISTER, 1843
Family **Asaphidae** BURMEISTER, 1843

Genus ***Niobina*** LAKE, 1946

T y p e s p e c i e s : *Niobina davidis* LAKE, 1946; Upper Tremadocian; Great Britain.

Niobina sp.

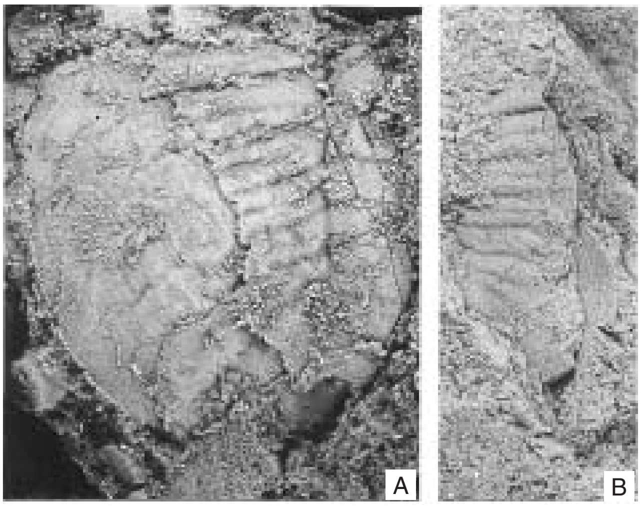
Text-fig. 25

1917 *Niobe* sp.; Klouček, p. 7.
1926a *Niobe* sp.; Klouček, p. 193.
1984a *Niobina*? sp.; Mergl, p. 27, pl. 7, fig. 5.
2001 *Niobina* sp.; Vaněk and Valíček, p. 16.

M a t e r i a l : Five fragments of pygidia.

D e s c r i p t i o n : The most complete pygidium is 40 mm wide and 23 mm long, but small fragments indicate even greater widths of about 70–80 mm. Pygidium broadly semi-elliptical, gently arched (tr.), with axis cca 20 % as wide as the pygidium. Axis gently convex (tr.), slightly tapering backward, 60–70 % as long as pygidium, with six distinct rings and rounded terminal piece. Pleural field with five distinct pairs of broadly S-shaped and backward inclined narrow pleural furrows and slightly less distinct but evenly long interpleural furrows, which are disconnected from narrow, well defined axial furrows. Pleural and interpleural furrows extend close to posterior margin, leaving only narrow smooth border. Pleural regions subhorizontal, with slightly downsloping margins. Doublure wide (sag. and tr.), at anterior margin almost 50 % as wide as pleural regions (tr.), covered by fine terrace ridges subparallel to posterior margin.

R e m a r k s : The species is imperfectly known due to its rarity and fragmentary preservation, though distinctly developed, interpleural furrows suggest the attribution of these fragments to *Niobina* LAKE, 1946. *Niobina* is a less common taxon. It is known in the Upper Tremadocian of Great Britain (Lake 1946) and Sweden (Tjernvik 1956), and in the Lower Tremadocian of Argentina (Harrington and Leanza 1957). The Bohemian specimens are characterised by less numerous axial rings and pleurae than other species of the genus.



Text-fig. 25. *Niobina* sp.
A – incomplete pygidium, latex cast of exterior, MM 129, ×2.5;
B – fragment of pygidium, internal mould, PCZCU 1581, ×2.5.
Mílina Formation, Olešná.

Two small fragments (part of an axis with an adjacent pleural area) of large pygidia were collected by Klouček in the Olešná locality. The label attached to these fragments indicates that they correspond to *Niobe* sp. in the compiled fossil lists (Klouček 1917, 1926a).

Occurrence: Mílina Formation; Olešná (very rare).

Family **Ceratopygidae** LINNARSSON, 1869

Genus ***Ceratopyge*** HAWLE et CORDA, 1847

Type species: *Olenus forficula* SARS, 1835; Tremadocian, Alum Shale Formation; Norway.

Ceratopyge mareki MERGL, 1984
Text-figs 26, 27

1922 *Ceratopyge* sp.; Klouček, p. 1.
1926a *Ceratopyge* sp.; Klouček, p. 192.
1937 *Ceratopyge* cf. *forficula* SARS; Koliha, p. 486.
1964 *Diceratopyge troedssoni* SDZUY, 1955; Vaněk, p. 108.
1965 *Diceratopyge troedssoni* SDZUY 1955; Vaněk, p. 276.
1984a *Ceratopyge mareki* sp. n.; Mergl, p. 27, pl. 8, figs 1–3, text-fig. 5.
2001 *Ceratopyge mareki* MERGL 1984; Vaněk and Valíček, p. 18.

Holotype: Complete specimen figured by Mergl (1984a) on pl. 8, fig. 1, re-figured here in text-fig. 26C, F, J, K, deposited in the collection of the National Museum, Prague (NM L 38496).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Úvaly, test-pit.

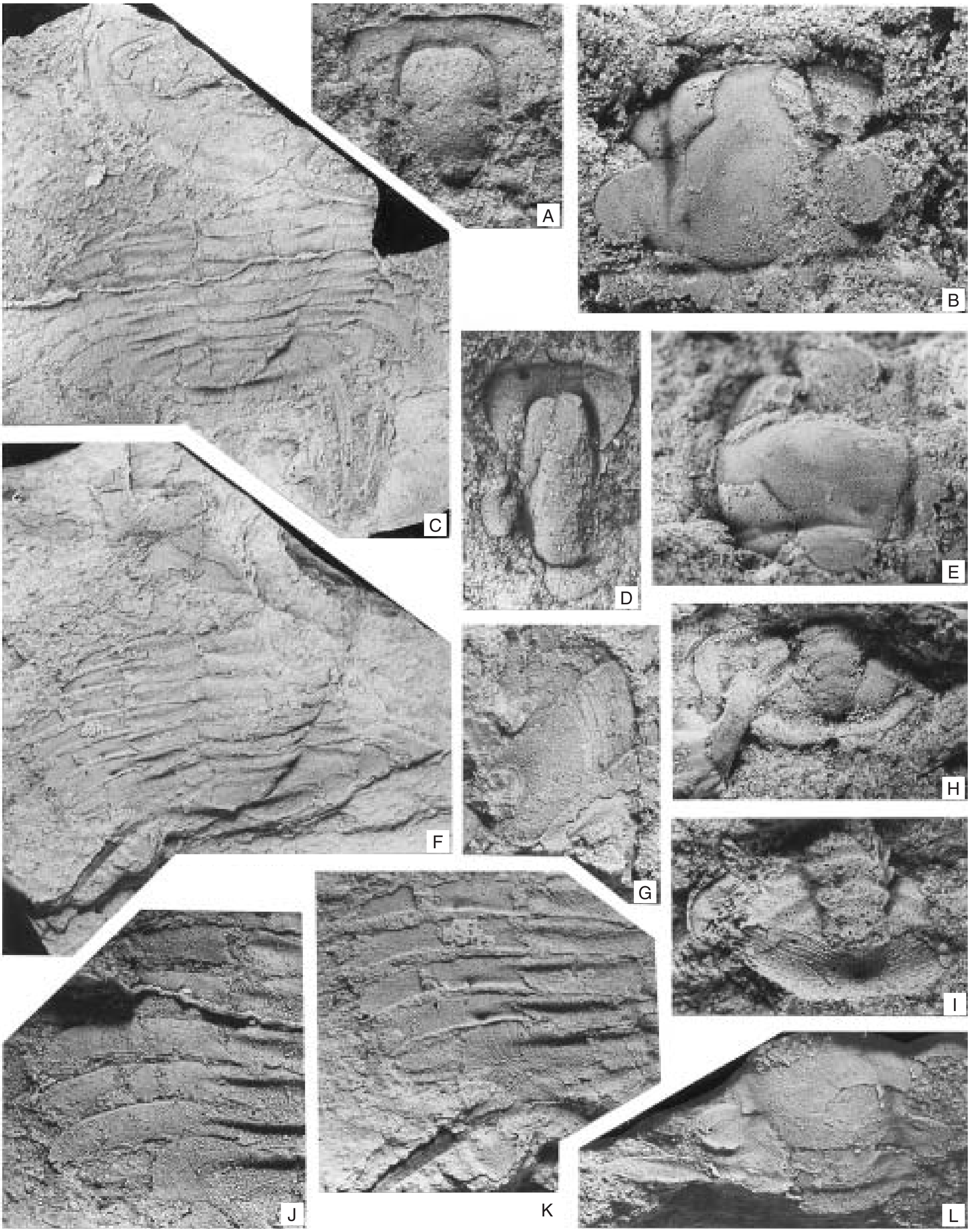
Material: One complete specimen, 4 complete cranidia, 2 librigenae, and 4 pygidia, all deformed in shale; one undeformed cranidium, one librigena, and four pygidia from cherts.

Diagnosis: *Ceratopyge* with broad (sag.) preglabellar field, evenly wide (tr.) glabella, transverse frontal lobe; distinct and weak S1 and S2, large palpebral lobes; relatively shorter (tr.) posterior fixigenae; posteriorly situated distinct median tubercle on glabella; slender, long, fairly backward directed genal spines; remarkably different length (tr) of pleurae, with long pleural spines; broad, rapidly tapering pygidial axis with four distinct rings and terminal piece; pygidial spines slender, long, directed posterodorsally, with diverging tips.

Description: See Mergl (1994).

Remarks: The undeformed material of *C. mareki* MERGL, 1984 is very rare and fragmentary. The numerous complete specimens are strongly deformed in shale, having obscure convexity and altered proportions. This preservation makes the comparison with other species difficult, especially to those preserved in limestones. Detailed data about the morphology and distribution of the Tremadocian ceratopygids from Scandinavia were insufficient until the work of Ebbestad (1999). He commented on the variable range and possible dimorphism of the species, and referred the species to *Ceratopyge* HAWLE et CORDA, 1847. The genus is restricted to the Tremadocian, with the earliest species *C. forficuloides* HARRINGTON et LEANZA, 1957 reported from the upper Lower Tremadocian of Argentina. This species differs from *C. mareki* by having a very short preglabellar field and a more forward curved anterior margin, a more posterior position of the glabellar median tubercle, four distinct glabellar furrows, and a longer pygidial axis. The Scandinavian *C. forficula* (SARS, 1835) is restricted to the upper Alum Shale Formation (Tremadocian). This species differs from *C. mareki* by having deeper S1, a shorter preglabellar field, a more anterior position of the glabellar median tubercle, more robust and curved genal spines, and a forward expanding glabellar frontal lobe bordered by a gently curved preglabellar furrow. The stratigraphically subsequent Scandinavian species *C. acicularis* (SARS et BOECK, 1838) from the Bjørkåsholmen Formation (Upper Tremadocian) differs from *C. mareki* by having less distinct S2, a more convex frontal margin of the cranidium, a less backward tapering axis of the thorax, a narrower (tr.), longer and less tapering pygidial axis with more numerous rings (five rings and axial piece) and less clearly defined axial rings. The pleural spines of the fifth and sixth thoracic segments are much longer in *C. mareki* than in *C. acicularis*. The species *Ceratopyge* sp. from the Alum Shale Formation of Norway (Ebbestad 1999) has a similarly rectangular outline of the pygidium, with a short and rapidly backward tapering axis, but *C.* sp. differs by having conspicuously stronger pleural spines. *Ceratopyge latilimbata* MOBERG et SEGERBERG, 1906 differs from *C. mareki* by having a much longer (sag.) preglabellar field, small palpebral lobes, and, according to the illustration of Moberg and Segerberg (1906: pl. 5, fig. 6), well developed, backward inclined eye ridges.

The first report on the presence of *Ceratopyge* in the Barrandian occurs in Klouček's fossil list (Klouček 1922) from the Úvaly area E of Prague. In the western part of the Prague Basin this genus is very rare, and its occurrence was only confirmed much later (Mergl 1984a). Despite the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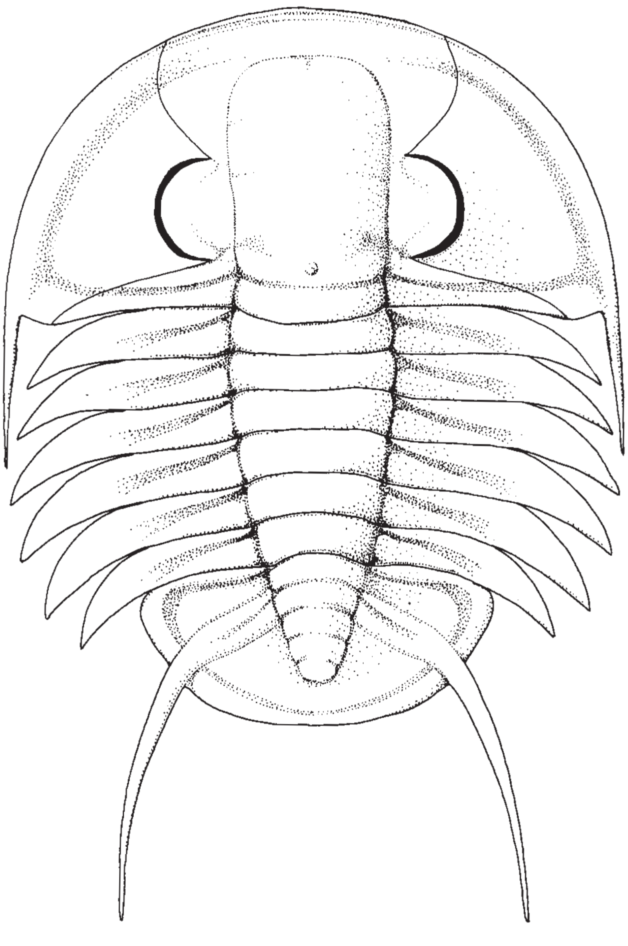
variable modes of preservation and abundance, specimens from both areas have the same morphology and certainly belong to the same species. Vaněk (1964, 1965) referred three specimens from the Úvaly area to *Diceratopyge troedssoni* SDZUY, 1955, but without providing any illustrations. This species is rare in the Leimitz Shales (Lower Tremadocian) of Bavaria, and is easily distinguished by the angular anterior border of the cephalon, and a longer pygidium with a longer (sag.) and narrower (tr.) axis (Sdzuy 1955).

Occurrence: Mílina Formation; Olešná (very rare), Kvaň (very rare), Úvaly, Vinice (abundant), Úvaly, test-pit (abundant).



Text-fig. 27. *Ceratopyge mareki* MERGL, 1984. Reconstruction of the exoskeleton. Approximately ×4.

Superfamily **Dikelocephaloidea** MILLER, 1889
Family **Dikelokephalinidae** KOBAYASHI, 1936

Genus ***Dikelokephalina*** BRØGGER, 1896

Type species: *Centropleura* ? *dicraeura* ANGELIN, 1854; Upper Tremadocian, Bjørkåsholmen Formation; Norway.

Remarks: An extensive discussion of the genus and the related genera *Ciliocephalus* LIU, 1977, *Asaphopsoides* HUPÉ, 1955, and *Asaphopsis* MANSUY, 1920 has arisen from the work of Kobayashi (1936), Jell and Stait (1985), Peng (1990), and Ebbestad (1999). Ebbestadt (1999) suggested that *Ciliocephalus* should be considered as a synonym of *Dikelokephalina* BRØGGER, 1896, but this opinion is not followed here. The relationship of the genus *Leimitzia* SDZUY, 1955 to other dikelokephalids was discussed by Peng (1990). The Bavarian species *Leimitzia bavarica* (BARRANDE, 1868) was also reported from the Mílina Formation of Bohemia by Vaněk (1965), but the validity of this report is questionable.

Dikelokephalina ulrichi RŮŽIČKA, 1935
Text-figs 28, 29

1935 *Dicellocephalina ulrichi* n. sp.; Růžička, p. 3, pl. 1, fig. 4.
1937 *Dicellocephalina ulrichi* RŮŽ.; Koliha, p. 486.
1965 *Dikelokephalina ulrichi* RŮŽIČKA, 1935; Vaněk, p. 108.
1965 *Dikelokephalina ulrichi* RŮŽIČKA, 1935; Vaněk, p. 276, pl. 24, fig. 22.
?1965 *Leimitzia bavarica* (BARRANDE, 1868); Vaněk, p. 108.
?1965 *Leimitzia bavarica* (BARRANDE, 1868); Vaněk, p. 276, pl. 24, fig. 23.
1970 *Dikelokephalina ulrichi* RŮŽIČKA, 1935; Horný and Bastl, p. 316.
1984a *Dikelokephalina ulrichi* RŮŽIČKA, 1935; Mergl, p. 26, pl. 8, figs 4, 5.
2001 *Dikelokephalina ulrichi* RŮŽIČKA, 1935; Vaněk and Valíček, p. 28.

Lectotype: Selected by Vaněk (1965), the cranidium figured by Růžička (1935) on pl. 1, fig. 4, re-figured here in text-figs fig. 28A, and 29A, deposited in the collection of the National Museum, Prague (NM L 18937).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

◄ **Text-fig. 26. *Ceratopyge mareki* MERGL, 1984.**
A – holotype, incomplete cranidium, internal mould, NM L 38497, ×5.5; B, E – incomplete cranidium, latex cast of exterior and its oblique view, PCZCU 1989, both ×7.5; C, F, J, K – tectonically deformed almost entire specimen; latex cast of exterior, internal mould, latex cast of pleural band and internal mould of the same area showing doublure with terrace ridges, NM L 38496, ×3, ×3, ×5.5, ×5.5; D – tectonically deformed cranidium, latex cast, NM L 38498, ×5.5; G – tectonically deformed librigena, internal mould, NM L 38499, ×5.5; H – pygidium, latex cast of exterior, PCZCU 1590, ×7.5; I – pygidium, internal mould showing doublure, PCZCU 1591, ×7.5; L – tectonically deformed cranidium, latex cast of exterior, NM L 38500, ×5.5; Mílina Formation, Olešná (A, H, I), Kvaň (B, E), Úvaly (Škvorec enclosure) (C, F, G, J, K, L) and Úvaly (Vinice) (D).

M a t e r i a l: Besides the lectotype, 4 incomplete cranidia and 7 pygidia.

D i a g n o s i s: *Dikelokephalina* with large palpebral lobes, shallow S1, 2S, and 3S furrows and small and shallow S4; pygidium transversely elliptical with five distinct axial rings and terminal piece and four distinct pleural furrows in pleural field; almost entire surface of cephalon and pygidium with prominent, irregularly anastomosing terrace ridges.

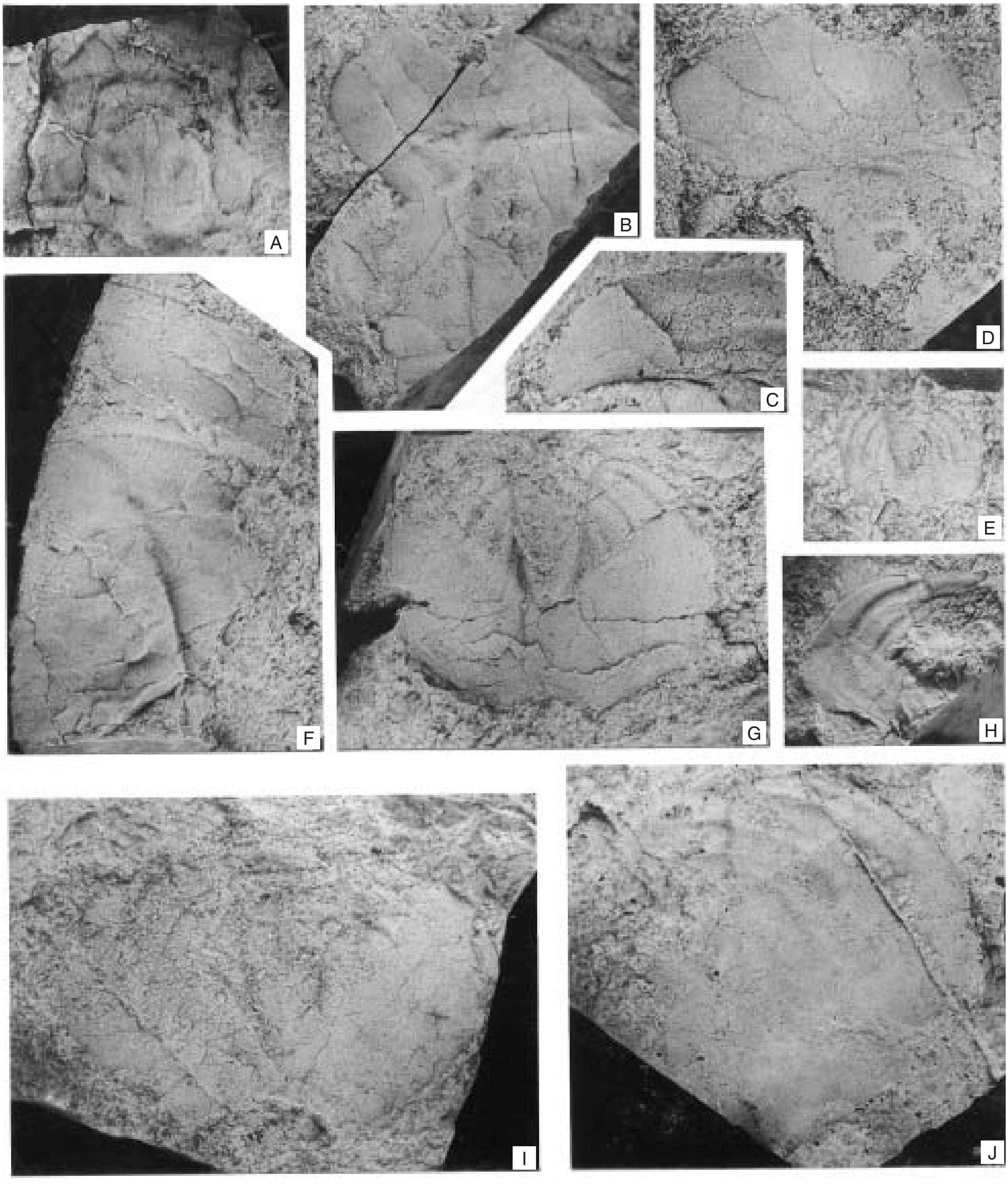
D e s c r i p t i o n: Glabella short (sag.), trapezoidal, weakly tapering anteriorly, anteriorly weakly rounded, weakly arched (tr.). Glabella length (sag.) is about three-fifths of the cranidium. Occipital ring transverse with weakly pointed median occipital tubercle. Occipital furrow distinct laterally, weak, and anteriorly arched medially. S1 shallow, large, pit-like, forked adaxially, situated in the posterior third of the glabella. S2 smaller, pit-like, shallow, transversally oval. S3 small, oval pits, situated close to eye ridges. All pits situated halfway between sagittal line and axial furrows. Axial furrows faintly indicated. Posterior adaxial part of fixigenae narrow (sag.) and long, gently curved backwards. Posterior branch of facial suture transverse. Anterior border furrow nearly in contact with glabella, broad (sag.) and shallow. Posterior border convex and broad (sag). Fixigena opposite to palpebral lobes wide and weakly arched (sag. and tr.). Palpebral lobes large, reniform, flat, measuring one-fourth of sagittal length, bordered by weak furrows. Eye ridges extending obliquely from anterior extremities of eyes to S3S, tapering and raised adaxially. Alae large, semicircular, situated between S1 and posterior border furrow. Preglabellar field large (sag. and tr.), feebly convex posteriorly and flat anteriorly. Anterior branch of facial suture diverges at an angle of 40–50° to the glabella, then turns inwards and forwards to meet at semi-elliptical anterior margin. Paradoublural line shallow, widening abaxially, merging with shallow preglabellar furrow. Doublure wide (sag.), bearing weak terrace lines. Preglabellar field and lateral border covered by distinct, fairly coarse, somehow anastomosing terrace ridges, which are densely packed near anterior margin but more distant, approximately with 0.5 mm apart, on resting surface. Occipital tubercle surrounded by concentric wavy ridges.

Thorax poorly known. Small fragments of pleurae that likely belong to the species have a shallow pleural furrow, low and evenly wide (exs.) anterior and posterior pleural bands. Adaxial portion of pleura slightly curved backward, being extended into shortly acute flat spine that bears oblique irregular terrace ridges on dorsal side and also on very broad (tr.) doublure.

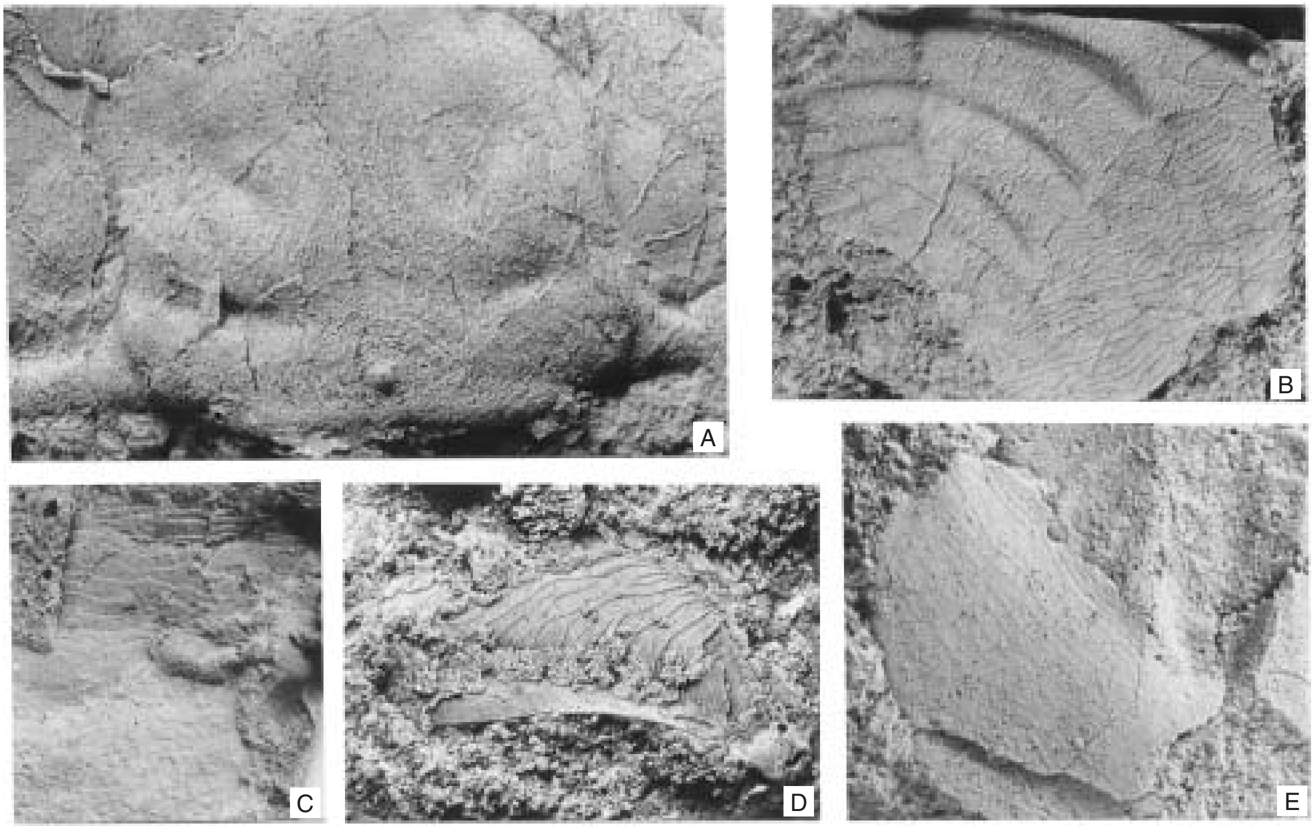
Pygidium transversely oval, weakly convex (sag.) with flattened postaxial portion. Axis 20–25 % as wide (tr.) and 70–80 % as long (sag.) as the pygidium, moderately convex (tr.) and weakly tapering posteriorly. Five rings and highly convex rounded terminal piece distinct. Axial furrows well defined, shallow and broad. Pleural field weakly convex, the border flat or weakly concave. Four pleural furrows present in large pygidia. Adaxial part of the first pair almost transverse, with abaxial part curved backward. The second and the third pairs of pleural furrows long, distinct, linear, curved more posteriorly. The fourth (last) pair of pleural furrow short, weakly diverging from each another. The doublure very long (sag. and exs.), weakly concave, bordering the end of the axis but rapidly expanding adaxially. Its surface covered by distinct terrace ridges parallel to posterior pygidial margin. About twenty terrace lines present on doublure ventral surface. Dorsal surface of the pygidium with fine anastomosing raised ridges, coarser marginally and finer adaxially on pleural regions, subparallel with pygidial margin. Posterior surface of pygidial and thoracic axial rings bear fine transverse raised ridges.

R e m a r k s: The species *D. ulrichi* RŮŽIČKA, 1935 fits well into the concept of the genus *Dikelokephalina* BRØGGER, 1899. The genus *Ciliocephalus* LIU, 1977 has a broadly conical and almost effaced glabella and a shorter preglabellar area. As stated by Ebbestadt (1999), the pygidium of *Ciliocephalus* is more transverse with a shorter axis, but other resemblances led Ebbestad (1999) to the conclusion that *Ciliocephalus* could be treated as a synonym of *Dikelokephalina*. *Asaphopsoides* HUPÉ, 1955 differs from the Bohemian species by the different position of the pygidial spines, and more numerous rings and pleural furrows on the pygidium. The species *D. ulrichi* is quite similar to *D. dicraeura* (ANGELIN, 1854) by having a longer pygidial axis, distinct S1, S2, and S3, and short pygidial spines. The cranidium of *D. dicraeura* differs from that of *D. ulrichi* by having deeper S1, S2, and S3, and smaller palpebral lobes. The pygidium of *D. dicraeura* is longer, with more than 8 rings and six distinct pleural furrows unlike the more transverse pygidium of *D. ulrichi* with only five rings, a terminal piece, and four pleural furrows. The shape of the pygidium of *D. ulrichi* is somewhat between those of *D. dicraeura* and *Ciliocephahus angulatus* LIU, 1977. The latter species has similarly short pygidial spines, and its pygidium is more transverse than that of *D. dicraeura*. Unlike *D. ulrichi*, the pygidium of *C. angulatus* has six pleural furrows, six rings, and the terminal piece. A broad and similarly shaped pygidium is seen in *D. firma* APPOLONOV et TSCHUGAEVA, 1983 from the Lower Tremadocian of Kazakhstan (Appolonov and Tschugaeva 1983). The Kazakhstan species differs by having a narrower (tr.) pygidial axis, smaller palpebral lobes, and less distinct glabellar furrows on a narrower (tr.) glabella. *D. amzassensis* (POLETAEVA, 1955) from the Tremadocian of the Sayan Altay area (Khalfin 1960) has a remarkably similar pygidium that differs only by having more numerous axial rings and a fifth pair of pleural furrows.

The species *D. ulrichi* RŮŽIČKA, 1935 is represented by poorly preserved and fragmented specimens. Therefore many of the morphological features of the exoskeleton are unknown. The cranidium has been described by Růžička (1935), and a separate hypostome of a nileid *Platypeltoides* was incorrectly referred to the same species. Vaněk (1965: pl. 24, fig. 22) figured a small fragment of the pygidium and



Text-fig. 28. *Dikelokephalina ulrichi* RŮŽIČKA, 1935.
A – lectotype, cranidium, latex cast of exterior, NM L 18937, ×2.2; B – incomplete cranidium, internal mould, PCZCU 1610, ×2.2; C – incomplete pleura, internal mould, PCZCU 1612, ×2.2; D – incomplete cranidium, internal mould, PCZCU 1611, ×2.2; E – small pygidium, internal mould, PCZCU 1613, ×2.2; F – incomplete cranidium, internal mould, NM L 38491 ×2.2; G – pygidium, internal mould, MM 131+, ×2.2; H – incomplete but weakly deformed pygidium, NM L 38492, ×2.2; I – large pygidium, internal mould, PCZCU 1614, ×2.2; J – incomplete large pygidium, latex cast of exterior, PCZCU 1615, ×2.2; Mílina Formation, Olešná.



Text-fig. 29. *Dikelokephalina ulrichi* RŮŽIČKA, 1935.
A – lectotype, cranidium, latex cast of detail exterior, NM L 18937, ×6.5; B – pygidium, latex cast of exterior with anastomosing ridges, NM L 38493, ×5; C – sculpture of anterior cephalic border, latex cast of exterior, NM L 38494, ×5; D – detail of pleura, NM L 38495, ×4; E – doublure of pygidium, internal mould, MM 131–, ×3.5; Mílina Formation, Olešná

re-figured the associated hypostome (Pl. 23, fig. 21). However, this hypostome belongs to *Platypeltoides perseis* sp. n., as seen below. Mergl (1984a) figured, but did not describe, a complete pygidium, and referred to the description of Vaněk (1965) for details. In addition to the figures noted above, Vaněk (1965; pl. 24, fig. 23) illustrated another fragment of a pygidium. This pygidium perhaps belongs to *D. ulrichi*, although Vaněk (1965) referred this specimen to the Bavarian species *Leimitzia bavarica* (BARRANDE, 1868). The locality data about this specimen is unreliable; though Vaněk indicated the Mílina locality, no trilobite remains are actually known from that site.

The species *D. ulrichi* is a rare species. It is known by mostly incomplete and mostly smaller pygidia at the Olešná locality, and a single poorly preserved pleura was collected at Kvaň. A very small fragment of a flat doublure with wavy terrace lines, which might belong to any dikelokephalinid, is known from the Třenice Formation in the Holoubkov locality. The rarity of *Dikelokephalina* in all its occurrences is characteristic of this genus (Jell and Stait 1985).

Occurrence: ? Třenice Formation; Holoubkov (very rare); Mílina Formation; Olešná (rare), Kvaň (very rare).

? Family **Eurekiidae** HUPÉ, 1953

Genus ***Holubaspis*** PŘIBYL, 1950

Type species: *Holubaspis bohemica* PŘIBYL, 1950 (= *Cheirurus Perneri* RŮŽIČKA, 1926); Upper Tremadocian, Třenice Formation; Barrandian, Bohemia.

Remarks: The systematic position of *Holubaspis perneri* (RŮŽIČKA, 1926) was long a matter of speculation. It was originally proposed as an olenid taxon (Klouček 1926a, 1931, Přibyl 1953). This suggestion was questioned by Henningsmoen (1957). Vaněk (1965) referred *H. perneri* to Hystricuridae HUPÉ, 1953, but misappropriated the pygidium of *H. perneri* to *Eulomina mitrata* (RŮŽIČKA, 1926), and instead referred a finely tuberculate pygidium of *Parabathycheilus krafti* sp. n. to *H. perneri*. The shape of cephalon and thorax of *H. perneri* is roughly consistent with hystricurids. It has an effaced tuberculate glabella, large palpebral lobes with prominent palpebral furrows, large librigenae with prominent border bearing several parallel terrace ridges, and a librigenal spine. The thorax has a broad axis and its pleurae are fulcrate with short, lateroventrally directed spines. However, the pygidium of *H. perneri* in unlike that of other hystricurids, being transversally rhomboidal, very short (sag.), with a highly raised axis, and small pleural fields with only one pair of deep anterior pleural furrows. The pygidial posterior border is inconspicuous and does not have terrace ridges. Other differences concern the preglabellar field and the glabella. Hystricurids have a distinctly convex preglabellar field between the preglabellar and anterior border furrows, and these furrows are not fused (see Jell and Stait 1985, Jell 1985, Dean 1989). The glabella of hystricurids is generally elliptical and not trapezoidal.

In view of cephalic and pygidial characters, *Holubaspis* is remarkably similar to the eurekiids, although this group is restricted to the late Cambrian of Laurentia (Moore 1959). The genus *Arcadiaspis* WESTROP, PALMER et RUNKEL, 2005 is especially similar to *Holubaspis,* although is relationship within the Eurekiidae is problematic (Westrop et al. 2005). Another eurekiid genus, *Corbinia* WALCOTT, 1924, has a similar trapezoidal glabella, prominent anterior border, short preglabellar field, and its librigena is nearly identical with that of *Holubaspis*, including a small laterally directed libriginal spine and fine terrace ridges on the anterior edge of the librigena. The main difference lies in the entire posterior margin of the pygidium of *Holubaspis*. However, pygidial spines are also unknown in *Arcadiaspis*, while the pygidium is entire and has a low border. The pygidial axes of eurekiids and *Holubaspis* are very similar. Both axes are very high, short, and broad (Dean 1989, Westrop et al. 2005). Therefore, it is now considered that *Holubaspis* may belong to the family Eurekiidae HUPÉ, 1953, as opposed to the Hystricuridae HUPÉ, 1953 as suggested by previous authors (Vaněk 1964, 1965, Mergl 1984a, 1994). The family Eurekiidae is restricted to the Upper Cambrian. However, the morphology of *Holubaspis* shares more characters of this family than can be explained only by homoeomophy. It is noteworthy that no rostral plate has been found among the numerous exoskeleton parts of *Holubaspis*. The adaxial tip of the librigenal doublure is very long and truncated, which may indicate the lack of a rostral plate and the presence of a median suture, as in the eurekiids (Whittington 1988).

Holubaspis perneri (RŮŽIČKA, 1926)

Text-figs 30–32

1914 *Olenid* sp.; Klouček, p. 2.
1917 *Olenid* I. n. sp.; Klouček, p. 6.
1917 *Olenid* II. n. sp.; Klouček, p. 6.
1922 Olenid n. sp.; Klouček, p. 1.
1924 *Olenid*; Koliha, p. 36.
1925 *Olenid* I. n. sp.; Klouček, p. 1.
1925 *Olenid* II. n. sp.; Klouček, p. 1.
1926a *Olenid* sp. I. ; Klouček, p. 192.
1926a *Olenid* sp. II.; Klouček, p. 192.
1926 *Euloma mitratum* n. sp.; Růžička, p. 5, pl. 1, figs 5, 6, not pl. 1, fig. 4.
1926 *Olenus* (*Cyclognathus*?) sp. I.; Růžička, p. 6, pl. 1, fig. 7.
1926 *Olenus* sp. II.; Růžička, p. 6, pl. 1, fig. 8.
1926 *Pliomera* sp.; Růžička, p. 15, pl. 1, fig. 11.
1926 *Cheirurus Perneri* n. sp.; Růžička, p. 12, pl. 2, figs 1–4, pl. 3, fig. 12.
1927 *Cheirurus Perneri*; Klouček and Koliha, p. 3.
1928 *Cheirurus Perneri* n. sp.; Růžička, p. 54.
1931 *Holubia bohemica* n. sp.; Klouček, p. 366, pl. 1, figs 1–4.
1937 *Holubia bohemica* KLOU.; Koliha, p. 485, 486.
1953 *Holubaspis bohemica* (KLOUČEK); Přibyl, p. 45.
1964 *Holubaspis perneri* (RŮŽIČKA, 1926); Vaněk, p. 107.
1965 *Holubaspis perneri* (RŮŽIČKA, 1926); Vaněk, p. 269, pl. 23, figs 12–17, pl. 26, figs 41–46.
1965 *Eulomina mitrata* (RŮŽIČKA, 1926); Vaněk, p. 286, pl. 25, figs 36, 37, not pl. 26, fig. 54.
1966 *Holubaspis perneri* (RŮŽ.); Havlíček and Vaněk, pl. 2, fig. 9.
1966 *Eulomina mitratum* (RŮŽ.); Havlíček and Vaněk, pl. 2, fig. 8.
1970 *Holubaspis perneri* (RŮŽIČKA, 1926); Horný and Bastl, p. 239.
1984a *Holubaspis perneri* (RŮŽIČKA, 1926); Mergl, p. 35, pl. 4, figs 1–9, text-fig. 8.
1994 *Holubaspis perneri* (RŮŽIČKA, 1926); Mergl, p. 16, pl. 4, figs 1–11.
2001 *Holubaspis perneri* (RŮŽIČKA, 1926); Vaněk and Valíček, p. 31.

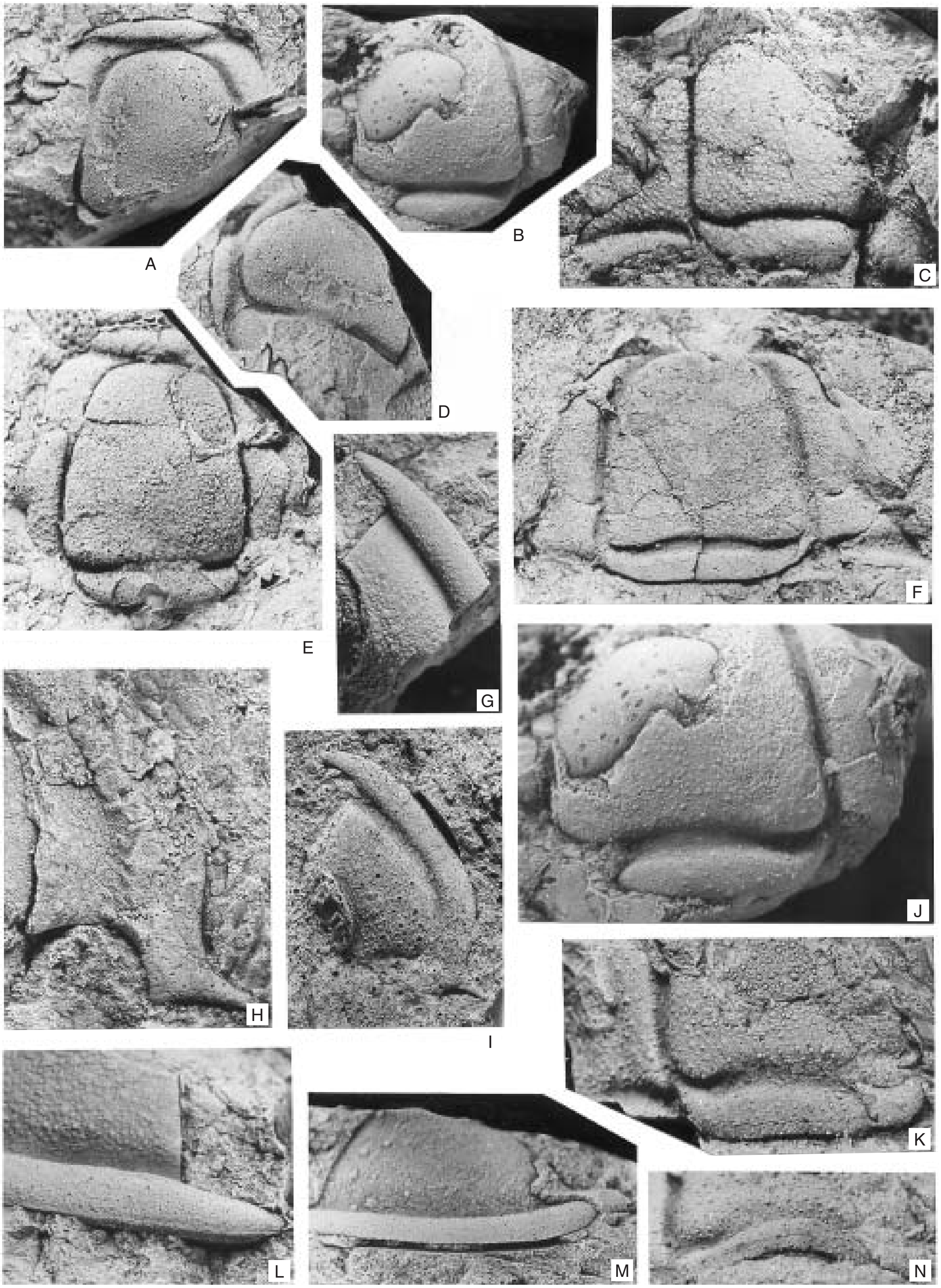
Lectotype: Selected by Vaněk (1965), incomplete cranidium figured by Růžička (1926) on pl. 2, fig. 1, deposited in the collection of the National Museum, Prague (NM L 18896).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the abandoned "V Ouzkém" iron ore mine.

Material: Over 30 cranidia and 60 free cheeks, 5 hypostoma, 17 pygidia, 3 nearly complete specimens and numerous fragments of segments and other parts of exoskeleton in various quality of preservation.

Description: Species with a cephalon width over 40 mm in the largest known specimen. This indicates an entire exoskeletal length of at least 70–80 mm.

Cephalon semi-circular, with almost transverse posterior margin and weak and broad anterior arch. Cranidium as long (sag.) as its width, with large roundly trapezoidal effaced glabella. Frontal part of glabella slightly rounded, steeply sloping toward deep border furrow. Sides of glabella with steeply downsloping sides toward deep, weakly diverging axial furrows. Central area almost flat. Occipital ring short (sag.), tapering abaxially, moderately convex dorsally, as wide (sag.) as glabella, bordered by deep, broad, forward curved occipital furrow. A low broadly conical occipital spine present. Fixigenae narrow in convex preocular and subhorizontal palpebral areas, with much longer (exs. and tr.) and almost horizontal posterior area. Anterior part of facial suture diverging toward border furrow, turned inwards at border, and converging at anterior side of anterior border. Lateral and posterior border furrows deep, with concave bottom. Posterior border high and narrow adaxially, rapidly expanding laterally. Posterior branch of facial suture oblique in postocular part, curved abaxial part cuts posterior margin almost at right angle. Palpebral lobe elongate reniform, large, in mid-length of the cranidium, with surface sloping adaxially. Palpebral furrow shallow, well defined. Librigena triangular, with evenly broad (tr.) and backward less convex border. Adaxial part of border acute, strongly convex. The outer, forward facing margin of lateral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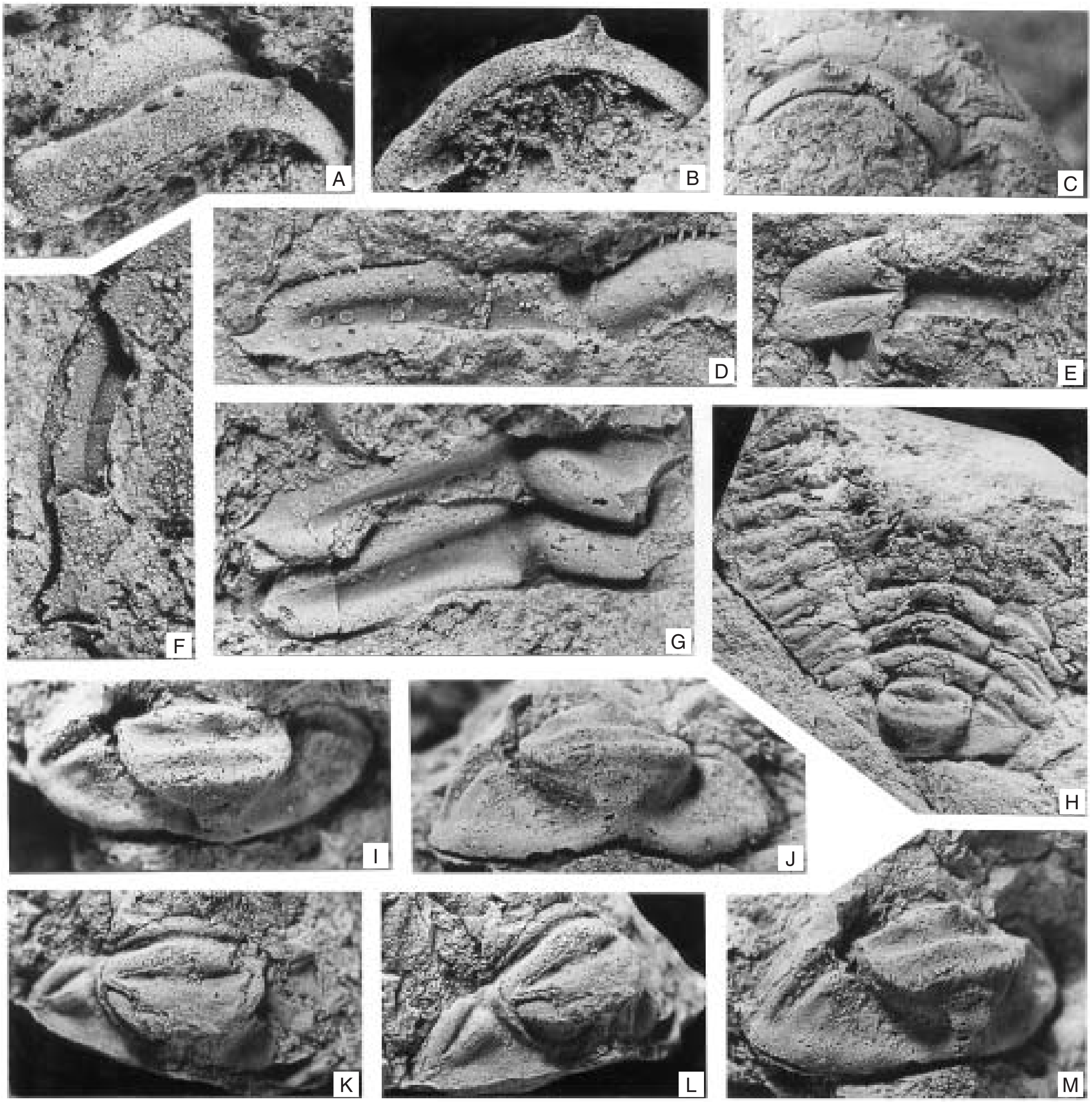


Text-fig. 31. ***Holubaspis perneri*** **(RŮŽIČKA, 1926).**
A, B, G – thoracic segments, latex cast of exterior showing axial spine in oblique and posterior views, and internal mould of the first and second pleura, PCZCU 1662, ×7.5, ×7.5, ×6.5; C – thoracic segment, internal mould showing axial spine, PCZCU 1663, ×5; D – pleura, internal mould showing spinose tip and infilling of pores, NM L 38522, ×6.5; E – pleura, in left showing its exterior and in right internal mould, NM L 38523, ×6.5; F – left librigena, internal mould showing hollow genal spine and ridge on the doublure, NM L 38527, ×6.5; H – posterior of thorax with pygidium, internal mould, PCZCU 1664, ×3; I, J, M – pygidium, internal mould and its posterior and oblique views, NM L 38524, all ×5; K, L – pygidium with partly preserved exoskeleton and its oblique view, NM L 38525, both ×5; Mílina Formation, Olešná (A–D, F–J, M) and Třenice Formation, Holoubkov (E, K, L).

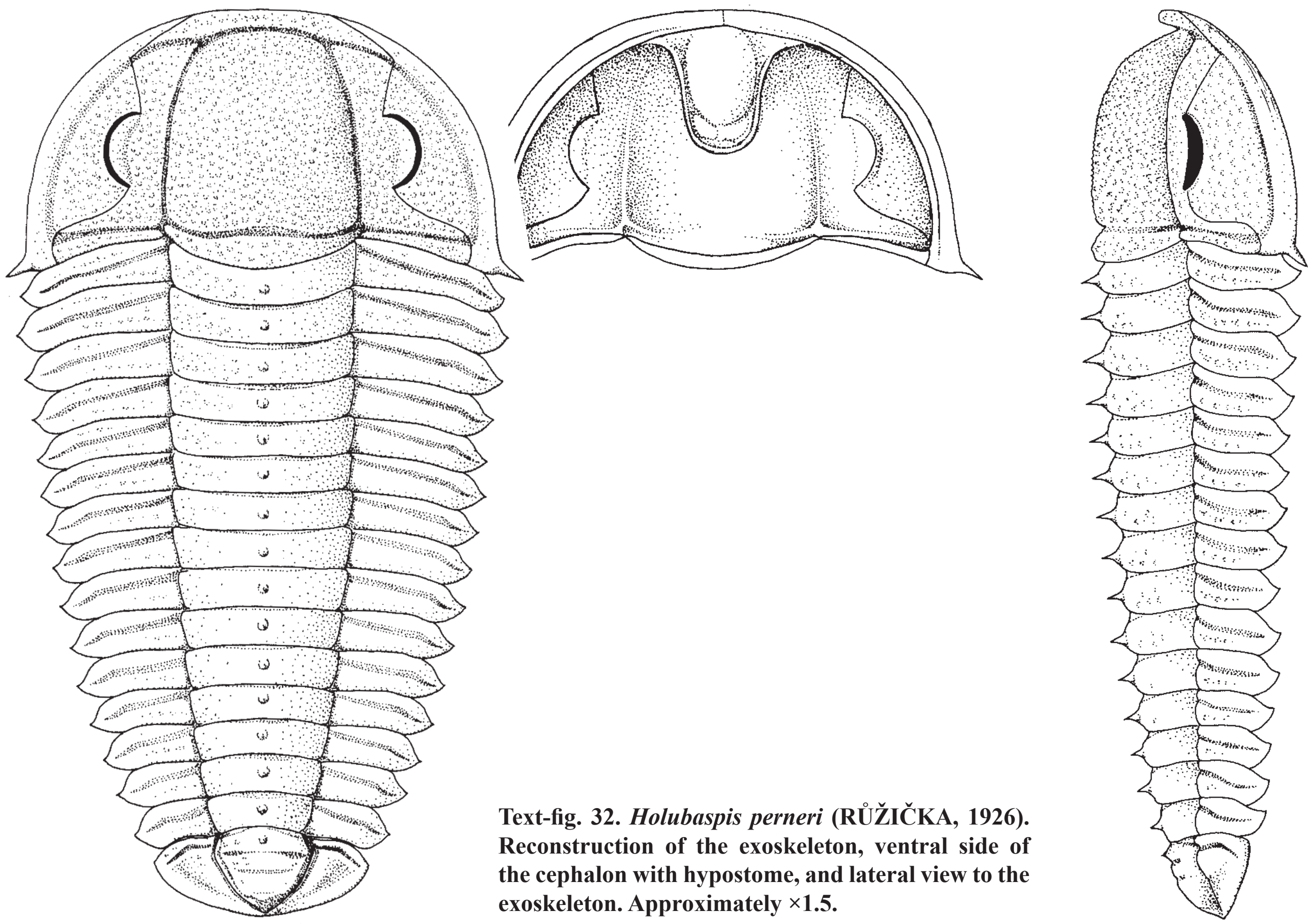
◀ **Text-fig. 30.** ***Holubaspis perneri*** **(RŮŽIČKA, 1926).**
A, D – cranidium, internal mould and its oblique view, PCZCU 1665, both ×3; B, J – cranidium, internal mould and detail of sculpture, JV 2471, ×3, ×5; C – incomplete cranidium, latex cast of exterior, PCZCU 1669, ×3; E – cranidium, latex cast of exterior, PCZCU 1666, ×3; F – cranidium, internal mould, PCZCU 1667, ×2.5; G, L – librigena and detail of lateral border, NM L 30829, ×5, ×10; H – genal angle with spine, NM L 38528, ×6.5; I – right librigena, latex cast of exterior, JV2477, ×3; K, N – detail of glabella, internal mould and its posterior view, PCZCU 1668, ×5; M – left librigena, side view with remain of exoskeleton (right), NM L 38529, ×6.5; Třenice Formation, Holoubkov (B, G, H, J, L, M) and Mílina Formation, Olešná (A, D–F, I, K, N), and Kvaň (C).

border acute, bearing three fine terrace ridges on the steep slope. Border furrow deeper adaxially, gently shallowing posterolaterally, meeting with posterior border furrow at facial suture. Genal field moderately convex, with large, crescent-shaped eye emargination. Eye socle low, surrounded by smooth surface. Genal spine shortly conical, directed posterolaterally. Doublure short, about two-thirds as long as occipital ring in axis, with smooth surface. Librigenal doublure subhorizontal, evenly wide, with fine furrow in mid-length (sag.), with long and truncated adaxial portion. Surface of cephalon covered by small spinose tubercles of variable size. Tubecles are finer on margins of border and on surface of palpebral lobes. Bottoms of border furrow, axial furrow, and occipital furrow lack tubercles.

Hypostome small, about 130 % as wide as its length, weakly tapering posteriorly. Hypostomal suture anteriorly moderately convex, posterior border rounded. Shoulders, lateral and posterior borders well defined, evenly wide (tr.), and strongly convex. Shoulders slightly arched ventrally. Anterior lobe of middle body elongate oval, nearly in contact with hypostomal suture, strongly convex (sag. and tr.), separated from lower and shorter posterior lobe by weak and only laterally distinct middle furrows. Maculae obscure. Anterior wings short, flat, extending and facing posteroventrally. Triangular posterior wings small, directed dorsally opposite middle furrows. Surface covered by fine tubercles.

Thorax of 13–14 fulcrate segments, tapering backward from the mid-length; the last three segments are distinctly narrower (tr.) than the more anterior ones. Axis strongly vaulted, of almost semicircular transverse profile. Articulating half ring long (sag.) and smooth. Articulating furrow deep and long (sag.). Axial doublure very short (sag.). Axial ring convex (sag.), with prominent axial spine having slightly transverse base. Axial spines present in all segments. It is noteworthy that the spine is weak on the occipital ring, but is already much higher on the ring of the first segment. The maximum height of spines is equal to arch of the axis, but spines are shorter posteriorly; the last segment has a low spine. Narrow inner portion of pleura is almost horizontal, with deep, narrow, backward weakly inclined pleural furrow that die out immediately at lateral end of pleura. Anterior and posterior bands evenly wide (tr.); anterior band slightly sinuous, less convex abaxially. Outer portion of pleura rapidly sloping, slightly depressed, with flat end extended into minute, anteroventrally directed spinose tip. Doublure narrow (tr.).

Pygidium widely triangular, 50 % as long as its width. Axis short, transverse, of subrhomboidal outline, very high, much higher and wider (sag.) than small, triangular pleural fields. Prominent articulating half ring followed by three rings. The first ring is dorsally considerably convex, bearing low acute axial spine of the same type as developed on the thorax. The second and third rings are subhorizontal,



Text-fig. 32. ***Holubaspis perneri*** **(RŮŽIČKA, 1926). Reconstruction of the exoskeleton, ventral side of the cephalon with hypostome, and lateral view to the exoskeleton. Approximately ×1.5.**

without spines, separated by weak and shallow ring furrows. The third ring extends backwards into triangular poorly defined terminal piece that steeply downslopes to contact with posterior border. Axial furrows anteriorly distinct, becoming shallower and rapidly converging backward. Pleural field small, triangular, with a pair of very deep, slightly backward inclined pleural furrows. Anterior band highly convex (exs.), posterior band lower and gradually passing into flat surface in posterior pleural field. Border weakly defined by weak border furrow. Border convex, continuing ventrally into short smooth doublure. Small posterior arch is distinct behind the axis. Surface of segments and pygidium finely tuberculate.

Remarks: Hammann and Sdzuy (in Sdzuy et al. 2001) reported *Holubaspis* aff. *perneri* (RŮŽIČKA, 1926) from the Vogtendorf Formation (Upper Tremadocian) of Bavaria, and commented on the distribution of the genus in Europe. The cephalon of *H.* aff. *perneri* differs, in addition to the characteristics noted by Hammann and Sdzuy (in Sdzuy et al. 2001), by having a less backward expanding genal field in the librigena.

The complicated history of *Holubaspis perneri* nomenclature has been discussed by Vaněk (1965) and Mergl (1984a, 1994). The species was first established on specimens from the Třenice Formation (Růžička 1926), though a different species, *Holubia bohemica* n. g. et n. sp., was soon established by Klouček (1931) based on specimens from the Mílina Formation. *Holubia bohemica* was subsequently synonymised with *Holubaspis perneri* by Vaněk (1965). The specimens from the Třenice Formation are indistinguishable from those of the stratigraphically younger Mílina Formation. This is surprising, because associated trilobite species in both formations are mostly different. The search for minute differences on the exoskeleton of *H. perneri*, such as a tuberculate ornament pattern, the number of terrace ridges on the librigena, the size and shape of the librigenal and pleural spines, was not successful. There are no obvious differences other than the generally larger exoskeletons and somewhat slender and longer librigenal spine of the stratigraphically younger specimens described originally as *H. bohemica* KLOUČEK, 1931; though the latter difference might be related to larger-sized individuals. These differences do not warrant the validity of *H. bohemica*, and it may be safest to regard all specimens as a single species.

Holubaspis perneri is the most common large trilobite in the Třenice and Mílina formations in the Komárov and Holoubkov areas, but it is rare at Úvaly (this was already known by Klouček in 1914). This trilobite was referred to the olenids by Klouček (1917, 1922, 1924, 1925, 1926a) and Koliha (1937), while Růžička (1926; pl. 1, figs 7, 8) referred it to the cheirurids (Růžička 1926, 1928, 1935). Other authors referred it to the hystricurids (Vaněk 1964, 1965, Mergl 1984a, 1994). Its fragments and the hypostome were also referred to other trilobite taxa or left undetermined (Růžička 1926; pl. 1, figs 5, 6, 11; pl. 3, fig. 11).

The species is known from numerous cranidia, librigenae, and pygidia; three more complete specimens were available to the present author. The first specimen, kept in a private collection (Mergl 1984a; pl. 4, fig. 5), is comprised of a cranidium with ten segments. The second, a more complete specimen (PCZCU 1664), shows a pygidium with seven posterior segments. Klouček (1931: p. 365) noted a damaged but complete specimen (NM L 18607), which is poorly preserved, without a pygidium, and shows 13 or 14 segments.

Occurrence: Třenice Formation, Holoubkov (abundant). Mílina Formation; Olešná (abundant), Kvaň (abundant), Úvaly, Vinice (rare).

Superfamily **Remopleuridoidea** HAWLE et CORDA, 1847

Family **Remopleurididae** HAWLE et CORDA, 1847

Genus ***Apatokephalus*** BRØGGER, 1896

Type species: *Trilobites serratus* BOECK, 1838; Upper Tremadocian, Bjørkåsholmen Formation, Norway.

Apatokephalus dagmarae MERGL, 1984

Text-figs 33, 34

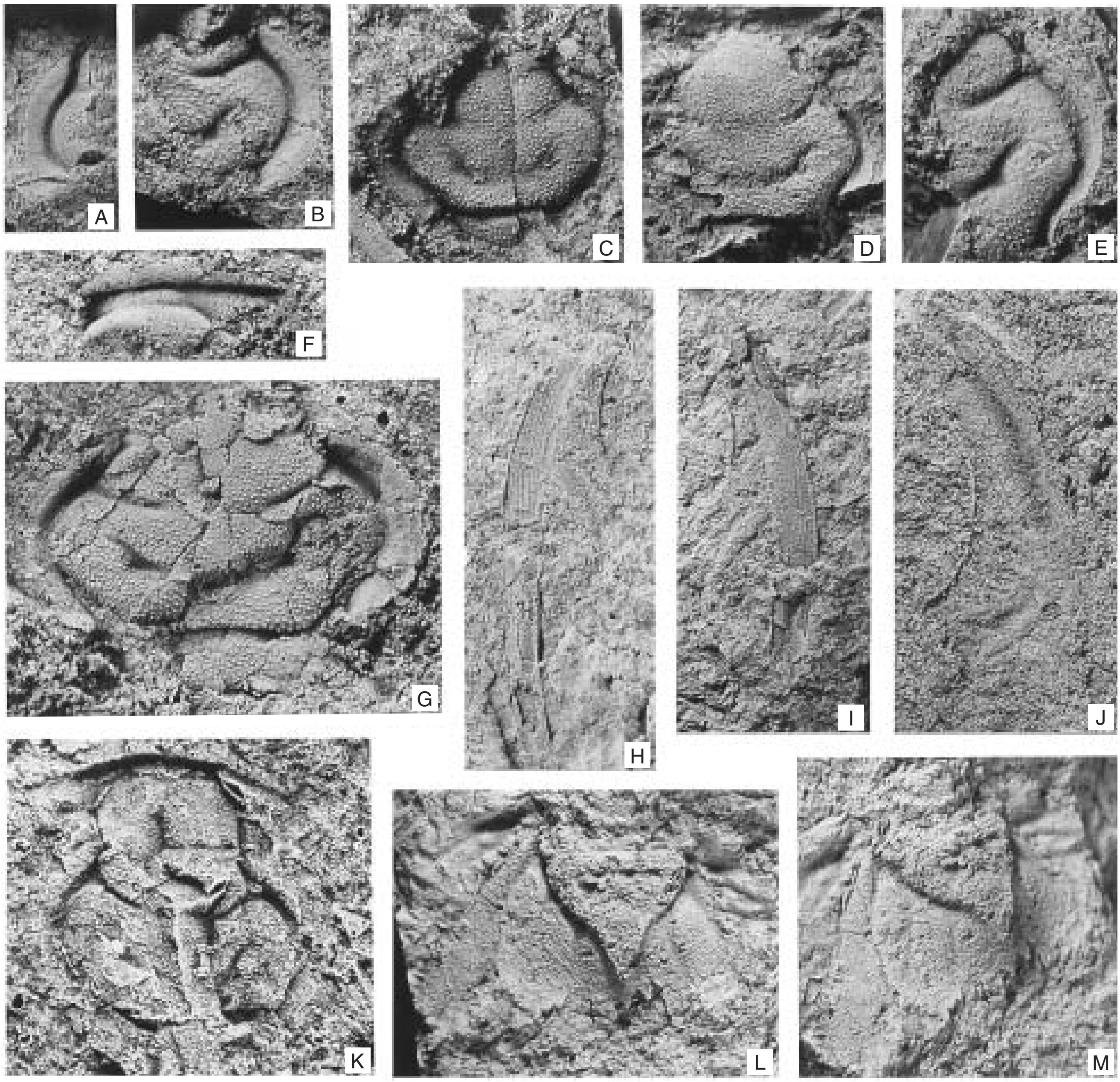
1922 *Apatocephalus* sp.; Klouček, p. 1.
1925 *Apatocephalus* sp.; Klouček, p. 1.
1926a *Apatocephalus* sp.; Klouček, p. 192.
1931 *Apatocephalus* aff. *serratus* (SARS et BOECK); Klouček, p. 364, pl. 1, figs 8, 9.
1937 *Apatocephalus* sp.; Koliha, p. 485.
1937 *Apatocephalus* cf. *serratus* (SARS et BOECK); Koliha, p. 485, 486.
1964 *Apatokephalus asarkus* SDZUY, 1955; Vaněk, p. 107.
1965 *Apatokephalus asarkus* SDZUY 1955; Vaněk, p. 271, pl. 23, fig. 18.
1970 *Apatokephalus asarkus* SDZUY 1955; Horný and Bastl, p. 282.
1984a *Apatokephalus dagmarae* sp. n.; Mergl, p. 39, pl. 3, figs 7–13; text-fig. 10.
2001 *Apatokephalus dagmarae* MERGL, 1984; Vaněk and Valíček, p. 40.

Holotype: Cranidium figured by Mergl (1984a) on pl. 3, fig. 7, re-figured here in text-fig. 33G, deposited in the collection of the National Museum, Prague (NM L 18601).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Material: Fifteen mostly incomplete cranidia, 10 librigenae, and 2 pygidia.

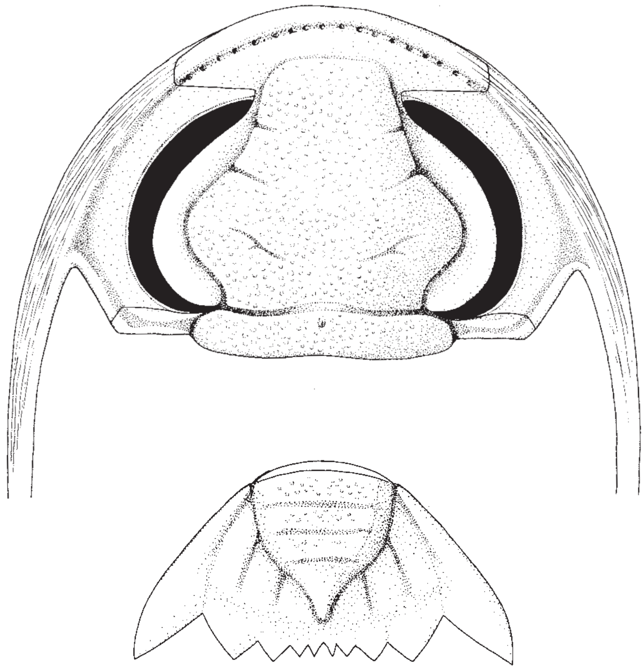
Diagnosis: *Apatokephalus* with cephalic sculpture of fine small tubercles, with short and rounded frontal glabellar node; S1 almost transverse, forked abaxially; large smooth palpebral lobes horizontal posteriorly, but steeply downsloping toward axial furrows in anterior part; genal field of librigena narrow (tr.) weakly widening backward; preglaberal field short, anterior border furrow with weak pits; occipital ring with small axial node; genal spine advanced, angle between posterior border and genal spine about 60°; surface of lateral border with fine terrace lines; pygidium with short and broad axis and three pairs of shallow pleural furrows and large flat pleural spine on the first pair.



Text-fig. 33. *Apatokephalus* aff. *dagmarae* MERGL, 1984.
A – fragment of cranidium, NM L 38478, ×6; B – fragment of cranidium, NM L 38479, ×6; Třenice Formation, Holoubkov (A, B).
***Apatokephalus dagmarae* MERGL, 1984.**
C – incomplete cranidium, latex cast of exterior, PCZCU 1635, ×7; D – incomplete cranidium, internal mould, PCZCU 1636, ×6; E – incomplete cranidium, internal mould, PCZCU 1637, ×6; F – anterior border, latex cast of exterior, PCZCU 1638, ×6; G – holotype, incomplete cranidium, latex cast of exterior, NM L 18601, ×7; H, I – incomplete librigena, internal and external moulds, PCZCU 1639, both ×6; J – incomplete librigena, internal mould, PCZCU 1640, ×6; K – almost complete cranidium, latex cast of exterior, NM L 38480, ×6; L, M – incomplete pygidium and its oblique view, MM 084, both ×7; Mílina Formation, Kvaň (C–F, H–I), Olešná (G, J–M).

Description: See Mergl (1984a).

Remarks: A new diagnosis is presented here based on new material that has revealed additional data on the morphology of the cephalon, and has partly corrected the original description of Mergl (1984a). Since the original description of *A. dagmarae* MERGL, 1984, several new species of the genus have been described, and the type species has been revised. Ebbestad (1999) discussed the morphology, taxonomy, and species referred to *Apatokephalus* BRØGGER, 1896, including *A. dagmarae*. Important new



Text-fig. 34. *Apatokephalus dagmarae* MERGL, 1984. Reconstruction of the cephalon and the pygidium. Approximately ×6.

data on the morphology of *A. serratus* BOECK, 1838 and other species from the Lower Ordovician of Norway reveals more information about the affinity of *A. dagmarae*. The species *A. serratus* from the Bjørkåsholmen Limestone (Upper Tremadocian) differs from *A. dagmarae* by having a coarsely tuberculate glabella sculpture, unforked S1 which are connected to axial furrows, evenly broad (tr.) palpebral lobes, and a shorter preglabellar field with much deeper pits in the border furrow. The librigenae of *A. serratus* are similarly narrow (tr.), but the genal spine is wider (tr.) and more curved inward than in *A. dagmarae*. The genal field of *A. serratus* bears a distinct narrow transverse ridge which is absent in *A. dagmarae*. The pygidium of *A. serratus* has a narrower (tr.) axis and probably a less transverse outline. The second Norwegian species, *A. dubius* (LINNARSSON, 1869) from the Bjørkåsholmen Limestone, resembles *A. dagmarae* by having an abaxially forked and less distinct S1, a wider (tr.) occipital ring, and forward tapering palpebral lobes. However, it differs from the Bohemian species by its lack of tubercles in sculpture; only fine raised lines cover its glabellar surface. The third Norwegian species, *A. dactylotypos* EBBESTAD, 1999, from the Bjørkåsholmen Limestone, has an anteriorly extended frontal lobe of the glabella, and its librigenae are much wider (tr.) and backward extended, while these of *A. dagmarae* are narrower and almost evenly wide along their length. The glabellar sculpture of fine tubercles resembles the sculpture of *A. dagmarae*.

Apatokephalus sarculum FORTEY et OWENS, 1991 is similar to *A. dagmarae* by the shape and finely tuberculate surface of the glabella. Although poorly known, the pygidium of *A. dagmarae* has a similarly short and broad axis, and its outline is probably similarly transverse as the pygidium of *A. sarculum*. Ebbestad (1999) referred to *A.* cf. *sarculum* specimens from the Alum Shale Formation (Tremadocian) of Norway. The British and Norwegian specimens show subangular anterior borders covered by prominent terrace lines. The border of *A. dagmarae* is less angular, being weakly and evenly rounded and lacking terrace lines. Librigenae of *A. sarculum* are wider (tr.), with posterior and lateral border furrow enclosing about 110°, and the eye socles are strongly curved. In *A. dagmarae* the contact of lateral and posterior border furrows is almost at a right angle, and the eye socle is less curved, indicating a less curved eye outline. Pillet (1992) reported three taxa of the genus from the Upper Tremadocian and the Lower Arenig of the Montagne Noire, France. Of these, *A. serratus fedoui* (PILLET, 1992) and *Deanokephalus brevifrons* (THORAL, 1935) differ by having smaller frontal lobes of the glabella, unforked S1, and palpebral lobes covered by small tubercles. The Upper Tremadocian species *A. tibicen* PŘIBYL et VANĚK, 1980 from Argentina, formerly referred to *A. serratus* by Harrington and Leanza (1957), is very similar to *A. dagmarae* but has posteriorly wider (tr.) librigenae and the anterior border of the cephalon is covered by distinct terrace lines, while the border of *A. dagmarae* is smooth or nearly smooth. The species *A. canadensis* KOBAYASHI, 1953 from the McKay Group (equivalent to the British Upper Tremadocian, the *Shumardia pusilla* and *Angelina sedgwicki* Zones; Dean 1989) of British Columbia, Canada, has a similar outline and finely tuberculate glabella surface, but differs by having a shorter (sag.) preglabellar field and a less transverse S1. Other Tremadocian species of the peri-Gondwanan area listed by Harrington and Leanza (1957) and Peng (1990) are less similar, and therefore not discussed here.

The species was originally compared with *A. serratus* (BOECK, 1838) by Klouček (1931), and was subsequently referred (Vaněk 1965) to the Bavarian species *A. asarkus* SDZUY, 1955. The Bavarian species is poorly illustrated (Sdzuy 1955), and some parts of its exoskeleton are unknown. This Bavarian species differs by having a narrower and only weakly expanded glabella between palpebral lobes, with two pairs of glabellar furrows. Only two glabellar furrows and a narrow glabella indicate a relationship between *A. asarkus* and the genus *Pseudokainella* HARRINGTON, 1938.

The species *A. dagmarae* is abundant in the Mílina Formation, but the exoskeletons are very fragmental or fractured (Text-fig. 33G). Fossilized parts of the cephalon are mostly represented by the genal field of the librigena and palpebral lobes with the adjoined small parts of the glabella. It is likely that these parts were the most resistant to the breakage. This indicates the very fragile nature of the cephalon.

Two fragments of *Apatokephalus* were found among the trilobite remains in the ores of the Třenice Formation at Holoubkov. The presence of this genus in the Třenice

Formation was noted by Klouček (1925, 1926a). One of the fragments (NM L 38478) was figured by Klouček (1931; pl. 1, fig. 8, re-figured herein in text-fig. 33A). The outline, finely tuberculate glabellar surface, and transverse sigmoidal S1 of another fragment from Holoubkov (Text-fig. 33B) are similar to *A. dagmarae*. Nevertheless, the tubercles are slightly larger and arranged in more distinct transverse rows. These two fragments provisionally named *A.* aff. *dagmarae* probably represent a separate species.

Occurrence: Třenice Formation, Holoubkov (very rare). Mílina Formation; Olešná (abundant), Kvaň (abundant), Úvaly, Vinice (rare).

Superfamily **Cyclopygoidea** RAYMOND, 1925
Family **Cyclopygidae** RAYMOND, 1925
Subfamily **Pricyclopyginae** FORTEY et OWENS, 1987

Genus ***Pricyclopyge*** RICHTER et RICHTER, 1954

Type species: *Aeglina prisca* BARRANDE, 1872; Llanvirnian, Šárka Formation; Barrandian, Bohemia.

Pricyclopyge oceanitis sp. n.

Text-fig. 35

1965 *Niobella innotata* (BARRANDE, 1868); Vaněk, p. 272, pl. 23, fig. 19.

2001 *Niobella* cf. *innotata* (BARRANDE, 1868); Vaněk and Valíček, p. 16 (part).

Holotype: Pygidium figured in text-fig. 35I deposited in the palaeontological collection of the University of West Bohemia at Plzeň (PCZCU 1574).

Paratype: Cephalon figured in text-fig. 35A, deposited in the palaeontological collection of the University of West Bohemia at Plzeň (PCZCU 1571).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Name: *Óceanitis*, from Greek mythology, the daughther of the Ókeanos.

Material: Two imperfect cephala and 10 pygidia.

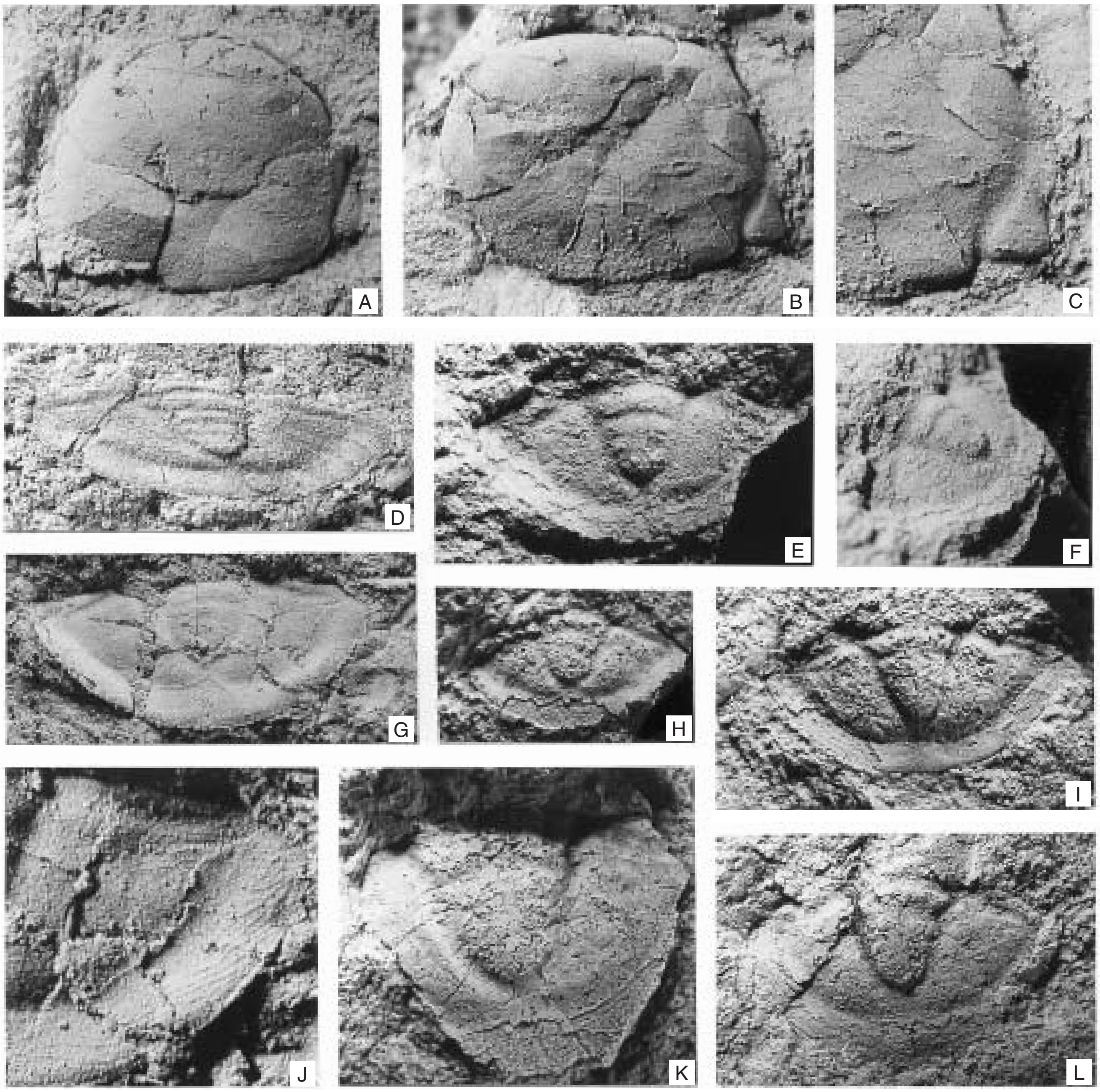
Diagnosis: *Pricyclopyge* with broadly pyriform glabella, narrow anteriorly tapering palpebral rim, and preserved posterior border furrows; pygidium broadly semi-elliptical with evenly curved posterior margin; deep anterior pleural furrows on pygidium; pygidial axis broadly triangular, rapidly tapering backwards with four rings and rounded terminal piece; pygidium with fine raised ridges on dorsal surface and coarse terrace ridges on doublure.

Description: Estimated length of entire exoskeleton is 25–40 mm. Cranidium broadly pyriform, cca 80 % as long as wide, widest at anterior one-third. Glabella moderately convex (sag. and tr.), with broad, strongly convex and steeply sloping anterior face. Palpebral rims narrowly crescent, tapering anteriorly and disappearing at anterior one-third of cephalon. Postocular fixigenae small, short, triangular, with distinct border furrow. Eyes unknown. Axial furrows shallow, slightly sigmoidal in course. Preoccipital tubercle distinct at mid-length of the glabella. Small oval impressions near the centre of glabella, which are characteristic of other species of the genus, are unknown.

Pygidium broadly semi-elliptical, 60 % as long as its width, gently convex (tr.). Axis distinct, rapidly tapering backward, moderately convex (tr.), about 60–70 % as long as the pygidium. Axial furrows distinct, wide, enclosing each other at about 45–50°. Four rings and high rounded axial piece distinct. Anterolateral edges of the pygidium acute, with short small articulating facets occupying about half of pleural width. Anterior margin raised, separated from pleural field by wide and distinct anterior pleural furrows which continue into broad, adaxially shallower posterior border furrow. Pleural field weakly convex (tr.), with two ill-defined pairs of pleural furrows. Narrow postaxial surface between adaxial lobes of pleural fields gently depressed. Border flattened, broad, evenly wide. Doublure slightly wider (tr.) than border, subhorizontal, evenly wide along whole length. Ventral surface of doublure covered by evenly distant, coarse terrace lines parallel to pygidial posterior margin. Dorsal surface of the pygidium nearly smooth except for very fine, oblique, often irregular terrace ridges. These ridges are more distinct on the border, being generally more transverse and distant anteriorly than posteriorly.

Remarks: The oldest known cyclopygids are those referred to *Prospectatrix* FORTEY, 1981, a genus with nileid-like morphology. Apart from the British type species *P. genatenta* (STUBBLEFIELD, 1927) from the Shineton Shales (Upper Tremadocian), the species *P. exquisita* ZHOU et al., 1994 has been described from the Lower Tremadocian (*Dichelepyge sinensis* Zone) of Xinjiang, China. *Pricyclopyge superciliata* DEAN, 1973 from the Sobova Formation (early Arenig) of Turkey, and a nearly identical cranidium from the late Arenig of Wales (Fortey and Owens 1987), have also been referred to *Prospectatrix* (Fortey 1981). Finally, the pygidia figured by Courtessole and Pillet (1975) from the Lower Tremadocian of the Montagne Noire, France, and referred to *Proteuloma geinitzi* (BARRANDE, 1868) probably belong to an unnamed species of *Prospectatrix*. The genus *Prospectatrix* has preserved a cephalic median suture, whereas the existence of this feature is unknown in the new species. All described species of *Prospectatrix* have large remnants of fixigenae. However, the new species *Pricyclopyge oceanitis* has distinctly narrower fixigenae (tr.), being similar to *Prospectatrix* cf. *genatenta* from North Wales (Fortey 1981: pl. 1, fig. e). The type species *P. genatenta* also retains three pairs of shallow glabellar furrows, which are unknown in the new species. The pygidium of *P. genatenta* has two pygidial axial rings, whereas *P. exquisita* has three rings. The new species of *Pricyclopyge* have four rings and the terminal piece. Although the form of *Prospectatrix* is more variable than was originally suggested by Fortey (1981), in view of the presence of already narrow fixigenae and the lack of glabellar furrows, the new species is referred to *Pricyclopyge*.

Another Lower Ordovician cyclopygid has been described by Tjernvik (1956) from the grey Ceratopyge



Text-fig. 35. *Pricyclopyge oceanitis* sp. n.
A – collapsed cranidium, internal mould, PCZCU 1571, ×4; B, C – deformed cranidium, internal mould and detail of fixigena, NM L 38503, ×4, ×6; D – tectonically deformed pygidium, NM L 38505, ×4; E, F – pygidium, internal mould and its oblique view, PCZCU 1572, both ×4.7; G, J – pygidium, latex cast of exterior and detail of sculpture, NM L 38504, ×6, ×12; H – small pygidium, internal mould, PCZCU 1573, ×4.7; I – holotype, pygidium, internal mould showing terrace lines on doublure, PCZCU 1574, ×4.7; K – largest gathered pygidium, internal mould, PCZCU 1575, ×4.7; L – pygidium, internal mould, PCZCU 1576, ×4.7; Mílina Formation, Olešná.

Limestone (= Bjørkåsholmen Limestone) of Öland, Sweden. The species *Cyclopyge latifrons* TJERNVIK, 1956 has been subsequently referred by Marek (1961) to the genus *Pricyclopyge* RICHTER et RICHTER, 1954. *Pricyclopyge latifrons* is a rare species, being known only from a single cranidium, while its pygidium remains unknown. Ebbestad (1999) did not report this species from Norway, although the trilobite fauna is almost identical with that described by Tjernvik (1956) from Öland. The early Arenig species *C. gallica* TJERNVIK, 1956 is locally very common in the uppermost part of the *Megistaspis planilimbata* Zone (Hunneberg), and another but unnamed *Cyclopyge* sp. is common in the Komstad Limestone of Scandinavia. Their abundant occurrences coincide with rising of sea-level at the base of the Billingen Stage (Nielsen 1995).

It is somewhat difficult to compare the Bohemian species with other earliest cyclopygids because of their less complete preservation and absence of data concerning the eyes and the presence of paired axial tubercles. This is the case for the new species and the formerly described taxa. The cranidium of *P. latifrons* is about half the size of *P. oceanitis* sp. n., and the axial furrows of the former are evenly curved and not sigmoidal as in *P. oceanitis*. The succeeding Scandinavian species, *C. gallica*, is much smaller, with a pygidium only 5.0–5.3 mm wide (Tjernvik 1956), while the pygidial width of *P. oceanitis* ranges from 12 to 16 mm. The larger size of the *P. oceanitis* exoskeleton suggests the stratigraphically younger species of *Pricyclopyge*, in which the width of the pygidium attains nearly 20 mm. The new species differs from the Arenigian to Darriwillian species *P. binodosa binodosa* (SALTER, 1859), *P. binodosa prisca* (BARRANDE, 1872), *P. binodosa eurycephala* FORTEY et OWENS, 1987, and *P. binodosa longicephala* (KLOUČEK, 1916) by the rounded posterior margin of the pygidium, and by having an anteriorly wider (tr.) and more rapidly tapering pygidial axis. The stratigraphically earliest specimen of *P. binodosa eurycephala* (Fortey and Owens 1987; fig. 56: f, g) from the early Fennian (Arenig) of Wales shows a more rounded outline with a shorter axis than those of the specimens higher in the stratigraphical sequence. This feature is consistent with the suggested gradual change of the pygidial outline from semi-elliptical to broadly triangular during the phylogenetic history of the genus. The subspecies *P. binodosa cyanea* MERGL, 1991 from the upper part of the Klabava Formation (upper Arenig) of Bohemia differs by having a smaller (about one third) size, and a less rounded pygidium with a narrower axis. The fixigenae of the cranidium of *P. oceanitis* has a very similar outline and size to that of *Microparia grandis* SALTER, 1859, which is reported from the early Arenig of Wales (Fortey and Owens 1978). The main difference is the shape of the pygidium; it is less transverse, with a narrow border defined by a faint border furrow, which is obscure behind the axis in *M. grandis*. The axis of *M. grandis* has only two rings, but this may be owing to the poor preservation of the specimens available to Fortey and Owens (1978).

Fortey (1981) noted the presence of fine terrace ridges on the dorsal surface of the pygidium of *Prospectatrix*. The new species has fine terrace ridges on the pygidial dorsal surface, similar to the pattern seen in nileids, exemplified e. g. by *Nileus exarmatus* TJERNVIK, 1956 (Schrank 1972). *Pricyclopyge oceanitis* is one of the stratigraphically earliest cyclopygids, and it is the earliest observed cyclopygid in the Prague Basin. The pygidium assigned to *Niobella innotata* (BARRANDE, 1868), figured by Vaněk (1965: pl. 23, fig. 19) belongs to *P. oceanitis.* This pygidium has a remarkably transverse outline, a distinct border, and a postaxial depression between weakly convex pleural fields.

Occurrence: Mílina Formation; Olešná (moderately abundant), Úvaly, Škvorec enclosure (rare).

Family **Nileidae** ANGELIN, 1854

Genus ***Platypeltoides*** PŘIBYL, 1948

Type species: *Platypeltis croftii* CALLAWAY, 1877; Tremadocian; Shropshire, England.

Platypeltoides perseis sp. n.

Text-figs 36A-K, 37

?1917 *Nileus* n. sp. ?; Klouček, p. 1.
?1922 *Nileus* sp.; Klouček, p. 1.
?1926 *Nileus*? sp.; Koliha, p. 36.
?1926a *Nileus* sp.; Klouček, p. 192.
1935 *Dicellocephalina ulrichi* n. sp.; Růžička, p. 3, pl. 1, fig. 5.
1964 *Niobella innotata* (BARRANDE, 1868); Vaněk, p. 107.
1965 *Niobella innotata* (BARRANDE, 1868); Vaněk, p. 272, pl. 23, fig. 20.
1965 *Dikelokephalina ulrichi* RŮŽIČKA 1935; Vaněk, p. 276, pl. 23, fig. 21.
1984a *Niobella* sp.; Mergl, p. 26, pl. 7, fig. 6.
2001 *Niobella* cf. *innotata* (BARRANDE, 1868); Vaněk and Valíček, p. 16 (partim).

Holotype: Pygidium figured in text-fig. 36I deposited in the palaeontological collections of the Czech Geological Survey, Prague (MM 130).

Paratypes: An incomplete cranidium figured in text-fig. 36A, deposited in the palaeontological collection of the Czech Geological Survey, Prague (MM 092b), and a librigena figured on text-fig. 36C, D, deposited in the palaeontological collection of the National Museum, Praha (NM L 38506).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

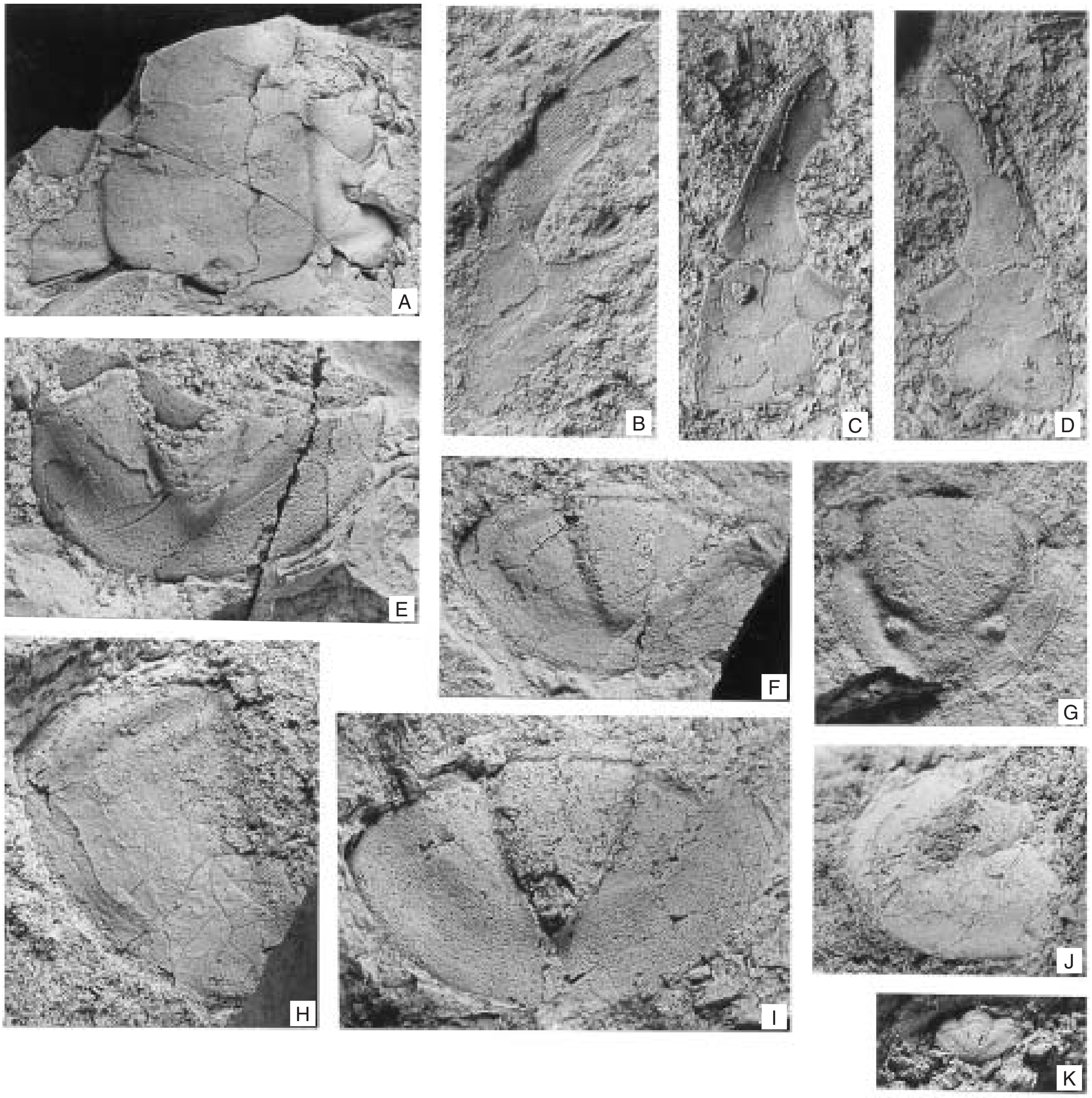
Material. Three imperfect cranidia, 7 librigenae, and 15 pygidia.

Name: *Perseis*, from Greek mythology, a daughter of Ókeanos.

Diagnosis: *Platypeltoides* with glabella weakly expanding in front of palpebral lobes, almost acute genal angle without spines, large palpebral lobes; transverse broadly elliptical pygidium, rapidly tapering pygidial axis without distinct rings; distinct anterior pleural furrow and shallow and distinct border furrow; long (exs.) pygidial doublure.

Description: Species of moderate size, with estimated length of exoskeleton between 50–60 mm. The largest known pygidium is 29 mm wide, but some glabellar fragments indicate even larger sizes.

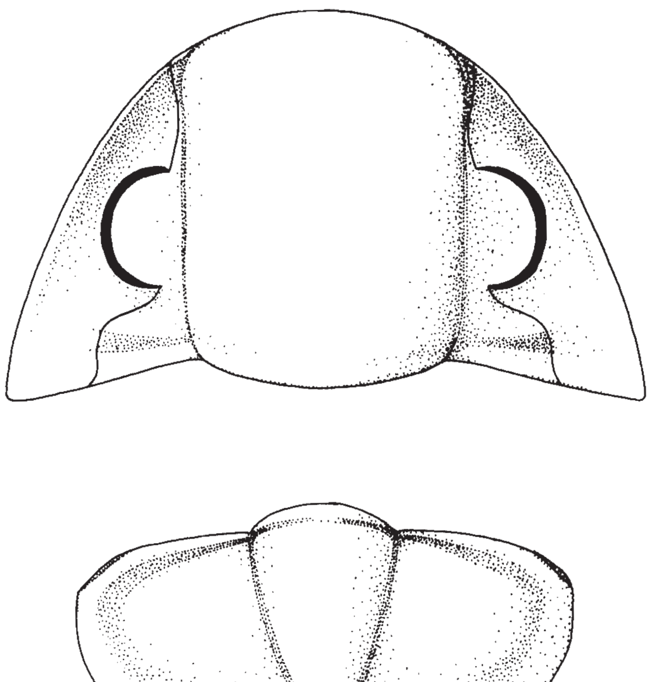
Cranidium gently convex, with weakly convex (tr.), effaced glabella. Glabella about 120 % as long (sag.) as its width, weakly expanding forwards in front of eyes, almost straight with anterior gently sloping toward the forward curved shallow anterior border furrow. Axial furrows almost parallel sided, weakly divergent, and becoming shallower forwards. Occipital furrow absent. Glabellar tubercle not discovered. Palberal lobes large, without rims, approaching axial furrows anteriorly, nearly horizontal. Total length of eye (exs.) about one-third of cephalic length. Postocular facial suture diverging about 45° to sag. line, rapidly curving



Text-fig. 36. ***Platypeltoides perseis*** **sp. n.**
A – incomplete cranidium, internal mould, MM 092b, ×2; B – tectonically deformed left librigena, internal mould showing doublure, NM L 38502, ×5.5; C, D – left librigena, latex casts of external and ventral surfaces, NM L 38506, both ×5.5; E – pygidium showing doublure, internal mould, PCZCU 1577, ×3.5; F – pygidium, internal mould, PCZCU 1578, ×3.5; G – hypostome, internal mould, PCZCU 1579, ×4; H – incomplete large pygidium, internal mould, PCZCU 1580, ×3.5; I – holotype, pygidium, internal mould, MM 130, ×3.5; J – pygidium, internal mould in oblique view, PCZCU 1643, ×2; K – meraspid pygidium, internal mould, PCZCU 1644, ×8; Mílina Formation, Olešná (A, C–J), Úvaly (Škvorec enclosure) (B), and Kvaň (K).
Platypeltoides **sp.**
L – right librigena, NM L 38507, ×3.8; Třenice Formation, Holoubkov.

abaxially to almost 90° angle toward posterior margin but deflected and cutting posterior margin at an acute angle (S-shaped). Postocular fixigena short (exs. and tr.), occupying about 40 % of glabellar width. Posterior border furrow broad and shallow, abaxially slightly running forward. Posterior margin of fixigenae straight, gently inclined backward. Librigena about half as wide (tr.) as its length (exs.), with weakly convex postocular genal field which continues forward into narrower, moderately concave, broad lateral border with acute edge at anterolateral margin. Genal angle acute, only the very tip rounded. Doublure wide (tr.), occupying most of ventral surface of librigenae. Doublure subhorizontal near genal angle, becoming progressively ventrally convex forwards. Eye socle low, semi-circular. Doublure surface covered by distinct, oblique, slightly backward curved terrace ridges.

Hypostome subcircular, slightly wider than long (Lh/Wh = 83 %), gently convex. Anterior lobe of middle body subpentagonal, equally as long as wide, separated by oblique deep middle furrow from low, short, transverse posterior lobe of middle body. Maculae small, elevated, located in posterior one-third. Lateral notches small. Anterior border short, anterior wing short, flat, moderately inclined dorsally. Shoulder of the same is low, of the same width (tr.) as ventrally weakly convex lateral and posterior borders. Anterior margin almost transverse. Lateral margins evenly rounded, posterior margin with shallow anteriorly rounded.



Text-fig. 37. *Platypeltoides perseis* sp. n. Reconstruction of the cephalon and the pygidium. Approximately ×2.

Pygidium broadly oval, 65–70 % as long as its width, gently convex (sag. and tr.). Axis distinct, slightly tapering posteriorly, 62–75 % as long, and 25 % of pygidial length, with blunt point. Axial furrows shallow and wide. Pleural field poorly convex, undivided, separated from broad and flattened border by weak and adaxially shallow border furrow. Anterior pleural furrows deep near axial furrows, widening and shallowing abaxially. Articulating facets well developed, tapering adaxially, forming broadly rounded anterolateral edge of pygidium. Posterior margin with acute edge. Doublure broad, tightly adjacent to the dorsal exoskeleton, occupying nearly 60 % of the pygidial length (exs.), with a broad emargination in sagittal axis, but extended slightly forward below the tip of the axis. Ventral surface of doublure covered by nearly thirty fine terrace ridges in the widest (exs.) part of the doublure.

Ontogeny: A single, only 1.0 mm long pygidium, that can be referred to the species (Text-fig. 36 K) has a defined axis, an obscure transverse pleural furrow, and a narrow doublure.

Remarks: The genus *Platypeltoides* PŘIBYL, 1948 ranges from the Upper Cambrian to the Arenig, with several species in Great Britain (Callaway 1877, Lake 1942), Sweden (Tjernvik 1956), Kazakhstan, and China (Troedsson 1937, Appolonov and Tschugaeva 1983, Peng 1990). The new species, *P. perseis* sp. n., is similar to the type species *P. croftii* (CALLAWAY, 1877) from the British Tremadocian (Owens et al. 1982). *Platypeltoides croftii* differs from *P. perseis* by having a rounded genal angle, longer (tr.) fixigenae, less parallel terrace ridges on the anterior portion of the librigenal doublure, and very forward-divergent preocular parts of the axial furrows. The pygidial axis of *P. perseis* is undivided and shorter than that of *P. croftii*, which has two distinct rings. *Platypeltoides wimani* (TROEDSSON, 1937) from the Panjiazui Formation (Lower Tremadocian) of South China (Peng 1990), differs from *P. perseis* by having wider (tr.) fixigenae, smaller palpebral lobes, and axial furrows in the postocular part that slightly converge, while in *P. perseis* the axial furrows are parallel to each another. *Platypeltoides marginulatus* APPOLONOV et TSCHUGAEVA, 1983 from the Upper Cambrian of Kazakhstan has a similar cranidium, but the pygidium has a shorter and less backward tapering axis than *P. perseis*. The Arenig species *P. serus* TJERNVIK, 1956 has a very similar cranidium outline, but its pygidium has three or four pleural ribs unlike the smooth pleural field of *P. perseis*.

Platypeltoides perseis is the only Bohemian species of the genus. Klouček (1922, 1924) referred some nileid-like trilobite remains to *Symphysurus* GOLDFUSS, 1843 and to *Nileus* DALMAN, 1827. His *Symphysurus* report concerns *Ottenbyaspis broeggeri* (RŮŽIČKA, 1926), *Hemibarrandia holoubkovenis* (RŮŽIČKA, 1926), or *H. klouceki* sp. n. Only the isolated left librigena from the Olešná locality, stored in the National Museum, Prague, which is from Klouček's collection (Text-fig. 36C, D) belongs to *P. perseis* sp. n. The species has been referred to *Niobella innotata* (BAR-

RANDE 1868), but the previously illustrated pygidia with a broad (exs.) doublure and weakly defined axis (Vaněk 1965: pl. 23, fig. 21; Mergl 1984a: pl. 26, fig. 6) are identical with the new material of *P. perseis*. The hypostome of *P. perseis* has been confused with *Dikelokephalina ulrichi* RŮŽIČKA, 1935 by previous authors (Růžička 1935, Vaněk 1965). The species is moderately abundant in the Olešná locality, being represented almost exclusively by pygidia, while librigenae, hypostomes, and cranidia are rare.

Occurrence: Mílina Formation; Olešná (abundant), Kvaň (rare), Úvaly, Vinice (abundant), Úvaly, test pit (rare).

Platypeltoides sp.

Text-fig. 36L

?1926a *Niobe* (?) sp.; Klouček, p. 193.

Material: One librigena (NM L 38507).

Remarks: The librigena of the same morphology has been observed in material from the Třenice Formation of the Holoubkov locality. It differs from librigena of *P. perseis* by wider (tr.) genal field. Whether this librigena concerns *Niobe* sp. in the fossil list of Klouček (1926a) is unclear.

Occurrence: Třenice Formation, Holoubkov (very rare).

Superfamily **Trinucleoidea** HAWLE et CORDA, 1847
Family **Orometopidae** HUPÉ, 1955

Genus ***Celdometopus*** nov. gen.

Type species: *Orometopus klouceki* Vaněk, 1965; Upper Tremadocian, Mílina Formation; Barrandian, Bohemia.

Diagnosis: Orometopid with high, anteriorly widening, subglobose glabella; large palpebral lobes highly raised above fixigena; librigenae with very high, subvertical fringe with prominent crests on inner and outer margins; long posterodorsally directed occipital spine; pygidium without border, border furrow, or pleural furrows; pygidial axis smooth, with rings distinct only on inner surface; weak posterior arch present.

Remarks: The new genus is especially characterized by a long, posterodorsally directed occipital spine, and a high subvertical brim bordered by prominent crests on its inner and outer margins. The brim of the librigenae is extended far backwards; thus, instead of thin genal spines, the librigena extends into a plate-like (tr.) structure, tapering backwards into a long genal spine. The genal spine bears a distinct crest between the subhorizontal genal field and the subvertical brim, and along the outer edge of the ventral side of the brim.

The new genus has many features that are characteristic of the family Orometopidae HUPÉ, 1955: wide (tr.) librigenae; an axial spine on the axial part of the cephalon; conspicuously raised, large palpebral lobes; finely pitted fixigenae; pairs of fossulae in the preglabellar furrow and adaxial part of the posterior border furrows; inflated bacculae; and a small, almost effaced transverse pygidium. Although orometopids are restricted to the late Tremadocian and the early Arenig, they have a wide geographic distribution; they occur from subequatorial Gondwana (Harrington and Leanza 1957) and Siberia (Petrunina 1960) to temperate Baltica (Angelin 1854, Størmer 1920, Tjernvik 1956, Ebbestad 1999) and high-latitude peri-Gondwana (Salter 1866, Lake 1907, Bulman and Rushton 1973).

The genus *Orometopus* BRØGGER, 1896 differs from *Celdometopus* by having a backward spine extended from the axial area of the glabella instead of from the occipital ring, externally distinct rings on the pygidial axis, a pair of transverse anterior pleural furrow on the pygidium, and a strikingly narrower (tr.) brim on the librigenae. However, both genera share numerous features indicating close phylogenetic affinity: the large palpebral lobes with eyes, fossulae in the preglabellar groove and at the ends of posterior border furrows, the very short pygidia lacking the border, and numerous but weak axial rings. Fortey and Chatterton (1988) and Ebbestad (1999) stated that the genus has a conservative morphology representing the primitive trinucleoideans. *Pagometopus* HENNINGSMOEN, 1959 lacks an occipital spine, has smaller and much posterior palpebral lobes, and its anterior margin is rounded with forward strongly converging facial suture. This genus is represented by the only type species from the Bjørkåsholmen Formation (Upper Tremadocian) of Norway. *Pyrimetopus* PŘIBYL et VANĚK, 1980, based on *O. pyrifrons* HARRINGTON, 1938 from the Upper Tremadocian of Argentina (Přibyl and Vaněk 1980, Waisfeld and Vaccari 2003), differs from *Celdometopus* by the absence of the occipital spine, and by having a distinct transverse anterior pleural furrow on a significantly longer pygidium. The pygidium of *Pyrimetopus* has a weakly but distinctly defined, wide, and downsloping border, which is absent in the new genus.

Celdometopus klouceki (VANĚK, 1965)

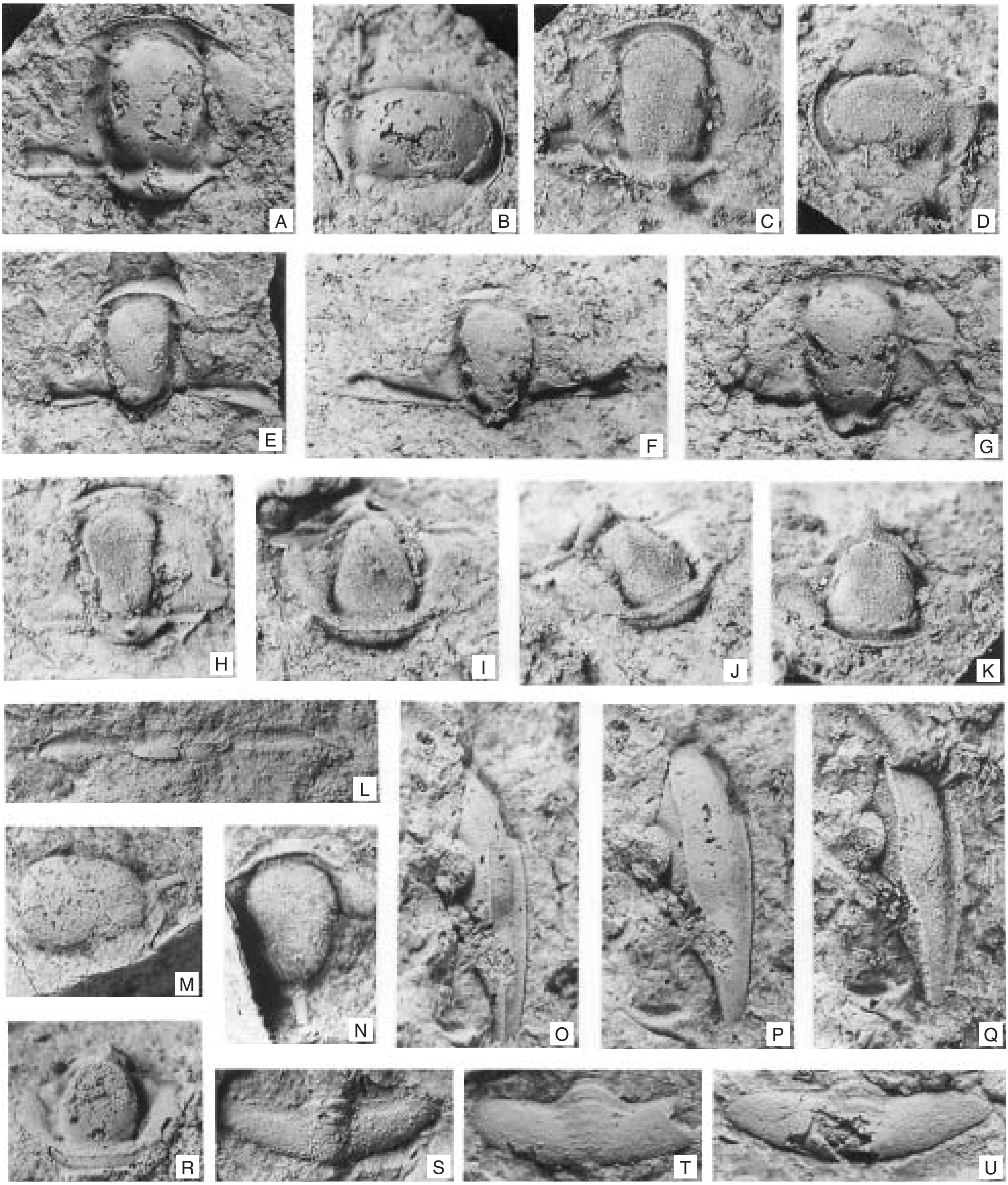
Text-figs 38, 39

1931 *Orometopus* aff. *elatifrons* (ANG.); Klouček, p. 364, pl. 1, figs 6, 7.
1931 *Orometopus* aff. *praenuntius* (SALTER); Klouček, p. 365, pl. 1, fig. 15.
1964 *Orometopus klouceki* n. sp.; Vaněk, p. 108.
1965 *Orometopus klouceki* n. sp.; Vaněk, p. 277, pl. 24, fig. 26.
1970 *Orometopus klouceki* VANĚK, 1965; Horný and Bastl, p. 125, 246.
1984a *Orometopus klouceki* VANĚK, 1965; Mergl, p. 30, pl. 3, figs 1–6, text-fig. 6.
2001 *Orometopus klouceki* VANĚK, 1965; Vaněk and Valíček, p. 37.

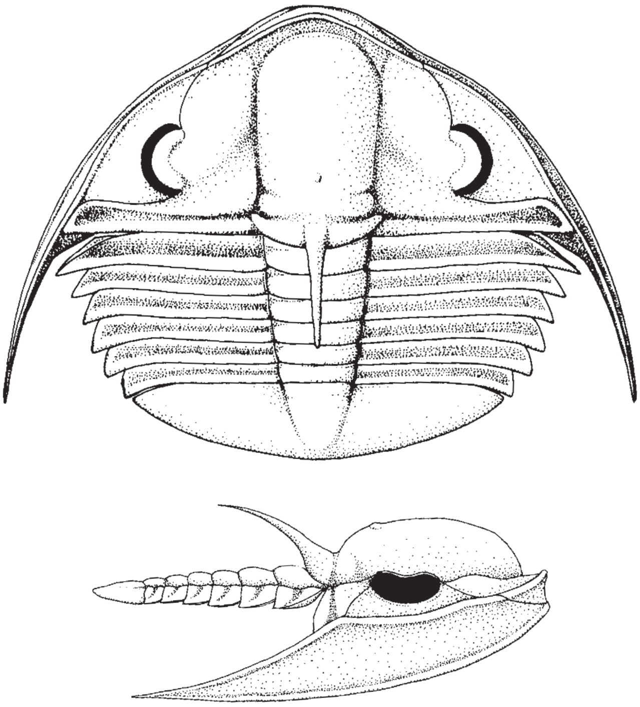
Holotype: Cranidium (external mould) figured by Vaněk (1965) on pl. 24, fig. 26 deposited in the collection of the National Museum, Prague (NM L 18602).

Type horizon and locality: Upper Tremadocian, Mílina Formation; Bohemia, Barrandian, Olešná, the abandoned quarry E of the village.

Material: Forty mostly incomplete cranidia, 10 librigena and 7 pygidia.



Text-fig. 38. ***Celdometopus klouceki*** **(VANĚK, 1965).**
A–D, K – cranidium, internal mould and latex cast in dorsal, oblique and anterior views, PCZCU 1592, all ×8; E – cranidium, internal mould, PCZCU 1593, ×8; F – cranidium, internal mould, PCZCU 1594, ×8; G – cranidium, internal mould, PCZCU 1594, ×8; H–J – cranidium, latex cast of exterior in dorsal, anterior and oblique views, PCZCU 1596, ×8; L – thoracic segment, internal mould, PCZCU 1597, ×8; M, N – glabella with occipital spine, internal mould and its latex cast, PCZCU 1598, both ×8; O–Q – librigena, internal mould in dorsal and oblique views and latex cast of exterior, MM 083, all ×9; R – cranidium, internal mould in anterior view, PCZCU 1599, ×8; S – pygidium, internal mould, PCZCU 1607, ×8; T – pygidium, internal mould, PCZCU 1608, ×8; U – pygidium, internal mould, PCZCU 1609, ×8; Mílina Formation, Olešná.



Text-fig. 39. *Celdometopus klouceki* (VANĚK, 1965). Reconstruction and lateral view to the exoskeleton. Approximately ×10.

D e s c r i p t i o n: See Mergl (1984a).

R e m a r k s: The cephalic characters have been described in detail by Mergl (1984a). A new reconstruction is presented here, although the number of segments of *C. klouceki* remains unknown, and the number of pleural segments in the reconstruction is adopted from other orometopids (Harrington and Leanza 1957, Moore 1959). The segments are very short (sag.), with narrow (tr.) horizontal pleurae that are low and adaxially acutely pointed. The articulating facet is short (exs.) and long (tr.), and is distinctly differentiated from the anterior pleural band. The pleural furrows are shallow and broad. The pygidial axis is smooth on the dorsal surface. Depending on a size of the pygidium, there are six or seven rings, laterally with small raised impressions, preserved on the inner surface. These imprints are common on other trinucleoid pygidia (Whittington 1965).

Celdometopus klouceki (VANĚK, 1965) was observed by Klouček (1931), who only had two poorly preserved cranidia. Vaněk (1965) stated that *C. klouceki* is a rare species, but this is not consistent with the new observations. *C. klouceki* is locally very frequent, sometimes even the dominant species among small trilobites in the upper part of the trilobite-bearing sequence at the Olešná locality. Apart from the mostly fragmentary cranidia, librigenae, broken genal spines, and pygidia are quite abundant. The species is very rare in the Kvaň locality, with only one librigena found. The species is unknown in the Úvaly area.

O c c u r r e n c e: Mílina Formation; Olešná (abundant), Kvaň (very rare).

Order **Ptychopariida** SWINNERTON, 1915
Superfamily **Harpina** MATTHEW, 1887
Family **Harpididae** RAW, 1949

Genus ***Harpides*** BEYRICH, 1846

T y p e s p e c i e s: *Harpides hospes* BEYRICH, 1846; Tremadocian; ? Bohemia.

Harpides grimmi BARRANDE, 1872

Text-fig. 40

1872 *Harpides Grimmi* BARR.; Barrande, p. 22, pl. 1, figs 11–14.
1920 *Dictyonema* sp.; Klouček, p. 123.
1922 *Harpides cf. rugosus* ?; Klouček, p. 1.
1926a *Harpides* sp.; Klouček, p. 192.
1931 *Harpides* sp. (cf. *grimmi* BARR. ?); Klouček, p. 364, pl. 1, figs 10, 11.
1964 *Harpides grimmi* BARRANDE, 1872; Vaněk, p. 108.
1965 *Harpides grimmi* BARRANDE, 1872; Vaněk, p. 277, pl. 24, figs 24, 25; pl. 26, fig. 50.
1966 *Harpides grimmi* BARR.; Havlíček and Vaněk, pl. 3, fig. 10.
1970 *Harpides grimmi* BARRANDE, 1872; Horný and Bastl, p. 150.
1980 *Harpides* (*Dictyocephalites*) *grimmi* BARRANDE, 1972; Pillet and Courtessole, p. 415, figs 1, 2:c.
1984a *Harpides grimmi* BARRANDE, 1872; Mergl, p. 29, pl. 7, fig. 7, pl. 8, figs 6–8.
2001 *Harpides grimmi* BARRANDE, 1872; Vaněk and Valíček, p. 31.

H o l o t y p e: Almost complete specimen, figured by Barrande on pl. 1, figs 11–14, deposited in the collection of the National Museum, Prague (NM L16606).

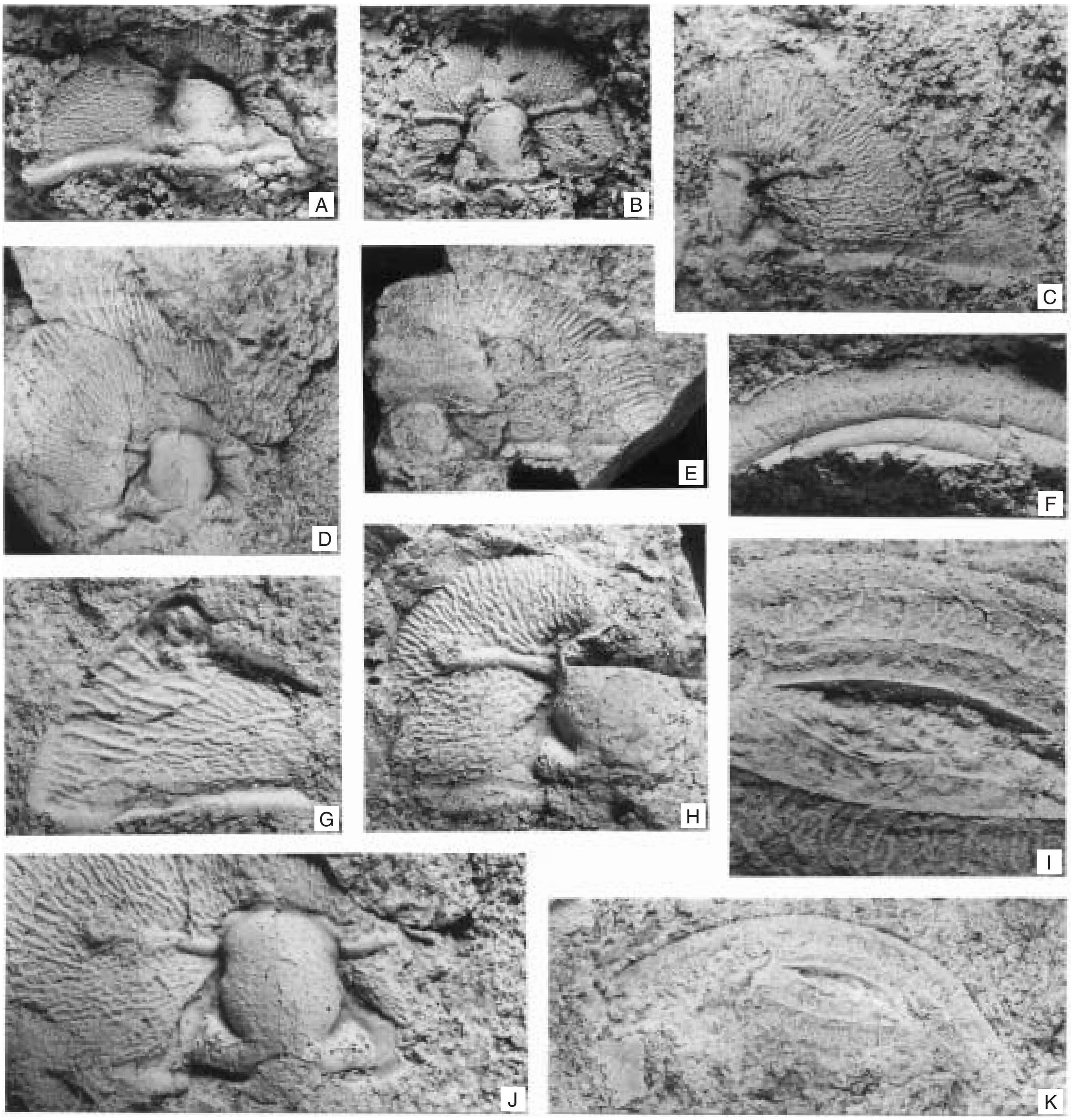
T y p e h o r i z o n a n d l o c a l i t y: Upper Tremadocian, probably Mílina Formation; Bohemia, Barrandian, Komárov area ?

M a t e r i a l: Besides the holotype, 15 incomplete cranidia including small specimens, 3 doublures and numerous small fragments of cephalon.

D i a g n o s i s: *Harpides* with semicircular, almost transverse posterior border and broadly angular genal angle without long spines; convex cephalon with transverse occipital furrow; glabella trapezoidal, with distinct S1 and S2, and obscure S3; preglabellar boss distinct; regular and rarely anastomosing genal caeca near marginal rim; doublural plate with weak genal caeca; anterior brim distinctly longer (sag.) than second and third brims; girder prominent; small high eye tubercles in one-fourth of fixigena; eye ridges directed anterolaterally.

D e s c r i p t i o n: Barrande (1872).

R e m a r k s: The affinity of *H. grimmi* BARRANDE, 1872 to other species has been commented on by several authors (Raw 1949, Harrington and Leanza 1957, Henningsmoen 1959, Pillet and Courtessole 1980, Peng 1990, Ebbestad 1999), all of whom noted the close morphological similarity of the Bohemian species to *H. rugosus* (SARS et BOECK, 1838), or suggested that they may be conspecific. Both species are undoubtedly closely related, but *Harpides grimmi* has more regular genal caeca in the proximity of the marginal rim, while these are more branching and anastomo-



Text-fig. 40. *Harpides grimmi* BARRANDE, 1852.
A – small cranidium, internal mould, PCZCU 1582, ×5; B – small cranidium, internal mould PCZCU 1583, ×5; C – incomplete small cranidium, internal mould, PCZCU 1584, ×5; D, J – incomplete cranidium, internal mould, and detail of glabella, MM 093, ×2.2, ×3.5; E – incomplete cranidium, internal mould, PCZCU 1585, ×2.2; F – doublure of small specimen, external mould, PCZCU 1586, ×6; G – part of fixigena, internal mould, PCZCU 1587, ×3.5; H – glabella and part of fixigena with eye ridge, internal mould, PCZCU 1588, ×3.5; I, K – doublure, internal mould, detail and complete preserved part, MM 132, ×4, ×1.8; Mílina Formation, Olešná.

sing (Ebbestad 1999: fig. 77A, E) in *H. rugosus*. The genal angle of *H. grimmi* is less acute, and only small specimens of sizes up to about 20 mm of the cranidial width show an acute angle similar to the genal angle of *H. rugosus*. The almost entire posterior border of *H. grimmi* is transverse, while in *H. rugosus* the abaxial portions of the posterior margin are slightly curved backward. Eye ridges of *H. grimmi* are longer, with a more lateral position of the eye tubercles; these are placed at about one-fifth of the fixigenal width in *H. rugosus*, but at one-fourth in *H. grimmi*. S2 and S3 are very distinct in *H. rugosus* but very obscure in *H. grimmi*. The doublural plates show important differences. The marginal brim in *H. grimmi* is about double the length (sag.) of the inner brim, while in *H. rugosus* the external brim is distinctly narrower, being only slightly longer (sag.) than the inner bands (Henningsmoen 1959). This feature, distinct in both the holotype and newly collected specimens from the Mílina Formation, confirms the presence of only a single species in the Barrandian. This identity was questioned by Klouček (1931), but it is indirectly evinced by the stratigraphical position in the Mílina Formation and the Bohemian provenience of the holotype. The dorsal surface of the cephalon, external rim, and the doublural plate are covered by fine, regularly spaced spinose tubercles. It seems unlikely that *H. grimmi,* referred to the subgenus *Dictyocephalides* by Pillet and Courtessole (1980)*,* is more closely related to *H.* (*D.*) *villebruni* (BERGERON, 1895) than to other species. The reconstruction of the cephalon by Pillet and Courtessole and (1980) is incorrect, because the existence of the genal spines is doubtful in *H. grimmi*. As seen in a preserved doublural plate, the genal angle of H. *grimmi* is likely to be without any genal spines, and this distinguishes the species also from *H. rugosus*. A small genal spine was drawn by Barrande (1872) on the holotype, and was redrawn by subsequent authors (e.g. Moore 1959). However, new observations of the holotype indicate that the reconstructed spine probably does not exist. *Harpides* (*D.*) *villebruni* has a wholly different pleurae morphology, and the genal angle is situated at mid-length of the cephalon, quite unlike its posterior position in *H. grimmi*. This led Ebbestadt (1999) to reject the subgeneric division of *Harpides* proposed by Pillet and Courtessole (1980). However, spinose pleurae and the unique morphology of the cephalon justify the validity of the genus *Dictyocephalus* BERGERON, 1895.

Various species of *Harpides* are known almost worldwide in the Tremadocian. Apart from morphologically distinct species (for instance *H. neogaeus* HARRINGTON and LEANZA, 1957, *H. atlanticus* BILLINGS, 1865, and *H. nodorugosus* POULSEN, 1965), other species are very similar to *H. grimmi*. In addition to the *H. rugosus* from the type area, incomplete cephala of *H. rugosus* are also reported from the Sayan Altai mountain region (Petrunina et al. in Khalfin 1960), and these are indistinguishable from the Bohemian material. The other three species from the Tremadocian of the same area are morphologically different.

The locality of the holotype of *Harpides grimmi* and its stratigraphic level have been unknown for over 150 years. Its locality has been inferred indirectly, suggesting the abandoned iron ore mine near Mirošov (Purkyně 1914, Prantl 1945) or Komárov (Vaněk 1965, Mergl 1984a). Therefore, when Klouček found the fragmentary material of this genus (Klouček 1920, 1922, 1931) in the Mílina Formation, this unique specimen was referred to that formation (Vaněk 1965). There are no differences between the holotype and the newly collected specimens from the cherts of the Mílina Formation. However, some important characteristics (such as the genal caeca of the dorsal surface near the marginal rim, and the morphology of the glabella) are unknown from the holotype of *H. grimmi*. Klouček (1931) only had small fragments of genae showing the general morphology, eye tubercle (Klouček 1931: pl. 1, fig. 10), and a strongly deformed cephalon with eye ridge and glabella. This rare material was not described by Klouček (1931). Because this material was not sufficient for critical comparison, Klouček referred the specimens to *Harpides* sp. (cf. *grimmi* Barr.?).

Occurrence: Mílina Formation; Olešná (abundant), Kvaň (very rare), Úvaly, test pit (rare); Mirošov (?).

? Order **Proetida** FORTEY et OWENS, 1965
Family unknown

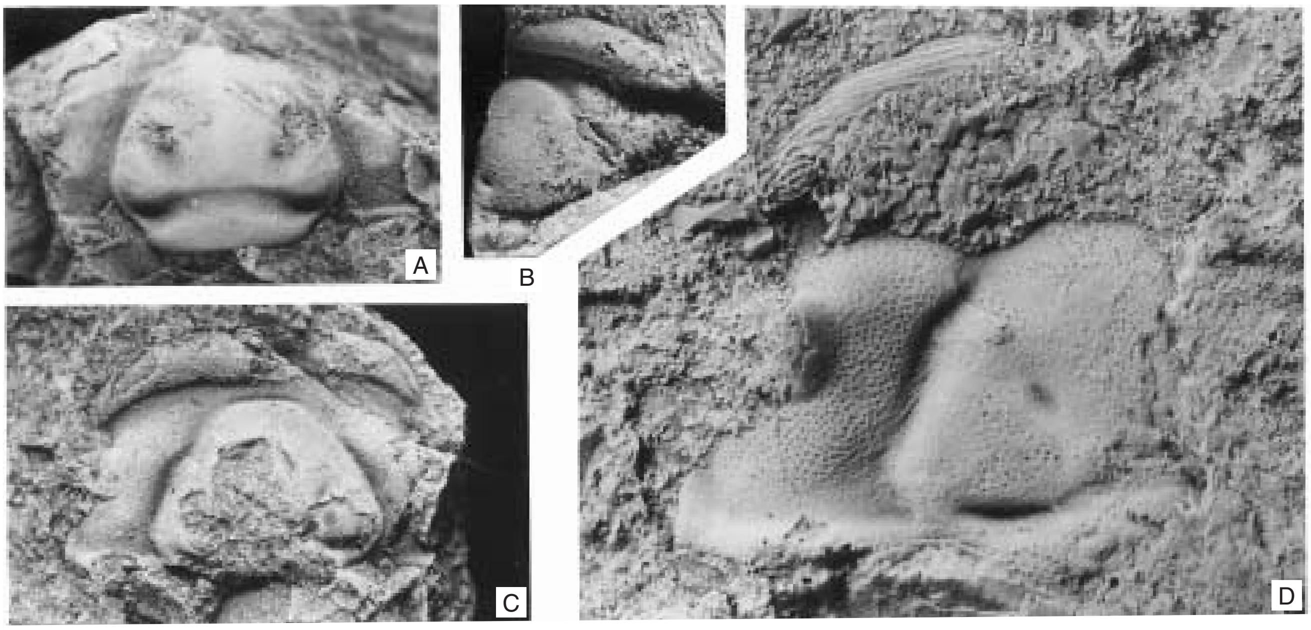
Genus ***Eulomina*** RŮŽIČKA, 1931

Type species: *Euloma mitratum* RŮŽIČKA, 1926; Upper Tremadocian, Třenice Formation; Barrandian, Bohemia.

Remarks: *Eulomina* RŮŽIČKA, 1931 has several remarkable features: a finely pitted external surface of cephalon and anterior border with unevenly raised ridges, smooth and highly raised palpebral lobes, externally obscure glabellar furrows, and the absence of a paraglabelar field. The inner surface of the glabella shows distinct S1 and less distinct S2. S3 is obscure, marked by a short and very weak thickening on the inner surface. The dorsal surface of the glabella is almost effaced; S1 and S2 are marked by weakly depressed, oblique oval, smooth spots disconnected from the axial furrows, while the pair of S3 is not discernible. These spots are distinct by their lack of the fine pits that cover the remaining surface of the glabella. Another remarkable character of *Eulomina* is a row of shallow minute pits, observed on the inner surface below the anterior border furrow. This row although less distinct than in other eulomids, should indicate an affinity to the Eulomidae KOBAYASHI, 1955. The anterior border is high and densely covered by anastomosing raised ridges.

Eulomina is a small trilobite, with a maximum length around 25 mm. There are some smaller early Ordovician eulomids with nearly effaced glabella, e.g. *Karataspis* ERGALIEV, 1983, but they have a long preglabellar field and much narrower (tr.) glabella. The pygidium of *Eulomina* was hitherto unknown, as Vaněk (1965) misidentified the pygidium of *Holubaspis perneri* (RŮŽIČKA, 1926). The species *Holoubkocheilus granulatus* (RŮŽIČKA, 1926), formerly referred to *Eulomina* by Vaněk (1965), has a quite different morphology and is referred to the hystricurids.

The taxonomic position of *Eulomina* has been uncertain since its establishment (Růžička 1926, Moore 1959). Unlike the calymenoideans, *Eulomina* lacks a tuberculate sculpture and paraglabellar fields, has strongly divergent anterior branches of facial sutures, and its glabellar furrows are unusually weak; only homalonotids that are otherwise entirely different among calymenoideans lack the glabellar furrows. On the other hand, *Eulomina* shows some resemblance to the proetid genus *Analocaspis* OWENS, 1970 from the Lower Chasmops Shale of Norway. A short preglabellar field, divergent facial sutures, wide (tr.) posterior fixigena, and nearly smooth surface in *Analocaspis* are similar to *Eulomina*. Owens (1970) commented on the similarity of *Analocaspis* to the calymenids, emphasizing the small, for-



Text-fig. 41. ***Eulomina mitratum*** **(RŮŽIČKA, 1926).**
A – lectotype, cranidium, internal mould, NM L 18886, ×7; B – incomplete cranidium, internal mould of exterior, NM L 38501, ×7; C, D – almost complete cranidium, internal mould and latex cast of exterior, NM L 18928, ×7, ×15; Třenice Formation, Holoubkov.

wardly placed eyes and deep axial furrows; but he considered *Analocaspis* to be a proetid. However, *Eulomina* differs by having a high anterior border, while its glabellar furrows are very weakly defined.

Eulomina mitratum (RŮŽIČKA, 1926)

Text-fig. 41

1926 *Euloma mitratum* n. sp.; Růžička, p. 5, pl. 1, fig. 4.
1927 *Euloma mitratum* n. sp.; Klouček and Koliha, p. 1.
1928 *Euloma mitratum* n. sp.; Růžička, p. 53.
1931 *Eulomina* n. g. *mitratum* n. sp.; Růžička, p. 390, pl. 1, fig. 6.
1931 *Olenus* sp. III; Růžička, p. 393, pl. 1, fig. 13.
1953 *Eulomina mitratum* (RŮŽIČKA); Přibyl, p. 42.
1964 *Eulomina mitrata* (RŮŽIČKA, 1926); Vaněk, p. 108.
1965 *Eulomina mitrata* (RŮŽIČKA, 1926); Vaněk, p. 285, pl. 26, figs 54, 55.
1965 *Pharostomina oepiki* SDZUY 1955; Vaněk, p. 283, pl. 26, fig. 59.
1970 *Eulomina mitrata* (RŮŽIČKA, 1926); Horný and Bastl, p. 206, pl. 16, fig. 2.
1994 *Eulomina mitratum* (Růžička 1926); Mergl, p. 15, pl. 8, figs 4–9.
2001 *Eulomina mitrata* (Růžička 1926); Vaněk and Valíček, p. 16.

Holotype: Cranidium figured by Růžička (1926) on pl. 1, fig. 4, re-figured here in text-fig. 41A,, deposited in the collection of the National Museum, Prague (NM L 18886).

Type horizon and locality: Upper Tremadocian, Třenice Formation; Bohemia, Barrandian, Holoubkov, dumps of the abandoned "V Ouzkém" iron ore mine.

Material: Six incomplete cranidia.

Remarks: Both Růžička (1926) and Vaněk (1965) confused the pygidium of *Eulomina mitratum* with the species *Holubaspis perneri* (RŮŽIČKA, 1926); this was pointed out by Mergl (1984a, 1994). Although Klouček (1925) listed two species of *Euloma* from the Holoubkov locality, Klouček and Koliha (1927; p. 3) subsequently considered *E. mitratum* to be invalid, as a synonym of *Euloma granulatum* RŮŽIČKA, 1926 (= *Holoubkocheilus granulatus*).

Occurrence: Třenice Formation, Holoubkov (rare).

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