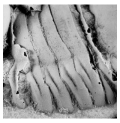
The effaced Ordovician trilobite *Svobodapeltis* and the earliest history of illaenimorph trilobites in the Ordovician of the Prague Basin (Bohemia)

MICHAL MERGL & VLADISLAV KOZÁK



Revision of the Middle Ordovician (Darriwilian) illaenimorph trilobite *Svobodapeltis avus* (Holub, 1908) results in a substantially emended diagnosis of the genus *Svobodapeltis* Šnajdr, 1957 and its assignment to the Family Hemibarrandiidae Courtessole & Pillet, 1975. The general illaeniform morphology of *Svobodapeltis* and its relative *Hemibarrandia* Prantl & Přibyl, 1949, with effaced cephalon and pygidium, the connective suture on the cephalic doublure indicating the presence of a rostral plate, no articulating furrows in the axis, and the fulcrate thorax are in distinct contrast with the presence of pleural furrows on all thoracic segments. The glabella that is defined anteriorly, the presence of border furrows on the cephalon, lack of the lunette, and furrowed segments are regarded as convincing evidence for separation of the Hemibarrandiidae from other illaenoids. The illaenid *Caudillaenus advena* (Barrande, 1872), a specimen of which was previously assigned to *S. avus* that influenced the concept of the genus, is redescribed together with its ancestor *C.* aff. *advena*. • Key words: trilobites, Illaenidae, *Svobodapeltis*, *Hemibarrandia*, Darriwilian, Ordovician, Czech Republic.

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Svobodapeltis avus (Holub, 1908) is a poorly known illaenimorph trilobite from the Šárka Formation (Darriwilian) of the Prague Basin, Czech Republic. It combines an illaenid-like morphology with furrowed thoracic pleurae, representing an unusual combination for the Illaenoidea. The species is very rare. Despite 120 years of intensive sampling of fossils in siliceous nodules of the Šárka Formation, only eighteen specimens have been found, with six of them showing some degree of articulation. Šnajdr (1957) erected *Svobodapeltis* on a few disarticulated specimens that he assigned to *S. avus*, the only included species, but his concept of the genus was partly misleading because one of the specimens, a cephalon with seven attached thoracic segments, actually belongs to the illaenid *Caudillanus advena* (Barrande 1872). On this basis, *S. avus* was assumed to be a member of the illaenid clade.

Newly available material, showing some previously unknown features of *Svobodapeltis* Šnajdr, 1957, makes possible a revised diagnosis and re-assessment of its relationship with other illaenimorph genera, especially *Hemibarrandia* Prantl & Přibyl, 1949.

Geological setting

The early Darriwilian Šárka Formation, the only formation in which *Svobodapeltis avus* occurs in the Prague Basin, ranges in thickness from 50 m to 300 m in the deepest part of the basin. The formation is characterised by its extraordinarily diverse fauna of trilobites, molluscs, echinoderms, brachiopods, and other benthic fossils (Havlíček & Vaněk 1966, Havlíček 1998). Most of the fossils come from siliceous loose nodules, which weather from the shales and have been sampled over a period of more than 150 years; unfortunately, detailed biostratigraphical data are missing. A few outcrops of the Šárka Formation and the most fossiliferous localities with nodules are aligned along the NW margin of the basin and in its western part. Almost all of the specimens of *S. avus*, coming from the local *Corymbograptus retroflexus* Biozone (Kraft & Kraft 1999), have been collected in siliceous nodules that are locally abundant in the soil of ploughed fields in the vicinity of Rokycany, Osek, Mýto, Těškov, Pětidomky, Praha-Vokovice, Popovice, and Úvaly (Klouček 1916). Fossils have rarely been sampled from shales of the Šárka Formation in natural outcrops, but temporary outcrops and brickyards have provided abundant fossils, especially in the vicinity of Prague (Klouček 1916).

Material and methods

Except for one poorly preserved, entire but strongly flattened dorsal exoskeleton in shale, other specimens are preserved in siliceous nodules. Some of these specimens are found on the external surface of nodules and often lack the edges of the particular shield. Silicified remains of the originally calcareous exoskeleton are sometimes preserved on the surface of nodules. Preservation in nodules favourably retains the original convexity and proportions of the exoskeleton. All known specimens have been studied, including some from private collections that are not figured.

Collections. – Czech Geological Survey in Prague, collections of Vladislav Kozák (CGS CW), Michal Mergl (CGS MM), Filip Novotný (CGS FN), Jan Peršín (CGS JP), and Jiří Vaněk (CGS JV); Museum of Dr. B. Horák at Rokycany (MR); West Bohemia Museum in Plzeň (WBM S); National Museum in Prague (NM L).

Terminology. – Follows Whittington & Kelly (1997).

Abbreviations. – H – height, L – length, W – width, ce – cephalon, cr – cranidium, lb – librigena, p – pygidium, exs. – exsagittal, sag. – sagittal, tr. – transversal.

Systematic palaeontology

Order Corynexochida Kobayashi, 1935
?Suborder Illaenina Jaanusson, 1959
?Superfamily Illaenoidea Hawle & Corda, 1847
Family Hemibarrandiidae Courtessole & Pillet, 1975

Diagnosis (emended). – Illaenimorph trilobites with dorsal surface smooth or finely pitted, with terrace ridges restricted to the peripheral rim of the cephalon; weakly defined axial furrows on cranidium and pygidium; no median pit or node on posterior part of glabella; no occipital furrow, no lunette; fixigenae almost effaced, with weak lateral border furrow, palpebral lobes small. Eyes small, posterior border furrow distinct. Raised rim on anterior margin of cranidium and adjacent part of librigenae. Thorax of nine segments, fulcrate, with pleural furrows on all segments; articulating process on segments weak. Pygidium effaced, with weakly defined axis; pygidial doublure short (sag.), with distinct terrace ridges.

Remarks. – Courtessole & Pillet (1975) erected the Hemibarrandiinae within the Nileidae Angelin, 1854, referring only *Hemibarrandia* Prantl & Přibyl, 1949 to the new subfamily. However, Mergl (1994) excluded *Hemibarrandia* from the Nileidae, allying it instead with *Panderia* and *Ottenbyaspis* within the Illaenidae. The main reasons for this reassignment were the presence of a rostral plate, the outline of the cephalic doublure with a connective suture and the pitted surface of the exoskeleton, resembling the pitting in other illaenids. *Hemibarrandia* was compared with *Ottenbyaspis*, the roughly contemporraneous genus represented by two rare, much smaller and insufficiently known species. However, the family name is maintained, because *Hemibarrandia* and *Svobodapeltis* share a combination of morphological features that does not fall within the diagnosis of other similarly effaced Ordovician trilobite families, especially the Illaenidae, Panderiidae and Nileidae.

The rejection of *Hemibarrandia* from the Nileidae was further promoted by Mergl (2006). This step was based on the nature of the connective suture on the ventral cephalic doublure. Although the rostral plate of *Hemibarrandia* is still unknown, the connective suture is apparently oblique and converges backwards (Mergl 2006, text-figs 12E, 13), suggesting that *Hemibarrandia* is not a nileid (see also Whittington 2003). The ventral cephalic doublure of *Svobodapeltis* is inadequately known, similarly as in *Hemibarrandia*, but a short (sag.) and wide (tr.) preserved part of the cephalic doublure (Fig. 3B–D) likely represents the rostral plate with backward converging connective suture. That *Hemibarrandia* has unusual morphology within the Nileidae has been stated already by Poulsen (1959). *Hemibarrandia* differs from other Nileidae also in the transverse outline of the cephalon, the presence of a lateral border furrow, the pitted surface of the exoskeleton, the lack of terrace lines on the dorsal surface, except on the marginal rim, and absence of lirae, which are a commom feature on some nileids (*Symphysurus*, *Kodymaspis*).

Unlike the illaenids, *Hemibarrandia* has distinct border furrows on the fixigenae and librigenae, and these continue adaxially into a shallow but distinct furrow separating the frontal lobe of the glabella from a raised marginal rim. A cephalic marginal rim with terrace lines similar to that in *Hemibarrandia* is present in some illaenids (*e.g. Illaenus alveolatus* Raymond, 1925, *I. marginalis* Raymond, 1925; see Whittington 1965), but in the majority of illaenids this structure is absent. The well-developed thoracic pleural furrows in *Hemibarrandia* are a distinct difference from the generally effaced pleurae of illaenids.

The Hemibarrandiidae is also distinguished from the Illaenidae by the absence of the lunette and of terrace ridges on the dorsal surface of the exoskeleton (with the exception of the peripheral rim), and the weak articulating processes on the ventral surface of the thoracic segments. The pygidial doublures of *Svobodapeltis* and *Hemibar-*

randia are narrow (exs.), with no median projection or notch, which are often present in some of the earliest illaenoids (Jaanusson 1954, 1957; Fortey & Bruton 2013).

Panderiids represent the earliest illaenoids. They are generally of small size (Bruton 1968) with a strongly convex cephalon with horseshoe shaped muscle scar on the glabella, forwardly diverging dorsal furrows running close to the palpebral lobes, and a small median glabellar tubercle (Bruton 1968, Whittington 1997a). All panderiids lack pleural furrows on the thoracic segments (Bruton 1968, Whittington 1997a), a feature present in *Hemibarrandia* and *Svobodapeltis*.

Bumastines also resemble hemibarrandiids in the effaced exoskeleton, but the former have a broad axis with narrow (tr.), non-fulcrate pleurae without pleural furrows, and backwardly facing terrace ridges on the effaced cephalon. Muscle scars on the glabella, weakly expressed on bumastines, are unknown on glabellae of *Hemibarrandia* and *Svobodapeltis*, although the mode of preservation is sufficiently favourable for their expression in these genera.

Genera assigned. – *Hemibarrandia* Prantl & Přibyl, 1949; *Svobodapeltis* Šnajdr, 1957.

Genus *Svobodapeltis* Šnajdr, 1957

Type species. – *Bumastus avus* Holub, 1908; Middle Ordovician, Darriwillian, Šárka Formation; Prague Basin, Czech Republic.

Diagnosis (emended). – Hemibarrandiid with thin exoskeleton and almost smooth dorsal surface. Cephalon strongly convex (sag., tr.); axial furrow weak, slightly diverging forwards immediately in front of posterior cephalic margin, thereafter converging, broadly parabolic in outline anteriorly. Marginal rim on cephalon short (sag.), having several terrace ridges. Palpebral area narrow (tr.), palpebral lobes and eyes small, situated very far forward. Posterior area of fixigena narrow (tr.), with distinct border furrow, librigenae with broad and weakly defined border furrow. Genal angle rounded. Doublure narrow (exs.), with prominent terrace ridges. Rostral plate short (sag.) and very wide (tr.), with backwardly coverging connective suture. Thorax with nine segments, with broad (tr.), weakly convex and gently backwardly tapering axis and narrower fulcrate pleural region. Articulating furrows are not differentiated from the rest of the axial rings; axial articulating processes on posterior edges of segments transversely elongated. Pleural furrows distinct. Pygidium effaced, with broad, weakly defined parabolic axis, and with postaxial region shorter (sag.) than the axis. Small and short (tr., exs.) articulating facet. First pleural furrow distinct, others absent. Pygidial doublure short (sag.), comprising about half postaxial length of pygidium, ventrally convex, without median emargination.

Discussion. – Pleural furrows: Holloway (2007) noted that thoracic pleural furrows are present in the styginids *Perischoclonus* Raymond, 1925 (see Whittington 1963) and *Bronteopsis* Salter, 1866 (see Ingham & Tripp 1991), but these genera are exceptions in comparison with others referred to the Illaenoidea. Unlike the majority of illaenoids, the pleural furrows are clearly developed in all thoracic segments of a holaspid specimen of *Svobodapeltis* (Fig. 1E, F). Pleural regions of other Furongian and Tremadocian illaenimorph genera (*e.g.* *Ottenbyaspis* Bruton, 1968) are poorly known. The somewhat problematical species *Ottenbyaspis* (?) *broeggeri* (Růžička, 1926) from the Tremadocian of Bohemia definitely lacks pleural furrows. It is one of the stratigraphically earliest illaenids worldwide (Mergl 1994, 2006). All post-Tremadocian illaenines, bumastines, and panderiines lack pleural furrows (Jaanusson 1954; Bruton 1968; Whittington 1965, 1997a; Fortey & Bruton 2013).

Border furrows: Unlike illaeinids and panderiids, in which cephalic border furrows are absent, a shallow but distinct lateral border furrow is present in *Svobodapeltis* (Figs 2, 3A).

Preglabellar area and muscle scars: Anterior slope of glabella and preglabellar field are indistinguishable in *Illaenus* and other illaenids. The flat area between anterior of glabella and marginal rim is distinct in *Svobodapeltis* (Fig. 2). Four pairs of muscle scars on the inner surface of glabella, generally distinguishable in illaenines, were not observed in *Svobodapeltis*. This difference could be explained by the different modes of preservation in limestone and clastic rocks, respectively. However, it is worth noting that *Ectillaenus* and *Caudillaenus* collected at the same localities as *Svobodapeltis* have the muscle scars often well preserved.

Articulating furrows and process: The poorly differentiated articulating furrows in the thorax are another shared feature of illaenids and *Svobodapeltis*. Articulating processes on the internal surface of segments are typical of illaenids but in *Svobodapeltis* they are poorly developed as low, short (tr.) ridges at the posterior edge of the ventral surface of segments (Fig. 3J). This may have been why Vaněk & Valíček (2001) assigned *Svobodapeltis* to the Bumastinae.

External surface: The external surface of the dorsal exoskeleton of *Svobodapeltis* lacks terrace ridges except on the marginal rim and ventral doublures. Very fine uniform pitting is preserved on the external surface of the cephalon and pygidium. Fine pitting also covers the internal surface of the exoskeleton (Fig. 3F). Fine external pits are more or less distinctly developed in illaenids such as *Illaenus* (see *e.g.* Whittington 1965) and *Ectillaenus* (see

Bruthansová 2003). The external surface of panderiids is smooth. Bruton (1968) noted that moulds of the internal surface of the dorsal exoskeleton of *Panderia* are pitted. Pitting of internal moulds of the *Illaenus* exoskeleton was noted by Whittington (1965). *Hemibarrandia*, the supposed relative of *Svobodapeltis*, has distinct external pitting similar to that of some illaenines (*e.g. Ectillaenus benignensis*).

Doublures: The part of the ventral cephalic doublure preserved in *Svobodapeltis* likely represents the rostral plate (Fig. 3B–D). This plate has an oblique lateral termination likely representing the backwardly converging connective suture. The plate has a smooth anterior band and a posterior band covered by a few terrace ridges. The rostral plate is curved dorsally along its posterior edge. The pygidial doublure is generally wide (sag.) in illaenids (Jaanusson 1954, Whittington 1997a) but is relatively narrower in *Svobodapeltis* and *Hemibarrandia*.

Slavíčková (1999) referred *Svobodapeltis* to the Styginidae without any discussion, but later (Bruthansová 2003) she referred *Svobodapeltis* to the Illaenidae.

Hemibarrandia is remarkably similar to *Svobodapeltis*. Both are of similar size, have similarly effaced cephala, cranidia that are weakly but clearly outlined anteriorly, and axial furrows that are distinct posteriorly but become weaker anteriorly. Other shared features are as follows: absence of lunette and terrace ridges, narrow (tr.) fixigenae with distinct border furrow, rounded librigenae with shallow border furrow, small eyes, similarly raised cephalic marginal rim with terrace ridges, backwardly convergent connective suture, fulcrate thorax, broad (tr.) axis, and pleural furrows in all segments. The pygidium of *Hemibarrandia* is similarly effaced (Mergl 2006, text-fig. 12M, N), but is distinctly wider transversely in *Svobodapeltis* (Lp/Wp 0.52 to 0.66 as opposed to 0.75 in *Svobodapeltis*). The dorsal surface of *Svobodapeltis* is generally smooth, devoid of pitting and terrace ridges, but in *Hemibarrandia* it is distinctly pitted, also on thoracic axial rings (Mergl 2006, text-figs 11G, I, M, 12J). *Svobodapeltis* has nine segments in the thorax (Šnajdr 1957; Fig. 1A herein). Another almost complete specimen (Fig. 1E, F) displays only eight segments, but the first segment is likely displaced beneath the cranidium. *Hemibarrandia* was reconstructed with only eight segments but the reconstruction was based on a single trunk (Mergl 2006, text-fig. 12) with partially displaced segments, and it is possible that it also has nine segments.

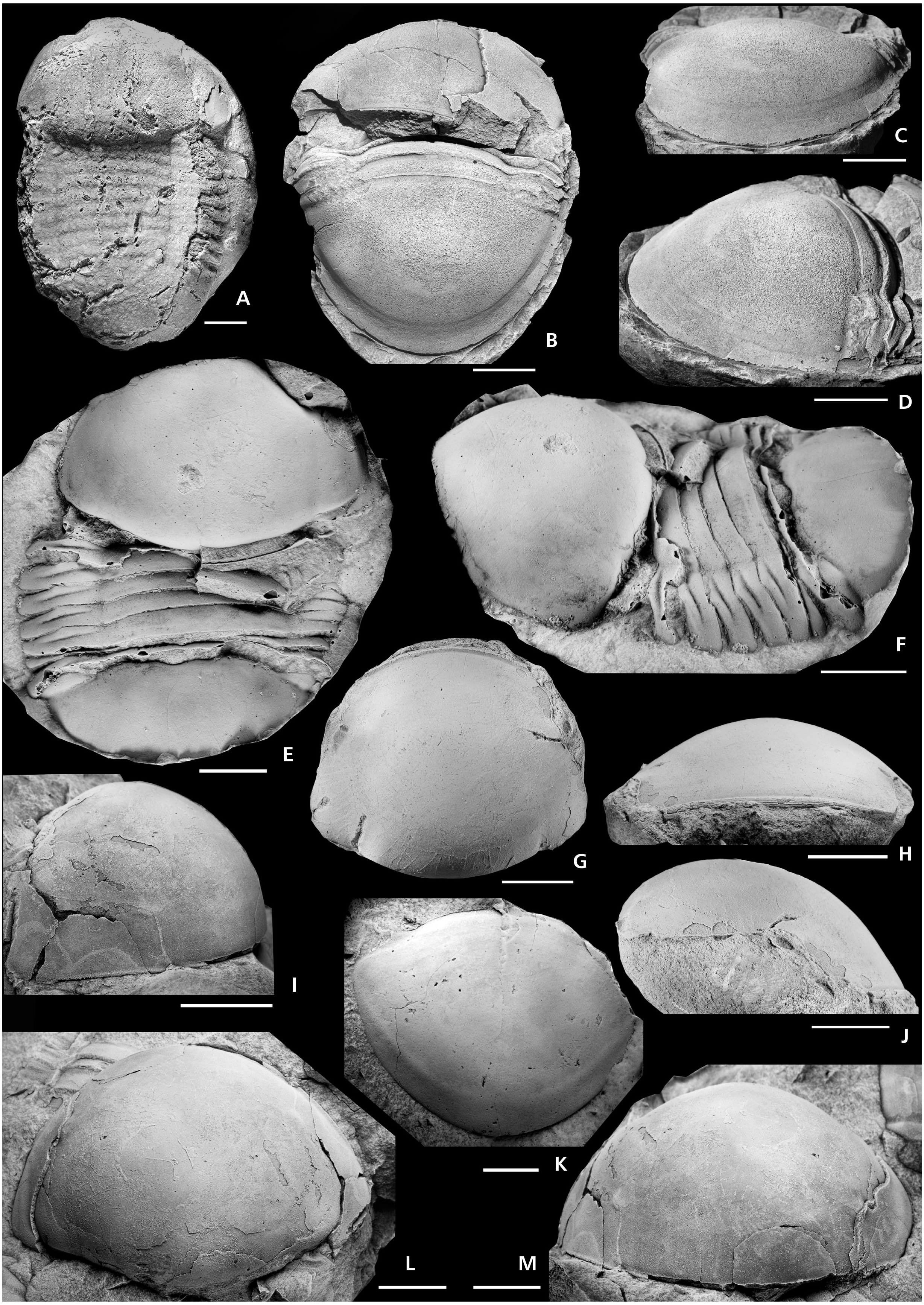
Remarks. – The genus is monospecific. *Svobodapeltis* is similar to other illaenimorph trilobites in its generally effaced exoskeleton but there are other subtle but important differences. Whittington (1997a) critically refined the definition of the Illaenidae. He concluded that the main features, shared by all (including the earliest) illaenids are: effacement, absence of preglabellar field, four pair of glabellar muscle scars, trapezoidal rostral plate, external surface with sculpture of backward facing terrace ridges, and lack of pleural furrows in the trunk. Primitive characters of the Illaenina are also listed by Holloway (2007, pp. 3–4). These comprise, among others, the presence of lunette adjacent to L1 and absence of preglabellar field. The lunette is not developed and a bordered preglabellar area is present in *Svobodapeltis* (Fig. 2). Adopting Holloway's (2007) definition, *Svobodapeltis* could not belong to the Illaenina.

Svobodapeltis avus **(Holub, 1908)**
Figures 1–3

1908 *Bumastus avus* Holub, p. 12, pl. 1, fig. 2.
1916 *Bumastus avus*? Holub. – Klouček, p. 10.
1957 *Svobodapeltis avus* (Holub, 1908). – Šnajdr, p. 119 (partim), fig. 37, pl. 12, fig. 2 [(*non* text-fig. 36, pl. 6, fig. 1, pl. 12, fig. 1 = *Caudillaenus advena* (Barrande, 1872)].
1970 *Svobodapeltis avus* (Holub, 1908). – Horný & Bastl, p. 66 (partim), pl. 8, fig. 5.
1972 *Svobodapeltis avus* (Holub, 1908). – Kraft, p. 5, pl. 3, fig. 2.
1989 *Illaenus pragensis* (Klouček). – Pek & Vaněk, p. 17 (partim).
1999 *Svobodapeltis avus* (Holub, 1908). – Slavíčková, p. 361.
2001 *Svobodapeltis avus* (Holub, 1908). – Vaněk & Valíček, p. 33.
2003 *Svobodapeltis avus* (Holub, 1908). – Bruthansová, p. 187 (*partim*), fig. 16a [*non* fig. 16b = *Caudillaenus advena* (Barrande, 1872)].

Holotype. – By monotypy; pygidium preserved as internal mould in a siliceous nodule, figured by Holub (1908, pl. 1, fig. 2), re-figured by Kraft (1972, pl. 3, fig. 2), and in Fig. 1A herein; MR 2875, old label MR 1-21.

Figure 1. *Svobodapeltis avus* (Holub, 1908), lower Darriwilian, Šárka Formation, localities Praha-Vokovice (A–D), Těškov (E, F), Osek (G–J, L, M), and Rokycany (K). Scale bar 10 mm. • A – incomplete, very poorly preserved dorsal exoskeleton, CGS JV 1479. • B–D – pygidium with three thoracic segments and incomplete, deformed cephalon, internal mould in dorsal, oblique posterior and oblique posterolateral views, NM L 19296. • E, F – incomplete dorsal exoskeleton, latex cast of external mould, CGS JP 32. • G, H, J – cranidium with silicified exoskeleton in dorsal, anterior and lateral views, CGS CW 9. • I, L, M – cephalon, internal mould in lateral, dorsal and anterior views, MR 2879. • K – pygidium, holotype, internal mould, MR 2875.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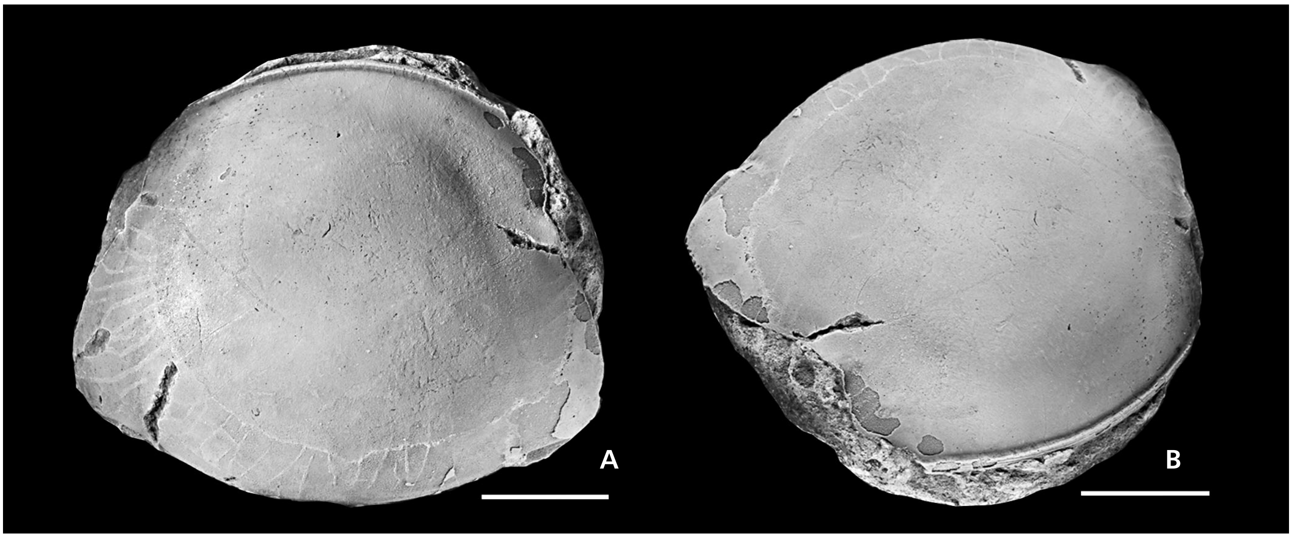

Figure 2. *Svobodapeltis avus* (Holub, 1908), lower Darriwilian, Šárka Formation, locality Osek. Scale bar 10 mm. Internal mould of the cranidium with remains of silicified exoskeleton at right posterior corner of the fixigena. Low angle illumination is used to show the outline of glabella and preglabellar area, CGS CW 9.

Type horizon. – Lower Darriwilian, Šárka Formation.

Type locality. – Osek near Rokycany.

Material. – Locality Osek: Cephalon, internal mould in siliceous nodule, MR 2879; cranidium, internal mould on siliceous nodule, CGS CW 9; cephalon with fragment of thorax, WBM S 4592. Locality Praha-Vokovice: Deformed cephalon with part of thorax and pygidium, NM L 19296 (old label ČD 355); incomplete pygidium, internal and external mould in siliceous nodule, GS JV 1450; incomplete pygidium, internal and external mould in siliceous nodule, CGS JV 1450; complete specimen on surface of siliceous nodule, CGS JV 1479, incomplete pygidium, internal and external mould in siliceous nodule, CGS JV 1476; a poorly preserved dorsal exoskeleton in shale, from Praha-Vokovice (Ke Dvoru), in the private collection of Luboš Henkl. Locality Rokycany: Incomplete cranidium, incomplete thorax and fragment of pygidium, internal mould in siliceous nodule, MR 2876; pygidium, internal mould in siliceous nodule, MR 2878. Locality Těškov: Almost complete specimen, external mould in broken siliceous nodule, GS JP 32; cranidium with detached rostral plate, internal and external moulds in siliceous nodule, GS FN 1; three cranidia and a pygidium preserved in siliceous nodules, from Těškov, in the private collection of the second author (V.K.).

Diagnosis. – As for genus.

Description. – Exoskeleton thin, having nearly smooth dorsal surface, with terrace ridges present only on the anterior rim of cephalon. Cephalon semielliptical in outline (tr.), highly convex (sag., tr.) with somewhat flatter anterior part; anterior margin evenly curved in dorsal view and slightly arched in anterior view. Glabellar outline very weakly visible on the internal surface of the cranidium, externally being even more indistinct. Glabella parabolic in outline in anterior two-thirds, narrowing slightly backwards in posterior third, occupying 80% of the cranidium (sag.), anterolaterally marked by weak change of convexity from fixigenae and the preglabellar area. In its posterior portion, the glabella distinctly marked by short and shallow axial furrows. Distinct axial furrows disappear at one-sixth length of the cranidium (exs.). Occipital furrow absent. Fixigenae steeply sloping abaxially, weakly convex (tr.), narrowest (tr.) opposite palpebral lobes, expanding anteriorly and posteriorly. Posterior border furrow distinct, broad and deep (Fig. 3B), running parallel with the posterior margin and disappearing before meeting the suture. Preocular branch of the facial suture initially diverges weakly forwards in front of eyes, then turns inward, crosses the anterior rim, runs along marginal rim of the cranidium and apparently meets a short (sag., exs.) rostral plate. Posterior branch of the facial suture broadly arcuate, diverging backwards from the eye and subsequently converging in its most posterior part. Palpebral lobes small, situated at 30% of length of cephalon in plan view. Eyes very small, elongate-oval (Figs 1I, 3F), with the visual surface steeply sloping and facing anterolaterally. Librigenae narrow (tr.) in dorsal view, steeply sloping abaxially, with broad and very shallow (tr.) border furrow (Fig. 3A), with rounded genal angle. Connective suture short, converging backward (Fig. 3C, D). Hypostome is unknown. Presumed rostral plate short (sag.), wide (tr.), with smooth anterior and ridged posterior bands on its exterior. Interior

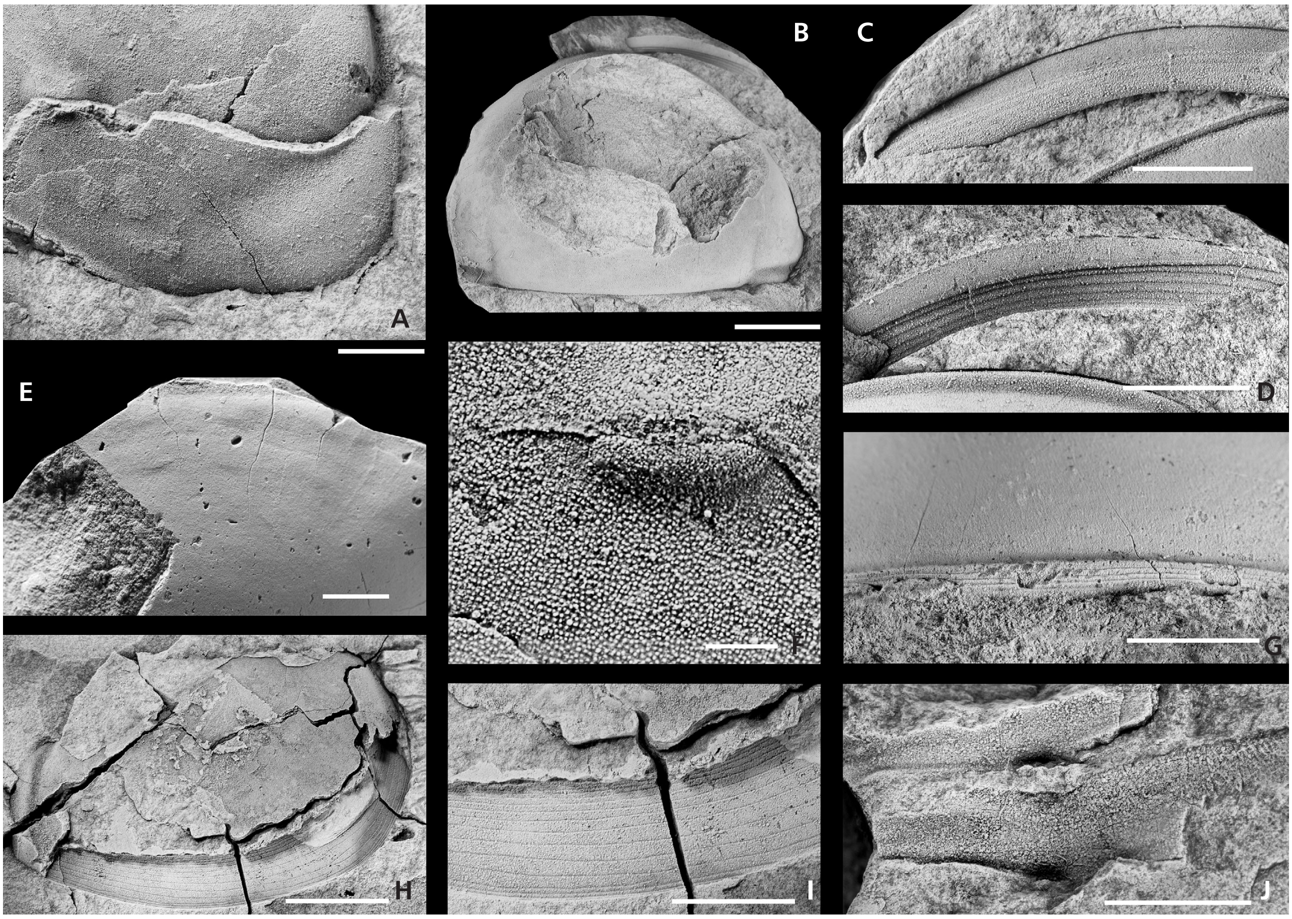

Figure 3. *Svobodapeltis avus* (Holub, 1908), lower Darriwilian, Šárka Formation, localities Osek (A, F, G), Těškov (B–D), Praha-Vokovice (H, I), and Rokycany (E, J, K). Scale bar 10 mm (A, B, H), 5 mm (C–E, G, I, J), and 1 mm (F). • A, F – cephalon, detail of left librigena with border furrow and detail of eye, internal mould, MR 2879. • B–D – cranidium with displaced rostral plate, and details of rostral plate, internal and external moulds, CGS FN 1. • E – pygidium, internal mould showing axial rings, MR 2878. • G – elevated rim at anterior margin of the cranidium, CGS CW 9. • H, I – pygidium, internal mould in posterolateral view, and detail of doublure with terrace ridges, CGS JV 1450. • J – detail of thoracic segments, internal mould showing low articulating processes, axis at right, MR 2876.

surface of glabella without distinct imprints of muscle areas.

Thorax of nine segments, with the first and last three segments slightly narrower (tr.) than second to sixth segments (Fig. 1A). Axis broad, occupying more than 60% width of the thorax, weakly tapering backwards, width of last axial ring 90% that of the first axial ring; axial furrow weak. Axial rings gently convex transversely and weakly convex sagittally, of uniform length (sag., exs.). Articulating furrow not defined. Doublure very short (sag., exs.). Pleurae fulcrate, inner and outer parts equal in width (tr.) on all segments. Pleural furrows narrow (exs.), distinct, dying out rather abruptly beyond fulcrum. Anterior pleural band is narrower than posterior band proximally, at the fulcrum they are of about equal length. Articulating facet narrowly triangular, weakly defined. Low, triangular articulating processes present at the posterior inner edges of each segment (Fig. 3J). Pleural tips bluntly rounded.

Pygidium broadly semielliptical, 75% as long as wide, gently convex (tr.), with more flattened axial part than the pleural regions. Axis poorly defined, parabolic in outline, occupying two-thirds pygidial length (sag.). Axial furrow absent. Pygidial segmentation not defined on exterior of exoskeleton but very weak ridges and paired muscle impressions that are barely visible on interior suggest the presence of about six axial rings and five pleural ribs (Figs 1K, 3E). Strongly raised anterior pleural band of first pygidial segment separated from remaining smooth portion of pleural region by shallow pleural furrow (Figs 1B, D, 3H); marginal zone of pleural region weakly concave outside distinct paradoublural line. Pygidial doublure convex, narrow, less than 20% of pygidial length (sag.), gently tapering anterolaterally, without median emargination or projection. Terrace ridges on doublure (Fig. 3I), and fine pitting on inner surface of dorsal shield are present.

The reconstructed size of exoskeletons indicates a length of approximately 100 mm and width of about 50 mm width in the majority of available specimens. The fragments indicate that some individuals may have been larger.

Remarks. – Klouček (1916, p. 10) based his new species *Bumastus pragensis* on a large cephalon with seven articulated thoracic segments (Fig. 4A–C). The same specimen was assigned to *Svobodapeltis avus* by Šnajdr (1957, text-fig. 36, pl. 12, fig. 1) and Bruthansová (2003, fig. 16b) but we consider that it belongs to *Caudillaenus advena* Barrande, 1872. Our conclusion is based on the following features:

(i) Presence of distinct muscle impressions on internal surface of glabella (Šnajdr 1957, text-fig. 36, pl. 6, fig. 1), which are characteristic for *C. advena,* and large palpebral lobes (Fig. 4A, E, F).

(ii) The forward convergence of the cephalic axial furrows behind the lunette was apparently exaggerated by compression of the cephalic shield (Fig. 4A); this feature probably led Šnajdr to differentiate the cephalon from all species of *Ectillaenus*, but other compressed cephala of *C. advena* show the same anterior convergence of the axial furrows (Fig. 4E).

(iii) The presence of a short (sag.) rostral plate with prominent terrace lines of the same outline as present in *C. advena* (Fig. 4C), and the presence of terrace ridges on cephalon (Fig. 4F) and segments (Fig. 4G) are further important features.

The seemingly broad axis and narrow pleural fields in the holotype of *B. pragensis* is probably the result of deformation. The steeply sloping part of the thoracic pleurae lateral to the fulcrum is not preserved in the siliceous nodule, because these parts were outside the nodule during its formation. The short horizontal part of the pleural field on the first and second segments is a characteristic feature of *C. advena* (Fig. 4D). Other segments of *C. advena* have this horizontal part slightly longer. In the holotype of *B. pragensis* (Fig. 4A), the thoracic pleurae are preserved only on the first to fifth segments, and the abaxial parts of the pleurae are truncated. As a result, the apparent width (tr.) of the axis is exaggerated, giving a bumastine appearance to the specimen.

Occurrence. – Middle Ordovician, lower Darriwilian, Šárka Formation, *Corymbograptus retroflexus* Biozone; Czech Republic, localities Osek, Praha-Vokovice, Rokycany and Těškov.

Suborder Illaenina Jaanusson, 1959
Superfamily Illaenoidea Hawle & Corda, 1847
Family Illaenidae Hawle & Corda, 1847

Genus *Caudillaenus* Rábano, Gutiérrez-Marco & García-Bellido, 2014

Type species. – *Caudillaenus nicolasi* Rábano, Gutiérrez-Marco & García-Bellido, 2014; Middle Ordovician, Darriwilian, Taddrist Formation, Anti-Atlas, Morocco.

***Caudillaenus advena* (Barrande, 1872)**
Figures 4, 5H

1872 *Illaenus advena* Barrande, p. 66, pl. 6, figs 5–10, pl. 14, figs 37, 38.
1884 *Illaenus advena* Barrande, 1872. – Novák, p. 17.
1916 *Illaenus advena* Barrande, 1872. – Raymond, p. 12.
1916 *Illaenus* cf. *advena* Barrande, 1872. – Klouček, p. 11.
1916 *Bumastus pragensis* Klouček. – Klouček, p. 10.
1918 *Illaenus advena* Barrande, 1872. – Novák *in* Perner, p. 26.
1953 *Bumastus pragensis* Klouček. – Přibyl, p. 29.
1957 *Ectillaenus advena* (Barrande, 1872). – Šnajdr, p. 203, pl. 2, fig. 8, pl. 6, text-figs 21, 22.
1957 *Svobodapeltis avus* (Holub, 1908) (partim). – Šnajdr, p. 243, pl. 12, fig. 1, text-fig. 36.
1970 *Ectillaenus advena* (Barrande, 1872). – Horný & Bastl, p. 53.
1989 *Ectillaenus advena* (Barrande, 1872). – Pek & Vaněk, p. 17.
1999 *Ectillaenus advena* (Barrande, 1872). – Slavíčková, p. 361.
2001 *Ectillaenus* (n. subg.?) *advena* (Barrande, 1872). – Vaněk & Valíček, p. 32.
2003 *Ectillaenus advena* (Barrande, 1872). – Bruthansová, p. 172, fig. 6a–e.
2003 *Svobodapeltis avus* (Holub, 1908) (partim). – Bruthansová, p. 187, fig. 16b [non fig. 16a = *Svobodapeltis avus* (Holub, 1908)].

Lectotype. – Designated by Šnajdr (1957); NM L 16740, enrolled specimen preserved as internal mould in siliceous nodule, figured by Barrande (1872, pl. 66, fig. 5), refigured by Bruthansová (2003, fig. 6a, c).

Type horizon. – Lower Darriwilian, Šárka Formation.

Type locality. – Osek near Rokycany.

Material. – More than sixty specimens (articulated dorsal exoskeletons, cephala, pygidia, librigenae) and two hypostomes, all preserved in siliceous nodules.

Remarks. – Apart from *Zbirovia arata* (Barrande, 1872) from the Dobrotivá Formation (Upper Darriwilian), all Middle Ordovician illaenids from Bohemia revised by

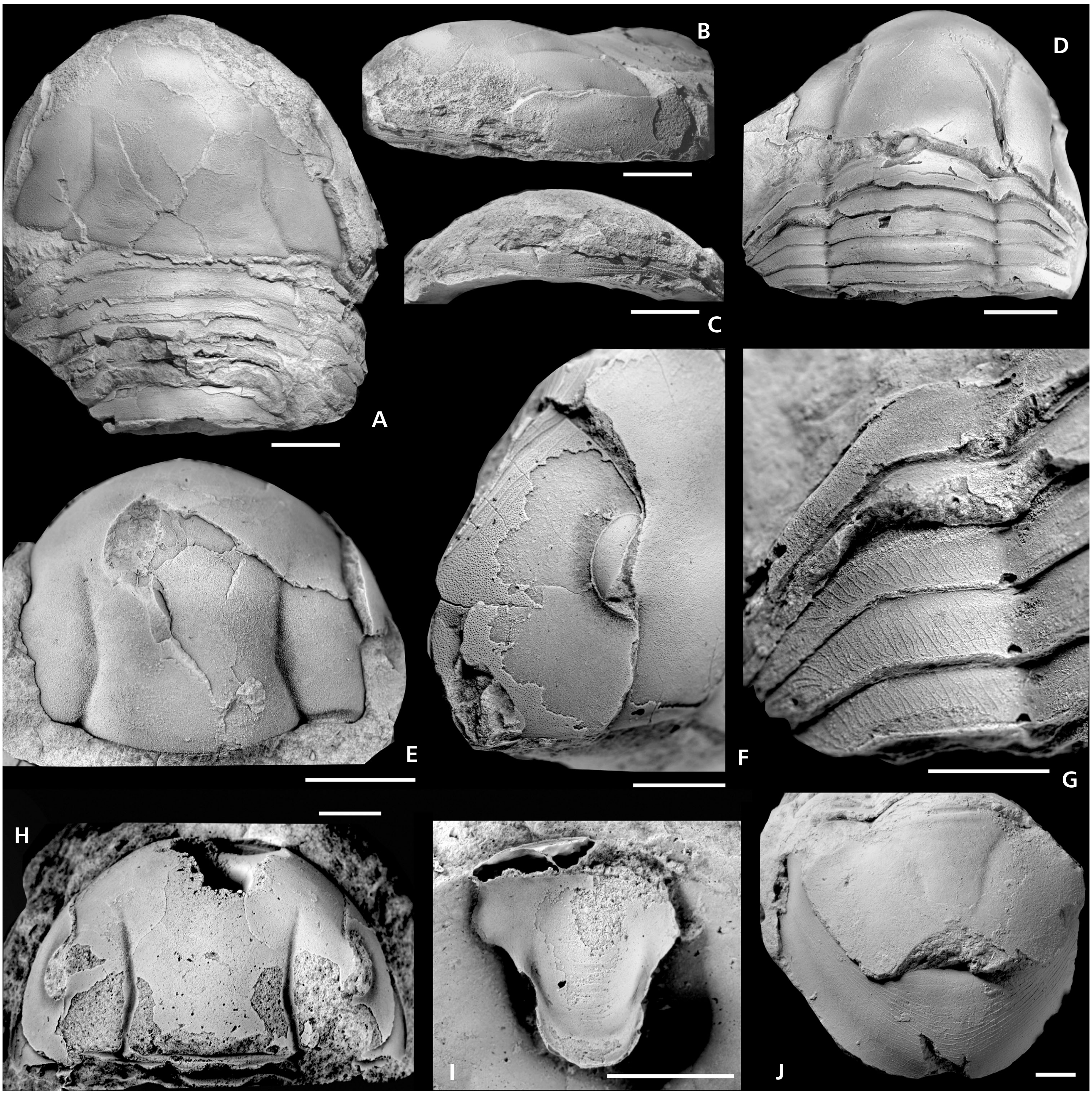

Figure 4. *Caudillaenus advena* (Barrande, 1872), lower Darriwilian, Šárka Formation, localities Praha-Vokovice (A–C), and Osek (D–G), Rokycany (H, I), Rokycany-Litohlavy (J). Scale bar 10 mm (A–E) and 5 mm (F–J). • A–C – cephalon with seven segments, internal mould, NM L19281. • D, G – cephalon with six segments, and detail of pleural region with terrace ridges of the silicified exoskeleton, CGS CW 6. • E – compressed cephalon, internal mould, CGS CW 7. • F – left librigena with eye, internal mould with partly silicified exoskeleton showing terrace ridges, CGS CW 8. • H, I – cephalon with hypostome *in situ*, internal mould, and latex cast of the hypostome, MR 12658. • J – pygidium showing doublure, internal mould, MR 156.

Šnajdr (1957) and Bruthansová (2003), including *Illaenus advena* Barrande, 1872, have been referred to *Ectillaenus* Salter, 1867. However, *Ectillaenus advena* is clearly distinct from other species of *Ectillaenus* in its larger eyes, comparatively longer axial furrows in the cephalon, broader axis and narrower pleural fields in the thorax, and in the shape of the hypostome. Doubts about the assignment *E. advena* to *Ectillaenus* have already been expressed by Vaněk & Valíček (2001). Bruthansová (2003) outlined its similarity to *Parillaenus* Jaanusson, 1954, apart from the shape of the pygidium, which in its parabolic outline is more similar to pygidia of *Ectillaenus*. We suggest that, on the basis of the features mentioned below, that *Ectillaenus advena* and its suggested ancestor *E.* aff *advena* can be reliably referred to the genus *Caudillaenus* Rábano, Gutiérrez-Marco & García-Bellido, 2014.

The eyes of *C. advena* are large and reniform, whereas in most species of *Ectillaenus*, except *E. giganteus* (Burmeister, 1843) (see Rábano 1990), the eyes are tiny or absent (Fortey & Owens 1987, Bruthansová 2003). The distinct subocular furrow that is characteristic of *C. nicolasi* is present also in *C. advena* (Fig. 5H).

The cranidium of *C. advena* like that of *C. nicolasi* is more strongly and more evenly convex (sag.) than in species of *Ectillaenus*, and the cephalic axial furrows are long and converge forwards behind the lunette and diverge forwards in front of it, whereas in *Ectillaenus* the axial furrows are subparallel and restricted only to the posterior part of the cranidium. The hypostome of *Ectillaenus* is triangular with nearly transverse anterior margin and long, rather narrow anterior wings (Šnajdr 1957, pl. 2, fig. 10, pl. 3, fig. 4; Fortey & Owens 1987). The hypostome of *C. advena* is longer (sag.), with broad anterior wings (Šnajdr 1957, pl. 6, fig. 2; see Fig. 4I herein). Its morphology is similar to the hypostome of *Illaenus sarsi* Jaanusson, 1954 from the Kundan Stage (Darriwilian) of Sweden. However, the hypostome of *C. nicolasi* is poorly known (Rábano *et al.* 2014).

Caudillaenus advena as well as *C. nicolasi* have a relatively wide (tr.) thoracic axis (Fig. 4D), and the horizontal part of the pleurae adaxial to the fulcrum is very narrow (tr.) on the first segment but much wider on the next segment (Fig. 4G; Rábano *et al.* 2014, fig. 3A).

Caudillaenus nicolasi has a triangular pygidium that is much longer than the cephalon and has a vincular furrow on the doublure. The pygidium of *C. advena* is parabolic in outline (Bruthansová 2003, fig. 6e) but is not as elongated as that of *C. nicolasi*, and the doublure is weakly sigmoidal in longitudinal section with a more poorly defined (but present) vincular furrow than in *C. nicolasi* (Fig. 4J). The shape and length of the pygidial axis is almost the same in *C. nicolasi* and *C. advena*. Despite the difference in the posterior outline of the pygidia we suggest that *C. advena* should be referred to *Caudillaenus*.

Occurrence. – Middle Ordovician, lower Darriwilian, Šárka Formation, *Corymbograptus retroflexus* Biozone; Czech Republic, localities Osek, Rokycany, Drahouš, Sirá, Těškov, Mýto (Svatoštěpánský pond), and Praha-Vokovice.

***Caudillaenus* aff. *advena* (Barrande, 1872)**
Figure 5A–I

1991a *Ectillaenus* sp. – Mergl, p. 197, pl. 1, figs 6, 7.
2004 *Ectillaenus* aff. *advena* (Barrande, 1872). – Doubrava & Vokáč, p. 125, fig. 1.

Material. – Internal mould of a cranidium with displaced right librigena (WBM S 06019); and internal mould of a pygidium with external mould of the doublure exposed, and with librigena and fragments of thoracic segments on the same slab (CGS MM 406).

Remarks. – We have examined the newly prepared cranidium with displaced librigena that was originally figured by Doubrava & Vokáč (2004, fig. 1). The specimen is not deformed and shows, though not evident in the original illustration, the entire posterior margin and posterior part of the axial furrows. The axial furrows are subparallel posteriorly but clearly diverge forward from a point opposite the front of the palpebral lobes. The glabella is narrowest at the lunette. The transition from the parallel part to gently diverging part of the axial furrows is gradual in *C.* aff. *advena* (Fig. 5A, B), unlike *C. advena* in which the transition from the forwardly convergent posterior part of the axial furrow to the forwardly divergent anterior part is abrupt (Fig. 4H). There are other shared features between *C. advena* and *C.* aff. *advena*, which distinguished both from *Ectillaenus*, namely the same strong convexity (sag.) of cranidium (Fig. 5G), size and location of palpebral lobes (Fig. 5B, C), and distinct terrace ridges on exterior of the anterior slope of the cranidium (Fig. 5F).

A fragmentary pygidium, of which only the external mould of the doublure is preserved (Fig. 5E), comes from the same locality and horizon as the cranidium of *C.* aff. *advena* and is assumed to belong to the same species. The doublure is broad with distinct terrace ridges, and is gently convex (sag.) in its posterior part. The outline, strength of the terrace ridges and low, ventrally convex sagittal ridge near the anterior margin of the doublure are the same as in *C. advena* (Fig. 4J).

The available data show that *C.* aff. *advena* represents a closely related, but likely a different species which was ancestral to *C. advena. Caudillaenus* aff. *advena* is the stratigraphically earliest illaenid in the Prague Basin.

Occurrence. – Middle Ordovician, Dapingian, Klabava Formation (volcano-sedimentary Komárov Complex), locality Malá Víska, dumps of abandoned iron ore mine Hlava.

Svobodapeltis and the earliest illaenoids

Despite the overall illaenimorph configuration of *Svobodapeltis*, there are important differences, which distinguish it from members of the Illaenidae and the Panderiidae. Bruton (1968) demonstrated the absence of pleural furrows in *Panderia*, one of the earliest illaenoids. Pleurae of similar form, with a single longitudinally convex band lacking the pleural furrow, are typical of Illaenidae (Jaanusson 1954, Whittington 1997a) and other Illaenina (Styginidae: Whittington 2000, Holloway 2007),

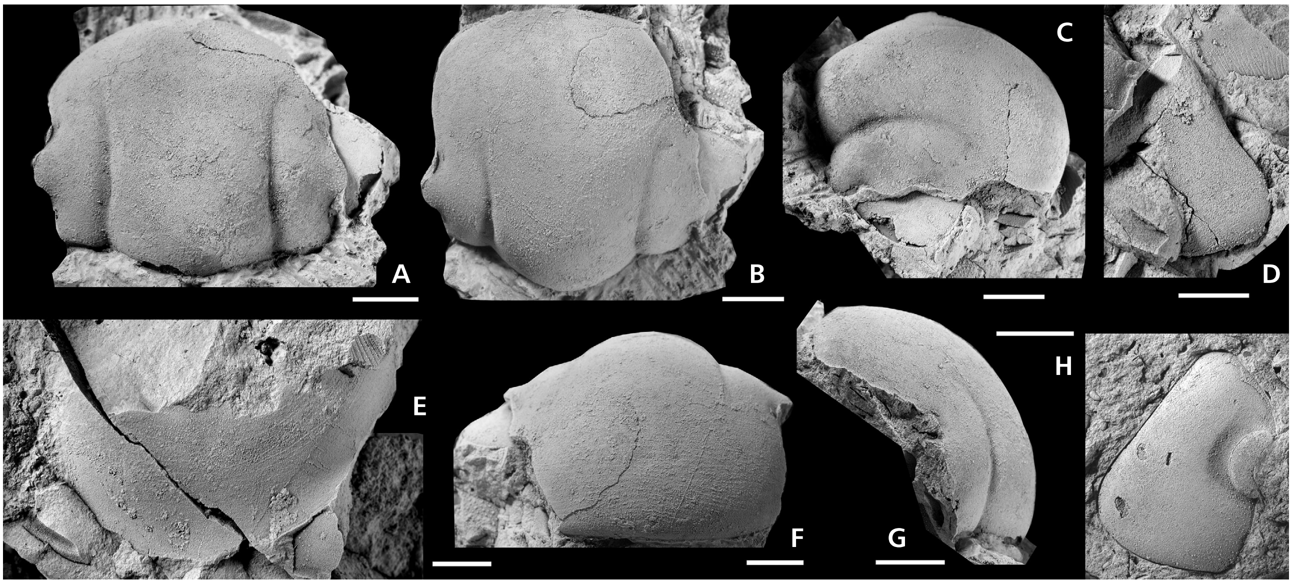

Figure 5. *Caudillaenus* aff. *advena* (Barrande, 1872), Dapingian, Klabava Formation, locality Hlava near Malá Víska (A–G). Scale bar 5 mm. • A–C, F, G – cranidium, internal mould in dorsal and anterodorsal views, in oblique view showing right librigena, anterior and anterior views, WBM S 6019. • D – incomplete right librigena, internal mould, GS MM 406. • E – pygidial doublure, internal mould, GS MM 406. • H – *Caudillaenus advena* (Barrande, 1872), Darriwilian, Šárka Formation, locality Cekov (H). Scale bar 5 mm. Left librigena, internal mould, MR 367.

The earliest known illaenids come from the late Tremadocian or earliest Floian of Scandinavia (Moberg & Segerberg 1906, Tjernvik 1956, Bruton 1968) and North China (Zhou & Fortey 1986). These early species are known only from cranidia and pygidia, and thoracic segments are unknown. The next stratigraphically younger (Darriwilian) illaenids [*e.g. Illaenus sarsi* Jaanusson, 1954, *Illaenus* (*Parillaenus*) *primoticus* Fortey & Bruton, 2013] lack glabellar and occipital furrows, the posterior border furrow of the cephalon, and pleural furrows within the trunk (Jaanusson 1957, pl. 4, figs 1–9; see also Whittington 1997a, figs 7.1–7.6). Whittington (1997a) suggested that the absence of glabellar, occipital and pleural furrows is a primitive character of this group.

Presence of pleural furrows in the thorax and pygidium is one of the earliest and most typical characters of the trilobite clade (Whittington 1997b). Lack of pleural furrows seems likely to be a synapomorphy of illaenids, panderiids, scutelluids and styginids, but pleural furrows are present in *Perischoclonus* and some species of *Bronteopsis*, suggesting that they were also present in the ancestor of these groups (Whittington 2000). However, in *Svobodapeltis*, as well as in *Hemibarrandia*, the pleural furrows are distinctly developed in large holaspides (Fig. 1E, F). This suggests that ancestors of *Svobodapeltis* must have separated from the last common ancestor of illaenids and panderiids before the development of effaced pleurae. If the styginid-scutelluid group originated independently from illaenids and panderiids (Whittington 1997a), smooth pleurae also developed independently, by parallel evolution. As mentioned above, the earliest members of this clade have the pleural furrows present, at least in young growth stages (Whittington 1950, 1963; Holloway 2007).

Furongian illaenimorph trilobites that could be ancestors of illaenids were discussed especially by Whittington (1997a). *Parakoldinia* Rozova, 1960 from the Furongian of Siberia (Rozova 1968, 1977) and Turkey (Shergold & Sdzuy 1984) closely resembles *Panderia*. If *Parakoldinia* and its late Cambrian relatives (Shergold & Sdzuy 1984, Lu & Zhou 1990) are early panderiids or illaenids, then the illaenid resemblance of *Hemibarrandia* and *Svobodapeltis* derived from their shared ancestors by parallel evolution in the late Cambrian. Thus, the Hemibarrandiidae could be the sister group of the Illaenidae and the Panderiidae, and may represent a separate illaenoid group in which furrowed pleurae were retained.

Gondwanan relatives of *Svobodapeltis*

The combination of illaenimorph features and furrowed pleurae is known in several species, which stratigraphically preceded *Svobodapeltis avus.* These species, all referred to *Hemibarrandia* Prantl & Přibyl, 1949, occur exclusively in the Lower Ordovician of West Gondwana (present Central Europe). *Hemibarrandia* includes large-sized trilobites having an effaced glabella bounded by weakly developed, subparallel, short axial furrows, narrow fixigenae with a small palpebral lobe, distinct posterior and lateral border furrows on the cephalon, the anterior marginal rim with terrace ridges, rounded genal angle, broad axis, fulcrate thorax, almost effaced pygidium with short (exs.)

ventrally convex doublure, and shallow but distinct pleural furrows in the thorax.

Hemibarrandia stratigraphically precedes *Svobodapeltis* as well as illaenines and bumastines, but is approximately contemporaneous with the earliest panderiines (Jaanusson 1954, 1957; Whittington 1965; Bruton 1968). *Hemibarrandia holoubkovensis* (Růžička, 1926) and *H. klouceki* Mergl, 2006 are known from the Tremadocian of the Czech Republic (Růžička 1926; Mergl 1994, 2006), and *H. triangula* Sdzuy, 1955 and unnamed species are known from Bavaria (Sdzuy 1955; Hammann & Sdzuy *in* Sdzuy *et al.* 2001). There are no reports of *Hemibarrandia* from the Floian or Dapingian.

Although the distinctly pitted external surface of *Hemibarrandia* differs from the much more finely pitted surface of *Svobodapeltis*, there are many shared features indicating that *Hemibarrandia* is the probable evolutionary ancestor of *Svobodapeltis*. Restriction of *Hemibarrandia* to the Tremadocian of Central Europe and *Svobodapeltis* to the Darriwilian of Bohemia indicates that evolution of the Hemibarrandiidae took place in a restricted area within high-latitude West Gondwana, independent of the early evolution of the Illaenidae and Panderidae in temperate Baltica, tropical Laurentia and tropical East Gondwana.

Earliest illaenimorph trilobites in the Prague Basin

The earliest illaenimorph trilobite in the Prague Basin is the poorly known *Ottenbyaspis* (?) *broeggeri* (Růžička, 1926). This small species comes from haematites of the Třenice Formation, imprecisely referred to the mid- or early late Tremadocian (Mergl 1994, 2006). *Ottenbyaspis* (?) *broeggeri* has an effaced glabella with median glabellar tubercle, it lacks pleural furrows on the thorax (erroneously stated to be present by Mergl 2006), and has no distinct articulating half rings on the thoracic segments. The species can be referred to the Panderiidae on the basis of its small size, the thickened ventral surface of the thoracic axial rings and pleurae, the presence of moderately long eyes indicated by distinct palpebral lobes, and the presence of a marginal rim on the cephalon. The dorsal surface of the pygidium of *O.* (?) *broeggeri* is smooth externally with a post-axial ridge but its inner surface retains traces of several axial rings. The same features were illustrated by Bruton (1968) in *Ottenbyaspis oriens* (Moberg & Segerberg, 1906) from the Bjørkasholmen Limestone (late Tremadocian) of Öland, Sweden.

No panderiids and hemibarrandiids are definitely known in the Floian in Bohemia. The earliest known illaenid is the poorly known *Caudillaenus* aff. *advena* from the upper Klabava Formation (?late Dapingian, see Doubrava & Vokáč 2004). This illaenid belongs to the *Pliomerops* Association, indicative of a moderately deep-water environment comparable with the Illaenid-Cheirurid Biofacies (Mergl *et al.* 2007).

Four illaenid species are known from the Šárka Formation (lower Darriwilian): *Ectillaenus katzeri katzeri*, *E. katzeri parabolinus*, *E. sarkaensis* (see Šnajdr 1957, Bruthansová 2003) and *Caudillaenus advena*. The illaenimorph *Svobodapeltis avus* is very rare in the Šárka Formation. These trilobites are associated with a taxonomically diverse fauna of the atheloptic assemblage (Havlíček & Vaněk 1966, Havlíček 1998). The presence of cyclopygids and *Girvanopyge* indicates a deeper-water, light-deficient habitat for these illaenoids.

Conclusions

Hemibarrandia and its descendant *Svobodapeltis* represent one of the earliest Ordovician trilobites of illaenimorph type. Both genera, here referred to the redefined family Hemibarrandiidae, differ from illaenids and panderiids in the presence of pleural furrows on all segments of the trunk. Hemibarrandiids have a broad preglabellar area and peripheral rim on the cephalon, lack a lunette, and a short and broad rostral plate is present. Despite the overall morphological similarity to illaenids, panderiids and nileids, hemibarrandiids are considered to represent an independent evolutionary clade. The presence of thoracic pleural furrows is a plesiomorphy retained from the Cambrian ancestor, and distinguishes hemibarrandiids from other illaenioids in which lack of pleural furrows is an important synapomorphy. The suprafamiliar affinity of the Hemibarrandiidae is unclear.

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