

A new Late Ordovician echinoderm Lagerstätte in the Prague Basin (Barrandian area, Czech Republic)

OLDŘICH FATKA, ÉLISE NARDIN, PETR BUDIL, MARTINA NOHEJLOVÁ, ONDŘEJ ZICHA, BERNARD PITTET†, RADEK MIKULÁŠ, MARTINA AUBRECHTOVÁ, MARIKA POLECHOVÁ, JAKUB VODIČKA, FRÉDÉRIC CHRISTOPHOUL, FARID SALEH & BERTRAND LEFEBVRE



A new Late Ordovician locality yielding abundant, remarkably preserved skeletal remains of marine invertebrates was excavated at the southern slope of the Blýskava hill near Chrustenice, Barrandian area, Czech Republic. The fossil association represents a new echinoderm Lagerstätte dominated by mass occurrences of fully articulated specimens of the solutan *Dendrocystites barrandei* Bather, 1913, associated with undescribed asteroid, coronate, crinoid, diploporitans, the enigmatic genus *Hexedriocystis* Sumrall & Zamora, 2011, rhombiferans, and stylophorans. In several levels, abundant articulated ophiuroids were found. The associated skeletal fauna comprises common, usually disarticulated remains of trilobites, abundant but poorly preserved brachiopods, as well as bivalves, small bryozoans, cephalopods, conulariids, foraminiferans, gastropods, machaeridians, and rare tentaculitoid tubeworms. The brachiopod fauna corresponds to the lower part of the *Bicus spina* Community. Ichnologically, the locality represents a *Teichichnus* Ichnofacies and a depauperate *Cruziana* Ichnofacies. The skeletal fauna commonly shows articulated remains of abundant organisms that were either living or freshly killed at the time of deposition. The assemblage represents an echinoderm Lagerstätte with prevailing specimens of the genus *Dendrocystites* Barrande, 1887. • Key words: Central Bohemia, echinoderm Lagerstätte, Letná Formation, Ordovician, taphonomy, ecology.

FATKA, O., NARDIN, E., BUDIL, P., NOHEJLOVÁ, M., ZICHA, O., PITTET, B., MIKULÁŠ, R., AUBRECHTOVÁ, M., POLECHOVÁ, M., VODIČKA, J., CHRISTOPHOUL, F., SALEH, F. & LEFEBVRE, B. 2025. A new Late Ordovician echinoderm Lagerstätte in the Prague Basin (Barrandian area, Czech Republic). *Bulletin of Geosciences* 100(2), 95–122 (12 figures, electronic supplementary material). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received April 4, 2024; accepted in revised form June 23, 2025; published online July 13, 2025; issued July 13, 2025.

Oldřich Fatka (corresponding author) & Jakub Vodička, Charles University, Institute of Geology and Palaeontology, Albertov 6, 128 43 Praha 2, Czech Republic; fatka@natur.cuni.cz • Petr Budil, Martina Nohejlová & Marika Polechová, Czech Geological Survey, Klárov 3, 118 21 Prague 1, Czech Republic • Elise Nardin & Frédéric Christophoul, Géosciences Environnement Toulouse, CNRS/UT/IRD/CNES Observatoire Midi-Pyrénées, 31400 Toulouse, France • Ondřej Zicha, BioLib, z. s., Jugoslávských partyzánů 34, 160 00, Prague 6, Czech Republic • Bernard Pittet† & Bertrand Lefebvre, Université Claude Bernard Lyon 1, ENSL, CNRS, LGL-TPE, F-69622, Villeurbanne, France • Martina Aubrechtová & Radek Mikuláš, Institute of Geology, Academy of Sciences of the Czech Republic, Prague, Czech Republic • Farid Saleh, Institute of Earth Sciences, University of Lausanne, Geopolis, CH-1015, Lausanne, Switzerland

Our current knowledge of the early diversification of most metazoan phyla in Cambrian–Ordovician times remains largely hampered by historical, sampling and taphonomic biases (e.g. Saleh *et al.* 2020, Whitaker & Kimmig 2020). Echinoderms are not an exception to this rule, although they acquired the possibility to mineralize their polyplated, high-magnesium calcite endoskeleton characterized by its diagnostic three-dimensional microstructure (stereom) as early as Cambrian Stage 3 (Bottjer *et al.* 2006, Kouchinsky *et al.* 2012). Taphonomic experiments made on extant taxa indicate that, under quiet environmental conditions, most echinoderm skeletons are disarticulated within a few days or weeks following their

death (e.g. Meyer 1971, Donovan 1991, Nebelsick 1995, Kerr & Twitchett 2004). This implies that the preservation of fully articulated specimens (*i.e.* those on which most taxonomic work can be done) generally requires their burial, when alive or soon after their death, by obrution deposits such as those generated by storms or turbidites (see Seilacher *et al.* 1985; Brett *et al.* 1997; Ausich 2001, 2021). Smith (1988) coined the term “echinoderm Lagerstätten” for such levels preserving fully articulated echinoderms. Most echinoderm Lagerstätten are Konzentrat-Lagerstätten *sensu* Seilacher (1970), *i.e.* exceptionally dense accumulations of skeletal remains (e.g. the Middle Ordovician Postolonnec Formation;

Hunter *et al.* 2007; the Upper Ordovician Ouine-Inirne, Lower Ktaoua, Cantera Shale and Fombuena formations; Lefebvre *et al.* 2010, Cole *et al.* 2017, Nohejlová & Lefebvre 2022). However, some of them can be also considered as Konservat-Lagerstätten *sensu* Seilacher (1970), *i.e.* levels yielding exceptionally preserved soft or lightly sclerotized tissues and organisms (*e.g.* the Lower Ordovician Fezouata Shale, the Lower Devonian Hunsrückschiefer; Glass & Blake 2004, Lefebvre *et al.* 2019). The discovery of new echinoderm Lagerstätten, providing snapshots of past communities, is critical to better evaluate not only the diversification of echinoderms in time and space but also their morphology and their palaeoecology.

In this context, the Prague Basin (Czech Republic) represents, along with France, Morocco and Spain (Fig. 1), one of the most favourable areas to document the Ordovician diversification of echinoderms in Gondwanan and peri-Gondwanan areas belonging to the high-latitude Mediterranean Province (Lefebvre & Fatka 2003; Lefebvre *et al.* 2013, 2022). More than 150 years of active field work and scientific activity in the Prague Basin have resulted in the discovery of echinoderm Lagerstätten in most Ordovician lithostratigraphic units and the description of particularly diverse and well-known assemblages. For example, the Lower Ordovician Třenice and Mílina formations yielded one of the earliest faunas dominated by diploporitans and rhombiferans (Mergl & Prokop 2006) and particularly rich and diverse echinoderm assemblages, including asterozoans, crinoids, solutans and stylophorans, were described from concretions collected in the shales of the Šárka (Darriwilian) and Dobrotivá (late Darriwilian–early Sandbian) formations (*e.g.* Barrande 1872, 1887; Prokop & Petr 1999, 2003; Lefebvre *et al.* 2012, 2022). In the overlying Libeň Formation, articulated stylophorans occur in black shales; this group dominates echinoderm assemblages in deeper settings of Vinice and large parts of the Bohdalec and Králův Dvůr formations (Barrande 1887, Prokop & Petr 1999, Lefebvre *et al.* 2022). The latter also contains abundant articulated rhombiferans and blastozoans restricted to iron ore lenses near the base of the formation and to layers of impure carbonate in the upper part of the Králův Dvůr Formation (Mikuláš & Prokop 2002).

In contrast to the aforementioned discoveries, obrution layers yielding abundant exceptionally preserved echinoderms covering bedding planes have been documented in only three levels: (i) the late Sandbian Letná Formation with several localities yielding mass occurrences of ophiuroids or solutans (Noailles *et al.* 2014); (ii) the early Katian Zahořany Formation, especially in the stratotype section near the Zahořany municipality (Barrande 1887); and (iii) the middle Katian Bohdalec Formation, which yielded a brittlestar bed with abundant

in situ preserved specimens of *Taeniaster bohemicus* Petr, 1989 (Petr 1989, Mikuláš *et al.* 1995). Such obrution deposits correspond to snapshots documenting the occurrence of autochthonous, gregarious and possibly opportunistic benthic communities, generally dominated (numerically) by one echinoderm taxon (Lefebvre 2007). In such echinoderm-dense beds, the associated fauna is generally rare and poorly diverse (Fig. 1).

A new section yielding another echinoderm Lagerstätte was recently excavated at the Blýskava hill near the Chrštenice municipality in the upper levels of the Letná Formation. The aim of this contribution is thus to provide the first detailed sedimentological and palaeontological analysis of this echinoderm-dominated Konzentrat-Lagerstätte (for preliminary remarks, see Nohejlová *et al.* 2019 and Lefebvre *et al.* 2022), to better understand the taphonomy and palaeoecology of shallow marine palaeocommunities in the Late Ordovician of the Prague Basin.

Geological setting

Geographic and stratigraphic context

The Prague Synform is a narrow, about 200 km long, NE–SW trending denudation relic of the original sedimentary area called the Prague Basin. It is located in the central part of the Teplá-Barrandian Unit in the central Bohemian Massif (Czech Republic, Central Europe) (Fig. 2). The Prague Basin comprises Tremadocian (earliest Ordovician) to Givetian (late Middle Devonian) sedimentary deposits (Havlíček 1981, Chlupáč *et al.* 1998). Fine- and coarse-grained clastic sediments are characteristic of the Ordovician sequences. Thick accumulations of conglomerates and sandstones originated in proximal, rather shallow-water environments, while dark greywackes and shales are characteristic of more distal, deeper parts of the basin (Havlíček 1998). The sedimentation was accompanied by a rather intensive volcanic activity concentrated around several volcanic centres (including the Ordovician Komárov Volcanic Complex), which locally resulted in thick accumulations of lavas and pyroclastics (Havlíček 1998, Patočka & Štorch 2004). The vertical and lateral alternation of sandstones, greywackes and shales, with locally developed lens-like bodies of oolitic ironstones is typical of the Upper Ordovician in the Prague Basin.

In the high-latitude West Gondwanan area, including the Prague Basin, the correlation of Upper Ordovician rocks has been problematic due to the absence of graptolites and conodonts combined with a high provinciality of other fossil groups like brachiopods and trilobites. Consequently, five regional chronostratigraphic units

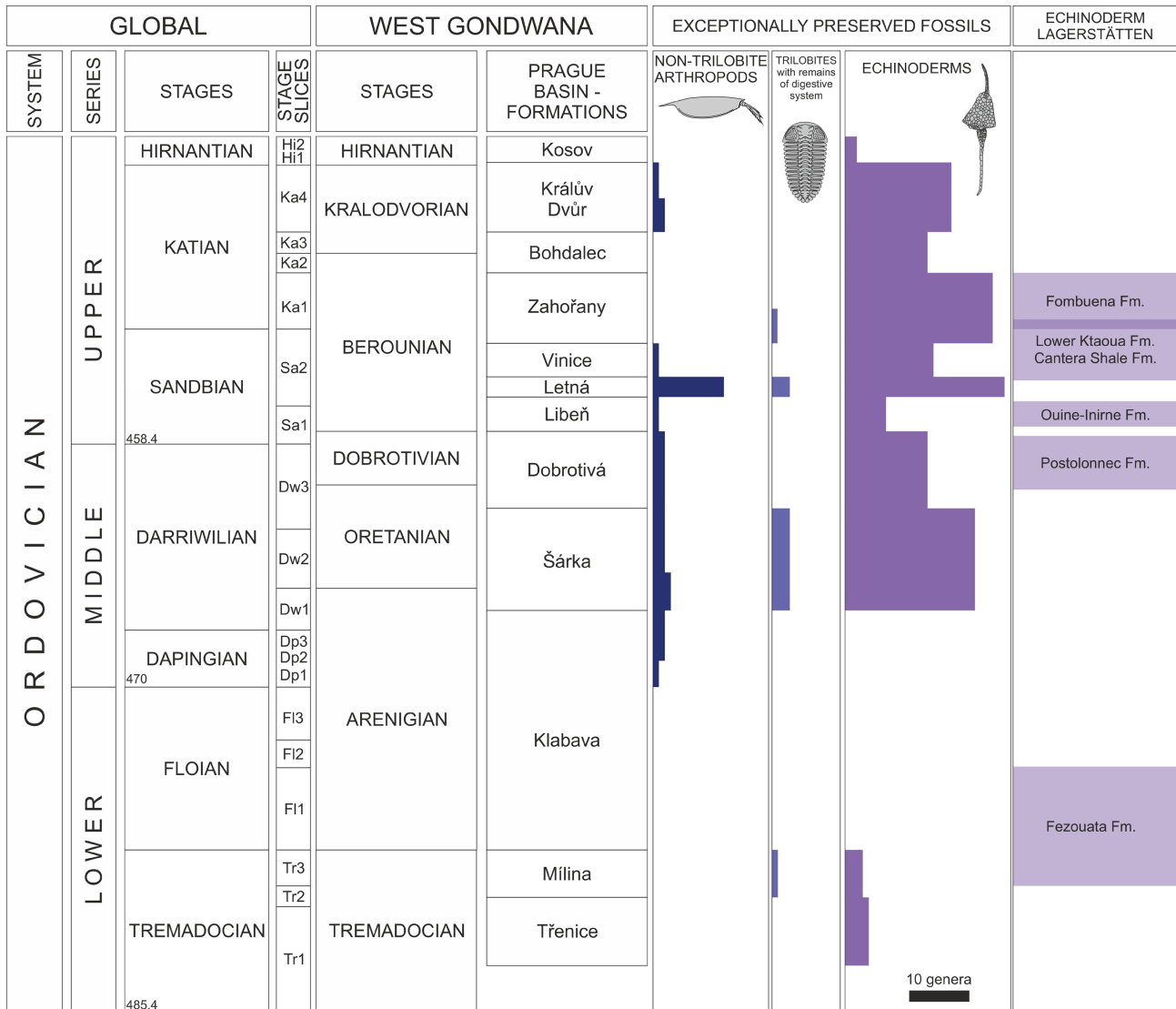


Figure 1. Chronostratigraphy and lithostratigraphy schemes, at the global and regional scales (modified from Fatka & Budil 2022). Generic diversity of exceptionally preserved arthropods and echinoderms in the Czech Republic (modified from Budil & Fatka, 2022). Stratigraphic occurrences of the main echinoderm Lagerstätten in the high latitude regions during the Ordovician (Fezouata Lagerstätte, see Lefebvre *et al.* 2016; Postolonnec Formation, see Hunter *et al.* 2007; Cantera Shale Formation, see Gutiérrez-Marco *et al.* 2018; Taflalt Lagerstätten in the Ouine-Inirne and Lower Ktaoua formations, see Lefebvre *et al.* 2008, 2010 and Hunter *et al.* 2010; Fombuena Formation, see Ausich *et al.* 2002, 2007 and Cole *et al.* 2017). Abbreviation: Fm. = Formation.

were established for this margin of the West Gondwana by Havlíček & Marek (1973) and Gutiérrez-Marco *et al.* (1995): the Middle Ordovician Oretanian and Dobrotivian regional stages (Darriwilian–earliest Sandbian), the Late Ordovician Berounian (early Sandbian–early Katian), the Kralodvorian (late Katian) and the Kosovian (Hirnantian) regional stages (Fig. 1).

The Berounian Regional Stage in the Prague Basin includes the Sandbian Libeň, Letná and Vinice formations, and the Katian Zahořany and Bohdalec formations (Gutiérrez-Marco *et al.* 2017; Fig. 1). In the Libeň and Letná formations, quartzose sandstones originated in a shallow-water environment, while fine-grained dark

shales are typical for the deeper part of the Libeň to Vinice formations. Siltstones and greywackes intercalated with lenses and thinner shales and impure carbonates are typical for the Zahořany Formation; shales and greywackes dominate the Bohdalec Formation. Sedimentary strata of these five formations yielded diverse skeletal faunas, which are characterized by the dominance of dalmanitid and trinucleid trilobites and the common occurrence of brachiopods like *Aegiromena*, *Drabovia* and *Paterula* (Havlíček & Vaněk 1966, 1990; Havlíček 1982). These are usually associated with common bivalves, gastropods, ostracods, locally abundant bryozoans, cephalopods, conulariids, cornulitids, echinoderms and hyoliths.

Graptolites, machaeridians and non-trilobite arthropods are generally rare but can be abundant in restricted layers. Representatives of other groups of invertebrates are not as well-known and the fossil content is highly variable (Havlíček *et al.* 1994, Fatka & Mergl 2009).

Letná Formation

The Letná Formation has been proposed by Šuf & Prantl (1946) and Kettner & Prantl (1948) for a thick complex of quartzose sandstones, greywackes, siltstones and pelites repeatedly alternating vertically. The current concept of the Letná Formation was formalized and detailed by Havlíček & Vaněk (1966) and Havlíček (1982, 1998) (for a historical overview see Chlupáč 1999). The Letná Formation is the thickest lithostratigraphic unit of the Ordovician of the Prague Basin (its thickness varies between 650 m in the axis of the basin and 40–70 m in the western part of the basin). The lower boundary of the Letná Formation corresponds to the onset of thick, rhythmically bedded quartzose sandstones, bioturbated quartzose sandstones, siltstones, and greywackes (Kukal 1958, 1998). The boundary with the stratigraphically overlying Vinice Formation is characterized by the occurrence of several-metres-thick lenses of ooidal ironstone of the Zdice-Nučice Iron Ore Horizon (Petránek *et al.* 1988, Fatka & Budil 2012). The area was historically subjected to intensive mining activity. Apart from abandoned quarries, an exposition of several mining galleries is accessible in the Chrštenice Mine Museum.

In the studied area, the Letná Formation forms a SW–NE oriented, about 600–650 m wide belt north of the Loděnice and east of the Chrštenice municipalities (Fig. 2). Structurally, this belt belongs to the NW wing of the Prague Synform (Melichar 2004). The inclination of beds ranges from 35° to 75° to the SE. The real thickness of the formation is approximately 500 m. On the 1 : 25,000 scale geological map, the Upper Ordovician rocks are tectonically undisturbed, except for two transverse normal faults situated NE and SW of the studied temporary excavation (Havlíček *et al.* 1993; Fig. 2). The northwestern part of the basin was dominated by a rather shallow-water environment in the Late Ordovician (Havlíček 1982, 1998).

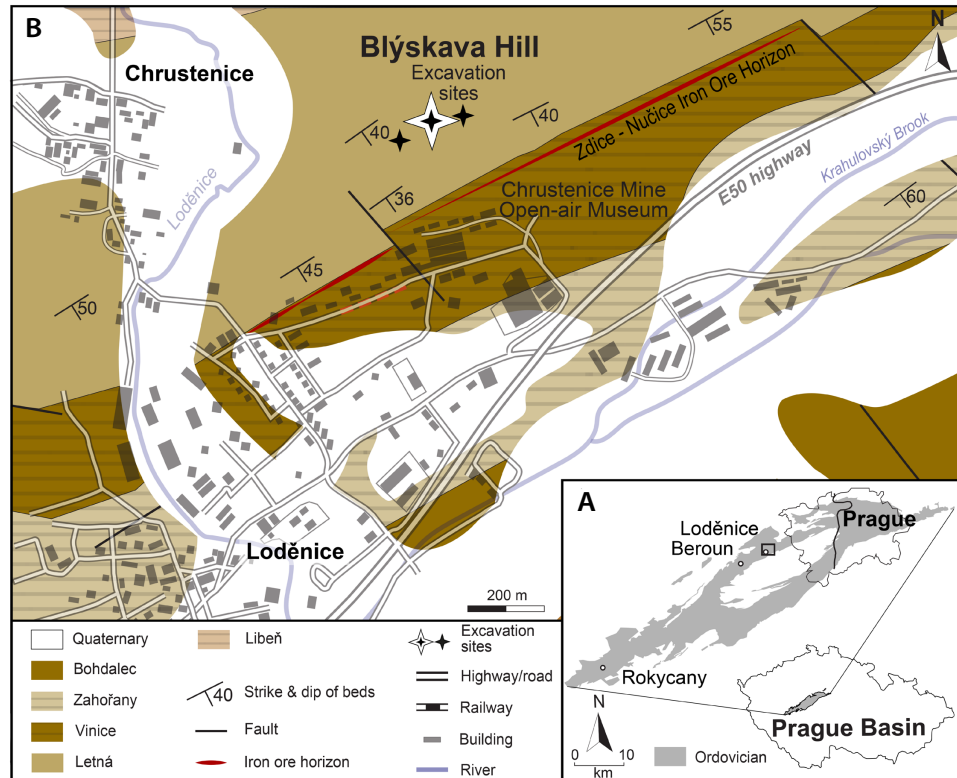
Abundant fossils with a dominance of benthic taxa (e.g. brachiopods, conulariids, echinoderms, ostracods, trilobites) are known to occur at several tens of natural outcrops and excavations in different stratigraphic levels of the Letná Formation (Havlíček & Vaněk 1966, Chlupáč 1965). Fossils are mostly preserved as fragmentary internal and external moulds of skeletal organisms associated with angular claystone fragments within quartzose sandstones to siltstones. Articulated specimens are generally

rare or are confined to several horizons only, including echinoderm-dense beds (Noailles *et al.* 2014, Lefebvre *et al.* 2022, Nohejlová, pers. comm. 2022). They represent cases of Konzentrát-Lagerstätten *sensu* Seilacher (1970) and Seilacher *et al.* (1985) and sometimes, Konservat-Lagerstätten (also called “Letná Fossil Lagerstätte”; Fatka *et al.* 2011). Such levels are rarely associated with exceptionally preserved fossils, like non-mineralized to slightly mineralized non-trilobite arthropods (for a recent review see Van Roy *et al.* 2021) and trilobites preserving parts of their digestive systems (Fatka *et al.* 2013, Budil & Fatka 2022). Accumulations of fossil remains commonly occur in thick-bedded quartzose sandstones of light-grey and yellow or grey-brown colour (Šnajdr 1990), which were interpreted as deposits of areas sheltered from wave activity by sand bars (Chlupáč 1965).

Fossil associations of the Letná Formation have been studied by Havlíček (1982), Havlíček & Vaněk (1966, 1990) and Havlíček & Fatka (1992), and recently summarized by Fatka & Mergl (2009) and Kraft *et al.* (2023). The brachiopod-based *Drabovia–Aegiromena* Association *sensu* Havlíček (1982) is distinguished into two communities: the *Drabovia redux* Community which is characteristic of shallow water, well-sorted quartzose sandstones, and the *Bicuspina* Community which occurs in slightly deeper environments of the poorly sorted greywackes of the higher levels of the Letná Formation. The trilobite-based *Dalmanitina–Deanaspis* Association including *Birmanites? ingens* (Barrande, 1852) and *Selenopeltis buchi* Barrande, 1846 is characteristic of proximal environments, while atheloptic assemblages or the Cyclopygid Biofacies are more characteristic of distal settings (see Fatka *et al.* 2013). Finally, the bivalve-based *Modiolopsis draboviensis* Association was established in coarse quartzose sandstones of the Letná Formation (Polechová 2022).

Diverse ichnofossils of the Letná Formation (but also the underlying Libeň Formation) play an important role in the understanding and interpretation of the environment and faunal diversity (Mikuláš 1998a, b; 1999). The ichnological content of the Letná Formation is disparate, despite the rather monotonous lithology in its lower and middle parts. The upper levels are more diversified with more than fifty ichnospecies, among them, the ichnogenera *Cruziana*, *Didymaulichnus*, *Palaeophycus*, *Planolites* (most common), *Rhizocorallium*, *Rusophycus* and *Teichichnus*. In some localities, the ichnogenus *Rusophycus* is considered as the trace of the trilobite *Deanaspis goldfussii* (Barrande, 1846) (Mikuláš & Budil 2013). The taxonomic composition of ichnotaxa suggests the occurrences of the *Cruziana* Ichnofacies and the *Skolithos* Ichnofacies in the Chrštenice and Beroun areas (see Mikuláš 1998a). The *Teichichnus* ichnofacies, suggesting fluctuating salinity conditions, was recognized

Figure 2. Geographic and geological location of the study area. • A – sketch map of the Barrandian area. • B – detailed map of the area of the Loděnice and Chrutenice municipalities showing the positions of the studied excavations, indicated by the stars ($50^{\circ} 00' 20.0''$ N, $14^{\circ} 10' 00.6''$ E). (Adapted after Kovanda et al. 1984).



in the dark grey clayey and sandy siltstones of the upper part of the Letná Formation, on the southeastern side of the Prague Basin (Mikuláš 2019). The spatial distribution of the ichnofacies indicates the possible simultaneous existence of a delta in the southeastern part of the Prague Basin and shallow, fully marine occurrences of the *Cruziana* Ichnofacies at the presently studied site.

Blýskava hill section near Chrutenice

Along the slopes of the Blýskava hill, the Letná Formation is exposed in numerous natural outcrops and old strip mines. Forested slopes are usually covered by rock debris ranging in thickness from several centimetres to several decimetres. Fossils occurring in mine galleries and mine dumps have been known since Barrande's time (Barrande 1852, Vála & Helmhacker 1872). Similarly, the occasional occurrence of articulated echinoderms and trilobites on the slopes of Blýskava hill has been known for a long time. However, the generally moderate to poor preservation of fossils did not attract palaeontological research to this area. More recently, Krůta in Kovanda et al. (1984) and Schallreuter & Krůta (2001) described a highly diverse and uniquely preserved ostracod fauna collected from the long excavation and loose blocks at the Ovčácký vrch hill situated approximately 500 m west from the current excavation (Fig. 2C).

Material and methods

In the years 2018–2019, one of the authors (OZ) discovered abundant articulated echinoderms associated with other skeletal fauna on the steep southern hillside of the Blýskava hill, (coordinates $50^{\circ} 00' 20.0''$ N, $14^{\circ} 10' 00.6''$ E; Fig. 2). The owner of the southern hillside of the Blýskava hill, the 'Lesy České Republiky, s.p.' (Forest of the Czech Republic, s.p.) granted permission for palaeontological research for the period of July–August 2019. Because of the difficult accessibility of the steep hillside, the excavation was opened manually. In early July 2019, a ~1.4-metre-thick sedimentary succession was exposed in a small temporary excavation about 5 meters wide and 7 metres high to a depth of 1.5 m (Fig. 3).

The temporary excavation is located about 30 m below the base of the overlying Vinice Formation. The exposed sedimentary succession was divided into eight separate bedsets (subdivided into individual layers named a–e during fieldwork) orientated $30\text{--}40^{\circ}$ to the SE (see Fig. 3). Where possible, the beds were subdivided into individual layers reaching several centimetres in thickness (e.g. Bed 7, 7a, b, c, d, etc.). Several smaller pits were examined within approximately 150 metres from the temporary excavation to better understand the general setting. Several taxa, which were not collected in the temporary excavation but were collected in the

smaller pits mentioned above, are also briefly discussed herein.

Lithological samples, remains of fossils and ichnofossils were collected during the excavation, and carefully attributed to each layer (see Appendix 1). The sedimentological evaluation of the excavated section was made in the field (BP, EN, FS). The identification of ichnofossils has been realized both in the field and in the lab based on the collected samples (RM). All field samples are housed in the Czech Geological Survey under Accessite No. 351/2021 (coll. BL). As all specimens are preserved as empty moulds, they had to be cast with latex to reveal their original three-dimensional morphology. For photographic purposes, latex casts were coated with ammonium chloride (NH_4Cl). All specimens were photographed with a NIKON D 300 camera (with Tamron SP 35mm F/1, 8 Di VC USD Macro Lenses). The exhaustive counting of body-fossil, made in the field, is synthesized in Appendix 2. The degree of fragmentation of body-fossil remains has been assessed later in the lab. Different aspects of the faunal diversity have been explored using the taxonomic richness at the generic level (S), the body fossil abundance (A) and the Simpson's Dominance Index (D), calculated on both the complete dataset and the articulated-remains dataset. The Dominance Index informs on the relative importance of the taxa in a community. It varies from 0 (all taxa are equally present) to 1 (one taxon dominates the community), see Simpson (1949). Those metrics have been computed using R (R Core Team 2023) and the package *vegan* (v. 2.7, Oksanen *et al.* 2025). Due to the non-normality of the data, the correlation between diversity metrics and the fragmentation degree is based on Spearman's Rank correlation (r_s). The influence of environmental, sedimentological and stratigraphic parameters is tested using the Kruskal-Wallis rank sum test and the pairwise Wilcoxon rank sum test. The faunal similarity between the considered echinoderm-dominated Konzentrát-Lagerstätten from the mid-late Ordovician of the high-latitude peri-Gondwanan area is assessed via a Hierarchical Cluster Analysis based on the unweighted average linkage algorithm and the Jaccard similarity index (package *Cluster*, v.2.1.8, Maechler *et al.* 2024).

Results

Sedimentology

The study section of the upper Letná Formation at Chrštenice exposes 140 cm of claystones, pale grey to brownish medium-grained sandstones (sometimes quartzose) to siltstones (locally containing a rich mica

admixture), grouped into two lithofacies (Fig. 3). The cross-stratified lithofacies (F1) consists in grey fine to medium-grained sandstone to siltstone with trough cross-stratification, sometimes truncated by the overlying layer. The thickness of the beds varies from 3 to 12 cm, while the trough ranges from 3 to 40 cm. The flaser- to wavy-laminated lithofacies (F2, Reineck & Wunderlich 1968) is composed of muddy to silty draping of internal laminations in heterolithic fine-grained layers. Flaser bedding consists predominantly of sand, with thin discontinuous lenses of mud that occurring in ripple cross-laminated sand layers. It forms in environments with stronger currents, where sand deposition dominates but brief slack-water periods allow mud to settle. Wavy bedding shows a more equal proportion of sand and mud, forming alternating layers of both in a continuous, wave-like pattern. It develops under moderate energy conditions, where sand and mud deposit more regularly during tidal cycles.

Beds contact for the latter facies is rather sharp at their bottom and lenticular at their top. These layers are 4 cm in thickness on average. F1 is interpreted to be deposited in a distal intertidal environment in a sand-dominated flat, because of the abundant complete or truncated cross-stratifications, with sometimes thin mud drapes (attributed to tidal ripples to megaripples), the bidirectional orientation of undisturbed body-fossils (mostly *Dendrocystites* specimens), and the coarsening- and thickening-upward organisation of the layers. F2 is interpreted as deposited slightly deeper, probably in a proximal subtidal environment, because of the wavy-bedding and the finer heterogeneous lithology.

The thickening-upward bedding, the orientation of bioturbations, and the relative proportion of the two facies along the succession distinguish three sedimentary units in the study section. Unit 1 contains beds 1 to 4, dominantly composed of truncated cross-bedded lithofacies F1, vertically and horizontally bioturbated. Bed 1, about 12 cm thick, is composed of massive, pale grey quartzose sandstones. Bed 2, about 23 cm thick, contains two unequal layers. Bed 2a is formed by 3 cm of flaser-laminated silty claystone (F2) overlain by 14 cm of massive sandstone (F1; Fig. 3). Bed 2b contrasts with 6 cm of brownish bioturbated and micaceous siltstone (F1). Bed 3, about 19 cm thick, is equally subdivided into two layers. Both are composed of bioturbated and micaceous, greyish to brownish siltstones (F1). Bed 4 is developed as a clayey siltstone (F1) with 2 cm of flaser-type laminations at its base (F2; Fig. 3). Intra-bed planes in beds 1, 2a, 3a and 3b are covered by numerous specimens of *Dendrocystites* orientated in multiple directions (Fig. 3). Unit 2 contains the horizontally bioturbated beds 5 and 6, showing a thicker representation of Facies 2 (almost 40% of the total thickness). Bed 5 is decomposed into 5 relatively thinner beds. Bed 5a is formed of 5 cm of flaser-laminated

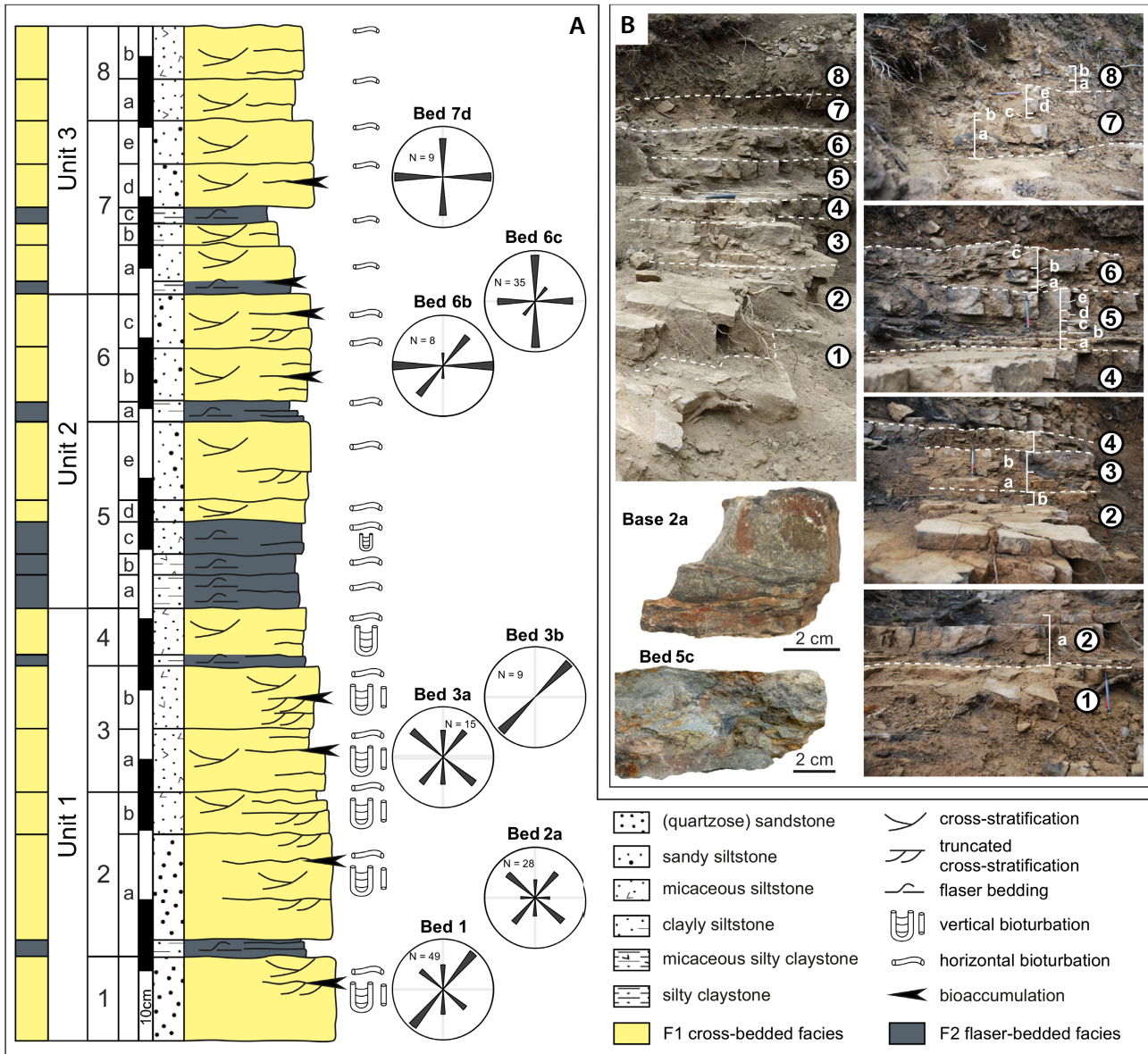


Figure 3. Temporary excavation at Blýskava hill, Letná Formation (Sandbian). • A – detailed sedimentary log with orientation of specimens from the fossiliferous lenses. • B – pictures of the temporary excavation, showing the numbering of beds and layers, and an example of a flaser-laminated layer at the bottom of the Bed 4 and a fossil of *Teichichnus* isp. (Bed 5c).

orange silty claystone (F1) bearing deformed fossil remains. Bed 5b is composed of 3 cm of flaser-bedded silty and micaceous claystone (F2), overlain by the Bed 5c (5 cm thick), showing more bioturbated (vertically and horizontally), micaceous, and slightly coarser Facies 2. Bed 5d (3 cm thick) and Bed 5e (11 cm thick) are both formed by cross-laminated brownish sandy siltstones (F1). Bed 6 is subdivided into 3 beds. Bed 6a is enhanced by flaser-laminated silty claystones (F2), about 4 cm thick. Beds 6b and 6c, each 8 cm thick, are composed of cross-bedded greyish sandy siltstones (F1). They both contain an accumulation of specimens of *Dendrocystites* showing

a bidirectional orientation (Fig. 3). Unit 3 includes beds 7 and 8, dominantly composed of cross-bedded lithofacies F1, but less bioturbated than the previous units. Bed 7 contains 5 unequal beds. Bed 7a is composed of flaser-laminated silty claystones (F2) overlain by 5 cm of cross-laminated siltstones, also observed in Bed 7b (F1). Bed 7c, devoid of body-fossils, fully expressed the lithofacies F2 over its 2 cm of thickness. Beds 7d and 7e are both composed of 6 cm of orange-grey silty sandstones (F1). Bed 8 is formed by two layers (6 and 8 cm thick, respectively) of brownish micaceous siltstones, showing well-preserved cross-laminations.

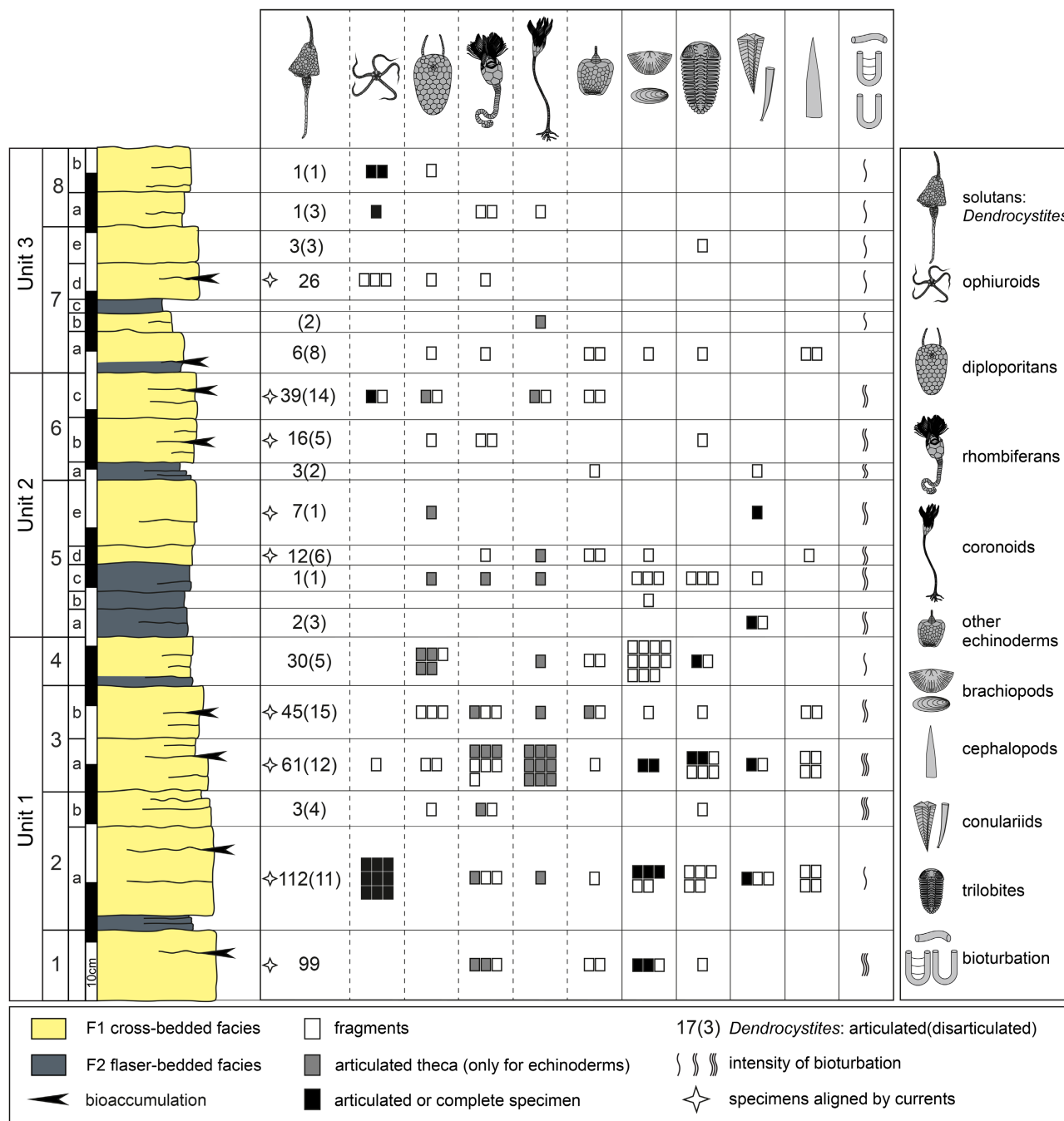


Figure 4. Log of the excavation with marked occurrence and abundance of selected taxonomic groups at the Blýskava hill (Letná Formation; Sandbian, Upper Ordovician).

Palaeontology

The excavation on the slopes of the Blýskava hill provided abundant, often remarkably preserved assemblages with a conspicuous dominance of echinoderms. From the stratigraphical point of view, the excavation is situated in the uppermost part of the Letná Formation. Thus, from the faunal list compiled by Havlíček & Vaněk (1966),

only a small part of taxa typical for the Letná Formation is present in the studied section. The following review compares the occurrence and relative abundance of taxa observed in the Blýskava hill excavation with the overall diversity of faunal groups known from the whole Letná Formation. It is noteworthy, that among the nearly twenty fossil groups known from the early Late Ordovician of the Prague Basin, no graptolites, hyoliths, non-trilobite

arthropods, palynomorphs (acritarchs and chitinozoans) and sponges could be documented in the temporary excavation (Fig. 4).

Brachiopods. – Only nine distinct brachiopod species (4% of the total faunal association) could be identified from several outcrops on the Blýskava hill, out of more than thirty known species in the Letná Formation (see Havlíček 1967, 1977). The Blýskava hill excavation yielded *Aegiromena* cf. *praecursor* Havlíček, 1952 (Fig. 5E), *Bicuspina multicostellata* Havlíček, 1951 (Fig. 5D), *Blýskavomena blýskavensis* (Havlíček, 1967) (Fig. 5A), *Drabovia redux* (Barrande, 1848) (Fig. 5C), *Drabovia* sp., *Drabovinella* sp., *Gelidorthis gemina* Havlíček, 1977 and *Hirnantia* cf. *ulrichi* Havlíček, 1951 (Fig. 5B). One poorly preserved specimen of *Rafanoglossa* sp. was found in Bed 5a of the temporary excavation (see Appendix 1). Most orthids are indeterminable because of their moderate to poor preservation, despite their high abundance (2% of the total faunal association). This could explain partly the apparent low taxonomic diversity of brachiopods in the study section.

Two bryozoan species were mentioned by Ernst *et al.* (2014) in the Letná Formation, one of which is the fenestrate *Chasmatopora havliceki* (Prantl, 1956), originally found in other outcrops on the Blýskava hill. At least two other species were found in the temporary excavation as epifauna or encrusting the shells of other invertebrates like brachiopods (Fig. 5C) and cephalopods (Fig. 5H, I). The cephalopod encruster *Ceramopora vadosa* Počta, 1894 was originally known from the slightly younger Zahořany Formation; and it also occurs on cephalopod shells collected from temporary excavation (Fig. 5J). This discovery, together with the finding of Marek *et al.* (2023a), extends the range of this taxon to the Letná Formation. The second species is an indeterminable branching bryozoan, previously observed in older sandstone levels of the Letná Formation.

Bivalves. – The bivalves of the Letná Formation were revised by Polechová (2022). In the temporary excavation, they are very rare, their remains are crushed and poorly preserved. The only determinable specimen is assigned to *Praenucula* sp. and is associated with the ichnofossil *Arachnostega* isp. (Fig. 5G).

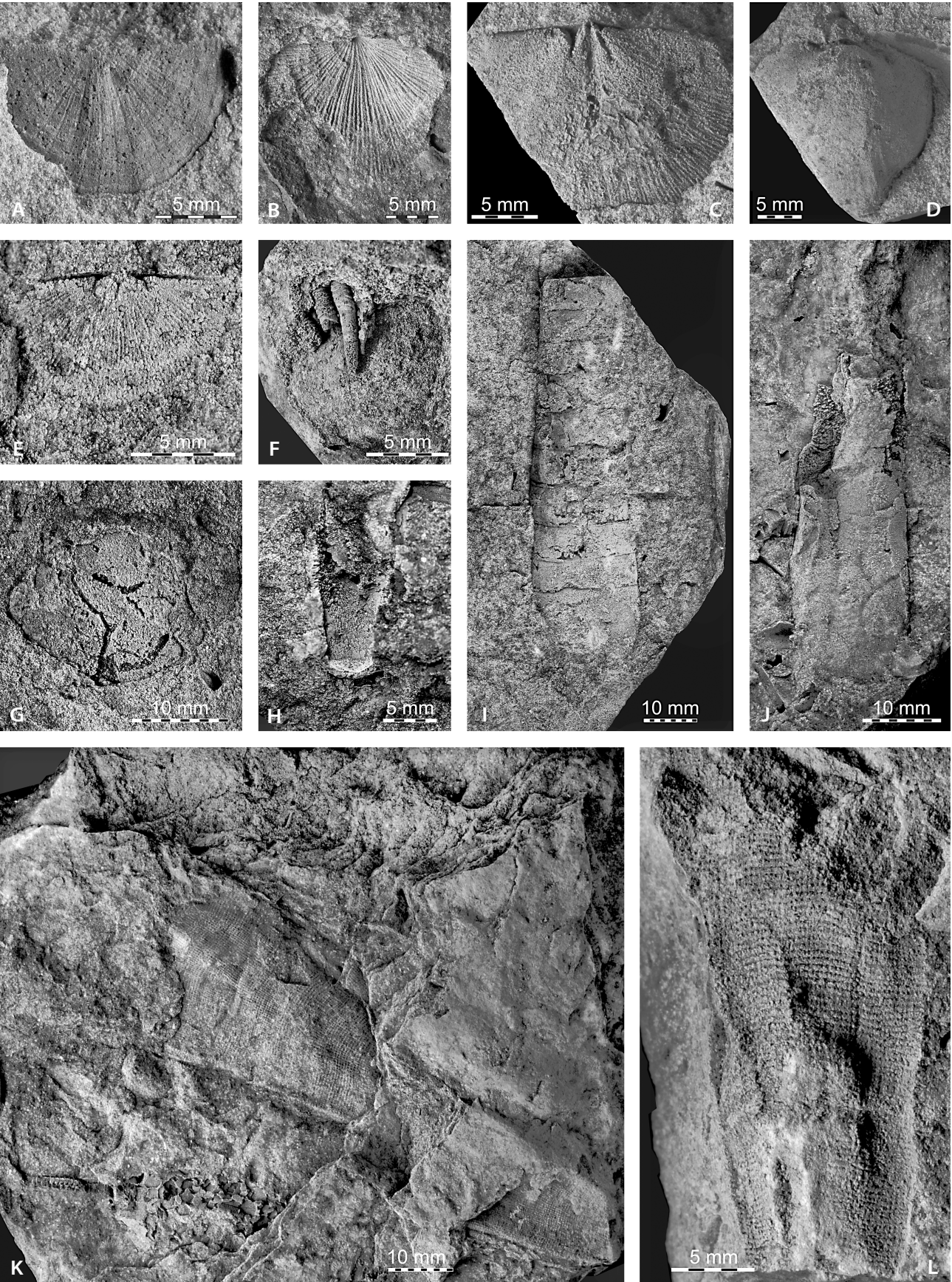
Cephalopods. – Cephalopods of the Letná Formation have never been studied comprehensively. The only species known from this formation is *Orthoceras? fractum* Barrande, 1870 (see also Marek *et al.* 2023a). Apart from that, the presence of cephalopods in the Letná Formation has only been briefly mentioned, including in the summary by Marek (1999). The Blýskava hill excavation yielded two cephalopod specimens (identified herein as

Orthoceras? fractum and Cephalopoda indet.) bearing the ichnofossil *Arachnostega* isp. and encrusting bryozoans (Fig. 5I). Ordovician gastropods, paragastropods and tergomyans of the Prague Basin were studied by Horný (1999). None of these groups were found in the temporary excavation or the Blýskava hill area. Only the gastropod *Nonorios pater* (Barrande, 1903) in Perner (1903) was collected (Fig. 6C); this species is common in other localities of the area.

Cnidarians. – Of the 11 cnidarian species recorded from the Letná Formation (Bouček 1928, Brabcová 2001), a few incomplete conchs of the conulariid *Archaeoconularia* and their fragments were found (Fig. 5K, L). Two specimens of the genus *Sphenothallus* were also discovered in the studied temporary excavation. Although this taxon is locally abundant in outcrops of the Blýskava hill, it is rare elsewhere in the upper part of the Letná Formation (Bruthansová & Van Iten 2020).

Foraminiferans. – In the Letná Formation, several specimens of agglutinated foraminiferans were collected from nearby localities. They are morphologically close to those described by Bubík (1997) from other levels of Berounian age in the Prague Basin and possibly belong to the family Psammosphaeridae. The temporary excavation yielded only one poorly preserved specimen of indeterminable agglutinated foraminiferan. Machaeridian annelids are represented by one incomplete specimen collected from a nearby excavation and attributed to *Plumulites folliculum* Barrande, 1872, which is quite common at numerous localities, including the section studied herein. Although no articulated specimen of *P. folliculum* was found in the temporary excavation, one poorly preserved specimen was collected from a nearby outcrop (Fig. 6A, B). The single species of encrusting tentaculitoid tubeworms, *Conchicolites confertus* (Barrande, 1867), is quite common at numerous localities of the upper part of the Letná Formation, including the section studied herein (Fig. 5F). Příbyl (1979), Vannier (1987) and Schallreuter & Krůta (2001) reported 16 ostracod species from the Blýskava hill area. Unfortunately, specimens from the temporary excavation are too poorly preserved to be determined.

Echinoderms. – The Letná Formation yielded abundant and diverse echinoderm assemblages, including asteroids (unpublished taxa), ophiuroids (*Bohemura*), coronates (*Mespilocystites*), crinoids (*Caleidocrinus*, isolated columnals), diploporitans (*Aristocystites*, *Fungocystites*, *Glaphocystis*), edrioasteroids (*Agelacrinites*, *Argodiscus*, *Hemicystites*), eocrinoids (*Ascocystites*), paracrinoids (*Letenocrinus*), rhombiferans (*Echinosphaerites*, *Macrocystella*, *Rhombifera*), solutans (*Dendrocystites*),



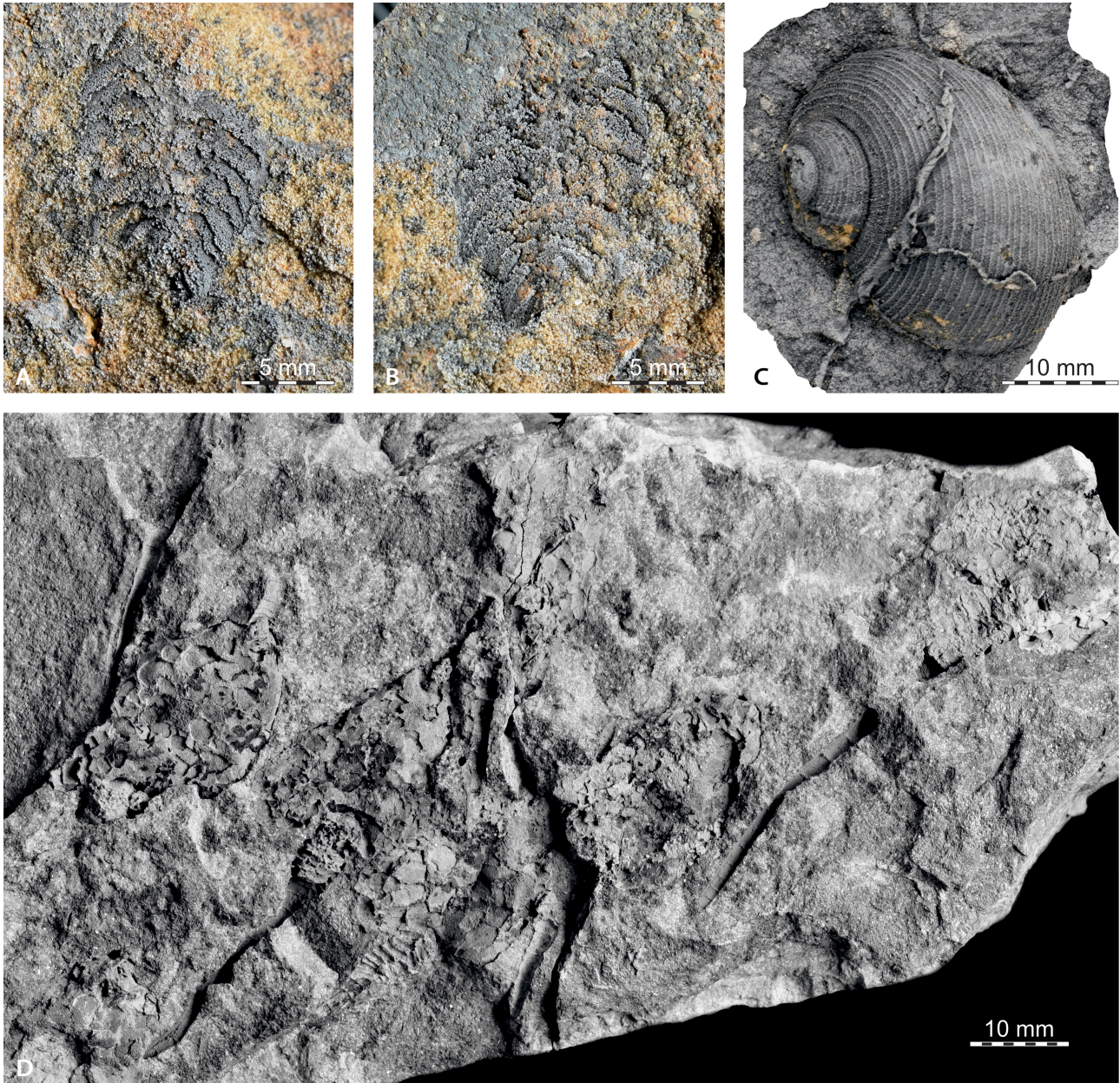


Figure 6. Blýskava hill assemblage, Letná Formation (Sandbian): plumulitid machaeridian (A–B), gastropod (C) and solutan blastozoan (D). • A, B – *Plumulites folliculum* Barrande, 1872, CGS BL 208; small exposure near the main excavation. • C – *Nonorios pater* (Barrande, 1903) in Perner (1903), CGS BL 23; small exposure near the main excavation. • D – mass occurrence of the echinoderm *Dendrocystites barrandei*; CGS BL 197; Bed 1.

< **Figure 5.** Blýskava hill assemblage, Letná Formation (Sandbian): brachiopods (A–E), bryozoans (C, H–J), encrusting tentaculitoid tubeworm (F), bivalve (G), orthoconic cephalopods (H–J), and conulariida (K, L). • A – *Blyskavomena blyskavensis* (Havlíček, 1967), dorsal valve, CGS BL 1a; Bed 2a. • B – *Hirnantia* cf. *ulrichi* Havlíček, 1951, dorsal valve, CGS BL 2b; Bed 5b. • C – *Drabovia redux* (Barrande, 1848), external surface of dorsal valve with encrusting bryozoans (or *Berenicea*-like organism), CGS BL 3; Bed 2a. • D – *Bicuspina multicostellata* Havlíček, 1951, ventral valve, CGS BL 4; Bed 2. • E – *Aegiromena* cf. *praecursor* Havlíček, 1952, dorsal valve, CGS BL 5; Bed 1. • F – *Conchicolites* cf. *confertus* (Barrande, 1867), several specimens attached to remains of indeterminable mollusc, internal mould, CGS BL 6; excavated material. • G – *Praenucula* sp., internal mould of the right valve with partially preserved hinge and traces of *Arachnostega*, CGS BL 9; excavated material, most probably Bed 1. • H – fragment of indeterminable bryozoan encrusting the outer surface of a cephalopod shell. CGS BL 10; Bed 3a. • I – shell of an orthoconic cephalopod classified as *Orthoceras? fractum* Barrande, 1870 with the ichnofossil *Arachnostega* isp. and remains of encrusting bryozoans, CGS BL 7; excavated material. • J – conch of Cephalopoda indet. with the ichnofossil *Arachnostega* isp. and surface is partially coated by encrusting bryozoans (*Ceramopora vadosa* Pošta, 1894), CGS BL 8; Bed 3a. • K – *Archaeoconularia* sp., several current-oriented specimens, and articulated theca of *Dendrocystites barrandei*, CGS BL 11; Bed 3b. • L – *Archaeoconularia* sp., remains of theca, CGS BL 12; Bed 2a.

and stylophorans (*Anatifopsis*, *Aspidocarpus*, *Barrandeocarpus*, *Thoralicarpus*) (see Barrande 1872, 1887; Prokop 1965; Ubahgs 1979; Prokop & Petr 1990, 1999; Noailles *et al.* 2014; Lefebvre *et al.* 2022). In the temporary excavation, echinoderms dominate in diversity and abundance (Fig. 4) – together they make up more than 89% of the collected specimens. Four layers (1, 2a, 3a, and 3b) in the lower part of the excavation are characterized by mass occurrences of the fully articulated solutan *Dendrocystites barrandei* Bather, 1913 (Fig. 6D). Other layers (6c, 7c, 8a and 8b) in the upper part of the excavation yielded abundant ophiuroids, commonly associated with *D. barrandei* and other echinoderm taxa (Fig. 4). *Dendrocystites* represents about 76% of the total faunal association (Figs 7A, 8D). At Blýskava hill, common echinoderm taxa (each representing between 2.5% and almost 4% of the total association) include the coronate *Mespilocystites bohemicus* Barrande, 1887 (Fig. 8G), the diploporitan *Glaphocystis cf. globulus* Chauvel, 1966 (Fig. 7C), and the rhombiferan *Echinospaerites infaustus* Barrande, 1887 (Fig. 8C). Less abundant echinoderms are undescribed asterozoans (Nohejlová & Hunter 2021; Fig. 7E), undescribed ophiuroids (Fig. 7D), the crinoid *Caleidocrinus multiramus* Waagen & Jahn, 1899 (Fig. 8E), two distinct diploporitans (*Codiacystis* sp. and *Fungocystites* sp.), edrioasteroids (*Hemicystites bohemicus* Barrande, 1887 and undetermined specimens), the rhombiferans *Homocystites cf. alter* (Barrande, 1887) (Fig. 7A), *Macrocystella bohémica* Barrande, 1887 and *Rhombifera bohémica* Barrande, 1867 (Fig. 8B), and the stylophorans *Anatifopsis* sp. and *Thoralicarpus prokopi* Lefebvre *et al.*, 2022 (Fig. 7B). Finally, one specimen of the enigmatic echinoderm *Hexedriocystis* sp. (Fig. 8F) was also recovered from an outcrop close to the temporary excavation.

Trilobites. – Out of twenty six trilobite species reported from the Letná Formation (for a more recent review see Vaněk & Valíček 2001, Pereira *et al.* 2017), only seven taxa were collected on the slopes of the Blýskava hill. Common trilobites at the temporary excavation site are *Cekovia cf. transfuga* (Barrande, 1852) (Fig. 9B, C, F), *Prionocheilus mendax* (Vaněk, 1965) (Fig. 9E), *Selenopeltis buchi* and *Vysocania cf. moravecii* Pereira *et al.*, 2017 (Fig. 9A, D). Disarticulated remains of *Eccoptochile clavigera* (Beyrich, 1845), *Eccoptochiloides tumescens* (Barrande, 1852) and *Primaspis primordialis* (Barrande, 1846) are

rare. Rare articulated exoskeletons are moderately to poorly preserved, common isolated exoskeletal elements are typically crushed and fragmentary.

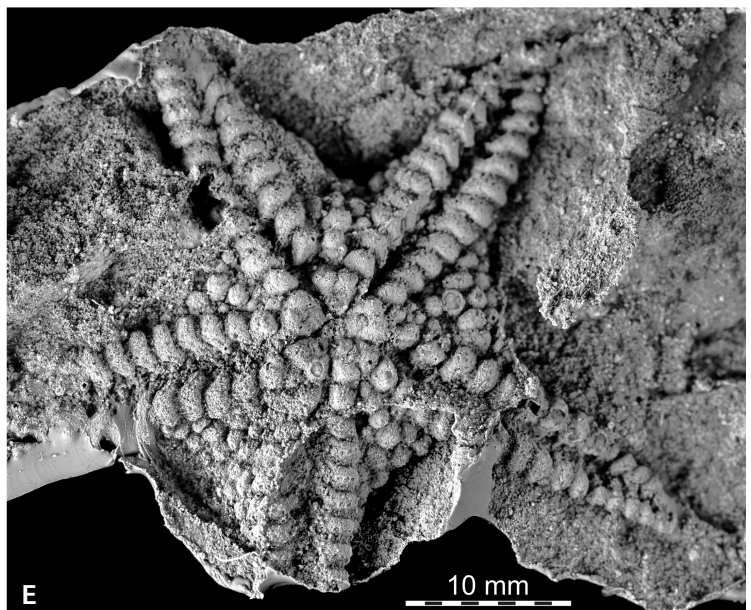
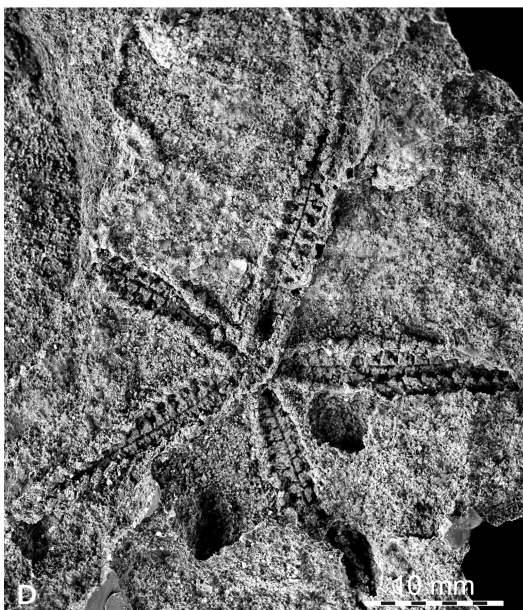
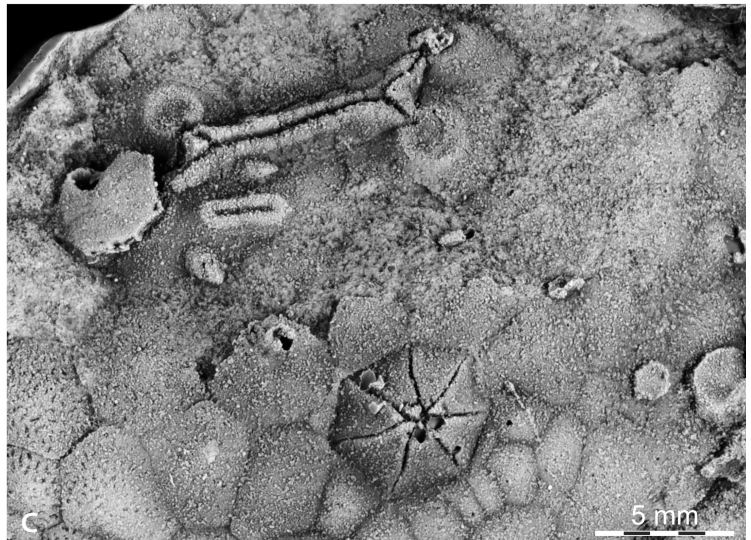
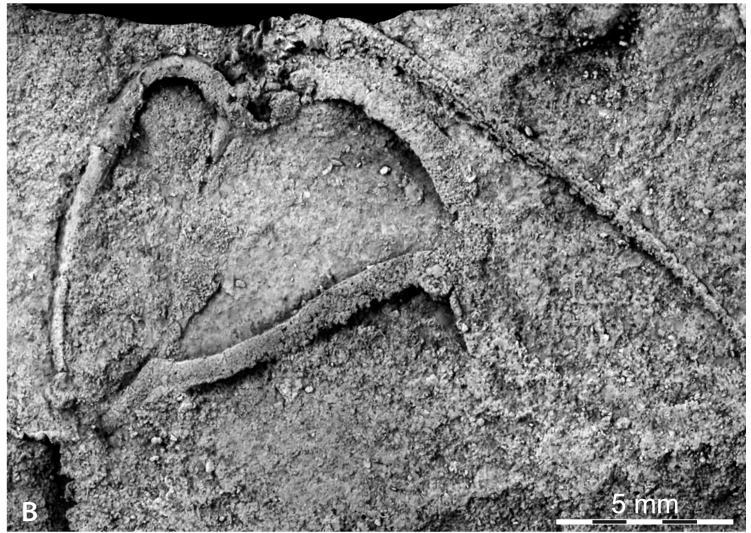
The locality “Blýskava” of Mikuláš (1998a) covered a much larger area when compared with the herein-studied temporary excavation. The recurrent presence of spreiten-structures is rather uncommon for the Letná Formation. *Planolites* isp. is the most common ichnotaxon, often preserved only as poorly discernible circular to oval cross-sections of tunnels. Unit 1 is characterized by a high ichnofabric index (ii = 3–4 *sensu* Droser & Bottjer 1986), consisting in the horizontal tunnels (attributed to *Planolites* isp.), vertical spreiten-structures (*Teichichnus*) and isolated vertical tunnels (cf. *Skolithos*, *Arenicolites*). Bed 4 is less bioturbated but its associated ichnofossils (mostly *Teichichnus* and *Planolites*) are preserved in full relief. These assemblages suggest the expression of *Teichichnus* ichnofacies *sensu* Gingras *et al.* (2024) also called a mixed *Cruziana*–*Skolithos* Ichnofacies (cf. Buatois & Mángano 2011). An internal mould of a cranium of *Vysocania cf. moravecii* filled with *Tomaculum* isp. and a co-occurrence of *Rusophycus* isp. and unfragmented specimen of *Cekovia* were collected from Bed 2 and 3a, respectively (Fig. 9A). Unit 2 shows an abundant but monotonous ichnoassemblage, characterized by intersecting horizontal and subhorizontal tunnels (e.g. *Planolites*). Bed 5c uniquely preserved a small-size *Teichichnus* (Fig. 3). Unit 3 fully preserves rare ichnofossils, only present on bedding planes as concave epireliefs and convex hyporeliefs of horizontal tunnels (and to a lesser extent some horizontal spreiten-structures such as *Syringomorpha* and *Zoophycos* in Bed 8). The prevalence of horizontal structures in Units 2 and 3 may indicate a depauperate *Cruziana* Ichnofacies, slightly more diversified but less abundant in Unit 3 (cf. Buatois & Mángano 2011).

Discussion

Stratigraphy

The temporary excavation yielded abundant skeletal remains, some of which made it possible to uncover its stratigraphic position within the upper part of the Letná Formation. In particular, the presence of the brachiopods *Aegiromena praecursor* and *Blýskavomena blýskavensis*,

Figure 7. Blýskava hill echinoderms, Letná Formation (Sandbian): solutan (A), stylophoran (B), diploporitan (C), ophiuroid (D) and asteroid (E). • A – *Dendrocystites barrandei* Bather, 1913 (left), together with the *Homocystites cf. alter* (Barrande, 1887) (right). CGS BL 28; small exposure near the main excavation. Scale bar = 1 cm. • B – *Thoralicarpus prokopi* Lefebvre *et al.*, 2022, CGS OZ 150, paratype; excavated rock debris. Scale bar = 5 mm. • C – *Glaphocystis cf. globulus* Chauvel, 1966, CGS BL 29; excavated rock debris. Scale bar = 5 mm. • D – Ophiuroidea indet. CGS BL 30; small exposure near the main excavation. Scale bar = 5 mm. • E – Asteroidea indet. CGS BL 31; small exposure near the main excavation. Scale bar = 5 mm.



associated with several other species including *Drabovia redux* (M. Mergl, pers. comm. 2022), indicates the lower part of the *Bicuspina* Community range of the *Drabovia–Aegiromena* Fauna of Havlíček (1982). The temporary excavation is situated in levels where *Bicuspina multcostellata* of the eponymous association occurs in adjacent exposures on slopes of the Blýskava hill. This taxon was also very rarely recorded in the studied temporary excavation (Bed 2). Ascertained trilobite species support the stratigraphic position discussed above.

Palaeoenvironment

The combination of the sedimentological and ichnological information suggests that the Blýskava hill sedimentary succession was deposited in a tide-dominated environment. Unit 1 is characterized by the lithofacies F1 with high micaceous content, the *Teichichnus* ichnofacies, and an ichnofabric index relatively high. This unit was deposited in the proximal intertidal zone, with periods of coarse terrigenous inputs and/or salinity stress due to freshwater inputs, as suggested by the ichnoassociation *Teichichnus* and *Planolites* (Mángano *et al.* 2023). The multiple orientations of the specimens of *Dendrocystites* may suggest a relatively high hydrodynamism. Both the abundant infaunal traces and the sedimentological characteristics of the layers indicate an oxygenated organic-rich soft substrate (softground). Unit 2 shows an alternation of the two lithofacies (with almost no micaceous content), a lower ichnofabric index and a monotonous depauperate *Cruziana* ichnofacies (except in Bed 5c). This unit shows a shallowing-upward trend, starting from a slightly deeper environment (probable proximal subtidal conditions), with rarer and finer terrigenous inputs (except in Beds 5e, 6b and 6c). Unit 3 records mainly the cross-bedded lithofacies F1 associated with a low ichnofabric index and a slightly more diverse ichnofacies, suggesting the return to the intertidal environment. Bioturbation is evidenced mostly by bulges or depressions and semi-cylindrical convex hyporelief or concave epirelief, only present on bedding planes. This suggests a higher sedimentation rate and short breaks in sedimentation. In the upper Unit 2 and the lower Unit 3, the few extensive fossiliferous lenses show bidirectionally-oriented articulated specimens of *Dendrocystites* and/or conulariids, recording tidal processes (Fig. 3). The decline of bioturbation and faunal frequency towards the top of the profile may reflect a decrease in organic content and habitability of the substrate and the seafloor. It may be linked to the shallowing-upward trend (recorded from Unit 2) leading to more unstable conditions due to increasing sedimentation rates associated with minor continental inputs.

Taphonomy

Taphonomic and biostratinomic processes including transportation can be assessed from the preservation of morphological details and the fragmentation of skeletons. The percentage of skeletal fragmentation is relatively low in Unit 1 (mostly lower than 25% except in Bed 2b), while it is more variable and reaches 50% and 75% in Units 2 and 3, respectively. The low skeletal fragmentation suggests that fauna can be considered autochthonous to parautochthonous in Unit 1 and in Bed 6c, where diversity and abundance are higher (Fig. 10A, B).

The preservation state varies among the taxonomic groups. Brachiopods are mostly preserved as internal and external moulds of disarticulated valves, except in Beds 1 and 2. Conulariids may be preserved as complete shells mostly in Unit 1 (but also in Beds 5a and 5e), and they are more fragmented in Unit 2 (except in Beds 5a and 5e). Their qualitative state of preservation may indicate that they are (para-)autochthonous. Shells of cephalopods are represented by rather long fragments of shells, suggesting that they were transported toward shallower environments.

Trilobite preservation is variable. Specimens of *Cekovia* are almost complete in the upper Unit 1 and in Bed 7e, while other occurrences consist of disarticulated elements (cranidium, pygidium and fragments of thorax). Representatives of other genera are mostly preserved as isolated skeletal parts in all layers in which they occur. No enrolled specimens were discovered in the study excavation. In a small side excavation, a complete specimen of *Prionocheilus mendax* was found with its hypostome (Fig. 9E). Therefore, only *Cekovia*, *Eccoptochiloides* and *Prionocheilus* might be considered autochthonous in these strata, while other genera might have lived nearby (Speyer & Brett 1986).

In the qualitative taphonomic classification of echinoderms proposed by Brett *et al.* (1997), asteroids, edrioasteroids, ophiuroids, solutans and stylophorans belong to the most fragile Type 1, whereas coronates, crinoids, diploporitans and rhombiferans are generally assigned to Type 2. Type-1 taxa are characterized by a delicate endoskeleton composed of weakly sutured plates. Decay experiments made on Recent Type-1 echinoderms (*e.g.* ophiuroids) suggest that their endoskeleton is completely disarticulated into isolated plates within days or a few weeks after death (Meyer 1971, Kerr & Twitchett 2004). The preservation of complete specimens is generally associated with obrution deposits, *e.g.* by rapid *in situ* burial of live individuals (*i.e.* by storm or turbidity flows; see *e.g.* Brett *et al.* 1997, Hunter *et al.* 2007, Lefebvre 2007, Lefebvre *et al.* 2022). Taphonomic experiments on modern ophiuroids further suggest that, although obrution deposits are a pre-requisite for the

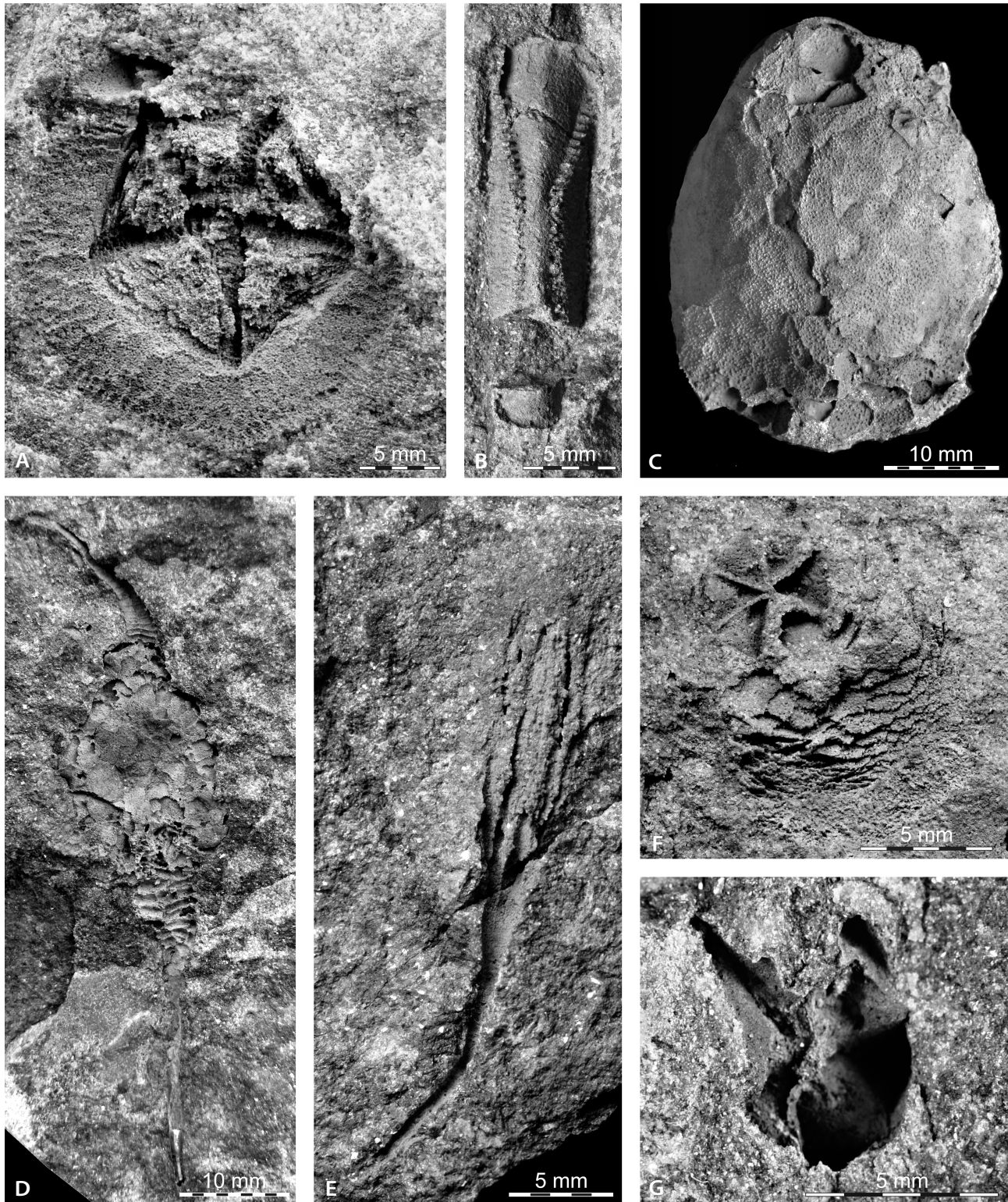


Figure 8. Blýskava hill echinoderms, Letná Formation (Sandbian): edrioasteroid (A), glyptocystitid rhombiferan (B, C), solutan (D), crinoid (E), *Hexedriocystis* (F), and coronate (G). • A – *Edrioasteroidea* indet. CGS BL 203; excavated rock debris. • B – *Rhombifera bohémica*. CGS BL 198; Bed 3a. • C – *Echinospaerites infaustus* Barrande, 1887. CGS BL 199; excavated rock debris. • D – *Dendrocystites barrandei* Bather, 1913. CGS BL 24; Bed 1. • E – *Caleidocrinus multiramus* Waagen & Jahn, 1899. CGS BL 25; excavated rock debris. • F – *Hexedriocystis* sp. CGS BL 26; excavated rock debris. • G – *Mespilocystites bohemicus* Barrande, 1887. CGS BL 27; excavated rock debris.

preservation of Type 1 echinoderms, massive occurrences of fully articulated individuals, in life position and without any evidence of escape postures or high stress (e.g. arm autotomy) could result from the anaesthetic effect of the sudden influx of fresh water into the marine realm (Fraga & Vega 2024). Most echinoderm specimens collected at the Blýskava hill are complete and fully articulated (e.g. ophiuroids, most solutans and stylophorans). Most individuals of the cornute stylophoran *Thoralicarpus prokopi* are preserved with slightly ajar or closed cover plates in their distal aulacophore, suggesting that they were probably buried alive (Lefebvre *et al.* 2022) by tidal processes. In solutans (*Dendrocystites*), the absence of brachioles oriented perpendicularly to the theca also confirms the *in situ* rapid burial of the specimens after a short period of freshwater input (cf. Marek *et al.* 2023a). Complete thecae of diploporitans and rhombiferans, sometimes articulated to stems for the latter, suggest a short transportation *via* similar processes (Brett *et al.* 1997).

The preservation of complete fragile echinoderms (the solutan *Dendrocystites*, stylophorans, and ophiuroids), and unenrolled articulated trilobites (e.g. *Cekovia*, *Prionocheilus*) at the top of the layers suggests that they may represent the autochthonous assemblage of the taphocenoses in Unit 1 and the upper Unit 3. The occurrence of thecae of Type-2 echinoderms (e.g. *Glaphrocystites*, *Mespilocystites* or *Echinospaerites*), the slightly incomplete cnidarians (e.g. *Archeoconularia*, *Sphenothallus*), and brachiopods (e.g. *Bicuspina*, *Drabovia*) may reflect a slightly transported parautochthonous assemblage in Unit 1 and sporadically in the rest of the study section (e.g. Beds 5c, 5d, 6c). Autochthonous assemblages were episodically buried alive, while parautochthonous assemblages were slightly reworked from shallow subtidal environments to the distal intertidal zone via tidal processes in Unit 1, Bed 6c, and the upper part of Unit 3. Body-fossils are mainly preserved on the layer planes in Unit 1 and in F1-Beds 6b, 6c, and 7d, where they are preferentially preserved as articulated skeletons. The short breaks in sedimentation within the intertidal Unit 1 have gathered multiple living organisms to be rapidly buried as bioaccumulations, lowering the skeletal fragmentation degrees and freezing the autochthonous assemblages (most likely due to the freshwater input).

The rest of Unit 2 and the lower part of Unit 3 have relatively thin layers, especially F2-beds, with erosional surfaces, possibly limiting the preservation of body fossils. The poor preservation of the scarce fauna suggests its short transportation and reworking in a distal intertidal environment.

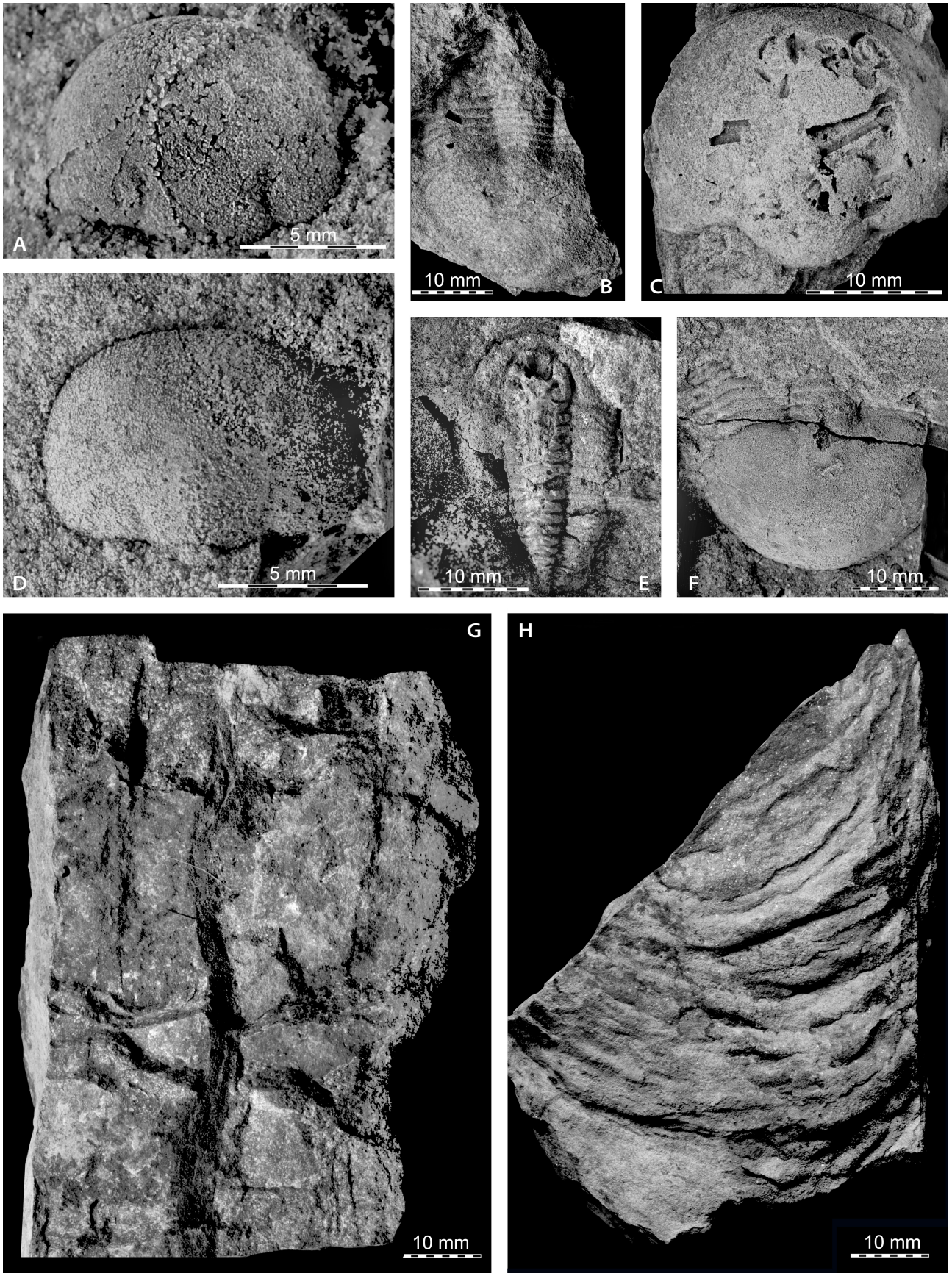
Biodiversity

The taxonomic composition of the overall marine taphocenoses is relatively homogeneous through the study section, with a total richness of 35 identifiable genera distributed in 19 classes belonging to 7 phyla (Fig. 4). Generic diversity and body-fossil abundance are positively correlated ($r_s = 0.86$; Fig. 10A, C). The fauna is dominated by seven classes of echinoderms representing about 89% of the gathered specimens. Brachiopods (three classes) and trilobites respectively represent about 4% and 3% of the total association (Fig. 4). Cnidarians and molluscs compose each about 2% of the total association, while the other phyla are represented by a few specimens, mostly allochthonous. Taxonomic richness and abundance are significantly higher in Unit 1 for both the total and the non-allochthonous assemblages and in cross-bedded facies F1 for the total assemblages (Fig. 11, Appendix 3). Assemblages are less abundant and less diverse in fine-grained layers, but taxa are more equally represented (lower Dominance Index, Fig. 11). Assemblages in sandy layers are significantly dominated by specimens of solutans and ophiuroids (high Dominance Index, Fig. 11, Appendix 3). Specimens of *Dendrocystites* represent more than 80% of the total abundance per coarse-grained layer.

Palaeoecology

Preserved benthic communities are composed mainly of surficial and erect fauna ranging from suspension-feeders (e.g., echinoderms, brachiopods, conulariids) to predators (Appendix 4). Among echinoderms, the slow vagrant solutan *Dendrocystites* is by far the most abundant taxon, representing 76% of the total association. Specimens are abundant and well preserved in almost all F1-layers (interpreted as intertidal environment), contrarily to

Figure 9. Blýskava hill assemblage, Letná Formation (Sandbian): trilobites (A–F) and ichnofossils (G, H). • A – *Vysocania* cf. *moraveci* Pereira *et al.*, 2017, cranium filled by *Tomaculum* sp., internal mould, CGS BL 13; Bed 2. • B – *Cekovia* cf. *transfuga* (Barrande, 1852), incomplete dorsally flattened specimen, internal mould, CGS BL 14a; Bed 3b. • C – *Cekovia*? sp., incomplete large cephalon filled by organic debris, internal mould, CGS BL 15; Bed 7e. • D – *Vysocania* cf. *moraveci* Pereira *et al.*, 2017, incomplete holaspide cephalon, internal mould, CGS BL 16; Bed 2. • E – *Prionocheilus mendax* (Vaněk, 1965), complete specimen with hypostome preserved *in-situ* and with possible remnants of the digestive system, CGS OZ 170; small exposure near the main excavation. • F – *Cekovia* cf. *transfuga* (Barrande, 1852), incomplete dorsally flattened specimen, internal mould, CGS BL 17a; excavated rock debris. • G – *Arenicolites* isp., CGS BL 18a; excavated rock debris, most probably Bed 1. • H – *Zoophycos* isp., CGS BL 19a; excavated rock debris.



F2-layers (interpreted as proximal subtidal environment). The new occurrence and dominance of *Dendrocystites* confirm that it was adapted to very shallow waters, and it was not restricted to storm-influenced environmental settings as it was previously supposed (Gil Cid *et al.* 1996; Lefebvre *et al.* 2007, 2010; Hunter *et al.* 2010; Gutiérrez-Marco *et al.* 2018; Nohejlová & Lefebvre 2022). The abundance of fully articulated *Dendrocystites* specimens in tidal deposits confirms their previous interpretation as opportunist taxa living in high energy and eutrophic water (Noailles *et al.* 2014).

Stylophorans are unexpectedly and extremely rare in the study section. Solutans and stylophorans may have been competing as low-tier (surficial), gregarious and opportunistic feeders (Sprinkle & Guensburg 1997, Lefebvre 2007, Noailles *et al.* 2014). The co-occurrence and/or partial overlap of fully articulated *Dendrocystites* specimens with exquisitely preserved ophiuroids (Beds 2a, 7d and 8a) reinforces the possible predatorial feeding mode for the latter (Petr 1989, Hunter *et al.* 2010, Noailles *et al.* 2014). In this case, ophiuroids would also be considered opportunists, hunting their prey in very shallow waters (Fatka *et al.* 2023). Sessile surficial or erect suspension-feeding echinoderms (coronates, diploporitans, edrioasteroids, rhombiferans) each represent between 2 and 4% of the total abundance and occur across the entire section in various states of preservation. Parautochthonous diploporitans and rhombiferans may also have competed as sessile +5 tiers (*sensu* Ausich & Bottjer 1985) in proximal subtidal environments. A similar hypothesis can be made for the parautochthonous coronate *Mespilocystites* and rhombiferan *Echinospaerites*, both interpreted as a +10 tier (*sensu* Ausich & Bottjer 1985).

When excluding *Dendrocystites* individuals, brachiopods and trilobites represent about 37 and 25% of the faunal association. The remaining dominant groups (cephalopods and other molluscs, conulariids, bryozoans) have a very equal representation, despite a certain taxonomic diversity, typical for the higher levels of the Letná Formation. All these groups constitute a relatively diverse association, mainly comprised of sessile suspension feeders, either epibenthic surficial to erect (brachiopods, bryozoans, conulariids) or encrusting (bryozoans, tentaculitoid tubeworms). Rhynchonellid brachiopods do not co-occur with strophomenid brachiopods in the study section, suggesting a possible niche repartition between these taxa. Apart from echinoderms, the vagrant benthos is represented by trilobites, sometimes fully articulated (e.g. upper Unit 1, Bed 7e) but typically preserved as isolated cephalon or pygidium. They represent shallow burrowers or surface ploughers; all occurring forms (most probably) correspond to scavengers/occasional predators with well-developed eyes, indicating colonization of the photic zone.

No attached epibionts on conulariid shells were observed in the material coming from the excavation but these are present at other sites of the Blýskava hill area (cf. also Marek *et al.* 2023a, b). The common occurrence of drilling ichnofossils (e.g. *Arachnostega*) on cephalopod shells (Fig. 5I) is remarkable, together with that of bryozoans (especially *Ceramopora vadosa*) and tentaculitoid tubeworms (*Conchicolites confertus*) that typically form relatively thick coatings on brachiopod or cephalopod shells (Fig. 5F, J, cf. also Marek *et al.* 2023a, b). Such “frozen interactions” can document that the shells rested on the seafloor for some time, offering a firm substrate for these encrusting taxa (the sandy sea floor was relatively unstable but suitable for some groups, such as rhynchonellid brachiopods).

The rare and rather long fragments of cephalopod shells (most likely allochthonous in Beds 2a, 3a and 7a) may represent the only possibly nektonic or demersal forms.

The three sedimentary units preserved similar ecological communities, for both the whole and the non-allochthonous assemblages. Nektonic or demersal predatory and encrusting fauna are interpreted as allochthonous in all units. The abundant *Planolites* ichnofabrics suggests the suite of direct, horizontally moving sediment eaters, possibly tracing the presence of opportunistic K-strategist invertebrates. Unit 1 preserves the most balanced trophic structure in the intertidal environment. Its faunal assemblage composes 10 (par-)autochthonous Cambrian guilds (Fig. 11). Benthic scavengers and predators, represented by the autochthonous trilobites and ophiuroids, were supposedly moving relatively fast on the seafloor, while the slow vagrant fauna is dominated by the autochthonous deposit-feeder solutan *Dendrocystites*. The latter might have fed on the high organic content of the sediment, expected from the ichnofauna.

The suspension feeders are represented by the autochthonous surficial brachiopods and the parautochthonous erect conulariids, diploporitan and some rhombiferan echinoderms. The recurrent vertical component of the ichnofabrics confirms the existence of infaunal filter feeders. Similar but strongly impoverished guilds exist in the two other units (Fig. 11). Unit 2 shows more complete erect suspension feeders and the disappearance of autochthonous predators. Suspension feeders in an erect position are consistent with the slightly deeper environment and the lower coarse terrigenous inputs. Unit 3 is characterized by the absence of any autochthonous attached or resting (suspension-feeding) fauna and the return of predators (ophiuroids only), leading to a dominance of *Dendrocystites* despite its relative infrequency. The rapid sedimentation rate and the poor organic content of the sediment may have prevented

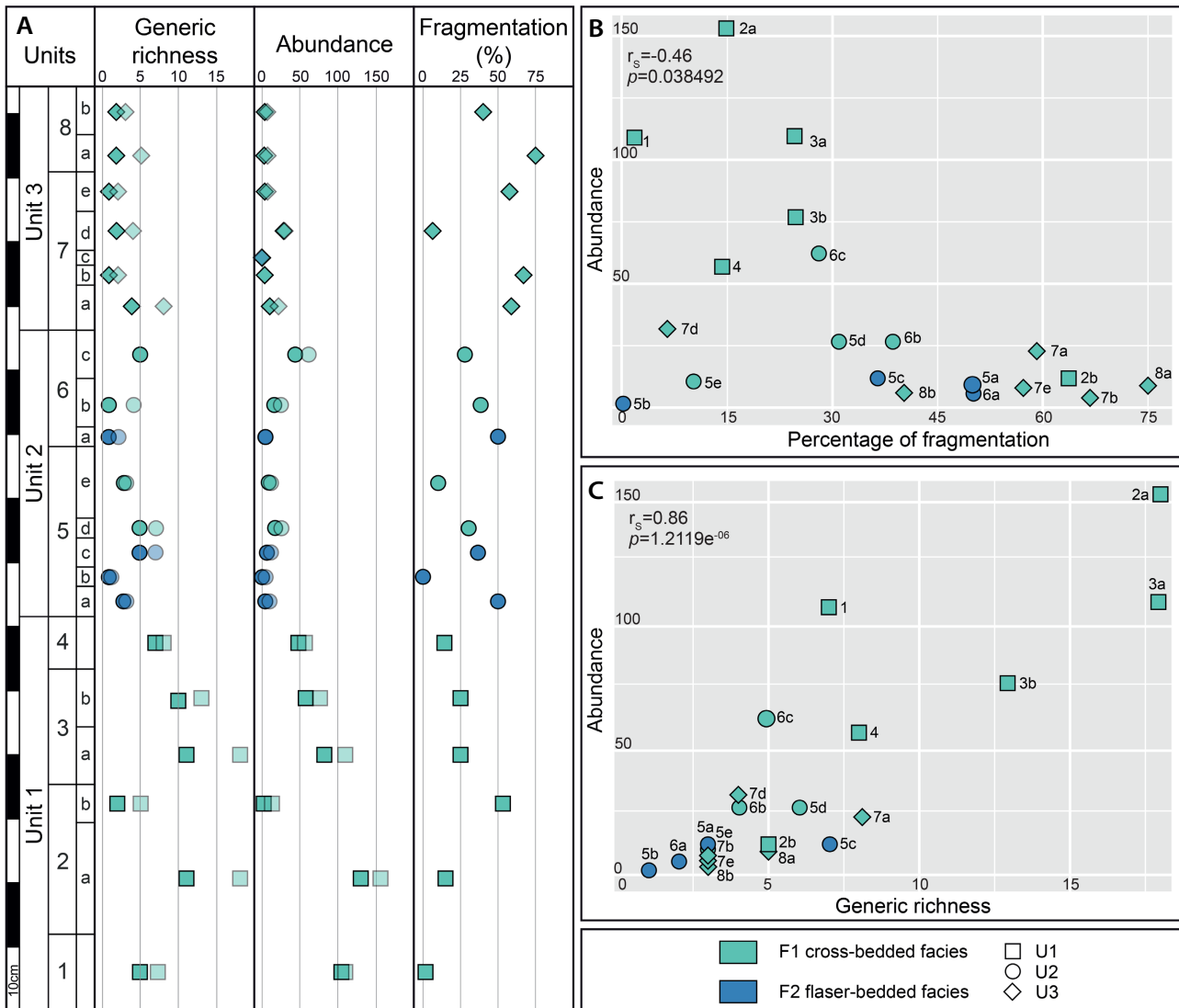


Figure 10. Blýskava hill diversity, Letná Formation (Sandbian). • A – generic rich, abundance and skeletal fragmentation per layer for the whole preserved fossil assemblage (points in transparency) and for the non-allochthonous assemblage (plain points) • B – scatter plot of the percentage of skeletal fragmentation and the body-fossil abundance. • C – scatter plot of the body-fossil abundance and the generic richness.

the extensive colonization of the intertidal zone by the deposit-feeders while predators might have hunted for prey during the short breaks in sedimentation. Activities of surficial grazers or deposit-feeders are confirmed by the horizontal fossil traces preserved as reliefs in Units 2 and 3. The absence of vertical trace fossils tends to support the scarcity of suspension feeders in Unit 3.

Comparison with other Ordovician echinoderm Lagerstätten in the high-latitude Mediterranean Province

Relatively comparable echinoderm dense beds dominated by the solutan *Dendrocystites* are known from strati-

graphically younger localities in the Upper Ordovician of the Prague Basin, including the Zahořany stratotype section, which is the historical type locality of numerous Barrande's echinoderm taxa, including *Dendrocystites sedgwicki* (see Barrande 1867, 1887; Bather 1913; Petr 1989; Noailles *et al.* 2014; Marek *et al.* 2023a). Relatively similar benthic associations dominated by the solutan *Dendrocystites* were also reported in shallow, high-energy, siliciclastic settings in the Upper Ordovician of Morocco (Lefebvre *et al.* 2007, Hunter *et al.* 2010, Nohejlová & Lefebvre 2022). In the eastern Anti-Atlas, the Tizi n'Mourghi locality (upper part of the Lower Ktaoua Formation, early Katian) yielded an almost monospecific assemblage of *Dendrocystites*, associated with rare other echinoderms comprising crinoids,

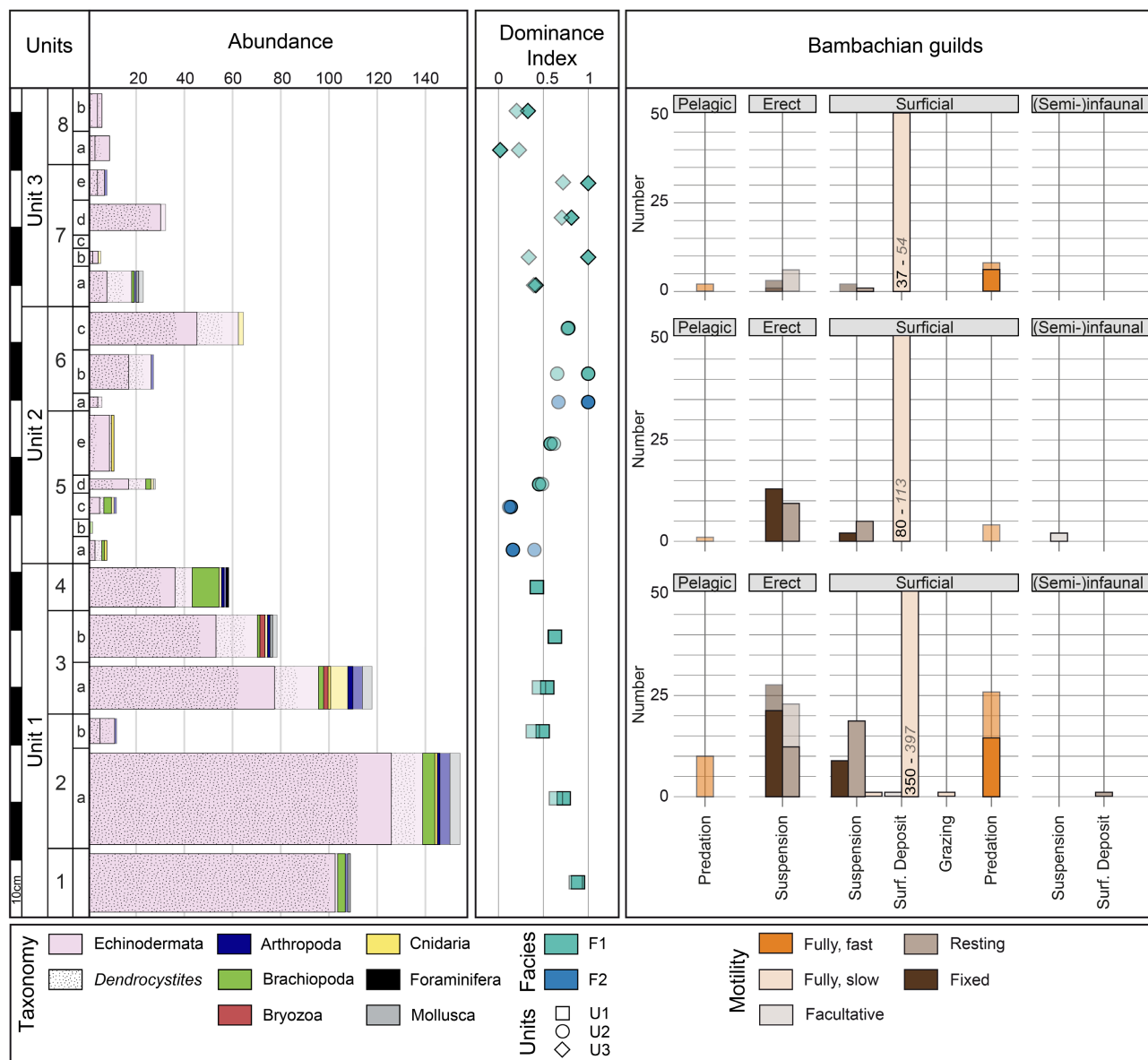


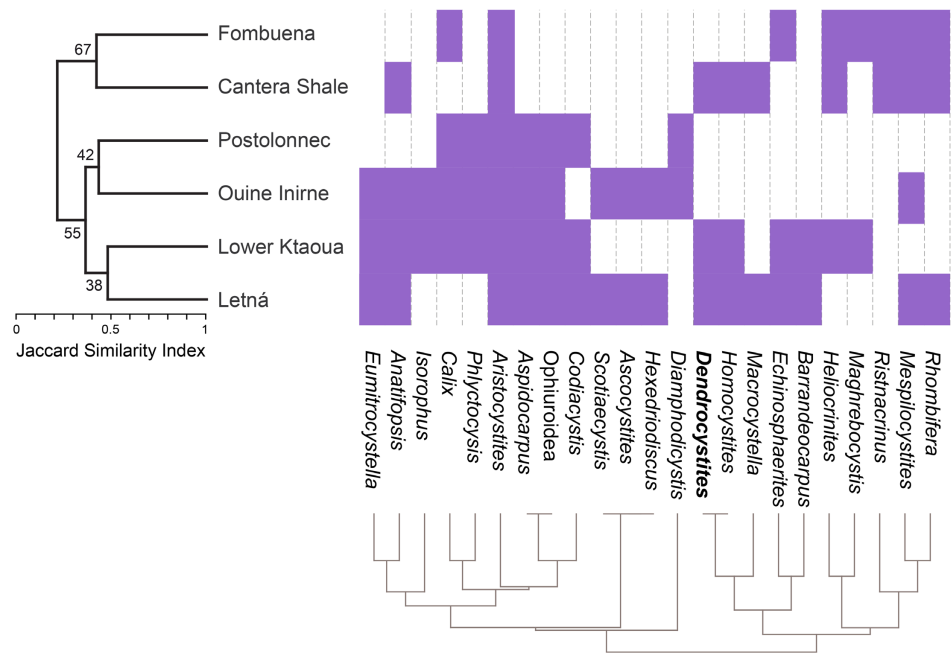
Figure 11. Blýskava hill ecology, Letná Formation (Sandbian). Body-fossil abundance of the taxonomic phyla, Dominance Index based on the generic abundance per layer and filling of the ecological guilds (*sensu* Bambach *et al.* 2007) for the three sedimentary units of the Blýskava hill excavation (Letná Formation; Sandbian, Upper Ordovician). Transparency indicates the whole preserved assemblages while plain color indicates the non-allochthonous fauna.

diploporitans (*Asterocystis*), glyptocystitid rhombiferans (*Homocystites*), ophiuroids and mitrate stylophorans (Lefebvre *et al.* 2007, Hunter *et al.* 2010, Nohejlová & Lefebvre 2022; Fig. 12). In the same area, another locality (Jbel Taklimt) provided a stratigraphically slightly older *Dendrocystites*-dominated dense bed (earliest Katian), associated to a more diverse benthic fauna including brachiopods, conulariids, edrioasteroids, ophiuroids and trilobites (Nohejlová & Lefebvre 2022). Fully articulated remains of the solutan *Dendrocystites* are also known from several other late Sandbian to early Katian localities in the Czech Republic (Vinice and Bohdalec

formations; Prokop & Petr 1999, Noailles *et al.* 2014), Morocco (Lower Ktaoua Formation; Lefebvre *et al.* 2007, Hunter *et al.* 2010, Nohejlová & Lefebvre 2022) and Spain (Cantera Shale; Gil Cid *et al.* 1996, Gutiérrez-Marco *et al.* 2018, Nohejlová & Lefebvre 2022). Most of these occurrences correspond to echinoderm-dominated benthic communities occurring in proximal, high-energy, siliciclastic settings, but contrary to the situation at Blýskava hill and Tizi n'Mourghi, *Dendrocystites* is a rare component of these assemblages (Fig. 12).

Solutan-dominated dense beds are not restricted to the genus *Dendrocystites* and/or the Upper Ordovician

Figure 12. Faunal similarities between the echinoderm-dominated Konzentrat-Lagerstätten from the mid-late Ordovician of the high-latitude peri-Gondwanan area. Similarities are based on an exhaustive database of generic occurrences (Appendix 5). Hierarchical Cluster Analysis based on the unweighted average linkage algorithm and the Jaccard similarity index.



of the Prague Basin and the eastern Anti-Atlas (Lefebvre 2007). However, such massive occurrences have been seldom described in shallow, high-energy environments. In the Central Anti-Atlas (Morocco), storm-generated accumulations of the solutan *Plasiacystis mobilis* were reported in some levels of the upper part of the Fezouata Shale (Floian) (Lefebvre et al. 2016, Dupichaud & Lefebvre 2022). In most cases, solutan-dominated assemblages occur in more distal settings, at or below the storm-wave base (Lefebvre 2007). This is the case, for example, in another locality (Taichoute) of the Central Anti-Atlas (Morocco), which yielded a *Plasiacystis*-dominated assemblage, also including brachiopods, cephalopods, gastropods, graptolites, glyptocystitid rhombiferans, somasteroids, stylophorans and trilobites (Saleh et al. 2022). Other examples of solutan-dominated echinoderm dense beds are stratigraphically older and outside of Gondwana: they include some levels of the Wheeler (*Coleicarpus sprinklei*) and Marjum (*Castericystis vali*) formations in the Drumian of Utah (Ubaghs & Robison 1985, 1988; Daley 1995, 1996).

Echinoderm dense beds occurring in proximal, high energy, siliciclastic settings are relatively common in the Ordovician of high-latitude regions of the Mediterranean Province, although most of them are not dominated by solutans. For example, eocrinoid- and stylophoran-dominated echinoderm Lagerstätten were described in the Lower Ordovician of Morocco (see e.g. Parsley & Gutiérrez-Marco 2005, Lefebvre et al. 2016, Allaire et al. 2017) and the Montagne Noire, France (e.g. Vizcaïno & Lefebvre, 1999, Lefebvre 2007, Nardin 2007). Similarly,

the late Darriwilian Ouine-Inirne Formation at Des-tombes locality no. 1698 (Tizi n'Tanekfoult, Morocco) yielded a low diversity assemblage dominated by the mitrate *Eumitrocystella savilli*, associated with few other taxa comprising relatively common other mitrates (*Aspidocarpus discoidalis* and *Anatifopsis* sp.), as well as rare eocrinoids and hyoliths (Cripps 1990, Beisswenger 1994, Lefebvre 2007). Numerous echinoderm dense beds dominated by eocrinoids, ophiuroids and/or stylophorans were recently described in the Upper Ordovician of the eastern Tafilalt, Morocco (Bou-Nemrou; see Lefebvre et al. 2007, 2008, 2022; Hunter et al. 2010; Sumrall & Zamora 2011, 2022; Nardin & Régault 2015, Botting 2022; Zamora & Sumrall 2022; Zamora et al. 2022). These Late Ordovician echinoderm Lagerstätten from the Tafilalt area are taphonomically and taxonomically very close to the Blýskava hill assemblage (Fig. 12), thus supporting the existence of strong faunal affinities between high-latitude peri-Gondwanan regions in the Late Ordovician (see e.g. Lefebvre 2007, Lefebvre et al. 2013, Nohejlová & Lefebvre 2022).

Conclusions

(1) The skeletal fauna in the studied excavation belongs to the lower parts of the brachiopod *Bicusplina* Community range of the *Drabovia–Aegiromena* Fauna of Havlíček (1982). In the temporary excavation at the southern slope of the Blýskava hill near Chrštenice, the relative composition of the fauna was documented and this study is one of the few works (see Mergl 1994) dealing with

quantitative data in the Ordovician of the Prague Basin, which are not based on museum or private collections.

(2) Studied section in the Blýskava hill provided the highest echinoderm diversity in the Letná Formation. The faunal association is dominated by echinoderms, representing more than 89% of specimens. The dominant taxon (the solutan *Dendrocystites*) represents about 76% of the assemblage and co-occurs with diverse asteroids, coronates, crinoids, diploporitans, edrioasteroids, ophiuroids, rhombiferans and stylophorans. The non-echinoderm part of the assemblage is comprised of mostly brachiopods, bryozoans, cephalopods, conulariids and trilobites, associated with rare bivalves, gastropods, foraminiferans and tentaculitoid tubeworms.

(3) The dominance of complete, fully articulated echinoderms makes it possible to classify the studied skeletal fauna as an echinoderm-dominated Konzentrat-Lagerstätte with prevailing specimens of the genus *Dendrocystites*.

(4) Sediments in the studied sequence were deposited in a very shallow-water environment of tidal flats with dominant tidal wave activity. The new occurrence and dominance of *Dendrocystites* in these levels confirm that it was adapted to very shallow waters, and it was not only restricted to storm-influenced environmental settings as previously thought.

Acknowledgements

Authors would like to express many thanks to William Ausich, handling editor Štěpán Manda and an anonymous reviewer for their constructive criticism of the early version of the manuscript. This study was supported by Czech Science Foundation (GACR) project no. 18-14575S, by the program Cooperatio GEOL of the Ministry of Education, Youth and Sports of the Czech Republic (OF), Strategic Research Plan of the Czech Geological Survey DKRVO/ČGS 2023-2027, internal task no. 311410 (PB, MN, MP). The study was partly funded by the PICS project n°246099 of the CNRS of France (EN). FS work is supported by a Swiss National Science Foundation Ambizione Grant (PZ00P2_209102). Lesy České Republiky, s.p. (Forest of the Czech Republic, s.p.) are acknowledged for access to the field area. Research Plan of the Institute of Geology of the Czech Academy of Sciences RVO67985831 (RM and MA). Milan Chroust, Eva Kadlecová, Radko Šarič (Czech Geological Survey), Vojtěch Kovář, Zuzana Kozlová, Veronika Veselá, Jana Čepičková, Barbora Švůgrová, Marta Letícia Hereino Kerkhoff (Charles University Prague), private collectors Václav Micka, Filip Novotný, Martin David are acknowledged for help in field. Michal Mergl (University of West Bohemia, Plzeň) is acknowledged for the generous help

with the determination of brachiopods. Andrej Ernst (University of Hamburg) is acknowledged for consultation of bryozoans. This paper is a contribution to IGCP project 735 “Rocks and the Rise of Ordovician Life: Filling knowledge gaps in the Early Palaeozoic Biodiversification”.

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Supplementary Electronic Material

- Appendix 1.** List of occurrences in the main excavation plus list of occurrences in the rock debris gathered from the measured excavation.
- Appendix 2.** Abundance matrix at the generic level.
- Appendix 3.** Results of the statistical tests.
- Appendix 4.** Ecological parameters for the genera.
- Appendix 5.** Presence/absence matrix of echinoderm genera in the selected echinoderm-dominated Konzentrat-Lagerstätten.