

Palaeoecology of a volcanically influenced Silurian sea floor in the Central Prague Basin, and its regional setting

JIRÍ KŘÍŽ†, LESLEY CHERNS & ŠTĚPÁN MANDA



The palaeoecology of a volcanically influenced Silurian sea floor is analysed from the Smoking Quarry, Kozolupy, Czech Republic. Platy limestones with small coral-stromatoporoid reefs developed around the Svatý Jan volcanic centre in the Prague Basin, alternating with atrypid brachiopod-rich tuffitic shales. The reef building organisms are preserved *in situ* or very little disturbed, as are the brachiopod assemblages, indicating limited reworking. Extrinsic climatic factors and diagenesis are considered with regard to the sedimentary cyclicity. Limestone firmgrounds and hardgrounds indicate early shallow cementation and exposure of irregular, probably nodular beds enhanced by diagenetic segregation of carbonate. In the volcanic setting, limestones may represent periods of greater current activity, when volcanoclastic sediment was washed into deeper areas, while shales represent more quiescent periods. The Kozolupy section studied represents the uppermost Gorstian volcano-sedimentary facies of the Kopanina Formation going up into shallow water limestones in the early Ludfordian. The succession is compared in its regional context with other sections in the Amerika Anticline, illustrating the spatial development of biofacies along the axis of the Prague Basin and the effects of global eustatic oscillations. • Key words: palaeoecology, small coral-stromatoporoid build-ups, volcano-sedimentary facies, Ludlow.

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The Teplá-Barrandian Unit of the Barrandian area formed the core of the small terrane of Perunica, separate from Gondwana in the Rheic Ocean from early mid Cambrian to Devonian times (Krs *et al.* 1987; Havlíček *et al.* 1994; Kříž *et al.* 2003; Patočka *et al.* 2003; Tasáryová *et al.* 2014, 2018; Franke *et al.* 2017; Žák & Sláma 2018; Torsvik & Cocks 2019; Žák *et al.* 2025). Silurian sedimentation in the Prague Basin was influenced by syn-sedimentary volcanism from centres along deep growth faults and at their intersections (Horný 1965; Kříž 1991, 1992). Following late Ordovician Hirnantian glacial lowstand, early Silurian transgression and flooding spread a blanket of clastic muds and anoxic conditions, represented by graptolitic, black shale facies. However, through late Llandovery and into Wenlock times sedimentation in those trough environments was increasingly carbonate-rich. Extensional, syn-sedimentary faulting was accompanied by volcanic activity, which introduced large volumes of volcanoclastic sediments as well as intrusions and lava flows. Around volcanic centres, accumulation of volcanoclastic sediments resulted in local areas of shallow-water environments, colonised by a rich shelly benthos

during periods of reduced sediment supply. Volcanic activity decreased in the late Gorstian and terminated close to the Gorstian–Ludfordian boundary when carbonate sedimentation extended across those volcanic sea floor highs. It is notable that abundant coral faunas are known only from late Wenlock (Homerian) and early Ludlow (Gorstian) volcano-sedimentary facies, corals are rare in the late Ludlow limestones.

In this paper we examine the facies development of an early Ludlow (Gorstian) limestone–tuffitic shale sequence in the vicinity of the Svatý Jan volcanic centre, which was sited along the Tachlovice Fault (Horný 1965; Kříž 1991, figs 4 and 5; Fig. 1). The locality at Kozolupy lies in the fault-bounded central segment of the Prague Basin, exposed in the Amerika Anticline, which represents a tectonic window in the Devonian rocks that cover most of the Silurian rocks between the Tachlovice and Koda faults to the north and south, and the Tobolka and Barrandov faults to west and east, respectively. The authors JK and LC studied the lower part of the section in detail in the late spring and early summer 1977. The complete section was measured in 1992 by JK and

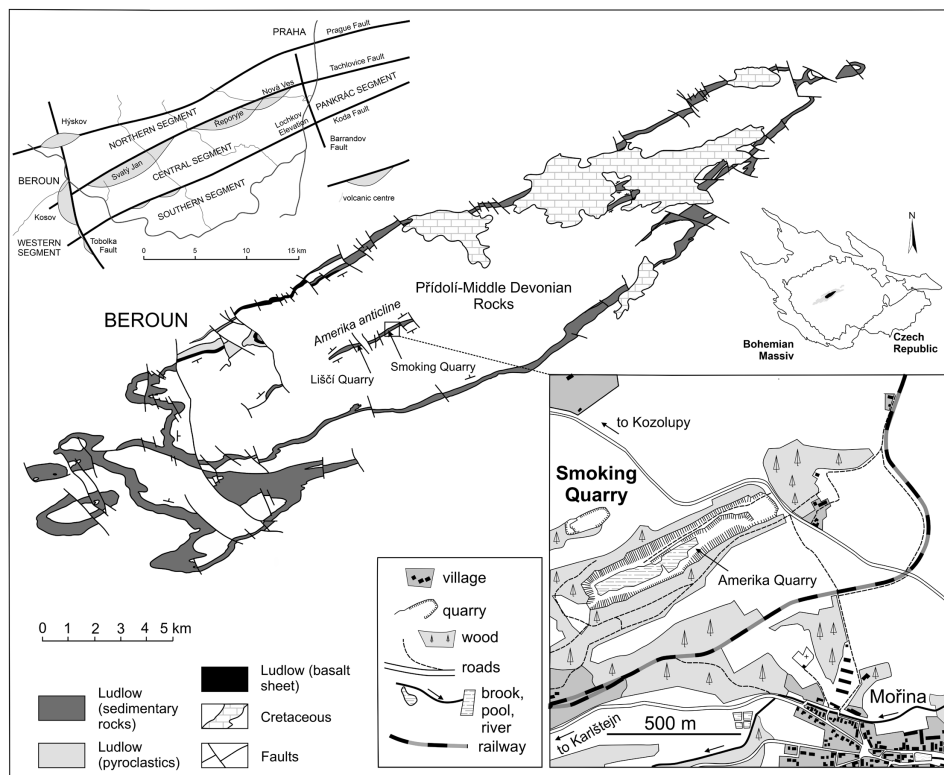


Figure 1. Distribution of Silurian Ludlow rocks and Kopanina Formation in the Prague Basin (after Manda & Kříž 2006) and position of study area in the Amerika Anticline, with positions of Smoking Quarry and Liščí Quarry marked. Silurian syn-sedimentary tectonics, volcanic and tectonic elevations, and segments (sub-basins) in the preserved parts of the Prague Basin shown in upper left corner (after Kříž 1991). Enlarged map of Smoking Quarry locality shown in lower right corner.

re-studied in 2007 by JK and ŠM. Subsequently the quarry was designated a protected Nature Monument (Kříž 1994). Material from the quarry is deposited in the collection of Jiří Kříž and Radek Mikuláš in Czech Geological Survey (prefix JK and RM) and National Museum in Prague (prefix NM L, collected by Pavel Lukeš).

We analyse the Gorstian faunal succession on a shallow carbonate sea floor that developed around the volcanic centre, replacing dark shales of a deeper basinal setting.

Smoking Quarry, Kozolupy

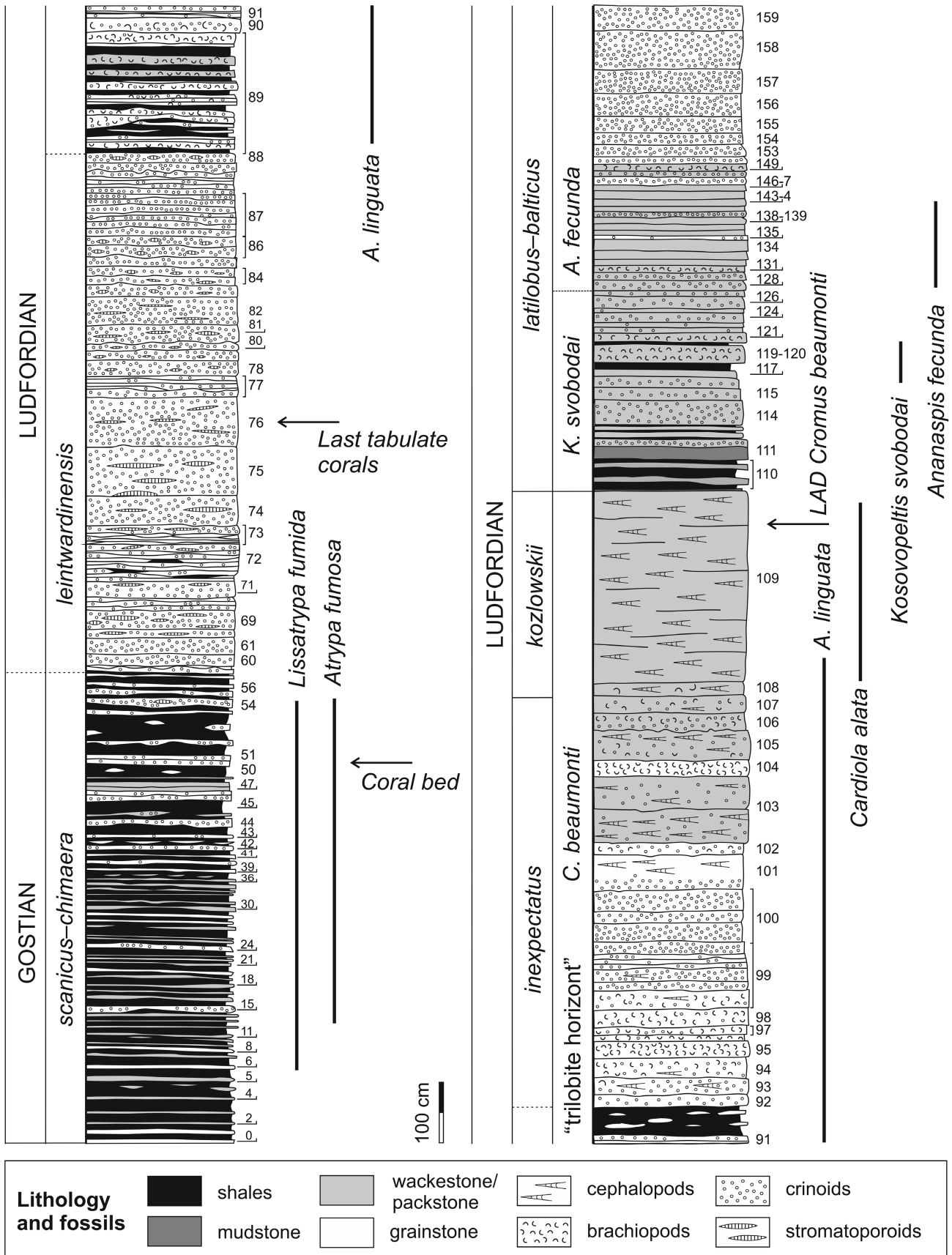
This small disused quarry (grid ref. 49° 57' 37" N, 14° 11' 35" E) is located NW of Mořina, in the Amerika Anticline (Fig. 1). This locality and section were described first by Horný (1955, pp. 368, 369, Amerika–east, Northern deposit). Galle (1973) described favositid corals. Kříž & Pek (1975) and Mikuláš (2019) described lower Ludlow trace fossils from there, and the section was measured and described by Kříž (1992) and Kříž *et al.* (1993). Havlíček & Štorch (1990) and Havlíček (1995) commented on the lower Ludlow benthic fauna, and the trilobite fauna was

described by Slavičková & Kocourek (2000) and Vaněk & Vokáč (2004).

The thickness of the Ludlow Kopanina Formation (Fig. 2) in the quarry is *c.* 40 m. The section starts with 7.8 m of thin bedded limestone–tuffitic shale alternations (bed Nos 1–57) with trilobites, brachiopods and cephalopods that indicate a late *Lobograptus scanicus*–*Saetograptus chimaera* Biozone Gorstian age. An 8.5 m succession (beds 58–88) of dolomitised, light grey fine-grained, thin to medium bedded (10–50 cm) crinoidal limestones includes fining-up and cross-bedding structures. There are abundant stromatoporoids, and corals are also present in some beds. Colonies are re-worked, usually fragmented and rounded. This part of the succession is studied in detail below.

The following *c.* 22 m Ludfordian sequence (beds 89–159) is predominantly bioclastic limestones (Kříž 1992; Fig. 2). It starts with a *c.* 3 m interval of thin bedded, platy limestones with crinoids and brachiopods intercalated with calcareous shale (beds 89–91). Abundant *Atrypa linguata* (von Buch, 1834) (usually disarticulated smaller valves) is accompanied by less abundant *Lissatrypa*, *Cyrtia* and *Sporinella* brachiopods.

Figure 2. Sedimentary log of succession in Smoking Quarry, showing bed numbers, amended from Kříž (1992). The study section encompasses the upper Gorstian succession beds 0–57; note that only limestones are numbered, intercalated shales are referred to those. Note, in the absence of graptolites, positions of biozonal boundaries are based on benthic macrofaunal assemblages (and re-interpreted since Kříž 1992).



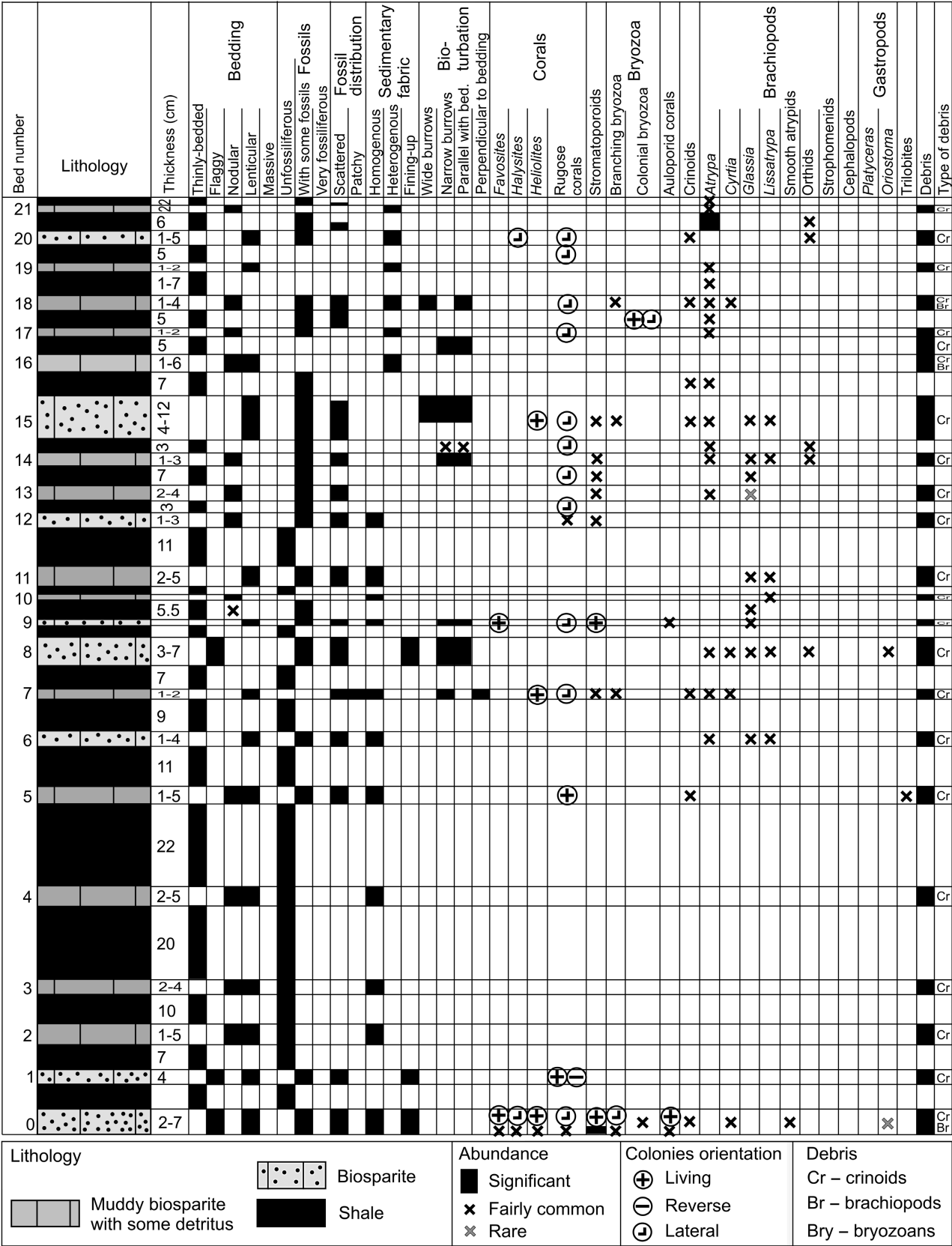


Figure 3. Detailed lithological and faunal log for the Gorstian succession in Smoking Quarry, lower part, beds 0–21. Note that only limestones are numbered on the log.

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Figure 4. Detailed lithological and faunal log for the Gorstian succession in Smoking Quarry, upper part, beds 22–49. Note that only limestones are numbered on the log.

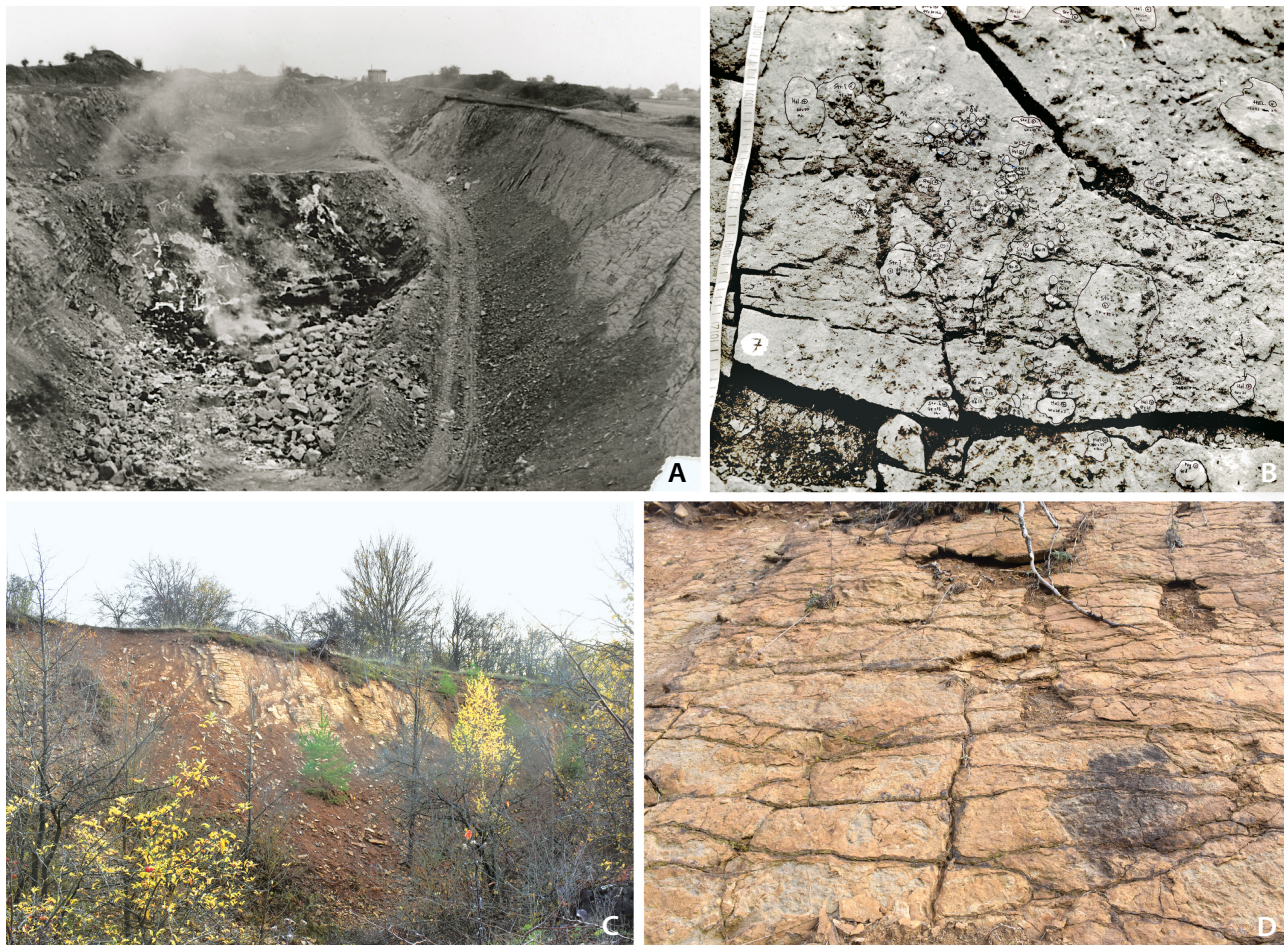


Figure 5. Smoking quarry, SW wall, Kopanina Formation, upper Gorstian. • A, C – condition in 1977 (A, photo by J. Kříž) and present day (C, photo by Š. Manda). • B, D – example of bedding surfaces with fossils for quadrat studies in 1977 (B) and current state (D).

The section continues in c. 6.7 m (beds 92–107) of light grey crinoidal, brachiopod and cephalopod limestones with *A. linguata*. Two beds (3.4 m, beds 108, 109) of grey cephalopod limestones have abundant pelagic cephalopods, while bivalves are represented by common *Cardiola alata* Barrande, 1881, *Dualina longiuscula* Barrande, 1881 and *Tenka* sp. A 0.4 m thick unit of grey laminated shales and muddy limestones (beds 109–110, 110) forms a sharp contact with the cephalopod limestones and is a local correlation marker; scolecodonts are abundant in both shales and limestones, strophomenid brachiopods are uncommon.

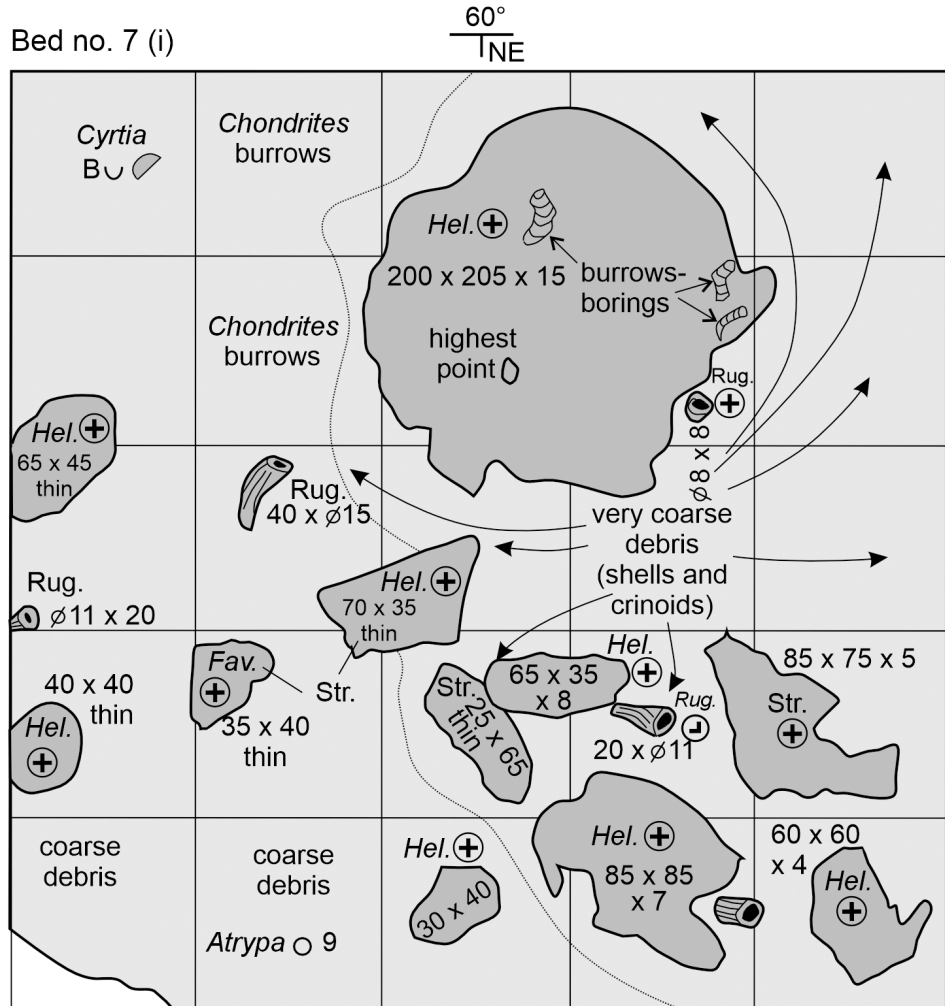
The succession continues with 5.2 m of dark grey, thin bedded, usually crinoidal platy limestones, sometimes separated by very thin shale intercalations (beds 111–149). Erosional basal surfaces overlain by fining-up crinoidal limestone are characteristic. In some beds disarticulated brachiopods are common, while the trilobite *Kosovopeltis svobodai* Šnajdr, 1960 is rare in the lower part of the interval and *Ananaspis fecunda* (Barrande, 1846) is uncommon in the higher part. The uppermost c. 2.5 m of

the section is light grey and rusty, fine-grained crinoidal grainstones (beds 150 to 159), with abundant *Atrypodea modesta* (Nikiforova, 1970) in some beds that indicates a latest Ludfordian age.

Description of late Gorstian strata – termination of volcano-sedimentary facies

The upper Gorstian part of the succession was logged in steeply dipping strata with exposed bedding surfaces (c. 32 m; Kříž 1992, fig. 62; Fig. 5). Correlation with a nearby trench section logged from the uppermost Wenlock Motol Formation up into the lower Kopanina Formation indicates that the logged quarry sequence starts c. 9.5 m above the base of the Kopanina Formation (Kříž 1992, figs 61, 62; Kříž *et al.* 1993, fig. 15). In this study an interval of c. 7.8 m of limestone–tuffitic shale alternations was logged in detail (Figs 3, 4). The lower Kopanina Formation succession is shales and tuffites that continue from the Motol Formation (Wenlock). These pass up through

Figure 6. Quadrat (50 cm square) of limestone bedding plane fauna, bed 7. Thin heliolitid and stromatoporoid colonies, right-way-up on surface of very coarse skeletal and crinoidal debris, crossed by feeding burrows of *Chondrites*. Abbreviations for Figs 6–10 – Fossils: Aulac. – aulopod coral; Bry. – bryozoans; Cr. – crinoids; Fav. – *Favosites*; Hal. – *Halysites*; Hel. – heliolitid corals; Orio. – *Oriostoma*; Rug. – rugose coral; Str. – stromatoporoid. Fossil orientations: + right way up; – over-turned; L on side – see key in Fig. 3. Brachiopods: B – brachial valve; P – pedicle valve; A – articulated.



increasingly carbonate rich, very thin limestone–shale alternations into thicker, bioclastic limestones. Lateral facies and thickness changes are rapid; many limestone beds are wavy-bedded and lenticular. Faunal records were compiled bed by bed, together with palaeoecological data on shell orientations, articulation, and distribution across long, steep bedding surfaces (now with very limited accessibility for study).

The limestones are variably muddy and crinoidal wackestones and packstones, mostly very thin (< 5 cm), nodular and lenticular, and generally muddier through the lower part of the measured section. The nodular nature suggests that many beds are secondary or diagenetically enhanced (e.g. Munnecke & Samtleben 1996, Wright *et al.* 2025). Through the lower part of the section (Fig. 3), sedimentary fabrics are rarely evident. Limestones have a mottled or homogeneous texture which, since macrofossils are typically scattered through, suggests a high degree of bioturbation (e.g. Taylor & Goldring 1993). Higher in the section (Fig. 4) where limestones become more common, discrete *Chondrites* networks

and other, broader shallow *Helminthopsis* traces evident against bedding fabric suggest a lower bioturbation index, possibly due to increased sedimentation rate. Macrofossils are still typically scattered through beds, but bioclastic debris shows a patchy concentration in burrow fills. The bioclastic sand component, which is generally high, is composed chiefly of fine pelmatozoan grains. Occasional graded beds (fining-up) indicate event deposits. In the upper part of the measured section, lenticular limestone beds become common and bedding is characteristically wavy. Some beds are cross-laminated, and a wave-rippled (tidal) surface was recorded directly below thicker packstones which become increasingly massive higher in the Kopanina Formation. Several packstone beds with rich coral-stromatoporoid faunas have irregular surface relief that appears to represent firmground areas, diagenetically enhanced by nodular carbonate growth. Direct encrustation on the sediment indicates episodes of hardground formation. Overall coarsening of limestones and increased current influence suggest hallowing-up.

Bed no. 15

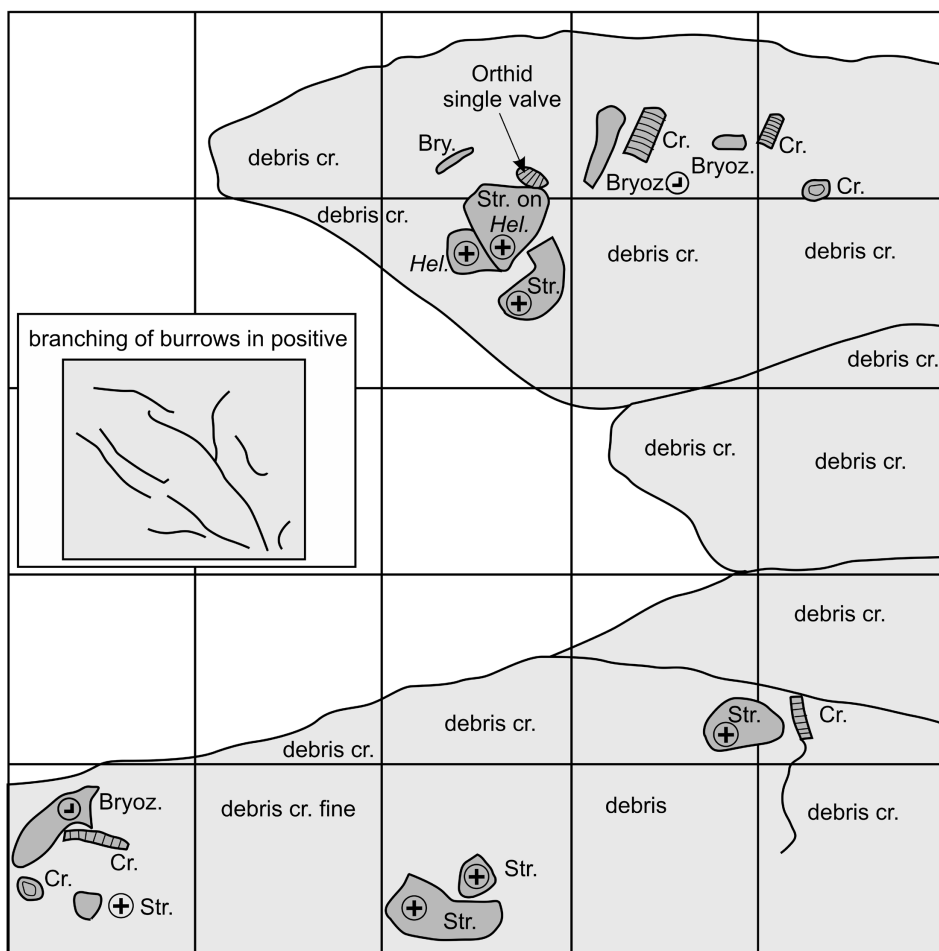


Figure 7. Quadrat (50 cm square) of limestone bedding plane fauna, bed 15. Small thin stromatoporoids with borings, apparently *in situ* on surface of coarse crinoidal debris, branching bryozoans, crinoid stem segments. Chondritic burrows cross the surface, preserved in relief. Abbreviations – see Fig. 6 caption.

Limestones are interbedded with very thin to thin (1–22 cm, mostly < 10 cm), dark tuffitic, and increasingly calcareous shales. These are relatively poor in macrofossils and bioclastic debris, especially in the lower part of the section. A high degree of bioturbation is indicated by the generally homogeneous texture, with few discrete burrow traces. A lack of bedding fabric means that no current structures are preserved.

Faunal associations (Figures 3–11, 15–17)

Nota bene on the logs (Figs 3, 4) only the limestone beds are numbered and intervening shales are referred to as a span between limestones.

The bioturbate texture of most shales and limestones indicates an active soft-bodied infauna. Through the lower 1.7 m of section (up to shale 11–12, Fig. 3), the shales lack body fossils, but in higher beds the brachiopod *Atrypa fumosa* Havlíček, 1990 in Havlíček & Štorch (1990) (Figs 15A–D, F–H; 17K) becomes increasingly common in limestones and also in shales from 14–15.

The limestone faunas are rich in colonial reef-building organisms typically associated with shallow and clear water habitats, such as tabulate corals, stromatoporoids and chaetetids ‘*Barrandeolites*’ *bowerbanki* (Milne-Edwards & Haime, 1851), many of which were apparently in life orientation and *in situ*. Only through the interval near the base of the section (*c.* 0.2–0.9 m, beds 2–4) were macrofossils sparse. The limestone faunas were referred to the Coral-crinoid Community by Havlíček & Štorch (1999), associated with brachiopods that indicated a Benthic Assemblage 3 (BA3; Boucot 1975, Boucot & Lawson 1999) position, *i.e.* in mid-shelf environments within wave base. The most common tabulate corals are heliolitids (e.g. *Heliolites*, Fig. 15I, J; *Propora*, *Stelliporella*, Fig. 16A), halysitids (*Halysites*, Fig. 16F), favositids (*Favosites*, Fig. 16G) and sarcinulids (*Thecia*, Figs 15–17). Stromatoporoids are also numerous. Colonies of both groups are relatively thin and platy; corals are mostly < 20 cm thick, stromatoporoids much thinner, and colonies are < 50 cm wide, but mostly < 30 cm. They typically have irregular, uneven lower surfaces that mould the form of the substrate. Aulopodid corals (*Aulopora*

Bed no. 44 (iv)

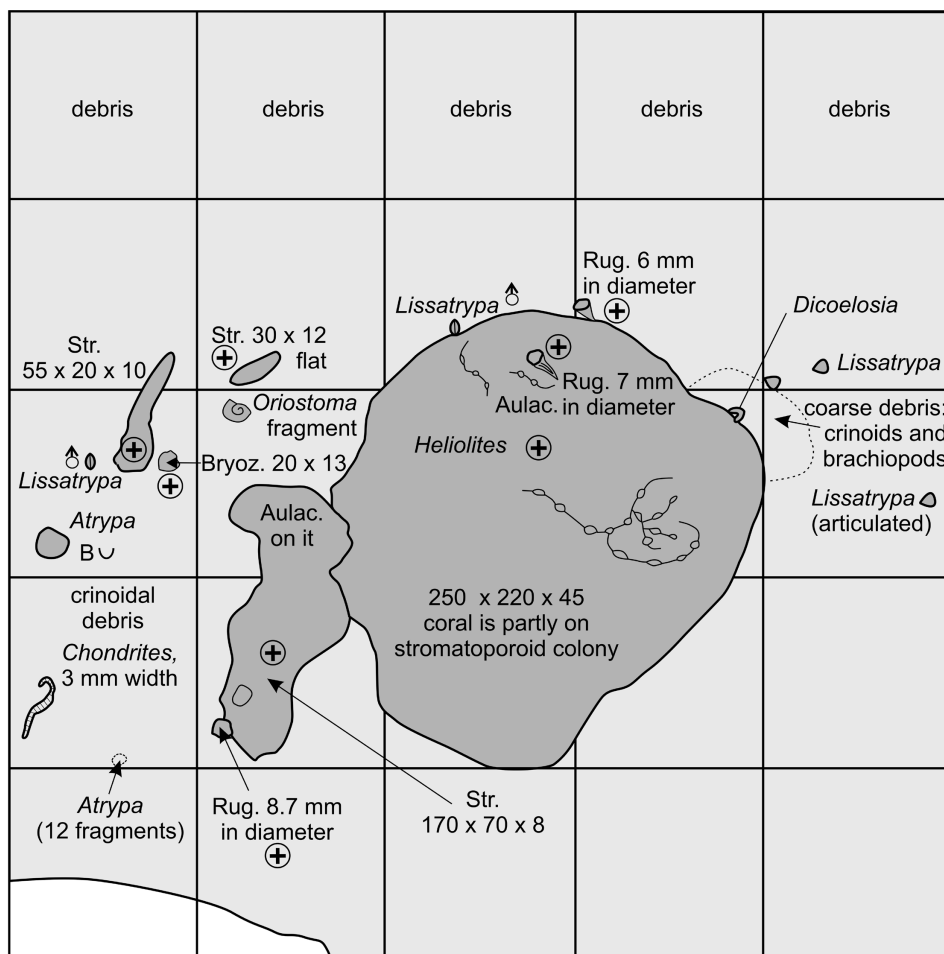


Figure 9. Quadrat (50 cm square) of limestone bedding plane fauna, bed 44. *In situ* large thin *Heliolites* coral colony encrusted by auloporid corals on coarse bioclastic crinoidal debris, scattered rugose corals and brachiopods. Abbreviations – see Fig. 6 caption.

spp.), which were hard-substrate encrusters, commonly overgrow other colonial and solitary skeletal organisms (heliolitids: Figs 15I, J; 16D; 17K; favositids: Figs 16G, K; 17G; atrypids: Figs 15D, G–H; 17K). Where they extend across bioclastic debris on bedding surfaces, it indicates that these were hardgrounds (Fig. 16E, K). One auloporid coral colony overgrows a small, flat and slightly rounded coral colony on both surfaces, indicating reworking before final deposition. Overgrowth between colonies of corals and stromatoporoids is also quite common, providing an organic framework in low mounds or biostromes (e.g. Figs 8–10). The associated fauna includes colonial and solitary rugose corals (including *Entellophyllum*, Fig. 16A, I; *Cystiphyllum*; *Syringaxon*; *Kodonophyllum*, Fig. 16H). Bryozoans include encrusting (Figs 16B, J, L; 17I) and attached fenestellate forms (Fig. 17F). Pelmatozoan (crinoid) debris is abundant, but articulated crowns are very rare (Fig. 17K). Some crinoid roots are found attached to colonial organisms (Fig. 17B). Among the brachiopods, *A. fumosa*, *Lissatrypa fumida* Havlíček, 1984, *Strophoprion euglypha relata* Havlíček, 1990 in Havlíček & Štorch

(1990) (Fig. 17A), *Cyrtia* sp. and *Dicoelosia biloba* (Linnaeus, 1758) (Fig. 15E) are most common, with *Isorthis* (*Arcualla*) *nummiformis* Havlíček, 1977. *Atrypa fumosa*-rich assemblages become increasingly common up through the succession. Gastropods (*Oriostoma* sp., Fig. 17H; platyceratids) are rare, trilobites including *Cromus beaumonti* (Barrande, 1846), *Kettneraspis geinitziana* (Hawle & Corda, 1847) (Fig. 17E), *Interproetus* aff. *coinsobrinus* Šnajdr, 1980 (Fig. 17H), *Leonaspis* (Fig. 17K), *Sphaerexochus*, *Scharyia* are present in low numbers. Occasional cephalopods [*Dawsonoceras annulatum* (Sowerby, 1818) (Fig. 17C); *Cyrtocycloceras ibex* (Sowerby) in Murchison (1839), *Peismoceras asperum* (Barrande, 1865) and *Geisonoceras* sp.] represent demersal swimmers.

Quadrat surveys (0.5 m²) were made of exposed areas of limestone bedding surfaces to assess skeletal distribution, breakage and shell orientations, and trace fossils (Figs 6–10, bedding planes of beds 7, 15, 40, 44, 51). Patchy distribution of skeletal organisms contributes to a mean areal coverage by macrofossils of < 20% (n = 31, s.d. = 15%). This mean figure masks variation

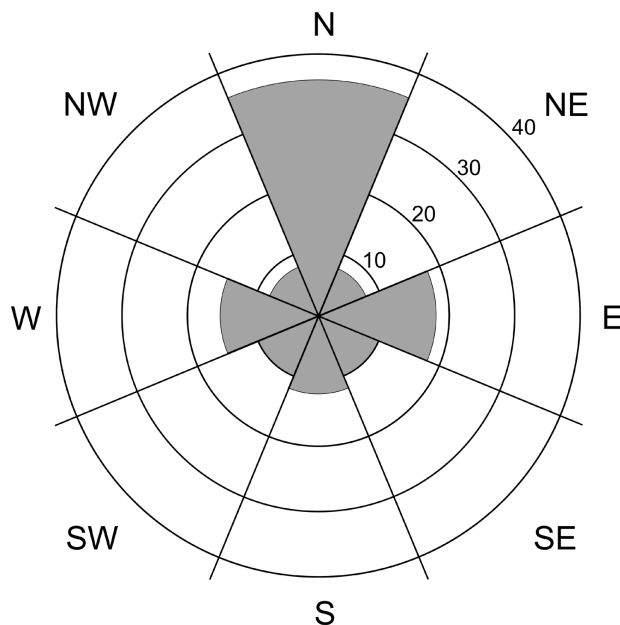
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By contrast, the atrypid-dominated brachiopod assemblages found both in shales and increasingly also in



Figure 11. Chondrites, SW wall of Smoking Quarry, left half of slab figured Kříž & Pek (1975, pl. 2, Fig. 4 traces type B), photo by J. Kříž 1974.

> **Figure 12.** Rose diagram of rugose coral orientations from a single bed (51) in 45° segments. Note the strong preferred orientation of corals, indicating the effects of currents.



the higher limestones, are level-bottom faunas typically from soft, muddy substrates. The broad thin trail on *A. fumosa*, which is commonly preserved in atrypid valves, was interpreted already by Ivanova (1962, text-figs 23–27) as functioning to prevent the brachiopod sinking into soft sediment. In other palaeobiogeographical realms, Boucot & Lawson (1999) noted the general association of fine-grained sediment, whether siliciclastic or carbonate, with his long-ranging (late Llandovery–Frasnian) North American *Atrypa reticularis* Community, and Watkins' (1979; Lawson 1999) late Gorstian *A. reticularis*–Coral Association from the Welsh Basin is associated with low energy, muddy carbonates. Valve ratios, orientations and sizes were noted (Figs 13, 14) from beds with

a high proportion of articulated shells, and data were also obtained from others where valves were chiefly disarticulated. Of the former, populations from four beds through c. 0.7 m of the limestone–shale alternations (beds 24–25 to 29–30) include up to 72% (mean 67%, s.d. = 5) of articulated shells (Fig. 14). Among assemblages with mostly disarticulated shells, the proportions of pedicle and brachial valves are fairly similar, but with the stable, convex-up orientation easily dominant. For example, 3 additional quadrats on bed 26–27 comprised 80% disarticulated shells, had a pedicle valve:brachial valve ratio of 0.8, and convex-up:concave-up ratio of 16.5. Left- (negatively) skewed and broad size-frequency distributions suggest both assemblages of articulated

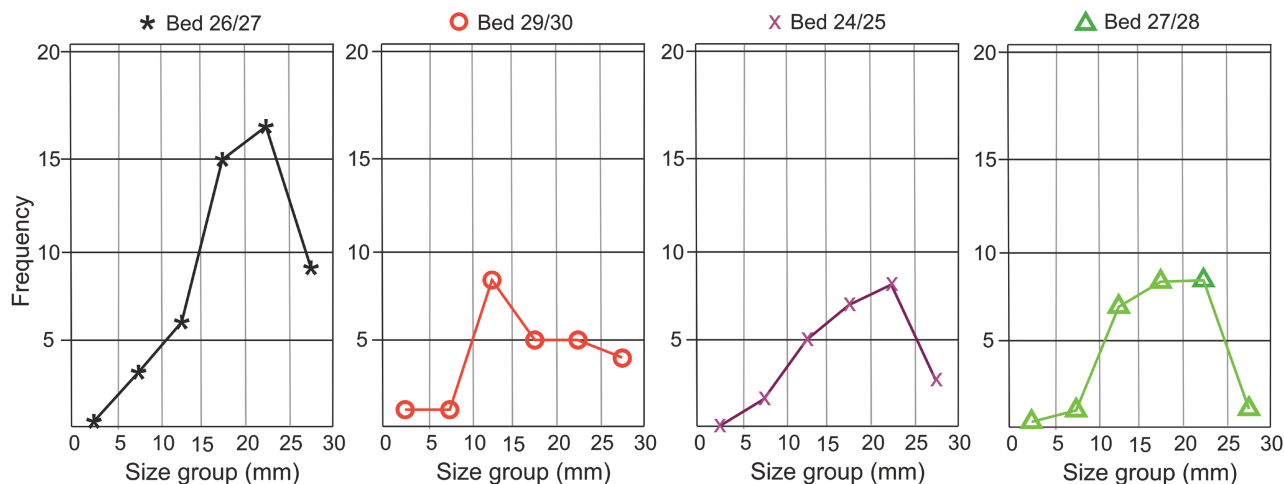


Figure 13. Size-frequency graphs for atrypids in quadrats from the four shale beds 24–25, 26–27 (two samples), 28–29 and 29–30. Note the left skew of all except 29–30, indicating mature populations with little reworking, although a scarcity of small individuals suggests some losses.

and disarticulated valves represent mature, *in situ* or neighbourhood populations (Fig. 13). It appears that sorting and transport were limited, although there are few small individuals among the populations. If these atrypid assemblages represent indigenous fauna, they occupied tracts of soft substrate adjacent to the firmgrounds where the small, patch reefs developed. It is notable that relatively few atrypids co-occur among the reef assemblages, chiefly clustered in pockets between framework areas.

Smoking Quarry coral-stromatoporoid build-ups

In the limestones, overgrowth of coral and stromatoporoid colonies (Figs 6–10) demonstrates a pattern of succession from the pioneer halysitid and rugose corals, through stromatoporoids, chaetetids and tabulate (heliolitid and favositid) corals, to auloporids and sarcinulids as encrusters, in minor, open frame reefs (Riding 2002). Chaetetids and crinoids are also associated with the build-ups.

The bedding surfaces are uneven and hummocky, with the colonial organisms based on low elevations formed by lenses of bioclastic (largely pelmatozoan) sand and gravel. These small Kozolupy reefs compare with Riding's (1981, Fig. 23) Silurian Axelsro-type from Gotland, which represent the lowest energy build-ups formed in marginal, more offshore zones of the carbonate ramp. In the upper Llandovery of Gotland, halysitid corals dominate with rugose corals in thin, laterally extensive build-ups (Stel 1978, Nield 1982), and occur among other more diverse, tabulate coral-stromatoporoid assemblages in small, thin patch reefs (< 1 m wide, < 0.4 m high). In the Kozolupy setting fringing a volcanic island a narrow shallow carbonate shelf supported the development of small reefs and biostromes in the wider basinal setting. Halysitid corals act as 'baffles' to stabilize muddy carbonate substrates. Riding (1981, p. 58) noted an ecological gradation between small dense reefs defined by some intergrowth of organisms and isolated colonial organisms among level-bottom communities. Similarly, at Kozolupy, the thin coral-stromatoporoid build-ups of intergrown and

Figure 14. Atrypid population histograms for the four beds as in Fig. 13, showing a high proportion of articulated shells (< 72%, average 67%), a further indication of these representing neighbourhood assemblages that have been little transported.

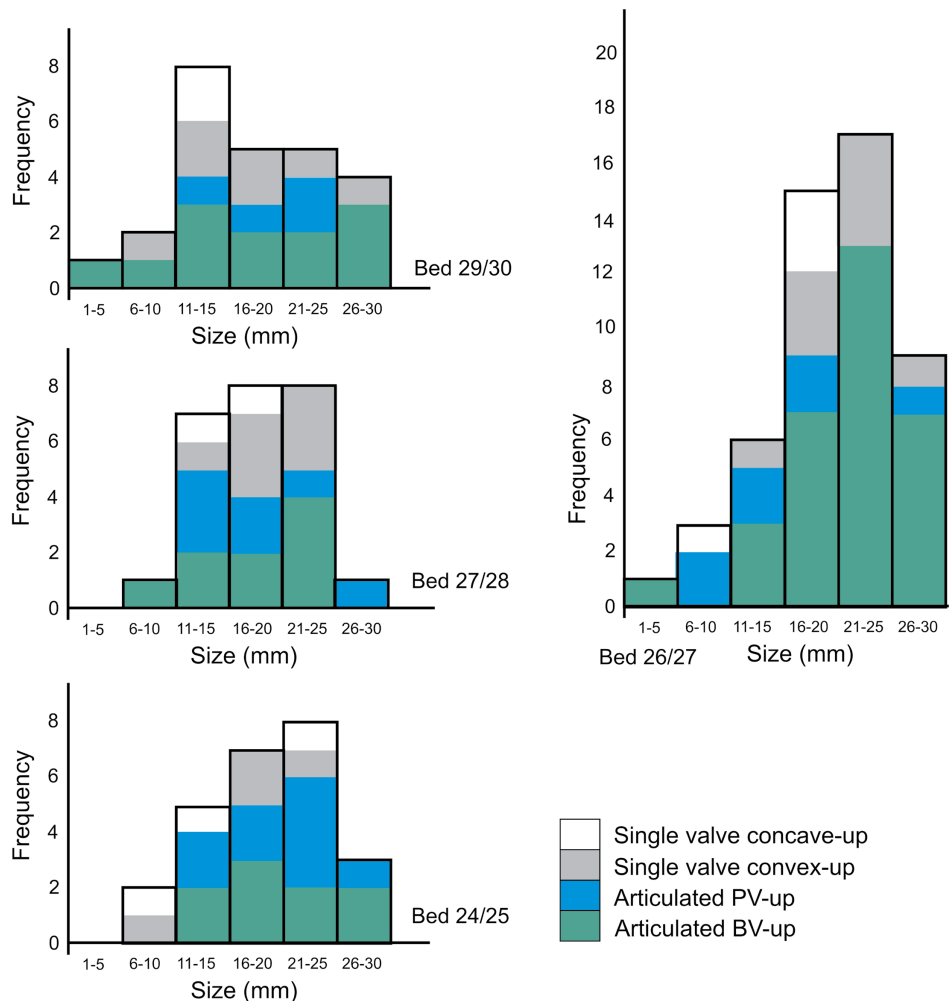
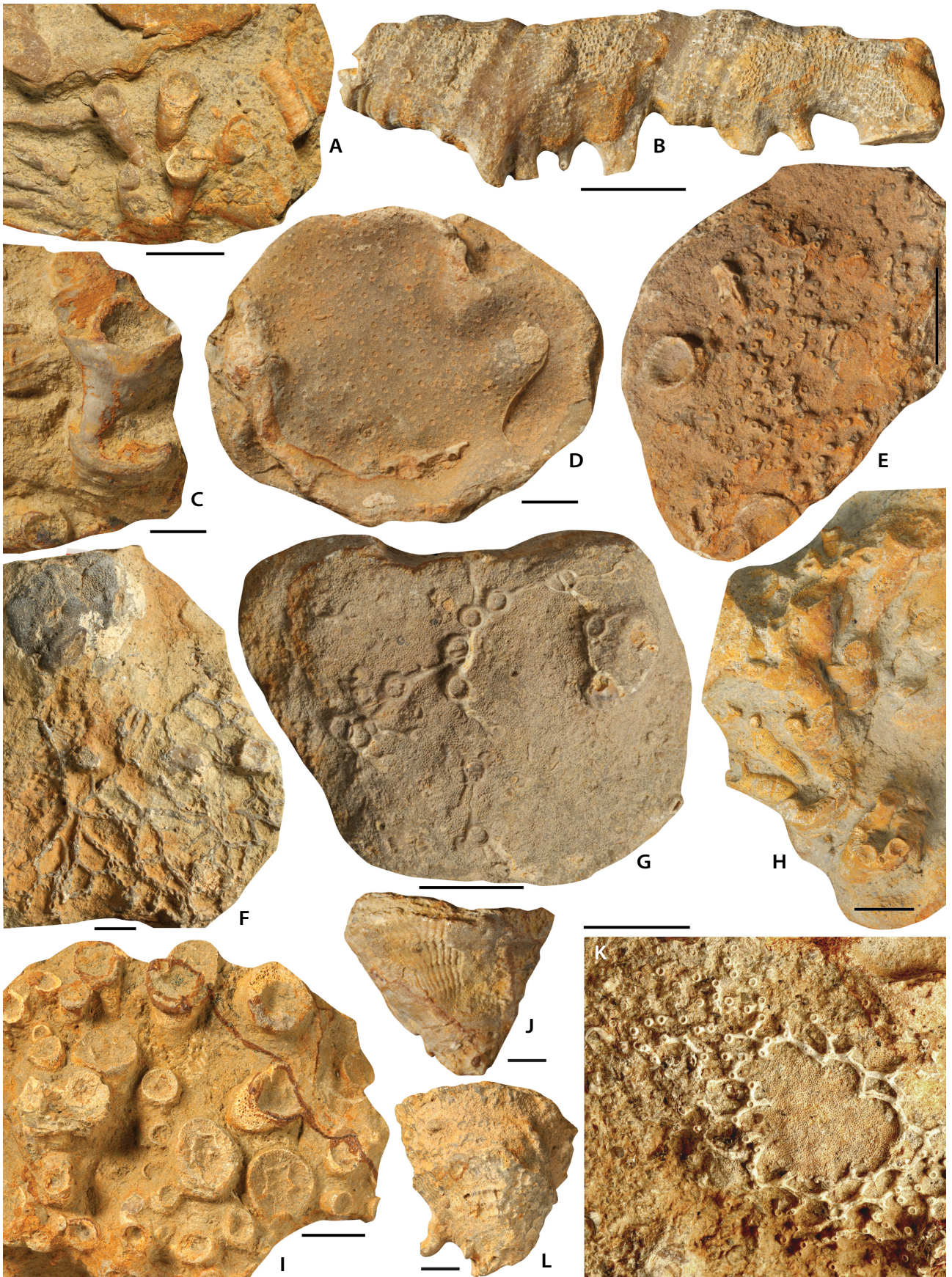




Figure 15. Fossils on bedding planes and isolated fossils from tuffitic shales, Smoking Quarry. In the uppermost Gorstian section fossils were collected mainly from debris below the outcrop, with only a limited number of finds from numbered beds. Brachiopods and a coral from tuffitic shales. • A–D, F–H – *Atrypa fumosa* Havlíček, the most abundant brachiopod in the coral-crinoid fauna. A, B, F – small specimen; A – brachial valve; B – pedicle valve; F – anterior view, NM L 40616. C, G – mature specimen; C – anterior view; G – brachial valve with initial stage of auloporid coral encrustation, NM L 40615. D, H – mature specimens encrusted by auloporid corals; D – pedicle valve, NM L 40618; H – brachial valve, NM L 40617. • E – five specimens of *Dicoelosia biloba* (Linnaeus) on *Favosites* colony, NM L 40603. • I, J – small coral colony of *Heliolites* encrusted by auloporid coral; I – corallum surface; J – lateral view of epitheca, NM L 40613. Scale bars: A–H = 5 mm; I, J = 10 mm.

> **Figure 16.** Corals from limestones among tuffitic shales, Smoking Quarry. • A – fasciculate rugosan colony (*Entellophyllum*) growing on corallum surface of tabulate coral *Stelliporella* sp., NM L 40610. • B – lateral view of solitary rugose coral with projecting tubules, encrusted by a bryozoan, NM L 40602. • C – budding of solitary rugose coral, NM L 40607. • D – coral *Heliolites* sp. with encrusting auloporid coral parallel to margin, NM L 40599. • E – dense colony of an auloporid coral apparently encrusting a hardground or thin stromatoporoid in association with small rugose coral preserved in life position, NM L 40605. • F – *Halysites* tabulate coral corallum surface partially encrusted by a thin stromatoporoid and encasing a small solitary rugose coral in life position, NM L 40614. • G – *Favosites* tabulate coral corallum surface encrusted by an auloporid coral mostly across elevated parts of colony, NM L 40601. • H – fasciculate rugosan coral colony (*Kodonophyllum*) growing on favositid colony (for lower part of colony see Fig. 17L), NM L 40612. • I – fasciculate rugosan coral colony (*Entellophyllum*) preserved in living position, NM L 40608. • J, L – two examples of solitary rugose coral epitheca encrusted by bryozoan (J), and favositid coral (L) and bryozoans, NM L 58112 (J) and NM L 40609 (L). • K – an auloporid coral encrusting directly onto a hardground substrate and spreading onto a favositid tabulate coral, the more elevated central part of the favositid is not encrusted, NM L 40598. Scale bar = 10 mm.



encrusted colonies differ only in scale from isolated encrusted colonies which also occur quite commonly in the same beds (e.g. Fig. 9). Many colonies have uneven undersurfaces which mirror an irregular substrate, lying directly on coarse bioclastic sand that formed a firmground for colonization. Direct aulopodid encrustation confirms the early lithification of some substrates. A generally high proportion of *in situ* colonies among the thin build-ups makes it probable that reef development and colony growth were not halted by current disturbance. More probable is blanketing by mud through subsidence, or the toxic effects of influx of fine volcanic material.

Prague Basin evolution and sea level

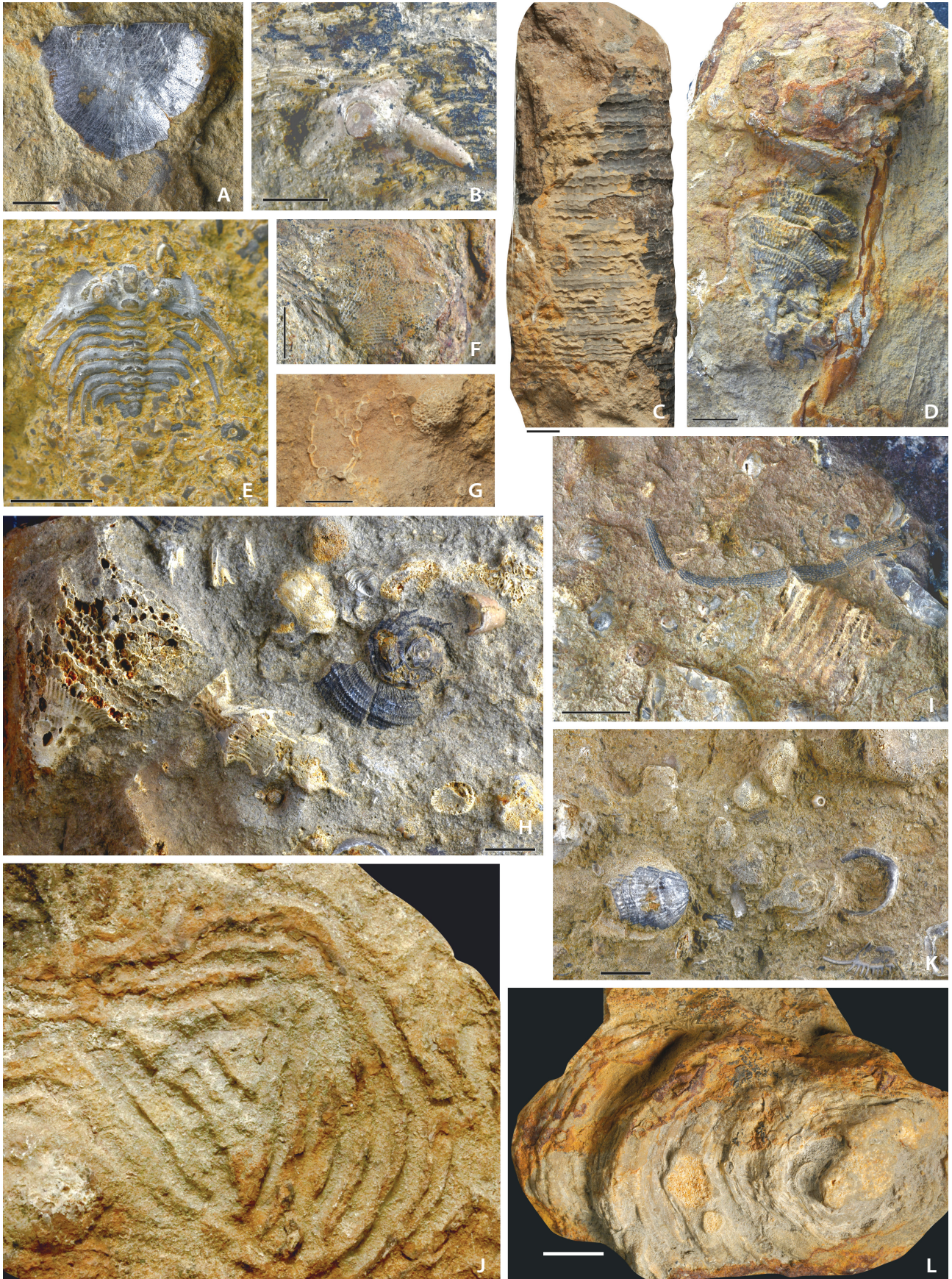
Silurian sea-levels in the Prague Basin were controlled regionally by syn-sedimentary tectonic activity and volcanism along major fault lineaments, superimposed on the global eustatic cyclicity that is documented across palaeocontinents (e.g. Johnson 1996, 2006, 2010; Melchin *et al.* 2020). In the Prague Basin (Fig. 1), tectonic movements and volcanic activity (Tachlovice, Koda and Tobolka faults; Kříž 1991, 1992) accompanied differential subsidence of central and outer segments of the Basin through Wenlock and into early Ludlow times. The wider eustatic pattern (Fig. 18) shows late Wenlock (Homerian, *Colonograptus ludensis* Biozone; = *Colonograptus ludensis*–*Colonograptus gerhardi* Biozone; Štorch 2023) regression, followed by early Ludlow (Gorstian, *Neodiversograptus nilssoni* Biozone) transgression, and then two further pulses of regression through later Ludlow times (Ludfordian, *Saetograptus leintwardinensis* and *Neocucullograptus kozlowskii*–*Formosograptus formosus* biozones). Facies succession and progradation/retrogradation of limestone facies in the Prague Basin show a more complex eustatic pattern; tectonic uplift/subsidence probably controlled regional eustatic oscillations and may even have masked global oscillations (Kříž 1991, 1992; Manda & Kříž 2006). Cephalopod limestone biofacies is a widespread indicator

of periods of regression in late Silurian–Devonian times across the equatorial Proto-Tethyan region (Bohemia, Carnic Alps, Montagne Noire, Sardinia; Kříž 1984, 1998, 1999a; Ferretti & Kříž 1995). This biofacies was deposited around sea-floor volcanic elevations in the Prague Basin between episodes of volcanic activity (e.g. Motol Formation of Nová Ves volcanic centre) and indicates when shallowing and basin inversion affected the various basin segments (Kříž 1992).

In the central segment of the Prague Basin, despite greater subsidence than in segments to the north and south (Kříž 1991, text-figs 2, 4, 9), late Wenlock regression and intense volcanic production led to temporary emergence of the Svatý Jan volcanic centre in middle Sheinwoodian and middle Homerian times during lowstands or periods of tectonic uplift (Horný 1955, 1965; Kříž 1991; Bek *et al.* 2022). Shallowing in the late Wenlock *Pristiograptus parvus* Biozone is documented by widespread carbonate sedimentation in the Svatý Jan volcanic centre (Kozel Limestone Member of Frýda & Frýdová 2014; formerly Kozel facies in Horný 1955, Kříž 1992). Thick lava sheets (< 60 m; Fiala 1982) remained emergent from mid Gorstian through Ludfordian and into latest Přídolí times (so called Svatý Jan island of Horný 1955 and Kříž 1992). Around the volcanic centre, basalt flows and coarse volcanoclastics were replaced laterally by shallow water carbonates with tuffs, while muds with tuffs were deposited further away from the volcanic islands in the early Ludlow (Horný 1955, 1965; Kříž 1991, text-fig. 5; Havlíček & Štorch 1999, fig. 15.2).

In the Amerika Anticline area (Smoking Quarry and Kozolupy trench sections), in the uppermost Motol Formation, a c. 1 m fossiliferous bioclastic limestone unit above and within tuffites represents carbonate deposition during late Wenlock lowstand and quiescence in eruptive activity (Horný 1955; Havlíček & Štorch 1990; Kříž 1992, fig. 62; Kříž *et al.* 1993, fig. 15). This correlates with the first development of cephalopod limestone biofacies in the Basin, in the late *Cyrtograptus hundertgreni* Biozone (Motol Formation) around the Nová Ves volcanic centre, farther NE along the Tachlovice Fault. The lower Kopanina

Figure 17. Fossils on limestone bedding planes (A, G–L) and tuffitic shales (B, C–E, F), Smoking Quarry. • A – a limestone bedding plane with sparse debris and *Strophoprion euglypha relata* (Havlíček), brachial valve, JK 18217. • B – pelmatozoan (crinoid) root on tabulate corals, JK 18210. • C – orthocone cephalopod *Dawsonoceras annulatum* Sowerby, lateral view, NM L 40600. • D – a rugose coral lying on a limestone bedding plane with offsets in the theca overgrown by a stromatoporoid, JK 18212. • E – nearly complete trilobite *Kettneraspis geinitziana* (Hawle & Corda) on bedding plane covered by fine crinoidal debris, JK 18240. • F – rare example of an fenestellate bryozoan attached to a coral colony, JK 18210. • G – favositid tabulate corallum surface encrusted with aulopodid coral and small favositid tabulate coral (on the most elevated parts), NM L 40604. • H – richly shelly limestone bedding plane with rugose and small tabulate corals, a solitary rugose coral with theca overgrown by a favositid coral (on the left), gastropod *Oriostoma* sp., partly articulated trilobite *Interproetus* aff. *coinsobrinus* Šnajdr, 1980 and a fragment of a crinoid stem, JK 18205. • I – erect and narrow zoarium of a bryozoan on limestone bedding plane with associated juvenile brachiopods and fragment of halysitid tabulate coral, JK 18202. • J – trace fossil type A of Kříž & Pek (1975), *Helminthopsis* isp. after R. Mikuláš, concave epirelief on bedding plane, collected by Radek Mikuláš, RM 217. • K – a limestone bed bedding plane with abundant small tabulate corals and brachiopod *Atrypa fumosa* Havlíček (note disarticulated brachial valve), rare example of articulated minute pisocrinid crown, kettneraspid trilobite free cheek JK 18146. • L – an inverted colony of heliolitid tabulate coral overgrown with small rugose, tabulate and aulopodid corals, NM L 40612. Scale bars: E = 5 mm; A–D, F–L = 10 mm.



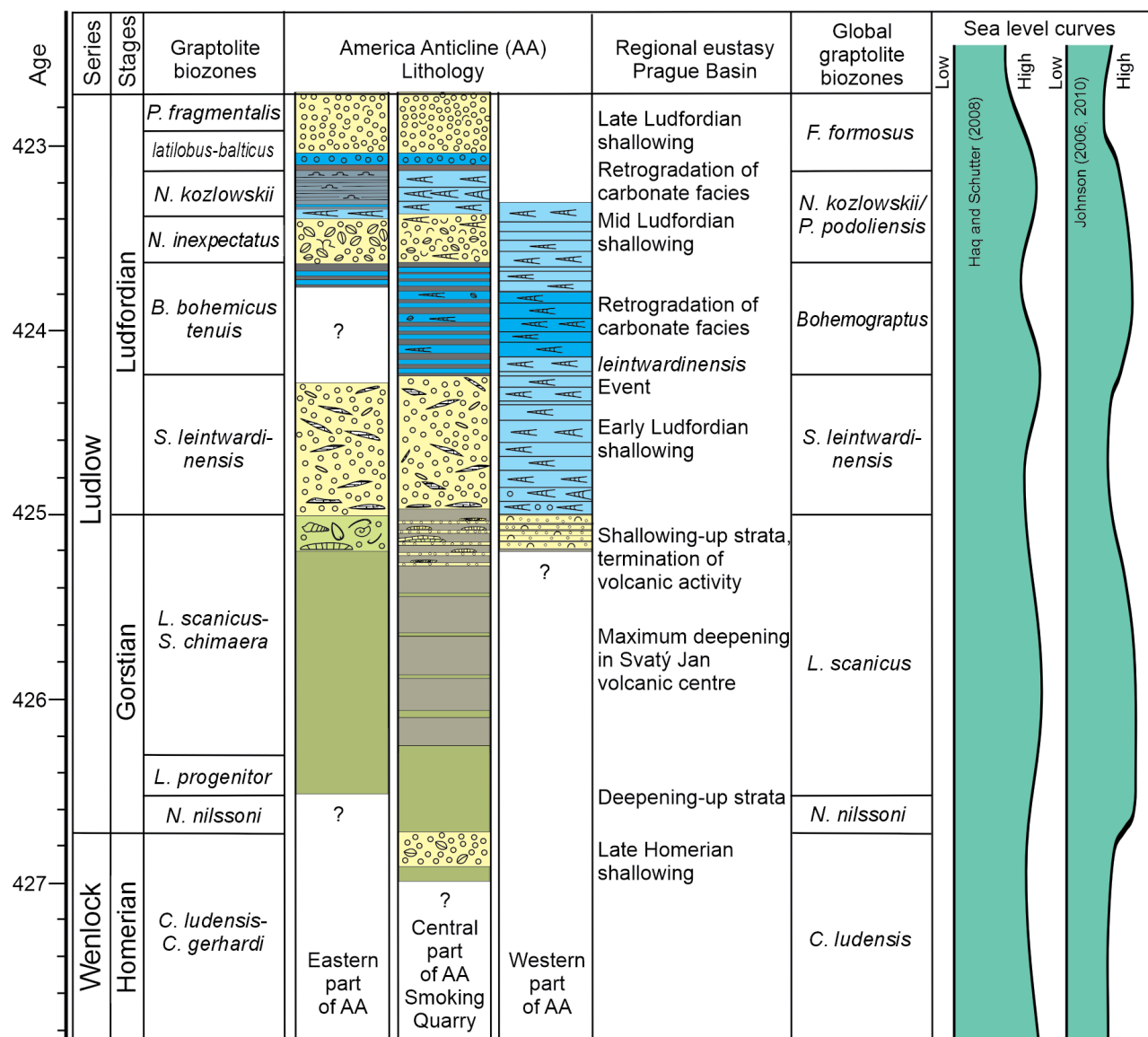


Figure 18. Stratigraphical diagram of volcano-sedimentary and limestone-dominated sequences in the Amerika Anticline illustrating the east–west lateral facies variation from shallower into deeper areas of the Basin, compared with the regional eustatic patterns of the Prague Basin, and with global sea level curves after Melchin *et al.* (2020). Graptolite biozones after Štorch (2023), global zonation after Melchin *et al.* (2020).

Formation succession at Kozolupy (trench section; Kříž *et al.* 1993, fig. 15) represents initial Ludlow (Gorstian) transgression, with an upward transition through tuffites into tuffitic shales (24 m), then passing up into the Smoking Quarry volcanoclastic section studied here showing latest Gorstian shallowing-up before termination of volcanic activity by early Ludfordian times. Overlying stromatoporoid-rich shallow water limestones correspond to the *S. leintwardinensis* Biozone lowstand (Figs 2, 18). Renewed deepening indicated by the overlying platy limestones and shales probably corresponds with that documented in the eastern Central segment in the *B. tenuis* Biozone, e.g. Mušlovka Quarry (Manda & Kříž 2006,

Štorch *et al.* 2014). However, higher limestones with *A. linguata* are considered again as shallow water facies and are known from several sections across the basin in the *Neocucullograptus inexpectatus* Biozone (Horný 1955, Havlíček & Štorch 1990, Manda & Kříž 2006). The two episodes of shallowing, in the early Ludfordian and then in the *N. inexpectatus* Biozone, correspond with the eustatic curve of Haq & Schutter (2008) rather than the single shallowing shown in Johnson (2006, 2010; Melchin *et al.* 2020; Fig. 18).

Cephalopod limestone biofacies first appears in Smoking Quarry at Kozolupy (Fig. 2) in the middle Ludfordian, late *N. inexpectatus*–*N. kozlowskii* biozones

documented by the *Cardiola alata* Community, Kříž, 1999a, b; figs 2, 18). It indicates continuous uplift of the central segment of the Prague Basin through later Ludlow times during a period of global highstand (Kříž 1991, text-figs 2, 6, 10). Shales and mudstones with scolecodonts just above the cephalopod limestones represent renewed deepening. They are overlain by dark to light grey, platy limestones passing up into fine-grained crinoidal grainstones of the upper Kopanina *Ananaspis fecunda* trilobite horizon (Horný 1955) which corresponds to the latest Ludfordian shallowing and lowstand of Johnson (2006, 2010). This correlates with the Kozłowski/Lau Bioevent and mid Ludfordian Carbon Isotope Excursion (Figs 2, 18; Manda & Kříž 2006; Lehnert et al. 2007; Frýda & Manda 2013; Frýda et al. 2021a, b; del Rey et al. 2023).

The regional development of volcanic/carbonate sedimentation along the Prague Basin axis, deepening from SW to NE within the window of the Amerika Anticline (Figs 1, 18) may be demonstrated by comparison of the localities Liščí and Mořina with the sequence at Smoking Quarry described above.

Kříž (2008) described the stratigraphic equivalent of the lowermost Smoking Quarry section (beds 1–30) in the western part of the Amerika Anticline at the Liščí Quarry locality 1.6 km SW, near the Amerika gamekeeper's lodge, Karlštejn, where it is developed as so-called gastropod layers (Bouček 1931, Horný 1955; Fig. 1). A very shallow water reduced section (5.55 m) of yellow, brown, violet and rusty, partly unconsolidated limestones with tuffaceous admixture and volcanic glass contains the most diverse Silurian benthic community in the Prague Basin with more than 202 species, consisting of crinoids (12), ostracods (2), trilobites (11), cephalopods (13), gastropods (60), bivalves (32), rostroconchids (4), tergomyans (1), polyplacophorans (1), microconchids (1), bryozoans (3), brachiopods (26), corals (31), stromatoporoids (3), algae (1) and sponges.

The gastropod beds contain the highly diverse *Janicula potens* Community composed of 32 species of bivalves analogous and homologous with the upper Wenlock Bivalvia communities described by Barrande (1881) from the vicinity of Loděnice, Tachlovice, Svatý Jan, Kozel near Beroun and Lištice in the Prague Basin, i.e. from local coral-rich limestones in volcano-sedimentary facies. It corresponds as well to the Bivalvia community described by Watkins (1996) from the upper Wenlock Racine Formation from Wisconsin and Illinois, North America. The Liščí Quarry bivalves occur in a bioturbated environment of partly unconsolidated biotrital limestone with a high tuffaceous admixture together with abundant crinoids, corals, gastropods, commonly articulated brachiopods and other benthic and nektobenthic fauna. The intercalating relatively thick layers (15–30 cm), of

grey green tuffites containing common lapilli (< 10 mm long) represent periodic disturbance of the environment by volcanic activity of the nearby (c. 2.5 km) Svatý Jan Volcano (Kříž 2008, p. 276, fig. 1, section No. 942, bed 2).

The co-occurring well-diversified brachiopod community (26 species) is dominated by *A. fumosa* (Havlíček & Štorch 1990), which is also frequent at the Smoking Quarry locality although only *Dictyonella* sp. from the other brachiopod species has been found there. Most of the brachiopods were found articulated in the tuffaceous limestones together with bivalves and gastropods. The relatively large brachiopod *Meristina mora* Michalík, 1970 is mostly found articulated in life position, in groups, forming nests in small channels and depressions filled with green tuffite (Michalík 1970). According to Havlíček & Štorch (1990) the brachiopod community inhabited the top of a submarine elevation built up of volcanoclastic rocks.

The benthic organisms from Liščí Quarry most probably inhabited well-ventilated shallow-water flats, overgrown locally by algae, with biotrital carbonate sedimentation influenced and periodically interrupted by direct ash fall and by the subsequent sedimentation of volcanoclastics by currents around the volcanic archipelago. The environment was likely protected against direct wave action by bars of crinoidal sands with local organic frames built by tabulate (mainly favositids, halysitids, and heliolitids) and rugose (microplasmid) coral colonies. The occurrence of quite abundant isolated sclerites of polyplacophoran molluscs indicates proximity to high energy, tidal, reef-shoal environments (Cherns 1999). The section continues into 10.27 m of pinkish-grey, greyish-brown to rusty-brown, mostly massive biotrital dolomitic limestones with crinoid detritus and stromatoporoid colonies, described macroscopically and microscopically by Kukal (1955, formation No. 3, 11 m thick, p. 248). These represent the equivalent of > 7 m of stromatoporoid limestones in the Kozolupy section. The Liščí Quarry section No. 942 is terminated by greenish tuffites (Kříž 2008, fig. 1, bed 31).

In the eastern part of the Amerika Anticline, 1.3 km NE, a section north of Mořina (Fig. 1) is developed in a deeper environment than the Smoking Quarry section. The poorly exposed and discontinuous section starts with > 5 m of rusty brown crinoidal limestones with abundant *A. fumosa* with large frills and includes the relatively rare brachiopod *Leptostrophia nebulosa* (Barrande, 1848). An overlying thin layer of shale is followed by 20 cm of grey biotrital limestone with an irregular lower bedding surface, a quite diverse assemblage of brachiopods and common graptolites of the *Saetograptus chimaera*–*Lobograptus scanicus* Biozone. Above the basal bed are grey cephalopod limestones with abundant *Cardiola*

docens Barrande, 1881 and common large cephalopods. The section continues in 1.95 m of cephalopod limestone with common *Cromus beaumonti* trilobites at the base and with relatively abundant *Cardiola pectinata* Barrande, 1881 in upper parts. The cephalopod limestone represents a very reduced sequence corresponding stratigraphically to the lower Ludfordian limestones with stromatoporoids in the Smoking Quarry.

In the north and south segments of the Basin, the Motol and lower Kopanina formations are developed entirely in shales and occasional thin beds of tuffites (Kříž *et al.* 1993, fig. 16). Those trough areas (*e.g.* southern, western and Pankrác segments; Kříž 1991, text-figs 2, 6, 10) continued to subside slowly until Přídolí times.

Discussion of cyclic limestone–shale alternations

The origin of cyclic, limestone–shale alternations has been a long-term subject of debate. Different faunas in the alternating lithologies may indicate original sedimentary rhythmicity, which becomes enhanced by diagenetic segregation of carbonate, relating to extrinsic climate cyclicity (*e.g.* Weedon 1986, Weedon & Jenkyns 1999). The correlation of rhythmic successions with external environmental triggers has however been questioned (Bohm *et al.* 2003, Westphal *et al.* 2004). In the Prague Basin the role of periodic volcanic activity is an additional factor. A diagenetic origin for the typically nodular limestones of offshore ramp shale environments is increasingly recognised, *e.g.* for the Silurian of the Gotland carbonate platform (Munnecke & Samtleben 1996) and Lower Jurassic in the UK (*e.g.* Wright *et al.* 2003). Munnecke & Samtleben (1996) proposed that limestone–marl alternations were the product of diagenetic dissolution and migration of carbonate sourced from aragonitic mud (also Hallam 1986). An analogue is provided by early diagenetic differentiation into alternating cemented and uncemented layers in Pliocene periplatform carbonates (Westphal *et al.* 2000). Cherns & Wright (2000; also Wright *et al.* 2003, Wright & Cherns 2016) proposed that skeletal aragonite dissolution, particularly affecting molluscs, may have been an important factor in diagenetic alternation of carbonates in offshore ramp settings.

In the Kopanina Formation, the succession shows a shallowing trend from the underlying transgressive Gorstian tuffite–shale sequence through very thinly bedded uppermost Gorstian limestone–shale alternations and up into limestones in the Ludfordian. Through the limestone–shale sequence, there is an upward change in the limestone faunas with an increase in colonial skeletons and local development of minor organic build-ups on patches of hard, early lithified carbonate substrate.

Atrypid-dominated brachiopod assemblages apparently thrived in soft, level-bottom mud environments through this transition. Both types of assemblages are apparently *in situ* or neighbourhood, *i.e.* little disturbed, even in higher limestones where current influence is more evident. Through the lower part of the section the muddy nature of both limestones and shales indicates subtidal areas where environmental energy was generally fairly low. Kříž (1992) suggested that the shallow, volcanically influenced limestone deposition represented periods when fine clastics were washed out into deeper areas, as seen at the railway cutting section described above north of Mořina, approximately 3.7 km from the Svatý Jan Volcano north of Bubovice, and that tuffitic shales were deposited in the area closer to the volcano during quiescent periods of current stagnation. In the Liščí Quarry section closest to the volcano north of Bubovice (2.8 km), the gastropod beds intercalate with 15–30 cm thick, green tuffites with common lapilli < 10 mm in size, and an irregularly shaped volcanic bomb up to 15 cm in diameter was also found there. However, although skeletal faunas are sparse through the lower part of the limestone–shale alternations, the presence of an active burrowing infauna throughout argues against anoxic or dysaerobic environments. The upward transition through from an atrypid-dominated muddy sea floor to episodic growth of minor organic, coral-stromatoporoid frame structures is accompanied by increased bioclastic debris and sand in the limestones, and more current influence (cross-lamination, rippling), indicating conditions within wave-base. The low build-ups indicate periods of clear, shallow waters, low net sedimentation rate and periodic seafloor exposure of early-cemented layers.

Do the alternating lithologies represent original depositional differences? The faunas of the tuffitic shales, except in the lowermost beds, are dominated by calcitic, frilled atrypid brachiopods, apparently tolerant of soft, muddy carbonate substrates. The lower limestones are muddy nodular wackestones, that likely represent diagenetic segregation of carbonate. Higher limestones are associated with richer, more diverse benthic assemblages, and some supported low organic build-ups. Colonisation by reef organisms forming low organic mounds indicates exposure of firmground or hardground surfaces, which had already been cemented in the shallow subsurface and then exhumed, and whose irregular topography confirms nodular diagenetic hardening.

Conclusions

The small coral-stromatoporoid build-ups in carbonates of volcano-sedimentary facies described from Smoking Quarry and the development of stratigraphically equivalent

successions along the Amerika Anticline illustrate a shallower to deeper trend from SW towards NE. In the Prague Basin, coral-rich faunas with their small reef build-ups are confined to late Wenlock to Early Ludlow times and to volcano-sedimentary shelves bordering the several volcanic centres. Carbonate-rich deposition marked periods of reduced net sedimentation when early lithified limestones became exposed on the seafloor forming firmgrounds and hardgrounds where colonial reef-builders flourished between episodic influxes of volcanoclastic sediment. Faunas are diverse and faunal changes are rapid across the volcano-sedimentary centres. Volcanic activity terminated in the Ludfordian. It is notable that these are only coral-rich faunas of this age in the southern Rheic Ocean of peri-Gondwanan Europe.

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