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Epibionts of mollusc shells from the Korycany limestones (Upper Cenomanian, Czech Republic)

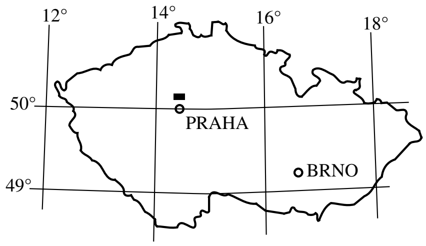
JIŘÍ ŽÍTT[1] – MARIE KOPÁČOVÁ[2] – ČESTMÍR NEKOVAŘÍK[3]

[1]Institute of Geology, Academy of Sciences of the Czech Republic, Rozvojová 135, 165 00 Praha 6, Czech Republic
[2]Institute of Geology and Palaeontology, Charles University, Albertov 6, 128 43 Praha 2, Czech Republic
[3]Czech Geological Survey, Klárov 3, 118 21 Praha 1, Czech Republic

A b s t r a c t. Abundant internal moulds of gastropod shells and imprints of bivalve shells were collected from the Korycany limestones (Korycany Member, Late Cenomanian) exposed in the gas-main excavations near Korycany in central Bohemia. The specimens are unique in that they comprise encrusters of inner shell surfaces, preserved after the shells were diagenetically dissolved or otherwise destructed. The preserved cemented component of an encrusting community consists of oysters, worms and bryozoans. In gastropods, predominantly apertural and adjacent parts of inner shell surfaces were colonized. Oysters, often in preferred orientations, prevail on inner surfaces of bivalve shells. A direction of coiling of oyster shells was proved to be a useful tool for a correct interpretation of the original position of encrusters on the host shells. Taphonomic and palaeobiological features of the encrusters indicate that the postmortem colonization of mollusc shells was only a short-lasting one, with possible slight environmental disturbances and episodic rapid burials. Later formation of gastropod moulds corresponded with shell dissolution and lithification rates of the rock. In this connection, two extreme mould types were distinguished with a series of stages in epibiont preservation between them.

A b s t r a k t. Z korycanských vápenců (korycanské vrstvy, svrchní cenoman), odkrytých ve výkopech pro plynovod poblíž Korycan ve středních Čechách, byl získán bohatý materiál gastropodů a mlžů, zachovaných většinou ve formě vnitřních jader a otisků. Povrchy jader gastropodů a otisky vnitřních povrchů izolovaných misek mlžů nesou zajímavé zbytky epibiontů, zastoupených ústřicemi, červy a mechovkami. Tito epibionti původně kolonizovali vnitřní povrchy schránek, po jejichž rozpuštění (u gastropodů) či rozpadu (hlavně u mlžů) zůstali zachováni v povrchových částech jader a otisků. U gastropodů jsou epibionti soustředěni hlavně v aperturální a adaperturální části tělesného závitu. Vnitřní povrchy misek mlžů nesly hlavně ústřice, často jednotně orientované. Pro správnou interpretaci původní pozice epibiontů na schránkách gastropodů i mlžů se ukázal být důležitý směr stáčení přisedlých spirálovitých misek ústřic (viz text). Tafonomické a paleobiologické rysy přisedlého společenstva indikují krátkodobou kolonizaci postmortálně zpřístupněných vnitřních částí schránek a epizodické rychlé pohřbívání. Pozdější vznik jader gastropodů byl závislý na vztahu rychlosti rozpouštění schránek a lithifikace horniny. V této souvislosti byly odlišeny dva krajní typy jader s odpovídajícím gradientem v zachování epibiontů mezi nimi.

K e y w o r d s: Gastropoda, Bivalvia, shells, encrusting fauna, internal moulds, taphonomy, Korycany Member, Upper Cenomanian, Bohemian Cretaceous Basin



Introduction

In spring 2000, the gas-main excavations near the Korycany village in central Bohemia offerred interesting exposures in the Late Cenomanian Korycany limestones with interesting sedimentological phenomena and extremely rich macrofauna (see Žítt and Nekovařík 2002a, b, Žítt et al. 2001). This type of fauna was collected and studied as early as in 19th century already and at the beginning of the last century (e.g. Reuss 1845–1846, Frič 1869, 1911, Weinzettl 1910, a. o.), but the specimens were derived from somewhat differrent rocks (limestones with higher $CaCO_3$ content) exposed in small temporary quarries. In 1970's the area was cut by two lines of gas-main excavation works situated several tens of metres north of the present one. All these new excavations partly transected old ash and debris fillings of the mentioned small quarries (southwest of Korycany). The results of geological and palaeontological documentations of the first two gas-main excavation works were not published immediately (see MS report of Houša et al. 1977), but an overall situation was later briefly described by Houša (1994). This author was the first who reported the occurrence of epibionts on the bivalve (*Inoceramus*) shell inner surfaces in the Korycany limestones. Encrusters of the inner surfaces of bivalve but mainly gastropod shells are described in detail herein, on the basis of more numerous newly found specimens.

Geographical and geological settings

The study areas are situated south of Korycany and north of Veliká Ves (Fig. 1), lying about 11 km north of Prague. The furrow excavated for the gas-main, exposed relatively thin limestone bodies, underlain and overlain by sandstones (Fig. 2). This sedimentary unit forms a part of the Korycany Member of the Peruc-Korycany Formation (Čech et al. 1980). In several places (see sites I–IV in Fig. 1) and mostly in the top parts of limestone bodies, abun-

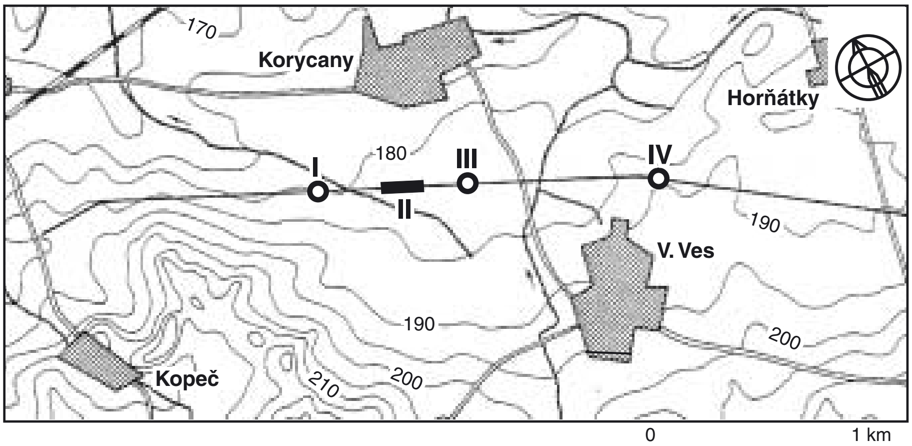


Fig. 1. A map showing the course of the gas-main near Korycany. I–IV – collection sites of the studied gastropods and bivalves; geological situation at site II shown by a geological section (see Fig. 2).

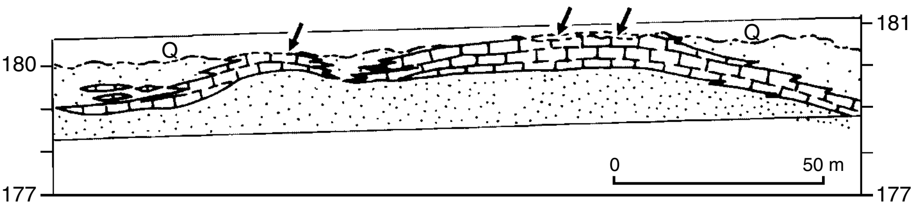


Fig. 2. Geological section (site II) as viewed in northern wall of the excavated furrow (depth of furrow about 2.3 m). Sandstones with bodies of sandy limestones were exposed; the studied gastropods and bivalves were collected in top parts of the limestones (arrows). For location of the section on the gas-main see Fig. 1. Vertical vs. horizontal scale ratio of the section is 10 : 1. Vertical scale shows altitudes in metres above sea level.

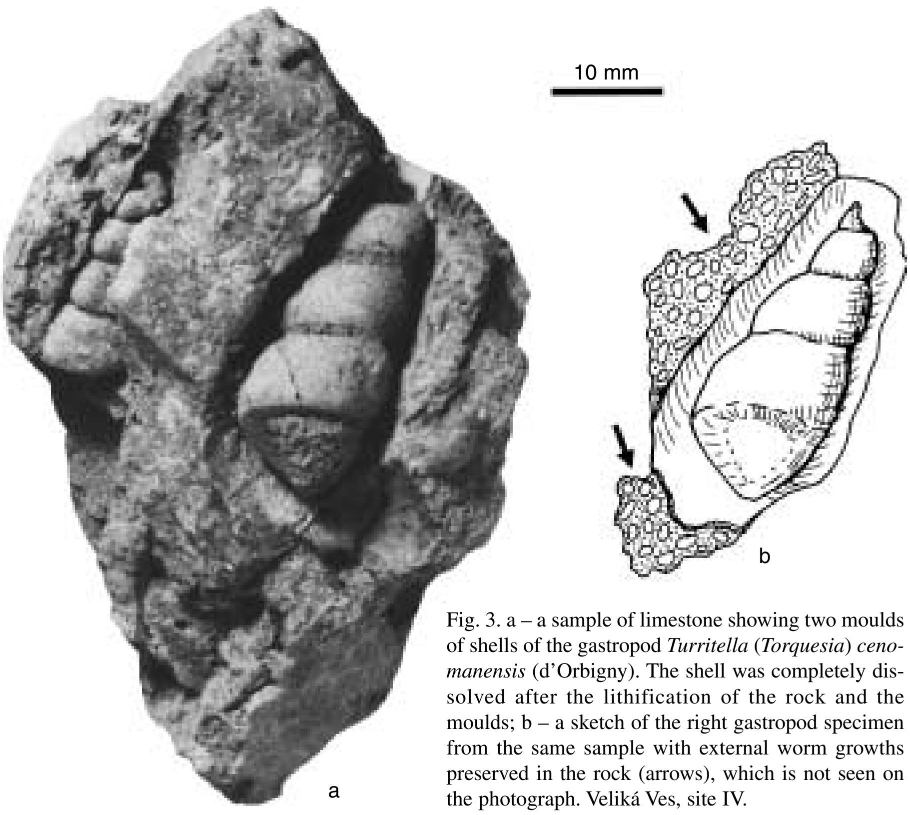


Fig. 3. a – a sample of limestone showing two moulds of shells of the gastropod *Turritella* (*Torquesia*) *cenomanensis* (d'Orbigny). The shell was completely dissolved after the lithification of the rock and the moulds; b – a sketch of the right gastropod specimen from the same sample with external worm growths preserved in the rock (arrows), which is not seen on the photograph. Veliká Ves, site IV.

dant macrofauna occurred with highly dominating gastropods and bivalves, rarely accompanied by corals and some other faunal groups (Žítt and Nekovařík 2002a). The Late Cenomanian age of these deposits was adopted by Pražák and Valečka 1990, Pražák 1994 and Svoboda 1999, while the Middle Cenomanian age was referred to by Houša (1994).

A variable admixture of sand particles and Proterozoic rock clasts classified as granules and fine pebbles (0.2–0.8 cm; classification of Blair and McPherson 1999) was found in the limestones. These very small clasts often form subhorizontal local streaks in the rock. The clasts of 1.6–5.0 cm size (coarse to very coarse pebbles) may be very rarely disseminated throughout limestone bodies, similarly as small (1 cm at a maximum) abraded fragments of coalified wood. Fillings of ichnofauna burrows also occur rarely (*Thalassinoides*? sp.). Thin sections of limestone show rich proportion of bivalve bioclasts, both abraded and angular.

Study material

The material studied consisted of gastropods (one shell and fourteen internal moulds) and bivalves (seven internal imprints of valves). These specimens are relatively well preserved while many smaller fragments or poorly preserved moulds were excluded from this study. Nevertheless, the taxonomic pertinence of gastropod moulds is only tentative. The species *Ampullospira* cf. *substantoni* Pchelintsev, 1953, *Ampullospira* sp., *Aporrhais* sp., *Natica gentii* (Sowerby, 1874), *Nerinea*(?) sp., *Tritonium*(?) sp., *Turritella* cf. *multistriata* Reuss, 1845, *Turritella* sp., and *Tylostoma*(?)

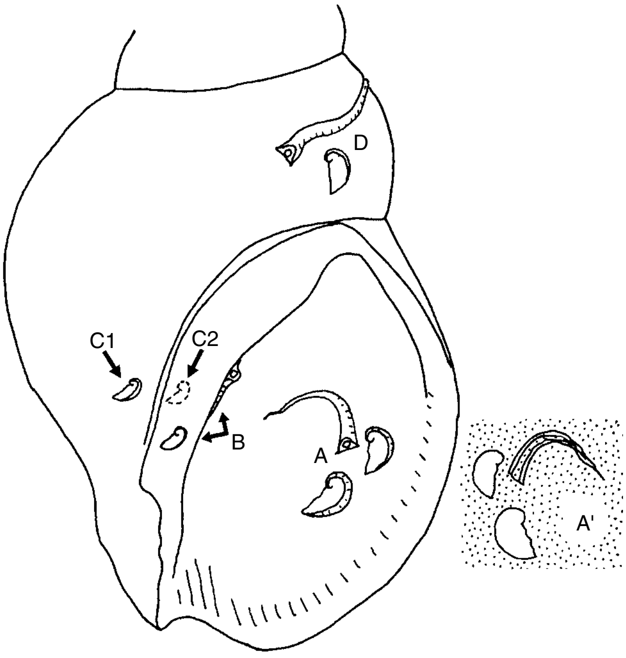


Fig. 4. A gastropod shell as a habitat of epibionts during the life of the host and after its death. A, B – epibionts on inner surface; C, D – epibionts on outer surface. A' – epibionts of group A as observed on the surface of internal mould (dotted) after the dissolution of the host shell (most of the studied epibionts are preserved in this manner). Epibionts of group B are unlikely to be observed as they are locked inside the mould on the adaxial side of the spire. Epibiont C2 settled shortly before the death of the snail, as it was yet overgrown by the apertural part of the whorl. Epibionts C1 and D may be coeval with C2, but they may well be postmortem, like groups A, B.

Fig. 5. The gastropod *Turritella* (*Torquesia*) *cenomanensis* (d'Orbigny) with a preserved shell colonized (most probably postmortem) by epibionts. Arrow – serpulid tube. Korycany, site III.

sp. were preliminarily identified. Most of the specimens have their apertures or closely adjacent body-whorl parts preserved. Bivalves were determined as *Neithea* sp., *Perna* (?) sp. and *Protocardia hillana* (Sowerby). The valves of the last two species were completely dissolved. The fillings of borings of *Entobia* sp., originally formed within the shell wall, were found in *Perna*(?) closely adpressed or fused with the surface of the shell imprint (Fig. 13). Identically preserved borings were also observed on one fragmentary mould of a gastropod shell (Fig. 11a).

The gastropods and bivalves were collected either from relatively hard rock that formed bottom parts of limestone bodies, or from their often sandier, soft and weathered topmost parts, where they were locally most concentrated. The preservation of gastropods was probably controlled by local, macroscopically often indetectable differences in carbonate content of the deposit. Higher $CaCO_3$ contents were favourable for shell preservation while in sandier parts the shells were completely dissolved. Dissolution of carbonate (aragonite) shells in sandier types of limestone must have been faster than the rock lithification as the moulds are often deformed (sometimes even drastically compressed) by sediment compaction. Some effect of external shell morphology on the shaping of these moulds is probable though hardly demonstrable. The moulds are often poorly defined in their surfaces, which complicates their release from fresh rock. Moulds of this type (i.e. type 1) have relatively coarse surfaces (e.g. Fig. 7c). Nevertheless, epibionts of originally inner shell surfaces are often (partly?) preserved. Most frequently, the mould surfaces bear irregularities probably reflecting local differences in dissolution of different parts of shells. In parts with a lower dissolution rate, the mould precisely reflects the inner shell surface. Such part of the surface is smooth, sometimes even slightly glossy, and most suitable for the inner shell surface epibionts to be preserved. In these parts, the moulds are well defined in the rock. Sometimes, very thin remains of shells are preserved here. Moulds, the surfaces of which are completely of this type are, however, very rare. In the figured extreme example (Fig. 3), the shell as a whole was dissolved after a sufficient lithification of the rock. As a result, the internal mould lies as a free object in the cavity imprinted by external shell surface. Both the smooth surface of this mould (i.e. type 2) and the men-

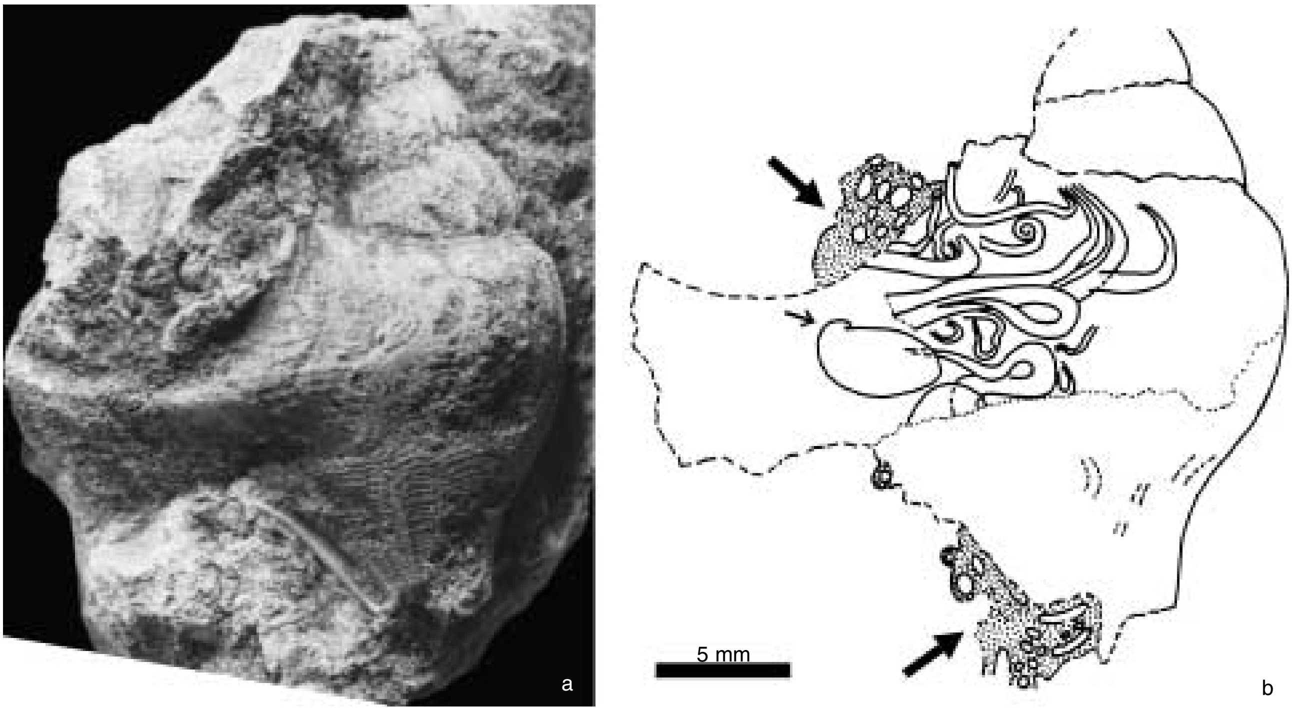


Fig. 6. The gastropod *Aporrhais* sp. with partly preserved shell. a – specimen in the rock; b – epibionts on the surface of the mould in areas disclosed by shell removal. Note the reverse spiral coiling of the oyster (small thin arrow). Epibionts on the inner shell surface possibly partly grew over the shell margin on its outer surface and partly onto the bottom substrate (thick arrows). Korycany, site II.

tioned imprinted outer surface may bear similarly preserved epibionts (for discussion see below).

The outer colonizers were preserved in rare cases, when the shell was not dissolved. The epibionts on inner shell surfaces are, however, masked by the shell itself and its internal filling. They may be, however, revealed due to mechanical separation of a mould from the shell, e.g. during gathering fossils from the rock. In such cases, the inner epibionts on the mould surface are generally very well preserved.

Bivalve shells were found mostly disarticulated. The valves and their fragments were completely dissolved only exceptionally (e.g. in *Protocardia*). Nevertheless, gathering of mere internal imprints with only some adhered fragmentary remains of valves was by far the most frequent due to their fragility (particularly in *Neithea*). The epibionts on inner valve surfaces were thus relatively well preserved on the imprint surfaces. Internal moulds of complete articulated specimens were also found deprived of the shell in the same manner (i.e. artificially due to their fragility), but some moulds were formed by dissolution in rocks with higher sand proportion. Nevertheless, all these finds show tight junction of shell valves that were apparently buried when the bivalves were still alive or soon after their death. Logically, no epibionts could settle on their inner surfaces.

Description of epibionts

The preserved encrusters are represented by oysters, worms, and bryozoans.

Oysters

Oysters are most important among the preserved epibionts to recognize the true position of the cementing community on shell surfaces. That is, the attached lower (left) valve is a clockwise spiral if viewed from the side of upper (right) valve (A in Fig. 4). When viewed from the opposite direction, i.e. on the attachment bases exposed on the mould surface, the coiling is apparently reverse, i.e. of counter-clockwise direction (A' in Fig. 4). Regarding the relative abundance, the oysters are intermediate among species of the cemented epibiont community. The bases are often preserved completely, which is extraordinary considering their thin central parts (Figs 7a, b, 12). Only the thicker side valve parts are better preserved more frequently (Fig. 14). Not only the aragonite shell, but also the calcite shell of oysters and other epibionts were sometimes completely dissolved in gastropods deposited in rocks with high sand content (partly possibly due to Quaternary weathering) (Fig. 11b).

The studied oysters are due to their small sizes hard to determine, but probably only *Amphidonte* (*Amphidonte*) *reticulatum* (Reuss) and *A.* (*A.*) *haliotoideum* (Sowerby) could be present. Predominance of the latter species is, however, more probable, as its isolated valves prevail in the sediment also.

Worms

Serpulid worms are the most common encrusters of the studied substrates. The thin basal attachment parts of tubes

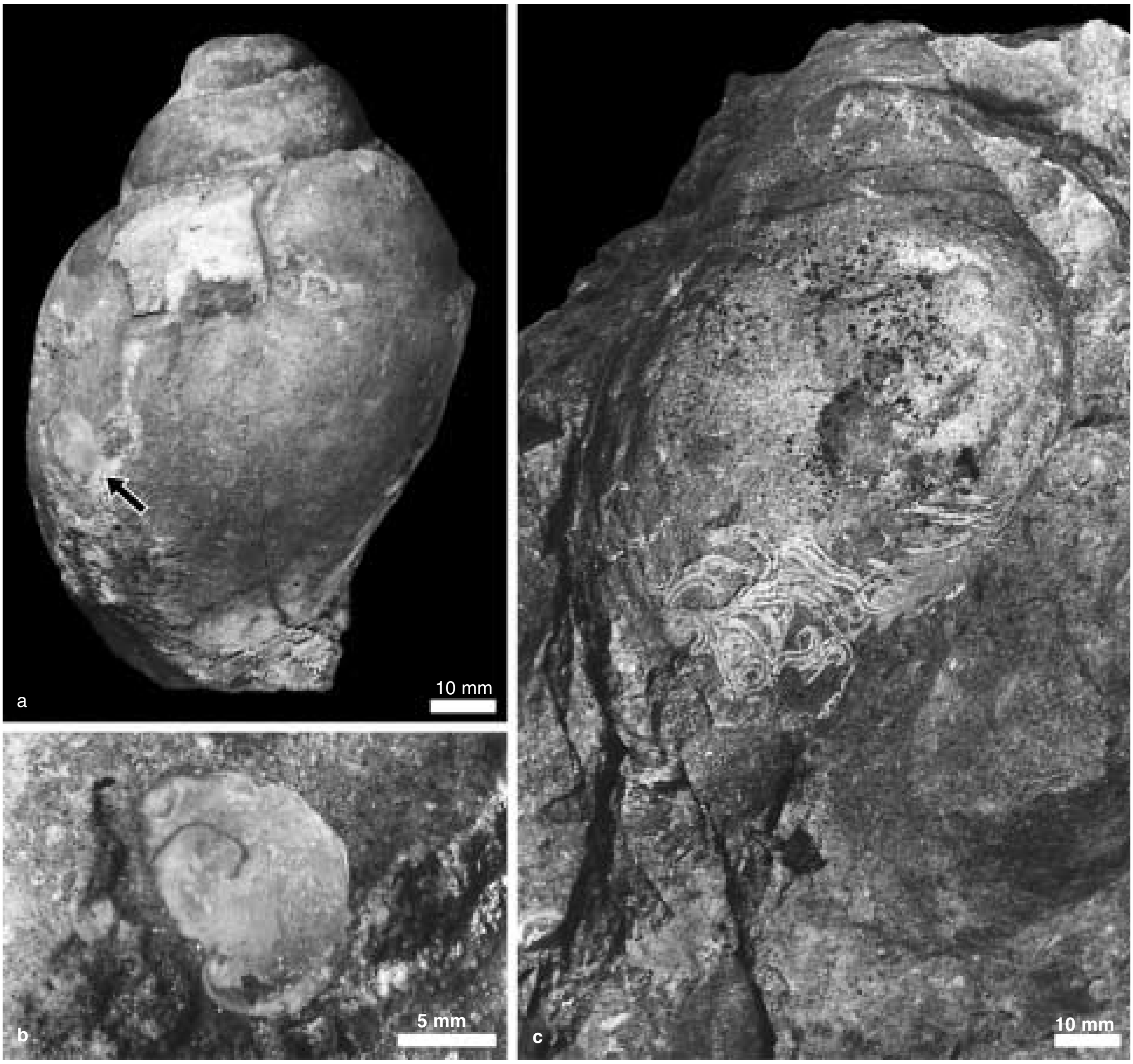


Fig. 7. a – internal mould of *Ampullospira* (?) sp. with an oyster originally cemented to the inner shell surface (arrow); b – attached oyster in close-up view. Note reverse orientation of the spirally coiled shell; c – internal mould of another specimen of the same species, showing rich worm encrusters on originally inner shell surface near the shell aperture. Korycany, site III.

are often destructed and tube fillings partly removed, thus exposing interiors of tubes (Figs 7c, 6b). Worms were mostly growing as solitary individuals but in some cases they formed rather dense coverings growing across shell margins on the sedimentary substrate or perhaps even on outer shell surface (Fig. 6b). Probably the same worm species were found on outer parts of preserved gastropod shells (Figs 3b, 5), sometimes forming very massive build-ups (Fig. 3b).

Bryozoans

At least three bryozoan species (Figs 9a-d) were found to colonize the gastropod and bivalve shells. They partly belong to cheilostomes (so far indetermined), which coated substrates by their relatively thin zoaria. While the specimens are relatively rare on the studied substrates and form only isolated zoaria, they may sometimes cover relatively large areas (Figs 10a, 11a, 13c). However, their areal extent was originally yet larger on the substrate because marginal parts of their colonies are mostly destructed. The most interesting colonization and species pattern is documented by the above mentioned Fig. 9. The growth pattern of the largest two zoaria (A in Fig. 9b) with lateral outgrowths should be noted (if there is no other overgrowing generation of the same or different taxa).

One of the so far indetermined gastropod moulds yielded several small and flat circular objects on the prolongation of the aperture (siphonal canal) (Figs 8a, b). These are isolated from one another and their structure is

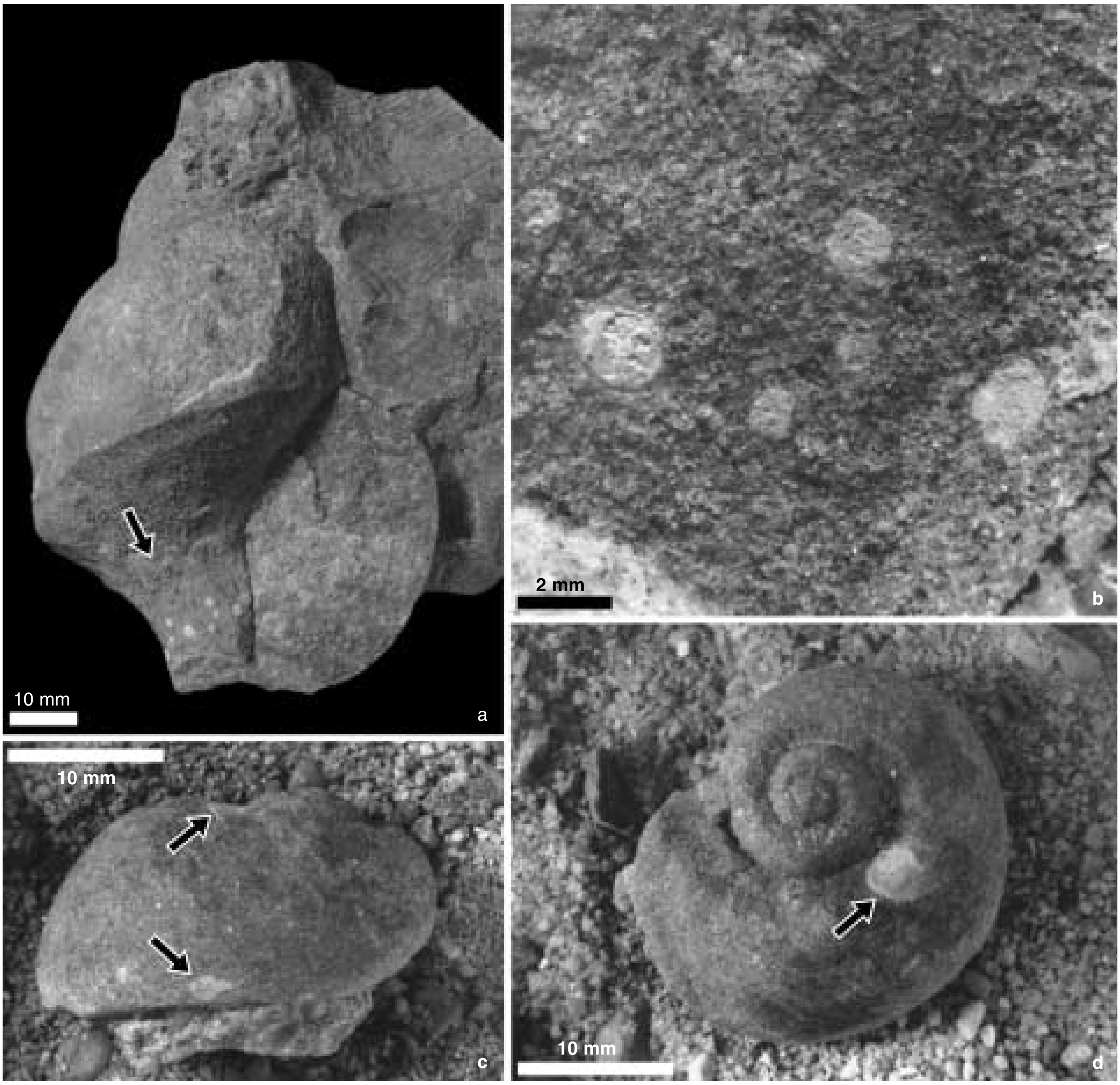


Fig. 8. a – internal mould of indetermined gastropod shell, showing tapering central parts (columella) with small circular objects (arrow) on its surface (bryozoans?; see b for a close-up view). They most probably settled on outer shell surface and were overgrown by younger shell parts later. c, d – internal mould of *Natica gentii* (Sowerby) in lateral and apical views. Arrows indicate oysters originally cemented to the inner shell surface. Korycany, site I.

mostly indiscernible. A structure resembling that of a bryozoan was slightly visible in only two of them.

Discussion

Gastropods

While the preservation of gastropods in the form of mere moulds represents a distinct loss of data for taxonomists, it may be favourable for other specialists, such as taphonomists. If the shell is preserved, its internal features are mostly not visible (e.g. epibionts colonizing inner shell surfaces) because of the sedimentary fill. When the aragonite shell is removed by natural dissolution (or mechanically), however, its inner calcite epibionts may be preserved in surficial parts of the mould. The loss of shells is thus an important prerequisite for the study of inner shell surfaces and their epibionts.

Unfortunately, inner epibionts on the external body whorl parts (outer lip) are only visible (A in Fig. 4) because those on axial parts (columella surface) are hidden in the mould matter (B in Fig. 4). The distribution of epibionts on inner shell surfaces shows that they were concentrated near shell apertures (Fig. 10) and in adjacent, somewhat proximal parts of the body whorl. This distribution apparently corresponds with the best accessibility of these shell parts for settlement of epibiont larvae and further nutrition of growing organisms.

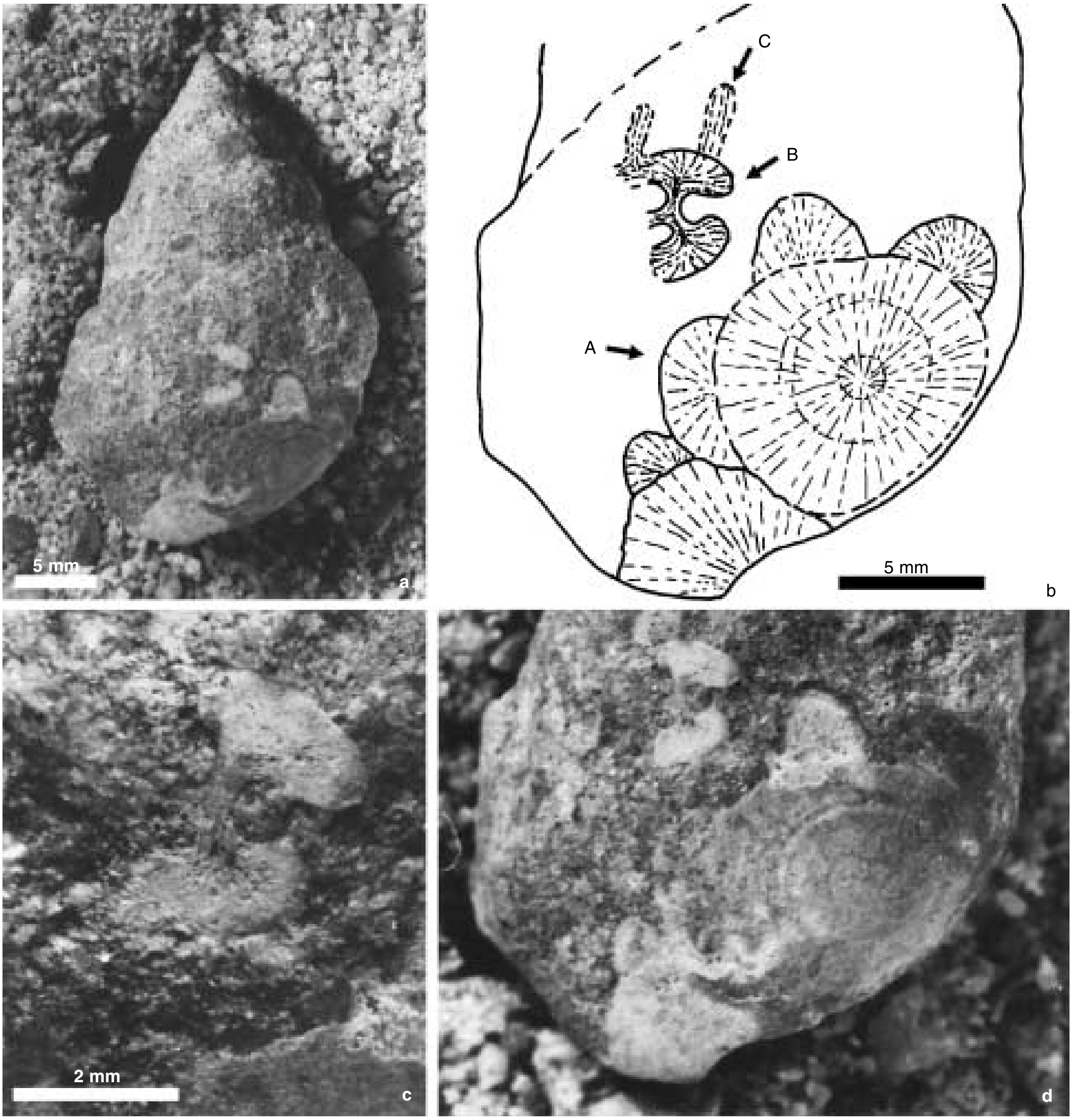


Fig. 9. Internal mould of *Tylostoma* sp. with bryozoan epibionts originally attached to the inner shell surface. a – lateral view of the mould; b, d – a close-up sketch and photo of several bryozoan zoaria probably belonging to about 3 different species (A-C in Fig. b); c – a close-up view of a bryozoan marked as B in previous figure.

The encrustation of shells was relatively poor not only regarding the epibiont species diversity but also the density of specimens. Epibiont species (at least oysters and worms) belong to common, relatively rapidly growing species. Oysters, however, obviously never reached maturity and decease in young stages. This indicates only a relatively short-time substrate (shell) exposure, which, on the other hand, was sufficient for growth of worms. Recolonizations of exhumed shells were not unambiguously evidenced. A good example of colonization is shown in an aporrhaid shell (Fig. 6). The marginal extension of outer lip (wing) ensured a position stability of empty shell on the bottom (with its aperture upwards) and offered large enough area for settlement of larvae. On the other hand, a sufficient stability of conditions (at least retaining the shell without sediment fill) was offered to the colonizers (bryozoans) even by morphologically different shells (e.g. *Tylostoma* sp., *Ampullospira* sp., see Figs 7, 9, 10).

The inner parts of gastropod shells might be generally considered as cryptic (micro-) habitats (see Kobluk 1988), though it was shown (see above) that epibionts

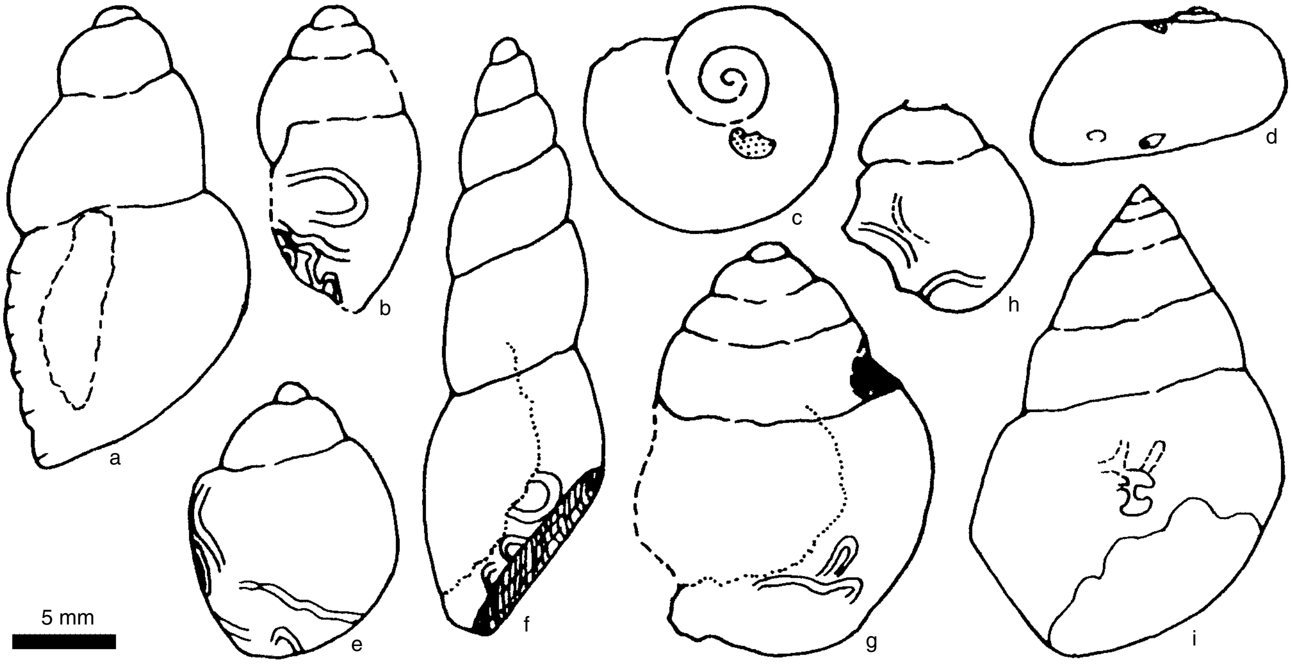


Fig. 10. Gastropod internal moulds with epibionts originally attached to inner shell surfaces. Note concentration of epibionts near the apertures of shells. a – *Tritonium* (?) sp.; b, e – *Ampullospira* cf. *substantoni* Pchelintsev; c, d – *Natica* gentii (Sowerby) in apical and lateral views (see also Figs 8c, d); f – *Turritella* sp.; g – *Tylostoma* (?) sp.; h – *Ampullospira* (?) sp.; i – *Tylostoma* sp. (see also Figs 9a-d). Korycany, site II (a, b, e-i), site I, (c, d).

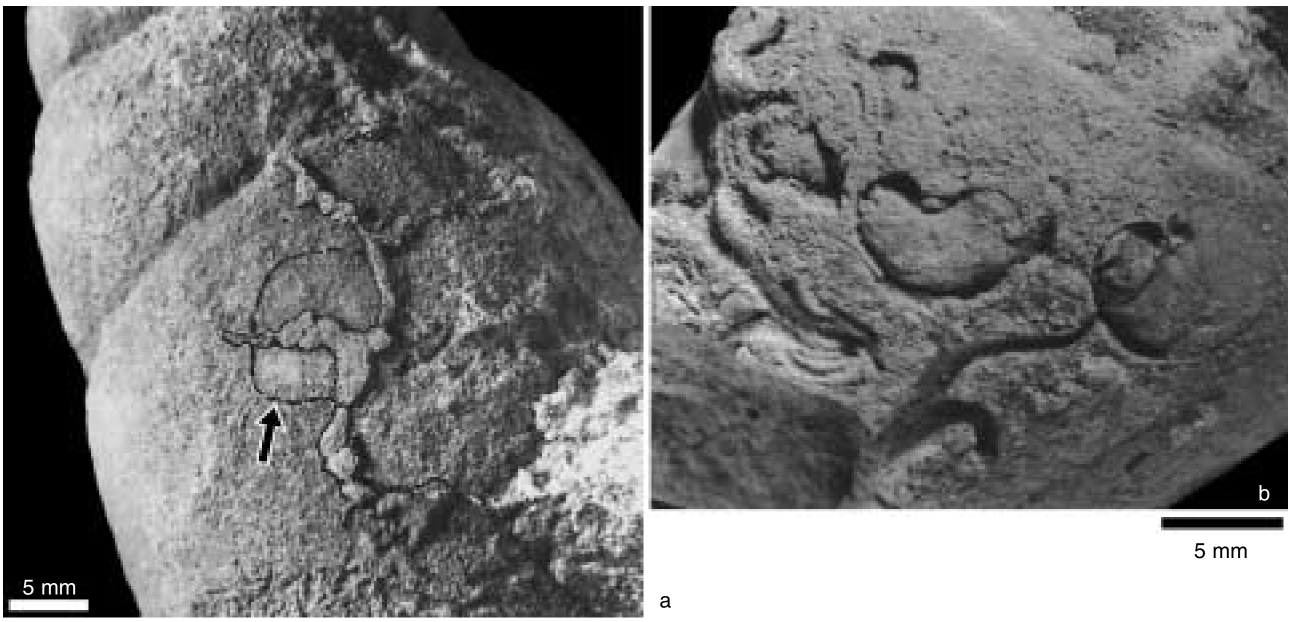


Fig. 11. a – internal mould of a probable nerineacean gastropod showing a zoarium of a cheilostome bryozoan originally attached to the inner shell surface (arrow). This epibiont is overlain by a filling of *Entobia* like borings originally formed within the shell matter (full line); b – fragment of an internal mould of indeterminable gastropod with dissolved remains of epibionts (mainly oysters) originally attached to inner surface of shell. Korycany, site II.

settled mostly inside the outermost parts of the body whorl. It may be speculated that the mobility of shells could markedly increase the intensity of offered shelter by, e.g. overturning the shells with their apertures close to the substrate. While oysters can often hardly survive such a change of life habit for longer periods (feeding, contact with sediment), serpulids could most probably continue their growth and overgrow or colonize the shells of just died oysters. In this sense, the case shown in Fig. 6b is very suggestive.

The studied moulds mostly belong to herbivore types of gastropods (e.g. *Tylostoma, Ampullospira, Tritonium*), but filter-feeders (*Turritella*) and carnivores (*Natica*) are also present. In the taphocoenose, the shells of open bottom forms and infaunal sand inhabitants were thus mixed together. Hundreds of moulds were observed in outcrops,

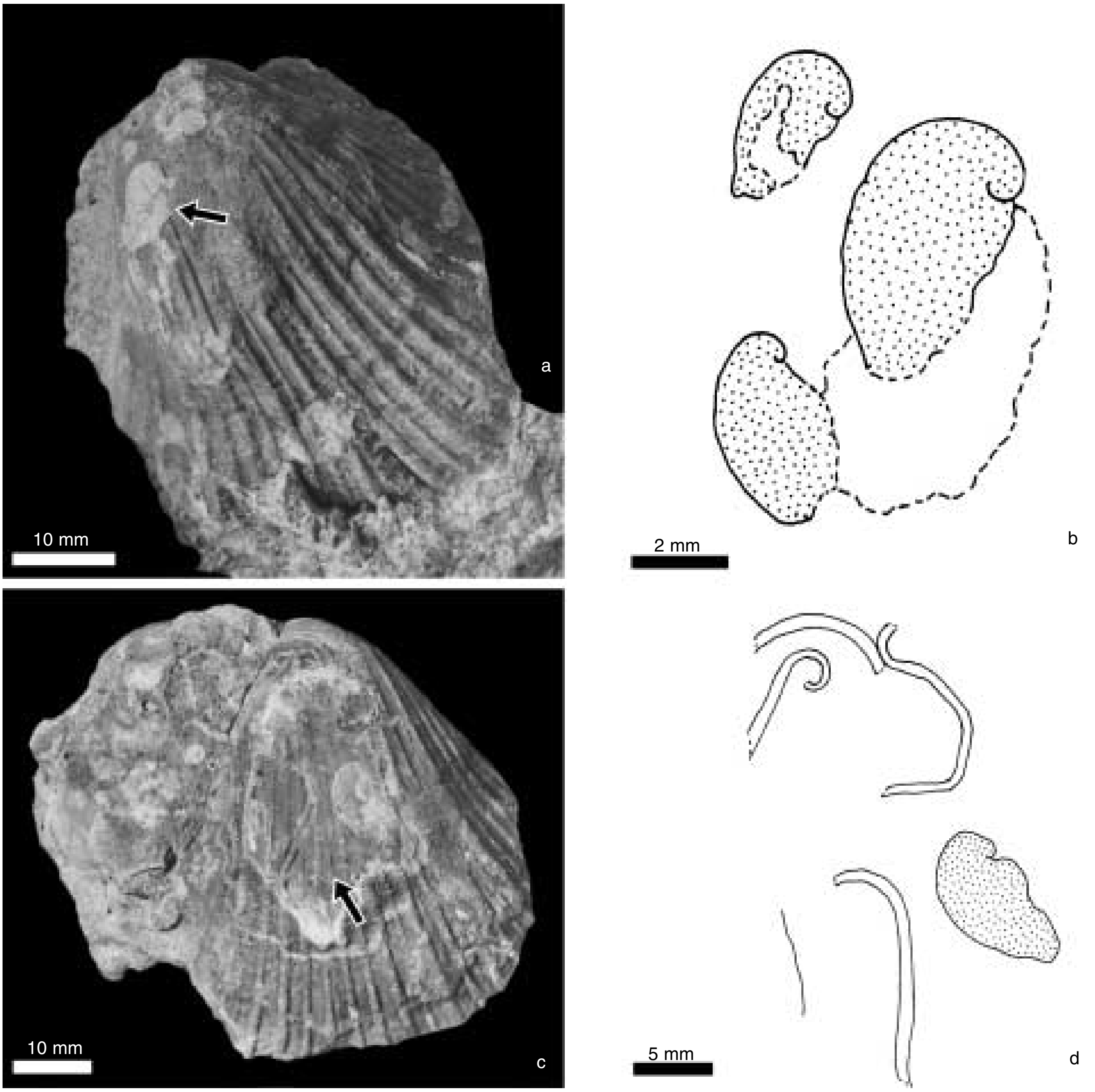


Fig. 12. a, c – internal moulds (imprints) of isolated valves of *Neithea* sp. with epibionts originally attached to the shell inner surfaces; a – whole specimen with an arrow marking a close-up view in Fig. 12b; b – group of oysters; individuals showing opposite spiral coiling; c – another example of the whole mould with an arrow marking a close-up view in Fig. 12d; d – a close-up view of worm and oyster remains. Korycany, site II

but their great majority could not be studied due to very poor preservation. Therefore, the proportion of colonized shells cannot be even estimated. The orientation in sediment was recorded in only a small part of the moulds, not showing signs of *in situ* encrustation.

The absence of epibionts on originally external shell surfaces was found during the study of internal moulds and imprints of molluscs. This may be explained by the fact that these epibionts are closed somewhere in the sediment surrounding internal moulds to which they were not adpressed so tightly to form a single body. These external epibionts can be supposed to have been at least as frequent as the inner ones as they also include those attached during the host life. However, a special case is represented by possible bryozoan epibionts mentioned above (Fig. 8a, b) found on a gastropod mould. Orientation of their attachment bases towards the mould interiors indicates that this case involves encrusters of outer shell surface. With regard to their positions on the shell and clear removal of an unknown part of the whorl, they have settled when the host was alive, because after a short period of growth they were overgrown by the whorl (for an example see C2 in Fig. 4). (The question of colonization relative to the host's life and death was repeatedly discussed in ammonite shells; see, e.g. Meischner 1968, Seilacher 1982, Rakús and Žítt 1993, a.o.)

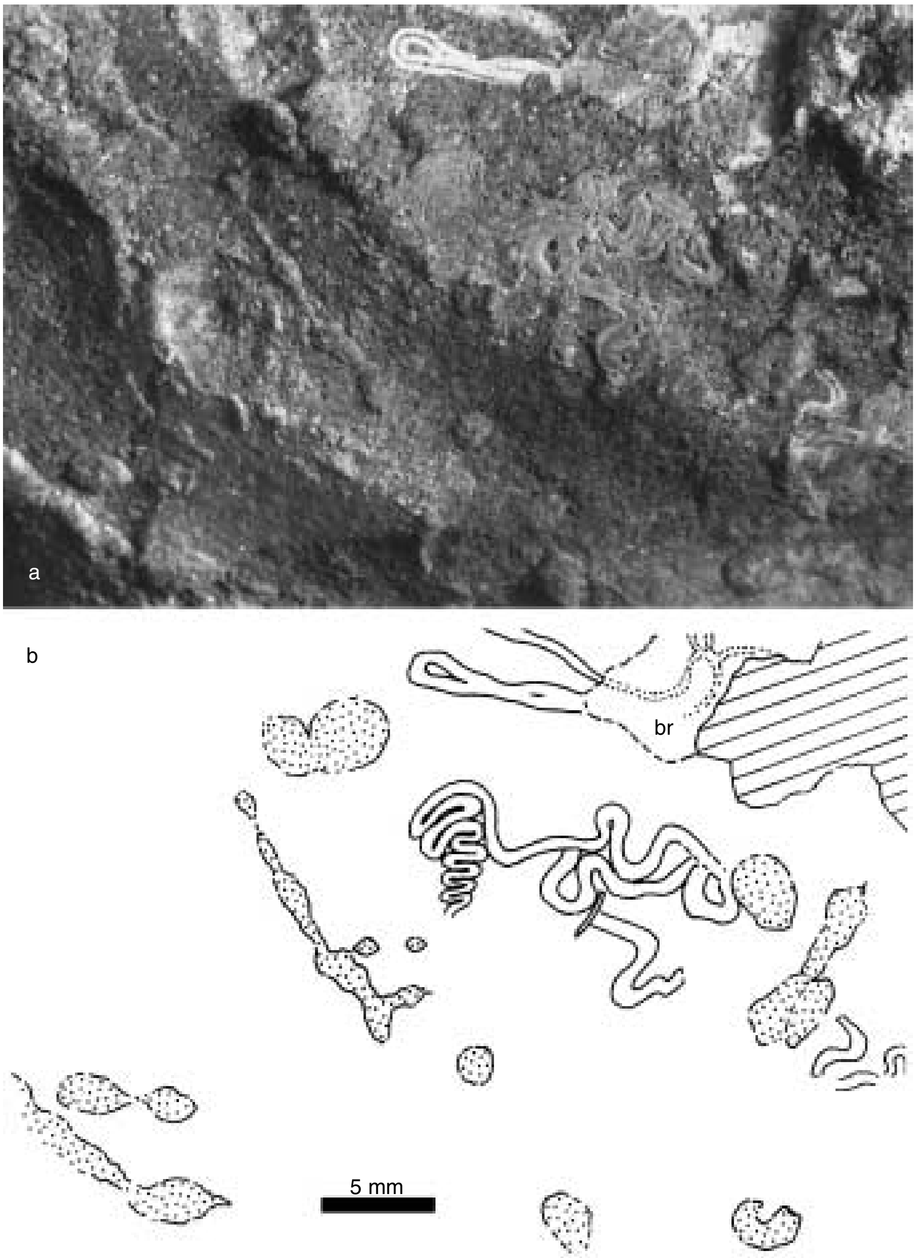


Fig. 13. A fragment of an internal mould of isolated valve of *Perna* (?) sp. with epibionts originally attached to the shell inner surface. a – photo; b – drawing of the same area: except tubes of worms and a bryozoan colony (br), the fillings of *Entobia*-like borings (stippled) of the original shell are adpressed to the mould. Hatched area – the rock originally in contact with outer surface of the shell adjoined to the mould after the dissolution of the shell. Korycany, site I.

Bivalves

Because bivalves are on average much more abundant than gastropods in the deposits of the Bohemian Cretaceous Basin, their encrusters are also more frequently found, mainly in the nearshore sedimentary settings. Even though they still have not been adequately described, their species spectrum in the shallow-water depositional environments seems to be roughly identical with that of hard-rock substrates (rocky bottom, rock clasts, intraclasts). The best finds of bioclast (mainly oyster and sponge) encrustations are being studied only now (localities Velim, Předboj, a.o.): the epizoan assemblages can be preliminary confirmed to consist of oysters, a spondylid, worms, bryozoans, thecidean brachiopods and foraminifers of mostly identical species as found by Žítt and Nekvasilová (1996). Altogether about 17 species were preliminarily distinguished, encrusting mainly larger oyster shells. These shells are mostly well preserved and, moreover, often free of sediment, which contrasts with those of now studied non-oyster bivalve species. Epibionts colonizing inner shell surfaces are therefore directly observable.

Isolated pelecypod valves from the Korycany limestones were very rarely gathered complete; hence no epibionts of their outer surfaces could be observed. As it was mentioned above, the internal moulds or imprints of valves bear basal attachment parts of epibionts preserved in the same way as they are preserved on gastropod internal moulds. The epibiont species are also identical. The presence of colonizers on inner shell surfaces clearly demonstrates the concave-up orientation of valves on the sandy bottom during epibiont settlement and most probably even their growth to the present size. Concave-up orientation of shells as a hydrodynamically unstable position indicates low rate of reorientation and thus only low energy of bottom currents (see Clifton 1971, Powell et al. 1989). Even though the importance of hydraulic reworking for orientation of shells on the sea bottom should not be overestimated (Kidwell and Bosence 1991), episodes of redeposition and reorientation are probable in the studied shallow water environment. When eventually deposited, the shells show roughly the same proportion of concave-up and convex-up orientations. Unfortunately, no bivalve shells studied on orientated rock samples were bearing epibionts.

The bivalve shells are, compared to the gastropods, more frequently colonized by oysters (Figs 12, 14). Moreover, these oyster epibionts often show preferred orientation within the extent of one cluster of individuals and sometimes on the whole shell (substrate) surface (Figs 12b, 14). This orientation is present even though the apparent local characters of concave substrate (shell surface) varied as for the slope dip and orientation. This indicates that, rather than local characters of the substrate, some parameters of the surrounding environment played a significant role in epibiont orientations. It is worth mentioning that all such identically orientated individuals attained similar sizes when they died and that they were most probably contemporaneous (see mutual contacts of specimens in Fig. 14). We suggest that settling larvae orientated themselves most probably under hydraulic conditions of a unidirectional bottom current, which was not, however, too strong to overturn shell substrates to hydrodynamically stable positions.

Compared with the investigations of modern fauna (particularly worms), the encrustation episodes of the Korycany shells (both gastropod and bivalve ones) were only short, lasting probably only several weeks (see Luckens 1976). Different growth stages of worms indicate that their settlement was probably not seasonally restricted (in modern species see Ralph and Hurley 1952). The relatively wide size range of the cemented oysters may be of similar nature. Oysters as organisms of essentially longer lifespan (at the Velim locality, several years can be estimated for fully grown specimens of *A.*(*A.*) *haliotoideum* about 5 cm long) were apparently killed at very early growth stages.

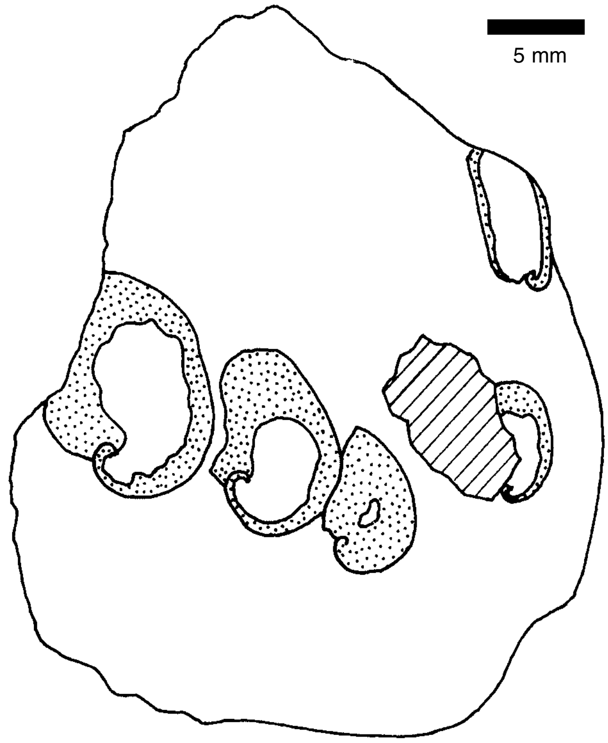


Fig. 14. An imprint of the inner surface of a bivalve shell showing its oyster epibionts. Note identical orientations of all specimens. Korycany, site III.

Results and conclusions

1. The sandy Korycany limestones (Peruc-Korycany Formation) near Korycany in central Bohemia (Late Cenomanian), yielded numerous gastropods and bivalves from excavations for the gas-main. The gastropods are preserved as internal moulds, bivalves mostly as valve imprints.
2. The formation of gastropod moulds was a process fully dependent on the shell dissolution and rock lithification rates. The slower dissolution relative to lithification, the more authentically were the internal moulds formed as for the shape and surface. In the continuous succession of mould quality parameters, two extreme members were distinguished as types 1 (coarse, deformed moulds) and 2 (smooth, undeformed moulds) with corresponding series of stages in epibiont preservation between them.
3. A distinctive loss of taxonomic data, caused by complete dissolution of gastropod shells and brittle character of bivalve shells, was compensated by a study of features which are not normally visible on well preserved specimens, here represented by epibionts originally attached to the inner shell surfaces.
4. The benthic community living attached to the studied substrates comprised only a low-diversity cementing component, consisting of one oyster species (*Amphidonte* (*A.*) cf. *haliotoideum* (Sowerby), one unidentified serpulid and about four bryozoan species. While the worm tubes are the most common, bryozoans are rare. All the epibionts preserved on each individual substrate were more or less contemporaneous, and record only a short-time (only several weeks are suggested) community development. Preferred orientation of oysters on inner surfaces of pelecypod valves is explained as a consequence of weak unidirectional bottom currents. Cryptic character of the micro-habitat in gastropod shell interiors is possible but not distinctive because only adapertural areas were mostly colonized.

The initial thanatocoenose comprising the gastropod shells of ecologically strongly different species (both epibenthic and infaunal) indicates redepositions and reworking of surficial bottom deposits. Encrustation of all these shells by identical epibionts points to the common area of encrustation under similar bottom conditions. Position of this area relative to the final bioclast deposition is hard to estimate, as the studied inner epibionts were sheltered in shell interiors (in gastropods) or on concave surfaces (in bivalves) and, as such could not be substantially damaged by reworking and transport. In gastropods, outer abrasion could not be studied due to later dissolution of shells. A postmortem mobility of empty shells is, however, indicated by their local current-induced preferred orientations. The studied bivalve shells do not seem to be substantially abraded but most of them show a complete disarticulation indicating their postmortem mobility as well. Lithology of the sediment on the final depositional site shows that only larger bioclasts (among them the gastropod and bivalve shells) could offer the cementing benthos a suitable substrate. However, only short-time windows for survival of epibionts existed, as indicated by the low species diversity and individual abundance, as well as by the high juvenile mortality (especially among oysters).

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