

A Middle Miocene gastropod shell with epifauna from the locality Buituri (Transylvanian Basin, Romania)

by
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Abstract — Abundant epifauna (bivalves, bryozoans, sessile worms), settled on gastropod shell (*Cerithium crenatum* BROCCHI), was studied from the Badenian locality of Buituri. Several epifaunal attachment phases were recognized passing off partly either during the life of the gastropod or at the time when its empty shell was approximately in the same position as during its lifetime, partly after the death of the gastropod when its shell was turned over from the life position. Mutual interactions among various representatives of sessile benthos colonizing the shell were described and interpreted.

Keywords — Buituri, Transylvanian Basin, Romania, Badenian, Gastropoda, Bivalvia, Bryozoa, Vermes, epibionts.

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Introduction

One gastropod shell (*Cerithium crenatum* BROCCHI) with abundant epifauna (bivalves, bryozoans, and sessile worms), colonizing its surface, was found among the fossil molluscs from the Badenian locality of Buituri (Transylvanian Basin, Romania) in the collections of the Geolo-

gical and Palaeontological Department of the Hungarian Natural History Museum, Budapest. Various mutual relations among the gastropod shell and the encrusting fossil organisms were studied; the results are presented in this paper.

Geological setting

The locality Buituri is situated in the southwestern part of the Transylvanian Depression, 20 km southwards from the city of Deva within the Lower Strei-Hațeg Basin (western Romania, Hunedoara Region). An outcrop of Middle Miocene (Badenian) sediments with a very abundant paleontological content represents the locality (MOISESCU 1955, RADO 1960, 1969, STUDENCKA et al. 1998). It belongs to the famous Romanian Miocene fossiliferous sites (POPESCU & MARINESCU 1978) and its fauna is similar to those described from the localities Coștei, Lăpugiu, and Tusa (RADO 1960, 1969, POPA & IANOLIU 2000).

The Transylvanian Depression is a Tertiary intramountain basin lying within the internal zone of the Carpathian Mountains. Its major reorganization occurred in the Middle Miocene (Badenian, New Styrian Phase), when the basin acquired its present configuration, and it is linked to the complex of the East Carpathian nappes. Transgressive clastics, marls, and dacitic tuffs were followed by a regionally extensive deeper marine salt layer (MÉSZÁROS 1997).

From the lithostratigraphic point of view, the Campie Group with three distinct distinguishable units (Ciceu-Giurgești Formation, Dej Formation and Mireș Formation) is accepted for the Transylvanian Depression within the Badenian (FILIPESCU 1996, MĂRUNTEANU et al. 1999, CHIRA 2001). Ciceu-Giurgești Formation (Badenian–Moravian) is a transgressive unit starting from conglomerates or gravels, overlaid by siltic clays and thin tuff levels marking the base of a new sedimentation cycle (NN5 nannoplank-

ton zone). Tuffs, tuffites, clays, and silts form the Dej Formation (Badenian–Moravian to Lower Wielician) (NN5 nannoplankton zone). Mireș Formation is of Middle/Late Badenian age (Upper Wielician to Kosovian, NN5–NN6 nannoplankton zones). Evaporites (gypsum and salt), breccias, gypsiferous sandstones, and bituminous shales form its lowermost part (Upper Wielician; sometimes distinguished as Ocna Dejului Formation, NN5b and NN6a Subzones; CHIRA 2001). The upper part is constituted of argillaceous shales, marls, clays, sometimes limestones, sands and sandstones. By convention, the Borșa-Apahida-Turda tuff is considered as the marker between the Badenian and Sarmatian (CIUPAGEA et al. 1970).

According to MOISESCU (1955), in the wider surroundings of Buituri the Badenian sediments (Dej and Mireș Formations) are widespread, being deposited transgressively on the crystalline rocks. They are represented mainly by calcareous, slightly bedded sands and clays, higher even by gypsum reaching sometimes up to 12 m in thickness. In the S and SW of the Buituri area the Badenian sediments are cropping out, in the N being buried under Sarmatian sediments on many places.

Various groups of organisms have been studied from the locality Buituri: foraminifers, molluscs (bivalves, gastropods, scaphopods, chitons), corals, sponges (spicules), brachiopods, bryozoans, worms, ostracods, echinoids, crustaceans, fishes (teleosts) and algae (MOISESCU 1955, RADO 1960, 1969). Molluscs (bivalves and gastropods)

are probably the most important ones. The Buituri area belonged to the littoral part of the Transylvanian Basin (MOISESCU 1955). During the Badenian, this area communicated with the Pannonian Basin and, through it, even with the Vienna Basin that is proved by many mollusc species in common. The water was warm, sufficiently oxygenated and favourable enough for flourishing of the benthos. The presence of many stenohaline molluscs (*Anomia*, *Pecten*, *Cardites*, *Panopea*, *Haliotis*, *Nucula*, *Arca*, *Glycymeris*, *Turritella*, *Aporrhais*, *Strombus*, *Voluta*, *Conus*) confirms

that the salinity reached normal marine values at this locality. Among molluscs, the representatives of epifauna, living on the substrate surface, predominate, the substrate being rather more sandy than clayey. Suspension feeders (*Turritella*) and predators (*Natica*, *Conus*, *Murex*) are abundant (MOISESCU 1955). STUDENCKA et al. (1998) made the last revision of the bivalves at Buituri based on the material from museum collections (Bucharest, Iași, Warszawa). They presented a list of 135 bivalve species ranging the locality to the Upper Badenian of the Central Paratethys.

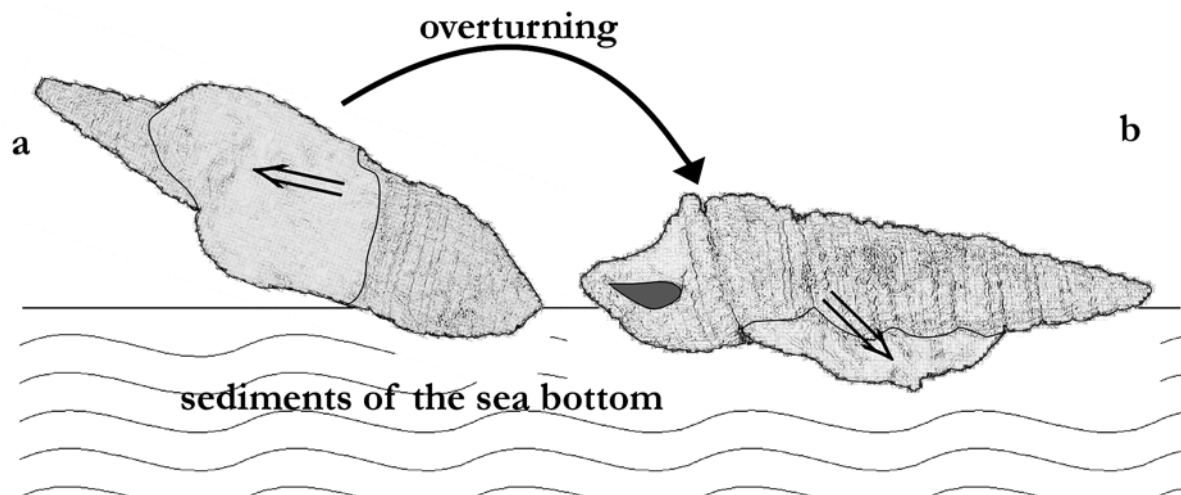


Figure 1 — Probable position of the gastropod shell — **a**: during the first series of attachment phases (the “living” position) — **b**: during the second series of attachment phases (the overturned position) — **Arrows**: the left valve of oyster *Ostrea digitalina* DUBOIS (specimen A).

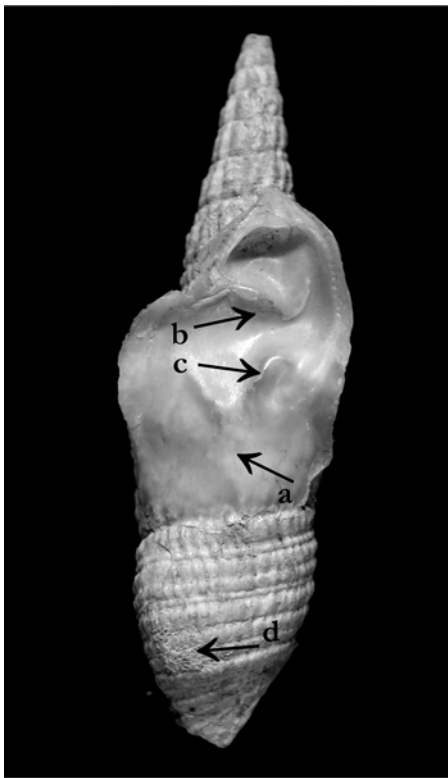
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Explanation to Plate I

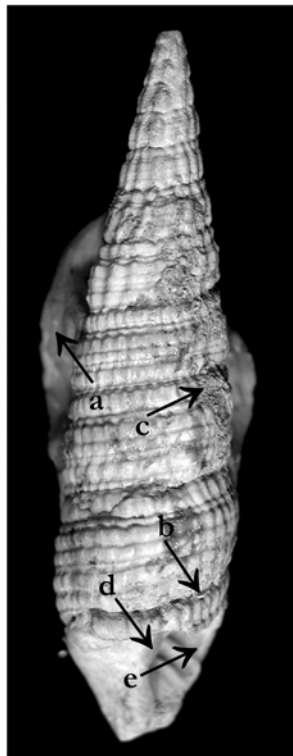
- Global view of the gastropod shell of *Cerithium crenatum* BROCCHI (opposite to the aperture) with several specimens of epifauna on the surface (arrows)** — $\times 1.9$; **a**: the left valve of oyster *Ostrea digitalina* DUBOIS (specimen A). Its inner surface is conspicuously indented, it is probable that it entirely overgrows at least two other probably oyster valves (specimens A1 and A2) — **b**, **c**, **d**: the bryozoan colony *Schizoporella tetragona* (REUSS) (specimen L) evident on the body whorl of the gastropod shell.
- Global view of the gastropod shell of *Cerithium crenatum* BROCCHI (apertural side). Several specimens of epifauna are evident on the shell surface (arrows)** — $\times 1.9$; **a**: oyster *Ostrea digitalina* DUBOIS (specimen A) — **b**: serpulid worm *Pomatoceros* sp. (specimen O) — **c**: bryozoan colony *Schizoporella tetragona* (REUSS) (specimen J) — **d**: oyster *Ostrea* sp. (specimen C) — **e**: serpulid worm *Pomatostegus* cf. *comatus* (ROVERETO) (specimen N).
- Global view of gastropod shell, *Cerithium crenatum* BROCCHI (apertural side) with several specimens of encrusting epifauna (arrows)** — $\times 4$; **a**: the left valve of oyster *Ostrea* sp. (specimen E), its inner surface is entirely covered by a colony of bryozoan *Schizoporella tetragona* (REUSS) (specimen J) — **b**: the left valve of oyster *Ostrea* sp. (specimen D) surrounded and slightly encrusted by a colony of bryozoan *Schizoporella tetragona* (REUSS) (specimen J) — **c**: the left valve of oyster *Ostrea* sp. (specimen F) attached to the inner valve surface of the specimen D — **d**: the bryozoan colony *Schizoporella tetragona* (REUSS) (specimen J) — **e**: the rest of the calcareous tubular shell of serpulid *Pomatoceros* sp. (specimen O) — **f**: the left valve of oyster *Ostrea digitalina* DUBOIS (specimen A).
- Surface details on the apertural side of the shell of *Cerithium crenatum* BROCCHI (compare with photograph 3)** — $\times 7.2$; **a**: the left valve of oyster *Ostrea* sp. (specimen E), its inner surface is entirely covered by a colony of bryozoan *Schizoporella tetragona* (REUSS) (specimen J) — **b**: the left valve of oyster *Ostrea* sp. (specimen D) surrounded and slightly encrusted by a colony of bryozoan *Schizoporella tetragona* (REUSS) (specimen J), it is evident that a part of the colony imitates the outer shape of specimen D — **c**: the left valve of oyster *Ostrea* sp. (specimen F) attached to the inner valve surface of specimen D — **d**: the bryozoan colony *Schizoporella tetragona* (REUSS) (specimen J).
- Remains of the calcareous tubular shell of serpulid *Pomatoceros* sp. (specimen O details)** — $\times 6.2$; the tube (arrow a) is attached to the upper margin of the body whorl of the gastropod shell (compare with photographs 2 and 3), just right of oyster *Ostrea* sp. left valve (specimen I — arrow b).
- Rest of the calcareous coiled tubular shell of serpulid worm, *Pomatostegus* cf. *comatus* (ROVERETO)** — $\times 35.2$; (specimen N) attached inside the aperture of the gastropod shell (detail — compare with photograph 2).
- Details of the shell aperture of *Cerithium crenatum* BROCCHI (the aperture side)** — $\times 4.4$; **a**: oyster *Ostrea* sp. (specimen C) attached just in the aperture of the *Cerithium* shell (on its inner lip) — **b**: *Schizomavella* cf. *tenella* (REUSS), a small bryozoan colony growing within the siphonal canal (specimen K).
- The surface detail of gastropod shell *Cerithium crenatum* BROCCHI** — $\times 4.8$; **a**: oyster *Ostrea* sp. (specimen B) attached about 1 mm right of the apex of specimen A — **b**: a small bryozoan colony of genus *Lagenipora* (specimen M) — **c**: the left valve of oyster *Ostrea digitalina* DUBOIS (specimen A).

All photos are taken by L. PLCHOVÁ

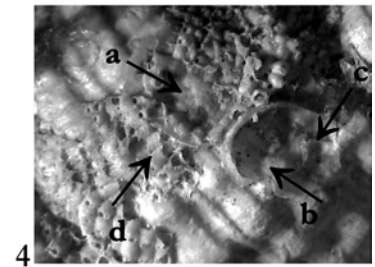
Plate I



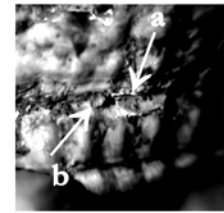
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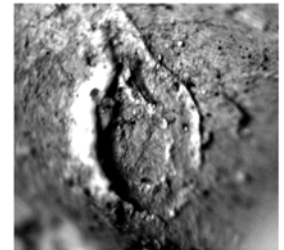
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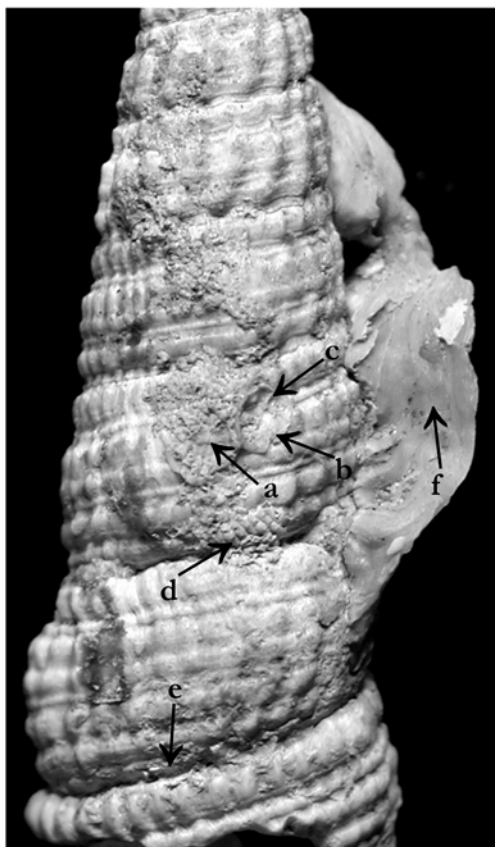
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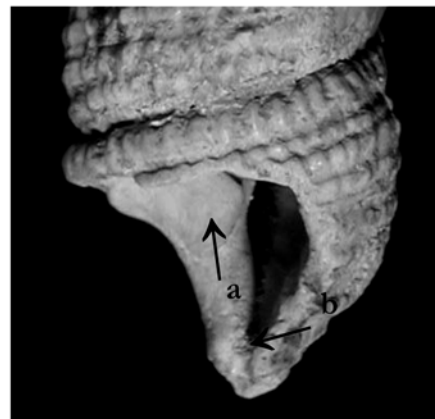
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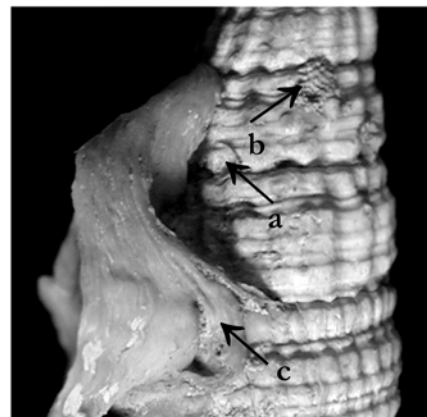
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RADO (1965, non vidi, fide in RADO 1969) and GHIURCA (1961, 1973) studied bryozoans from the locality Buituri. GHIURCA recognized a total of 25 species, but he neither described nor illustrated any of them. The modern revision of this fauna seems to be essential.

Sessile worms (serpulids) were, up to now, studied from the locality Buituri by RADO (1960). Our presented results, based on publications by ROVERETO (1904) and SCHMIDT (1955) can probably be regarded as additional modern descriptions of serpulids from this locality.

Material, methods

The studied epifauna encrusted a shell of *Cerithium crenatum* BROCCHI (Figure 1, Plate I: 1–8), collected from the locality of Buituri. The specimen is deposited in the paleontological collections of the Hungarian Natural History Museum (Magyar Természettudományi Múzeum), Budapest, and labelled as M.59.1789. *Cerithium crenatum*

BROCC. Bujtúr, Torton, Erdély, Vétel: Streda Rezső.

The study was made by binocular microscope Nikon SMZ-1, digital camera Olympus CAMEDIA C-3030 ZOOM and by digital color video camera JVC ½ INCH CCD TK-C1381.

Results

Gastropod shell (Plate I: 1–8) — The shell is 4.9 cm high and maximally 1.2 cm wide. The body whorl (number 0) and totally eleven spiral whorls (numbers 1–11, counted from the body whorl) are preserved, while the uppermost part of the spire is missing. The shell aperture is slightly damaged, its margins and the lower part of the siphonal canal are broken off, but the broken edges are slightly rounded. In the following text the aperture and the opposite sides of the shell are distinguished. The shell surface is rather strongly weathered and, probably due to the absence of other hard substrate, encrusted by numerous specimens of sessile benthos (epifauna): bivalves, bryozoans and worms.

Oysters — *Specimen A* (Plate I: 1–3, 8) — *Ostrea digitalina* DUBOIS, left valve with the apex oriented towards the juvenile part of the gastropod shell. The attachment point of the oyster shell is situated between the 4th and 5th spiral whorls, on the opposite side of the gastropod shell, the valve covering the following 4 whorls towards the body whorl. The oyster valve is 2.2 cm long and 1.5 cm wide. Its inner surface is conspicuously indented. With regard to the shape of the roughness as well as to the fact that the attached valve generally closely imitates the configuration of the substratum, it is probable that the valve of *specimen A* entirely overgrows at least two other probably oyster valves (*specimens A1 and A2*).

Specimen B (Plate I: 8) — *Ostrea* sp., juvenile stadium of the left valve about 1 mm long; it is attached about 1 mm right of the apex of *specimen A* at the boundary between the 3rd and 4th spiral whorl, with the apex orientated to the right.

Specimen C (Plate I: 2, 7) — *Ostrea* cf. *digitalina* DUBOIS, left valve with the visible adductor imprint, the length of the valve is 0.7 cm and the width is 0.5 cm. The valve is attached to the inner lip of the *Cerithium* peristome, with the apex oriented to the left. The marginal parts of the valve are missing; the broken parts have sharp edges.

Specimen D (Plate I: 3–4) — *Ostrea* sp., left valve (2 mm long and 2 mm wide) with the attachment point situated at the 3rd whorl of the gastropod shell merely on the aperture side and with the apex oriented downwards. The valve is surrounded by bryozoans (*specimen J*), on the left side of its inner surface a small area of about 0.1 square mm is covered by a bryozoan colony.

Specimen E (Plate I: 3–4) — *Ostrea* sp., left valve with the length about 2.5 mm and width 2 mm and with the apex oriented downwards. The valve is attached to the 3rd spiral whorl close to *specimen D* on the aperture side of the gastropod shell. The inner valve surface is entirely covered by a bryozoan colony (*specimen J*).

Specimen F (Plate I: 3–4) — *Ostrea* sp., juvenile left valve few tenths of mm long and wide attached to the inner surface of *specimen D* valve with the apex oriented to the left.

Specimens G, H and I — *Ostrea* sp., juvenile left valves, few tenths of mm long and wide, attached at the boundary between the spire and the body whorl. *Specimen G* is situated on the right side of the ventral margin of *specimen A*, with apex oriented to the left. *Specimen H* is attached further 5 mm right from *specimen G*, with apex oriented slightly obliquely left downwards.

Specimen I (Plate I: 5) is settled about 1 cm left of the ventral margin of *specimen A*, with apex oriented to the right. Close to *specimen I*, a tubular shell of the worm *Pomatoceros* sp. (*specimen O*) is visible.

Bryozoans — *Specimen J* (Plate I: 2–4) — *Schizoporella tetragona* (REUSS), the largest bryozoan colony on the gastropod shell surface. The colony covers an almost continuous area of about 2×0.5 cm on 4 whorls up from the boundary between spire and body whorl. The colony is partly intensively abraded, but its larger part is well preserved, about 30 zooecia (individuals) are not damaged. The colony grows along the spire, slightly in the direction to the siphonal canal. The colony encrusts also inner surfaces of the neighbouring oysters (*specimen E* and partly *specimen D*). It is evident that a part of this colony imitates the outer shape of *specimen D*.

Specimen K (Plate I: 7) — *Schizomavella* cf. *tenella* (REUSS), a small colony consisting of three complete zooecia and three to four remnants of damaged zooecia. The colony grows inside the aperture of the gastropod shell, within the siphonal canal, covering an area of about 1×1 mm. The colony is poorly preserved, so the correct identification is not possible. The colony grows alone; no interactions with other epibionts are observable.

Specimen L (Plate I: 1) — *Schizoporella tetragona* (REUSS), the colony covers an area of about 2×2 mm on the outer side of the body whorl (right from the gastropod aperture),

with evident abrasion traces on its surface. About 20 zooecia are well preserved, another 15 to 20 individuals are preserved as mere remains. No interactions with other organisms are visible.

Specimen M (Plate I: 8) — *Lagenipora?* sp., a very small poorly preserved colony consisting of about 3–4 zooecia and about 10 remains of damaged individuals. The colony grew alone on the upper part of the spire; no interactions with other epibionts are observable.

Serpulids — *Specimen N* (Plate I: 2, 6) — *Pomatostegus* cf. *comatus* (ROVERETO), the remnant of a calcareous, coiled tubular shell is attached to the inner side of the outer lip of the gastropod shell. The maximal tube cross-section diameter is about 0.5 mm. The lumen is circular, no internal sculpture developed; the cellular layers of serpulids are very well preserved, they developed as a composite, undulating layer. The aperture is preserved only partially; it is funnel-

shaped and oriented towards the peristome of the gastropod. The other parts of the tube are not preserved. This specimen is adult and seems to be 2–3 years old by development of the cellular layers. It could settle inside the gastropod shell only after the gastropod had died and its shell had turned over the oyster valve (*specimen A*).

Specimen O (Plate I: 2–3, 5) — *Pomatoceros* sp., remain of a calcareous, tubular shell of about 3 mm length. The tube is attached to the upper margin of the last whorl of the gastropod shell, closely right to the oyster valve (*specimen I*). The tube is only partly preserved and having a circular to triangular cross section. The anterior and the posterior parts of the tube are not preserved; the low comb developed on the dorsal part of the tube. The diameter of tube cross-section is about 0.2 mm. This specimen is young; it can be one year old because the cellular layers are not completely developed.

Discussion

We can positively assume that the described epifauna as a whole represents several distinguishable attachment phases constituting greater sequences immediately connected with the instantaneous (i.e. minimally two) gastropod shell positions. These sequences, as well as their possible individual attachment phases are discussed in the following. Nevertheless, the chronological succession of individual attachment phases within the sequences cannot be described and interpreted unambiguously due to the scarcity of evident interactions among the individual epibionts.

The first sequence of attachment phases (generally connected with the “living” position of the shell) —

This sequence originated when the gastropod shell was generally in the living position or in the position very close to that during the life (the aperture downwards, the apex obliquely upwards, see: Figure 1a). There is no reason to exclude the possibility that these attachment processes occurred during the life of the gastropod. Nevertheless, there are still other possibilities: the empty shell could be occupied secondarily by other organisms, for example hermit crabs, or partly buried in the sediments with its apical part rising obliquely upwards above the bottom.

The following attachment phases can be included into this sequence:

Phase 1A — *Oysters A1* and *A2*, attached between the 4th to 5th spiral whorls, might represent the very first epibiont generation. Probably after their death, oyster *specimen A* fully overgrew them representing therefore potentially the first visible sessile organism on the gastropod shell surface. Considering its valve size, it can be concluded that *specimen A* is about one year old (the comparable material was described from the locality Rudoltice v Čechách, see details in HLADÍLOVÁ & PEK 1998). The attachment points of all these oyster valves are situated relatively high on the spire, on the side opposite to the aperture. This fact supports the interpretation that the gastropod shell was oriented with aperture generally downwards and spire obliquely upwards during the attachments of specimens

A1, *A2*, and *A*. This corresponds more or less to the life position when just the above mentioned parts of the shell surface were accessible for the settlement of epibionts.

Phase 1B — Besides the mentioned oysters, bryozoan *specimen L* also could settle on the gastropod shell during this time interval. *Specimen L* is attached to the opposite side of the shell and this position, as well as the relatively abundant abrasion traces on its surface, confirms the inference that the settlement could have taken place generally during this first sequence of attachment phases. In such a case, *specimen L* may represent the oldest bryozoan, occurring on the surface of the studied gastropod shell. Since there are no interactions among bryozoan *L* and other organisms (e.g. oysters *A*, *A1*, *A2*), the exact attachment timing of the bryozoan colony within this sequence cannot be determined with certainty.

The second sequence of attachment phases (generally connected with the overturned position of the shell) —

After the death of the gastropod (or abandonment of its shell by possible secondary inhabitants, for example hermit crabs) as well as after the death of oyster *A*, the empty gastropod shell was evidently turned over from its life position while the left valve of oyster *A* served most probably as a new “base” (Figure 1b). Consequently, the apertural side of the gastropod shell surface became exposed to the epifauna for settlement. This position is unequivocally regarded as the most stable for the studied specimen anyway. The gastropod shell probably persisted for a relatively long time approximately in this overturned position, at a guess for more than 2 years considering the maximal individual age of the epifauna found (see below).

The following attachment phases can be distinguished within this sequence:

Phase 2A — *Oyster C* (situated in the interior of the gastropod shell), the bryozoan colony *K*, and *serpulid N* [growing inside (or close to) the gastropod siphonal canal] undoubtedly colonized the gastropod shell just after its overturning because they are attached to places which were

inaccessible during the life of the gastropod. *Oyster C* grew minimally for 7–8 months (this conclusion is based on the comparison of its size to that of *specimen A*), *serpulid N* is minimally 2 years old.

From the attachment points of the sessile worms (*specimens N* and *O*), it can be generally inferred that they have not settled the shell most probably until its overturning. The mutual attachment succession, as well as the chronological attachment sequence relative to the oysters and bryozoans cannot be reconstructed accurately because of the total lack of evidences. Both serpulids settled into sheltered places. The reason could be either self-protection and/or the possibility of an easy food acquisition.

Phase 2B — The smaller oysters (*specimens D* and *E*) probably represent a separate attachment phase. Their ages are of only 1–2 months concluded from their sizes. The shell of *specimen E* is somewhat greater, therefore it grew longer than *specimen D*. Considering the fact that *valve E* is fully overgrown by the bryozoans (*specimen J*), which are imitating and only partly overgrowing the shape of *valve D*, it is highly probable that *specimen E* is somewhat older than *D*. Rather likely, *specimen E* was already dead in time of the bryozoan colonization, whereas *specimen D* was still alive. According to their interactions and positions of settlement (the apertural side of the gastropod shell), it can also be supposed that these oysters did not attach to the gastropod shell until its overturning, i.e. generally during the second sequence of attachment phases.

Phase 2C — The bryozoan *specimen J* is unequivocally younger than *oysters D* and *E* because they serve as basement for the colony (*oyster E* completely, *oyster D* only partly are overgrown by *specimen J*). Moreover, this bryozoan colony imitates the outline of *oyster D*. Simultaneously, *specimen J* is undoubtedly older than *oyster F* because its valve is not covered by the bryozoans at all.

Thus it is possible to suppose that *specimen J* represents more than one generation of bryozoans and that the colony partly covering the inner surface of oyster *specimen D* is most probably younger than the bryozoans covering *specimen E* (furthermore, this conclusion is supported by the fact that this colony covers only a small part of the inner surface of *specimen D* and that the bryozoans are entirely missing on the inner surface of *specimen F*). Therefore it might represent the youngest bryozoan colony on the gastropod shell.

Phase 2D — *Oysters F, G, H* and *I* are markedly smaller and younger than *specimens D* and *E*. Considering their sizes and developments it can be concluded that their ages make to about one month (early postlarval stadium). *Specimen F* is unequivocally younger than *specimen D*, being attached to its inner surface and being not overgrown by the bryozoans. *Oysters F, G, H* and *I* therefore probably represent a separate attachment phase (or phases) and they were attached probably as the very last elements to the gastropod shell.

Unclear attachment phases — An explicit inclusion of the remaining part of the epifauna (*specimens B, M*) into the above mentioned attachment phases (1A–2D) is problematic. The size and age of the oyster (*specimen B*) correspond with those of *specimens D* and *E*. However, it is impossible to decide doubtlessly whereas its attachment to the gastropod shell took place still before its overturning or after it (and maybe approximately together with *specimens D* and *E*), since the valve of *specimen B* is attached to such a place on the gastropod shell surface which was accessible in both time intervals mentioned.

The same conclusion is also valid for the bryozoan *specimen M*. Its attachment point is on the upper part of the spiral whorls and more or less on the aperture side of the gastropod shell, i.e. in such a place that was also accessible in both time intervals.

Conclusion

From the locality of Buituri (Badenian, Transylvanian Basin, Romania), the gastropod shell (*Cerithium crenatum* BROCCHI) with a rich epifauna (bivalves, bryozoans, sessile worms) was studied. In total 15 specimens of epibionts were found and their attachment phases were analysed. Among these organisms specimens of different individual ages (months–years) can be recognized.

From the total amount of the sessile species found, as well as from the places and types of their attachment to the gastropod shell, it can be concluded generally that:

a) the shell of species *Cerithium crenatum* probably persisted for a longer time (3 years minimally) on the surface of the sea bottom without being buried in its sediment and it was utilized for a long-term as solid substrate for settlement of larvae of the sessile benthos;

b) considering the fact that the sessile benthos was forced to utilize shells of other organisms for the settlement

of its larvae, the sea bottom in the place of the gastropod shell occurrence was probably represented by rather loamy sediments;

c) the processes of the epifaunal attachment to the gastropod shell, at least partly, did not take place until the death of the gastropod, when its shell had become empty, because some specimens of the epifauna were attached inside the gastropod shell, namely to places where the attachment was impossible during the life of the gastropod;

d) the studied epifauna represents several settlement phases constituting minimally two sequences of the shell colonization closely connected with the momentary gastropod shell position (the “living” one and the overturned one); the chronological succession of individual attachment phases within the sequences cannot be distinguished and interpreted unambiguously due to the scarcity of evident interactions among the epibionts.

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