Bulletin of Geosciences, Vol. 78, No. 4, 423–429, 2003
© Czech Geological Survey, ISSN 1214-1119

Shell morphology and palaeoecology of *Praenatica gregaria* Perner, 1903 from the Koněprusy Limestone (Lower Devonian) of Bohemia (Czech Republic)

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Abstract. *Praenatica gregaria* Perner, 1903 is an Early Devonian (Pragian) gastropod that is judged to be adapted to a stationary living habit on the tegmen of camerate crinoids. More than one thousand specimens were examined in order to describe and explain the occurrence of different morphological forms. The variability of the shells was found to be closely dependent on the attachment surface. Rapid growth changes during an ontogeny demonstrate the ability to move, perhaps even change hosts. Traces of colour patterns, epizoans *in situ* and repaired shell fractures were observed in some cases. The reconstructed colour pattern consists of longitudinal bands often transversally crossed by growth lines lacking pigment and probably serving a sheltering function. Various epizoans showed that the empty conch served as an appropriate base for the attachment of small and fragile organisms, most commonly bryozoan colonies. The majority of the studied shell fractures were formed passively in the surf, only some of them show evidence of the activity of molluscivorous predators.

Key words: Lower Devonian, Prague Basin, Gastropoda, Platyceratidae, morphological variability, colour patterns, epizoans, shell breakage

Introduction

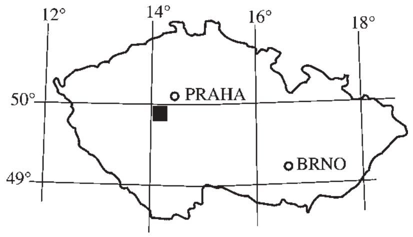
Praenatica gregaria Perner, 1903, an Early Devonian (Pragian) gastropod, belongs to the family Platyceratidae of the Neritimorpha (Bandel and Frýda 1999). The group is well known for the relationship between its representatives and crinoids (Keyes 1888, Bowsher 1955, Lane 1978, 1984, Mironova and Eltysheva 1978, Rollins and Brezenski 1988, Horný 2000). Common occurrences of the gastropod shells always in the similar way affixed atop the crinoid calyx often led to discussions about its meaning. The scientific view upon this fossil association has changed a lot over more than 150 years.

According to Bowsher (1955) the earliest note of an association between molluscs and crinoids comes from the half of the 19th century. It was believed that the crinoids were carnivorous and that some of them were buried in sediment just in the act of feeding on a gastropod or on the other hand the gastropod was judged to be a carnivore that fed on crinoids.

For a long time the association of platyceratid gastropods and crinoids was considered as an example of coprofagous commensalism (Bowsher 1955, Lane 1978, 1984). The gastropod affixed atop the crinoid tegmen commonly covering the anus was thought to have fed (in a harmless manner) on excrements expulsed by the host.

A rather unconventional interpretation that platyceratids were possibly gametophagous parasites was suggested recently (Lane 1984). Predation on living crinoids may have even played a role in the evolution of the crinoids themselves.

New evidence (Rollins and Brezinski 1988) of the nature of the platyceratid-crinoid interaction supports another interpretation of the traditionally accepted coprofagous model. The most common and most important trophic strategy was possibly based on taking advantage of aerosol filtration by the crinoid and elevation above the substrate. Coprophagy, gametophagous parasitism or even real predation where thus, if ever, minor and accessory feeding strategies.



The apertural margin often closely corresponds to the surface of the crinoid calyx which demonstrates that the snails lived in this way for most of their lives. The gastropods, nevertheless, were not limited to the advantageous coexistence strictly. The attachment of some Silurian platyceratids also on various firm objects lying at the sediment surface (empty shells of orthocone nautiloids, brachiopod shells, lithified parts of bioclastic sediment) was proved by Horný (2000).

Horný (1992, 1995) noticed sporadic cases of feed-suffering of *Praenatica gregaria* (rare dwarfed forms in facies far from the reef), probably due to the absence of an appropriate host. In the Koněprusy area (a reefal facies), the species is abundant to dominant, which corresponds with the developed gardens of camerate crinoids taking advantage of a local high concentration of biosuspension (Prokop 1999).

Material and methods

The examined fossil material consists of more than one thousand specimens and comes from various sources. The

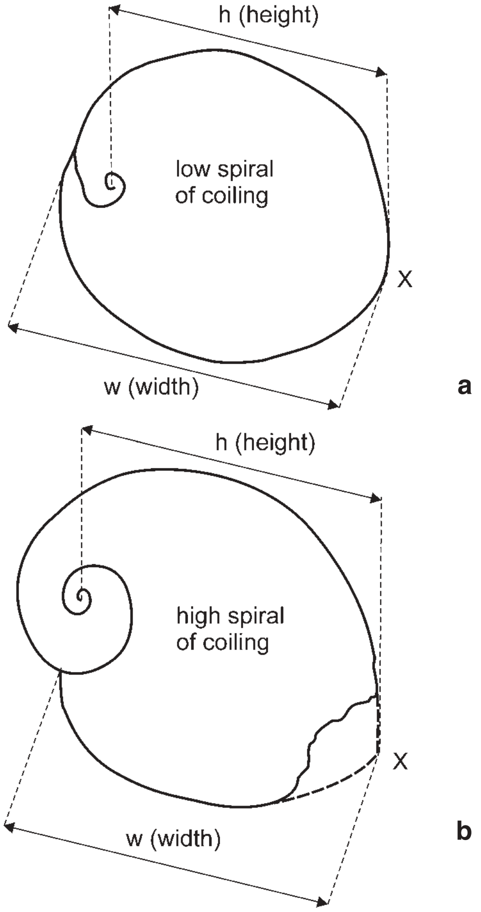


Fig. 1. Width (w) = max. aperture width, height (h) = the distance between the apex and the most distant point on the aperture (X).

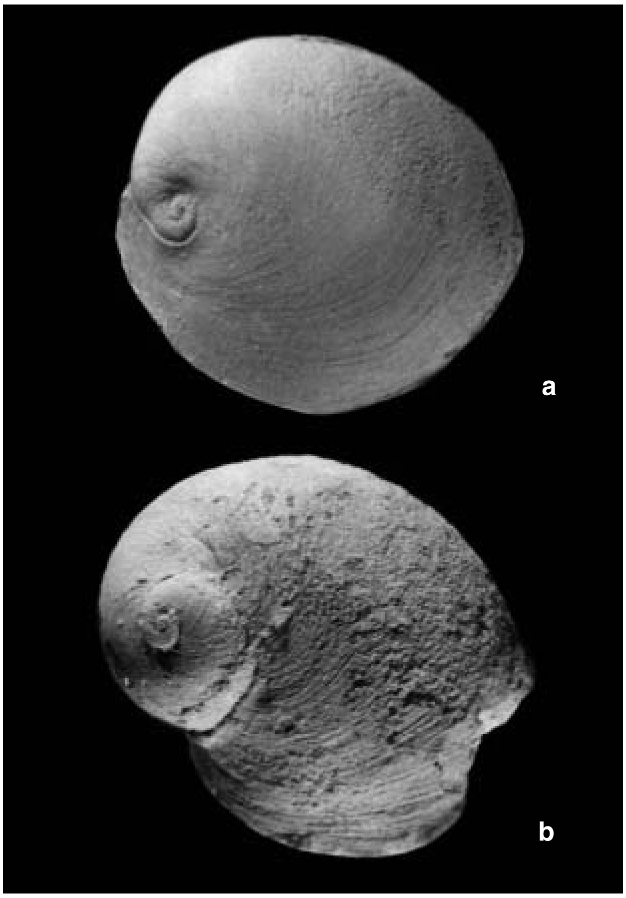


Fig. 2. *P. gregaria*, whitened with ammonium chloride. a – p 922 (CGS), b – p 6147 (CGS); oblique apical views of the shells with the low (a) and high (b) spiral of coiling; × 2.2 (a, b).

majority (ca 70 %) belongs to the National Museum in Prague (NM) collections and the author's acquisition (kept in the IGP Charles University collections) from the Plešivec Quarry near Měňany (ca 4 km SE of Koněprusy). The remaining 30 % come from the palaeontological collections of the Czech Geological Survey (CGS), the Institute of Geology and Palaeontology of the Charles University (IGP CU) and the Museum of Bohemian Karst in Beroun (MBK).

An additional mechanical preparation was necessary in most cases. The measurements were carried out on 847 selected, only completely preserved specimens. The basic description of shell morphology involved mutual comparison of the maximum aperture width and the height of the conch expressed by the distance between the apex and the aperture (Fig. 1).

Results and discussion

Morphological variability and its palaeoecological interpretation

The morphological variability was described by the relative height of the growth spiral. Individuals strongly vaulted with revealed premature whorls and therefore relatively high coiling (Fig. 2a: width/height = 17 mm/26 mm, see Fig. 1) were observed as well as very broad and flat individuals with a superficially dominating last whorl and an almost hidden spira, the relative height of which is very small (Fig. 2b: width/height = 25 mm/22 mm, see Fig. 1). A continuous series of transitional specimens exists between both extremes (Fig. 4, correl. coeff. = 0.98). The distribution of the whole set (Fig. 3a, b) is asymmetrical (fast build-up towards the most frequent classes and apparently a more gentle decrease towards larger sizes) and unimodal (moderate drop around 30 mm may be caused by a higher predator pressure on that class). The increase in height was somewhat faster than the increase in size. Younger and smaller individuals are generally slightly flatter, and become more vaulted during their growth. This trend can be generally interpreted as an effort of a growing gastropod to adjust to the life in constantly straightened conditions on a more slowly growing crinoid.

Growth changes during ontogeny were sometimes observed. The change can be either very immediate, documented by a sharp boundary line (Fig. 5) or rather slow, when it does not document a rapid event in the gastropod's life (Fig. 6). Last whorls of slowly changing specimens are always straight, loose and not further widening. Such specimens may have lived on crinoids whose calyxes were no more growing. A nutrient-dependent gastropod had to adapt its growth to given conditions. The rapid changes in growth are clearly marked in the shell morphology, and document a sudden event (maybe the loss of the crinoid host). Different conditions affected new morphology in various ways (by widening or contraction of aperture diameter). This demonstrates that *Praenatica gregaria*, though undoubtedly profiting from the stationary living habit, was able, at least partly, to move (maybe to change its hosts).

Original colour patterns

Preservation of colour patterns in Paleozoic fossils is generally rare. The problem in platyceratids was described, e.g., by Yochelson and Kříž (1974), Kříž and Lukeš (1974), Horný and Henry (1999).

Relicts of different quality of preservation were observed in 2–3 % of the specimens. These are mostly very poorly visible spirally running bands, max. 1 mm wide; almost always on specimens with dark-fossilized shells. On less dark-fossilized specimens, the bands are light and better visible, often transversally crossed by growth lines lacking pigment (Fig. 7a, b). A specimen (Fig. 7c) uniformly covered with light spots of equal size passing to parallel lines documents an imperfect preservation of originally continuous longitudinal bands (Stehli 1955 – a similar case on a brachiopod conch).

The pigmentation received the form of more or less regularly arranged spiral bands and represented – with respect to the excellent gastropod's adaptation to the stationary life mode on a crinoid tegmen – a passively protective (sheltering) function. This interpretation conforms with the idea of Kříž and Lukeš (1974) that radial and spiral colour bands are developed preferably on less mobile and sessile molluscs.

Epizoans

A limited number of specimens show evidence of an epizoan fixation. Bryozoan colonies were most common. A cyclostomate bryozoan *Hederella obscura* (Fig. 8f, g) overgrew the specimen of *Praenatica* from both the outer and inner surfaces (Horný 1985 – bryozoan zoarium overgrowing the inner shell surface of *Orthonychia*); a detailed view of the base of a cornet-like zoarium of a fenestellid bryozoan *Hemitrypa linotheras* (Fig. 8h) demonstrates its life position, and also a specimen bearing a small crinoid holdfast (Fig. 8i) documents a trace of a bryozoan growth. The inner shell surface of one specimen revealed the attachment of an inarticulate brachiopod *Petrocrania* (Fig. 8a, b). A cluster of small isolated spots (Fig. 8d, e) observed on three specimens remain undetermined. A cross section revealed no relief on the outer and inner shell surfaces. It probably originated by the attachment of a sessile organism, perhaps a brachiopod (Nekvasilová 1975, R. Mikuláš pers. comm.). Fig. 8c gives evidence of borings representing a hitherto unknown ichnotaxon (Wahlman 1992, Horný and Peel 1995, Horný 1997c, R. Mikuláš pers. comm.).

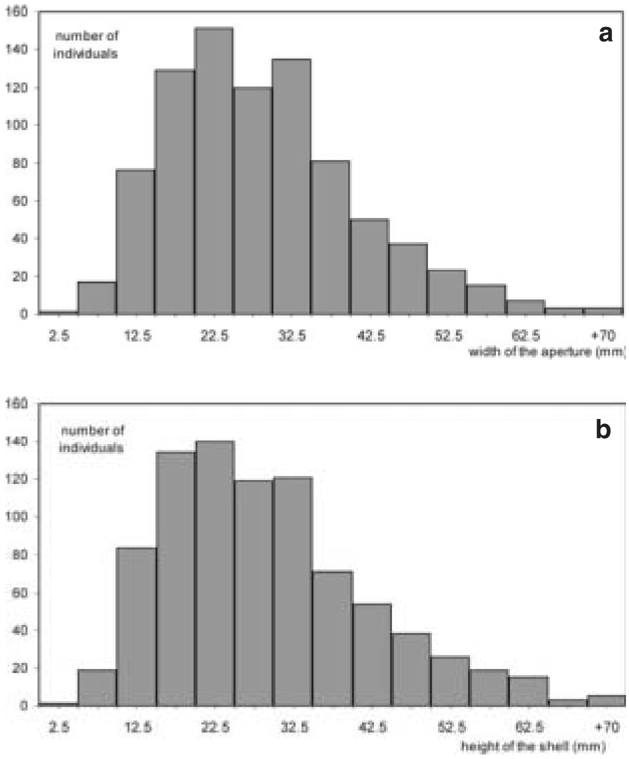


Fig. 3. Histograms showing the distribution of both measured sizes: a – "width" (see Fig. 1), n = 847, Ø = 28 mm, min. = 2 mm, max. = 118 mm, skewness = 1.1207, kurtosis = 3.3229; b – "height" (see Fig. 1), n = 847, Ø = 28 mm, min. = 2 mm, max. = 99, skewness = 1.0225, kurtosis = 1.5819.

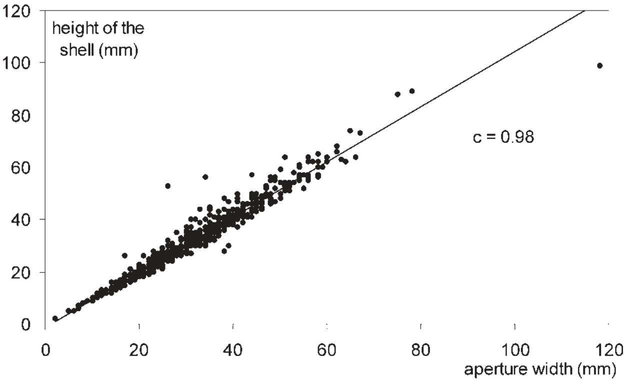


Fig. 4. The dependence graph. Regression line input. Correlation coefficient (Spearmen) = 0.98.

All the indicated cases most probably represent attachment on already empty shells. The life atop the crinoid calyx would not be advantageous for fragile branches of bryozoan colonies. Empty shell accumulations offered a welcomed protection against predators or forceful wave action.

Shell breakage and repair

A mechanical injury of the conch can be of two different types (Lindström and Peel 1997). The first type is a non-biological damage (wave-induced stress, abrasion in the surf zone), the second and dominant agent is predation.

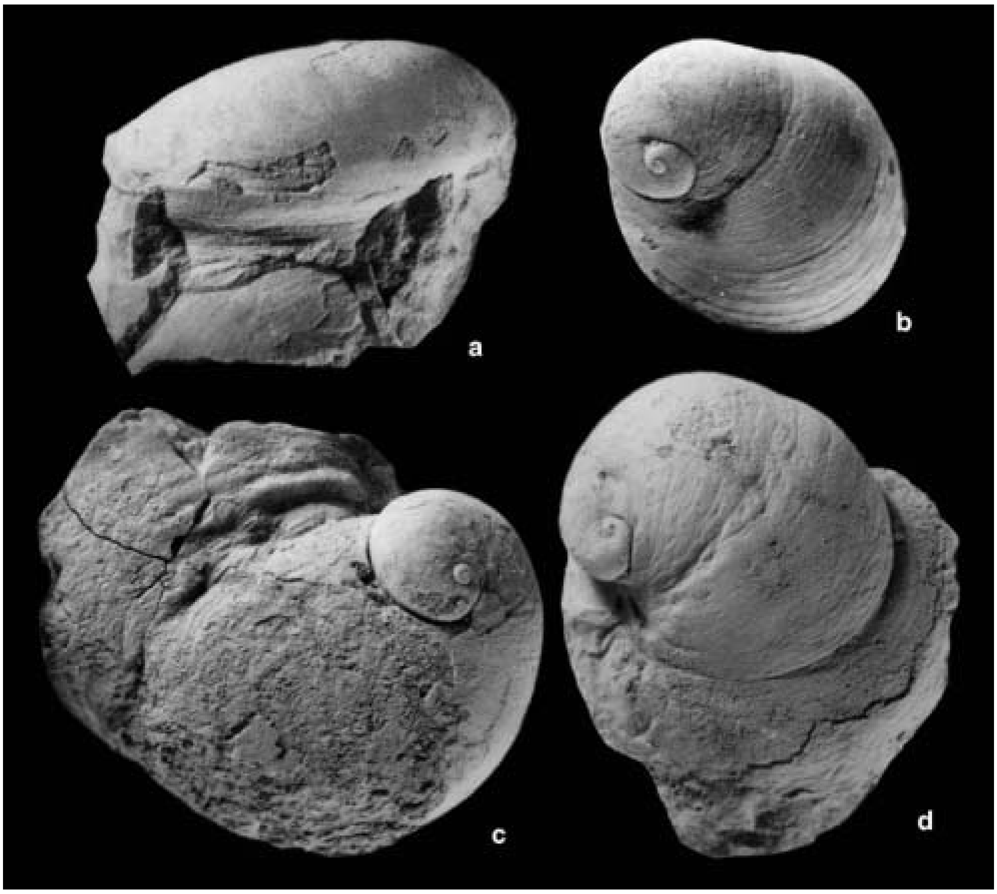


Fig. 5. *Praenatica gregaria*, whitened with ammonium chloride.
a – p 6150 A (CGS),
b – NM L 12 333 (NM),
c – NM L 36 307 (NM),
d – NM L 36 156 (NM);
oblique posterior (a), oblique apical (b, d) and oblique anterior (c) views of the shells showing rapid growth changes marked by sharp boundary lines; × 2.1 (a), × 2 (b), × 2.5 (c), × 1.8 (d).

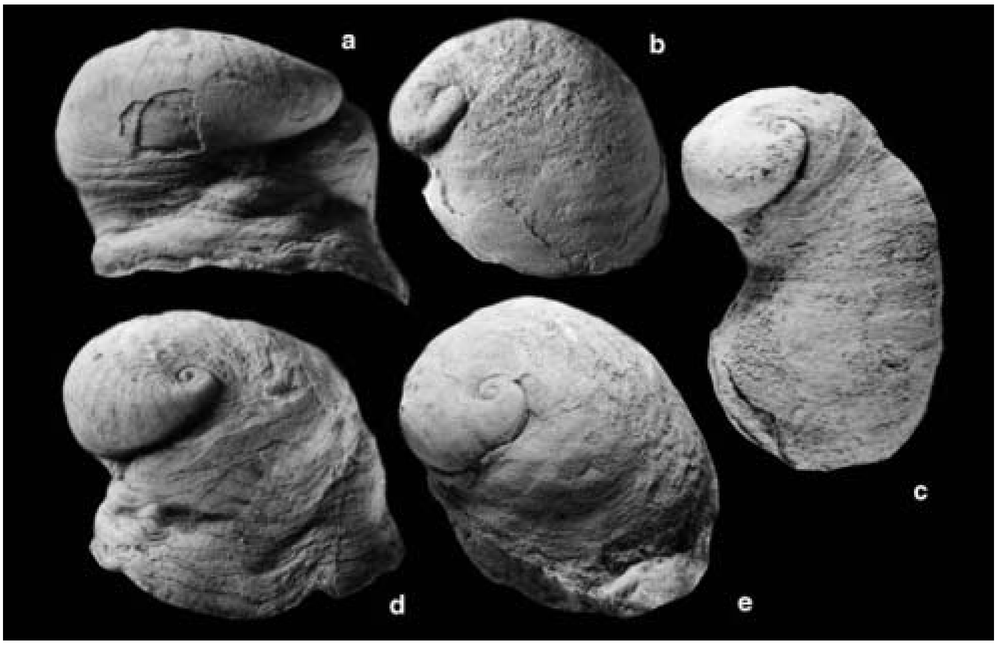


Fig. 6. *Praenatica gregaria*, whitened with ammonium chloride.
a, b – NM L 12 386 (NM),
c – NM L 36 153 (NM),
d – IGP K 2871 (IGP CU),
e – IGP K 9 (IGP CU);
oblique basal anterior (a), oblique anterior (b), anterior (c, d) and oblique apical (e) views of the shells showing rather slow, continuous growth change. Note straight, loose and not further widening last whorl and more or less pronounced spirally arranged ridges documenting life in straightened conditions among crinoid arms; × 2.2 (a–e).

The shell of *Praenatica gregaria* was showing typical antique features as for its resistance to breakage (Vermeij 1977, 1983a, b): large, round aperture, relatively thin wall, absence of more pronounced ornamentation. It was, therefore, extremely fragile. The Koněprusy reef represents a high-energy environment (Chlupáč et al. 1992). The gastropods were probably often torn off the host in the storms and easily damaged in the surf zone. Nevertheless, the origin of the breakage can be sometimes widely speculated. Fig. 9a does not show marks of repair but the lethal effect is not probable judged by the position (compared with the assumed position of vital organs) and small extent of the breakage. It probably originated after the gastropod's death, maybe as a consequence of a sharp clash in the surf.

Fig. 9b–g shows repaired fractures, possibly caused by predation activity. The most probable predators were nautiloid cephalopods (Vermeij 1977, Peel 1984, Horný 1997a, b), phyllocarids and eurypterids (Selden 1984). Primitive fish-like vertebrates should be also considered, for at that time they did not possess specialized pavement-like dentition enabling to crush shells (Vermeij 1982).

Conclusions

- Morphological variability of *Praenatica gregaria* was found to be continuous – extremes are connected by transitional members (Fig. 4).
- *Praenatica gregaria* was able to adjust to different characters of a substrate – by slow or even rapid changes of growth (Figs 5, 6). The rapid changes suggest its ability to move, maybe even change hosts.
- An original colour pattern consisting of spiral bands, often transversally crossed by growth lines lacking pigment, was described and interpreted as a protection against predators (Fig. 7).
- Empty shells of *Praenatica* obviously served as an appropriate substrate for epizoans, e.g., bryozoan colonies and inarticulate brachiopods (Fig. 8).
- The shell itself was relatively easily breakable. Different fractures and deformations were studied and the majority of them (ca 80 %) were found to be a result of a high-energy environment in a reef habitat. The other most probably demonstrate the activity of molluscivorous predators (Fig. 9).

Acknowledgements. The author thanks Dr. Radvan J. Horný, Dr. Jiří Frýda and Assoc. Prof. Jaroslav Marek for their kind and valuable comments to the manuscript. A special thank belongs to Dr. Rudolf J. Prokop and Dr. Radek Mikuláš for important consultations and to Štěpán Rak and Ladislav Zedník for their nice help during the fieldwork stage.

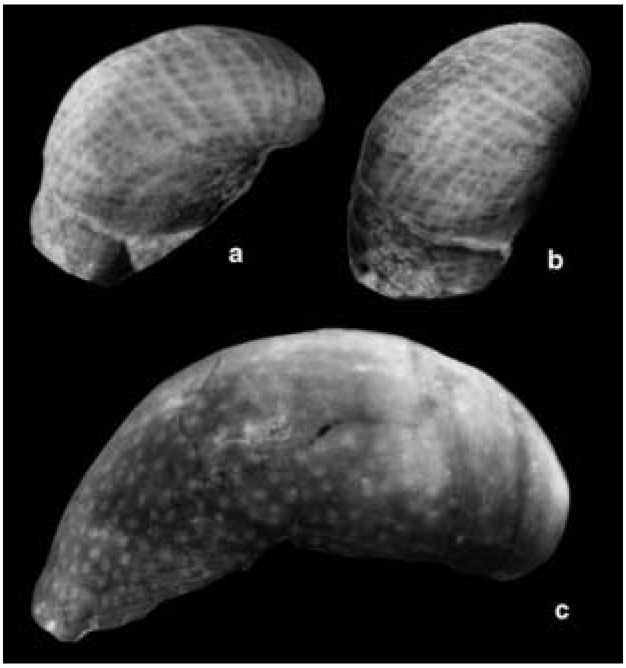


Fig. 7. *Praenatica gregaria*, immersed in glycerin. a, b – NM L 36 177 (NM), c – NM L 36 377 (NM), oblique basal (a, c) and dorsal (b) views of the shells bearing traces of colour markings; a, b – the net of light longitudinal bands transversally crossed by the growth lines lacking pigment, c – light, equally large spots as the rest of imperfectly preserved, originally continuous bands; × 2.2 (a, b), × 2 (c).

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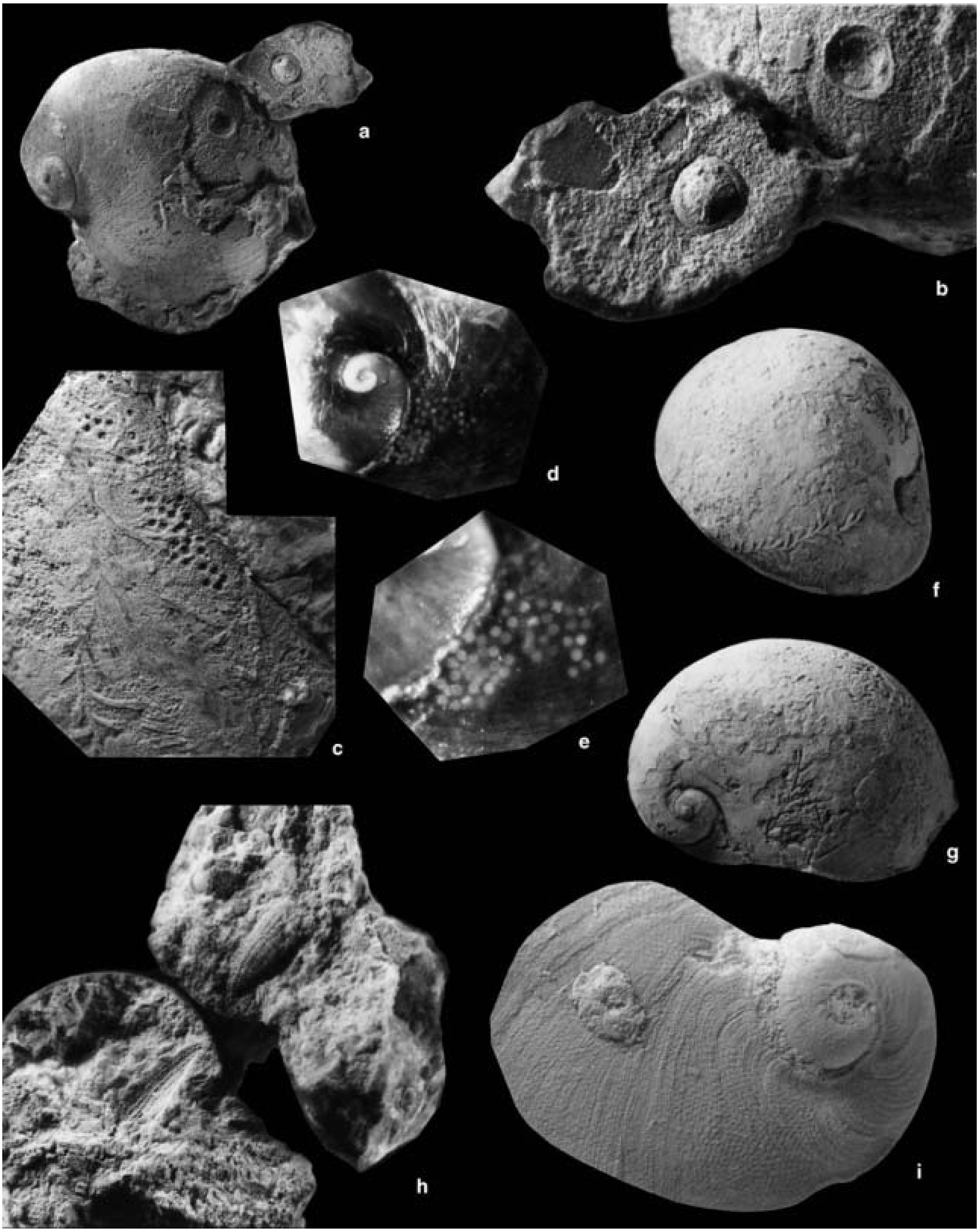

Fig. 8. *Praenatica gregaria*, whitened with ammonium chloride except d and e. a, b – NM L 36 385 (NM), c, f, g – IGP H 295 (IGP CU), d, e – IGP H 232 (IGP CU), h – NM L 36 220 (NM), i – IGP H 222 (IGP CU); anterior (a), detailed (b), partial oblique basal (c), partial apical (d, e, i), oblique apical (f), oblique dorsal (g) and interior (h) views of specimens documenting epizoan fixation; a, b – inarticulate brachiopod *Petrocrania*, c, g, f – cyclostome bryozoan *Hemitrypa linotheras* demonstrably overgrowing both the outer and inner (f – note the exfoliated part) shell surfaces, d, e – accumulation of small spots probably as the consequence of the attachment of an unknown sessile organism, i – trace of growth of an undetermined bryozoan and a small crinoid holdfast; × 0.8 (a), × 2 (b, d), × 3.2 (c, i), × 4 (e), × 1.3 (f, g), × 1.9 (h).

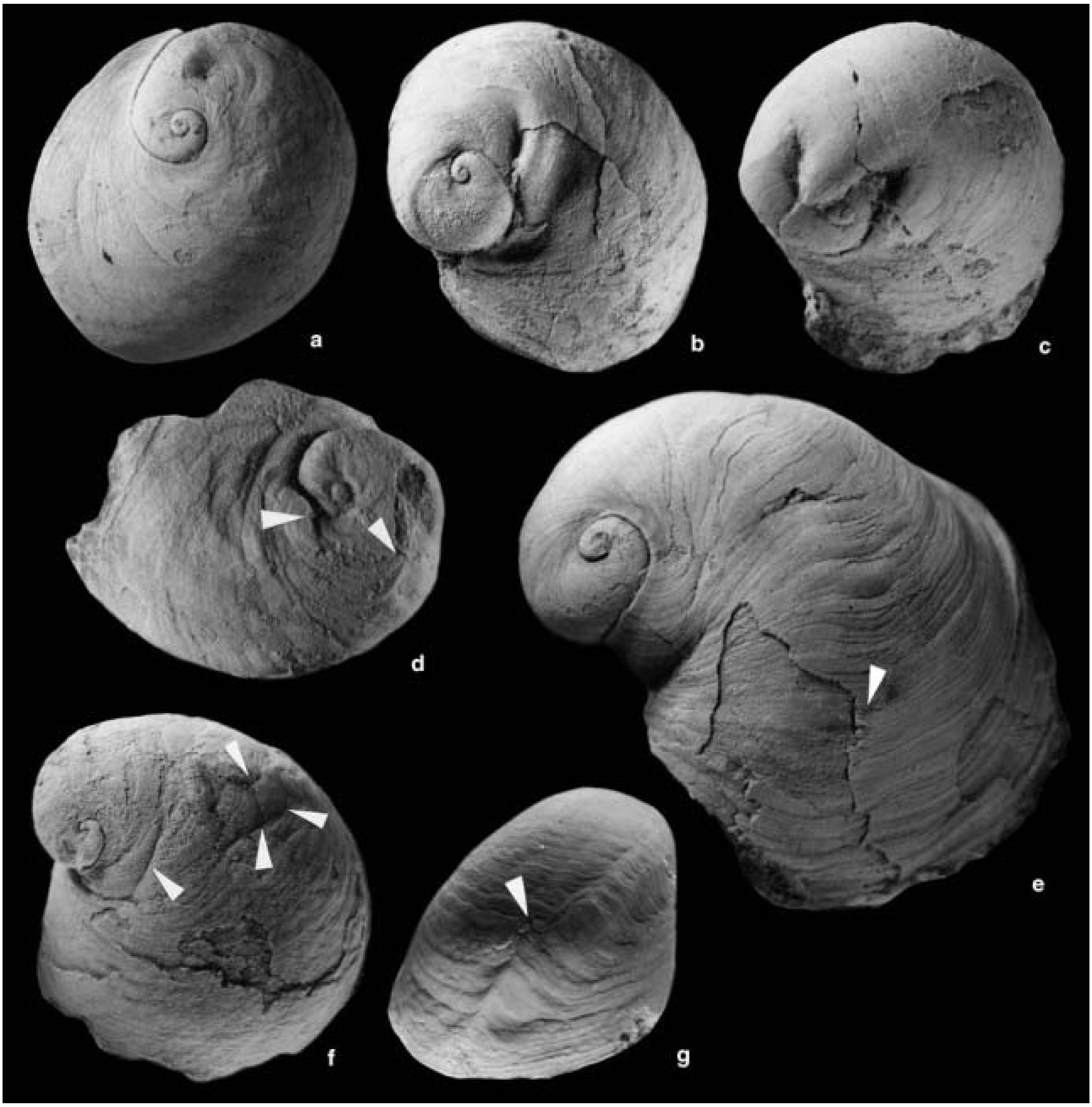

Fig. 9. *Praenatica gregaria*, whitened with ammonium chloride. a – IPG H 174 (IPG CU), b – NM L 36 297 (NM), c – NM L 36 164 (NM), d – p 6 148 C (CGS), e – IPG K 20 (IGP CU), f – NM L 36 307 (NM), g – NM L 12 332 (NM); apical (a, c, d), oblique apical (b, f), anterior (e) and dorsal (g) views of specimens bearing marks of shell breakage; a – probably postmortem fracture, maybe a consequence of a sharp clash in the surf, b–g – various strong but repaired fractures (probably resulting of failed predation). Note g – new shell, growing from below the fracture, bears differently oriented growth lines. At place (arrowed), where the palial margin was injured, a characteristic feather-like sculpture originated; × 1.8 (a, b), × 2 (c), × 2.5 (d), × 2.2 (e), × 1.3 (f), × 1.7 (g).

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Handling editor: Zdeněk Kukal