BASTERIA, 52: 77-100, 1988

On morphology, function and taxonomic importance of the shell ribs in Clausiliidae (Mollusca: Gastropoda Pulmonata), with special reference to those in Albinaria

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In Clausiliidae, Urocoptidae and a few other groups the shell ribs are not solid, but hollow and provided with complicated structures inside. These structures are described and illustrated. Their presence may be correlated with a certain habitat, at least within a polymorphic species. Several physical consequences of ribs are suggested and some are experimentally tested. Especially shell weight and strength, surface water adhesion, shell permeability and warming up after insolation are dealt with. The possible adaptive value is discussed.

Key words: Gastropoda Pulmonata, Clausiliidae, *Albinaria*, shell ribs, shell structure, shell formation, adaptation, taxonomy.

CONTENTS

1. INTRODUCTION

Gastropod shells are often provided with ribs (costae), which are transverse elevations on the shell surface, different from e.g. the remains of former apertural lips (varices) and growth-lines. The relatively prominent and more or less regularly spaced sculptural elements treated as ribs in the present article, are genetically determined. They differ from occasionally thickened growth-lines, which may develop due to climatic circumstances related to shell-growth.

Generally ribs are thought of as solid structures. However, in all the shells of Clausiliidae that were investigated, belonging to various species, the ribs proved to be hollow and often provided with more or less complicated membranous septa with adhering crystalline structures. In the present paper a morphological analysis of these special ribs is given, together with some considerations concerning their development, taxonomical interpretability and imaginable functional relevance.

Among the Clausiliidae many (sub)species are characterized by ribbed shells. The taxa belonging to the Mediterranean Alopiinae exemplify the wide range of variation in shell sculpture, between totally smooth and very prominently ribbed, independently in several genera and sometimes even in a single species. Especially within the speciose genus *Albinaria* Vest, 1867, represented in Greece and neighboring countries, this variation is evident. The epitome in ribbing are subspecies of *A. praeclara* (Pfeiffer, 1853), *A. adrianae* Gittenberger, 1979 and *A. olivieri* (Roth, 1839).

While discussing the transverse shell sculpture in Clausiliidae, the following terminology has been used: smooth [without any sculpture discernible with the naked eye], weakly sculptured [e.g. *A. contaminata incommoda* (O. Boettger, 1878) (fig. 1)], finely ribbed [e.g. *A. senilis* (Rossmässler, 1836) (fig. 2)], moderately ribbed [e.g. *A. praeclara drakakisi* (Maltzan, 1884) (fig. 3)], prominently ribbed [e.g. *A. adrianae dubia* Gittenberger, 1979 (fig. 4)], and very prominently ribbed [e.g. *A. a. adrianae* (fig. 5) and *A. p. praeclara* (fig. 5a)]. The various qualitative categories can only subjectively be distinguished from each other; exact quantitative measurements proved to be impossible in practice.

Only in species characterized by relatively large, prominently ribbed shells [e.g. *A. adrianae*, *Chilostoma cingulata gobanzi* (Frauenfeld, 1867)] it proved to be possible to determine unequivocally with the naked eye whether or not the ribs were hollow. Usually a microscope was needed. To study details of the rib-structure, a JEOL-840A scanning electron microscope (SEM) was used. Unless stated otherwise, all SEM-photographs have been made of gold-coated specimens kept in the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

In order to minimize uncontrolled damage to internal structures, shell fragments were used, that had never been cleaned ultrasonically. However, to investigate the internal structure of a rib, its roof at least had to be partly removed, inevitably resulting in artefacts. At sites with "natural" fractures many morphological details proved to be destroyed, evidently because of their fragility.

The observations concerning *Albinaria* species of Kephallinía have been made by both authors, independently; those on species of the island of Crete originate from Ms. E.C. Flach, Mr. N. Reitsma and the second author, partly independently.

2. MATERIAL

The material for study, listed below, was obtained from the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands. In the text the various samples may be

Figs. 1-5. Transverse sculpture in *Albinaria* (sub)species; 3 & 5a and 4 & 5 are conspecific, 5 and 5a are not. 1, weakly sculptured *A. contaminata incommoda* (O. Boettger) (sample 7); 2, finely ribbed *A. s. senilis* (Rossmässler) (sample 21): 3, moderately ribbed *A. praeclara drakakisi* (Maltzan) (sample 17); 4, prominently ribbed *A. adrianae dubia* Gittenberger (sample 4); 5, 5a, very prominently ribbed *A. a. adrianae* Gittenberger [5] (sample 1) and *A. p. praeclara* (L. Pfeiffer) [5a] (sample 15). All figures c. × 3. Photographs by G.


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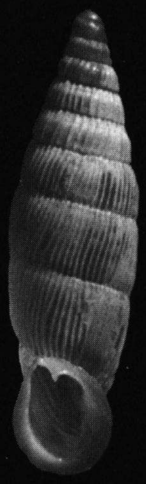
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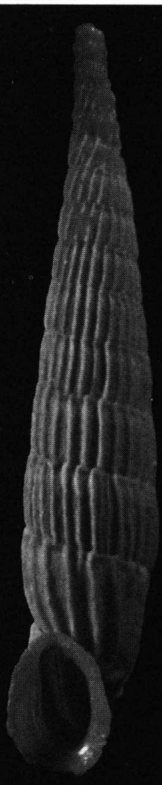
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referred to by means of the station numbers preceding the localities. Unless stated otherwise, the localities are situated in Greece.

2.1. Species with shells with hollow ribs

Clausiliidae

Albinaria a. adrianae Gittenberger; (1) Poros, Kephallinía, 25 m alt.; (2) Poros, Kephallinía, 30 m alt.; (3) Poros, Kephallinía, 50 m alt.

A. adrianae dubia Gittenberger; (4) Ag. Georgios, N. of Pastra, Kephallinía, 275 m alt.; (5) Atsoupades, NW. of Valerianos, Kephallinía, 260 m alt.; (6) Arginia, Kephallinía, 520 m alt.

A. contaminata incommoda (O. Boettger); (7) Tzanata, W. of Poros, Kephallinía, 130 m alt.; (8) Charakti, NW. of Digaleto, Kephallinía, 485 m alt.

A. idaea (L. Pfeiffer); (9) Kamaras-Nidda, Crete.

A. inflata turgida Wagner; (10) prov. Lasithi, Crete.

A. jonica (L. Pfeiffer); (11) Assos, Kephallinía, 25 m alt.

A. o. olivieri (Roth); (12) Rhodos, Rhodos; Karpathos.

A. olivieri famosa (O. Boettger); (13) Kasos.

A. olivieri oertzeni (O. Boettger); (14) Kasos.

A. p. praeclara (L. Pfeiffer); (15) Ag. Nicolaos, Crete, 50 m alt.; (16) S-side Vroukas, 14 km N. of Ag. Nicolaos, Crete, 250 m alt.

A. praeclara drakakisi (Maltzan); (17) E. of Gournia, 19 km SE. of Ag. Nicolaos, Crete, 10 m alt.; (18) Kalo Horio, S. of Ag. Nicolaos, Crete, 110 m alt.; (19) Sfaka, NE. of Kavousi, Crete, 300 m alt.; (20) Gorge entrance 1 km NE. of Monastiraki, Crete, 120 m alt.

A. s. senilis (Rossmässler); (21) 3.9 km SE. of Argostoli, Kephallinía, 10 m alt.

A. senilis flavescens (O. Boettger); (22) 7 km W. of Lixouri, Kephallinía, 200 m alt.

A. sublamellosa obliterata (O. Boettger); (23) Crete.

A. sublamellosa ssp.; (24) Sfakia, Crete.

A. teres nordsiecki Zilch; (25) Gorge entrance 1 km NE. of Monastiraki, Crete, 120 m alt.

A. teres extensa (L. Pfeiffer); (25a) Prov. Lasithi, Crete.

Cristataria s. strangulata (L. Pfeiffer); (26) Nahr el Kelb, Libanon.

C. strangulata calopleura (Westerlund) [figured in Nordsieck (1971: 259), from Hari el Mir, Libanon].

Isabellaria haessleini (Fauer); (27) Niata, Prov. Lakonia, Peloponnisos, 250 m alt.

Clausilia dubia grimmeri (L. Pfeiffer); (28) Deutsch-Feistritz, Steiermark, Austria.

C. dubia otvinensis Gallenstein; (29) Otvinskogel, Kärnten, Austria.

Charpentieria (Itala) stenzii letochana (Gredler); (30) Schönleitental, Mte. Cristallo, Belluno, Italy, 1500 m alt.

Muticaria macrostoma scalaris (L. Pfeiffer); (31) 2.5 km SE. of Mellicha, Malta.

Ruthenica filograna (Rossmässler); (32) Tolmin, Slovenija, Jugoslavia, 250 m alt.

Agathylla lamellosa (Wagner); (33) Lokrum, Hrvatska, Jugoslavia.

Sericata albicosta (O. Boettger); (34) Olympus, Prov. Pieria, Thessalia, 1500 m alt.

Macrogastra plicatula (Draparnaud); (35) Nièvre, St.-Saulge, France, 300 m alt.

Andinia taczanowskii (Lubomirski); (36) Bambamarca, Cerro Machaipungo, Dept. Cajamarca, Peru, 3000 m alt.

Temesa a. albocostata Weyrauch; (37) Alis, Dept. Lima, Peru, 3300 m alt.

Urocoptidae

Gongylostoma (Callonia) lowei (Torre); (38) Sierra de Guane, Prov. Pinar del Rio, Cuba.

G. (C.) ellioti (Poey); (39) Mendoza, Prov. Pinar del Rio, Cuba.

G. (C.) dautzenbergiana (Crosse); (40) Cuba.

G. (?) *blainiana* (L. Pfeiffer); (41) Cuba.

Idiostemma uncata (L. Pfeiffer); (42) Cuba.

Oleacinidae

Varicella acuticostata horrida Pilsbry; (43) Cuba.

2.2. Species with shells with massive ribs

Chondrinidae
Chondrina centralis (Fagot); (44) Laruns, Pyrénées-Atlantiques, France, 1400 m alt.

Helicidae
Hemicycla plicaria (Lamarck); (45) Tenerife, Canary Is., Spain.
Helicopsis cyclodon (Webb & Berthelot); (46) Gran Canaria, Canary Is., Spain.
Cochlicella (?) *liebetruti* (Albers); (47) Cyprus.
Chilostoma cingulatum gobanzi (Frauenfeld); (48) Valle Toscolano, W. of Gargnano S. Garda, Brescia Italy, 500 m alt.

Endodontidae
Foxidonta stevensoni Clench; (49) Fin. Mala, Salomon Is.

Cerionidae
Cerion marielinum Pilsbry; (50) Lighthouse Mariel, Cuba, 450 m alt.
C. uva (L.); (51) Malmok, Bonaire, The Netherlands Antilles.
C. watlingense Dall; (52) N. of Cockburn Town, Watling, Bahama Is.

Bulimulidae
Bostryx eremothauma (Pilsbry); (53) Chile.
B. lizarasoae Weyrauch; (54) Vechaycoto, Dept. Huanuco, Peru, 2000 m alt.
Naesiotus fernandezae Weyrauch; (55) Balsas, Rio Marañon, Peru, 850 m alt.
Scutalus costulatus Weyrauch; (56) Inca Parca, 34 km N. of Junin, Dept. Junin, Peru, 4200 m alt.

Streptaxidae
Gonospira callifera Morelet; (57) Curepipe, Mauritius, 600 m alt.
Gulella pretiosa nyiroensis (Preston); (58) W.-rim Lake Paradise, Mt. Marsabit, Kenya, 1500 m alt.

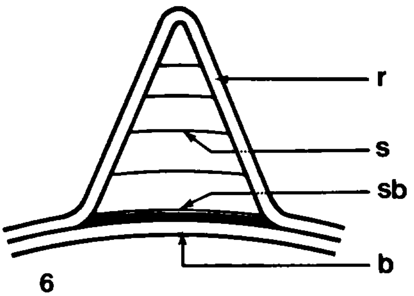
3. MORPHOLOGY OF THE HOLLOW RIBS

3.1. The general structure

The ribs consist of three main parts, viz. (1) the outer roof, (2) the inner base and (3) the interior, which is either empty or provided with complicated structures (figs. 6, 8, 9, 12, 13, 16, 19).

The roof consists of a few layers which are usually not clearly discernible. According to e.g. Cox (1960: I122), the outermost calcareous layer will be covered by the organic periostracum, "at least at some period during growth". In *Albinaria* a periostracum has not been observed, however. Probably because of its fragility and vulnerability it is not persistent. The base of the ribs consists of at least two layers, which often cannot be distinguished properly. The innermost layer is the nacreous one, which is in contact with the soft parts of the snail. Both the roof and the base layers remain discernible also in the shell segments between the ribs, where they are in direct contact (figs. 6, 8).

Within a rib there may be up to six suspended septa, situated more or less parallel to the inner shell surface. In addition there may be one or more septa attached to the rib base or each other, respectively (figs. 6, 9). The septa consist of an organic membrane with calcium carbonate particles (figs. 6, 9-11). Usually such a particle may be observed at both sides of the membrane, as if the septum runs through it (figs. 7A, 10). Sometimes septa are found with particles which are covered by the membrane at one



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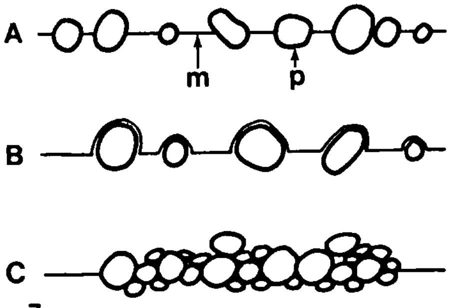

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Figs. 6, 7. Schematic views of a hollow rib. 6, cross-section; 7A-C, details of three types of septa and particles. For explanation see the text. Abbreviations: b, rib-base; i, intercostal segment; m, organic membrane; p, particle; r, roof; s, septum; sb, several septa fused on the rib-base; t, thread-like elevations (microsculpture) on the shell surface.

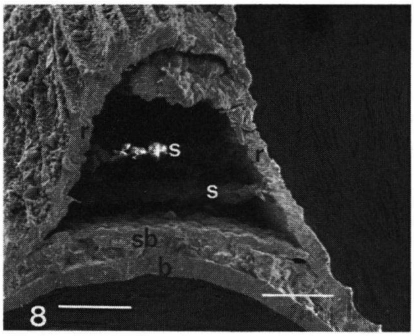
side (figs. 7B, 11). The organic membrane can be (1) provided with only a few particles, which do not touch (fig. 7A, B), (2) completely covered with particles, which remain individually recognizable (figs. 9, 12), (3) covered with a layer of fused particles (fig. 16), or (4) covered with a basal layer of fused particles and additional ones on both sides (figs. 7C, 13, 14). These four main types cannot be clearly distinguished. They might exemplify stages in a process, which does not run equally far in every case. In the types 3 and 4 the septa have become rigid plates and the membranous parts cannot be seen anymore.

Many incomplete, perhaps ruptured membranes have been observed which are not covered with particles, as well as threads (fig. 20), which either connect isolated parts of a septum or run between particles belonging to one or more septa.

In the majority of clausiliid shells there are two types of ribs, viz. the cervical ribs on the neck or cervix [after Rossmässler (1835: 34) and Pilsbry (1920: vii)] and the other ones. Often the former are more prominent and more widely spaced than the latter. If so, the cervical ribs differ additionally from the other ones by the presence of more internal septa, which are usually also more rigid (figs. 15, 16) (see above, stages 3 and 4). Thus both the number and the structure of the septa are related to the absolute size of the ribs. This is underlined by the fact that there are no obvious internal differences between cervical and other ribs if these are not differentiated externally (as e.g. in *A. a. adrianae*).

Generally the shape and size of the ribs are carefully described in (sub)species diagnoses. Differences in these characters are often a major argument for recognizing new taxa. In contrast with this variation, the internal rib morphology is remarkably unspecific and only correlated with the absolute rib size.

Figs. 8-11. Details of hollow ribs in *A. a. adrianae* Gittenberger (8) (sample 1) and *A. a. dubia* Gittenberger (9-11) (sample 4). 8, 9, cross-sections; 10, 11, details of septa. Scale bars 100 μm (8) or 10 μm (9-11). Abbreviations: see legends to figs. 6, 7. Photographs by K.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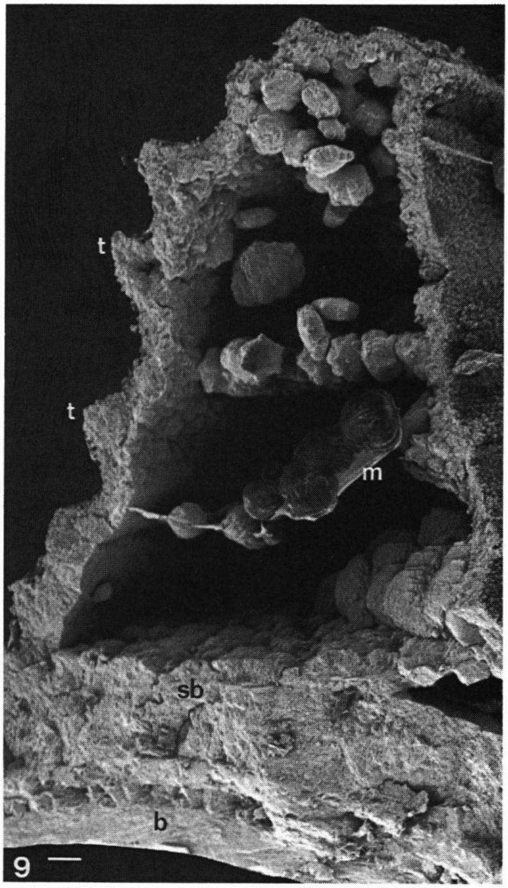
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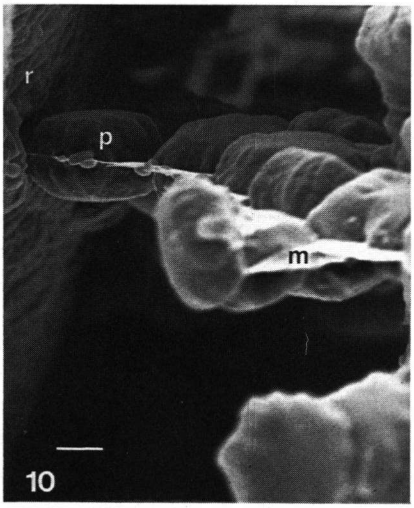
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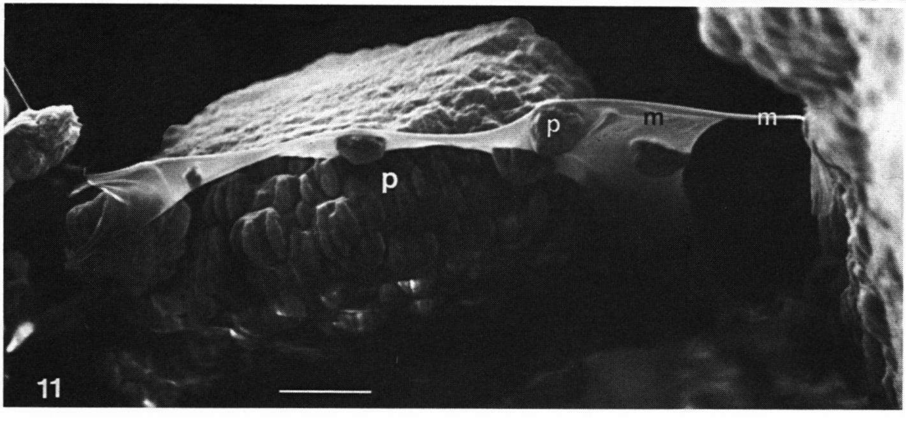
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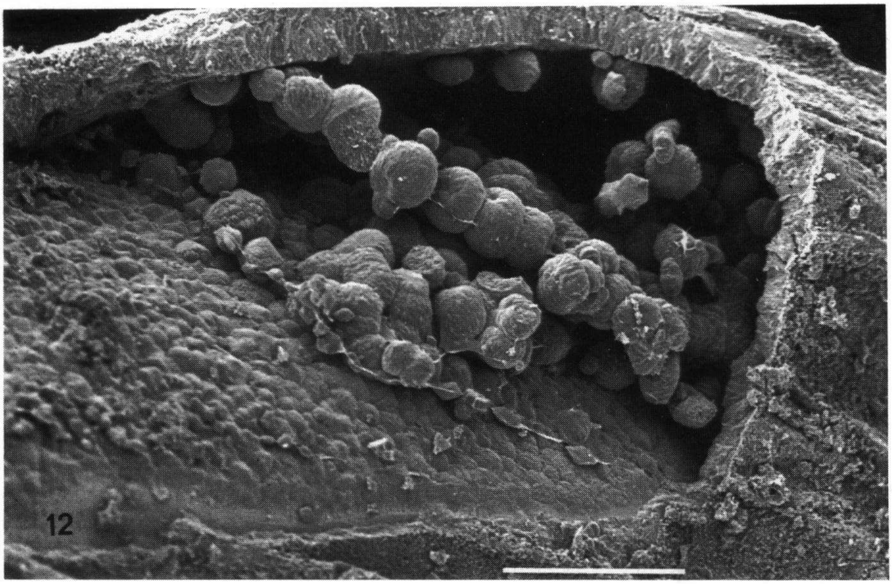


Fig. 12. Cross-section of a rib in *A. a. adrianae* Gittenberger (sample 1), with a septum provided with many individual sub-spherical particles (type 2). Scale bar 100 µm. Photograph by K.

3.2. The septal particles

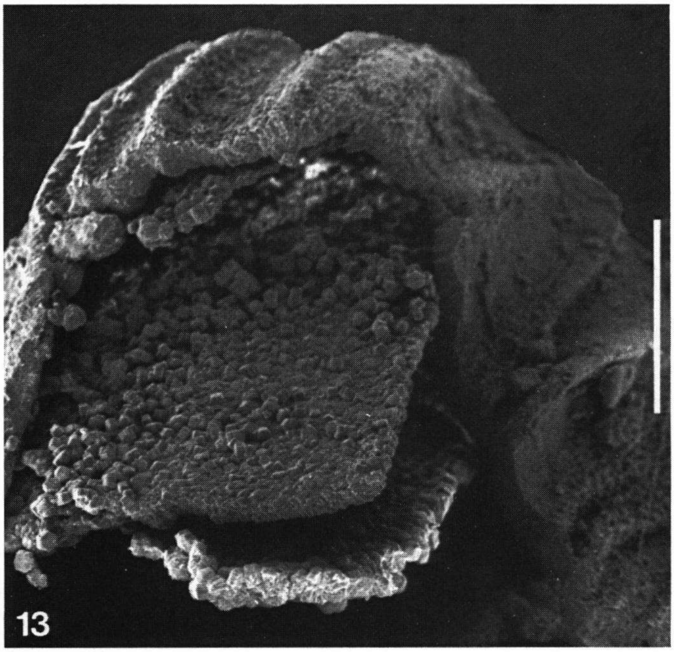
Clusters of crystals are indicated by the neutral term particles, regardless of their composition. Several types of particles are more or less arbitrarily recognizable. They should probably at least partly be interpreted as stages in a process of growing. There are (1) sub-spherical particles, (2) cubical or hexagonal particles, and (3) particles composed of blade-shaped crystals.

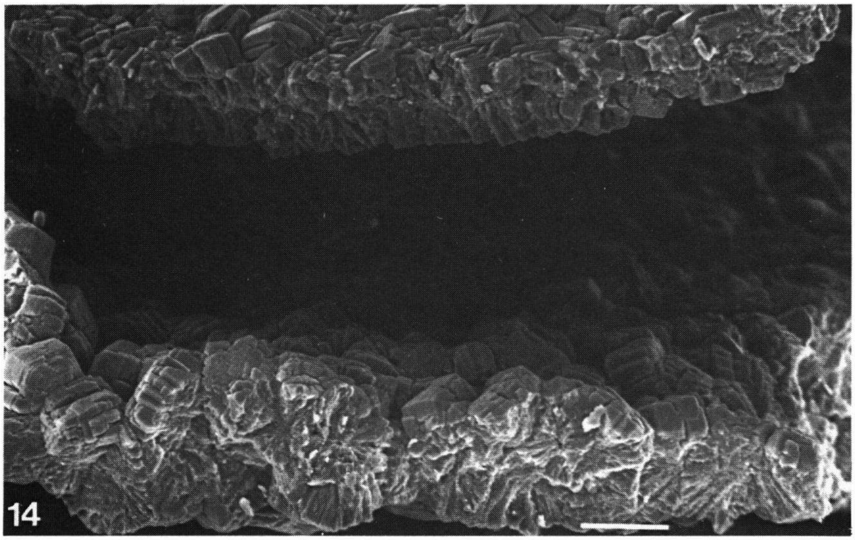
The more or less spherical particles are composed of bar- or grain-like crystals (fig. 17), which vary in length and shape. In a presumed developmental sequence, the particles may be arranged as discoidal (fig. 10) (often somewhat star-like), cylindrical, and sub-spherical (fig. 17). Their axial poles are flattened or slightly concave. The particles might start their development from an initial crystal-bar, deposited in the organic membrane. Additional bars are clustered against the longitudinal sides of this central structure, resulting in discoidal particles; when crystals are also deposited on the axial sides of the discs, the other shapes will eventually be formed.

The cubical or hexagonal particles, occurring in isolation or mixed with other types, might be only a special category among the initial stages of the previous ones (fig. 18).

Quite remarkable are the sub-spherical particles composed of clusters of crystals which are similar to those formed in gypsum. These are found mainly in the rib-ends or on the inside of the roof and are always mixed with other types (figs. 19, 20).

The calcified parts of gastropod shells are usually formed in a very orderly way, resulting in the wealth of specific details used by taxonomists for the identification of





Figs. 13, 14. Cross-section of a rib in *A. a. adrianae* Gittenberger (sample 1), with a detail, showing septa forming rigid plates (type 4). Scale bars 100 µm and 10 µm, respectively. Photographs by K.

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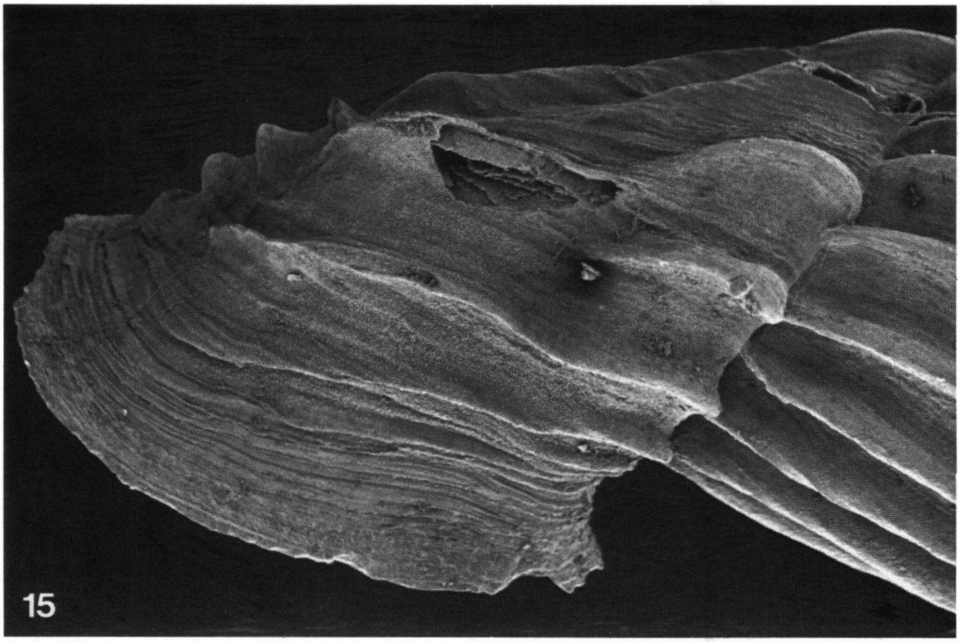

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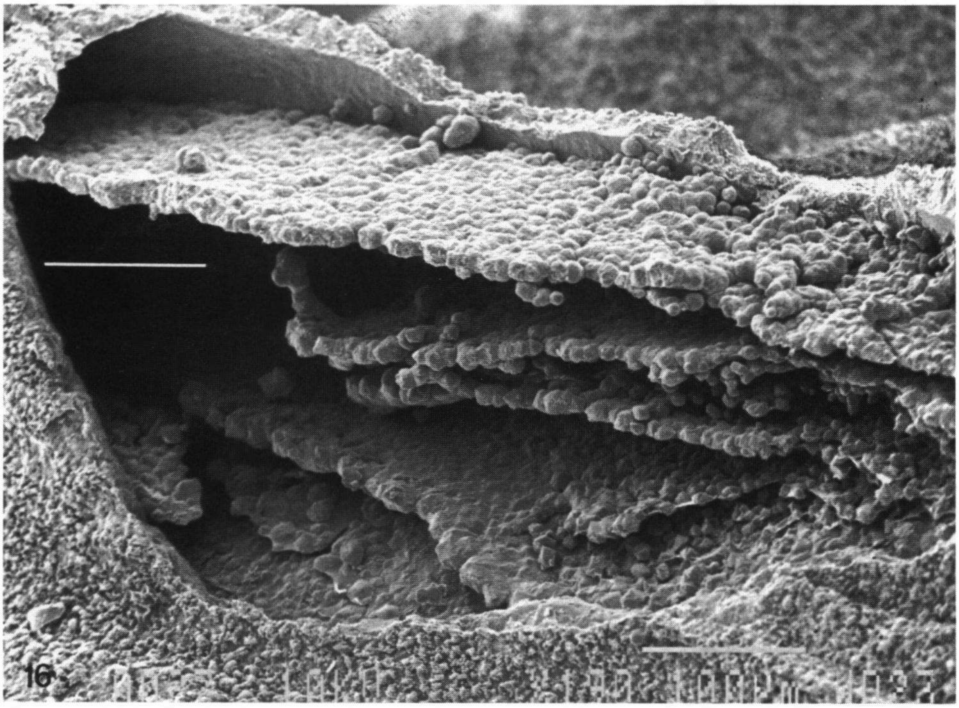
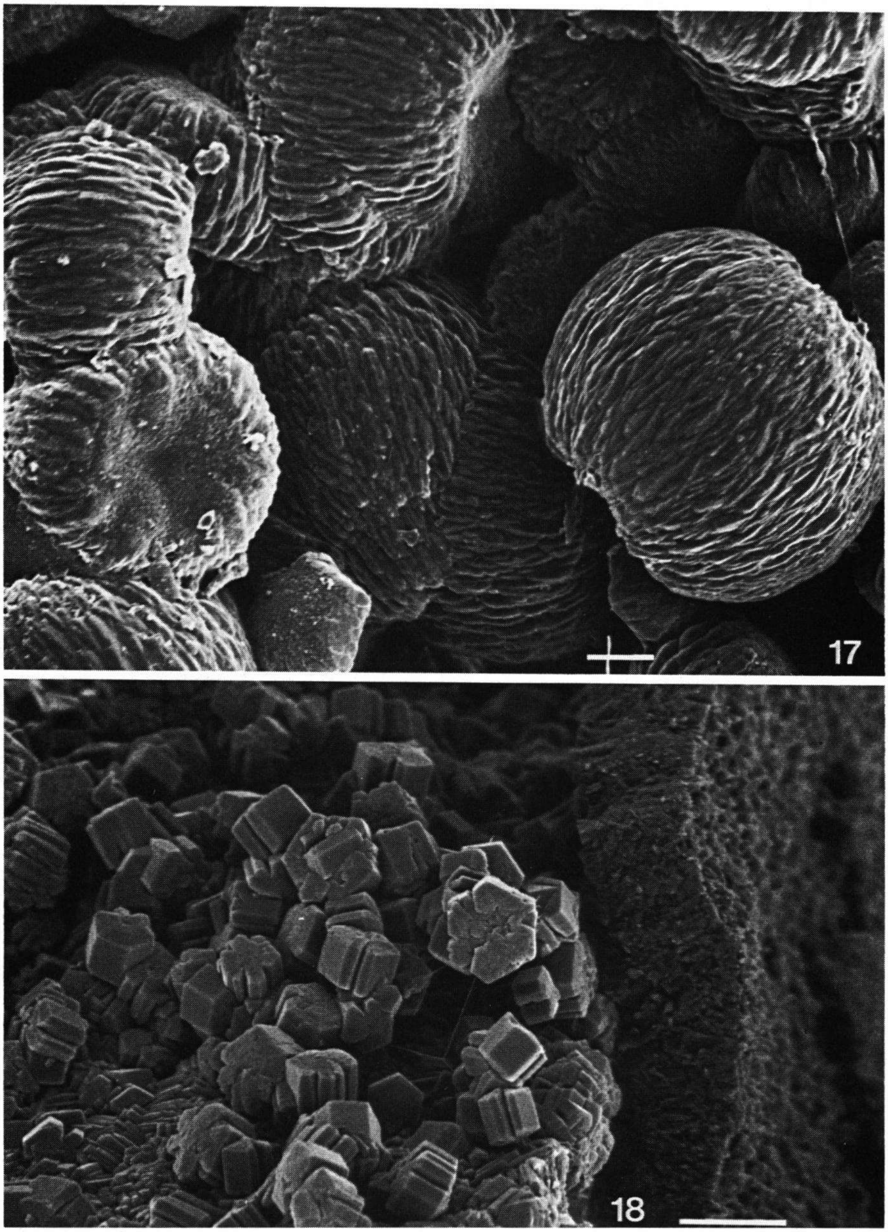
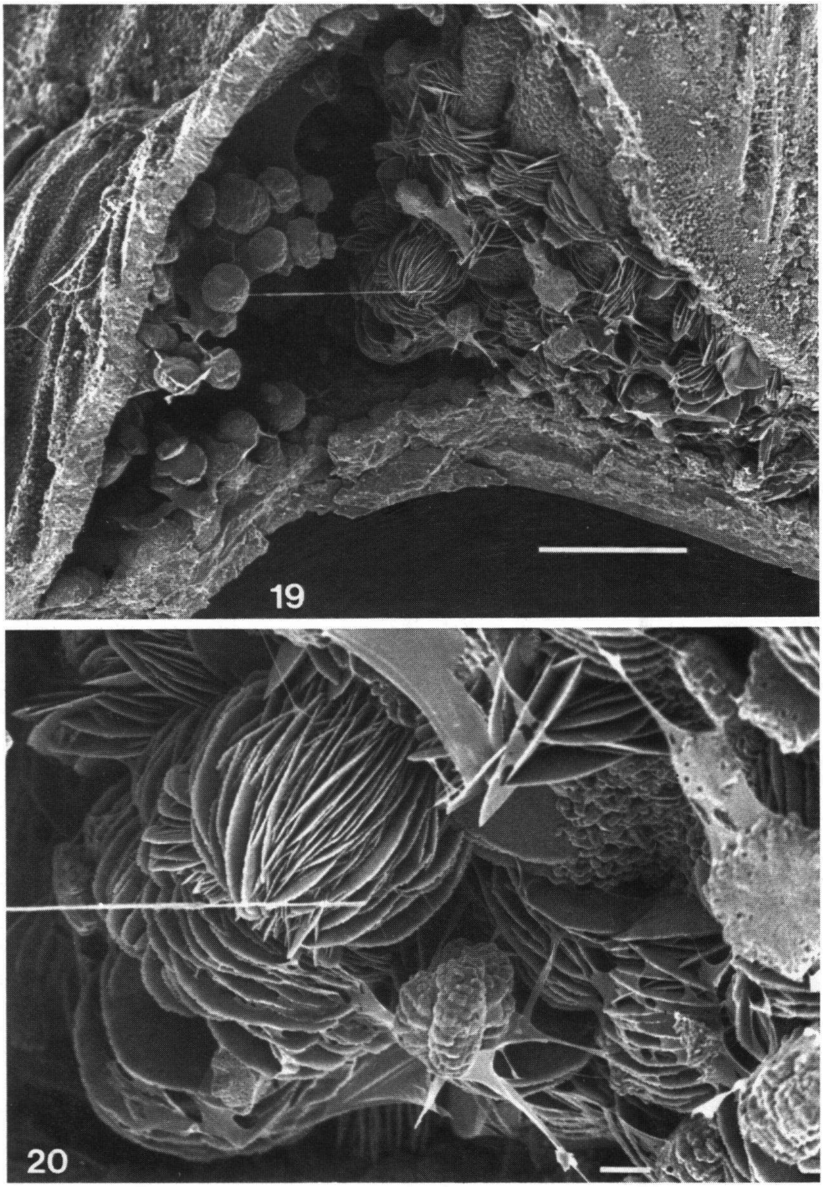


Figs. 15, 16. The cervical part of the shell in *A. sublamellosa obliterata* (O. Boettger) (sample 23), with a detail of a rib which has been opened, showing some septa composed by a layer of fused particles (type 3). Scale bar in fig. 16, 100 µm. Photographs by K.



Figs. 17, 18. Sub-spherical [17] and hexagonal [18] septal particles in *A. a. adrianae* Gittenberger (sample 1). Scale bars 10 µm. Photographs by K.



Figs. 19, 20. Cross-section of a rib in *A. a. adrianae* Gittenberger (sample 1), near its adapical end, showing sub-spherical and gypsum-like particles, with a detail of the latter ones. Scale bars 100 µm and 10 µm, respectively. Photographs by K.

species. The higgledy-piggledy arrangement of the septal particles is quite different. Evidently their axial orientation, probably that of the initial crystal-bar, is largely independent of the plane of the organic membrane. If particles are added on top of those already formed, as in the most rigid septa, this occurs without any regular pattern.

3.3. Chemical composition of the crystals

Most probably the crystals that build the particles are composed of aragonite. The hexagonal and gypsum-like forms, as well as the bar-like subunits of the sub-spherical particles, are most frequently seen in aragonite. This is also regarded in general as the most common crystal-type in pulmonate shells (Bøggild, 1930: 240). However, there is no absolute certainty while judging on only these data. All the registered crystal-forms do also exist as calcite pseudomorphs, albeit far less common (Zwaan, personal communication).

4. DEVELOPMENT OF THE RIBS

From only the SEM-photographs it is far from clear how the septa inside the ribs are actually formed. Some possible steps in this process may be suggested, however.

The width of the shell segments between the individual ribs is of about the same magnitude as the width of the ribs themselves. The formation of a complicated, hollow rib will take more time than that of a connecting segment. Nevertheless, nearly all of the juvenile individuals collected randomly for study (71 of 80), had shells provided with apertural borders showing that rib formation was not going on. This suggests that rib formation is usually finished quickly, once it has been started, probably to avoid structural damage. This would reduce the probability that a specimen is collected while a rib is formed. A factor that is of importance to explain the rarity of unfinished ribs in the studied material, might be that shell-growth is concentrated in certain parts of the seasons, e.g. in the wet winter months. Our material was collected during the periods 1-12 November and 16 March-26 May.

Formation of the roof, the septa inside and the bottom plate of a rib are different steps. Ribs do run parallel with the growth-lines or cross them. Specimens of the former category (*A. adrianae*) could be studied, in which the roof was almost finished, or just completed, without either septa or a bottom plate being formed (fig. 21A). In shells representing the latter group (*A. adrianae* [fig. 5a]), specimens with partly developed ribs were seen, in which the roof was accompanied by septa and a bottom plate only in its uppermost part. It can be assumed that after the roof is (partly) formed, a free hanging organic membrane is attached deep inside the ridge of the future rib.

Additional membranes may follow (fig. 21B). Then the formation of the particles on the membrane will start, the initial ones with their centers of gravity on the level of the membrane; on top of these additional particles may be deposited (see before). A final step in rib formation might be the construction of its base, or the development of adhering septa on the base (fig. 21C).

Several authors have published SEM-photographs to illustrate molluscan shell formation. Studying shell repair, Saleuddin (1979: 75, fig. 47) and Wilbur (1973: 17, 18, 20, figs. 5, 6) figured structures, in *Helix* and *Otala* (Gastropoda Pulmonata: Helicidae), which are strikingly similar to the septal particles discussed above. Wilbur (1964: 276) found similar particles in *Elliptio* (Bivalvia: Unionidae). After experimen-

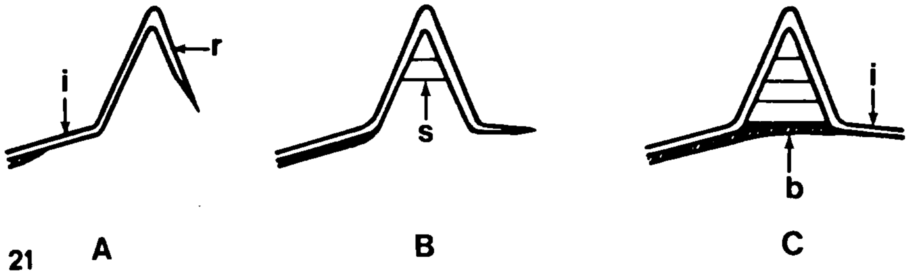


Fig. 21A-C. Schematic views of cross-sections of a developing rib in *Albinaria*, showing subsequent stages of development (from A to B). Abbreviations: see legends to figs. 6, 7.

tal removal of small parts of the shell, these authors observed the formation of an organic membrane on which crystals started to grow, resulting in cubical and sub-spherical particles. Normal shell-growth starts in a similar way with an organic membrane on which crystallization takes place (Wilbur, 1973: 19-23). Inside the hollow ribs we may observe structures exemplifying phases in the calcification process which occur only temporarily during shell regeneration and normal shell-growth of molluscs.

5. HOLLOW RIBS AND PHYLOGENY

Apart from some remarks in species descriptions (Nordsieck, 1979: 64) and general reviews (Pilsbry, 1903) hollow ribs have received no attention in the literature. Yet, they cannot be considered rare structures. All the clausiliid ribs that were investigated with the SEM proved to be (partly) hollow. Even in fine riblets hollow spots were found, sometimes provided with the characteristic sub-spherical particles. Most probably it is a family character of the Clausiliidae that the transverse elevations of the shell surface that have sufficient prominence to be called ribs, are (partly) hollow.

Shell ribs of representatives of various other pulmonate families have been investigated to find out whether hollow ribs are restricted to the Clausiliidae or not (see above sub "Material"). It turned out that they may also occur at least in Urocoptidae and Oleacinidae. The structure of the ribs in these two families, the arrangement of the septa and the occurrence of sub-spherical particles on an organic membrane, are all largely similar to what has been observed in Clausiliidae. Only the gross structure of the ribs may be somewhat different, i.e. they may have prominent, blunt protrudings, which have often lost the ribroof on top (damage), thus allowing a view into the inside. The septal particles might be less variable in shape than they proved to be in the Clausiliidae, where much more species have been investigated, however. Pilsbry (1903: xiv) considered the urocoptid hollow ribs "the acme of sculptural development". According to his view, the occurrence of hollow ribs in the genera *Holospira* Martens, 1860, *Idiostemma* Pilsbry & Vanatta, 1898, *Tetrentodon* Pilsbry, 1903, *Callonia* Crosse & Fischer, 1870 and *Brachypodella* Beck, 1837, classified with two different subfamilies, is based on convergent evolution, since in each case these taxa are (1903: xvii) "related far more nearly to forms with normal sculpture than to each other". It remains unclear whether he presumed that urocoptid species may also have solid ribs. All the ribbed shells of Urocoptidae studied for the present paper proved to have hollow ribs, suggesting this to be a family character, as it is in the Clausiliidae. The same might apply to the Oleacinidae; for this family, in which heavily sculptured shells are rare, there are data for two (sub)species with conspicuous ribs, viz. *Spiraxis (Dignaxis) mirabilis* (C.B. Adams, 1849) (see Pilsbry, 1907: 16, pl. 1, fig. 3) and *Varicella acuticostata horrida* Pilsbry, 1907, both of them with hollow ribs.

Wind & Wise (1974: figs. 9-10) described the shell-spines in *Guildfordia* Gray, 1850 (Gastropoda Prosobranchia: Turbinidae) as hollow and provided proximally with one or two septa, subdividing the interior into separate cavities. Some of the aragonite structures show similarities with sub-spherical particles on clausiliid septa.

Partly because of the uncertainty with regard to the phylogenetic relations between the higher taxa of the Gastropoda, it remains unclear how frequently hollow ribs have evolved independently. It is still unclear whether the character state in question should be considered the apomorphic or plesiomorphic condition. The occurrence in both Clausiliidae and Urocoptidae could be considered an autapomorphy, i.e. indicative of a common ancestor of these two taxa, which are considered closely related by Schileyko (1979) and Tillier (1985: 167), but not so by Nordsieck (1985: 19). However, hollow ribs do also occur in at least two other families of snails. The Oleacinidae are generally considered far less closely related, whereas the Turbinidae are even classified in another subclassis. Both convergent evolution and symplesiomorphy might be suggested to explain this, meanwhile leaving the possibility open to consider Clausiliidae and Urocoptidae sister-groups, derived from a common ancestor with hollow ribs. The extremely large ribs in a few *Albinaria* species may be considered a result of parallelism. A symplesiomorphic occurrence, implying the former distribution of this character over a wide geographic range and its subsequent disappearance in many independent evolutionary lines, cannot be totally excluded, but seems to be less probable. Apart from the rib characters, there are no additional data supporting the view that an autapomorphic character state is involved (Nordsieck, 1977).

6. HOLLOW RIBS AND HABITAT

Boettger (1932) and Rensch (1932) have published initial studies on the adaptational character of shell ribs and their ecological and geographical distribution in Europe. According to Rensch (1932: 805) the percentage of species characterized by prominently transversely sculptured shells in the western Palaearctic, is highest (37.2%) in the circum-Mediterranean countries, lower (21.1%) in northern and central Europe, and lowest (15.6%) in the alpine region. However, these results cannot be interpreted easily, partly because the taxonomic diversity in the various areas is not taken into account. This diversity is relevant because of the unequal evolutionary potential of various taxa. A single speciose genus with (like *Albinaria*) or without many prominently sculptured species may influence a percentage considerably. Furthermore Rensch lumped a heterogenous group of forms together, not distinguishing genetically determined regular ribs, either hollow or solid, from other kinds of prominent transverse sculpture, like more irregularly spaced thickened growth-lines, which may be formed in relation with climatic circumstances. Unfortunately it has not been indicated clearly how exactly Rensch calculated the various percentages, i.e. what (sub)species were actually counted for a certain category.

Without going into more detail and quite in contrast to Rensch (1932: 805), Boettger (1932: 209) mentioned that strongly ribbed shells are relatively common in the large, geologically young, mountain ranges. His definition of a rib is more similar to the one accepted in the present paper than is that of Rensch.

Gould & Woodruff (1978, 1986), dealing with shell sculpture in *Cerion* Röding, 1798, on islands of the Bahamas, found a strong correlation of geography with morphology. To explain the observed pattern they suggested that at a time of emergent Bahama banks during the Pleistocene the ribbed populations inhabited the coasts and those with a less prominent sculpture the interior of the islands of that period. It might be not simply coincidental that we observed a similar intraspecific variation in *Albinaria* (see below).

Considering the western Palaearctic terrestrial gastropod fauna as a whole, it becomes evident that the occurrence of shell ribs is not concentrated in a single type of habitat. In e.g. the genus *Chondrina* Reichenbach, 1828, with all the 22 species occurring in mountainous parts of western Europe on rock-faces, shells with the most prominent (solid) ribs are found in (1) *C. centralis* (Fagot, 1891), known from the central part of the western Pyrenees, between 1000 and 1700 m altitude, and probably evolved in a glacial refuge, (2) *C. calpica* (Westerlund, 1872), known from southernmost Spain and the opposite part of Morocco, between sea-level and over 1000 m altitude, and (3) *C. lusitanica* (L. Pfeiffer, 1848), from western Portugal, occurring at sea-level and at higher elevations. Other *Chondrina* species, found at various altitudes, have more or less striate or smooth shells. In the Clausiliidae too, prominently ribbed (sub)species may occur in a series of habitats, varying from rocks in very cold alpine valleys, exposed to the North [*Charpentieria stenzii letochana* (Gredler, 1874)], to hot Mediterranean rock-faces just above sea-level, exposed to the South (e.g. several *Albinaria* species).

Because of the confusing results in elucidating a possible relation between shell sculpture and habitat by an approach in which different species, with more or less equal types of shell sculpture, from a vast range, are grouped together and compared ecologically, another strategy was tried, studying a relatively small area and concentrating on the intra- instead of the interspecific variation in shell sculpture.

The very prominently ribbed *A. a. adrianae* (fig. 5) occurs near the eastern Kephallinian port Poros, exclusively on high rock-faces, starting slightly above sea-level, both in a narrow valley and facing the sea (Gittenberger, 1979). *A. adrianae dubia* (fig. 4), the prominently ribbed adjoining subspecies, which is also restricted to open rock-faces, lives in the hills which flank the southern slopes of the Oros (= Mtn.) Aenos, and has never been found below 200 m. The populations of the two subspecies remain apart for a few kilometers. In their combined range *A. contaminata incommoda* (fig. 1) is found among limestone rocks on the bottom.

A. p. praeclara (fig. 5a), with very prominently ribbed shells, occurs in coastal areas near Ag. Nikolaos on E. Crete. West of Ag. Nikolaos this subspecies may be found both on open rock-faces and among limestone rocks on the bottom, without any accompanying *Albinaria* species. North of the city, where large quantities of smooth-shelled *A. moreletiana* (O. Boettger, 1878) dominate the open rock-faces, *A. p. praeclara* is a strict bottom dweller (Gittenberger, unpublished data). The adjoining *A. p. drakakisi* (fig. 3) with shells with only moderately prominent ribs, is linked to the nominate subspecies by a narrow zone of intermediate forms. Generally, but not exclusively, it is found at higher altitudes in the hills or mountains. Surprisingly some isolated populations of *A. p. praeclara* were found at high altitudes, separated from its main range at lower altitudes by populations of *A. p. drakakisi* (after Flach & Reitsma, unpublished data). It can be hypothesized that this is a secondary pattern, resulting from an expansion of the range of the latter subspecies into the once continuous range of the former one. This would imply that *A. p. praeclara* has an inferior fitness at higher altitudes.

A very prominently ribbed, still undescribed subspecies of *A. sublamellosa* (O. Boettger, 1883) (Wiese, in litt., 1987), lives near the coast in western Crete, while moderately ribbed *A. s. sublamellosa* inhabits the mountains above Sfakion.

Among the many forms of *A. teres* (Olivier, 1801), inhabiting the coastal area and higher zones in eastern Crete, as well as the surrounding islets, *A. t. manselli* (O. Boettger, 1883), is characterized by shells with prominent ribs (Pfeiffer, 1956: pl. 7 fig. 60). The other subspecies have (much) less conspicuously ribbed shells. *A. t. manselli* is only known from the very small (and low) Kavalli islets opposite SE. Crete.

Pfeiffer (1956: 102, 105) has clearly described the occurrence of both *A. olivieri famosa* (O. Boettger, 1889) (see Pfeiffer, 1956: pl. 8 figs. 71-74) and *A. o. olivieri* on the islands of Kasos and Scarpantos. On Kasos *A. olivieri famosa* is represented from the seaside up to about 100 m altitude, on a hot, rocky and sandy slope with a very poor vegetation; on the much cooler rock-faces of an adjoining narrow cleft, situated at a higher altitude, *A. o. olivieri* is found. Pfeiffer emphasized that heavy rains will regularly wash specimens of the latter form into the area of the former one, surprisingly without any observable effect on their ranges, which prove to be sharply delimitated. From Scarpantos a very similar situation is reported. *A. o. famosa*, the subspecies occurring at low elevations, on the bottom in a hot habitat, has prominently ribbed shells, whereas *A. o. olivieri* has shells which are much less conspicuously sculptured. The two taxa are conspecific according to Zilch (1977: 339), but not so after Pfeiffer (1956). The exact distribution of the very prominently ribbed *A. o. oertzeni* (O. Boettger, 1889) (see Pfeiffer, 1956: pl. 8 fig. 75), also reported from the island of Kasos, is still unknown; one might predict that this form will be found somewhere in the coastal area. Another low-altitude island form of *A. olivieri* is the (very) prominently ribbed *A. o. camura* (O. Boettger, 1889) from the island of Armathia, where it occurs with *A. o. famosa* (after Zilch, 1977: 339).

The most prominently ribbed subspecies that have been studied have relatively small ranges within the species to which they belong. This suggests that their optimal habitats do also occur only (very) locally. Evidently, the presence of (very) prominent ribs generally reduces the possibility to inhabit a large range, probably because among the *Albinaria* species it results in optimal fitness in only an extreme, very localized habitat. It can be considered a general rule that if a subspecies with (very) prominent ribs exists next to conspecific subspecies without them, the former taxon will be found at the lowest altitudes.

Since there is an intraspecific correlation between rib-prominence and altitudinal distribution or coastal proximity, it is logical to attribute an adaptive value to rib-size. Conspicuously convergent evolution (figs. 5, 5a) points in the same direction. The exact mechanism behind this is still far from clear, but some preliminary notes concerning certain consequences of (prominent) ribs can be presented.

7. PHYSICAL CONSEQUENCES AND BIOLOGICAL RELEVANCE OF SHELL RIBS

It is obvious that differences in shell sculpture, i.e. smooth versus prominently ribbed, may have physical consequences for the animals inside these shells. Big ribs may considerably enlarge the shell surface. They will have mechanical consequences and influence e.g. the air turbulence in the micro-environment and the reflection of radiation. Some effects of ribs could be demonstrated and measured experimentally. Undamaged shells of various (sub)species were used for comparison. (The consequences of an experimental removal of ribs are not yet described).

Most certainly in *Albinaria* shell weight and strength, i.e. the resistence against fatal damage, are important, as well as surface water adhesion and permeability of the shell wall. The snails live in a rocky environment with occasional heavy rain showers which may wash them away more or less suddenly. Most of the year the environment will be dry and (very) warm and desiccation will be a most serious threat. In many *Albinaria* species the animals do not hide, but expose themselves freely to the open air, remaining inactive for long periods. Detailed information as to the actual length of these periods, based on field observations, is lacking. Doing so they appear to be vulnerable with respect to predators (very poorly known) and water-loss because of insolation, but on the other hand they get most easily wet and may optimally profit from relatively short rain showers. As can be frequently observed during field work, such rains often have hardly any effect in more sheltered places, which may remain dry as will the creatures hidden there.

The various consequences of being prominently sculptured will result in morphological compromises, balanced by factors within the niches occupied by the subspecies in question. Some of these possible consequences are mentioned below, with a few preliminary results of illustrative experiments. In several cases the question remains, whether the magnitude of the differences observed between more or less prominently sculptured shells, could be relevant for their owners in borderline situations.

7.1. Shell weight and strength

In a classical experiment, Boettger (1932) demonstrated most convincingly that in the helicid species *Chilostoma cingulata* (Studer, 1820) specimens provided with prominent ribs (*C. c. gobanzi*) can be artificially broken less easily than shells of equal shape, size and weight, but without any ribs, found in an adjoining subspecies [*C. c. colubrina* (Cristofori & Jan, 1832)]. At least with the solid ribs in *C. c. gobanzi*, low weight and high strength can be combined. This is an advantageous combination with respect to potential shell damage. Nevertheless, in *C. cingulata*, living in a rocky, mountainous habitat, where the snails may easily tumble down or get hit by rocks, prominent ribs are found in only one of the subspecies, which inhabits a very small section of the total species range. In the smooth *C. c. colubrina* overall shell thickness may be such that the shells are even stronger than equally sized, but much lighter shells of *C. c. gobanzi*.

In *Albinaria*, prominently ribbed specimens may be lighter than finely ribbed or smooth ones of a comparable size (table 1). The second factor, shell strength, cannot be measured as in *Chilostoma cingulata*, because the ribs are hollow and start breaking before the entire shell is seriously damaged. Obviously this kind of ribs acts as a buffer. In nature, many *Albinaria* shells have one or more ribs partly broken, indicating former

subspec.	height (mm)	width (mm)	cone (mm^2)	weight (mg)	weight /cone	n
1	14.73	3.30	86.12	38.39	0.44	30
2	12.63	2.79	62.59	24.69	0.39	22
3	15.57	4.50	127.91	65.73	0.51	38
4	19.68	4.20	144.65	81.86	0.56	5
5	18.28	3.41	107.59	49.56	0.47	5

Table 1. Measurements and weights of *Albinaria* shells.

accidents, which proved to be not really harmfull for the animal because the interior of the shell was left intact.

In several specimens belonging to five *Albinaria* subspecies shell height and width (minus the protruding rib-surfaces) were measured and converted into the surface of an ideal cone. The individual shell weight was also determined. Finally a weight index was calculated. The following subspecies have been used: 1, *A. a. adrianae* (very prominent ribs) [samples 1, 2, 3]; 2, *A. a. dubia* (prominent ribs) [samples 4, 5, 6]; 3, *A. contaminata incommoda* (weakly ribbed) [samples 7, 8]; 4, *A. teres nordsiecki* Zilch, 1977 (weakly ribbed) [sample 25]; 5, *A. praeclara drakakisi* (moderately ribbed) [sample 19].

As may be concluded from table 1, there is not (only) a simple relation between shell size and wall thickness. The weakly sculptured shells have the thickest walls. Because shell widths were measured without counting the protruding ribs, the weight of the material constituting these ribs is automatically added to that of the ideal cone. This implies that the ratio weight/cone (table 1), indicating the mean shell wall thickness, is in fact calculated too high in heavily sculptured specimens. Thus the wall of the intercostal shell segments in prominently sculptured shells is even more different (thinner) from the shell wall in (nearly) smooth shells than might be concluded from table 1 at first sight.

7.2. Surface water adhesion

It has been demonstrated by Neuckel (1981: 19, 61) in the genera *Chondrina* and *Pyramidula* Fitzinger, 1833 (Pulmonata, Pupillacea), that these snails react relatively quickly to (artificial) rain by becoming active. This concerns species represented on open rock-faces, the habitat of many *Albinaria* species. Neuckel (1981: 28, fig. 17) also tested several pulmonate gastropods occurring in other habitats. He found that snails belonging to the latter category become active only after 50 to 85 minutes, whereas those of the former group generally react on water within 30 minutes. It turned out that *Chondrina avenacea* (Bruguière, 1792) deals most effectively with water, by immediate water uptake through the end-gut and the pneumostome (Neuckel, 1981: 61). Nothing is known about the reaction to sudden wetness (rain) in *Albinaria*. However, some similarity with *Chondrina* might be hypothesized because of the similarity in habitat.

In a preliminary single experiment it could only be demonstrated that different *Albinaria* species may react differently on water. Specimens of both *A. teres nordsiecki* and *A. praeclara drakakisi*, collected the same day, sympatrically on rocks, and kept exactly the same way in the laboratory, were sprinkled with water after two months of dormancy. The former subspecies is characterized by weekly sculptured shells, in the latter these are moderately ribbed. After 11 minutes the first *A. t. nordsiecki* started crawling about and within 35 minutes 20 (87%) of the 23 specimens were active. Quite in contrast, the first *A. p. drakakisi* showed its tentacles only after 35 minutes and it took 55 minutes until 19 (95%) of the 20 specimens were active. This result was surprising, because the shells of the latter subspecies catch more water than do those of the former (see below).

Short rain showers during the end and the beginning of the dry season, or within the dry season itself, might be important for snails in relatively arid areas to reduce the length of their period of obligatory dormancy. Fitness might be related to the effectiveness in benefitting from such rains. It could be shown that the extent of the periods of increased humidity in the snail's micro-climate, and thus the lengths of its periods of potential activity, are influenced by the shell sculpture. In a simple, preliminary experiment it became evident (Reitsma & Gittenberger, unpublished data) that the most prominently ribbed *Albinaria* shells catch more water than do e.g. smooth shells; the latter ones remain wet a shorter time. The amount of water caught and thus available for storage within the animal, vitally important to endure a long period of drought, will vary with the shell sculpture. This water quantity might also be relevant with regard to the critical values concerning wetness to be attained for the induction of activity itself.

Several shells of (1) moderately to very prominently ribbed species (*A. praeclara drakakisi* [sample 17] and *A. p. praeclara* [sample 15]), and (2) more weakly sculptured species (*A. inflata turgida* A. J. Wagner, 1924 [sample 10] and *A. teres extensa* (L. Pfeiffer, 1864) [sample 25a]), were soaked in water in such a way that the interior of the shells remained dry. Immediately after this the water-soaked specimens were observed under a microscope, while being lighted, and thus warmed up, from a distance of 10 cm by two 5 V microscope lamps with fully opened diaphragms. The end of the process of drying is accompanied by an abrupt change in shell colour and thus easily observable. It could be directly observed that the surface of the moderately or very prominently ribbed shells remained wet 2.5 to 3 times longer than that of the other ones, evidently because relatively much water was caught between the ribs. In *A. praeclara drakakisi* the shells became dry after c. 3.0 minutes, in *A. p. praeclara* after c. 2.5 minutes, in *A. teres extensa* after c. 1.5 minutes and in *A. inflata turgida* after c. 1.0 minute. How these figures change with a milder warming up and a varying air turbulence (in relation to the shape of the shell surface), will be investigated and shells of other (sub)species will be tested as well. The variation in microsculpture, e.g. presence or absence of reticulate threads (fig. 9, 13) between the main ribs, enlarging the shell surface, will be taken into account then.

Direct observations suggest that in shells with large ribs more water is retained between the shell surface and the substratum than in smooth shells.

Evidently differences in the attraction of surface water, related to shell sculpture, are a fact. It could not be demonstrated that there is storage of water inside the hollow ribs. Different (sub)species will have unequal properties with respect to this quality. There will also be a shift in both absolute and relative amount of surface water adhesion during the growing phase of an individual snail in those (sub)species that have shells which are not homogeneously sculptured all over. Even in shells which appear to be smooth at first sight, the initial teleoconch whorls are often provided with relatively prominent riblets. In that case juvenile specimens will be better equipped to attract water than will be adult ones.

7.3. Evaporation and shell permeability

Apertural size and shape, shell thickness and structure of the epiphragma determine the rate of water-loss in dormant snails (Machin, 1967). Water-loss through the shell and shell thickness correlated with the relative humidity of the habitat have been reported by various authors (e.g. Riddle, 1983: 433; Goodfriend, 1986: 216).

To investigate water-loss, individual water-filled shells, with sealed apertures, of both *A. a. adrianae* and *A. contaminata incommoda* were put on a balance of precision and then lighted (warmed up) and weighted continuously. The former subspecies is characterized by the presence of very prominent ribs; in the latter one the shells are nearly smooth. No significant differences in speed or way of water-loss was observed. This implies that the supposed relatively high water permeability of the thin intercostal shell segments in *A. a. adrianae* is compensated by the much lower permeability of the segments with broad hollow ribs. This assumption will be tested by artificially removing the ribs and repeating the experiment.

7.4. Ribs and insolation

It is reasonable to suppose that in conchiferous snails the effects of insolation might to some extent depend upon shell shape and sculpture. A start was made to test this principle. A water-filled shell, with its aperture sealed, was fixed in a natural, vertical position on a sand-coloured cardboard substratum. A 0.1 mm thick copper-constantan thermocouple was mounted in the shell through a very narrow artificial hole, made in the ventral side of the second adapertural whorl. This way it became possible to measure exactly the temperature inside the shell. The temperature could be continuously registered graphically. A 5 V microscope lamp with open diaphragma, placed at a distance of 15 cm from the shell was switched on and off, after the maximum temperature being reached. The effects of this "insolation" on the inside of the shell were registered with a temperature curve. The experiment was repeated to check the constancy of the results. In addition, the position of the lamp was changed, to check how different angles of radiation influenced the temperature curves and the maximum temperatures reached inside. Specimens of the two subspecies mentioned in the preceding paragraph were used, because of the conspicuously different shell sculpture.

After switching on the lamp, the inside temperature of the shells always increased, first quickly and then, rather abruptly, much slower, finally reaching a maximum. Without changing the position of the lamp, this maximum temperature proved to be the same in both *A. a. adrianae* and *A. contaminata incommoda*, as had to be expected. However, after starting the experiment, the temperature in the former shell did rise twice as fast as in the latter one. After switching off the lamp, the temperature did fall back to the initial level about equally quickly in both. Changing the angle of illumination, resulted in a different maximum inside temperature of the shells.

It would lead beyond the scope of the present introductionary paper to present and discuss all available data here at length. Moreover, work is still in progress. We may content ourselves with the conclusion that the time-span required to attain the maximum temperature inside an *Abinaria* shell may depend upon the shell's sculpture, directly or indirectly (in relation to the correlated shell wall thickness).

8. ACKNOWLEDGEMENTS

For valuable help of various kinds we are grateful to L.J.M. Butot (Bilthoven), Ms. E.C. Flach (Leiden), J.H.W. Krom (Leiden), N. Reitsma (Leiden), V. Wiese (Cismar), Prof. Dr. P.C. Zwaan (Leiden).

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10. SAMENVATTING

Morfologie, functie en taxonomische betekenis van schelpribben bij Clausiliidae, met speciale aandacht voor *Albinaria*

Ribben zijn algemeen voorkomende schelpstructuren, die bij Clausiliidae, Urocoptidae en enkele andere groepen gastropoden niet massief zijn. Bij vertegenwoordigers van deze families bleken de schelpribben niet alleen hol te zijn, maar bovendien voorzien van ingewikkelde membraneuze septa met aangehechte kristallijne structuren. In dit artikel wordt in de eerste plaats een morfologische beschrijving van deze complexe holle ribben gegeven. Daarna volgen overwegingen aangaande de ontwikkeling, de taxonomische betekenis en de functie ervan. Bij het morfologische onderzoek werd veel gebruik gemaakt van een rasterelektronenmicroscoop. Zie blz. 80-81 voor een overzicht van het onderzochte materiaal, waarbij in aparte lijsten respectievelijk soorten met holle en met massieve ribben worden vermeld.

Holle ribben bestaan uit een dak, een bodem en een hierdoor omsloten ruimte die leeg is of voorzien van septa, organische membranen waarop kristallen zijn afgezet. De septa "hangen" in de ribben als vloeren in een flatgebouw en/of zijn opeen gestapeld op de bodem. Het aantal septa is afhankelijk van de absolute afmetingen van de betreffende rib. De aangehechte (samengestelde) kristallen kunnen in vorm en aantal sterk verschillen. Het is mogelijk om min of meer bolvormige (fig. 17), hoekige (fig. 18) of rozetvormige (fig. 20) aanhechtsels te onderscheiden. Bij de vorming van de ribben wordt eerst het dak gemaakt, daaronder worden vervolgens septa aangebracht en uiteindelijk wordt het geheel afgesloten met de bodemplaat.

Holle ribben zijn een familiekenmerk voor zowel de Clausiliidae als de Urocoptidae en mogelijk ook voor de Oleacinidae. Met name het voorkomen bij zowel Clausiliidae als Urocoptidae is opvallend, aangezien het steun geeft aan de opvatting van enkele auteurs die deze families op andere gronden als nauw verwant beschouwen.

Het valt op, tenminste binnen het genus *Albinaria*, dat als er binnen een soort duidelijke verschillen bestaan in grootte en aantal van de ribben, de vormen met de grootste en tevens de minste ribben in de laagst gelegen gebieden (veelal zeeniveau) worden gevonden. Bovendien zijn de huisjes van soorten met grote ribben vaak lichter dan die van soorten die niet of nauwelijks geribd zijn. De holle ribben vormen een gewichtsbesparende versteviging, die vooral het voordeel biedt als buffer te kunnen werken in situaties waar bij ribloze of met massieve ribben bezette schelpen gemakkelijk het inwendige van de schelp beschadigd zou kunnen worden.

Er is sprake van een verhoogde wateradhesie bij schelpen met (grote) ribben, waardoor optimaal gebruik kan worden gemaakt van het soms schaarse water (regen, dauw). Dit zou een verlenging van de actieve periode(n) kunnen betekenen.

Het is bekend dat er dwars door de schelpwand heen verdamping van water plaats kan vinden. Er kon evenwel geen correlatie worden aangetoond tussen de mate van een dergelijk vochtverlies en de aanwezigheid van meer of minder grove ribben.

Het is nog onduidelijk in hoeverre de sculptuur van het schelpoppervlak een rol speelt bij de reflectie van stralingswarmte.